

BRAUN-BLANQUETIA

RECUEIL DE TRAVAUX DE GEOBOTANIQUE/ REVIEW OF GEOBOTANICAL MONOGRAPHS

46

CENTENAIRE DE LA PHYTOSOCIOLOGIE

par

Farid Bensettiti, Frédéric Bioret,
Vincent Boullet, Franco Pedrotti

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CAMERINO
2010

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BRAUN-BLANQUETIA

Un héritage est enrichissant et ouvre de nouvelles possibilités créatrices. Mais il en découle en contre partie l'obligation de ne pas gaspiller le patrimoine reçu. Ceux qui, aujourd'hui étudient la végétation grâce à la phytosociologie peuvent utiliser des méthodologies bien au point et tirer profit d'un ensemble cohérent de connaissances.

C'est le résultat du travail méthodique de nombreux chercheurs de qualité pendant plusieurs décennies. Aujourd'hui, nous nous trouvons face à des problèmes qui ne sont sans doute pas tout à fait nouveaux mais qui paraissent infiniment plus graves que dans le passé: primauté de la technique, spécialisation, pénurie de matières premières, d'énergie et d'espace, crise de l'environnement...

Il se développe ainsi des problèmes spécifiques divers pour lesquels il est nécessaire de trouver des réponses nouvelles. Les chercheurs sont placés devant un véritable défi et il dépend de leur savoir et de leur imagination de montrer si la Science de la végétation est capable d'apporter une contribution appréciable à la solution de ces problèmes.

La tradition phytosociologique dans ce contexte constitue une base essentielle. La conception typologique de la végétation et la clarté du système qui en découle, l'habitude des chercheurs de vivre en contact étroit avec la végétation, les recherches basées sur l'observation condition antithétique de l'expérimentation, sont les traits caractéristiques de la phytosociologie. Les lignes directrices qui nous ont été transmises par les maîtres de la Science de la végétation, Josias Braun-Blanquet et Reinhold Tüxen avant tout, constituent actuellement une part importante de notre patrimoine d'idées. Notre but est de valoriser cet héritage et d'honorer la mémoire du premier de ces maîtres et fondateur de la phytosociologie moderne par une nouvelle série de publications.

Pourront y trouver place des monographies étudiant concrètement la végétation selon les enseignements de J. Braun-Blanquet et R. Tüxen qui, à travers la créativité des auteurs, produiront de nouveaux fruits.

Disciples nous-mêmes de J. Braun-Blanquet et ayant collaboré à son activité, nous pensons qu'à travers cette série de publications son héritage restera vivant dans l'esprit originel et avec de nouvelles idées.

Mise en page et préparation pour l'impression: Massimo Maccari

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Centenaire de la phytosociologie. Braun-Blanquetia, 46, 2010.

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Tipografia Editrice TEMI - via Maccani 108/12 - 38121 TRENTO, Italia

E-mail: temi@temieditrice.it

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J. BRAUN-BLANQUET, 1954

Drawn from a photograph by Françoise M. Danserau

Ce volume de Braun-Blanquetia (n. 46) est édité par l'Amicale Internationale de Phytosociologie, en collaboration avec la Société Française de Phytosociologie.

Il symbolise le passage de relai de l'Amicale vers la SFP qui devient à partir de 2011 l'éditeur de la revue Documents Phytosociologiques.

Il est dédié au Professeur Jean-Marie Géhu, maître de la phytosociologie européenne moderne, à l'occasion du Colloque international du Centenaire de la Phytosociologie, qui s'est tenu à l'Université de Brest, du 3 au 5 novembre 2010.

Franco Pedrotti et Frédéric Bioret

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À PROPOS DU CENTENAIRE DE LA PHYTOSOCIOLOGIE

CENTO ANNI DI FITOSOCIOLOGIA

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ABSTRACT

A historical sketch of the development of phytosociology during one century of activity. The conceptual contribution of Braun-Blanquet and the controversy with the Scandinavian School are described. In the foundation period, Phytosociology is proposed as a formalised method to describe the plant cover and the concept of plant community (association) is analysed. After World War II Phytosociology develops in Europe due to a strong collaboration between Braun-Blanquet and Tüxen, two quite different personalities with different scientific interests, but both interacting in a very constructive way. In the 60ies and 70ies the group around Tüxen with participants to the symposia in Stolzenau and later in Rinteln, allows a fruitful collaboration among different research centres. The initiative for the redaction of the Prodromus of European Plant Communities has been often discussed but never realised. The 80ies are a period of dramatic developments. After the death of Braun-Blanquet and Tüxen new trends develop: the use of methods for automatic data processing and data banks and the expansion of phytocociological investigation in other continents. The re-born International Association for Vegetation Science and its Journal promote a new background for phytosociological research. Applied phytosociology works mainly for conservation and withj the study of global change. Indeed until now Phytosociology remains a prevalently descriptive method and the problem because and why plants are grouped in communities still remains not resolved. The author describes in detail his first encounter with Braun-Blanquet, the difficult development of Phytosociology in Italy and the last scientific testaments of the two leading personalities of Phytosociology.

KEYWORDS: Century of phytosociology, plant association, the Braun-Blanquet approach, S.I.G.M.A., Tüxen, Italian phytosociology, International Association of Vegetation Science, applied

Phytosociology, Vegetation mapping, Landscape Ecology.

INTRODUZIONE

La fitosociologia viene definita, cento anni orsono, come lo studio delle associazioni vegetali, intese come “comunità vegetali di composizione floristica definita” (FLAHAULT e SCHROTER, 1910). Una dichiarazione interlocutoria, che rimanda il problema alla definizione dell’oggetto di questo studio, cioè della comunità vegetale.

Qui si apre un problema importante: queste comunità vegetali esistono realmente, oppure sono una creazione del nostro intelletto? Se il secondo corno del dilemma è vero, la fitosociologia non può diventare oggetto di ricerca scientifica: dunque, se vogliamo affermare l’esistenza delle comunità vegetali, come una realtà naturale (paragonabile ad es. alla specie), dobbiamo darne una definizione basata su una sana applicazione del metodo della scienza sperimentale: definire un paradigma. Nella moderna concezione della scienza sperimentale, questo viene identificato in un insieme di esperimenti ripetibili, che stanno alla base della teoria. Un simile paradigma, per la fitosociologia, dopo 100 anni di attività ancora non esiste.

Dunque, il dilemma, dopo un secolo di sviluppo, non è ancora risolto, come vedremo nel capitolo conclusivo: quindi, fino ad ora, non siamo ancora in grado di considerare la fitosociologia una teoria scientifica che sviluppa un paradigma di valore generale. Possiamo però constatare che l’applicazione del metodo fitosociologico ha avviato un processo di acquisizione di conoscenze, che è ancora in pieno sviluppo. Dunque, anche se la base teorica è ancora incompleta, siamo certamente di fronte ad un metodo che ha dato ottimi risultati. Così la fitosociologia viene anche indicata come “The Braun-Blanquet approach” (WESTHOFF e VAN DER MAAREL, 1973), dal nome dello studioso che più di ogni altro ha contribuito al suo iniziale sviluppo.

Queste preoccupazioni erano pre-

senti ai primi sostenitori della fitosociologia, e me ne rimane il chiaro ricordo anche da conversazioni, negli anni ’50 del secolo scorso, con Braun-Blanquet, Furrer, Gams ed altri che avevano partecipato a quel periodo fondativo. Infatti, fin dal principio, la fitosociologia non viene accolta con entusiasmo dalla comunità scientifica, anzi, con un certo sospetto di deviazione idealistica oppure addirittura come pura fantasia: un’idea che esiste solo nella testa di pochi visionari. Per questo, durante i primi decenni del secolo scorso, quelli che operano nel campo della fitosociologia si mantengono sulla difensiva, cercando ogni occasione per dimostrare la validità della sua base scientifica; intanto, le conoscenze acquisite mediante ricerche fitosociologiche si sviluppano rapidamente. Molti studiosi autorevoli, soprattutto tra i cultori della tassonomia e tra quelli di lingua inglese, restano però scettici nei riguardi di questo metodo durante tutto il periodo della loro attività scientifica. Ricordo una delle prime riunioni organizzate per la Flora Europaea, a Genova nei primi anni ’60, durante la quale si discusse quali informazioni dare sull’habitat delle singole specie ed uno dei presenti propose di inserire anche dati fitosociologici, ma la proposta non venne nemmeno presa in considerazione.

La fitosociologia negli anni ’20 e ’30 rimane circoscritta all’ambiente centroeuropeo (Svizzera, Germania, Polonia) e non trova riconoscimenti nei paesi di lingua anglosassone; anche in Germania, stenta ad affermarsi ad es. a Berlino, allora uno dei massimi centri mondiali della botanica sistematica. Queste sono probabilmente vicende abbastanza normali, quando si tratta di affermare una nuova idea, e le cose non erano andate in maniera molto diversa anche quando, mezzo secolo prima, si era discussa la teoria darwiniana dell’evoluzione. Anche per la fitosociologia pesavano alcuni fattori: la nuova teoria era stata presentata da uno studioso isolato, estraneo ai gruppi riconosciuti in quel campo della ricerca scientifica, senza una chiara collocazione accademica, e non aveva una base spe-

rimentale chiara. Mancava l'perimentum crucis, uno come Mendel che fin dall'inizio dimostrasse in maniera indiscutibile la necessità di una nuova teoria.

Tra coloro che affrontano seriamente il problema, si delinea quindi una netta divisione in due gruppi, fieramente opposti l'uno all'altro: da un lato gli studiosi più vicini a Braun-Blanquet, indicati come "scuola Zurigo-Montpellier" che sviluppano soprattutto l'aspetto descrittivo, mentre dall'altro la scuola scandinava, che fa capo a Du Rietz propone metodi sperimentalni di analisi della vegetazione. I primi dimostrano facilmente come i metodi sviluppati sulla uniforme vegetazione scandinava siano inapplicabili nell'ambiente estremamente diversificato delle Alpi e del Mediterraneo, i secondi criticano l'approccio tipologico come una proiezione di idee preconcette. La divisione rimarrà netta fino agli anni '50, quando, nella fortunata occasione di un'escurzione internazionale in Svezia, studiosi dell'uno e dell'altro campo si troveranno assieme sul terreno ed avranno il piacere di constatare come i rispettivi metodi di ricerca dessero risultati del tutto compatibili: da quel momento, nessuno parlerà più di due scuole per la fitosociologia.

In realtà, è un fatto di percezione immediata, come i vegetali abbiano la tendenza a formare aggruppamenti che si ripetono in luoghi diversi, con piccole differenze, quando le condizioni ambientali siano simili. Questo è ben noto a chi vive a contatto con l'ambiente: chi lavora nel bosco, chi raccoglie funghi e frutti selvatici, i cacciatori, i forestali. Questi conoscono molto bene i "posti" dove si trovano i porcini e dove si raccolgono le fragole, altri sanno riconoscere dove si annida il gallo cedrone oppure dove la farnia soffre la siccità e perde le foglie. Il punto essenziale, in questo caso, è la connessione tra il popolamento vegetale e l'ambiente e la ripetibilità dell'esperienza: in questo modo, il fatto biologico diviene l'indicatore dei fattori ambientali. La ripetibilità è il punto essenziale, perché si tratta di un fatto soltanto probabilistico e non di uno stretto legame di causa-effetto. Dunque, tra l'esperienza che si raccoglie in questo modo e quella che si ottiene attraverso la sperimentazione (ad es.: il calore dilata i corpi) esiste una differenza profonda. Ma sono entrambi modi di conoscere la realtà.

Lo studio delle piante, sia nell'antichità, sia dopo la ripresa degli studi botanici nel sec. XVI con Mattioli e la fondazione dei primi Orti universitari si

era sempre concentrato sulle singole specie; l'approccio non è cambiato con Linneo, che anzi ha dato un contributo importante alla comprensione della specie, come unità biologica fondamentale. A questo approccio rimane ancora legata la Géographie Botanique di A. P. De Candolle.

Durante il sec. XIX si sviluppa invece lo studio delle formazioni, e non è un caso che questo avvenga proprio attorno all'ambiente alpino e le connessioni con le zone fredde dell'Europa settentrionale (Unger, Kerner), infatti qui si dispone di conoscenze floristiche accurate, ed i gradienti di altitudine (dal piano alle cime) e latitudine (Alpi - Scandinavia) permettono paragoni istruttivi. Le formazioni vegetali sono intrinsecamente differenti dagli aggruppamenti vegetali che forniranno la base della fitosociologia, tuttavia introducono un concetto nuovo: le condizioni ambientali selezionano gruppi di specie, che si ripetono dovunque si abbiano simili condizioni ambientali. I fatti già noti ai boscaioli e cacciatori sono riproposti con linguaggio scientifico, analizzati e, quando possibile, spiegati.

Fin dall'inizio, molti, tra coloro che sono impegnati in questo tipo di studio, sentono la necessità di dare ad esso una chiara base logica. La ricerca di una adeguata definizione per questo metodo di ricerca, e per il suo oggetto (la comunità vegetale) viene sentita come esigenza primaria per garantire l'accettazione della fitosociologia da parte di una comunità scientifica inquadrata nelle discipline tradizionali e scarsamente sensibile, scettica o spesso addirittura decisamente polemica, nei riguardi di questa nuova idea.

Ma questa esigenza di idee chiare e distinte forse è soltanto una espressione di perfezionismo. Ricordo che, dopo una decina d'anni di ricerche con il metodo fitosociologico, anch'io mi ponevo spesso il problema della definizione rigorosa. Mi capitò in quel tempo di leggere nell'Abriss der Psychoanalyse di S. Freud una frase che sembrava adattarsi bene alla mia situazione: ...una definizione precisa della psicanalisi è inutile: basta ricordare che essa permette di scoprire fenomeni che prima non si conoscevano e che, date determinate condizioni, si ripetono con regolarità... Lo stesso si può ripetere per la fitosociologia.

In effetti, la possibilità euristica (previsione basata sull'esperienza per risolvere agevolmente un problema) è una caratteristica essenziale della fitosociologia e chiunque abbia esperienza ne può raccontare molti esempi. Ne

ricordo uno solo: nel luglio 1986 la Società Estalpino-Dinarica di Scienza della Vegetazione tiene la sua riunione annuale in Germania, a Monaco. Durante l'escurzione nel Bayern Wald ci si ferma per un rilievo in un consorzio semi-naturale di abete bianco e faggio. Completata la lista delle specie si discute la composizione della cenosi, tutti sono d'accordo che si tratta di una cenosi ampiamente diffusa, ma uno dei partecipanti sloveni osserva che in questo contesto si sarebbe aspettato di trovare *Blechnum spicant*: si allarga la ricerca ed infatti, pochi metri al di fuori della superficie rilevata, viene trovata la specie mancante. Lo stesso modello in Baviera ed in Slovenia, ed in entrambi i casi la presenza di una specie erbacea, rara e poco appariscente, come fine indicatore ambientale.

Aver previsto la presenza di una specie soltanto sulla base del contesto vegetazionale circostante è un'esperienza molto frequente per chi si occupa di ricerche in campo e può essere considerata una sorta di base fenomenologica della fitosociologia.

Questo aspetto euristico si sviluppa particolarmente, durante la fase fondativa, dallo studio di ambienti estremi: la vegetazione costiera degli ambienti salati, delle dune, la vegetazione della fascia nivale, di suoli particolarmente basici oppure acidi. In condizioni ecologiche estreme, la selezione agisce con maggiore intensità, mettendo in evidenza le specie meglio adattate; queste, a loro volta, possono essere usate come indicatori che portano un'informazione ecologica particolarmente significativa. Lo studio comparato di questi ecosistemi in varie parti d'Europa (ad es. Alpi e Tatra oppure coste mediterranee ed atlantiche) mette nuovamente in evidenza questa capacità di previsione, insita negli schemi astratti della fitosociologia.

È importante ritornare sull'elaborazione dei concetti fondamentali, perché, dopo un secolo di attività, gli interessi di chi è attivo nel campo della fitosociologia si rivolgono ormai soprattutto verso la definizione di modelli ecologici, le applicazioni, il paesaggio.

BRAUN-BLANQUET - IL PARADIGMA SCIENTIFICO

Nel periodo fondativo della fitosociologia la figura centrale è Josias Braun-Blanquet (1884-1980), svizzero, nato e cresciuto a Coira, in una cultura di stretta osservanza evangelica, e predestinato a continuare un'atti-

vità bancaria su base familiare; piccolo di statura e magro, ma forte e tenace, negli anni giovanili è un coraggioso arrampicatore solitario sulle vette oltre i 3000 delle Alpi svizzere. La sua preparazione all'attività commerciale gli è utile anche per lo studio della vegetazione di vetta (ed in seguito per quella mediterranea) in un'epoca nella quale la statistica non era ancora entrata nella biologia. Nell'ambiente alpino delle Alpi Retiche e Lepontine ha l'intuizione della possibilità di interpretare la copertura come Gestalt, cioè che la infinita variabilità della vegetazione possa venire semplificata ad un modello costante, e questo diventerà il pensiero trainante durante tutta la sua vita: per un approfondimento sul significato dell'insegnamento di Braun-Blanquet si rimanda a PIGNATTI E. e PIGNATTI S. (1981).

TESTIMONIANZE E RICORDI 1. IL PRIMO INCONTRO CON BRAUN-BLANQUET

Nel 1950-51 si sapeva che d'estate Braun-Blanquet, assieme alla moglie, era in giro nelle vallate alpine, spesso anche in Italia, e qualcuno l'aveva incontrato, forse Fenaroli. Restava una figura mitica, inaccessibile per un giovane laureando. Quando nell'estate 1952 rientravo da Barcellona con un lento treno notturno, ad una fermata, sono svegliato dall'altoparlante della stazione che annuncia "Montpellier, Montpellier..." e mi viene in mente che mi trovo, sia pure per pochi minuti, nella stessa città nella quale vive il Maestro. Poi mi addormento nuovamente.

L'anno successivo, pochi giorni dopo Pasqua, arrivo nel primo mattino a Montpellier; sbrigò rapidamente le formalità (un paese dove il Comité d'Accueil per i borsisti stranieri funziona!), mi indicano dove sia la SIGMA e mi avvio a piedi: è una mattinata primaverile, gradevole dopo la nebbia di Pavia. Percorro il lungo Chemin du Pioch de Boutonnet ed arrivo, quasi in periferia, ad una villa in un giardino alberato. All'ingresso mi dicono di andar sulla destra; arrivo ad una veranda, la porta è aperta ed un signore anziano, seduto al tavolino, mi fa un cenno d'entrare: così, in maniera del tutto informale mi trovo di fronte allo scienziato, autore dei lavori che avevo tante volte studiato. Un uomo piccolo, un po' curvo, del quale ricordo le spesse lenti degli occhiali, un ciuffo di capelli bianchi che scendeva sulla fronte, l'espressione amichevole. Il tavolo davanti a lui era colmo di libri, carte, fogli di appunti: scriveva a mano;

sulle pareti interne della veranda c'erano scaffali con libri ed altro materiale di documentazione, nel naturale disordine di un momento d'attività operosa. Stava lavorando al suo libro sulle valli aride centroalpine. Abbiamo una lunga conversazione, e lui s'informa sulle ricerche avviate a Pavia ed in generale sulla situazione italiana. Un ambiente tranquillo, senza il via vai e le telefonate degli istituti universitari. Mi guida nella sala accanto, detta "la cartographie" e mi fa conoscere altri giovani borsisti stranieri. Da quel momento capisco di esser di fronte ad una personalità rilevante, non solo come studioso, ma anche come uomo.

L'assunto che BRAUN-BLANQUET (1928) propone come base per la fitosociologia, è che la vegetazione è composta da unità discrete, riconoscibili mediante la loro composizione floristica, studiata mediante una precisa tecnica di rilievo; in linea generale, la vegetazione può essere analizzata con metodo quantitativo (biomassa), oppure qualitativo (flora), mentre il rilievo fitosociologico è quali-quantitativo, e permette di integrare i due tipi di approccio (PIGNATTI E. e PIGNATTI S., 1981). In questo senso essa viene indicata da Braun-Blanquet, nei suoi lavori teorici, come metodo "floristico-statistico"; la tecnica di rilievo è un punto essenziale.

Rivista con l'esperienza attuale, questa problematica si può riassumere nelle proposizioni seguenti:

- 1) ogni specie ha una propria ecologia, differente da quella di ogni altra specie, dunque non si conoscono due specie che abbiano esattamente la stessa distribuzione sulla Terra (salvo rari casi di parassitismo obbligato);
- 2) tuttavia la distribuzione delle specie non è casuale, perché esse hanno la tendenza a riunirsi in "fitocenosi": comunità che si ripetono nel tempo e nello spazio;
- 3) le fitocenosi che hanno composizione relativamente stabile e sono riconoscibili in luoghi ed in tempi differenti quando si abbiano le stesse condizioni al contorno, sono interpretate come "associazioni vegetali";
- 4) l'associazione vegetale corrisponde a regole di efficienza nell'utilizzazione del flusso energetico in base alle risorse stazionali, dunque quando questo sia possibile, la fitocenosi tende a trasformarsi verso la condizione ottimale;
- 5) ergo: nel continuum vegetazionale si possono definire unità elementari discrete e ripetibili, la cui composizione può essere stabile, ma variare nel tempo.

Possiamo condensare queste af-

fermazioni con il seguente paradigma "la vegetazione ha composizione specifica discontinua, pur essendo dipendente dai fattori ecologici che hanno variazione continua tra un minimo ed un massimo, in quanto le specie si integrano in maniera tale da formare unità discrete: fitocenosi inquadrabili in associazioni".

Definizioni:

- vegetazione: può essere genericamente definita come "a system of largely spontaneously growing plants", VANDER MAAREL (2005)
- fitocenosi: "the concrete stand of vegetation", WESTHOFF e VAN DER MAAREL (1978);
- associazione "a piece of vegetation in a uniform environment with a relatively uniform floristic composition and structure that is distinct from the surrounding vegetation", VAN DER MAAREL (2005).

Il fondamentale contributo personale di Braun-Blanquet a questa teoria può venire così sintetizzato (PIGNATTI E. e PIGNATTI S., 1980):

- a) rilievo, nel quale si ha la connessione tra l'informazione floristica e la valutazione quantitativa;
- b) descrizione univoca dell'associazione sulla base di rilievi riuniti in tabella;
- c) denominazione univoca per ciascuna associazione;
- d) costruzione di un sistema, fondato sulle informazioni indicate in a).

La struttura di questa teoria è largamente paragonabile ad altre ben note; ad es. con la geologia: la vegetazione corrisponde al substrato geologico in generale, la fitocenosi ad un singolo strato riconoscibile sul terreno, l'associazione alla serie geologica nella quale lo strato viene inserito. La serie geologica viene riconosciuta mediante fossili guida, ed analogamente l'associazione viene riconosciuta mediante specie guida (o specie caratteristiche). Più avanti cercheremo di approfondire questo punto.

Nel quadro delle moderne conoscenze sugli ecosistemi (ecosistemica), l'associazione può essere interpretata come un canale che trasmette informazioni sopra l'ambiente; queste informazioni devono essere ricevute, comprese correttamente e rese disponibili nell'interesse del mantenimento della vita sulla terra (PIGNATTI E. e PIGNATTI S., 1980).

L'edificio di conoscenze che oggi costituisce la fitosociologia, si costruisce storicamente attraverso una serie lunga di esperienze, di Braun-Blanquet e di altri studiosi che sono in contatto

con lui, e che vengono man mano pubblicate. Il metodo rimane fondamentalmente descrittivo, ma è basato su una tecnica di rilevamento condivisa, che rende pienamente confrontabili i dati raccolti in tempi e luoghi diversi dai differenti ricercatori. La fitosociologia si sviluppa quindi come l'esplorazione di un continente ancora sconosciuto, ma i risultati si integrano formando progressivamente un ordinato edificio di conoscenze. Vanno ricordati alcuni eventi importanti: il lavoro di W. KOCH (1926) che per primo realizza la articolazione in unità fitosociologiche dell'intero manto vegetazionale a scala regionale; oppure Pawłowski *et al.* (1928) che ritrovano in Polonia le stesse unità vegetazionali già note per le Alpi. Braun-Blanquet, che aveva iniziato la sua attività a Zurigo, fonda nel 1927 a Montpellier la Station Internationale di Phytosociologie Méditerranéenne et Alpine (SIGMA) sorretta da un gruppo internazionale di istituti scientifici, ma che conserverà sempre lo status di istituzione privata. L'anno successivo viene pubblicata la prima trattazione generale su metodi e risultati della ricerca fitosociologica, alla quale seguiranno due edizioni ampliate (BRAUN-BLANQUET, 1928 e 1964). La SIGMA diviene il punto d'incontro tra gli studiosi di geobotanica del mondo intero. Uno dei colleghi in questa esperienza, raccontava di essere entrato nella SIGMA con una valigia piena di rilievi e di esserne uscito, dopo un periodo di duro lavoro, con una monografia pronta per la stampa. Per decenni Braun-Blanquet mantiene contatti personali con tutti i più attivi corrispondenti esteri, assicurando in questo modo una completa unità per quanto riguarda basi scientifiche e stile redazionale a tutta la produzione fitosociologica fino agli anni '50 ed oltre.

La componente essenziale della base sperimentale della fitosociologia è il singolo rilievo. Nei primi saggi pionieristici i rilievi erano poco più che liste di specie con annotazioni di rarità o abbondanza, come risulterebbero dagli appunti di campagna. In seguito si affermava la pratica di eseguire rilievi di 100 m², con valutazione ad occhio della copertura di ciascuna specie, espressa con una scala di 5 valori: un insieme di 5 a 10 rilievi, tra loro coerenti e riuniti in tabella, veniva ritenuto sufficiente per definire un'associazione.

Questo procedimento veniva criticato dagli studiosi scandinavi, che procedevano con rigido metodo di campionamento statistico (noto in Italia come

"rilievo secondo Raunkiaer"): lanciare a caso un cerchietto delimitante una superficie standard di pochi decimetri quadrati ed eseguire il censimento delle sole specie crescenti nell'area delimitata dal cerchietto. Il lancio veniva ripetuto una cinquantina di volte in modo da poter assegnare a ciascuna specie un valore di frequenza statisticamente significativo.

Su questi differenti metodi di rilevamento si sviluppò una discussione che continuò fino agli anni '50. Gli studiosi di scuola scandinava rimproveravano a quelli della scuola Zurigo-Montpellier, la soggettività nella scelta delle superfici da rilevare e l'imprecisione dei valori stimati ad occhio. Al contrario, i secondi opponevano la macchinosità dell'analisi mediante il cerchietto che nel caso di vegetazione complessa (ad es. nei boschi) poteva richiedere un giorno intero di lavoro per rilevare un singolo popolamento, e comunque dava sempre risultati incompleti, in quanto le specie rare e di piccola taglia hanno probabilità scarsa o quasi nulla di rientrare nelle aree circoscritte dal cerchietto (e spesso si tratta proprio degli indicatori più significativi). E poi, come rilevare con il cerchietto un ninfeo, oppure la vegetazione di una parete verticale? Progressivamente, le distanze vennero a ridursi: oggi per i rilievi fitosociologici vengono applicate tecniche uniformi, così da poterli trattare con metodi statistici, e nei casi che richiedono grande precisione (ad es. per le associazioni di muschi e licheni) sono applicati metodi di campionamento con superfici standard di pochi dm quadrati, poco differenti dai rilievi sec. Raunkiaer.

Un punto delicato è quello della scelta della superficie per il rilievo, che secondo la prassi della fitosociologia avviene per libera decisione del rilevatore: allora, si obbletta, non si tratta di campionamento casuale, ed i risultati non hanno valore scientifico. Però, in questi termini la critica è male impostata. Il dato rilevante è la composizione specifica della vegetazione esaminata, e questa non è mai nota a priori: infatti, nello scegliere la superficie, il rilevatore non conosce quali siano tutte le specie effettivamente presenti, ma soltanto controlla l'uniformità della vegetazione ed il contesto ecologico generale. Trattandosi dell'inventario su superfici la cui flora, volta per volta, non è nota a priori, il procedimento ha il carattere di campionamento casuale. Tutt'al più potrà esserci soggettività nell'inserire un dato rilievo in una tabella piuttosto che in un'altra, ma oggi questo avviene

in base a procedimenti automatizzati, e quindi al di fuori dall'arbitrio del ricercatore. In molti casi - a scopo didattico - si è provato ad eseguire i rilievi secondo le regole del campionamento casuale, ad es. lungo un percorso rettilineo a distanza predefinita: i risultati non differivano da quelli ottenuti per scelta arbitraria delle superfici da rilevare, però il lavoro comportava una grande perdita di tempo a causa della presenza di superfici a vegetazione eterogenea, inadatte per eseguirvi un rilievo.

Si può concludere, riconoscendo che sia l'idea di base che il procedimento applicati nello studio della vegetazione sono scientificamente corretti. Su questo si basa la teoria scientifica che prende il nome di fitosociologia. Una teoria che è stata applicata in innumerevoli casi da moltissimi studiosi in condizioni diverse e con interessi diversi senza arrivare a dimostrare che essa sia falsa. Soltanto la dimostrazione che la teoria sia falsa (falsificazione) può autorizzare a rifiutarla e sostituirla con un'altra teoria migliore. Questo finora non è avvenuto, però non è detto che non possa avvenire in futuro, come è successo a teorie ben più fondamentali di questa, basti pensare all'etere.

Per renderci conto del significato di questa constatazione, si può esaminare un altro esempio di teoria scientifica, scelto tra quelli più vicini: il concetto della specie in Linneo. Qui abbiamo un chiaro paradigma "Species tot sunt diversae quot diversas formas ab initio creavit infinitum Ens" *Fundamenta botanica* N. 157 (1736), e c'è un procedimento (inserimento nelle Clas- ses plantarum). Questa semplice base concettuale ha permesso di descrivere mezzo milione di specie e riunire un immenso patrimonio di conoscenze. Oggi sappiamo che il paradigma linneano, superato dalla teoria dell'evoluzione, non è più sostenibile, tuttavia il concetto di specie ancora rimane fondamentale. In questo senso, possiamo concludere che il paradigma proposto da Braun-Blanquet per la conoscenza della vegetazione abbia avuto un significato paragonabile a quello del paradigma linneano per la conoscenza delle specie.

LA FITOSOCIOLOGIA NELLA DIMENSIONE CONTINENTALE (DAGLI ANNI '50 AGLI ANNI '70)

Negli anni '30 e fino alla seconda guerra mondiale si ha un periodo di fecondo sviluppo della fitosociologia, che trova nuovi studiosi interessati in

Austria (Aichinger, Wagner), Belgio (Lebrun, Noirfalise), Cecoslovacchia (Klika, Hadač), Francia (Molinier, Sugnuglas), Jugoslavia (Horvat, Horvatić), Scandinavia (Dahl, Nordhagen), Svizzera (Lüdi), Ungheria (Soó, Zolyomi) e soprattutto in Olanda (Sissingh, Vlieger, Diemont, Westhoff) ed in Germania (Ellenberg, Oberdorfer, Volk). Nelle opere di questi Autori e dei loro allievi e collaboratori, la vegetazione viene descritta mediante tabelle, secondo il modello già sviluppato ai primordi della ricerca fitosociologica: esse però diventano progressivamente più ampie e comprensive, riportando in qualche caso fino ad una cinquantina di rilievi, il che richiede l'inserimento di costose tavole fuori testo. La tabella rappresenta la struttura della vegetazione, essa però di regola è accompagnata da un accurato studio ecologico, che spesso sconfinava nella pedologia ed ecofisiologia. La comparazione dei dati di diversi Autori rivela interessanti analogie, ma risulta difficile per la complessità dei dati e la stretta dipendenza dalle condizioni locali o addirittura stazionali.

Così matura l'evento più importante nello sviluppo delle conoscenze fitosociologiche dell'anteguerra: la pubblicazione della prima grande sintesi a carattere regionale (TÜXEN, 1937). Quest'opera riguarda la Germania nord-occidentale, cioè grosso modo, un'area compresa tra il Reno e la Weser: essa contiene la sintesi di migliaia di rilievi, eseguiti da autori diversi in tempi diversi. Negli anni precedenti Tüxen aveva diretto un centro di studi sulla vegetazione, a Hannover. Con questa pubblicazione, Tüxen entra nella ristretta cerchia dei leader nel campo della fitosociologia.

Reinhold Tüxen è nato nel 1900, nella Germania settentrionale, vicino al confine con la Danimarca. Dopo gli studi universitari in chimica, si sviluppa l'interesse per la botanica. Nel 1926 ha l'opportunità di partecipare ad un corso tenuto da Braun-Blanquet a Zurigo, e da questo momento si dedica completamente alle ricerche con il metodo fitosociologico e sviluppa un programma di cartografia della vegetazione come base per la pianificazione territoriale nel nord-ovest della Germania. Guida un efficiente gruppo di lavoro, al quale partecipano anche studiosi olandesi, e questo svolge una intensa attività di rilevamenti e cartografia su tutta la regione. Nella sintesi del 1937 i dati sono esposti in maniera sinottica, in un centinaio di liste nelle quali ogni specie entra soltanto con la frequenza percentuale. Si rinuncia alla pubblicazione delle

tabelle con molte colonne, che talvolta potrebbero raggiungere un tale numero di rilievi e specie, da risultare illeggibili; ogni tipo di vegetazione è dunque rappresentato da un'unica colonna. Una drastica riduzione, che ovviamente comporta una perdita d'informazione, però in questo modo si raggiunge una facile e piena comparabilità tra l'una e l'altra tabella e con le tabelle rilevate nei paesi limitrofi. Viene descritta la vegetazione di un'ampia area, paragonabile all'intera Italia Settentrionale, frutto di un immenso lavoro sul campo, che viene reso facilmente accessibile. La sintesi del 1937 inventa un nuovo linguaggio, che apre la possibilità di ampie comparazioni, ed in pochi anni vengono pubblicate analoghe sintesi regionali per Olanda, Belgio, Francia mediterranea, Grgioni; per l'Italia il primo esempio riguarda la vegetazione della pianura veneta (PIGNATTI S., 1953).

Durante la seconda guerra mondiale la SIGMA rimane il punto di riferimento per chi pratica la fitosociologia, e vi si svolge un'attività continua, benché ridotta: nella zona di Montpellier non ci sono combattimenti, e Braun-Blanquet, cittadino svizzero, gode della protezione di un paese neutrale. Anche il centro di ricerche diretto da Tüxen, fissato a Stolzenau, un piccolo paese nella zona agricola presso Hannover, rimane indenne e dopo la fine delle ostilità il lavoro viene ripreso intensamente nel quadro delle attività per la ricostruzione.

A questo punto, la fitosociologia ha due poli: Montpellier e Stolzenau, dove sono attivi rispettivamente Braun-Blanquet e Tüxen. I due hanno poco in comune: il primo è taciturno e riflessivo, avvezzo al dialogo nel contatto personale; facondo ed estroverso il secondo, abituato a parlare in pubblico ed a trascinare l'uditore; anche il contesto culturale è diverso: Braun-Blanquet è un montanaro che parla Schwytzer-deutsch mentre Tüxen è cresciuto ai confini tra Germania e Danimarca, dove la faggeta arriva quasi alla costa, e si parla Plattdeutsch; è interessante il fatto che né l'uno né l'altro ha avuto un curriculum di studi centrato fin dal principio sulla botanica, né una carriera accademica in questo campo. Rispetto all'establishment accademico, entrambi rimangono outsiders. Tuttavia, si intendono molto bene e c'è una stima reciproca: in molti anni di dimostrazione con entrambi non ho mai udito una critica dell'uno verso l'altro. In realtà i loro rapporti erano essenzialmente epistolari, perché si sono incontrati molto raramente: l'unico caso del quale sono stato

spettatore è stato il Congresso internazionale di Botanica a Parigi (1954). Hanno collaborato raramente, ma pubblicano assieme la definizione delle prime classi di vegetazione, una pietra miliare per il successivo sviluppo della fitosociologia. In sostanza, negli anni '50-'60 esiste una sorta di diaarchia: si va a Montpellier per un periodo di raccolto, ad es. preparare una tesi di dottorato discutendo punto per punto con il Maestro, e seguirlo nelle escursioni negli ambienti del Midi, che spesso diventavano vere e proprie lezioni itineranti; si va a Stolzenau (successivamente l'istituto viene trasferito a Rinteln) per partecipare a frequenti sedute di lavoro o congressi e consultare l'immenso quantità di dati disponibili.

Nel periodo 1954-1960, quasi senza che ce ne rendessimo conto, si attua un importante cambio di prospettiva: la fitosociologia raggiunge in Europa la dimensione continentale. Superate le incertezze e polemiche iniziali, molti ricercatori cresciuti con l'esperienza fitosociologica sono ormai arrivati alla maturità scientifica ed a loro volta stanno educando una nuova generazione di giovani ricercatori. L'editore Junk pubblica il periodico *Vegetatio*, con l'ampia collaborazione di Braun-Blanquet, e questo periodico si afferma come la voce più autorevole nel campo della fitosociologia. In Germania, Oberdorfer sviluppa a Freiburg un centro attivo di studi fitosociologici, che in questo caso è inserito nell'Università, con la possibilità di avere allievi qualificati: non è in alternativa all'attività di Tüxen, perché i due lavorano su binari paralleli. Oberdorfer continua la tradizione aperta da Tüxen nel 1937, con il volume sulle associazioni vegetali della Germania di sud-ovest, pubblicato nel 1957: questo si svilupperà in una seconda edizione in 5 volumi pubblicata negli anni '80. Durante la guerra veniva inviato in Grecia ed altre zone dei Balcani con il compito di studiare la vegetazione, e negli anni successivi una lunga residenza nel Cile meridionale gli offriva una prima occasione di paragoni intercontinentali. Il suo contributo più importante, secondo me è la "Pflanzensociologische Exkursionsflora" (OBERDORFER, 1949), un piccolo volume tascabile, nel quale tutte le specie sono definite su base ecologica ed anche fitosociologica: un esempio, rimasto unico, di una sorta d'etologia delle piante, che ha avuto un successo inimmaginabile (nel 2001 era arrivata all'ottava edizione!). Si sviluppano così relazioni incrociate ed attivi gruppi del tutto indipendenti, ma in stretto contatto tra loro.

Anche il miglioramento delle condizioni politiche ed economiche nell'Europa occidentale favorisce la possibilità di spostamenti e scambi d'idee ed esperienze. E naturalmente ci sono molte iniziative spontanee per strutturare questa tendenza.

Nella seconda metà degli anni '50 si sviluppa l'attività della Società Internazionale di Fitosociologia (guidata, in maniera del tutto informale, da Tüxen) con escursioni annuali e convegni. Una delle prime escursioni si svolge proprio a Pavia nel 1958, con la partecipazione di Braun-Blanquet e rappresenta un primo riconoscimento della presenza in Italia di un gruppo che collabora nel campo della fitosociologia: una importante iniezione di ottimismo per il futuro. I convegni, organizzati da Tüxen, si tengono a Stolzenau (e successivamente a Rinteln) nella settimana prima di Pasqua, con tempi diversi anno per anno. La partecipazione è intensa e si forma un gruppo di lavoro internazionale con gli studiosi europei più attivi (molti giovani e giovanissimi) e di giapponesi ed americani. Fin dal principio ho frequentato questi convegni, nei quali spesso ero l'unico italiano; negli anni '60 il viaggio in treno durava 20 ore, quasi il tempo che oggi ci vuole per arrivare in Australia; agli ultimi convegni si andava in aereo. Per un ventennio questi convegni saranno il centro per la proposta, discussione e rielaborazione delle nuove idee; all'ultimo di questi convegni, a Rinteln nel 1980, Tüxen, gravemente ammalato, non potrà partecipare personalmente.

Durante questo periodo di oltre due decenni la fitosociologia continua dunque a svilupparsi in Europa (successivamente anche in Giappone) in maniera ben integrata, con frequenti contatti tra gli studiosi più attivi, e viene elaborato un corpus di conoscenze che rimane tuttora la base indiscussa per l'interpretazione dei lineamenti generali della vegetazione europea.

TESTIMONIANZE E RICORDI 2. LA FITOSOCIOLOGIA IN ITALIA NEGLI ANNI '50

La fitosociologia in Italia si è sviluppata relativamente tardi. Infatti negli anni '30 in Italia quasi soltanto gli studiosi della scuola di Firenze si occupavano di studi sulla vegetazione, sotto l'influenza del professor Giovanni Negri, torinese, che in pubblicazioni del periodo precedente aveva preso una posizione del tutto critica nei riguardi della fitosociologia. Così, gli studi sulla

vegetazione comparsi nel periodo tra le due guerre e fino all'inizio degli anni '60, anche quelli di più ampio respiro¹ come ad es. i lavori riguardanti la vegetazione delle Pinete Ravennati (ZANGHERI, 1936), la Laguna di Venezia (BÉGUINOT, 1941), il Comelico (ZENARI, 1941), le ofioliti toscane (PICHI SERMOLLI, 1948), il Terminillo (MONTELUCCI, 1953), Maretto (FRANCINI e MESSERI, 1956), la Sila (SARFATTI, 1955, 1959, 1965) hanno carattere meramente descrittivo oppure sperimentano una difficile applicazione dei metodi di rilievo sec. Raunkjaer alla vegetazione mediterranea; la chiusura nei riguardi di chi veniva proponendo le nuove idee anche in Italia era netta. In realtà anche prima degli anni '50 qualcuno aveva portato almeno il nome della fitosociologia nella ricerca in Italia: va citata anzitutto la prof. Luzzatto, attiva a Milano negli anni '30, che però non ha pubblicato quasi nulla in questo campo; qualche contributo episodico si può trovare in alcuni lavori di Gabrielle Braun-Blanquet e di Josias Braun-Blanquet. Le nuove idee arrivano grazie all'iniziativa di Valerio Giacomini, che alla fine degli anni '30, da poco laureato a Pavia, entra in contatto con studiosi germanici che lavorano in questo campo, e cerca

¹ Studi monografici nei quali non è utilizzato il metodo fitosociologico:

FRANCINI E., MESSERI A., 1956 - *L'isola di Maretto nell'arcipelago delle Egadi e la sua vegetazione*. Webbia 11: 607-846.

MARCHESONI V., 1959 - *Importanza del fattore storico-climatico e dell'azione antropica nell'evoluzione della vegetazione forestale dell'Appennino Umbro-Marchigiano*. Ann. Acc. It. Sc. Forestali, VIII: 327-343.

MONTELUCCI G., 1953 - *La vegetazione del Monte Terminillo (Appennino centrale)*. Webbia 9: 49-359.

PICHI-SERMOLLI R., 1948 - *Flora e vegetazione delle serpentine e delle altre ofioliti dell'alta valle del Tevere (Toscana)*. Webbia 6: 1-380.

SAPPA F., 1951 - *Illustrazione ed esemplificazione sui quercei delle Langhe di un metodo biocenotico proposto da E. Schmid*. N. Giorn. Bot. It. n. s., 58: 195-236.

SAPPA F., RIVAS GODAY S., 1954 - *Contributo alla interpretazione della vegetazione dei Monegros (Spagna, Aragona)*. Allionia 1: 1-32.

SARFATTI G., 1955 - *Notizie sulla Sila e la sua vegetazione*. N. Giorn. Bot. Ital., 62: 505-515.

SARFATTI G., 1959 - *Prodromo della flora della Sila (Calabria). Parte I*, Webbia, 15(1): 169-248, Parte II, Webbia, 20(2): 355-425 (1965).

ZANGHERI P., 1936 - *Flora e vegetazione delle Pinete di Ravenna*. Bologna: Arnaldo Forni Editore, pp. 421.

ZENARI S., 1941 - *La vegetazione del Comelico (Alto Cadore)*. Nuovo Giorn. Bot. Ital., 48: 1-388.

di introdurre l'approccio fitosociologico anche in Italia; però la guerra gli impedisce di sviluppare il discorso. Ritornato dalla prigionia in Germania, riprende questa azione, così a Pavia si forma un primo nucleo di giovani (al quale posso partecipare, ancora laureando, dal 1948) che lavorano con il metodo della fitosociologia. La reazione del gruppo accademico fiorentino è immediata: nel primo momento si tratta di una vera e propria lotta della quale sono stato spettatore. Va però precisato che il contrasto era soprattutto al livello accademico, mentre tra i giovani del gruppo di Pavia e quelli di Firenze si sono presto stabilite condizioni di serena collaborazione tendente ad un confronto costruttivo. Nel 1953, Zangheri, direttore dell'Archivio Botanico, pubblica la mia sintesi fitosociologica della vegetazione della Laguna Veneta: vado a Forlì per illustrargli il lavoro, e mi presento con un po' di batticuore, ma trovo un interlocutore interessato, che discute con competenza sulla base della sua esperienza riguardante la Pineta di Ravenna; nasce così un'amicizia che si manterrà nel tempo. Ruggero Tomaselli, allora giovane assistente a Pavia, alla fine degli anni '40 va a Montpellier per un lungo periodo di specializzazione sotto la guida di Braun-Blanquet. Già la mia tesi di laurea, elaborata a partire dal 1949 e presentata a Pavia nel luglio 1951, riguardante la vegetazione psammofila del litorale veneto, è un lavoro eseguito integralmente secondo il metodo fitosociologico (anzi: si tratta della prima ricerca eseguita in Italia, da un italiano, con questo metodo); successivamente queste ricerche fitosociologiche sono allargate alla vegetazione litorale nel Maghreb, poi a Beyrouth, Barcellona (1952, con il prof. Antonio de Bolòs ed assieme a Oriol, suo figlio) ed a Montpellier (1953, con Braun-Blanquet, il Maestro).

Alla fine del luglio 1953, una piccola Fiat 500 arrancava sulla salita da Bormio verso lo Stelvio: alla guida Giacomin, assieme a me e Pirola; alla Terza Cantoniera organizziamo una modesta base per ricerche, con libri, carte topografiche, erbario ed un microscopio. Presto ci raggiungeranno Credaro e Vido (per le analisi di suoli), e si lavorerà intensamente fino alla prima spruzzata di neve; al ritorno a Pavia, portiamo con noi la carta di vegetazione in scala 1:12.500 dell'area tra quota 2200-2800 (la prima carta fitosociologica realizzata in Italia, ed anche la prima in assoluto a quote così elevate). Nessuno avrebbe potuto immaginare che quella piccola pattuglia fosse l'avanguardia

delle centinaia di ricercatori che in seguito in Italia esploreranno tutto il territorio, descrivendone la vegetazione mediante il metodo fitosociologico, dalle Dolomiti a Capo Passero e Pantelleria.

Nel 1955 Giacomini viene chiamato alla cattedra di botanica a Sassari e quindi a Catania dove si fermerà per diversi anni: in questa sede promuove ricerche coordinate, nelle quali sono impegnati molti giovani, tra i quali Furnari, Gentile, Pirola, Poli. Giacomini qui si rende conto dell'importanza di una ricerca che abbia anche interesse applicativo e sviluppa un ampio progetto di cartografia della vegetazione, anche se questo era lontano dai suoi interessi scientifici precedenti, come specialista nel campo della briologia. Nel 1958 il gruppo di Pavia organizza l'Escursione annuale della Società Internazionale di Fitosociologia: si stabiliscono amicizie e collaborazioni che dureranno nel tempo con i colleghi che vengono da Spagna, Portogallo, Francia, Olanda, Germania, Svezia. Intanto, l'uso del metodo fitosociologico continua ad espandersi: trasferitomi a Padova nel 1956, trovavo subito un ambiente favorevole, molti giovani si impegnavano negli studi sul terreno e si aprivano collaborazioni con Palermo: Di Martino e Pedrotti andavano a specializzarsi a Montpellier, seguiti poco dopo da Lorenzoni, Lausi e Poldini, Cristofolini a Zurigo con Ellenberg, Rizzi a Vienna con Hannes Mayer. Nel 1963 ero chiamato alla cattedra di botanica a Trieste e qui si sviluppava un centro di studi sulla sociologia ed ecologia delle alghe marine. Tra Padova e Trieste si forma nel 1961-63 un gruppo di lavoro molto attivo in stretta collaborazione internazionale con i colleghi della Jugoslavia (Max Wraber) ed Austria (Erwin Aichinger) e di altre zone vicine; da questo gruppo in seguito si svilupperà la Società Estalpino-Dinaria per lo studio della vegetazione (Fig. 1), tuttora attiva: alle prime riunioni partecipa anche Braun-Blanquet, onorato da tutti come il capo-scuola della sociologia vegetale. A questo gruppo aderiscono anche Renzo Agostini e Alberto Hofmann, che hanno modo di rendersi conto dell'utilità di questo nu-

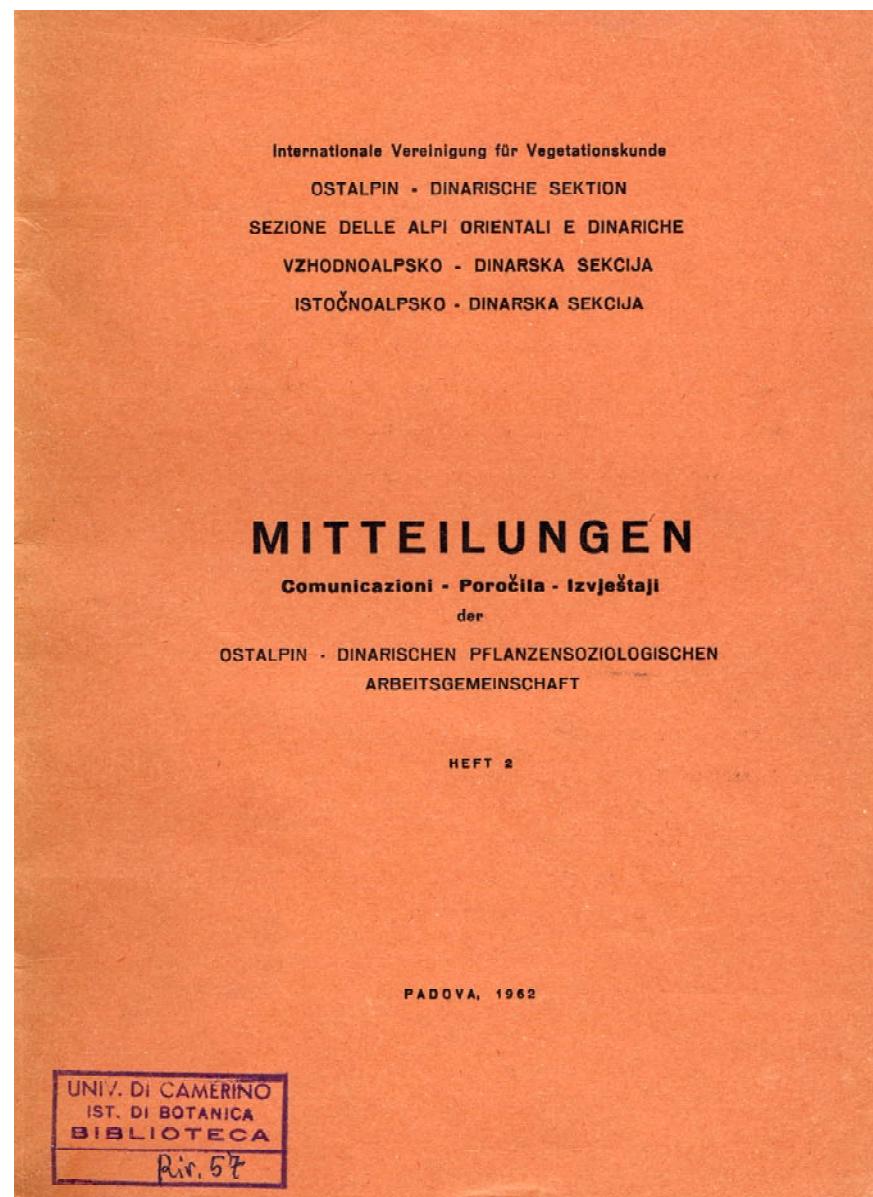


Fig. 1 - Copertina del fascicolo n. 2 delle "Mitteilungen...".

vo approccio nella pratica forestale. Vengono pubblicati i primi studi monografici sulla vegetazione italiana²: la fitosociologia in Italia era ormai decollata.

Però il decennio 1953-1963 non va considerato un periodo di tranquillo sviluppo: la fitosociologia continuava a rimanere in Italia avversata dall'establishment accademico: questo si traduceva in osservazioni ironiche o critiche durante le riunioni scientifiche, e nella difficoltà per chi lavorava in questo campo a pubblicare e ad ottenere riconoscimenti di carriera e fondi di ricerca.

Tra gli opposenti più leali è gradito ricordare Francesco Sappa, studioso serio e fortemente motivato, attivo a Torino già dal periodo pre-bellico, che in diversi lavori cercava di proporre un metodo alternativo per il rilievo della vegetazione, sperimentato nei suoi studi sulla vegetazione delle Langhe (SAPPA, 1951) e dell'Aragon (SAPPA e RIVAS GODAY, 1954). Fortemente influenzato dalle idee di Emil Schmid, ottiene risultati molto interessanti e comparabili a quelli delle indagini fitosociologiche, ma una fine immatura, ancora nel pieno dell'attività scientifica, gli ha impedito

² Monografie fitosociologiche riguardanti l'Italia (in ordine temporale):

GIACOMINI V., 1951 - Ricerche sulla flora briologica xerotermica delle Alpi Italiane. *Vegetatio*, 3: 1-123.

GIACOMINI V., PIGNATTI S., 1955 - Flora e vegetazione dell'alta valle del Braulio. *Mem. Soc. Ital. Sc. Nat. Mus. Civ. Storia Nat.* Milano, 11(2-3): 1-194.

PIGNATTI S., 1959 - Ricerche sull'ecologia e

Ven. Sc. Lett. Arti, 32(3): 1-134.
GIACOMINI V., PIROLA A., WIKUS E., 1962 - I Pascoli dell'alta Valle di S. Giacomo (Spluga). *Flora et Vegetatio Italica*, 4: 1-115.
POLI E., 1965 - La vegetazione altomontana dell'Etna. *Flora et Vegetatio Italica*, 5: 1-241.
PIGNATTI S., 1966 - La vegetazione alofila della Laguna Veneta. *Mem. Ist. Ven. Sc. Lett. Arti*, 33(1): 1-174.

di arrivare ad una conclusione. Come ultimo tentativo di contrastare lo sviluppo delle ricerche con metodo fitosociologico va ricordato il saggio duramente polemico di SUSMEL (1959). Quando l'ho ricevuto, mi sono studiato accuratamente il testo, rilevando alcuni errori concettuali di base, ed ho scritto "di getto" una risposta animata da una forte vis polemica: riletta serenamente, e con il consiglio del direttore dell'Istituto Botanico di Pavia (Raffaele Ciferri) si è preferito lasciar perdere, per non dare troppa importanza agli oppositori, quando ormai la fitosociologia stava affermandosi: risponderà GIACOMINI (1960) con una pacata messa a punto. Nel 1968 l'Escursione della Società Botanica Italiana (della quale nel frattempo ero stato eletto Presidente) si svolge in Gargano: durante la visita a Valle Carbonara, si decide, su proposta del Segretario Giacomo Sarfatti, di rilevare collegialmente (con la guida di

Montelucci) un tipico esempio di prato steppico, sia con il procedimento fitosociologico che con quello di Raunkiaer. Il primo metodo in poco più di mezz'ora permette di registrare una lista esaurente delle specie presenti, mentre il secondo richiede oltre due ore, non arriva ad una lista completa, però permette di valutare le frequenze in maniera più accurata. Vantaggi e svantaggi dei due metodi sono confrontati serenamente, e da questo momento, anche in Italia cesserà ogni discussione aprioristica contro o in favore della fitosociologia.

Nel 1963 si è arrivati alla fondazione della Società Italiana di Fitosociologia ad opera del primo gruppo di studiosi italiani di essa; da allora funziona come agente propulsore delle ricerche sulla vegetazione nel nostro paese; dal 1964 essa pubblica il Notiziario della Società Italiana di Fitosociologia (Fig. 2), che nel 1990 è diventato la

rivista Fitosociologia.

LA CONFUSIONE DEI LINGUAGGI

Nella nuova dimensione continentale, durante il periodo dal dopoguerra alla fine degli anni '70, il patrimonio di conoscenze nel campo della fitosociologia si sviluppa impetuosamente in Europa, e singoli studiosi lo allargano anche ad altri continenti. In Europa i rapporti sono difficili a causa della divisione in due blocchi, ed i colleghi dei paesi orientali raramente possono partecipare alle escursioni e convegni: così, spesso sono gli studiosi dell'Europa occidentale che visitano i colleghi dell'est per mantenere i contatti. A Trieste si sviluppa la Società Estalpino-Dinarica che stabilisce un ponte tra italiani, austriaci, tedeschi e svizzeri da un lato, e sloveni, croati, bosniaci, macedoni, ungheresi e polacchi dall'altro.

In questa situazione, la formazione di singoli gruppi locali poteva considerarsi uno sviluppo positivo, però in qualche caso l'isolamento portava qualche studioso a dare importanza a idee che non lo meritavano: ricordo qualche caso estremo, come quello di uno che pensava di rinnovare la fitosociologia derivando i nomi delle associazioni da 3 specie, anziché 1-2 come di regola, oppure un altro che si batteva perché, nello schema gerarchico della vegetazione, al di sopra della classe venisse introdotto un livello superiore: la "divisione". A parte questi aspetti quasi folcloristici, con l'espandersi delle conoscenze ai paesi dell'est e del bacino Mediterraneo, ci si doveva continuamente confrontare con nuove interpretazioni delle strutture vegetazionali, di cui era per lo più impossibile valutare il reale significato. Il fatto che queste novità venissero pubblicate nelle lingue nazionali non facilitava la comprensione; infatti, in precedenza, tutta la letteratura che contava, era pubblicata in francese o tedesco.

Va tenuto presente che durante i primi 50 anni (ca. 1910-1960) lo sviluppo della fitosociologia e la descrizione di nuove unità, dall'associazione alla classe, erano frutto di una stretta collaborazione, sotto la guida, benevola ma ferma, di Braun-Blanquet, e questo aveva garantito una completa coerenza di quanto si veniva man mano pubblicando. I lavori più significativi erano distribuiti nella serie delle Communications SIGMA e delle Mitteilungen, con l'editing rispettivamente di Braun-Blanquet e di Tüxen. Era ben raro il caso che uno studioso pubblicas-

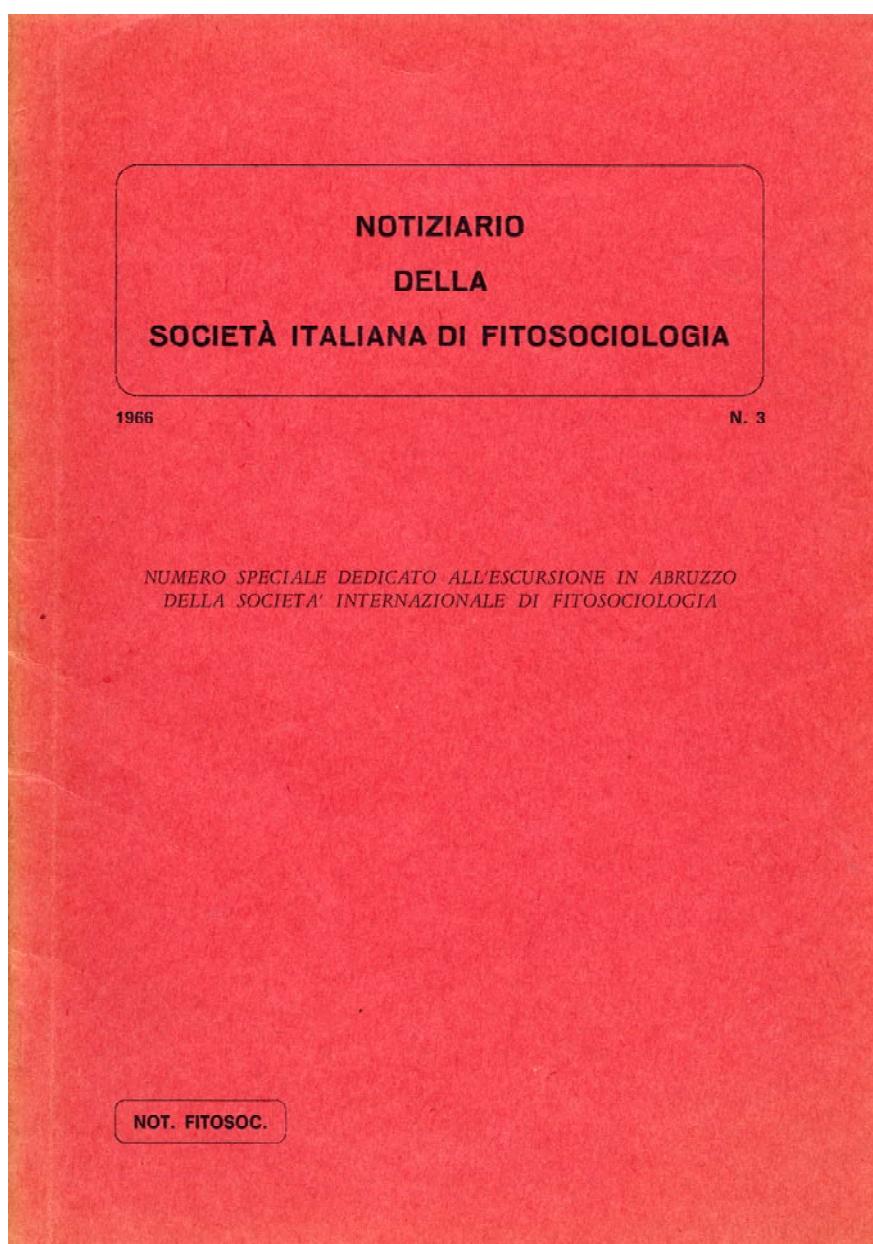


Fig. 2 - Il n. 3 del Notiziario; i numeri 1 e 2 sono stati pubblicati negli Annali di Botanica.

se una nuova associazione o altra unità sociologica senza un preventivo controllo di uno dei due, in quanto solo a Montpellier ed a Stolzenau esisteva la necessaria bibliografia di riferimento. Con lo sviluppo di molti centri indipendenti di ricerca la situazione cambia, perché mancano i rapporti personali per stabilire le necessarie relazioni. Inoltre, spesso esiste l'esigenza di pubblicare per dimostrare laboriosità oppure, nei paesi ad economia socialista, per rispettare le norme dei piani governativi. La conseguenza è una imprevista proliferazione di nuove associazioni, alleanze, a volte anche ordini e classi, che venivano ad appesantire e talora sconvolgere l'edificio faticosamente costruito nei decenni precedenti. In molti casi si arriva ad una forma di autoreferenzialità, un rischio al quale molti naturalisti sono esposti, ma che in questo caso è diventato particolarmente effettivo a causa dell'isolamento e delle barriere politiche e linguistiche. Si aggiunga che, nei paesi allora sottoposti all'influenza russa nel quadro dell'Unione Sovietica, la fitosociologia era ufficialmente ignorata, anche se gran parte dei contenuti ne venivano riproposti come fitocenologia.

Così, nel convegno annuale di Stolzenau del 1964, io stesso, pur appartenendo alla giovane generazione, presentavo una nota (PIGNATTI S., 1968) sul processo indicato come "inflazione delle unità di vegetazione", che sarà molto citata negli anni seguenti come indicazione di un rischio imprevisto, da evitare. Nelle discussioni che ne seguirono, Tüxen ha proposto che, per evitare la confusione delle lingue, si procedesse alla redazione di un'opera a carattere generale con l'inquadramento della vegetazione europea: la parola chiave era "Prodromus". Infatti, un "Prodrome des groupements végétaux" era stato iniziato a cura di Braun-Blanquet già negli anni '30, con la pubblicazione di una decina di fascicoli, ma la serie si era interrotta durante la guerra e non ripresa successivamente. In quel momento sarebbe stato probabilmente possibile arrivare in tempi brevi ad un risultato: nella mia ipotesi avrebbe potuto consistere in un volume, agile e di facile consultazione, redatto in larga collaborazione, dividendo il lavoro tra una ventina di specialisti, ciascuno dei quali fosse responsabile di una classe di vegetazione (oppure di un ordine o alleanza nel caso delle classi maggiormente diversificate). Dopo lunghe discussioni si decise invece di percorrere una via più lunga, con diverse azioni preliminari: 1) analisi esauriente della bibliografia; 2) partecipazione allo Handbook of

Vegetation Science; 3) referaggio in continuo della nuova letteratura sul nuovo periodico *Excerpta Botanica*; 4) fissazione di norme precise di nomenclatura e priorità. Tutte cose utili ed importanti, però in questo modo il problema veniva spostato ad un indefinito futuro. Vediamo come questi obiettivi siano stati sviluppati nella realtà:

1) analisi della bibliografia - si è risolta nella faticosissima compilazione di interminabili liste di citazioni, pubblicate ad opera di Tüxen negli anni '70, di scarso interesse e difficile consultazione, e ben presto divenute obsolete per il diffondersi dell'informazione on line;

2) Handbook, opera di ampio respiro, con disparità di livello tra i vari volumi, nei quali la fitosociologia ha un posto marginale; fa eccezione l'ottima sintesi teorica di WESTHOFF e VAN DER MAAREL (1978);

3) referaggio, mi sono battuto inutilmente per avere una presentazione degli articoli che venivano man mano pubblicati (sul modello di Biological Abstracts) ed invece si è preferito pubblicare bibliografie nazionali: una sintesi del passato senza aperture verso l'avvenire, anche questa rapidamente obsoleta;

4) nomenclatura, un punto che merita un approfondimento, di cui si tratterà più avanti.

Volendo dare un giudizio retrospettivo, devo purtroppo concludere che negli anni '70 sono state percepite le cause che avrebbero potuto portare ad una crisi, però nel tentativo di superarla si è avviata un'attività troppo ambiziosa e con pretese di perfezionismo, che non ha dato i frutti sperati, e che non ha neppure avviato il Prodromus, che pure era rimasto fino all'ultimo nei desideri di Tüxen. L'argomento sarà ripreso in un'altra ottica negli anni '90. Tuttavia, la confusione dei linguaggi non è stata superata, anzi, oggi è probabilmente più grave di allora.

La mia opinione attuale è che in realtà la confusione dei linguaggi deriva dalla natura stessa della fitosociologia. Infatti: cos'è la fitosociologia? possiamo affermare che la fitosociologia può essere inclusa tra le scienze della natura? La mia risposta è negativa. Infatti, le scienze della natura, come fisica, chimica, geologia e biologia, hanno una base concreta nel mondo fisico, del quale sono in grado di spiegare ed eventualmente prevedere i fenomeni. Nello studio della vegetazione, la base concreta sono le fitocenosi, ma l'oggetto della fitosociologia sono le associazioni vegetali, cioè un'immagine astratta di queste. In sostanza, la fitosociologia lavora

su immagini della nostra mente, come, appunto, la psicanalisi. In altre parole, quando si fa un rilievo, l'oggetto non sono i singoli individui vegetali (l'unica realtà concreta presente) ma la particolare condizione di equilibrio che tra essi si stabilisce. Possiamo spiegare le cause dalle quali questo equilibrio dipende e, come si è visto, prevedere dove e come esso potrà ripresentarsi, ma non la posizione e le dimensioni del singolo individuo nell'ambito della fitocenosi. Probabilmente questa critica sarebbe stata considerata cavillosa dai fondatori della fitosociologia, però essa ci spiega perché, successivamente la fitosociologia venisse indicata come "The Braun-Blanquet approach" (WESTHOFF e VAN DER MAAREL, 1978). Dunque, la fitosociologia appare soprattutto un approccio, basato su un particolare metodo di lavoro, più che un ramo della scienza naturale.

Invece, la fitosociologia è nata come una via per conoscere la natura, utilizzando un metodo a carattere sperimentale. Siamo a cavallo tra il sec. XIX e XX e la scienza a base meccanicista di derivazione illuministica è dominante. Teniamo presente inoltre che Braun-Blanquet ha una base di matematica applicata e Tüxen di chimica. Quindi essi ed i loro colleghi, organizzano le conoscenze "come se" la fitosociologia fosse una scienza della natura. Questo viene espresso chiarissimamente da Braun-Blanquet nel suo trattato del 1928 (pag. 18), dove si afferma testualmente: Le ultime parti "atomistiche" (le virgolette sono sue) di ogni associazione sono i singoli individui. Dunque il fondamento della fitosociologia, nella concezione di Braun-Blanquet, sono individui concreti che formano l'associazione, come gli atomi che formano la molecola. Questo però mi sembra una chiara contraddizione con il concetto dell'associazione basata su un equilibrio immateriale.

Per analogia, Braun-Blanquet trae ispirazione dalla più prossima tra le scienze naturali: la sistematica dei vegetali: l'associazione come analogo della specie, la nomenclatura latina, l'inquadramento in uno schema gerarchico. Però rimane una differenza fondamentale: l'oggetto della botanica sistematica è la specie, formata a sua volta da individui concreti, studiabili con metodi fisico-chimici e conservabili come viventi in orto botanico oppure come esemplari d'erbario ed in casi particolari surgelati o mediante trattamento chimico; l'oggetto della fitosociologia è l'associazione, composta da fitocenosi concrete, che però non sono

conservabili, nemmeno come viventi, perché gli individui che le compongono sono inseriti in un continuo turnover.

Di questo si deve tener conto quando vogliamo esaminare più attentamente il problema della nomenclatura. L'idea di denominare le singole associazioni dal nome delle specie più significative è addirittura più antica della fitosociologia, perché si trova già in qualche lavoro riguardante la vegetazione alpina, risalente alla seconda metà del sec. XIX. Qualche regola sommaria veniva data negli anni '30 per il Prodrome, e successivamente in uno dei primi numeri di *Vegetatio* degli anni '50. In generale si era andati avanti con buon senso e senza problemi particolari. In relazione al progetto di *Prodromus* è iniziata una faticosa discussione che dopo quasi due decenni ha portato ad un codice, che contiene norme a mio vedere inutilmente vessatorie e talvolta addirittura illogiche. Anche qui si è voluto imitare la nomenclatura botanica, sorvolando sulle differenze tra i due casi. È stabilito il principio di priorità, in base al quale la descrizione valida spesso è quella di un autore che aveva soltanto un'idea vaga o erronea; si applica di routine il nome del primo descrittore, e questo è risultato uno stimolo poderoso a descrivere nuove associazioni. Un'altra differenza importante rispetto alla tassonomia delle specie vegetali è la questione del typus, cioè del materiale di riferimento per stabilire l'identità della specie, oppure, nel caso nostro, dell'associazione. Per le specie, il problema è facilmente risolto: il typus è un campione d'erbario contenente un esemplare essiccato di un individuo della data specie (in generale si tratta del materiale originale che è servito per descrivere la specie), dunque ha esistenza oggettiva. Ma per l'associazione il problema si complica: ricordiamo che l'associazione è fondata su un particolare equilibrio, dunque il typus è immateriale; pertanto, si considera typus un rilievo, generalmente inserito in una tabella con più rilievi. La differenza è essenziale: per la specie, nei casi dubbi è sufficiente l'esame del materiale originale (autopsia), eventualmente all'estremo delle tecniche disponibili (microscopio elettronico, DNA) ma cosa fare per l'associazione? Il rilievo potrebbe contenere un errore di determinazione (cosa che avviene molto spesso). È stato proposto di stabilire degli "stand typus", ad es. in un parco nazionale, ma non sarebbero gli stessi studiati dall'autore che ha descritto l'associazione, inoltre la vegetazione tende na-

turalmente a variare, per effetto di fluttuazioni casuali oppure di successione. Il risultato è che il typus dell'associazione non ha esistenza oggettiva, ma viene definito sulla base di un'asserzione dell'autore, del tipo "...nel giorno tale e nel posto tale ho osservato: etc." ma non vi è possibilità di verifica autopatica. Se qualche buontempone descrivesse una combinazione "nonsense", ad es., un *Leontopodio-Quercetum ilicis*, quale argomento logico ci sarebbe per negarne la validità? Nella prassi, si preferisce passar sopra a questo aspetto, ma si tratta di un'importante salto logico, perché il typus è l'architrave di tutto l'edificio tassonomico.

In sostanza, la confusione dei linguaggi deriva dall'impostazione in senso meccanicista che i pionieri nello studio della vegetazione (soprattutto Braun-Blanquet e Tüxen) hanno dato alla fitosociologia. Entrambi avevano una conoscenza straordinariamente profonda della vegetazione, come oggetto di osservazione: quando è stato necessario dare una base teorica a queste conoscenze, essi hanno cercato di inquadrarle nella cultura positivista allora predominante in biologia, dopo il superamento del vitalismo ottocentesco. Questa impostazione implica la definizione di catene di causa -> effetto per la spiegazione dei fenomeni. Ricordo una affermazione pronunciata da Tüxen in seduta plenaria nel congresso internazionale di Botanica a Parigi (1954): "Come ogni cavallo si tira dentro una coda, così ad ogni associazione segue un corrispondente profilo di suolo". L'affermazione fu subito contestata da Westhoff, ed in seguito Tüxen accettò la critica: infatti è errato parlare di associazione e profilo - entrambe astrazioni; bisogna partire da "piante" e "componenti del suolo" che si condizionano a vicenda; il processo lineare associazione -> profilo si risolve in un processo ciclico di azioni e reazioni: il continuum-suolo-vegetazione (PIGNATTI E. e PIGNATTI S., *in pubbl.*). Spezzando arbitrariamente il processo ciclico in singole componenti lineari, si perde il contatto con il "fenomeno primordiale" che viene frammentato in singoli stadi tra loro non comparabili. Di qui la confusione dei linguaggi, causa prima dell'inflazione.

In maniera molto generale, nello studio della natura si possono distinguere due metodi che corrispondono a due impostazioni differenti (PIGNATTI E. e PIGNATTI S., 1980): I - il metodo visuale (morfologico), derivato dal pensiero idealistico, come osservazione statica che porta alla defi-

nizione di tipi. Nel caso della vegetazione, i tipi sono le associazioni, definite sulla base di specie caratteristiche; II - il metodo sperimentale (riduzionistico) derivante dal pensiero meccanicistico, come definizione di gradienti, in una visione dinamica.

Non si può dire che l'una delle due impostazioni sia giusta e l'altra sbagliata, ma piuttosto che i risultati dell'una devono integrarsi con quelli dell'altra. Nella fitosociologia si è avuta finora la prevalenza della prima.

IL RINNOVAMENTO DEGLI ANNI '80

Sempre negli anni '70, nella discussione si inserisce un nuovo elemento: l'apertura verso metodi statistici e le nuove opportunità offerte dai calcolatori. Avevo da tempo la convinzione che i dati fitosociologici potessero rappresentare un materiale adatto da analizzare, per chiarire le relazioni sulle quali si appoggia il concetto di associazione vegetale, ma non ero riuscito ad andare molto avanti. Una nuova idea nasce una sera, nel 1961, quando discutetti con l'amico Mario Dolcher, professore di analisi matematica a Trieste, semplici procedimenti di calcolo per chiarire le relazioni quantitative tra l'una e l'altra specie e lui mi obietta, che in città è arrivato il primo calcolatore elettronico (alle Assicurazioni Generali), che viene usato anche per ricerca scientifica, allora "perché limitarsi ad una specie rispetto ad un'altra e non prendere invece in considerazione tutte rispetto a tutte? Questo oggi è diventato possibile" Per il momento non se ne fece nulla, ma l'idea continuò ad interessarmi. Il primo incontro con Eddy van der Maarel è del 1964, in uno dei simposi organizzati da Tüxen: si apre questo discorso, che viene approfondito in incontri successivi, assieme a Cristofolini e Lausi (eravamo indicati come "il Trio di Trieste", da un trio di pianoforte, violino e violoncello, molto celebre a quel tempo); in seguito si aggiungeranno Orloci, Beeftink, Feoli, Romane ed altri e nel 1969, sempre durante uno dei simposi da Tüxen, sarà costituito lo "Working group for data processing", che sarà attivo durante tutto il decennio degli anni '70, con riunioni di lavoro e simposi a Trieste, Nijmegen e Montpellier.

Di questi anni sono i primi esperimenti di analisi multivariata dei dati fitosociologici, intanto sia la hardware che la software fanno progressi rapidissimi e ben presto il trattamento dei dati

fitosociologici mediante analisi multivariata diviene routine (VAN DER MAAREL *et al.*, 1980). Da questo approccio statistico mi aspettavo un progresso decisivo per il Prodromo. Infatti, mi ero già reso conto delle difficoltà che la fitosociologia stava incontrando a causa dell'approccio positivista che minacciava di ridurla ad una mera catalogazione di associazioni (PIGNATTI S., 1975): partendo da questa prima intuizione si trattava di trovare un procedimento ottimale per la definizione dell'associazione, che spazzasse dal tavolo le infinite discussioni che portavano all'inflazione di unità fitosociologiche soprallmentata.

In realtà, l'applicazione dei metodi di trattamento automatico ha portato a grandi progressi nella realtà quotidiana di chi lavora sulla vegetazione, però succede anche che, mediante i metodi di analisi, risulta agevole mettere in evidenza le differenze ed in questo modo alla fine si fanno ancora più associazioni, aumentando la confusione. D'altra parte, la pretesa di sostituire il cervello umano con quello elettronico non si è realizzata - e non possiamo che rallegrarcene. Il tentativo di trovare un livello di similarità che possa essere considerato di soglia per definire con procedimento unitario le associazioni e le altre unità sintassonomiche si è rivelato irrealizzabile. Invece, l'utilizzo del computer per le banche di dati ha avuto una ricaduta molto positiva, ma anche in questo caso, non decisiva. In ogni caso la potenza di calcolo del computer si è dimostrata un fattore essenziale per il trattamento di sistemi complessi, in modo da superare l'impostazione meccanica insita nella metodologia originale della fitosociologia.

Queste idee vengono proposte anche nei simposi annuali di Rinteln. Sull'uso dei calcolatori, Tüxen rimane scettico: ha sempre diffidato degli algoritmi astrusi e i suoi massicci schedari zeppi di tabelle e rilievi gli danno più fiducia di un calcolatore nel quale, premendo un tasto per sbaglio, si può cancellare tutto. Ci considera dei giovani scanzonati da trattare con paterna tolleranza: il gruppo dei "Mathematiker" (un titolo del tutto usurpato, almeno per quanto mi riguarda). Invece, proprio negli anni '70, si incrocia la traiettoria di un nuovo astro, che viene ad arricchire il sistema bipolare del periodo precedente.

Heinz Ellenberg (n. 1913) a differenza di Braun-Blanquet e di Tüxen, ha effettuato un regolare curriculum di studi nel campo dell'ecologia vegetale, con un periodo di specializzazione a Montpellier, ed arrivando al dottorato in

botanica; successivamente in carriera universitaria come assistente di Walter a Stoccarda, in seguito professore a Zurigo e quindi a Göttingen. Frequentava i simposi organizzati da Tüxen (al quale era legato da lunga amicizia), dedicando i suoi interventi soprattutto a problemi ecologici da risolvere con ricerche sperimentali: le descrizioni di nuove associazioni e gli schemi sintassonomici lo annoiavano. Spesso metteva in evidenza gli aspetti che legano la vegetazione all'habitat umano, e questo non solo da un punto di vista antropocentrico (l'ambiente in funzione dell'uomo) ma anche nel senso opposto: rimangono classiche le sue ricerche sulla forma delle case coloniche in Germania. A Zurigo aveva anche sperimentato con Cristofolini i primi programmi di elaborazione automatica con un calcolatore a schede perforate, senza però arrivare a risultati operativi.

Come presidente per molti anni della Società tedesca di Ecologia e successivamente primo Presidente della International Association for Vegetation Science, Ellenberg ha avuto una posizione centrale negli sviluppi recenti della fitosociologia. Il suo contributo più importante (relativamente al tema che stiamo trattando) è l'introduzione dei valori di bioindicazione (*Zeigerwerte*, ELLENBERG, 1974) che permettono di inserire una specie in uno spazio ecologico a 7 dimensioni corrispondenti ai fattori ecologici fondamentali (luce, calore, pH etc.): si tratta di un geniale esempio di expert system, che Ellenberg ha saputo realizzare per tutte le specie della flora della Germania (oltre 2000). Su questa idea aveva lavorato già negli anni '50, ma al momento della pubblicazione (1974) essa non ha suscitato particolare interesse, forse perché era troppo avanzata rispetto alla cultura ed interessi del momento. Del resto, anche negli anni successivi, lo stesso ideatore non è andato molto oltre singoli saggi di applicazione: solo negli anni '90, con la possibilità di gestire mediante calcolatore l'immensa quantità di informazioni resa disponibile, ci si renderà conto che un nuovo, potente strumento di ricerca era stato messo a disposizione della comunità scientifica. Adesso ne esiste una versione ampliata per le specie della flora italiana (PIGNATTI, MENEGONI e PIETROSANTI, 2005), tuttavia le potenzialità dei valori di bioindicazione sono state finora utilizzate solo in parte. Maggiore fortuna ha avuto il suo trattato sulla vegetazione dell'Europa Centrale (ELLENBERG, 1988).

Nel 1980, a pochi mesi di distanza

l'uno dall'altro, Tüxen e Braun-Blanquet ci lasciavano. Nei primi contatti tra colleghi, ci si sente dei sopravvissuti, e prevale lo sbigottimento, nel constatare che erano venuti a mancare due punti di riferimento insostituibili: la sensazione che le cose mai potranno tornare ad essere come prima. Nella prima riunione, nella primavera successiva, ci si ritrova con un senso di smarrimento: ...e adesso? ma la situazione viene presa in mano dai più esperti, in particolare il gruppo degli olandesi (Westhoff, Barkman e van der Maarel tra i primi), e si decide di dare nuova vita all'associazione internazionale di fitosociologia (esistente già dagli anni '30). Essa viene riproposta come International Association for Vegetation Science (da qui in avanti indicata come IAVS), con una decisa proiezione intercontinentale, con Ellenberg come presidente ed un gruppo promotore che riunisce gli abituali frequentatori dei simposi organizzati da Tüxen; questi simposi continuano, con una rotazione tra diverse sedi europee ed in seguito anche extraeuropee; Vegetatio, organo ufficiale della società, è affidato a van der Maarel che in poco tempo lo fa diventare un periodico d'avanguardia. Anche in Italia si muove qualcosa: per iniziativa di Franco Pedrotti e Jean-Marie Géhu nel 1984 viene avviata Braun-Blanquetia, come serie di studi monografici, attualmente quasi una cinquantina (Fig. 3). Il popolo di coloro che praticano la fitosociologia si inserisce progressivamente nelle moderne strutture della comunità scientifica. Negli anni '80 si tengono diversi corsi per diffondere i metodi di elaborazione automatica dei dati fitosociologici, alcuni di questi a Roma.

APPLICAZIONI

Nelle pagine precedenti è stato riassunto criticamente lo sviluppo delle idee portanti della fitosociologia, durante un periodo di quasi un sessantennio, nel quale sono stato di caso in caso spettatore o attore comprimario. Tutti questi avvenimenti sono il risultato della dinamica interna di un gruppo nel quale si sono avuti momenti di forte confronto e sviluppo di nuove idee. Però, durante questo periodo, la fitosociologia ha ricevuto uno stimolo importante anche dall'esterno. Braun-Blanquet aveva sempre ricercato contatti con le pubbliche amministrazioni e con il mondo produttivo, per evitare che la fitosociologia rimanesse confinata entro una stretta cerchia di teorici. Il punto d'incontro è stato trovato nella possibilità di

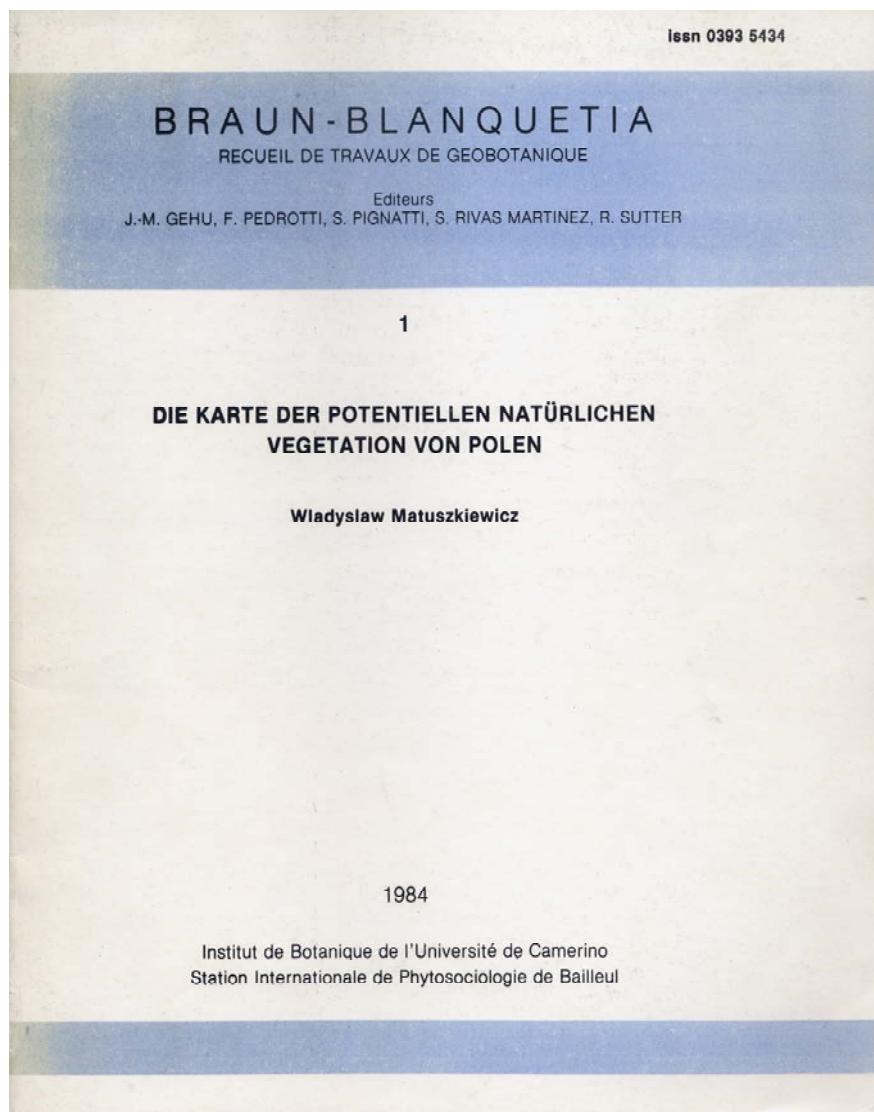


Fig. 3 - Copertina del primo volume di Braun-Blanquetia.

ottenere attraverso la fitosociologia una conoscenza approfondita del territorio, dalla quale ricavare le informazioni necessarie per una corretta gestione.

Per questo scopo, l'esigenza essenziale è di poter trasferire le conoscenze acquisite attraverso l'analisi fitosociologica, comprensibili soltanto a pochi studiosi, ad un pubblico più ampio di tecnici ed amministratori. Da qui nascono le prime carte fitosociologiche, generalmente a grande scala (1:10.000 - 1:25.000), già negli anni '30, nella Francia meridionale. Il metodo viene ripreso e sviluppato in Germania, dove in quel periodo è in corso un complesso programma di pianificazione territoriale: nasce così il centro di cartografia della vegetazione diretto da Tüxen, prima a Hannover e poi, negli anni di guerra e nel dopoguerra a Stolzenau ed a Rinteln, sempre nei dintorni di questa città. Dobbiamo sostanzialmente a Tüxen ed ai suoi collaboratori, se la cartografia fitosociologica si è evoluta dal risultato di ricerca individuale ad un metodo di lavoro in grado di fornire risultati confrontabili a scala

continentale.

Anche in Italia la cartografia della vegetazione diventa una motivazione importante per lo sviluppo della fitosociologia. Se ne occupa soprattutto Giacomini, già nelle prime esperienze alpine allo Stelvio ed allo Spluga; durante i suoi successivi periodi a Napoli e a Roma inserisce in questa attività giovani geologi (Bruno, De Marco, Avena, Blasi), che portano un'esperienza ormai ben maturata nel campo delle carte geologiche, e questo permette di raggiungere in poco tempo un buon livello tecnico anche nelle carte realizzate in Italia. In maniera del tutto indipendente, anche Pedrotti produce una serie di documenti cartografici in varie zone dell'Appennino ed in Trentino; a lui dobbiamo anche l'unico manuale di cartografia geobotanica pubblicato in Italia (PEDROTTI, 2004).

Negli ultimi anni si diffondono le tecniche per l'utilizzazione a scopi civili dei dati satellitari: nelle fasi dell'avvio di Carta della Natura, nel 1995-96, ho partecipato ai primi tentativi di rileggere i dati satellitari con il linguaggio

della fitosociologia, trovando tali difficoltà da farmi dubitare che per questa via si potesse realmente arrivare a carte di vegetazione. Nel frattempo, la qualità dei dati di base è molto migliorata ed oggi la parte più noiosa del lavoro cartografico è ormai affidata al computer. Anche qui, però, la partecipazione impegnata del ricercatore in campagna rimane indispensabile.

Negli anni '50 si riteneva possibile trarre dai risultati della ricerca fitosociologica nuove tecniche per la gestione dei coltivi, prati stabili e dei pascoli: ricerche in questo senso si sviluppano a Pavia sulle marcite e sulla vegetazione infestante di risaie e campi di cereali. Uno studio approfondito dei prati permanenti del Trentino (PEDROTTI, 1963) mette in evidenza le particolari caratteristiche ecologiche di questo ecosistema semi-naturale realizzato dall'uomo nei secoli passati. Tuttavia, l'impetuoso sviluppo della meccanizzazione in agricoltura e dell'impiego di prodotti di sintesi come fertilizzanti o biocidi ha purtroppo svuotato l'interesse di queste ricerche, che potrebbero essere la base per un approccio soft all'agricoltura biologica. Nel campo forestale, invece, le conoscenze derivanti dall'approccio fitosociologico sono rapidamente entrate nella prassi, dapprima in Svizzera, Paesi Bassi, Austria e Germania e quindi anche da noi ed in generale in Europa, Giappone e Sudafrica.

La fitosociologia si apre ad un pubblico più vasto con l'approvazione della Direttiva "Habitats" del 1992, che prevede uno standard europeo per la definizione delle unità vegetazionali. In quel momento ci si è potuto rendere conto di quanto sarebbe stato utile disporre del Prodromus, sul quale si era tanto (troppo) discusso. Infatti, la Comunità presenta Corine, uno standard preparato in poco tempo ed in maniera sommaria da persone incompetenti, con vistose incongruenze e gravi lacune per quanto riguarda la vegetazione dei territori mediterranei ed alpini. Alle nostre proteste, si risponde che è necessario, anzitutto far partire il programma, rimandando la revisione ad un periodo successivo, che non è mai arrivato. Così, nelle sue varie versioni come Corine e Eunis, tutta l'importante attività della conservazione è vincolata all'uso di un documento difettoso, sul quale, nella prassi è stato necessario affrontare continue discussioni, redigere manuali interpretativi e introdurre una buona percentuale di confusione in argomenti che sembravano chiariti in maniera definitiva.

Nonostante queste difficoltà, la ri-

cerca fitosociologica ha potuto portare un contributo fondamentale nel campo della conservazione. Nelle riserve e parchi terrestri (che sono la grande maggioranza), la carta fitosociologica è la base insostituibile per l'inventario del patrimonio naturale (vegetale ed animale) da proteggere; il monitoraggio delle comunità vegetali fornisce l'informazione per le azioni da svolgere, nel quadro di una conservazione che non sia soltanto attività inventariale, ma tenda verso l'interazione con la naturale dinamica degli ecosistemi. Non è un caso, che Valerio Giacomini, l'araldo della fitosociologia in Italia, negli ultimi anni della sua vita si sia dedicato con successo a sviluppare la coscienza del grande patrimonio naturale concentrato nel nostro paese e della necessità di conservarlo e trasmetterlo alle prossime generazioni.

Un discorso particolare merita l'Ecologia del Paesaggio, che si è sviluppata inizialmente nell'Europa Centrale in stretta collaborazione con la fitosociologia; oggi costituisce un campo di azione e ricerca specializzato, ma il contatto rimane, grazie alla fecondazione incrociata tra le due culture, ad un comune patrimonio di conoscenze ed a parallele prospettive di sviluppo. Lasciamo la parola su questo argomento a Vittorio Ingegnoli.

FITOSOCIOLOGIA ED ECOLOGIA DEL PAESAGGIO (UN CONTRIBUTO DI VITTORIO INGEGNOLI)

Come noto, fra la fine del XIX secolo e l'inizio del XX la scienza ha incominciato a presentare dei cambiamenti epocali che l'hanno messa in crisi. La Fisica ha perduto le sue certezze meccanicistiche, a causa del progredire della fisica delle particelle sub-atomiche (Meccanica quantistica), la sua fede in un tempo e in uno spazio "assoluto", a causa della Teoria della Relatività e nella reversibilità dei processi, a causa degli studi sulla termodinamica (e.g. Boltzmann). Inoltre, la convinzione positivista che i dati dell'esperienza possano tradursi in conoscenza scientifica di per sé, è stata decisamente smentita. Infatti, come aveva dimostrato Einstein (1918, 1923), questo punto di vista è sbagliato e può portare a una catalogazione, non a un sistema teorico.

Al pari di tutti gli studi di ecologia, gli studi sulla vegetazione portati avanti da Braun-Blanquet sono stati indubbiamente utili e importanti, ma non sono riusciti a stare al passo con gli stravolgiamenti dei paradigmi scientifici. Per tali

ragioni, gli studi di fitosociologia (Braun-Blanquet) presentano ovvi vantaggi per quanto riguarda la descrizione (la catalogazione) della vegetazione, ma anche sicure limitazioni, essendo basati su una epistemologia positivista e su concetti ecologici oggi superati.

Diamo una rapida sintesi dei limiti principali (PIGNATTI S., BOX e FUJIWARA, 2002; INGEGNOLI, 2002, 2005; INGEGLI e PIGNATTI S., 2007): a) riferimento ad un concetto di naturalità che esclude in ogni caso l'uomo; b) dinamica basata sul concetto di successione ecologica intesa ancora come lineare e deterministica; c) riferimento ad uno "spazio ecologico" che non considera il principio delle proprietà emergenti; d) ricorso al concetto di "vegetazione potenziale" che non considera il ruolo dei disturbi nei sistemi ecologici; e) ignoranza delle funzioni di sistema complesso e scaladipendenti, pretendendo di poter studiare il paesaggio col metodo deterministico basato sul "sigmetum" (TÜXEN, 1956; RIVAS-MARTÍNEZ, 1987).

Un confronto con lo studio del paesaggio, specifico livello di organizzazione della vita sulla Terra (INGEGLI, 2002), mostra inoltre che (f) il livello di organizzazione a cui ci si riferisce è diverso: la comunità/ecosistema in un caso, l'unità di paesaggio nell'altro; g) esistono limiti alla capacità rappresentativa delle specie. Inoltre, ogni metodo di stima della "distanza ecologica" tra vegetazione potenziale e reale presuppone il paesaggio ottimale come omogeneo, implicando l'insieme di tutte le componenti di una serie di vegetazione arrivate allo stadio climacico, il che è contrario a tutti i principi di ecologia del paesaggio, e al concetto stesso di biodiversità.

Mentre, quindi, da un lato la fitosociologia è stata un buon elemento propulsore degli studi sul paesaggio, che senza una appropriata descrizione delle fitocenosi sarebbero stati in difficoltà, dall'altro essa ha impedito la formulazione di alcune domande basilari, quali: 1) come considerare il contributo di una tessera vegetata alla metastabilità generale di una unità di paesaggio?; 2) come paragonare i dati ecologici di una macchia forestata con quelli di un altro tipo di vegetazione?; 3) come utilizzare i caratteri ecologici dei diversi tipi di vegetazione per arrivare a una valutazione diagnostica riferita a una certa unità di paesaggio?; 4) come integrare in modo sistemico gli altri parametri ecologici con quelli relativi alla vegetazione?

Le risposte coerenti alla bionomia del paesaggio iniziano con la proposta

del nuovo concetto di "the fittest vegetation for" (per una bibliografia su questo argomento cfr. INGEGLI e PIGNATTI S., 2007) per superare quello di vegetazione potenziale. Questa reinterpretazione del concetto di vegetazione potenziale sta ad indicare "la vegetazione più calzante: in condizioni climatiche e geomorfiche di un limitato periodo di tempo in un certo luogo definito; in funzione della storia dello stesso e con un certo insieme di disturbi incorporabili (compresi quelli umani); in condizioni naturali e non naturali". Le implicazioni sono diverse: ad esempio, i concetti di vegetazione primaria o secondaria perdono di significato; inoltre, in regioni fortemente antropizzate non ha più senso paragonare la vegetazione reale con quella potenziale, dati i cambiamenti ambientali in atto. Il concetto di "the fittest vegetation", unito al principio che "...il comportamento di un sistema dipende non soltanto dai suoi elementi componenti, ma anche dal modo in cui essi sono assemblati e disposti..." (Principio delle Proprietà Emergenti) evidenzia un grande cambio di prospettiva anche nelle applicazioni.

TESTIMONIANZE E RICORDI 3. IL SIMPOSIO SUI COMPLESSI DI VEGETAZIONE (1977)

Alla fine degli anni '70 si sentiva che una nuova visione della fitosociologia, ormai necessaria, stava maturando, nel metodo e nei concetti di base. Molti di noi pensavano che questo rinnovamento potesse venire fondato sull'applicazione dei procedimenti automatici di analisi dei dati, che già stavano producendo i primi frutti, oppure attraverso una fecondazione incrociata con la ricerca biotassonomica: sullo sfondo stava la prospettiva di un passo decisivo verso l'elaborazione del Prodromus. Così, quando Tüxen convocava il simposio annuale per il 1977 con il titolo "Complessi di vegetazione (Vegetationskomplexe)" molti di noi vissero una sorta di brain storming, nel tentativo di trovare una via metodologicamente ineccepibile per rielaborare l'esperienza fitosociologica dal punto di vista della complessità. Era un argomento del quale, fino a quel momento, non si era mai parlato. Fin dal primo giorno si apriva una vivace discussione sulla relazione introduttiva di Tüxen e sulle idee che altri tra i partecipanti venivano presentando. Le differenze nei punti di vista e nei risultati facevano prevedere un confronto costruttivo. Invece Tüxen

sembrava considerare la discussione metodologica una perdita di tempo e proponeva direttamente una nomenclatura formalizzata da introdurre per classificare i complessi in un sistema gerarchico parallelo a quello già utilizzato per le associazioni. Sembrava quasi che volesse arrivare alle conclusioni, prima ancora di aver discusso su quali premesse fondare il nuovo concetto. Quella sera molti dei partecipanti venuti da lontano continuarono a discutere fino a tardi, su cosa si potesse realmente intendere per complesso di vegetazione.

Il giorno successivo, Tüxen prendeva la parola per spiegare come avesse avuto un'idea: in breve, il complesso è una somma di associazioni, che in matematica viene indicata con la lettera greca Σ , dunque un "sigmetum"; l'assonanza con il nome della SIGMA di Montpellier (al quale erano legati i ricordi giovanili di tanti fra i presenti) rendeva familiare questa parola, da posporre, come una desinenza, a tutti i nomi di complessi. Il discorso suscitava reazioni discordanti: alcuni davano un'approvazione entusiastica, però molti altri (anch'io tra questi) restavano perplessi. Si faceva subito notare come quello che stavamo cercando non fosse un nome, ma un concetto scientifico, senza il quale anche il nome restava privo di significato. Inoltre, facevamo notare come il termine usato fino a quel momento (complesso) avesse un significato (= insieme di fattori interagenti) ben più profondo che una semplice sommatoria. Ma queste proteste rimanevano senza seguito.

Nei commenti successivi ci si rendeva conto come si stesse avviando la possibilità di creare una quantità di nuovi nomi da applicare a oggetti che mancavano di una definizione scientifica: una sbandata in senso nominalistico di cui nessuno sentiva il bisogno. Infatti, in mancanza di una non ambigua definizione, si danno giudizi soggettivi, cioè si esce dall'oggettività, necessaria perché un linguaggio possa dirsi scientifico.

Inoltre, veniva criticato lo stesso nome "sigmetum", un neologismo privo di senso, inadatto per il linguaggio scientifico. A questo si rispondeva che nel progresso scientifico ci si era ormai abituati a simili neologismi: neutrino, buchi neri, i quark. Certo, ma questi termini si basavano sul formidabile edificio concettuale della fisica teorica: come avremmo potuto spiegare in una discussione con colleghi fisici, chimici, matematici, geologi o biologi cosa fosse un sigmetum? Queste sono le prime obiezioni che si sono immediatamente

presentate nella prima discussione su questo argomento. Non è stato possibile troncare il discorso sul nascere: è abbastanza paradossale che quando i sigmeti sono stati proposti, l'unico italiano presente fossi io, di parere contrario, ma oggi proprio l'Italia è uno dei pochi posti nei quali si continua a parlarne. Comunque, devo osservare che mentre scrivo queste righe, noto come in rete cliccando su sigmetum si ottengano 5.000 voci, mentre per vegetation complex ce ne sono 10 milioni. In questa sede dobbiamo limitarci su questo punto ad argomenti di carattere molto generale: per chi volesse approfondire, consigliamo la lettura dell'autorevole confutazione in ELLENBERG (1996, pag. 916 e segg.).

Alla fine del convegno, commento l'accaduto con l'amico Gerhard Helmut Schwabe, ecologo di grande saggezza e con lunghe esperienze in vari continenti, e lui esce in questa riflessione: "È un fatto ben noto che i popoli con culture animiste, quando si trovano di fronte ad un evento che non riescono a comprendere, gli danno un nome, e con questo ritengono di essere in grado di dominarlo".

FITOSOCIOLOGIA IN AMBIENTI EXTRAEUROPEI

I primi tentativi di estendere l'analisi fitosociologica al di fuori dell'Europa risalgono agli anni '30, tuttavia per arrivare ad una completa applicazione del metodo si devono attendere gli anni '60, quando Tüxen ospita ripetutamente studiosi giapponesi, e quindi si reca lui stesso in Giappone dove Miyawaki (che in precedenza si era specializzato sotto la sua guida) ha preparato un gruppo di collaboratori esperti, che applicano i metodi della fitosociologia con un particolare moltiplicatore, intrinsecamente giapponese, di precisione, laboriosità e senso artistico. Nella prima escursione fitosociologica transcontinentale (1974), che si sviluppa su Hokkaido, Honshu e Kyushu,abbiamo la possibilità di conoscere una comunità di studiosi giapponesi competenti e molto motivati: la quantità di pubblicazioni ricevute in omaggio mette in crisi le nostre possibilità di trasporto. Successivamente, studiosi provenienti dalla Germania diffondono questo nuovo modo di far ricerca in varie zone dell'America latina e si formano centri locali nei quali si pratica la fitosociologia, in Argentina, Cile, Brasile, mentre sarà Pedrotti che negli anni '80 effettuerà le prime prospettive alle alte quo-

te della Bolivia. Con la dissoluzione dell'Unione Sovietica gli studiosi russi hanno avviato ampi programmi di ricerca in Siberia e fino alla Kamchatka, altri gruppi europei hanno iniziato l'esplorazione dei deserti centro-asiatici e del Gobi. Nell'America Settentrionale un centro attivo è nel Quebec, mentre negli USA soltanto negli ultimi anni sono iniziate ricerche con metodi comparabili. I colleghi olandesi, con Westhoff e Werger trasmetteranno l'esperienza fitosociologica nell'Africa meridionale, ed in seguito si avranno più o meno approfondate ricerche in molti altri paesi. La prima difficoltà nelle ricerche oltremare è la mancanza delle indispensabili conoscenze sulla flora, in paesi dove i botanici sono rari e mancano flore pubblicate; per questo, in alcuni casi i risultati di approfondate ricerche non sono arrivati alla pubblicazione. Ellenberg ha lavorato molto in Sudamerica, compiendo molte volte la traversata dalla costa atlantica a quella pacifica e viceversa, con ricche raccolte, però non è riuscito a terminare lo studio di questo materiale; anche i risultati delle nostre prospettive in Australia Occidentale (Erika e Sandro Pignatti, attualmente oltre 1500 rilievi) soltanto in minima parte sono arrivati alla pubblicazione.

Queste ricerche hanno sicuramente arricchito l'esperienza fitosociologica ed integrato la teoria con nuovi punti di vista. Anche in questo caso è confermato il valore predittivo delle conoscenze fitosociologiche: infatti in molti ambienti si possono individuare casi impressionanti di strutture parallele, ad es. la foresta subalpina di conifere che in Europa è costituita da *Picea abies*, in Giappone da *Picea jezoensis* e sulle Montagne Rocciose da *Picea engelmannii* e *Pseudotsuga menziesii*. In tutta la fascia circumboreale questi casi sono frequenti, però a volte si scoprono analogie anche su lunghe distanze, ad es. le faggete con sottobosco di bambu nani: in Giappone c'è *Fagus crenata* con varie specie di *Sasa* e *Arundinaria*, nelle Ande meridionali *Nothofagus* con il piccolo bambu *Chusquea*. Ricordo una bella formazione sempreverde a Cape Naturaliste, all'estremo sud-ovest del continente australiano con tutto l'aspetto di una pineta mediterranea, dove la specie arborea invece era una *Melaleuca* (mirtacee) a foglie aghiformi, che anche nel portamento e ramificazione aveva l'aspetto di un pino (in Australia non esistono specie indigene di *Pinus*). Così, i paragoni intercontinentali arricchiscono anche le nostre conoscenze sugli ecosistemi nostrani:

ad es., per quanto riguarda il problema dell'incendio come fattore naturale dell'ecosistema, l'esperienza accumulata dagli studiosi locali in California ed in Australia ci ha permesso di interpretare meglio il problema nella vegetazione mediterranea.

Tuttavia esistono anche differenze profonde; la più impressionante secondo me è il fatto che il suolo nella foresta tropicale è privo della strutturazione in orizzonti che si nota nelle nostre foreste. In generale questo viene attribuito al clima caldo e umido, che permette una rapida demolizione della materia organica, ed essa non ha la possibilità di accumularsi nel suolo. Questo sicuramente è un fatto accertato, tuttavia in Australia occidentale questi suoli non strutturati si hanno anche nell'area a clima temperato caldo di tipo mediterraneo. A questo proposito va tenuto presente che le aree attualmente a clima tropicale caldo-umido sono in queste condizioni almeno dall'inizio del Pliocene e lo stesso vale per le aree a clima mediterraneo dell'Australia. Dunque, siamo di fronte ad un problema che non si può risolvere soltanto con analisi chimiche, ma che richiede una visione fondata su tempi lunghi.

Un altro importante progresso portato dall'esperienza sulla vegetazione di altri continenti è il distacco dalla specie come componente elementare dell'associazione. Infatti, la ricerca fitosociologica su scala regionale, come quella effettuata in Europa fino agli anni '50, è strettamente legata alle specie, come componenti elementari della comunità. Il rilievo si risolve in un catalogo di specie e la valutazione del rilievo avviene sulla base delle specie caratteristiche. Invece, in un paragone intercontinentale le specie in comune sono pochissime o (più spesso) nessuna. In qualche caso si passa ai generi, alle famiglie, ma il significato di paragoni a questo livello diviene sempre più opinabile. Bisogna dunque staccarsi dal linguaggio di derivazione linneana, introdotto per scopi completamente diversi, e crearne uno nuovo, basato sugli adattamenti ecomorfologici (consistenza della foglia, cuticola, distribuzione degli stomi etc.) ed ecofisiologici (periodicità, disseminazione, impollinazione etc.); si tratta di quelli che oggi vengono indicati come i "traits" delle piante: un discorso che tuttora rimane ancora in gran parte da sviluppare. In altri termini, nella fitosociologia classica si identificava un elemento in comune tra la vegetazione delle spiagge mediterranee ed atlantiche nella presenza in entrambi i casi di *Ammophila*; oggi pos-

siamo allargare il paragone ad altri ecosistemi dove si hanno graminacee con simili adattamenti, come *Spinifex* nelle isole dell'Indonesia e *Triodia* nel deserto sabbioso australiano. Dalla vicarianza tassonomica si passa alla vicarianza strutturale, ecologica, funzionale.

Concludiamo questo rapido sguardo sui paragoni intercontinentali notando come le ricerche fitosociologiche che hanno avuto maggiore successo in territori extraeuropei siano quelle riguardanti paesi a clima temperato o freddo, sia nell'emisfero boreale che in quello australe. Nella fascia intertropicale si hanno dati sulla vegetazione della savana, mentre per quanto riguarda la foresta pluviale, l'unico studio complessivo è di Borhidi, sulla vegetazione di Cuba. In effetti, lo studio fitosociologico nella foresta tropicale urta contro grandi ostacoli, come ho constatato personalmente in tentativi eseguiti nella Cina meridionale, Thailand, Indonesia e Messico: anzitutto, l'estrema difficoltà di riconoscere le specie, la struttura arborescente pluristratificata, la mancanza di esemplari in fiore. Per eseguire un censimento credibile sarebbe necessario costruire impalcature per raggiungere tutti gli strati della vegetazione e ritornare sullo stesso posto in tutte le stagioni.

È possibile che queste difficoltà dipendano dall'insufficienza del ricercatore singolo, che ha fatto il suo training sulla vegetazione delle fascie temperate: forse potrebbero essere superate con lavoro di gruppo ed ampia disponibilità di mezzi tecnici. Però esiste anche la possibilità che tra la vegetazione delle zone temperate e fredde e quella tropicale vi sia realmente una differenza di principio, in quanto la prima esiste solo da poco più di 10.000 anni (Olocene), mentre la seconda da parecchi milioni di anni, durante i quali il suolo è stato dilavato da tutti i materiali solubili ed ha perduto la capacità di accumulare humus.

Se questo è vero, se ne dovrebbe concludere che le associazioni vegetali sono una caratteristica dei climi temperati e freddi, e rimane il dubbio se abbia realmente un senso tentare di usare il metodo fitosociologico per lo studio della vegetazione tropicale. In conseguenza, la fitosociologia andrebbe ridimensionata come una caratteristica della vegetazione di climi extratropicali. Oggi abbiamo la tendenza a considerare la foresta pluviale come un caso limite o un'eccezione rispetto alle condizioni delle zone temperate e fredde, ma non è un'eccezione da poco, in quanto si tratta del più complesso ecosistema

forestale del globo. La vegetazione dell'ambiente tropicale è una challenge anche per chi lavora sulla vegetazione europea.

TESTIMONIANZE E RICORDI 3. DUE MESSAGGI

Uno sguardo sulla situazione attuale ci rende chiaro il fatto che lo sforzo di rinnovamento degli anni '80 ha realizzato una nuova situazione, nella quale una comunità di studiosi, diffusa in tutto il globo, sviluppando autonomamente iniziative individuali, ma mantenendo il background unitario della tradizione fitosociologica, è in grado di operare, con continui progressi nei metodi e nelle conoscenze. Si è avviato un ciclo, che non si è ancora concluso. Prima di esaminare la situazione attuale e le prospettive vorrei tuttavia inserire un breve intermezzo con una testimonianza personale.

Lo sviluppo della fitosociologia, dal dopoguerra in poi, per oltre 30 anni è stato largamente condizionato, come si è visto, dall'attività di due grandi personalità scientifiche: Braun-Blanquet e Tüxen. Avendo avuto la possibilità di uno scambio d'idee con l'uno e poi con l'altro pochi giorni prima che ci lasciassero, può essere rilevante prendere conoscenza delle loro opinioni, con tutto il rispetto e reverenza che si impongono, date le condizioni nelle quali esse vennero espresse.

Durante il convegno svoltosi a Rinteln nell'aprile 1980, il figlio di Tüxen mi ha dato il permesso di avere un breve scambio d'idee con il padre: era molto indebolito, e mi era chiaro che ci stavamo incontrando per l'ultima volta. Alla conclusione del colloquio, quando trovai il coraggio di chiedergli, quale ritenesse il compito più importante per lo sviluppo della fitosociologia, risponde con chiarezza: "Prodromus machen" (fare il Prodromus). Questo è il messaggio che ci viene dallo studioso che per decenni ha maggiormente contribuito allo sviluppo di una comunità scientifica dedicata allo studio della fitosociologia.

Pochi mesi più tardi, nel settembre dello stesso anno, il Gruppo di Lavoro per lo studio delle successioni su aree permanenti si riunisce a Montpellier assieme al Working group for data Processing per il suo meeting conclusivo: questa volta non si viene alla SIGMA, ma nella moderna struttura di ricerca del CEFE dove lavora Romane. Durante il discorso d'apertura, in maniera del tutto inaspettata compare la figlia Mi-

reille Braun-Blanquet assieme al padre, che cammina con passo pesante, ma fermo, fra lo stupore di tutti. In questa occasione ha detto soltanto poche parole, e così pure quando alla sera tutti i partecipanti sono invitati per una breve visita alla SIGMA. Il giorno successivo siamo invitati a cena, Erika ed io, e c'è la possibilità di un contatto diretto: ma è difficile intendersi, a causa della sorridità ormai quasi completa. Alla fine decido di scrivere qualche bigliettino, anche con Beethoven negli ultimi anni avevano fatto così, e pongo la stessa domanda rivolta a Tüxen. La risposta mi stupisce: spiega faticosamente che ritiene prioritario uno studio dettagliato per chiarire le penetrazioni di specie e associazioni mediterranee nelle valli dell'Appennino e definire il limite di queste verso l'Italia settentrionale; insiste: un'analisi sul terreno, portando come modello la sua ricerca sulle valli aride delle Alpi. Pochi giorni più tardi, il 20 settembre 1980, arriva in visita il suo allievo ed amico Oriol de Bolós di Barcellona, con la moglie: lui li accoglie sulla scala davanti alla porta di casa, cade e non si rialzerà più: non è chiaro se la caduta abbia causato un malore oppure sia avvenuto il contrario.

Due risposte molto differenti. Quella di Tüxen dimostra quanto avesse tenuto al Prodromus e lo considerasse un'opera necessaria, ma ancora incompiuta. La risposta di Braun-Blanquet sul primo momento mi aveva deluso: sembrava tutt'al più un buon titolo per una tesi di dottorato. Ripensandoci, in seguito, mi son reso conto che questo è un argomento di ricerca pura, che investe temi di grande significato, sia attualistici (il gradiente climatico ed ecologico) che storici: scambi floristici durante le glaciazioni, la recente orogenesi appenninica, il significato del complesso M. Antola - M. Lesima - M. Maggiorasca come punto di snodo, ed ancora più indietro nel tempo, il rapporto con la Corsica. Sono dei temi sui quali oggi non ne sappiamo più di quanto ne sapesse Braun-Blanquet trent'anni fa. Col senno di poi potrei aggiungere altri temi paralleli, come i rapporti transadriatici (Dinaridi - Appennino Centrale - Gargano), quelli transegeici (Grecia - Puglia) e transmediterranei (Maghreb - Sicilia). Questi sono "buchi neri" che ci impediscono di impostare in maniera oggettiva la spiegazione della straordinaria biodiversità dell'Italia, e che oggi potrebbero essere chiariti con l'aiuto dell'analisi molecolare. Pecato non averli messi all'ordine del giorno per l'anno della biodiversità che si sta concludendo.

SITUAZIONE ATTUALE E PROSPETTIVE

Nelle risposte degli studiosi che hanno maggiormente contribuito alla crescita della fitosociologia nel secolo passato, troviamo le due principali motivazioni per chi ha lavorato in questo campo: il contributo ad una generale visione del mondo e l'esplorazione dell'ignoto, il "natural desiderio del sapere" come Federico Cesi scriveva, all'inizio della rivoluzione scientifica, quattro secoli orsono.

Alla fine degli anni '80 cadono le barriere che per 45 anni avevano diviso l'Europa in due sistemi politici tra loro quasi incomunicanti ed il mondo si è aperto allo stile di vita della globalizzazione, con la facilità degli spostamenti ed i collegamenti on line. La IAVS ha accentuato il carattere di società internazionale a diffusione globale, con oltre un migliaio di Soci attivi in tutti i continenti ed alla presidenza si sono succeduti Ellenberg (Germania), lo scrivente, quindi Box (USA) seguito da Peet (USA). Dopo la cessazione della casa editrice Junk, Vegetatio, che per oltre 30 anni era stata il periodico di riferimento per la fitosociologia, viene posizionata nel settore dell'ecologia vegetale: essa è sostituita come organo ufficiale dal Journal of Vegetation Science, creazione di van der Maarel oggi arrivato ormai al 20esimo volume, con 2 sezioni ed elevato impatto. Ogni anno viene organizzato un simposio ed una escursione, che di volta in volta sono stati ospitati nei più importanti centri di ricerche sulla vegetazione. Il passaggio dalla dimensione continentale a quella globale è compiuto.

È il progresso verso la condizione di una moderna società scientifica, che però porta un problema imprevisto. Durante il periodo dei simposi di Rinteln, la lingua d'uso corrente era il tedesco e questo aveva limitato la partecipazione di chi non poteva esprimersi bene in questa lingua: minima, ad es., la partecipazione italiana. Con la creazione della IAVS si passa all'inglese e questo costringe molti (me per primo) ad esprimermi in questa lingua. Uno sviluppo che considero positivo: esso però provoca la reazione di spagnoli e francesi, che non accettano l'inglese come lingua internazionale, e formano in alternativa la "Association Amicale de Phytosociologie" francofona per iniziativa del prof. Jean-Marie Géhu (Lille-Bailleul), alla quale aderisce anche la Società Italiana di Fitossociologia: una decisione antistorica, che esclude gran parte degli studiosi di lingua neo-

latina dal più avanzato filone della ricerca internazionale. Una divisione che ancora oggi pesa negativamente sulla presenza degli studiosi mediterranei nella IAVS.

Per quanto riguarda i problemi dei quali mi sono più strettamente interessato, il messaggio contenuto nelle ultime parole di Tüxen mi è rimasto sempre presente, così nel 1991-1992 nell'ambito della IAVS veniva deliberata (su proposta di Grabherr e Mucina, fortemente appoggiata da me, come presidente) la costituzione del gruppo di lavoro European Vegetation Survey (EVS), che da allora si riunisce in primavera in forma di workshop presso l'Orto Botanico di Roma (ed in altre sedi, in anni alterni), continuando la tradizione dei simposi tüxeniani. Si sperimentano con successo metodi adatti di raccolta dei rilievi in banche dati e programmi di elaborazione. Ai principi i progressi sono rapidi, anche favoriti dalla contemporanea pubblicazione di importanti esempi di survey a carattere nazionale, come quelli per Austria (GRABHERR, MUCINA *et al.*, 3 vol.), Paesi Bassi (SCHAMINÉE *et al.*, 5 vol.), Regno Unito (RODWELL, 5 vol.) e la Germania nord-occidentale (OBERDORFER, 5 vol.). Dapprima sembra che basti scegliere uno di questi esempi e proiettarlo su base continentale per risolvere il problema, ma presto ci si rende conto che siamo di fronte ad un problema ben più complesso: anche con una drastica semplificazione, e rinunciando ad alcune zone ancora incompletamente studiate, per l'intera Europa ci vorrebbero almeno 20-30 volumi: chi è capace di scriverli? chi li pubblica? e, soprattutto: chi li legge? La pubblicazione di un'opera generale, in larga collaborazione e con molti volumi appare sempre più un ritorno al passato, destinato al fallimento. Così ci si orienta verso la possibilità di realizzare un sito in internet nel quale riunire le conoscenze, ma anche su questo finora non si è andato molto oltre le dichiarazioni di principi.

Allora, per fissare l'esperienza raccolta durante i primi workshop, viene pubblicato il catalogo delle unità superiori della vegetazione europea (RODWELL *et al.*, 2002): un libretto di meno di 200 pagine: la montagna ha partorito un topolino? Forse, però sta di fatto che un'opera del genere non era mai stata realizzata prima, nemmeno quando le alleanze note per l'Europa erano un decimo di quelle attuali. E negli 8 anni successivi, nessuno è stato in grado di produrre un'opera che superasse questo primo risultato. Il gruppo EVS ha 20 anni di attività: è ormai maggiorenne ed

ha ancora un ampio compito davanti a sé.

Per quanto riguarda le applicazioni della fitosociologia, un campo interamente nuovo si sta aprendo negli ultimi anni a causa del progressivo peggioramento della situazione ambientale, ormai a livello globale. Gli interventi sull'ambiente finora sono condotti con applicazioni tecnologiche, che nella maggior parte dei casi provocano danni gravissimi e spesso irreversibili: il consumo di territorio si estende con dinamica progressivamente accelerata, e lo stesso avviene per l'esaurimento delle risorse marine, la distruzione delle foreste tropicali, la dissipazione della biodiversità. La causa sta nel fatto che l'ambiente (ed in particolare la vegetazione) sono considerati superfici o biomasse, con un ottuso riduzionismo meccanico: la complessità dell'ecosistema non entra nei calcoli economici. L'applicazione dell'approccio di Braun-Blanquet e del concetto di complesso di vegetazione, in molti casi potrebbero permettere di proporre soluzioni adeguate e sostenibili. Vanno indicati alcuni campi nei quali siamo ancora agli inizi:

- agricoltura biologica, controllo delle specie commensali (egoisticamente indicate come "malerbe"), organizzazione di agro-ecosistemi;
- le nozioni ricavate dalla fitosociologia come base per l'inserimento della componente naturale nelle realizzazioni urbanistiche in modo da attenuarne l'effetto alienante (seguendo l'esempio largamente sviluppato in Giappone);
- per gli studiosi più anziani, ormai a riposo, ritornare sui posti nei quali hanno effettuato i primi rilievi, negli anni giovanili, e ripeterli, in modo da poter documentare e interpretare le variazioni del manto vegetale nel corso di parecchi decenni;
- studiare sperimentalmente le condizioni che si verranno a stabilire per effetto del cambio climatico e possibili interventi di mitigazione.

Le prime proposte di applicazioni delle conoscenze fitosociologiche risalgono agli anni '30 ed allora si immaginavano applicazioni ingegneristiche, o addirittura a scopo bellico, che non sono divenute realtà. Adesso si aprono campi per interventi soft, su base culturale e volontaristica, mirati ad un generale miglioramento delle qualità della vita.

Ritorniamo ora alla definizione iniziale della fitosociologia come studio delle associazioni vegetali, e conside-

riamo le prospettive attuali della ricerca per chiarire che cosa veramente si intende come associazione vegetale.

Va qui aperta una seria riflessione sui dati esposti nel già citato catalogo delle alleanze nelle quali si articola la vegetazione europea prodotto dall'EVS (RODWELL *et al.*, 2002). Da questo studio, risultano note per l'Europa ben 928 alleanze. Ipotizzando una media di 5 associazioni per alleanza, questo significa che nel continente si potranno avere circa 5.000 associazioni - ed è una previsione prudentiale. Teniamo conto che l'intera flora europea è censita in poco più di 10.000 specie: il rapporto è 1:2. Nella monografia della vegetazione delle Dolomiti attualmente in pubblicazione (PIGNATTI E. e PIGNATTI S., *in pubbl.*), si hanno 112 associazioni con 2.400 specie: un rapporto di 1:20, che appare ragionevole. Come è possibile che a livello europeo si vada invece verso una situazione di circa una associazione ogni due specie? Allora, non sarebbe più conveniente studiare i rapporti ecologici delle singole specie (autoecologia) e lasciar perdere la sinecologia? Gli svantaggi di questa situazione sono di fronte a tutti. Non è soltanto il fastidio dello studioso, che in ogni pubblicazione si deve confrontare con una quantità di nuovi nomi e con un continuo rimescolamento della classificazione. Siamo di fronte ad una relativizzazione del concetto di associazione, che viene ridotto al livello della singola fitocenosi ed applicato a unità di significato locale. In questo modo, l'analisi della vegetazione viene limitata alla sola attività descrittiva, un compito evidentemente senza fine, perché infinite sono le possibilità di combinazioni tra le specie. Si perde la possibilità di arrivare al livello dell'associazione, come questa era stata concepita da Braun-Blanquet, cioè si perde la possibilità di generalizzare: l'approccio di Braun-Blanquet è ridotto al solo procedimento per i rilievi e manca la possibilità di ricavarne una teoria scientifica.

Dunque, sembra che anche qui si stia profilando una nuova versione dell'inflazione da me denunciata oltre 40 anni orsono. Il concetto di associazione era stato inizialmente introdotto per dare una immagine sintetica del manto vegetale, rispetto all'enumerazione delle singole specie, ma sembra che questo obiettivo, con il progredire delle conoscenze, si stia allontanando, e se il numero delle unità descritte si avvicina al numero delle specie, questa visione è perduta. Insomma, per il momento sembra che il problema del Prodromus non sia stato risolto, ma che soltanto si sia

imparato a convivere con esso.

Cerchiamo di approfondire questo punto. In realtà, si può notare come la proliferazione di alleanze sia circoscritta ad alcuni argomenti: la vegetazione rupestris (*Asplenietea*, 75 alleanze), dei ghiaioni e macereti (*Thlaspietea*, 48), sinantropica (*Stellarietea*, 44), dei prati aridi (*Festuco-Brometea*, 65). Tutte queste sono condizioni particolari come l'endemismo frammentato delle alte montagne mediterranee, l'azione dell'uomo, e le steppe, dove la frammentazione geografica, l'evoluzione postglaciale e l'impatto della pastorizia si sommano. Forse dobbiamo concludere che l'inquadramento sintassonomico basato sui risultati dell'approccio fitosociologico sia inadatto, oltre che alla vegetazione tropicale, anche alla vegetazione degli ambienti con endemismo conservativo oppure esposti all'impatto umano. Teniamo presente che anche questi sono ambienti nei quali non si ha lo sviluppo di un suolo maturo, con orizzonti ben definiti. Sembra dunque che l'informazione ricavata dalla composizione specifica sia soltanto l'aspetto più immediatamente percepibile dell'associazione, che tuttavia va integrato con meta-dati (forme biologiche, corotipi, bioindicazione sec. Ellenberg, traits).

Arriviamo così a quello che mi sembra sia il problema irrisolto, che sta a monte di queste riflessioni: perché le piante si riuniscono in comunità, e come avviene questo? In effetti, esistono rapporti che favoriscono la presenza di individui di due o più specie in vicinanza gli uni degli altri, ma si tratta per lo più di fatti del tutto ovvi, come ad es. le liane che crescono in vicinanza di alberi. Altrimenti, la formazione delle comunità viene attribuita a competizione o concorrenza (BRAUN-BLANQUET, 1928). Tuttavia bisogna tener conto che un ambiente pianeggiante e con la varietà di ecotopi che può esser considerata normale alle nostre latitudini, può ospitare alcune centinaia di specie, un numero che aumenta vistosamente se vi sono dislivelli altitudinali. Attraverso i normali processi di disseminazione esiste in teoria la possibilità per ogni specie di potersi sviluppare in qualsiasi punto della superficie considerata, e se la distribuzione delle specie fosse integralmente casuale dovrebbe proprio esser così. Invece sappiamo che non è così: le specie si aggregano in comunità, cioè assumono una distribuzione altamente improbabile. In altri termini, si può affermare che gli individui delle specie tendono ad assumere una distribuzione ordinata. Questo fatto è in controtenden-

denza rispetto al II Principio della termodinamica, ma non ci deve stupire: moltissimi processi biologici hanno il carattere di passaggio verso uno stato improbabile, ordinato. Questo avviene quando gli atomi si collegano nella sintesi di molecole complesse, le molecole nella formazione di membrane, le membrane nella cellula, nei tessuti etc. In tutti questi casi l'ordinamento avviene grazie a processi, nei quali una componente materiale fornisce la base per raggiungere la condizione di ordine. Se una base di questo genere esista anche nel caso delle associazioni non è noto, ma sembra quasi una necessità logica. Competizione o concorrenza sembrano ipotesi molto deboli, perché richiederebbero un processo del tipo trial and error, ma sembra poco verosimile che tutte le specie abbiano effettivamente provato ad inserirsi in ogni associazione, prima di insediarsi stabilmente in una nella quale risultano meglio adattate. Una serie di domande senza risposta. Noi osserviamo l'aggregarsi delle piante in comunità però, annebbiati dall'ansia di descrivere tutte le possibili forme di convivenza tra le piante, abbiamo dimenticato di chiederci perché questo avvenga e darne una spiegazione verificabile con il metodo sperimentale.

Questa situazione mi ha inquietato già da tempo. La necessità del passaggio dalla visione meccanicista ad una visione sintetica era stata affermata già da tempo, almeno in maniera generica, (PIGNATTI S., 1975). Su questo siamo ritornati successivamente, alla ricerca del nuovo paradigma (PIGNATTI S., Box, FUJIWARA, 2002). Nel frattempo, la scienza ha continuato a progredire ed offre oggi nuove possibilità sperimentali, che 35 anni fa non si potevano nemmeno sognare, e nuovi paradigmi di interpretazione. Si può discutere se coloro che si occupano di fitosociologia abbiano saputo utilizzare queste possibilità. In questo momento, mi sembra che il problema più urgente sia la verifica se, ed in quale misura, la fitosociologia possa ricavare vantaggi dai rapidi progressi della genomica, soprattutto in una visione della continuità tra vegetazione e suolo. Nuovi metodi e nuovi punti di vista sono necessari per dare la necessaria base sperimentale all'approccio di Braun-Blanquet.

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UN SIÈCLE DE PHYTOSOCIOLOGIE SIGMATISTE EN FRANCE: DU TEMPS DES PIONNIERS AUX APPLICATIONS MODERNES

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ABSTRACT

The aim of this presentation is to show the evolution of the sigmatist phytosociology in France, from the Bruxelles international botanical congress and the publications of Josias Braun-Blanquet, up to recent applications and issues of the 21st century, especially in topics relevant to decision making and management. After the first regional monographies, teams of phytosociologists set up in the sixties within different french universities and schools. The outcoming publications are mainly dedicated to the description of the vegetation of natural and semi-natural habitats. From the late sixties, the Amicale de phytosociologie which became in 1982 the Association Amicale francophone de Phytosociologie and the Station internationale de phytosociologie of Bailleul, created by Jean-Marie et Jeannette Géhu, will play a major role in the influence, valorisation and spread of the scientific knowledge related to phytosociology in Europe. Since four decades, professors Jean-Marie Géhu and Franco Pedrotti are the editors of two international journals, «Colloques Phytosociologiques» and «Documents Phytosociologiques» which represent an inestimable documentation about european vegetations. The modern applications of the phytosociology, in several topics such as cartography, landscape phytosociology and habitats typology are presented.

KEYWORDS: Century of phytosociology, French phytosociology, Géhu, Station Internationale de Phytosociologie, Bailleul, Association Amicale Francophone Phytosociologie, Documents Phytosociologiques, Colloques Phytosociologiques, Société Française Phytosociologie.

RÉSUMÉ

L'objet de cette présentation est de montrer comment la phytosociologie sigmatiste a évolué en France, depuis le Congrès international de Botanique à

Bruxelles, et les travaux de Josias Braun-Blanquet, jusqu'aux applications et enjeux récents du XXIe siècle, notamment dans les domaines de l'aide à la décision et de l'aménagement du territoire. Après les premiers travaux essentiellement consacrés à des monographies régionales, des équipes de phytosociologues se structurent à partir des années 60, au sein de différentes universités et écoles françaises. Les nombreux travaux qui en découlent permettent la description phytosociologique de la végétation de la plupart des grands types de milieux naturels et/ou semi-naturels. À partir de la fin des années soixante, l'Amicale de phytosociologie qui devient en 1982 l'«Association Amicale francophone de Phytosociologie» et la Station internationale de phytosociologie de Bailleul, fondée par Jean-Marie et Jeannette Géhu, jouent un rôle essentiel pour le rayonnement, la valorisation et la diffusion de la connaissance scientifique relative à la phytosociologie en Europe. D'autre part, depuis quatre décennies, les professeurs Jean-Marie Géhu et Franco Pedrotti sont les principaux instigateurs de la publication de deux revues internationales, les «Colloques Phytosociologiques» et les «Documents Phytosociologiques» qui constituent une source inestimable de données sur les végétations européennes. Les applications modernes de la phytosociologie, notamment dans les domaines de la cartographie, de la phytosociologie paysagère et de la construction d'un référentiel typologique des habitats sont présentées.

Dès 1891, le terme même de phytosociologie était utilisé par Józef Paczkowski qui proposait de le substituer à celui de *florologie* (DASZKIEWICZ, 2004). Même si cet auteur donne le premier une définition de l'association végétale, il faudra attendre 1910 et le Congrès international de Botanique à Bruxelles, pour que le terme d'association végétale soit précisé par Schröter et Flahault, puis dans la thèse de Josias Braun en 1915 (GÉHU, 1997) et dans le «Vocabulaire de sociologie végétale» (BRAUN-BLANQUET, PAVILLARD, 1928). C'est cet-

te phytosociologie moderne là, qualifiée de sigmatiste, dont nous célébrons le centenaire en 2010. Une présentation récente très détaillée et documentée de l'histoire de la phytosociologie (GÉHU, 2010) rappelle les fondements de cette science et retrace son évolution jusqu'au début du XXIe siècle.

Même si nous célébrons son centenaire en 2010, en même temps que l'année internationale de la biodiversité, la phytosociologie sigmatiste doit être considérée comme une discipline scientifique moderne, par comparaison avec d'autres disciplines, notamment la taxonomie. L'objet de cette présentation est de montrer comment cette science a évolué en France depuis l'époque des pionniers jusqu'aux applications et enjeux récents du XXIe siècle, notamment dans les domaines de l'aide à la décision et de l'aménagement du territoire, et des changements climatiques.

Réaliser une synthèse exhaustive d'un siècle de phytosociologie sigmatiste en France est une vaste entreprise que cette contribution n'a pas la prétention d'atteindre. Nous ne saurions citer ici la totalité des auteurs et des références bibliographiques relatives à la phytosociologie française.

LE TEMPS DES PIONNIERS ET LE MAÎTRE BRAUN-BLANQUET

Dès le début du 19^e siècle, avec Alexander von HUMBOLDT (1807), l'étude des communautés végétales était essentiellement fondée sur une approche physionomiste.

Il est impossible de faire un historique de la phytosociologie en France et en Europe, sans évoquer d'une part l'œuvre de Josias Braun-Blanquet (1884-1980), père fondateur de la phytosociologie moderne, et d'autre part la Station Internationale de Géobotanique Méditerranéenne et Alpine (S.I.G.M.A.) créée en 1935 à l'initiative de W.C. De Leuw et de R. Combes et dirigée dès son origine par J. Braun-Blanquet. Dans la continuité de la pensée de ses maîtres Schröter et Flahault, Braun-Blanquet développera une nouvelle science, la

géobotanique, qui rassemble de manière indissociable la phytosociologie, la phytogéographie et la synécologie. Comme l'écrit GÉHU (1997), ce maître à penser de la phytosociologie moderne et fondateur de l'école géobotanique Züricho-MontPELLIÉRaine, structurera la phytosociologie en définissant les modalités typologiques hiérarchisées. Braun-Blanquet et la SIGMA contribueront à l'essor de la phytosociologie en Europe et dans le monde pendant un demi-siècle (1935-1980).

Cette époque est marquée d'un grand nombre de publications: dans un premier temps, les travaux phytosociologiques étaient consacrés à des monographies régionales: sans être exhaustifs, nous pouvons citer les nombreux travaux de BRAUN (1915) sur le massif de l'Aigoual, LAURENT (1921) sur la végétation de la Champagne crayeuse, IMCHENETZKY (1926) émigré russe suite à la révolution bolchevique, et professeur à l'université de Besançon, CHATEAU (1926-1929) sur la végétation de Saône-et-Loire, HAGÉNE (1931) pionnier de la phytosociologie et de l'écologie qui a étudié la végétation de la région de Dijon, ALLORGE (1922, Vexin), LUQUET (1926, Monts-Dore, 1937, Limagne), MALCUT (1929, vallées vosgiennes), DE BANNES-PUGIRON (1933, Valentinois), MOLINIER (1934, environs de Marseille), QUANTIN (1935, Jura sud), LEMÉE (1937, Perche), JOVET (1949, Valois).

LE DÉVELOPPEMENT DE LA PHYTOSOCIOLOGIE EN FRANCE

Pour la seconde moitié du XX^e siècle, on peut citer les travaux de BRETON (1956, région de Dijon), GÉHU (1959, Avesnois), FRILEUX (1977, Pays de Bray), BOTINEAU (1985, Vallée de la Vienne), MULLER (1986, Pays de Bittche), BIORET (1989, îles de Bretagne).

À partir des années 60, la phytosociologie a connu un certain développement dans différentes universités et écoles françaises, permettant à des équipes de se structurer: Lille (J.-M. Géhu, J. Géhu-Franck, A. Delelis, B. De Foucault, V. Bouillet, J.-L. Mériaux), Orsay (M. Guinochet, A. Lacoste), Paris VIII (R. Braque), INRA Versailles-Grignon (R. Delpech), Amiens (J.-R. Wattez), Strasbourg (R. Carbiener), ENGREF Nancy (J.-C. Rameau), Metz (S. Muller), Besançon (M. Bidault, J.-M. Royer), Marseille (R. Molinier, P. Quézel, M. Barbero, R. Loisel, R. Nègre, M. Gruber, J. Gamisans), Nice (G. Lapraz, R. Salanon), Corte (G. Paradis, C. Piazz-

za), Toulouse (A. Baudière), Limoges (A. Ghistem, M. Botineau), Clermont-Ferrand (J.-E. Loiseau, G. Thébaud), Rennes (J. Touffet, B. Clément, J. Harry), Brest (F. Bioret), Bordeaux I (J.-J. Lazare), Caen (M. Provost, A. Lecointe), Angers (R. Corillion, M. Guerlesquin), Rouen (P.-N. Frileux).

Il importe de revenir sur l'objet d'étude de la phytosociologie, c'est-à-dire l'association végétale. Le syntaxon élémentaire n'est pas toujours l'association végétale, c'est le plus souvent une variante ou une sous-association.

En 1891, Paczoski définit le terme d'association végétale comme «*un groupement de plantes, diverses génétiquement, écologiquement et biologiquement. Dans une association, les individus d'après leur caractère occupent une place bien définie, ils se développent à diverses périodes de l'année, l'ensemble couvre le sol comme une véritable couverture, en utilisant le terrain occupé le plus efficacement, mais sans risque pour son existence, les éléments de l'ensemble créent un milieu social*

Plusieurs auteurs ont proposé des définitions de l'association végétale, en s'inspirant de la définition historique de BRAUN (1915), libérée de l'approche physionomique:

«*L'association végétale est un groupement végétal plus ou moins stable et en équilibre avec le milieu ambiant, caractérisé par une composition floristique déterminée dans laquelle certains éléments exclusifs ou à peu près (espèces caractéristiques) révèlent par leur présence une écologie particulière et autonome... L'association végétale répond à des conditions stationnelles déterminées*

GUINOCHET (1973) propose une définition fondée sur la composition floristique et la notion d'espèce caractéristique «*l'association végétale est une organisation originale d'espèces dont certaines dites caractéristiques lui sont plus particulièrement liées, les autres étant qualifiées de compagnes*

Pour GÉHU (1987, 2000), l'association se dégage d'un ensemble d'individus d'associations (ou relevés) possédant en commun, sur une surface de même ordre de grandeur - mais variable selon les types de végétation - à peu près les mêmes: caractéristiques floristiques (combinaisons d'espèces caractéristiques); caractéristiques statistiques (répétitivité de la combinaison); caractéristiques structurales (physionomie, stratification); caractéristiques écologiques (homogénéité du milieu stationnel); caractéristiques chorologiques

(aire de répartition déterminée); caractéristiques historiques (origine, dynamique).

Cette définition de l'association végétale, fondée sur l'approche floristico-écologique, traduit d'une part la nécessité de prendre en compte un faisceau d'informations complémentaire au relevé floristique proprement dit, et d'autre part met l'accent sur la dimension dynamique et historique des phytocénoses (GÉHU, 1987).

La notion de combinaison caractéristique d'association a progressivement remplacé celle d'espèce(s) caractéristique(s), notamment pour les milieux soumis à de fortes contraintes écologiques, tels que les milieux montagnards et littoraux (BIORET, GÉHU, 2008).

La méthode phytosociologique repose sur un certain nombre de principes et de critères. Si les relevés ne sont pas réalisés de manière très rigoureuse sur le terrain, leur analyse et leur interprétation seront difficiles voire impossibles. L'approche floristico-écologique sur le terrain doit guider le phytosociologue pour le choix de ses relevés, et la délimitation des contours des individus d'association. La notion d'aire de végétation homogène a quelque peu évolué depuis un siècle, par rapport à l'échelle spatiale d'apprehension de l'homogénéité physionomique, floristique et écologique. Jusque dans les années 1960, les relevés concernant les végétations non forestières étaient souvent effectués sur de vastes surfaces, rassemblant parfois des variations importantes de certains facteurs écologiques tels que la topographie ou l'hydrographie. Actuellement, les relevés de végétations herbacées ou chaméphytiques sont effectués sur des surfaces plus réduites, tenant compte des variations fines de la topographie, de l'orientation ou de la nature du substrat. Cette approche plus fine permet de décrire les végétations organisées en mosaïques ou s'exprimant le long de gradients écologiques (GÉHU, RIVAS-MARTÍNEZ, 1981). C'est par exemple le cas des végétations des vases salées (*Thero-Suaedetea splendentis*, *Asteretea triploli*, *Salicornietea fruticosae*) dont l'expression de la diversité phytocénotique est conditionnée par des gradients en interaction: salinité, topographie, durée et fréquence d'immersion, nature du sédiment, piétinement, pâturage, trophie...

LA PLUPART DES GRANDS TYPES DE MILIEUX ONT ÉTÉ CA-

RACTÉRISÉS D'UN POINT DE VUE PHYTOSOCIOLOGIQUE.

La végétation de la plupart des grands types de milieux a été décrite d'un point de vue phytosociologique, à l'exception de la végétation rudérale et de la végétation messicole qui restent peu étudiées en France. Les 12 premiers colloques phytosociologiques, consacrés à des thématiques écologiques, ont largement contribué à diffuser la connaissance et à la réalisation de monographies régionales ou de synthèses synsystématiques.

Les végétations côtières terrestres ont fait l'objet de nombreux travaux, sur les littoraux atlantiques et méditerranéens (Baudière et collaborateurs). Après quelques monographies régionales consacrées au Pays Basque (Jovet), au littoral du Centre-Ouest (Kunholtz-Lordat), les très nombreux travaux de GÉHU (1975b, 1976, 1979a, 1981...); GÉHU, GÉHU-FRANCK (1969); GÉHU, TÜXEN (1972) ont largement contribué au développement de la connaissance détaillée de la phytosociologie littorale française, en préconisant la réalisation de relevés sur des surfaces homogènes, intégrant les variations fines des facteurs microclimatologiques, microtopographiques, édaphiques, dynamiques, anthropiques et historiques. D'autres auteurs l'ont accompagné dans cette approche: WATTEZ (1968, 1975), LAHONDÈRE (2005), BIROET (1989, 1994, 2008), BIROET, GÉHU (2008).

Les landes ont fait l'objet de synthèses régionales, notamment dans le domaine atlantique. Les landes littorales ont été étudiées par GÉHU (1975a) GÉHU, GÉHU-FRANCK, 1975a, 1975b); les landes intérieures par CLÉMENT (1978).

Les pelouses et ourlets préforestiers, ont fait l'objet de nombreux travaux: la classe des *Trifolio-Geranietae* a particulièrement été étudiée par ROYER, RAMEAU (1983); DE FOUCault *et al.* (1983); DE FOUCault, FRILEUX (1983a, 1983b, 1988); BRAQUE (1983, 2001); BRAQUE, LOISEAU (1972, 1994).

Les fourrés et manteaux ont particulièrement été étudiés sur les littoraux atlantiques (GÉHU, GÉHU-FRANCK, 1983; GÉHU, 2007; BIROET, 2008), et les manteaux calcicoles dans le nord de la France (DE FOUCault, DELElis-DUSSOLIER, 1983).

Les milieux forestiers ont fait l'objet de nombreux travaux monographiques et de synthèse, avec notamment RAMEAU (1994, 1997), RAMEAU *et al.* (2000), GÉGOUT *et al.* (2008). Les végétations forestières on d'abord été

étudiées par les forestiers qui optaient pour une approche écologique, sans adhérer aux concepts de la phytosociologie sigmatiste. Il faudra attendre les années 60 pour que des études phytosociologiques soient menées de manière plus systématique (JACAMON, 1988). Les nombreux travaux de RAMEAU (1988) ont contribué très largement à ce rapprochement.

Les travaux en phytosociologie forestière concernent les forêts alluviales (RAMEAU, SCHMITT, 1984), les forêts planitaires (FRILEUX, 1975; BARDAT, 1993; CLÉMENT *et al.*, 1975; TIMBAL, LAZARE, 2005 ; DUMÉ, 1978; BOTINEAU, 1985; MULLER, 1978; JULVE, 1988; RAMEAU, 1974, 1980; BOEUF *et al.*, 2000, 2005); les forêts littorales (GÉHU, GÉHU-FRANCK, 1988), les forêts des Pyrénées orientales (BAUDIÈRE, 1975)...

Les milieux herbacés de pelouses et de prairies, ont fait l'objet d'une remarquable synthèse historique de DELPECH (1989). Divers travaux de FRILEUX (1966), de BOULLET (1986) et de ROYER (1987, 1991) portent sur les pelouses sèches de la classe des *Festuco-Brometea*, ceux de GAULTIER (1989) sur les pelouses supraméditerranéennes des *Ononidetalia striatae*. Les pelouses sèches de la Classe des *Tuberarietea guttatae* ont été étudiées dans la plupart des régions biogéographiques: l'est de la France (ROYER, 1978), la vallée de la Loire (CORILLION, COUDERC, 1978), le nord-ouest de la France (DE FOUCault, FRILEUX, 1983, 1988b; PROVOST, 1978), le bassin parisien (BOURNÉRIAS *et al.*, 1978; MAUBERT, 1978; BARANGER, 1978).

Les milieux prairiaux ont fait l'objet d'un colloque spécifique en 1976 dédié aux prairies inondables, et ont été étudiés dans plusieurs régions (FRILEUX, 1977; DIDIER, ROYER, 1989; DELPECH, 1994; GÉHU, BIONDI, 1995; DUVIGNEAUD 1986; TRIVAUDEY 1995; FERREZ 2007).

Les végétations aquatiques ont été étudiées par quelques auteurs: (MÉRIAUX, 1978) a notamment étudié la classe des *Potametea*. SCHAEFER-GUIGNIER a effectué de nombreux travaux sur les milieux aquatiques de Franche-Comté, notamment dans une thèse publiée dans les *Dissertationes Botanicae* en 1994. FELZINES (1982) s'est consacré à l'étude des étangs du Centre-Est.

Les végétations de tourbières proprement dites ont été étudiées par MALCUIT (1929), KAULE, (1974), BICK (1985) pour les Vosges, GALLANDAT (1982), ROYER *et al.* (1980) pour le Jura. De nombreux travaux concernent le Massif Central (VANDEN BERGHEN, 1963; THÉBAUD *et al.*, 2003...). Les végéta-

tions de marais ont été étudiées dans les nombreuses monographies régionales, ainsi que dans des travaux plus synthétiques avec GALLANDAT (1982); DE FOUCault (1984); ROYER, DIDIER (1996, marais tufeux); GIUGNI(Haute-Savoie); WATTEZ (1968, Picardie); VANDEN BERGHEN, (1964, 1969a, 1969b, Aquitaine); BRESSOUD (1989, marais artico-alpins)...

Les milieux rocheux et d'éboulis ont fait l'objet de quelques synthèses régionales (LAVAGNE, 1963; ROYER, 1983; FERREZ 2000; KORNECK, 1974). Leur étude est le plus souvent dispersée dans les monographies locales des régions montagneuses.

Les milieux montagnards, subalpins et alpins ont été beaucoup étudiés jusque dans les années 80 mais très inégalement d'un massif à l'autre.

Bien que surtout étudiées d'un point de vue floristique et géobotanique par l'école de Toulouse et notamment par Henri Gaussen de 1921 à 1966, les Pyrénées ont fait l'objet de plusieurs monographies phytosociologiques: le Massif du Néouvielle (CHOUARD, 1926); BRAUN-BLANQUET (1948) consacre une monographie à la végétation alpine des Pyrénées orientales. Il faut également citer les travaux de Baudière et collaborateurs; GRÜBER (1978)...

Les végétations des Alpes ont surtout été étudiées par BRAUN-BLANQUET, (1954, 1961...); GUINOCHE (1938); LACOSTE (1964, 1965, 1967, 1972, 1975); BARBERO (1970, 1972); BARBERO, BONO (1967); BARBERO, LOISEL (1971); BARBERO *et al.*, (1972); BARBERO, QUÉZEL (1975).

Pour le Massif central, on peut citer les travaux de BRAUN (1915); LUQUET (1926, 1937); LEMÉE, CARBIENER (1956); LEMÉE (1959); VAN DEN BERGHEN (1963); BRAUN-BLANQUET (1971); THÉBAUD (1988); MICHALET *et al.* (1989); BILLY (1988, 1997, 2000, 2002).

Le massif jurassien est bien connu suite aux écrits de POTTIER-ALAPETITE (1942); QUANTIN (1935) et surtout aux nombreux travaux du laboratoire de Bidault (SIMERAY, 1976; GILLET, 1982; RAMEAU, SCHMITT, 1984; ROYER, 1987; FERREZ, 2000, 2007...) et de celui de Neuchâtel (BÉGUIN, 1972; GALLANDAT, 1982; RICHARD, 1961). La végétation vosgienne a été étudiée par des précurseurs (MALCUIT, 1929; ISSLER, 1929), plus récemment par CARBIENER (1966); RAMEAU, BOEUF et plusieurs botanistes allemands (KORNECK, 1974; KAULE, 1974; BICK, 1985).

Après les nombreux travaux de MOLINIER (1934, et jusqu'en 1970) et de BRAUN-BLANQUET sur le Languedoc, les

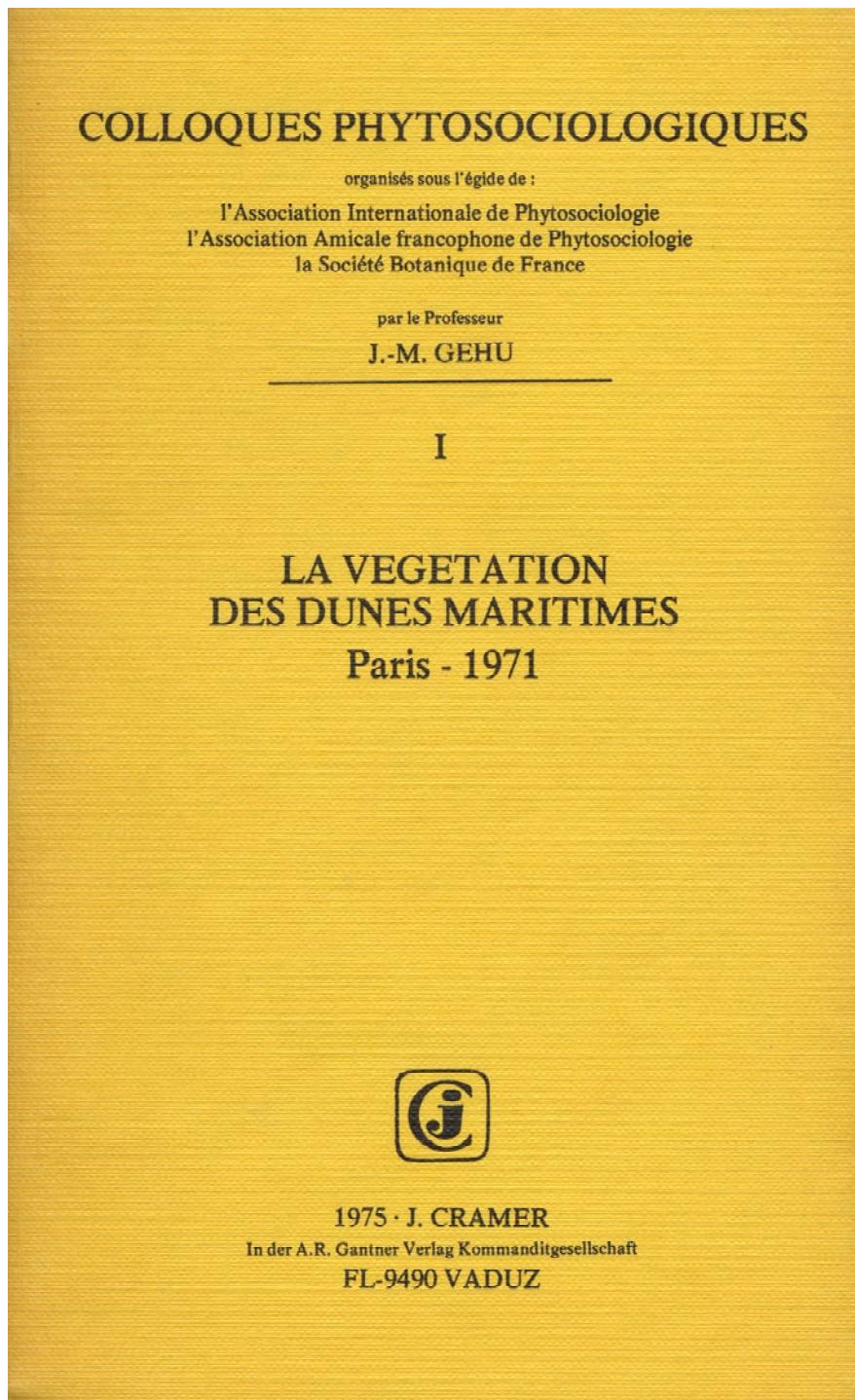


Fig. 1 - Le premier volume des "Colloques Phytosociologiques".

végétations méditerranéennes ont surtout été étudiées entre les années 50 et 80, avec les synthèses de TCHOU (1948, 1949); BRAUN-BLANQUET *et al.* (1952); BARBERO, LOISEL (1971); BARBERO *et al.* (1974); BARBERO, QUÉZEL (1983); LAPRAZ (1977, 1979, 1982, 1984); AUBERT, LOISEL (1971); LOISEL (1971, 1976). La végétation de la Corse a surtout été étudiée au début du XXe siècle par LITARDIÈRE et MALCUIT dans leurs nombreuses «Contributions à l'étude phytosociologique de la Corse» de 1926 à 1940, puis de manière synthétique par GAMISANS (1975, 1991). Les végétations littorales terrestres ont fait l'objet de nombreux travaux: MOLINIER (1959);

GAMISANS, MURACCIOLE (1985); GÉHU, BIONDI (1994), ainsi que les nombreux travaux de Paradis et collaborateurs (PIAZZA, PARADIS, 1997, 1998...) qui ont également étudié les végétations des îlots satellites de la Corse. Les Classes des *Rosmarinetea* et des *Cisto-Lavanduletea* ont fait l'objet d'une synthèse récente (ROUX, 2005).

En dehors des végétations dominées par les plantes vasculaires, les végétations dominées par les Cormophytes n'ont fait l'objet que de rares travaux dans le domaine de la phytosociologie.

Bien qu'encore trop peu développés les travaux de bryosociologie (Hé-

BRARD, 1973; LECOINTE, 1975, 1978; CLÉMENT, TOUFFET, 1979, 1980) ont permis d'aboutir à la publication récente d'un Synopsis bryosociologique pour la France (BARDAT, HAUGUEL, 2002; BARDAT, 2003), couvrant le territoire métropolitain et dont la structure inclut à la fois des unités supérieures relevant du synsystème des végétations vascu-laires, mais également des Classes strictement bryosociologiques.

L'application de la méthode phyto-sociologique aux communautés algales a fait l'objet de quelques travaux sur les associations d'algues marines en Méditerranée (BOUDORESQUE, 1967). Un synsystème a été proposé à l'échelle nationale (JULVE, 1992).

LE RÔLE ESSENTIEL JOUÉ PAR L'AMICALE FRANCOPHONE DE PHYTOSOCIOLOGIE ET LA STATION INTERNATIONALE DE PHYTOSOCIOLOGIE DE BAILLEUL

Il est essentiel de mentionner le rôle majeur joué par deux structures pour le rayonnement, la valorisation et la diffusion de la connaissance scientifique relative à la phytosociologie en Europe: d'une part l'Amicale de phytosociologie, née en 1969, d'un groupe informel de phytosociologues français autour d'un projet commun de recherche sur la végétation de la Brenne, qui devient officiellement en 1982 l'«Association Internationale Amicale Francophone de Phytosociologie»; d'autre part, la Station internationale de phytosociologie de Bailleul, fondée par Jean-Marie et Jeannette Géhu, qui devient Centre régional de Phytosociologie en 1986, puis Conservatoire botanique national en 1991.

Depuis quatre décennies, les professeurs Jean-Marie Géhu et Franco Pedrotti sont les principaux instigateurs de la publication de deux revues internationales qui constituent une source inestimable de données sur les végétations européennes.

Jean-Marie Géhu, secrétaire général de l'Amicale est le rédacteur des Colloques Phytosociologiques (Fig. 1). À partir de 1971, les «Colloques Phytosociologiques» ont été publiés par l'Amicale de phytosociologie, dans le but de soutenir et de développer la phytosociologie en Europe «franco-latino-phone». La majorité d'entre eux se sont déroulés en France. De 1971 à 2005, quelque 29 colloques de dimen-sion internationale ont été organisés et leurs actes publiés dans la série des livres jaunes des «Colloques phytosocio-

logiques» qui compte 30 volumes (Tableau 1). Ces véritables ouvrages de référence pour la communauté des phytosociologues, ont d'abord été consacrés à des types de végétations: dunes maritimes, landes, tourbières, prairies inondables, forêts alluviales, pelouses sèches, végétations aquatiques et amphibiennes... Ils ont ensuite été consacrés à des thématiques appliquées à la conservation de la nature, la foresterie, le pastoralisme, la typologie des habitats en lien avec la directive européenne Habitats...

Depuis l'année de sa création en 2002, la Société française de Phytosociologie a pris le relais de l'Amicale, et organisé ou co-organisé trois colloques internationaux.

Les Documents Phytosociologiques constituent l'autre revue francophone de phytosociologie (Fig. 2). Lancée en 1969 par l'Amicale de Phytosociologie, cette revue est parrainée par J. Braun-Blanquet et R. Tüxen. Jusqu'en 1976, la première série compte 20 fascicules. De 1977 à 1981, les volumes I à V de la nouvelle série de la revue sont édités par l'éditeur allemand Cramer. En 1982, Les «Documents Phytosociologiques» deviennent la revue officielle de l'«Association Internationale Amicale Francophone de Phytosociologie». À partir de 1981, sur un accord intervenu entre les Professeurs Jean-Marie Géhu et Franco Pedrotti, président de l'Amicale, la revue «Documents Phytosociologiques» est imprimée par les presses de l'Université de Camerino (Italie) et publiée conjointement par la Station de Phytosociologie de Bailleul et l'Institut de Botanique de Camerino, sous l'égide de l'«Association Amicale Internationale Francophone de Phytosociologie». De 1981 à 2010, 18 tomes correspondant aux volumes VI à XX, puis les volumes XXI et XXII de la nouvelle série sortiront des presses de Camerino (Fig. 3), à l'exception du volume XVII (1996), consacré à la bibliographie des fascicules 1-20 et des volumes NS I-XIV, et publié par Gebrüder Borntraeger, Berlin.

En décembre 2009, un accord passé entre l'Amicale internationale de Phytosociologie et la Société française de Phytosociologie (Fig. 4), précise que la SFP, en collaboration avec le Conservatoire botanique national du Massif central, prendra en charge la publication de la revue à partir de 2011. Les actes du colloque de Brest de novembre 2010 constitueront le premier volume de cette nouvelle série de la revue.

LES APPLICATIONS MODERNES

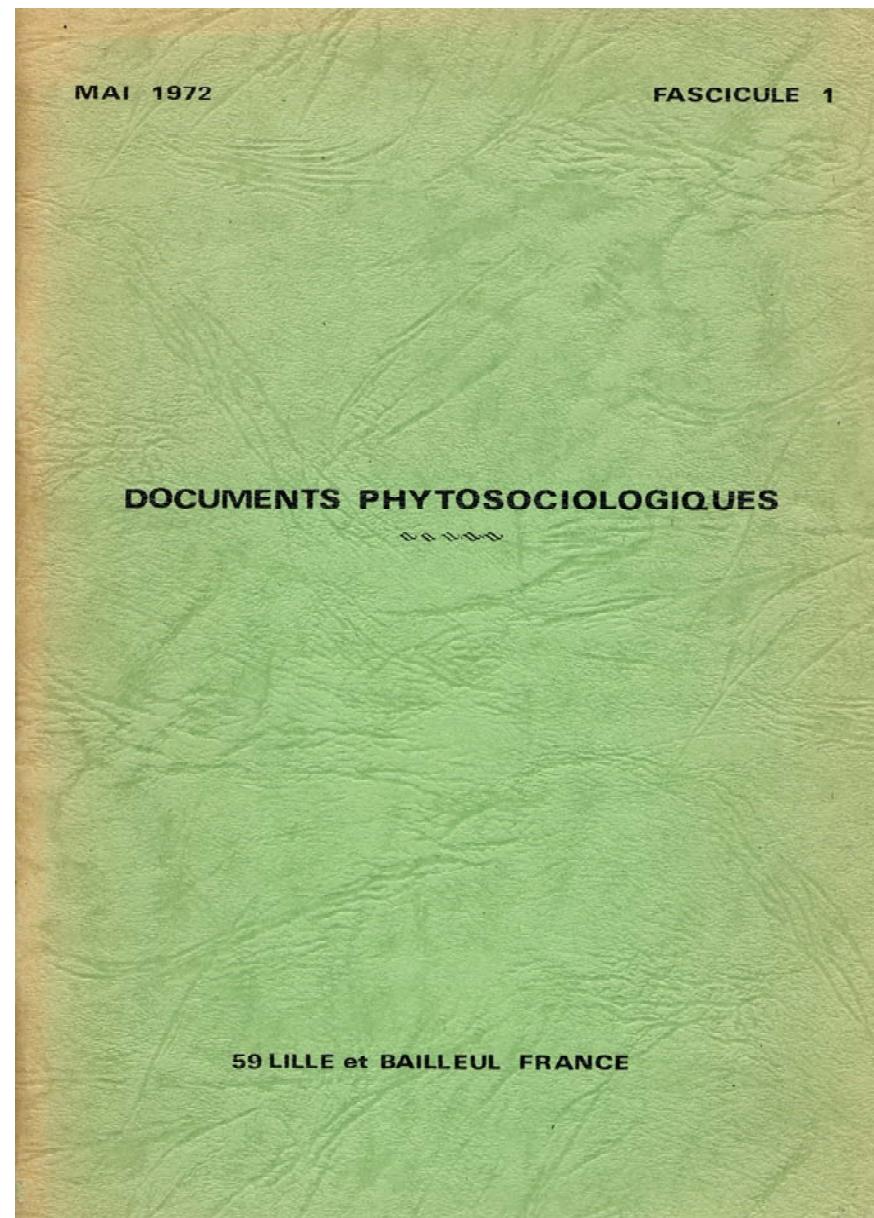


Fig. 2 - Le premier volume des "Documents Phytosociologiques".



Fig. 3 - Visite de la délégation de la Société Française de Phytosociologie au Département de Botanique et Ecologie de l'Université de Camerino en décembre 2009, pour discuter du transfert de la revue *Documents Phytosociologiques* de l'Association Internationale Amicale Francophone de Phytosociologie à la Société Française de Phytosociologie. De gauche à droite: Franco Pedrotti, Frédéric Bioret, Farid Bensettiti, Vincent Boullet (photo F. Bensettiti).

Tableau 1 - Liste des Colloques Phytosociologiques et des colloques organisés ou co-organisés par l'Amicale internationale de Phytosociologie (1970-1999) et par la Société française de Phytosociologie (2002-2010).

Année	Lieu	Thème	Année de publication	Revue, tome
1971	Paris	La végétation des dunes maritimes	1975	Colloques Phytosociologiques I
1973	Lille	La végétation des landes d'Europe occidentale	1975	Colloques Phytosociologiques II
1974	Lille	La végétation des forêts caducifoliées acidiphiles	1975	Colloques Phytosociologiques III
1975	Lille	La végétation des vases salées	1976	Colloques Phytosociologiques IV
1976	Lille	La végétation des prairies inondables	1978	Colloques Phytosociologiques V
1977	Lille	La végétation des pelouses sèches à thérophytés	1978	Colloques Phytosociologiques VI
1978	Lille	La végétation des sols tourbeux	1980	Colloques Phytosociologiques VII
1979	Lille	Les lisères forestières	1983	Colloques Phytosociologiques VIII
1980	Strasbourg	La végétation des forêts alluviales	1984	Colloques Phytosociologiques IX
1981	Lille	Les végétations aquatiques et amphibiennes	1983	Colloques Phytosociologiques X
1982	Strasbourg	La végétation des pelouses calcaires	1984	Colloques Phytosociologiques XI
1983	Bailleul	Les végétations nitrophiles et anthropogènes	1985	Colloques Phytosociologiques XII
1984	Bailleul	Séminaire mégaphorbiaies	1985	Colloques Phytosociologiques XII
1985	Bailleul	Végétation et géomorphologie	1986	Colloques Phytosociologiques XIII
1985	Nancy	Phytosociologie et foresterie	1988	Colloques Phytosociologiques XIV
1987	Strasbourg	Phytosociologie et conservation de la nature	1988	Colloques Phytosociologiques XV
1988	Paris	Phytosociologie et pastoralisme	1989	Colloques Phytosociologiques XVI
1989	Versailles	Phytosociologie et paysage	1991	Colloques Phytosociologiques XVII
1989	Bailleul	Phytosociologie littorale et taxonomie	1992	Colloques Phytosociologiques XVIII
1989	Cagliari	Végétation et qualité de l'environnement côtier en Méditerranée	1992	Colloques Phytosociologiques XIX
1991	Bailleul	Phytodynamique et biogéographie historique des forêts	1993	Colloques Phytosociologiques XX
1992	Camerino	Ecologia del Paesaggio e Progettazione Ambientale	1995	Colloques Phytosociologiques XXI
1993	Bailleul	La syntaxonomie et la systématique européennes, comme base typologique des habitats	1994	Colloques Phytosociologiques XXII
1994	Bailleul	Large Area Vegetation Surveys	1995	Colloques Phytosociologiques XXIII
1995	Camerino	Fitodinamica	1996	Colloques Phytosociologiques XXIV
-	-	Bibliographie des Colloques phytosociologiques	1996	Colloques Phytosociologiques XXV
1996	Orsay	Données pour un prodrome des végétations de France	2005	Colloques Phytosociologiques XXVI
1997	Bailleul	Les données de la phytosociologie sigmatiste	2000	Colloques Phytosociologiques XXVII
1998	Camerino	La végétation postglaciaire du passé et du présent	2004	Colloques Phytosociologiques XXVIII
2002	Limoges	Les landes et la Directive Habitats	2008	Acta Botanica Gallica, vol. 155, n°1
2005	Rabbi	Biodiversità, dinamica del paesaggio e gestione delle aree montane	sous presse	Colloques Phytosociologiques XXIX
2008	Nancy	La Phytosociologie face aux défis de la connaissance et de la gestion durable des espaces naturels. Hommage au Professeur Jean-Claude Rameau	2010	Revue Forestière Française
2010	Brest	Centenaire de la phytosociologie	2011	Documents Phytosociologiques



Fig. 4 - Le Conseil d'Administration de la Société Française de Phytosociologie, réuni à Paris en février 2004. De gauche à droite: Jean-Marie Royer, Jacques Bardat, Jean-Roger Wattez, Jean-Marie Géhu, Vincent Boulet, Huguette Duquef (non membre du CA), Jacques Haury, Frédéric Bioret, Michel Botineau, René Delpech, Alain Lacoste (photo F. Bensettiti).

DE LA PHYTOSOCIOLOGIE

CARTOGRAPHIE DE LA VÉGÉTATION

Après les premiers essais de cartographie phytosociologique de la région de Pontarlier par GUINOCHE (1955) et de Clermont-Ferrand (LEMÉE, 1959), depuis quelques décennies, la typologie phytosociologique est utilisée comme base de la cartographie de la végétation (PEDROTTI, 2000; VIGO *et al.*, 2000; BLASI *et al.*, 2004). Elle est le fondement méthodologique de la cartographie des habitats naturels et semi-naturels des espaces protégés: les méthodologies employées pour la cartographie par exemple des habitats des réserves naturelles (RNF, CHIFFAUT, 2006) ou des sites Natura 2000 (HARDEGEN *et al.*, 2001) s'inspirent très largement de la méthode et la classification phytosociologique.

La cartographie phytosociologique fournit de précieux documents qui permettent, dans le cadre d'une approche

diachronique, l'évaluation de la dynamique de la végétation ou de l'évolution de l'état de conservation d'un site. À partir de la cartographie phytosociologique de la végétation actuelle d'un territoire, il est possible de définir les cartographies de la végétation potentielle, des tendances dynamiques, de la naturalité, et la cartographie symphytoscopique ou phytosociologique intégrée (PEDROTTI, 2004).

LE DÉVELOPPEMENT RÉCENT DE LA PHYTOSOCIOLOGIE PAYSAGÈRE

La phytosociologie paysagère ou symphytosociologie permet de définir des sigmetum ou des géosigmetum, correspondant aux séries de végétation capables de s'exprimer sur des territoires respectivement écologiquement ou géomorphologiquement homogènes.

La symphytosociologie s'est développée à partir de la fin des années 70 en France, sous l'impulsion de J.-M. GÉHU (1979b, 1991b). Une synthèse récente retrace l'évolution de la symphytosociologie (GÉHU, 2004).

Si le développement récent de la phytosociologie paysagère n'a pas fait l'objet de nombreux travaux académiques, il aura, en revanche, permis de nombreuses applications dans le domaine de la bioévaluation et de l'aménagement du territoire (GÉHU, 1995). L'approche symphytosociologique permet de réaliser l'évaluation de la dégradation paysagère d'un site, de l'état de conservation des habitats, de l'artificialisation ou de la naturalité des communautés végétales ou des paysages, ou encore des risques d'incendie... (GÉHU, GÉHU-FRANCK, 1991; BOULLET, GÉHU, 1991; BIORET *et al.*, 1991).

LA PHYTOSOCIOLOGIE ET LES RÉFÉRENTIELS DES HABITATS

Depuis 1981, la typologie des habitats naturels et semi-naturels de l'Europe est majoritairement fondée sur la typologie phytosociologique (CORINE Biotopes, 1991). En 1992, la Directive européenne Habitats Faune-Flore, identifie des habitats naturels et semi-naturels d'intérêt communautaire. (Manuel EUR 27). La mise en œuvre de cette directive, via la réseau Natura 2000, n'aura fait que renforcer le rôle de la phytosociologie pour la description des habitats dans les différents pays membres de l'Union européenne (POTT, 2000).

Une étape importante fut marquée

par le XXVI^e Colloque Phytosociologique, intitulé «*Données pour un prodrome des végétations de France*» organisé à Orsay en 1996 par le professeur Alain Lacoste. Il fut notamment l'occasion de présenter plusieurs synthèses régionales (BARDAT *et al.*, 2005; LAHONDÈRE, 2005). Sous l'impulsion du Professeur Jean-Marie Géhu, un «groupe des experts» rassemblant une dizaine de phytosociologues français, était constitué: sa mission fut la construction et la validation du Prodrome des végétations de France. La Société française de Phytosociologie, créée en 2002 (Fig. 2), devient logiquement la structure porteuse de ce projet. Devant l'importance de la tâche qui leur incombaient, et afin de ne pas reporter la publication du Prodrome aux calendes grecques, les auteurs ont très rapidement renoncé à l'ambition initiale de décliner le sysystème jusqu'aux associations, arrêtant la déclinaison au niveau des sous-alliances. Le Prodrome des végétations de France (BARDAT *et al.*, 2004) constitue le premier référentiel national (France métropolitaine) des végétations ordonnées dans le sysystème de la phytosociologie sigmatiste. Il comporte 712 syntaxons de rang supérieur (classes à sous-alliances) répartis en 76 classes, 141 ordres, 7 sous-ordres, 361 alliances et 127 sous-alliances.

Dans le cadre de la mise en œuvre de la directive européenne Habitats Faune-Flore, le Ministère chargé de l'environnement confiait dès 1997 au Muséum national d'Histoire Naturelle de Paris, la réalisation des cahiers d'habitats. Les 5 tomes des cahiers d'habitats consacrés aux habitats rocheux, côtières, forestiers, humides et agro-pastoraux (BENSETTITI *et al.*, 2001-2005), décrivent les habitats génériques de l'annexe I de la Directive Habitats, déclinés en habitats élémentaires, selon un déterminisme biogéographique, écologique, ou lié aux modalités de gestion. L'ensemble des associations végétales caractérisant chaque habitat générique est mentionné, ainsi que la correspondance avec le sysystème du Prodrome des végétations de France.

LA PHYTOSOCIOLOGIE, OUTIL DE BIOÉVALUATION

Pour le gestionnaire d'un espace naturel, la richesse phytocénétique d'un territoire est une information tout aussi intéressante que la richesse spécifique ou le nombre d'espèces menacées ou protégées. L'évaluation patrimoniale d'un site intègre, aux côtés des espèces

animales et végétales remarquables, les syntaxons d'intérêt patrimonial majeur pouvant faire l'objet de listes ou livres rouges (GÉHU, 1991a).

Deux concepts peuvent être utiles à l'évaluation patrimoniale des syntaxons. La notion de géosynvicariance permet d'expliciter le remplacement d'une unité syntaxonomique par une autre dans un milieu écologiquement similaire mais dans un territoire biogéographique différent (GÉHU, 1978). La notion de synendémisme désigne un syntaxon dont l'aire de répartition est circonscrite à un territoire géographique limité (GÉHU, GÉHU-FRANCK, 1985; GÉHU, 1986).

Dans le domaine de l'écologie de la restauration, la phytosociologie est un outil pertinent qui permet de caractériser les étapes de dégradation du tapis végétal (BIORET *et al.*, 1991), et de réaliser des relevés dont l'analyse statistique permet de décrire les écosystèmes de référence et les trajectoires de restauration de la végétation des sites faisant l'objet d'opérations de restauration (SAWTSCHUCK, 2010).

PÉDAGOGIE

La transmission du savoir et la formation à la science phytosociologique sont des préoccupations qui se sont notamment traduites par la publication d'ouvrages méthodologiques et pédagogiques, destinés à des publics divers. Après les ouvrages de GUINOCHE (1955, 1973), DE FOUCALUT (1986a, 1986b) publia le «Petit manuel d'initiation à la phytosociologie sigmatiste», premier ouvrage à vocation pédagogique. Il sera suivi par LAHONDÈRE (1997) et ROYER (2009). D'autres ouvrages présentent la méthode phytosociologique (LACOSTE, SALANON, 1999; BOUZILLÉ, 2007).

Il faut également citer l'article de référence méthodologique que constitue «Notions fondamentales de Phytosociologie» de GÉHU et RIVAS-MARTÍNEZ (1981).

Il faut également citer le Vocabulaire de phytosociologie et de synécologie végétale (DELPECH, 1996), puis le récent Dictionnaire de synécologie végétale et de phytosociologie (GÉHU, 2006) qui rassemble quelque 12.000 entrées relatives à la phytosociologie et à l'étude de la végétation.

En France, la situation de l'enseignement universitaire et de la recherche en phytosociologie est largement préoccupante. Si l'enseignement de la phytosociologie est encore assuré dans quelques universités, en tant qu'outil métho-

dologique de description et d'analyse de la végétation, en revanche très peu de scientifiques ont la possibilité d'afficher la phytosociologie comme une thématique de recherche à part entière, les instances d'évaluation des enseignants-chercheurs et des chercheurs privilégier les disciplines telles que la biologie moléculaire ou la génétique. Sans parler de discipline sinistrée, ce constat alarmant se traduit depuis les années 80 par un volume de publications réduit par comparaison avec par exemple nos collègues espagnols, portugais ou italiens.

Paradoxalement, de nombreuses structures publiques ou privées liées à l'environnement et à l'aménagement du territoire recherchent des phytosociologues de terrain pour effectuer des inventaires et des évaluations.

Des sessions et des stages de terrain sont organisées par la Société botanique du Centre-Ouest (depuis 1986), la Société française de Phytosociologie (depuis 2003), le Centre d'étude et de conservation des ressources végétales (CECRV), certaines universités (Limoges...), l'Atelier technique des espaces naturels (ATEN), et les conservatoires botaniques nationaux.

QUELS ENJEUX ACTUELS POUR LA PHYTOSOCIOLOGIE EN FRANCE?

Un des enjeux actuels majeurs lié au domaine de la connaissance concerne l'aboutissement du projet de déclinaison du prodrome des végétations de France jusqu'au niveau des associations.

Le projet actuel, baptisé «Prodrome des végétations de France 2» (PVF 2), a pour but de poursuivre le travail réalisé entre 1996 et 2004 (BIORET, ROYER, 2009). Initié en 2006, il répond à des objectifs multiples: poursuivre la déclinaison jusqu'au niveau des syntaxons élémentaires que représentent les associations végétales, faciliter l'identification des syntaxons, et permettre l'identification des correspondances avec les classifications européennes des habitats naturels et semi-naturels (CORINE Biotopes, EUR 27...). Les synthèses des premières classes ont été publiées en 2010 dans le Journal de Botanique (DE FOUCault, 2009, 2010; DE FOUCault, BIORET, 2010). Des classes complexes comme celle des *Querco-roboris-Fagetea sylvatica* font l'objet d'un groupe de travail.

A l'issue de ce projet, les phytosociologues de terrain, ainsi que les

personnes impliquées dans la gestion conservatoire des espaces naturels et de la biodiversité végétale disposeront d'un référentiel national des végétations de la France métropolitaine, à l'instar des autres référentiels nationaux européens (par exemple RIVAS-MARTÍNEZ *et al.* (2001, 2002) pour la péninsule ibérique), du Synopsis des végétations de la Bourgogne et de la Champagne-Ardenne (ROYER *et al.*, 2006), ou des référentiels régionaux des habitats présentés par les conservatoires botaniques nationaux (CATTEAU *et al.*, 2009).

Ce projet permettra notamment de valider un synsystème pour certaines végétations qui nécessitent une mise au point synsystématique nationale: c'est le cas des forêts caducifoliées tempérées des classes des *Querco-Fagetea* et des *Quercetea ilicis*. Il en est de même pour les végétations de matorrals, dont la synthèse nationale devra intégrer les synsystèmes italiens et ibériques.

Dans le domaine de la bioévaluation, la phytosociologie devient un outil incontournable de l'aménagement du territoire. Il devrait être naturellement pris en compte dans l'élaboration des méthodologies d'évaluation de l'état de conservation et de cartographie des habitats naturels et semi-naturels à l'échelle nationale.

Dans le domaine de l'évaluation patrimoniale, des listes rouges d'habitats élaborées selon des critères de rareté et de menaces, aux échelles régionale et nationale, permettraient de justifier scientifiquement par la suite des listes d'habitats protégés. Ce vaste chantier avait d'ailleurs été proposé dans les recommandations du second colloque de Brest sur la flore menacée de France (BIORET, BOULLET, 1999). Le développement d'un tel outil aurait pour avantage de faire entrer dans le champ réglementaire de la protection de la nature les habitats qui n'ont pas été retenus dans l'annexe I de la Directive européenne Habitats Faune Flore de 1992.

Un des enjeux récents pour la phytosociologie est de s'ouvrir largement à d'autres réseaux de scientifiques et de gestionnaires, dans le domaine de l'écologie végétale, de la restauration écologique et de la gestion conservatoire du patrimoine naturel, et de la connaissance et de l'évaluation de la biodiversité (BLASI, 1995; LODI, 2004). Les gestionnaires d'espaces naturels pourraient utiliser des protocoles de suivis standardisés à l'échelle nationale, intégrant la méthode phytosociologique, de manière à permettre des approches diachroniques et synchroniques, notamment dans le cadre de l'évaluation de

l'impact des changements globaux sur la biodiversité.

D'un point de vue de la connaissance phytosociologique des territoires et de l'évaluation patrimoniale, il serait utile d'encourager à nouveau le développement de monographies et de synthèses régionales.

REMERCIEMENTS

L'auteur remercie sincèrement Jacques Bardat et Jean-Marie Royer pour leurs remarques et les renseignements qu'ils lui ont fournis.

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ROMANIAN PHYTOSOCIOLOGY: RESULTS AND PERSPECTIVES

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ABSTRACT

The present paper approaches a general presentation of the main stages and achievements of the Romanian phytosociology, starting from the opinion according to which phytosociology is an inter- and pluridisciplinary, analytic and synthetic, fundamental and alike practical domain, in more than 75 years of its existence. A general survey of the researchers and phytosociologists from this part of Europe is given by this synthesis. But, taking into consideration the fact that a balance should be positive to the future, the author proposes 6 future target directions, which should support the modernization of the Romanian phytosociology and give a better involvement in solving out certain socio-economical problems.

KEYWORDS: Romanian phytosociology.

INTRODUCTION

Almost a quarter of a century younger than French-Swiss "mother phytosociology", the science of plant communities in Romania is, like many other biological fields, at a critical time, when its reformation and modernization become necessary conditions for its survival.

The 2010 anniversary (100 years since the Brussels Congress) was a very good opportunity for phytosociologists to assess results and particularly, to point out the future directions of development, under the conditions of the pressure of globalization, of increasing competition between the various branches of science, as well as in the context of the multiple crises that affect contemporary mankind.

Although the history of science is not the most appreciated field, we must admit that it offers us a multitude of ideas, it helps us better understand the roads taken and follow better roads in the future; that it teaches us, like Mircea Eliade emphasized, that "...nothing is destroyed by criticism, no existence or meaning can be justified by reason...",

but "...a value is only suppressed by the creation of another value...", with a life that is "...more extensive, denser, more fertile".

This is why we attempted to synthesize in a few lines the achievements of Romanian phytosociologists and to point out several directions necessary for the future evolution of this discipline. A science with a strong inter- and multidisciplinary character, considered as "...both an analytical and synthetic discipline, fundamental through the evidenced laws and applicative through the information and solutions provided to the various socio-economic sectors" (CRISTEA *et al.*, 2004, p. 26).

BEGINNINGS AND DEVELOPMENT OF PHYTOSOCIOLOGY IN ROMANIA

The defining years for the beginnings of Romanian phytosociology remain 1931 and 1934, although in the first two decades of the past century, a number of articles on vegetation signed by A. Borza, Nyáradi E.I., I. Grintescu, M. Gușuleac, G. Bujoreanu, Soó R., etc., were published.

The 6th International Phytogeographic Excursion (organized in Romania by Prof. Alexandru Borza and its collaborators; July 1931) was also intended to stimulate phytosociological research, as recommended only one year before by the resolution of the Cambridge Congress (1930). The *Guide* of this Excursion included a number of published contributions on the vegetation of the areas visited by the participants (see BORZA, 1931).

The paper published by BORZA (1934) on the Retezat Mountains, considered by POP E. (1972) as being "...of crucial importance not only for the results that it contains, but also for the doctrine clarifications and for the crystallization of the working method..." (p. 27) undoubtedly represents the "birth certificate" of Romanian phytosociology. It was also a model for young botanists, some of whom had the possibility to train at SIGMA-Montpellier

(e.g. N. Zitti, E. Soroceanu, A. Paucă, E. Țopă and V. Borza).

Over the following two decades, important phytosociological contributions were brought by A. Borza, T. Săvulescu, E. Ghișa, S. Pașcovschi, A. Buia, I. Morariu, M. Răvărău, E. Țopă etc. (see SANDA *et al.*, 1998a).

The socio-political changes of 1946-1947 affected many fields of biology (particularly genetics), but botanists continued the series of floristic and phytosociological researches, even if the latter were called "geobotanical" or "phytocoenological" researches, because plant sociology was not admitted by the unique party.

In spite of his brutal removal from the university (in 1947), Prof. Borza offered Romanian botanists a model of monographic work (in 1959), which was followed with slight changes for more than four decades.

Then, BORZA & BOȘCAIU (1965) provided Romanian naturalists with a basic treatise for the study of the plant cover, which is still valid to a large extent, a treatise that stimulated the extension of researches in this area, the development of phytosociology as a science by itself in Romania.

There followed four decades during which phytosociological studies performed by specialists from both the universities and the new institutes of biological researches from Cluj, Bucharest, Iași and Timișoara were extended and diversified.

MAIN ACHIEVEMENTS OF ROMANIAN PHYTOSOCIOLOGY

Without intending to present an exhaustive picture of what has been achieved in Romanian phytosociology, we believe that emphasizing the main directions of the work of our phytosociologists can give a general view of the role and importance of this science in Romanian education and research:
a) Being included in the curriculum of the Faculties of Biology and Agriculture, at first only as a chapter of General Botany, later as a discipline by itself,

phytosociology required **handbooks** for the theoretical and practical training of students and PhD students, entitled either “geobotany” (between 1950-1960), or “phytocoenology” (in the period 1970-1990), or “phytosociology” (6 such handbooks were published after 1990). Most of these were based on the conception of the French-Swiss school (J. Braun-Blanquet’s “Bible”, 1951 and 1964);

b) Today, the **general study of the Romanian vegetation has practically ended**, only small “white spots” being left, which will be approached in future studies. The decisive role in this work has been played by PhD theses, elaborated particularly at the universities and institutes subordinated to the Romanian Academy of Cluj-Napoca, Bucharest and Iași;

c) **Monographs** on the flora and vegetation or only the vegetation of the main regions or mountain massifs of Romania have been published, with an increase in the number of publications over the past 15-20 years (more than 20 such monographs published after 1990, mainly written by young people), as a result of several factors: 1) the opening generated by the socio-political changes at the end of 1989, 2) the appointment of new PhD directors, 3) the need for young specialists in higher education and research, 4) even the inclusion of the publication of a treatise or a monograph in the promotion criteria.

Although there does not exist a strictly specialized journal in Phytosociology, most of the vegetation papers were published and are being published in botanical **journals**. The most popular of them are: *Contribuții Botanice* (“Botanical Contributions”, edited in Cluj-Napoca; Fig. 1), *Acta Horti Botanici Bucurestiensis*, *Romanian Journal of Biology-Plant Biology* (both edited in Bucharest), *Journal of Plant Development* (edited in Iași) etc.;

d) The series of **critical syntheses** on the Romanian vegetation was initiated and is ongoing, including: COLDEA (1991), COLDEA et al. (1997), IVAN (red.), (1992), IVAN et al. (1993), SANDA (2002), SANDA et al. (1998, 1999, 2005, 2008), CHIFU et al. (2006) etc.;

e) **Collaborations** with specialists in the fields of zoology have been initiated, in order to evidence the structure of biocoenoses from protected areas in particular, an important aspect for the management planning of these areas;

f) Although timid, there are some researches focused on the **evidencing of the functions** of various types of phytocoenoses, with emphasis on the produc-

tion and protection function, such as: POPESCU-ZELETIN-ed. (1971), BÂNDIU (1985), CRISTEA & PREDA (1981), CHIFU et al. (1986) etc. The information function of phytocoenoses, particularly the bioindicator role, has not been neglected either (e.g. CSÚRÖS & CSÚRÖS, 1966; RESMERITĂ & POP, 1987);

g) A number of Romanian phytosociologists (not very many, it is true) were or are involved in **European research projects**, as part of the FP6 program (e.g. the *IntraBioDiv* and *EcoChange* grants, coordinated by the “J. Fourier” University, Grenoble, and at national level, by ICB Cluj-Napoca), or as part of programs such as PHARE (e.g. CBC 2005 Romania-Bulgaria, coordinated by “Ovidius” University Constanța; see FĂGĂRAȘ-coord., 2008) or PIN/MATRA (financed by the Netherlands Government, coordinated in Romania by the Bucharest University; see SÂRBU et al., 2004, SÂRBU -coord., 2007);

h) In 1991, the **Romanian Society of Phytosociology was founded**, through the efforts of the regretted Acad. Nicolae Boșcaiu (PEDROTTI, 1999) and under the stimulation of Prof. F. Pedrotti (Camerino University) and Prof. J-M. Géhu, (Lille University), a society including 83 specialists, which institutionally committed in 2010 to carry out research projects, such as the project regarding the Natura 2000 site from Căian (Cluj county), co-financed by the European Regional Development Fund;

i) The three **international phytosociological excursions** organized in Romania (in 1993, 1998 and 2000), as well as a series of **international conferences and symposia** (e.g. “*Phytosociology at landscape ecology service*”, 20-25 May, 2003, “*Conceptions and methods of nature conservation in Europe*”, 16-19 September, 2004), were also important. The Fifth *Planta Europa* Conference, hosted in Cluj-Napoca in September 2007, where the new plant conservation strategy in EU was finalized, should also be mentioned;

j) **The description of new coenotaxa** was and is a constant concern of phytosociologists. Thus, compared to the many associations specific for this biogeographical area that have been described by Romanian phytosociologists [e.g. *Quercetum robori-petraeae* Borza (1928)1959, *Carpino-Quercetum petraeae* Borza 1941, *Galio rotundifolio-Fagetum* Boșcaiu 1971, *Telekio speciosae-Alnetum incanae* Coldea (1986)1990, *Seslerio haynaldiana-Saxifragetum rocheliana* Boșcaiu 1971, *Dryadetum octopetalae* Csúrös et al. 1956, *Bruckenthalio-Vaccinietum*

Coldea 2008, *Poëtum mediae* Csúrös et al. 1956 etc.] or even by specialists from other countries (e.g. *Sympyto cordato-Fagetum* Vida 1959, 1963), the contributions of our phytosociologists with regard to higher coenotaxa are relatively modest.

Thus, the following were described as new for science:

- a vegetation class (*Puccinellio-Salicornietea* Țopă 1939);
- 6 orders [*Stipo eriocaulis-Festucetalia pallentis* Pop I. (1968)1989, 1991, *Seslerietalia rigidae* Gergely 1967, *Juniper-Pinetalia mugo* Boșcaiu 1971, *Betuletalia pendulae* Resmerită & Pop 1986, *Artemisietalia petrosae* Sanda et al. 2001, *Tamaricetalia* (Borza & Boșcaiu 1963) Popescu & Sanda 1992];
- and 17 alliances [e.g.: *Veronicofficinalis-Quercion* Pop I. 1971, *Thymo comosi-Festucion rupicolae* Pop I. 1968, *Papavero-Thymion pulcherrimi* Pop I. 1968, *Veronicion baumgartennii* Coldea 1991, *Micromerion pulegii* Boșcaiu (1971)1979, *Danthonio-Brychypodion* Boșcaiu 1972, *Betulion pendulae* Resmerită & Pop 1986, *Quercion pedunculiflorae* Doltu, Popescu & Sanda 1980, *Querco-Carpinion orientalis* Csúrös et al. 1968, *Cakilion maritimae* Morariu 1957, *Scolymion hispanici* Morariu 1967, etc.].

FUTURE DEVELOPMENT DIRECTIONS

Neither in 1993 nor in 2004 did we try to answer the question “*Quo vadis Phytosociologia?*”, and nor will we attempt to answer it now. The reason is simple: in the first place, the current evolution of science is spectacular and difficult to predict, and phytosociology (if it is to remain a science by itself) should also follow this evolution and find its own solutions and modalities in order to be more convincing and more useful. In the second place, in our opinion, very many phytosociologists are so blinded by the complexity of the problems posed by the structure and dynamics of phytocoenoses that they set out on a road which is difficult to understand even by a naturalist in the absence of phytosociological training.

This is why, hoping that phytosociology in general and Romanian phytosociology in particular will not destroy themselves, we would like to suggest several future directions for our colleagues in this Carpathian-Danubian-Pontic area:

- a) Developing at national (and subsequently, continental) level unitary lu-

crative databases that can allow modern comparative analyses and, from here, veridical nomenclatural and coenotaxonomic structural changes that can be easily identified and useful for other fields of activity. This can only be achieved by national projects and by setting up teams of experts in present and potential vegetation, as well as information tools;

b) In parallel to the extension of studies on landscape phytosociology (geo-synphytosociological studies, according to Géhu and Rivas-Martínez), the participation of ecologists is required, as well as the development of population studies (including phylogeographic studies) and ecophysiological studies for both the dominant species of various eco-coenotic environments, and species with special phytogeographical value;

c) Harmonizing forest and grassland typologies with the coenotaxonomic system, in order to facilitate the collaboration of specialists in these fields and increase the applicability of phytosociological contributions. A determinator of coenotaxonomic units in Romania (similar to the determinator elaborated for Austria by Willner & Grabbherr-eds., 2007) is more than necessary;

d) The extension of researches aimed at clarifying the intimate mechanisms of the association of plants in well structured dynamic communities, including by experimental methods, is a premise for the understanding of the functioning of various types of ecosystems;

e) Collaborations oriented towards the evaluation of the specific and ecological biodiversity of all types of habitats in Romania, with particular emphasis on those included in various protected area networks;

f) Last but not least, we believe that phytosociologists should restructure their language and simplify the coenotaxonomic system so that it can be understood by those who can or must use information on the structure and dynamics of plant groups.

While BORZA & BoșCAIU (1965) showed that Romanian phytosociological researches started in Cluj, we believe that today, this university center has the responsibility to initiate the reform and the modernization of Romanian phytosociology, and that young people are the most entitled to do this!

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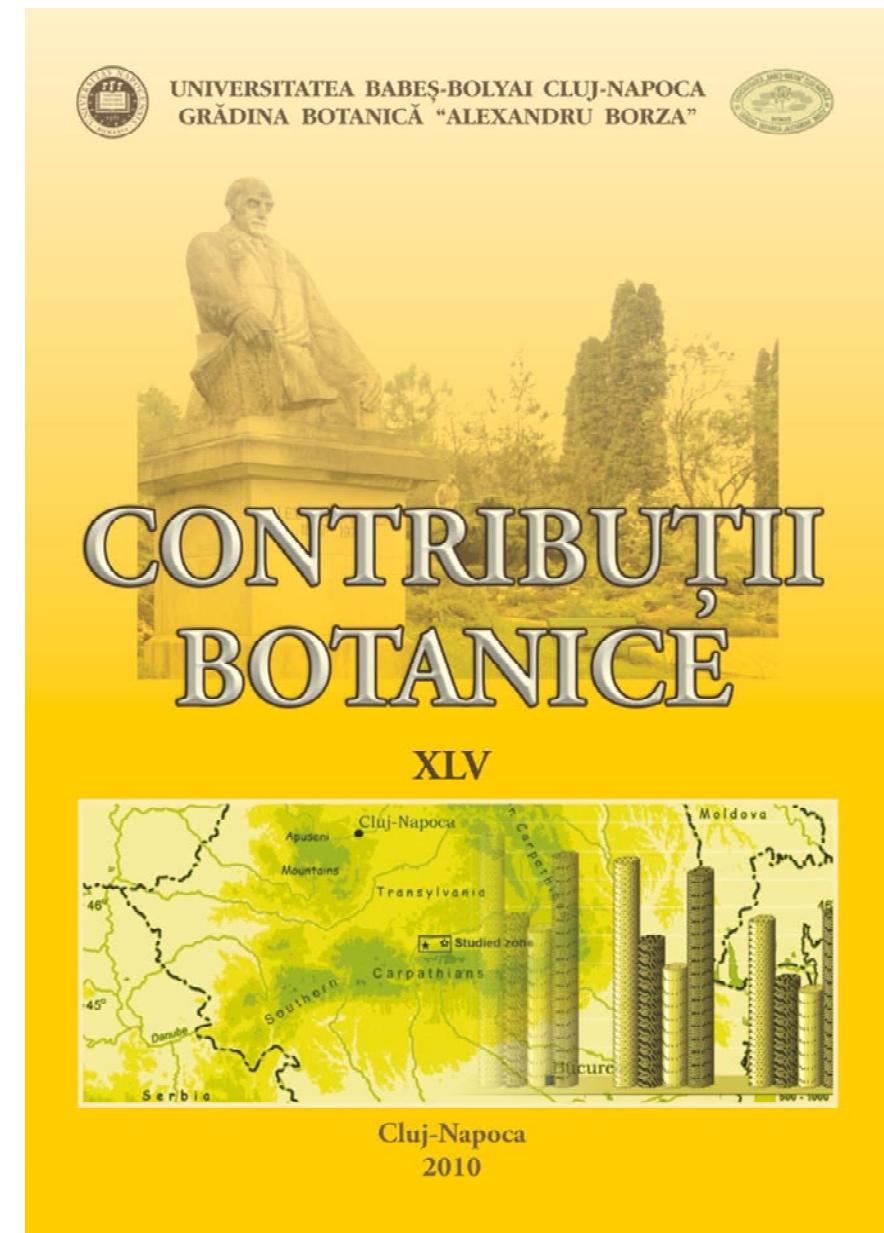


Fig. 1 - Contribuții Botanice (cover of the last issue, 2010), are indexed in 12 international data bases.

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THE HISTORY OF THE BRAUN-BLANQUET APPROACH APPLICATION AND THE MODERN STATE OF SYNTAXONOMY IN RUSSIA

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ABSTRACT

History of syntaxonomy development in Russian and the former USSR has been reviewed. Acceptance of the Braun-Blanquet approach by Russian phytosociologists in the 1980s was conditioned by realization of advantages of floristic criteria for evaluation of vegetation features as compared with the traditional dominant approach. Several periods of the Braun-Blanquet method acceptance and spreading were analyzed. The main results of syntaxonomy in Russia are related with the successful development of classification systems for vegetation types in geographically large areas. A brief characterization of modern syntaxonomic centers in Russia is given.

KEYWORDS: Century of Phytosociology, Soviet Geobotany, History of Braun-Blanquet approach, Russian Phytosociology, Syntaxonomy in Russia, Centers of Modern Syntaxonomy in Russia, Classification Systems of Vegetation.

INTRODUCTION

Protection of biological diversity has become one of the most important social and scientific challenges in the last century due to fast industrial evolution of Humanity. It explains progress in development of syntaxonomy, which plays fundamental role in the organization of monitoring and conservation of biodiversity. Syntaxonomy based on the Braun-Blanquet approach has been dominating in Europe since the 1920s (especially in the second half of the last century) and later in other countries (e.g. in Japan). In Russia, this approach has been used only since the 1980s, however it has produced remarkable results. It can be explained by high diversity of vegetation in Russia, as well as by many geobotanists with excellent knowledge of flora and plant-geographical traditions, all of which played an important role in the acceptance of the Braun-Blanquet's ideology.

PREREQUISITES FOR THE ESTABLISHMENT OF SYNTAXONOMY IN RUSSIA

Traditionally, Russian geobotanists followed the ecological-physiognomic method (dominant approach) of plant community classification referred to as a northern tradition (WHITTAKER, 1962). This approach was simple and the knowledge of complete floristic compositions in phytocoenoses was not required. It allowed for the creation of names for plant communities directly in field. The ecological-physiognomic method of classification was successfully used for plant communities with stable dominants (boreal forests, deserts, dry steppes and swamps), but it was not suitable for poly-dominant types, and especially for such types where permanent changes of dominants were observed (meadows, ruderal, and weed vegetation). Nevertheless, the latter were also classified into associations similar to spruce forests and deserts according to the principle of predominance of one or several species. Moreover, plant communities were grouped into formations according to one main dominant species. As a result, a syntaxonomic position of a certain community could be changed several times over the course of several years or even one growing season. Hundreds of associations were established with this approach. All descriptions of associations and higher units were accompanied by very short incomplete lists of the most abundant species however the table with complete species lists were rarely published.

Consequently, results of this approach aroused a scientific discontent among many Soviet geobotanists. They looked for alternatives to the orthodox dominant classification and sometimes tried to use ecological indicators as additional features. These modified approaches were discussed during the Third All-Union conference on vegetation classification (Leningrad, 1971). The resolution of this conference contained a proposal to establish associations using both dominants and indica-

tor species and recommended to publish tables with complete relevés. However, the outcomes from the conference were useless because Soviet scientific journals did not publish papers with phytosociological tables. Soviet publishers also refused to incorporate tables with original relevés into monographs.

The absence of a unified method and attempts of scientists to overcome draw backs of the dominant approach resulted in striking disagreements among the classification systems elaborated by various authors. At that time, there was only one specialist in floristic classification - Grebetshchikov, who returned to the USSR after emigration. However, he dared not get involved in any discussions with leaders of Soviet geobotany (Sukachov, Shennikov, Lavrenko, Sochava) on the subject.

One of the reasons that negatively influenced the expansion of the Braun-Blanquet approach was unfavorable political climate in the country. All scientific directions were divided into "socialist" and "bourgeois" ones. The Braun-Blanquet approach was considered as a "bourgeois" one and could not be widely used by socialist scientists. Nevertheless, in the 1960s it was obvious that the disdain of European phytosociologists' experience damaged the progress of Soviet geobotany. Shennikov, who opposed the Braun-Blanquet approach for a long time, made a step forward the positive evaluation of this method as an achievement of international phytosociology in his latest paper "Development of unified natural classification of vegetation" (SHENNICKOV, 1962).

There he wrote that plants, their communities and habitats have been very successfully characterized by European phytosociologists (Braun-Blanquet, Ellenberg, Tüxen, etc.). He also recognized that use of ecological indicators and characteristic species as an advantage of the Braun-Blanquet method and recommended publication of phytosociological tables for description of plant communities. Thus, by the 1960s, many Soviet geobotanists were ready to accept the principles of

the Braun-Blanquet method.

INITIAL PERIOD OF THE BRAUN-BLANQUET METHOD ACCEPTANCE (PRIOR TO 1990)

Slovak phytosociologist Ruzhchka introduced new ideas to Soviet geobotany in 1961-1962 when he visited Komarov Botanical Institute in Leningrad (now St-Petersburg) and gave a series of lectures about the Braun-Blanquet approach. His excellent lectures were well attended and were followed with long discussions with those who were interested in the Braun-Blanquet method. Undoubtedly, Ruzhchka's lectures inspired a keen interest in some Russian geobotanists to the approaches of Central European syntaxonomists. After that, KARAMYSHEVA (1967) applied the method of phytosociological tables to the classification of steppe communities. ALEXANDROVA (1969) published a special chapter in her monograph on vegetation classification approaches that was a Russian translation of Ellenberg's method of relevés treatment. These first publications played a prominent role in the popularization of syntaxonomy among Soviet geobotanists. But until the 1980s, the dominant approach remained to be most commonly used method for vegetation classification.

The 6th All-Union conference on vegetation classification, which was held in Ufa in 1981, had essential importance on further development of the Braun-Blanquet approach in the former Soviet Union. About one hundred and fifty participants from all regions of Russia, Estonia, Lithuania, Latvia and Ukraine took part in this meeting. An enthusiastic atmosphere created by the strong influence of European approaches predominated the sessions, and as a result, the accepted resolution confirmed the necessity of the Braun-Blanquet method's intensive use. A famous Estonian historiographer TRASS called the resolution a "historic event for geobotany in the former USSR".

After that conference, the monograph "Classification of vegetation of the USSR" (1986) was published. It included the first results of the vegetation classifications using the Braun-Blanquet method prepared by Dyrakov, Shergunova, Korotkov, Shelyag-Sosonko, Solomakha, Sapegin, Dymina, Korzhenevskiy, Golub, Kononov, Gogoleva and others. The quality of syntaxonomic analysis provided by different authors in this monograph

was not equal, because Soviet geobotanists made only the first steps in the use of the Braun-Blanquet approach. Another set-back that restricted the quality of those publications was the extremely limited access to West European syntaxonomical literature. Nevertheless, that monograph was a large step forward in mastering a new method. The number of Russian phytosociologists following the Braun-Blanquet method increased, but there were no good opportunities to publish their results because Soviet journals did not accept papers with phytosociological tables.

The only available option to make phytosociological tables publicly available was through the All-Union Institute of Scientific and Technical Information (VINITI). This Institute rapidly and very cheaply distributed manuscripts all over the country and the abstracts of the manuscripts were published separately in the special Abstract Journal (*Referativnyi Zhurnal*). According to SOLOMESHCH *et al.* (1994), more than 150 manuscripts containing about 15000 relevés were published in this way during the period of 1986-1991. They included phytosociological tables and descriptions of syntaxa of steppe, meadow, forest, tundra, swamp, ruderal and weed vegetation from various regions of the former USSR. Those manuscripts were not reviewed and the scientific level of publications was not always very high. Nevertheless, those publications in VINITI allowed Soviet geobotanists to start practicing the Braun-Blanquet approach and to develop the first vegetation syntaxonomical concepts for the vast area from Baltic Sea to Far East. However, Russian syntaxonomists had to stop publishing their results in VINITI after 1992, because VINITI did not accept requests for manuscripts from foreign phytosociologists to send the manuscripts abroad. All of these resulted in non-recognition of conformity of classifications published by Russian scientists with Code of Phytosociological Nomenclature. Moreover VINITI significantly increased prices on publications and copies of manuscripts, which made it impossible to exchange the materials quickly.

First Russian methodic center where phytosociologists from the former USSR could study the Braun-Blanquet approach was established in Ufa (Laboratory of Geobotany in Bashkir State University and in the Institute of Biology of RAS. Among those who studied method in Ufa were prominent phytosociologists from the Moscow (Onipchenko, Petelin, Minaeva), St-Peter-

sburg (Matveyeva, Zanokha, Neshatava), Murmansk (Koroleva), Syktyvkar (Teteriuk & Turubanova), Khabarovsk (Achtyamov), Yakutia (Kononov, Gogoleva, Cherosov, Sleptsova, Pestriakov), Volgograd (Golub), Bryansk (Bulokhov), Novosibirsk (Dymina, Ermakov, Koroljuk, Taran) as well as phytosociologists from Ukraine (Korzhenevsky, Solomakha, Krichfalushy, Gamor, Sipailova) and Belorussia (Sapegin). Syntaxonomists from Ufa (Solomeshch, Abramova, Ishbirdin) in collaboration with colleagues from Moscow (Korotkov & Onipchenko) arranged the All-Union School teaching the Braun-Blanquet approach for more than 40 young plant ecologists from all over the country.

Originally, the Braun-Blanquet approach was based on the concept of discreteness of vegetation. Therefore the syntaxonomy was considered as adequate and *unequivocal* reflection of natural patterns of plant communities. Some Russian geobotanists followed the concept of continuum in vegetation previously developed by Ramenskiy. They used classification as a tool to reduce the endless diversity of plant communities along vegetation continuum to a limited number of discrete units and considered this as conventional process that can be accomplished in several different ways (less conventional for forests classification and more conventional for ruderal and vegetal vegetation). Mirkin, as a representative of continual ideas of vegetation, elaborated a set of theoretical concepts, such as the influence of paradigms in phytocoenology on results of classification (MIRKIN, 1987); differences between syntaxonomy and taxonomy (MIRKIN, 1989); explanations of the causes of plurality of syntaxonomic solutions and overcoming this plurality on the basis of conventional agreements among syntaxonomists (MIRKIN, 1985, 1989). These contributions were noticed and appreciated by other prominent advocates of continual nature of vegetation (e.g. McINTOSH, 1993).

At the end of that period first monographs on syntaxonomy, symphytotsociology, and vegetation dynamics that covered various vegetation types from different regions of Russia were published including those in international journals. Among them publications about ecology and syntaxonomy of Yakutian alases (MIRKIN *et al.*, 1985; GOGOLEVA *et al.*, 1987), ruderal vegetation of Bashkortostan Republic (ISHBIRDIN *et al.*, 1988; MIRKIN *et al.*, 1989a,b), meadow classification (MIRKIN & SHEL-

YAG-SOSONKO, 1984; SHELYAG-SOSONKO *et al.*, 1987), and surveys of vegetation of delta of the Volga river (GOLUB & MIRKIN, 1986; GOLUB & TCHORBADZE, 1989). A valuable contribution in the cataloguing diversity of plant communities was made by East German scientists studying vegetation in the South Urals (SCHUBERT *et al.*, 1979, 1981; KLOTZ & KÖCK, 1984, 1986). They described several associations of meadows, steppes, forests and flood-plain vegetation.

SPREADING THE BRAUN-BLANQUET METHOD IN 1990S

Very fast spreading the Braun-Blanquet approach over all Russian Federation was observed in 1990s. At that time, the intensive study of Siberian vegetation diversity started along with the further development of syntaxonomy in European part of Russia. The main peculiarity of classification approach of Siberian phytosociologists was related with incorporation of plant-geographical ideas in syntaxonomy. They have studied vegetation through the vast area of Northern Asia and have made comprehensive comparisons with classification systems existing in Europe and Japan. As a result, several new high level units (classes and orders) were described for forests, meadows, steppes and high mountain vegetation on the basis of geographically wide data sets (classes *Calamagrostetea langsdorffii* Mirkin in Achtyamov *et al.* 1985, *Brachypodio-Betuletea pendulae* Ermakov *et al.* 1991, *Rhytidio-Laricetea sibiricae* Korotkov & Ermakov 1999, *Querco-Betuletea davuricae* Ermakov & Petelin 1997, etc.). Important contributions in development syntaxonomy of Siberian vegetation was made by the group of Czech and Slovak phytosociologists leaded by Milan Chtry (Masaryk University, Brno) who in collaboration with their colleagues from Buryatia studied vegetation of the Baikal region. They published several comprehensive surveys of various vegetation types from Eastern Siberia and gave some important ideas on higher unit statuses (CHTRY *et al.*, 1993; DANIHELCA & CHTRY, 1995; ANENKNONOV & CHTRY, 1998). New syntaxonomic centers in Novosibirsk and Vladivostok were established at that time.

An extensive development of Russian syntaxonomy was closely related with historical politic event - the fall of "iron curtain". It resulted in an establishing of permanent scientific contacts between Russian geobotanists and

their European colleagues. Invaluable role for establishment of cooperation between East and East European scientists played an international project "Safeguarding biodiversity in East Europe" headed by Prof. Jonh Rodwell and supported by the UK Darwin Initiative (1996-1999). J. Rodwell organized several international workshops in Lancaster University where many Russian and East European scientists had opportunity to study modern methods of vegetation science including organization of data bases of phytosociological information. As a result of this project activity, a new Red Data Book of Plant Communities in the former USSR (SOLOMESHCH *et al.*, 1997) was published. This book contains the complete list of the higher syntaxa and their evaluations performed for geographically wide territory of Northern Eurasia.

A very important contribution for the further development of Russian phytosociology was made by S. Hennekens and J. Scaminée (the Netherlands) giving an opportunity to use the Turboveg - software for storing and processing phytosociological data. The latter made possible to exchange big data sets among all members of European phytosociological community and realization of new international projects on vegetation diversity. As a result, numerous surveys on vegetation diversity of various Russian regions were published during 1990s according. Among them were such contributions as surveys of swamp forests of North Western Russia (BOCH & SMAGIN, 1993); meadows of flood-plain of the Amur river, North Eastern Asia (ACHTYMOV, 1995); forests of European part of Russia (KOROTKOV, 1991); high mountain vegetation of the Urals (ISHBIRDIN *et al.*, 1996); classification of halophytic and desert vegetation of Eurasia (GOLUB, 1994a,b), diversity of flood-plain meadows of the Lena river (MIRKIN *et al.*, 1992a,b); classification of Arctic vegetation published in the special issue of Journal of Vegetation Science (KOROLEVA, 1994; MATVEEVA, 1994; RAZZHIVIN, 1994). At the end of this period, the monograph Vegetation Science (history and modern state of concepts) by MIRKIN and NAUMOVA (1998) was published. This monograph contains methodology of the Braun-Blanquet approach including sym-phytosociology and Conspectus of higher units (class-alliance) of vegetation of the former USSR.

A BRIEF CHARACTERIZATIONS

OF MODERN SYNTAXONOMIC CENTERS IN RUSSIA IN 2000-PRESENT TIME

A. EUROPEAN PART

Komarov Botanical Institute, Saint Petersburg. Expansion of the Braun-Blanquet approach in the former USSR started from this institute in the 1960s. After 2000 a series of contributions on syntaxonomy of Arctic and sub-Arctic vegetation (MATVEYEVA, 2006; KHOLOD, 2007; SEKRETARYOVA, 2001, 2003; ZANOKHA, 2001, 2003) and swamp vegetation (SMAGIN, 2003; SMAGIN & NAPRIYENKO, 2003) appeared.

Bashkirian State University and Institute of Biology, Ufa. This center is oriented dominantly on vegetation of the Urals where high diversity of plant communities is determined by unique position of this mountain system in the contact zone between Europe and Asia and by altitudinal zonation. A series of regional monographs characterizing syntaxonomic diversity of all zonal and azonal vegetation types has been published (MARTYNENKO *et al.*, 2003, 2005; Flora and vegetation ..., 2008, etc.). The special attention was paid to classification of forests vegetation. Currently the classification system includes 48 associations of 3 classes (*Querco-Fagetea* Braun-Blanquet & Vlieger in Vlieger 1937; *Vaccinio-Piceetea* Braun-Blanquet in Braun-Blanquet, Sissingh. et Vlieger 1939; *Brachypodio pinnatifidetulae pendulae* Ermakov *et al.*, 1991). Four new alliances characterizing European nemoral forests at the eastern limit of their ranges were originally described there: *Lathyro-Quercion roboris* Solomeshch *et al.*, 1989; *Aconito septentrionalis-Tilion cordatae* Solomeshch *et al.*, 1993; *Aconito septentrionalis-Piceion obovatae* Solomeshch *et al.*, ex Martynenko *et al.*, 2008; *Trollio europaei-Pinion sylvestris* Fedorov ex Ermakov *et al.*, 2000. Syntaxonomy of forests in the South Urals has an important role for elaboration of unified forest classification for Northern Eurasia because this mountain system links two large subcontinents - Europe and Asia.

Diversity of meadow, steppe and synantropic vegetation in the Urals was represented in contributions by GRIGOREV *et al.*, 2002; FILINOV *et al.*, 2002; YAMALOV *et al.*, 2003; YAMALOV, 2005; ZIROVA, 2007; Synantropic vegetation of the Zauralie ..., 2008; YAMALOV & KUKARINA, 2009. Classifications of moss and lichen communities were elaborated there for the first time in Russia

(BAISHEVA *et al.*, 1994, 2004; BAISHEVA, 1995, 2000; ZHURAVLYEVA *et al.*, 2004). **Institute of ecology of the Volga river basin, Tolyatti.** A special attention of syntaxonomists from this center was concentrated for the development of classification system of halophytic vegetation. The surveys of plant communities with predominance of hemi-cryptophytes in saline sites (classes *Salicori-nietea fruticosae* Braun-Blanquet et Tüxen ex de Bold & Vayreda 1950, *Festuco-Puccinellietea* Soó ex Vicherek 1973) of inner part of Northern Eurasia were published (GOLUB *et al.*, 2001a,b, 2005c). Some important contributions on classification of halophytic communities were made for various regions of Eastern Europe (FREITAG *et al.*, 2001; KARPOV *et al.*, 2003; LYSENKO *et al.*, 2003; KARPOV & YURITSYNA, 2006) as well as for vegetation of sea shores of Baltic (GOLUB *et al.*, 2005 a,b), White (GOLUB *et al.*, 2003; SOROKIN & GOLUB, 2006), Azov and Black seas (GOLUB & SOKOLOV, 1998; GOLUB *et al.*, 2006, 2009).

Bryansk State University. The group of phytosociologists from this center study diversity of vegetation in the west of European part of Russia. They published results of classifications of meadows (BULOKHOV, 2001), forests (BULOKHOV & SOLOMESHCH, 2003), weed vegetation (BULOKHOV & KHARIN, 2008; SEMENISHCHENKOV, 2009). Three new alliances (*Querco roboris-Tilion cordatae* Solomeshch et Laivinsh ex Bulokhov et Solomeshch 2003, *Vaccinio myrtillii-Quercion roboris* Bulokhov et Solomeshch 2003) characterize regional peculiarities of zonal East European broad-leaved forests. An essential contribution for development of European boreal and nemoral forests classification has been made by phytosociologists from Institute of Geography and Center of problems of ecology and productivity of forests (ZAUGOLNOVA & BRASLAVSKAYA, 2003; ZAUGOLNOVA & MOROZOVA, 2004; MOROZOVA *et al.*, 2008; ZAUGOLNOVA *et al.*, 2009). Classification of European tundra communities were developed by KOROLEVA (2001, 2006) from Polar botanical Garden.

Syntaxonomy of aquatic vegetation of Komi Republic were developed by TETERYUK & SOLOMESHCH (2003). Communities of hydrophytes and alga were studied by BOBROV *et al.* (2005). Some syntaxa of alpine vegetation of the Caucasus were described by ONIPCHENKO (2002) from Moscow State University and KOROTKOV & BELONOVSKAYA (1998).

B. SIBERIA AND RUSSIAN FAR EAST

Central Siberian Botanical Garden, Novosibirsk. Traditionally Siberian geobotanists studies diversity vegetation of vast territories of Northern Asia. Therefore the application of the Braun-Blanquet method was initially based on plant-geographical concepts and syntaxonomic analysis was made using comprehensive comparisons of floristic peculiarities of zonal vegetation types. As a result, the original concepts of the higher units for boreal forests, steppes, meadows and high mountain vegetation have been elaborated since 1990s. Among them, the concepts of geographical corresponding classes of North Asian hemiboreal forests - *Brachypodio pin-nati-Betuletea pendulae* Ermakov *et al.*, 1991, *Rhytidio-Laricetea* Korotkov & Ermakov, 1999, *Querco mongolicae-Betuletea davuricae* Ermakov & Petelin, 1997 as well as corresponding classes of meadows - *Molinio-Arrhenatheretea* R. Tüxen. 1937 and *Arundinello anomala-Agrostetea trinii* Ermakov & Krestov, 2009 demonstrate an importance of special climatic regimes and roles of influences of Atlantic and Pacific oceans for the formation of floristic differences of the higher units of vegetation in western and eastern parts of Eurasia (ERMAKOV *et al.*, 1991, 2000, 2002; ERMAKOV, 2003, 2010; ERMAKOV & KRESTOV, 2009). Classification system of boreal forests of the Eurasian class *Vaccinio-Piceetea* Braun-Blanquet in Braun-Blanquet *et al.*, 1939 was added by two new orders - *Ledo-Laricetalia cajanderi* Ermakov in Ermakov & Alsynbayev, 2004 and *Lathyrum humiles-Laricetalia cajanderi* Ermakov *et al.*, 2002 representing special forest types formed in ultracontinental bioclimate and permafrost (ERMAKOV *et al.*, 2002).

Results of analyses of diversity of Euro-Siberian and Central Asian steppes of the classes *Festuco-Brometea* and *Cleistogenetea squarrosae* were published in contributions by Korolyuk (GADZHIEV *et al.*, 2002), ERMAKOV *et al.*, 2008. Classification of high mountain tundra and tall-forb meadows is represented in papers by ERMAKOV *et al.* (2005); ZIBZEYEV (2009); TELYATNIKOV (2009).

Development of syntaxonomy in Southern Siberia was also closely related with the results of numerous international expeditions of Russian, Czech and Slovak phytosociologists leaded by Chytry and Valakhovic in the Baikal region and Altai-Sayanian Mountains (ANEKHONOV & CHYTRY, 1998; ERMAKOV

et al., 2006).

Institute of Biology and Soil Science, Vladivostok. The classification of forests of the sub-Pacific part of North Asia was intensively developed during last 20 years. Currently the comprehensive characterizations of higher units of boreal and nemoral vegetation are represented in contributions by KRESTOV & NAKAMURA (2002) - dark-coniferous forests of the *Abieti-Piceetalia* Miyawaki *et al.*, 1968; GUMAROVA (1993); KRESTOV *et al.* (2006) - broad-leaved forests of the *Quercetea mongolicae* Song ex Krestov *et al.*, 2006 and *Querco-Betuletea davuricae* Ermakov & Petelin, 1997; KRESTOV *et al.* (2009) - boreal larch forests of the *Ledo-Laricetalia cajanderi* Ermakov in Ermakov & Alsynbayev, 2004 and *Lathyrum humiles-Laricetalia cajanderi* Ermakov *et al.*, 2002. A new concept of classification of sub-Pacific meadows (*Arundinello anomala-Agrostetea trinii* Ermakov & Krestov, 2009) was created by ERMAKOV & KRESTOV (2009). All results of syntaxonomy of Russian Far East are based on plant-geographical comparisons of vegetation types of Eurasia and North America and on small-scale bioclimatic patterns developed by KRESTOV (2007).

Yakutsk State University and Institute of Biology of Cryolitic Zone, Yakutsk. Yakutian phytosociologists produced classifications of various vegetation types occurring in middle boreal subzone of ultracontinental climatic sector of Eurasia. Extazonal steppes and meadows of the classes *Cleistogenetea squarrosae* and *Hordeetea brevisubulati* Mirkin 1986 were classified by MIRKIN *et al.*, 1985; GOGOLEVA *et al.*, 1987. Antropogenous vegetation types were studied by CHEROSOV *et al.* (2005). Characterizations of syntaxa of zonal forests (*Vaccinio-Piceetea*) and high mountain dwarf-shrub vegetation (*Loiseleurio-Vaccinietea*) were published by ERMAKOV *et al.* (2002); ERMAKOV & CHEROSOV (2005).

A special importance for understanding diversity of North-East Asian vegetation (Magadan region) represents a monograph by SINELNIKOVA (2009) from Institute of Biology, Magadan. It contains a comprehensive data on high-mountain vegetation (*Loiseleurio-Vaccinietea*), forests (*Vaccinio-Piceetea*, *Rhytidio-Laricetea*), steppes (*Cleistogenetea squarrosae*), swamps and swamp forests (*Oxycocco-Sphagnetea*).

The Braun-Blanquet approach has predominated since 2000 in Russia. An important positive event for Russian phytosociology was an appearance of

new journal "Vegetation of Russia (Russian Geobotanical Journal)" published by Russian Botanical Society together with Komarov Botanical Institute in St-Petersburg after 2001. This journal (Eds: N. Matveyeva and B. Gannibal) has given an opportunity for Russian geobotanists to publish contributions on vegetation classifications using the Braun-Blanquet approach with the complete phytosociological tables. Currently, 70 contributions published in 15 volumes of this journal contain comprehensive information on diversity of various vegetation types and several thousand relevés. This journal also plays an important role of handbook on syntaxonomy for young phytosociologists starting to work with the Braun-Blanquet method.

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PHYTOSOCIOLOGY IN JAPAN. THE PAST, PRESENT AND FUTURE FROM THE FOOTSTEPS OF ONE PHYTOSOCIOLOGIST

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ABSTRACT

In the first half of the 20th century a movement for nature preservation arose in Japan influenced by the knowledge of vegetation science in Europe. In spite of introduction of synecology and Braun-Blanquet method, Japanese vegetation scientists had difficulty in getting away from physiognomy and decision of community units by dominant species because of lack of information. I learned phytosociology including the way of vegetation field surveys, table work to systematize plant communities, the knowledge of actual and potential natural vegetation and vegetation mapping, under Prof. Tüxen in Germany, beginning in 1958. After returning to Japan, I systematized vegetation of Japan through phytosociological field surveys all over the country and published the results. During surveys I recognized the loss of indigenous forests and began reforestation based on phytosociology. Until now more than 40,000,000 trees were planted at about 1700 sites in Japan as well as overseas. Today experimental, metric and analytical approaches are prevailing in vegetation science. However, phytosociology is fundamental and significant science in globally comparative researches and reforestation as basic solution to the present environment problems worldwide. Phytosociology is the future-oriented science.

KEYWORDS: Century of Phytosociology, Japanese Phytosociology, Potential Natural Vegetation, Japanese Indigenous Forests.

THE DAWN

Europe has a long history in *Vegetationskunde* (vegetation science), *Geobotanik* (geobotany) and *Pflanzensoziologie* (phytosociology) (SCHMITTHÜSEN, 1961; ELLENBERG, 1980; POTT, 1992 and many other publications). In Japan, traditional herbalism prevailed until the beginning of the 20th century. Manabu Miyoshi, professor of Tokyo Universi-

ty and other scientists learned vegetation science in Germany and brought the new knowledge of vegetation science and the concept of *Naturdenkmal* (natural monument) to Japan.

At first precious individual pieces of nature like old big trees or strangely shaped rocks were designated as natural treasures. A movement for nature preservation arose, and before long the Law of National Parks was enacted and the Nature Conservation Society of Japan was established. Vegetation scientists came to be concerned about assemblages of green plants, and taxonomy took root in Japan.

Vegetation scientists in those days, including Harufusa Nakano and Yoshiji Yoshii, studied plant communities. Those days were hard times before the World War II, however, and they could only see a bit of the new science in the literature from Europe. That literature introduced taxonomy based on dominant species, advocated by so-called the Scandinavian School of Du Rietz and H. Osvald, and by the older knowledge of plant geography from Alexander von Humboldt. Those early Japanese scientists tried field vegetation surveys and made plant community units based on dominant species following the literature. Their method, however,

was almost indistinguishable from plant geography, taxonomy, or synecology.

It was Tokio Suzuki who first introduced synecology and the Braun-Blanquet method of vegetation field surveys. For the first time in Japan he used classification terms such as "association" and "alliance" in his book "Vegetation in Eastern Asia" (SUZUKI, 1952). The fundamentals of phytosociology consist of minute vegetation field surveys, drawing relevé and community tables, deciding on the appropriate rank of community unit based on species combination, and their systematization. Japanese vegetation scientists were interested in the new concept of plant community science, synecology, but they did not know exactly how and where to set quadrats in the field, how to make community tables from their data, nor how to decide on community units objectively through species combinations in the tables. Therefore they could not get away from physiognomy and decided community units by dominant species.

STUDY OF WEED COMMUNITIES

At Hiroshima University, I studied weed communities growing under hu-



Prof. R. Tüxen and A. Miyawaki at an IAVS symposium, Rinteln, Germany, April 1971
(photo A. Miyawaki).

man impact in agricultural areas or along roadsides. In those days weeds were not generally a topic of concern, nor regarded as a subject of research. Yoshiwo Horikawa, my university professor, encouraged me to study on weeds, however, saying that weeds are an important subject, occurring on the boundary between green nature and humans activities. After graduation, I made field surveys of weed communities all over Japan.

In September 1958, I went to Germany to study, accepting Reinholt Tüxen's invitation. He was the director of the *Bundesanstalt für Vegetationskartierung* (Federal Institute for Vegetation Mapping) at Stolzenau along the Weser River in (then) West Germany. The day after my arrival, I was taken out to the *Liineburgerheide* (heath) and other sites in Niedersachsen, and was taught the phytosociological concrete method of vegetation field survey. In the laboratory, I was amazed at the table work, which included making community tables from relevés, deciding the rank of community units from species combination, not only from dominant species, and systematizing communities into associations, alliances, orders and classes. It was not quantitative, but qualitative and deeper insight into vegetation. I met the quintessence of phytosociology.

At the same time, I compared the data of weed communities I had brought from Japan with those of paddy field weed communities of Europe that W. Koch and other scientists had researched. I compiled them into the *Oryzea sativae* class, based on community composition, and published the result in *Vegetatio* (MIYAWAKI, 1960).

POTENTIAL NATURAL VEGETATION

R. Tüxen delivered a new concept of vegetation "potential natural vegetation" in 1956. Before that there were only two concepts of vegetation, original vegetation (vegetation before humans influenced it) and actual vegetation (vegetation we can see and touch now). Potential natural vegetation is the third theoretical vegetation that all the natural conditions in a given area are considered to support, ultimately, if it were not for human impacts.

First it was very difficult for me to understand the concept. It seemed almost magic. I was taught how to figure out the potential natural vegetation through field work both in Germany

and after coming back to Japan. The potential natural vegetation recognized through minute vegetation field surveys is available in drawing accurate maps for land use and protecting or more positively regenerating native forests for green environments.

Many Japanese vegetation scientists may not understand the systematization of data from field surveys in phytosociology, especially the concept of the potential natural vegetation, which they consider to be hypothesis.

DEVELOPING PERIOD OF JAPAN'S PHYTOSOCIOLOGY

At the IA VS Congress in Rinteln in 1960, V. Westhof showed the progress of phytosociology in each country by drawing circles of various sizes. He drew big circles for many European countries, but just a small dot for Japan. Since I introduced phytosociology to Japan in 1960s, however, it has developed steadily. Many Japanese vegetation scientists came to have an interest in phytosociology, either directly or indirectly, and published research papers and books.

In 1974 the IA VS Congress and international excursion were held in Japan for the first time, and top vegetation scientists in the world participated from more than 20 countries (MIYAWAKI & TÜXEN, 1977). Again in 1984 the IA VS Congress was held in Tokyo (MIYAWAKI *et al.*, 1987). Over the twenty years from the day Japan was indicated as a dot, phytosociology in Japan can be said to have reached the world level.

I continued vegetation field surveys all over the Japanese Archipelago as well as in other areas of the world. Based on the results of the surveys around Japan, the "Vegetation of Japan" was published, in 10 volumes, with the help of over a hundred researchers nationwide. Each volume includes maps of both actual and potential natural vegetation, together with community tables (MIYAWAKI *et al.*, 1980-1989). In 1994 a book "Vegetation in Eastern North America. Vegetation System and Dynamics under Human Activity in the Eastern North American Cultural Region in Comparison with Japan" was compiled in cooperation with E. O. Box and other scientists (MIYAWAKI *et al.*, 1994). Japan and Eastern North America are located mostly in the same vegetation zones, so we conducted comparative research on vegetation communities and species com-

bination through phytosociological field surveys.

The (then) Japanese Environmental Agency accepted my suggestion and completed maps of the actual vegetation of the Japanese Archipelago, at a scale of 1:50000, taking 10 years, though there were some defects.

By the 1990s most countries of Europe had already decided on their vegetation units, based on species combination from vegetation field surveys, and plotted concrete distributions of systematized vegetation communities on maps. Some countries, including Germany, Italy and Czechoslovakia, could also identify their potential natural vegetation from remaining vegetation and complete its mapping.

Afterward ecology became concerned primarily with measurement. Experimental metric approaches came in from America, and now it is in full flower. The earlier ecology based on fieldwork, phytosociology, developed mainly by Braun-Blanquet, Géhu, Pignatti, Pedrotti, Rivas-Martinez and many other European scientists, came to be one branch of vegetation ecology. In other words, Ökologie is now changed into ecology.

REFORESTATION BASED ON PHYTOSOCIOLOGY

While I studied weeds growing under human influence, I thought most actual vegetation except weeds was really natural vegetation. As I investigated all types of vegetation in the field in Germany, however, I understood that most actual vegetation is really a substitute changed under long-term human impact. It can be said that actual vegetation is the result of human civilization. Especially recent urbanization, industrialization and large-scaled commercial plantation by monoculture have destroyed natural forests both in developed countries and in developing countries.

Japan was not an exception. For about 10 years after I came back from Germany, I kept conducting vegetation field surveys throughout Japan with young researchers, and compiled 608 associations into 133 alliances, 73 orders and 44 classes (MIYAWAKI *et al.*, 1980-1989). They were mostly substitute vegetation. I was surprised that so many indigenous forests had been destroyed. Actually about 98% of the area of Japan was originally covered with indigenous forests. I aspired to form quasi-natural forests, that is, native fo-

rests of native trees, as the foundation for human existence, through the phytosociological method.

Around the end of the 1960s and in the 1970s, the problems of environmental pollution and nature destruction hit Japan, accompanying the rapid economic growth. Private companies and national and local governments began asking us to help make green environments.

Japan is the only one country in the world that preserved and built native forests for 4000 years, though on the other hand it destroyed nature in developing new villages and agricultural land. Wise men in old days protected indigenous forests on ridges and river edges from destruction by leading people to believe these forests were the home of deities of Shinto and Buddhism, and not to incur divine wrath.

Today Japanese people have lost their religious spirit, and many indigenous forests have been destroyed. Still we can see collections of green plants, though, not only in rural areas but also in urban and industrial areas, where they look like green oases in the concrete desert. These are the so-called Chinjuno-mori, native forests in and around shrines and temples. We can identify the potential natural vegetation by catching faint information from these forests.

In the regeneration of native forests, we first conduct phytosociological field surveys around the planting site and choose the appropriate tree species to plant. These are the main tree species from the potential natural vegetation and as many other component tree species as possible. Then we nurse potted saplings with fully developed root systems from seeds, and mix and plant densely following the system of natural forests. We phytosociologists write the scenario for reforestation, and local citizens are the main agents and participants. Private companies, public administrations and other groups like NPOs work as directors or play background roles of reforestation.

The company that began regeneration of native forests by the phytosociological method, in 1970, was Nippon Steel Corporation, which was followed by other companies including Honda Motor Co., Mitsui Real Estate, Mitsubishi Corporation, Torei, and others. Today, not only leading companies such as Toyota, Yokohama Rubber, AEON, The Bank of Kyoto, and Toyoda Gosei, but also many small and mid-sized companies, national and local governments, and public schools are planting saplings

for regeneration of native forests. The leaders of each body have far-sightedness, decisiveness, energy and patience.

It is epoch-making that the Forestry Agency, MAFF Japan, began phytosociological reforestation in 2009. So far they were making coniferous monoculture forests for lumber production. As for me, I have always insisted that the tree species to plant for reforestation should be indigenous trees, which are evergreen laurel trees in warm temperate zones and summer green broad-leaved oaks and beeches in cold temperate zones. I heard they regarded me as a nuisance, getting in their way. But eventually they began to plant indigenous trees to restore devastated areas of coniferous forests.

I also made reforestations based on phytosociology in Malaysia, Thailand, the Brazilian Amazon, China, Inner Mongolia, Kenya, Tasmania and other areas in the world. Until now the number of planting site is about 1,700, and the total number of planted saplings is over 40,000,000.

INDIGENOUS FORESTS OF JAPAN

More than half of Japan's land area is in the laurel forest zone, and the main tree species include *Castanopsis cuspidata*, *Persea thunbergii*, and various evergreen *Quercus* species. These have deep taproots and are difficult to fall knock down in strong wind, floods, heavy rain, and landslides from typhoons, earthquakes and tsunami. The roots hold water in the soil after rainfall. These trees also have fresh evergreen,

water-rich leaves that will not support fire. The indigenous forests are multi-layered and protect residents from air and noise pollution. After all they have local functions of environmental protection and disaster mitigation. Globally, they help reduce climatic warming by absorbing and fixing CO₂. Half the dry weight of trees is carbon. When young seedlings grow into tall trees and form a multi-layered forest in about 10-20 years in Japan, a large amount of carbon is fixed within the forest. Indigenous forests also restore and maintain biodiversity in their natural environments.

Laurel and deciduous broad-leaved forests can be lumbered in 80 to 120 years. Emergent trees are logged selectively and carefully, and used as furniture or building materials. They must not be burnt or disposed of, since this would release their stored carbon rapidly. As successors in a lower storey grow quickly and occupy the space of logged emergent trees, the system of a whole forest is sustained through time.

On the other hand, coniferous forests mono-cultured for lumber production require permanent management. When they are not well managed because of downturns in demand due to cheap imported lumber, they deteriorate, and become devastated. Their roots are generally shallow, and they easily fall down in typhoons and earthquakes. Fallen trees and dirt sometimes back up water and cause disaster in downstream areas. Besides, many Japanese people suffer from cedar and cypress allergies, as plants produce much pollen when they die slowly (MIYAWAKI & Box, 2006).



Josias Braun-Blanquet and his wife Gabrielle, SIGMA, Montpellier, 1959 (photo A. Miyawaki).

THE FUTURE OF PHYTOSOCIOLOGY

In June 1959, with Tüxen, I visited Braun-Blanquet and his wife in Montpellier. He welcomed me saying "It was sweet of you to come all the way from Japan", shaking my hand firmly. Géhu came to Japan together with his associates to attend the IAVS Congress and Excursion held in Japan, and gave me a lot of advice. At one time, after a one-month-long field survey tour throughout Japan in 1984, he said, "Japanese people often say their country has a lot of green forests. But natural forests remain only on islands beyond the sea or deep in the mountains where people rarely visit. As for urban areas, France has more forests, as you see in Strasbourg, on the banks of the Seine and as house forests". Since then, I have kept these words in mind and devoted myself to regeneration of urban and industrial forests.

In January 1990, I visited Tüxen after the IAVS Symposium in Rinteln. It was some months before he passed away. He reached over and took my hand, saying in a dim voice "Braun-Blanquet sowed a seed of phytosociology, and grew it into a big tree. I produced flowers of vegetation mapping in the tree, and you bore fruit of reforestation far in the East". This was the first compliment from the solemn and strict professor.

If it had not been for Braun-Blanquet's phytosociology, Tüxen's severe teaching, and Géhu's casual advice, my study could not have produced adequate results. I would not have been able to regenerate native forests of native trees in urban and industrial areas like today.

Phytosociology is now at a crossroads in a sense. Experimental ecology and other individual metric approaches in vegetation science have developed covering a wide range theoretically and practically, due to new measurement instruments and techniques. These individual researches are of course very important from now on. On the other hand, phytosociology may be considered to have served its purpose but it is the foundation of vegetation science and global comparative researches.

Especially it is the basic research for immediate environmental problems of today. For the sake of regeneration of green environment it is necessary to reexamine the vegetation units and systems in each area, through field vegetation surveys and to draw vegetation maps. Objective phytosociological identification and definition of vegetation

units will become increasingly significant. I am convinced phytosociology will continue to develop for the certain future of humans.

Lastly, to Prof. Jean-Marie Géhu, Congratulations on your 80th Birthday! You are still young and cheerful enough to pursue phytosociological studies with your fellow researchers in Europe and other areas of the world. I wish you good health and research progress.

I express my sincere gratitude to my friend Prof. Franco Pedrotti (Camerino) and the professors who planned and organized this special issue.

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THE CONTRIBUTION TO PHYTOSOCIOLOGY OF THE JOURNAL *PHYTOCOENOSIS* OF JANUSZ B. FALIŃSKI

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ABSTRACT

The journal *Phytocoenosis* was founded in 1972 by Janusz B. Faliński (Białowieża Geobotanical Station - University of Warsaw) and published until 2005. The main subjects published in *Phytocoenosis* were population biology, phenology, vegetation dynamic processes, secondary successions, the role of woody dioecious species in secondary succession and regeneration, dynamism of vegetation based on permanent quadrats, synanthropization, alien species, neophytism, geobotanical cartography (floristic and vegetational), and geobotany applied to nature conservation.

KEYWORDS: *Phytocoenosis*, Janusz B. Faliński, Białowieża, population biology, phenology, dynamic processes of vegetation, synanthropization of vegetation, alien species, neophytism, geobotanical cartography (floristic and vegetational), nature conservation.

The journal *Phytocoenosis* was founded in 1972 by Janusz B. Faliński and published until 2005; it was very important because it reported the results of studies conducted at the Białowieża Geobotanical Station, regarding various aspects of Phytosociology, and, more in general, Geobotany and Plant Ecology. Prof. Janusz Bogdan Faliński (1934-2004) was an assiduous participant in the phytosociological colloquia of Bailleul and Camerino (Fig. 1). It seemed appropriate to provide in this volume of *Braun-Blanquetia*, dedicated to the centenary of Phytosociology, the list of the volumes of the journal he founded and directed for many years. After his death, the University of Warsaw was not able (or was unwilling) to continue publishing *Phytocoenosis*, to the detriment not only of science, but also of the great Polish tradition of botany.

Faliński's research, which span-

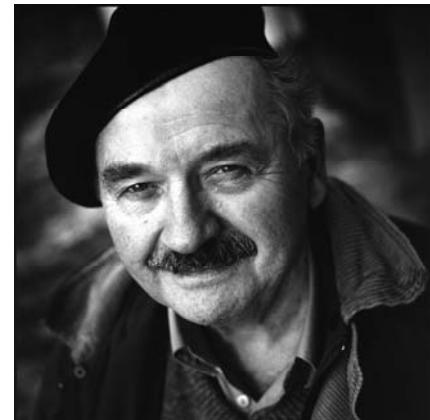


Fig. 1 - Janusz Bogdan Faliński (foto Ulrich Lebeuf).

ned many sectors of Geobotany, has been analyzed in the biographies dedicated to him and in other works (ZARYCKI, 1995, 1998; MIREK and HOLEKSA, 2006; HOLEKSA, MIREK, WOJCICKI, 2006; PEDROTTI, 1998, 2005a, 2005b, 2006;

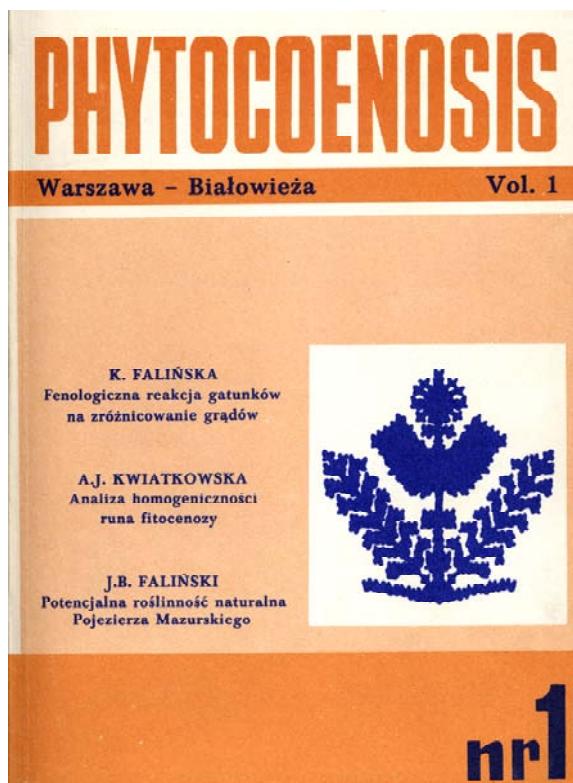


Fig. 2 - *Phytocoenosis*, cover of the first number (1972).

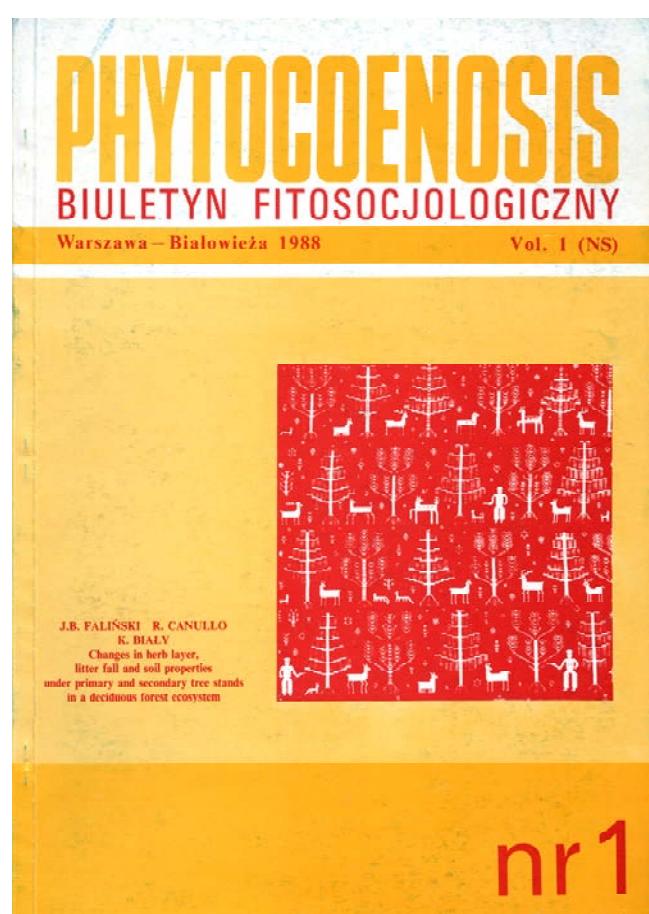


Fig. 3 - *Phytocoenosis N.S.*, cover of the first number (1988).

Tab. 1 - Volumes index of *Phytocoenosis*.

- PHYTOCOENOSIS, BIULETYN FITOSOCIOLOGICZNY (1972-1978)
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 Vol. 16 - Archivum Geobotanicum 10, 2004, pp. 71
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GÉHU, 2005; CANULLO, 2005, 2006; AUTORI VARI, 2005; FALIŃSKI, KWIAŁKOWSKA FALIŃSKA, CANULLO, 2006; DIPARTIMENTO BOTANICA ECOLOGIA UNIVERSITÀ CAMERINO, 2006). The volume published by the Department of Botany and Ecology of the University of Camerino in 2006 also contains an Italian translation of the last article by Falinski, edited by Roberto Canullo, recounting his impressions of an excursion to the Torricchio Natural Reserve of the University of Camerino. The original

article had been published in the Polish journal of Ecology, *Wiadomości Botaniczne* (FALIŃSKI, 2005, 2006; CANULLO, 2006).

Geobotanical cartography is a field to which Falinski dedicated a two-volume manual that is certainly the most complete treatise in the world of its kind, for many reasons: its definition of the field of study, dealing contemporaneously with all the types of geobotanical, floristic, and vegetational cartography, which normally are addressed

by different specialists, the subdivision of the subject, the detail of the chapters, and the originality of the interpretations and illustrations (FALIŃSKI, 1990-1991). The manual was published in Polish, and thus is little known; Falinski would have published it in English as well, but for his untimely death.

THE JOURNAL MATERIAŁY ZAKŁADU FITOSOCJOLOGII STOSOWANEJ U.W.

In the period 1960-1972 Włodzisław Matuszkiewicz and Janusz B. Falinski edited the series entitled **Materiały Zakładu Fitosocjologii Stosowanej U.W.** (*Materials of the Department of Applied Phytosociology of the University of Warsaw*). The series was published by the Department of Applied Phytosociology of the University of Warsaw; a total of 28 issues was published, with 70 contributions by 33 authors, totaling about 1400 pages, not counting inserts and maps.

THE JOURNAL PHYTOCOENOSIS

In 1972 FALIŃSKI (1972) announced that the old series would continue with the name **Phytocoenosis, Biuletyn Fitosociologiczny** (*Phytocoenosis, Phytosociological Bulletin*); this new journal was published by the Department of Phytosociology and Plant Ecology and by the Białowieża Geobotanical Station, both institutions of the University of Warsaw. The format of the journal was 20.5 x 15 cm (Fig. 2) and it was published from 1972 to 1978 with 7 volumes and 2 supplements (see Tab. 1). FALIŃSKI (1972) stated *Phytocoenosis is focused on disseminating the results of studies conducted by the Białowieża Geobotanical Station and other scientific institutions cooperating with the Station in research programmes and activities.*

THE NEW SERIES OF PHYTOCOENOSIS

After a hiatus of several years, in 1988 Prof. Falinski was able to resume publication of *Phytocoenosis*, now in a new format (29.5 x 21 cm) more suitable for geobotanical maps (Fig. 3). This time the journal was edited by the Białowieża Geobotanical Station, which Falinski directed until 2004. The 17 volumes of 36 numbers (see Tab. 1) were divided into the following series

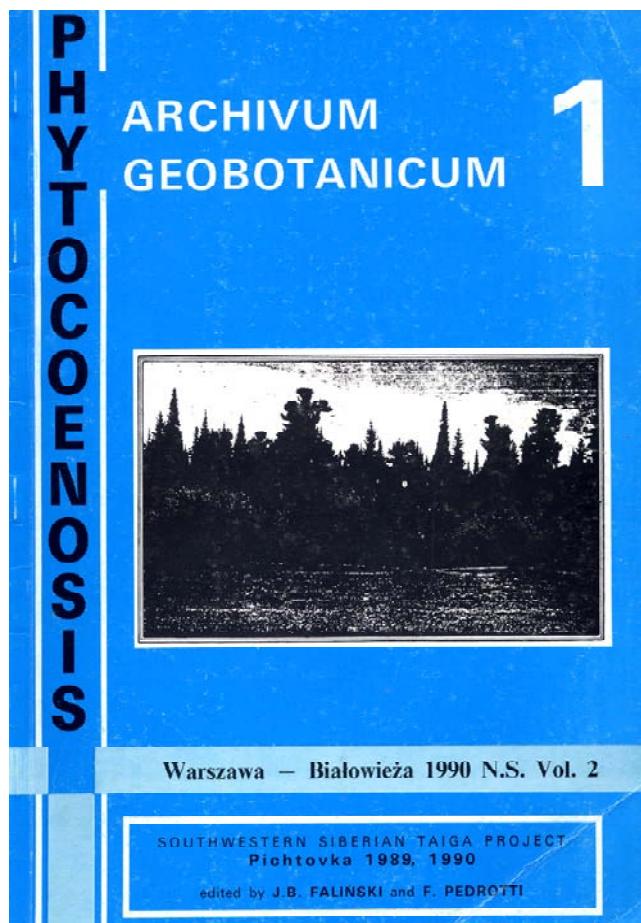


Fig. 4 - Archivum Geobotanicum, cover of vol. 2, n. 1 (1990).

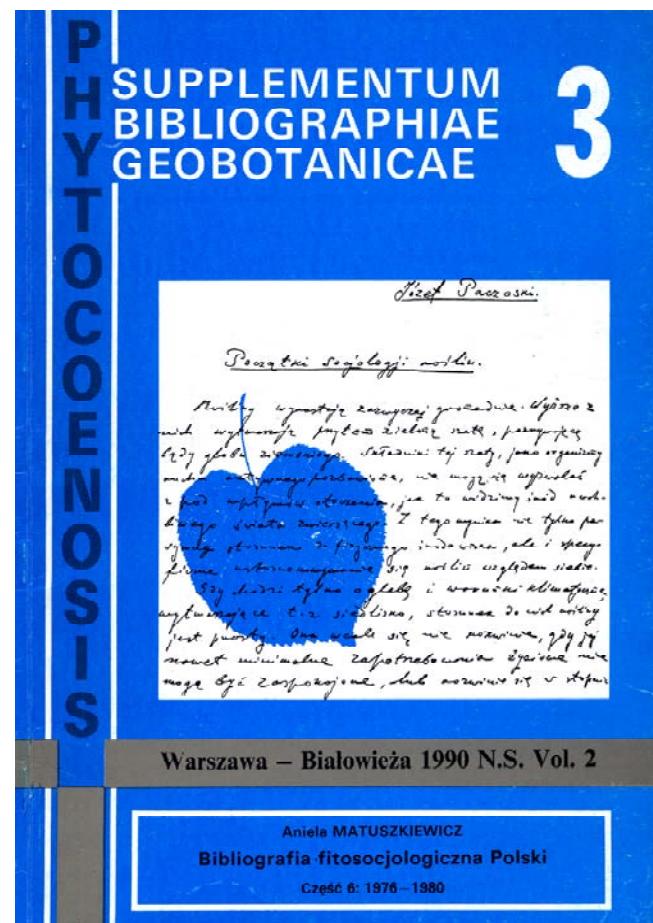


Fig. 5 - Supplementum Bibliographiae Geobotanicae, cover of vol. 2, n. 3 (1990); the cover features a facsimile of a manuscript by Józef Paczoski, the first scientist to use the term "Phytosociology." Paczoski is the author of an important monograph on the woods of Białowieża (PACZOSKI, 1930).

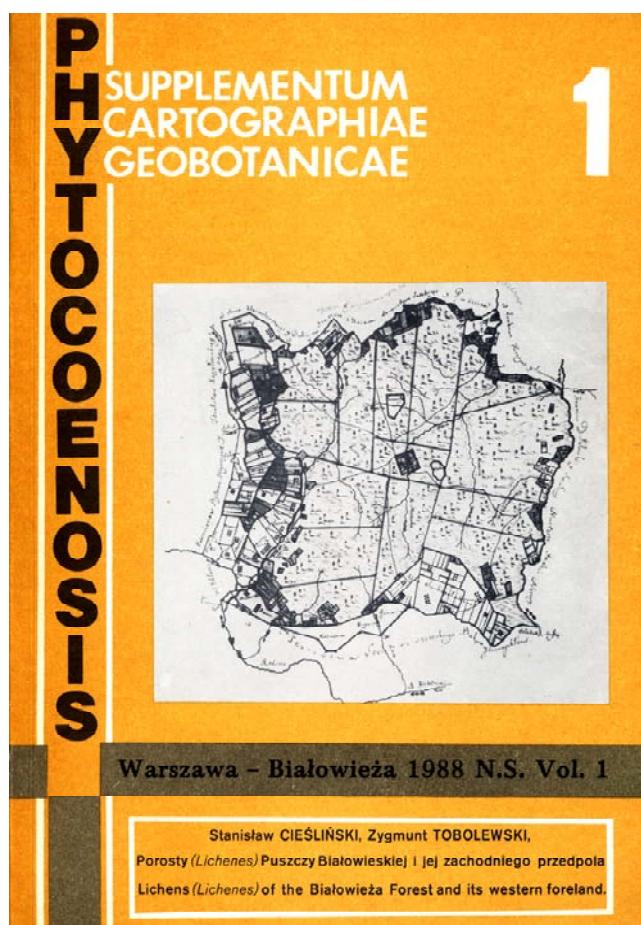


Fig. 6 - Supplementum Cartographiae Geobotanicae, cover of vol. 1, n. 1 (1991); the cover shows a late XVIII century map of the Białowieża forest.

based on research topics addressed at the Geobotanical Station (FALIŃSKI, 1991): **Archivum Geobotanicum**, publishing basic scientific documentation of the research conducted by the Białowieża Geobotanical Station (Fig. 4), **Supplementum Cartographiae Geobotanicae**, publishing maps and map collections, geobotanical atlases, as well as papers and material about geobotanical cartography (Fig. 5), **Supplementum Bibliographiae Geobotanicae**, publishing the current phytosociological bibliography, the bibliography of maps, and other sources of information on similar subjects (Fig. 6) and **Seminarium Geobotanicum**, publishing research notes, methodological and theoretical papers, material prepared for the seminars, reviews, scientific chronicle, and reports (Fig. 7).

SUBJECTS ADDRESSED

The main subjects addressed in the journal *Phytocoenosis* were population biology, phenology, dynamic processes of vegetation, secondary successions, the role of woody dioecious spe-

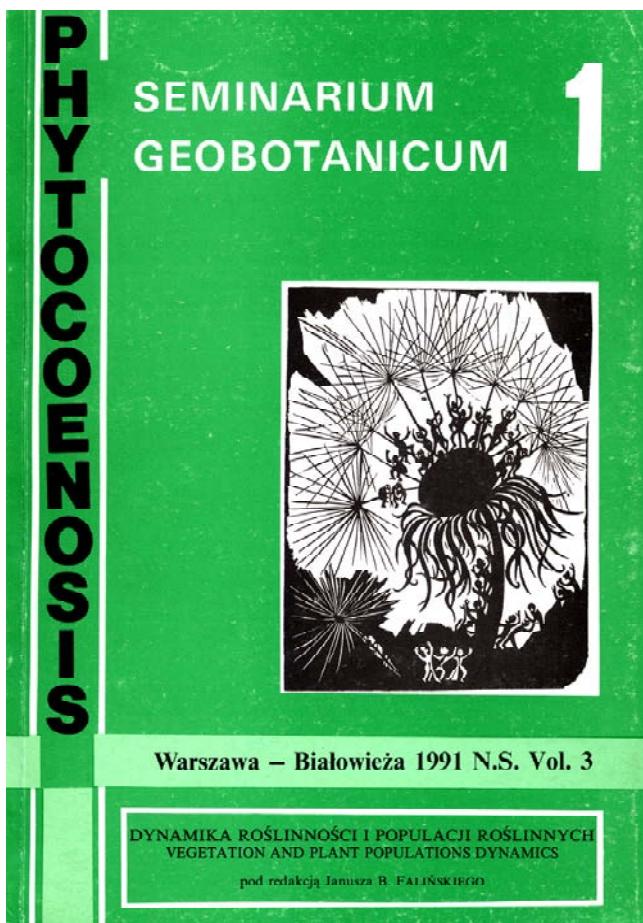


Fig. 7 - Seminarium Geobotanicum, cover of vol. 3, n. 1 (1991).

cies in secondary succession and regeneration, long term studies on the dynamism of vegetation based on permanent quadrants, synanthropization of vegetation, alien species, neophytism, geobotanical cartography (floristic and vegetational), and geobotany applied to nature conservation.

After the death of Prof. Faliński, his collaborator Wojciech Adamowski, a member of the *Phytocoenosis* editorial board, supervised the printing of a special number of the Supplementum Bibliographiae Geobotanicae (FALIŃSKI & ADAMOWSKI, 2004) with a complete index of all the works published in the old and new series of *Phytocoenosis*. With these words ADAMOWSKI (2004) concluded his presentation of this number: *This bibliographic issue of Phytocoenosis provides documentation of and closes a certain stage in the history of the Białowieża Geobotanical Station, ended with the passing away of Professor Faliński.*

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RICORDANDO IL MIO MAESTRO JOSIAS BRAUN-BLANQUET

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ABSTRACT

Braun-Blanquet is recorded in this essay as imprinted in the memory of one of his grateful disciples similar to Pictures in an Exhibition:

- The first encounter in Switzerland with Braun-Blanquet in 1951 describes him in the middle of a fascinating village scene.
- During 1952/53 the postdoctorate at the SIGMA in Montpellier getting to know Braun-Blanquet's personality, his life style, family life, contact with scientists, colleagues and students.
- On excursions with students of different countries Braun-Blanquet as a geobotanist, with a profound knowledge of the flora, vegetation and ecology of the Midi.
- An excellent teacher with dedication towards his students, with the constant aim to unify them in working groups; to them he reveals the real study of nature like an open book to be read with reverence, devotion and humbleness.
- How to perform an exact relevé and how to study and understand plant communities, their structures and method of statistic approach and elaboration.
- Respect for plants and animals, sympathy for his little goat, conservation of a pristine environment and its natural evolution.
- Taking care of his own vineyard.
- Openminded and with a great sense of hospitality for visitig colleagues and students and keeping a huge amount of handwritten correspondence with scientists all over the world.
- Finally during the last hundred years after its foundation, Braun-Blanquet's Plantsociology with its still unsurpassed statistic method is used by hundreds of geobotanists in the world in order to better understand the environment and its plant communities.

KEYWORDS: Braun-Blanquet, Montpellier, SIGMA.

Lo incontrai per la prima volta nel lontano 1951 a Zernez, in Engadina. Ero studentessa del 6° semestre della

Facoltà di Filosofia a Vienna, e un bel giorno, dopo la lezione di Pflanzensoziologie (Fitosociologia) il prof. Höfler mi disse: *Signorina Wikus, venga un momento in Istituto, che avrei una proposta da farle.* La proposta era la seguente: *Finisca al più presto gli esami, e dopo vada da Braun-Blanquet nell'Engadina dove passa le estati, e gli mostri le sue tabelle delle Dolomiti.* È

una persona dalla quale lei potrebbe imparare molto... Seguii il suo consiglio, presi il treno ai primi di agosto e arrivai a Zernez, piccolo villaggio di montagna nei Grigioni (Unterengadin), verso il tramonto. Nel piccolo albergo del paese chiesi se sapessero dirmi come trovare il dr. Braun, e la signora che lo gestiva mi prese per mano e uscendo dalla porta indicò due signori nella



Josias Braun-Blanquet

piazzetta e disse: *Il più piccolo è il dr. Braun.* Uno dei due era alto e magro, sulla cinquantina (e si rivelò essere il lichenologo Frey), l'altro era più basso di una testa, capelli folti bianchissimi, di età più avanzata, e tutti e due avevano lo sguardo attento e incuriosito rivolto verso la strada che scendeva dalla montagna. Stavano aspettando qualcuno o qualcosa? Non riuscivo ancora a intuire il motivo, lo capii poco dopo: ci fu un tintinnio di campanelle ed ecco, dalla strada che sbucava nella piccola piazza del paese, arrivò un gregge di capre che scendeva a passetti spediti, in testa il caprone con aria fiera e maestosa, e dietro a lui (come il Pifferaio di Hameln) il suo seguito di caprette che camminavano in fretta e sembravano ben affiatate. In quello scampanio di cento-duecento campanelle, gli animali man mano arrivavano davanti alla propria stalla e svoltavano a destra o a sinistra verso la propria dimora scomparendo ai nostri occhi. Al tintinnio delle campanelle del gregge, poi, si aggiunse la campana della chiesetta con i suoi rintocchi sonori preludendo ai vespri. I due signori in attesa, quindi, volevano godersi proprio questo spettacolo del rientro del gregge dai pascoli di montagna accompagnato dal tintinnio delle loro campane e sui loro volti leggevo godimento e ammirazione.

A questo ricordo di un'immagine di pace e serenità associo per sempre il primo incontro con la persona che doveva diventare il mio grande maestro e amico paterno, Maestro con la M maiuscola, direi.

Il dr. Braun aveva coltivato un legame speciale con una capra del tutto particolare. La chiamava Biquette ed era un animale dal pelo bianco a grosse chiazze brune, con una barba lunga e due boccoli laterali, che per queste caratteristiche non tanto comuni e il suo incedere leggero ed elegante, sembrava muoversi come una gran dama, una persona davvero; il dr. Braun la accarezzava sempre sotto il mento quando attraversava il giardino della SIGMA (Station Internationale de Géobotanique méditerranéenne et Alpine) a Montpellier, dove lui abitava con moglie e figlia e dove Biquette pascolava durante la giornata. Biquette gli andava sempre incontro, scodinzolando e, ricevuta la solita carezza, lo guardava con i suoi placidi occhi da capra pieni di affetto e gratitudine. E in una di queste occasioni, in mia presenza, il dr. Braun riferendosi alla capra, disse: *Nous nous comprenons sans parler!* A lei era permesso tutto, gustare tutte le erbe che le piacevano, correre, insomma, Biquette ave-

va più concessioni nel giardino della figlia del Maestro, Mireille, alla quale era persino proibito attraversare il giardino in bicicletta per non disturbare la successione della vegetazione che era in procinto di evolvere verso il *Quercetum ilicis galloprovinciale*. *Biquette est intelligente*, disse il dr. Braun, *conosce molto bene le piante, distingue in modo eccellente Urospermum dalechampii da Reichardia picroides, ed io ho imparato da lei.* (Il dr. Braun, per esempio, distingueva i germogli o le rosette basali di varie specie di Asteraceae assaggiandole).

Ma ora vorrei tornare alla persona del mio maestro e descrivere come era il suo carattere e come insegnava durante le escursioni.

Pochi mesi dopo la mia laurea a Vienna nell'autunno del 1952 su invito del dr. Braun ero andata a Montpellier (oggi si direbbe per un post-dottorato) e lì trascorsi un annetto, finanziandomi il soggiorno come "au-pair" al Sacré Coeur di Montpellier, poco distante dalla SIGMA da cui la separava soltanto un immenso vigneto e la strada. La SIGMA era frequentata da giovani dottori di tutta l'Europa, soprattutto dall'Olanda, Germania, Svizzera, Polonia, Turchia, e nella primavera del 1953 venne anche un italiano di nome Sandro Pignatti, che tre anni dopo divenne mio marito. Tutti questi giovani venivano a Montpellier per osservare attentamente la vegetazione, imparare la Fitossociologia, come fare rilievi, come elaborare le tabelle. Quello che io ammiravo in questo maestro era il suo modo di essere umile, semplice, sincero e modesto, severo con se stesso, risparmiatore, ma esuberante, però cortese. Durante le escursioni non avrebbe mai mancato di dare la mano a sua moglie quando si doveva attraversare un punto difficile, scavalcare un muretto e mai tornava a casa senza un pacchetto di dolcetti di pasticceria, anche dopo la fine di escursioni estremamente lunghe e faticose. E come insegnava: non si metteva mai al centro dell'attenzione, ma il centro erano le persone alle quali era diretta la sua parola, non era invadente, ma molto semplice, partiva sempre dalla natura, dalla specie, dalla vegetazione del Midi per inserirsi in essa, lui, tu e io, in quest'ordine, nel bosco, nel prato, nella comunità di specie della spiaggia a Palavas, ad Aigues Mortes, mete delle escursioni, e la natura davanti a noi come un libro aperto nel quale tutti noi impariamo a leggere, noi inseriti come piccoli granelli pensanti in questa catena infinita dell'Universo, attenti e interessati ad imparare e partecipi nell'os-

servare la natura con reverenza.

Negli anni che seguirono non mancarono occasioni di rivedere il Maestro durante congressi ed escursioni, su nostro invito personale a lui ed a sua moglie Gabrielle a Lienz, oppure noi nuovamente alla SIGMA. Il dr. Braun teneva una vasta corrispondenza con colleghi e allievi di tutto il mondo e rispondeva sempre alle nostre lettere. Non usava la macchina da scrivere, lui scriveva a mano. Tutt'al più dettava le lettere alla segretaria.

Noi abbiamo conservata una mappa con tutta la corrispondenza di Braun-Blanquet a noi e anche qualche lettera in copia inviata da noi a lui. Le lettere e cartoline inviate a uno di noi o a tutti e due e conservate sono 93, più tre telegrammi. La corrispondenza iniziò il 1° agosto del 1951 con una cartolina a me, precisando il villaggio del nostro primo incontro.

Era sempre felice di ricevere notizie della nostra famiglia in crescita e le foto dei bambini, che inseriva nel suo album degli ospiti. Ma voleva anche vedere i nostri figli. Un'unica volta questo è stato possibile: un incontro non esattamente programmato, ma felice, nel Parco Nazionale Svizzero. Eravamo alla ricerca del dr. Braun-Blanquet e di sua figlia insieme al prof. Erwin Aichinger e sua moglie. Sapevamo che il dr. Braun-Blanquet doveva essere circa in una determinata zona ed infatti, con il mio "occhio di lince" (come disse qualcuno) vidi tre persone sedute al bordo del bosco, erano i Braun-Blanquet, il padre assieme alla figlia Mireille, ed il loro fedele amico Ernst Furrer. Misi sul prato, su una tovaglia tirolese, scelta per l'occasione, una Thuringertorte che avevo preparato, e questa venne gustata da tutti poco dopo. Mireille prima di congedarci dava ad alcuni dei nostri bimbi una bottiglietta (vuota?) di génepi che loro conservarono a lungo come una reliquia. Quel giorno, nell'estate del 1974, era il 90esimo compleanno del dr. Braun-Blanquet. Così è anche facile ricostruire la data: il 3 agosto.

Nel 1980 durante un viaggio fino a Madrid nella nostra VW combi rossa, con 2 dei nostri figli, sulla via del ritorno volevamo partecipare a un convegno della "Arbeitsgruppe über Sukzessionsforschung" della International Association for Vegetation Science a Montpellier. Il Maestro e sua figlia ci mandano un telegramma a Trieste, prima della nostra partenza: "ATTENDONS AVEC JOIE 4 PIGNATTI LE 16 SEPTEMBRE POUR COUCHER. MIREILLE ET JOSI BRAUN BLANQUET". Eravamo commossi. E duran-

te il convegno apparve il dr. Braun-Blanquet, 96enne, una grande sorpresa per tutti i partecipanti. Invitò tutti i presenti ad un breve ricevimento nella SIGMA durante il pomeriggio. Me lo vedo ancora, su una poltrona di paglia davanti all'ingresso della villa, mentre sua figlia offriva uva della loro vigna dietro la casa.

Mentre i nostri figli avevano fretta di tornare a casa in treno, mio marito e io eravamo invitati a casa del Maestro a cena. Il tavolo del soggiorno nel piano di sopra era festosamente apparecchiato e spicavano grandi tovaglioli di lino finissimo con un monogramma vistoso ricamato con le iniziali N.P. *Questo è il monogramma della famiglia Pavillard*, spiegò la figlia (professore di medicina interna e dietologa alla Facoltà di Medicina), *un regalo della signora Pavillard a mia madre* (Gabrielle Blanquet, botanica anche lei e, da giovane, allieva di Pavillard). Il prof. Pavillard era uno dei due grandi maestri del dr. Braun-Blanquet: Pavillard a Montpellier, Schröter a Zurigo.

Il dr. Braun-Blanquet con gli anni era diventato quasi sordo, e talvolta la conversazione si svolgeva per iscritto, ma riusciva molto bene a leggere le labbra di sua figlia. Il Maestro, che ancora vedeva bene, rispondeva a voce. Quella sera il mio posto a tavola era di fianco a lui ed ero commossa della sua attenzione continua e pronta nel servirmi e nel versare il vino (della sua propria vigna). La figlia Mireille curava molto il lato dietetico di suo padre e ci raccontò che proprio in questi anni della sua vecchiaia lei si godeva il padre (ormai vedovo dal 1966) finalmente, perché quando era più giovane e attivo, non aveva mai avuto tempo per lei come avrebbe desiderato.

Con la posta dello stesso giorno il Maestro aveva ricevuto un libro di Elias Landolt di Zurigo sulla Conservazione della Natura in Svizzera. Il dr. Braun-Blanquet era curioso di sfogliare questo lavoro appena arrivato e dopo un po' si scusò e congedò da noi, e disse di volersi ritirare e dare un'occhiata al libro arrivato, salutandoci affettuosamente con un: *Esperons nous de nous revoir encore quelques fois!*

Purtroppo la speranza espressa non doveva realizzarsi. Solo due giorni dopo la nostra partenza, nel ricevere la visita molto gradita del prof. Bolós e moglie da Barcellona, il dr. Braun-Blanquet cadde dalle scale salendo al primo piano e siruppe la spina dorsale. Con il passare degli anni gli era venuta una gobba pronunciata, e pare sia stata questa a non sopportare le conseguenze della

caduta. Voleva che le sue spoglie riposassero nella terra della sua patria, a Coira.

Nei decenni che seguirono il mio soggiorno a Montpellier e fino ad oggi molti sono i botanici che hanno imparato il metodo e le tecniche di rilevamento in campo del mio maestro Josias Braun-Blanquet e lui rimane il fondatore riconosciuto di una scuola i cui allievi si può dire siano diffusi in tutto il mondo. Mi sento privilegiata di appartenere ormai ai pochissimi allievi diretti ancora viventi che hanno imparato da lui personalmente come eseguire un rilievo, non in fretta e furia, ma con grande precisione ed esattezza e, scritto l'elenco delle specie, i valori di presenza, copertura e sociabilità, i particolari del luogo, del terreno, la data ecc., ecco, il Maestro riteneva il rilievo concluso se alla fine, durante l'ultimo quarto d'ora, non venivano trovate e aggiunte nuove specie.

Sulla domanda *È necessario annotare la sociabilità* (infatti oggi non sono pochi i fitosociologi che la tralasciano) scrive: *Bei + kann in der Regel die Soziabilität wegfallen. Bei den höheren Abundanzzahlen muss man es jedem einzelnen überlassen, ob er es fuer gut findet die Soziabilität beizugeben. Ich tue es in der Regel und zwar deshalb, weil die Soziabilität manchmal guten Aufschluss ueber die soziologische Bedeutung der Art gibt. Sie sehen auch, dass Leute wie Fu..., Pa..., Eg... keine sehr gewiegt Soziologen sind. Es kann vorkommen, dass eine Art mit ganz verschiedener Soziabilität in die Gesellschaft eintritt und solche Unterschiede beleuchten wieder die Vitalität und Konkurrenzkraft der Art* (dalla lettera del 9 novembre 1961).

Non risparmiava anche critiche acute sull'andamento di convegni ed alla fine di un "Colloque méditerranéen" a Montpellier (negli anni '70) scrisse che questo non aveva messo alla luce troppe novità. *Viele Worte und mässige Ideen. Manche Leute sprechen um gehört und gedruckt zu werden* (dalla lettera del 9 giugno 1974).

La scienza non si è fermata, la tecnica e l'elaborazione dei dati hanno pure fatto progressi, gli studiosi di fitosociologia si sono moltiplicati prima come funghi, e man mano (anche con deviazioni in varie direzioni specialistiche), con arricchimenti nel campo dell'ecologia e degli ecosistemi. Però in molte università gli studenti non ricevono più una solida base di sistematica e tassonomia, molti studenti non imparano e non conoscono più le piante, ahimè! Vengono prospettate molte ipotesi futuristiche, molti castelli per aria come si presenterà probabilmente la



Josias Braun-Blanquet con Erika Pignatti Wikus al Passo di Sella, luglio 1961 (foto Franco Pedrotti).

nostra vegetazione su questo pianeta tra 20, 50, 100 anni. Ricordiamo pure il cambio climatico, il calo della biodiversità, ed ancora la probabilistica d'abord! Il mio maestro forse a questo punto avrebbe da dire: *Ricordatevi che alla base della nostra scienza ci sta la volontà di imparare dalla natura, studiare con grande umiltà le sue leggi intrinseche e approfondire il sapere ad infinitum, sempre cominciando dal piccolo, pars pro toto. Fertig, lustig!* (tradotto dal tedesco circa: *finito, allegria!*). Spesse volte disse queste due parole quando un obiettivo importante era stato raggiunto).

Il 3 agosto del 1984 sarebbe stato il centesimo compleanno del mio maestro. Quel giorno eravamo in Giappone riuniti assieme a 200 e più studiosi della vegetazione, provenienti da tutto il mondo. Mio marito ha voluto che io ricordassi il nostro grande maestro Josias Braun-Blanquet davanti ai partecipanti del Congresso della IAVS a Tokyo. Un ricordo che mi ha commosso, ma che nel contempo riempie ancora il mio cuore di gratitudine per quanto ho imparato da lui, il dr. Josias Braun-Blanquet. Mi riempie di gioia constatare come dal suo insegnamento si sia formata una scuola di pensiero scientifico, diffusa in tutto il mondo, impegnata a studiare e interpretare gli ecosistemi come unità che evolvono nella loro interezza. In questo modo il Maestro ha additato la via per evitare di cadere nella tentazione riduzionista di disarticolare la vegetazione nei singoli componenti, per poterla dominare e sfruttare. Dal pensiero di Braun-Blanquet nasce la moderna concezione della vegetazione, come sistema complesso auto-organizzante.

REINHOLD TÜXEN SOCIETY (RTG) - SCIENTIFIC SOCIETY FOR VEGETATION SCIENCES

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ABSTRACT

The Reinhold Tüxen Society (RTG) is the German-language scientific society for vegetation sciences. It is named after Prof. Dr. Drs. h.c. mult. Reinhold Tüxen (1899-1980), the father and advocate of phytosociology primarily in Germany, and also in numerous other countries around the world as well. The RTG is registered at the Institute of Geobotany at the Leibniz Universität Hannover. The director is currently Prof. Dr. Richard Pott. The RTG establishes science working groups. It has published the annual "Reports of the Reinhold Tüxen Society" (*Berichte der Reinhold Tüxen Gesellschaft*) since 1989 to communicate its activities and results. It advises and assists the city of Rinteln in awarding the Reinhold Tüxen Prize, an international science award, every three years. This prize has been awarded since 1987 by the city of Rinteln in memory of its honorary citizen Reinhold Tüxen. It has a value of 5,000 euro and is considered to be the only science prize worldwide that is awarded exclusively for significant achievements in research and practice in the field of vegetation sciences.

KEYWORDS: German Phytosociology, Nomenclature, Syntaxonomy, Reinhold Tüxen Society.

HISTORICAL BACKGROUND

It is thanks to the outstanding achievements of our promotor of vegetation sciences, and in particular phytosociology, Reinhold Tüxen, that up until his death in Rinteln in 1980, the state of Lower Saxony was an international center for vegetation science and geobotanical research for many years. This is demonstrated by, for instance, the founding of the Reich Center for Vegetation Mapping in Hannover in 1938, which later became the German Federal Agency for Vegetation Science (1955), and which today is based in Bonn-Bad Godesberg and is now called the German Federal Agency for Nature Conserva-

tion.

The office of what is currently known as the International Association for Vegetation Sciences (IAVS), as well as the International Symposia for Vegetation Sciences held annually from 1954 to 1981 in Rinteln that attracted 150-200 participants from all around the world each year still testify to the central, lasting importance Reinhold Tüxen had for global vegetation science (Fig. 1).

In recognition of the research center set up by R. Tüxen and of his scientific-political significance at that time, following his death the state government of Lower Saxony acquired his scientific estate in 1981 and it was then brought to the North-German Academy for Nature Conservation (NNA, Lunenburg Heath, Schneverdingen) - today known as the Alfred Toepfer Academy for Nature Conservation - to ensure the continuation of all scientific research there. These libraries and the Tüxen Archive are currently the most complete collections of phytosociological data and literature.

Afterwards, in 1989, Lower Saxony's Minister of Agriculture and Forestry decided to transfer this collection of literature and documents to the Institute of Geobotany at the Leibniz Universität Hannover and charge them with

keeping and endeavoring to build upon it (POTT, 1999).

The proceeds from the purchase of the scientific estate of Tüxen together with its textbook collection (Fig. 2), more than 40,000 offprints, their cards, the phytosociological original tables and their irreplaceable diapositives were entrusted to the Reinhold and Johanna Tüxen Foundation as according to the testament of R. Tüxen. The purpose of the foundation as per its charter is the promotion of phytosociology in research, teaching and application, as well as the oversight and financial support of scientific research on the basis of the scientific principles developed by R. Tüxen.

After Tüxen's death in 1980 the Reinhold Tüxen Society was founded. Following German reunification the RTG was subsequently reconfigured and newly established in 1990 as a "Scientific Society for Vegetation Sciences". It currently boasts about 350 members.

SCIENTIFIC PROGRAM OF THE RTG

Phytosociology as a scientific method has its origins in vegetation geography, as can be seen from the geographical descriptions of vegetation

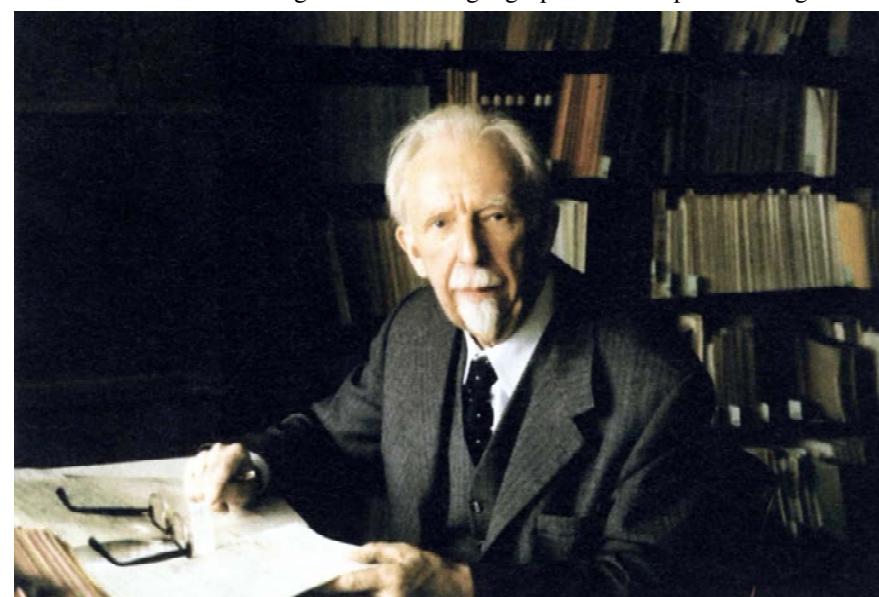


Fig. 1 - Professor Dr. Reinhold Tüxen (1899-1980).

from Carl von Linné (1707-1778) and Alexander von Humboldt (1769-1859), for example. It was first developed in the early decades of the twentieth century, and then finally developed to a scientifically based method practical in the field in 1928 by Josias Braun-Blanquet (1884-1980). This is known as the "Zurich-Montpellier School" of phytosociology and has in the meantime prevailed worldwide over the other schools, such as the "Uppsala School" of Gustaf Einar Du Rietz (1895-1967). Phytosociology after Braun-Blanquet was primarily advanced by Reinhold Tüxen in northern Germany, and by Erich Oberdorfer (1905-2002) in southern Germany. Phytosociological methods are widely used today as a means of working primarily in geobotany, geography, in agricultural and

forestry sciences as well as in landscape planning, and in gathering vegetation science data.

After the system of phytosociology had been worked out to a large extent for Central Europe in the early 1970s, its influence spread and fundamentally affected aspects of ecology and nature conservation. At the same time quantitative approaches and GIS-driven programs were developed to align and subject the phytosociological methods to the criteria of an exact science with the aid of statistical significance analyses. The "International Code of Phytosociological Nomenclature, 3rd edition" by WEBER *et al.* (2000), for instance, traced its origins to one of our annual conferences from March 21-23, 1991 in Rinteln, and afterwards from February 26-27, 1997 in Hannover; it was created by

a "Standing Committee" of the IAVS and the *Fédération Internationale de Phytosociologie (FIP)*. This now represents an important foundation for all issues of nomenclature and the syntaxonomy of vegetation types of phytosociology and their rank and position. In their working groups and at international symposia - such as the one held September 13-17, 2011 in Valencia/Spain - members of FIP discuss and advance these new topics (www.scienzadellavegetazione.it).

The RTG is able to still today provide a forum for the consideration of the older scientific, technological, social and ecological challenges of researching, collecting and describing the many vegetation types and vegetation landscapes of the earth. Interdisciplinary work and research, connecting geobotanical knowledge with the cultures of various countries, tackling topic points of especially current or regional significance, as well as an openness for topics and participants are the important fundamental principles of our work.

The scientific program of the RTG therefore addresses the notion that our actions are fully comprehensible first in connection with their historical and cultural context. In light of this we have established the following three scientific working groups: Vegetation History (Palynology and Archaeobotany); Vegetation Dynamics; Biomonitoring and Global Change.

The topic of "landscape" is a new field to which we will be dedicating an interdisciplinary annual conference from April 2 to 4, 2011 in Hannover and on which we will be founding this new working group. As of the winter semester of 2010 there is even a master's degree course in "Landscape Sciences" at the Leibniz Universität Hannover, which is unique in Germany (www.geobotanik.uni-hannover.de). At all of our conferences we deal with past and current developments and observe, examine, discuss and evaluate their place in both the present and the future.

Our activities at the RTG comprise several program points: One central format are the previously mentioned annual conferences, working group meetings and scientific symposia that deal with current topics and offer new forums for discussion and review. The scientific program of the annual conference in Hannover - or every three years in Rinteln - is rich in diversity, whereby the diversity of all disciplines and of the active participants are brought together in accordance with our guiding principle of networking. We provide such



Fig. 2 - Dr. Silje Berger in the Tüxen-Library, Institute of Geobotany, Leibniz-University Hannover.



Fig. 3 - The former university town Rinteln, with its famous Weser-Renaissance-architecture.

services primarily to RTG members (<http://de.wikipedia.org/wiki/Reinhold-Tüxen-Gesellschaft>, www.reinhold-tüxen-gesellschaft.de/kontakt.htm). At a higher level, the RTG is mostly involved with the activities of the FIP.

A further central program point comprises the expert discussions within the working groups, which are also offered as outdoor events and international excursions. Our well-attended exclusive lecturer and professor excursions to the East Frisian Island (1995), to northern Germany (1997, 1999), to the Canary Islands (1997-2009), to China (2009) and Kamtchatka (2010) have become legendary.

REINHOLD TÜXEN (1899-1980)

Professor Dr. Drs. h.c. mult. Reinhold Tüxen (* May 21, 1899 in Ulsnis; † May 16, 1980 in Rinteln) was an important vegetation scientist and above all a phytosociologist. He grew up in the rural north of Schleswig-Holstein, in the Schlei region before Angeln, between the cities of Schleswig and Kappeln, where he was able to play in beech forests set aside as farmland as a child. (TÜXEN, 1986) These childhood impressions prefaced a career in science that eventually made Reinhold Tüxen one of the pioneers of phytosociology. He studied chemistry, botany and geology in Heidelberg, and then phytosociology with J. Braun-Blanquet at the ETH Zurich and in Montpellier.

In the 1930s he was employed by the Provincial Office for Nature Conservation in Hannover and developed - together with Ernst Preising (1911-2007) and Heinz Ellenberg (1913-1997), among others - a vegetation mapping for the province of Hannover. This office became the "Central Office for the Vegetation Mapping of the Reich" in 1939, which then later became - as previously mentioned - the "Federal Agency for Vegetation Mapping", of which Tüxen was the director for 25 years until 1964. This in turn became the present-day "Federal Agency for Nature Conservation".

In April, 1963 R. Tüxen moved into a house in Rinteln-Todenmann. Starting in 1965 this was where he organized annual international symposia in Rinteln. This made the former university town of Rinteln (Fig. 3) well-known as the site of scientific conferences. In 1979 the city granted him honorary citizenship. Reinhold Tüxen is Rinteln's sole honorary citizen to date.

R. Tüxen received numerous other honors for his scientific accomplishments: 1954 - Culture Award from the city of Kiel; 1959 - Dr. h.c. University of Montpellier; 1964 - German Federal Cross of Merit; 1965 - Dr. h.c. University of Lille; 1975 - Dr. h.c. University of Gießen; 1976 - Alexander v. Humboldt Gold Medal; 1977 - Dr. h.c. University of Freiburg; 1978 - Dr. h.c. University of Toulouse; 1978 - Lower Saxony Award; 1979 - Dr. h.c. University of Hannover.

Reinhold Tüxen had a long and productive life.

A list of his scientific output comprises 542 publications (BARKMAN, 1981). The most important of these examine the climax problems in northwestern Europe (TÜXEN, 1930, 1970), the plant communities of northwestern Germany (1952, 1975), the higher syntaxo-

nomic units of Europe (1958), the vegetation of Ireland (1952), the vegetation of Spain (1958), and the plant communities of Japan (1979), just to provide a brief overview of his diverse work. He had always been mostly interested in the Pleistocene landscapes of northwestern Germany and their coasts and islands, the bogs and the geest with their old wood pastures, the moor and juniper landscapes, and the distinctive sandy and loamy soils and their legendary "script" as an indicator of natural and anthropogenic influences in the past and present (TÜXEN, 1957; POTT, 1995; POTT, 2005; POTT & HÜPPE, 2007).

REPORTS OF THE RTG AND OF THE RINTELN SYMPOSIA

A further important focus of the



Fig. 4 - The first volume "Berichte der Reinhold-Tüxen-Gesellschaft, 1989".

Tab. 1 - Volumes index of Berichte der Reinhold Tüxen Gesellschaft.

- 1989 - Vol. 1, Rintelner Symposium I, Tüxen-Price: Erich Oberdorfer: Beech forests of Europe.
 1990 - Vol. 2, Hannover: Vegetationstypen in statu nascendi, Vegetation-complexes; *Stellarietea mediae*-Synsystematic comparison; Molinio - Arrhenatheraea synsystematic Comparison; *Pteridio-Rubion* and *Prunetalia* - New classification; *Carpinion betuli* - Forests of SW- Germany. [Vegetation types in statu nascendi, Vegetation-complexes; *Stellarietea mediae*-Synsystematic comparison; Molinio-Arrhenatheraea synsystematic Comparison; *Pteridio-Rubion* and *Prunetalia* - New classification; *Carpinion betuli* - Forests of SW-Germany]
 1991 - Vol. 3, Rintelner Symposium II, Tüxen-Price: Victor Westhoff: Coastal Vegetation of Europe.
 1992 - Vol. 4, Hannover: Stipendiaten der Reinhold- und Johanna- Tüxen-Foundation: Federsee-Fen-Ecosystems: *Magnocaricion*, *Scheuchzerietalia*, *Oxycocco-Sphagnetea* - Tofieldietalia - Associations; Dwarf shrub Heathland of Island; *Asplenietea*-Associations of Central Europe, *Quercion roburi-petraeae*-woodlands of Central Europe; Montio-Cardaminetea-Ass. of Central Europe u.a. [Awardees of the Reinhold and Johanna Tüxen Foundation: Federsee-Fen-Ecosystems: *Magnocaricion*, *Scheuchzerietalia*, *Oxycocco-Sphagnetea* - Tofieldietalia - Associations; Dwarf shrub Heathland of Island; *Asplenietea*-Associations of Central Europe, *Quercion roburi-petraeae*-woodlands of Central Europe; Montio-Cardaminetea-Ass. of Central Europe and more]
 1993 - Vol. 5, Rintelner Symposium III, Tüxen-Price: Ernst Preising: Heathlands of Europe. [Rinteln Symposium III, Tüxen-Price: Ernst Preising: Heathlands of Europe]
 1994 - Vol. 6, Hannover: Stipendiaten der Reinhold und Johanna-Tüxen-Foundation: Vegetations- und Landschaftswandel im Schwarzwald, *Ranunculion fluitantis* - Standortfaktoren, Biocenology of *Coenagrion mercuriale*, Ecology of *Caricetalia davallianae*; Rivulets in urban areas, *Xerobrometum* Br. -Bl.15 em 31; Life history of *Aposeris foetida*; Wild Rabbits and *Carici arenariae-Empetretum*; Seed bank of *Arrhenatherion* and *Trisetetum*" u.a. [Awardees of the Reinhold and Johanna Tüxen Foundation: Vegetation and landscape change in the Black Forest, *Ranunculion fluitantis* - location factors, Biocenology of *Coenagrion mercuriale*, Ecology of *Caricetalia davallianae*; Rivulets in urban areas, *Xerobrometum*, Br. -Bl.15 em 31; Life history of *Aposeris foetida*; Wild Rabbits and *Carici arenariae-Empetretum*; Seed bank of *Arrhenatherion* and *Trisetetum* and more]
 1995 - Vol. 7, Rintelner Symposium IV, Tüxen-Price: Akira Miyawaki: Revitalisierung gestörter und zerstörter Lebensräume. [Rinteln Symposium IV, Tüxen-Price: Akira Miyawaki: Revitalizing disturbed and destroyed habitats]
 1996 - Vol. 8, Hannover: Stipendiaten der Reinhold und Johanna Tüxen-Foundation: Oligotrophe Kleinmoore; *Narthecium ossifragum* - Heidemoore; *Campylopus introflexus* - Küstendünen; Kiefernwälder der Erico-Pinetea u.a. [Awardees of the Reinhold and Johanna Tüxen Foundation: Oligotroph small bogs; *Narthecium ossifragum*- Heather moors; *Campylopus introflexus* - Coastal dunes; Pine forests of the Erico-Pinetea and more]
 1997 - Vol. 9, Rintelner Symposium V, Tüxen-Price: Konrad Buchwald: Vegetationskunde als Grundlage für Natur- und Landschaftsschutz. [Rinteln Symposium V, Tüxen-Price: Konrad Buchwald: Vegetation sciences as a foundation for nature and landscape preservation]
 1998 - Vol. 10, Hannover: Mechanismen der Konkurrenz - Überlegenheit; Klassifikationen nach Hemerobiestufen; Serra Estrela; Portugal; Simeonof Islands; Southwestern Alaska; u.a. [Mechanisms of competition - Superiority; Classifications according to hemeroby levels; Serra Estrela; Portugal; Simeonof Islands; Southwestern Alaska; and more]
 1999 - Vol. 11, Hannover: 100 Jahre Reinhold Tüxen. [100 years of Reinhold Tüxen]
 2000 - Vol. 12, Rintelner Symposium VI, Tüxen-Price: Dieter Müller-Dombois: Biodiversity. [Rinteln Symposium VI, Tüxen-Price: Dieter Müller-Dombois: Biodiversity]
 2001 - Vol. 13, Wien [Vienna]: 50 Jahre numerische Methoden in der Vegetationsökologie - ein Rückblick. [50 years of numerical methods in vegetation ecology - a review]
 2002 - Vol. 14, Hannover: Vegetationsökologie außereuropäischer Regionen. [Vegetation ecology of regions outside of Europe]
 2003 - Vol. 15, Rintelner Symposium VII, Tüxen-Price: Otti Wilmanns: Pflanzengesellschaften als Lebensraum für Tiere - Interaktionen von Flora und Fauna. [Rinteln Symposium VII, Tüxen-Price: Otti Wilmanns: Plant communities as habitats for animals - interactions of flora and fauna]
 2004 - Vol. 16, Hannover: International Plant Protection Convention (IPPC); Seed Persistence; Monitoring of Mountain Peaks; Palaeo-botanical Research Geo-Biosphere during the last 15,000 years; Plant diversity of Mediterranean Ecosystems; and more.
 2005 - Vol. 17, Hannover: Biologische Invasionen, Langzeit-Dynamik Schynige Platte; Schweiz; Savannen Tanzania; Mount Kinabalu; Jordan River; Ephemeral wetlands in the world; u.a. [Biological invasions, Long-term dynamics of the Schynige Platte; Switzerland; Savannas Tanzania; Mount Kinabalu; Jordan River; Ephemeral wetlands in the world; and more]
 2006 - Vol. 18, Rintelner Symposium VIII, Tüxen-Price: Frank Klötzli: Angewandte Vegetationskunde in den Trockenräumen der Erde. [Rinteln Symposium VIII, Tüxen-Price: Frank Klötzli: Applied vegetation science in the earth's dry spots]
 2007 - Vol. 19, Hannover: Historische, palynologische und biogeographische Aspekte der Vegetation u.a. von SE-Tibet; Alpen; Grönland; Australien; Northeast Asia. [Historical, palynological and biogeographical aspects of vegetation from, for example, Southeastern Tibet, the Alps, Greenland, Australia, Northeast Asia]
 2008 - Vol. 20, Hannover: Die aktuelle und künftige Bedeutung der Geobotanik bei der FFH-Gesetzgebung in Europa - Neue Wege in Natur- und Landschaftsschutz. [The current and future significance of geobotany in flora, fauna and habitat legislation in Europe - new paths in nature and landscape conservation]
 2009 - Vol. 21, Rintelner Symposium IX, Tüxen-Price: Heinrich E. Weber: Eine Natur-Biotische Vielfalt. [Rinteln Symposium IX, Tüxen-Price: Heinrich E. Weber: A nature-biotic diversity]
 2010 - Vol. 22, Hannover: Klimawandel und Vegetationsveränderungen - Phantom oder Wirklichkeit? [Climate change and changes to vegetation - phantom phenomenon or reality?]

RTG besides the annual encounters in Hannover, the symposia in Rinteln and the excursions is the member journal "Reports of the Reinhold Tüxen Society" [Berichte der Reinhold Tüxen Gesellschaft]. It appeared for the first time in 1989 (Fig. 4). In the meantime 22 annual volumes have been published,

which we briefly list in the following with important content details and topic areas (Tab. 1). Complete content details can be found at <http://www.reinhold-tuxen-gesellschaft.de>.

The reports of the RTG are now regarded as one of the leading, predominantly German-language geobotani-

cal journals and reach a broad international readership with an edition of about 500 copies. They serve as a national and international journal of exchange, and also to keep the Tüxen Library at the Institute of Geobotany up to date. Many of our members regularly contribute to the success of the volumes with intere-

sting review articles and new research results. They provide a basis for scientific debate not to be underestimated, even in the age of electronic communication and media. The papers from our reports are often cited in textbooks and other journalistic essays. This reflects the fact that they represent a sound, long-lasting foundation of vegetation sciences research.

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PHYTOSOCIOLOGY IN THE BRITISH ISLES

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ABSTRACT

Though so long on the margins of European vegetation science, the United Kingdom has for twenty years used a phytosociological approach for the description of plant communities, the evaluation of sites and the designation, management and monitoring of protected areas. All state environment agencies, wildlife NGOs and corporate industries also accept the UK National Vegetation Classification (NVC) as a standard for environmental impact assessment, landscape restoration and interpreting the Habitats Directive. Moreover, it is widely used as a basis for ecological teaching and research and the interpretation of biodiversity and habitats for the general public. This paper summarises the development of phytosociology in the UK and the background to the NVC, describes the methods adopted and provides examples of how phytosociology has been applied¹.

KEYWORDS: Century of Phytosociology, British Phytosociology, UK National Vegetation Classification, British Plant Communities.

THE BEGINNINGS

The first detailed account of the vegetation types of the British Isles was published in the early years of the 20th century (TANSLEY, 1911). Sadly, the intentions of the British Vegetation Committee, which coordinated this publication, to describe and map the vegetation of the whole country foundered with the First World War. It was not until 20 years later (TANSLEY, 1939) that a much more extensive account of the plant communities of the country was published. This work acquired enormous authority among British ecologists but it was not comprehensive in its coverage

nor systematic in the way the vegetation types were described. Indeed, it rather self-consciously avoided the rigorous taxonomy of plant associations that had been developing for some time elsewhere in Europe in the tradition of phytosociology. This attitude reflects a difference in the scientific temperament of British ecologists who are generally more interested in how vegetation works than how it might be named and classified. This remained a continuing hindrance in developing any consensus in Britain about how plant communities ought to be described, or whether they exist at all.

In fact, the first demonstration of the value of phytosociology for understanding the vegetation of the north-western edge of temperate Europe came with the 1949 International Excursion to Ireland after which the two masters of this tradition published an account of Irish plant associations (BRAUN-BLANQUET & TÜXEN, 1952). However, it was not until the young ecologist Duncan Poore visited Germany in the years immediately following and then went on to apply the phytosociological approach to the vegetation of the Scottish mountains that a convincing account of the methodology appeared in the British ecological literature (POORE, 1955a, b, c; POORE & MCVEAN, 1957). To him, and to most of his readers, it seemed however that the real value of phytosociology was not so much the hierarchical definition of plant associations, as the meticulous sampling of homogeneous stands and the use of such observations for understanding the ecology of vegetation. When MCVEAN & RATCLIFFE (1962) extended this phytosociological approach to the huge and complex landscape of the Scottish Highlands, they related the plant communities they defined to those described from Scandinavia (NORDHAGEN, 1943; DAHL, 1956), but they were more interested in understanding climatic, edaphic and biotic influences on the vegetation than in syntaxonomy.

In the years following, there was no attempt to extend McVean & Ratcliffe's work to the rest of the British

Isles and much of the energy of ecologists in this country was consumed by arguments about subjectivity in sampling and the relative merits of classification or ordination as analytical techniques. However, some workers found it quite possible to combine phytosociology with numerical methods, as with IVIMEY-COOK & PROCTOR's, (1966) work in western Ireland. Also, new generations of research students began to be inspired by the phytosociological tradition, producing accounts of particular groups of vegetation types - for example, calcicolous grasslands (SHIMWELL, 1968), heaths (BRIDGEWATER, 1970), rich fens (WHEELER, 1975) and salt-marshes (ADAM, 1976) - and of particular places, as with studies of the vegetation of the Isle of Skye (BIRKS, 1969), the Cornish cliffs (MALLOCH, 1970, Fig. 1) and Upper Teesdale (BRADSHAW & JONES, 1976). At the Macaulay Institute in Aberdeen, workers extended the phytosociological approach in extensive studies of the vegetation of the lowlands and southern Uplands of Scotland (BIRSE & ROBERTSON, 1976; BIRSE, 1980, 1984).

Despite such enthusiastic activity, these data were accumulating without



Fig. 1 - *Crithmo-Spergularietum rupicolae* Géhu 1964 occurs widely on the spray-splashed cliffs of southern Britain.

¹ Full details of the background and methodology of the UK NVC are in the General Introduction to each of the five volumes of British Plant Communities (RODWELL, ed., 1991 et seq.).

an overall framework of classification of British vegetation. Also, without standardised accounts of plant communities, it was impossible to describe and map nature reserves in any systematic way and so compare their value for nature conservation. Ecological researchers also lacked a basis of community ecology in which to locate the very considerable amounts of autecological research that were taking place in the country. Dr Derek Ratcliffe, the Chief Scientist of the Nature Conservancy (the state agency for nature protection) and Professor Donald Pigott, the eminent university plant ecologist, therefore proposed a research programme to carry out a National Vegetation Classification (NVC) of the whole country. In 1975, funded by the UK government, this work began with a team of five surveyors and a supervisor panel of seven expert ecologists. I was myself the coordinator of the project.

THE UK NATIONAL VEGETATION CLASSIFICATION

The UK NVC aimed to cover all parts of England, Scotland and Wales. The vegetation types of all natural, semi-natural and major artificial habitats were to be included and there was to be no special focus on rare, interesting or threatened plant communities. At the start of the work, systematic searches were made for high quality data: apart from the few classic phytosociological studies, the biggest source of relevés was the postgraduate theses of particular vegetation types or localities. We were also able to encourage others outside the project team to begin collecting relevés of compatible format. Annual monitoring of accumulating data over the three years of field work (1975–78) enabled us to ensure good coverage of the country and the range of British vegetation types.



Fig. 2 - In woodlands like this British equivalent of the *Endymio-Carpinetum* Noirfalise & Sougnez 1963, the UK NVC used relevés of 50x50 m for the canopy and understorey and 4x4 m for the field and ground layers.

For what we considered very good reasons, the data standards of the UK NVC were not entirely those of traditional SIGMA phytosociology:

- 1) We located our relevés using only the criterion of homogeneity of the vegetation – its floristic and structural uniformity. The presence of character species in the vegetation was never used because we believe that this introduces a dangerous circularity in the process of definition of syntaxa. In fact, many of the species characteristic of particular associations or alliances defined in central Europe are not so faithful as you approach the Atlantic fringe of the Continent.
 - 2) We used different sizes of relevé according to the structural scale of the vegetation because it is well known that plot-size has a considerable influence in the definition of syntaxa (for example, DENGLER *et al.*, 2009). We thought that 1x1 m is very often too small to provide representative data and, for woodlands, a 10x10 m quadrat for the canopy is certainly inadequate. Thus we used 2x2 m for grasslands, 4x4 m for heaths, 10x10 m for tall herb vegetation and so on. With woodlands, we used two nested quadrats, one at 4x4 m or 10x10 m for the ground and field layer, one at 50x50 m for the canopy and understorey (Fig. 2). Where vegetation occurred in very small stands – as in springs or temporary pools, we used the whole stand as the relevé. Streamsides, riverbanks and hedgerows were sampled using linear quadrats of 1x10 m.
 - 3) We recorded all vascular plants, bryophytes and macrolichens (*sensu* DAHL, 1968) but not epiphytic or epilithic cryptogams.
 - 4) Cover-abundance was estimated using the Domin scale (*sensu* DAHL & HADAC, 1941) rather than Braun-Blanquet scales as this measure had been employed previously in British surveys.
 - 5) Basic environmental data were recorded for every relevé: location (using the UK National Grid); altitude; slope; aspect; geology; soil type; the percentage cover of bare rock, bare soil or litter and for aquatic vegetation the depth, speed and turbidity of the open waters and the nature of the bed. Biotic features like signs of grazing, mowing, burning, trampling or other kinds of disturbance were noted in a qualitative way. Notes, sketches and diagrams were used to supplement this basic information and to provide some indication of the wider landscape context of the relevé.
- At the close of the three sampling seasons, the survey team had collected 13,000 relevés. To these we added about

20,000 further compatible relevés from existing sources. Altogether, data were available from about 80% of the 10x10 km grid squares of the British mainland and many islands (Fig. 3).

Data were analysed using a variety of multivariate computational techniques (mainly in those days TWINSPAN, HILL, 1979) to produce end groups equivalent to Braun-Blanquet associations. Again, we had some guiding principles: 1) As in traditional phytosociology, only the floristic data - the cover-abundance records of the vascular plants and cryptogams - were used for the analysis. The environmental data collected were used afterwards to understand the ecological meaning of the distinctions recognised in the analysis.

2) However, this was to be a new classification built from the 'bottom up'. As we proceeded, it became clear that many of the plant communities emerging from the analysis were similar to associations already defined elsewhere in Europe but we did not simply allocate relevés to such existing syntaxa in a discriminant fashion.

3) Also, we rejected no relevés before or during the data sorting because they were nondescript or troublesome in character. Our classification was intended to be of practical value for a wide variety of users and had to include much ill-defined vegetation as well as 'good examples' of syntaxa.

From the start of the project, we were concerned that the work gained wide support among ecologists of various British traditions in universities and research institutes and among potential users in many different kinds of agencies and organisations. We therefore established regular exchanges of information and ideas through project progress reports circulated widely in the UK and across Europe and by giving papers at scientific meetings. As the work progressed, drafts of particular sections of the classification were produced with preliminary descriptions of the plant communities. Even before final publication, many people were therefore using the UK NVC.

THE PUBLICATION OF BRITISH PLANT COMMUNITIES

The results of the UK NVC were published in five volumes of *British Plant Communities* (RODWELL, ed., 1991 *et seq.*, Fig. 4). The presentation of the results gives priority to the description of the plant communities, rather than the construction of a hierarchical classi-

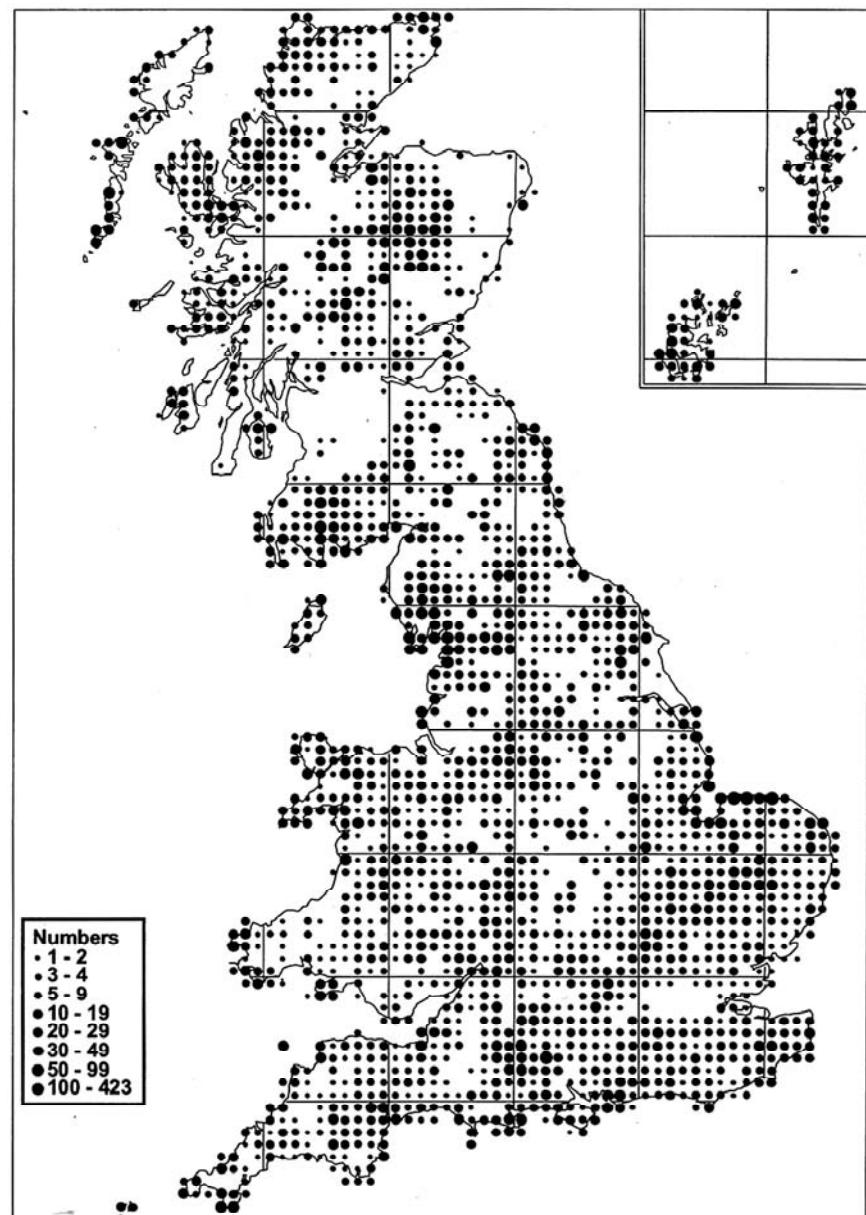


Fig. 3 - The distribution and density of relevés at the close of the programme of field survey for the UK NVC.

fication, and the communities are arranged in broad formations: Woodlands and Scrub (Volume 1, 1991), Heaths and Mires (Volume 2, 1991), Grasslands and Montane Communities (Volume 3, 1992), Aquatics, Swamps and Tall-herb Fens (1994) and Maritime Communities and Vegetation of Open Habitats (2000). Each major group of communities has a general introduction and a key.

A total of 293 plant communities are described and, where these are obviously identical with associations already described, the name and author citation of such a syntaxon is used, eg. *Centaureo-Cynosuretum cristati* Braun-Blanquet & Tüxen 1952. Otherwise we have not formally named the syntaxa in a phyto-sociological style but used names that would be appealing to the British users, eg. *Anthoxanthum-Geranium* hay meadow. In that sense, there-

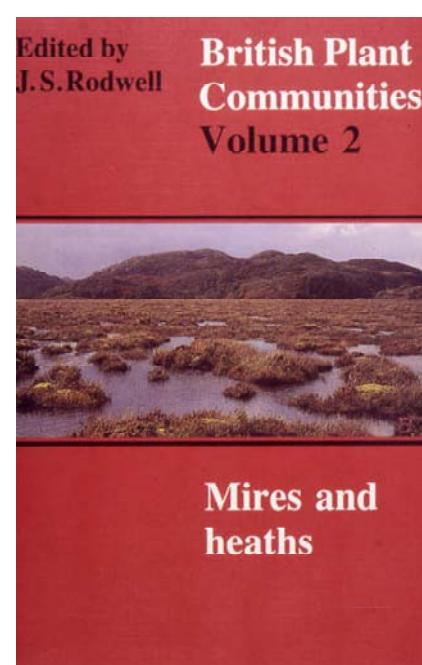


Fig. 4 - The five volumes of *British Plant Communities* are available in hardback and paperback from Cambridge University Press.

fore, the communities are not validly published associations. Always, though, the phytosociological affinities of the communities are noted and there is a conspectus in the final volume which uses a framework of classes, orders and alliances.

The core of the descriptions are the floristic tables for the communities and their sub-communities in which all constant, preferential and common associate species are tabulated using constancy classes. The accounts of the communities follow a modular style and the emphasis is on the description of the floristics and structure of the vegetation in each community and its sub-communities and on the relationships between the vegetation and the habitat. Much of

the material is based on observations made during sampling but existing ecological information has also been included from the published and 'grey' literature. Bibliographies provide full details of these references. Particular attention has been given to the climatic, edaphic and biotic factors influencing the vegetation and separate sections of text detail the common zonations and successions in which the communities occur.

Throughout the descriptions of the communities, particular places and regions are often referred to as characteristic or classic sites where the vegetation can be seen but there are also details of the overall distribution with maps of the locations of the relevés of all

communities and sub-communities.

THE APPLICATIONS OF PHYTOSOCIOLOGY IN THE UK

The UK NVC was quickly adopted as the standard by all statutory environmental agencies in the country (for wildlife, agriculture, forestry), by scientists in research institutes, by non-governmental organisations, by business and utilities. For all of these it provides a common language that is used for the description, evaluation, monitoring and management of sites that are of particular interest or concern, for research into plant species or ecosystems, for restoration and designing of new habitats and landscapes and for understanding the relationships between nature and culture.

From the start, it was clear that, with such a complex new scheme for describing vegetation, a training programme would be necessary for helping users understand the potential and limits of the approach for its various applications. Also, without a strong phytosociological tradition in the UK, it was necessary to instruct those users who wished to collect new data how to make high quality relevés. In the past twenty years, I have myself and with others taught over 2500 people how to use the classification and make relevés in more than 150 short courses of two to three days in many different parts of the country. Often now such courses are ‘tailor-made’ to meet particular needs in different situations (Fig. 5). The NVC is also taught in undergraduate courses and MSc programmes at some universities and a *User’s Handbook* (RODWELL, 2006) is available as a pdf download for any who wish to use the approach (<http://www.jncc.gov.uk/page-3724>). Guides to particular sections of the NVC have been produced (eg. HALL *et al.*, 2004) and bespoke toolkits to address particular user needs (RODWELL & SKELCHER, 2007).

A major application of the UK NVC is for the description and mapping of sites of importance for biodiversity and many nature reserves and other sites of special environmental interest have now been mapped at various scales (usually 1: 2,500 or 1: 5,000) and described in a standard phytosociological fashion - in particular, most coastal cliffs and sand dunes, many woodlands, great stretches of the uplands. With the development of GIS, such standardised meta-data have become very flexible and important in their applications.



*Fig. 5 - Training courses for farmers apply phytosociology to understand how less intensive agriculture might diversify *Cynosurion* pastures and meadows.*

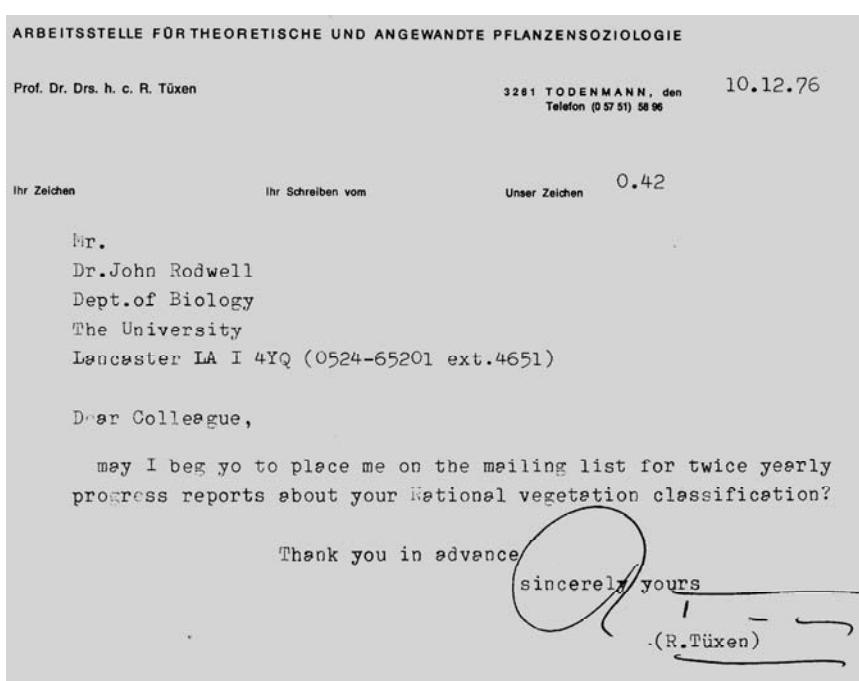


Fig. 6 - A letter of recognition from Professor Dr Drs Reinhold Tüxen at the start of the UK NVC

The wide dispersal of expert skills also means that many new relevés are available and authoritative and detailed accounts can now be produced of local and regional vegetation in the UK. For example, we have impressive new accounts of the vegetation of British mountains and collines (AVERIS *et al.*, 2004) and of the lowland grasslands of Wales (STEVENS *et al.*, 2010). In Wales, an interesting development is the translation of the NVC plant community names into Welsh, a language used there by 40% of the people, and for all government and official business (RODWELL *et al.*, in press). Although Northern Ireland was not included in the original NVC project, many relevés have since been collected there and syntaxa defined from the vegetation of the province, for example, on the maritime vegetation of its sea-cliffs, sand-dunes and salt-marshes (COOPER *et al.*, 1992).

The NVC is also used as a phytosociological basis for the interpretation of the UK's international obligations, as under the Habitats Directive, and particular studies have applied the NVC for a detailed scientific understanding of British vegetation in a wider European context - as with our Scottish pinewoods (RODWELL & COOPER, 1995), broadleaf woodlands (RODWELL & DRING, 2001) and lowland grasslands (RODWELL *et al.*, 2006). The NVC was also used in the British contribution to the phytosociological interpretation of the legend of the European Vegetation Map (BOHN *et al.*, 2000).

The NVC is also used as a phytosociological standard for environmental impact assessment, for evaluating habitat condition and for reporting on the success or otherwise of policy objectives, for example, in agri-environment programmes for restoration of *Cynosurion* and *Triseto-Polygonion* meadows. For monitoring the impacts of air-quality on *Mesobromion* grasslands, a national network of permanent relevés was established in 14 distinct communities across the whole country (RODWELL *et al.*, 1993).

Using the NVC, phytosociology has also been applied for understanding habitat patterns and processes, for example, in a study of the impacts of ground water in the *Cynosurion*, *Alopecurion* and *Calthion* meadows of flood-plains (GOWING *et al.*, 2002) and the relationships between below-ground microbial populations and transitions between *Violion* and *Lolio-Plantaginion* grasslands (GRAYSON *et al.*, 2004). It has also proved invaluable for understanding the ecological behaviour of parti-

cular species by providing a community context to physiological research (eg. MILNES *et al.*, 1998).

As a practical tool, the UK NVC has been used in a manual produced by the state forest agency to provide a phytosociological basis for advice on planting sustainable mixtures of native trees and shrubs, for example along the edges of motorways (RODWELL & PATTERSON, 2004). It has also been applied in landscape design for restoration schemes, as in flood-plains where there is an interest in shifting from intensive agriculture into more diverse landscape with semi-natural elements (RODWELL *et al.*, 2005).

When the UK NVC was published in the five volumes of *British Plant Communities*, we accepted that the scheme was a first approximation with weaknesses and gaps. A subsequent exercise in assessing the adequacy of coverage has suggested various revisions with some new sub-communities to those originally described and has identified a further 60 new communities, providing an outline description of each (RODWELL *et al.*, 1998, pdf download at <http://www.jncc.gov.uk/page-2312>).

It is only 35 years since the UK NVC began and our presence was acknowledged by one of the founding fathers of phyto-sociology (Fig. 6). After a late start, we have been able to take our place among practitioners and made rapid progress in the application of this approach, sometimes pioneering novel ways to use such data. We were quickly invited to be among the first members of the European Vegetation Survey, a Working Group of the International Association for Vegetation Science, and contributed to an early demonstration of the value of sharing data and developing European overviews of vegetation (ZUIDHOFF *et al.*, 1996). It is clear (SCHAMINÉE *et al.*, 2010) that the UK holds one of the more substantial sources of relevés in Europe and we continue trying to play a leading part in the exchange of ideas, the sharing of skills and the development of common standards in phytosociology.

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LES APPROCHES PHYTOSOCIOLOGIQUES DANS LA PRÉSERVATION DES HABITATS. APPLICATION À QUELQUES SITES DES PARCS DE L'AHAGGAR ET DU TASSILI

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ABSTRACT

Phytosociology or the study of plant communities is a science that has developed over a hundred years ago. It reached its apogee in the last five decades by many studies worldwide and by its applicability in the typology of plants communities in different regions of the planet.

With the impetus given by many authors in the mid fifties and sixties, knowledge of plant communities by the phytosociological relevé method called "sigmatist" method was particularly imposed. Sectoral or regional works in Algeria have emerged.

Scientific tool acquired the "sigmatist" method applications appeared and deployed in particular area that is to say in the preservation and conservation of fragile or vulnerable habitats and plant communities.

In this context, we apply the phytosociology approach to monitoring floristic diversity of some wadis of the Ahaggar and Tassili.

KEYWORDS: Habitats preservation, phytosociological approach, Algeria, Ahaggar, Tassili.

RÉSUMÉ

La phytosociologie ou étude des associations végétales est une science qui se développe depuis une centaine d'années. Elle a atteint son apogée ces

cinq dernières décennies par les nombreux travaux à travers le monde et par son applicabilité dans la typologie des communautés végétales de différentes régions de la planète.

Grâce à l'essor donné par de nombreux auteurs vers le milieu des années cinquante et soixante, la connaissance des communautés végétales par la méthode du relevé phytosociologique dite méthode "sigmatiste" s'est particulièrement imposée. Les travaux, sectoriels ou régionaux, en Algérie ont vu le jour.

Outil scientifique maîtrisé, les applications de la méthode "sigmatiste" se révèlent et se déploient dans un domaine particulier c'est-à-dire dans la préservation et la conservation des habitats et des phytocénoses fragiles ou fragilisées.

Dans ce cadre, nous appliquons l'approche phytosociologie au suivi de la diversité floristique de certains oueds de l'Ahaggar et du Tassili.

INTRODUCTION

La végétation de l'Ahaggar et du Tassili est assez connue au point de vue floristique depuis les travaux de MAIRE (1933) et ceux de QUEZEL et SANTA (1962-63). Viennent ensuite ceux de OZENDA (1977, 1983) où sont collationnées les descriptions des principaux taxons de ces contrées du Sahara central.

En termes d'approche phytoécologique, les travaux de LEREDDE (1957)

demeurent encore une référence particulière pour le Tassili N'Ajers.

Quant aux travaux de syntaxonomie, QUEZEL (1957; 1965) a proposé une diagnose autour de laquelle s'articulent les études récentes. A cela s'ajoutent celles de BARRY *et al.*, de 1973 à 1986 sur la base ceux de MONOD (1957) concernant notamment la chorologie de ces territoires sur les supports climatiques, bioclimatiques et phytogéographiques.

De manière très partielle, les études actuelles gravitent autour de la détermination d'unités particulières dans les habitats singuliers (ABDELKRIM, 1992; BENHOUHOU *et al.*, 2004; KAABEACHE *et al.*, 1997). Des flores ciblées ont vu le jour. Les auteurs visent essentiellement les principales espèces habituellement exploitées par les populations nomades (SAHKI *et al.*, 2004; BENCHELAH *et al.*, 2000; GAST, 2000). Ils existent, par ailleurs, des révisions taxonomiques sur les endémiques sahariennes tels que les articles de BAALI CHÉRIF *et al.*, (2005); BESNARD (1999); BESNARD *et al.* (2001) sur le Genre *Olea*¹ du groupe *europea*.

Les études d'impact ont été développées dans un cadre visant l'état actuel de sites à préserver. Les années 2000 ont été mises à contribution pour asseoir une approche méthodologique de suivi de la biodiversité (ABDELKRIM, 2008; ABDELKRIM, 2006; ABDELKRIM *et al.*, 2007).

¹ Les flores utilisées sont celles de QUEZEL et SANTA (1962-63) et de OZENDA (1977 et 1983).

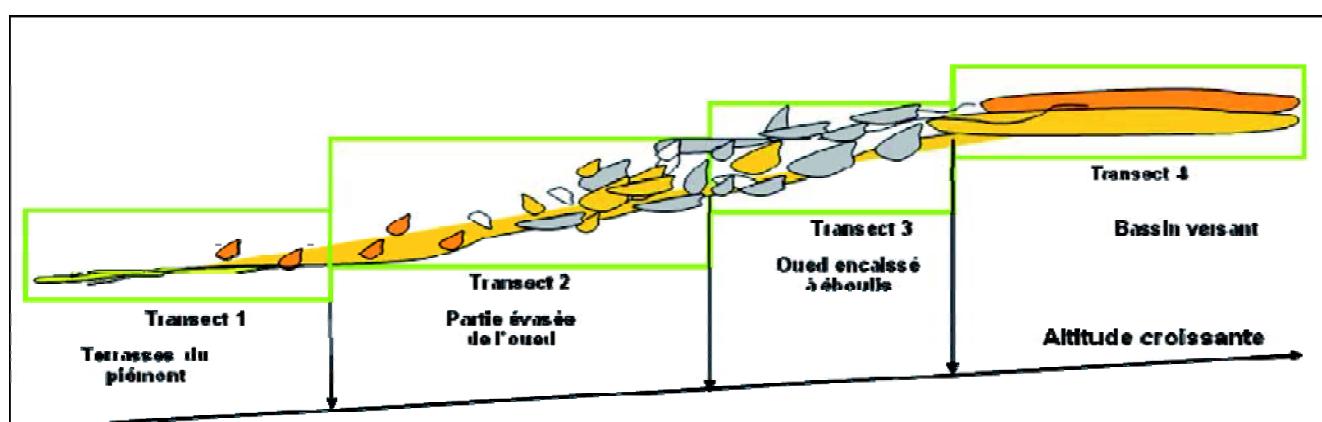


Fig. 1 - Coupe schématique d'un transect parcellaire.

Tableau 1 - Suivi d'un transect parcellaire selon l'altitude.

Transect 1		Transect 2		Transect 3		Transect 4	
Altitude : 1700 m		1720 m		1776 m		1838 m	
Taxons	%	Taxons	%	Taxons		Taxons	%
<i>Myrtus nivellei</i> (2)	60	<i>Pituranthus chloranthus</i> ,	20	<i>Ephedra altissima</i>		<i>Asparagus altissima</i>	60
<i>Maerua crassifolia</i> (+) (un seul individu),		<i>Artemisia campestris</i> ssp <i>glutinosa</i>		<i>Trichosodesma africanum</i>		<i>Rhus tripartitum</i>	
<i>Typha elephantina</i> (+) (Oued)		<i>Rumex vesicarius</i> ,		<i>Grewia populifolia</i>		<i>Helianthemum lippii</i>	
<i>Nerium oleander</i> (+) (Oued)		<i>Echium pychnanthum</i> ssp. <i>humile</i> ,		<i>Ficus salicifolia</i>		<i>Cymbopogon schoenanthus</i>	
<i>Rhus tripartitum</i> (+)		<i>Reseda villosa</i> ,		<i>Ficus ingens</i> (1 individu)		<i>Fagonia glutinosa</i>	
<i>Tamarix africana</i> (qq pieds)		<i>Linaria sagittata</i> ,		<i>Capparis spinosa</i>		<i>Salvia chaudaei</i>	
<i>Acacia arabica</i> (1 individu)		<i>Lotus jolyi</i> ,		<i>Olea laperrini</i>		<i>Centaurea pungens</i> ,	
<i>Globularia alypum</i>		<i>Moricandia arvensis</i> ssp. <i>robusta</i> ,		<i>Rhus tripartitum</i>		<i>Teucrium polium</i> ssp. <i>geyrii</i> ,	
<i>Artemisia campestris</i> (+)		<i>Chrysanthemum macrocarpum</i> ,		Individus éparses sur les parois et falaises		<i>Pinnesetum setaceum</i> ssp. <i>orientale</i> ,	
<i>Caralluma venenosa</i> (+)		<i>Helianthemum lippii</i> (Individus vigoureux)				<i>Lavandula antinea</i> ,	
<i>Caralluma demaisena</i> (+)		<i>Teucrium polium</i> ssp. <i>geyrii</i>				<i>Tribulus terrester</i> ,	
		<i>Reseda villosa</i>				<i>Launaea nudicaulis</i>	
		<i>Periploca laevigata</i>				<i>Matricaria pubescens</i>	
						<i>Silene hoggariensis</i> (endémique)	
						<i>Cleome amblyocarpa</i>	
						<i>Heliotropium undulatum</i>	

Sur la base des résultats obtenus, notre contribution se rapporte à une adaptation de l'approche inspirée de la méthodologie utilisée en phytosociologie.

MATÉRIEL ET MÉTHODES

«Un ensemble cohérent de types biologiques crée un paysage; la plus ou moins grande répétition de l'un d'eux personnalisé la formation végétale» (BARRY et CELLES, 1972-73). Cette définition nous permet de situer quelques phytocénoses reconnues au cours de nos investigations, brèves et très localisées. La cohérence reconnue nous incite à définir, à déterminer et à reconnaître les lieux et les milieux support de communautés végétales susceptibles d'entretenir les formes bio-diversifiées actuelles et les mêmes formes à préserver ou à améliorer pour une préservation durable.

Les travaux de nombreux auteurs, depuis MAIRE (1933) concluent à une stabilité paysagère et à une répétition des communautés végétales en fonction des variables oro-topographiques et édaphiques. Toutefois, au niveau supérieur, les classes, déjà définies par QUEZEL (1965), demeurent la référence.

Nous avons initié, depuis 2006, une approche méthodologique basée sur un échantillonnage selon le principe de transects (échantillonnage systématique) par une méthode linéaire com-

binée aux parcellaires c'est-à-dire aux surfaces pour lesquelles il convient de suivre la végétation en revenant aux mêmes points de manière périodique (Fig. 1).

Au niveau de chaque parcelle retenue où chacun des rectangles correspond à une topo-séquence et admis comme individu d'association, un relevé floristique est exécuté selon le principe du relevé sigmatiste ou selon la recherche d'informations sur la composition phytocénotique comme élément de base de la dynamique trophique.

Les Oueds sont des refuges; ils abritent des communautés encore préservées. Cette structure est un exemple de la complexité d'habitat où il est parfois difficile de percevoir les individus d'associations car les intrications sont importantes.

RÉSULTATS ET DISCUSSION

Nous avons appliqué ces transects parcellaires au niveau des oueds des massifs montagneux de l'Ahaggar. A titre d'exemple, nous avions suivi la progression de la végétation de quelques oueds dans les massifs de la Taessa (oued Akaiour, oued Ilamène) et de la Tefedest (Oueds Amghah, Ouhat et Adjelil) jusqu'à leur impluvium respectif (ABDELKrim, 2006; ABDELKrim et al., 2007, 2008).

Nous développons cette approche pour l'oued Akaiour dans le massif de

la Taessa.

A 1500 m, les terrasses de l'oued, dans sa course finale, sont caractérisées par une végétation assez dense dont le recouvrement atteint 60%. Les principales espèces sont: *Myrtus nivellei* (dominant, 10-20%), *Maerua crassifolia* (un seul individu), *Typha elephantina* (abondant, 5-10%), *Rhus tripartitum* (abondant, 40%), *Nerium oleander* (5-10%), *Acacia arabica* (deux pieds), *Teucrium polium* ssp. *geyrii*, *Globularia alypum* ssp. *eriocephala*, *Tamarix articulata* (quelques pieds). De nombreux taxons se retrouvent à cette altitude et persistent encore jusqu'à 1720 m (*Pituranthus chloranthus*, *Artemisia campestris* ssp. *glutinosa*, *Rumex vesicarius*, *Echium pychnanthum* ssp. *humile*, *Reseda villosa*, *Linaria sagittata*, *Lotus jolyi*, *Moricandia arvensis* ssp. *robusta*, *Chrysanthemum macrocarpum*, *Helianthemum lippii*, *Cymbopogon schoenanthus*, *Heliotropium undulatum*, *Cleome amblyocarpa*, *Caralluma venenosa* et *C. decaisneana*).

La richesse spécifique s'atténue vers les altitudes élevées et laisse place à des taxons endémiques des falaises rocheuses. Nous citons *Ficus salicifolia* ssp. *telukat*, *F. ingens* (un seul pied). Les taxons chasmophiles des éboulis rocheux *Grewia populifolia*, *Olea laperrini* et *Rhus tripartitum* (Tableau 1).

En terme d'approche syntaxonomique, chacune des parcelles inclurait une ou plusieurs unités de niveau élé-

mentaire difficilement extirpables. Au commencement, vers l'aval, là où l'oued Akaiour se perd, les terrasses alluviales se fondent dans l'oued Idikel dont la végétation est déjà décrite (ABDELKRIM, 1992) avec l'association relictuelle *Pistacio atlanticae-myrtetum nivellei* Abdelkrim 1992.

Cette succession en transects parcellaires correspondrait à des points relevés intégrant des syntaxons que seule une analyse identifierait. Ce sont des végétations d'oueds parfois fermées où des syntaxons sur substrat rocailleux sont superposables. On distinguerait, selon QUEZEL (1965), des sous associations au sein de l'association à *Olea laperrini* et *Crambe krakili var. garamas* ou celle où domineraient *Myrtus nivellei* et *Pennisetum setaceum* ssp. *orientale* voire l'association à *Olea laperrini* et *Myrtus nivellei* décrite par KAABECHÉ et GHARZOULI en 1997 (Figs. 2a et 2b).

Le transect 4, à 1838 m d'altitude correspondrait à une pelouse d'altitude se rapportant aux *Helianthemo-Polygonychiea* Quezel 1965 équivalent des *Helianthemetea lippii* Barry, Celles, Manière 1985. C'est une végétation de plateaux d'altitude avec *Helianthemum lippii*, *Asparagus altissima*, *Cymbopogon schoenanthus*, *Fagonia glutinosa*, *Salvia chaudaei*, *Centaurea pungens*, *Teucrium polium* ssp. *geyrii*, *Tribulus terrester*, *Launaea nudicaulis*, *Matricaria pubescens*, *Silene hoggariensis* (endémique), *Cleome amblyocarpa*, *Heliotropium undulatum*. Une nette dominance de *Helianthemum lippii*, *Paronychia arabica* var. *brevista*, *P. chlorothyrsa* var. *saharicum*, *Echium humile* var. *sahariensis* constitue l'ossature de la phytocénose.

La classe des *Lavanduletea antineae* Quezel 1965 et particulièrement le *Lavandulion antineae* se rapporte aux végétations des lits d'oueds et des éboulis vers les altitudes supérieures à 1700 m avec une originalité des éléments floristiques de souche méditerranéenne. Elle abrite les taxons endémiques du Sahara central. C'est à cette classe que les phytocénoses des différents transects se rattacherait.

CONCLUSION

Le choix des transects au niveau de l'oued Akaiour (massif de la Taessa) est une illustration de l'application inspirée de la méthode phytosociologique pour connaître les phytocénoses de base constituant le début de la chaîne trophique pour les espèces animales herbivores en voie d'extinction (le mouflon à



Fig. 2a - Aspect de la végétation fermée de l'oued Akaiour (massif de la Taessa, Ahaggar).



Fig. 2b - Groupement à *Myrtus nivellei* en aval de l'oued Akaiour (massif de la Taessa, Ahaggar).

manchettes et la gazelle dorcas) indispensables au maintien du guépard dans cette partie du Sahara central.

L'ordre des *Lavanduletalia antineae* et l'alliance *Lavandulion antineae* constituent les syntaxons où les espèces de la strate arbustive sont à retenir (*Olea laperrini*, *Rhus tripartitum*, *Myrtus nivellei*, *Pistacia atlantica*). Les Oueds sont des refuges et abritent des communautés encore préservées et dont l'étude est à promouvoir pour un approfondissement ou une révision syntaxonomique des groupements végétaux du Sahara central en recomposant les informations données par les relevés de l'ensemble de ces transects parcellaires. L'essentiel dans cette approche est la proposition d'une méthode pour un sui-

vi périodique de l'état des végétations de certains sites considérés comme prioritaires pour le suivi de la diversité faunistique et floristique dans les parcs de l'Ahaggar et du Tassili.

REMERCIEMENTS

Nous remercions l'ensemble des personnes des Offices des Parcs Nationaux de l'Ahaggar (OPNA) et du Tassili (OPNT) pour leur aide substantielle sur le terrain au cours des missions dans le cadre du projet PNUD 0034575 "Préservation et utilisation de la diversité biologique d'intérêt mondial dans les parcs nationaux de l'Ahaggar et du Tassili". Nous saisissons cette occasion

pour évoquer la mémoire de Sid Ali Ramdane, coordonnateur du projet, arraché trop vite à la vie et ravi aux siens.

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MATORRALES SUCULENTOS Y DESÉRTICOS DEL DESIERTO CENTRAL DE BAJA CALIFORNIA AFECTADOS POR LA MARESÍA

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ABSTRACT

In this contribution we studied the coastal succulent and desertic scrubs plant communities of inland areas but still affected by sea salt spray, on the pacific coast of "Valle de los Cirios" (Baja California, Mexico), using the phytosociologic method. Three associations were recognized: *Bergerocactus emoryi*-*Agavetum shawii* Peinado, Alcaraz, Aguirre & Delgadillo 1995, *Ferrocactus fordii*-*Euphorbietum miserae* Alcaraz & Delgadillo ass. nova and *Atriplici julaceae-Yuccetum validae* Alcaraz & Delgadillo ass. nova; the last one with two subassociations of geographical character, one in the north area of the association (subass. *agavetosum goldmaniana* (Peinado, Alcaraz, Aguirre & Delgadillo 1995) Alcaraz & Delgadillo comb. nova), and the typical subassociation, of southern distribution. Those three associations belong to the class *Prosopido torreyanae-Foquierietea splendens* and order *Parkinsonietalia florido-microphyllae*, but the first one is included in the Californian alliance *Agavion shawii*, and the other two are included in the Sonora desert alliance *Idrio columnaris-Pachycormion pubescens*. In the work we argue the criteria to classify, using the phytosociology, these kind of plant communities, in the transition between a special gradient, as the determined by sea salt spray intensity, and a main gradient, or a slope gradient.

KEYWORDS: Coastal succulent scrubs, desertic scrubs, new associations, Valle de los Cirios, Baja California, Mexico.

RESUMEN

En esta contribución se ha estudiado la vegetación más interior de la afectada por la maresía en las costas pacíficas del Valle de los Cirios (Baja California, Méjico). Se han reconocido tres asociaciones vegetales de matorral suculento: *Bergerocactus emoryi*-*Agavetum shawii* Peinado, Alcaraz, Aguirre y Delgadillo 1995, *Ferrocactus fordii*-*Euphorbietum*

miserae Alcaraz y Delgadillo ass. nova y *Atriplici julaceae-Yuccetum validae* Alcaraz y Delgadillo ass. nova, está última con dos subasociaciones de carácter geográfico, una norteña (subass. *agavetosum goldmaniana* (Peinado, Alcaraz, Aguirre y Delgadillo 1995) Alcaraz y Delgadillo comb. nova), y la subasociación típica, de área más meridional. Estas tres asociaciones se consideran incluidas en la clase *Prosopido torreyanae-Foquierietea splendens*, orden *Parkinsonietalia florido-microphyllae*, si bien la primera asociación corresponde a la alianza *Agavion shawii*, propia de territorios californianos infra y termomediterráneos semiáridos, y las otras dos en la alianza *idrio columnaris-Pachycormion pubescens*, de zonas sonorenses termomediterráneas áridas e hiperáridas. Se discuten razonadamente en el trabajo los criterios para abordar desde un punto de vista fitosociológico la clasificación de este tipo de comunidades en la transición entre un gradiente especial, como el marcado por la intensidad de la maresía, y los gradientes principales o de vertientes.

INTRODUCCIÓN

La maresía o hálito marino es el aporte de sal a las tierras costeras debido a las salpicaduras de agua marina y de gotas de agua salada en suspensión en la atmósfera. Este rocío salino tiene dos orígenes: el estallido de burbujas en la superficie del océano lanza gotitas de agua salada al aire marino, con un radio medio comprendido entre los 0,5 y 5 mm para las menores y de 3 a 50 mm para las mayores (ZHANG *et al.*, 2005); otra fuente de agua salada es la separación de gotas de más de 20 mm de radio en la cresta de las olas causadas por vientos suficientemente intensos (PIAZZOLA *et al.*, 2002; ZHANG *et al.*, 2005).

La maresía es un factor de alteración abiótico que juega un papel ecológico crítico para muchas plantas costeras (GRIFFITHS y ORIANS, 2003a, 2003b; WELLS y SHUNK, 1938), siendo sus efectos más conocidos la alteración del

balance hídrico de las plantas (MUNNS, 1993), la necrosis o incluso la pérdida de hojas (KARSCHON, 1958; PARSONS y GILL, 1968), alteraciones en la reproducción (HESP, 1991; CHEPLICK y DEMETRI, 1999) y reducción del crecimiento (GRIFFITHS y ORIANS, 2003b; TOMINAGA *et al.*, 1991).

No obstante, algunos estudios han revelado que el rocío marino es una fuente significativa de cationes esenciales para los suelos (WHIPKEY *et al.*, 2000); de hecho, la maresía podría proveer de la mayoría de los cationes esenciales a rocas y suelos pobres en nutrientes en los ambientes litorales. En cualquier caso, hay plantas tolerantes a estas alteraciones (OOSTING, 1945; SÁNCHEZ-BLANCO *et al.*, 2003; YURA, 1997; ZHU, 2001) que pueden obtener ventajas en la competencia bajo tales condiciones adversas.

Como resultado de todos estos efectos, la maresía suele tener una gran influencia en la zonación y sucesión en los ecosistemas litorales, dados diferentes niveles de tolerancia de las especies vegetales al rocío salino (BARBOUR, 1978; BARBOUR Y DE JONG, 1977; BOYCE, 1954; GRIFFITHS y ORIANS, 2003a, 2003b; MALLOCH, 1972; OOSTING, 1945; OOSTING y BILLINGS, 1942; TYNDALL *et al.*, 1987; SYKES y WILSON, 1988).

La zonación de la vegetación en las costas del Pacífico de Norteamérica ha sido estudiada en dunas y acantilados (BARBOUR, 1978; OOSTING, 1945; OOSTING y BILLINGS, 1942; PEINADO *et al.*, 2005, 2008), pero hay muy escasa información sobre las comunidades vegetales que se asientan en los tramos del gradiente en transición entre la cubierta vegetal típicamente litoral y la de zonas más interiores, protegidas del hálito marino (ALCARAZ, 1996). Dicha vegetación muestra una llamativa confluencia de especies bien adaptadas a soportar la maresía y las más tolerantes a este factor con óptimo en zonas interiores (ALCARAZ y DELGADO, 1998).

En el seno de un estudio más amplio sobre la vegetación del desierto central de la península de Baja California (Méjico), también denominado como «Desierto Cochimí» (DELGADIL-

LO, 1998), se han podido muestrear fitosociológicamente los matorrales de tales zonas de transición, los cuales muestran la predicha confluencia de las especies menos tolerantes a la maresía dentro del ámbito litoral con las más tolerantes dentro del ámbito interior. Esta situación de transición revela interesantes aspectos que plantean no pocos problemas desde el punto de su interpretación fitosociológica, por la ubicación entre comunidades de clases de vegetación litorales y clases de vegetación climáticas (ALCARAZ, 1996); todo ello convierte a estos estudios en una fuente de datos para un campo teórico muy interesante de la fitosociología en la búsqueda de patrones y soluciones que podrían aplicarse a situaciones similares en todo el Mundo.

MATERIAL Y MÉTODOS

ÁREA DE ESTUDIO

Los mapas que ilustran este apartado se han realizado con la aplicación GMT (2010), complementados con la aplicación de dibujo vectorial INKSCAPE (2010). El área de estudio se ubica en la

costa pacífica de la parte centro-norte de la península de Baja California (Méjico), entre los paralelos 28.00°-31.00° Norte y los meridianos 113.70°-116.00° Oeste (ver Fig. 1).

El territorio tiene un clima que va desde un mediterráneo semiárido a un desierto e hiperdesierto con lluvias de invierno (PEINADO *et al.*, 1995). Los materiales geológicos son diversos, con representación de sedimentarios, principalmente limolitas en la parte norte del área de estudio, algunos metamórficos (gneises) y finalmente también los hay magnéticos, que son los predominantes, tanto de carácter ácido (granitos y tonalitas) como básico (sobre todo basaltos). Las acumulaciones de carbonato cálcico no son raras en las depresiones y partes bajas de las laderas (bajadas) donde la roca originaria es básica, pero tienen un origen edáfico (liberación de calcio de las rocas, fijación en forma de carbonatos por combinación con el CO₂ del aire y acumulación en zonas topográficamente deprimidas por lavado lateral.

Una escasa población humana y el difícil acceso a las zonas costeras, que en general sólo puede ser realizado a través de interminables pistas de terra-

cería, frecuentemente en muy malas condiciones debido al escaso mantenimiento que se les da, han permitido un buen estado de conservación de la vegetación, por lo que frecuentemente es fácil observar una vegetación más o menos primitiva en gran parte del territorio objeto de estudio.

La detección de las zonas afectadas por la maresía se ha llevado a cabo a través de métodos directos, como son la observación *in situ* de las acumulaciones de sal, tanto sobre el suelo como sobre las plantas, e indirectos, entre los que se puede destacar el estado de las plantas, con alteraciones manifiestas en las partes de los órganos que miran hacia el mar, crecimiento unidireccional en sentido contrario al de la costa, plantas muertas debido al estrés salino, presencia de líquenes aerohalófilos, particularmente de los géneros *Niebla* y *Vermilacinia* (SPJUT, 1996, 2003, 2005) sobre suelo, rocas y como epifleos (sobre las cortezas de plantas vivas), especialmente sobre los troncos y ramas de *Euphorbia misera* y *Lycium californicum*. Igualmente la presencia de plantas que son conocidos indicadores de maresía (PEINADO *et al.*, 1995), aunque con coberturas mucho menores que en las áreas inmediatas al mar, fueron elementos considerados para decidir las zonas a muestrear.

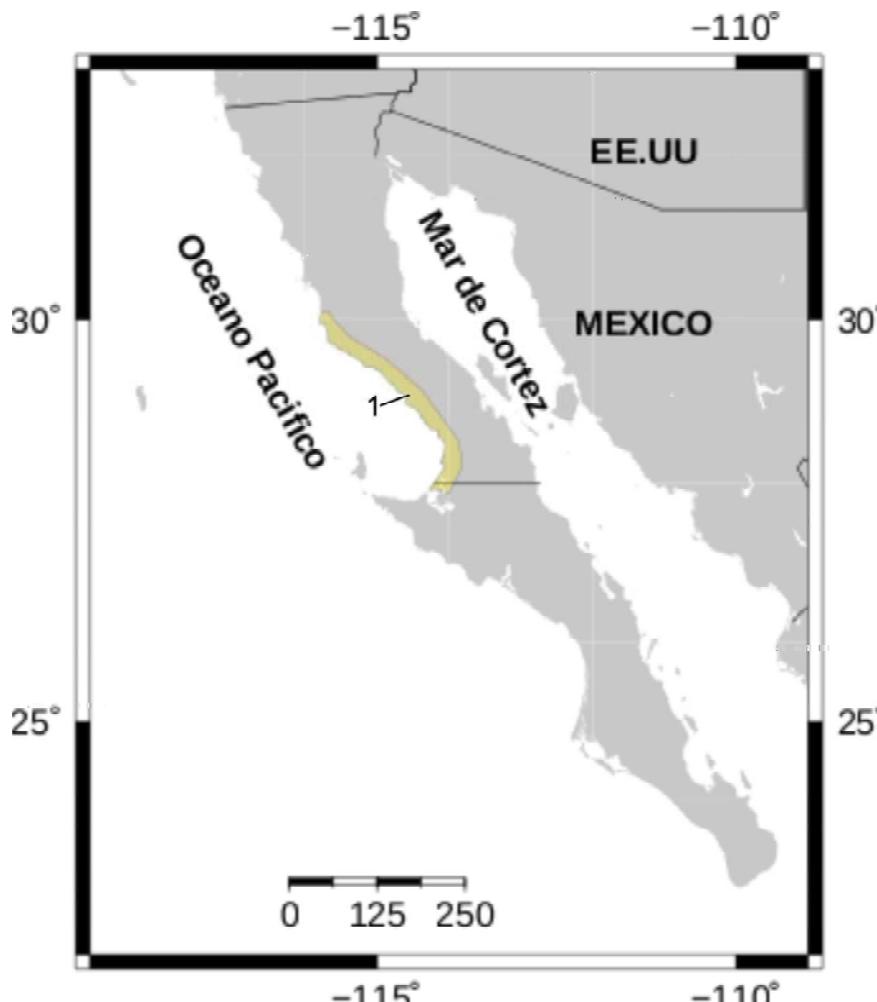


Fig. 1 - Península de Baja California (Méjico) con indicación del área estudiada (1).

NOMENCLATURA TAXONÓMICA Y SINTAXONÓMICA

La determinación de las plantas vasculares ha sido realizada usando como base la obra de WIGGINS (1981), actualizada en la base de datos de BAJAFLORA (2010). La validación taxonómica se consultó en ITIS (2010) y TROPICOS (2010).

Para la nomenclatura de líquenes ha seguido a siguió a SPJUT (1996, 2003, 2005).

La nomenclatura fitosociológica se ha analizado de acuerdo con el Código Internacional de Nomenclatura Fitossociológica (WEBER *et al.*, 2000).

MUESTREO

La vegetación de tipo matorral succulento (DELGADILLO, 1998) entre las zonas de transición de las áreas intensamente influenciadas por la maresía y las interiores fue estudiada entre 2004 y 2009. Se tomó un total de 39 inventarios fitosociológicos realizados de acuerdo con el método sigmatista de la tradición Zürich-Montpellier (WE-

STHOFF y VAN DER MAAREL, 1978). El área mínima fue calculada usando la curva especies / área (área mínima cuantitativa), arrojando valores que oscilaron entre los 80 y los 150 metros cuadrados. En los inventarios fitosociológicos cada una de las especies de plantas fue cuantificada usando el índice de abundancia dominancia (WESTHOFF y VAN DER MAAREL, 1978). Además de esta información básica, se anotaron algunas variables ambientales fácilmente identificables, como la orientación, pendiente, grado de alteración, tipo de sustrato y cobertura por parte de líquenes aerohalófilos terrestres y epífitos. Los inventarios fueron georreferenciados por medio de un GPS Garmin modelo Oregon 400t, dando las coordenadas de un punto en una ubicación centrada (centroide) dentro de la superficie del inventario.

ANÁLISIS DE LOS DATOS

Se realizó un análisis complementario de los datos (KENT y BALLARD, 1988), utilizando tanto métodos numéricos como fitosociológicos.

Para el análisis numérico los valores de abundancia-dominancia fueron transformados en la escala ordinal de van der Maarel (WESTHOFF y VAN DER MAAREL, 1978). La matriz original, compuesta por 39 inventarios y 68 taxones, fue sometida a análisis numérico con el programa «R» (2010) complementado con la librería «Vegan» (OKSANEN *et al.*, 2010). La matriz original (39x68) fue mecanizada en una hoja de cálculo del programa OpenOffice.org Calc (ORACLE, 2010) y exportada a un archivo en formato «csv», apropiado para su carga por parte del programa «R».

El análisis numérico realizado fue de componentes principales (PCA), el cual es apropiado para el tipo de datos utilizado (OKSANEN *et al.*, 2010), caracterizado por comprender un gradiente ecológico corto (rango parcial de mareas desde la costa hacia el interior) y otro gradiente florístico suave en la dirección Sur-Norte.

Paralelamente se llevó a cabo una clasificación fitosociológica tradicional usando la función «vegemite» de la librería «Vegan» para reordenar la matriz original en función de la similitud florística de los inventarios. Los resultados de ambos análisis (el numérico y el tradicional) se usaron para reordenar la disposición de los inventarios y de las especies. Complementariamente se confeccionó un cuadro sintético en el que se utilizaron además de los datos obte-

nidos en este trabajo los publicados previamente por PEINADO *et al.* (1995), los cuales sirvieron para destacar las diferencias y similitudes entre los distintos cuadros de vegetación generados con los procesos anteriores. Algunas de las decisiones tomadas en este proceso se basaron en el conocimiento de las áreas de distribución de las especies más relevantes, obtenidas gracias a la base de datos BAJAFLORA (2010).

RESULTADOS

INVENTARIOS REALIZADOS Y ANÁLISIS DE LOS MISMOS

La situación de los puntos de muestreo se muestran en la Fig. 2, resultando un total de 39 inventarios (relevés) y 68 taxones.

Muchas zonas costeras tienen accesos muy difíciles, a través de caminos en muy mal estado, o incluso es necesario ir en embarcación por la costa para llegar a las mismas y trepar por acantilados con grandes pendientes, por lo que hay tramos de costa a los que no se ha podido acceder de momento.

El análisis de componentes principales, que se muestra en la Fig. 3, destaca la clara distinción de las parcelas de posición más septentrional, correspondientes a las zonas de clima semiárido al norte de la localidad de El Rosario (1) mientras que el resto de unidades se disponen en la mitad inferior del diagrama, marcando un gradiente desde la parte central izquierda del mismo hasta la inferior derecha. Se ha delimitado de forma aproximada la separación entre dos tipos de vegetación que se comentan en los resultados del análisis fitosociológico que se detalla más adelante, correspondiendo las unidades incluidas en el grupo «2» a las parcelas situadas entre el sur de El Rosario (Agua Blanca) y el oeste de Puerto Catarina, y las del grupo «3» las situadas desde Puerto Catarina hasta las proximidades de Guerrero Negro.

La tabulación de los inventarios realizada con la función «vegemite» coincide en buena medida con los resultados del PCA (Fig. 3). El grupo 1 está bien diferenciado por taxones como *Agave shawii* subsp. *shawii*, *Bergerocactus emoryi*, *Encelia californica*, *Opuntia littoralis* y *Eriogonum*

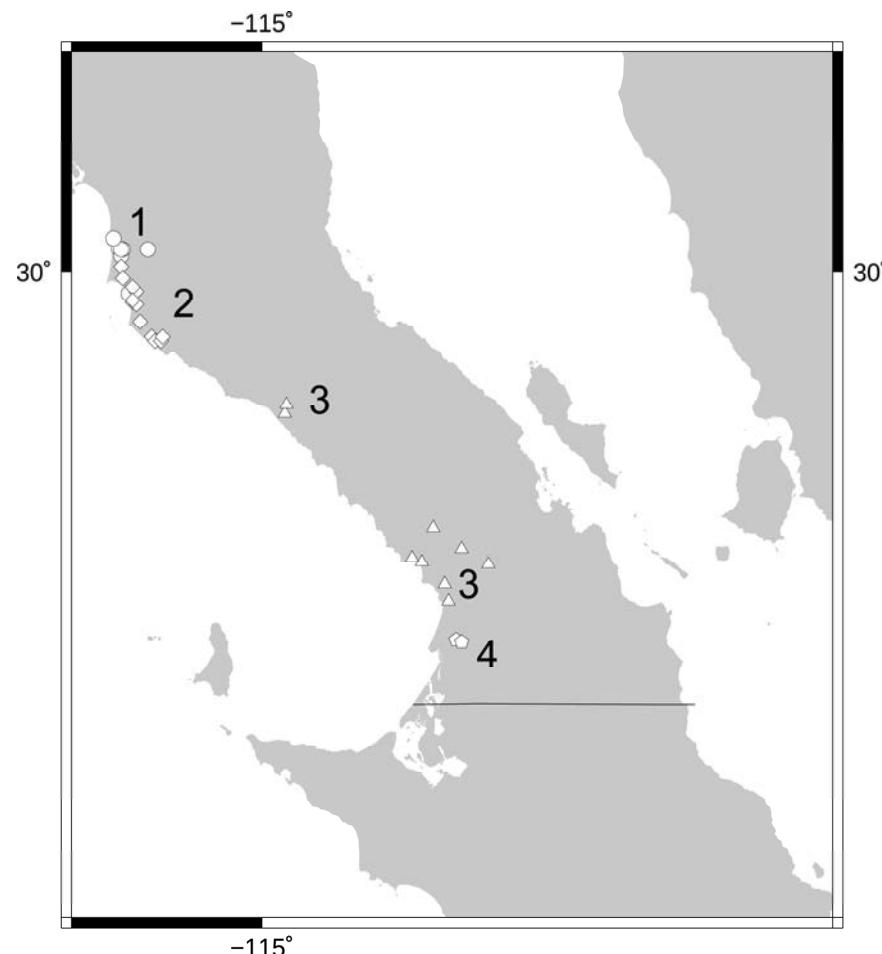


Fig. 2 - Localización de los puntos de muestreo: 1. Unidades muestrales correspondientes a la asociación *Bergerocactus emoryi*-*Agavetum shawii*; 2. *Ferocacto fordii*-*Euphorbietum miserae*; 3. *Atriplici julaceae*-*Yuccetum validae* subass. *agavetosum goldmaniana*; 4. *Atriplici julaceae*-*Yuccetum validae* subass. *yuccetosum validae*.

fastigiatum, encajando en lo que se ha llamado matorral costero suculento bajocaliforniano.

En el grupo 2 del PCA se resaltan las mayores relaciones florísticas con el grupo «3» que con el «1», destacando taxones como *Hesperoyucca peninsularis* e individuos dispersos de *Pachycereus schottii*. Finalmente el grupo «3» está bien definido por taxones como *Yucca valida* y *Dudleya acuminata*, pero muestra cierta heterogeneidad, habiéndose puesto de manifiesto a través de «vegemite» que hay un grupo de inventarios que comparten un conjunto de taxones más norteños (*Agave shawii* subsp. *goldmaniana*, *Ferocactus gracilis* y sus variedades *coloratus* y *gracilis*) frente a otro más meridional, del entorno de Guerrero Negro, diferenciado por taxones como *Cylindropuntia calmalliana* y *Ferocactus peninsulae* var. *viscainensis*, junto con la ausencia de los del subgrupo norteño.

En la revisión bibliográfica realizada se ha comprobado las grandes relaciones de los inventarios del grupo «1» con la asociación ya descrita *Bergerocacto emoryi-Agavetum shawii* descrita por PEINADO *et al.* (1995), mientras que los más septentrionales del grupo «3» tienen una alta coincidencia con los incluidos en la asociación *Yucca validae-Fouquierietum diguetii* subasociación *agavetosum goldmaniana*

(PEINADO *et al.*, 1995).

De acuerdo con los análisis numéricos y los más propios de la fitosociología clásica realizados, se considera que los inventarios realizados pueden ser agrupados en tres tipos base de comunidad vegetal (asociaciones), una de ellas (grupo 3) representada por dos subasociaciones (Cuadros 1 a 3). La síntesis comparativa de estas unidades, junto con las previamente descritas relacionadas, se muestra en el Cuadro 4, donde es posible apreciar mejor las semejanzas y diferencias entre las distintas unidades.

mentos crasicaules destaca la viznaga *aerohalófila Ferocactus fordii* variedad *fordii*.

Esta asociación se desarrolla principalmente en suelos formados a partir de limolitas en zonas próximas al mar entre Punta Colonet y Punta Baja (El Rosario). Este tipo de roca es especialmente favorable a la acumulación de las sales procedentes de la maresía, pero al tiempo dificulta la instalación de líquenes aerohalófitos, que sólo se presentan en zonas de crestas con cantos rodados (*Niebla podetiforma*, *Vermilacinia paleoderma*, etc.), donde el fenómeno de la maresía es más intenso y donde se concentran cantos de roca, principalmente de tipo basáltico. Sin embargo los tallos de corteza lisa de *Euphorbia misera* suelen estar densamente cubiertos del líquen *Vermilacinia leopardina*.

La asociación se desarrolla en zonas termomediterráneas semiáridas influenciadas por la maresía, suponiendo la transición entre matorrales costeros californianos y sonorenses.

Ass. *Bergerocacto emoryi-Agavetum shawii* Peinado, Alcaraz, Aguirre y Delgadillo in J. Veg. Sci., 6: 84 (1995) Cuadro 1, inventarios 1 a 8

Matorral dominado por plantas suculentas, ya sea crasifolias (*Agave shawii* subsp. *shawii*, *Dudleya attenuata* subsp. *attenuata*, *Dudleya cultrata*), crasicaules (*Bergerocactus emoryi*, *Echinocereus maritimus*, *Mammillaria dioica*, *Stenocereus gummosus*, etc.), caméfitos maresícolas (*Atriplex julacea*, *Frankenia palmeri*) o no (*Ambrosia chenopodifolia*, *Euphorbia misera*, *Eriogonum scalare*, etc.). Entre los ele-

Matorrales dominados por *Frankenia palmeri* y *Euphorbia misera*, mostrando generalmente esta última especie las ramas cubiertas de líquenes aerohalófilos (sobre todo *Vermilacinia leopardina*); entre estos caméfitos resaltan las rosetas de grandes hojas semisuculentas de *Hesperoyucca peninsularis*. La cobertura de la comunidad no es muy alta y en los claros suelen abundar líquenes terrícolas aerohalófilos del género *Niebla* (particularmente *Niebla arenaria*). Otras especies comunes son las aerohalófilas *Atriplex julacea* y *Ferocactus fordii* var. *fordii*; también merece destacarse la participación en la asociación de ejemplares dispersos de cardo barbón (*Pachycereus schottii*).

Se desarrolla en zonas poco alejadas del mar desde el Este de Punta Baja (El Rosario) hasta Puerto Catarina, sobre conglomerados poligénicos en los que predominan cantos de rocas basálticas; más raramente se asienta sobre limolitas.

Florísticamente es pobre, pero son más comunes los elementos sonorenses que los californianos, los cuales quedan reducidos a contados individuos de *Cylindropuntia prolifera*.

No hay estaciones meteorológicas en el área de la asociación, pero dada la

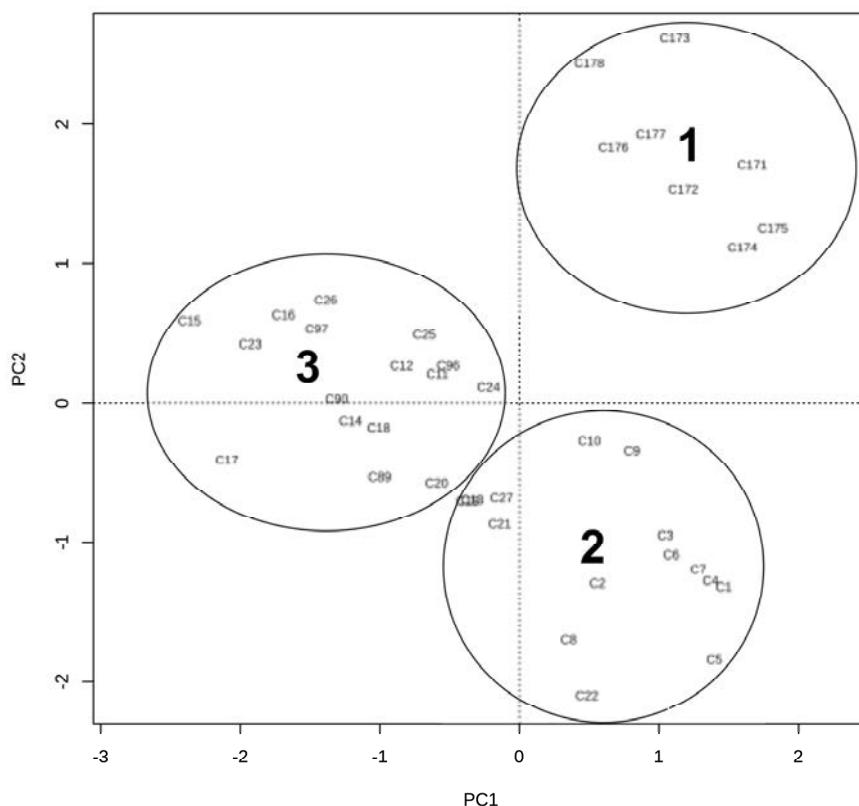


Fig. 3 - Resultados del análisis de componentes principales: 1. Unidades muestrales correspondientes a la asociación *Bergerocacto emoryi-Agavetum shawii*; 2. Unidades muestrales incluidas en la asociación *Ferocacto fordii-Euphorbiatum miserae*; 3. Unidades muestrales de la asociación *Atriplicae-Yuccetum valida*.

Cuadro 1 - Bergerocacto emoryi-Agavetum shawii Peinado, Alcaraz, Aguirre & Delgadillo 1995.

Nº Orden	1	2	3	4	5	6	7	8	P
Registro	R9-1	R9-4	R7-96	R7-102	R7-103	R7-104	R7-106	R7-108	
Altitud (m)	150	53	117	182	152	156	164	57	
Orientación	W-NW	-	N-NW	W	S-SW	S-SW	-	SSW	
Inclinación (º)	15	-	5	35	15	15	-	30	
Área (m ²)	100	100	150	90	80	70	50	80	

Características territoriales de asociación y alianza (*Agavion shawii*)

Agave shawii s. shawii	2	2	3	2	2	2	2	3	V
Dudleya cultrata	1	+	+	1	1	1	1	.	V
Aesculus parryi	+	.	.	1	+	.	.	.	II
Bergerocactus emoryi	+	+	+	.	+	+	+	.	IV
Dudleya attenuata s. attenuata	+	.	.	+	.	.	1	1	III

Plantas maresícolas

Frankenia palmeri	3	3	2	2	3	+	.	1	V
Atriplex julacea	.	+	.	.	+	1	.	+	III
Ferocactus fordii v. fordii	+	+	+	.	.	.	+	.	III

Características de orden (*Parkinsonietalia florido-microphyllae*)

Echinocereus maritimus	1	.	+	1	+	1	2	+	V
Euphorbia misera*	2	3	2	2	3	3	2	2	V
Mammillaria dioica	1	.	1	1	1	1	1	1	V
Ambrosia chenopodifolia	1	2	2	.	.	+	.	2	IV
Stenocereus gummosus	1	+	+	1	III
Cylindropuntia alcahes v. alcahes	.	.	2	.	+	.	.	+	II
Eriogonum scalare	1	2	.	II
Lycium californicum	.	+	+	II

Addenda: Inv. 2: *Cylindropuntia molesta* +, *Cylindropuntia prolifera* 1, *Ribes tortuosum* +; Inv. 3: *Cylindropuntia cholla* 1, *Ferocactus gracilis* v. *gracilis* +; Inv. 6: *Harfordia macroptera* 1, *Lycium andersonii* v. *andersonii* +; Inv. 7: *Encelia californica* +, *Eriogonum fasciculatum* v. *fasciculatum* 3, *Niebla* sp. pl. 3.

Cuadro 2 - Ass. *Ferocacto fordii-Euphorbietum miserae* Alcaraz & Delgadillo ass. nova hoc loco (relevé tipo nº 4).

Nº Orden	1	2	3	4	5	6	7	8	9	10	11	12	13	14	P
Registro	R9-2	R9-3	R9-5	R9-6	R9-7	R9-9	R9-10	R9-11	R9-12	R9-13	R9-14	R9-8	R9-15	R9-16	
Altitud (m)	154	109	87	58	66	99	95	86	20	43	122	73	130	138	
Orientación	W-NW	W-NW	W-NW	NW	NW-N	SW	N	W	S	SW	SW	-	SW	SE	
Inclinación (º)	15	15	10	20	30	20	10	10	5	15	20	-	5	5	
Área (m ²)	50	70	100	50	50	80	80	50	60	100	70	150	100	100	

Características territoriales de asociación y alianza (*Idrio columnaris-Pachycormion pubescens*)

Hesperoyucca peninsularis	.	.	.	1	+	1	+	.	+	1	1	+	1	2	IV
Dudleya cultrata	1	+	1	1	+	+	+	III
Ambrosia bryantii	+	.	I
Fouquieria columnaris	1	+	1	I

Plantas y líquenes maresícolas

Ferocactus fordii v. fordii	.	+	.	1	.	+	.	+	1	+	+	+	+	+	IV
Niebla sp. (sobre suelo)	2	3	+	+	2	1	2	3	+	IV
Frankenia palmeri	3	.	3	3	3	2	2	.	2	2	.	1	.	.	IV
Atriplex julacea	+	.	+	.	I

Características de orden, clase y transgresivas

Euphorbia misera	2*	2*	2*	1*	1*	2*	3*	2*	2*	2	2	+	2	2	V
Stenocereus gummosus	.	.	+	.	.	+	+	.	2	2	.	+	.	.	III
Ambrosia chenopodifolia	+	+	2	+	2	.	II
Echinocereus maritimus	+	+	+	+	+	+	+	+	+	+	+	+	+	+	II
Lycium californicum	1	.	+	1	.	.	.	3	.	.	II
Mammillaria dioica	1	2	.	.	.	+	+	II
Pachycerus schottii	.	.	+	.	.	+	.	.	+	.	.	+	+	+	II
Atriplex canescens v. linearis	.	.	+	.	.	+	1	1	1	I
Cylindropuntia prolifera (transgresiva)	.	.	+	.	.	+	+	.	.	I
Lycium andersonii v. andersonii	*	*	*	*	*	*	*	*	*	1	*	*	*	*	I

Addenda: Inv. 1: *Mammillaria brandegeei* +; Inv. 3: *Cylindropuntia cholla* +, *Encelia asperifolia* +; Inv. 9: *Aesculus parryi* +, *Dudleya attenuata* s. *attenuata* +, *Simmondsia chinensis* +; Inv. 14: *Cylindropuntia alcahes* v. *alcahes* +, *Fouquieria splendens* +, *Pachycormus discolor* v. *pubescens* 2.

* Con tallos y ramas cubiertos de *Vermilacinia leopardina*.

Cuadro 3 - Ass. *Atriplici julaceae-Yuccetum validae* Alcaraz & Delgadillo ass. nova hoc loco (relevé tipo nº 1): a) subass. *yuccetosum validae* (typicum); b) subass. *agavetosum goldmaniana* (Peinado, Alcaraz, Aguirre & Delgadillo 1995) Alcaraz & Delgadillo nova comb.

Nº Orden	1	2	3	4	5	6	7	8	9	10	11	12	13	Pa	Pb		
Registro	R8-110	R8-111	R8-112	R4-35	R4-40	R4-41	R7-79	R7-80	R4-37	R8-124	R9-34	R9-35	R9-33				
Altitud (m)	47	39	40	260	135	50	210	158	57	60	105	105	168				
Orientación	-	-	-	-	-	-	-	-	-	-	NW	NW	W-SW				
Inclinación (º)	-	-	-	-	-	-	-	-	-	-	20	25	10				
Área (m ²)	100	100	120	200	150	150	100	150	120	100	150	80	100				
Características territoriales de asociación y alianza (<i>Idrio columnaris-Pachycormus pubescens</i>)																	
<i>Yucca valida</i>	+	1	1	.	1	+	.	.	+	1	+	+	+	3	II		
<i>Fouquieria columnaris</i>	.	1	+	.	1	.	1	1	2	II		
<i>Fouquieria diguetii</i>	1	+	.	.	+	1	.	.	.	1	II		
<i>Pachycormus discolor</i> v. <i>pubescens</i>	+	.	1	1	.	1	.	.	.	0	II		
<i>Euphorbia lomelii</i>	+	+	0	I		
Diferenciales de subasociaciones																	
<i>Cylindropuntia calmalliana</i>	+	+	+	.	+	+	+	+	+	+	+	+	+	3	.		
<i>Dudleya acuminata</i>	+	-	+	2	.		
<i>Agave shawii</i> s. <i>goldmaniana</i>	.	.	.	1	1	2	2	1	2	1	1	1	+	2	V		
<i>Dudleya cistriformis</i>	.	.	.	+	.	1	+	+	+	+	+	+	.	.	III		
<i>Xylonagra arborea</i> s. <i>wigginsii</i>	1	.	.	.	2	.	2	3	.	1			
Plantas y líquenes maresícolas																	
<i>Atriplex julacea</i>	+	1	1	2	2	2	2	1	+	1	2	+	1	2	V		
<i>Frankenia palmeri</i>	2	2	.	.	+	.	.	+	2	2	3	2	.	2	III		
<i>Niebla</i> sp. pl.	.	.	.	1	.	.	1	.	1	.	2	3	.	IV			
<i>Ferocactus fordii</i> v. <i>fordii</i>	+	.	.	.	+	I		
Características de orden, clase y transgresivas																	
<i>Euphorbia misera</i>	1	1	1	2	1	2	1	1	1	1	2	1	2	3	V		
<i>Mammillaria dioica</i>	+	+	+	1	+	+	+	+	+	+	.	.	+	3	IV		
<i>Ambrosia chenopodiifolia</i>	1	2	2	+	2	1	+	1	+	1	2	2	2	3	III		
<i>Stenocereus gummosus</i>	+	1	+	+	2	1	+	1	+	+	+	+	+	3	IV		
<i>Echinocereus maritimus</i>	+	+	1	1	.	1	+	+	1	3	III		
<i>Ferocactus gracilis</i> v. <i>gracilis</i>	.	.	.	1	+	+	+	1	.	.	+	+	+	0	III		
<i>Lycium andersonii</i> v. <i>andersonii</i>	1	1	1	0 II		
<i>Lycium californicum</i>	+	1	+	1	+	1	.	+	+	+	+	+	+	3	III		
<i>Cylindropuntia cholla</i>	2	1	+	1	+	+	+	+	+	0	II		
<i>Encelia asperifolia</i>	.	.	.	1	1	.	2	.	+	+	+	+	+	0	II		
<i>Pachycereus pringlei</i>	.	.	.	1	1	.	1	1	1	1	1	1	1	0	II		
<i>Cylindropuntia tesajo</i>	.	.	.	1	1	1	1	1	1	1	1	1	1	0	I		
<i>Jatropha cinerea</i>	+	.	+	.	.	1	1	1	1	1	1	1	1	2	.		
<i>Myrtillocactus cochal</i>	1	1	1	1	1	1	1	1	1	0	I		
<i>Pachycereus schottii</i>	1	1	1	1	1	1	1	1	1	0	I		
Características de clase																	
<i>Fouquieria splendens</i>	.	.	.	+	1	1	1	1	1	1	1	1	1	1	0		
<i>Zephyranthes longifolia</i>	+	+	+	1	1	1	1	1	1	1	1	1	1	1	1		
Compañeras														4	2	0	1
<i>Chloracantha spinosa</i>																	

Addenda: Inv. 3: *Ferocactus peninsulae* v. *viscainensis* +; Inv. 4: *Atriplex barclayana* 1, *Bursera microphylla* +, *Harfordia macroptera* +, *Hesperoyucca peninsularis* +; Inv. 7: *Cylindropuntia molesta* +, *Fagonia laevis* +, *Tillandsia recurvata* +; Inv. 8: *Ambrosia camphorata* +, *Prosopis glandulosa* v. *torreyana* +, *Stenocereus thurberi* +, *Trixis californica* +; Inv. 9: *Ferocactus gracilis* v. *coloratus* 1, *Ferocactus peninsulae* v. *peninsulae* +; Inv. 11: *Lotus scoparius* v. *scoparius* +; Inv. 13: *Ambrosia dumosa* +.

información existente en su entorno, muy probablemente se desarrolle en territorios termomediterráneos áridos superiores.

Ass. *Atriplici julacea-Yuccetum validae* Alcaraz y Delgadillo ass. nova hoc loco

Cuadro 3, inventarios 1 a 13, typus inventario (relevé) 1 [Arroyo El León, al norte de Villa Jesús María, 28° 17' 52" N, 115° 58' 58.5" W] (subass. *typicum*)

subasociación *agavetosum goldmaniana* (Peinado, Alcaraz, Aguirre y Delgadillo 1995) Alcaraz y Delgadillo comb. nova (inventarios 4 a 13) [Basionym: *Yucca validae*-*Fouquierietum diguetii* Peinado et al., 1995 subass. *agavetosum goldmaniana* Peinado, Alcaraz, Aguirre y Delgadillo in *J. Veg. Sci.* 6: 87 (1995), holotype table 7, rel. 9]

Matorrales relativamente diversos en los que fisionómicamente destaca un estrato superior, discontinuo, de fanerófitos más o menos leñosos (*Fouquieria columnaris*, *Fouquieria diguetii*, *Yucca valida*, etc.), algunas veces con

cardones (*Pachycereus pringlei*) y otro de caméfitos y nanofanerófitos entre los que hay plantas suculentas (*Agave shawii* subsp. *goldmanina*, *Euphorbia lomelii*, *Euphorbia misera*, *Mammillaria dioica*, *Stenocereus gummosus*, etc.) y las típicas indicadoras de maresía (*Atriplex julacea*, *Frankenia palmeri*, *Ferocactus fordii* var. *fordii*) y los líquenes aerohalófilos (*Niebla* sp. pl. y *Vermilarcinia* sp. pl.). Como en las asociaciones anteriores, los tallos y ramas más gruesas de las especies de corteza lisa están recubiertos de líquenes.

El aspecto más empobrecido de la asociación se da en las extensas llanuras de Vizcaíno y el entorno de Guerrero Negro, territorio en el que no obstante hay elementos endémicos locales como *Cylindropuntia calmalliana* y *Dudleya acuminata* que pueden ser usadas como diferenciales geográficas de la raza o subasociación típica (ALCARAZ, 1996). Más al norte, desde Villa Jesús María hasta las proximidades de Puerto Catarina, hay un nutrido grupo de taxones diferenciales que permiten reconocer una subasociación geográfica septentrional en la que destaca por su gran

porte y regularidad el mezcal *Agave shawii* subsp. *goldmaniana*.

Climáticamente se desarrolla en territorios desérticos pero aún con régimen de lluvias no tropical (precipitaciones máximas invierno) bajo ombroclimas áridos (subasociación *agavetosum goldmaniana*) o incluso hiperáridos (subasociación típica).

Al describir la subasociación *agavetosum goldmaniana* dentro del *Yucco valideae*-*Fouquierietum diguetii*, Peinado et al. (1995: 87, tabla 7, tipo inventario 9) presentan cuatro inventarios de zonas afectadas por maresía, fácilmente detectables por las especies maresícolas *Atriplex julacea* y *Frankenia palmeri* que incluyen. Sin embargo el tipo de la asociación (tabla 7, inventario 3) corresponde a una vegetación no maresícola que representaría la clímax de los llanos de Vizcaíno. La separación entre la vegetación no maresícola y la de transición, objeto del presente este trabajo, por coherencia con los criterios que se mantienen en el mismo, lleva a tener que separar unas comunidades de las otras en el rango de asociación; por ello se propone desgajar fito-

Cuadro 4 - Tabla sintética.

Nº de inventarios
Nº Orden

4	8	14	3	4	10
1	2	3	4	5	6

Características territoriales de *Bergerocacto-Agavetum shawii*

Agave shawii s. *shawii*
Bergerocactus emoryi
Encelia californica (dif.)
Opuntia littoralis (dif.)
Eriogonum fastigiatum

4	V
4	IV
1	I
3	II
1	II

Características territoriales de *Ferocacto-Eunhorbietum miserae*

Hesperoyucca peninsularis
Pachycereus schottii

.	.	IV	.	.	I
.	.	II	.	.	.

Características territoriales de *Atriplici-Yuccetum validae* y diferenciales de sus subasociaciones

Dudleya acuminata
Yucca valida
Zephyranthes longifolia
Cylindropuntia calmalliana (a)
Ferocactus peninsulae v. *viscainensis* (a)
Agave shawii s. *goldmaniana* (b)
Ferocactus gracilis v. *coloratus* (b)
Ferocactus gracilis v. *gracilis* (b)
Xylonagra arborea v. *wigginsii* (b)

.	.	.	1	.	I
.	.	.	3	4	IV
.	.	.	3	.	I
.	.	.	2	.	.
.	.	.	1	.	.
.	.	.	.	4	V
.	.	.	.	2	I
.	I	.	.	2	III
.	I

Especies maresícolas

Atriplex julacea
Ferocactus fordii v. *fordii*
Frankenia palmeri
Niebla sp. pl.

1	III	I	3	2	IV
4	III	IV	.	.	I
.	V	IV	2	3	V
.	I	IV	.	.	III

Características de la alianza *Agavion shawii*

Aesculus parryi
Cylindropuntia prolifera
Dudlea attenuata v. *attenuata*
Mammillaria brandegei

1	II	I	.	.	.
4	I	I	.	.	.
.	III	I	.	.	.
.	.	I	.	.	.

Características de la alianza *Idrio-Pachycormion pubescens*

Ambrosia camphorata
Euphorbia lomelii
Ferocactus peninsulae v. *peninsulae*
Fouquieria columnaris
Fouquieria diguetii
Pachycormus v. *pubescens*

.	.	.	1	.	.
.	.	.	2	.	II
.	.	I	.	.	II
.	.	.	.	1	I
.	.	.	.	1	II
.	I

Características del orden (*Parkinsonietalia florido-microphyllae*)

Ambrosia chenopodifolia
Atriplex barclayana
Bursera microphylla
Cylindropuntia alcáhes v. *alcáhes*
Cylindropuntia cholla
Cylindropuntia molesta
Cylindropuntia tesajo
Dudleya cultrata
Echinocereus maritimus
Encelia asperifolia
Euphorbia misera
Fagonia laevis
Harfordia macroptera
Jatropha cinerea
Mammillaria dioica
Mvtillocactus cochal
Pachycereus pringlei
Simmondsia chinensis
Stenocereus gummosus
Stenocereus thurberi

4	IV	II	3	3	IV
.	I
.	.	.	1	.	I
.	II	.	.	3	.
.	I	I	.	.	II
.	I	.	.	.	I
.	.	.	.	2	I
.	V	III	.	.	III
4	V	III	3	4	III
.	.	I	.	.	II
4	V	V	3	4	V
.	I
1	I	.	.	.	I
.	.	.	2	.	.
4	V	II	3	.	IV
1	II	.	.	.	I
.	.	.	.	2	II
2	.	I	.	.	.
2	III	III	3	4	IV
.	I

Características de clase

Fouquieria splendens
Prosopis glandulosa v. *torreyana*

.	.	I	.	.	I
.	I

1) *Bergerocacto emoryi-Agavetum shawii* Peinado et al. 1995, tabla 2 (Inv. 1, 2, 3, 6); 2) *Bergerocacto emoryi-Agavetum shawii* (Cuadro 1 en este trabajo); 3) *Ferocacto fordii-Euphorbiatum miserae* (Cuadro 2 en este trabajo); 4) *Atriplici julaceae-Yuccetum validae* subass. *yuccetosum validae* (Cuadro 3 en este trabajo, inventarios 1 a 3); 5) *Yucco validae-Fouquierietum diguetii* subass. *agavetosum goldmanianae* Peinado et al. 1995 (tabla 7, inventarios 7 a 10); 6) *Atriplici julaceae-Yuccetum validae* subass. *agavetosum goldmanianae* (Cuadro 3 en este trabajo, inventarios 4 a 13).

sociológicamente los matorrales con *Agave shawii* subsp. *goldmaniana* afectados por la maresía del *Yucca validae-Fouquierietum diguetii* y llevarlos a las comunidades maresícolas norteñas con *Yucca valida*, con la que comparte un cuerpo de especies común importante; el conjunto constituirían una asociación particular con dos razas o subasociaciones geográficas; de ahí la propuesta de combinación nueva, ya que el rango de la unidad inicialmente propuesta por Peinado y colaboradores no varía.

DISCUSIÓN

Las comunidades vegetales de zonas sublitorales sometidas al rocío salino procedente del mar, pero lo suficientemente alejadas de la línea de costa como para que las especies más halotolerantes de la vegetación zonal puedan tener una cierta capacidad de competencia con las estrictamente maresícolas, comparten especies de ambos ambientes; esto produce problemas cuando se intenta ubicarlas en un modelo fitosociológico de clasificación (ALCARAZ, 1996; ALCARAZ y DELGADO, 1998). En este sentido sería posible ubicarlas tanto en las clases de vegetación que incluyen formaciones aerohalófilas, como en las más relacionadas con la vegetación zonal. En su análisis de las geoseries especiales ALCARAZ (1996), al tratar las maresícolas resalta la importancia de la última banda, en el sentido de la costa hacia el interior, donde se asientan comunidades ricas en especies zonales, siendo de una mayor riqueza florística, por lo que aconseja como criterio básico el incluirlas ya dentro de la clase de vegetación zonal que corresponda, puesto que dicha banda presenta además aspectos sucesionales muy relacionados con los propios de la vegetación zonal.

En este orden de cosas, estos tipos de vegetación en la zona estudiada podrían inscribirse o bien en la clase de comunidades maresícolas *Atriplici julacea-Frankenietea palmeri* Peinado, Aguirre, Delgadillo y Macías in Plant Ecol., 196: 55 (2008), de la clase zonal mediterránea *Heteromelo arbutifoliae-Quercetea agrifoliae* Rivas-Martínez in Itineraria Geobotanica, 10: 17(1997), donde se ubicaron originariamente las comunidades de matorral costero suculento bajocaliforniano con *Agave shawii* subsp. *shawii*, o bien en la de vegetación leñosa y suculenta sonorense *Prosopido torreyanae-Fouquierietea splendens* Rivas-Martínez in Itineraria Geo-

botanica, 10: 92(1997). Los comentarios vertidos en el párrafo anterior apoyan a la decisión de descartar la primera clase, maresícola y halófila, y centrarse en la discusión de las otras dos alternativas.

Cuando RIVAS-MARTÍNEZ (1997) describe la clase de chaparrales californianos *Heteromelo arbutifoliae-Quercetea agrifoliae* incluye en la misma los matorrales costeros suculentos bajocalifornianos, presididos por *Agave shawii* subsp. *shawii*, considerándolos como chaparral leñoso bajo, rico en cactáceas y plantas crasifolias arrosetadas; para ellos describe una nueva alianza (*Agavion shawii* Rivas-Martínez in Itineraria Geobotanica, 10: 44-45(1997)) que incluye dentro del orden *Adenostomo fasciculati-Rhamnetalia crenulatae* Rivas-Martínez in Itineraria Geobotanica, 10: 433(1997). Sin embargo las cuatro asociaciones descritas de matorral costero suculento (PEINADO et al., 1995: *Bergerocactus emory-Agavetum shawii*, *Roso minutifoliae-Aesculetum parryi*, PEINADO et al., 2008: *Cneoridio dumosae-Agavetum shawii*, *Trixido californicae-Stenocereetum gummosum*) tienen una escasa representación de elementos de la clase *Heteromelo arbutifoliae-Quercetea agrifoliae* (*Rhus integrifolia* en cuatro de los inventarios originales del *Bergerocactus-Agavetum* y uno en la original del *Roso minutifoliae-Aesculetum parryi*), siendo sin embargo muy numerosos los de *Prosopido torreyanae-Fouquierietea splendens* (*Euphorbia misera*, *Ferocactus gracilis* var. *gracilis*, *Mammillaria dioica*, *Myrtillocactus cochal*, *Simmondsia chinensis*, *Solanum hindsianum*, *Stenocereus gummosus*, etc.), incluso algunos son dominantes en ciertos inventarios.

Descartado pues, por las razones expresadas, el ubicar estas comunidades en la clase aerohalófila costera, la clase donde mejor parecen poderse ubicar los matorrales costeros suculentos bajocalifornianos es la sonorense *Prosopido torreyanae-Fouquierietea splendens* por evidentes criterios florísticos.

Una vez seleccionada la clase más apropiada de las actualmente descritas, en cuanto a la ubicación dentro de los órdenes descritos se plantea un doble problema. Por un lado PEINADO et al. (1995: 56) crearon un orden *Bergerocactus emory-Agavietalia shawii* Peinado, Aguirre, Delgadillo y Macías in Plant Ecol., 196: 56(2008) dentro de la clase halófila *Atriplici julacea-Frankenietea palmeri*, para incluir exclusivamente la alianza *Agavion shawii*, dado que al ubicarla en tal clase, difícilmente

podría integrarse en los órdenes que se incluían en la misma. Por otro lado, dentro de la clase *Prosopido torreyanae-Fouquierietea splendens* RIVAS MARTÍNEZ(1997) considera dos órdenes, uno de las áreas occidentales de los territorios sonorenses (*Orden Parkinsonietalia florido-microphyllae* in Itineraria Geobotanica, 10: 94(1997)), donde se ubica el área del presente estudio, y otro sonorense oriental (*Guajaco angustifolii-Parkinsonietalia texanae* in Itineraria Geobotanica, 10: 101(1997)).

En el orden occidental considera una alianza de las zonas subcontinentales y semicontinentales sonorenses (*Prosopido velutinae-Carnegion giganteae* Rivas-Martínez in Itineraria Geobotanica, 10: 95(1997)), que quedan fuera del área de estudio, y otra alianza propia de la mayor parte de la península de Baja California más o menos afectada por el Pacífico (*Idrio columnaris-Pachycormion pubescens* Rivas-Martínez in Itineraria Geobotanica, 10: 99(1997)), pero excluyendo los matorrales costeros suculentos del *Agavion shawii*, a los que sin embargo considera muy relacionados.

Los elementos del *Idrio columnaris-Pachycormion pubescens* son muy escasos en las comunidades del *Agavion shawii* y suelen darse en las zonas de ecotonos (*Bergerocactus emory-Agavetum shawii* subass. *idrietosum columnaris* Peinado, Alcaraz, Aguirre y Delgadillo in J. Veg. Sci., 6: 85(1995)), por lo que unir ambas alianzas, en cuyo caso el nombre prioritario sería el de *Agavion shawii*, no tiene una sólida base florística. Diferenciar otro tercer orden (el ya mencionado *Bergerocactus emory-Agavietalia shawii*) supondría una unidad de gran rango para un contingente relativamente reducido de comunidades vegetales. Sin embargo y dado que hay un cierto número de taxones comunes entre *Agavion shawii* y *Parkinsonietalia florido-microphyllae*, en el presente trabajo se ha optado por la alternativa de transferir la alianza de matorral costero suculento bajocaliforniano al mencionado orden, que pasaría a estar integrado por tres alianzas:

- *Agavion shawii*: termomediterránea (como vegetación permanente) - infra-mediterránea semiárida;
- *Idrio columnaris-Pachycormion pubescens*: infra-termomediterránea árida-hiperárida, termotropical árida-hiperárida;
- *Prosopido velutinae-Carnegion giganteae*: mesotropical árida-hiperárida.

La asociación *Ferocactus fordii-Euphorbiatum miserae* presenta una baja

riqueza florística, pero con abundancia de elementos aerohalófilos. No obstante la abundancia de *Euphorbia misera*, especie considerada en algunas publicaciones como estrictamente maresícola (PEINADO *et al.*, 2008: 44), en realidad este taxón está ampliamente distribuido en zonas interiores de la península de Baja California, lejos de la influencia del hálito marino, por lo que aquí se considera como una especie zonal halotolerante; esto junto con la representación, ciertamente que con escasos individuos, de diversas plantas sonorenses (*Ambrosia chenopodifolia*, *Echinocereus maritimus*, *Mammillaria dioica*, *Pachycereus schottii*, *Simmondsia chinensis*, *Stenocereus gummosus*), los cuales apoyan su inclusión en la alianza *Idrio columnaris-Pachycormion pubescens*, dentro de la cual representan la asociación aerohalófila más norteña.

Por último hay que destacar la gran abundancia de elementos del *Idrio columnaris-Pachycormion pubescens* en la asociación *Atriplici julaceae-Yuccetum validae*, que dejan bien a las claras dónde debe incluirse desde el punto de vista sintaxonómico.

De acuerdo con todas estas consideraciones, las comunidades tratadas en el presente trabajo quedarían encuadradas en el siguiente esquema sintaxonómico (ver cuadro sintético 4):

Clase Prosopido torreyanae-Fouquieretea splendens Rivas-Martínez in Itinera Geobotánica, 10: 92-93(1997)

Orden Parkinsonietalia florido-microphyllae Rivas-Martínez in Itinera Geobotánica, 10: 94(1997)

Alianza Agavion shawii Rivas-Martínez in Itinera Geobotánica, 10: 44(1997)

Asociación Bergerocactus emoryi-Agavetum shawii Peinado, Alcaraz, Aguirre y Delgadillo in J. Veg. Sci., 6: 84-85(1995)

Alianza Idrio columnaris-Pachycormion pubescens Rivas-Martínez in Itinera Geobotánica, 10: 99(1997)

Asociación Ferocactus fordii-Euphorbiatum miserae Alcaraz y Delgadillo ass. nova

Asociación Atriplici julaceae-Yuccetum validae Alcaraz y Delgadillo ass. nova

subasociación *yuccetosum validae* (*typicum*)

subasociación *agavetosum goldmaniae* (Peinado, Alcaraz, Aguirre y Delgadillo 1995) Alcaraz y Delgadillo comb. nova

El tratamiento fitosociológico de la vegetación fundamentado en muestras que consideren los gradientes ambientales y en criterios para «rom-

per» de forma razonada y consensuada el continuum, es una aproximación muy interesante para abordar estudios con la metodología sigmatista en territorios donde la continuidad de la vegetación es muy manifiesta, como es el caso de muchas áreas bien conservadas.

En los gradientes especiales (ALCARAZ, 1996) pueden darse situaciones de transición entre tipos de vegetación muy diferentes, azonales y zonales, en el extremo del gradiente donde los factores que lo determinan tienen menor incidencia. En tales casos se plantea un problema adicional al del continuum, que es el de tener unidades muestrales (inventarios) que por la composición florística están a caballo entre una clase de vegetación azonal y otra zonal; al analizar esos inventarios se corre el riesgo de valorar la abundancia de las especies para inclinarse hacia su encuadre en una u otra clase, por lo que se podría acabar proponiendo dos comunidades que cualitativamente son muy similares pero cuantitativamente observadas pudieran ir a hacia un lado u otro. Para estos casos, que se dan en el extremo de muchos gradientes ecológicos especiales en la superficie terrestre, se propone dar más importancia a las especies de la clase zonal, independientemente de su mayor o menor abundancia, como criterio a aplicar en todas las situaciones, para así realizar un tratamiento homogéneo y generar clasificaciones fitosociológicas más homogéneas.

CONCLUSIONES

La zona de transición o ecotono entre la vegetación maresícola y el matorral costero suculento de las costas pacíficas en el Valle de los Cirios (Baja California, México) muestra las características predichas para tales situaciones en la teoría sobre geoseries (ALCARAZ, 1996), estructurándose unas comunidades vegetales en las que conviven las especies más estenoicas de las maresícolas con las más halotolerantes de la vegetación zonal.

Desde las proximidades de El Rosario (30° N) hasta Guerrero Negro (28° N), al sur, hay un gradiente florístico que afecta a la vegetación de esta zona, de modo que es posible reconocer tres comunidades en el rango de asociación (*Bergerocactus emoryi-Agavetum shawii*, *Ferocactus fordii-Euphorbiatum miserae* y *Atriplici julaceae-Yuccetum validae*), la última además con dos subasociaciones geográficas, una sureña (*typicum*) y otra más norteña (*agavetosum*

goldmaniae).

Estas comunidades de transición entre dos gradientes (el marcado por la maresía y el de vertientes) pueden fitosociológicamente incluirse o bien como un extremo bajo menor rocío salino de las clases de vegetación maresícolas o, por el otro lado, como el aspecto más halotolerante de clases de vegetación zonales. Dada la importancia que la fitosociología dinámica y catenal otorga a los elementos de la vegetación zonal y la existencia de un dinamismo muy activo, a diferencia de los restringidos aspectos sucesionales que se observan en las zonas de más intensa maresía, se ha optado por considerar estas comunidades como propias de las clases de vegetación zonales, en este caso las tres asociaciones se incluyen en la clase *Prosopido torreyanae-Fouquierietea splendens*. En situaciones similares en el sureste de la península Ibérica, en este caso en un entorno más degradado, los tomillares o matorrales camefíticos mostraron un comportamiento similar (ALCARAZ y DELGADO, 1998) y la solución adoptada para encuadrar estas comunidades fue equivalente.

Los matorrales suculentos más nortenos, incluidos en la alianza *Agavion shawii*, muestran un componente florístico más relacionado con la clase de óptimo neotropical *Prosopido torreyanae-Fouquierietea splendens*, que con la clase *Hetermelo arbutifoliae-Quercetea agrifoliae*, en la que inicialmente fue incluida, por lo que se propone su transferencia a la primera.

En las siguientes páginas, se observan algunas especies de la flora y algunos aspectos de la vegetación de Baja California, México (Fig. 4-15).



Fig. 4 - Ejemplar de *Atriplex julacea*.



Fig. 5 - Aspecto en flor de *Ferocactus fordii* var. *fordii*.



Fig. 6 - Aspecto en flor de *Frankenia palmeri*.

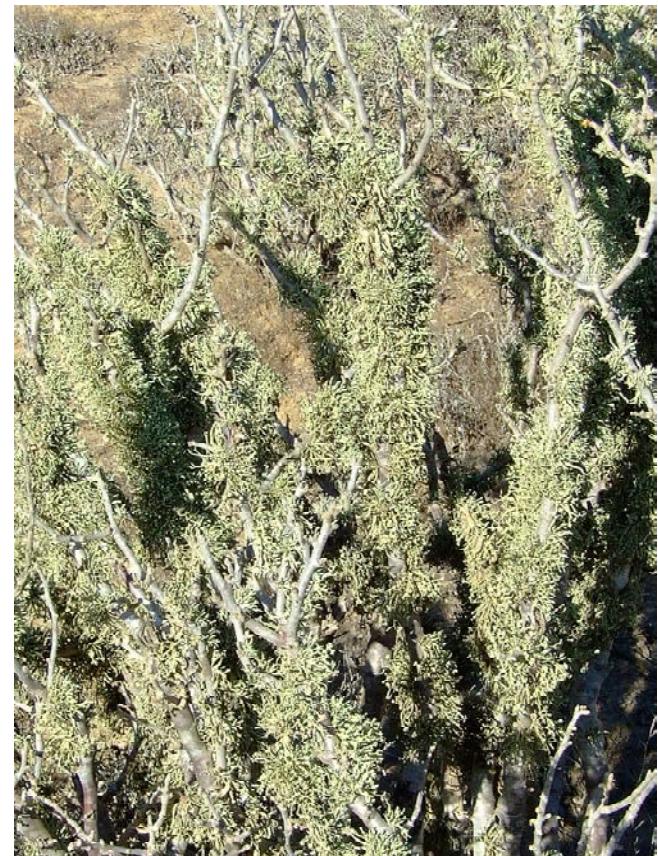


Fig. 7 - Ramas y troncos de *Euphorbia misera* cubiertos por el liquen *Vermilacinia leopardina*.



Fig. 8 - Líquenes maresícolas sobre conglomerados en cresterías de lomas cerca de El Rosario, los más abundantes son *Vermilacinia paleoderma* y *Niebla podetiforma*.



Fig. 9 - Matorral del *Atriplici julaceae-Yuccetum validae* subass. *agavetosum goldmanianae* cerca del Faro de San José, con líquenes maresícolas (especialmente *Vermilacinia paleoderma*) cubriendo las rocas más directamente expuestas al viento procedente del mar.



Fig. 10 - Aspecto general de los matorrales del *Bergerocacto emoryi*-*Agavetum shawii* cerca de El Rosario.



Fig. 11 - *Bergerocacto emoryi*-*Agavetum shawii*, con ejemplares en flor de *Agave shawii* subsp. *shawii* en Valle Tranquilo, al norte de El Rosario.



Fig. 12 - *Ferocactus fordii*-*Euphorbietum miserae*, faciación sobre conglomerados rica en *Frankenia palmeri*.



Fig. 13 - *Ferocactus fordii*-*Euphorbietum miserae* en laderas, con rosetas de *Hesperoyucca peninsularis*.



Fig. 14 - Aspecto más degradado, por ganadería extensiva, del *Ferocacto fordii-Euphorbietum miserae* sobre limolitas, destaca entre los líquenes terrícolas la abundancia de *Niebla arenaria*.



Fig. 15 - *Atriplici julacea-Yuccetum valida subass. typicum*, llanuras al norte de Guerrero Negro.

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L'ASSOCIAZIONE LUNULARIETUM CRUCIATAE GIACOMINI 1951 NELLA CITTÀ DI CAMERINO (MARCHE, ITALIA CENTRALE)

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ABSTRACT

The association *Lunularietum cruciatae* Giacomini 1951 has been recorded for the bryophyte flora of the town of Camerino (Marches, Central Italy). This association grows in the pavement of some roads of the historic center.

KEYWORDS: *Lunularia cruciata*, *Pellia endiviifolia*, *Lunularietum cruciatae*, Camerino.

INTRODUZIONE

La flora e la vegetazione briofitica degli ambienti urbani presentano un notevole interesse sia dal punto di vista floristico che fitosociologico e fitogeografico e non di rado è possibile scoprire in tali ambienti specie e associazioni considerate rare o poco diffuse per il territorio italiano.

I centri urbani ospitano, infatti, in maniera molto più rilevante di altri ecosistemi, una varietà di microambienti che permettono una maggiore colonizzazione da parte delle briofite.

La flora briologica della città di Camerino è stata oggetto di studio da parte di CORTINI PEDROTTI (1989), la quale ha rilevato la presenza di 71 briofite (7 epatiche e 64 muschi). L'area presa in considerazione per tale ricerca corrispondeva al centro storico, cioè a quella parte della città compresa all'interno delle mura castellane. In particolare, gli ambienti più comuni esplorati sono quelli rappresentati dai vecchi muri, le grotte che si aprono alla base delle antiche mura della città, il suolo dei giardini e le fessure della pavimentazione di alcuni vicoli del centro storico.

L'ASSOCIAZIONE LUNULARIETUM CRUCIATAE GIACOMINI 1951

Di particolare interesse briosociologico è il recente ritrovamento dell'associazione *Lunularietum cruciatae* Giacomini 1951 (Tab. 1). Largamente diffusa a causa della sua ampia valenza

ecologica, l'associazione è stata rilevata principalmente negli interstizi del selciato di alcuni vicoli del centro storico di Camerino, in condizioni di umidità e nitrificazione piuttosto elevate (Fig. 1).

Nel complesso tale associazione si può definire una comunità terricola, meso-xerofila, sciafila, nitrofila. Dal punto di vista fisionomico e floristico, la comunità è caratterizzata da *Lunularia cruciata*, epatica tallosa appartenente all'elemento oceanico-mediterraneo, facilmente riconoscibile per la presenza sulla superficie del tallo di coppette propagulifere a forma di semiluna, contenenti al loro interno gemme lenticolari della riproduzione vegetativa. La specie cresce sui terreni umidi, alla base di muri, pareti rocciose, nei giardini, ai margini delle strade e nell'interstizio dei selciati stradali (Fig. 2), come pure in prossimità di sorgenti e lungo i corsi d'acqua, sia in ambienti naturali che antropizzati. In Italia tale specie è ampiamente diffusa in quasi tutte le regioni (ALEFFI *et al.*, 2008).

Tra le specie di unità superiore rinvenute si segnalano *Didymodon vinealis* e *Barbula unguiculata*, due specie tipiche di ambienti antropizzati appartenenti alla Famiglia delle *Pottiaceae*

ae, Sottofamiglia delle *Barbuleae* (CORTINI PEDROTTI, 2001, 2005). Fra le specie compagne, significativa è la presenza di *Pellia endiviifolia* e di alcune specie del genere *Bryum*. Per quanto riguarda l'area di distribuzione, il *Lunularietum cruciatae* è diffuso prevalentemente nell'area mediterranea con irradiazioni nel centro Europa. In Italia tale associazione è stata segnalata in passato da LO GIUDICE (1995) per l'ambiente urbano della città di Catania, dove assume caratteristiche più marcatamente xerofile.

Circa la sintassonomia, il *Lunularietum cruciatae* viene inserito nell'alleanza *Grimaldion fragrantis* Smarda e Hadac 1944, che comprende associazioni di muschi mediterranei presenti nel centro Europa (HÜBSCHMANN, 1986).

Recentemente ROS e GUERRA (1987) hanno proposto il *Mannion androgynae* quale vicariante mediterranea di detta alleanza, caratterizzata dalla presenza di comunità terricole xerofile, non nitrofile, dominate da epatiche tallose. La comunità a *Lunularia cruciata* individuata nel centro storico di Camerino, a carattere mesofilo e nitrofilo, pur essendo povera di elementi caratteristici del *Grimaldion fragrantis*, può tuttavia essere a pieno titolo inserita nell'ordine *Barbulealia unguiculatae*.



Fig. 1 - L'associazione *Lunularietum cruciatae* (Tab. 1, ril. 4).

Tab. 1 - *Lunularietum cruciatae* Giacomini 1951.

	1	2	3	4	5	P r e s e n z a
Numero rilievo						
Copertura (%)	70	70	90	80	80	
Superficie (dmq)	4	4	4	4	4	
Numero di specie	5	5	5	5	6	
Caratt. ass.						
Lunularia cruciata	3.4	2.3	4.5	3.4	1.2	5
Caratt. alleanza, ordine e classe (<i>Grimaldion fragrantis</i>, <i>Barbuletalia unguiculatae</i>, <i>Barbuletea unguiculatae</i>)						
Didymodon vinealis	2.3	1.2	2.3	1.2	1.2	5
Barbula unguiculata	-	+	+ .2	+	1.2	4
Altre specie						
Bryum bicolor	+	1.2	+	+ .2	+	5
Bryum ruderale	+	+	+	-	-	3
Barbula convoluta	-	-	-	+	+	2
Pellia endiviifolia	+	-	-	-	-	1
Bryum capillare	-	-	-	-	+	1

culatae v. Hüb schmann 1960 della classe *Barbuletea unguiculatae* Mohan 1978 (PRIVITERA e PUGLISI, 2004).

POPOLAMENTO A *PELLIA ENDIVIIFOLIA*

In alcune grotte che si aprono all'interno dell'Orto botanico "Carmela Cortini" dell'Università di Camerino, alla base delle vecchie mura della città, in parte di origine naturale ed in parte scavate dall'uomo, la presenza di stillicidio permanente ha determinato la formazione di un popolamento a *Pellia endiviifolia*, di cui viene qui riportato un rilievo (ril. n. 1): superficie cmq 40,

grado di ricoprimento 90%; *Pellia endiviifolia* 3.4, *Lunularia cruciata* 2.3, *Eurhynchium pumilum* 1.2, *Rhynchosstiella tenella* 1.2, *Fissidens limbatus* +.2. Tale popolamento presenta alcune caratteristiche che lo avvicinano all'alleanza del *Pellion endiviifoliae* Bardat 1998, caratterizzata dalla prevalenza di epatiche tallose (BARDAT e HAUGUEL, 2002).

Pellia endiviifolia è stata trovata in passato, in condizioni analoghe, da CORTINI PEDROTTI (1982) sul fondo di una piccola nicchia posta all'ingresso della Grotta di Frasassi (Ancona, Marche). LOCALITÀ E DATA DEI RILIEVI

Tab. 1 - Camerino (Marche, Italia cen-

trale), centro storico, 4 ottobre 2009; ril. n. 1: "grottoni" dell'Orto botanico, 6 ottobre 2009.

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Fig. 2 - Vicoli di Camerino in cui si sviluppa l'associazione *Lunularietum cruciatae*.

EMPLEO DE LOS HÁBITATS NATURALES Y SEMINATURALES EN LA EVALUACIÓN DE LAS SIERRAS DEL LEVANTE ALMERIENSE (ALMERÍA, ESPAÑA)

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ABSTRACT

The natural and seminatural habitats used in the Spanish Strategy for the conservation of Biodiversity have been revealed as important diagnostic elements. Since the promulgation of the Habitats Directive 92/43 EEC, Spain and specially the Autonomous Community of Andalusia have developed a detailed cartography (E. 1:5000) of the natural protected areas as well as other new ones allowing their recognition as SCI. (Sites of Community Importance).

In this paper, the results presented were obtained in the cartography and evaluation of the vegetation in the mountains of the Levante Almeriense (Almería, Spain) used as a basis for their declaration as SCI.

KEY WORDS: cartography, conservation, Habitats Directive, Sierra of Levante almeriense.

RESUMEN

Los hábitats naturales y seminaturales utilizados en la Estrategia española para la conservación de la Biodiversidad, se han revelado como elementos diagnósticos de importancia. Desde la promulgación de la Directiva Hábitats 92/43 CEE, España y más concretamente la Comunidad Autónoma de Andalucía, han desarrollado una cartografía de detalle (E. 1:5000) tanto de los espacios naturales protegidos como de otros nuevos que han permitido su reconocimiento como LIC (Lugares de interés comunitario). Los estudios incorporan, además de la transcripción del programa CORINE (inspirado en la metodología fitosociológica de la escuela europea), modelos de evaluación, estado de conservación, prevención de riesgos, caracterización de impactos y, en algunos casos, modelos de restauración de la vegetación en áreas degradadas y/o sometidas a procesos de desertificación.

En este trabajo se presentan los resultados obtenidos en la cartografía y

evaluación de la vegetación en las sierras del Levante almeriense (Almería, España) que sirvieron de base para su declaración como LIC.

INTRODUCCIÓN

La Directiva Hábitats 92/43/CEE del Consejo de las Comunidades Europeas establece que los Estados integrados en la Unión Europea contribuirán a la constitución de una red ecológica de zonas especiales de conservación (Red Natura 2000) en función de la representación que tengan en su territorio los tipos de hábitats naturales y las especies que se relacionan en los anexos corre-

spondientes.

La diagnosis y clasificación de los hábitats naturales se fundamenta en el programa CORINE que se recoge en el Corine biotopes manual Habitat of the European Community y en la actualización parcial de éste contenida en Relation between the Directive Habitat 92/43 and the Corine Habitat List, donde la caracterización y sistematización de los hábitats está ampliamente inspirada en la metodología fitosociológica europea.

En lo que respecta a España su elevada biodiversidad y el amplio conocimiento de sus comunidades vegetales ha contribuido a desarrollar la Directiva Hábitats en varias fases. La primera consistió en la cartografía de los

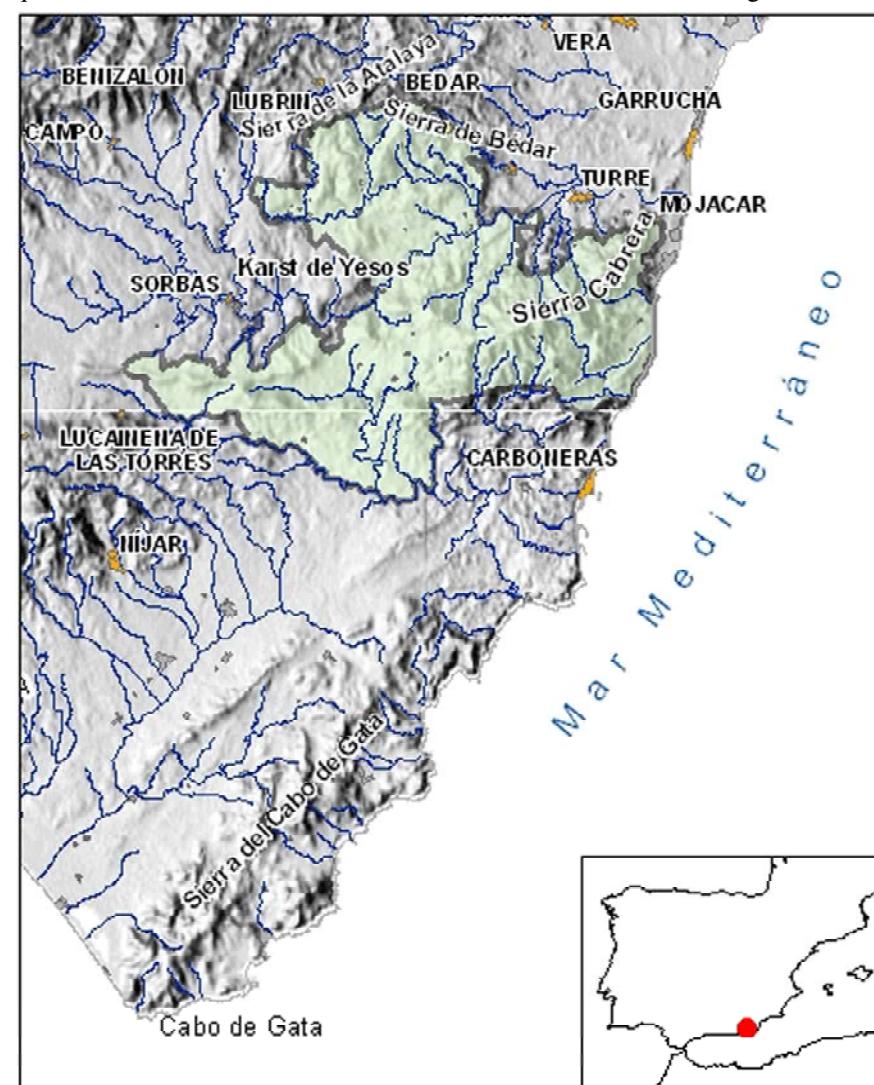


Fig. 1 - Mapa de situación.

tipos de hábitats en las 1080 hojas del Mapa 1:50.000 del Servicio Geográfico del Ejército. Para alcanzar el nivel de asociación (a veces subasociación) se incorporaron dos nuevos dígitos alfanuméricos al código de cuatro dígitos recogidos en el Anexo I Habitat types tal como se expresa en RIVAS-MARTÍNEZ *et al.* (1994). La segunda fase amplió el proceso de inventariación a otros tipos de hábitats significativos y no recogidos en la Directiva lo que dio origen al Atlas y Manual de los Hábitats de España (RIVAS-MARTÍNEZ *et al.*, 2003). Con esta base de datos se han digitalizado, cartografiado y referenciado buena parte de los hábitats en el territorio español y generalizado su empleo como elementos fundamentales en los estudios de evaluación y ordenación del territorio.

El objetivo de este trabajo es presentar los modelos de cartografía y evaluación que se están realizando en los espacios naturales de Andalucía, tomando como ejemplo las sierras del Levante de Almería y la información que se obtiene de las bases de datos asociadas.

ÁREA DE ESTUDIO

Bajo el nombre de sierras del Levante almeriense se incluyen fundamentalmente las sierras de Cabrera y Béjar, situadas en la parte oriental de la provincia de Almería, así como algunas zonas adyacentes: Karst de yesos en Sorbas, Riscos del Tesorero y Sánchez y cerros volcánicos entre Carboneras y Mojácar (Fig. 1).

En el área están representadas las estribaciones más orientales de la Sierra de los Filabres y, como apéndice de ésta, la Sierra de Béjar con alturas no superiores a los 600 m donde son característicos los materiales de naturaleza esquistosa. Hacia el este, se encuentra Sierra Cabrera, emplazada entre la Cuenca de Sorbas-Vera, al norte, y la depresión del Campo de Níjar, al sur. Es una alineación orientada OSO-NE que presenta altitudes medias de 200-300 m y se eleva hasta casi los 1.000 m en la zona central de la sierra (Mezquita, 960 m). Está constituida por materiales del Complejo Alpujárride (micasquistos, esquistos, cuarcitas) y una cobertura de rocas carbonatadas que aflora en las zonas más elevadas de la sierra. Connecta, a la altura de Mojácar, con las últimas colinas volcánicas de la Sierra de Cabo de Gata. La parte suroccidental contacta con las estribaciones de la Sierra Alhamilla (cerros próximos a Lucentina de las Torres).

Entre estas sierras del Levante almeriense se localizan una serie de depresiones o cuencas, que de norte a sur son: la Cuenca de Vera drenada por el río Antas, la de Sorbas, drenada por el río Aguas y situada entre la Sierra de Béjar al norte y las sierras Alhamilla y Cabrera, al sur. Por último, la de Níjar, drenada por el río Carboneras y sólamente representada por la margen izquierda del río que limita con la Sierra Cabrera.

El carácter distintivo de estos ríos y ramblas es su irregularidad e intermitencia pues sus aguas funcionan con gran rapidez a raíz de las precipitaciones. Las fuertes pendientes y la ausencia de vegetación determinan que, en poco tiempo, estos lechos transporten grandes cantidades de agua. Las pendientes, los suelos desprovistos de vegetación y la torrencialidad con que se producen las lluvias les otorgan su gran capacidad de erosión.

De especial interés son las colinas de origen volcánico adosadas al macizo montañoso de Sierra Cabrera y separadas tectónicamente por un sistema de fallas. Estas rocas volcánicas forman parte de la prolongación hacia el NE del volcanismo calcoalcalino del área de Cabo de Gata, que en este territorio están formadas por una sucesión de aglomerados, andesitas en masa, tobas, conglomerados poligénicos, cenizas y dacitas (anfibólicas y piroxénicas).

Los suelos más generalizados corresponden a regosoles y litosoles, desarrollándose en la parte meridional de Sierra Cabrera suelos más profundos: cambisoles. Los fluvisoles calcáreos ocupan los cauces de ramblas y ríos. También se presentan yermosoles hápicos en zonas con afloramientos de yesos.

El análisis de los datos termoplviométricos referentes a las precipitaciones muestra la escasez de las mismas en toda el área con valores inferiores o próximos a los 400 mm anuales. El bioclima mayoritario es de tipo Mediterráneo xérico oceánico y sólo las zonas más elevadas por encima de 800 m de altitud presentan un bioclima pluviestacional oceánico (RIVAS-MARTÍNEZ, 2007). El termotipo dominante es el termomediterráneo y el ombrotipo semiárido.

SERIES Y GEOSERIES DE VEGETACIÓN

La vegetación del territorio ha sido descrita, en su estructura y dinamismo, por diversos autores (ALCARAZ *et al.*,

1989; PEINADO *et al.*, 1992; ASENI y DÍEZ-GARRETAS 1996a, 1996b, 2000). En la actualidad y siguiendo los criterios de RIVAS-MARTÍNEZ *et al.* (2010) se distinguen las siguientes series y geoserries:

- Climatófilas, determinadas por las condiciones climáticas generales del territorio, sin desviaciones topográficas o de naturaleza edáfica.

- Serie valenciana y alicantino-murciana termo-mesomediterránea seco-subhúmeda de los bosques de *Quercus rotundifolia* (*Rubio longifoliae-Querco rotundifoliae* sigmetum). Faciación almeriense de *Phlomis purpurea* subsp. *almeriensis*.

- Serie murciano-almeriense termo-mediterránea semiárida de *Rhamnus lycioides* con *Chamaerops humilis* (*Chamaeropo humilis-Rhamno lycioidis* sigmetum).

- Faciación típica murciana de *Rhamnus oleoides* subsp. *angustifolius*

- Faciación almeriense occidental de *Phlomis purpurea* subsp. *almeriensis*

- Faciación almeriense oriental gipsícola de *Santolina viscosa*.

- Serie almeriense oriental y charidemá infra-termomediterránea árida de *Periploca angustifolia* con *Maytenus europaea* (*Mayteno europaei-Periploco angustifoliae* sigmetum).

- Serie almeriense infra-termomediterránea árido-semiárida de *Ziziphus lotus* (*Zizipho loti* sigmetum). Faciación almeriense oriental de *Rhamnus oleoides* subsp. *angustifolius*.

- Edafófilas, ligadas a factores edáficos excepcionales o desviantes, tanto por xericidad (edafoxerófilas) como por hidromorfía (edafohigrófilas).

- Serie de ramblas almeriense infra-termomediterránea de *Nerium oleander* (*Zizipho loti-Nerio oleandri* sigmetum).

- Geoserie fluvial murciano-almeriense termomediterránea de los bosques de *Populus alba* (*Lonicero biflorae-Populo albae* geosigmetum).

MATERIAL Y MÉTODOS

La fotointerpretación se ha realizado sobre fotografía de infrarrojo color (escala 1:20.000). Las unidades delimitadas sobre la fotografía aérea y posteriormente reconocidas y restituidas, se han definido a escala 1:5.000, sobre la ortofoto de referencia. Se ha utilizado la base del Mapa Topográfico de Andalucía a escala 1:10.000, en formato digital. Cada una de las “unidades o polígonos” lleva incorporada información referente a la composición florí-

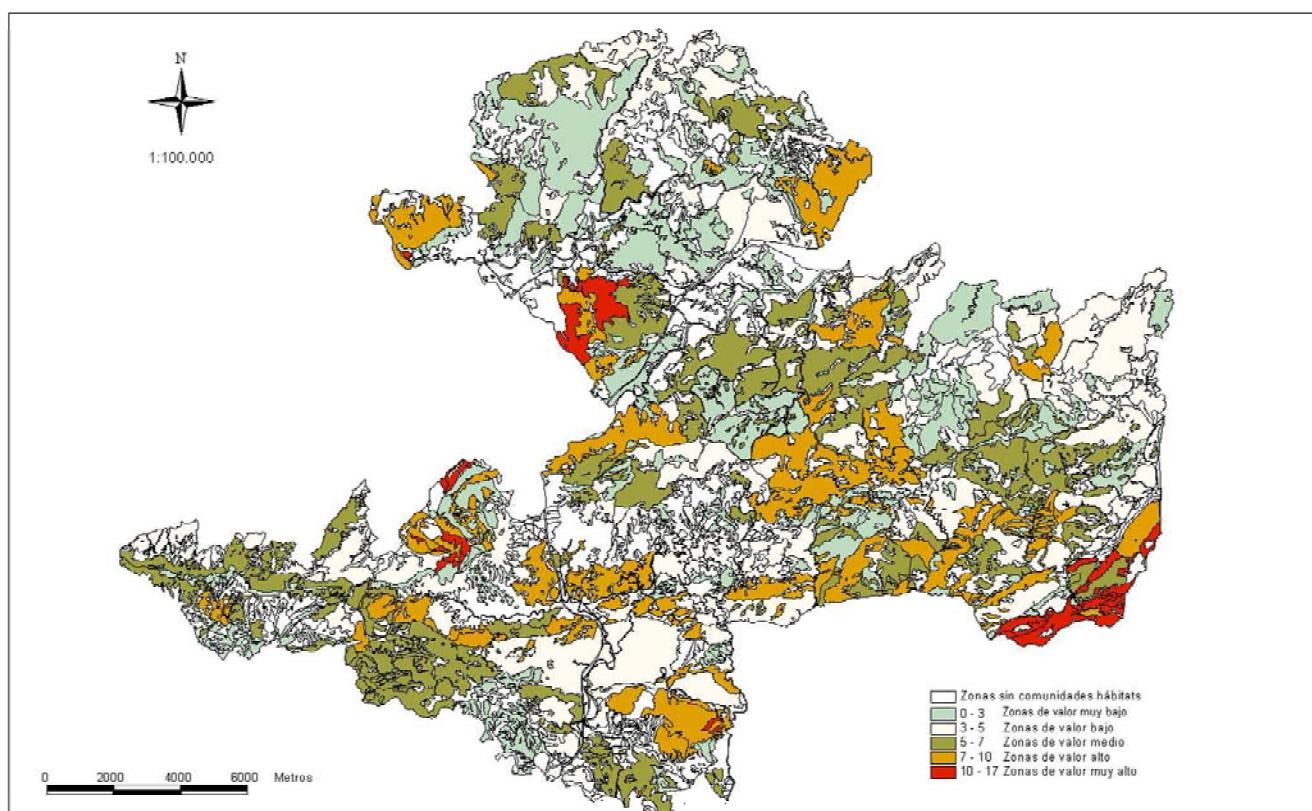


Fig. 2 - Mapa de evaluación.

stica e inventarios fitosociológicos según la metodología de BRAUN-BLANQUET (1979) que permite identificar las comunidades presentes en cada unidad, su preponderancia, porcentaje de ocupación y nivel evolutivo considerado dentro de la serie o geoserie de vegetación correspondiente. Se incluyen datos de carácter geomorfológico, biogeográfico, bioclimático (termotipo y ombrotipo), edáfico y tipo de uso del suelo. En la estructura de la vegetación se han considerado parámetros como cobertura, naturalidad, formas vitales predominantes en los distintos estratos, proporción de suelo desnudo y, en algunos casos combustibilidad forestal. En la codificación de hábitat se ha seguido la propuesta de seis dígitos tal como aparece en el Atlas y Manual de Hábitat de España que permite distinguir hasta el nivel de subasociación (RIVAS-MARTÍNEZ *et al.*, 1994, 2003). En los aspectos nomenclaturales de los taxones y sintaxones se ha tenido en cuenta las recientes revisiones de RIVAS-MARTÍNEZ *et al.* (2001, 2002, 2010). La información alfanumérica generada se grabó utilizando la base de datos propuesta por la Consejería de Medio Ambiente de la Junta de Andalucía.

En lo que respecta a la metodología de evaluación que combina datos florísticos y fitocenóticos, los pioneros de estos estudios utilizaron diversos parámetros como originalidad, rareza, índice global de valor biológico vege-

tal, etc., en comunidades del litoral atlántico francés (GÉHU, 1979; GÉHU y GÉHU-FRANK, 1980). Estos valores cuantitativos aplicados en biotopos concretos (saldares, acantilados, etc.) se emplearon posteriormente en áreas más complejas con diversos ecosistemas de ámbito territorial, como parques naturales (MARTÍN OSORIO y ASENSI, 1988). En la actualidad, algunos autores utilizan criterios intrínsecos semicuantitativos (LOIDI, 1994; DÍAZ GONZALEZ *et al.*, 1996; ASENSI y DÍEZ-GARRETAS, 2000) como: 1. endemidad, que valora la distribución geográfica exclusiva tanto del hábitat como de los grupos syntaxonómicos superiores a los que pertenece (escala 0-5). 2. Rareza, pondera la existencia del hábitat en una determinada unidad biogeográfica (escala 0-4). 3. Relictismo, expresa la expansión o regresión por causas naturales y su tendencia futura (escala 0-4). 4. Fragilidad o probabilidad de desaparición del hábitat por posibles modificaciones de las condiciones medioambientales. 5. Vulnerabilidad, factor extrínseco que evalúa la tendencia actual a una reducción del área de distribución del hábitat (escala 0-3). En cada polígono se ha ponderado asimismo, el porcentaje de cobertura de cada comunidad (P_j), la consideración de prioritario o no en la Directiva Habitat (H_j), la suma (V_{ij}) de los valores intrínsecos (i) de cada comunidad (j) y el valor de conservación de cada comunidad en su polígono correspondiente

(C_j).

El resultado es un algoritmo $V_k = \sum [P_j \times H_j + \sum V_{ij} + C_j]$ que permite correlacionar espacios biogeográficos afines que presentan series de vegetación comparables en unidades geomorfológicas definidas (BEGUIN y THEURIL-LAT, 1982).

RESULTADOS Y CONCLUSIONES

Se han delimitado 2160 polígonos donde se encuentran representados un conjunto de sintaxones, marcados con el código que corresponde a los indicados en el Plan Nacional de Cartografía de Hábitat. Con un asterisco se han señalados los prioritarios de acuerdo con la Directiva Habitat. Se incluyen también las comunidades que no han sido consideradas como hábitat (n.h.): (522243) *Aristido coerulescentis-Hyparrhenietum sinaicae*, (n.h.) *Artemisia barrelieri-Salsoletum genistoidis*, (n.h.) *Asphodelo fistulosi-Hordeetum leporini*, (143011) *Atriplicetum glauco-halimi*, (143012) *Atriplici glaucae-Suaedetum pruinosa*e, (433522) *Bupleuro gibraltarici-Ononidetum speciosae*, (n.h.) *Carduo bourgeani-Silybum marianii*, (n.h.) *Carthamo arbore-scentis-Ballotetum hirsutae*, *(522212) *Dactylido hispanicae-Lygeetum sparti*, (821011) *Equiseto ramosissimi-Saccharum ravennae*, (n.h.) *Emeci spinosae-Malvetum parviflorae*, (121015) *Erynnis*

gio maritimi-Sporoboletum arenarii, (n.h.) *Gasouletum crystallino-nodiflori*, (143034) *Haloxyllo tamariscifolii-Atriplicetum glaucae*, *(152031/152032) *Helianthemo alypoidis-Gypsophiletum struthii*, (433421) *Helianthemo almeriensis-Sideritidetum pusillae*, (n.h.) *Inulo viscosae-Oryzopsietum miliaceae*, (721135) *Lafuenteo rotundifoliae-Teucrietum intricati*, *(522224) *Lapietro martinezii-Stipetum tenacissimae*, (433525) *Lavandulo dentatae-Genistetum retamoidis*, (82D011) *Lonicerо biflorae-Populetum albae*, (303057) *Lavandulo stoechadis-Genistetum equisetiformis*, (433410) *Limonietum estevei*, *(422011/857012) *Mayteno europaei-Periplocetum angustifoliae*, (n.h.) *Moricandio arvensis-Carrichteretum annuae*, (n.h.) *Nicotiano glaucae-Onopordetum micropteri*, *(522034) *Plantagini ovatae-Chaenorhinetum grandiflori*, (834043) *Rubio longifolie-Quercetum rotundifoliae*, (121014) *Salsolo kali-Cakiletum aegyptiacae*, (433424) *Sideritido osteoxyliae-Teucrietum charidemi*, *(52207B/56297B) *Teucrio pseudochamaeptytis-Brachypodietum ramosi*, (433528) *Thymelaeo tartonraiae-Genistetum ramosissimae*, (621123) *Typho-Schoenoplectetum glauci*, *(422013) *Ziziphetum loti*, (82D030) *Zizipheto loti-Nerietum oleandri*.

El resultado cuantitativo de la evaluación biológica de los polígonos, con los criterios anteriormente expuestos, ha sido posteriormente ordenado en una escala de valores que permiten separar aquellos territorios con valor biológico muy alto (10-17), alto (7-10), medio (5-7), bajo (3-5), sin interés (0-3) y, finalmente, aquellos otros donde no se encuentran comunidades reconocibles como hábitats (Fig. 2). Estas evaluaciones ponen de relieve las zonas que presentan un alto valor biológico como son los cerros volcánicos del Cabo de Gata donde se concentran un buen número de taxones y comunidades endémicas (*Mayteno angustifoliae-Periploco angustifoliae sigmetum*). Presentan también valor muy alto algunas áreas gipsícolas localizadas en las proximidades del Karst de yesos de Sorbas (*Chamaeropo humilis-Rhamno lycoidis sigmetum*, faciación gipsícola con *Santolina viscosa*). Zonas de valor alto y medio se reconocen en algunas áreas occidentales de Sierra Cabrera (*Chamaeropo humilis-Rhamno lycoidis sigmetum*, faciación con *Phlomis almeriensis*) y en la Sierra de Bédar (*Chamaeropo humilis-Rhamno lycoidis sigmetum*, faciación con *Rhamnus angustifolia*).

AGRACEDIMIENTOS

Estudio subvencionado por el proyecto 8.06/03.1850-51 (Junta de Andalucía-Universidad de Málaga. Cofinanciado con fondos de la Unión Europea).

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LA ALIANZA *SEDION PYRENAICI* TÜXEN EX RIVAS-MARTÍNEZ ET AL. 1994 EN EL NORTE DE NAVARRA (ESPAÑA)

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ABSTRACT

Succulent *Crassulaceae* chamaephyte dominated communities living on siliceous lithosols of northern Navarra are studied in this paper. They are included in the *Sedion pyrenaici* alliance and two associations are recognized: one in the Pyrenean area and another one in the Basque-Cantabrian area. For the first one we found *Sileno rupestris-Sedetum pyrenaici*, an association described from the Benasque area, in central Pyrenees, which is represented in Navarra by the new western subassociation *agrostietosum durieui*. In the Basque-Cantabrian territories, the new association *Festuco hirtulae-Sedetum pyrenaici* is described, which is diversified into two subassociations: typicum, and *agrostietosum durieui* for the highest summits of the surveyed area.

KEYWORDS: succulent communities, lithosols, *Sedum anglicum* subsp. *pyrenaicum*, *Agrostis durieui*, northern Iberian Peninsula.

RESUMEN

En el presente estudio se aborda el estudio de las comunidades silicícolas sobre litosuelos dominadas por caméfitos crasicaules de la alianza *Sedion pyrenaici* en la Navarra septentrional. Se constata la existencia de la asociación ya conocida del Pirineo Central (Benaque) *Sileno rupestris-Sedetum pyrenaici*, y de la que se describe la nueva subasociación *agrostietosum durieui* propia del Pirineo occidental. En el ámbito territorial del sector Cántabro-Vascónico, distrito Vascónico oriental, se describe la nueva asociación *Festuco hirtulae-Sedetum pyrenaici*, en la que se diferencian dos subasociaciones, la típica, y *agrostietosum durieui*, de las montañas más elevadas del tramo oriental del territorio.

INTRODUCCIÓN

La clase *Sedo-Sclerantheseta* agru-

pa comunidades primocolonizadoras de baja cobertura, formadas por plantas de pequeño porte, a menudo suculentas de la familia de las *Crassulaceae*, que, junto con algunos terófitos, caméfitos y geófitos, habitan sobre litosuelos y protosuelos de estaciones rupestres, en general poco inclinadas. Esta vegetación, rica en endemismos y con alta capacidad de retención de las partículas de los suelos esqueléticos, se extiende tanto por la Región Eurosiberiana como por la Mediterránea. Las comunidades silicícolas de la Península Ibérica se incluyen en el orden *Sedo-Sclerantheseta*, que en las montañas silíceas del área de estudio está representado por la alianza orófila *Sedion pyrenaici*, de distribución pirenaico-orocantábrica y mediterránea ibérica occidental (RIVAS-MARTÍNEZ *et al.*, 2001, 2002).

MATERIAL Y MÉTODOS

Este estudio abarca las montañas navarras de los sectores Cántabro-Vascónico y Pirenaico occidental (Fig. 1). La sectorización biogeográfica sigue, en lo esencial, los límites y categorías establecidas por BERASTEGI *et al.* (1997).

En el primero de los dos sectores gran parte de las montañas son silíceas, mientras que en el Pirenaico occidental predominan las calizas. El único macizo silíceo del Pirineo navarro donde se alcanza el piso orotemplado es el Monte Lakora, formado por esquistos y cuarcitas paleozoicas.

Para la realización de los inventarios se ha utilizado la metodología fitosociológica (BRAUN-BLANQUET, 1979) y para la identificación y nomenclatura de los taxones se han seguido Flora Iberica (CASTROVIEJO *et al.*, 1986-2010) y las Claves ilustradas de la flora del País Vasco y territorios limítrofes (AIZPURA *et al.*, 1999), excepto en los casos de *Agrostis durieui* y *Sedum anglicum* subsp. *pyrenaicum*, para los que hemos seguido a CASTROVIEJO y CHAPPIN (1999) y LAÍNZ (1963) respectivamente.

RESULTADOS Y DISCUSIÓN

Las comunidades de la alianza *Sedion pyrenaici* encuentran una amplia representación en el ámbito cántabro-vascónico mientras que en el pirenaico se ciñen al macizo de Lakora. Por otro

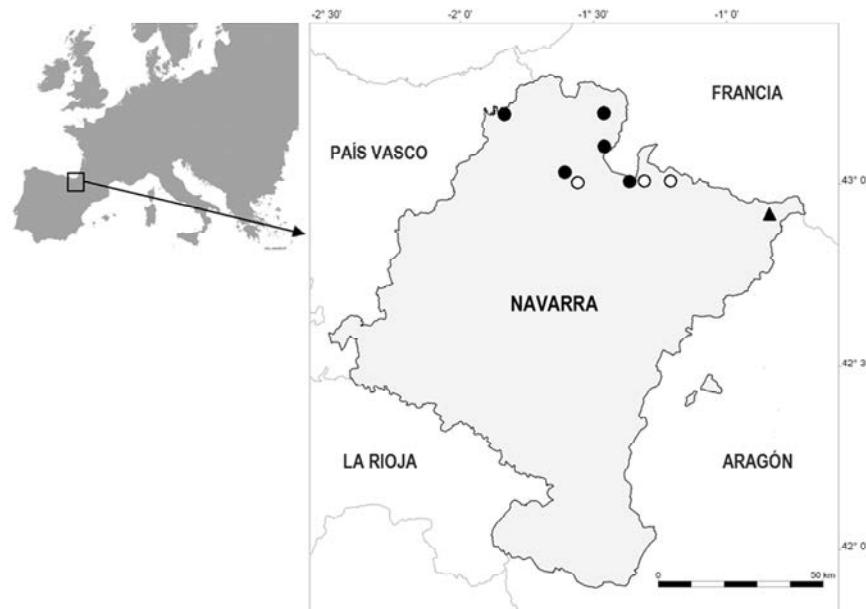


Fig. 1 - Área de estudio. Los puntos indican la localización de los inventarios: ● *Festuco hirtulae-Sedetum pyrenaici typicum*; ○ *Festuco hirtulae-Sedetum pyrenaici agrostietosum durieui*; ▲ *Sileno rupestris-Sedetum pyrenaici agrostietosum durieui*.

Tabla 1 - *Festuco hirtulae-Sedetum pyrenaici ass. nova*; inv. 1-9: *typicum*; inv. 10-17 subass. *agrostietosum durieui subass. nova*.

Altitud (1=10 m)	50	52	101	145	125	85	130	81	80	129	129	120	145	147	151	150	151
Área (m ²)	2	1	4	9	8	3	10	1	1	9	4	10	10	9	9	9	9
N. Especies	5	8	2	12	11	12	6	9	9	9	6	12	14	7	7	7	8
N. Orden	1	2	3	4	5	6	7	8	9*	10	11	12	13*	14	15	16	17

Características de asociación y unidades superiores	2	1	.	1	1	2	1	2	1	1	+	2	1	.	.	2	.
<i>Sedum anglicum</i> ssp. <i>pyrenaicum</i>	2	1	.	1	1	2	1	2	1	1	+	2	1	.	.	2	.
<i>Festuca ovina</i> ssp. <i>hirtula</i>	.	.	.	2	2	+	1	.	1	3	2	.	1	2	2	3	3
<i>Sedum hirsutum</i> ssp. <i>hirsutum</i>	.	.	2	.	.	+	1	.	1	.	2	1	1

Diferenciales de las subasociaciones	3	3	.	.	.	3	.	.	1	.	2	+	1	2	2	2	1	1
<i>Rumex acetosella</i> ssp. <i>angiocarpus</i>	3	3	.	.	.	3	.	.	1	.	2	+	1	2	2	2	1	1
<i>Agrostis durieui</i>

Compañeras	.	1	.	2	.	2	.	1	1	1	.	.	1	1	+	.	2	.
<i>Festuca nigrescens</i> ssp. <i>microphylla</i>	.	1	.	2	.	2	.	1	1	1	.	.	1	1	+	.	2	.
<i>Deschampsia flexuosa</i>	.	.	1	1	+	+	+	.	1	1	2	1
<i>Agrostis curtisii</i>	.	.	.	+	.	+	+	2	1	1	.	.	+	+	.	.	+	.
<i>Galium saxatile</i>	1	.	.	2	+	.	.	+	2	2	1	2	.
<i>Jasione laevis</i>	.	.	.	3	+	+	+	+	2	.	+
<i>Calluna vulgaris</i>	.	.	.	+	.	+	+	+	.	.	1	+	.
<i>Erica cinerea</i>	+	+	.	1	+	.	.	.	+	+
<i>Carex pilulifera</i>	.	.	.	+	+	1	.	.	+	+
<i>Hypochoeris radicata</i>	+	+	.	.	.	+	+
<i>Vaccinium myrtillus</i>	.	.	.	1	+	+	.	.	.
<i>Genista pilosa</i>	.	.	.	+	1	+
<i>Luzula</i> sp.	1	+	.	+	.	.	.
<i>Ornithopus perpusillus</i>	2	1
<i>Danthonia decumbens</i>	.	1	+
<i>Agrostis capillaris</i>	.	2	+
<i>Leontodon pyrenaicus</i>	.	.	.	+	+
<i>Ulex gallii</i>	+
<i>Erica vagans</i>	+	.	.	+
<i>Avenula sulcata</i>	+	.	.	+	.	.	+
<i>Carex caryophyllea</i>	+	.	.	+	.	.	+

lado, las cumbres de las montañas más elevadas del sector Cántabro-Vascónico no alcanzan el piso orotemplado, de modo que esta vegetación se ubica principalmente en el piso supratemplado, mientras que, en el Pirineo Navarro, el monte Lakora alcanza mayor altitud dando lugar a que haya una representación orotemplada silícea, lo que permite la presencia de una asociación propia de este piso. En consecuencia, tenemos dos espacios ecológico-biogeográficos para el desarrollo de las comunidades de esta alianza: el pirenaico orotemplado y el cántabro-vascónico supratemplado. En cada uno de ellos vive una asociación distinta (Fig. 1).

Sileno rupestris-Sedetum pyrenaici agrostietosum durieui subass. nova *hoc loco*

Comunidades comofíticas silíceas orotempladas con *Agrostis durieui* y *Sedum anglicum* ssp. *pyrenaicum*.

En el piso orotemplado, en hábitats rupestres sobre rocas silíceas con escaso desarrollo edáfico, se desarrolla esta comunidad de la que presentamos el siguiente inventario: Monte Lakora (Navarra) a 1750 m de altitud, en 10 m², con *Agrostis durieui* 2, *Silene rupestris* 1, *Sedum anglicum* ssp. *pyrenaicum* 1, *Antennaria dioica*

+, *Calluna vulgaris* 1, *Campanula scheuchzeri* 1, *Festuca eskia* 1, *Festuca nigrescens* subsp. *microphylla* 1, *Genista pilosa* 1, *Lotus corniculatus* +, *Omalotheca supina* +, *Pilosella officinarum* +, *Plantago alpina* +, *Trifolium alpinum* 1, *Vaccinium myrtillus* +, *Veronica fruticans* subsp. *cantabrica* +, *Veronica officinalis* 1, *Carex* sp. 1.

Se caracteriza por la presencia de *Sedum anglicum* subsp. *pyrenaicum*, *Silene rupestris* y *Agrostis durieui*, taxones característicos de la *Sedo-Scleranthetea*. Si bien están ausentes en el inventario, otras especies propias de estas comunidades que viven en el entorno son *Sedum brevifolium*, *Sedum hirsutum* subsp. *hirsutum*, *Sempervivum montanum*, *Sempervivum tectorum* subsp. *tectorum* y *Paronychia polygonifolia* (BERASTEGI, 2010; LORDA, 2001). Como compañeras destacan algunas especies acidófilas características de las comunidades de *Festucion eskiae* Braun-Blanquet 1948, como *Festuca eskia* y *Veronica fruticans* subsp. *cantabrica*, que marcan el contacto de estas comunidades de *Agrostis durieui* con los pastizales de *Festuca eskia*. Por otro lado, y a favor de un gradiente de profundidad y humedad edáfica crecientes, estas comunidades entran en contacto con los pastizales mesófilos y acidófilos de *Nardion strictae* Braun-Blanquet in Braun-Blanquet y Jenny 1926.

En cuanto a la sintaxonomía, esta comunidad se corresponde bien con la asociación descrita por TÜXEN y OBERDORFER (1958) de los alrededores de Panticosa (Pirineo central) y señalada posteriormente del Pirineo occidental (RIVAS-MARTÍNEZ *et al.*, 1991; LODI *et al.*, 1997). El inventario que aportamos procede del Pirineo occidental navarro (Fig. 1), y ello tiene como consecuencia la aparición de *Agrostis durieui*, hecho de importancia biogeográfica porque esta gramínea, de distribución noroccidental ibérica, está ausente de los tramos centrales y orientales de la cordillera pirenaica (ROMERO, 1988, sub. *A. truncatula* subsp. *commista*). Por eso, estimamos oportuno describir la subasociación *agrostietosum durieui* subass. *nova* *hoc loco* designando como holotipo el inventario que se transcribe más arriba. En este contexto, tipificamos también la asociación y la subasociación típica mediante la elección de un inventario en la tabla original. Lectotypus: *Sileno rupestris-Sedetum pyrenaici* Tüxen y Oberdorfer 1958, Veröff. Geobot. Inst. Rübel Zürich 32: 153, Tabla 45, inv. 32 [designado aquí].

Desde el punto de vista dinámico, estas comunidades evolucionan hacia un brezal pobre en especies formado básicamente por *Calluna vulgaris* y *Vaccinium myrtillus*, que en las zonas más altas se enriquece con *Vaccinium uliginosum*.

nosum subsp. *microphyllum* (LORDA y REMÓN, 2003). Es una vegetación que se encuadra en la serie orotemplada pirenaica de los pinares de pino negro (*Pinus uncinata*), en una facies silicícola particular del monte Lakora (LOIDI y BÁSCONES, 2006).

Festuco hirtulae-Sedetum pyrenaici ass. nova hoc loco (Tabla 1)
typicum subass. *nova hoc loco*
agrostietosum durieui subass. *nova hoc loco*

Comunidades comofíticas silicícolas supratempladas con *Festuca ovina* subsp. *hirtula* y *Sedum anglicum* subsp. *pyrenaicum*.

En el piso supratemplado cántabro-vascónico, sobre rocas silíceas, esquistos, granitos, areniscas, etc., en litosuelos, se desarrolla una comunidad caracterizada por la presencia de *Sedum anglicum* subsp. *pyrenaicum*, *Sedum hirsutum* subsp. *hirsutum* y *Rumex acetosella* subsp. *angiocarpus*, además de *Festuca ovina* subsp. *hirtula* y *Genista pilosa*. Se encuentran también algunas especies de los pastizales acidófilos (*Violion caninae* Schwickerath 1944) y brezales (*Daboecion cantabricae* (Dupont ex Rivas-Martínez 1979) Rivas-Martínez, Fernández González y Loidi 1999) circundantes como *Agrostis curtisii*, *Erica cinerea*, *Calluna vulgaris*, *Gaulium saxatile*, etc., así como algunas especies de las comunidades de *Thero-Airion* Tüxen y Oberdorfer 1958 em. Rivas-Martínez 1978 como *Aira prae-cox*, *Vulpia bromoides*, *Ornithopus perpusillus*, etc.

Los primeros antecedentes de esta comunidad se remontan a ALLORGE (1941), que menciona la combinación de *Sedum hirsutum* con *S. anglicum* en los roquedos silíceos vascos. CATALÁN (1987) aporta, en su monografía sobre la cuenca del río Bidasoa, una tabla sobre la “comunidad con *Sedum anglicum* y *S. hirsutum*”, que se desarrolla en las repisas someras de los roquedos silíceos. Estos inventarios corresponden a un aspecto local de estas comunidades y su propuesta, sin designación de tipo ni publicación efectiva, resulta inválida (arts. 1, 3c, y 5 CPN, WEBER, MORAVEC y THEURILLAT, 2000). El muestreo realizado en este trabajo comprende un ámbito geográfico mayor (Fig. 1, Tabla 1). De esta manera, según se extrae del conjunto de los inventarios aportados, y tras haberse avanzado sustancialmente en el conocimiento del género *Festuca* en la Península Ibérica (FUENTE y ORTÚNEZ, 1998), el taxón

característico de este tipo de comunidades es *Festuca ovina* subsp. *hirtula*, que es una gramínea de fuerte carácter atlántico (Fig. 2), frecuente también en brezales de *Daboecion cantabricae* y en los pastizales del *Carici piluliferae-Agrostietum curtisii* Darquistade, Berastegi, Campos y Loidi 2004 (*Violion caninae*) (DARQUISTADE et al., 2004). Su distribución conocida en la Península Ibérica se restringe al ámbito cántabro-vascónico, principalmente al distrito Vascónico oriental (ORTÚNEZ y FUENTE, 1994; FUENTE et al., 1997).

El área total de distribución de esta subespecie abarca un amplio espacio en la provincia Atlántica europea, desde las Islas Británicas y el oeste de Francia hasta alcanzar el territorio peninsular en los distritos mencionados.

En consecuencia, estimamos que esta combinación de especies, circunscrita a un territorio definido y repetida bajo unas condiciones mesológicas similares, merece la descripción de una asociación nueva, *Festuco hirtulae-Sedetum pyrenaici ass. nova hoc loco* (holotipus inv. 9, Tabla 1), posiblemente de amplia jurisdicción atlántica. Representa una asociación geovicaria del *Sedetum micranthro-pyrenaici* Rivas-Martínez, Díaz, Prieto, Loidi y Peñas 1984, carente de *Festuca ovina* subsp. *hirtula* y que, desde los territorios orocantábricos, se extiende hasta el distrito Santanderino-Vizcaíno (LOIDI et al., 1997).

El área principal de distribución de la nueva asociación se concentra en el sector Cántabro-Vascónico, distrito Vascónico oriental. Está presente en las montañas del tercio septentrional del territorio navarro: montes de Auza, Bianditz, Saioa, Gartzaga, Alkurruntz,

Aiako harria, Ortzanzurieta, Lauñamendi, etc. (Fig. 1). Se desarrolla principalmente en el ambiente de la serie acidófila del haya *Saxifrago hirsutae-Fago sylvaticae* sigmentum, aunque también puede aparecer en los tramos más elevados de la serie acidófila del roble pedunculado *Hyperico pulchri-Querco roboris* sigmetum.

En lo relativo a su variabilidad, destaca la presencia de *Agrostis durieui* en aquellas estaciones con elevaciones superiores a los 1200 m de altitud, lo cual sucede en algunas de las montañas de mayor altitud en la mitad oriental del distrito Vascónico oriental, como son Gartzaga (Baztan), Astobizkar y Lauñamendi (Luzaide) y Mendimotz y Ortzanurieta (Orreaga). La presencia de esta gramínea y su significación biogeográfica han sido ya comentadas más arriba, y parece estar ligada principalmente a la elevada altitud de estas montañas vascónicas orientales, las cuales están agrupadas en los tramos más cercanos al Pirineo. Todo ello confluye en una combinación característica y repetida de taxones con una biogeografía y unas condiciones ecológicas definidas, lo que permite agrupar estas comunidades con *Agrostis durieui* en la subasociación *agrostietosum durieui* subass. *nova hoc loco* (holotipus inv. 13, Tabla 1).

También cabe mencionar que hay una facies de esta comunidad, que conocemos por ahora sólo en el seno de su subasociación típica, en la que es predominante *Rumex acetosella* subsp. *angiocarpus* y que aparece muy frecuentemente asociada a suelos removidos, más o menos alterados, en zonas de secano del ganado, bordes de camino, etc.



● Material estudiado

■ Área de distribución

Fig. 2 - Distribución de *Festuca ovina* subsp. *hirtula* en la Península Ibérica (FUENTE et al., 1997).

ENCUADRE SINTAXONÓMICO

SEDO-SCLERANTHETEA Tüxen 1937
 Sedo-Scleranthetalia Braun-Blanquet
 1955
Sedion pyrenaici Tüxen ex Rivas-Martínez, Díaz, Prieto, Loidi y Penas 1984
 in Díaz y Prieto 1994
Sileno rupestris-*Sedetum pyrenaici*
 Tüxen in Tüxen y Oberdorfer 1958
agrostietosum durieui subass. nova
Festuco hirtulae-*Sedetum pyrenaici*
 ass. nova
typicum
agrostietosum durieui subass. nova

Tabla 1

Además: **Inv. 2:** *Scleranthus polycarpus* 2, *Veronica officinalis* 2; **Inv. 3:** *Sagina procumbens* +; **Inv. 5:** *Allium ericetorum* +, *Daboezia cantabrica* +, *Festuca gr. ovina* +; **Inv. 6:** *Aira praecox* 1, *Vulpia bromoides* +; **Inv. 8:** *Festuca gr. ovina* 1; **Inv. 10:** *Thymus praecox* ssp. *polytrichus* 1; **Inv. 12:** *Festuca* sp. 2; **Inv. 13:** *Nardus stricta* +, *Thymus pulegioides* +.

Localidades: **1)** Baztan. Pto. Otsondo, 30TXN2187 (NA); **2)** Lesaka. Citó. Ari-txulegi, 30TWN9891 (NA); **3)** Baztan. Pto. Belate a Saioa, 30TXN1366 (NA); **4)** Orreaga. Mte. Mendimotz, 30TXN3965 (NA); **5)** Luzaide. Mte. Lauñamendi, 30TXN3568 (NA); **6)** Baztan. Pto. Izpegi, 30TXN2981 (NA); **7)** Baztan. Mte. Autza, 30TXN2878 (NA); **8)** Bera. Mte. Bianditz, 30TWN9888 (NA); **9)** (*hohsyntypus*) Bera. Mte. Bianditz, 30TWN9889 (NA); **10)** Baztan. Mte. Gartzaga, 30TXN1566 (NA); **11)** Anue. Hirumugeta, 30TXN1566 (NA); **12)** Orreaga. Pto. Ibañeta, 30TXN3765 (NA); **13)** (*hohsyntypus*) Luzaide. Mte. Astobizkar, 30TXN3865 (NA); **14)** Luzaide. Mte. Astobizkar, 30TXN3866 (NA); **15)** Orreaga. Mte. Ortzanzurieta, 30TXN4064 (NA); **16)** Orreaga. Mte. Ortzanzurieta, 30TXN4164 (NA); **17)** Orreaga. Mte. Ortzanzurieta, 30TXN4064 (NA).

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THE HALOPHILOUS RETRO-DUNE GRASSLANDS OF THE ITALIAN ADRIATIC COASTLINE

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For Jean-Marie Géhu, our “maestro”, who made exceptional contributions to the development of syndynamic phytosociology that is particularly relevant to the study of the coastal vegetation

ABSTRACT

This paper shows a concise overview of the phytosociological analysis conducted on the coastal hyperhalophilous brackish vegetation in the Italian Adriatic coast. Despite the enormous changes that this stretch of coast has endured over the years there are still a significant presence in terms of biogeographic and phytocoenosis relevance, nevertheless these habitats are highly fragmented. A framework about these vegetation types is provided for the most important vegetation classes: *Thero-Suaedetea*, *Salicornietea fruticosae* and *Spartinetea maritimae*. The presentation ends with the overall syntaxonomical scheme and it also shows published and unedited data.

These are derived from analyses that the authors have carried out in the southern Italian Adriatic coast, which have particularly investigated the mouths of Ofanto and Candelaro rivers in the area immediately south of the Gargano promontory, a stretch of the coast of Brindisi and some resorts of Salento, in the southernmost part of Puglia.

For these areas association already described for other localities and some new ones have been found: *Bassio hirsutae-Suaedetum splendentis*; *Suaedo splendentis-Salicornietum venetae*; *Suaedo splendentis-Salicornietum dolichostachyae*.

In the conclusions the importance of hyperhalophilous vegetation of the Italian Adriatic coast is underlined, highlighting the need for an accurate census of the habitats (in the sense of Directive 92/43/EEC) and the definition of the management plans of Natura 2000 sites in which these fall.

The article is dedicated by the authors to Jean-Marie Géhu, in the year of his eightieth birthday, as we recognize him the merit of having contributed more than any other to the analysis of coastal European and North African vegetation.

KEYWORDS: Italian Adriatic Sea, phytosociology, coastal habitat, hyperhalophilous vegetation.

INTRODUCTION

The aim of this article is to present the diversity of the retro-dunal halophilous grasslands of the Italian Adriatic coastline, even though in a synthetic form. There remain a significant amount of these grasslands, and even although they are greatly fragmented, they represent an important aspect of this type of biodiversity. These grasslands cannot be said to be fully known even today, despite having been the focus of many studies. The most important of these studies come from the 1930's, with the excellent work of Sandro Pignatti (1952; 1966) on the north Adriatic, and later with numerous contributions from the research group of Giovanni Giorgio Lorenzoni, who concentrated particularly on the southern section of the basin (CHIESURA LORENZONI & LORENZONI, 1977; CANIGLIA *et al.*, 1978, 1984; LORENZONI, 1967, 1978; LORENZONI & GHIRELLI, 1988; LORENZONI *et al.*, 1984). Particular developments were then made in the phytosociological research of this Italian coastal vegetation, and in particular of that of the Adriatic coastline, with the analyses carried out following an investigation organised by Jean-Marie Géhu in 1982, for the whole of the Italian coastline (GÉHU *et al.*, 1984). This expedition was particularly significant because many young Italian researchers also participated, some of whom have continued the studies of the Mediterranean coasts and described with Géhu the various typologies of the coastal vegetation, establishing synviciants and geosynviciants of great biogeographical relevance. Further studies were then carried out by Géhu again, and by other Italian experts (GÉHU, SCOPOLA *et al.*, 1984; GÉHU, COSTA *et al.*, 1984; GÉHU & BONDI, 1996; ANDREUCCI *et al.*, 1999; BRULLO *et al.*, 2001; BONDI, 1986; BONDI *et al.*, 2006; BONDI, 2007; SBURLINO *et al.*, 2008).

The halophilous grasslands of the western Adriatic have survived more or less intact only in small sections that are mainly confined to the high Adriatic of the Venezia Lagoon, and to the mouth of the River Po. These then disappear

altogether and then reappear further south, down to Gargano, near the Lesina and Varano Lakes, at the mouth of the Ofanto and Candelaro Rivers in Puglia, and along other parts of the Puglia coast. These ecosystems have been well studied in parts, and mainly in the northern Adriatic (ANDREUCCI *et al.*, 1999; BONDI, 1999; CORBETTA, 1968, 1976; CANIGLIA *et al.*, 1997; FERRARI *et al.*, 1985; FORNACIARI, 1968; GÉHU & BONDI, 1996; GÉHU *et al.*, 1984a and b; GERDOL & PICCOLI, 1984; LORENZONI, 1983; PICCOLI, 1995; PICCOLI *et al.*, 1991; PICCOLI *et al.*, 1994; PIGNATTI, 1952, 1953, 1966; POLDINI *et al.*, 1999), while the southern sections have been investigated mainly along the Salento coast (CANIGLIA *et al.*, 1984; CURTI & LORENZONI, 1968; GÉHU *et al.*, 1984; LORENZONI, 1967; LORENZONI, 1983; LORENZONI & GHIRELLI, 1988; LORENZONI *et al.*, 1980). In contrast, the haophilous grasslands of Gargano and around Brindisi have been little studied, which are those for which on this occasion we wish to present some aspects using unpublished data. These data refer to some ecosystems with salty vegetation for which, as well as the associations already reported, we have identified new plant communities of great phytogeographical and phytosociological interest.

MATERIALS AND METHODS

This study focussed in particular on some biotypes of the northern sections of the Puglia coast, with reference to the mouth of the Ofanto River and the mouth of the Candelaro River in the Province of Foggia, to the south of the Gargano promontory. The study area more to the south was instead a section of the Brindisi coastline, which is characterised by low sandy coasts, and some Salento resorts.

The Ofanto River is the main water course in Puglia, both for its length and its water flow. Its mouth forms a sort of delta, with its inner sections comprising the very interesting wet zones that are used in part for salt extraction (the stretch between Margherita di Savoia and Tri-

nitapoli). Within this area, the Natural Reserve for Animal Repopulation (*Riserva naturale di ripopolamento animale*) of the salt lakes (covering 4,000 hectares) has been established, which is managed by the Ramsar Convention relative to the Wet Areas of International Importance (*Zone umide d'importanza internazionale*).

The Candelaro River, which is situated a few kilometres to the north, empties out at Manfredonia, and in the area of its mouth there are even today wet zones of great conservational interest due to the rare plant species and communities found there. More to the south, in the Province of Brindisi, there are large alternating sections of rocky coasts and beaches of various lengths, within which there are still the dunal and retro-dunal ecosystems. In particular, in Torre Canne Sud and in Lido Morelli, there are well conserved retro-dunal halophilous grasslands. Finally, some of the communities described have been found in some resorts in Salento, and more precisely near '*le Cesine*'.

This study was conducted according to the classical phytosociological method (BRAUN-BLANQUET, 1964; TÜXEN, 1956, 1977, 1979; GÉHU & RIVAS-MARTÍNEZ, 1981; THEURILLAT, 1992; BIONDI, 1994; RIVAS-MARTÍNEZ, 2005),

concentrating in particular on the choice of the homogeneous area for the sampling through careful observation of the structure of the vegetation and the geomorphology of the area covered by the various vegetation typologies (BIONDI *et al.*, 2004).

The bioclimate classification of the main Adriatic coastal stations was conducted according to the method proposed by RIVAS-MARTÍNEZ *et al.* (2005), and elaborated through the classification system available on-line at www.globalbioclimatics.org. Through the input of analytical climate data (average, maximum and minimum monthly temperatures and monthly precipitation with reference to the whole of the historic series of each station), this has allowed a 'bioclimate diagnoses' to be obtained (macrobioclimate, bioclimate, possible bioclimate variants, thermotype and ombrotype), simultaneously with the thermo-pluviometric diagram.

BIOGEOGRAPHICAL AND GEOGRAPHICAL CLASSIFICATION

The Adriatic Sea basin has a length of approximately 800 km and an average width of 150 km, giving an area of about 132,000 km², with a maximum

depth of 1,230 m. The Italian Adriatic coastline stretches for about 1,436 km, and represents about 20% of the total length of the Italian coastline, which is estimated as 7,458 km. The average salinity is 3.8%, with strong differences between the northern (less salty) and the southern sections.

From a morphological point of view, the Adriatic coastline can be divided into three areas (BIONDI, 1986):

- 1) The northern section, where there are the mouths of the River Po and other alpine rivers, which do not exceed a depth of about 75 m;
- 2) The central section between the town of Ancona and the Gargano peninsula, which is characterised by the presence of the 'meso-Adriatic deep-sea trench' (about 266 m deep);
- 3) The southern section, with an average depth of 1,000 m and a maximum depth of about 1,200 m.

In the Otranto Channel, which separates the Adriatic Sea from the Ionian Sea, the depth is reduced to about 800 m.

The Adriatic has the largest area of continental platform of the Mediterranean, providing a sort of 'marigraph' that has recorded the phases of the raised global sea levels. Due to the low depth, most of this area emerged during the last glacial maximum (LGM) and then was progressively submerged over the last 17,000 years. When the ice of the LGM began to melt, the low slope of the platform helped the horizontal transfer of the coastal deposits and their progressive submersion during the various stages of the postglacial transgression.

Recent studies on the Italian peninsula have taken into account some important additions to the field of phytosociology. Therefore, for the recognition of the phytogeographical territories, additions have been made to the traditional chorological considerations, including synchorological considerations concerning the *syntaxa* distributions, and in particular the vegetation series (*sigmeta*) and geoseries (*geosigmeta*). According to these concepts, Rivas-Martínez created the Biogeographical Map of Europe (RIVAS-MARTÍNEZ *et al.*, 2004). Within this, the Italian territory is included within the Eurosiberian and the Mediterranean regions (Fig. 1).

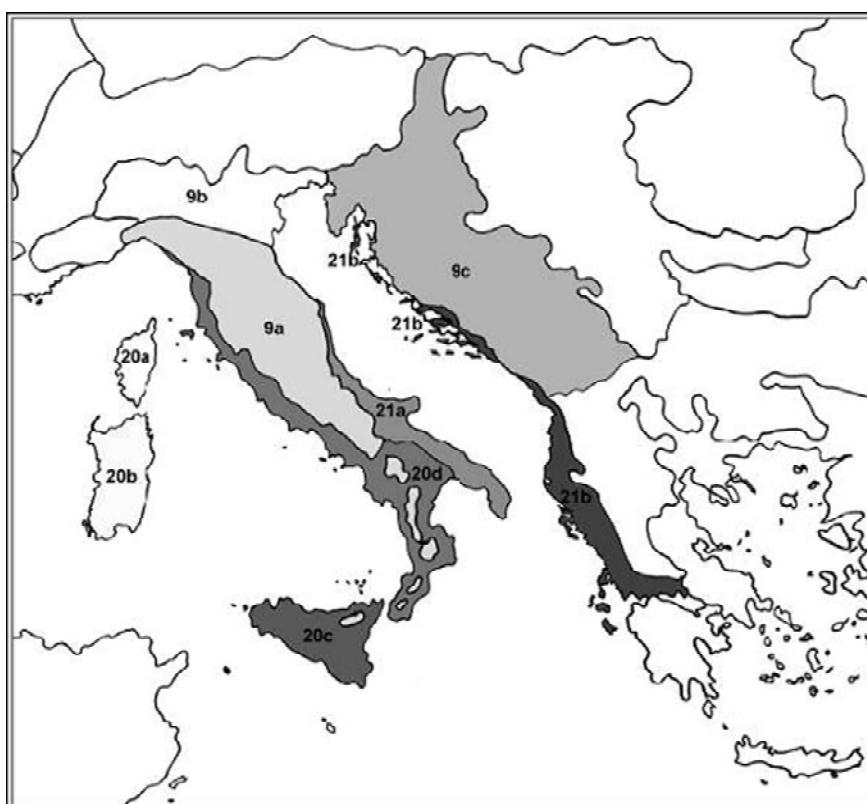


Fig. 1 - The Eurosiberian region, which includes the northern Adriatic basin with the Apennino-Balkan province in which the following sub-provinces can be recognized: 9a, Apennine subprovince; 9b, Padanian subprovince; 9c, Illyrian sub-province. The Mediterranean region includes the Adriatic province (21) with the following sub-provinces: 21a, Apulia sub-province; 21b, Epiro-Dalmatian sub-province; 21c, Peloponnesian sub-province.

BIOCLIMATE CLASSIFICATION

The results of the classification shown in Tab. 1 highlight a north-south gradient that starts from the oceanic temperate bioclimate of the northern-

most stations (e.g. Trieste, Venice) and moves through its Mediterranean subvariant, to end up in the south with the Mediterranean pluviseasonal bioclimate (Fig. 2).

THE ADRIATIC HALOPHILOUS PLANT COMMUNITIES

The retro-dunal coastal vegetation is affected by the amount of salt that remains on the surface of the soil. The vegetal communities are distributed such that each one follows its own ecological needs in terms of moisture and, above all, salinity, always making up a mosaic of phytocoenoses. Although they are almost always in very close contact with each other, these phytocoenoses come from different vegetation classes, among which the most significant are: *Spartinetea maritimae*, *Thero-Suaedetea* and *Salicornietea fruticosae*.

THE GRASSLANDS OF THE CLASS *SPARTINETEA MARITIMAE*

Due to tides of some importance in

Tab. 1 - Bioclimate classification of the main Italian Adriatic thermopluvio-metric stations.

Station	Macrobioclimate	Bioclimate	Bioclimatic belt	thermotype horizons	ombrotype horizons
Trieste	Temperate	Oceanic	low mesotemperate	upper subhumid	
Venezia	Temperate	Oceanic	upper mesotemperate	low subhumid	
Ravenna	Temperate	Oceanic	upper mesotemperate	low subhumid	
Rimini	Temperate	Oceanic (submediterranean)	upper mesotemperate	low subhumid	
Ancona	Mediterranean	Pluviseasonal-oceanic	upper meso-mediterranean	low subhumid	
Pescara	Mediterranean	Pluviseasonal-oceanic	upper meso-mediterranean	low subhumid	
Lesina	Mediterranean	Pluviseasonal-oceanic	low meso-mediterranean	upper dry	
Vieste	Mediterranean	Pluviseasonal-oceanic	low meso-mediterranean	upper dry	
Bari Palese	Mediterranean	Pluviseasonal-oceanic	low meso-mediterranean	low subhumid	
Brindisi	Mediterranean	Pluviseasonal-oceanic	upper thermomediterranean	upper dry	
Lecce	Mediterranean	Pluviseasonal-oceanic	upper thermomediterranean	upper dry	
Otranto	Mediterranean	Pluviseasonal-oceanic	upper thermomediterranean	low subhumid	

the northern Adriatic, there is a particular phytocoenosis that is dominated by *Spartina maritima*. This is an Atlantic species that penetrates into the Mediterranean only along the northern Adriatic coast. The substrates on which this phytocoenosis develops are muddy-sandy and subjected to the alternating tidal fluctuations that are much more pronounced in the northern Adriatic (90-100 cm) than in the rest of the Adriatic basin (30 cm in the south) and the Mediterranean. The floristic composition of the vegetation of *Spartina maritima* includes *Limonium narbonense* and *Puccinellia festuciformis* ssp. *festuciformis*, the differential species of the

Adriatic coenosis, called *Limonio narbonense-Spartinetum maritimae*, with respect to that Atlantic. This association is found in Italy only in the Veneta Lagoon.

THE HALOPHILOUS ANNUAL GRASSLANDS OF THE CLASS *THERO-SUAEDETEA*

In the composition of the salty grassland vegetation, great importance is seen for the species of the genus *Salicornia*, which exclusively include annuals, and of the genera *Sarcocornia*, *Arthocnemum* and *Halocnemum*, to which the perennial species belong.



Fig. 2 - Ombothermic diagrams of the main Adriatic coastal locations. There is a particularly evident north-south bioclimate gradient that indicates the change from the temperate macrobioclimate of the northern Adriatic, through the Submediterranean conditions in the middle section, to the Mediterranean macrobioclimate in the south.

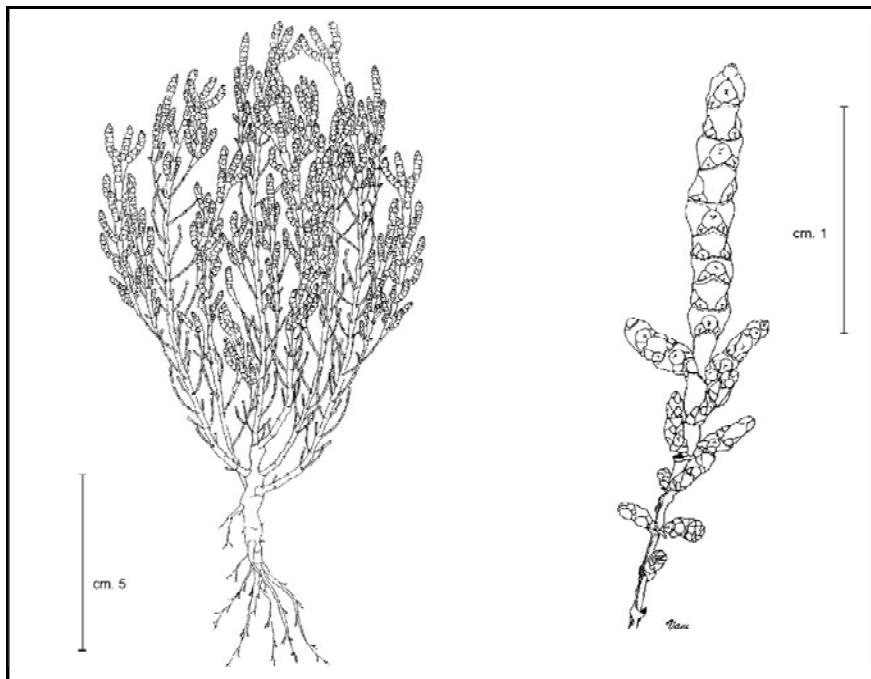


Fig. 3 - *Salicornia patula* Duval-Jouve. The drawing shows the plant as a whole, for its overall structure, and a detail of a branch and the inflorescence (original drawing).

Tab. 2 - *Suaedo maritimae-Salicornietum patulae* (Brullo & Furnari 1976) Géhu & Géhu-Franck 1984.

	Rel. n.	1	2	3	4	5	6	Pres.
	Area (m ²)	10	8	5	2	2	2	
	Coverage (%)	80	50	80	100	80	80	
Charact. species of the association								
T scap	Salicornia patula Duval-Jouve	4,4	3,3	3,4	5,5	4,4	4,4	6
T scap	COSMOP.	1,2	+2	2,3	.	.	.	3
Other species								
H caesp	Puccinellia borri (Bab.) Hayek	1,2	1,2	2
G rhiz	Aelropus littoralis (Gouan) Parl.	.	.	1,3	.	.	1,2	2
T scap	Atriplex hastata Auct. non L.	.	.	.	1,2	.	.	1
H caesp	Puccinellia festuciformis (Host) Parl.	+2	.	1
H bienn	Aster tripolium L.	+	1

Tab. 3 - *Suaedo splendens-Salicornietum patulae* Rivas-Martínez, Costa, Castroviejo & Valdeés-Bermejo 1980 corr. Rivas-Martínez 1990.

	Rel. n.	1	2	3	Pres.
	Area (m ²)	5	15	20	
	Coverage (%)	80	95	90	
Charact. species of the association					
T scap	Salicornia patula Duval-Jouve	4,4	5,5	5,5	3
T scap	C-ASIAT.-N-MEDIT.	2,2	2,2	2,3	3
Other species					
He	Phragmites australis (Cav.) Trin.	.	1,1.0	+0	2
G rhiz	Juncus subulatus Forsskal	.	+0	.	1

In Italy, the *Salicornia* genus includes diploid and tetraploid species. Among the diploids, only *Salicornia patula* (Fig. 3) is known for the Adriatic. It forms a plant community that develops in positions that are higher than the vegetation of *Salicornia* tetraploids, and so on substrates that dry more quickly in the summer, and are therefore more salty. In all of Italy, the vegetation of *Salicornia patula* is in the *Suaedo-Salicornietum patulae* association (BRULLO & FURNARI, 1976) GÉHU & GÉHU-FRANCK, 1984. Tab. 2 gives some of the unpub-

blished relevés attributed to this association from various resorts in Puglia.

The association *Suaedo-Salicornietum patulae* is widely distributed in Italy, and in terms of the Italian Adriatic coast, it is found from the north of the basin down to the more southern sections of Salento. Moreover, in Puglia, *Salicornia patula* is part of the association *Suaedo splendens-Salicornietum patulae* described for the Iberian peninsula which is characterised by *Suaeda splendens*. At present, for the Italian Adriatic coastline, this association is

only reported for the mouth of the Candelaro River, although this does not exclude the possibility of it being found in other sites. This association develops in the presence of wet and salty clay, in the areas that are a little raised. Tab. 3 gives some of the unpublished relevés attributed to this association, carried out at the mouth of the Candelaro River.

Among the tetraploid *Salicornia*, in the northern Adriatic, Pignatti & Lausi described *Salicornia veneta* (Fig. 4), which was considered endemic to the northern Adriatic. In recent decades the species was found in the ponds of Cagliari (BIONDI *et al.*, 1997) and at the pond of S'Ena Arrubia (BIONDI *et al.*, 2000, 2001) in the Gulf of Oristano. In the present work is presented a new resort where the species has been found, at the mouth of the Candelaro River, to the south of the Gargano promontory, therefore, *Salicornia veneta* can be considered endemic having an Italian Adriatic-Tyrrhenian distribution.

Salicornia veneta is part of a community of few species, *Salicornietum venetae* Pignatti 1966, that develops in the depressions that are water-covered for most of the summer season. The association has been widely found in the Adriatic: in Friuli-Venezia Giulia, in some locations in Veneto, in many places in Emilia Romagna (BIONDI, 1999), and recently in some locations in Puglia, both for the Ionian coast of Salento near to the Capitano marshes, and for the Adriatic at the mouth of the Candelaro River (Tab. 4, unpublished relevés). In this last, moreover, *Salicornia veneta* is part of another, newly described association, named *Suaedo splendens-Salicornietum venetae* (Tab. 5, relevé type n. 3), which is characterised by *Suaeda splendens* and *Salicornia veneta*. This association has also been found in many nuclei within the perennial vegetation of *Arthrocnemum macrostachyum* in lower areas with respect to those occupied by these last species.

Salicornia dolichostachya is another tetraploid species of great size, like *S. veneta*, although in comparison it has some differential characteristics, such as the ends of the branches with pointed parts at the distal extremes, while the branching along the stem is always higher than that of *S. veneta*, which occurs nearer the collar. Another discriminatory character that is not seen in the most important descriptions of the flora, is the presence of groups of branches on the same point of the stem, as shown in Fig. 5.

Along with *S. veneta*, *S. dolicho-*

stachya belongs to the group of *Salicornia procumbens*, which includes a total of four species in Europe (*S. fragilis*, *S. nitens* as well as *S. dolichostachya* and *S. veneta*) and it has a mainly Atlantic distribution, and less so in the Mediterranean (DAVY *et al.*, 2001). In Italy, this species has only been reported for two Tyrrhenian stations: in the National Park of Circeo (IBERITE & MACARIO, 1992) and near Cagliari (BIONDI *et al.*, 1997). A population in a good state of conservation was also found recently at the mouth of the Candelaro River, to the south of the Gargano promontory, in the Province of Foggia.

From the phytosociology point of view, for the French Atlantic coast, the association *Salicornietum dolichostachyae* Géhu & Géhu-Franck 1984 has been described, while for Sardinia, the association *Salicornietum emerici-dolichostachyae* Biondi 1997 has been identified, which is the vicariant of the former association in the Mediterranean. The surveys carried out in the only Adriatic station known for this species, the mouth of the Candelaro River, has allowed us to recognize a new association, called *Suaeda splendens-Salicornietum dolichostachyae* (Tab. 6, relevé type n. 3), which is characterised by *Suaeda splendens*, a species with a central Asian and northern Mediterranean distribution (Mediterranean coast of Spain, the Balearic Islands, the Portuguese Atlantic coast, Sardinia, southern Italy, Albania and Greece; Fig. 6), which has been reported for the Italian peninsula only for Bagnoli, near Naples, and for Salpi Lake, near Margherita di Savoia (PIGNATTI, 1982).

Moreover, we have recently found this species in the new station of Lido Morelli, near Torre Canne (Brindisi). This new association therefore represents the Adriatic vicariant of the Tyrrhenian community *Salicornietum emerici-dolichostachyae*. This community develops in areas characterised by a depressed micromorphology where the salty water remains stagnant for long periods after the tides, and it therefore represents the phytocoenosis that is most resistant to being water-covered. This is a community of few species in which, as well as *Salicornia dolichostachya* and *Suaeda splendens*, there is also often *Atriplex hastata*, and as the contact species, *Puccinellia festuciformis* and *Alimione portulacoides*.

In the Adriatic, there is also another species of significant biogeographical interest, *Bassia hirsuta*, which forms coenoses of limited areas. This species

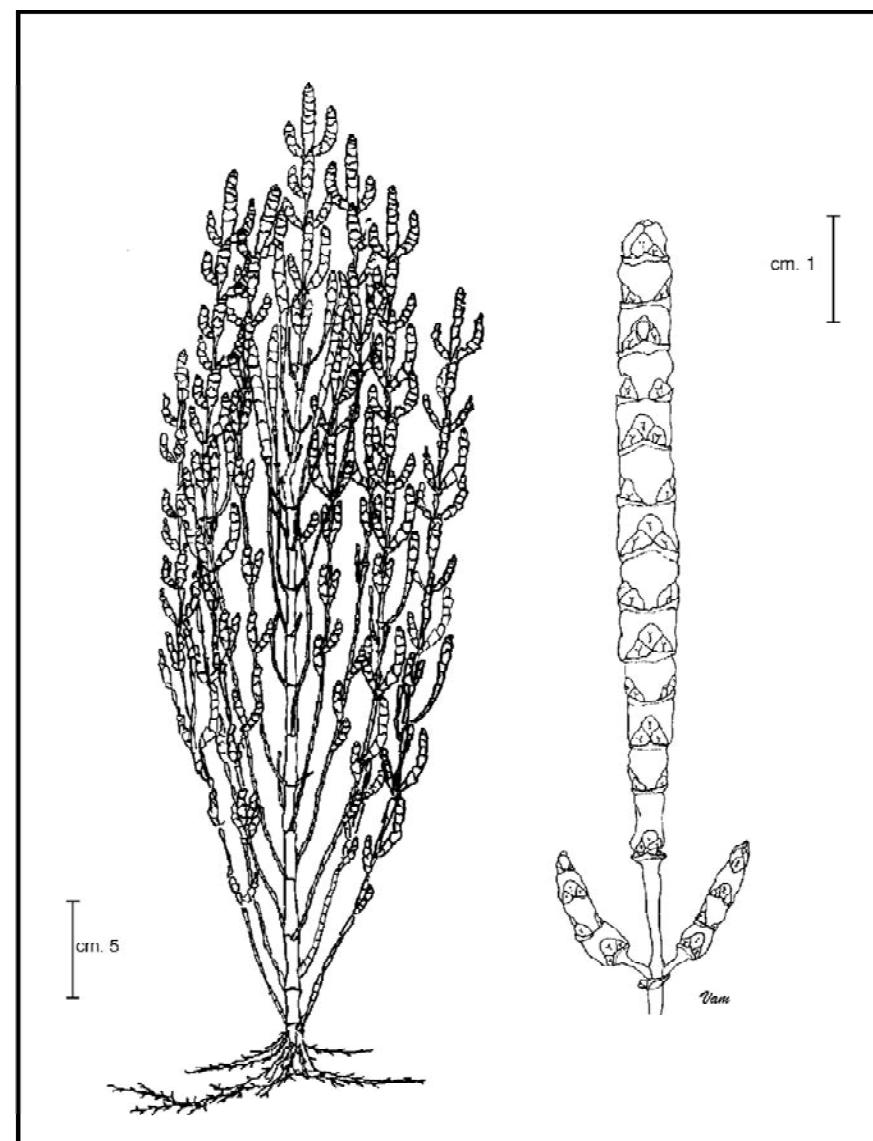


Fig. 4 - *Salicornia veneta* Pign. et Lausi. The drawing shows the plant as a whole, for its overall structure, and a detail of a branch and the inflorescence (original drawing).

Tab. 4 - *Salicornietum venetae* Pignatti 1966.

		Rel. n.	1	2	3	4	5	6	7	Pres.
		Area (m ²)	3	3	10	25	15	30	10	
		Coverage (%)	95	90	80	95	95	85	85	
T scap	ENDEM.	Charact. species of the association								
		<i>Salicornia veneta</i> Pign. et Lausi	5,5	4,5	5,5	5,5	5,5	5,5	5,5	7
H caesp.		Other species								
		<i>Puccinellia festuciformis</i> (Host) Parl.	+2	.	.	.	2,2	2,3	.	3

Tab. 5 - *Suaedo splendens-Salicornietum venetae ass. nova.*

		Rel. n.	1	2	3*	4	5	Pres.
		Area (m ²)	2	5	10	8	8	
		Coverage (%)	80	80	90	80	85	
T scap	ENDEM.	Charact. species of the association						
T scap	C-ASIAT.-N-MEDIT.	<i>Salicornia veneta</i> Pign. et Lausi	4,4	4,4	4,5	4,5	4,5	5
H caesp		<i>Suaeda splendens</i> (Pourret) G. et G.	1,2	1,2	2,2	2,2	1,2	5
Ch frut	CIRCUMBOR.	Other species						
H caesp	MEDIT. ATL.	<i>Puccinellia festuciformis</i> (Host) Parl.	.	.	+2	+2	1,2	3
T scap		<i>Halimione portulacoides</i> (L.) Aellen	.	.	+2	.	+	2
H bienn	EURASIASIT.	<i>Puccinellia borrii</i> (Bab.) Hayek	.	+2	.	.	.	1
		<i>Atriplex hastata</i> Auct. non L.	.	.	.	1,2	.	1
		<i>Aster tripolium</i> L.	.	.	.	+	.	1

has a fragmented distribution along the Italian Adriatic coast, as it is found in the north in Friuli-Venezia Giulia and Veneto and in Emilia Romagna, and in

Puglia near the Lesina and Varano Lakes (PIGNATTI, 1982; Fig. 7). Recently, we have found this species also to the south of Gargano, near the mouth of the Can-

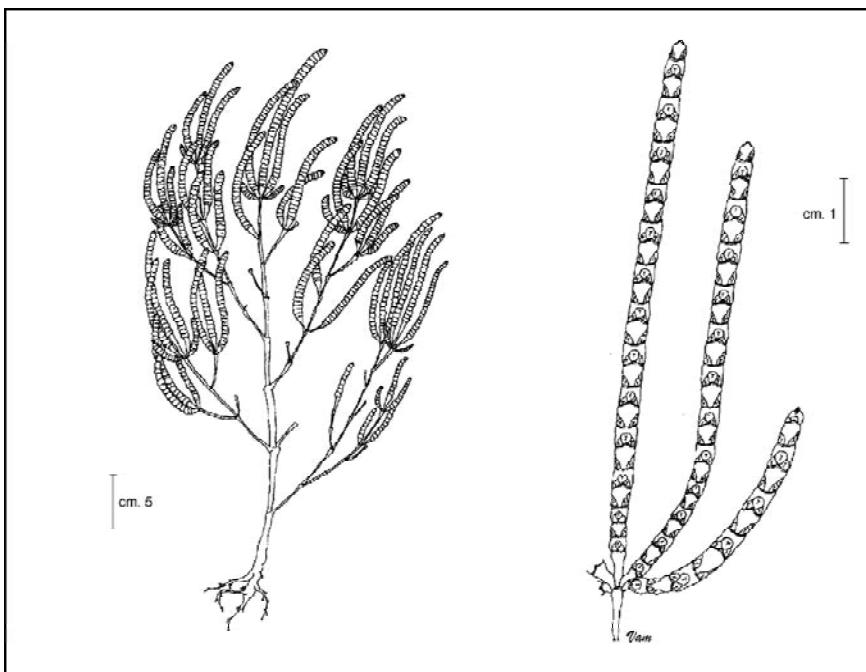


Fig. 5 - *Salicornia dolichostachya* Moss. The drawing shows the plant as a whole, for its overall structure, and a detail of a branch and the inflorescence (from BIONDI, 1999).

Tab. 6 - *Suaedo splendensis-Salicornietum dolichostachyae ass. nova.*

		Rel. n.	1	2	3*	4	5	6	7	Pres.
		Area (m ²)	5	10	10	9	8	8	7	
		Coverage (%)	85	90	90	90	80	80	90	
Charact. species of the association										
T scap		<i>Salicornia dolichostachya</i> Moss	4,4	4,5	4,5	5,5	4,4	5,5	5,5	7
T scap	C-ASIAT.-N-MEDIT.	<i>Suaeda splendens</i> (Pourret) G. et G. cfr.	3,3	2,3	2,2	1,2	2,3	.	.	5
T scap		Charact. species of the upper units								
		<i>Atriplex hastata</i> Auct. non L.	.	1,2	1,2	.	2,3	.	.	3
		Other species								
H caesp		<i>Puccinellia festuciformis</i> (Host) Parl.	1,2	1,2	+	2,2	+2,2	2,3	.	6
Ch frut	CIRCUMBOR.	<i>Halimione portulacoides</i> (L.) Aellen	+	(+)	.	.	+2	.	.	3
Ch suffr	MEDIT. ATL.(STENO)	<i>Inula crithmoides</i> L.	.	.	+2	1
He	SUBCOSMOP.	<i>Phragmites australis</i> (Cav.) Trin.	.	.	+0	1
H bienn	EURASIAS.	<i>Aster tripolium</i> L.	+2	.	1

delaro River and at 'le Cesine' in Salento. *Bassia hirsuta* includes dense nitrophilous communities, mainly monospecific, and often with a linear structure and located at the edges of small pools or channels, and in the clearings of the *Salicornieto* where there are deposits of dead organic matter, like the accumulation of hydrophites (e.g. *Ruppia maritima*, *Posidonia oceanica*).

Braun-Blanquet described in 1928 for the Camargue and Languedoc the association *Suaedo-Kochietum hirsutae* n.n. (=*Suaedo-Bassietum hirsutae*) characterised by *Bassia hirsuta* and *Cressa cretica* (BRAUN-BLANQUET, 1933; BRAUN-BLANQUET *et al.*, 1952). This association has been reported several times in the Adriatic, from the Friuli-Venezia Giulia coastline (POLDINI *et al.*, 1999), the Venice Lagoon (CORBETTA & PIRONE, 1999), in the Emilia-Romagna at the Po River Delta (PICCOLI, 1995), to Puglia in the lakes of Lesina and Varano (CORBETTA, 1970), in the last years we have found two new resort at the mouth of the River Candelaro and in Salento of which some unpublished re-

levés are reported in Tab. 7.

Here, the institution of the new association ***Bassio hirsutae-Suaedetum splendensis*** (Tab. 8, relevé type n. 2) is proposed. It is a pioneer nitrophilous association that develops in the wet clay at the edges of small pools and of the areas frequented by pasture animals, dominated by *Suaeda splendens*. This phytocoenosis that also colonises the abandoned fields after farming, is always on clayey and wet soils, and it has been found at the mouth of the Candelaro River, where it is also in the subassociation *salicornietosum patulae* (relevé type n. 10) and around Brindisi near Torre Canne.

In the literature the association *Suaedo splendensis-Bassietum hirsutae* Braun-Blanquet 1928 is reported for the Camargue and Languedoc (GÉHU *et al.*, 1992; GÉHU, 1991) but it is not clear to which work of Braun-Blanquet it refers, but anyway, in 1952 in the work "Les Groupements végétaux de la France Méditerranéenne" it is indicated only the association *Suaedo maritimae-Bassietum hirsutae* and in the table *Suaeda*

splendens never appears. It is therefore considered that the latter references should be reported to the association *Suaedo maritimae-Bassietum hirsutae*.

As well as the vegetation typologies already presented here, in the Adriatic it is also possible to find sporadically the association ***Salsoretum sodae***, described for the Venice Lagoon (PIGNATTI, 1952) and later found also in many other parts of the north Adriatic, in the area of the Po delta, and in Puglia near the Lesina and Varano Lakes (GÉHU *et al.*, 1984a). This is an annual halonitrophilous community that develops along the borders of the salty pools with deposits of organic matter that dry out during the summer season. As an example, Table 9 includes two unpublished relevés carried out in Puglia, near Brindisi, and on the island of San Pietro opposite Taranto, in the Ionian Sea.

It is interesting, finally, to mention the presence in the Adriatic coasts of the ***Atriplicetum tatarici*** association, described for the Venice Lagoon (PIGNATTI, 1966) and also present at the mouth of the Candelaro River in Puglia, in Tab. 10 an unpublished relevé is shown.

THE PERENNIAL HALOPHILOUS GRASSLANDS OF THE CLASS *SALICORNIETEA FRUTICOSAE*

The perennial *Salicornia*, *Sarcocornia fruticosa*, *Arthrocnemum macrostachyum* and *Halocnemum strobilaceum* grow mainly to the north and south of the basin. These three species make up various typologies of chamaephyte and succulent nanophanerophyte vegetation which have found their ecological place on the salty and wet soils that are not always submerged (BIONDI, 1999). *Sarcocornia fruticosa* is a species distributed along the Mediterranean and European Atlantic coasts towards the north, up to Britany. In Italy, it is found along both the Adriatic and Tyrrhenian coasts. For the Adriatic, it forms a part of the associations that are now briefly described:

Puccinellio festuciformis-Sarcocornietum fruticosae (Braun-Blanquet, 1928) Géhu 1976: an association that is present along all of the Italian coastal territory that develops in the salty depressions with particularly high salt concentrations (the hypersaline areas) at medium and higher levels (BIONDI, 1999). As examples, Tab. 11 gives some unpublished relevés carried out in Puglia, at the mouths of the Candelaro and Ofanto Rivers, and in Salento in the Palude del Capitano.

Sarcocornietum deflexae (Braun-

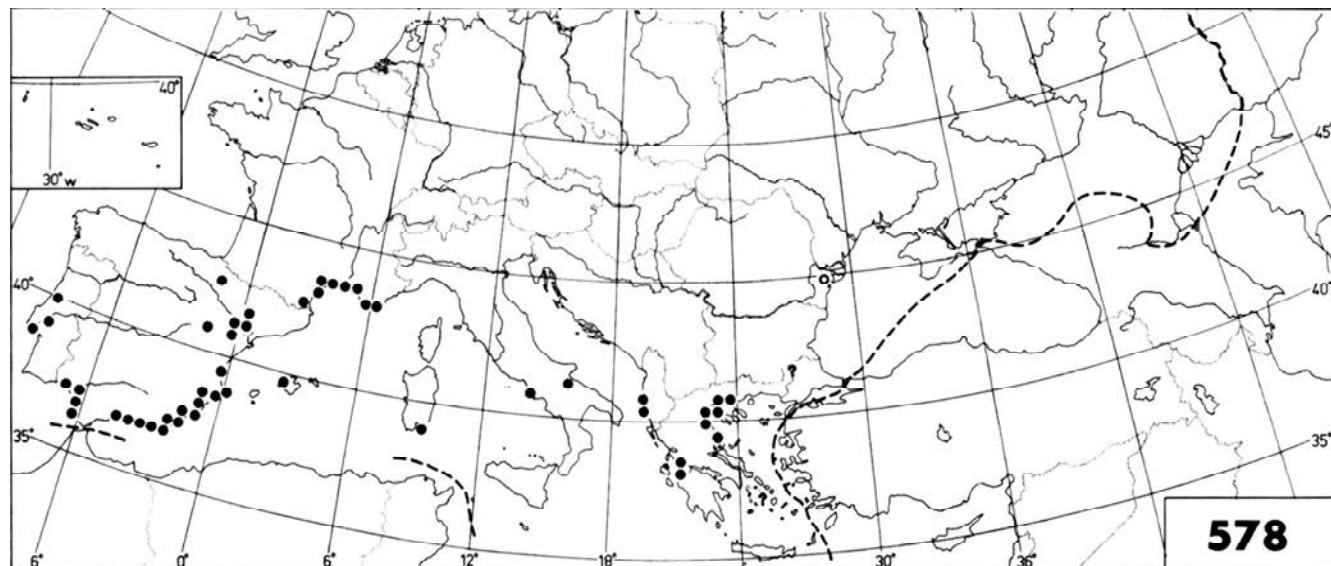


Fig. 6 - The distribution of *Suaeda splendens* (from JALAS & SUOMINEN, 1980).

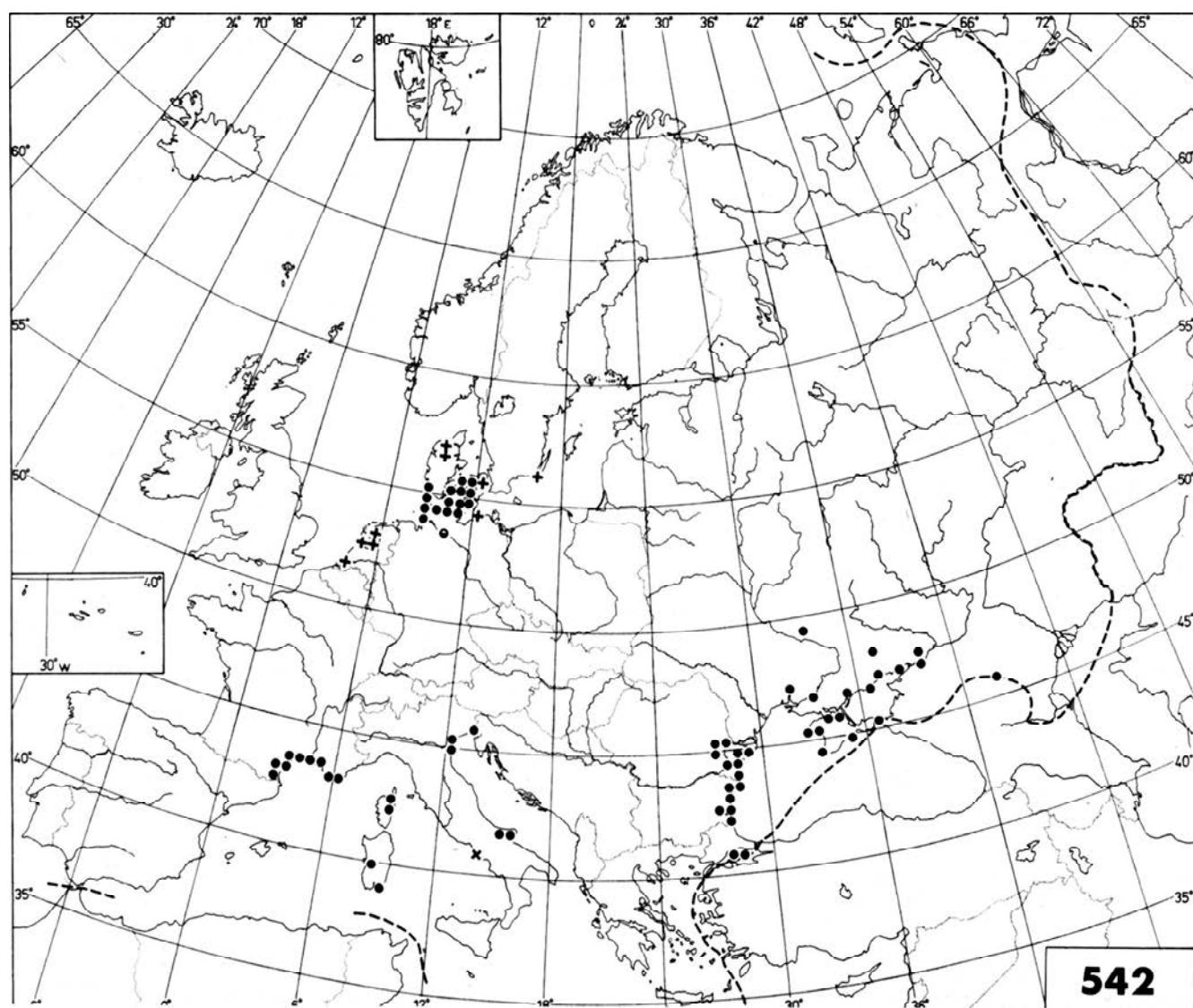


Fig. 7 - The distribution of *Bassia hirsuta* (from JALAS & SUOMINEN, 1980).

Blanquet, 1931) Lahondère, Géhu & Paradis 1992: an association dominated by *Sarcocorniafruticosa* var. *deflexa*: a ground-hugging chamaephyte association of few species found along the deeper salty depressions that remain

water-covered for most of the winter season and have high concentrations of salt. In Italy, it has been noted for the northern Adriatic, at the Sacca di Belluccio (the mouth of the Reno River) and in Sardinia, near Cagliari. Recen-

tly, we have also found this association in Puglia, in Salento, and the island of San Pietro of Taranto. Tab. 12 gives the unpublished relevés from these Puglia resorts.

A. macrostachyum is a succulent

Tab. 7 - *Suaedo maritimae-Bassietum hirsutae* Braun-Blanquet 1928.

		Rel. n.	1	2	3	4	Pres.
		Area (m ²)	40	6	5	15	
		Coverage (%)	80	80	60	50	
		Charact. species of the association					
T scap	S-EUROP.-SUDSIB.	Bassia hirsuta (L.) Asch.	5,5	4,5	3,3	3,3	4
		Charact. species of the upper units					
T succ		Salicornia patula Duval-Jouve	+	.	.	1,2	2
T scap	COSMOP.	Suaeda maritima (L.) Dumort.	.	.	.	1,1	1
		Other species					
G rhiz	ANFI ATL.	Spartina juncea (Michx.) Willd.	1,1	.	.	+	2
Ch succ	EURIMEDIT.	Arthrocnemum fruticosum (L.) Moq.	.	1,1	+	.	2
Ch suffr	MEDIT.ATL.(STENO)	Inula crithmoides L.	1,2	.	.	.	1
T scap	MEDIT.ATL.(EURI)	Cakile maritima Scop.	+	.	.	.	1
Ch frut	CIRCUMBOR.	Halimione portulacoides (L.) Aellen	.	+2	.	.	1
T scap	W-EURIMEDIT.	Hordeum marinum With.	.	.	1,2	.	1
P scap		Tamarix sp. plantule	.	.	.	+	1

chamaephyte that is more widely distributed than the last, as it is also found on rocky substrata near the sea. This species is dominant in some types of communities and is part of the composition of other plant associations, as a species of higher syntaxonomic levels. The following give brief descriptions of the Adriatic communities:

Puccinellio convolutae-Arthroc nemetum macrostachyi (Braun-Blanquet, 1928) Géhu ex Géhu, Costa, Scopola, Biondi, Marchiori, Peris, Géhu-Franck, Caniglia & Veri 1984: a widely spread association along the Italian coasts, both for the Adriatic and the Tyrrhenian. This develops within salty depressions, and it can tolerate both high salt levels and water stress (BIONDI, 1999). Tab. 13 reports some unpublished relevés for this association that were carried out in Puglia, for the Ionian Sea in Salento.

Limonio virgati-Arthroc nemetum macrostachyi Biondi, Casavecchia & Guerra 2006: this association has been described for Salento (BIONDI *et al.*,

2006), and it develops on the rocky calcarenite cliffs where there are sandy deposits among the rocks.

A. macrostachyum is also part of the association ***Agropyro elongati-Inuletum crithmoidis*** Braun-Blanquet (1931) 1952, described for the Languedoc and present, than in France, at the mouth of the Ebre River in Spain and Italy in Sicily and in the Venice Lagoon (BRAUN-B LANQUET *et al.*, 1952). These are haophilous grasslands with a dominance of *Inula crithmoides* and *Limonium serotinum* with *Agropyron elongatum*, *Arthrocnemum macrostachy whole* and *Halimione portulacoides*, which develop on wet sand of average saltiness. Tab. 14 reports some unpublished relevés for this association, carried out in different resorts of Puglia.

In the north Adriatic, near the Sacca di Bellocchio and the Valli of Comacchio there is the only Adriatic station of *Halocnemum strobilaceum*, that gives origin to the association ***Arthroc nemero glauci-Halocnemetum strobilacei*** (CORBETTA, 1976; ANDREUCCI *et al.*,

1999). This is a community that can resist very high salt concentrations, in that it develops at the bottom of retro-dunal depressions occupied by the hypersaline vegetation.

A recent publication (PAPINI *et al.*, 2004) presented phylogenetic analyses conducted on the internal transcribed spacers of the ribosomal genes that have shown that in the *Salicornieae* tribe, the three tetraploid species of *Salicornia* in Italy (*S. emerici*, *S. veneta* and *S. dolichostachya*) share complete identity (100%) in the nucleotide sequence of this region. The same genetic analyses carried out on samples of *Halocnemum strobilaceum* of the north Adriatic and of the stagnant pools of Cagliari has allowed the recognition of as many as 17 transitions and 9 transversions, which supports the existence of two subspecies, or even of two different species. Therefore, taxonomic studies are needed to reveal the morphological differences that can allow the description of the differences between these two taxonomic entities.

CONCLUSIONS

Research carried out to date on the hyperhalophilous coastal and retro-dunal vegetation of the Italian Adriatic coast has allowed the description of the great phytocoenotic biodiversity that includes associations specialised at different levels and with different biogeographical and bioclimate characters. The conservation of these vegetation typologies represents a highly relevant political choice that needs to be made soon, as the human pressure on the habitats of

Tab. 8 - *Bassio hirsutae-Suaedetum splendens ass. nova.*

		Rel. n.	1	2*	3	4	5	6	7	8	9	10**	11	12	Pres.
		Area (m ²)	12	8	10	15	5	4	20	8	30	60	15	7	
		Coverage (%)	60	80	80	60	90	60	80	80	90	80	85	85	
		Charact. species of the association													
T scap	C-ASIAT.-N-MEDIT.	Suaeda splendens (Pourret) G. et G. cfr.	3,3	3,4	4,5	3,3	4,5	3,4	4,5	4,4	5,5	4,4	4,4	4,5	12
T scap	S-EUROP.-SUDSIB.	Bassia hirsuta (L.) Asch.	1,2	2,2	2
		Diff. species of the subass. <i>salicornietosum patulae</i>													
T scap		Salicornia patula Duval-Jouve	1,2	1,2	+	4
		Charact. species of the upper units													
T scap	CIRCUMBOR.	Atriplex hastata Auct. non L.	1,2	1,2	2,3	.	.	1,2	2,2	3,3	6
T scap		Salicornia dolichostachya Moss	+	1
T scap	S-EUROP.-SUDSIB.	Atriplex tatarica L.	3,3	1
T scap	COSMOP.	Suaeda maritima (L.) Dumort.													
		Other species													
Ch frut	CIRCUMBOR.	Halimione portulacoides (L.) Aellen	.	.	+	.	.	+2	.	.	.	+2	.	+	4
H ros	EURIMEDIT.	Limonium serotinum (Rchb.) Pign.	.	.	+	1,2	+	3
Ch suffr	MEDIT.ATL.(STENO)	Inula crithmoides L.	+	+	2
Ch succ	EURIMEDIT.	Arthrocnemum fruticosum (L.) Moq.	+	.	.	.	+	2
H caesp		Puccinellia festuciformis (Host) Parl.	.	.	1,2	1
Ch succ		Arthrocnemum macrostachy whole (Moric.) C. Koch	.	(+)	1
H caesp	EURIMEDIT.	Juncus acutus L.	.	.	.	1,2	1
T scap	EURIMEDIT.	Hainardia cylindrica (Willd.) Greuter	.	.	.	+2	1
T scap	SUBCOSMOP.	Spergularia marina (L.) Griseb.	.	.	.	+	1
T scap	AVV.	Aster squamatus (Sprengel) Hieron.	.	.	.	+	1
G rhiz	SUBCOSMOP.	Juncus maritimus Lam.	+2	.	.	.	1

these typologies is particularly high. This involves, in particular, habitats defined in the European Union Directive 92/43/CEE (1310 "Salicornia and other annuals colonizing mud and sand", 1320 "Spartina swards (Spartinum maritima)" and 1420 "Mediterranean and thermo-Atlantic halophilous scrubs (Sarcocornetia fruticosi)", that are for the major part extremely rare, and are located throughout Italy and along the Adriatic coast. Their protection therefore requires management plans for SCI and SPA that pay particular attention to the ecology of these communities, with the aim of avoiding their disappearance or strong reduction, as has already happened in a large part of this territory. Therefore, it would be very useful an accurate census for the entire Adriatic of these small plant communities at risk of disappearing as carried out in the French coast by GÉHU (1991) through the implementation of a detailed atlas, with geo-referenced stations so that they can be adequately monitored in time.

SYNTAXONOMICAL LIST OF THE ADRIATIC HALOPHILOUS VEGETATION WITH REFERENCE TO THE THREE CLASSES DISCUSSED IN THE TEXT

Thero-Suaedetea Rivas-Martínez 1972
Thero-Suaedetalia Braun-Blanquet & O. de Bolòs 1958

Thero-Suaedion Braun-Blanquet in Braun-Blanquet, Roussine & Nègre 1952

Salsoletum sodae Pignatti 1953

Suaedo maritimae-Bassietum hirsutae
Braun-Blanquet 1928

Bassio hirsutae-Suaedetum splendens ass. nova

Thero-Salicornietalia Tüxen in Tüxen & Oberdorfer ex Géhu & Géhu-Franck 1984

Salicornion patulae Géhu & Géhu-Franck 1984

Suaedo maritimae-Salicornietum patulae (Brullo & Furnari 1976) Géhu & Géhu-Franck 1984

Suaedo splendens-Salicornietum patulae Rivas-Martínez, Costa, Castroviejo & Valdeés-Bermejo 1980 corr.

Rivas-Martínez 1990
Suaedo splendens-Salicornietum venetae ass. nova

Suaedo splendens-Salicornietum dolichostachyae ass. nova

Salicornietum venetae Pignatti 1966
Salicornietum emericii (O. de Bolos 1962) Brullo & Furnari 1976

Salicornietea fruticosae Braun-Blanquet

Tab. 9 - *Salsoletum sodae* Pignatti 1953.

		Rel. n.	1	2	Pres.
		Area (m ²)	2	10	
		Coverage (%)	70	100	
		Charact. species of the association			
T scap	PALEOTEMP.	Salsola soda L.	3,3	5,5	2
T scap		Charact. species of the upper units			
		Atriplex hastata Auct. non L.	2,3	1,2	2

Tab. 10 - *Atriplicetum tataricae* Pignatti 1966.

		Rel. n.	1
		Area (m ²)	20
		Coverage (%)	95
		Charact. species of the association	
T scap	S-EUROP.-SUDSIB.	Atriplex tatarica L.	5,5
T scap	COSMOP.	Charact. species of the upper units	
T scap	PALEOTEMP.	Suaeda maritima (L.) Dumort.	+2
T scap	AVV.	Salsola soda L.	+2
Ch succ		Other species	
Ch frut	CIRCUMBOR.	Aster squamatus (Sprengel) Hieron.	1,2
T scap	W-EURIMEDIT.	Arthrocnemum fruticosum (L.) Moq. var. deflexa	1,1
T scap	SUBTROP.	Halimione portulacoides (L.) Aellen	+
		Hordeum marinum With.	+
		Polygonum monspeliacum (L.) Desf.	+

Tab. 11 - *Puccinellio festuciformis-Sarcocornietum fruticosae* (Braun-Blanquet 1928)
Géhu 1976.

		Rel. n.	1	2	3	4	5	Pres.
		Area (m ²)	15	30	40	40	50	
		Coverage (%)	100	100	100	95	90	
		Charact. species of the association						
Ch succ	EURIMEDIT.	Arthrocnemum fruticosum (L.) Moq.	4,5	4,5	5,5	5,5	4,5	5
H caesp		Puccinellia festuciformis (Host) Parl.	+2	+2	1,2	2,2	2,2	5
		Charact. species of the upper units						
Ch frut	CIRCUMBOR.	Halimione portulacoides (L.) Aellen	3,4	1,2	+2	1,2	1,2	5
H ros	EURIMEDIT.	Limonium serotinum (Rchb.) Pign.	1,2	2,2	+	.	.	3
Ch suffr	MEDIT. ATL.-STENO)	Inula crithmoides L.	+2	+2	.	.	.	2
T scap		Triglochin barellieri Loisel.	+	+	.	.	.	2
Ch succ		Arthrocnemum macrostachyum (Moric.) C. Koch	.	.	.	1,2,0	2,2	2
H ros	EURIMEDIT.	Limonium virgatum (Willd.) Fourr.	.	1,2	.	.	.	1
		Other species						
T scap	COSMOP.	Suaeda maritima (L.) Dumort.	.	.	+	.	.	1

Tab. 12 - *Sarcocornietum deflexae* (Braun-Blanquet 1931) Lahondère, Géhu et Paradis 1992.

		Rel. n.	1	2	3	Pres.
		Area (m ²)	20	10	40	
		Coverage (%)	90	98	100	
		Charact. species of the association				
Ch succ		Sarcocornia fruticosa (L.) A. J. Scott var. deflexa	5,5	5,5	5,5	3
		Charact. species of the upper units				
Ch frut	CIRCUMBOR.	Halimione portulacoides (L.) Aellen	1,2	.	.	1
		Arthrocnemum macrostachyum (Moric.) C. Koch	.	.	+2	1
		Other species				
Ch suffr	ENDEM.	Limonium japyicum (Groves) Pign.	1,1	.	.	1

& Tüxen ex A. & O. de Bolòs 1950	1992
Sarcocornietalia fruticosae Braun-Blanquet 1933	Sarcocornenion fruticosae Rivas-Martínez 1980
Salicornion fruticosae Braun-Blanquet 1933	<i>Puccinellio festuciformis-Sarcocornietum fruticosae</i> (Braun-Blanquet 1928)
Sarcocornenion deflexae Rivas-Martínez, Lousa, Diaz, Fernandez-Gonzalez & Costa corr. Géhu & Biondi 1966	Géhu 1976
<i>Sarcocornietum deflexae</i> (Braun-Blanquet 1931) Lahondère, Géhu et Paradis	Arthrocnemenion macrostachyi Rivas-Martínez 1980
Salicornietea fruticosae Braun-Blanquet	<i>Puccinellio convolutae-Arthrocnemum macrostachyi</i> (Braun-Blanquet

Tab. 13 - *Puccinellio convolutae-Arthrocnemetum macrostachyi* (Braun-Blanquet 1928) Géhu ex Géhu, Costa, Scoppola, Biondi, Marchiori, Peris, Géhu-Franck, Caniglia & Veri 1984.

		Rel. n.	1	2	3	4	5	Pres.
		Area (m ²)	80	40	15	15	50	
		Coverage (%)	95	90	100	100	100	
Charact. species of the association								
Ch succ		Arthrocnemum macrostachy whole (Moric.) C. Koch	5.5	5.5	5.5	5.5	5.5	5
H caesp		Puccinellia festuciformis (Host) Parl.	2.2	2.2	2.2	+2	+	5
Charact. species of the upper units								
H ros	EURIMEDIT.	Limonium serotinum (Rchb.) Pign.	1.1	1.2	1.2	1.1	.	4
T scap		Triglochin barellieri Loisel.	.	1.1	.	.	.	1
Ch frut	CIRCUMBOR.	Halimione portulacoides (L.) Aellen	2.2	1
Other species								
H caesp	EURIMEDIT.	Agropyron elongatum (Host) Beauv.	.	.	+	.	.	1
Ch suffr	MEDIT.ATL.(STENO)	Inula crithmoides L.	.	.	+	.	.	1
G rhiz	S-MEDIT.	Juncus subulatus Forsskal	2.3	1
T scap		Atriplex hastata Auct. non L.	+	1

Tab. 14 - *Agropyro-Inuletum crithmoidis* Braun-Blanquet (1931) 1952.

		Ril. n.	1	2	3	4	5	6	7	8	9	10	Pres.
		Sup.	50	30	20	20	30	60	60	15	50	40	
		Ric.	100	100	90	90	100	90	100	90	100	100	
Charact. and diff. species of the association													
Ch suffr	MEDIT.ATL.(STENO)	Inula crithmoides L.	4.5	2.2	3.4	2.3	3.3	3.3	1.2	4.4	4.4	3.3	10
H ros	EURIMEDIT.	Limonium serotinum (Rchb.) Pign.	2.2	5.5	4.4	4.5	5.5	4.4	4.4	3.3	2.3	4.4	10
H caesp	EURIMEDIT.	Agropyron elongatum (Host) Beauv.	1.2	+	1.2	+	+2	1.2	2.2	1.2	2.3	.	9
Charact. species of the upper units													
Ch succ	STENOMEDIT.	Arthrocnemum macrostachy whole (Moric.) C. Koch	+2	1.2	1.2	1.2	.	2.2	2.2	+	1.2.0	2.3	9
Ch frut	CIRCUMBOR.	Halimione portulacoides (L.) Aellen	2.2	+2	+	.	1.2	2.3	.	1.2	.	+2	7
H caesp	STENOMEDIT.	Puccinellia festuciformis (Host) Parl.	.	+	1
H bienn	EURASIAT.	Aster tripolium L.	1.2	.	1	
Other species													
H caesp	EURIMEDIT.	Juncus acutus L.	4.4	2.2	2.3	2.3	+2	+2	1.2	2.2	.	1.2	9
T scap	C-ASIA-T.-N-MEDIT.	Suaeda splendens (Pourret) G. et G. cfr.	.	+	1.1	+	.	.	+	.	+	.	5
He	SUBCOSMOP.	Phragmites australis (Cav.) Trin.	.	.	.	+	1.1	+2	.	.	1.2.0	.	4
H ros	S-EUROP.-SUDSIB.	Plantago maritima L.	+2	.	.	.	2.3	.	2
T scap	AVV.	Aster squamatus (Sprengel) Hieron.	+	+	2
G rhiz	SUBCOSMOP.	Juncus maritimus Lam.	1.2	1
T scap	CIRCUMBOR.	Atriplex hastata	+	1
T scap	SUBCOSMOP.	Bromus hordeaceus L.	+	1
H caesp	STENOMEDIT.	Oryzopsis miliacea (L.) Asch. et Schweinf.	+2	1
G rhiz	S-MEDIT.	Juncus subulatus Forsskal	+	.	1

1928) Géhu ex Géhu, Costa, Scoppola, Biondi, Marchiori, Peris, Géhu-Franck, Caniglia & Veri 1984

Limonio virgati-Arthrocnemetum macrostachyi Biondi, Casavecchia & Guerra 2006

Agropyro elongati-Inuletum crithmoidis Braun-Blanquet (1931) 1952

Halocnemenion strobilacei Géhu e Costa in Géhu, Costa, Biondi, Peris e Arnold 1984

Arthrocnemo glauci-Halocnemetum strobilacei Oberdorfer 1952

Spartinetea maritimae Tüxen in Beftink & Géhu 1973

Spartinetalia maritimae Conard ex Beftink & Géhu 1973

Spartinion maritimae Conard ex Beftink & Géhu 1973

Limonio narbonense-Spartinetum maritimae (Pignatti 1966) Beftink & Géhu 1973

In the next pages some aspects of the halophilous retro-dune grasslands of the Italian Adriatic coastline (Figs. 8-16).



Fig. 8 - An aspect of the State Natural Reserve of Sacca di Bellocchio in the Northern Adriatic Sea, at the mouth of the River Reno.



Fig. 9 - *Halocnemum strobilaceum* vegetation in the hyperhaline depressions behind dunes, in the resort Sacca di Bellocchio.



Fig. 10 - A detail of *Halocnemum strobilaceum* in the resort Sacca di Bellocchio.



Fig. 11 - *Salicornietum venetae* in Sacca di Bellocchio.



Fig. 12 - An aspect of the landscape of the mouth of the Candelaro River, south of the Gargano Promontory. The violet color is given by the flowering of a population of *Limonium narbonense*.



Fig. 13 - An other aspect of the halophilous vegetation of the mouth of the Candelaro River.



Fig. 14 - *Salicornia patula* at the mouth of the Candelaro River.



Fig. 15 - *Suaeda splendens* in the resort Torre Canne (Brindisi).



Fig. 16 - *Suaedo maritimae-Bassietum hirsutae* in the resort Le Cesine.

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LES VÉGÉTATIONS À *FRANKENIA LAEVIS* ET À *LIMONIUM* À NERVURES PARALLÈLES DES HAUTS SCHORRES SABLONNEUX ET DES FALAISES DU LITTORAL ATLANTIQUE FRANÇAIS

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ABSTRACT

Six new plant associations with *Frankenia laevis* and parallel nervures *Limonium* are described. They grow on mud and sandy substrates, at the highest part of salt marshes and on maritime cliffs of the atlantic seashore.

KEYWORDS: atlantic seashore, phytosociology, *Frankenia laevis*, *Limonium* spp.

RÉSUMÉ

Six nouvelles associations végétales à *Frankenia laevis* et *Limonium* à nervures parallèles des hauts schorres sablonneux et des falaises du littoral atlantique français sont décrites.

INTRODUCTION

Sur le littoral armoricain, *Frankenia laevis*, espèce méditerranéenne-atlantique, se développe préférentiellement sur les hauts schorres sablonneux et sur les pans de falaises exposées le plus souvent au sud. Fréquent sur les côtes sud et ouest armoricaines, il devient plus discret sur le littoral nord armoricain, de la pointe occidentale du Finistère au Cotentin (PROVOST, 1993).

Sur le littoral atlantique français, les végétations halophiles à *Frankenia laevis* et à *Limonium* à nervures parallèles des vases salées ont fait l'objet de plusieurs travaux (KUHNHOLTZ-LORDAT, 1926a; LAHONDÈRE, 1971; GÉHU et GÉHUAU, 1975; GÉHU, 1976; LAHONDÈRE et BOUZILLÉ, 1983; GÉHU et BIORET, 1992; LAHONDÈRE, 1996; LAHONDÈRE et BIORET, 1995, 1997a, 1997b). Les végétations à *Limonium* spp. des falaises maritimes ont été également étudiées (KUHNHOLY-Z-LORDAT, 1926b; LAHONDÈRE, 1971; GÉHU et al., 1984; LAHONDÈRE et al., 1991; LAHONDÈRE et BIORET, 1995, 1997b; BIORET et GÉHU, 2008).

L'étude des végétations littorales armoricaines et du Centre-Ouest, nous a permis de remarquer des végétations

halophiles originales, caractérisées par *Frankenia laevis* et divers taxons de *Limonium* à nervures parallèles, sur les zones supérieures du schorre atteintes par le flot au moment des grandes marées de vives eaux, ainsi que sur certaines falaises basses régulièrement aspergées par les embruns.

MÉTHODE

La méthodologie suivie est celle de la phytosociologie sigmatiste (GÉHU et RIVAS-MARTÍNEZ, 1981; GÉHU, 1987), c'est-à-dire l'approche floristico-éco-logique: les 103 relevés phytosociologiques analysés dans le cadre de ce travail ont été effectués sur des aires de végétation homogènes d'un point de vue écologique, physionomique et floristique. La nomenclature des taxons suivie est celle de KERGUÉLEN (1993).

RÉSULTATS

VÉGÉTATIONS DES VASES SALÉES

1. *Parapholido strigosa-Limonietum occidentalis* (Lahondère et Bioret 1995) ass. *nova hoc loco* (Tableau 1). Cette végétation se développe à la partie supérieure du schorre, sur un substrat vaso-sableux constitué de tangues plus ou moins indurées, et inondé aux grandes marées de vives eaux. Il s'agit d'une communauté paucispécifique (nombre spécifique moyen de 7,7), caractérisée par une combinaison floristique associant régulièrement *Parapholis strigosa*, *Limonium occidentale*, et *Limonium normannicum*. Décrite initialement par LAHONDÈRE et BIORET (1995) sous le nom de *Parapholido strigosa-Limonietum binervosi* nom prov., nous proposons de considérer cette phytocénose comme une association originale: *Parapholido strigosa-Limonietum occidentalis*

Tableau 1 - *Parapholido strigosa-Limonietum occidentalis* (Lahondère et Bioret 1995) ass. *nova hoc loco*.

N. relevés	1	2	3	4	5	6	7	Σ
Surface (m ²)	3	2	10	2	5	4	3	
Recouvrement (%)	70	80	60	60	40	50	50	
Nombre spécifique	9	7	9	9	7	6	7	
Nombre spécifique moyen								7,7

Combinaison caractéristique d'association	33	12	11	23	34	34	23	V
<i>Limonium occidentale</i>	33	12	11	23	34	34	23	V
<i>Parapholis strigosa</i>	22	55	44	22	11	11	11	V
<i>Limonium normannicum</i>	+	.	.	2	.	.	12	III

Différentielle de sous-association	.	.	+	+	2	11	11	V
<i>Elytrigia atherica</i>	.	.	+	+	2	11	11	V

Spécies des unités supérieures	+	11	.	+	22	11	.	V
<i>Spergularia marina</i>	+	11	.	+	22	11	.	V
<i>Plantago maritima</i>	12	.	+	+	2	.	11	V
<i>Puccinellia maritima</i>	11	.	.	12	+	+	.	IV
<i>Festuca rubra</i> subsp. <i>litoralis</i>	11	.	+	11	.	.	+	IV
<i>Spergularia media</i>	.	+	I
<i>Armeria maritima</i>	+°	I
<i>Suaeda maritima</i>	.	+	I

Autres	+°	+	.	22	+°	2	12	V
<i>Halimione portulacoides</i>	+°	+	.	22	+°	2	12	V
<i>Salicornia ramosissima</i>	.	11	I
<i>Matricaria maritima</i>	.	.	11	I
<i>Beta vulgaris</i> subsp. <i>maritima</i>	.	.	+	I
<i>Sedum acre</i>	.	.	+	I
<i>Leymus arenarius</i>	.	.	+	I

dentalis (Lahondère et Bioret 1995) ass. *nova hoc loco* (holosyntype: relevé n. 2, Tableau 1).

Deux variations écologiques correspondent à des sous-associations:

- variation typique: *typicum subass. nova hoc loco* (holosyntype: relevé n. 2, Tableau 1);
- variation liée au contact supérieur des végétations du haut schorre caractérisée par *Elytrigia atherica*: *elytrigietosum athericae subass. nova hoc loco* (holosyntype: relevé n. 5, Tableau 1).

Cette association est connue seulement dans la partie occidentale de la baie du Mont Saint-Michel, mais serait à rechercher ailleurs sur le littoral nord armoricain.

2. *Frankenio laevis-Limonietum occidentalis ass. nova hoc loco* (Tableau 2). Cette végétation se développe sur un substrat vaso-sableux, plus ou moins fortement compacté, au niveau des zones de contact entre les dunes et les vases salées, dans la partie supérieure de l'estran atteinte seulement par les marées hautes de vives eaux. Elle se développe au contact inférieur de l'*Agropyro pungentis-Suaedetum verae* Géhu 1976. Cette communauté paucispécifique (nombre spécifique moyen de 7,2) est caractérisée par une combinaison floristique associant régulièrement *Frankenia laevis* et *Limonium occidentale*. Compte tenu de ses caractéristiques floristiques et écologiques,

il est proposé de la considérer comme une association originale, nommée *Frankenio laevis-Limonietum occidentalis ass. nova hoc loco* (holosyntype: relevé n. 1, Tableau 2).

Deux sous-associations peuvent être distinguées:

- variation typique: *typicum subass. nova hoc loco* (holosyntype: relevé n. 1, Tableau 2);
- variation sur substrat sableux et séchard, caractérisée par des éléments des *Saginetea maritimae*: *Parapholis strigosa*, *Sagina maritima* et *Limonium dodartii*: *parapholidetosum strigosae subass. nova hoc loco* (holosyntype: relevé n. 5, Tableau 2).

Cette association observée sur les littoraux de Loire-Atlantique et des Côtes d'Armor, serait à rechercher ailleurs sur les côtes nord et ouest armoricaines.

3. *Frankenio laevis-Limonietum auriculiersifolii ass. nova hoc loco* (Tableau 3). Cette statice se développe à la partie supérieure des schorres, au contact avec l'arrière-dune, sur un substrat sablo-vaseux compact et humide (Fig.1), dont l'humidité est entretenue par de l'eau phréatique (LAHONDÈRE et BIORET, 1997b). Il s'agit d'une communauté paucispécifique (nombre spécifique moyen de 7,4), caractérisée par une combinaison floristique associant régulièrement *Frankenia laevis* et *Limonium auriculiersifolium* (Fig.2). Il est

proposé de considérer cette phytocène comme une association originale, nommée *Frankenio laevis-Limonietum auriculiersifolii ass. nova hoc loco* (holosyntype: relevé n. 6, Tableau 3).

Trois variations correspondant à des sous-associations peuvent être distinguées:

- variation typique: *typicum subass. nova hoc loco* (holosyntype: relevé n. 6, Tableau 3);
- variation liée aux substrats plus secs et plus sablonneux, caractérisée par *Limonium dodartii* et *Honckenya peploides*: *limonietosum dodartii subass. nova hoc loco* (holosyntype: relevé n. 11, Tableau 3);
- variation plus hygrophile, liée à des suintements phréatiques latéraux, caractérisée par *Juncus maritimus*, *Phragmites communis* et *Elytrigia atherica*: *juncetosum maritimi subass. nova hoc loco* (holosyntype: relevé n. 2, Tableau 3).

Le *Frankenio-Limonietum auriculiersifolii* se différencie du *Limonietum lychnidifolio-dodartii* Géhu et Géhu-Franck 1975, par la présence de *Sarcocornia fruticosa* var. *deflexum*, la moindre fréquence de *Limonium dodartii*, *Elytrigia atherica* et *Suaeda vera*, et l'absence de *Puccinellia maritima* et de *Festuca rubra* subsp. *litoralis*.

Sa répartition géographique est limitée au littoral sud du Morbihan et autour du bassin d'Arcachon. Cette association est absente du littoral de Vendée et de Charente-Maritime, où elle est remplacée par le *Frankenio laevis-Limonietum ovalifolii*.

4. *Frankenio laevis-Limonietum ovalifolii* (Lahondère 1996) ass. *nova hoc loco* (Tableau 4). À la partie supérieure du schorre, au contact de la dune, sur un substrat vaso-sableux, se développe une végétation linéaire discontinue, largement dominée physionomiquement par *Limonium ovalifolium*, longtemps confondu par certains auteurs avec *Limonium auriculiersifolium*. *Limonium ovalifolium* forme très souvent des touffes denses, ce qui n'est pas le cas de *Limonium auriculiersifolium*.

Cet ensemble paucispécifique (nombre spécifique moyen de 5,8) est caractérisé par une combinaison floristique originale, associant régulièrement *Frankenia laevis* et *Limonium ovalifolium*. Il faut remarquer que *Limonium dodartii* apparaît parfois à la partie supérieure de ce groupement. Compte tenu de l'originalité de la combinaison floristique et de sa synécologie, il est proposé de considérer ce groupement comme une association végétale origi-

Tableau 2 - *Frankenio laevis-Limonietum occidentalis ass. nova hoc loco*.

N. relevés	1	2	3	4	5	Σ
Surface (m ²)	2	1	3	5	3	
Recouvrement (%)	50	30	50	60	40	
Nombre spécifique	5	3	10	12	6	
Nombre spécifique moyen						7,2

Combinaison caractéristique d'association

Limonium occidentale	34	23	33	33	23	V
Frankenia laevis	13	12	12	34	33	V

Différentielles de sous-association

Parapholis strigosa	.	.	+	11	+	III
Sagina maritima	.	.	.	+	11	II
Limonium dodartii	.	.	+	12	.	II

Espèces des unités supérieures

Spergularia marina	22	11	12	2	12	V
Armeria maritima	.	.	+°	+	12	III
Puccinellia maritima	2	.	2	+	.	III
Suaeda maritima	.	.	+	+	.	II
Limonium vulgare	.	.	.	j	.	I

Espèces des *Salicornietea fruticosae*

Halimione portulacoides	j°	.	12	+2°	.	III
Suaeda vera	.	.	+	11°	.	II



Fig. 1 - Le *Frankenio laevis-Limonietum auriculiformis* se développe dans la zone de rencontre entre la partie supérieure du pré salé et la dune, au contact supérieur du *Junc maritimi-Caricetum extensae* traduisant la présence de suintements phréatiques (Morbihan).

nale que Lahondère avait pressentie sur les côtes de Saintonge (1996). Nous proposons de la nommer *Frankenio laevis-Limonietum ovalifolii* (Lahondère 1996) ass. *nova hoc loco* (holosyntype: relevé n. 13, Tableau 4).

Deux sous-associations peuvent

être distinguées:

- variation typique: *typicum subass. nova hoc loco* (holosyntype: relevé n. 13, Tableau 4);
- variation sur substrat plus sec au contact de l'*Agropyro-Suaedetum verae* Géhu 1976, caractérisée par *Limonium*

dodartii: limonietosum dodartii subass. nova hoc loco (holosyntype: relevé n. 16, Tableau 4).

Là où nous avons pu observer les étapes du développement de cette association, nous avons noté que la croissance du *Limonium* précède celle de



Fig. 2 - *Limonium auriculiforme* (Pourr.) Druce (Plouharnel, Morbihan).

Tableau 3 - *Frankenio laevis-Limonietum auriculiursifolii ass. nova hoc loco.*

N. relevés	1	2	3	4	5	6	7	8	9	10	11	Σ
Surface (m ²)	3	10	3	10	2	10	20	3	30	3	5	
Recouvrement (%)	90	100	90	80	90	95	60	30	90	70	65	
Nombre spécifique	9	7	5	4	8	8	5	5	7	7	7	7,4
Nombre spécifique moyen												

Combinaison caractéristique d'association

Limonium auriculiursifolium	3	5	+	3	3	4	3	33	2	44	44	V
Frankenia laevis	.	1	4	.	3	11	II	

Différentielles de sous-associations

Limonium dodartii	.	.	3	1	1	+	II
Honckenya peploides	.	+	1	3	.	2	II
Parapholis strigosa	.	.	.	+	+	+	II
Arenaria leptoclados	+	+
Arenaria serpyllifolia subsp. lloydii	.	.	.	+	+
Juncus maritimus	+	.	+	1	11	32	III
Elytrigia atherica	3	22	4	.	33	II
Phragmites australis	+	11	.	I

Espèces des unités supérieures

Suaeda maritima	+	1	.	+	22	+	III
Plantago maritima	2	+	.	.	.	1	II
Spergularia marina	1	+	I
Glaux maritima	3	.	+	I
Salicornia ramosissima	+	+	.	.	I
Limonium vulgare	+	+	.	
Carex extensa	+	+	

Espèces des *Salicornietea fruticosae*

Halimione portulacoides	+	+	.	.	j	.	+	2	.	j	.	III
Suaeda vera	.	+	3	j	+	II
Arthrocnemum fruticosum var. deflexum	1	.	.	.	j	+	II
Inula crithmoides	1	.	.	+

Autres espèces

Plantago coronopus	+	.	.	+	.	I
Atriplex littoralis	+	+

Frankenia laevis. Dans le stades de dégénération de l'association, due à la remontée du niveau de la mer, ou à l'invasion de celle-ci suite à la modification du trait de côte, *Limonium ovalifolium* se maintient plus longtemps que les autres éléments structurants du groupement, comme nous l'avons noté dans une zone de forte érosion, à la pointe de Gatseau et à Saint-Trojan, sur l'île d'Oléron: de petits monticules couronnés de touffes plus ou moins dégradées du *Limonium*, témoignent de l'ancienne occupation de l'association.

Cette association se développe entre l'*Agropyropungentis-Suaedetum vegae* Géhu 1976 et la végétation arrière-dunaire.

Le *Frankenio laevis-Limonietum ovalifolii* présente une répartition géographique très limitée, du sud de la Vendée à la pointe Espagnole en Charente-Maritime; il n'atteint pas les côtes

de Gironde. Cette association est particulièrement bien représentée à l'île d'Oléron et sur le littoral de Saintonge. *Limonium ovalifolium* disparaît des côtes françaises au niveau de Saint-Palais-sur-mer, et ne réapparaît qu'au niveau des côtes de Santander (ERBEN, 1993).

VÉGÉTATIONS DES FALAISES MARITIMES

5. *Frankenio laevis-Limonietum dodartii* (Lahondère et Bioret 1997) *ass. nova hoc loco* (Tableau 5). Ce type de végétation présente une physionomie de pelouse très rase assez recouvrante, interrompue par quelques microclairières de sol nu. Elle se développe à la partie sommitale de falaises calcaires basses et exposées, dont l'altitude n'excède pas 5 m. Le substrat, de nature argilo-calcaire, mêlé de cailloutis, correspon-

dant parfois à des placages sableux, et pouvant atteindre une trentaine de centimètres, recouvre directement la roche mère. Au moment des tempêtes, les paquets de mer projetés par les vagues au sommet de ces falaises, peuventasperger directement la végétation et y déposer des fragments d'algues d'échouage. Ce niveau bionomique confère à cette phytocénose un caractère hyperhalophile subnitrophile.

Il s'agit d'une communauté pauci-spécifique (nombre spécifique moyen de 6,1), caractérisée par une combinaison floristique associant régulièrement *Frankenia laevis*, *Limonium dodartii*, et *Plantago coronopus*.

Quelques espèces théophytiques de la Classe des *Saginetea maritimae* sont présentes: *Parapholis incurva*, *Sagina maritima*, *Desmazeria marina*. Sur les placages sableux, on note la présence de *Eryngium campestre* et *Aethorhiza bulbosa*.

Par rapport aux deux associations des falaises du littoral du Centre-Ouest, également caractérisées par *Limonium dodartii*, le *Spergulario rupicolae-Limonietum dodartii* Géhu, Géhu-Franck et Scoppola 1984 et le *Dactylo oceanicae-Limonietum dodartii* (Lahondère 1979) Géhu, Géhu-Franck et Scoppola 1984 nom. corr. Bioret et Géhu 2008, deux espèces sont absentes dans le groupement à *Frankenia laevis* et *Limonium dodartii*: *Spergularia rupicola* et *Armeria maritima*.

Ce type de végétation avait déjà été signalé sur le littoral de Charente-Maritime, à l'île d'Aix et Saint-Palais-sur-Mer (LAHONDÈRE et BIORET, 1997b; LAHONDÈRE, 2005). Compte tenu de ses caractéristiques écologiques et de sa combinaison floristique originales, nous proposons de l'élever au rang d'association: *Frankenio laevis-Limonietum dodartii* (Lahondère et Bioret 1997) *ass. nova hoc loco* (holotype: relevé n. 2, Tableau 5).

Diverses variations écologiques correspondent à des sous-associations:

- variation typique: *typicum subass. nova hoc loco* (holotype: relevé n. 2, Tableau 5);
- variation hyperhalophile, située au contact supérieur des végétations chamo-halophiles, caractérisée par *Crithmum maritimum*; *crithmetosum maritimi subass. nova hoc loco* (holotype: relevé n. 9, Tableau 5);
- variation subnitrophile, liée au dépôt régulier de laisses de mer projetées par les vagues au moment des tempêtes, caractérisée par *Beta vulgaris* subsp. *maritima* et *Cochlearia danica*; *betosum maritimae subass. nova hoc loco*

Tableau 4 - *Frankenio laevis-Limonietum ovalifolii* (Lahondère 1996) ass. nova hoc loco.

N. relevés	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	Σ
Surface (m ²)	5	5	5	5	20	15	10	20	50	10	25	20	15	6	10	15	20	5	10	
Recouvrement (%)	65	80	50	65	90	80	80	90	70	90	80	100	80	70	60	90	80	60	70	
Nombre spécifique	8	5	5	8	7	4	5	6	7	3	6	4	7	3	8	6	6	7	7	
Nombre spécifique moyen																			5,8	

Combinaison caractéristique d'association

Limonium ovalifolium	23	43	34	22	5	4	3	4	3	5	5	5	4	4	23	4	4	22	23	V
Frankenia laevis	22	33	34	22	+	1	4	3	+	3	3	5	4	+	23	4	2	12	34	V

Différentielles de sous-association

Limonium dodartii	1	1	23	+	II
Elytrigia atherica	+	1	.	.	I

Espèces des unités supérieures

Suaeda maritima	11j	11j	.	+	.	.	+	1	1	.	+	.	2	.	+	.	.	.	+	III
Puccinellia maritima	+	12°	.	+	+	.	+	II
Spergularia marina	+	.	.	+	1	I
Salsola soda	+	.	.	+	I
Limonium vulgare	+	+

Espèces des *Salicornietea fruticosae*

Suaeda vera	11°	.	+°	11°	1	1	+	3	1	2	+	1	+	.	2	1	1	.	.	IV
Halimione portulacoides	23°	12	+	22	+	.	.	2	.	.	+	1	2	.	2	1	.	.	.	III
Sarcocornia fruticosa	+°	.	.	+°	.	.	.	2	.	.	1	.	1	1	12	.	1	.	.	III
Inula crithmoides	1	+	

Autres espèces

Matricaria maritima	+	+	12	I
Parapholis strigosa	.	.	+	+	.	I
Arenaria serpyllifolia	+	+	I
Calystegia soldanella	+	+
Cakile maritima	+	+
Salicornia ramosissima	+	+	.	.	+
Desmazeria marina	+	+	.	.	+
Beta vulgaris subsp. maritima	+	+	.	.	+

(holosyntype: relevé n. 13, Tableau 5).

Cette association présente une aire de répartition géographique limitée au littoral calcaire de Saintonge: Île d'Oléron, Île d'Aix, Saint-Palais-sur-mer.

6. *Spergulario rupicolae-Frankenietum laevis ass. nova hoc loco* (Tableau 6). Cette végétation rase et très recouvrante, forme des draperies dominées physionomiquement par *Frankenia laevis*. Elle se développe au niveau de falaises rocheuses exposées aux embruns, sur un substrat argilo-limoneux, au niveau de replats ou de corniches adossés aux blocs rocheux, où peuvent également s'accumuler des arènes d'altération de la roche mère de nature granitique ou micaschisteuse. Les stations présentent le plus souvent une exposition chaude.

La combinaison floristique associe régulièrement *Frankenia laevis*, *Armeria maritima* et *Spergularia rupicola*, accompagnés par *Cochlearia danica*.

Compte tenu de ses originalités écologiques et floristiques, il s'agit

d'une association originale qu'il est proposé de nommer *Spergulario rupicolae-Frankenietum laevis ass. nova hoc loco* (holosyntype: relevé n. 2, Tableau 6).

Deux sous-associations peuvent être distinguées:

- variation typique: *typicum subass. nova hoc loco* (holosyntype: relevé n. 2, Tableau 6);
- variation hyperhalophile, située au contact supérieur des végétations chamo-halophiles, caractérisée par *Crithmum maritimum*: *crithmetosum maritimi subass. nova hoc loco* (holosyntype: relevé n. 11, Tableau 6);

Dans les sites les plus fréquentés et piétinés, les placages quasi-monospécifiques à *Frankenia laevis* observés à la partie sommitale des falaises, peuvent être considérés comme des groupements secondaires, se développant en substitution des pelouses aérohalines de l'*Armerio maritimae-Festucetum pruinosa* Géhu 2008, ou de la pelouse écorchée de l'*Armerio maritimae-Plantaginetum coronopodis* (Vanden Berghe 1965) Bioret et Géhu 2008.

Le *Spergulario rupicolae-Frankenietum laevis* se développe au contact inférieur ou latéral du *Crithmo maritti-Limonietum ovalifolii* (Kunholtz-Lordat 1926) Lahondère, Bioret et Botineau 1991, ou du *Spergulario rupicolae-Critchmetum maritimi* (Roux et Lahondère 1960) Géhu 1962 nom. inv.

Cette association végétale a été recensée sur le littoral sud et ouest armoricain, de la Loire-Atlantique au Finistère. Elle est très probablement présente également sur les littoraux rocheux de Vendée et serait également à rechercher sur les falaises du littoral nord armoricain.

SYNDYNAMIQUE

En raison de leur caractère hyperspecialisé lié aux contraintes mésologiques, ces associations correspondent à des végétations permanentes et ne présentent aucune dynamique particulière. Sur les hauts schorres, leur maintien est plus lié à des phénomènes de dynamique sédimentaire: accrétion, érosion,

Tableau 5 - *Frankenio laevis-Limonietum dodartii* (Lahondère et Bioret 1997) ass. nova hoc loco.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Σ		
N. relevés	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20			
Surface (m ²)	3	0,5	1	2	3	1	3	3	3	2	2	3	2	2	1	2	1	1	1	1			
Recouvrement (%)	75	75	65	75	90	70	75	75	70	60	80	95	50	65	80	80	80	80	60	75	95		
Nombre spécifique	5	6	3	4	3	4	4	4	4	6	6	8	6	7	8	8	7	10	8	12	9		
Nombre spécifique moyen																					6,4		
Combinaison caractéristique d'association																							
Limonium dodartii	23	23	34	44	44	23	33	33	33	23	2	23	23	23	33	12	23	33	11	V			
Frankenia laevis	44	34	23	33	11	44	12	12	33	34	55	55	12	44	55	34	55	44	44	55	V		
Plantago coronopus	12	12	11	12	12	+	11	.	+	.	11	+	+	11	III		
Différentielles de sous-associations																							
Critchmum maritimum	34	13	34	33	22	II		
Beta vulgaris subsp. maritima	i°	+°	12°	11	2	+	2	i°	2	+°	+°	III		
Cochlearia danica	+	2	+	11	+	+	.	II		
Espèces des Saginetea maritimae																							
Parapholis incurva	+	.	.	+	.	11	+	+	+	11	.	+	11	11	+	.	+	+	+	22	IV		
Sagina maritima	.	2	+	.	+	+	.	+	.	+	.	+	II		
Desmazeria marina	.	+	+	.	.	+	+	.	+	+	.	+	2	II		
Autres espèces																							
Elytrigia atherica	+	22	12	11	+	+	+	2	11	11	+	+	11	+	IV		
Eryngium campestre	11	+	.	12	.	I		
Aethorhiza bulbosa	+	+	.	+	+		
Convolvulus linneatus	+	r			
Phleum arenarium	+	.	r			
Polycarpon tetraphyllum	+	.	r			
Cynodon dactylon	+	.	r			

Tableau 6 - *Spergulario rupicolae-Frankenietum laevis* ass. nova hoc loco.

	1	2	3	4	5	6	7	8	9	10	11	Σ
N. relevés	1	3	2	3	2	1	2	2	3	2	1	
Surface (m ²)	100	85	90	100	80	80	85	85	75	75	80	
Recouvrement (%)	100	85	90	100	80	80	85	85	75	75	80	
Nombre spécifique	5	7	7	6	7	10	9	8	9	5	8	
Nombre spécifique moyen												7,4

Combinaison caractéristique d'association

	55	45	33	55	55	45	45	55	45	45	55	V
Frankenia laevis	2	23	33	12	12	12	.	23	+	11	V	

Différentielles de sous-association

	+	i	2	12	13	III
Crithmum maritimum	

Especes des Armerio maritimae-Festucetea pruinosa

Armeria maritima	12	+	23	.	12	11	.	2	11°	2	IV
Festuca rubra subsp. pruinosa	2	.	2	I
Inula crithmoides	.	.	2	+	.	
Plantago maritima	.	.	+	.	23	I
Limonium occidentale	.	.	.	+	.	.	11	.	.	.	I
Limonium ovalifolium	.	2	+	.	

Especes des Saginetea maritimae

Cochlearia danica	22	11	11	22	+	11	22	22	.	+	+	V
Desmazeria marina	.	+	.	+	22	.	11	.	+	.	III	
Sagina maritima	22	11	+	.	.	.	II	
Parapholis incurva	.	.	11	.	.	11	11	.	.	.	II	
Cerastium diffusum	11	.	.	+	.	.	I	
Bromus feronii	+	+	.	

Autres espèces

Plantago coronopus	.	2	+	.	.	11	21	21	+	.	+	IV
Beta vulgaris subsp. maritima	.	.	2	.	.	+	+	+	.	.	II	
Cynodon dactylon	+	+	.	.	.	+	I	
Atriplex littoralis	11j	+		
Atriplex prostrata	+	+		
Sonchus oleraceus	+	+		

ou de dégradation de cette étroite et fragile bande de transition entre le substrat vaseux du haut schorre et le substrat sableux des milieux arrière-dunaires. À la partie sommitale des falaises exposées les plus fréquentées, ces végétations peuvent être menacées par un piétinement trop intense.

SYNSYSTÉMATIQUE

En suivant BARDAT *et al.* (2004), l'ensemble des végétations des hauts schorres sableux du littoral atlantique français, ainsi que le *Frankenio-Limonietum dodartii* peuvent être regroupées dans l'alliance de l'*Armerion maritimae* Braun-Blanquet et de Leeuw 1936, et la sous-alliance du *Frankenio laevis-Armerienion maritimae* Géhu et Géhu-Franck ex Géhu 1976 (Tableau 7).

Trois autres associations du haut schorre sableux du littoral atlantique, non étudiées dans le cadre de ce travail, font partie de la même sous-alliance: le *Frankenio laevis-Limonietum normanicum* (Lemée 1952) Géhu et Bioret 1992, association synendémique du Golfe normanno-breton, notamment présent dans les hâvres de la côte occidentale du Cotentin (DELASSUS, 2009), et le *Cochleario anglicae-Frankenietum laevis*

Géhu 1976 du littoral ouest-armoricain (GÉHU, 1976). Quant au *Limonietum auriculiursifolii-dodartii* (Kunholtz-Lordat 1926) J.-M. et J. Géhu 1975 corr. hoc loco décrit initialement du littoral du Centre-Ouest, son statut et sa répartition restent à préciser. Ce syntaxon n'existe pas en Charente-Maritime, où c'est le *Frankenio laevis-Limonietum ovalifolii* qui est présent; il existe peut-être sur le littoral de Loire-Atlantique à Pen-Bron.

Le *Spergulario rupicolae-Frankenietum laevis* est quant à lui rattaché à l'alliance de l'*Armerion maritima* Braun-Blanquet et de Leeuw 1936, la sous-alliance du *Frankenio laevis-Armerienion maritima* Géhu et Géhu-Franck ex Géhu 1976, au sein de la classe des *Armerio-Festucetea* Bioret et Géhu 2008.

Le synsystème s'organise de la manière suivante:

Asteretea tripolii Westhoff et Beeftink in Beeftink 1962

Végétation des prés salés atlantiques à dominance d'hémicryptophytes.

Glauco maritimae-Puccinellietalia maritimae Beeftink et Westhoff in Beeftink 1962

Prairies salées des côtes atlantiques européennes (cantabro à boréo-atlantiques), plus accessoirement des bassins salifères subatlantiques.

Armerion maritima Braun-Blanquet et de Leeuw 1936

Communautés des niveaux supérieurs et hauts de schorre.

Frankenio laevis-Armerienion maritima Géhu et Géhu-Franck ex Géhu 1976

Communautés des hauts schorres sabloux secs du littoral cantabro-atlantique.

Parapholido strigosae-Limonietum occidentalis (Lahondère et Bioret 1995) ass. *nova hoc loco*, staticaie des hauts schorres sablo-tangueux du littoral nord-est armoricain.

Frankenio laevis-Limonietum occidentalis ass. *nova hoc loco*, staticaie des hauts schorres vaso-sableux de Loire-Atlantique et des Côtes d'Armor.

Frankenio laevis-Limonietum auriculiursifolii ass. *nova hoc loco*, staticaie des hauts schorres sableux du Morbihan et du bassin d'Arcachon.

Frankenio laevis-Limonietum ovalifolii (Lahondère 1996) ass. *nova hoc loco*, staticaie des hauts schorres vaso-sableux de Vendée et de Charente-Maritime.

Frankenio laevis-Limonietum dodartii (Lahondère et Bioret 1997) ass. *nova hoc loco*, staticaie sur placages limoneux et sableux des falaises calcaires

Tableau 7 - Tableau synthétique des associations à *Frankenia laevis* et *Limonium à nervures parallèles* du littoral atlantique français.

Associations N. relevés	1	7	8	6	4	2	3	9	5
Limonium normannicum	III	V
Limonium occidentale	V	.	I	.	V
Spergularia rupicola	.	.	V
Cochlearia anglica	.	.	III
Limonium ovalifolium	.	.	.	+	V
Limonium auriculiursifolium	V	V	.	.
Limonium dodartii	II	II	II	V	V
Frankenia laevis	.	I	V	V	V	V	II	IV	V
Parapholis strigosa	V	.	.	I	III	II	V	.	.
Elytrigia atherica	V	.	III	.	I	.	II	V	IV
Halimione portulacoides	V	.	V	.	III	III	III	V	.
Puccinellia maritima	IV	.	V	.	II	III	III	III	.
Spergularia marina	V	.	III	.	I	V	I	III	.
Plantago maritima	V	.	V	I	.	.	II	.	.
Sagina maritima	.	.	.	II	.	II	.	II	II
Armeria maritima	I	.	V	IV	.	III	.	.	.
Suaeda maritima	I	.	V	.	III	II	III	.	.
Beta vulgaris subsp. maritima	I	.	.	II	+	.	.	III	.
Plantago coronopus	.	.	.	IV	.	.	I	II	III
Suaeda vera	IV	II	II	V	.
Festuca rubra subsp. littoralis	IV	.	II	II	.
Salicornia ramosissima	.	.	III	.	+	.	I	.	.
Spergularia media
Desmazeria marina	.	.	.	III	+	.	.	.	II
Inula crithmoides	.	.	.	+	+	.	+	.	.
Limonium vulgare	+	.	+	.	.
Parapholis incurva	.	.	.	II	IV
Cochlearia danica	.	.	.	V	II
Crithmum maritimum	.	.	.	III	II
Matricaria maritima	I	I	.	.	.
Glaux maritima	.	.	II	.	.	.	I	.	.
Atriplex littoralis	.	.	.	+	.	.	+	.	.
Arenaria serpyllifolia subsp. lloydii	I	.	+	.	.
Salicornia pusilla	.	.	I
Arthrocnemum perenne	.	.	+
Cerastium diffusum	.	.	.	I
Cynodon dactylon	.	.	.	I
Festuca rubra subsp. pruinosa	.	.	.	I
Sonchus oleraceus	.	.	.	+
Atriplex prostrata	.	.	.	+
Bromus ferronii	.	.	.	+
Sarcocornia fruticosa	III
Salsola soda	I
Cakile maritima	+
Calystegia soldanella	+
Sedum acre	I	.	.	.
Leymus arenarius	I	.	.	.
Juncus maritimus	III	.	.
Phragmites australis	I	.	.
Sarcocornia fruticosa var. deflexum	II	.	.	.
Honckenya peploides	II	.	.	.
Arenaria leptoclados	+	.	.
Carex extensa	+	.	.

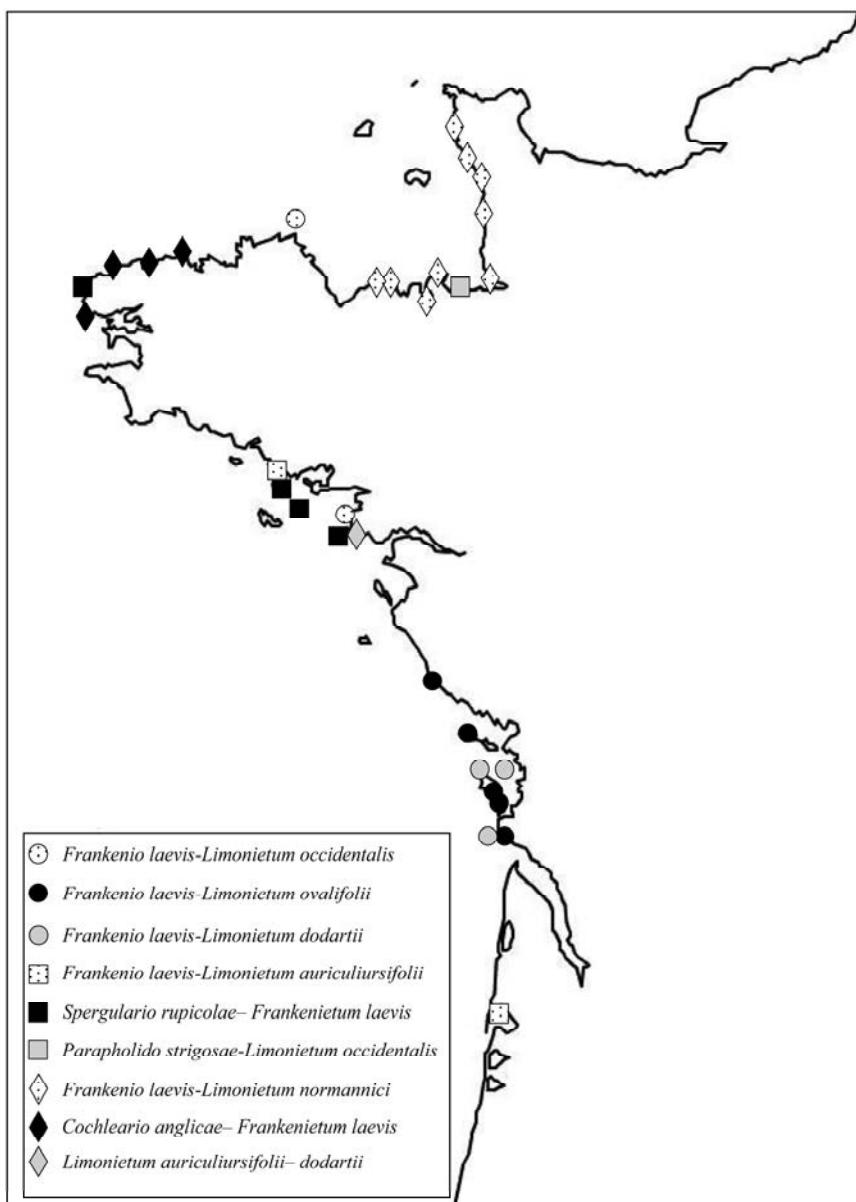


Fig. 3 - Répartition géographique des végétations à *Frankenia laevis* et *Limonium* à nervures parallèles du littoral atlantique français.

basses hyperexposées de Saintonge. *Frankenio laevis-Limonietum normannici* (Lemée 1952) Géhu et Bioret 1992, statice des hauts schorres sableux du Golfe normanno-breton.

Cochleario anglicae-Frankenietum laevis Géhu 1976, frankéniaie des hauts schorres sableux de l'extrême ouest armoricain (Finistère).

Limonietum auriculiursifolii-dodartii (Kunholtz-Lordat 1926) J.-M. et J. Géhu 1975 corr. *hoc loco*, statice des hauts schorres sableux du littoral du Centre-Ouest.

Armerio maritimae-Festucetea pruinosa Bioret et Géhu 2008

Chasmo-chomophytes, pelouses et ourlets de l'étage aérohalin des falaises atlantiques européennes.

Critchmo maritimi-Armerion maritimae Géhu 1964

Chasmo-chomophytes, pelouses et ourlets aérohalins des falaises médio et cantabro-atlantiques.

Critchmo maritimi-Armerion maritimae Géhu 1968

Chasmo-chomophytes, pelouses et ourlets aérohalins des falaises médio et cantabro-atlantiques.

Critchmo maritimi-Limonienion binervosi Géhu et Géhu-Franck 1984

Végétations chasmo-chomophytiques pionnières de la base de l'étage aérohalin des falaises atlantiques médio et cantabro-atlantiques, fortement aspergées d'embruns.

Spergulario rupicolae-Frankenietum laevis ass. nov. *hoc loco*, drapérie à *Frankenia laevis* des hauts de falaises granitiques et micaschisteuses exposées de Loire-Atlantique et du Morbihan.

CONCLUSION

Les végétations à *Frankenia laevis* et *Limonium* à nervures parallèles des hauts schorres sablonneux du littoral atlantique français, intégrées à la sous-alliance du *Frankenio laevis-Armerienion maritimae*, peuvent être rattachées à l'habitat d'intérêt communautaire 1330 Prés salés atlantiques (*Glauco-Puccinellietalia maritimae*). Le *Spergulario rupicolae-Frankenietum laevis* peut quant à lui être rattaché à l'habitat d'intérêt communautaire 1230 Falaises avec végétation des côtes atlantiques et baltiques.

Toutes ces associations végétales correspondent à des syntaxons synendémiques du littoral atlantique français, eu égard à leur aire de répartition très limitée géographiquement, même si des prospections complémentaires permettraient probablement de compléter leur chorologie (Fig. 3). Ce synendémisme leur confère un intérêt patrimonial de premier ordre, et des mesures de gestion conservatoire seraient nécessaires, notamment dans le cadre de l'élaboration et la mise en œuvre des documents d'objectifs des sites Natura 2000 où elles sont présentes. Il s'agit essentiellement de soustraire du piétinement l'étroite zone de contact entre vases salées et dunes. Comme nous l'avons remarqué pour le *Frankenio laevis-Limonietum ovalifolii*, ces syntaxons pourraient constituer de bons indicateurs pour l'évaluation de l'impact des changements globaux sur la biodiversité phytocœnotique littorale.

LOCALISATION DES RELEVÉS

Tableau 1 - *Parapholido strigosae-Limonietum occidentalis* (Lahondère et Bioret 1995) ass. *nova hoc loco*. Baie du Mont Saint-Michel (35), 1995: 1) Isle Bernard; 2), 3), 5), 6) Hirel; 4), 7) Crevelin.

Tableau 2 - *Frankenio laevis-Limonietum occidentalis* ass. *nova hoc loco*: 3), 4) Mesquény (44), 1998; 1), 2), 5) Île Lavrec (Bréhat) (22), 2000.

Tableau 3 - *Frankenio laevis-Limonietum auriculiursifolii* ass. *nova hoc loco*: 2), 3), 6), 4), 1) Plouharnel (56); 5) Plouharnel (relevé Y. Guillevic); 7), 9), 10), 11) Clauouey, entre Lège et Cap Ferret (33), anse du Sangla, 1996; 8) Arcachon (33), 2000.

Tableau 4 - *Frankenio laevis-Limonietum ovalifolii* (Lahondère 1996) ass. *nova hoc loco*: 2), 3) La Perrotière, Île d'Oléron (17), 2000; 4) La Gautrelle, Île d'Oléron, 2000; 5) La Couarde, Île de Ré (17); 1), 6), 7), 8), 9) Baie de Gatseau, Saint-Trojan, Île d'Oléron; 10), 11), 12), 13), 14) La Perrotine, Boyardville, Île d'Oléron; 16), 17) Le Galon d'Or, Ronce-les-Bains, La Tremblade

- (17); 15), 18), 19) Le Veillon (Talmont Saint-Hilaire) (85), 1997.
- Tableau 5 - *Frankenio laevis-Limonietum dodartii* (Lahondère et Bioret 1997) ass. *nova hoc loco*; 1), 2), 3), 10), 11), 12), 13), 14) La Combe (SW de la pointe de Chassiron, Île d'Oléron) (17), 2000; 4), 16), 17), 15), 18), 19) La Nègrerie (SW de la pointe de Chassiron, Île d'Oléron), 2000; 8), 9) île d'Aix (17) (Lahondère et Bioret, 1997); 5), 7) La Grande côte, Saint-Palais-sur-mer (17) (Lahondère et Bioret, 1997); 6) Combat Les Mattes (17), 2004; 20) Corniche de Saint-Palais-sur-mer (17), (2004). Tableau 6 - *Spergulario rupicolae-Frankenietum laevis ass. nova hoc loco*; 1), 2), 3), 4) Le Croisic (44), côte sauvage (Rocher de l'ours), 2008; 5), 9) Houat (56), 1999; 6) Le Croisic, Baie du Scal (44), 2001; 7), 8), 10) Porspoder (29), 1991; 11) Hoëdic (56), 2006.
- Tableau 7 - Tableau synthétique des associations à *Frankenia laevis* et *Limonium* à nervures parallèles du littoral atlantique français:
- 1) *Parapholido strigosae-Limonietum occidentalis* (Lahondère et Bioret 1995) ass. *nova hoc loco*
 - 2) *Frankenio laevis-Limonietum occidentalis ass. nova hoc loco*
 - 3) *Frankenio laevis-Limonietum auriculursifolii ass. nova hoc loco*
 - 4) *Frankenio laevis-Limonietum ovalifolii* (Lahondère 1996) ass. *nova hoc loco*
 - 5) *Frankenio laevis-Limonietum dodartii* (Lahondère et Bioret 1997) ass. *nova hoc loco*
 - 6) *Spergulario rupicolae-Frankenietum laevis ass. nova hoc loco*
 - 7) *Frankenio laevis-Limonietum normannici* (Lemée 1952) Géhu et Bioret 1992
 - 8) *Cochleario anglicae-Frankenietum laevis* Géhu 1976
 - 9) *Limonietum auriculursifolii-dodartii* (Kunholtz-Lordat 1926) J.-M. et J. Géhu 1975 corr. *hoc loco*.
- EXPLICATION DES TABLEAUX**
- ° vitalité réduite
j juvénile
- BIBLIOGRAPHIE**
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FORÊTS VIERGES EN ROUMANIE

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ABSTRACT

The severe deterioration of the environment registered in the last century and its consequences have conducted to the conclusion that unaltered status of the environment is a prerequisite for a sustainable development. Virgin forests play a key role in this process. These forests have accumulated an important informational inheritance over the time and have a huge potential for the research of ecological phenomena in ecosystems unaltered by anthropic actions. According to a recent study, Romania has the highest area of virgin forests in the temperate region of Europe (app. 218 000 ha), which is rather poor in such forests. The largest area of virgin forests (98%) has been preserved in the remote areas of the Carpathian

Mountains. They represent a priceless natural capital, with a special scientific and cultural value belonging, not only to Romania, but also to the entire world. These forests must be preserved using the national network of protected areas, the forest management certification process and the zoning system adopted by forest management planning. The article presents a series of data and information concerning Romanian virgin forests distribution, structure and biodiversity.

KEYWORDS: Virgin forests, distribution, structure, biodiversity, Romania, Carpathian Mountains.

La Roumanie, pays située au centre géographique de l'Europe, possède encore 6400000 ha de forêts, la plus grande superficie dans les montagnes

(Carpates) (Fig. 1). Les forêts de Roumanie ont une grande diversité due, d'une part, à la position géographique du territoire sous l'influence de trois climats régionaux - le climat océanique, frais et humide, de l'ouest, le climat continental, sec, de l'est et le climat chaud et sec du sud de l'Europe, et, de l'autre part, à la présence de la chaîne des Carpates, au centre du pays, déterminant les climats des montagnes plus froides et plus humides que les climats des plaines.

Sur la carte suivante on peut voir cette diversité des forêts roumaines (Fig. 2). En effet en Roumanie il y a des forêts boréales d'épicéa dans les hautes montagnes, des forêts némorales du sapin, du hêtre dans les montagnes, chêne rouge et chêne pédonculé dans les collines, des forêts subméditerranéennes avec *Quercus cerris* et *Q. frainetto*

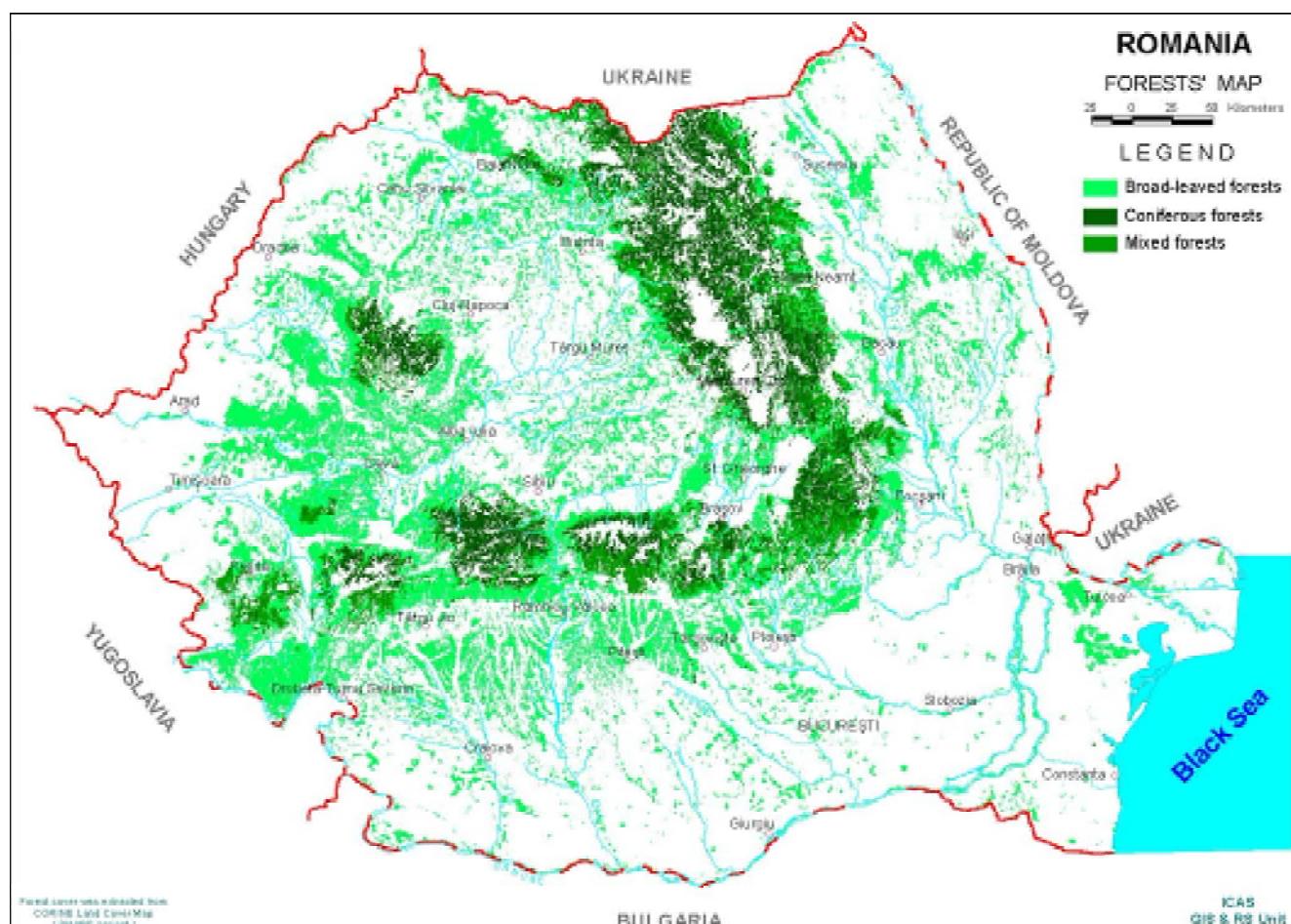


Fig. 1 - Carte des forêts roumaines.

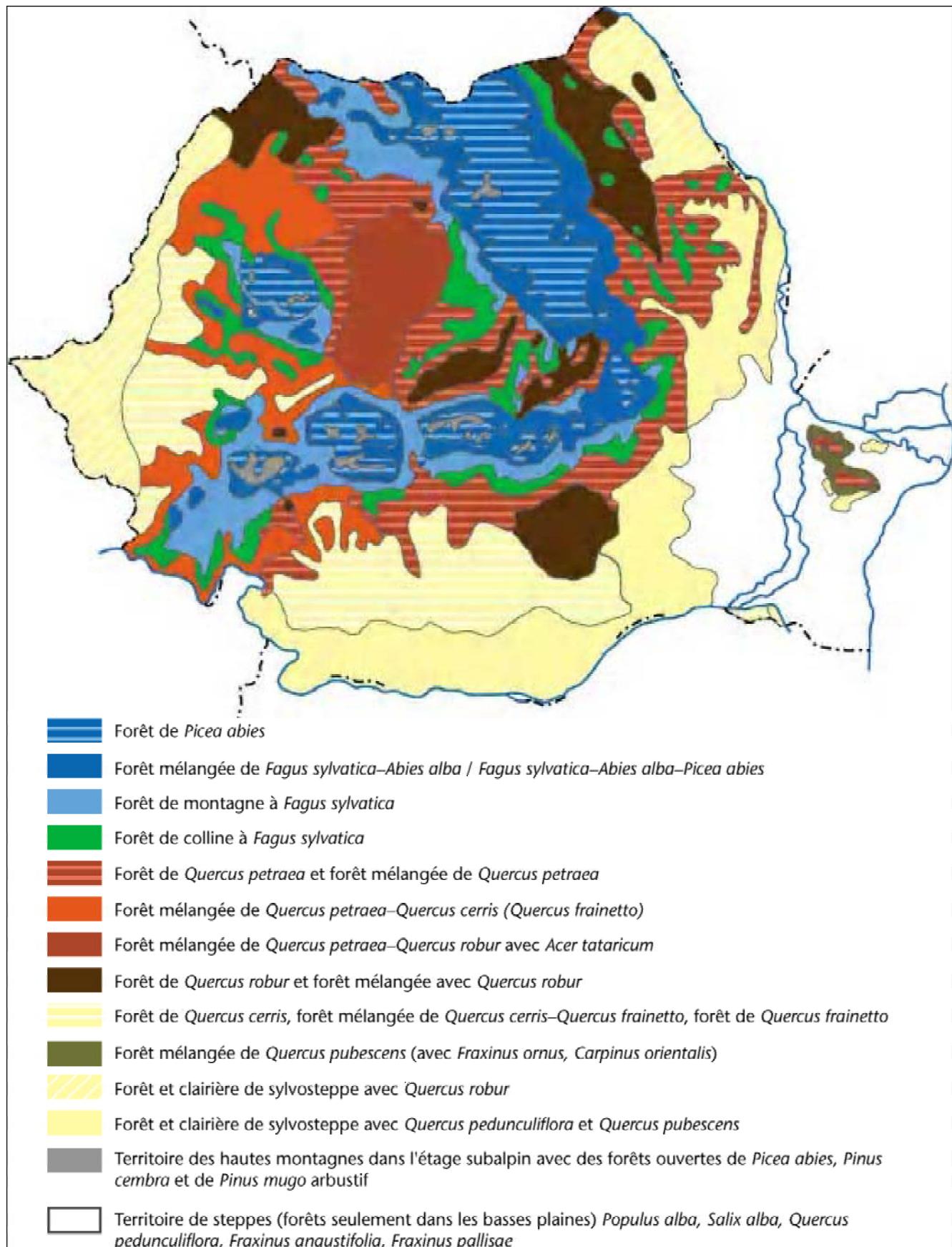


Fig. 2 - Principales formations forestières de Roumanie (d'après DONIȚĂ *et al.*, 1981).

dans les plaines et de forêts et forêts claires xériques avec *Quercus pedunculiflora* et *Q. pubescens* dans la steppe forestière.

Parce qu'en Roumanie l'industrialisation a commencée seulement à la fin du XIX^e siècle,

beaucoup de ces forêts étaient encore vierges au début du XX^e siècle. En 1903, le professeur P. Antonescu, de la Faculté de Sylviculture, écrivait: «Dans notre pays il y a des nombreuses forêts, surtout dans la région montagneuse, dont, à cause de l'absence des routes

forestières, n'ont pas été exploitées. Dans ces forêts les peuplements possèdent l'aspect de la futaie jardinée irrégulière, c'est à dire les dimensions et les âges des arbres sont presque partout confus, mélangés et où ils se présentent sous la forme de petits

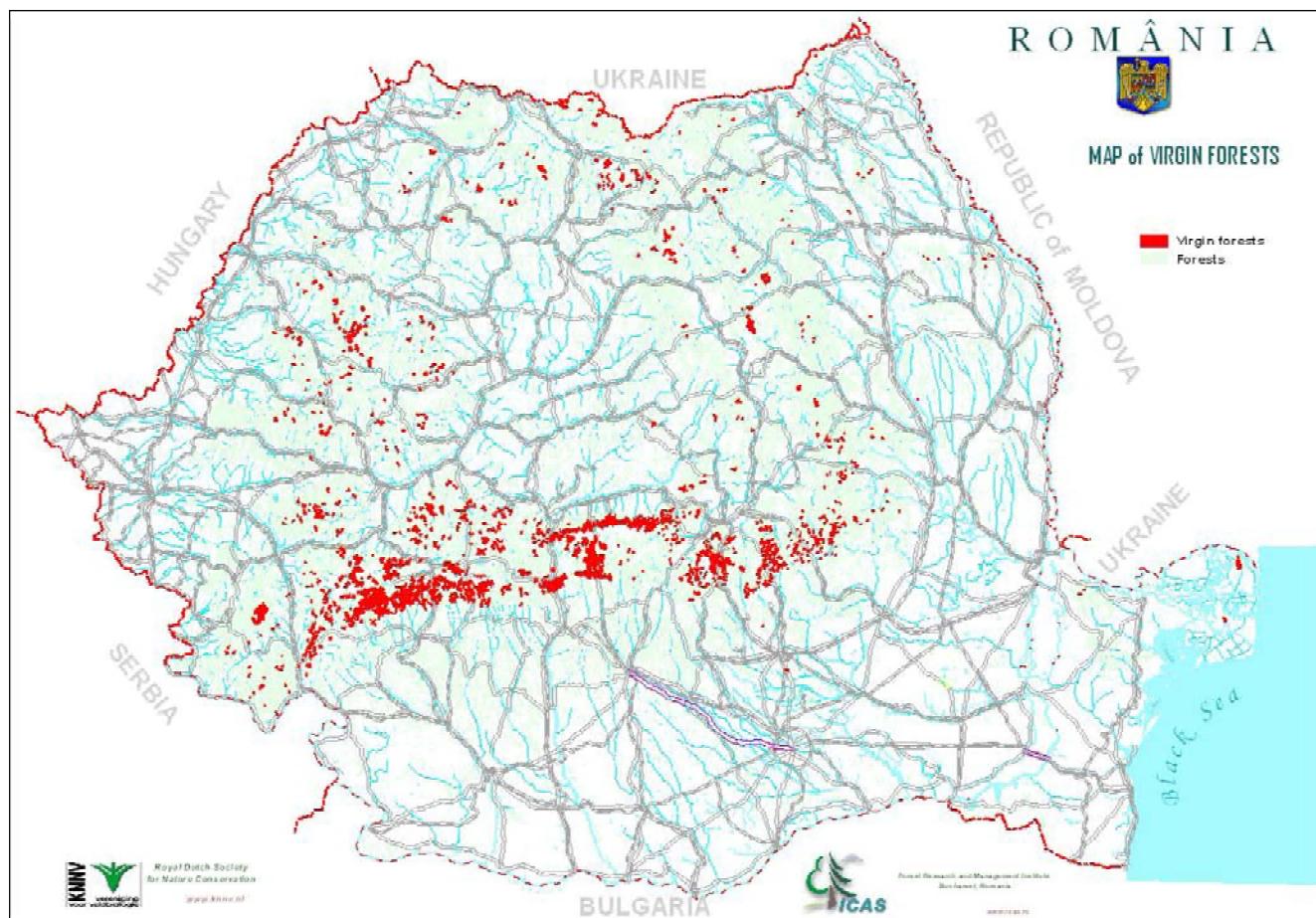


Fig. 3 - La répartition des forêts vierges en Roumanie (BİRİŞ et VEEN, 2005).

bouquets au groupes d'âges plus ou moins uniforme, régulièrement distribuées sur la plupart de la superficie de la forêt» (ANTONESCU, 1903).

P. Antonescu a étudié la structure de ces forêts dans les Carpates Méridionaux, mais il n'a pas publié les résultats. Quelques valeurs synthétiques ont été publiées par RUBNER (1934, 1960).

J. Fröhlich, qui a étudié aussi des nombreux forêts vierges dans les Carpates, a publié une série de ses inventaires et une synthèse (1954).

D'autres études sur ces forêts ont été publiés par POPESCU-ZELETIN (1936, 1958), RUCĂREANU (1939), PRODAN (1944), PREDESCU (1953), DISSESCU (1958), COSTEA (1962), TÂRZIU (1970), LEAHU (1971, 1972), GIURGIU (1974, 1984), CENUŞĂ (1992), SMEJKAL *et al.* (1995), IACOB *et al.* (1998). En 2001 a été publiée, en français et en roumain, un volume sur quelques forêts vierges du Roumanie (GIURGIU *et al.*, 2001).

Mais qu'est ce que s'est une forêt vierge? C'est une forêt naturelle que n'a pas souffert d'influence anthropiques significatives capable d'altérer la composition, la structure et les processus biocénotiques, les caractéristiques du habitat.

Malheureusement l'industrialisation rapide pendant le XX^{ème} siècle et spécialement pendant les années 1960-

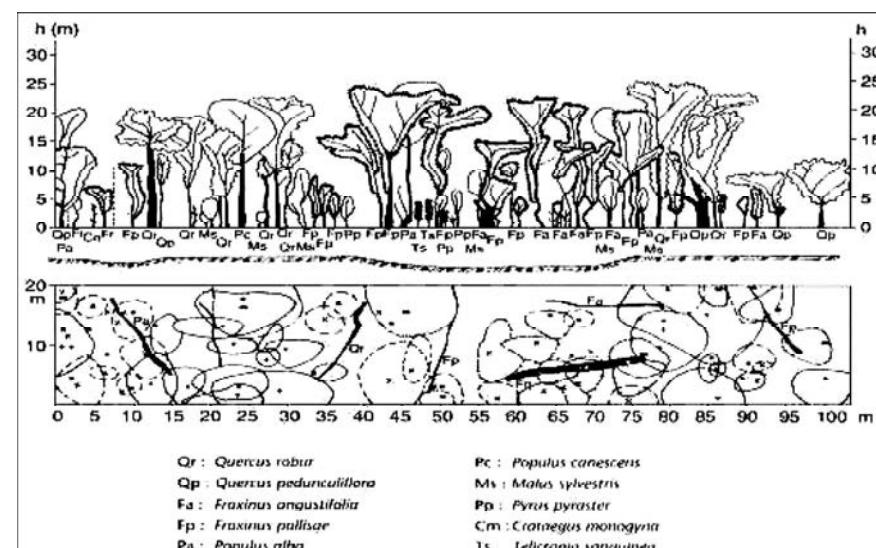


Fig. 4 - Structure d'un peuplement ripicole dans la réserve naturelle de la forêt de Letea.

1989, et le développement d'un réseau de chemins forestiers ont été les causes d'une sévère réduction de la surface des forêts vierges. En 1970 on comptait encore 400.000 ha. Un récent inventaire n'a trouvé que 218.500 ha des forêts vierges (ayant les surfaces de plus de 50 ha). Presque toutes ces forêts se trouvent dans les montagnes, au fond des vallées, où l'accès est encore difficile. Mais un récent programme de construction de 20.000 km de nouvelles chemins forestières, pour visiter toutes les forêts, menace les forêts vierges qui ne sont

pas incluses dans les zones protégées.

Le projet d'inventarier les forêts vierges de Roumanie a été financé par la Société Royale Hollandaise de Protection de la Nature, et a été réalisé par l'Institut de Recherches et d'Aménagement Forestier Roumain, dans le programme MATRA, pendant les années 2001-2005, (BİRİŞ et VEEN, 2005).

La répartition de ces 218.500 ha des forêts vierges est la suivante (Tableau 1). En ce qui concerne la répartition des unités de relief de grande envergure, environ 98% des forêts vierges de

Tableau 1 - Répartition des forêts vierges grandes unités typologiques.

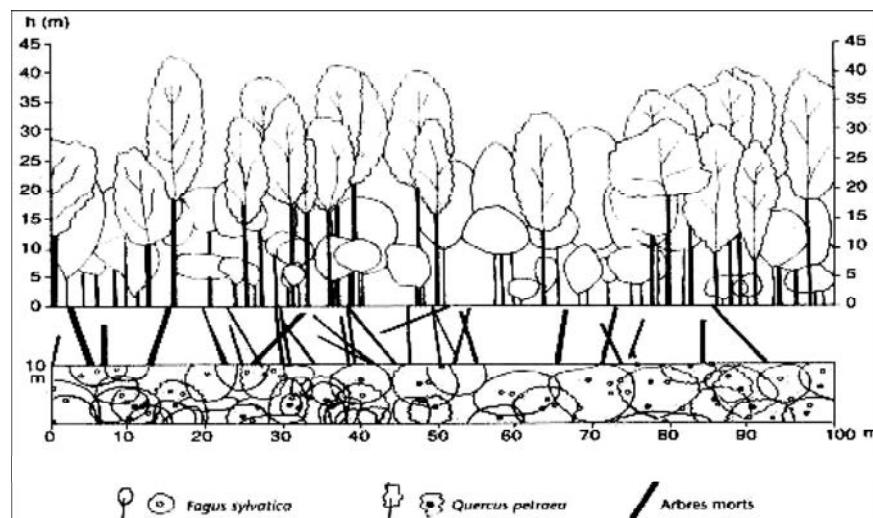
	Grande unité typologique	Surface (ha)
1	Forêts et forêts claires boréales (<i>Picea abies</i> , <i>Larix decidua</i> , <i>Pinus cembra</i>)	46933
2	Forêts némorales (<i>Abies alba</i> , <i>Picea abies</i> , <i>Fagus sylvatica</i>)	46645
3	Forêts némorales de <i>Fagus sylvatica</i> des montagnes	92437
4	Forêts némorales de <i>Fagus sylvatica</i> des collines	20867
5	Forêts némorales de <i>Quercus petraea</i>	3563
6	Forêts némorales de <i>Quercus robur</i>	378
7	Forêts subméditerranéennes de <i>Quercus cerris</i> et <i>Q. frainetto</i>	66
8	Forêts et forêts claires de sylveste forestière	66
9	Forêts ripariennes	931
10	Autres forêts	6408
	Total	218494

Tableau 2 - Structure des peuplements par phase d'évolution de la forêt vierge de Giumalău.

Phase d'évolution	Nombre d'arbres par ha	Diamètre des arbres (cm)	Hauteurs des arbres (m)
Initiale	1546	18,6	15,6
Optimale	1000	27,1	19
Optimale tardive	665	27,5	19,3
Terminale avec de la régénération	913	22,5	14,5
De dégradation	320	30,5	20,3

Tableau 3 - Volume du bois mort par phases d'évolution de la forêt vierge de Giumalău.

Phase d'évolution	Volume du bois mort (m ³)	Proportion du bois mort au volume total du bois (%)
Initiale	71	8,7
Optimale	167	29,2
Optimale tardive	75	14,6
Terminale avec de la régénération	119	19,6
De dégradation	108	32,1

Fig. 5 - Structure d'un peuplement de chêne rouvre (*Quercus petraea*) et de hêtre (*Fagus sylvatica* ssp. *moesiaca*) dans la réserve naturelle de Runcu.

Roumanie se trouvent dans les Carpates et seulement une fraction (0,6%) dans les collines et dans les plaines et la prairie et Delta du Danube (1,3%). Les grandes surfaces de forêts vierges se trouvent dans les Carpates Méridionales (environ 79%), suivie par Carpates Orientales (11%), les Carpates Occidentales (8%) (Fig. 3).

Les forêts vierges sont le plus grand réservoir de la biodiversité forestière. Elles abritent la plus grande partie des champignons et des insectes, 84% des mammifères, 62% des oiseaux, 87% des reptiles,

les, 94% des amphibiens, 62% des poissons du pays.

Actuellement, 75% des forêts vierges sont incorporées dans les parcs naturels et nationaux, mais seulement 18% se trouvent dans les zones de protection spéciales où l'accès est interdit. Or, précisément la protection absolue de ces forêts est la condition de leur développement naturel sans aucune intervention de l'homme, sauf la recherche scientifique.

La structure de quelques forêts vierges est rendue de suite (d'après GIURGIU

et al., 2001).

La réserve naturelle de la forêt de Letea se trouve sur une île de sable dans le Delta du Danube (altitude 1-5 m, climat aride avec des températures annuelles de 11,3 °C et des précipitations de 350 mm). Des longues lanières étroites de forêt occupent les dépressions parmi les dunes de sable où l'humidité permet le développement des arbres.

La végétation des forêts est complexe: des chênes (*Quercus robur*, *Q. pedunculiflora*), des frênes (*Fraxinus angustifolia*, *F. pallisae*), des peupliers (*Populus alba*, *P. tremula*, *P. canescens*), des nombreux arbisseaux et surtout des rideaux des lianes (*Vitis sylvestris*, *Periploca graeca*, *Hedera helix*, *Clematis vitalba*) (Fig. 4).

La réserve naturelle de la forêt de Runcu se trouve dans la région des collines au centre du pays (altitude 550 m, climat chaud et humide avec des températures annuelles de 8,2 °C et des précipitations de 850 mm). C'est une forêt de chêne rouvre (*Quercus petraea*), de 120-200 ans (les arbres ayant une hauteur en plus de 40 m), mélangée avec le hêtre (*Fagus sylvatica* ssp. *moesiaca*) (Fig. 5).

La réserve naturelle de Nera est située au sud-ouest de la Roumanie (altitude entre 700 et 1400 m, climat frais et humide, avec des températures

annuelles de 6,5 °C et des précipitations annuelles de 1100 mm). Située dans les montagnes au sud-ouest du pays, c'est la plus remarquable des forêts vierges de Roumanie, bien connue dans tout l'Europe. L'arbre dominant c'est le hêtre (*Fagus sylvatica*). L'âge des arbres est de 20 à 280 ans et les hauteurs jusqu'à 50 m (Fig. 6).

La réserve naturelle de Slătioara dans les Carpates Orientales (altitude 850 m, climat frais et humide avec températures annuelles de 5 °C et précipitations annuelles de 820 mm). Une forêt séculaire de hêtre, sapin et épicéa avec des arbres de plus de 40 m en hauteur (Fig. 7).

La réserve naturelle de Giumalău, aussi dans les Carpates Orientales (altitude 1250-1280 m, climat froid et humide avec des températures annuelles de 3,0 °C et des précipitations annuelles de 910 mm). Une forêt d'épicéa avec des arbres âgées de 20 à 200 ans ayant une hauteur dépassant 40 m (Fig. 8).

Pendant les dernières années, dans quelques forêts vierges, on étudie la composition et la structure des biocénoses, leur dynamique.

Dans la réserve de Giumalău on a établi le nombre, le diamètre et la hauteur des arbres par phase d'évolution de la forêt vierges (Tableau 2).

On a déterminé aussi le volume du bois mort (Tableau 3).

Étudiant les insectes du sol et saptoxyliques on a trouvé 239 espèces de *Coleoptera*, 86 espèces de *Collembola*, 25 espèces de *Araneae* (NIRZU *et al.*, 2008, 2009). La plus part des insectes sont détritivores (125). On a trouvé aussi 99 espèces de *Briophytes* (42 *Hepaticae* et 57 *Musci*) (BIRIŞ *et al.*, 2008).

Les forêts vierges de la Roumanie ont une grande importance comme témoignes de la grande forêt qui couvrait jadis les Carpates et les territoires conjoints, comme réservoir d'une riche bio et éco diversité, mais aussi comme objet d'études de la structure et des processus éco systémiques de la forêt naturelle. Leur sauvegarde s'impose pour ne pas perdre cette richesse inestimable.

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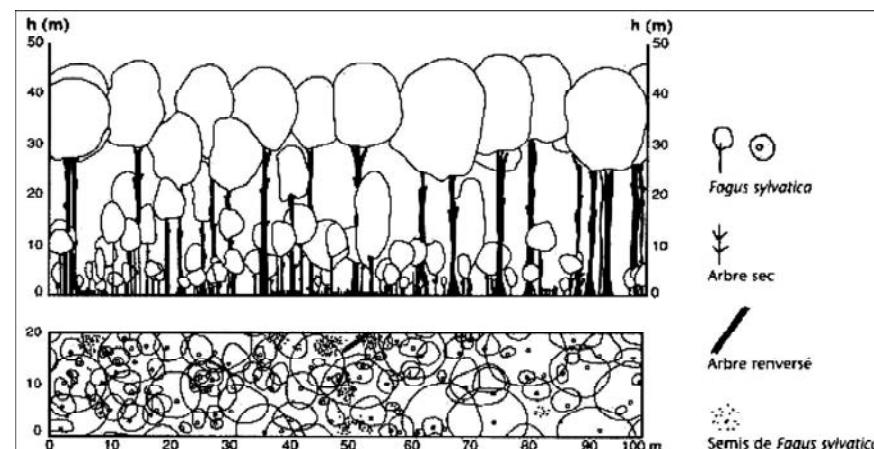


Fig. 6 - Structure d'une hêtraie de montagne dans la réserve naturelle d'Izvoarele Nerei.

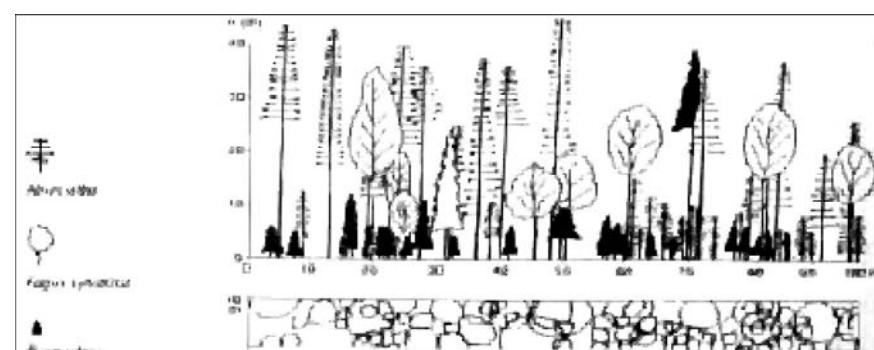


Fig. 7 - Structure d'un peuplement mélange hêtre-sapin-épicéa dans la réserve naturelle de Slătioara.

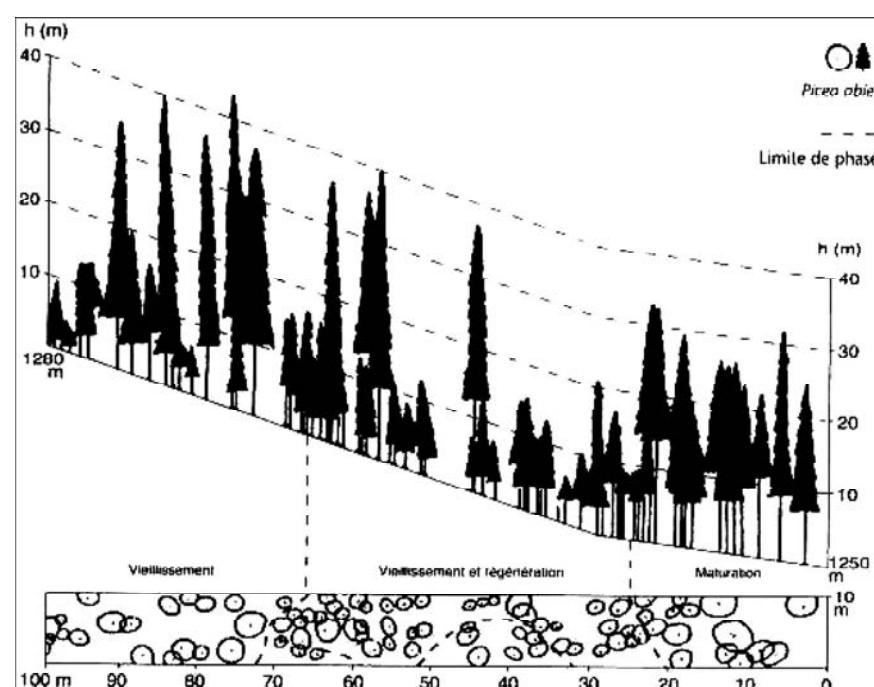


Fig. 8 - Structure d'une pessière dans la réserve naturelle de Giumalău.

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WHAT ELSE CAN BE DONE WITH RELEVÉ DATA: EASTERN NORTH AMERICA?

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ABSTRACT

Braun-Blanquet relevés provide not only species information for phytosociological classification but also description of vegetation structure and often ancillary environmental data, which can be included to analyze other vegetation aspects. The Eastern North American Vegetation Survey provided a large, geographically extensive relevé data-base that can be used for various other purposes, including study of vegetation structure and determinants of species richness. A limited phytosociological classification was already done, as well initial statistical study of species richness. This paper suggests some other uses of large plot data-bases, including a non-taxonomic methodology that may yield insight into vegetation structure and richness.

KEYWORDS: relevé data-base, ancillary plot data, substrate characterization, qualitative plot analysis, species richness, Eastern North American Vegetation Survey.

INTRODUCTION

Phytosociology can be viewed as a three-step procedure, involving field data collection, tabletop to identify community groupings, and placement of these groupings into a general hierarchy of types. Braun-Blanquet relevés collected in the field provide not only species composition, however, but also three-dimensional descriptions of vegetation structure, which can be analyzed in various ways to gain insight into the processes and relations that may govern the structure, dynamics, and species richness of vegetation. One might thus legitimately ask what else can be done with such data. Further uses are not limited to analyses that require species identification.

Individual relevés can suggest future vegetation dynamics and dominant species based on regeneration by overstorey species found in understorey layers. Small numbers of relevés can be

used as permanent quadrats for monitoring plant growth or vegetation change over time. More general insight requires large numbers of relevés collected over and adequately representing the geography of large areas. Among the uses of such larger data-bases are:

- Geographic inventory of taxon distribution, frequency and abundance;
- Identification of factors related to vegetation dimensions, such as height and cover;
- Study of structural relationships within the vegetation, such as between the cover of the individual vegetation layers, or between cover and species richness;
- Study of diversity and species richness in vegetation, in total or by layer; and
- Study of the autecology of the plants that compose the vegetation.

Most of these endeavors require building large vegetation data-bases that include not only relevé data but also ancillary data such as for climate and substrate properties.

In 1988-90, the so-called Eastern North American Vegetation Survey (ENAVS) provided the relevé basis for one such large, geographic vegetation data-base. ENAVS was and probably still is the most geographically extensive vegetation survey ever done in eastern North America by Braun-Blanquet methodology, gathering about 1,400 relevés of mostly natural vegetation. Transects were made from south Florida to Ontario to Québec in June 1988, from Québec to west Florida to Louisiana in September-October 1989, and from New England to the Florida Keys in September-October 1990 (see Fig. 1 in MIYAWAKI *et al.*, 1994). The survey, under the direction of Prof. Akira Miyawaki, was a follow-up to the ten-year "Vegetation of Japan" project (MIYAWAKI, ed., 1980-89) and was funded by Monbushō (the Japanese Ministry of Science, Education and Culture), in order to gather data for comparison with comparable geographic situations in Japan.

The ENAVS data were classified phytosociologically by the Japanese team, as far as number of relevés would permit, and results were published by

MIYAWAKI *et al.* (1994). Of course, for such a large area, not all vegetation types had enough relevés for valid phytosociological classification, and in fact almost 10% of the taxa identified in the field as "species" were not identified completely until later (some never). Even so, after publication of the book, the data had served their immediate purpose in Japan. The question remained, though, what else could be done with such a large data-base. One immediate suggestion is to look at patterns and correlates of the number of species in the plots, which can be done even with taxa that are not all completely identified. The purpose of this paper is to describe the ENAVS data-base, how it was computerized and amplified with ancillary data, and how it has been and can be used further to study vegetation patterns in eastern North America, especially patterns of species richness and abundance, and vegetation diversity.

FIELD METHODOLOGY AND DATA

Field itineraries were organized by Box in the USA, by Miroslav Grandtner in Québec, and by Paul Maycock in Ontario (Box, 1994). In the USA, many local experts suggested study sites and helped with species identifications. Sampling always sought natural, more or less stable vegetation, but ruderal and other vegetation was also sampled as opportunities arose. The relevés were recorded by traditional Braun-Blanquet methodology, using cover and sociability scales of 1-5, as described in detail by FUJIWARA (1987). Plots were of course not square, but sizes generally followed the rule-of-thumb that one side of an equivalent square plot should be similar to canopy height. Each relevé was recorded on a separate relevé form, designed by the Japanese team. Data recorded for each plot, in addition to the species data, include date and relevé number, layer heights and cover amounts, region and closest city or town, elevation, slope and aspect, relevé size, personnel (scribe underlined), and verbal descriptions of

Topography: summit, ridge, slope (upper middle lower concave convex), valley, flat, depression, floodplain, alluvial, marsh, fen/bog, swamp.
Soil type: podzol, brown, red, yellow, black, white-sand, humic-sand, gley, pseudogley, sandy-loam, silt, gravel, rubble, rocky, submerged, other: _____.
Soil moisture: dry, mesic, moist, hydric.
Soil depth: deep, shallow
Litter layer: _____.

Topographic and substrate properties of relevé sites were described, in the field, by circling the appropriate terms, sometimes also by providing additional notes in the spaces indicated. The data form was designed by the vegetation science group at Yokohama National University for ENAVS and all subsequent fieldwork.

ENAVS = Eastern North American Vegetation Survey (1988-1990).

Fig. 1 - Plot Environmental Features Recognized on ENAVS Field Data Forms.

vegetation type and more detailed location of the plot.

In 1989-90, topography and substrate information were also recorded for each site, by circling appropriate terms on the back side of relevé forms (see Fig. 1) that had been improved based on experience the first year. Topographic information includes slope position and other relevant features, such as location on a ridge or in a floodplain or other depression. Substrate information includes soil texture, color, humic content, and wetness, as well as depth and perhaps verbal description of a surface litter layer. A vegetation profile was also sketched by one team member, for most relevés, which helped greatly with later interpretations.

Forests and other woods were sampled in most states/provinces, but especially in Georgia and Florida, with their richness of upland and remaining bottomland and floodplain forests, includ-

ing swamps (see Tab. 1). Scrub and savanna vegetation, usually on sand, was sampled especially in the Carolinas and Florida. Wetlands were most sampled along the St. Lawrence estuary, in lower New England, in the Carolina coastal plain (pocosins), in the Pearl River basin and Mississippi delta in Louisiana, and in Florida. Coastal vegetation was sampled especially in Nova Scotia, on Cape Cod and Long Island, and along the North Carolina coast, the Georgia embayment (especially salt marshes), and both coasts of Florida. Mountain vegetation was sampled mainly in Québec and the southern Appalachians of North Carolina but also on Mt. Washington (New Hampshire).

DATA-BASE CREATION

The data were typed into computer files in 1990-91, at the University of

Tab. 1 - ENAVS Relevé Totals by Location.

	N	Forests/ Woods	Scrub/ Savanna	Dw-Scrub/ Herb	Wetlands	Mountains	Coastal	Other
Ontario	31	17	5		9			
Québec	157	15	5	40	53	40		2
New Brunswick	18	1			17			
Nova Scotia	28	6	1	5			15	1
Maine	14	7	2	4	1			
New Hampshire	7					7		
Massachusetts	66	4	1	9	5		47	
Connect. + Rhode I.	45	20	3	1	20			1
New York + N.Jersey	38	15	1	1		3	22	
Pennsylvania	12	12						
Maryland + Del.	41	33			8			
W. Virginia	15	8	1		5	[7]		1
Virginia	31	18			1	[6]	12	
N. Carolina	198	29	30	9	30	43	53	1
S. Carolina	30	6	13		8		4	
Georgia	146	80	13		2	49		2
Alabama	13	13						
Mississippi	22	8			4		10	
Louisiana	51	18	1		26		6	
Florida	188	70	23	1	14		40	2
S. Florida	6	4			4		23	1
Totals	1151	381	105	78	185	171	220	11

Relevés are from the region east of the Appalachian Mountains, from Laurentide Québec and the Saint Lawrence estuary to South Florida and west along the Gulf coastal plain to southeastern Louisiana. The numbers of relevés shown here, for different vegetation types, are based on an initial, algorithm-based classification. Forests are considered to be closed and relatively tall, while shorter or open tree-dominated stands are called woods. Scrub is generally shorter or more open, or both, and not necessarily dominated only by trees. Herbaceous stands include meadows and pioneer vegetation. Abbreviations: Dw-Scrub=dwarf-scrub. ENAVS=Eastern North American Vegetation Survey (1988-1990).

Georgia, in a format designed to facilitate the typing. The resulting data-base, built initially on a mainframe computer, was not designed for compatibility with other packages because others did not yet exist. Nor did standardized relevé-processing software (e.g. JUICE), geographic positioning systems, laptop computers, WORD, or even Windows exist; desktop computers and their first really useable language compilers were just then becoming generally available. Nevertheless, all relevé information on the field data forms was entered, but no attempt has been made to convert to EXCEL or other subsequent proprietary format.

The next step was to write programs for data management, specific to the data format: RELVIEW for data scanning and error suggestion, RELEVIN for re-formatting into consistent columns and into printable relevé format, RELSPP for itemizing species and counting their occurrence, RAWTABLR for creating raw tables for phytosociological tablework, RELSPECs for summarizing plot characteristics, and others. In the early 2000s, all relevé sites were relocated on maps and given geographic coordinates (hundredths of degrees). At this time, the climate at each site was also reconstructed, by three-dimensional triangulation (program POLATE) from nearby meteorological stations, and climatic water budgets were calculated (program SOLWAT). Finally, some site topographic and substrate characters were also coded, and a scheme for their quantification was explored.

The plots were classified initially by an automated physiognomic algorithm (subroutine STAND) that recognizes structural types such as forest, open woods, scrub, marshes, and bogs, based on height and cover values plus some keywords in the verbal vegetation descriptions. Geographic coverage in the data-base and representation of different general vegetation classes, as classified by the physiognomic algorithm, are shown in Tab. 1.

INITIAL ANALYSES

Some further uses of large, geographic relevé data-bases have already been suggested, but study of factors related to species richness in vegetation, at all scales, is perhaps of particular interest. Potential controls or at least correlates of species richness have been suggested, and main

hypotheses were summarized by PALMER (1994). Increasing species richness in larger areas is well understood, and it is generally expected that richness will increase with greater spatial heterogeneity of habitats. Even so, consistent relationships between environmental (or biotic) factors and total species richness, at plot scale, have not been shown over large, diverse geographic regions.

Statistical analysis of relationships between whole-plot species richness and environmental factors, including climate, was attempted for the whole ENAVS region. This included an attempt to quantify some of the most important substrate properties, such as soil texture (on the 0-3.5 SOLWAT scale). Even with this inclusion of substrate and exclusion of wetlands and other edaphically or topographically controlled plots, however, only weak relationships were found (SABIN, 2005). Quantification of substrate properties was subsequently abandoned as being too vulnerable to artifact. Instead it seems better simply to code the topographic and substrate features verbally, in abbreviated form, and rely on “expert system” processing and decision making by those who saw the sites and recorded the data.

Investigating controls of species richness does not require that all species have names, but it does require smaller, more summarizing data-bases. Since RELSPECs summarizes almost all the coded data except names and values for the individual species, it could be used to summarize plot structure and provide a summary table of both the verbal and quantitative characteristics for each relevé. In particular, the resulting summary table (too wide to show here) shows the height, cover and number of species, in a convenient side-by-side format, for each individual layer, as may be needed for identifying relations between vegetation attributes and substrate or topographic factors. Since each relevé is represented by a single line in the table, the relevés can be re-ordered easily by hand.

The relevés were then re-sorted manually, beyond the physiognomic algorithm, into more biotope-based vegetation types. This involved qualitative ecological interpretation of the sites and vegetation, based on vegetation structure and on the topographic and substrate information provided on the relevé forms (1989-90, inferred from other notes for 1988). Vegetation structure includes structural type, height, canopy closure, number of

Tab. 2 - Wooded Stand Types and Selected Main Subtypes Recognized in ENAVS Relevés, with Canopy Height and Cover, and Species Richness (excluding subtropical).

	Nrel	Ht	Cover	Nspp
Northern Deciduous Forests (BL/mixed)	37	45-18m	90-70	75-21
Bottomland/Floodplain Forests	11	33-20m	90-60	42-23
Forests on Rocky Terrain	19	30-15m	90-60	44-15
Urban Forests (mostly Northern)	10	40-25m	85-70	51-33
Southern Deciduous Forests (BL/mixed)	51	47-18m	90-70	66-22
Open-Canopy Forests (tall)	6	46-25m	60-50	52-22
Bottomland Forests (moist, less flooded)	8	38-28m	80-70	75-33
Floodplain Forests (inundated more)	35	38-20m	90-50	63-26
Forests on Rocky Terrain	5	28-15m	85-75	41-21
Forests on Humic/White Sand	19	42-20m	90-60	47-21
Mainly Evergreen Forests (broadleaf)				
Sclerophyll, on Humic Sand	23	30-18m	85-70	48-14
Sclerophyll, on White Sand	3	22-16m	80-70	25-17
Bottomland Forests (moist, less flooded)	6	32-20m	80-70	74-28
Floodplain Forests (inundated more)	13	30-22m	85-70	57-17
EG and Semi-EG Delta Forests	7	27-22m	90-80	43-17
Bay Forests (laurophyll)	7	35-22m	85-60	22-9
Swamps and other Inundated Woods				
Everwet/Long-Flooded	4	25-14m	75-40	9-2
Dry-Phase Swamps (sampled dry)	16	35-13m	90-40	46-14
Myakka River Dry Swamps (sampled dry)	4	23-20m	80	19-16
<i>Taxodium</i> Swamps (incl. dry-phase)	11	50-18m	90-20	31-15
Cedar Swamps (<i>Chamaecyparis thyoides</i>)	7	30-13m	70-40	27-7
Red-Maple Swamps (<i>Acer rubrum</i>)	7	28-15m	85-60	33-13
Woodlands (BL and mixed)				
Open Woodlands (15m or taller)	5	25-20m	60-40	60-44
Closed Oakwoods under Sparse Pine	3	18-12m	20	20-14
Sandhill Woods	14	13-8m	80-40	36-14
Short Woods on Dry White Sand	5	12-8m	70-60	21-10
Pine Forests and Woods				
Seral Pinewoods (non-sand substrates)	5	36-18m	50-30	54-44
White-Sand Pinewoods	6	26-14m	65-40	35-18
Short Pinewoods	10	15-10m	70-38	30-8
Open Pine Woods/Savannas	16	30-12m	40-10	42-22
Tsuga Forests	18	40-18m	90-70	47-5
Boreal Woods	6	24-17m	75-50	28-12
Boreal Woods on Sand	3	17-12m	70-60	26-8
Upland Subpolar analogs	5	20-15m	80-40	20-6
Cedar Woods (<i>Thuja occidentalis</i>)	6	24-11m	70-20	37-14
Aspen Forests (<i>Populus tremuloides</i>)	3	22-17m	70	46-32
Mountain Vegetation				
Mountain Forests (deciduous/mixed)	18	45-22m	90-70	60-29
Upper-Montane Low Woods (non-conifer)	5	15-14m	80-50	39-16
Subalpine Conifer Woods	11	17-10m	90-20	28-8
Treeline Conifer Krumholz	3	6-3m	80-70	19-9
Summit Scrub	10	8-4m	60-20	22-7
Scrub and Thickets				
Sand Scrub with Pine Overstorey	5	20-10m	90-60	26-9
Pocosin with Pine Overstorey (peat)	9	18-12m	100-80	37-8
Sandhill Scrub	4	12-5m	5	10-7
Low Pocosin (peat)	4	7-3m	10-5	24-6
Coastal Woods (terrestrial)				
Dune Forests	18	28-15m	85-40	36-15
Low Dune Woods/Hammocks	10	12-6m	80-20	27-10

Stands are classified by structure, topographic position, and substrate type and wetness. Nrel = number of relevés; Ht = canopy height; Cover = cover of main level; Nspp = number of species. ENAVS = Eastern North American Vegetation Survey (1988-1990).

levels, and cover of relevant understorey levels, such as a dense shrub layer that may reduce herb-layer richness. Site physical characteristics include not only the characters shown in Fig. 1 but also other noted indications of soil moisture and humic content, rockiness, and presence of standing water (and its supposed seasonality). The result is a classification by familiar physiognomic types (forests, marshes, etc.) at the first level, then by physiographic provinces (e.g. northern vs southern, with mountains and coastal grouped separately), and then by local topography and substrate characteristics, especially slope position and soil texture, humic content and wetness. A necessarily condensed summary of this result is shown in Tab. 2, for woody types only.

This classification of more ecological plot types includes entries such as floodplain forests or woods on rocky upper slopes, which are tied closely to substrate or topographic situations (or both). Ranges of values within each type are shown for canopy height, cover of the main vegetation layer, and total species richness. The widest ranges of species richness appear in open-canopy forests, woods on rocky terrain, forests and woods on sand, floodplain forests and dry-phase swamps, pocosin scrub, most kinds of dune vegetation, alpine vegetation, and herbaceous vegetation, especially ruderal, in wetlands, and on littorals. The general forest classes also show wide ranges, due to the larger numbers of stands. On the other hand, some vegetation types show rather little variation in species richness: pinewoods, longer-flooded floodplain forests such as *Taxodium* swamps, boreal woods, bogs, riparian and dry-phase littoral meadows, scrub of sandhills and other extreme substrates, and beach and aquatic vegetation.

CONCLUSIONS

Earlier analysis had shown little correlation between the total stand species richness and climatic variables, even when stands obviously controlled by other factors were excluded. Instead it appears that richness may be related more to vegetative cover in individual levels, and to substrate properties, than to climate. Some basic initial observations are that:

- There is often a wide range of total species richness within stands of the same vegetation type, with little appa-

rent relationship to the most obvious environmental conditions.

- The greatest total species richness appears in bottomland forests (especially in the South) but also in some upland forests, on sandstone, under open canopies, etc.

- There does not seem to be a large effect of plot size on species richness.

- There is consistently low richness in dense laurophyll forests (bay forests and *Tsuga* forests) and in vegetation on sand, especially if the humus content is very low.

In forests, understorey cover sometimes varies more widely in poorer than in richer stands.

Some relationships between layers were also suggested, such as between cover and richness in individual layers or an inverse relationship between overstorey and understorey cover. Richness in understorey layers may be controlled more by topography and substrate properties, and is thus related more closely to environmental conditions than is total richness.

The value in this qualitative approach to vegetation analysis is that it was done with a large, geographically extensive and representative data-base, with a high diversity of biotope conditions and vegetation types. It also involves ancillary data that can be recorded easily in the field. The sorting methodology is described in more detail in another short paper (BOX & FUJIWARA, submitted), which shows portions of the full table, with height, cover and species richness of each layer. The next step is a more rigorous scrutiny of this full summary table.

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DATOS SOBRE LA VEGETACIÓN PSAMÓFILA RUDERAL DE LA COSTA CANTÁBRICA

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ABSTRACT

Two new associations from the coastal sandy environments of the Basque-Cantabrian area (Iberian Peninsula) are described in this paper: *Plantagini coronopodi-Cynodontetum dactyli* and *Hordeo murini-Arctothecetum calendulae*. Both are related to intense human impact and bear populations of naturalized alien species. We include them respectively in *Potentillion anserinae* and *Sisymbrium officinalis* alliances, due to their ruderal nature and floristic composition.

KEYWORDS: coastal sand dunes, *Arctotheca calendula*, *Sporobolus indicus*, alien plants, northern Iberian Peninsula.

RESUMEN

En este trabajo se describen dos nuevas asociaciones de los arenales costeros cantábricos de la Península Ibérica: *Plantagini coronopodi-Cynodontetum dactyli* y *Hordeo murini-Arctothecetum calendulae*. Ambas están favorecidas por la actividad humana y albergan poblaciones de plantas alóctonas naturalizadas. Las incluimos en las alianzas *Potentillion anserinae* y *Sisymbrium officinalis*, respectivamente, a la vista de su carácter ruderal y composición florística.

INTRODUCCIÓN

Los hábitats dunares han sido de-

clarados como hábitats de interés para la conservación a nivel europeo (Directiva 92/43/CEE) y albergan un elevado porcentaje de especies amenazadas; en el área eurosiberiana del País Vasco la flora amenazada de los hábitats litorales (dunas, marismas y acantilados) supone el 27% de la flora amenazada (PRIETO *et al.*, 2007). Estos ecosistemas están sometidos a un fuerte impacto antrópico, lo que ha dado lugar a su profundo deterioro. Además, presentan un alto grado de invasión: el 19% de las plantas alóctonas del País Vasco está presente en los hábitats litorales (CAMPOS y HERRERA, 2009). Dentro de estos ecosistemas litorales, las dunas albergan el mayor número de especies alóctonas, algunas de ellas de carácter fuertemente invasor (CAMPOS *et al.*, 2004). Esto se debe en parte a que las características climáticas de estas áreas costeras permiten el establecimiento de especies de origen tropical y subtropical que poseen un elevado potencial invasor. En este trabajo se estudian dos fitocenosis ligadas a la actividad humana y a la invasión de especies alóctonas.

MATERIAL Y MÉTODOS

El área de estudio comprende la mitad oriental de la costa cantábrica en el norte de la Península Ibérica (España), desde el oeste de Cantabria hasta el suroeste de Francia (Fig. 1). Biogeográficamente se encuadra en el sector Cántabro-Vascónico de la provincia Cántabro-Atlántica, dentro de la región Eurosiberiana (RIVAS-MARTÍNEZ, 2007). Se

han realizado 78 inventarios de vegetación según la metodología fitosociológica (BRAUN-BLANQUET, 1979), en un total de 17 arenales a lo largo de más de 300 km de costa, todos entre 0 y 10 m de altitud.

Para la identificación y nomenclatura de los taxones se han seguido Flora Iberica (CASTROVIEJO *et al.*, 1986-2010) y las Claves ilustradas de la flora del País Vasco y territorios limítrofes (AIZPURA *et al.*, 1999), excepto para *Catapodium marinum* (L.) C.E. Hubb., *Elytrigia juncea* ssp. *boreoatlantica* (Simonet y Guin.) Hyl., *Elytrigia atherica* (Link) Kerguélen ex Carreras y *Festuca rubra* ssp. *arenaria* (Osbeck) Aresch. En las tablas se han simplificado los trinómenes correspondientes a las subespecies a binómenes: *Ammophila australis* (*Ammophila arenaria* ssp. *australis*), *Arrhenatherum bulbosum* (*Arrhenatherum elatius* ssp. *bulbosum*), *Cakile integrifolia* (*Cakile maritima* ssp. *integrifolia*), *Crepis haenseleri* (*Crepis vesicaria* ssp. *haenseleri*), *Daucus gummifer* (*Daucus carota* ssp. *gummifer*), *Elytrigia boreoatlantica* (*Elytrigia juncea* ssp. *boreoatlantica*), *Festuca arenaria* (*Festuca rubra* ssp. *arenaria*), *Festuca pruinosa* (*Festuca rubra* ssp. *pruinosa*), *Herniaria robusta* (*Herniaria ciliolata* ssp. *robusta*), *Hordeum leporinum* (*Hordeum murinum* ssp. *leporinum*), *Hordeum murinum* (*Hordeum murinum* ssp. *murinum*), *Linaria maritima* (*Linaria supina* ssp. *maritima*), *Poa irrigata* (*Poa pratensis* ssp. *irrigata*), *Poa feratiana* (*Poa trivialis* ssp. *feratiana*), *Polycarpon diphyllum* (*Polycarpon tetraphyllum* ssp. *diphyllum*), *Raphanus landra* (*Raphanus*



Fig. 1 - Área de estudio. Los puntos indican la localización de los arenales muestreados.

Tabla 1 - *Plantagini coronopodi-Cynodontetum dactyli ass. nova* (*Molinio-Arrhenatheretea*, *Plantaginetalia majoris*, *Potentillion anserinae*).

Altitud (1 = 10 m)	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Área (m ²)	30	6	40	8	30	15	16	16	8	15	15	30	8	20	12	10	12	16	25	25	25	25	10	
Nº Especies	7	8	17	5	8	13	15	9	12	15	26	30	9	18	17	13	16	11	12	15	18	25		
Nº Orden	1	2	3	4	5	6	7	8*	9	10	11	12	13	14	15	16	17	18	19	20	21	22		
Características de asociación y unidades superiores																								
<i>Sporobolus indicus*</i>	5	3	5	4	4	5	5	5	4	1	1	3	+	1	1	
<i>Cynodon dactylon</i>	.	.	1	2	3	2	1	2	.	3	3	.	5	2	2	2	2	1	2	3	2	3		
<i>Plantago coronopus</i>	.	.	+	.	+	.	1	2	2	.	.	+	1	2	1	3	3	3	4	3	3	3	+	
<i>Plantago lanceolata</i>	.	1	.	+	.	.	2	1	1	3	2	2	+	.	2	.	.	+	1	+	1	1		
<i>Medicago littoralis</i>	.	.	+	.	.	+	.	1	1	1	.	3	2	+	.	2	1	3	.	+	.	.		
<i>Lolium perenne</i>	1	.	+	.	3	.	.	3	3	+	2	1	1	1	1	1	+	
<i>Hainardia cylindrica</i>	+	.	1	.	.	1	1	2	2	2	.		
<i>Stenotaphrum secundatum*</i>	.	.	.	2	.	2	+	.	.	2	3		
<i>Bellis perennis</i>	1	1	.	+	1	1		
<i>Ranunculus bulbosus</i>	1	+	.	.	+	1		
<i>Taraxacum officinale</i>	+	+	+		
<i>Trifolium repens</i>	+	.	2	1		
<i>Paspalum dilatatum*</i>	+	+	1	.		
<i>Poa irrigata</i>	1	.	.	+		
<i>Plantago major</i>	1		
Compañeras																								
<i>Arctotheca calendula*</i>	.	.	.	+	.	.	1	+	+	.	.	.	3	3	3	3	3	3	3	3	3	3	2	
<i>Poa annua</i>	1	.	.	+	.	1	1	3	1	.	1	+	1	1		
<i>Lagurus ovatus</i>	.	1	.	.	1	1	.	.	2	.	1	.	+	.	.	+	.	+	.	+	1	1		
<i>Conyza bonariensis*</i>	+	1	+	.	.	+	3	.	.	+	1		
<i>Polycarpon tetraphyllum</i>	.	1	1	.	1	2	1	+	2		
<i>Eryngium campestre</i>	.	+	1	2	.	1	.	.	.	+		
<i>Hypochoeris radicata</i>	+	1	.	.	+	+	+	.	.	.	+		
<i>Lophochloa cristata</i>	.	.	1	2	.	1	+	2	+		
<i>Raphanus landra</i>	+	+	+	+	.	.		
<i>Catapodium marinum</i>	.	.	1	1	.	1	1	1	1		
<i>Dactylis glomerata</i>	1	.	.	2	+		
<i>Lavatera cretica</i>	1	.	.	+	.	+	+	+	.	.	.			
<i>Leontodon taraxacoides</i>	+	+	.	1	+	3	.		
<i>Medicago polymorpha</i>	+	1	1	1	.		
<i>Vulpia fasciculata</i>	.	1	1	2	1	.	1		
<i>Bromus diandrus</i>	+	+	1		
<i>Veronica arvensis</i>	1	.	.	.	1	1	+	.	.			
<i>Crepis haenseleri</i>	2	+	.	+	.	.		
<i>Geranium molle</i>	+	+	.	+	.	+		
<i>Rumex pulcher</i>	+	+	+	.	+	.	.	.		

raphanistrum ssp. *landra*), *Rumex hispanicus* (*Rumex bucephalophorus* ssp. *hispanicus*), *Thymus britannicus* (*Thymus praecox* ssp. *britannicus*).

La clasificación numérica de los inventarios se ha llevado a cabo mediante el análisis de agrupación jerárquico. La matriz de disimilitud se calculó con la distancia de Bray-Curtis, previa transformación de los índices de frecuencia-abundancia de Braun-Blanquet mediante el cálculo de su raíz cuadrada, para disminuir el peso de las especies de mayor cobertura. La estrategia de agrupamiento fue el algoritmo “flexible method”, disponible en el módulo GINKGO de la aplicación VEGANA (FONT *et al.*, 2003).

RESULTADOS Y DISCUSIÓN

El análisis comparativo del conjunto de inventarios realizados nos ha permitido reconocer dos asociaciones nuevas para este tipo de hábitats en el territorio estudiado. Son fitocenosis de carácter ruderal, que contactan frecuentemente entre sí en los ecosistemas dunares más degradados y que muestran elevados índices de invasión por algunas especies alóctonas (señaladas en las tablas mediante *) como *Arctotheca calendula*, *Sporobolus indicus*, *Conyza bonariensis*, *Paspalum dilatatum* o *Stenotaphrum secundatum*, a las que se les une un importante contingente de especies de *Stellarietea mediae*, en detrimento de las especies psamófilas propias de la clase *Ammophiletea* Braun-Blanquet y Tüxen ex Westhoff, Dijk y Passchier, 1946.

***Plantagini coronopodi-Cynodontetum dactyli ass. nova hoc loco* (Tabla 1)**

Holosyntypus: Tabla 1, inv. 8

[Pastizales vivaces psamófilos mesoxerófilos ruderados cántabro-atlánticos]

En los accesos y senderos de playas y dunas de la costa cantábrica se desarrollan pastizales graminoides dominados por *Sporobolus indicus*, en los que participan también otras especies

Tabla 2 - Hordeo murini-Arcothecetum calendulae ass. nova (Stellaria mediae, Sisymbriata officinalis, Sisymbrium officinale).

Tabla 2 - continuación.

Nº Orden	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56				
<i>Rumex hispanicus</i>																																																												
<i>Arenaria leptoclados</i>																																																												
<i>Carex lutescens</i>																																																												
<i>Festuca juncifolia</i>																																																												
<i>Orinus ramosissima</i>																																																												
<i>Aphanes arvensis</i>																																																												
<i>Oenanthe diffusa</i>																																																												
<i>Medicago lupulina</i>																																																												
<i>Allium vineale</i>																																																												
<i>Calystegia soldanella</i>																																																												
<i>Conyza bonariensis*</i>																																																												
<i>Elytrigia atherica</i>																																																												
<i>Ranunculus bulbosus</i>																																																												
<i>Rumex crispus</i>																																																												
<i>Silene nocturna</i>																																																												
<i>Trifolium dubium</i>																																																												
<i>Vicia angustifolia</i>																																																												
<i>Aethiochrysa bulbosa</i>																																																												
<i>Anagallis arvensis</i>																																																												
<i>Arenaria serpyllifolia</i>																																																												
<i>Beta maritima</i>																																																												
<i>Cutandia maritima</i>																																																												
<i>Erodium cicutarium</i>																																																												
<i>Festuca pruinosa</i>																																																												
<i>Parapholis incurva</i>																																																												
<i>Phleum arenarium</i>																																																												
<i>Soliva pterosperma*</i>																																																												
<i>Trifolium repens</i>																																																												
<i>Urtica dioica</i>																																																												
<i>Vulpia myuros</i>																																																												

invasoras como *Stenotaphrum secundatum* y *Conyza bonariensis*, y que se enriquecen en *Paspalum dilatatum* cuando aumenta la humedad edáfica. Pastizales similares fueron incluidos por HERRERA y PRIETO in DÍAZ y PRIETO (1994) en el sintaxis *Plantagini coronopodi-Trifolietum fragiferi* Tüxen in Tüxen y Oberdorfer ex Díaz 1975 *sporobletosum indicum* Herrera y Prieto in Díaz y Prieto 1994, a través de la alianza *Trifolio-Cynodontion* Braun-Blanquet y de Bolòs 1958. En opinión de dichos autores se trataría de un pastizal dominado por *Cynodon dactylon* y *Trifolium fragiferum*, desarrollado en suelos sometidos a hidromorfía temporal con desecación estival y que representa una versión termo-mesotemplada frecuente en sistemas dunares frente a la subasociación típica. Posteriormente RIVAS-MARTÍNEZ *et al.* (2001) propusieron como más adecuada su reubicación en la alianza *Agrostion stoloniferae*.

En la tabla de HERRERA (1995: Tabla 69) que dio pie a definir dicha subasociación, se observa que ésta puede dividirse claramente en dos grupos que se diferencian florística y ecológicamente: los primeros cinco inventarios (Tabla 69: inv. 1-5), dominados por *Trifolium fragiferum* y que presentan *Agrostis stolonifera* y *Lotus glaber*, se localizan preferentemente en depresiones dunares en contacto con juncales del *Carici arenariae-Juncetum acutum* Herrera 1995, donde el nivel freático es elevado gran parte del año, pero se produce una notable sequía estival superficial, lo que favorece a estas especies higrófilas; los cinco restantes (Tabla 69: inv. 6-10) se hallan dominados por *Sporobolus indicus* y *Plantago coronopus* y en ellos faltan las otras especies comentadas. Por tanto, esta facies se separa florísticamente del tipo designado de la subasociación (Tabla 69: inv. 1) y, a diferencia de la versión típica, tapiza de manera generalizada los senderos y accesos a las dunas en situaciones no deprimidas, siendo la comunidad más extendida en los pastizales pisoteados de los sistemas dunares del Cantábrico oriental. La tabla que presentamos (Tabla 1) recoge inventarios de estas situaciones realizados a lo largo de la costa del sector Cántabro-Vascónico, y en ella puede observarse también una total ausencia de las especies higrófilas antedichas.

En nuestra opinión existen suficientes diferencias florísticas, ecológicas y catenales para distinguir estas dos versiones como asociaciones independientes, que por supuesto entran a menudo en contacto a lo largo de una

estrecha franja alrededor de las depresiones dunares. En consecuencia, proponemos la nueva asociación *Plantagini coronopodi-Cynodontetum dactyli* para representar los pastizales psamófilos termo-mesotemplados cántabro-vascónicos dominados por *Sporobolus indicus* y/o *Cynodon dactylon*, y la incluimos en la alianza *Potentillion anserinae*.

En la Tabla 1 se observa una graduación desde las posiciones de las zonas retrasadas de los complejos dunares, con suelos compactados y pisoteados, con un contenido elevado en elementos finos, donde contactan y se intercalan con frecuencia con los herbazales subnitrófilos de *Arctotheca calendula*, a las situaciones más xéricas, dominadas por *Sporobolus indicus*, donde se hacen menos frecuentes especies de *Potentillion anserinae* y *Sisymbrium officinalis*.

Hordeo murini-Arctothecetum calendulae ass. nova hoc loco (Tabla 2)

Holosyntypus: Tabla 2, inv. 45
[Herbazales psammonitrófilos cántabro-atlánticos de *Arctotheca calendula*]

Sobre las arenas nitrificadas algo removidas y poco pisoteadas de los accesos a las playas y dunas del área de estudio, se desarrolla una comunidad de fenología primaveral y carácter subnitrófilo dominada por el terófito de origen surafricano *Arctotheca calendula* (HERRERA *et al.*, 2008), al que accom-

pañan especies como *Hordeum murinum* subsp. *leporinum*, *H. murinum* subsp. *murinum*, *Lophochloa cristata*, *Rumex pulcher*, *Hirschfeldia incana* y más puntualmente *Anacyclus radiatus*, *Asphodelus fistulosus*, *Cardaria draba* y *Emex spinosa*, que la aproximan a las comunidades ibéricas más termófilas de la alianza *Hordeion leporini* Braun-Blanquet in Braun-Blanquet, Gajewski, Wraber y Walas 1936 corr. de Bolòs 1962. Estos herbazales psammófilos con *Arctotheca* ya fueron señalados por AEDO (1985) del occidente cántabro.

En la Tabla 2 se han reunido 56 inventarios realizados en diferentes ecosistemas dunares del sector Cántabro-Vascónico, desde Irún (SS) hasta San Vicente de la Barquera (S).

El análisis de agrupación realizado con un total de 97 inventarios inéditos (CAMPOS, 2010) pertenecientes a herbazales subnitrófilos de *Sisymbrium officinalis* en el territorio, revela la existencia de dos grandes grupos (Fig. 2): los inventarios psamófilos con presencia de *Arctotheca calendula* (B) y los inventarios no psamófilos, que pertenecen a la asociación *Sisymbrio officinalis-Hordeetum murini* Braun-Blanquet 1967 (A).

A la vista de los resultados, creamos que hay suficientes diferencias florísticas y ecológicas para separar los herbazales subnitrófilos psamófilos primaverales en una asociación diferente, al igual que ya hicieran GÉHU y GÉHU-FRANCK (1985) en Francia. Dentro de la

alianza *Sisymbrio officinalis*, dichos autores señalaron la presencia de la asociación *Laguro ovati-Hordeetum leporini* Géhu y Géhu-Franck 1985 en las inmediaciones de las dunas armoricanas, diferenciándola de la más general *Bromo-Hordeetum murini* (Allorge, 1922) Lohm. 1950 y la más halófila *Laguro-Raphanetum maritimi* (Géhu J.-M. y Géhu-Franck J., 1969) Géhu y Géhu-Franck 1985.

Si bien las comunidades cántabro-vascónicas muestran una gran similitud florística y ecológica con el *Laguro-Hordeetum leporini*, la ausencia en las comunidades armoricanas de especies más meridionales como *Arctotheca calendula*, *Lavatera cretica*, *Rumex pulcher* o *Lophochloa cristata*, nos inducen a describir la nueva asociación, *Hordeo murini-Arctothecetum calendulae*, que tipificamos en el inventario 45 de la Tabla 2.

ENCUADRE SINTAXONÓMICO

Molinio-Arrhenatheretea Tüxen 1937
Plantaginetalia majoris Tüxen y Preising in Tüxen 1950

Potentillion anserinae Tüxen 1947
Plantagini coronopodi-Cynodontetum dactyli ass. nova

Stellarietea mediae Tüxen, Lohmeyer y Preising ex von Rochow 1951
Chenopodio-Stellarienea Rivas Goday 1956

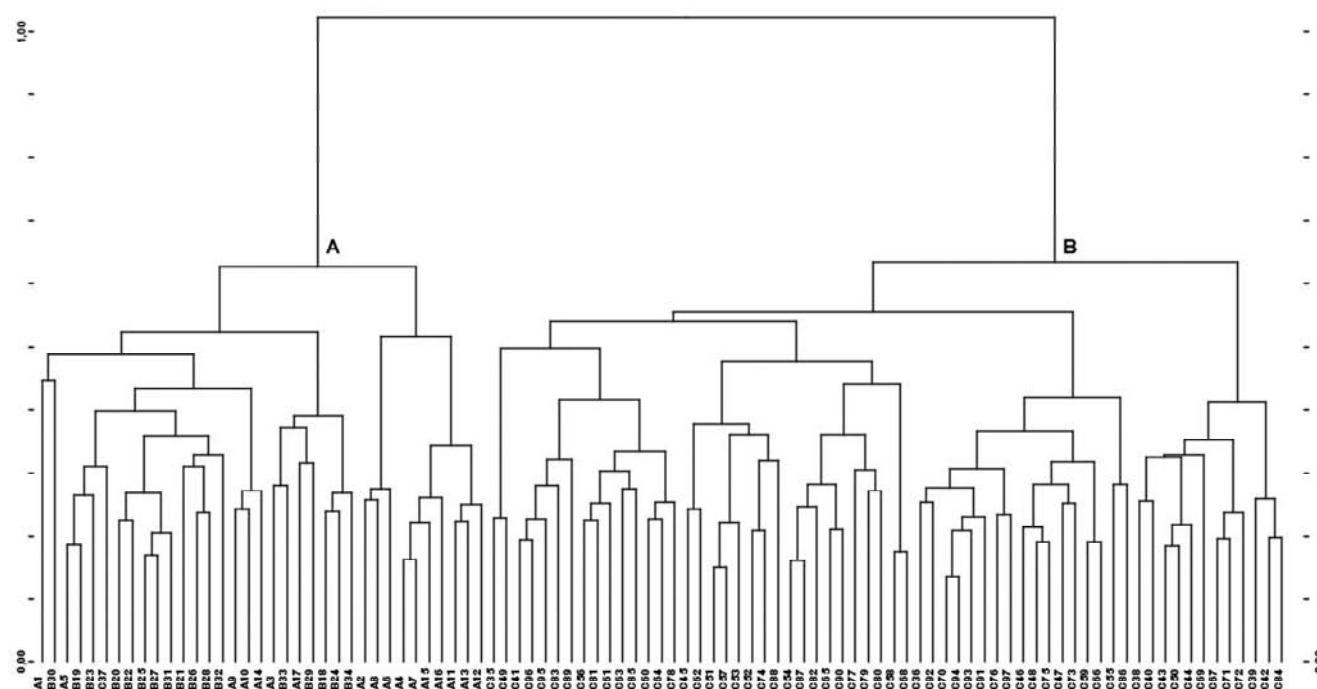


Fig. 2 - Dendrograma resultante del análisis de agrupación jerárquico de los herbazales terofíticos subnitrófilos de la alianza *Sisymbrio officinalis* en el territorio: *Sisymbrio-Hordeetum murini* (A), *Hordeo murini-Arctothecetum calendulae* (B). En la matriz especies-inventarios se eliminaron las especies de baja frecuencia, presentes en uno o dos inventarios. El resultado fue una matriz de 103x97 (especies x inventarios).

Sisymbrietalia officinalis J. Tüxen in Lohmeyer *et al.* 1962 em. Rivas-Martínez, Báscones, Díaz, Fernández-González y Loidi 1991
Sisymbrium officinale Tüxen, Lohmeyer y Preising in Tüxen 1950
Hordeo murini-Arctothecetum calendulae ass. nova

Tabla 1

Además: Inv. 1: *Calystegia soldanella* +, *Ononis ramosissima* +, *Daucus gummifer* +, *Elytrigia atherica* 1; Inv. 2: *Oenothera gr. biennis** +, *Lobularia maritima** +, *Thymus britannicus* 1; Inv. 3: *Arenaria serpyllifolia* 1, *Calyptegia soldanella* +, *Eryngium maritimum* +, *Melilotus indicus* +, *Oenothera gr. biennis** +, *Paspalum vaginatum** 1, *Elytrigia boreoatlantica* +, *Lepidium virginicum** 1, *Petrorhagia nanteuilii* +; Inv. 5: *Ononis ramosissima* +, *Festuca vasconensis* +, *Polygonum arenarium* +; Inv. 6: *Daucus carota* +, *Avena barbata* 1, *Dianthus hyssopifolius* +; Inv. 7: *Conyza sumatrensis** +, *Verbascum* sp. +, *Allium vineale* +, *Oenothera glazioviana** +; Inv. 8: *Bromus catharticus** +; Inv. 9: *Paspalum vaginatum** +, *Medicago arabica* +, *Trifolium dubium* 1; Inv. 10: *Convolvulus arvensis* +, *Conyza sumatrensis** 1, *Crepis capillaris* 1, *Festuca arenaria* 2, *Linaria maritima* 1; Inv. 11: *Bromus hordeaceus* 1, *Catapodium rigidum* 1, *Crepis capillaris* 2, *Daucus carota* +, *Festuca arenaria* 1, *Medicago lupulina* 2, *Trifolium scabrum* +, *Gaudinia fragilis* +, *Lotus glaber* 1, *Picris echioides* +, *Silene nocturna* +, *Trifolium campestre* 1, *Trifolium pratense* +; Inv. 12: *Arenaria serpyllifolia* 1, *Catapodium rigidum* 1, *Eryngium maritimum* +, *Hordeum leporinum* +, *Phleum arenarium* +, *Trifolium scabrum* +, *Aethrorhiza bulbosa* +, *Cerastium diffusum* +, *Poa bulbosa* +, *Rosa sempervirens* +, *Sinapis arvensis* +; Inv. 14: *Bromus hordeaceus* +, *Hordeum murinum* s.l. +, *Vulpia myuros* 1, *Geranium pyrenaicum* 1; Inv. 15: *Erodium moschatum* 1, *Hordeum murinum* 1, *Melilotus indicus* +, *Anacyclus clavatus** 1, *Malva nicaeensis* 1; Inv. 16: *Hordeum murinum* 1, *Trifolium resupinatum* 1; Inv. 17: *Festuca pruinosa* +, *Hordeum leporinum* 1, *Verbascum* sp. +, *Rumex crispus* +; Inv. 18: *Sisymbrium officinale* +; Inv. 19: *Bromus catharticus** +, *Phleum arenarium* +, *Carex arenaria* 1; Inv. 20: *Vulpia myuros* +; Inv. 21: *Hordeum murinum* s.l. +; Inv. 22: *Convolvulus arvensis* 1, *Erodium moschatum* +, *Festuca pruinosa* +, *Medicago lupulina* 1,

Anagallis arvensis 1, *Anthemis arvensis* +, *Rumex hispanicus* +.

Localidades: 1,4 y 7) Castro Urdiales, 30TVP7305 (S); 2) Zumaia, 30TWN6194 (SS); 3) Hendaya, 30TWP9803 (FR); 5) Santoña, 30TVP6212 (S); 6) Zierbena, 30TVP9100(BI); 8(*holosyntypus*), 13, 16 y 17) Muskiz, 30TVN9099 (BI); 9) San Vicente de la Barquera, 30TUP8705 (S); 10, 11 y 12) Gorliz, 30TWP0407 (BI); 14) Santoña, Berria, 30TVP6212 (S); 15) Santoña, 30TVP6309 (S); 18) Ibarrangelu, 30TWP2706(BI); 19, 20 y 21) Noja, 30TVP5715 (S); 22) Somo, 30TVP3911 (S).

Tabla 2

Además: Inv. 1: *Elytrigia boreoatlantica* 1, *Polygonum maritimum* 1; Inv. 2: *Elytrigia boreoatlantica* 1, *Cardaria draba* +; Inv. 3: *Desmazeria rigida* +; Inv. 4: *Pancratium maritimum* +; Inv. 7: *Daucus gummifer* +, *Echium vulgare* 1; Inv. 9: *Scirpoides holoschoenus* +, *Silene vulgaris* +; Inv. 11: *Chenopodium ambrosioides** 1, *Hypochoeris radicata* +, *Oenothera glazioviana** 1, *Picris echioides* +; Inv. 13: *Hypochoeris radicata* +, *Medicago sativa** +; Inv. 14: *Juncus bufonius* 1; Inv. 18: *Hordeum distichon** +, *Poa trivialis* +; Inv. 19: *Poa irrigata* 2, *Geranium pyrenaicum* +; Inv. 20: *Coronopus didymus** +, *Lotus corniculatus* +, *Polygonum maritimum* +, *Ammophila australis* +; Inv. 21: *Trifolium resupinatum* 2; Inv. 22: *Aster squamatus** +, *Verbena officinalis* +; Inv. 23: *Trifolium resupinatum* 2; Inv. 27: *Conyza canadensis** +, *Holcus lanatus* +, *Paspalum vaginatum** 1, *Rumex* sp. +, *Avena sterilis* 1, *Euphorbia portlandica* +, *Ononis reclinata* +, *Trifolium campestre* 1, *Trifolium scabrum* 1, *Vicia cordata* 1; Inv. 29: *Lolium multiflorum* 2; Inv. 30: *Conyza canadensis** +, *Anacyclus clavatus** +, *Avena sativa** +, *Filago pyramidata* +, *Gaudinia fragilis* +; Inv. 31: *Asphodelus fistulosus** 1, *Atriplex prostrata* +, *Cakile integrifolia* 1, *Herniaria robusta* 1, *Matthiola sinuata* +; Inv. 33: *Desmazeria rigida* 2; Inv. 34: *Parietaria judaica* 1; Inv. 35: *Emex spinosa** 4, *Geranium purpureum* +; Inv. 36: *Chenopodium ambrosioides** +; Inv. 37: *Pancratium maritimum* +; Inv. 38: *Holcus lanatus* +, *Rumex x pratensis* 1, *Malva nicaeensis* +, *Polygonum aviculare* +; Inv. 39: *Eryngium maritimum* +, *Lolium rigidum* +, *Pittosporum tobira* pl.* +; Inv. 40: *Arum italicum* +, *Carex divulsa* 1, *Melilotus indicus* 1,

Scilla verna 1, *Stenotaphrum secundatum** 1; Inv. 41: *Arum italicum* +; Inv. 42: *Poa irrigata* 1, *Daucus carota* +; Inv. 43: *Agrostis stolonifera* +, *Euphorbia helioscopia* 1, *Paspalum vaginatum** +, *Senecio mikanioides** +; Inv. 44: *Agrostis stolonifera* 1, *Juncus bufonius* 1, *Medicago arabica* 2, *Papaver rhoes* 1, *Rumex x pratensis* +, *Arrhenatherum bulbosum* +, *Cerastium glomeratum* +, *Polycarpon diphyllum* 1, *Ranunculus sardous* +, *Rhinanthus mediterraneus* +, *Silene gallica* +; Inv. 45: *Papaver rhoes* +, *Poa feratiana* +, *Fumaria capreolata* +; Inv. 46: *Polygonum arenastrum* +, *Sagina apetala* +, *Silene conica* +; Inv. 48: *Carex divulsa* +, *Euphorbia helioscopia* +, *Linum bienne* +, *Minuartia hybrida* 1, *Sherardia arvensis* +, *Verbascum thapsus* +; Inv. 49: *Scirpoides holoschoenus* +; Inv. 50: *Paspalum dilatatum** +; Inv. 51: *Medicago arabica* 1, *Malva neglecta* +; Inv. 53: *Linum bienne* 2, *Lotus corniculatus* 1; Inv. 54: *Poa feratiana* 1; Inv. 55: *Coronopus didymus** +, *Chamomilla suaveolens** +, *Sagina maritima* +, *Spergularia rubra* 1; Inv. 56: *Melilotus indicus* 1, *Rumex* sp. +, *Arrhenatherum elatius* s.l. +, *Ononis maritima* 1, *Senecio vulgaris* +.

Localidades: 1 y 42) Santoña, Berria, 30TVP6112 (S); 2, 4, 15, 16, 30, 32, 50, 51, 52 y 53) Noja, 30TVP5715 (S); 3, 9, 18 y 38) Laredo, 30TVP6406 (S); 5, 33, 34, 35, 36 y 40) Ibarrangelu, playa de Laga 30TWP2706 (BI); 6 y 17) Santoña, Berria, 30TVP6212 (S); 7 y 19) Piélagos, 30TVP2211 (S); 8 y 37) Noja, 30TVP5615 (S); 10) Laredo, 30TVP6306 (S); 11) Laredo, 30TVP6308 (S); 12) Somo, 30TVP4011 (S); 13, 39 y 56) Muskiz, 30TVN9099 (BI); 14) Noja, 30TVP5814 (S); 20) Piélagos, 30TVP2111 (S); 21 y 23) San Vicente de la Barquera, 30TUP8705 (S); 22) Oriol, 30TWN7093 (SS); 24, 43, 45 (*holosyntypus*), 46, 47 y 48) Castro Urdiales, 30TVP7305 (S); 25, 26 y 54) Galizano, 30TVP4514 (S); 27) Somo, 30TVP3911 (S); 28) San Vicente de la Barquera, 30TUP8805 (S); 29) Valdáliga, Oyambre, 30TUP9205 (S); 31 y 41) Noja, 30TVP5913 (S); 44) Castro Urdiales, 30TVP7404 (S); 49) Gorliz, 30TWP0407 (BI); 55) Castro Urdiales, 30TVP7405 (S).

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VEGETATION ALONG MOUNTAIN STREAMS IN THE SOUTHERN PART OF THE REPUBLIC OF MACEDONIA

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ABSTRACT

The work deals with vegetation along mountain streams in the southern part of the Republic of Macedonia. Spring vegetation of *Montio-Cardaminetea* appears at sources in the subalpine zone and tall herb communities of *Cirsion appendiculati* are found along streams down to the montane zone. The floristic composition of vegetation along the altitudinal gradient is presented and analyzed. The vegetation has also been classified into a syntaxonomic system and the following syntaxa have been established: *Pedicularis limnogenae-Saxifragetum stellaris* subsp. *alpigenae* (*Pinguicula balcanicae-Cardaminion raphanifoliae* subsp. *acris*, *Montio-Cardaminetalia*, *Montio-Cardaminetea*); *Doronico-Cirsietum appendiculati* and *Geo coccinei-Rumicetum alpinae* (*Cirsion appendiculati*, *Adenostyletalia*, *Mulgedio-Aconitetea*).

KEYWORDS: Balkan, gradient, *Mulgedio-Aconitetea*, *Montio-Cardaminetea*, spring, syntaxonomy, stream, tall herb, vegetation.

INTRODUCTION

The vegetation along high mountain streams in Macedonia has attracted researchers since the beginning of the 20th century. Several endemic plant species exist in the area and many of them have been described here (MATEVSKI & KOSTADINOVSKI, 1996). The earliest researcher of vegetation in the area was ADAMOVIĆ (1909), who first described this kind of vegetation. HORVAT (1935, 1936, 1937, 1960) and HORVAT *et al.* (1974) subsequently elaborated this vegetation and wrote several papers; Horvat also initiated other research into this type of vegetation, for instance with Em (HORVAT & EM, 1949). Studies were also conducted by RUDSKI (1938) and, in recent times, by MICEVSKI (1994).

The aim of the study was to sample the vegetation along mountain streams in the southern part of the Republic of Macedonia. The vegetation was sam-

pled along streams from sources at an altitude of 1,800 to 2,200 m, to the lower part, where the water is captured at an altitude of about 1,200 m and used to supply drinking water for the population. The vertical zonation of vegetation is elaborated; the communities were classified into a phytosociological system and the system has been harmonized with international standards (WEBER *et al.*, 2000).

The article is dedicated to the 80th anniversary of Prof. dr. dr. h. c. Jean-Marie Géhu, with whom the first author of this article had the opportunity to work at the beginning of his scientific career. He is grateful for the knowledge acquired, which enabled him further work in the field of vegetation science.

METHODS

The investigation was conducted according to the standard Braun-Blanquet method (BRAUN-BLANQUET, 1964). Numerical analyses (classification and ordination) were performed by the SYNTAX (PODANI, 2001) and CANOCO (TER BRAAK & ŠMILAUER, 2002) programs. Braun-Blanquet cover values were transformed to the ordinal, as proposed by VAN DER MAAREL (1979). The nomenclature of plant species is according to CĚKOVA (2005) and TUTIN *et al.* (1960-1980).

RESEARCH AREA

The research area is situated in the southern part of Macedonia, between Prespa Lake in the west and Pelagonia in the east. In the center is Baba Mountain, with its peak Pelister at an altitude of 2,601 m. The Pelister massive is composed of several peaks higher than 2,000 m. The bedrock is composed of rock of various origin: metamorphic rock, paleozoic granite, granitic greis (STOJADINović, 1970).

The vegetation is fairly diverse. The following forest communities can be found on the vertical profile: *Quercetum frainetto cerris*, *Fagetum monta-*

num, *Abieti-Fagetum* and *Fagetum subbalpinum*. In extreme sites there are forests of a relict tree species *Pinus peuce*. Above the timberline appear natural grasslands of *Caricetea curvulae* (HORVAT, 1949; HORVAT, 1960; HORVAT *et al.*, 1974; FUKAREK & JOVANOVIĆ, 1986).

The vegetation was sampled on the Pelister massif, along the mountain rivers Sapundžica, Crvena reka, Brajčinska reka, Ezerska reka, Šemnica and Caparska reka (Fig. 1). Relevés were sampled during the optimum development of the vegetation; at the end of June and beginning of July. The vegetation was sampled along the river from sources, where typical vegetation of springs appears, and along the streams, where tall herb communities appear. Rivers are captured for drinking water at an altitude of about 1,200 m.

RESULTS

The relevés were divided at the beginning into two floristically and ecologically different groups, one representing spring vegetation and the other tall herb communities. We elaborated these two groups separately. Since the spring vegetation is represented only by a few relevés, we did not proceed with any analysis of this material. The floristic composition is presented in Tab. 1. The tall herb communities were sampled more extensively, since they cover larger surfaces and the relevés are presented in Tabs. 2 and 3. These communities were the subject of numerical analysis.

We first elaborated a classification of the tall herb communities. The dendrogram (Fig. 2) shows two main clusters, which represent two associations, one dominated by *Cirsium appendiculatum* and the other one by *Rumex alpinus*. Both associations are presented in Tabs. 2 and 3. The *Cirsium appendiculatum*-dominated group is further divided into two subgroups, one typical and the other characterized by species of lower altitudes, e.g. *Mentha spicata*, *Brachythecium rivulare*, *Telekia speciosa*, etc. (c.f. Tab. 2).

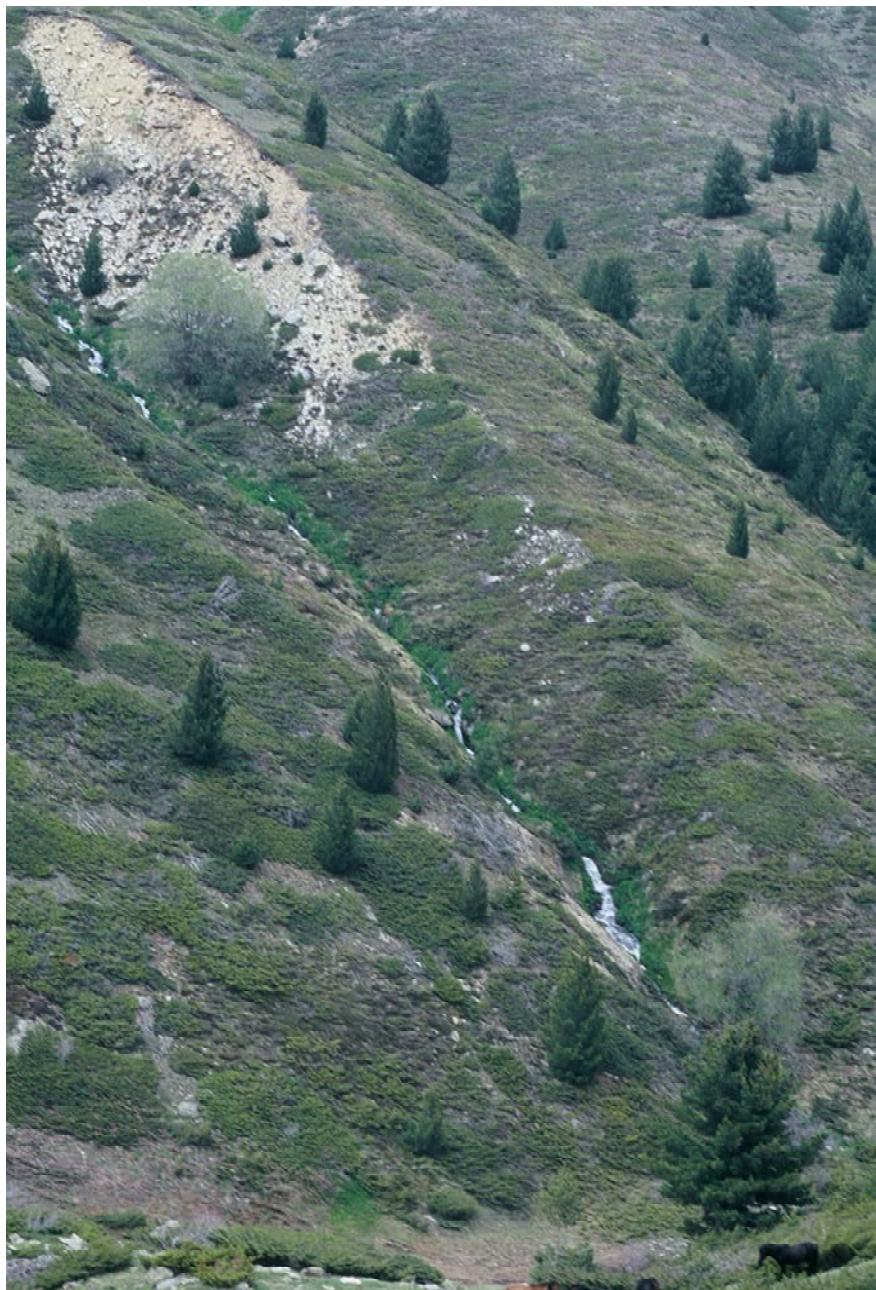


Fig. 1 - View of mountain streams in early spring. We cannot recognise tall herb communities, because they will develop later in the early summer.

We then tried to detect the ecological factor that contributes most to the diversity of tall herb communities. The Monte Carlo permutation test showed that the most important factor is altitude (Tab. 4), which was also confirmed by the Box-Wiskers diagram (Fig. 3). A zonation can be observed from the lowest *Doronicico-Cirsietum appendiculati telekietosum* through *Doronicico-Cirsietum appendiculati typicum* to *Geococcinei-Rumicetum alpini* and *Pedicularis limnogeneae-Cardaminetum raphanifoliae* subsp. *acris*, which can be found at the highest altitudes.

The same zonation is also evident from the diagram showing the DCA of the relevés of tall herb communities (Fig. 4). The species composition (Fig. 5) shows that, at higher altitudes, high mountain species, such as *Rumex alpi-*

nus, *Caltha palustris* subsp. *laeta*, *Brachythecium plumulosum*, *Saxifraga stellaris* etc. can be found. The central position in the diagram and, at the same time, also in ecological conditions, is held by species such as *Athyrium filix-femina*, *Geranium sylvaticum* and *Angelica pannicaria*. At lower altitudes, lowland species, such as *Poa nemoralis*, *Doronicum austriacum* and *Myosotis sylvatica*, can already be detected.

DISCUSSION

VEGETATION OF SPRINGS

The class *Montio-Cardaminetea* comprises vegetation that appears around springs and streams. The vegetation is limited in space and includes

many communities of limited distribution. The floristic composition is a result of the permanent flow of water, which maintains the temperature of the site relatively stable. The vertical structure is built by cormophytes and the lower of mosses. *Montio-Cardaminetea* and *Montion-Cardaminetalia* are the syntaxa of vegetation of cold springs, commonly dominated by bryophytes (ZECHMEISTER & MUCINA, 1994, RODWELL *et al.*, 2002).

The *Saxifraga stellaris* dominated communities that can appear around springs in the southern Balkans were first mentioned by HORVAT (1935), who found these communities at small sources on silicate bedrock in the area of Kajmakčalan, Jakupica and Šar planina (Fig. 6). He later (1960) classified the *Saxifraga stellaris*-dominated communities as the association *Philonotidi seriatae-Saxifragetum stellaris* Horvat 1949 in *Montio-Cardaminion* (*Montio-Cardaminetalia*). Unfortunately, Horvat's manuscript of 1949 about the mountain vegetation of Macedonia was not published. The first published relevés assigned to *Philonotidi seriatae-Saxifragetum stellaris* Horvat 1949 were published by ROUSSAKOVA (2000), from the Rila Mountains in Bulgaria. HÁYEK *et al.* later (2005) published relevés dominated by *Saxifraga stellaris* from the Vitosha Mountains in Bulgaria and assigned them to *Saxifragetum stellaris* DREYL 1940 (alliance *Philotodinion* Hinterlang 1992). They consider that this association is probably distributed throughout the whole of Europe, from the boreal zone, through the eastern Carpathians and Balkans to southernmost Europe.

Since we do not have Horvat's original relevés; and the communities under consideration are of different floristic composition than the relevés published by ROUSSAKOVA (2000) and HÁYEK *et al.* (2005); it was decided to describe a new association: *Pedicularis limnogenae-Saxifragetum stellaris* subsp. *alpigenae*. At the same time, it can be recognized that endemic species, e.g., *Cardamine raphanifolia* subsp. *acris*, *Pedicularis limnogenae*, *Pinguicula balcanica*, *Carex rigida* var. *macedonica*, as well as *Geum coccineum*, *Angelica pannicaria* and *Alchemilla indivisa*, build a large proportion of the floristic composition of these communities, and we thus propose a new alliance: *Pinguiculaceae-Cardaminion raphanifoliae* subsp. *acris*. The alliance comprises the oligotrophic spring vegetation of high montane and subalpine zones in the southern Balkans.

Table 1 - Analytical table of *Pedicularis limnogenae-Saxifragetum stellaris* subsp. *alpigenae*.

	1	2	3	4	5	6	7	8	9	10	11	12	13
Relevé number													
Surface (m ²)	5	4	4	9	10	8	5	5	8	5	9	5	3
Cover of vegetation (%)	80	70	70	75	75	95	90	95	85	80	80	80	80
Inclination	90	40	15	60	40	6	4	7	8	2	7	2	5
Aspect	E	E	E	E	NE	SE	SE	SE	N	N	N	NE	N
Altitude (m)	1800	1800	1790	1770	1750	2170	2171	2173	2180	1770	2180	1755	1550
Number of species	14	15	11	10	16	14	14	14	13	16	13	13	16
Ass. and all. diag. species													
Saxifraga stellaris ssp. <i>alpigena</i>	C	4.1	4.1	5.1	4.1	4.1	4.1	4.1	4.1	3.1	4.1	4.1	4.1
Cardamine raphanifolia ssp. <i>acris</i>	C	+	1.1	1.1	1.1	2.1	1.1	2.1	+	1.1	+	2.1	+
Pedicularis limnogenae	C	.	.	+	+	+	+	.	1.1	+	1.1	+	1.1
Geum coccineum (diff.)	C	+	+	+	+	1.1	+	+	+
Pinguicula balcanica	C	.	.	.	+	+	1.1	+	+	+	+	+	8
Carex rigida var. <i>macedonica</i>	C	1.1	+	+	+	+	1.1	.
Alchemilla indivisa (diff.)	C	1.1	3.1	1.1	+	+	.	.	.	+	.	.	6
Angelica pannicaria (diff.)	C	+	+	.	+	+	4
Montio-Cardaminetalia, Montio-Cardaminetea													
Caltha palustris ssp. <i>laeta</i>	C	+	+	+	1.1	+	+	+	+	+	+	+	1.1
Epilobium alsinifolium	C	1.1	2.1	3.1	3.1	3.1	1.1	1.1	.	+	.	+	.
Epilobium nutans	C	+	.	+	3
Stellaria alsine	C	1.1	2.1	.	+	.	.	3
Drepanocladus aduncus	D	3.2	3.2	2.2	2.2	3.2	3.2	3.2	3.2	2.2	2.2	.	.
Deschampsia caespitosa	C	+	1.1	+	1.1	1.1	+	1.1	1.1
Carex echinata	C	.	.	+	.	.	1.1	1.1	1.1	.	1.1	+	7
Luzula multiflora	C	+	+	+	+	+	+	6
Plagiomnium medium	D	2.2	2.2	+	1.2	+	.	.	1.2	1.2	1.2	.	5
Sphagnum sp.	D	1.2	1.2	1.2	.	1.2	.
Veratrum album	C	+	.	.	+	.	+	+	4
Pellia epiphylla	D	2.2	2.2	1.2	3
Anthoxanthum odoratum	C	+	.	+	3
Athyrium filix-femina	C	1.1	+	.	.	+	3
Carex serotina ssp. <i>serotina</i>	C	+	+	+	+	.	.	.	3
Saxifraga rotundifolia ssp. <i>Chrysosplenifolia</i>	C	3.1	2.1	+	.	.	.	3
Trifolium hybridum	C	+	.	+	+	3

TALL HERB COMMUNITIES ALONG STREAMS

The class *Mulgedio-Aconitetea* encompasses shrub and tall herb vegetation of high altitudes growing on moist and fertile soils that are under the influence of percolation water (RODWELL *et al.*, 2002). In Macedonia, such vegetation can be classified into the order *Adenostyletalia* and can be further divided

into three alliances *Cirsion appendiculati*, *Geion coccinei* and *Calamagrostidion villosae* (HORVAT, 1960). In the present work, we will deal only with *Cirsion appendiculati*, which was already characterized as “Bachbegleitvegetation” by ADAMOVIĆ (1909). This vegetation has a lot in common with vegetation that appears in central European mountains classified into *Adeno-*

stylion (MICH'L *et al.*, 2010). On the other hand, such vegetation is more limited to moist habitats, because of the drier global climate. This might also be why the role of bryophytes is lower here than in communities more to the north. The vegetation is thus well developed on Pelister, where the bedrock is silicate and there are quite a number of strong springs.

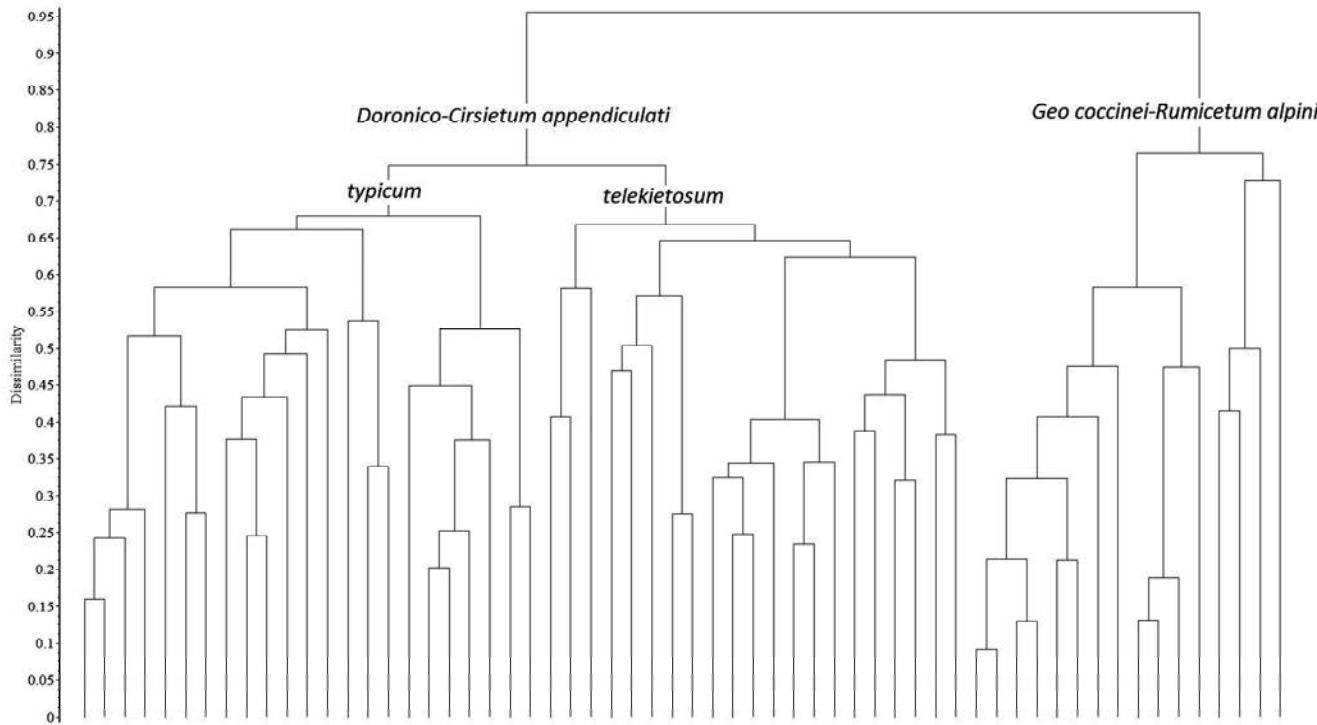


Fig. 2 - Classification of tall herb relevés. (complete link as method and similarity ratio as a measure of resemblance). The order of relevés corresponds to those in Tables 2 and 3, respectively.

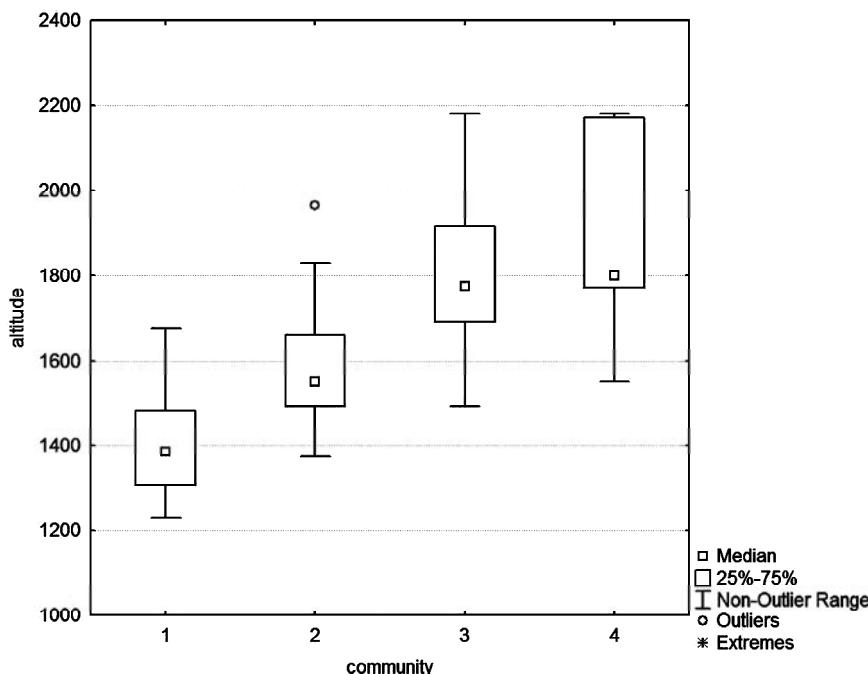


Fig. 3 - Box-Wiskers diagram showing the altitude of relevés. Legend: 1 - *Doronico-Cirsietum appendiculati telekietosum*, 2 - *Doronico-Cirsietum appendiculati typicum*, 3 - *Geo coccinei-Rumicetum alpini*, 4 - *Pedicularis limnogenae-Saxifragetum stellaris subsp. alpigenae*.

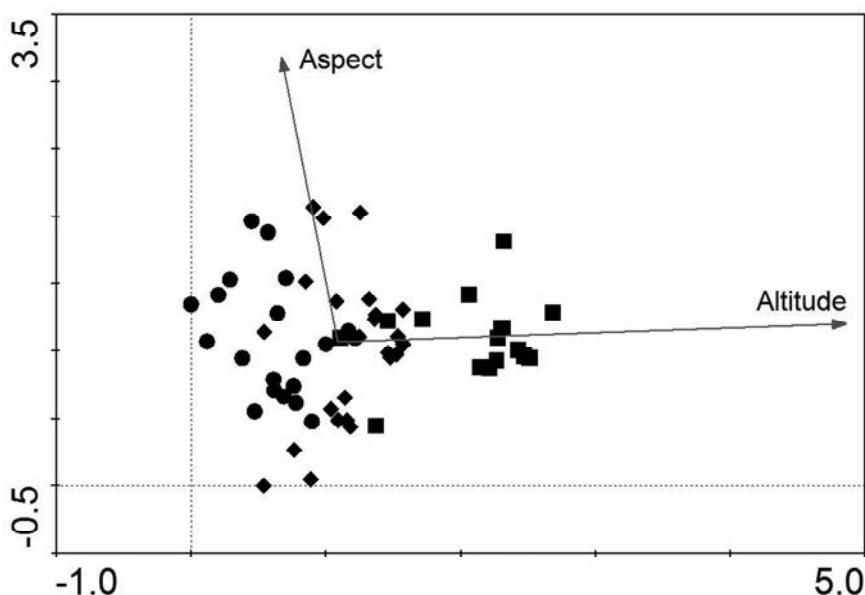


Fig. 4 - DCA of relevés of tall herb communities. Explanatory variables are passively projected onto the diagram. Circles represent *Doronico-Cirsietum appendiculati telekietosum*, diamonds *Doronico-Cirsietum appendiculati typicum* and squares *Geo-Rumicetum alpini*.

Numerical analysis shows two well defined groups. The main division is altitude and it is shown on the first axis in the ordination diagram (Fig. 4). *Rumex alpinus*-dominated communities (i.e. *Geo coccinei-Rumicetum alpini*) are found at higher altitudes (1,700-1,900 m), with *Doronico-Cirsietum appendiculati typicum* at lower altitudes (1,500-1,600 m) and *Doronico-Cirsietum appendiculati telekietosum* at the lowest, around 1,400 m, and it can even be found at 1,200 m (Fig. 3).

COMMUNITY

The plants of this community reach their optimum in the early summer (Fig. 7). They are up to two meters high and are quite attractive. They grow in the bottom of valleys and can already be recognized from a distance: two meter high yellow-red strips, a mixture of flowering *Cirsium appendiculatum* and *Doronicum austriacum* (Fig. 8).

The characteristic species of the association is *Cirsium appendiculatum*. It is the dominant species and gives the characteristic appearance to the community. In addition to this species, se-

veral diagnostic species appear, such as *Doronicum austriacum*, *Angelica paniculata*, *Geum coccineum*, *Mysotis scorpioides*, *Alchemilla indivisa*, *Milium effusum*, *Caltha laeta*, *Ranunculus sericus*, *Veratrum album* and *Cardamine raphanifolia* subsp. *acris*.

The association can be divided into two subassociations. At lower altitudes, *Doronico-Cirsietum appendiculati telekietosum* appears, with many species of nitrophilous tall herb communities of *Galio-Urticetea*, such as *Geranium robertianum*, *Geum urbanum*, *Vicia sepium*, *Mnium undulatum* and also species of the class of meadow vegetation *Molinio-Arrhenatheretea*, such as *Arrhenatherum elatius* and *Cynosurus cristatus*. The other subassociation, *Doronico-Cirsietum appendiculati typicum*, is found at higher altitudes and is characterized by a lack of species and can be treated as typical.

HORVAT (1935) first mentioned this community as a *Cirsium appendiculatum* dominated community in his report about investigations in Macedonia. He named it the following year (HORVAT, 1936) *Caltho laetae-Cirsietum appendiculati* and, in 1960 (HORVAT, 1960), in a work about high mountain vegetation in Macedonia, *Doronico orphaniidis-Cirsietum appendiculati*. *Doronicum orphaniidis* should be considered a synonym of *Doronicum austriacum* (FLORA EUROPAEA, 2010). Unfortunately, Horvat published no relevé of this community from Macedonia nor is there any indication that the name corresponds to an already published relevé. Later, MICEVSKI (1994) published two relevés from Bistra Mountain in Macedonia. These relevés are dominated by *Cirsium appendiculatum* and assigned to "*Orphanido-Cirsietum appendiculati* Horvat 1936".

When HORVAT *et al.* (1937) described the alliance *Cirsion appendiculati*, they also published a relevé of a community that is characterized by "an abundance of *Cirsium appendiculatum* and *Doronicum austriacum*" from the valley of Bistrica in the Rila Mountains in Bulgaria. In the same publication, there is also a relevé from Macedonia without any indication of cover values, representing *Caltho laetae-Cirsietum appendiculati*. In our opinion, *Caltho-Cirsietum* and *Doronico-Cirsietum* are the same associations. It has therefore been decided to accept Horvat's later opinion (HORVAT, 1960; MICEVSKI, 1994) and call the community *Doronico austriacae-Cirsietum appendiculati* and to choose as holotype the relevé published by HORVAT *et al.* (1937) from

the Rila Mountains.

RUMEX ALPINUS-DOMINATED COMMUNITY

Rumex alpinus dominated communities in the region are usually assigned to the association *Senecioni-Rumicetum alpini*, described by Horvat in 1949 in an unpublished manuscript and mentioned later (HORVAT, 1960) without proper relevé material. This association is found around sheepfolds, where is a lot of excrement, which enables the development of the species *Rumex alpinus* and also several other nitrophilous species, such as *Capsella bursa-pastoris*, *Polygonum aviculare*, *Poa annua*, *Chenopodium bonus-henricus* etc. These communities are widely distributed in the Balkans (PENEV, 1960; LAKUŠIĆ, 1966; ROUSSAKOVA, 2000). They have been classified within the frame of alpine nitrophilous high herb communities *Rumicion alpini* (ROUSSAKOVA, 2000; TZONEV et al., 2009) or *Chenopodion subalpinum* (HORVAT, 1960; LAKUŠIĆ, 1966).

The communities under consideration cannot be classified in the association *Senecioni-Rumicetum alpini*, because nitrophilous species are entirely missing. The elaborated stands are probably natural stands of the species *Rumex alpinus*, which later expanded in sites with a more nitrophilous char-

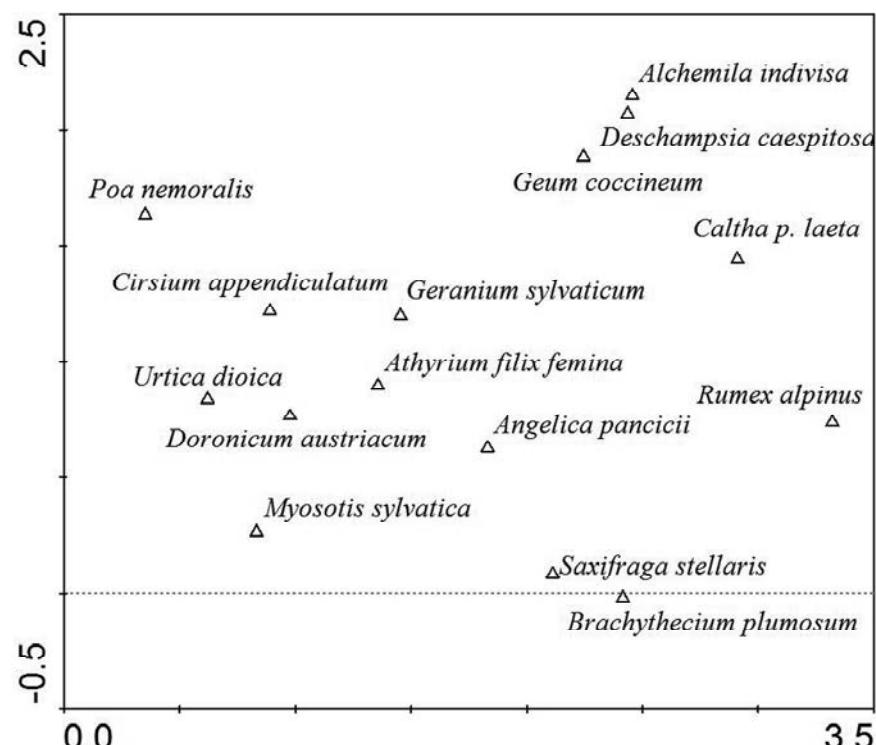


Fig. 5 - DCA of species composition of tall herb communities. Only species that meet a weight range of 20-100% are shown.

racter. Since there are no other species that enable classification into a syntaxon with a nitrophilous character (e.g. *Rumicion alpini*) and species of *Cirsion appendiculati* prevail, the community has been classified within this latter one, as a new association (Fig. 9).

An ecologically similar situation can also be found in the Carpathians,

where more natural *Rumex alpinus* dominated communities are classified into *Mulgedio-Aconitea* and those with a ruderal character into *Galio-Urticetea* (STACHURSKA-SWAKOŃ, 2009). In the northern part of Slovakia, the *Rumex alpinus*-dominated communities that are found on moist to wet concave slopes and in glens with a high level of ground



Fig. 6 - Vegetation dominated by *Saxifraga stellaris* subsp. *alpigena* thrives around sources in high altitudes.



Fig. 7 - In the early summer we can recognise very decorative red-yellow stripes along mountain streams.

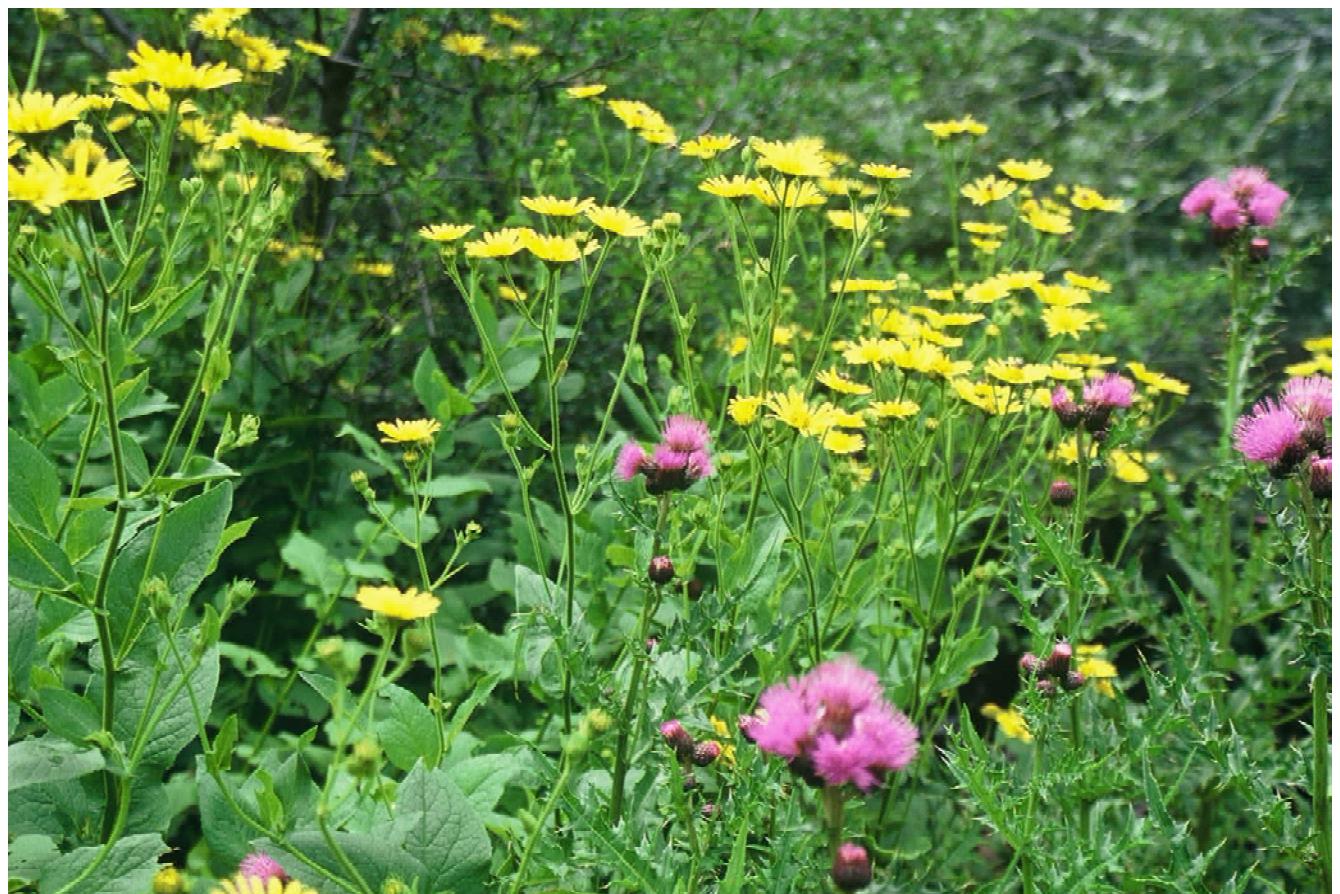


Fig. 8 - When we approach we can recognise yellow flowers of *Doronicum austriacum* and red flowers of *Cirsium appendiculatum*.

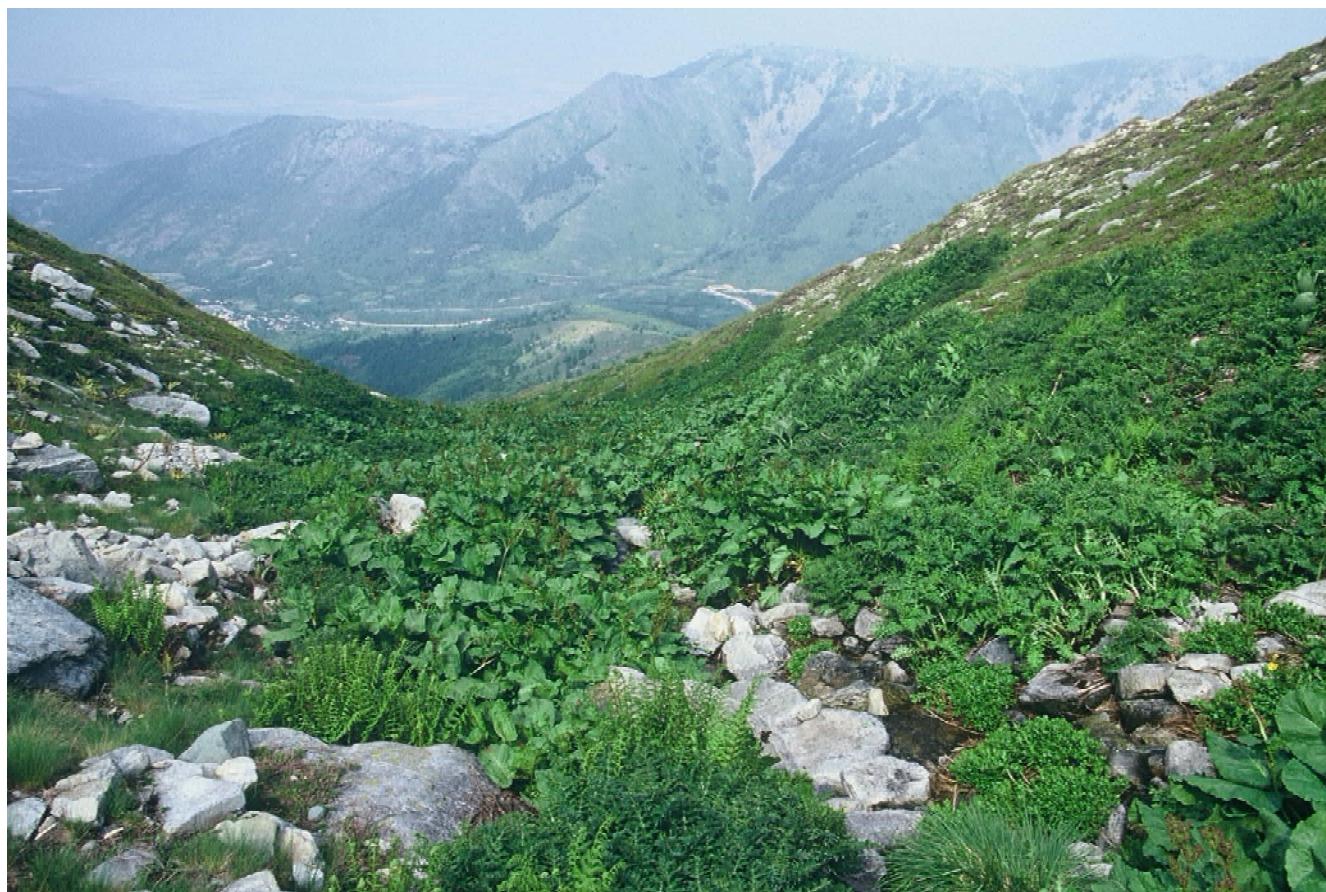


Fig. 9 - *Rumex alpinus*-dominated tall herb communities appear at the highest altitudes.

water and springs, are classified within *Petasition officinalis* (*Petasitio-Chaerophylletalia*, *Mulgedio-Aconitetea*), which comprises tall herb broadleaved natural riparian communities on alluvium and the banks of mountain streams (ŠIBÍKOVÁ et al., 2008).

DESCRIPTION OF NEW SYNTAXA

Pedicularis limnogenae-Saxifragetum stellaris ssp. *alpigenae* Čarni et Matevski ass. nova

Holotypus *hoc loco*: Tab. 1/8.

Diagnostic species: *Saxifraga stellaris* subsp. *alpigena*, *Alchemilla indivisa*, *Angelica pancicii*, *Cardamine raphanifolia* subsp. *acris*, *Carex rigida* var. *macedonica*, *Geum coccineum*, *Pedicularis limnogenae*, *Pinguicula balcanica*.

Ecological circumstances: spring vegetation on silicate bedrock in the subalpine zone in the Pelister mountain range.

Pinguicula balcanicae-Cardaminion raphanifoliae subsp. *acris* Čarni et Matevski all. nova

Holotypus *hoc loco*: *Pedicularis limnogenae-Saxifragetum stellaris* subsp. *alpigenae*

Diagnostic species: *Alchemilla indivisa*, *Angelica pancicii*, *Cardamine raphanifolia* subsp. *acris*, *Carex rigida*

var. *macedonica*, *Geum coccineum*, *Pedicularis limnogenae*, *Pinguicula balcanica*.

Ecological circumstances: spring vegetation on silicate bedrock in the subalpine zone in the southern Balkans.

Doronico austriacae-Cirsietum appendiculati Horvat ex Čarni et Matevski ass. nova

Holotypus *hoc loco*: HORVAT et al. 1937 - Table VI/1.

Diagnostic species (HORVAT et al. 1937): *Cirsium appendiculatum* (dom.), *Angelica pancicii*, *Heracleum sphondylium* subsp. *verticillatum*, *Anthriscus fumariooides*.

Ecological circumstances: tall herb vegetation along brook from the montane to subalpine zone in the southern part of the Balkans.

Doronico austriacae-Cirsietum appendiculati telekietosum Čarni et Matevski subass. nova

Holotypus *hoc loco*: Table 2/35.

Diagnostic species: *Brachythecium rivulare*, *Equisetum arvense*, *Geranium reflexum*, *Geranium robertianum*, *Mentha spicata* subsp. *spicata*, *Pellia epiphylla*, *Telekia speciosa*, *Vicia sepium*. Ecological circumstances: The subassociation is found at lower altitudes.

Geo coccinei-Rumicetum alpini Čarni et Matevski ass. nova

et Matevski ass. nova

Holotypus *hoc loco*: Table 3/9.

Diagnostic species: *Rumex alpinus* (dom.), *Cirsium appendiculatum*, *Alchemilla indivisa*, *Angelica pancicii*, *Geum coccineum*.

Ecological circumstances: tall herb vegetation along streams in the altimontane and subalpine zones in the southern part of the Balkans.

Cirsion appendiculati HORVAT 1937

Lectotype *hoc loco*: *Doronico austriacae-Cirsietum appendiculati*.

Diagnostic species (HORVAT et al. 1937): *Cirsium appendiculatum* (dom.), *Angelica pancicii*, *Heracleum sphondylium* subsp. *verticillatum*, *Anthriscus fumariooides*.

Ecological circumstances: tall herb vegetation along streams from the montane to subalpine zone in the southern part of the Balkans.

SYNTAXONOMICAL SCHEME

Pedicularis limnogenae-Saxifragetum stellaris subsp. *alpigenae* Čarni et Matevski ass. nova

Pinguicula balcanicae-Cardaminion raphanifoliae subsp. *acris* Čarni et Matevski all. nova

Montio-Cardaminetalia Pawłowski 1928

Table 2 - Analytical table of *Doronico austriacae-Cirsietum appendiculati*.

Table 2 - (continuation).

Relevé number	Surface of relevé (m ²)	Cover (%)	Inclination (°)	Altitude (m)	Aspect	Number of species	Presence
1	2	30	30	50	W	Veronica chamaedrys	23
1	2	100	100	100	W	Phragmites australis	21
1	2	1570	1530	1490	W	Epilobium obscurum	22
1	2	27	25	30	W	Stellaria graminea	20
1	2	27	25	40	W	Dryopteris filix-mas	30
1	2	27	25	50	W	Lamiastrum galeobdolon subsp. galeobdolon	30
1	2	27	25	50	W	Dactylis glomerata	30
1	2	27	25	50	W	Fallopia palustris	30
1	2	27	25	50	W	Althaea officinalis	30
1	2	27	25	50	W	Veronica urticifolia	30
1	2	27	25	50	W	Holcus lanatus	30
1	2	27	25	50	W	Lamium maculatum	30
1	2	27	25	50	W	Valeriana officinalis	30
1	2	27	25	50	W	Dactylorhiza cordigera subsp. bosniaca	30
1	2	27	25	50	W	Oxalis acetosella	30
1	2	27	25	50	W	Rumex obtusifolius subsp. subspinus	30
1	2	27	25	50	W	Arenaria agrimonoides	30
1	2	27	25	50	W	Cruciata laevipes	30
1	2	27	25	50	W	Heracleum sphondylium	30
1	2	27	25	50	W	Iuncus effusus	30
1	2	27	25	50	W	Tozzia alpina subsp. carpatica	30
1	2	27	25	50	W	Actaea spicata	30
1	2	27	25	50	W	Agrostis capillaris	30
1	2	27	25	50	W	Calamagrostis brachytricha	30
1	2	27	25	50	W	Carex leporina	30
1	2	27	25	50	W	Godium aparine	30
1	2	27	25	50	W	Stellaria alsine	30
1	2	27	25	50	W	Cynosurus cristatus	30
1	2	27	25	50	W	Dactylorhiza maculata	30
1	2	27	25	50	W	Armenatherum elatius	30
1	2	27	25	50	W	Poa trivialis subsp. trivialis	30
1	2	27	25	50	W	Vacconia myrrillus	30
1	2	27	25	50	W	Polystichum aculeatum	30
1	2	27	25	50	W	Carex vulpina	30
1	2	27	25	50	W	Sympetrum tuberosum	30
1	2	27	25	50	W	Ceratium caespitum	30
1	2	27	25	50	W	Euphorbia amygdaloides	30
1	2	27	25	50	W	Fragaria vesca	30
1	2	27	25	50	W	Poa annua	30
1	2	27	25	50	W	Viola canina	30
1	2	27	25	50	W	Fominia antipyretica	30
1	2	27	25	50	W	Fragaria viridis	30
1	2	27	25	50	W	Myosotis sylvatica	30
1	2	27	25	50	W	Bromus benekenii	30
1	2	27	25	50	W	Moehringia trinervia	30

Table 2 - (continuation).

Table 2 - (continuation).

Table 3 - Analytical table of *Geo coccinei-Rumicetum alpini*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16		
Relevé number	8	8	70	50	80	20	50	60	50	20	50	60	40	30	25	10		
Surface (m ²)	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100		
Inklinacija	5	3	15	4	8	5	8	8	15	3	10	5	3	6	10	5		
Altitude (m)	1490	1510	1630	1680	1950	1975	1780	1700	1750	1750	1770	1940	1800	1890	1850	2180		
Ekspozicija	NW	SE	E	NW	E	E	E	SE	E	E	E	E	SE	SE	N			
Number of species	27	25	21	31	18	14	15	26	21	25	21	17	15	18	21	18		
Char. Species	Layer															Presence		
Rumex alpinus		4.1	3.1	5.1	4.1	4.1	4.1	4.1	4.1	4.1	4.1	4.1	4.1	4.1	4.1	16		
<i>Cirsion appendiculati, Adenostyletalia, Mulgedio-Aconitetea</i>																		
<i>Cirsium appendiculatum</i>	C	+	+	1.1	+	1.1	1.1	2.1	+	1.1	1.1	1.1	1.1	1.1	+	+	16	
<i>Alchemilla indivisa</i>	C	1.1	+	+	2.1	1.1	+	+	.	1.1	2.1	+	1.1	+	+	1.1	+	15
<i>Angelica pannicifolia</i>	C	2.1	3.1	+	2.1	+	+	2.1	.	2.1	3.1	2.1	+	3.1	3.1	3.1	.	14
<i>Geum coccineum</i>	C	1.1	2.1	1.1	2.1	+	.	+	.	1.1	+	+	+	+	+	+	+	14
<i>Caltha palustris</i> subsp. <i>laeta</i>	C	.	.	2.1	1.1	1.1	1.1	2.1	.	2.1	2.1	2.1	1.1	3.1	2.1	2.1	2.1	13
<i>Doronicum austriacum</i>	C	1.1	2.1	.	2.1	+	.	+	+	2.1	+	1.1	.	1.1	+	+	.	12
<i>Veratrum album</i>	C	+	.	+	+	+	+	+	+	+	+	+	.	.	+	+	.	11
<i>Geranium sylvaticum</i>	C	1.1	+	+	2.1	.	.	+	+	.	+	.	.	+	+	+	10	
<i>Serophularia scopolii</i>	C	.	.	.	+	+	+	+	.	.	+	+	.	+	.	.	6	
Other species																		
<i>Athyrium filix-femina</i>	C	+	1.1	1.1	1.1	+	+	+	.	+	1.1	1.1	1.1	+	+	+	.	14
<i>Deschampsia caespitosa</i>	C	+	.	+	+	+	+	+	.	+	1.1	+	+	+	+	+	.	13
<i>Epilobium alsinifolium</i>	C	2.1	1.1	+	.	1.1	+	1.1	1.1	1.1	+	1.2	+	11
<i>Myosotis scorpioides</i>	C	1.1	2.1	.	+	.	+	+	+	1.1	1.1	+	+	+	.	.	11	
<i>Saxifraga rotundifolia</i> subsp. <i>chrysosplenifolia</i> var. <i>rhodopaea</i>	C	.	+	.	+	1.1	+	+	.	+	.	1.1	2.1	.	1.1	1.1	1.1	11
<i>Brachythecium plumosum</i>	D	1.2	.	.	1.1	1.2	1.2	.	+	.	1.2	.	1.2	.	1.2	.	1.2	9
<i>Cardamine acris</i>	C	.	+	+	.	.	1.1	.	1.1	.	1.1	.	1.1	+	1.1	2.1	2.1	9
<i>Urtica dioica</i>	C	.	.	+	+	+	+	+	+	.	+	.	+	+	+	.	8	
<i>Rubus idaeus</i>	C	+	.	.	+	.	.	1.1	+	.	+	+	.	+	.	+	.	7
<i>Pedicularis limnogena</i>	C	+	+	+	.	+	+	+	+	+	.	+	6	
<i>Saxifraga stellaris</i> subsp. <i>alpigena</i>	C	.	.	+	.	+	4.2	.	1.2	.	4.2	.	4.2	5
<i>Vaccinium myrtillus</i>	C	.	.	+	.	.	.	+	+	.	+	+	.	5
<i>Valeriana officinalis</i>	C	1.1	+	+	+	.	.	.	+	.	+	5	
<i>Festuca pratensis</i> subsp. <i>apennina</i>	C	+	.	.	1.1	.	.	.	+	.	+	+	4	
<i>Galium album</i>	C	.	.	.	+	+	.	+	+	.	+	+	4	
<i>Scapania undulata</i>	D	+	.	.	+	+	.	+	+	.	+	+	.	.	+	.	3	
<i>Chaerophyllum aureum</i>	C	+	.	.	+	+	.	+	+	.	+	+	3	
<i>Myosotis sylvatica</i>	C	.	.	.	+	+	.	+	+	.	+	+	.	.	+	.	3	
<i>Poa nemoralis</i>	C	.	1.1	.	1.1	.	.	+	+	.	+	+	3	
<i>Thalictrum aquilegifolium</i>	C	+	+	.	.	+	.	+	+	.	+	+	3	
<i>Vicia sepium</i>	C	+	+	.	.	+	.	+	+	.	+	+	3	

Table 4 - Results of unrestricted Monte Carlo test with 9999 permutation; testing of statistical significance of variables and canonical axes. Forward selection of explanatory variables was used to provide a ranking of relative importance of the specific variable (TER BRAAK & ŠMILAUER, 2002).

Variable	Lambda A	P	F
Altitude	0.19	0.002	2.97
Aspect	0.12	0.002	1.84
Surface	0.08	0.096	1.36
Inclination	0.08	0.238	1.13

Montio-Cardaminetalia Braun-Blanquet et Tüxen ex Klika et Hadač 1944

Doronico austriacae-Cirsietum appendiculati Horvat ex Čarni et Matevski ass. nova

Geo coccinei-Rumicetum alpini Čarni et Matevski ass. nova

Cirsion appendiculati Horvat et al. 1937
Adenostyletalia Gabrielle et Josias Braun-Blanquet 1931

Mulgedio-Aconitetea Hadač et Klika 1944

ACKNOWLEDGEMENT

For help in the preparation of the manuscript, we are grateful to Magdalena Cekova for identification of

mosses, Mitko Kostadinovski for identification of vascular plants and to Andrej Martinčič for identification of the genus *Alchemilla*. The authors acknowledge financial support from the state budget by the Slovenian Research Agency (project N. L1-9737 and P1-0236) and the Ministry of Education and Science of the Republic of Macedonia.

APPENDIX

Table 1 - Localities: 1-5 Ezerska reka 26.06.2002; 6-9, 11 Golemo ezero, 26.06.2002; 10, 12, 13 Sapundžica, 27.06.2002.

Designation of layers: C = herb layer, D = moss layer.

Species with lower frequency: *Brachythecium plumosum* D 11: 2.2, 12: 2.2; *Chiloscyphus polyanthus* D 13: 3.2; *Cirsium appendiculatum* C 9: +, 11: +; *Cystopteris fragilis* C 1: +, 2: +; *Dryopteris filix-mas* C 5: +; *Eriophorum latifolium* C 13: +; *Festuca rubra* subsp. *rubra* C 6: +, 13: +; *Juncus conglomeratus* C 3: +, 10: +; *Myosotis scorpioides* C 2: +; *Parnassia palustris* C 5: +; *Poa nemoralis* C 1: +, 2: +; *Rumex* sp. C 2: +; *Sagina procumbens* var. *procumbens* C 1: +.

Table 2 - Localities: 1. Orlovi Bari-Sapundžica, 17.7.2001; 2. Nižepole, Skrcko, 17.7.2001; 3. Nižepole, Skrcko, 17.7.2001; 4. Nižepole, Skrcko, 17.7.2001; 5. Nižepole-Crvena reka, 20.7.2001; 6. Crvena reka, 27.6.2002; 7. Crvena reka, 27.6.2002; 8. Crvena reka, 27.6.2002; 9. Crvena reka, 27.6.2002; 10. Crvena reka, 27.6.2002; 11. Crvena reka, 27.6.2002; 12. Ezerska reka, Debel rid, 26.6.2002; 13. Caparska reka, 26.6.2002; 14. Under Kajmakačalan, 40° 53,819' N, 21° 49,526' 29.6.2002; 15. Under Kajmakačalan, 40° 53,544' N, 21° 48,432' 29.6.2002; 16. Under Kajmakačalan, 40° 53,564' N, 21° 48,466' 29.6.2002; 17. Magarevska reka, česma Ilinden, between Kopanki and Jorgov kamen, 28.6.2002; 18. Magarevska reka, česma Ilinden, between Kopanki and Jorgov kamen, 28.6.2002; 19. Magarevska reka, below česma Ilinden, between Kopanki and Jorgov kamen, 28.6.2002; 20. Magarevska reka, below česma Ilinden, between Kopanki and Jorgov kamen, 28.6.2002; 21. Magarevska reka, below česma Ilinden, between Kopanki and Jorgov kamen, 28.6.2002; 22. Magarevska reka, 28.6.2002; 23. Magarevska reka, near Lastojčin kamen, 28.6.2002; 24. Brajčinska reka, v. Brajčino, in sha-

dow of beech tree, 25.6.2002; 25. Brajčinska reka, v. Brajčino, in shadow of beech tree, 25.6.2002; 26. Šemnica, 30.6.2002; 27. Šemnica, 30.6.2002; 28. Šemnica, 30.6.2002; 29. Šemnica, 30.6.2002; 30. Pisoderi, 40° 46,908' N, 21° 15,930' E, 29.6.2002; 31. Pisoderi, 29.6.2002; 32. Caparska reka, 1.7.2002; 33. Caparska reka, 1.7.2002; 34. Caparska reka, 1.7.2002; 35. Caparska reka, 1.7.2002; 36. Caparska reka, 1.7.2002; 37. Caparska reka, 1.7.2002; 38. Caparska reka, 1.7.2002; 39. Sapundžica, 2.7.2002; 40. Sapundžica, 2.7.2002; 41. Sapundžica, 2.7.2002; 42. Sapundžica, 2.7.2002; 43. Sapundžica, 2.7.2002; 44. Sapundžica, near to česma, 2.7.2002. Species with lower frequency: *Achillea grandifolia* C 25: +, 33: +, *Adenostyles alliariae* subsp. *hybrida* C 39: +, *Alopecurus pratensis* C 30: +, 31: +, *Arum maculatum* C 27: +, *Barbarea vulgaris* C 38: +, *Bellis perennis* C 27: +, 28: +, *Brachypodium pinnatum* C 43: +, *Brachythecium rutabulum* D 30: +, 44: +, *Brachythecium* sp. D 14: +, 15: +, 31: +, *Bruckenthalia spiculifolia* C 1: +, 2: +, 3: +, *Bryum capillare* D 22: 1.1, 27: 1.1, *Bryum pseudotriquetrum* D 16: +, *Calamintha grandiflora* C 21: +, 23: +, *Campanula glomerata* C 24: +, 42: +, 44: +, *Cardamine bulbifera* C 26: +, *Carex echinata* C 35: +, *Carex pallescens* C 41: +, 42: +, 43: +, *Carex paniculata* C 16: +, *Carex remota* C 24: +, 29: +, *Carex sylvatica* C 26: +, *Cerastium petricola* C 14: +, *Chaerophyllum temulum* C 15: +, 16: +, *Climacium dendroides* D 22: 1.1, 23: 1.2, *Clinopodium vulgare* C 5: +, *Cuscuta* sp. C 43: +, *Cystopteris fragilis* C 8: +, 14: +, 20: +, *Epilobium alpestre* C 13: 1.1, 25: +, 36: +, *Epilobium angustifolium* C 13: +, 22: +, *Epilobium nutans* C 41: +, *Epilobium roseum* subsp. *subsessile* C 8: +, 9: +, 37: +, *Euphorbia cyparissias* C 4: +, 27: +, 32: +, *Euphorbia stricta* C 28: +, 29: +, *Euphorbia verrucosa* C 8: +, 9: +, *Eurhynchium speciosum* D 27: +, 39: 1.2, *Fagus sylvatica* juv. C 24: +, 27: +, 37: +, *Festuca pratensis* subsp. *pratensis* C 44: +, *Geranium asphodeloides* C 26: +, 27: +, *Geranium cinereum* subsp. *subcaulescens* var. *rupestris* C 14: +, *Geranium pyrenaicum* C 11: +, *Glyceria plicata* C 31: +, *Hesperis dinarica* C 37: +, *Hypericum perforatum* var. *perforatum* C 27: +, 40: +, *Hypnum cupressiforme* D 27: +, *Knautia magnifica* C 1: +, 3: +, 5: +, *Lapsana communis* C 25: +, 29: +, *Lolium perenne* C 27: +, 29: +, *Lophocolea bidentata* D 26: 1.2, *Luzula forsteri* C 43: +, *Luzula luzuloides* C 14: +, 16: +, *Origanum vulgare* C 11: +, 24: +, *Philonotis marchica* D 12: +, 24: +, 25: +, *Philonotis seriata* D 41: +, 42:

+, *Poa pratensis* C 11: +, *Poa trivialis* subsp. *sylvicola* C 11: +, 28: +, 44: +, *Polygonum bistorta* C 15: +, 16: +, *Porella cordeana* D 13: +, 22: 1.1, *Potentilla reptans* C 24: +, *Primula veris* subsp. *columnae* C 27: +, *Prunella vulgaris* C 27: +, 28: +, *Pteridium aquilinum* C 31: +, 38: +, *Ranunculus oreophilus* C 14: +, 44: +, 2, *Rhizomnium punctatum* D 21: +, 26: +, 28: +, *Rhynchosciurus elephas* C 16: +, *Rosa nitidula* C 9: +, 11: +, *Rosa pendulina* C 24: +, 34: +, *Rumex patientia* C 27: +, 30: +, 38: +, *Salix caprea* C 2: +, 3: +, *Sambucus ebulus* C 25: +, *Sanicula europaea* C 21: +, *Saxifraga stellaris* subsp. *alpigena* C 3: +, 41: +, 42: +, *Secale montanum* C 24: +, *Senecio rupestris* C 14: +, 16: +, *Senecio subalpinus* C 16: +, *Stachys sylvatica* C 13: +, 24: +, 29: +, *Taraxacum officinale* C 9: +, *Thamnobryum alopecurum* D 21: +, *Thlaspikovatsii* C 14: +, 36: +, *Trifolium pratense* C 27: +, 32: +, 42: +, *Trifolium repens* C 24: +, 28: +, *Veronica beccabunga* C 11: +, 43: +, *Viola orphanidis* C 7: +, 14: +, 15: +.

Table 3 - Localities: 1. Sapundžica, 24.6.2002; 2. Sapundžica, 22.6.2002; 3. Markovo Bačilo-Crvena Reka, 20.7.2001; 4. Sapundžica, 2.7.2002; 5. Ezerska reka, between Debel Rid and Hrbet, 26.6.2002; 6. Ezerska reka, between Debel Rid and Hrbet, 26.6.2002; 7. Ezerska reka-Debel Rid, 18.7.2001; 8. Magarevska reka, near Jorgov kamen, 28.6.2002; 9. Ezerska reka-Debel Rid, 18.7.2001; 10. Sapundžica, 2.7.2002; 11. Ezerska reka-Debel Rid, 18.7.2001; 12. Ezerska reka, 26.6.2002; 13. Ezerskareka, 26.6.2002; 14. Ezerska reka, 26.6.2002; 15. Ezerska reka, 26.6.2002; 16. Golemo ezero, 26.6.2002.

Species with lower frequency: *Arenaria agrimonoides* C 2: +, *Arrhenatherum elatius* C 1: +, *Bromus benekenii* C 8: +, *Carex panicea* C 3: +, *Carex rigidula* var. *macedonica* C 16: +, *Chenopodium bonus-henricus* C 8: +, 12: +, *Cynosurus cristatus* C 2: +, *Dactylis glomerata* C 10: +, *Dactylorhiza cordigera* subsp. *bosniaca* C 13: +, *Dryopteris filix-mas* C 8: +, *Epilobium montanum* C 1: +, 8: +, *Epilobium obscurum* C 3: +, *Equisetum arvense* C 3: 1.1, *Euphorbia amygdaloides* C 1: +, 2: +, *Fragaria viridis* C 2: +, *Geranium macrorrhizum* C 8: +, *Geum urbanum* C 8: +, *Gymnocarpium dryopteris* C 11: +, *Holcus lanatus* C 2: +, *Juncus conglomeratus* C 3: +, *Juncus thomasi* C 3: +, 9: +, *Lamiastrum galeobdolon* subsp. *galeobdolon* C 8: +, *Lamium garganicum* C 15: +, *Lathyrus pratensis* C 1:

1.1, *Luzula multiflora* C 3: +, 10: +, *Mentha spicata* subsp. *spicata* C 1: +, *Milium effusum* C 4: +, 10: +, *Pellia epiphylla* D 4: +, 15: +, *Philonotis marchica* D 15: +, *Philonotis seriata* D 4: +, *Pimpinella saxifraga* C 16: +, *Plagiomnium medium* D 4: +, *Plagiomnium undulatum* D 2: 2.2, *Poa trivialis* subsp. *sylvicola* C 1: +, 2: +, *Pteridium aquilinum* C 2: +, *Ranunculus sericus* C 1: 1.1, 2: 1.1, *Rosa pendulina* C 8: +, *Rubus guentheri* C 2: +, 8: +, *Rumex arifolius* C 3: +, 4: +, *Senecio subalpinus* C 9: +, 10: +, *Silene asterias* C 4: +, 10: +, *Silene vulgaris* subsp. *vulgaris* C 4: +, 8: +, *Stachys thymphaea* C 8: +, 9: +, *Stellaria alsine* C 16: +, *Sympyrum tuberosum* C 8: +, *Tozzia alpina* subsp. *carpathica* C 1: +, 15: +, *Trifolium hybridum* C 10: +, *Veronica chamaedrys* C 4: +, *Viola orphanidis* C 3: +, 8: +.

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PLANT SPECIES DIVERSITY AND DISTRIBUTION ALONG ENVIRONMENTAL GRADIENTS IN A SUBMEDITERRANEAN FOREST LANDSCAPE (CENTRAL ITALY)

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ABSTRACT

A survey of a submediterranean forest landscape in central Italy was carried out to assess floristic diversity and species ecological behaviour in relation to some environmental gradients (altitude, aspect, light intensity on the undergrowth, soil pH, nitrogen content and texture). Diversity indices (species richness, Shannon-Wiener and Evenness) trends, calculated in relation to environmental parameters, showed to be mostly related to stress gradients. The highest diversity, in fact, is linked to the least stressful conditions. Redundancy analysis (RDA) allowed to identify six species sets, related to the environmental parameters, which were tested through bioindication values analysis. Intensity of stress factors and their combination select one or more groups of species with different ecological behaviour, leading to the local floristic differentiation of plant communities. This approach may be useful to predict floristic variation of forest ecosystems as a consequence of increasing stress levels, such as drought stress due to climatic changes, to the definition of plant diversity conservation guidelines and for biodiversity monitoring.

KEYWORDS: Diversity, environmental gradients, forest vegetation.

RIASSUNTO

È stata effettuata una campagna di rilievi in un paesaggio forestale submediterraneo nell'Italia centrale per valutare la diversità floristica ed il comportamento ecologico delle specie in relazione ad alcuni gradienti ambientali (altitudine, esposizione, intensità della luce nel sottobosco, pH, contenuto di azoto e tessitura del suolo). L'andamento degli indici di diversità (ricchezza di specie, Shannon-Wiener e Evenness), calcolati in relazione ai parametri ambientali, ha dimostrato di essere legato, per lo più, a gradienti di stress. La diversità più elevata è infatti associata alle condizioni meno stressanti. L'analisi della ridon-

danza (RDA) ha permesso di identificare sei gruppi di specie legati ai parametri ambientali, che sono stati testati con l'analisi dei valori di bioindicazione. L'intensità dei fattori di stress e la loro combinazione seleziona uno o più gruppi di specie con differente comportamento ecologico, portando alla differenziazione floristica locale delle comunità vegetali. Questo approccio può essere utile a predire le variazioni floristiche degli ecosistemi forestali come conseguenza dei crescenti livelli di stress come lo stress d'aridità dovuto ai cambiamenti climatici, alla definizione di linee guida per la conservazione della diversità vegetale e al monitoraggio della biodiversità.

INTRODUCTION

Since the classic studies of WHITTAKER (1956) and BRAY & CURTIS (1957), plant ecologists have sought to quantify the distribution of plant species along complex environmental gradients. Although over any large region the distribution of species richness is likely to be governed by two or more environmental gradients (MARGULES *et al.*, 1987; PAUSAS, 1994; PAUSAS & CARRERAS, 1995; AUSTIN *et al.*, 1996; PAUSAS & AUSTIN, 2001), species richness studies about this issue have been mainly single-factor studies (*e.g.* HUSTON, 1980; WILSON & KEDDY, 1988). Species diversity shifts in forest plant communities have been reported by several authors to be related to differences in environmental conditions, such as nutrients level, soil reaction, soil moisture and light intensity (*e.g.* FORMAN, 1995; ROSENZWEIG, 1995; BURNETT *et al.*, 1998; NICHOLS *et al.*, 1998; NASH SUDING, 2001; DECOCQ, 2002). These factors are, in turn, related to topography, bedrock geology, soil physic characteristics (soil depth, texture and drainage), overstory structure and land use history (HUTCHINSON *et al.*, 1999; DECOCQ, 2000). Moreover, floristic differentiation patterns in vegetation are usually too complex to be simplified in either strictly geographical differentiation or in a strictly edaphic

or local topo-climatic differentiation (WHITTAKER, 1975; TZONEV *et al.*, 2006). Often these patterns are scale-dependent, showing stronger edaphic effects at finer scales and stronger geographic distinctions on broader scales (CHYTRÝ *et al.*, 2002; KUŽELOVÁ & CHYTRÝ, 2004).

The aim of this work was to assess the floristic diversity and ecological behaviour of species in relation to some environmental gradients (altitude, aspect, light intensity on the undergrowth, soil pH, nitrogen content and texture) in a submediterranean forest landscape, taking into account the hierarchical approach to the landscape characterization (BLASI *et al.*, 2000) and the phytosociological placement of plant communities, in order to reduce the scale-dependent effects on floristic differentiation pattern.

MATERIALS AND METHODS

STUDY AREA

The study area is a hilly and mountainous territory, placed in the central-southern part of Umbria-Marche Apennines (around Camerino, Foligno and Fabriano - central Italy), at altitudes ranging from 150 to 2,300 m a.s.l. (coordinates 43°20'-42°50' N; 12°26'-13°23' E).

From a geological viewpoint, this territory is characterized by calcareous, marly-calcareous, marly-arenaceous and arenaceous substrata. The most common morphologies are represented by reliefs with slightly steep tops and moderately to very steep slopes, which give rise to small flat bottomed valleys (BISCI & DRAMIS, 1991).

The study area is located within a submediterranean context, at the border between Temperate and Mediterranean macroclimatic regions (RIVAS-MARTÍNEZ, 2005).

The forest landscape is featured by mixed woods, in which *Quercus ilex* subsp. *ilex*, *Quercus pubescens* s.l., *Ostrya carpinifolia*, *Quercus cerris*, *Castanea sativa* and *Fagus sylvatica* subsp. *sylvatica* play a dominant or a

Tab. 1 - Main features of the Upper Mesotemperate bioclimatic belt. Termotype and Ombrotype classification follows RIVAS-MARTÍNEZ (2004); for the calculation of n. of months of drought stress and cold stress MITRAKOS' indices (1980, 1982) were applied (from: ORSOMANDO & CATORCI 2000, modified).

Bioclimatic belt	Altitudinal range (m a.s.l.)	Average annual temperature (°C)	Average annual precipitation (mm)	Average monthly temperature < 10 °C (n. of months)	Average monthly min. temperature < 0 °C (n. of months)	Thermotype	Ombrotype	Drought stress (n. of months)	Cold stress (n. of months)	Vegetative period (n. of days with average monthly min. temperature > 6 °C)
Upper Mesotemperate	500/600-1000/1100	11-13	850-1100	5-6	1-2	Upper Mesotemperate	Lower Humid	0	6-7	180-210

Tab. 2 - Scales for the environmental parameters used in RDA.

Environmental parameter	Class	
Aspect	1	Southern (SE-WNW)
	2	Northern (NW-ESE)
Altitude (m a.s.l.)	1	500-800
	2	800-1100
Soil pH	1	< 6.0
	2	6.0-7.0
	3	> 7.0
Soil total nitrogen content (g/Kg)	1	< 2.0
	2	2.0-4.0
	3	> 4.0
Soil texture (sand %)	1	> 60.0
	2	40.0-60.0
	3	< 40.0
Light intensity ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	1	< 25.0
	2	25.0-50.0
	3	50.1-75.0
	4	> 75.0

codominant role. These woods are mainly managed as coppices with standards and cut down every 20-30 years.

EXPERIMENTAL DESIGN

To plan data collection, the study area was divided into homogeneous ecological units according to the BLASI *et al.* (2000) method, using the plant landscape geodatabase (G.I.S.) of Marches (CATORCI *et al.*, 2007a; PESARESI *et al.*, 2007) and Umbria (ORSOMANDO & CATORCI, 1999, 2000).

In order to reduce the number of environmental variables, woods belonging to the Upper Mesotemperate bioclimatic belt (BIONDI *et al.*, 1995; CATORCI *et al.*, 2007b) were selected; the main features of this belt are shown in Tab. 1.

The area was further divided into the main geologic systems (calcareous, marly-calcareous, marly-arenaceous and arenaceous), within each of them, two aspect classes regarding North-facing (from NW to ESE) and South-facing (from SE to WNW) slopes were distinguished. In fact, because of the transition between two macroclimatic contexts, on Southern aspects, characterized by higher temperature and insolation, summer drought stress increases and winter cold stress decreases (JACKSON, 1966; BONAN, 2008) compared to the mean conditions of the Upper Mesotemperate belt. Within each homogeneous ecological unit, five sampling plots (80 on the whole), covering 400

m^2 each (20x20 m), were randomly selected. In each of them floristic and field data were gathered.

DATA COLLECTION

Floristic and environmental data were collected in the period 2006-2007; species cover values were assessed using Braun-Blanquet classes (BRAUN-BLANQUET, 1964).

Each soil sample, collected in five locations in each plot within a depth ranging from 10 to 40 cm and thoroughly mixed, was analysed by a soils laboratory for pH, total nitrogen content (g/kg) and texture (sand, clay and silt %). Furthermore some field data (altitude and aspect) were also gathered. Measurements of light intensity on the undergrowth ($\frac{1}{4}\text{mol m}^{-2} \text{s}^{-1}$) were performed in June/July, at 50 cm above soil level, using a ceptometer.

Information about species bioindication values were gathered from PIGNATTI (2005).

DATA ELABORATION

For statistical elaborations, species abundances were expressed in percent values using the average cover values of Braun-Blanquet classes; environmental parameters values (aspect, altitude, soil pH, soil total nitrogen content, soil sand %, light intensity on the undergrowth) were expressed in classes (Tab. 2).

Species richness, Shannon-Wiener and Evenness indices were calculated on two matrices: relevés x species (cover %) and relevés x environmental parameters (classes).

Cluster analysis of floristic data set was run on the matrix relevés x species, using the complete link method, based on Euclidean distance, after transformation of Braun-Blanquet classes according to VAN DER MAAREL's (1979) scale. Groups of relevés were classified into *syntaxa* according to revision publications of Italian vegetation (BIONDI *et al.*, 2002, 2003; BLASI *et al.*, 2004), as well as local studies (CATORCI & ORSOMANDO, 2001; ALLEGREZZA *et al.*, 2002;

ALLEGREZZA, 2003; CATORCI *et al.*, 2003, 2008, 2010).

A Redundancy analysis (RDA) on the matrix relevés x variables (floristic units and environmental parameters) was run to understand the amount of total variability related to ecological factors affecting species distribution and to define ecologically homogeneous species sets.

Ecological behaviour of the resulting species sets was tested using light, temperature, soil moisture, soil reaction and soil nutrients bioindication values.

Diversity indices were calculated using PCORD 5.0 software (McCUNE & GRACE, 2002; McCUNE & MEFFORD, 2006); cluster analysis and RDA were performed using SYN-TAX 2000 package (PODANI, 2001).

RESULTS

PHYTOSOCIOLOGICAL PLACEMENT

The multivariate analysis (Fig. 1) shows two main clusters: I) woodlands of South-facing slopes, with a dominance of *Quercus pubescens* s.l. (subclusters Ia_{1b}, Ia₂ and Ib) or *Quercus ilex* (subcluster Ia_{1a}), placed in *Quercetalia pubescenti-petraeae* and *Quercetalia ilicis* orders; II) woodlands of North-facing slopes with a dominance of *Ostrya carpinifolia* (subcluster IIa), *Quercus cerris* or *Castanea sativa* (subcluster IIb), placed in *Quercetalia pubescenti-petraeae* and *Fagetalia sylvaticae* orders. Subclusters are divided into groups which correspond to the syntaxonomical levels of association and subassociation. These *syntaxa* are shortly described in Tab. 3.

SPECIES DIVERSITY

A total of 214 species was collected. Species richness, Shannon-Wiener and Evenness diversity indices values, related to each environmental parameter class, are reported in Tab. 4. The highest richness and Shannon-Wiener index values were recorded for North-facing slopes, altitudes ranging

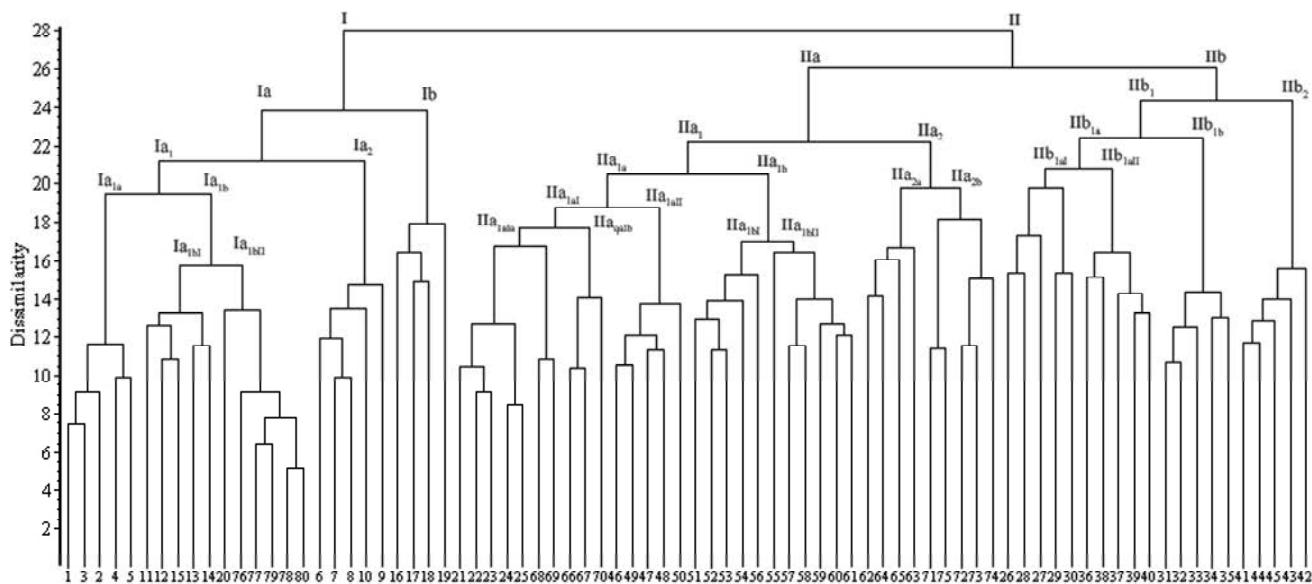


Fig. 1 - Dendrogram of phytosociological relevés (Ia_{1a} - *Cyclamino hederifolii*-*Quercetum ilicis cyclaminetosum hederifolii*; Ia_{1b1} - *Cytiso sessilifolii*-*Quercetum pubescens*; Ia_{1b2} - *Quercus cerris* and *Quercus pubescens* s.l. community; Ia₂ - *Erico arboreae*-*Quercetum pubescens ericetosum arboreae*; Ib - *Pucedano cervariae*-*Quercetum pubescens peucedanetosum cervariae*; IIa_{1a1} - *Aceri obtusati*-*Quercetum cerridis*; IIa_{1a2} - *Scutellario columnae*-*Ostryetum carpinifoliae prunetosum avium*; IIa_{1a3} - *Hieracio murorum*-*Ostryetum carpinifoliae hieracietosum murorum*; IIa_{1b1} - *Scutellario columnae*-*Ostryetum carpinifoliae cyisetosum sessilifolii*; IIa_{1b2} - *Scutellario columnae*-*Ostryetum carpinifoliae violetosum reichenbachianae*; IIa_{2a} - *Scutellario columnae*-*Ostryetum carpinifoliae fagetosum sylvaticae*; IIa_{2b} - *Carici digitatae*-*Ostryetum carpinifoliae*; IIb_{1a1} - *Aceri obtusati*-*Quercetum cerridis fagetosum sylvaticae*; IIb_{1a2} - *Carici sylvaticae*-*Quercetum cerridis*; IIb_{1b} - *Cephalanthero longifoliae*-*Quercetum cerridis*; IIb₂ - *Cyclamino hederifolii*-*Castaneetum sativae*).

Tab. 3 - Description of the forest syntaxa of the study area.

Ia_{1a} - *Cyclamino hederifolii*-*Quercetum ilicis* Biondi, Casavecchia et Gigante 2003 *cyclaminetosum hederifolii* Biondi, Casavecchia et Gigante 2003: woodlands with a dominance of *Quercus ilex* subsp. *ilex*, growing on calcareous South-facing very steep slopes.

Ia_{1b1} - *Cytiso sessilifolii*-*Quercetum pubescens* Blasi, Feoli et Avena 1982: woodlands with a dominance of *Quercus pubescens* s.l., growing on calcareous detritic South-facing, moderately to very steep slopes.

Ia_{1b2} - *Quercus pubescens* s.l. and *Quercus cerris* community (*Carpinion orientalis*): woodlands with a dominance of *Quercus pubescens* s.l. and *Q. cerris*, growing on marly-arenaceous South-facing, moderately to very steep slopes.

Ia₂ - *Erico arboreae*-*Quercetum pubescens ericetosum arboreae* Catorci, Ballelli, Iocchi, Paura et Vitanzi 2008: woodlands with a dominance of *Quercus pubescens* s.l., growing on sandstone South-facing, moderately to very steep slopes.

Ib - *Pucedano cervariae*-*Quercetum pubescens* (Ubaldi et al., 1984) Ubaldi 1988 *peucedanetosum cervariae* Allegrezza, Baldoni, Biondi, Taffetani et Zuccarello 2002: woodlands with a dominance of *Quercus pubescens* s.l., growing on marly-calcareous South-facing, slightly to moderately steep slopes.

IIa_{1a1} - *Aceri obtusati*-*Quercetum cerridis* Ubaldi et Speranza 1982: woodlands with a dominance of *Ostrya carpinifolia* and *Quercus cerris*, growing on marly-arenaceous North-facing, slightly to moderately steep slopes.

IIa_{1a2} - *Scutellario columnae*-*Ostryetum carpinifoliae* Pedrotti, Ballelli et Biondi ex Pedrotti, Ballelli, Biondi, Cortini-Pedrotti et Orsomando 1980 *prunetosum avium* Allegrezza 2003: woodlands with a dominance of *Ostrya carpinifolia*, growing on marly-calcareous North-facing, moderately to very steep slopes.

IIa_{1a3} - *Hieracio murorum*-*Ostryetum carpinifoliae* Catorci, Ballelli, Iocchi, Paura et Vitanzi 2008 *hieracietosum murorum* Catorci, Ballelli, Iocchi, Paura et Vitanzi 2008: woodlands with a dominance of *Ostrya carpinifolia*, growing on arenaceous North-facing, moderately to very steep slopes.

IIa_{1b1} - *Scutellario columnae*-*Ostryetum carpinifoliae* Pedrotti, Ballelli et Biondi ex Pedrotti, Ballelli, Biondi, Cortini-Pedrotti et Orsomando 1980 *cyisetosum sessilifolii* Biondi, Allegrezza et Taffetani 1990: woodlands with a dominance of *Ostrya carpinifolia*, growing on calcareous South-facing, moderately to very steep slopes.

IIa_{1b2} - *Scutellario columnae*-*Ostryetum carpinifoliae* Pedrotti, Ballelli et Biondi ex Pedrotti, Ballelli, Biondi, Cortini-Pedrotti et Orsomando 1980 *violetosum reichenbachianae* Allegrezza 2003: woodlands with a dominance of *Ostrya carpinifolia*, growing on calcareous North-facing, moderately to very steep slopes.

IIa_{2a} - *Scutellario columnae*-*Ostryetum carpinifoliae* Pedrotti, Ballelli et Biondi ex Pedrotti, Ballelli, Biondi, Cortini-Pedrotti et Orsomando 1980 *fagetosum sylvaticae* Pedrotti, Ballelli et Biondi 1982: woodlands with a dominance of *Ostrya carpinifolia* and *Fagus sylvatica*, growing on calcareous North-facing, moderately to very steep slopes.

IIa_{2b} - *Carici digitatae*-*Ostryetum carpinifoliae* Catorci, Gatti et Sparvoli 2003: woodlands with a dominance *Ostrya carpinifolia*, growing on calcareous North-facing slopes, with medium-high angle.

IIb_{1a1} - *Aceri obtusati*-*Quercetum cerridis* Ubaldi et Speranza 1982 *fagetosum sylvaticae* Allegrezza 2003: woodlands with a dominance of *Ostrya carpinifolia* and *Quercus cerris*, growing on calcareous North-facing, moderately to very steep slopes.

IIb_{1a2} - *Carici sylvaticae*-*Quercetum cerridis* Catorci et Orsomando 2001: woodlands with a dominance of *Quercus cerris*, growing on calcareous North-facing, slightly steep slopes.

IIb_{1b} - *Cephalanthero longifoliae*-*Quercetum cerridis* Scoppola et Filesi 1997: woodlands with a dominance of *Quercus cerris*, growing on sandstone North-facing, slightly steep slopes.

IIb₂ - *Cyclamino hederifolii*-*Castaneetum sativae* Allegrezza 2003: woodlands with a dominance of *Castanea sativa*, growing on sandstone North-facing, slightly to moderately steep slopes.

Tab. 4 - Richness, Shannon-Wiener and Evenness indices calculated for the environmental parameter classes.

Environmental parameter	Class	Species nr.	Shannon-Wiener index	Evenness index
Aspect	1	27,8	1,898	0,583
	2	36,6	2,157	0,603
Altitude	1	32,9	2,000	0,582
	2	34,9	2,327	0,658
Soil pH	1	30,5	1,972	0,582
	2	27,9	2,070	0,626
	3	38,4	2,133	0,593
Soil total nitrogen content	1	28,9	1,884	0,566
	2	32,2	2,111	0,616
	3	45,0	2,255	0,596
Soil texture (sand %)	1	27,1	1,879	0,577
	2	32,4	1,983	0,580
	3	38,8	2,304	0,635
Light intensity	1	19,0	1,267	0,431
	2	37,3	2,268	0,633
	3	38,6	1,928	0,530
	4	24,6	2,025	0,638

Tab. 5 - RDA axes summary statistics and intraset correlations for environmental parameters.

Axis	Eigenvalue	Eigenvalue as percentage of total	% variance of interset relation	Intraset correlations						
				Aspect	Altitude	Soil pH	Soil total nitrogen content	Soil texture (sand %)	Light intensity	
1	16,82	8,58	32,52	0,78	0,71	-0,03	0,43	0,31	0,53	
2	11,35	5,79	21,95	-0,30	-0,30	0,90	0,72	0,46	0,14	
3	8,14	4,16	15,75	0,16	-0,48	0,04	-0,15	-0,75	0,43	
4	7,11	3,63	13,75	-0,42	0,43	0,28	0,40	-0,12	0,17	
5	4,44	2,27	8,59	0,29	-0,02	0,02	-0,33	0,33	0,69	
6	3,85	1,96	7,44	0,12	-0,05	0,33	-0,12	-0,09	-0,12	

from 800 to 1,100 m a.s.l., neutral-basic and nitrogen-rich soils with a low sand content, intermediate light intensities on the undergrowth; the lowest values were recorded for South-facing slopes, altitudes ranging from 500 to 800 m a.s.l., neutral/neutral-acid, nitrogen-poor soils, with a high sand percentage, low light intensities on the undergrowth. Evenness index shows the same trends, except for acid soils (minimum index value), high light intensities, intermediate soil nitrogen content and neutral/neutral-acid soils (maximum index values). More in particular, the highest species richness (45.0) is linked to the highest soil nitrogen content ($>4\text{ g/kg}$), the lowest (19.0) to the lowest light intensity on the undergrowth ($<25\frac{1}{4}\text{ mol m}^{-2}\text{ s}^{-1}$). The highest Shannon-Wiener and Evenness indices are related to the highest altitudes (800-1,000 m a.s.l.)

and to the least soil sand percentage (2.30-2.33 and 0.64-0.66, respectively), the lowest to low light intensity (1.27 and 0.43, respectively).

SPECIES ECOLOGICAL BEHAVIOUR

RDA canonical axes explain 26.39% of total variance of species data set. The first axis, explaining 32.52% of variance of interset relation (8.58% of total variance) is particularly related to light intensity on the undergrowth, aspect and altitude; the second axis, explaining 21.95% (5.79% of total variance) is primarily linked to soil pH and secondarily to soil total nitrogen content; the third axis, explaining 15.75% of variance of interset relation (4.16% of total variance) is related to soil sand percentage (Tab. 5).

In the RDA triplot (Fig. 2) two groups of species can be distinguished: one group, near axes origin, not particularly linked to the analyzed combination of environmental features (about 53% of total species number) and another one directly linked to one or more of them (about 47%), which may be divided into six sub-groups (Tab. 6). The mean and median bioindication values, calculated for each of these groups (Tab. 7), are compared according to the main gradients highlighted by RDA. In comparison with the other species sets, groups A and F show the highest light and temperature bioindication values and the lowest soil moisture and nutrients ones, while they differ for soil reaction values. Groups B and E present the same light, temperature, soil moisture and nutrients bioindication values, but quite different soil reaction values. Groups C and D show similar light and soil reaction values; in fact they are nearer to axis 1 than the other groups, while they have quite different temperature mean values.

The ecological behaviour characterization of each group and the relations among species sets, environmental stresses and ecological factors are summarized in Tab. 8. Species belonging to group A are linked to high level of dryness (high solar radiation due to Southern exposure or draining substrata) and low or medium-low nitrogen content; those included in group F are also linked to acid, sandy soils. Both species of A and F groups are light-demanding.

Species of groups B and E mainly differ for soil pH and are both related to medium-low light intensity on the undergrowth. From an ecological viewpoint, species belonging to group B are linked to neutral, clayey, nitrogen-rich soils, while those included in group E are related to acid, sandy-clayey soils with intermediate nitrogen content. Both groups characterize plant communities of North-facing slopes.

Species belonging to groups C and D are both typically linked to low light intensity on the undergrowth. From an ecological viewpoint, species included in group C are related to neutral and clayey soils with high nitrogen content, while group D includes floristic units of subacid and sandy-clayey soils with intermediate nitrogen content. Species of the two groups are water-demanding and low light intensity-tolerators. Both groups characterize phytocoenoses of North-facing slopes.

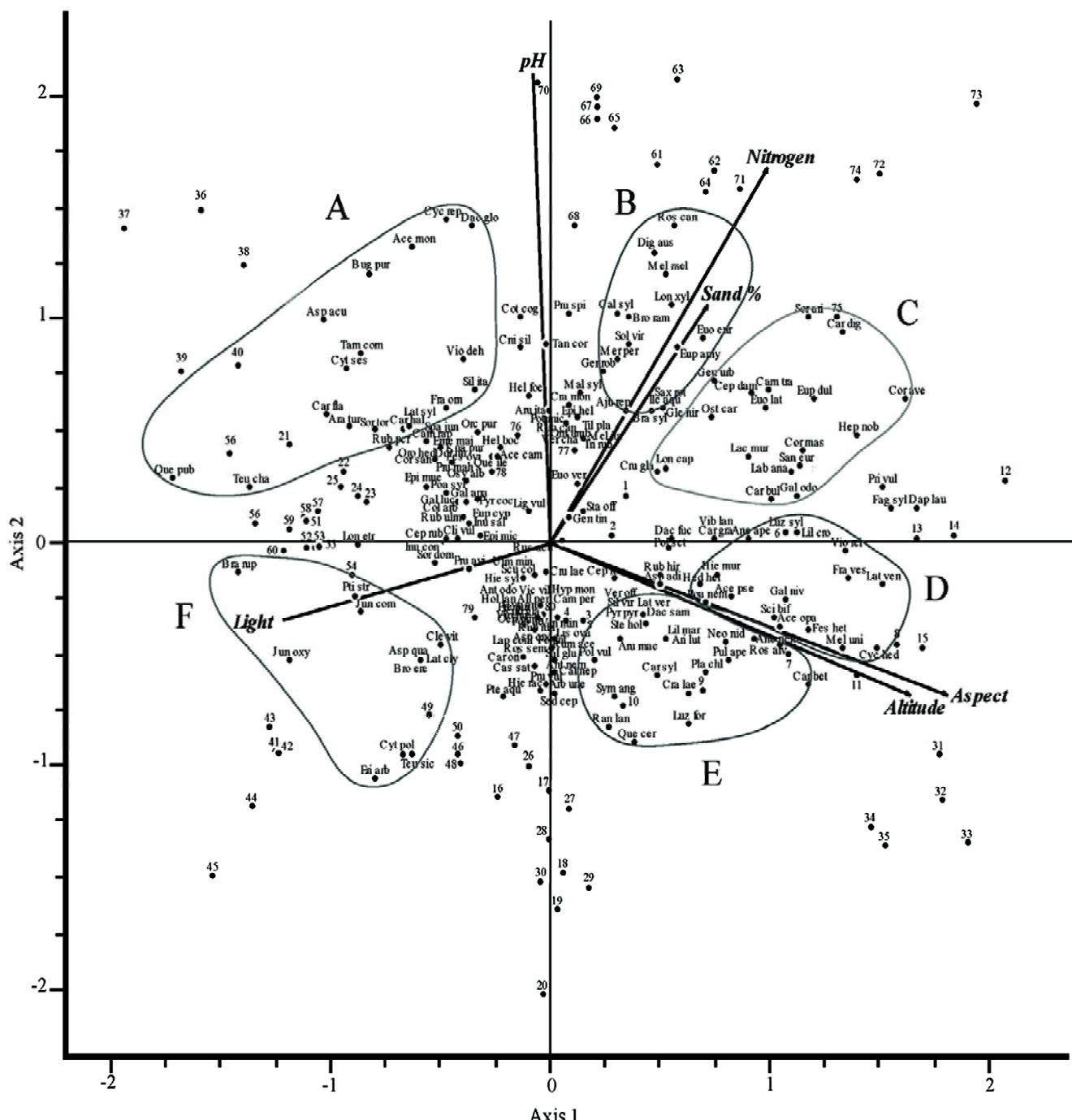


Fig. 2 - Ordination scatterogram from a Redundancy analysis on 80 objects (relevés) and 220 variables (214 species and 6 ecological parameters). Relevés are numbered, species are labelled. Letters A-F indicate species groups reported in Tab. 6.

DISCUSSION

Research findings highlight that in the study area the most important stress factors are soil dryness (related to aspect and soil texture), low nitrogen availability and acid pH. These results are in accordance with the ones of many authors (e.g. BURNETT *et al.*, 1998; NICHOLS *et al.*, 1998; SCHAFFERS, 2002; HÄRDITLE *et al.*, 2003). Also light intensity is important to determine the floristic composition of the undergrowth, as demonstrated also by MOORE & VANKAT (1986), COLLINS & PICKETT (1988) and SCHMIDT (2005).

From a floristic point of view, the

studied forest landscape is composed of two main species groups. The first one is made up of species whose distribution seems not to be linked to the local scale environmental features (species near axes origin), but, instead, to broader scale factors, such as macroclimatic conditions and biogeographic features; the second species group distribution, instead, is linked to local scale environmental features and to one or more of the considered environmental constraints. Furthermore, it is possible to state that intense stress (drought stress on South-facing slopes, nitrogen-poor soils with a high sand percentage or low light intensity) lowers richness and in-

duces the dominance of one or few species (low Shannon and Evenness indices values). The opposite trend is related to low stress level; as a matter of fact, the highest richness and Shannon-Wiener index values were recorded for the least stressful conditions. These results are in accordance with those emphasized by PAUSAS & CARRERAS (1995), BURNETT *et al.* (1998) and DECOCQ (2000).

The lowest richness was not found in relation to acid soils, but to neutral/neutral-acid ones, probably because of the overlapping of other environmental stresses (PAUSAS & AUSTIN, 2001) such as soil dryness and low nitrogen con-

Tab. 6 - Groups of species highlighted by Redundancy analysis (in brackets labels used in Fig. 2 are reported).

Group A. *Acer monspessulanum* subsp. *monspessulanum* (*Ace mon*), *Arabis turrita* (*Ara tur*), *Asparagus acutifolius* (*Asp acu*), *Buglossoides purpurocaerulea* (*Bug pur*), *Carex flacca* s.l. (*Car fla*), *Carex halleriana* (*Car hal*), *Cyclamen repandum* subsp. *repandum* (*Cyc rep*), *Cytisophyllum sessilifolium* (*Cyt ses*), *Dactylis glomerata* subsp. *glomerata* (*Dac glo*), *Fraxinus ornus* subsp. *ornus* (*Fra orn*), *Lathyrus sylvestris* (*Lat syl*), *Quercus pubescens* s.l. (*Que pub*), *Silene italica* (*Sil ita*), *Sorbus torminalis* (*Sor tor*), *Tamus communis* (*Tam com*), *Teucrium chamaedrys* subsp. *chamaedrys* (*Teu cha*), *Viola alba* subsp. *dehnhardtii* (*Vio deh*).

Group B. *Ajuga reptans* (*Aju rep*), *Brachypodium sylvaticum* (*Bra syl*), *Bromus ramosus* (*Bro ram*), *Calamintha nepeta* subsp. *sylvatica* (*Cal syl*), *Digitalis lutea* subsp. *australis* (*Dig aus*), *Euonymus europaeus* (*Euo eur*), *Euphorbia amygdaloides* subsp. *amygdaloides* (*Eup amy*), *Geranium robertianum* (*Ger rob*), *Glechoma hirsuta* (*Gle hir*), *Ilex aquifolium* (*Ile aqu*), *Lonicera xylosteum* (*Lon xyl*), *Melittis melissophyllum* subsp. *melissophyllum* (*Mel mel*), *Mercurialis perennis* (*Mer per*), *Rosa canina* s.l. (*Ros can*), *Saxifraga rotundifolia* (*Sax rot*), *Solidago virgaurea* subsp. *virgaurea* (*Sol vir*).

Group C. *Campanula trachelium* subsp. *trachelium* (*Cam tra*), *Cardamine bulbifera* (*Car bul*), *Carex digitata* (*Car dig*), *Cephalanthera damasonium* (*Cep dam*), *Cornus mas* (*Cormas*), *Corylus avellana* (*Cor ave*), *Cruciata glabra* subsp. *glabra* (*Cru gla*), *Euonymus latifolius* (*Euo lat*), *Euphorbia dulcis* (*Eup dul*), *Galium odoratum* (*Gal odo*), *Geum urbanum* (*Geu urb*), *Hepatica nobilis* (*Hep nob*), *Laburnum anagyroides* subsp. *anagyroides* (*Lab ana*), *Lactuca muralis* (*Lac mur*), *Lonicera caprifolium* (*Lon cap*), *Ostrya carpinifolia* (*Ost car*), *Sanicula europaea* (*San eur*), *Sorbus aria* subsp. *aria* (*Sor ari*).

Group D. *Acer opalus* subsp. *obtusatum* (*Ace obt*), *Acer pseudoplatanus* (*Ace pse*), *Anemone apennina* subsp. *apennina* (*Ane ape*), *Cyclamen hederifolium* subsp. *hederifolium* (*Cyc hed*), *Festuca heterophylla* (*Fes het*), *Fragaria vesca* subsp. *vesca* (*Fra ves*), *Galanthus nivalis* subsp. *nivalis* (*Gal niv*), *Hedera helix* subsp. *helix* (*Hed hel*), *Hieracium murorum* (*Hie mur*), *Lathyrus venetus* (*Lat ven*), *Lilium bulbiferum* subsp. *croceum* (*Lil cro*), *Luzula sylvatica* subsp. *sylvatica* (*Luz syl*), *Melica uniflora* (*Mel uni*), *Poa nemoralis* (*Poa nem*), *Scilla bifolia* (*Sci bif*), *Viola reichenbachiana* (*Vio rei*).

Group E. *Anemone nemorosa* (*Ane nem*), *Aristolochia lutea* (*Ari lut*), *Arum maculatum* (*Aru mac*), *Carex sylvatica* (*Car syl*), *Carpinus betulus* (*Car bet*), *Crataegus laevigata* (*Cra lae*), *Dactylorhiza sambucina* (*Dac sam*), *Lathyrus vernus* (*Lat ver*), *Lilium martagon* (*Lil mar*), *Luzula forsteri* (*Luz for*), *Neottia nidus-avis* (*Neo nid*), *Platanthera chlorantha* (*Pla chl*), *Polypodium vulgare* (*Pol vul*), *Pulmonaria apennina* (*Pul ape*), *Pyrus pyraster* (*Pyr pyr*), *Quercus cerris* (*Que cer*), *Ranunculus lanuginosus* (*Ran lan*), *Rosa arvensis* (*Ros arv*), *Silene viridiflora* (*Sil vir*), *Stellaria holostea* (*Ste hol*), *Symphytum tuberosum* subsp. *angustifolium* (*Sym ang*), *Veronica officinalis* (*Ver off*).

Group F. *Asplenium trichomanes* subsp. *quadrivalens* (*Asp qua*), *Brachypodium rupestre* (*Bra rup*), *Bromus erectus* subsp. *erectus* (*Bro ere*), *Clematis vitalba* (*Cle vit*), *Cytisus hirsutus* subsp. *polytrichus* (*Cyt pol*), *Erica arborea* (*Eri arb*), *Juniperus communis* (*Jun com*), *Juniperus oxycedrus* subsp. *oxycedrus* (*Jun oxy*), *Lathyrus clymenum* (*Lat cly*), *Ptilostemon strictum* (*Pti str*), *Teucrium siculum* subsp. *siculum* (*Teu sic*).

tent. Richness decrease in the most light condition corresponds to South-facing slopes (*Cytiso sessilifolii-Quercetum pubescens*, *Quercus cerris* and *Quercus pubescens* community and *Erico arboreae-Quercetum pubescens*), characterized in turn by the most intense drought stress. Shannon-Wiener and Evenness indices decrease in the range 50-75 $\frac{1}{4}\text{mol m}^{-2} \text{s}^{-1}$, is probably related

to the management kind (high forest) of *Quercus cerris* and *Carpinus betulus* woods (*Carici sylvaticae-Quercetum cerridis*) which tends to make tree canopy more homogeneous from a floristic viewpoint. Furthermore, evenness shows an increasing trend from high to low stressful conditions, in accordance with Shannon diversity and species number, except for soil pH and total

nitrogen concentration. In fact, at the highest nitrogen content and on neutral-basic soils, evenness decreases, unlike richness and Shannon index. It means that the higher value of nutrient availability in the study area probably is not enough to determine a richness decrease through competitive exclusion and the spread of dominant species (GRIME, 2001) but lead to a change in species abundances distribution pattern, making forest community species set less evenly distributed.

Stress gradients act not only on species diversity, but also on plant communities species composition. Species strongly related to the most stressful environmental conditions are those of A and F groups (Fig. 2, Tab. 6). From an ecological viewpoint species of group A would be considered nemoral, light-

Tab. 7 - Mean and median of bioindication values calculated for species groups highlighted by RDA.

	Light		Temperature		Soil moisture		Soil reaction		Soil nutrients	
	Mean	Median	Mean	Median	Mean	Median	Mean	Median	Mean	Median
Group A	5,7	6,0	6,9	7,0	3,9	4,0	6,4	7,0	4,2	4,0
Group B	4,9	5,0	5,2	5,0	4,7	5,0	6,6	7,0	5,1	5,0
Group C	4,2	4,0	5,7	5,0	4,7	5,0	6,5	7,0	5,4	5,0
Group D	4,5	4,0	5,2	5,0	4,9	5,0	6,5	7,0	5,5	5,0
Group E	4,7	5,0	5,5	5,0	4,9	5,0	5,8	6,0	5,2	5,0
Group F	6,7	7,0	7,0	7,0	3,8	4,0	5,7	6,5	3,4	3,0

Tab. 8 - Matrix summarizing the ecological characterization of each group highlighted by RDA (A-F) and the related environmental stresses and ecological factors.

Groups of species	A	B	C	D	E	F
Ecological behaviour	Dryness-tolerators, light-demanding species	Nitrogen-demanding midshadow species	Water and Nitrogen-demanding species, low light intensity-tolerators	Water and nitrogen-demanding species, low light intensity and slight acidity-tolerators	Low nitrogen-demanding, acidity-tolerator species	Dryness and acidity-tolerators, light-demanding species
Environmental stresses	Draining soils, strong insolation, low soil depth	Intermediate-low light intensity	Low light intensity	Low light intensity, slightly acid pH	Intermediate-low light intensity, acid pH	Low soil nitrogen content, acid pH, sandy soil texture
Light intensity	High	Intermediate-low	Low	Low	Intermediate-low	High
pH	Neutral	Neutral	Neutral	Subacid	Acid	Acid
Texture	Sandy-clayey	Clayey	Clayey	Sandy-clayey	Sandy-clayey	Sandy
Nitrogen	Intermediate	High	High	Intermediate	Intermediate	Low
Aspect	South	North	North	North	North	South

demanding species or living in forest edges and clearings, while those of group F are pioneer species of open habitats, ingressive in woods probably because of soil deterioration or for the excessive forest canopy openings due to forestry activity. In fact, light-demanding oaks, as *Quercus pubescens* s.l., and the related undergrowth species, have been often favoured by past forest management and by direct facilitation (MANTEL, 1990; WALLNÖFER & HOTTER, 2008).

Species belonging to group B can be considered edge or semipioneer floristic units. They live under the canopy of the forest edge and are probably favoured by the periodic wood cutting linked to the forest management (BARTHA *et al.*, 2008). Group E includes specialist sciophilous nemoral, acidophilous and relatively soil moisture-demanding species. This ecological behaviour type is very different from that of B group. The only joining point is the same light demand, but this similarity is probably due to different causes: forestry management history and structure (group B) and light permeability of woods canopy (group E).

Groups C and D may be considered to be composed by "ancient forest species" (HERMY *et al.*, 1999), which prefer cool and moist soils with intermediate pH.

CONCLUSIONS

The research results allowed to ascertain that, as stated by GRIME (1973), also in the submediterranean forest landscape, stress level acts to define species diversity. Moreover, results permit to hypothesize that, in homogeneous bioclimatic conditions, Shannon-Wiener, Simpson and Evenness indices could be used as stress indicators within a forest landscape.

From a floristic point of view, intensity and combination of stress factors select one or more groups of species with different ecological behaviour, leading to the local floristic differentiation of plant communities. Within the pool of species adapted to the different sets of environmental factors, forest management and land use history act, determining the temporal pattern of the different ecological behaviour type species groups (BARTHA *et al.*, 2008). In fact, the ingressions of edge and clearing nitrophilous (group B) or open habitat species (group F) in forest communities, could be interpreted as a result of frequent coppicing and/or past soil erosion. On the other hand, the prevalence

of nemoral species (groups D and E) indicates a higher forest soil cover because of longer turnover or higher forest topsoil cover after cutting down (HÄRDTLE *et al.*, 2004; REIF & GÄRTNER, 2007). Moreover, it can be hypothesized that the presence of such species also depends on land use history and in particular on the continuity of forest cover over the time (DECOCQ, 2003).

The results of this study represent a useful tool for future research, aimed to define plant diversity conservation guidelines and biodiversity monitoring. This approach will be useful in the future, because climatic change will certainly increase drought stress and the possibility to predict species shifting and floristic variation of forest ecosystems would be a very important goal for their future management. Moreover, it could be important also for plant communities phytosociological characterization, in order to better select the diagnostic group of species of each *syntaxon* taking into account their local meaning from an ecological point of view.

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LA “RECIPROCITÀ” NELLE CENOSI VEGETALI (*nota preliminare*)

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ABSTRACT

The reciprocity of phytocenosis is the report established in a habitat between one or more native species with one or more alien species (Neophytes). This relationship is realized in the respective environments in the different parts of the world, where at least one species is native. Thus in the first coenosis there will be autochthonous and exotic species, while the second coenosis, the species that were indigenous now are exotic and vice-versa. We can identify also three different kinds of reciprocity: finished, unfinished and universal. There are three types of reciprocity: complete, incomplete and universal. Inside the coenosis with reciprocity, we can identify species with three different roles: mutual species, witness species and universal species. There are other cases in which exotic plants are not able to

reproduce naturally, because of depending directly by man (cultivated), leading to a forced reciprocity.

KEYWORDS: Neophytes, reciprocity, autochthonous species, exotic species, phytocenosis.

RÉSUMÉ

La réciprocité des phytocoénoses est la relation qui s'établit dans un habitat entre une ou plusieurs espèces indigènes avec une ou plusieurs espèces exotiques (Néophytes); elle se réalise dans les environnements respectifs des différentes parties du monde, où au moins une espèce est originale. Ainsi, dans la première coenose il y aura des espèces indigènes et exotiques et par contre, dans la deuxième, les espèces qui étaient indigènes sont exotiques et

vice-versa. Il existe trois types de réciprocité: complète, incomplète et universelle. Dans ces coénoses les espèces possèdent trois rôles différents: espèces réciproques, espèces témoins et espèces universelles. Il y a d'autres cas dans lesquels des plantes exotiques ne sont pas capables de se reproduire naturellement, en dépendant directement de l'homme (espèces cultivées), conduisant à une réciprocité forcée.

RIASSUNTO

La reciprocità delle fitocenosi è la relazione che si stabilisce all'interno di un biotopo tra una o più specie autoctone e una o più specie esotiche (Neofite); essa si realizza nei rispettivi ambienti delle diverse parti del mondo, ove almeno una specie sia autoctona. In tal modo nella prima cenosi ci saranno



Fig. 1 - Johannesburg (Sudafrica), luogo erboso a prevalenza di *Trifolium repens* e *Duchesnea indica*, specie erbacee reptanti diffuse in tutti i continenti (foto K. Cianfaglione, 2008).

specie autoctone ed alloctone, mentre nella seconda le specie che prima erano esotiche ora sono autoctone e viceversa. Si possono distinguere tre tipi di reciprocità: compiuta, incompiuta e universale. All'interno delle cenosi con reciprocità possiamo individuare specie con tre ruoli diversi: specie reciproche, specie testimone e specie universali. Ci sono altri casi nei quali le piante esotiche non sono capaci di riprodursi naturalmente, dipendendo direttamente dall'azione dell'uomo (coltivate), determinando così una reciprocità forzata.

INTRODUZIONE

Le Neofite sono specie vegetali introdotte dall'uomo dopo la scoperta dell'America (GÉHU, 2006); esse tendono ad espandere il loro areale per diverse ragioni dipendenti soprattutto all'uomo, fenomeno noto come Neofitismo (FALIŃSKI, 1998). La loro diffusione induce sempre modificazioni nella vegetazione, provocando squilibri biologici più o meno marcati a livello delle associazioni vegetali. I principali fenomeni sono quelli della degenerazione delle associazioni per modifica della loro composizione floristica originaria e della loro struttura, la scomparsa di as-

sociazioni, la formazione di nuove associazioni, la sinantropizzazione generale della vegetazione e l'abbassamento del grado di naturalità della vegetazione (FALIŃSKI, 1975, 1986).

In questo modo si possono formare in tutto il mondo fitocenosi caratterizzate dalle stesse specie; ne costituisce un esempio il caso di Johannesburg, dove possiamo vedere due piante esotiche per l'Africa e con lo stesso adattamento morfologico (specie reptanti), *Duchesnea indica* (dell'Asia) e *Trifolium repens* (dell'Europa) (Fig. 1); questa cenosi - caratterizzata da due specie stolonifere e tappezzanti - può essere riscontrata in varie parti del mondo, ma con rapporti di reciprocità invertiti, come sarà specificato più avanti. In questo caso, in particolare, essendo la foto eseguita in Africa e non essendo presenti nella cenosi specie africane, possiamo parlare di reciprocità incompleta per l'Africa, ma tale cenosi in Europa o in Asia è un esempio di reciprocità compiuta.

LA RECIPROCITÀ DELLE CENOSI

Accanto alle modificazioni prima elencate, le fitocenosi acquistano una nuova proprietà come conseguenza del Neofitismo, che possiamo chiamare re-

ciproicità. Essa si instaura a seguito dell'introduzione di nuove specie, chiamate esotiche. La reciprocità delle fitocenosi è la relazione che si stabilisce all'interno di un biotopo tra una o più specie autoctone e una o più specie esotiche; essa si realizza nei rispettivi ambienti delle diverse parti del mondo, ove almeno una specie sia autoctona. Se esistono specie in comune in due cenosi simili e ubicate in diverse parti del mondo, nella prima cenosi ci saranno specie autoctone ed alloctone, mentre nella seconda le specie che prima erano esotiche ora diventano autoctone e viceversa. Le specie interessate presentano caratteristiche analoghe (quali ecologia, adattamento, forma biologica), pur essendo diverse dal punto di vista sistematico e con una differente provenienza geografica.

Ho cominciato ad intuire questo rapporto in Ecuador, ove ho potuto notare come i meliloti europei (*Melilotus albus* e *M. officinalis*) spesso si accompagnavano a specie locali come *Bidens aurea* del Centroamerica (PIGNATTI, 1982); la cenosi formata da queste specie è rinvenibile anche in Italia.

Si possono distinguere tre tipi di reciprocità: *compiuta, incompiuta e universale*.

La reciprocità è *compiuta* quando effettivamente le cenosi possono riscon-



Fig. 2 - Luogo erboso all'interno dell'Orto botanico di Kirstenbosch, Città del Capo, Sudafrica. Da sinistra a destra si osservano: *Geranium rotundifolium*, *Trifolium repens*, *Euphorbia peplus*, *Briza maxima*, *Cardamine hirsuta*, *Oxalis pes-caprae*, *Vicia sativa* (foto K. Cianfaglione, 2008).



Fig. 3 - Sudafrica, andando da Caledon verso Swellendam, formazione simile alla macchia mediterranea, con evidenti *Aloe africana* (cfr) e *Opuntia ficus-indica*. Questo è un esempio di reciprocità incompiuta o potenziale (foto K. Cianfaglione, 2008).



Fig. 4 - Montagne di Swellendam (Sudafrica), ove sorge la Marloth Nature Reserve, cenosi caratterizzata da: *Anagallis arvensis* var. *caerulea*, *Juncus* sp., *Pteridium aquilinum*, *Podocarpus falcatus*, con *Pteridium aquilinum* specie universale e *Podocarpus falcatus* specie testimone (foto K. Cianfaglione, 2008).



Fig. 5 - Clanwilliam (Sudafrica), cenosi ruderale con *Lactuca serriola* e un alberello di *Melia azederach*; si nota anche un ceppo di eucalipto (*Eucalyptus* sp.) (foto K. Cianfaglione, 2008).

trarsi in varie parti del mondo nelle quali siano presenti naturalmente (autoctone) le specie interessate nella cenosi con reciprocità.

Durante un viaggio in Africa meridionale, nell'Orto botanico di Kirstenbosch, ho notato una cenosi con *Briza maxima* (dell'Europa mediterranea) e *Oxalis pes-caprae* (dell'Africa). Come la precedente, questa cenosi è esattamente riscontrabile all'inverso in Italia; cioè con la stessa composizione floristica, ove però si invertono i ruoli delle specie: ciò che è esotico diviene autoctono e viceversa. All'interno di quest'ultima fitocenosi, che è di tipo prativo, sono presenti: *Cardamine hirsuta*, *Briza maxima*, *Oxalis pes-caprae*, *Geranium rotundifolium*, *Trifolium repens*, *Vicia sativa* ed *Euphorbia peplus* (Fig. 2). Queste sono tutte specie con adattamenti simili e - tranne l'*Oxalis* - sono tutte specie esotiche per l'Africa (BROMILOW, 2001). Tramite il principio della reciprocità, in Italia troviamo le stesse specie in una cenosi affine, ma con rapporti invertiti: cioè tutte le specie che in Africa erano esotiche sono ora autoctone tranne *Oxalis* che invece diviene esotica, pur mantenendo lo stesso grado di relazione tra le altre specie. In Italia è possibile trovare cenni con queste caratteristiche floristiche negli uliveti lungo la costa o negli agrumeti della Sicilia

ove POLI (1961) segnala una cenosi dominata da *Oxalis pes-caprae* (=*O. cornuta*), nella quale crescono anche *Geranium rotundifolium* ed *Euphorbia peplus*. Si evince pertanto come il rapporto di reciprocità rimanga sempre dello stesso grado, benché sia soggetto ad una specularità (reciprocità compiuta).

La reciprocità è da considerarsi incompiuta quando in un biotopo, pur essendoci condizioni idonee, non è ancora possibile individuare una reciprocità compiuta; cioè perché non sono ancora arrivate le specie (ad esempio per mancanza di propaguli), ma teoricamente potrebbero arrivarci. Questa è una reciprocità che allo stato dei fatti rimane ipotetica ed essendo proiettata nel futuro è una reciprocità potenziale.

La reciprocità è applicabile non solo alle specie dello strato erbaceo ma anche a quelle arboree ed arbustive (Fig. 3); in questa fitocenosi sudafricana in un ambiente caldo e xerico crescono due specie con simile adattamento (succulente) come *Opuntia ficus-indica* e *Agave africana* (COATES PALGRAVE, 2002); tali specie potrebbero riscontrarsi anche in Messico, dove *Opuntia* è indigena e l'*Aloe* sarebbe esotica, pur non evidenziando variazioni dei loro rapporti fitocenotici. In questo caso possiamo inoltre notare alcuni arbusti africani non segnalati in Messico: que-

sti sono un esempio di specie testimone, le quali testimoniano la provenienza della cenosi in questione (Sud-Africa), non essendo ancora caratterizzate dal rapporto di reciprocità. Se anche queste piante venissero ritrovate in una cenosi simile nel Messico, allora non sarebbero più considerabili come specie testimone ma come specie reciproche.

La reciprocità universale si ha invece quando all'interno del biotopo viene coinvolta almeno una specie autoctona in ciascuna cenosi vegetale analizzata; trattasi di specie cosmopolite o semi-cosmopolite (a livello globale), ma questo concetto può esser applicato per estensione anche a livelli più locali.

Sulle montagne di Swellendam (Sud-Africa), notiamo una cenosi con *Anagallis arvensis* var. *caerulea*, *Pteridium aquilinum*, *Podocarpus falcatus* (Fig. 4). Una cenosi con gli stessi rapporti di reciprocità potrebbe essere rinvenibile anche in Italia, trovando però in tal caso come specie indigene *Anagallis arvensis* var. *caerulea* e *Pteridium aquilinum*, mentre il *Podocarpus* sarebbe esotico. In questo caso *Pteridium aquilinum* è specie universale, mentre *Podocarpus falcatus* è specie testimone.

Pertanto ne conseguе che all'interno delle cenni con reciprocità possiamo individuare specie con tre ruoli di-

versi: *specie reciproche*, *specie testimone* e *specie universali*.

Le *specie reciproche* sono quelle specie che si scambiano di valore all'interno della cenosi (le piante alloctone di un sito divengono autoctone in un altro e viceversa), mentre le *specie testimone* sono quelle specie autoctone che non si possono scambiare all'interno delle cenosì. Le *specie universali* sono le specie riscontrabili in ciascun sito individuato, sempre come autoctone, come può accadere con le specie cosmopolite.

Un ultimo caso è quello delle piante esotiche che non sono capaci di riprodursi naturalmente dipendendo direttamente dall'intervento dell'uomo, determinando così una *reciprocità forzata*.

In una cenosi d'ambiente ruderale del Sud-Africa (Fig. 5) possiamo vedere una *Melia azederach* (India), un ceppo di *Eucaliptus* sp. (Australia) e *Lactuca serriola* (Europa). In Sud-Africa *Melia azederach* riesce a spontaneizzarsi (BROMILOW, 2001), mentre in Italia non è mai del tutto spontanea (PIGNATTI, 1982), pertanto in Italia troveremo queste specie in reciprocità solo dove l'uomo ha piantato gli eucalipti e la *Melia* (*reciprocità forzata*).

In una cenosi più o meno complessa possiamo distinguere contemporaneamente anche più tipi di reciprocità, in base al numero e alla provenienza delle specie coinvolte. In una fitocenosi la reciprocità è una proprietà dinamica, potendo evolversi continuamente assieme al grado e alla ricorrenza del disturbo subito. In Africa ho notato molti altri esempi simili, come la ricorrenza di cenosì tropicali (ad esempio a *Lantana camara*) riscontrabili inversamente in Sud America e in Asia tropicale.

CONSIDERAZIONI CONCLUSIVE

Le cenosì che hanno una reciprocità riscontrata sono caratteristiche di ambienti più o meno degradati (visto l'ingresso di specie alloctone) e possono essere utili anche allo studio della naturalità dell'ambiente e delle formazioni vegetali, nonché allo studio dei biotopi (loro equilibri, come essi possono evolvere a seguito dell'ingresso di altre specie, resilienza, ecc.).

Questo principio in particolare è di ampia valenza biogeografica in quanto si può attualizzare per ogni tipo di cenozi (piante superiori, funghi, alghe, ecc.) presenti in un determinato ambiente e ripetibile in maniera speculare nelle parti del mondo ove le specie componenti in esame sono indigene.

Inoltre lo studio di questo rapporto è utile come ulteriore dato per le analisi climatologiche, basandosi anche su parametri biotici, non solo abiotici.

RINGRAZIAMENTI

Ringrazio il prof. Franco Pedrotti (Camerino) per i viaggi di studio in America latina e in Sud-Africa e per i consigli per la stesura di questa nota preliminare.

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THE RICCIOCARPETUM NATANTIS ASSOCIATION IN THE SPRINGS OF CAPO PESCARA, ABRUZZO (ITALY)

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ABSTRACT

The presence of *Ricciocarpos natans* was reported in the springs of "Sorgenti di Capo Pescara" near Popoli (Abruzzo) on April 19, 1956 and was confirmed on November 24, 2010; 54 years later. This work describes the associations of the *Lemnetea* class in the springs of Capo Pescara and reports for the first time in Abruzzo the *Ricciocarpetum natantis* association. Today these springs are part of a protected area, the Riserva Naturale Guidata "Sorgenti del Pescara" [The "Pescara Springs" Guided Nature Reserve].

KEYWORDS: *Ricciocarpos natans*, *Lemna*, *Lemnetea*, Capo Pescara springs, Abruzzo.

RIASSUNTO

La presenza di *Ricciocarpos natans* è stata segnalata nelle sorgenti di Capo Pescara, vicino a Popoli (Abruzzo) il 19 aprile 1956 ed è stata confermata il 24 novembre 2010, dopo 54 anni. Questo lavoro descrive le associazioni della classe *Lemnetea* nelle sorgenti di Capo Pescara e l'associazione *Ricciocarpetum natantis*, segnalata qui per la prima volta in Abruzzo. Oggi queste sorgenti sono comprese in una zona protetta: la Riserva Naturale Guidata "Sorgenti del Pescara".

INTRODUCTION

The presence of *Ricciocarpos natans* was reported in the springs of Capo Pescara near Popoli (Abruzzo) on April 19, 1956, as attested by a sample of this species deposited in the herbarium of the Camerino University Department of Botany and Ecology (CAME), without the name of the collector. The sample, conserved in a test tube, was later identified and made known by PEDROTTI (1979). After a long period in which this species was no longer found in the area, it was sighted again on November 24, 2010; in three points of

the spring, 54 years after the first reporting. This aquatic liverwort often appears irregularly in the same location, as reported by PEDROTTI (1979) for the marshes of Colfiorito in Umbria Region and ALEFFI & CORTINI-PEDROTTI (1995) for the Colfiorito plain in the Marche Region.

The present note reports on the finding of this species and presents the associations of the *Lemnetea* class

present in the springs of Capo Pescara.

ENVIRONMENTAL CHARACTERISTICS

The springs of Capo Pescara are located at the foot of Colle di Capo Pescara (452 m on sea level). They constitute a vast spring-marsh-river area



Fig. 1 - *Ricciocarpetum natantis*, Capo Pescara springs (Abruzzo). November 24, 2010 (photo K. Cianfaglione).

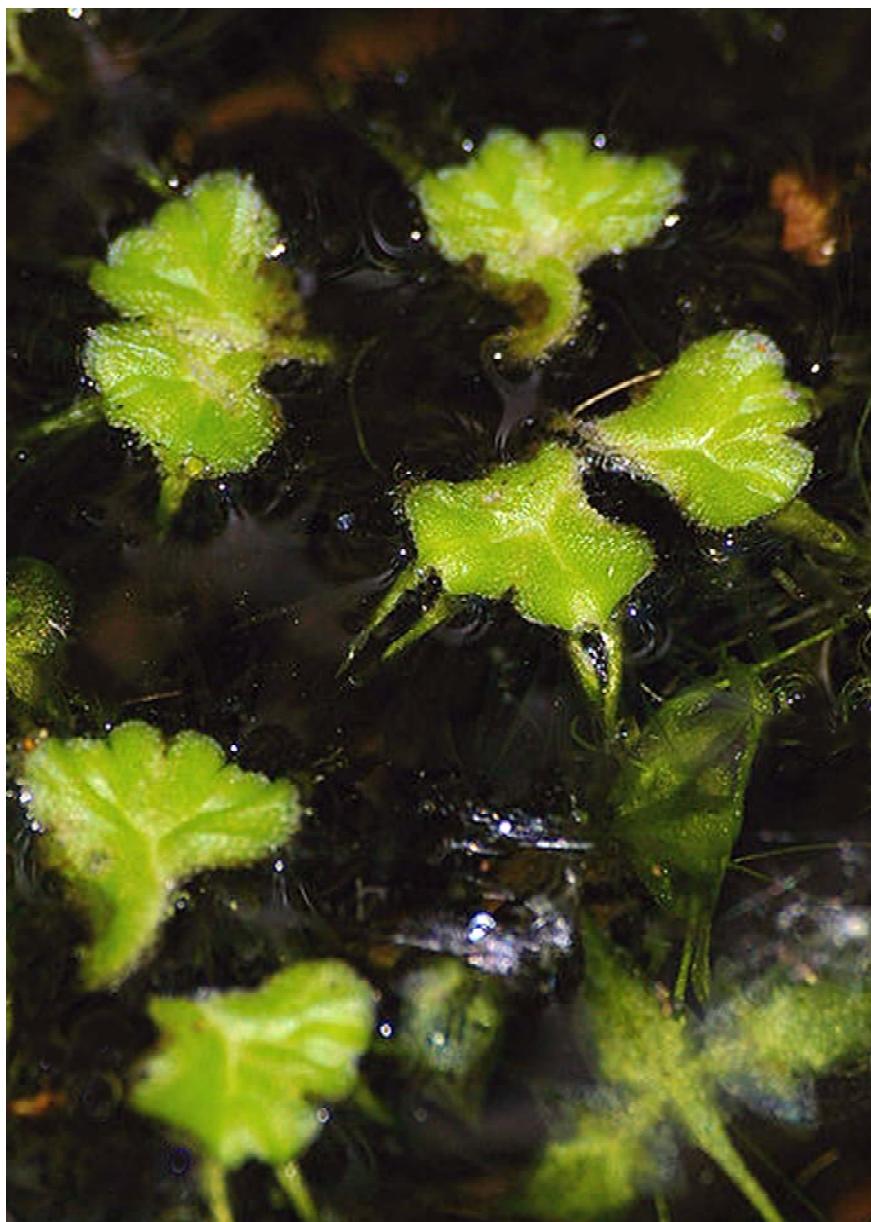


Fig. 2 - *Ricciocarpus natans* with *Lemna trisulca*, Capo Pescara springs (Abruzzo). November 24, 2010 (photo K. Cianfaglione).

Tab. 1 - Records of the *Lemnetea* class.

Relevé number	1	2	3	4	5	6	7	8
Surface (cm ²)	40	20	40	40	30	20	100	100
Cover of vegetation (%)	90	40	95	100	100	95	100	90
<i>Ricciocarpus natans</i>	5.5	2.2	+
<i>Lemna minor</i>	.	.	5.5	5.5	5.5	5.5	.	.
<i>Lemna trisulca</i>	.	1.2	.	.	1.1	+	5.5	5.5
<i>Ceratophyllum demersum</i> *	+	.	.

* only floating living fragments.

Records executed November 24, 9 and December 10, 2010. Springs of Capo Pescara, Abruzzo.

with over 60 widely distributed springs that come from the surrounding mountains such as the Gran Sasso d'Italia, the Sirente and the Majella-Morrone group; after a few meters, they flow into the

Aterno River to give rise to the Pescara River. The flow of this complex water system is fairly constant all year, with oscillations from 6,500 litres/second in April to 7-8,000 in August and January.

This area, located entirely within the municipal territory of Popoli (Pescara), covers about 50 ha, in the northern part of the Peligna Valley.

PRESENCE OF *RICCIOCARPOS NATANS* IN THE SPRINGS OF CAPO PESCARA

Ricciocarpus natans is distributed with three nuclei that are not very far from each other, at about 300 m below the first spring. They grow amidst the swamp reeds (*Phragmitetum vulgaris*) in such a way as to be protected from the water flow. The groups observed were composed of few individuals and only one of these populations had a certain density of individuals, as noted during the inspection on November 24, 2010. As in other parts of Europe, *Ricciocarpus natans* is not a common species (BALEVIČIENĖ & BALEVIČIUS, 2006) and is subject to the natural oscillations in aquifer levels.

The Capo Pescara site is the only one known for Abruzzo for this aquatic liverwort (ALEFFI *et. al.*, 2008).

THE ASSOCIATIONS OF THE *LEMNETEA* CLASS OF THE CAPO PESCARA SPRINGS

In the springs of Capo Pescara the following floating pleustophyte species are present (between liverworts and angiosperms): *Ricciocarpus natans* (L.) Corda, *Lemna minor* L., *L. trisulca* L., *L. minuta* Kunt. (still being studied). They form the following associations of the *Lemnetea* Bolòs et Masclans 1955 class, *Lemnetalia minoris* de Bolòs et Masclans 1955 order, *Lemnion minoris* de Bolòs et Masclans 1955 alliance: *Ricciocarpetum natantis* R. Tüxen 1974, *Lemnetum minoris* Oberdorfer ex T. Müller et Görs 1960 and *Lemnetum trisulcae* (Kelhofer 1915) Knapp et Stoffers 1962. These associations are more easily found among reed beds like cane thickets (*Phragmitetum vulgaris*) and *Scirpetum lacustris*, where they find shelter among the helophytes.

RICCIOCARPETUM NATANTIS (TAB. 1, RECORDS 1-2)

Of the two observations of *Ricciocarpetum natantis*, only one was a monospecific population (Fig. 1) while the other also had *Lemna trisulca* (Fig. 2).

This association is reported here

for the first time for Abruzzo.

Lemnetum trisulcae (Tab. 1, records 7-8).

This association grows very substantially with very extended agglomerates, reaching a thickness of some centimeters, prevalently in *Phragmites* stands and in reed beds (Figs. 3, 4). This association is also present rarely in the drainage ditches ("le forme") of the Peligna Valley, was reported nearby (Tirino River) by BUCHWALD (1994) and in Capo Pescara by PIRONE et. al. (1997) [sub "population of *Lemna trisulca*"]. *Lemna trisulca* is very rare in Abruzzo (CONTI, 1998).

Lemnetum minoris (Tab. 1, records 3-4-5-6).

This association was found only in three groups in the reed bed, in four bends where the water is more stagnant and eutrophic because of numerous plant remains. The association is almost always monospecific (record 4), but sometimes there is a sporadic occurrence of *Ricciocarpos natans* (Fig. 5, record 3) or *L. trisulca* [subass. *lemnethosum trisulcae* Th. Müller et Görs 1960, cited by ČERNOHOUS and HUSÁK (1986) for north-east Bohemia and by HRIVNÁK R. (2002) for Slovakia and Hungary as "variant with *Lemna trisulca*"] (record 5). Another layer variant with *Cera-*

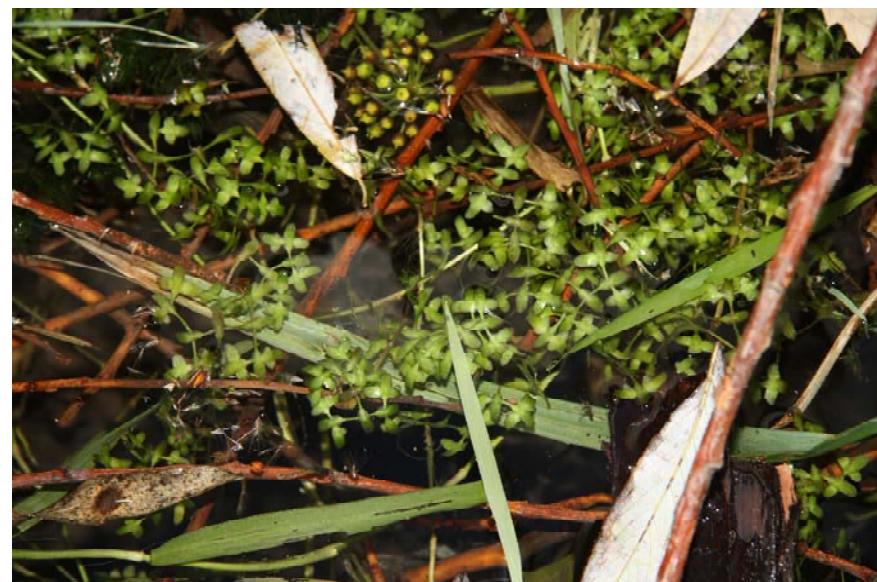


Fig. 3 - *Lemnetum trisulcae*, abundant in particular among reed beds (*Phragmitetum vulgaris* and *Scirpetum lacustris*), in Capo Pescara springs (Abruzzo). December 9, 2010 (photo K. Cianfaglione).

tophyllum demersum, like in HRIVNÁK R. (2002) was find in Capo Pescara springs (record 6). This association was reported in the past by CORBETTA & PIRONE (1989) in the Tirino River [sub "grouping of *Lemna minor*"] and by PIRONE et al. (1997) for Capo Pescara [sub "population of *Lemna minor*"]; it is also present in other sites of the Peligna Valley (CIANFAGLIONE, 2009), specifically in the springs of the marshy woods (*Carici ripariae-Alnetum glutinosae*) 2008, surface area 30 cm²; degree of coverage 100%; *Lemna minor* 5.5.

Record 2 - Bagnaturo di Pratola Peligna (L'Aquila), springs on the alder woods (*Carici ripariae-Alnetum glutinosae*) 2008, surface area 30 cm²; degree of coverage 70%; *Lemna minor* 4.4.



Fig. 4 - An extensive and dense layer of *Lemnetum trisulcae* at the center of strong currents; in this case it is favored by *Schoenoplectus lacustris* (interpenetrated into the *Scirpetum lacustris*), in the Capo Pescara springs (Abruzzo). December 9, 2010 (photo K. Cianfaglione).



Fig. 5 - *Lemnetum minoris* with *Ricciocarpus natans*, Capo Pescara springs (Abruzzo). November 24, 2010 (photo K. Cianfaglione).

CONCLUDING CONSIDERATIONS

In the Capo Pescara springs, the margin areas, often held to be less important than the rest of the body of water, have at some points over time been reworked (earth removed or brought, creation of simple structures, buildings, roads and reclamation) as reported by TAMMARO (1998). Near the shore, the water level is less deep, varying from soil level to a meter. The surrounding shores are occupied by dense cane thickets that constitute an interesting landscape element. The area hosts a diversified avifauna, whose establishment or temporary presence is related to the fact that the biotope is one of the few wet zones protected by the Abruzzo Region. Like others floating pleustophytes, *Ricciocarpos natans* provides food for various birds and fish and habitat for insects and other aquatic invertebrates. This plant has often appears irregularly in the same locality, probably because of alterations in the shorelines and excessive cutting of the reed beds repeated over the years. In addition, in some cases, the presence of this plant is promoted by aquatic birds that can spread it or carry it where it could have disappeared. Today these springs belong to a protected area: the Riserva Naturale Guidata "Sorgenti del Pescara" ["Pescara Springs" Guided Nature Reserve], established in 1986.

ACKNOWLEDGEMENTS

Special thanks are due to Prof. em. Franco Pedrotti (University of Camerino) for his precious support in the editing of this paper and at the Dr. Piera

Lisa Di Felice, director of the Reserve, for the logistical support.

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LES PRAIRIES MESOXEROPHILES DE L'ALLIANCE *CIRSIOS-BRACHYPODION* HADAČ ET KLIKA EX KLIKA 1951 DE ROUMANIE

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ABSTRACT

The paper is focused on the results of the floristic and ecological analysis of mesoxerophile grasslands from Romania. 277 relevées have been processed and are grouped in the following 6 associations: *Carici humilis-Brachypodietum pinnati*, *Polygalo majori-Brachypodietum pinnati*, *Danthonio alpinae-Brachypodietum pinnati*, *Rhinantho rumelic-Brometum erecti*, *Ferulago campestris-Caricetum humilis* and *Thymio comosoi-Caricetum humilis*. Each association is characterized by one or more regional species, endemic or ponto-balcanic, which differentiates them from the associations described in Central Europe. As the association described by *Bromus erectus* contains most of the species characteristic for the alliance *Cirsio-Brachypodion*, and the species characteristic for the alliance *Bromion erecti* are few, we have included the association *Rhinantho rumelic-Brometum erecti* together with the meso-xerophile associations described by *Brachypodium pinnatum*. In the paper we validate the associations specific to the studied region according to the Phytosociological Nomenclature Code.

Keywords: mesoxerophile grasslands, *Cirsio-Brachypodion*, Romania.

Les prairies mésoxérophiles de Roumanie sont répandues notamment dans l'ouest et le centre du pays (Transylvanie), où le climat régional subit de faibles influences océaniques (Pop G., 2001) et sont présentes seulement de façon isolée, sur de petites surfaces dans la partie sud-est du pays au climat continental modéré (CIOCÂRLAN, 1969; STEFAN, 1996).

Ces prairies dominées par *Brachypodium pinnatum*, *Carex humilis*, *Botriochloa ischaemum*, *Dorycnium herbaceum* et rarement par *Bromus erectus* dans l'Europe de l'Est sont rangées dans l'alliance *Cirsio-Brachypodion pinnati* Hadač et Klika ex Klika 1951 (CHYTRÝ et al., 2007; BORHIDI, 1996; MUCINA et al., 2003) un syntaxon vica-

riant dans l'alliance *Bromion erecti* de l'ouest et du centre de l'Europe (OBERDÖRFER, 1978; POTT, 1995; DIERSCHKE, 1997; GÉHU et GÉHU-FRANCK, 1984).

La plupart des sites de Roumanie peuplés par ces prairies sont secondaires et se sont répandues dans la zone collinaire (350-850 m) après la coupe des forêts de feuillus mésophiles de chêne rouvre (*Quercus petraea*) au charme commun (*Carpinus betulus*).

Dans la structure floristique de ces prairies, les espèces dominantes mentionnées sont accompagnées par certains éléments régionaux pontico-balcaniques et endémiques tels *Chamaecytisus albus*, *Rhinanthus rumelicus*, *Phleum montanum*, *Ferulago campestris*, *Ferulago sylvatica*, *Dianthus membranaceus*, *Thymus comosus*, *Linaria dalmatica* ssp. *transsilvanica*, *Cephalaria radiata*, *Cephalaria uralensis*, *Seseli gracile*, qui apportent aux associations identifiées une touche phytogéographique distincte et permettent une bonne caractérisation floristique par rapport aux associations de l'Ouest et du centre de l'Europe.

Dans les régions étudiées en Roumanie, de telles phytocoénoses mésoxérophiles viennent souvent en contact avec les phytocoénoses xérophiles de l'ordre *Festucetalia valesiacae*, ce qui

fait que la structure de ces phytocoénoses contient de nombreuses espèces caractéristiques de cet ordre.

Nous allons analyser sous leur aspect floristique et écologique les six associations végétales des prairies mésoxérophiles présentes en Roumanie. Pour mettre en évidence le degré de ressemblance floristique entre les associations nous avons dressé un dendrogramme basé sur le coefficient de similarité Jaccard (Fig. 1). La composition floristique de chaque association est présentée dans le tableau synthétique par des chiffres romains (I-V) qui représentent les classes de constance des espèces. La nomenclature des espèces est celle de CIOCÂRLAN (2009).

1. Ass. *Carici humilis-Brachypodietum pinnatum* Soó ex Pop et al. 2002 (tableau 1, colonne 1) Lectotype: Soó 1949, tab. 19, rel. 3;

Syn.: *Carex humilis-Brahypodium pinnatum* Soó 1942 (Art. 1), *Cariceto humilis-Brachypodietum pinnati transsilvaticum* Soó 1947, 1949 (Art. 34).

Les phytocoénoses de cette association peuplent les crêtes et le tiers supérieur des versants ensoleillés et à faible inclinaison du plateau de Transylvanie et des piémonts occidentaux à une altitude de 350-900 m. Les sols où

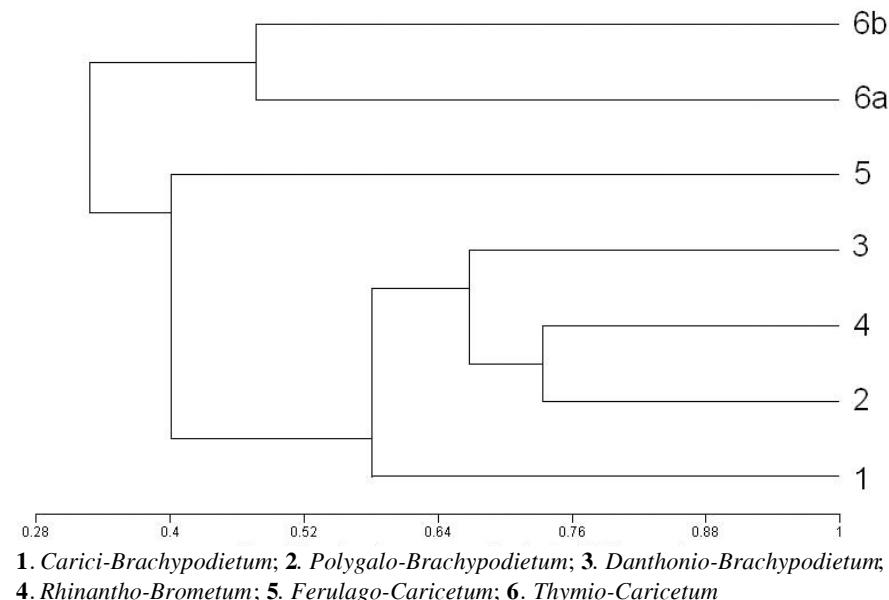


Fig. 1 - Le dendrogramme de similarité Jaccard.

Tableau 1 - Les associations d'alliance *Cirsio-Brachypodion*.

Associations nr.	1	2	3	4	5	6a	6b
Nombres des relevés	98	70	18	38	15	32	6
Altitude m.s.m. (en 10 m)	37-90	38-62	38-57	38-65	40-85	52-90	58-70

Caract. d'ass.

Phleum montanum	II	-	I	-	-	I	I
Leontodon crispus	III	-	I	-	II	III	I
Polygala major	II	IV	III	II	III	-	I
Chamaecytisus albus	II	III	II	II	-	I	I
Rhinanthus rumelicus	-	III	III	II	II	-	I
Danthonia alpina	-	I	IV	I	-	-	I
Bromus erectus	I	I	I	V	-	I	-
Ferulago campestris	-	-	-	-	III	-	-
Dianthus membranaceus	-	-	-	-	III	-	-
Thymus comosus	II	-	-	-	-	IV	V
Linaria d. * transsilvanica	-	-	-	-	-	IV	IV
Diff. sous.							
Hyacinthella leucophaea	-	-	-	-	-	-	V
Taraxacum erythrospermum	-	-	-	-	-	-	V
Ornithogalum o. * kochii	-	-	-	-	-	I	V
Cirsio-Brachypodion et Brometalia							
Inula ensifolia	II	I	I	I	I	II	III
Brachypodium pinnatum	V	V	V	III	I	I	-
Centaurea scabiosa	II	II	I	II	I	I	-
Onobrychis viciifolia	II	IV	II	III	II	I	-
Carex humilis	IV	-	II	I	V	V	V
Trifolium montanum	II	III	III	II	III	I	-
Linum flavum	II	III	I	I	I	-	-
Dorycnium herbaceum	IV	V	IV	III	III	-	-
Campanula glomerata	I	I	I	I	I	-	-
Helianthemum canum	I	-	-	-	-	III	III
Scorzonera purpurea	I	I	I	I	-	II	-
Trifolium alpestre	I	-	II	I	II	I	-
Prunella grandiflora	I	I	I	I	I	-	-
Polygala comosa	I	I	I	I	-	-	-
Briza media	II	IV	IV	IV	-	-	-
Orchis tridentata	I	I	I	I	-	-	-
Linum tenuifolium	I	I	I	-	I	-	-
Trifolium pannonicum	-	II	I	II	I	-	-
Gentiana cruciata	I	I	-	I	I	-	-
Carex tomentosa	I	I	I	I	-	-	-
Orchis morio	I	I	I	I	-	-	-
Hypochoeris maculata	II	-	I	I	II	-	-
Veronica teucrium	I	I	-	I	-	-	-
Linum perenne	-	I	I	I	-	-	-
Cephalaria radiata	I	-	I	-	-	-	I
Seseli annuum	I	-	I	I	-	-	-
Scorzonera austriaca	I	-	-	-	-	III	III
Thesium linophyllum	II	-	-	I	-	-	-
Carex montana	I	-	-	-	II	-	-
Carlina acaulis	I	I	-	-	-	-	-
Orchis militaris	I	-	I	-	-	-	-
Cirsium pannonicum	I	-	-	-	-	-	-
Orchis purpurea	I	-	-	-	-	-	-
Orchis ustulata	-	I	-	-	-	-	-
Festucetalia valesiacae							
Festuca rupicola	III	I	II	I	III	IV	V
Scabiosa ochroleuca	II	IV	III	II	III	II	II
Campanula sibirica	II	III	II	II	II	III	II
Adonis vernalis	II	I	I	I	II	II	III
Onobrychis arenaria	I	-	I	I	II	I	II
Centaurea biebersteinii	III	I	-	-	IV	III	III
Jurinea m. * transsilvanica	II	I	I	-	-	III	III
Thymus glabrescens	I	I	I	I	I	-	-
Festuca valesiaca	I	-	I	II	III	II	-
Seseli pallasi	I	-	I	-	I	II	III
Allium flavum	I	I	-	-	-	II	-
Achillea collina	III	-	-	I	II	II	-
Verbascum phoeniceum	I	I	-	I	-	I	-
Astragalus monspessulanus	II	I	II	II	-	-	-
Thymus pannonicus	II	I	-	-	IV	I	-

elles se développent sont des rendzines ou bruns jaunâtres, à squelette riche et à réaction neutre ou faiblement acide. Les espèces que nous désignons comme caractéristiques pour l'association et qui en conditionnent une distribution carpato-balkanique sont *Phleum montanum* et *Leontodon crispus*. Cette particularité phytogéographique est renforcée par les espèces régionales *Thymus comosus*, *Jurinea mollis* ssp. *transsilvanica*, *Viola jooi*, *Seseli gracile*, *Onosma pseudoarenaria*, *Allium albidum* et *Ferulago silvatica* qui malgré leur présence sporadique dans l'association la différencient floristiquement des associations *Scabioso-Brachypodietum* Klika 1933 (CHYTRÝ *et al.*, 2007), *Careci montanae-Brachypodietum* Soó 1949 (BORHIDI, 1996) et *Onobrychido-Brachypodietum* Eijsink *et al.* 1978 (MUCINA et KOLBEK, 1993) décrites dans les régions avoisinantes. Dans les zones étudiées, les phytocoénoses de cette association viennent au contact de celles de l'association *Salvio-Festucetum rupicole* Zoly. ex Soó 1964.

2. Ass. *Polygalo majori-Brachypodietum pinnati* Wagner 1941 (Tableau 1. colonne 2.).

Dans cette association sont rangées les phytocoénoses xéromésophiles de *Brachypodium pinnatum* végétant sur les terrasses et les versants ensoleillés et faiblement inclinés, aux sols bruns eumésobasiques ou rendzines dans le bassin des vallées Târnava Mare, Târnava Mica et Gurghiu (SĂMĂRGHITAN, 2005; OROIANU *et al.*, 2007). Le caractère xérophytique plus atténué de cette association par rapport à l'association précédente est mis en évidence d'une part par l'absence des espèces xérophiles *Carex humilis*, *Thesium linophyllum*, *Achillea collina*, *Helianthemum canum*, *Teucrium montanum*, d'autre part par une présence importante des espèces mésophiles caractéristiques pour la classe *Molinio-Arrhenatheretea*. Les espèces d'identification de l'association sont *Polygala major* et *Chamecytisus albus*. Elles ont une présence élevée dans l'association et atteignent souvent un recouvrement de 5-10%. Le caractère secondaire de ces phytocoénoses est mis en évidence par la présence, dans leur structure floristique, des espèces de reconnaissances pour la classe *Trifolio-Geranietea*, pareillement à celle de la République Tchèque (CHYTRÝ *et al.*, 2007). Dans les zones étudiées, de telles phytocoénoses viennent en contact avec celles de l'association *Danthonio-Brachypodietum* Soó ex Pop *et al.* 2002.

3. Ass. *Danthonio-Brachypodietum pinnati* Soó ex Pop et al. 2002 (Tableau 1, colonne 3) Lectotype: Soó 1949, tab. 20, rel. 6.

Syn.: *Danthonio-Brachypodietum pinnati* Soó 1947, 1949 (Art. 3, b.).

Les phytocoénoses de cette association végétent sporadiquement dans les zones collinaires de Transylvanie sur les versants faiblement inclinés et sur les terrasses ensoleillées à exposition sud-ouest où elles se sont installées à la place des forêts de *Quercus petraea* et *Quercus robur*. Elles végétent dans des sols bruns jaunâtres, faiblement acides, humides ou semi-secs, pauvres en substances nutritives. Les espèces d'identification de l'association sont *Danthonia alpina* et *Brachypodium pinnatum*. Elles atteignent un recouvrement de 45-55% et sont accompagnées par des espèces régionales et continentales telles: *Chamaecytisus albus*, *Rhinanthus rumelicus*, *Salvia transsilvanica*, *Jurinea mollis* ssp. *transsilvana*, *Echium maculatum*, *Adonis vernalis*, *Salvia nutans* qui la distinguent floristiquement de l'association *Danthonio-Scorzonerenetum villosae* Horvatić 1949 de Croatie. Le caractère mésoxérophile de cette association est relevé par une présence importante des espèces xérophiles caractéristiques pour la classe *Festuco-Brometea* et des espèces mésophiles spécifiques pour la classe *Molinio-Arrhenatheretea*. Dans les sites étudiés du centre de la Transylvanie, de telles phytocoénoses viennent en contact avec les prairies xérophiles de l'association *Danthonio-Festucetum rupicolae* (Csürös et al., 1961).

4. Ass. *Rhinantho rumelici-Brometum erecti* Sanda et Popescu 1999 (tableau 1, colonne 4) Lectotype: SANDA et al., 1976, tab. 1, rel. 1.

Les phytocoénoses mésoxérophiles édifiées par *Bromus erectus* sont réparties sporadiquement seulement en Transylvanie, où le climat régional subit encore une faible influence subatlantique. De telles phytocoénoses ont été identifiées, intra-zone, dans les prairies mésoxérophiles à *Brachypodium pinnatum*, raison pour laquelle dans leur structure dominent les espèces xérophiles par rapport aux espèces mésophiles (RESMERITĂ et SPĂRchez, 1984). Les espèces caractéristiques de l'alliance *Bromion erecti* mentionnées dans l'Europe centrale (OBERDORFER, 1978; MUCINA et al., 1993) et occidentale (GÉHU et GÉHU-FRANCK, 1984; ROYER, 1991) sont presque totalement absentes des phytocoénoses décrites en Roumanie. C'est la raison pour laquelle nous avons

Tableau 1 - (continuation).

Associations nr.	1	2	3	4	5	6a	6b
Nombres des relevés	98	70	18	38	15	32	6
Altitude m.s.m. (en 10 m)	37-90	38-62	38-57	38-65	40-85	52-90	58-70
Astragalus onobrychis	I	I	-	I	II	-	-
Veronica prostrata	I	-	-	I	-	II	II
Asyneuma canescens	-	I	-	I	-	I	-
Hieracium bauhinii	II	-	I	I	-	-	-
Salvia austriaca	I	-	I	I	-	-	-
Achillea setacea	III	-	II	-	II	-	-
Centaurea rhenana	-	II	I	I	-	-	-
Silene otites	I	-	-	-	I	III	-
Veronica jacquinii	I	-	-	-	I	-	-
Stipa pulcherrima	-	-	-	-	-	II	II
<i>Festuco-Brometea</i>							
Asperula cynanchica	III	IV	IV	III	IV	IV	V
Medicago falcata	III	I	III	III	V	II	I
Euphorbia cyparissias	III	II	II	II	II	IV	V
Teucrium chamaedrys	IV	III	I	III	IV	V	V
Fragaria viridis	I	III	II	II	I	II	II
Galium verum	II	IV	IV	III	II	II	II
Stachys recta	II	II	II	II	III	IV	IV
Veronica orchidaea	II	III	III	I	I	I	III
Anthericum ramosum	II	III	I	I	-	III	II
Helianthemum nummularium	I	I	I	I	-	II	V
Salvia pratensis	III	II	II	III	-	III	II
Thalictrum minus	I	II	I	I	-	III	I
Filipendula vulgaris	II	III	IV	III	III	I	-
Botriochloa ischaemum	II	I	-	I	III	II	V
Koeleria macrantha	III	-	II	II	III	IV	IV
Dianthus carthusianorum	II	III	I	III	I	I	-
Poa angustifolia	I	I	-	I	II	I	I
Teucrium montanum	II	-	I	II	-	IV	II
Eryngium campestre	III	III	II	III	I	-	-
Phleum phleoides	I	I	I	I	I	II	-
Galium glaucum	I	I	I	-	-	II	V
Anthyllis vulneraria	II	II	I	II	-	II	-
Acinos arvensis	I	-	I	-	I	II	III
Sanguisorba minor	I	I	I	I	-	-	-
Pimpinella saxifraga	II	III	II	II	-	-	-
Prunella laciniata	I	I	II	I	-	-	-
Stipa capillata	-	-	-	-	I	III	V
Ajuga genevensis	I	-	I	I	-	-	-
<i>Molinio-Arrhenatheretea</i>							
Plantago media	III	II	III	III	IV	I	-
Knautia arvensis	II	IV	III	III	I	I	-
Plantago lanceolata	II	II	III	III	II	-	-
Tragopogon orientalis	I	III	II	I	II	-	-
Achillea millefolium	II	IV	III	III	II	-	-
Leucanthemum vulgare	II	IV	III	III	I	-	-
Trifolium pratense	I	I	I	II	II	-	-
Lotus corniculatus	II	IV	III	III	-	-	-
Daucus carota	I	II	II	III	-	-	-
Vicia cracca	II	I	I	II	-	-	-
Senecio jacobaea	I	II	II	I	-	-	-
Linum catharticum	I	II	II	II	-	-	-
Campanula patula	-	II	I	I	-	-	-
Rumex acetosa	I	I	I	-	-	-	-
Leontodon hispidus	I	I	-	II	-	-	-
Holcus lanatus	-	I	I	I	-	-	-
Stellaria graminea	-	II	I	-	-	-	-
Poa pratensis	-	I	-	II	-	-	-
<i>Trifolio-Geranietae</i>							
Dictamnus albus	I	I	I	-	-	II	II
Verbascum lychnitis	-	-	I	I	I	IV	IV
Geranium sanguineum	I	-	I	-	-	III	V
Vincetoxicum hirundinaria	I	I	I	-	-	II	-
Agrimonia eupatoria	-	IV	II	III	I	-	-
Peucedanum cervaria	II	IV	I	-	-	-	-
Clematis recta	I	I	-	-	-	-	-
Trifolium medium	-	II	-	I	-	-	-

Tableau 1 - (continuation).

Associations nr.	1	2	3	4	5	6a	6b
Nombres des relevés	98	70	18	38	15	32	6
Altitude m.s.m. (en 10 m)	37-90	38-62	38-57	38-65	40-85	52-90	58-70

Compagnes

Inula hirta	I	I	I	I	II	I	II
Salvia verticillata	II	IV	II	III	II	I	-
Echium vulgare	II	II	I	II	I	I	-
Artemisia campestris	I	I	I	I	-	III	III
Galium mollugo	I	II	I	II	-	II	II
Coronilla varia	II	V	II	III	II	II	-
Elymus hispidus	I	I	I	I	IV	II	-
Hypericum perforatum	I	III	-	II	II	II	IV
Bupleurum falcatum	I	III	I	II	-	I	-
Medicago lupulina	I	I	I	II	II	-	-
Genista tinctoria	-	II	I	I	-	II	I
Falcaria vulgaris	II	I	I	I	II	-	-
Dactylis glomerata	I	III	II	III	I	-	-
Prunella vulgaris	I	III	II	II	I	-	-
Ranunculus polyanthemos	I	I	III	III	II	-	-
Carlina vulgaris	I	I	I	I	II	-	-
Carex caryophyllea	I	I	-	II	II	I	-
Colchicum autumnale	I	I	I	I	I	-	-
Hieracium pilosella	I	I	I	I	I	-	-
Aster amellus	I	I	I	-	-	I	-
Amygdalus nana	I	-	I	-	-	I	III
Chamaecytisus nigricans	II	II	I	I	-	-	-
Linum hirsutum	I	I	I	III	-	-	-
Eryngium planum	I	III	I	I	-	-	-
Nonea pulla	II	II	I	I	-	-	-
Stachys germanica	I	II	III	I	-	-	-
Agrostis capillaris	I	II	II	II	-	-	-
Anthoxanthum odoratum	I	I	II	I	-	-	-
Cichorium intybus	I	III	I	III	-	-	-
Peucedanum oreoselinum	I	I	I	-	-	I	-
Echium maculatum	I	-	I	-	-	I	IV
Pulsatilla m. * australis	I	-	I	-	-	II	III
Plantago argentea	I	-	I	-	-	III	II
Alyssum allyssoides	-	I	-	-	II	III	I
Chamaecytisus austriacus	I	-	I	-	I	I	-
Arrhenatherum elatius	-	II	I	I	-	I	-
Festuca rubra	I	I	I	I	-	-	-
Centaurea a. * spinulosa	-	I	II	I	I	-	-
Potentilla recta	-	I	I	I	I	-	-
Arenaria serpyllifolia	-	-	-	I	I	III	I
Stachys officinalis	-	II	I	I	I	-	-
Origanum vulgare	I	II	-	I	I	-	-
Astragalus austriacus	I	I	-	I	-	-	-
Echinops sphaerocephalus	-	I	I	I	-	-	-
Salvia nutans	I	-	I	-	-	I	-
Melilotus officinalis	I	I	-	I	-	-	-
Tanacetum corymbosum	I	-	-	-	III	I	-
Rhinanthus angustifolius	II	I	-	I	-	-	-
Seseli gracile	I	-	I	I	-	-	-
Allium albidum	I	-	-	-	-	I	-
Ononis arvensis	-	III	III	II	-	-	-
Medicago minima	-	II	I	I	-	-	-
Cynosurus cristatus	-	I	II	I	-	-	-
Cerastium holosteoides	-	I	I	II	-	-	-
Pedicularis c. * campestris	I	-	I	I	-	-	-
Centaurium erythraea	-	I	I	I	-	-	-
Erigeron annuus	-	II	I	I	-	-	-
Astragalus glycyphyllos	-	II	-	I	-	I	-
Asparagus officinalis	-	I	I	I	-	-	-
Crepis biennis	-	I	I	II	-	-	-
Crambe tatarica	I	I	-	-	I	-	-
Veronica chamaedrys	-	I	-	I	-	I	-
Helianthemum n. * obscurum	II	-	-	-	-	II	-
Reseda lutea	I	-	-	I	-	-	-
Melampyrum cristatum	-	I	II	-	-	-	-
Sedum hispanicum	-	-	-	-	-	II	III

rangé les coénoses mésoxérophiiles à *Bromus erectus* de Transylvanie dans l'alliance *Cirsio-Brachypodion*, non pas dans l'alliance *Bromion erecti*, comme ont procédé récemment, à tort, les phytosociologues roumains (SANDA, 2002; SANDA et al., 1999, 2008; POP et al., 2002). Cet argument résulte aussi de la place qu'occupe l'association *Rhantino-Brometum erecti* dans le dendrogramme (Fig. 1). La particularité floristique des coénoses à *Bromus erectus* de Transylvanie consiste dans la présence dans leur structure d'espèces régionales ponto-pannonico-balkaniques telles *Chamaecytisus albus* et *Rhinanthus rumelicus* qui en délimitent une répartition sud-est européenne conforme au climat régional de type tempéré-continentale (ROYER, 1991). Dans les zones d'où l'on a décrit des coénoses à *Bromus erectus*, celles-ci viennent en contact direct avec les coénoses édifiées par *Brachypodium pinnatum* groupées dans les associations *Polygalo majori-Brachypodietum* et *Carici humilis-Brachypodietum* (SOÓ, 1949; POP et al., 2002).

5. Ass. *Ferulago campestris-Carice-tum humilis* (Ciocârlan 1969) nom. nov. h.l. (Tableau 1, colonne 5) Lectotype: CIOCÂRLAN, 1969, tab. 1, rel. 2).

Syn.: *Caricetum humilis subcarpaticum* Ciocârlan 1969 (Art. 34) *Brachypodietum pinnati* Ştefan 1993 non Libb. 1930 (Art. 36).

Les coénoses édifiées prépondéramment par *Carex humilis* dans la zone de courbure des Subcarpates à savoir le bassin Slănic du Buzău, le bassin Râmnicu Sărat et le bassin du Milcov (CIOCÂRLAN, 1969; ŞTEFAN, 1993; COROI, 2001) au climat subcontinental (température moyenne annuelle de 9-10 °C et précipitations de quelque 600 mm) nous les rangeons dans cette association. Les sols dans lesquels elles végétent sont des tchernozem lessivé, bruns argiloilluviaux ou pseudorendzines, à réaction faiblement acide vers faiblement basique. Les espèces que nous désignons comme caractéristiques pour cette association sont *Ferugalo campestris* et *Dianthus membranaceus*. A côté de ces éléments régionaux, dans la structure floristique de l'association apparaissent sporadiquement, à des altitudes plus basses (250-350 m.s.m.) des éléments pontiques (*Jurinea arachnoidea*, *Galium octonarium*, *Centaura orientalis*, *Taraxacum serotinum* et d'autres) spécifiques pour les prairies xérophiiles de steppe de l'Est de la Roumanie. Ces espèces distinguent du point de vue floristique les coénoses à *Carex*

humilis de la région par rapport à celles de Transylvanie et ne permettent pas de les ranger dans l'association *Carici humilis-Brachypodietum pinnati* (CHIFU et al., 2006).

6. Ass. *Thymio comosi-Caricetum humilis* Morariu et Danciu 1977 (Tableau 1, colonne 6a, 6b) Lectotype: MORARIU et DANCIU, 1977, tab. 1, rel. 5.

Syn.: *Caricetum humilis transylvanicum* Zoly. 1939 (Art. 34).

Les phytocoénoses collinaires et submontagnardes (500-900 m.s.m.) autour de la dépression de Brasov qui végètent abondamment sur les crêtes et les versants ensoleillés à inclinaison faible à moyenne (15° à 40°) ont été rangées dans cette association (MORARIU et DANCIU, 1977). Les sols sur lesquels se développent ces phytocoénoses sont des rendzines et para rendzines, superficiels, riches en humus et à réaction faiblement alcaline (pH: 7,4). Le climat de la zone se caractérise par des températures moyennes multi annuelles de 7,8-8 °C et des précipitations de 747 mm. Les espèces daco-balkaniques désignées comme caractéristiques pour l'association sont *Thymus comosus* et *Linaria dalmatica* ssp. *transsilvanica*, à côté desquelles sont présentes d'autres espèces régionales (*Phleum montanum*, *Allium albidum*, *Leontodon crispus*, *Chamaecytisus albus*, *Cephalaria urvensis*), celles-ci préfigurant pour l'association une répartition sud-est européenne. La présence dans l'association d'espèces thermophiles caractéristiques de la classe *Trifolio-Geranietea* relève le fait que les coénoses stépisées de *Carex humilis* se sont étendues dans la zone après la coupe des forêts mésothermophiles de quercinées.

La plupart des phytocoénoses à *Carex humilis* et *Thymus comosus* se range dans la sous-association *typicum* (colonne 6a). Les phytocoénoses situées autour des localités Hărman et Sâmpetreu qui se développent dans des stations au climat local plus continental dans la structure floristique desquelles sont présentes les espèces différencielles *Hyacinthella leucophaea*, *Taraxacum erythrospermum* et *Ornithogalum orthophyllum* ssp. *kochii* ont été rangées dans une sous-association distincte: *hyacynthelletosum leucophaeae* Morariu 1978 (colonne 6b, Lectotype: MORARIU, 1978, tab. 1, rel. 1).

CONCLUSIONS

Les prairies mésoxérophiles à *Brachypodium pinnatum* de Roumanie se

Tableau 1 - (continuation).

Associations nr.	1	2	3	4	5	6a	6b
Nombres des relevés	98	70	18	38	15	32	6
Altitude m.s.m. (en 10 m)	37-90	38-62	38-57	38-65	40-85	52-90	58-70
Centaurea triumfetti	I	-	-	-	-	II	-
Ornithogalum pyramidale	-	I	I	-	-	-	-
Allium sphaerocephalum	-	-	-	-	-	II	V
Euphrasia stricta	I	II	-	-	-	-	-
Minuartia setacea	-	-	-	-	-	II	IV
Stipa pennata	-	I	-	-	-	I	-
Astragalus cicer	-	I	-	I	-	-	-
Galium album	-	I	-	I	-	-	-
Thymus pulegioides	-	III	-	I	-	-	-
Gymnadenia conopsea	-	I	I	-	-	-	-
Orchis coriophora	-	I	I	-	-	-	-
Salvia transsilvanica	-	I	I	-	-	-	-
Ferulago sylvatica	I	-	I	-	-	-	-
Trifolium campestre	-	-	-	-	I	-	I
Salvia nemorosa	-	-	-	-	IV	-	IV
Euphorbia glareosa	-	-	-	-	II	-	II
Viola jooi	I	-	-	-	-	-	-
Onosma pseudoarenaria	I	-	-	-	-	-	-
Seseli osseum	I	-	-	-	-	-	-
Elymus h. * barbulatus	-	-	-	-	-	-	III
Allium scorodoprasum	-	I	-	-	-	-	-
Iris pumila	I	-	-	-	-	-	-
Serratula radiata	I	-	-	-	-	-	-
Centaurea atropurpurea	I	-	-	-	-	-	-
Poa badensis	-	-	-	-	-	II	-
Iris ruthenica	I	-	-	-	-	-	-

caractérisent par une richesse floristique élevée et par la présence dans leur structure d'espèces endémiques et ponto-balkaniques rares à grande valeur phytogénétique telles: *Cephalaria radiata*, *Cephalaria uralensis*, *Linaria dalmatica* ssp. *transsilvanica*, *Ferulago campestris*, *Hyacinthella leucophaea*, *Pulsatilla montana* ssp. *australis*, *Echium maculatum* et *Crambe tatarica*.

Certaines de ces prairies mésoxérophiles sont présentes aussi dans les sites "Natura 2000" proposés par la Roumanie. Pour une meilleure protection des espèces rares mentionnées plus haut il est nécessaire de mettre en œuvre le plan de management pour les sites principaux où se trouvent ces prairies et de créer des zones de protection spéciales pour les coénoses qui contiennent les espèces rares.

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COMMUNAUTÉS DE LICHENS DES MONTS PĂDUREA CRAIULUI (CARPATES DE TRANSYLVANIE): UNE APPROCHE NUMÉRIQUE À LEUR CLASSIFICATION SYNTAXONOMIQUE ET ORDINATION ÉCOLOGIQUE

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ABSTRACT

A total number of 139 relevés were performed along transects located about 2 km apart and along the steepest slope. The classification of relevés was done by hierarchical cluster analysis using the UPGMA (average) linkage applied on a Morisita resemblance matrix. The optimal number of clusters was decided based on the distribution of t^2 pseudo-statistics and a trade-off between size and homogeneity of clusters. The best discriminant (differential) species among relevés groups were assessed using the indicator species analysis. The indirect ordination of relevés was performed by non-metric multidimensional scaling (NMDS) in the reduced space of four axes.

Twelve groups of relevés (clusters) were finally retained and assigned to different lichen associations: two terricolous (*Cladonietum coniocraeae* and *Cladonietum mitis*), seven corticolous (*Physcietum adscendentis*, *Parmelietum acetabuli*, *Parmelietum caperatae*, *Pyrenuletum nitidae*, *Pertusarietum amarae*, *Lecanoretum subfuscæ*, *Pseudoverniagetum furfuraceae*) and three saxicolous (*Caloplacetum saxicolae*, *Verrucario-Placynthietum nigri*, *Toninietum candidae*). The terricolous communities have the highest distinctiveness in terms of species composition. The spatial configuration of relevés in the space of the first two NMDS axes reveals clearly the most important ecological factor involved in the specific differentiation of lichen communities, namely the substrate type. The ordination of relevés along the third and fourth axes is determined by substrate fertility and slope aspect. Elevation doesn't seem to have a significant effect on the specific composition, probably because of the limited altitudinal range (300 to 850 m). We concluded that the lichen community structure within the study area is mainly controlled by substrate properties and slope microclimate.

NOMENCLATURE BOTANIQUE: SANTESSON (1993).

NOMENCLATURE SYNTAXONOMIQUE: WIRTH (1995).

KEYWORDS: corticolous, dendrogramme, indicator species analysis, phytosociological associations, non-metric multidimensional scaling, saxicolous, slope aspect, substrate fertility, terricolous.

INTRODUCTION

Des études phytosociologiques, qui ont mis en évidence une différenciation des communautés de lichens en fonction du substrat et d'autres facteurs écologiques locaux, ont été effectuées soit de façon empirique (CODOREANU, 1971; ROTĂRESCU, 1978; SAVA, 1983; PRIGODINA LUKOŠIENĖ et REMIGIJUS NAUJALIS, 2006) ou bien numérique (BATES, 1992; GAUSLAA, 1995).

Les principales motivations de la présente étude ont été, d'une part, la manque d'une étude phytosociologique de la zone et d'autre part, la nécessité de parachever l'évaluation de la zone sous l'aspect de la diversité végétale, en complétant ainsi l'étude de la végétation cormophytique (GROZA, 2008). De cette manière, on va faciliter la clarification des rapports entre les communautés (microphytocoénoses) de lichens corticoles et terricoles, et les communautés de cormophytes où ceci se retrouvent encadrées. De plus, les données collectées contribueront à compléter les connaissances concernant la distribution des espèces de lichens, spécialement celles rares et menacées.

Les objectifs de la présente étude ont été les suivants: 1) la classification coenotaxonomique des communautés de lichens de l'étage collinaire des Montagnes Pădurea Craiului; 2) l'identification des facteurs écologiques de nature abiotique les plus importants qui ont contribué à la structuration floristique de ces communautés.

MATERIAUX ET MÉTHODES

AIRE D'ÉTUDE

Les Montagnes Pădurea Craiului, avec une superficie d'environ 730 km² (GROZA, 2008) se situent dans le Nord-

Ouest des Montagnes Apuseni (Les Carpates de Transylvanie, Roumanie). L'altitude de la zone étudiée varie entre 345-850 m, l'hauteur maximal de ces montagnes étant 1015 m. Le substrat géologique est principalement représenté par des roches carbonatées, spécialement des calcaires. Environ 57% de la surface du massif est couverte de forêts qui appartiennent à deux grandes formations forestières: des chênaies mixtes (*Querco cerris-Carpinetum* Boșcaiu *et al.* 1966; *Quercetum petraeae-cerris* Soó 1957; *Querco petraeae-Carpinetum* Borza 1941) à l'étage collinaire, respectivement des chênaies - hêtraies mixtes (*Querco petraeae-Fagetum silvaticae* Resmeriță 1974), des hêtraies (*Festuco drymeiae-Fagetum* Morariu *et al.* 1968) et des hêtraies mixtes avec charme (*Carpino-Fagetum silvaticae* Paucă 1941) à l'étage inférieur de la montagne. Les prairies, d'origine secondaire, sont utilisées par les indigènes en tant que foins et pâtures, en couvrant des superficies étendues du massif.

La zone ne présente pas des grandes agglomérations urbaines, étant présentes en particulier des petites localités (villages et assemblée de villages). L'influence anthropique est évidente en particulier par l'exploitation du bois dans les formations forestiers, activités économiques spécifiques dans la zone (l'élevage et l'agriculture de subsistance) et le tourisme, concentré le long de grandes rivières ou des formations karstiques. La pollution est très faible, parce que la principale source de pollution, dans le passé représenté par les mines, est désormais éliminé en raison des fermetures de mines.

COLLECTION DES DONNÉES

Afin de rédiger la présente étude, on a utilisé les résultats des recherches qu'on avait menées nous-mêmes, le matériel de lichens étant collecté et étudié au cours de 8 ans (1994-2001). Nos recherches ont été réalisées spécialement dans des forêts murs et on s'est concentré sur les communautés de li-

chens corticoles; secondairement on a étudié les communautés saxicoles et terricoles, aussi.

La méthode de travail adoptée dans l'étude de la végétation de lichens correspond aux principes phytosociologiques Central-Européens, avec les particularités spécifiques à la lichenosociologie (GÉHU, 2006). La composition des coénoses de lichens a été mise en évidence à travers des relevés effectués sur des superficies ayant la dimension de 0,5 m². Un numéro total de 139 relevés ont été effectués au long de certaines transectes placées de 2 à 2 km, perpendiculairement sur les courbes de niveau.

L'identification des associations de lichens a été faite aux termes de la composition spécifique, en tenant compte spécialement des espèces caractéristiques et des espèces dominantes. L'abondance-dominance des espèces a été appréciée visuellement en utilisant l'échelle de Braun-Blanquet. Le tableau synthétique des associations a été réalisé sur la base de la constance des espèces, exprimée comme pourcentage. Parmi les variables abiotiques, pour chaque relevé on a enregistré l'altitude, la pente du terrain, le type et l'exposition du substrat.

Afin d'identifier les espèces de lichens on a utilisé les déterminateurs de CIURCHEA (1998), PURVIS *et al.* (1992) et WIRTH (1995). Pour la détermination chimique des espèces, on a appliqué, conjointement à la méthode traditionnelle avec des colorants, la chromatographie à couche fine (CULBERSON et

KRISTINSSON, 1970; WHITE et JAMES, 1985).

LA TRANSFORMATION ET L'ANALYSE DES DONNÉES

L'abondance-dominance des espèces a été convertie en recouvrement relative (pourcentage) par rapport au milieu des classes de recouvrement correspondantes à l'échelle Braun-Blanquet (+=0,5%; 1=3%; 2=15%; 3=37,5%; 4=62,5%; 5=87,5%). De même, l'exposition du substrat a été transformée en une variable numérique aux termes de la méthode utilisée par WISER *et al.* (1996), conformément à la formule:

$$E' = \cos(E_{\max} - E) + 1,$$

où E_{\max} et E sont l'exposition avec le microclimat le plus microtherme (Nord-Est dans le cas de la zone étudiée) et respectivement, l'exposition mesurée avec la boussole (les deux exprimées en grades par rapport à la direction Nord).

La ressemblance floristique de toutes les paires de relevés a été évaluée à l'aide de l'indice de Morisita, qui est presque indépendant de l'aire du relevé et du numéro d'espèces, mais sensible à l'abondance des espèces dominantes (KREBS, 1999). La classification des relevés a été réalisée par une analyse cluster hiérarchique qui fait usage de l'algorithme UPGMA pour la construction de la dendrogramme (LEGENDRE et LEGENDRE, 1998). La mesure dans quel-

le celle-ci dernière altère les relations de ressemblance entre les relevés, exprimées initialement par l'indice Morisita, a été évaluée par la corrélation cophénétique (LEGENDRE et LEGENDRE, 1998). La stabilité des nœuds de la dendrogramme a été estimée comme pourcentage, en tenant compte de la proportion d'un total de 9999 de réplications simulées par bootstrapping, pour lesquelles les nœuds respectifs gardent la même composition que la dendrogramme originelle (HAMMER, 2010). Pour la sélection du numéro optimal de groupes (clusters) de la dendrogramme on a fait appel à la distribution de l'indice pseudostatistique t^2 , en vue de l'identification des valeurs minimales (SAS INSTITUTE INC., 2007). Parmi les solutions existantes on a choisi finalement la variante qui correspondait à un compromis entre l'homogénéité et la différenciation floristique des clusters.

L'identification des meilleures espèces discriminantes (à valeur différentielle) parmi les groupes de relevés distingués a été effectuée aux termes de l'analyse des espèces discriminantes, nommées de manière originelle par les auteurs, l'analyse des espèces "indicatrices" (DUFRENE et LEGENDRE, 1997). Celle-ci calcule le pouvoir discriminant spécifique (exprimé en pourcentage), qui résulte comme produit entre la fréquence relative et l'abondance relative de l'espèce en cause dans un certain group de relevés (syntaxone). La signification statistique du pouvoir discriminant maximal de chaque espèce a été établie par un test Monte Carlo basé sur 15999 permutations.

L'ordination indirecte des relevés a été réalisée par la mise à l'échelle non-métrique multidimensionnelle (NMDS), qui a utilisé comme input la même matrice de ressemblance floristique entre les relevés. On a extrait un numéro total de 4 axes, ce qui a permis d'obtenir une configuration spatiale stable (vérifiée par des roulages successifs) et d'une valeur réduite du stress, respectivement d'un coefficient de corrélation Pearson élevé entre la matrice de distances mesurées en l'espace d'ordination et la matrice de différence floristique entre les relevés (SAS INSTITUTE INC., 2007). En vue de l'interprétation écologique des 4 axes extraites, on a calculé les coefficients de corrélation Spearman entre les coordonnées des relevés, d'une part et les variables abiotiques et les recouvrements relatives des espèces, d'autre part. La signification des gradients écologiques dominants a été déduite, la plupart des fois, à travers les valences autécologiques des

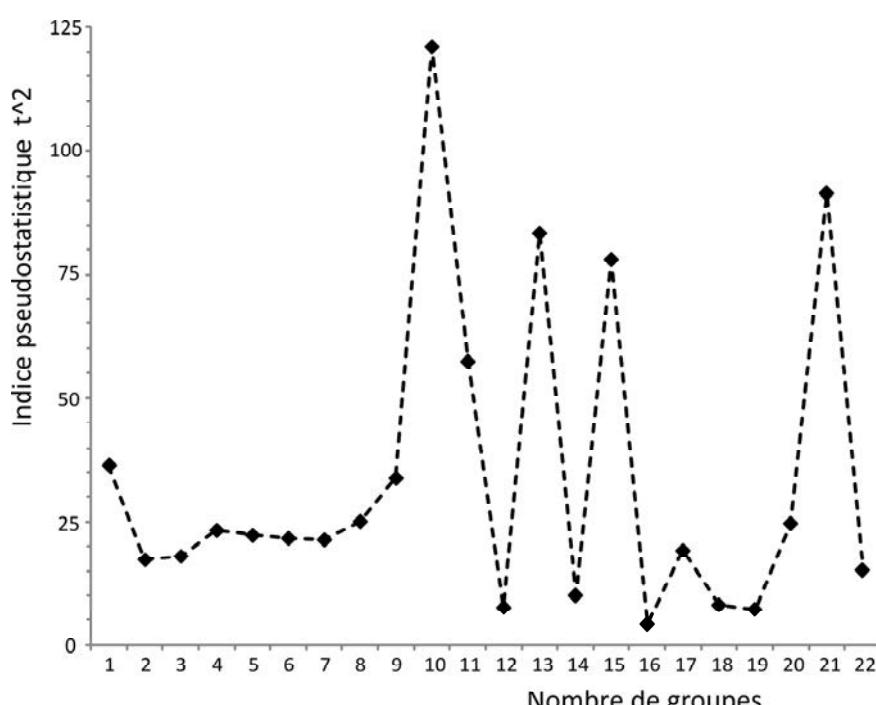


Fig. 1 - La variation de l'indice pseudostatistique t^2 en fonction du numéro des groupes de relevés qui résulte à la suite de l'analyse cluster, à mesure de leur agrégation hiérarchique.

espèces bien corrélées avec les axes d'ordination. En ce sens, on a fait appel aux valeurs indicatrices écologiques en rapport avec la lumière, l'humidité, la réaction chimique et la trophycité du substrat, conformément à l'échelle de ELLENBERG *et al.* (1992).

Les analyses numériques mentionnées auparavant ont été effectuées à l'aide des programmes SAS 9.2 (SAS INSTITUTE INC., 2007), PC-ORD 5.31 (McCUNE et MEFFORD, 2006) et PAST 1.99 (HAMMER *et al.*, 2001).

RÉSULTATS ET DISCUSSIONS

La variation de l'indice pseudostatistique t^2 en fonction du numéro des clusters met en évidence l'existence de plusieurs minimes, qui correspondent à des solutions avec 2, 12, 14, 16 et 19 groupes (Fig. 1). L'apparition de certains groupes formés de 1 ou 2 relevés, lorsque le numéro des clusters est élevé (> 12), fait que ceux-ci n'ont pas de signification eco-floristique et statistique détectable (Fig. 2). D'autre part, la solution avec 2 groupes a le désavantage d'un niveau très bas de la ressemblance floristique entre les relevés qui forment chaque cluster, bien que les probabilités bootstrap associées aux deux nœuds correspondants (de 100% et 93%) soient les plus élevées de la moitié supérieure de la dendrogramme (Fig. 2). Par conséquent, la solution avec 12 groupes est considérée optimale de la perspective du rapport entre la dimen-

Tableau 1 - Le pouvoir discriminant (en pourcentage) des meilleures espèces à valeur différentielle entre les associations distinguées (on ne présente que les espèces dont le pouvoir discriminant maximale dépasse 85%). Les valeurs en bold sont statistiquement significatives à un seuil critique de la probabilité alpha de 0,0001. Les abréviations des associations, de même que pour la Fig. 2.

Association	Pf	Cm	Pc	Vp	Pn	Tc	Cc	Ph_a	Pa	Cs	Ls	P_a
Nombre des relevés	7	15	12	11	12	8	11	18	13	10	11	11
<i>Parmelia saxatilis</i>	100	0	0	0	0	0	0	0	0	0	0	0
<i>Pseudevernia furfuracea</i>	99	0	0	0	0	0	0	0	0	0	0	0
<i>Platismatia glauca</i>	99	0	0	0	0	0	0	0	0	0	0	0
<i>Cladonia mitis</i>	0	100	0	0	0	0	0	0	0	0	0	0
<i>Flavoparmelia caperata</i>	0	0	100	0	0	0	0	0	0	0	0	0
<i>Placynthium nigrum</i>	0	0	0	100	0	0	0	0	0	0	0	0
<i>Graphis scripta</i>	0	0	0	0	100	0	0	0	0	0	0	0
<i>Toninia candida</i>	0	0	0	0	0	99	0	0	0	0	0	0
<i>Collema tenax</i>	0	0	0	0	0	88	0	0	0	0	0	0
<i>Cladonia coniocraea</i>	0	0	0	0	0	0	99	0	0	0	0	0
<i>Physcia adscendens</i>	0	0	0	0	0	0	0	97	1	0	0	0
<i>Pleurosticta acetabulum</i>	0	0	3	0	0	0	0	0	97	0	0	0
<i>Caloplaca saxicola</i>	0	0	0	2	0	1	0	0	0	95	0	0
<i>Lecanora subfuscata</i>	0	0	0	0	0	0	0	0	0	0	95	3
<i>Phlyctis agelaea</i>	0	0	0	0	1	0	0	0	0	0	6	89

Tableau 2 - Les coefficients de corrélation Spearman d'entre les quatre axes NMDS, d'une part et les variables abiotiques et les abondances des espèces, d'autre part (on ne retrouve listées que les variables et les espèces qui présentent les plus hautes corrélations positives et négatives avec au moins une des axes). Symboles: *** p<0,0001; ** 0,0001<p<0,001; * 0,001<p<0,01; NS=insignifiant.

Variables abiotiques/espèces	Axe 1	Axe 2	Axe 3	Axe 4
Pente du terrain	-0.653***	NS	NS	0.526***
<i>Lecidella elaeochroma</i>	0.608***	-0.501***	NS	-0.264*
<i>Protoblastenia rupestris</i>	-0.559***	NS	-0.218*	0.445***
<i>Caloplaca saxicola</i>	-0.552***	0.258*	-0.512***	0.327***
<i>Cladonia furcata</i>	NS	0.556***	0.456***	0.361***
<i>Lecanora subfuscata</i>	0.342***	-0.501***	NS	NS
<i>Cladonia mitis</i>	NS	0.441***	0.537***	0.279**
<i>Evernia prunastri</i>	NS	-0.357***	NS	-0.699***
Exposition du substrat	-0.459***	0.257*	NS	0.616***
<i>Placynthium nigrum</i>	-0.363***	NS	-0.223*	0.468***

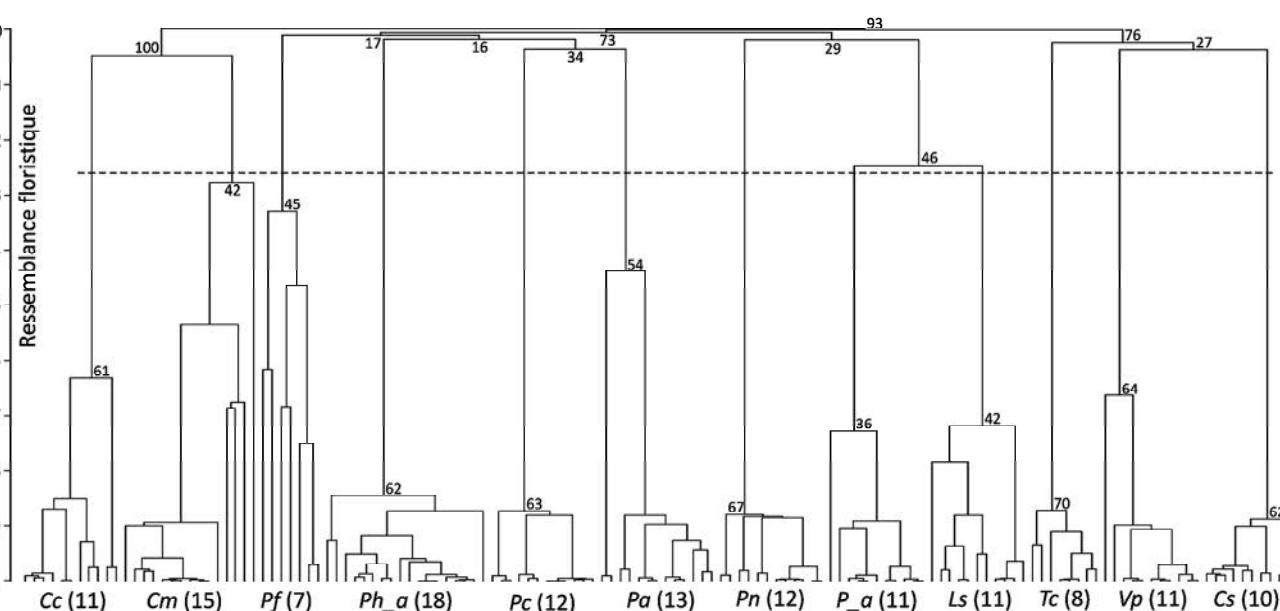


Fig. 2 - La dendrogramme des 139 relevés obtenu au moyen de l'algorithme UPGMA (la corrélation cophénétique = 0,9914). Les probabilités inscrites à côté des nœuds principaux sont proportionnelles avec la stabilité statistique de ceux-ci. La ligne interrompue correspond à la solution avec 12 groupes. Les parenthèses indiquent le nombre total des relevés du cluster correspondants. Abréviations: Cc=Cladonietum coniocraeae; Cm=Cladonietum mitis; Pf=Pseudevernetum furfuraceae; Ph_a=Physcietum adscendentis; Pc=Pamelietum caperatae; Pa=Pamelietum acetabuli; Pn=Pyrenuletum nitidae; P_a=Pertusarietum amarae; Ls=Lecanoretum subfuscatae; Tc=Toninietum candidate; Vp=Verrucario-Placynthietum nigri; Cs=Caloplacetum saxicolae.

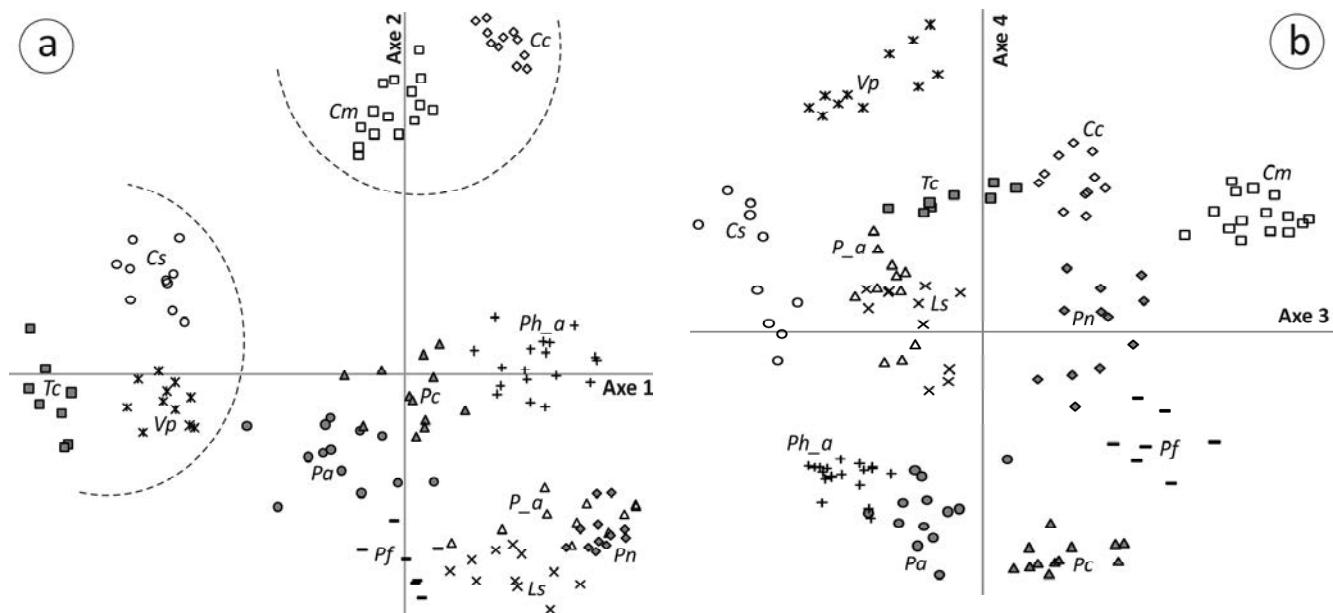


Fig. 3 - L'ordination NMDS des 139 relevés dans l'espace déterminé par les axes 1-2 (a) et 3-4 (b). La valeur résiduelle du stress est de 0,115, et la corrélation linéaire entre les distances originelles et celles mesurées dans l'espace d'ordination est de 0,953. La signification des abréviations est la même que pour la Fig. 2.

sion des groupes et leur homogénéité (Fig. 2).

Les 12 groupes de relevés ont été attribués à un numéro identique d'associations de lichens, à la base des espèces édificatrices (dominantes) et des celles caractéristiques pour les cénotaxones supérieurs (voir la tableau synthétique de l'Appendice). Le cadre syntaxonomique complet des communautés de macrolichens de la zone d'étude est présenté en ce qui suit.

Cl. *Verrucarietea nigrescentis* Wirth 1980
Ord. *Verrucarietalia* Klem. 1950
All. *Caloplacion decipientis* Klem. 1950
Ass. *Caloplacetum saxicolae* (Du Rietz 1925) Kaiser 1926 [Cs]

Cl. *Collematetea cristati* Wirth 1980
Ord. *Collematetalia cristati* Wirth 1980
All. *Collemat fuscovirens* (Klem. 1955) Wirth 1980
Ass. *Verrucario-Placynthietum nigri* Kaiser 1926 [Vp]
Ass. *Toninietum candidae* Kaiser 1926 [Tc]

Cl. *Hypogymnieteaphysodis* Föllm. 1974
Ord. *Alectoretalia* Dahl et Hadač 1944
All. *Hypogymnion physodis* Beschel 1958
Ass. *Pseudevernetum furfuraceae* Hil. 1925 [Pf]

Cl. *Arthonio-Lecidelletea elaeochromae* Drehwald 1993
Ord. *Graphidetalia scriptae* Hadač 1944
All. *Graphidion scriptae* Ochsner 1928
Ass. *Pyrenuletum nitidae* Hil. 1925 [Pn]
Ass. *Pertusarietum amarae* Hil. 1925

[P_a]

All. *Lecanorion subfuscæ* Ochsner 1928
Ass. *Lecanoretum subfuscæ* Hil. 1925 [Ls]
Cl. *Physcietea* Tomaselli et De Michelis 1957
Ord. *Physcietalia adscendentis* Hadač 1944 em. Barkman 1958
All. *Xanthorion parietinae* Ochsner 1928
Ass. *Physcietum adscendentis* Frey et Ochsner 1926 [Ph_a]
Ass. *Parmelietum acetabuli* Ochsner 1928 [Pa]
Ass. *Parmelietum caperatae* Felföldy 1941 [Pc]

Cl. *Cladonio digitatae-Lepidozietae reptantis* Jež. et Vondr. 1962
Ord. *Cladonio digitatae-Lepidozietalia reptantis* Jež. et Vondr. 1962
All. *Cladonion coniocraeae* Duvign. 1942 ex James et al. 1977
Ass. *Cladonietum coniocraeae* Duvign. 1942 ex James et al. 1977 [Cc]

Cl. *Ceratodontopurpurei-Polytrichea piliferi* Mohan 1978
Ord. *Peltigeretalia* Klem. 1950
All. *Cladonion arbusculae* Klem. 1955
Ass. *Cladonietum mitis* Krieger 1937 [Cm]

Les espèces avec le plus grand pouvoir discriminant pour les associations distinguées sont listées dans le Tableau 1. Comme prévu, une partie de celles-ci (*Platismatia glauca*, *Graphis scripta*, *Collemat enax*) sont des espèces caractéristiques pour les cénotaxones supérieurs (Tableau 1 et Appendice), pendant que d'autres peuvent être con-

siderées des espèces différentielles au niveau d'association: *Pseudevernia furfuracea* et *Parmelia saxatilis* (pour l'ass. Pf), *Cladonia mitis* (pour l'ass. Cm), *Flavoparmelia caperata* (pour l'ass. Pc), *Placynthium nigrum* (pour l'ass. Vp), *Toninia candida* (pour l'ass. Tc), *Cladonia coniocraea* (pour l'ass. Cc), *Physcia adscendens* (pour l'ass. Ph_a), *Pleurosticta acetabulum* (pour l'ass. Pa), *Caloplaca saxicola* (pour l'ass. Cs), *Lecanora subfuscæ* (pour l'ass. Ls), et *Phlyctis agelaea* (pour l'ass. P_a).

Le moins différencié est le group de relevés correspondant à l'association P_a, fait mis en évidence tant par l'existence d'une seule espèce avec un pouvoir discriminant de seulement 89% (Tableau 1), tant par la valeur la plus basse (36%) de la probabilité bootstrap associée au nœud correspondant de la dendrogramme (Fig. 2). De manière surprenante, le group de relevé appartenant à l'association Pf possède la plupart et les plus discriminantes espèces par rapport aux reste des associations, bien que la probabilité bootstrap associée au nœud correspondant soit seulement 45% (Fig. 2).

La configuration des relevés dans l'espace des premiers deux axes NMDS reflète clairement le facteur écologique dominant dans la structuration des communautés de lichens, c'est-à-dire le type du substrat. Cette liaison est suggéré par les bonnes corrélations que l'axe 1 et l'axe 2 ont avec les espèces *Lecidella elaeochrome* (corticole) et *Protoblastenia rupestris* (saxicole), et respectivement *Cladonia furcata* (terricole) (Tableau 2). Ainsi, au long de l'axe 1 sont enchaînées, de gauche à droite, les

communautés saxicoles (*Tc*, *Cs* et *Vp*), suivies par celles corticoles (*Pa*, *Pf*, *Pc*, *Ls*, *Ph_a*, *P_a* et *Pn*) (Fig. 3a). La corrélation négative entre la pente du terrain et l'axe 1 (Tableau 2) confirme la signification que l'on avait attribuée à la dernière, car les affleurements rocheux sont beaucoup plus répandus sur les versants abrupts que sur ceux faiblement inclinés. L'axe 2 sépare clairement les communautés terricoles de la partie supérieure (*Cc* et *Cm*) de celles corticoles de la partie inférieure (Fig. 3a).

Le positionnement des relevés dans l'espace bidimensionnel des axes 3 et 4 est déterminé par la trophicité minérale du substrat et par le microclimat des versants. L'axe 3 est superposé sur un gradient négatif de contenu en nutriments minéraux (Fig. 3b), comme le suggère la corrélation positive avec l'espèce oligotrophe *Cladonia mitis* et la corrélation négative avec l'espèce méso-eutrophe *Caloplaca saxicola* (Tableau 2). L'axe 4 correspond à un gradient d'humidité, fait suggéré par la corrélation négative avec *Evernia prunastri* (élément xéro-mésophile) et par la relation positive avec l'exposition (Tableau 2). Ainsi, les communautés de lichens de la partie supérieure de l'ordinogramme préfèrent les versants om-

brés, plus humides (le secteur N-NE), et celles de la partie inférieure occupent à préférence les versants ensoleillés, moins humides (le secteur S-SOU) (Fig. 3b). L'effet de l'exposition sur la différenciation structurelle des communautés de lichens est accentuée par la corrélation positive entre l'axe 4 et la pente du terrain (Tableau 2), ce qui indique le fait que les versants ombrés ont des pentes plus grandes que ceux ensoleillés. Il est intéressant à signaler un phénomène de compensation écologique entre le régime thermique des roches calcaires et l'humidité plus haute des versants ombrés, en le sens que le développement des communautés basiphiles de *Vp* est possible uniquement sur les versants plus humides, qui estompent le chauffage rapide et fort des calcaires (CODOREANU, 1971; COSTE, 1994).

Le degré de recouvrement des lichens ne présente qu'une faible, mais significative, corrélation avec l'axe 1, ce qui confirme un rapport facile à remarquer sur le terrain, c'est-à-dire que les communautés saxicoles présentent un degré de recouvrement plus bas que celles terricoles et, surtout, que celles corticoles, de même que l'avaient observé CODOREANU (1971), ROTĂRESCU

(1978) et SAVA (1983). Enfin, l'altitude ne joue pas un rôle important dans la différenciation floristique des communautés de lichens du territoire étudié, probablement à cause de son amplitude altimétrique relativement faible, entre les limites de l'étage collinaire.

CONCLUSIONS

Les communautés de macrolichens de la partie basse des Montagnes Pădurea Craiului peuvent être encadrées en 12 associations (deux terricoles, trois saxicoles et sept corticoles), qui s'individualisent assez bien, vu les abondances d'espèces édificatrices et les fréquences d'espèces caractéristiques/différentielles. Les communautés terriques appartenant aux classes *Cladonio digitatae-Lepidozietea reptantis* et *Ceratodont-Polytrichetea piliferi* se diffèrentient le plus clairement de point de vue floristique. La structure floristique des communautés de lichens de la zone étudiée est déterminée de manière prédominante par le type du substrat, à laquelle viennent s'ajouter la trophicité minérale et l'exposition du substrat, en temps que l'altitude n'a pas un effet détectable.

Appendice - Tableau synthétique des associations de lichens identifiées dans les Montagnes Pădurea Craiului. Les valeurs représentent la constance des espèces (en pourcentage), et les codes d'entre parenthèses font référence à l'abondance-dominance maximale des espèces (sur l'échelle Braun-Blanquet) enregistrée dans chaque association. Les abréviations des associations - les mêmes que pour la Fig. 2.

Appendice - (continuation).

Appendice - (continuation).

Association	Cc 500-620	Cm 300-650	Cs 380-500	Vp 300-600	Tc 300-550	Pn 400-540	P_a 300-420	Ls 300-420	Ph_a 300-540	Pa 350-700	Pc 350-450	Pf 520-850
Altitude min-max (m)	15-25	10-30	50-70	40-85	65-75	0-15	5-35	15-40	5-20	4-80	0-30	15-20
Pente min-max (grades)	65-80	60-80	45-70	50-80	65-85	70-85	70-85	65-90	60-90	65-80	70-80	50-75
Recouvrement min-max (%)												
Nombre de relevés	11	15	10	11	8	12	11	11	18	13	12	7
Cladonia fimbriata	55(1)	47(2)
Peltigera aphloides	45(1)	80(2)
Cladonia rangiformis	36(1)	40(+)
Dibaeis baeomycetes	27(+)	27(+)
Peltigera polydactyla	18(+)	13(+)
Peltigera horizontalis	18(+)	13(+)
Diploschistes muscorum	18(+)	13(+)
Lecidea leucodesma	.	.	30(1)	.	13(+)
Toninia sedifolia	.	.	.	36(+)	75(1)
Lobothalnia melanaspis	.	.	.	36(+)	38(1)
Collema crispum	.	.	.	36(+)	38(+)
Phlyctis argena	33(+)	64(2)
Ramalina fastigiata	17(+)	38(+)	.	.
Cladonia cenotea	73(1)
Cladonia pocillum	36(1)
Peltigera membranacea	18(+)
Peltigera praetextata	.	53(1)
Cladonia symphytaria	.	33(1)
Cladonia coccinea	.	33(1)
Peltigera elisabethae	.	13(+)
Dermatocarpon miniatum	.	.	60(1)
Lecania muralis	.	.	50(1)
Buellia venusta	.	.	30(1)
Buellia dubiana	.	.	30(+)
Verrucaria fusca	.	.	30(+)
Verrucaria calcicola	.	.	20(1)
Lecania nylanderiana	.	.	20(+)
Thryea confusa	.	.	55(2)
Collema limosum	.	.	36(+)
Collema undulatum	.	.	18(+)
Collema auriforme	.	.	18(+)
Verrucaria glauca	.	.	18(+)
Aspicilia contorta	.	.	.	75(1)
Leptogium teretiusculum	.	.	.	13(+)
Leproplaca xantholytha	.	.	.	13(+)
Xanthoparmelia conspersa	.	.	.	13(+)
Xanthoparmelia somolensis	.	.	.	13(+)
Thelotrema lepadinum	33(1)
Lepraria lobifrons	33(+)
Opegrapha atra	33(+)
Melanella subargentifera	36(+)
Ramalina obtusata	18(+)
Hypocenomyce scalaris	15(+)
Melanella elegantula	15(+)
Parmelia pastilifera	67(1)
Physcia dubia	33(+)	.	.	.
Vulpicida pinastri	17(+)	.	.	.
Cetrelia olivetorum	29(+)	.	.
Usnea filipendula	29(+)	.	.

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SUR L'EXTENSION À LA PHYTOSOCIOLOGIE D'UN CONCEPT DE LA PHYSIQUE, LE PHÉNOMÈNE D'HYSTÉRÉSIS

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ABSTRACT

The author analyses a concept going from physics and extended to plant sociology, hysteresis. It is illustrated with the dynamics of epiphytic lichenic vegetation under influence of acid atmospheric pollution, of the mesophilous meadow vegetation under influence of fertilization (eutrophication), with some consequences on ecological genius.

KEYWORDS: phytosociologie, hysteresis.

RÉSUMÉ

L'auteur analyse ici un concept issu de la physique étendu à la phytosociologie, l'hystérésis, en l'illustrant notamment avec la dynamique de la végétation épiphytique lichénique sous l'influence de la pollution atmosphérique acide, de la végétation prairiale mésophile sous l'influence de la fertilisation (eutrophisation), avec diverses conséquences au niveau du génie écologique.

En physique, le phénomène d'hystérésis (du grec *husterein*, être en retard) a surtout été mis en évidence dans le magnétisme. D'une manière générale, si une cause *C* produit un effet *E*, on dit qu'il y a hystérésis lorsque la courbe $E=f(C)$ obtenue à la croissance de *C* est différente de la courbe $E=\mathcal{f}(C)$ obtenue à la décroissance de *C*. Généralement, la raison en est que les variations de *E* ne sont pas totalement réversibles comme par exemple la magnétisation d'un matériau par un courant électrique qui persiste quand le courant a disparu. En cristallographie, sous un gradient de température, la transformation du fer $\alpha\beta$ (cubique centré) et fer γ (cubique à faces centrées) ou la transformation de l'austénite en martensite présentent aussi un tel phénomène.

L'extension à la phytosociologie apparaît dans les phénomènes de dynamique provoquée souvent par des causes humaines. L'introduction de ce concept physique dans notre science se lit

dès 1974 dans une publication de SCHMID (1974: 170) évoquant la reconstitution d'une formation climacique détruite tardant à se reconstituer, hystérésis qui peut s'expliquer par «*l'insuffisance des moyens de dispersion des espèces susceptibles de se substituer aux constituants de la formation initiale*».

Un premier exemple, assez bien connu (VAN HALUWYN et LEROND, 1993; DE FOUCault, 1992, 1993a) est offert par les effets de la pollution atmosphérique acide sur la végétation épiphytique lichénique, bien étudiée depuis les années 1970 (HAWKSWORTH et ROSE, 1970). D'une manière générale, selon un gradient croissant de pollution, on assiste à une modification progressive de cette végétation épiphytique, que l'on peut décrire en terme de série, c'est-à-dire une suite de syntaxons élémentaires floristiquement bien définis et ordonnés le long du gradient causal; la notion de série est un homologue qualitatif de la fonction quantitative $f(C)$ évoquée en physique. Une telle série peut être représentée d'une manière floristique, en mettant en évidence la disparition progressive des taxons selon leur sensibilité, ou d'une manière systémique (des noms de syntaxons reliés par une flèche systémique représentant la cause). Une telle série peut être utilisée en bioindication en associant à une flore épiphytique observée un intervalle de concentration en polluant.

Pourtant, depuis une vingtaine d'années, grâce aux avancées techniques dans le domaine industriel, cette pollution régresse et, si l'on veut continuer à utiliser l'échelle de bioindication établie dans l'étape précédente, il faut vérifier qu'elle reste valable en pollution décroissante et qu'on assiste à un retour des taxons épiphytes. Or l'inertie d'une réapparition risque d'être plus élevée que celle d'une disparition; pour un degré de pollution donné, la végétation présente pourra être différente de celle observée au même degré en pollution croissante. Ainsi l'hystérésis de la végétation lichénique traduit une résistance à l'effet de l'inversion du facteur causal, un frein à la réversibilité. La reconstitution d'une communauté liché-

nique est fonction de plusieurs facteurs dont la faiblesse peut expliquer ce frein: accessibilité (HEIMANS, 1954) des lichens aux phorophytes, qualité favorable des écorces qui ont pu garder le souvenir de l'histoire de la station, germination et croissance des lichens, persistance d'un polluant différent du polluant initial.

Le second exemple est moins connu de ce point de vue bien qu'il touche un facteur écologique souvent clairement identifié, l'eutrophisation, avec le cas des prairies mésophiles relevant de la classe des *Arrhenatheretea elatioris*¹.

Plusieurs travaux antérieurs utilisant l'approche systémique ont montré que, bien souvent, les prairies fauchées ou pâturées de cette classe dérivent de pelouses plus oligotrophiles relevant soit des *Nardetea strictae* ou des *Caricetea curvulae* sur substrats acides, soit des *Festuco-valesiaceae-Brometea erecti* ou des *Festuco-Seslerietea variae* sur des substrats basiques, souvent à faible biomasse et de médiocre qualité fourragère. La fertilisation (apport d'éléments minéraux et organiques) a pour but d'améliorer les performances des pelouses et de les transformer en prairies plus productives. Sur le plan synfloristique, on peut suivre ces modifications grâce à la mise en évidence de séries trophiques qui mènent des pelouses oligotrophiles initiales à des prairies mésotrophiles puis eutrophiles, voire à des friches nitrophiles à biomasse élevée (DE FOUCault, 1989). Au cours de telles séries, on assiste progressivement à la régression ou la disparition des espèces les plus sensibles, et souvent de valeur patrimoniale, et corrélativement l'apparition d'espèces eutrophiles plus banals favorisées par l'élévation du niveau trophique.

Mais récemment, les écologues et protecteurs de la biodiversité se sont inquiétés de la régression des taxons patrimoniaux et beaucoup d'organismes (parcs naturels régionaux, conservatoi-

¹ La nomenclature phytosociologique jusqu'au rang alliance suit le référentiel de BARDAT et al. (2004).

res régionaux d'espaces naturels...) tentent maintenant d'inverser la tendance généralisée vers l'eutrophisation et de mettre en œuvre diverses mesures «agri-environnementales» (chargement des prairies, baisse ou suppression des apports fertilisants, exportation de la biomasse organique) ayant pour finalité de relever la valeur patrimoniale des prairies en les faisant passer du stade eutrophile au stade mésotrophile au moins. Le problème est que cette inversion trophique présente de l'hystérisis: si en deux-trois ans d'amélioration pastorale une pelouse peut dériver vers une prairie eutrophile sans grande valeur patrimoniale, on ne sait guère, du moins dans les systèmes pastoraux de plaine, combien il en faut pour revenir à un stade mésotrophile, à défaut du stade initial oligotrophile. Dans certains systèmes de montagne en revanche, par exemple en Vanoise, DELPECH (1976) a observé un retour des pelouses à *Phleum alpinum* L. vers une nardaie oligotrophile un certain temps après l'arrêt des apports fertilisants et LACOSTE (1975: 234) précise que les *Nardetum alpigenum* Braun-Blanquet 1949 et *Festucetum spadiceae* Guinochet 1938 *centauretosum uniflorae* passent au *Meo athamantici-Trisetetum flavescentis* Lacoste 1975 par fertilisation et que la dynamique inverse est possible par oligotrophisation. On peut faire remarquer que cette hystérisis trophique est souvent incompatible avec le délai administratif des mesures agri-environnementales qui ne durent souvent que trop peu d'années pour révéler des résultats concrets.

On peut encore considérer d'autres exemples de dynamique et explorer leur degré d'hystérisis.

Une salinisation peut intervenir localement dans nos régions tempérées, soit par dépôt de sel (sur les routes en hiver, GÉHU, 1983; VANDEN BERGHEN, 1994), soit par réaction chimique aboutissant à une libération de Na_2CO_3 (MATYSIAK, 1993); sur le plan phytosociologique, ceci se traduit par l'apparition d'espèces oligohalophiles telles que *Puccinellia distans* (L.) Parl.; connaissant la mobilité de Na^+ , on peut penser que l'hystérisis est ici très faible et que, sans apport nouveau de sel, le retour à des communautés nettement glycophiles devrait être rapide. La récente tempête Xynthia conjuguée à de grandes marées sur les côtes atlantiques françaises (mars 2010), qui a eu pour effet l'entrée d'eau de mer sur les terres intérieures, offre une occasion de tester cette hystérisis en vraie grandeur.

En revanche, l'érosion du sol, qui

décape les horizons supérieurs et peut remettre à nu la roche mère, possède une très longue hystérisis car la reconstitution du sol initial peut exiger des dizaines, voire des centaines d'années; elle est d'ailleurs fonction du climat et de la végétation de substitution qui apportera la fraction organique du futur sol.

Le pâturage des prairies mésophiles induit la disparition des espèces sensibles au piétinement et aux coupes fréquentes (*Arrhenatherum elatius* (L.) P. Beauv., *Trisetum flavescens* (L.) P. Beauv., *Crepis biennis* L., etc.) et favorise l'apparition d'espèces considérées comme indicatrices (*Cynosurus cristatus* L., *Trifolium repens* L., *Lolium perenne* L., *Bellis perennis* L., etc.); l'abandon de cette pratique et le fauchage favorisent le retour des premières, mais laissent aussi persister longtemps les secondes, ce qui ne facilite pas toujours l'interprétation phytosociologique de telles prairies; mais ces taxons indicateurs de pâturage le sont-ils vraiment ou sont-ils plutôt des taxons plus largement caractéristiques de la classe des prairies, donc communs aux deux types de prairies?

Dans les études fondamentales comme appliquées (génie écologique; DE FOUCault, 1988) de dynamiques végétales, il convient donc de garder à l'esprit que les transformations mises en jeu peuvent présenter des phénomènes d'hystérisis analogues à ceux que l'on peut observer dans certains phénomènes physiques; avant de mettre en route des transformations écologiques, les ingénieurs devraient aussi penser à leur possible hystérisis. En outre, comme on l'a vu pour la végétation lichénique, les échelles de bioindication peuvent ne pas superposer en gradient causal croissant et décroissant, ce qui pourrait parfois limiter leur utilité. Là encore, un certain parallélisme existe avec la physique, des instruments de mesure de certaines grandeurs pouvant présenter une hystérisis, et on a montré par ailleurs que la bioindication est un acte de mesure qualitative (DE FOUCault, 1993a). On a là des arguments de plus pour considérer que la phytosociologie sigmatiste possède la valeur d'une physique qualitative (DE FOUCault, 1986, 1992).

Il serait d'un haut intérêt de dépasser ces considérations qualitatives et d'acquérir des informations quantitatives lors d'études cinétiques dans des conditions systémiques variées; on a vu par exemple qu'en montagne il semble que le retour de prairies mésotrophiles, voire de pelouses oligotrophiles soit

plus rapide qu'en plaine.

Il pourrait être aussi intéressant d'initier une modélisation énergétique de cette hystérisis: l'introduction dans un écosystème d'énergie (musculaire d'origine humaine ou animale, fossile par le biais d'engins) induisant une certaine dynamique pourrait ralentir la dynamique inverse si celle-ci ne s'accompagne pas d'une nouvelle injection d'énergie. Par exemple, le défrichement d'une strate arborée peut ne prendre que quelques heures avec les tronçonneuses actuelles, un incendie ou une tempête (injection d'énergie), alors que plusieurs dizaines d'années seront nécessaires pour assister à sa reconstitution spontanée (injection d'énergie nulle), sans même forcément atteindre le retour de la forêt mature. L'abandon du pastoralisme traditionnel (annulation de l'énergie injectée) sur les pelouses oligotrophiles se traduit par une dynamique progressive induisant la fermeture par les fourrés puis le retour de la forêt en quelques dizaines d'années; mais les travaux de défrichement des ligneux peut en quelques années seulement (injection d'énergie) ramener l'état de la végétation à des pelouses de plus grande valeur patrimoniale, même si l'état initial n'est pas complètement atteint. Ainsi l'homme peut réduire l'hystérisis et accélérer la vitesse dynamique en injectant de l'énergie.

Inversement l'existence de cette hystérisis peut posséder une certaine valeur heuristique, en permettant une conservation assez longue, une mémoire, de l'histoire qui s'est déroulée sur un site; l'archéologie peut par exemple s'appuyer sur des végétations inattendues dans un contexte édaphique donné pour en déduire des occupations humaines anciennes, des sites anciennement anthropisés. Ainsi, une végétation basiphile en contexte normalement acide peut révéler une alcalinisation ancienne par apport de matériau calcaire, alcalinisation présentant une hystérisis suffisante pour être encore perceptible des dizaines, voir quelques centaines d'années après l'abandon du site par ses occupants (GHESTEM, 2002; GHESTEM et al., 2003). De même, une végétation eutrophile en contexte normalement oligotrophe peut révéler une activité humaine passée intense (villages, pastoralisme...). Ou encore, en phytosociologie, une dynamique inverse présentant une certaine hystérisis peut permettre la conservation de taxons de stades précédents, ces taxons autorisant dès lors l'acquisition d'informations sur ces stades par la méthode des orbites systémiques (DE FOUCault, 1993b).

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HEATHY PEATLAND WITH *ERICA CILIARIS* IN THE SOUTHWESTERN MEDITERRANEAN AREA

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With our best wishes dedicated to Prof. Jean-Marie Géhu, on the occasion of his 80th birthday. He contributed enormously to the knowledge of heath vegetation in Atlantic Europe. By organizing the meetings in Bailleul over many years he offered an interesting scientific forum for phytosociologists and a wonderful ambiance for his colleagues

ABSTRACT

Habitats with fens and brooks are very rare in the SW Mediterranean, but of high conservational value because they shelter the southernmost outliers of Atlantic phytogeographic elements. Field studies were undertaken in the Serra de Monchique in Southern Portugal and on both sides of the Straits of Gibraltar (the Campo de Gibraltar in Spain respectively the Tangier Peninsula in Morocco) and 27 phytosociological relevés from heathy peatlands are presented. They are discussed on the basis of a comparative constancy table in a broader geographical context, covering the whole distribution area of *Erica ciliaris*. Two figures illustrate the vegetation mosaic and the contact series. Heath vegetation on peaty soils in the study area belongs to an impoverished *Genisto anglicae-Ericetum ciliaris*, the central association of the *Genistion micranthae-anglicae*. The following subassociations and variants can be observed: 1) *pinguiculatum lusitanicae* on wet open peat soil, 2) *ditrichietosum viscosae* subass. nov. on sites degraded by strong grazing and trampling (more common in Morocco), 3) an intact variant with *Genista tridens* and *Stauracanthus boivinii*, restricted to the Campo de Gibraltar, 4) a variant with *Erica erigena* and 5) a variant with *Stemmacantha longifolia* and *Schoenus nigricans*, a transition to a fen community. The comparison of *Erica ciliaris* heaths in SW Iberia and NW Morocco with those in NW Spain, Brittany and SW England showed that heath vegetation on peat soils (*Genistion micranthae-anglicae* and *Ulicion minoris*) has a clear azonal character. The increasing summer drought from Cornwall to the Tangier Peninsula is compensated by a shift to edaphic wet conditions. The phytogeographic contrast between the Eurosiberian and the Mediterranean area is reflected by transgressive species from the surrounding matrix vegetation.

Area, *Genistion micranthae-anglicae*.

INTRODUCTION

Heathlands of the class *Calluno-Ulicetea*, dominated by evergreen dwarf shrubs of Ericaceae and Genisteae, colonize acidic soils along the Atlantic façade of temperate and mediterranean Europe (CROSS, 2003). In the temperate atlantic zone of Western Europe, the hotspot of floristic and ecological diversification is Brittany (see synopsis in BOTINEAU & GÉHU, 2005; GÉHU, 1975). In the Mediterranean bioclimate, they

have their centre of floristic diversity in the most humid northwestern part of the Iberian Peninsula and become floristically more and more impoverished towards the southern and the continental parts of Spain (DÍAZ GONZÁLEZ, 1998; LOIDI *et al.*, 2007).

Heathland vegetation can occur on drained soils as well as on soils with stagnant water and peat formation. In the Southwest Mediterranean area, the communities on drained soils belong to the *Ericion umbellatae*, respective the suballiance *Stauracanthenion boivinii*. These communities have been studied in detail and a large number of phytoso-



Fig. 1 - Distribution of *Erica ciliaris* (after ROSE *et al.* 1996, modified) and localities of studied heathy peatland communities (Numbers correspond to columns in Tab. 2).

ciological relevés is available (see LOIDI *et al.*, 2007; DÍAZ GONZÁLEZ, 1998 and RIVAS-MARTÍNEZ, 1979 for synoptic views).

Heathy peatland vegetation is less well known. Habitats with fens and brooks are very rare in Southern Portugal, SW Andalusia and NW Morocco. They cover only very small and isolated patches. First observations about the vegetation of mires with partly mineral soils and partly peat soils are recorded by ALLORGE & ALLORGE (1945) from the Campo de Gibraltar (Cádiz Province, Andalusia). These authors give a floristic list with fen species such as *Erica ciliaris*, *E. erigena*, *Anagallis tenella*, *A. crassifolia*, and *Pinguicula lusitanica*. For the highest and most humid part of the Serra de Monchique in the Algarve hinterland (Portugal), MALATO BELIZ (1982) documented with several relevés a species combination with *Erica ciliaris*, *Anagallis tenella*, *Pinguicula lusitanica* and *Juncus rugosus*. In Morocco, first floristic lists of fen vegetation have been published by SAUVAGE (1961) and DAHLGREN & LASSEN (1972). These authors mapped the southernmost outliers of atlantic and boreal phytogeographical elements in NW Morocco. They describe a strong decline from the Tangier area towards the south and the east.

Erica ciliaris and *E. tetralix* are the most characteristic Ericaceae of heathy peatland in atlantic Europe. *Erica ciliaris* is limited to the most oceanic part, ranging from Ireland and SW England over Brittany, Galicia and Portugal up to NW Morocco (Fig. 1). *Erica tetralix* is less restricted to the hyperoceanic climate. It occurs also in the interior of the Iberian Peninsula and in the Cantabrian Mountains and the Pyrenees. In France *Erica tetralix* replaces *E. ciliaris* farther to the east (see distribution maps for Calluno-Ulicetea-communities in BOTINEAU & GÉHU, 2005). *Erica ciliaris* is considered as character species, *Erica tetralix* as differential species of the alliance *Genistion micranthae-anglicae* (*Ulicetalia minoris*, *Calluno-Ulicetea*) (DÍAZ GONZÁLEZ, 1998). A first synopsis about the *Genistion micranthae-anglicae*-communities in the SW of the Iberian Peninsula is presented by NETO (1997).

Plant communities with *Erica ciliaris* have been recorded from the coastal area of the Alentejo (NETO *et al.*, 1996; NETO, 1997, 2002) and from the Portalegre area (CASTRO ANTUNES, 1994) in southern Portugal, from wet dune valleys in the Doñana National Park in SW Spain (RIVAS-MARTÍNEZ *et al.*, 1980),

and from the coastal area near Larache (QUEZEL *et al.*, 1988) and the Prerif Mountains (ROMO, 2009) on the Tangier Peninsula in Morocco.

The observations on both sides of the Straits of Gibraltar are fragmentary (but see DEIL, 1997a for the occurrence of *Erica ciliaris* in an *Anagallido-Juncion* turf). A first aim of this contribution is to present new data about heathy peatlands in the Campo de Gibraltar (Spain), the Tangier Peninsula (Morocco) and the Serra de Monchique in the Algarve Province (Portugal). The comparison of the relevés from both sides of the Straits of Gibraltar should show whether the floristic composition of *Erica ciliaris* heathland reflects the stronger anthropo-zoogenic impact and ruderalisation in Morocco in comparison to SW Andalusia, as has been observed for example in alluvial shrub communities (*Rubo-Nerietum oleandri*) (DEIL, 1997b).

These regional observations are discussed in a broader geographical context to see if there is a phytogeographic pattern along the climatic gradient from SW England to NW Morocco. The hypothesis is that heath communities on peat soils (here *Erica ciliaris*-vegetation respectively the *Genistion micranthae-anglicae*) have a clear azonal character and that the phytogeographic contrast between the Eurosiberian and the Mediterranean area is better reflected by the transgressive species from the surrounding matrix vegetation on drained soils. We include a few communities with *Erica tetralix* in our analysis and a community with *Erica andevalensis* on ultramafic soils in the Huelva province (Spain) (CABEZUDO *et al.*, 1989).

STUDY AREA

GEOLOGY, SOIL AND CLIMATE

The study areas are the peninsulas at both sides of the Straits of Gibraltar and the Serra de Monchique in the hinterland of the Algarve province in Southern Portugal. These three areas have some abiotic features in common: 1) acidic bedrock material and 2) a thermomediterranean subhumid pluviseasonal-oceanic bioclimate (according to the classification of Rivas-Martínez, see www.globalbioclimatics.org). Both factors are favourable for the development of heathy peatlands and for hydro-morphic (pseudogley) and podzolic soils. In SW Spain and NW Morocco, fens and bogs are often linked to the spring

horizon line between the Aljibe Sandstone and the underlying Aljibe Clay. Both are part of the Cretaceous Flysch series of the "Unidad de Gibraltar" (= Unité numidienne on the Moroccan side) (ANDRÉ, 1971; DIDON *et al.*, 1973). In the Serra de Monchique, peat accumulations can be found on the one hand in the Foia summit area over syenite as bedrock material and on the other hand in lower areas over grauwackes and flysch bedrock, often near springs with soaking water.

PHYTOGEOGRAPHY

The common traits in substrate, soil and bioclimate and a land bridge across the Straits of Gibraltar until the Pliocene result in a great floristic similarity (GALÁN DE MERA & VICENTE ORELANA, 1997). VALDÉS (1991) and DEIL & GALÁN DE MERA (2003) underline the floristic and vegetation similarities by setting up a Tingitano-Onubo-Algarvian phytogeographic province. This is part of the Atlantic-Ibero-Moroccan superprovince *sensu* PÉREZ LATORRE *et al.* (1996). This phytogeographic unit is more or less identical with the "Coastal Lusitan-Andalusian Province" *sensu* RIVAS-MARTÍNEZ *et al.* (2002a). The unit includes those parts of the Iberian Peninsula and of NW-Africa which have an atlantic-mediterranean precipitation regime (GAUSSSEN *et al.*, 1958). These climatic conditions offer a migration road for Atlantic and Eurosiberian floristic elements towards Northern Africa (SAUVAGE, 1961; DAHLGREN & LASSEN, 1972).

HUMAN IMPACT

The influence on the vegetation cover by man and his livestock is quite different on the European and African sides. In general, human land use and pasture pressure are high in Morocco and low in SW Spain (DEIL, 2003). The Serra de Monchique is in an intermediate position (KROHMER & DEIL, 2003).

METHODS

Phytosociological relevés were sampled and classified according to the Braun-Blanquet-method (BRAUN-BLANQUET, 1964). 18 relevés from *Erica ciliaris* heaths were sampled (but not yet published) in the context of other floristic and phytosociological studies in the Campo de Gibraltar (Spain) and the

Tab. 1 - (cont.).

Column number	1 2	3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8	1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	1 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2
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Country	P P	8 5 5 5 3 5 5 5 5 7 1 2 3 4 5 6	4 0 0 0 4 4 4 4 1	O O a 2 1 3 6 9 0 5 7 a a a a a a a a
CS <i>Cisto-Lavanduletea</i>	1 1	1 2 2 2 1 1 1 1 1 1 1 1 1 1 1 1	2 3 2 1 3 2 1 2 2	7 8 1 6 2 0 3 5 0 4 6 1 2 3 2 1 1 1
Cistus salvifolius	.	.	1 + 1 1 1	.
Cistus crispus
Halimium halimifolium multiflorum
Lavandula stoechas s.str.
Cistus monspeliensis
Ornithogalum broteroi
Cytinus hypocistis macranthus
Cistus ladanifer + +
CS <i>Quercetea ilicis</i>	.	.	1 1 + 1 + + + . + + +	2 2 2 1 1 1 1 1 .
Myrtus communis	.	.	. + . +	1 1 . . 1 . . .
Phillyrea angustifolia	.	.	. + +
Calicotome infesta intermedia	.	.	. + +
Sanguisorba minor magnolii	+ + . + +
Quercus suber	.	.	. + . . . + + . +
Quercus lusitanica	+ . . . + . + . .
Daphne gnidium
Smilax aspera	.	.	. +
Companions	.	.	2 3 . 1 2 2 + 2 . . 1
Pteridium aquilinum	.	.	. +	1 + . + 1 + . .
Carex depressa
Lotus parviflorus
Pulicaria odora	.	.	. +	+ 1 . 1 1 .
Stachys officinalis
Bellis sylvestris +
Anthoxanthum aristatum macranthum	.	.	. + 1 +
Scirpus cernuus	+
Isoetes histrix
Exaculum pusillum +
Pinus pinaster (planted)
Arium nodiflorum + 1
Carex laevigata	1 + 1

Further rare species: Col. 1: Gnaphalium luteo-album +; Cyperus longus +; Lythrum salicaria +; Col. 2: Osmunda regalis +; Juncus bulbosus +; Holcus lanatus +; Col. 4: Genista linifolia +; Carlina corymbosa +; Elaeoselinum foetidum +; Col. 5: Briza maxima +; Carex distans 1; Col. 6: Paspalum dilatatum 1; Juncus hybridus 1; Col. 7: Erica arborea +; Arbutus unedo 1; Col. 8: Juncus articulatus 1; Lobelia urens +; Andryala integrifolia +; Col. 10: Cyperus mundtii +; Col. 11: Myosotis welwitschii +; Col. 12: Ulex borgiae :+; Rubia peregrina longifolia +; Col. 13: Festuca baetica +; Klasea alcalae +; Col. 14: Hydrocotyle vulgaris +; Col. 15: Pistacia lentiscus +; Col. 19: Hyparrhenia podotricha +; Crepis tingitana 1; Col. 20: Chamaerops humilis +; Calamintha nepeta glandulosa +; Leontodon longirostris +; Juncus conglomeratus +; Col. 21: Juncus tenagelia +; Col. 23: Teucrium afrum rubriflorum +; Lithodora prostrata lusitanica +; Col. 25: Urginea maritima +; Col. 26: Tolpis barbata +; Festuca caerulescens +; Col. 27: Ranunculus paludosus +; Plantago coronopus +; Cynara humilis +; Moenchia octandra +; Tuberaria guttata +; Trifolium angustifolium +; Plantago bellardii +; Festuca triflora +.

Country: M = Morocco, P = Portugal, S = Spain

Tangier Peninsula by GALÁN DE MERA (1993) and DEIL (1997b), two relevés are from the Serra de Monchique in Southern Portugal (Tab. 1). 9 relevés already published in DEIL (1997a) are included in this table. They are from a locality in the Tangier area, close to the Straits of Gibraltar, and represent a heath rich variant of the *Stemmacantho ericeticola-Schoenetum nigricantis*.

For a comparison with heathy peatlands in other parts of Atlantic Europe, a number of tables documenting vegetation with *Erica ciliaris* and/or *E. tetralix* have been taken from the literature and are presented and discussed here in a constancy table (Tab. 2). The regional distribution should cover the whole range of *Erica ciliaris*. Ireland is not represented in our data set. For

France, only a small portion of the available data has been selected. The full data set for France is presented and classified in BOTINEAU & GÉHU (2005).

The nomenclature of the vascular plants follows TUTIN *et al.* (1964-1980), VALDÉS *et al.* (1987) and VALDÉS *et al.* (2002). The nomenclature of the syntaxa is according to DÍAZ GONZÁLEZ (1998) and RIVAS-MARTÍNEZ *et al.* (2002a, b).

RESULTS

SW IBERIAN AND NW MOROCCAN HEATHY PEATLANDS

Fens and bogs are rare habitats in the landscapes on both sides of the Straits of Gibraltar and they only cover very small surfaces, often only a few square meters in size. They are either linked to the above mentioned spring horizon line or they occur in shallow depressions over stagnant loamy soils or pseudogley, where peat has accumulated. The permanently wet central part of these depressions is covered by herbaceous perennial vegetation, mostly belonging to *Anagallido-Juncion*-communities. At the outer fringes, these bogs are colonised by shrubs with 50 to 70% cover and up to 1.5 m height. The dominant and frequent shrubs are *Erica ciliaris*, *E. scoparia*, *Calluna vulgaris*, *Genista* spp. and *Stauracanthus boivinii* (Tab. 1). The tufted grass *Molinia caerulea* ssp. *arundinacea* is a constant companion. The heathy peatlands can be classified as an impoverished *Genisto anglicae-Ericetum ciliaris* QUÉZEL et al. 1988. *Genista anglica* (in Morocco always as ssp. *ancistrocarpa* (RAYNAUD, 1979)) is restricted to the southern part of the Tangier Peninsula near Larache (Tab. 1, col. 3), where the association has been described, and to bogs in the Prérif Mountains (DAHLGREN & LASSEN, 1972). The species is absent in the Northern part of the Tangier Peninsula, in the Campo de Gibraltar and in the Serra de Monchique.

The following subassociations and geographic variants can be observed:

1. The subassociation *pinguiculetosum lusitanicae* on wet open peat soil (Tab. 1, col. 1-2, 14, and 16). *Ulex minor* is restricted to the samples from the Serra de Monchique (col. 1-2).
2. The subassociation *ditrichietosum viscosa* subass. nov. (Tab. 1, col. 3-8, typus relevé col. 5). This is a degraded subtype, more common in Morocco, due to strong grazing and trampling. Indicators for the ruderalization are *Ditrichia viscosa*, *Mentha pulegium*, *Panicum repens* and *Daucus carota*. Such disturbed bogs are rich in unspecified species.

3. A less disturbed variant with *Genista tridens* and *Stauracanthus boivinii* (Tab. 1, col. 13-18) is restricted to the Campo de Gibraltar.
4. A variant with *Erica erigena* (col. 9-11) was observed at several localities, always close to the Gibraltar Straits. *Erica erigena*, first recorded for North Africa by STEFANESCO & VILHENA (1968),

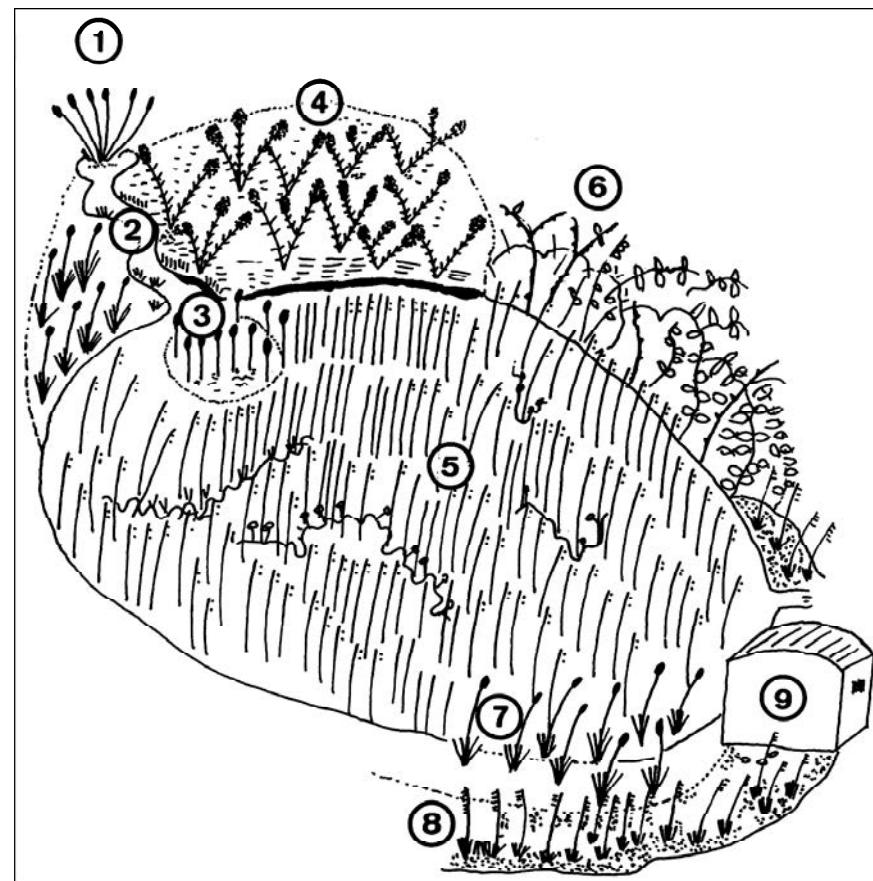


Fig. 2 - Vegetation mosaic at the Laguna Altos de Majada Escobar (Cádiz province, Spain). 1. *Lobelio urentis-Juncetum pedunculati schoenetosum nigricantis*; 2. *Anagallido tenellae-Juncetum bulbosi*, geographic race with *Anagallis crassifolia*; 3. *Glycerio declinatae-Eleocharitetum palustris*; 4. *Genisto anglicae-Ericetum ciliaris*; 5. *Juncus subnodulosus*-community; 6. *Lonicero hispanicae-Rubetum ulmifolii*; 7. *Lobelio-Lotetum pedunculati*, geographic race with *Juncus rugosus*; 8. *Gaudinio fragilis-Agrostietum castellanae*; 9. Water tank.

is in the study area always associated with the *Genisto-Ericetum ciliaris*. In other parts of its distribution area the species is linked to peaty soils and to *Molinio-Holoschoenion* fen vegetation like in the *Erico scopariae-ciliaris* in SW France (LAHONDÈRE & BIROUET, 1996). It is not strictly silicole, but can also grow on alkaline peat soils and is then associated with *Rosmarino-Ericion*-species (MANSANET et al., 1980). pH-analyses from the peat soils in the Gibraltar area however are not available at present.

5. The variant with *Stemmacantha longifolia*, *Euphorbia translagana* and *Romulea major* (col. 19-27) is a transition between a *Schoenus nigricans* fen and a heathy peatland.

VEGETATION MOSAICS AND CONTACT SERIES

Small-scale occurrence and short-distance transitions to other communities are peculiarities of the heathy peatlands (CABEZUDO et al., 1989). They are embedded into a fine-grained vegetation mosaic, triggered by soil water

content, depth of the peat layer and different inflammability and fire frequency. The small size of the *Erica ciliaris* patches is the reason for strong vicinity effects from the surrounding matrix vegetation. The short-distance transitions between *Anagallido-Juncion*, *Genistion micranthae-anglicae* and *Ericion umbellatae*-communities within a few meters of horizontal and several decimeters vertical distance result in introgressions between these units. This can be demonstrated by data sampling along transects. Such a transect is recorded by DEIL (1997a) from the Jebel Sanduc area near Meloussa (Tangier Peninsula, Morocco): *Erica ciliaris* occurs on the periodically moist fringe of a depression, situated between an *Erica umbellata*-heathland on the drained slope and the *Stemmacantho ericeticola-Schoenetum nigricantis* fen in the centre of the depression.

Two figures will illustrate the vegetation mosaic and the contact series around the *Genisto-Ericetum ciliaris*. Fig. 2 shows the vegetation mosaic at the Laguna Altos de Majada Escobar in the Aljibe Mountains (Cádiz Province, Spain), and Fig. 3 shows the catena

Tab. 2 - Heathy peatland communities along the Atlantic coast from Southern England to Northern Morocco.

Column number	1	2	3	4	5	6	7	8	9	0	1	1	1	1	1	1	1	1	1	2
Number of relevés	6	5	1	9	6	2	1	9	5	2	8	6	4	0	0	8	7	9	4	3
Region	S	M	S	M	M	S	P	P	M	P	I	F	F	E	E	S	S	S	S	S
CS Genisto-Ericetum ciliaris and Genistion micranthae-anglicae																				
Erica ciliaris	.	4	4	4	4	4	5	5	5	2	5	4	5	5	5
Genista anglica (incl. ancistrocarpa)	.	1	.	4	2	4	.	3	.	.	1	1	.	.	4	3	4	4	.	.
Genista micrantha	4	2	3	.	.	.
Erica lusitanica	2	4
Ulex minor lusitanicus	4	5	5
DS of associations, subassociations and variants																				
Erica andevalensis	4
Dittrichia viscosa (incl. revoluta)	.	5	1	4	3	1
Erica erigena	.	1	1	.	.	5	4
Stemmacantha longifolia ericeticola	.	.	4
Centaurea uliginosa	1	1	2
Cirsium welwitschii	2
Euphorbia uliginosa	4
Drosera intermedia	3
Pinguicula lusitanica	2	2	2	2	.
Cirsium grumosum	3
Serratula seoanei	2
Pseudarhenaterum longifolium	5
Carex asturica	1	2	.	.	2	.	.
Erica vagans	4
Genista hispanica occidentalis	1
Thymelaea dendryobryum	4
Genista carpetana	4
Myrica gale	3	4	3	.
CS Ulicetalia, Calluno-Ulicetea																				
Calluna vulgaris	.	4	1	4	1	2	4	5	1	2	.	3	3	3	5	4	4	4	4	.
Potentilla erecta	.	4	3	.	4	2	4	4	5	.	1	1	2	4	3	2	.	4	4	3
Agrostis curtissii	.	.	1	1	1	.	.	4	.	4	.	2	5	5	1	.	1	.	.	.
Danthonia decumbens	.	1	1	3	.	.	.	1	2	1	.	2	.	.	2	.	2	.	.	.
Erica scoparia	.	5	4	4	3	3	1	4	.	2	4	.	.
Erica umbellata	.	.	2	3
Erica cinerea	5	.	1	1	2	4	4	4
Genista triacanthos s.str.	.	5	2	.	1	2	4	.	1	1
Genista tridentata	.	.	1	1	3	1	.	.	.
Cistus psilosepalus	1	1	3	4	.	.	.
Stauracanthus boivinii	.	1	2	1
Avenula sulcata (incl. albinervis)	.	.	1	1	1	1	2
Pedicularis sylvatica lusitanica	.	.	1	1	.	1	1
Simethis planifolia	.	.	2	.	2	.	.	2	.	.	2
CS Ulicion minoris																				
Erica tetralix	4	1	4	2	.	1	4	4	3	.
Ulex minor s.str.	2	5	2	5	4
CS Nardo-Callunetea and elements of the Eurosiberian zone																				
Nardus stricta	1	4	4	.	.	
Carex pilulifera	3	1	1	1	.	.	.	
Gentiana pneumonanthe	1	.	.	.	2	1	.	.	.	
Ulex europaeus	1	3	1	
Ulex gallii	1	.	5	
Polygala serpyllifolia	1	.	3	
Hieracium pilosella	1	1	
Juncus squarrosum	2	4	.	.	.	

Tab. 2 - (cont.).

Tab. 2 - (cont.).

Column number	1	2	3	4	5	6	7	8	9	0	1	1	1	1	1	1	1	1	2	
Number of relevés	6	5	1	9	6	2	1	9	5	2	8	6	4	0	0	8	7	9	4	3
Region	S	M	S	M	M	S	P	P	M	P	I	F	F	E	E	S	S	S	S	S
Companions																				
Pteridium aquilinum	.	3	2	.	1	4	3	3	2	.	1	.	1	4	.	
Rubus ulmifolius	.	3	1	.	3	4	3	
Holcus grandiflorus	.	1	1	1	
Salix agg. Atrocinerea	1	2	2	
Osmunda regalis	.	.	.	2	.	.	3	1	
Briza minor	.	3	.	1	.	1	
Carex depressa	.	1	.	2	
Pulicaria odora	.	1	.	2	
Stachys officinalis	.	.	1	1	
Bellis sylvestris	.	.	1	1	
Scirpus cernuus	.	.	1	1	
Isoetes histrix	.	.	1	1	
Exaculum pusillum	.	1	.	1	
Apium nodiflorum	.	1	1	
Carex laevigata	.	.	1	2	
Galium palustre	1	.	2	
Frangula alnus	1	2	1	
Polygala vulgaris	5	1	
Lythrum salicaria	4	.	1	
Juncus bulbosus	3	.	1	3	
Quercus robur	2	2	
Hypericum pulchrum	1	.	1	.	1	
Teucrium scorodonia	1	.	1	
Hypnum cupressiforme s.l.	2	.	2	

Further rare species: Col. 1: Ulex eriocladus 1; Nerium oleander :1; Col. 2: Daucus carota s.str. 3; Anthoxanthum aristatum macranthum 3; Genista linifolia 1; Carlina corymbosa 1; Elaeoselinum foetidum 1; Briza maxima 1; Paspalum dilatatum 1; Juncus hybridus 1; Erica arborea 1; Arbutus unedo 1; Col. 3: Mentha suaveolens 1; Juncus articulatus 1; Andryala integrifolia 1; Cyperus mundtii 1; Myosotis welwitschii 1; Ulex borgiae 1; Rubia peregrina longifolia 1; Festuca baetica 1; Genista tridens 2; Klasea alcalae :1; Pistacia lentiscus 1; Col. 4: Ornithogalum broteroii 2; Lotus parviflorus 2; Euphorbia transtagana 1; Romulea major 1; Tuberaria lignosa 1; Linum bienne 1; Cistus crispus 3; Lavandula stoechas s.str. 1; Cistus monspeliensis 1; Sanguisorba minor magnoliifl 2; Juncus striatus 1; Pinus pinaster (planted) 1; Hyparrhenia podotricha 1; Crepis tingitana 1; Chamaerops humilis 1; Calamintha nepeta glandulosa 1; Leontodon longirostris 1; Juncus tenageia 1; Teucrium afrum rubriflorum 1; Lithodora prostrata lusitanica 1; Urginea maritima 1; Tolpis barbata 1; Festuca caerulescens 1; Ranunculus paludosus 1; Plantago coronopus 1; Cynara humilis 1; Moenchia octandra 1; Tuberaria guttata 1; Trifolium angustifolium 1; Plantago bellardii 1; Festuca triflora 1; Col. 5: Sphagnum sp. 1, Myosotis sicula 1; Col. 6: Cynodon dactylon 1; Scutellaria minor 1; Saccharum ravennae 1; Juncus maritimus 1; Iris pseudacorus 1; Col. 7: Cirsium vulgare 1; Rhynchospora rugosa 2; Phragmites australis 2; Arrhenatherum album 2; Cladium mariscus 1; Carex muricata lamprocarpa 1; Alisma plantago-aquatica 1; Carex paniculata lusitanica 1; Col. 8: Ulex australis 4; Drosophyllum lusitanicum 4; Lythrum portula 3; Lythrum tribracteatum 2; Oenanthe lachenalii 2; Stauracanthus genistoides 1; Dittichia graveolens 1; Cytisus striatus 1; Col. 9: Blechnum spicant 3; Oenanthe maroccana 2; Alnus glutinosa 2; Lotus hispidus 1; Col. 10: Gnaphalium luteo-album 1; Cyperus longus 1; Sibthorpia europaea 2; Col. 11: Daboezia cantabrica 1; Lithospermum diffusum s.str. 3; Hypericum linearifolium 1; Pyrus communis 1; Quercus pyrenaica 1; Physospermum aquilegiifolium 1; Col. 12: Cirsium filipendulum 2; Salix agg. aurita 1; Rubus sp. 1; Col. 13: Ulex minor x gallii 1; Scorzonera humilis 1; Carex pulicaris 1; Dicranum scoparium 1; Cladonia agg. furcata 1; Thuidium tamariscinum 1; Pyrus sp. 1; Castanea sativa 1; Sphagnum sp. 1; Betula verrucosa 1; Prunus spinosa 1; Rubus agg. discolor 1; Solidago virgaurea 1; Epilobium sp. 1; Dactylorhiza sp. 1; Viola agg. canina 1; Succisa praemorsa 1; Cirsium dissectum 1; Luzula multiflora 1; Cladonia agg. implexa 1; Salix agg. repens 1; Salix agg. cinerea 1; Cuscuta epithymum 2; Col. 14: Narthecium ossifragum 1; Rubus fruticosus agg. 1; Col. 15: Sphagnum subnitens 1; Cladonia portentosa 1; Col. 16: Cistus laurifolius 1; Thymus pulegioides 1; Luzula campestris 1; Brachypodium pinnatum 1; Galium pinetorum 1; Arenaria montana 1; Potentilla montana 3; Halimium umbellatum 1; Col. 17: Dianthus langeanus 1; Festuca iberica 2; Agrostis truncatula 3; Galium verum 1; Festuca indigesta 1; Plantago alpina 1; Teesdaliopsis conferta 1; Col. 18: Euphorbia polygalifolia 1; Deschampsia refracta 1; Carex binervis 1; Polytrichum attenuatum 1; Col. 19: Lotus pedunculatus 4; Carex vulpina 2; Scirpus pseudosetaceus 2; Cytisus scoparius 4; Narcissus pseudonarcissus 4; Col. 20: Carex nigra 2; Aulacomnium palustre 2; Sphagnum subsecundum rufescens 3.

Constancy classes: 1 = 1-20%, 2 = 21-40%, 3 = 41-60%, 4 = 61-80%, 5 = 81-100%

Regions: E = England; F = France; I = Iberia (Portugal and Spain); M = Morocco; P = Portugal; S = Spain.

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3. Genisto anglicae-Ericetum ciliaris (DEIL *et al.*, Tab. 1 this paper, col. 8-18). Campo de Gibraltar (Spain)
4. Stemmacantho ericeticolae-Schoenetum nigricantis (DEIL 1997a, Tab. 1pp). Tangérois (Morocco)

5. Genisto anglicae-Ericetum ciliaris (QUÉZEL *et al.*, 1988, Tab. 14). Tangérois (Morocco)
6. Erica ciliaris-Ulicetum lusitanici (RIVAS-MARTÍNEZ *et al.*, 1980, Tab. 60). Doñana-National Park, Huelva (Spain)
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8. Drosero intermediae-Ericetum ciliaris (CASTRO ANTUNES, 1994, Tab. 4). Portalegre (Portugal)
9. Genisto anglicae-Ericetum ciliaris pinguisetosum lusitanicae (ROMO, 2009, Tab. 5). Tangérois (Morocco)
10. Genisto-Ericetum pinguisetosum lusitanicae (DEIL *et al.*, Tab. 1 this paper, col. 1-2). Algarve (Portugal)
11. Cirsio filipenduli (grumosi)-Ericetum ciliaris (BRAUN-BLANQUET *et al.*, 1964). Serra do Gerês, Lugo (Portugal and Spain)
12. Ulici minoris-Ericetum tetricum (WATTEZ & GODEAU, 1986, Tab. 3). Région Guérandaise (France)
13. Ulici minoris-Ericetum ciliaris (WATTEZ & WATTEZ, 1995, Tab. 3). Brittany (France)
14. *Erica ciliaris* community; typical subass. with *Ulex minor*-*Agrostis curtisii* (RODWELL, 1991 H3 NVC in ROSE *et al.* 1996). Dorset (England)
15. *Erica ciliaris* community; *Erica tetralix* subtype (RODWELL, 1991 H4 NVC in ROSE *et al.*, 1996). Cornwall (England)
16. Genisto anglicae-Ericetum vagantis (RIVAS-MARTÍNEZ, 1979, Tab. 19). Burgos, Soria and Santander (Spain)
17. Thymelaeo dendrobryi-Genistetum carpetanae (RIVAS-MARTÍNEZ, 1979, Tab. 18). Zamora (Spain)
18. Genisto anglicae-Ericetum tetricum (RIVAS-MARTÍNEZ, 1979, Tab. 20). Santander and Zamora (Spain)
19. Erica tetricum-Myricetum gale (VELASCO NEGUERUELA, 1980, Tab. 1). Toledo (Spain)
20. *Erica tetralix*-*Myrica gale*-community (RIVAS GODAY, 1964: 470). Extremadura (Spain)

from wet peaty depressions and water courses to heathland and Cork Oak forests on drained Eocene sandstone on a coastal plain near Larache in Morocco. The *Genisto-Ericetum ciliaris* is towards the wet centre of the depression in contact with perennial rush meadows (*Anagallido-Juncetum bulbosi* when the water is stagnant, *Glycerio declinatae-Eleocharitetum palustris* and *Lobelio-Lotetum pedunculati schoenetosum nigrantis* when water is flowing or soaking). On the dry fringe Cork Oak forests of the *Myrto-Quercetum suberis*-type or its degradation stages (*Calicotomo-Genistetum lanuginosae*, *Genisto tridentis-Stauracanthetum boivinii*, *Drosophyllo-lusitanicae-Stauracanthetum boivinii* and *Erico umbellatae-Halimietum multiflori*) follow. A similar vegetation mosaic exists around the *Cirsio welwitschii-Ericetum ciliaris* in the littoral area of the Alentejo (Portugal) (see Fig. 13 in NETO, 2002).

Erica ciliaris heath can also be in contact with or embedded into a vegetation complex with *Rhododendron ponticum*, (*Rhododendro-Franguletem* in the Aljibe Mountains in Spain, *Campanulo primulifoliae-Rhododendretum* in the Serra de Monchique (Portugal) (MALATO BELIZ, 1982). In the Prerif Mountains of Morocco, *Erica ciliaris* occurs in mires (DAHLGREN & LASSEN, 1972), surrounded by mixed forest with *Quercus canariensis* and *Q. suber*, and in *Osmundo-Alnion*-riverine forests (ROMO, 2009).

HEATHY PEATLANDS IN A BROADER GEOGRAPHIC CONTEXT

On the basis of constancy Tab. 2, the *Erica ciliaris*-heathlands of the Serra de Monchique and the Gibraltar area are compared with similar communities in other parts of the Iberian Peninsula, and France and England. The localities of the vegetation samples and the bi-

bibliographic references are given in Fig. 1.

The data set demonstrates the azonal character of heathy peatland. A considerable number of species occur with high constancy from the perhumid climate zone of Southern England to the Mediterranean climate of Northern Morocco. They are character species of the *Genistion micrantho-anglicae* (first of all *Erica ciliaris* and *Genista anglica* (incl. ssp. *ancistrocarpa*) themselves) respectively of the *Ulicetalia* and *Calluno-Ulicetea* (*Calluna vulgaris*, *Potentilla erecta*, *Agrostis curtisii*, *Danthonia decumbens* a.o.). These species have their southernmost limits of distribution in peatlands in NW Morocco. The same azonal behaviours have some transgressives from mires with rushes (*Anagallido-Juncion* and *Holoschoenion*), which are often in contact with heathy peatland, such as *Anagallis tenella*, *Molinia caerulea* s.l., *Holcus lanatus*, and several perennial *Juncus*-species.

Other diagnostic taxa of the class *Calluno-Ulicetea* show a clear geographic pattern and react to this large-scale climatic gradient from Cornwall to the Tangier Peninsula. *Erica tetralix* and *Ulex minor* s.str. (character species of the *Ulicion minoris*), *Erica cinerea*, *Genista micrantha* and the *Daboecion*-species *Carex asturica* occur only in the central and northern part of the transect, whereas character species of the *Stauracanthenion boivinii* (*Stauracanthus boivinii*, *Genista triacanthos* s.str., *Ulex minor* ssp. *lusitanicus*, *Pedicularis sylvatica* ssp. *lusitanica* and *Erica lusitana*) are restricted to the SW Iberian Peninsula and NW Morocco. The latter taxa are elements of the Tingitano-Onubo-Algarvian phytogeographic province. This floristic differentiation is strengthened by three other species groups, which are transgressives from the surrounding matrix vegetation: The *Nardo-Callunetea*-species and Eurosiberian elements (*Nardus stricta* to *Juncus*

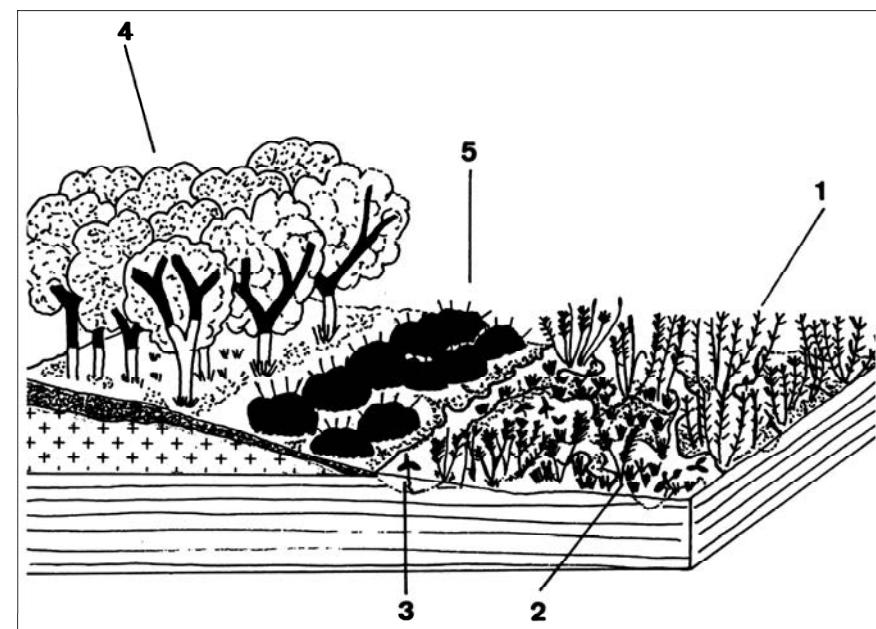


Fig. 3 - Wetland vegetation mosaic near Larache (Morocco). 1. *Genisto anglicae-Ericetum ciliaris*; 2. *Anagallido tenellae-Juncetum bulbosi*, geographic race with *Anagallis crassifolia*; 3. *Potamogeton polygonifolius*-community; 4. *Myrto communis-Quercetum suberis*; 5. *Erico umbellatae-Halimietum multiflori*.

squarrosum) on the one hand, occurring in our data set from NW Spain to England and the character species of the Mediterranean classes *Cisto-Lavanduletea* (*Cistus salvifolius* to *Cytinus hypocistis*) and *Quercetea ilicis* (*Myrtus communis* to *Erica australis*) on the other hand. They latter species occur in the heathy peatland habitat only in the southern part of the study area. The transition from the Atlantic-temperate to the Atlantic-Mediterranean climate is also reflected on the infraspecific level, for example by the shift from *Genista anglica* s.str. to *Genista anglica* ssp. *ancistrocarpa*.

The *Genisto anglicae* (*ancistrocarpa*)-*Ericetum ciliaris*, described by QUÉZEL *et al.* (1988) from the Sahel de Larache in Morocco (Tab. 2, col. 5), has the broadest distribution of the associations within the *Genistion micranthae-anglicae*. It is the central association (*sensu* DIERSCHKE, 1981) of this alliance. An edaphic subassociation on open turfs over wet peaty soil is the *Genisto-Ericetum pinguisetosum lusitanici*. It was recently described from the outer Rif Mountains in Morocco (ROMO, 2009, Tab. 2, col. 9), but is also known from the Serra de Monchique in Southern Portugal (MALATO BELIZ, 1982; DEIL *et al.*, this paper Tab. 1, col. 1-2, Tab. 2, col. 10,) and from the Campo de Gibraltar. There is a very similar ecology and species combination of this subassociation to the *Drosero intermediae-Ericetum ciliaris* (col. 8), described by CASTRO ANTUNES (1994) from the Northern Alentejo (Portugal).

The *Erica ciliaris*-stands on the Tangier Peninsula (col. 2) and in the Campo de Gibraltar (col. 3) can be considered as an impoverished variant of the *Genisto anglicae-Ericetum ciliaris* (*Genista anglica* is missing there). *Erica ciliaris* itself is transgressive into bog meadows of the *Anagallido-Junco*. A local variant, restricted to the Tangier Peninsula, is the *Stemmacantho ericeticola-Schoenetum nigricantis* (DEIL, 1997a) in a variant with *Erica ciliaris* (col. 4). The *Erico ciliaris-Ulicetum lusitanici* (RIVAS-MARTÍNEZ *et al.*, 1980), colonising wet dune valleys in the Coto de Doñana National Park (Huelva, Spain) (col. 6), is very similar to the *Genisto-Ericetum*. Somewhat isolated is the *Ulici eriocladi-Ericetum andevalensis* (= *Junco rugosi-Ericetum andevalensis ulicetosum eriocladi*) (col. 1). It is included by its authors into the *Genistion micrantho-anglicae*. This community, characterised by *Erica andevalensis*, a highly endemic species closely related to *Erica tetralix*, occurs

on soils with pyrite and heavy metal content on alluvial substrates in the Andevalo, a colline area north of Huelva (Spain) (CABEZUDO & RIVERA, 1980; CABEZUDO *et al.*, 1989).

Two further associations belong to the heathy peatland community group in the Atlantic part of the Iberian Peninsula: The *Cirsio welwitschii-Ericetum ciliaris* from the Sado area south of Lisbon (col. 7) (NETO *et al.*, 1996; NETO, 1997, 2002) and the *Cirsio grumosi-Ericetum ciliaris* (col. 11) (BRAUN-BLANQUET *et al.*, 1964) from the Serra de Gerês (Northern Portugal) and Lugo (Galicia, Spain). Both associations are characterised by stenochorous microspecies of otherwise widespread taxa: *Cirsium welwitschii* is closely related to *C. monspeliacum*, *C. grumosum* to *C. filipendulum*, and *Serratula seoanei* belongs to the *S. tinctoria*-aggregate. Comparable communities in the Cantabrian Mountains and their nomenclatural problems are discussed by LOIDI *et al.* (1996). The transitional character from the SW-Mediterranean community group to the NW-Iberian group at the border between northern Portugal and Galicia is reflected in the species composition of the *Cirsio grumosi-Ericetum ciliaris*, a mixture of *Genisto anglicae-Ericetum ciliaris*- and *Genisto anglicae-Ericetum vagantis*-species, enriched by local endemics (*Cirsium grumosum*, *Serratula seoanei*, *Pseudarrhenatherum longifolium*).

A selected number of relevés from NW France and SW England documents the floristic composition of heathy peatlands there (Tab. 2, col. 12 to 15) (for more data from NW France see BOTINEAU & GÉHU, 2005; GÉHU, 1975). This northern group includes the *Ulici minoris-Ericetum tetralicis* from the Lorient and the vicinity of Guerande (France) (WATTEZ & GODEAU, 1986) (col. 12), the *Ulici minoris-Ericetum ciliaris* from the Morbihan (Brittany) (WATTEZ & WATTEZ, 1995) (col. 13) and both *Erica ciliaris*-communities from Southern England (Dorset and Cornwall, col. 14 and 15) (RODWELL, 1991 in ROSE *et al.*, 1996). All these communities are very similar and can be arranged into the *Ulicion minoris* Malcuit 1929 (including the alliance *Ulici-Ericion ciliaris sensu* Géhu, 1975 and *sensu* RODWELL *et al.*, 2002) respectively the suballiance *Ericenion ciliaris-tetralicis* (BOTINEAU & GÉHU, 2005).

The heathy peatlands in the mountains of Northern Spain and in the continental parts of the Iberian Peninsula are more different (col. 16-20) (the same is true for heathlands on drained soils,

see LOIDI *et al.*, 2007). Strong Atlantic elements such as *Ulex* div. spec., *Centaura uliginosa*, *Euphorbia uliginosa* and *Erica ciliaris* are missing there. The following associations are known from the Cantabrian Mountains: *Genisto anglicae-Ericetum vagantis* (col. 16), recorded from Santander, Soria, and Burgos (RIVAS-MARTÍNEZ, 1979) (several subassociations in LOIDI *et al.*, 1996), the *Thymelaeo dendrobryi-Genistetum carpetanae* (col. 17) from the Province of Zamora (RIVAS-MARTÍNEZ, 1979) and the *Genisto anglicae-Ericetum tetralicis* (col. 18) from Zamora and Santander (RIVAS-MARTÍNEZ, 1979). They shelter endemics like *Genista micrantha*, *G. carpetana*, *G. hispanica* ssp. *occidentalis*, *Thymelaea dendrobryum*, *Euphorbia polygalphylla*, *Dianthus langeanus* and *Carex asturica*.

Erica tetralix-heaths with *Myrica gale* are recorded from the Montes de Toledo and the Extremadura in Central Spain (col. 19 and 20) (RIVAS GODAY, 1964; VELASCO-NEGUELU, 1980). The *Erico tetralicis-Myricetum gale* might also be interpreted as a historical relict form of the *Genisto anglicae-Ericetum tetralicis*. The holarctic element Sweet Gale (HULTEN & FRIES, 1986) is in Central Spain a relic from a pluvial epoch of the Holocene.

DISCUSSION

Habitats with fens and brooks are very rare in the SW Mediterranean, but of high conservational value because they shelter the southernmost outposts of Atlantic phytogeographic elements. They cover only very small and isolated patches and are therefore extremely sensitive to changes in climatic and hydrologic conditions. The field studies in the Serra de Monchique and on the peninsulas on both sides of the Straits of Gibraltar showed that intact stands of *Erica ciliaris* heathland still exist, but documented also a process of ruderalization by grazing and trampling, reflected in the floristic composition by the constant occurrence of *Dittrichia viscosa*, especially in Morocco.

The comparison of the southernmost *Erica ciliaris* heaths with those in Northern Spain, Brittany and SW England showed that heath communities on peat soils (*Erica ciliaris*-vegetation respectively the *Genistion micranthae-anglicae*) have a clear azonal character. The climatic gradient from SW England to NW Morocco and the phytogeographic contrast between the Eurosiberian and the Mediterranean area is

better reflected by the transgressive species from the surrounding matrix vegetation on drained, non-peaty soils. *Calluno-Ulicetea*-communities on mineral soils reflect the phytogeographic and bioclimatic pattern in Atlantic Europe and North Africa in the same way as the climax-vegetation (LOIDI *et al.*, 2007).

The increasing summer drought to the south from Cornwall to the Tangier Peninsula is compensated by *Erica ciliaris* and its associates by an increasing preference for edaphically wet environments. Such a shift in habitat preference was also noted by MOLINA & MORENO (1999) for *Oenanthe crocata*-communities in the gradient from Brittany to the Cadiz area in SW Andalusia. There is a stock of common species, but also a certain shift in the sociological behaviour (from *Agropyro-Rumicion* and *Filipendulion* in the Eurosiberian zone to *Glycerio-Sparganion* in the Mediterranean part).

LOCATION OF RELEVES

Tab. 1 - **1-2**: Dirty road between Cima-teira and Ribeira da Perna da Negra-valley, Serra de Monchique, Algarve (P); **3**: 20km north of Larache on the road to Tangier (M); **4-5**: Dehar Zirou, Tangier (M); **6**: Jebel Atba, Tangier (M); **7**: La Pena, Tarifa, Cádiz (S); **8-10**: Río Guadalmesí, Sierra de la Luna, Tarifa, Cádiz (S); **11**: Garganta de los Laureles, Alcalá de los Gazules, Cádiz (S); **12**: Sierra del Niño, Moheda del Muerto, Los Barrios, Cádiz (S); **13**: Hoya de los Calderos, Jerez de la Frontera, Cádiz (S); **14**: Altos de Majada Escobar, Alcalá de los Gazules, Cádiz (S); **15-18**: Cerro de las Callejuelas, Puerto de Gáliz, Jerez de la Frontera, Cádiz (S). **19-27**: Jebel Sanduc near Meloussa, Tangier (M).

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LESSONS FOR RESTORATION OF PROTECTED LANDS

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ABSTRACT

Primary succession requires amelioration, dispersal, establishment and development. Biotic interactions, landscape effects, changing safe-site qualities and chance all affect succession. Studies on many volcanoes (e.g. Etna, Fuji, St. Helens, Ksudach, Tarawera and Kilauea) reveal lessons to improve restoration of damaged habitats within protected areas. Successional trajectories develop at different rates due to stress and in alternative directions due to priority effects and dispersal limitations. Natural mosaics are the result. Recovery from major disturbances can be hastened by alleviating stress through appropriate fertilization, while taking care to avoid competitive effects. Even very short distances limit dispersal of most species, so managers must continually facilitate dispersal. Competition and herbivory can retard and deflect succession, so active management may be needed. Natural processes can produce several alternative, stable, but still natural, plant communities, so a mosaic of vegetation in protected natural areas should be encouraged. Monitoring through permanent plots is required to detect invasions by alien species and responses to climatic changes. The information from long-term monitoring has deepened the understanding of succession processes and can lead to more effective vegetation management.

KEYWORDS: Mount St. Helens, Plant dispersal, Primary succession, Volcanoes.

INTRODUCTION

Volcanoes occur throughout the world, at all latitudes and in most climates. They are concentrated on islands associated with spreading seafloors (Iceland; Rift Valley of Africa), where continental plates meet (the Sunda Arc near Indonesia; west coast of South America) and over geological hotspots (Galapagos Islands, Réunion, Yellowstone Park). Volcanoes are very diverse in

their environments. Mt. Etna, formed by the collision of Africa and Europe is in a Mediterranean climate (POLI MARCHESE & GRILLO, 2000). Mt. Kilauea, a young hot spot volcano is tropical at its base, alpine at its summit and supports rainforests and deserts (KITAYAMA *et al.*, 1995). Mt. Tarawera occurs in a populated warm temperate zone (CLARKSON & CLARKSON, 1995). Japan's Mt. Fuji reaches to permanent snows from a subtropical habitat (MASUZAWA, 1985) and is climbed by thousands of pilgrims each year. Mt. Ksudach, at the tip of the Kamchatka Peninsula is in a harsh, remote continental, sub-boreal zone (GRISHIN *et al.*, 1996) and is rarely visited. Mount St. Helens, in a cool temperate coniferous zone is the most studied volcano on the planet (DEL MORAL *et al.*, 2005). The biota of many volcanoes is protected by regulations, while others are protected by their isolation. Most have no legal or practical protection.

Volcanoes are important to biological complexity because they can provide refugia for many species, and their environments contrast with the surroundings. They also offer recreation and tourism values. Studies on many volcanoes have led to greater understanding of primary succession (cf. WALKER & DEL MORAL, 2003; DEL MORAL & WALKER, 2007), but more importantly, such studies are leading to greater understanding of restoration (WALKER *et al.*, 2006; DEL MORAL *et al.*, 2006). Without fundamental research into the

mechanisms of succession, restoration efforts will be inefficient and often unsuccessful.

This paper summarizes lessons learned during 26 years of study on Mount St. Helens. I will describe how some of these lessons can be applied to returning derelict lands to productive and efficient ecosystems.

SUCCESSIONAL MECHANISMS

The outline of primary succession mechanisms (Fig. 1) shows critical points, sometimes called bottlenecks, where community assembly may be delayed by natural processes or assisted by management efforts. Plant establishment after a major disturbance normally requires physical amelioration before colonizing seeds can survive. Nutrients may arrive as dust, pollen, non-viable seeds, excreta of passing birds or large animals and even in the form of insects and spiders who soon perish after descending into an inhospitable landscape. Erosion may remove unstable substrates to reveal suitable terrain, while cracks may develop to trap seeds. Such safe-sites are crucial in the early stages of community assembly.

Dispersal mechanisms continually feed the new landscape. At first, seeds are rare, and their main effect is to add nutrients to the substrate. The species pool is more limited than is usually appreciated (cf. DEL MORAL & ECKERT,

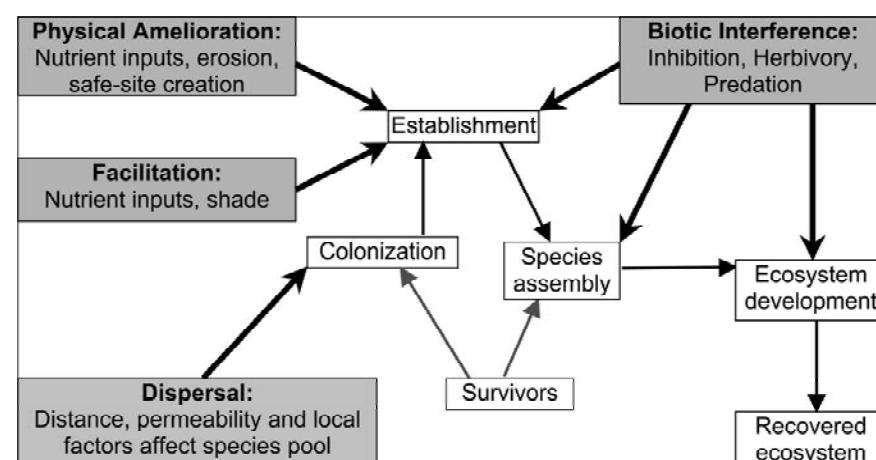


Fig. 1 - Mechanisms of primary succession, determined from studies on Mount St. Helens.

2004). A few tens of meters is sufficient to isolate a site from most invaders and distance alone leads to substantial heterogeneity in early communities because the seed rain is sparse and capricious (DEL MORAL & ELLIS, 2004). Landscapes differ in the degree to which they resist dispersal (called permeability). If favorable microsites dot the site, then dispersal will be more efficient (JONES & DEL MORAL, 2005). Wind direction, animal vectors and the local presence of species adapted to stressful conditions are among factors that affect dispersal rates and hence colonization.

In some sites, patches of survivors occur in refugia. On volcanoes, refugia occur on high ground that does not receive lava flows or on slopes protected from eruptive blasts. Survivors may contribute disproportionately to early colonization (FRANKLIN & MACMAHON, 2000), but this effect is restricted where surviving species are poorly adapted to the stressful conditions found after a major disturbance.

Once physical amelioration and dispersal have set the stage, seedlings can begin to establish. Survival may be enhanced by other species (facilitation), but the balance between positive and negative effects of neighbors is complex (WALKER, 1993; CALLAWAY & WALKER, 1997; BELLINGHAM *et al.*, 2001). Nutrient status, drought stress, plant density and substrate age are a few factors that determine this balance (DEL MORAL & ROZZELL, 2005). As the first colonists mature, they alter conditions so that additional colonists can estab-

lish. In addition, competitive inhibition, herbivory and seed predation (BISHOP, 2002) affect survivorship and the relative composition of the assembling community.

The rate of succession is normally determined by environmental stress (DEL MORAL, 2006), so even when the vegetation trajectory tends towards a stable equilibrium, a mosaic develops on the landscape. The mosaic represents the same community at different stages of successional development. On Mount St. Helens, permanent plots have recorded species composition changes on a ridge near the crater since 1984. Twenty plots are arrayed between 1218 and 1468 m. While the plots suffered the same devastation, differences in elevation and residual soils have led to different rates of development. DCA was applied to the matrix of plots by years and I aggregated the plots by their composition in 2005 into four categories that were strongly correlated with elevation. During the 22 years of development, individual plots developed through several associations. Early in the process, groups were sparse and poor in species. Through time, plots underwent transitions so that by 2005, they were in three groups, and seven groups were no longer present. Group H was the least developed and occurred at the highest elevations. Group I occurred in ten intermediate sites, while Group J, containing the best developed, most diverse plots was at the lowest elevations. DCA-1 scores are a good indicator of vegetation cover and composition. The mean

scores declined most rapidly in Group J, least in Group H (Fig. 2). A linear regression of plot age with DCA was significant in each case. The relationship was strongest in the two samples of Group I in which change was greatest. Group H changes only moderately, while most of the changes in Group J occurred by 1999. Other studies on Mount St. Helens have demonstrated similar differences in development rates based on environmental stress.

The mature vegetation that forms after major disturbances is often similar to that which once occupied the site, but this is not a requirement of succession. The degree to which there are survivors from before the disturbance may reduce initial variation and increases the similarities between pre- and post-disturbance vegetation. However, many factors can cause vegetation to form a stable community distinct from its surroundings and from earlier vegetation on the site (McCUNE & ALLEN, 1985). These factors include different available species pools (due to changes in surrounding land use, invasions by exotic species, etc.), changes in climate compared to the last establishment window, differences in the intensity of the initiating disturbance, patches of surviving plants, seeds or soil, and various stochastic factors. Development rates, trajectories and stable species composition after primary succession are less predictable than after secondary succession (TURNER & DALE, 1998). The main cause of this phenomenon is that surviving organisms are a signal from the previous community that conditions development and limits developmental options.

FACTORS THAT AFFECT TRAJECTORIES

On Mount St. Helens, similar sites have not necessarily developed towards similar composition (DEL MORAL & JONES, 2002). Two physically similar sites may retain dissimilar vegetation due to priority effects related to stochastic dispersal events, small differences in distance from colonists and subsequent unusual events that are not uniformly distributed on the landscape.

PRIORITY EFFECTS

To illustrate some of these processes, I selected data from a grid of contiguous 100 m² plots that have been sampled annually since 1989 (Fig. 3). The

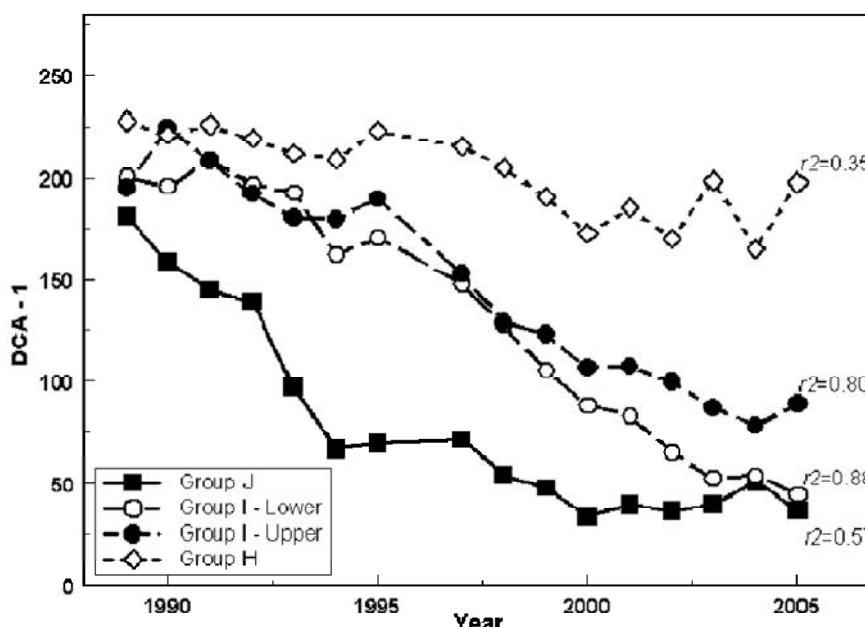


Fig. 2 - Changes in mean DCA-1 scores in four composite samples of vegetation on Studebaker Ridge, Mount St. Helens. Low elevation plots (J) changes most dramatically and stabilized by 2000; high elevation plots (H) changed little, and remain sparse. Intermediate plots (I, two samples) continue to develop; lower samples have progressed more quickly and may be converging with association J.

first five plots in each of 20 rows were analyzed in the years shown. Clearly, succession has occurred, as the strong decline in DCA-1 between 1989 and 2003; then, while DCA-1 changed little, DCA-2 increased strongly. There was a decline in standard deviations consistent with convergence from 1989 to 1995, but there was an increase in 1999 as mosses began to invade. The shift in DCA-2 was due to the unexpected crash of *Lupinus lepidus*. This was the result of an unusual climatic event and to the resumption of volcanic activity in late 2004 that has inhibited mosses. These unforeseen results also led to a reduction in the SD. These data illustrate that long-term monitoring is required and that stochastic geological and climatic events can influence the trajectory of recovering vegetation.

A particular site will develop in different directions if the first colonists differ. One indication of such effects comes from comparisons of lupine colonies with adjacent sites with only sparse lupines. The colonies were stratified by age, based on work by DEL MORAL & ROZZELL (2005), who compared structural differences in lupine colonies with the adjacent sites (Tab. 1). The data for one site were frequency determinations in 500 20 by 20 cm quadrats per site. Dominance (1 - Simpson's index) and diversity (H_p) were calculated from these data. To assess the effects on other species, calculations were also made after excluding lupines.

All sparse sites had significantly lower frequencies when lupines were included; but even excepting lupines, vegetation was denser in lupine colonies. Dominance was greater only in mature sites with lupines, while excluding lupines showed only stronger dominance in young, sparse sites. Diversity was greater in mature sparse sites when lupines were included. When lupines were excluded, diversity was greater in old and young colonies. These results demonstrate that the presence of lupines facilitates vegetation development and that this effect increases with age. However, the effect is complex because mosses are the major beneficiaries of lupine presence, and they tend to restrict the development of other species.

The effect of lupines clearly influenced vegetation trajectories (Fig. 4). Lupine colony composition changed with age, as did the adjacent sparse sites. Colonies differed moderately from adjacent sites, which is an effect that was due primarily to lupines, but also to changes in species composition among

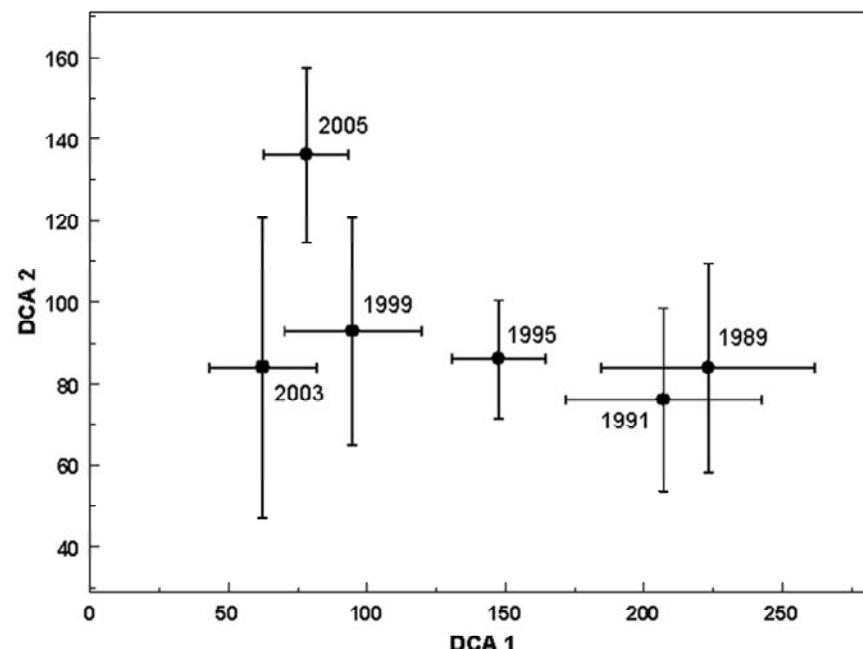


Fig. 3 - Changes in mean DCA ordination scores among contiguous plots on a sample grid, Mount St. Helens. Samples changed progressively from 1989 to 2003, then an unexpected, dramatic decline in the dominant species (*Lupinus lepidus*) resulted in a sharp deviation in the trajectory. Standard deviations remain large, indicating that convergence has not occurred.

the other species. Variation among the colonies was less than among sparse sites (note the very large SD in each set of sparse sites).

These and several other long-term studies on Mount St. Helens clearly demonstrate the importance of the species that first colonize a site. Pioneers alter the subsequent rules of establishment and affect the rate at which biomass and nutrients accumulate.

GRADIENT EFFECTS

The distance from a source of vegetation affects species composition. Based on an earlier study (FULLER & DEL MORAL, 2003), we showed that the effects of dense surviving vegetation attenuate sharply with distance (DEL MORAL & ECKERT, 2005). Beyond 8 m of surviving vegetation, there was little effect on percent cover or richness (Fig. 5) as both measures reached the background level. However, in that study, few surviving species were capable of invading the bare pumice, and the limited effect was due to pioneer species first establishing in the refugia, then dispersing copious seeds into the surroundings. The floristics changed significantly with distance from refugia, as demonstrated by DCA (Fig. 6). Sites adjacent to the refugia were diverse, but all occur on the right side of the graph, while those more distant occur scattered on the left side of the graph.

DEL MORAL & ELLIS (2004) also demonstrated the gradient effects of

distance in a different way. Four transects consisting of 100 m² plots were established at regular distances from the edge of intact vegetation on a large lahar deposited 23 years prior to the study. Transects were at increasing elevation, and thus each was more stressful than the previous. Species richness and plot cover declined with distance and with elevation. Heterogeneity (measured by percent similarity among 25 sub-samples and by standard deviations of these values) also declined significantly. Within plot similarity declined from 57.4% to 30% with elevation, while similarity between plots declined significantly (from 71.2% to 45.4%) and the SD doubled. There is no question that

Tab. 1 - Structural features within and outside of lupine patches established for over 20 years (Old), 12 to 15 years (Mature) and 5 to 10 years (Young). Data are shown for all species and without *Lupinus lepidus*. Frequency is the sum of individual percent frequency in the sample; dominance is the complement of Simpson's index and diversity is the Shannon-Wiener function.

Site	Frequency	Dominance	Diversity
All Species			
Old lupine patch	270	0.78	1.76
Old sparse site	159	0.75	1.78
Mature lupine patch	195	0.67	1.49
Mature sparse site	116	0.76	1.80
Young lupine patch	228	0.66	1.42
Young sparse site	137	0.64	1.34
No Lupines			
Old lupine patch	174	0.76	1.89
Old sparse site	121	0.70	1.67
Mature lupine patch	100	0.69	1.67
Mature sparse site	82	0.70	1.66
Young lupine patch	130	0.62	1.39
Young sparse site	87	0.50	1.14

distance alone contributes to landscape variation and to differences in successional trajectories.

UNUSUAL EVENTS

Superimposed on the effects of arrival order (priority) and landscape effects (gradually increasing isolation with disturbance size) are unpredictable and unique events. Studies by many individuals have demonstrated the wide array of these contingent events. They range from the date of the eruption at a time when much of this landscape was covered in snow and the unexplained

early arrival of *Lupinus lepidus* at a few severe, isolated sites within one year of the event. *Lupinus* has a large seed and is dispersed locally by explosive dehiscence and by ants, but the first seeds to establish on pyroclastic material crossed at least 4 km of inhospitable terrain. Many cases of unusual, even novel, and unforeseen joint occurrences of species rarely found together have been very common. The occurrence of *Lupinus latifolius* (a species of forest margins and lush meadows) with *L. lepidus*, a species of dry, subalpine habitats is most notable. These species continue to coexist at lower, drier elevations than either normally occupies and in expo-

sed habitats at higher elevations.

Most recently, an unusual climatic event occurred. Severe cold occurred above 900 m on Mount St. Helens before snow blanketed the terrain in 2004. Throughout its range, *Lupinus lepidus* (an herbaceous perennial) suffered nearly total dieback causing it to be sparse until mid-summer in 2005. The consequences of this event are still being investigated, but it appears that species suppressed by lupines expanded substantially.

LESSONS FROM LONG TERM STUDIES

THE VEGETATION MOSAIC IS NORMAL

Most mature vegetation exists as a variable mosaic. The mosaic is established early in primary succession by landscape factors that provide a heterogeneous propagule rain. Favorable microsites (safe-sites) are initially rare, so that colonization is not uniform, nor is it random. Spatial heterogeneity that affects levels of productivity and stress also contribute to the mosaic. Species composition varies and the rate of development is not synchronized on the terrain. A large suite of contingent factors enhances this mosaic. Subsequently, habitats become further differentiated by the actions of key species, of introduced herbivores and the nomadic behavior of herbivores such as elk. These large ungulates affect vegetation at Mount St. Helens in many ways, including, but not limited to, differential browsing, seed predation, internal and external seed predation, trampling, wallowing and creating safe-sites in their hoof prints.

Managers of protected landscapes should recognize that the mosaic is not only natural, but also desirable if biodiversity is to be preserved and augmented. A corollary is that there is rarely a single desirable stable end-point for vegetation. Multiple stable vegetation states have now been demonstrated in several habitats, and may well be the rule, not the exception.

DEL MORAL & LACHER (2005) reported on the vegetation pattern on Mount St. Helens after 23 years. It remains variable both between habitats and within habitats. There was substantial variation even within each of seven community types. The vegetation pattern was only loosely tied to environmental factors and these were all spatial. This result supports the hypothesis that at least during early succession, site

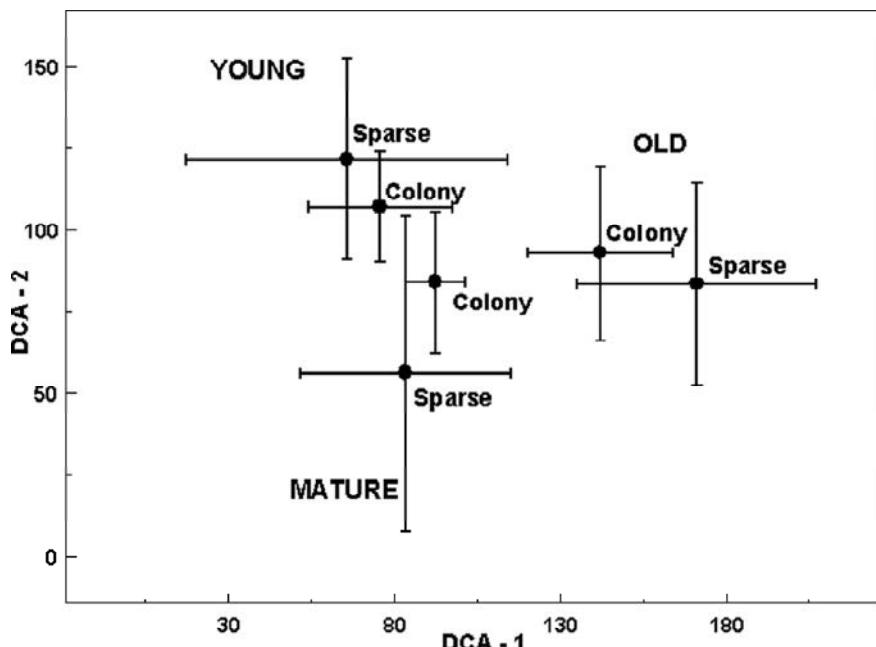


Fig. 4 - *Lupinus lepidus* affects trajectories both by the length of time it is present and by its density. Colonies and adjacent sparse sites differ strongly. Colonies are relatively similar, while adjacent sites differ from one other to a much greater degree. Sparse sites are much more variable.

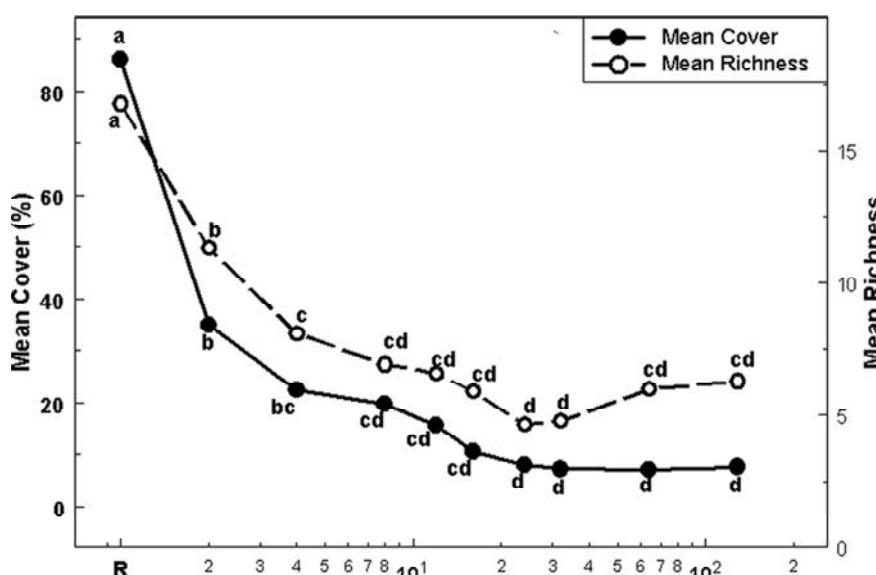


Fig. 5 - The effects of refugia on surrounding vegetation decline strongly with distance. Within 8 m of a dense colony of vegetation that survived the eruption, both cover and species richness reached a level similar to that at much larger distances. For each line, letters indicate membership in groups not distinguishable after analysis of variance, followed by a Bonferroni test.

location is the most important factor that determines species composition. Though it is too early to draw conclusions, there was no evidence that vegetation in similar habitats would converge to a relatively homogeneous state.

STRESS REDUCTION IS REQUIRED FOR INITIAL ESTABLISHMENT

Early in primary succession, nothing can occur until stress and infertility are reduced to levels where seedlings can establish. This process is initially dominated by physical processes (deposition of nutrients from outside the system, minor erosion) and usually includes a rain of such unlikely colonists as spiders. These predatory organisms soon perish, but add valuable carbon and nitrogen to the system. Restoration ecologists know that fertility must be managed for a successful outcome. However, as demonstrated where *Lupinus* achieves strong dominance, too much fertility can impede development and reduce diversity.

The conditions for establishment change as vegetation develops and the environment becomes less stressful. Where at first only a very few, particularly favorable, sites could support a successful seedling, a greater portion of the substrate becomes open to colonization as amelioration proceeds. As soon as plants establish and mature, the potential for biotic stresses to develop also increases. Not only do competitive interactions (see below) become prominent, but also herbivores begin to thrive (BISHOP, 2002), with complex implications for succession (FAGAN & BISHOP, 2000; FAGAN *et al.*, 2005). Long-term management of developing vegetation in protected areas must account for this fluctuating biotic environment.

COMPETITION AND FACILITATION OCCUR THROUGHOUT SUCCESSION

One standard concept of primary succession is that biological facilitation is crucial during the early stages and that competition is limited or balanced by other factors (KLANDERUB & TOTLAND, 2004). However, there is an increasing literature that indicates that competition is common in early succession and in stressful environments (FRANKS, 2003; TOTLAND *et al.*, 2004). The relative mix of positive and negative biotic forces changes space and time.

In the case of *Lupinus lepidus*, the accumulation of diversity and biomass

of other species may be retarded in dense patches, but promoted in adjacent sparse patches. Superimposed on this pattern is that of herbivory, which can be intense on the dense, vibrant margins of lupines, but restricted both in sparse populations and in dense, senescent colonies.

Herbivores can arrest succession by restricting facilitation effects. *Salix* spp. could develop moderately dense colonies on pumice at Mount St. Helens, but a stem borer kills most shrubs before they can produce significant facilitation for less stress-tolerant plant species. When variations in competition, facilitation and herbivory occur in both space and time, a vegetation mosaic is likely to develop and persist. A major challenge for maintaining vegetation in protected lands is to manage the biotic environment to preserve biodiversity and the vegetation mosaic.

MOSAICS PERSIST

Once formed, vegetation mosaics tend to persist through time. The effects of priority can be profound. On lahars at Mount St. Helens, mosaics have developed that appear to be stable. An open woodland consisting of several species of conifers has invaded where exposed rocks facilitated seedling establishment. The diversity of conifers, many of them already reproductive after less than 20 years, exceeds that in adjacent mature forests. Vegetation beneath the canopies is sparse and distinct from open surroundings. Where conifers have not become established, a carpet of *Raco-*

mitrium, punctuated by *Lupinus* and the prostrate shrub *Penstemon* dominate large areas. In addition, there are patches of *Populus* with a distinct understory, thickets of the nitrogen-fixing shrub *Alnus viridis* and large patches of *Arctostaphylos nevadensis* (related to *A. uva-ursi*) that cover many square meters. While some of these elements may not persist, they will alter the local course of succession. While the mosaic may or may not be permanent, it will be an important feature of the vegetation for centuries. It is neither reasonable nor desirable to suppress this heterogeneity in an attempt to hasten the development of "climax" vegetation.

Based on an exploration of montane meadows on 400 year-old lahars on Mount St. Helens, mosaics may indeed persist. Consider that conifers may invade and establish rapidly close to sources of seeds, but in many places, no seed source occurs. In these places, open meadows develop. Meadows can resist the invasion of conifers on Mount St. Helens because summers are dry and soils infertile. Conifer seeds arrive in small numbers and a few germinate. Seedlings have been noted to persist for a few years, but slow growth due to nitrogen deficient (GILL *et al.*, 2006) soils pre-dispose seedlings to death from the inevitable extreme drought. The meadows also become differentiated into patches dominated by grasses and those dominated by low woody shrubs.

MONITORING IS REQUIRED

A major lesson for proper manage-

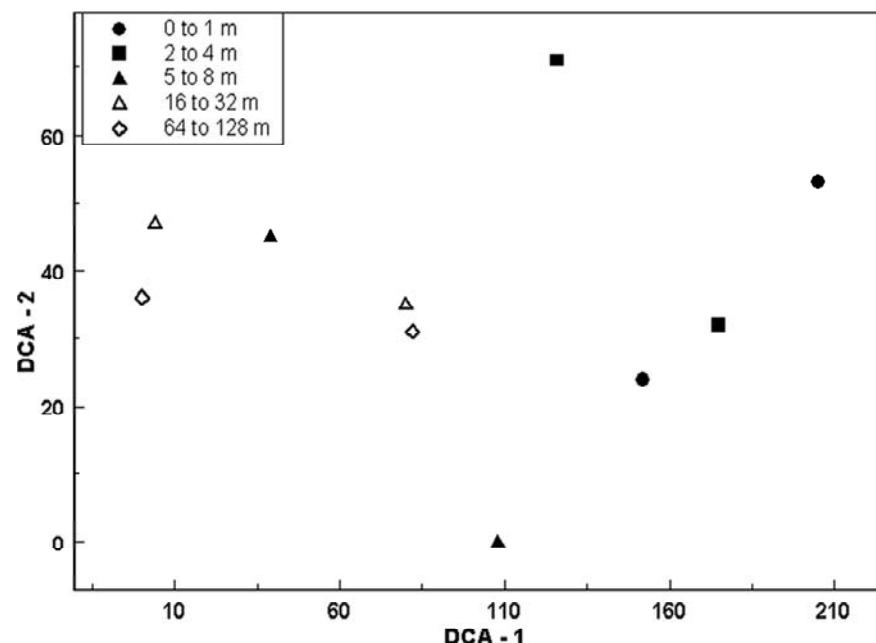


Fig. 6 - The composition of plots changed significantly with distance as shown by DCA of the mean composition. Sites 64 to 128 m distant share less than 50% of the species with those adjacent to the refugia.

ment of protected lands is that conditions must be continually monitored. Short-term fluctuations in climate, unusual disturbances (e.g., volcanic eruptions, insect plagues) can adversely affect vegetation. In some cases, remedial action may limit the damage. Monitoring can also provide crucial knowledge for restoration of damaged habitats and to curtail mechanisms that may generate undesirable deflection of succession trajectories.

Long-term monitoring also permits testing hypotheses. Short-term studies conducted under a particular set of conditions can lead to one conclusion. This conclusion may not be valid over the range of conditions to be expected over many years on a site. For example, it appeared that vegetation on a lahar at Mount St. Helens had reached a stage of very slow development and minimum heterogeneity after 20 years. However, subsequently (years 2002 and 2004 in Fig. 7), a major shift in the trajectory direction and sample heterogeneity occurred (cf. 1993 to 1999 with 2002 and 2004). In this case, an unexpected explosion in *Lupinus lepidus* in many, but not all, plots of the sample led to dramatic increases in biomass in several species. The result was dramatic. Had the study terminated in 1999, the conclusion would have been that a stable meadow community had been established and that further significant change would require the invasion of conifers.

A more important reason for monitoring is to be alerted to events triggered by global warming. Global climate

change associated with anthropogenic factors may lead to average temperature increases of 2-3 °C by 2100 (WESTOBY & BURGMAN, 2006). Such dramatic changes will require many species to migrate away from the pole or upwards (if possible). It is unlikely that species linked through facilitation, pollination or mycorrhizal association will be able to migrate at the same rates, so disruptions are inevitable. Monitoring may permit early warnings of impending disassociations so that intervention may occur. For example, species complexes could be translocated into more favorable habitats, after due considerations for rainfall patterns as well. The target species would require their associates (e.g. mycorrhizae, soil bacteria, pollinators) and would require assistance against competitors. While this is a daunting challenge, it would be impossible without long-term monitoring. The most effective method to preserve species in protected habitats is, however, not biological. Every social and political effort must be undertaken to reduce CO₂, dramatically... and soon.

CONCLUSION

The study of recovery from the effects of Mount St. Helens has many lessons for the restoration of damaged protected lands. Some lessons are cautionary, while others provide lessons for the kinds of proactive. Succession trajectories are unlikely to follow paths similar to those that previously occur-

red. Climatic factors are changing, landscape conditions differ, the biota may be different due to recent introductions and chance events may create unusual initial conditions. Thus, managers of protected lands should not attempt to force trajectories into predetermined, arbitrary paths.

Intrinsic habitat heterogeneity should be welcomed and preserved. This allows for variations in the vegetation that support biodiversity and offer a buffer to climate variation and change. Competition favors established plants, so the importance of arrival order cannot be overemphasized. The biotic variation imposed by strong competitors persists until life history events or disturbance permits transitions to other species (CONNELL & SLATYER, 1977). Initially sites are quite variable, with patterns dictated in large part by stochastic events (DEL MORAL, 1999). Eventually, deterministic processes lead to stronger relationships among species and between species and their environment. For example, in the early stages, many species can establish on a barren site, but after many years, only those that are more efficient under the developing regime can survive competition and herbivory. These processes result in associations that are more predictable, yet heterogeneity, once established, appears to persist.

Rehabilitation, restoration and protection of vegetation all require subtle and profound understanding of how communities assemble, where the bottlenecks occur and how trajectories can be modified to meet specific goals. Monitoring natural recovery from devastating disturbances has provided some of this understanding.

ACKNOWLEDGEMENTS

I thank Prof.ssa Emilia Poli Marchese for the kind invitation to participate in the Symposium on Ecology, Conservation and Management of Ecosystems in Protected Areas at the XVIIth International Congress, Vienna. I also thank the U.S. National Science Foundation for funding since 1981 and the University of Washington Graduate School for travel funds.

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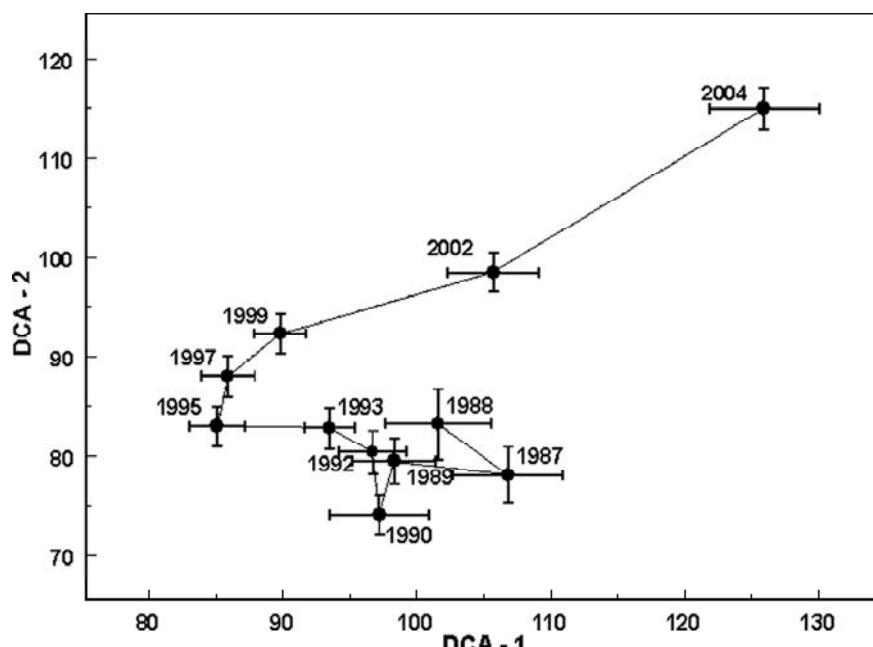


Fig. 7 - Long term monitoring can provide surprises. Repeat sampling of 64 plots on a lahar demonstrated moderate, consistent change from 1987 to 1999. Variation (standard error) decreased. However, the trajectory abruptly shifted direction and rate in 2002, and by 2004, variation was large. The years 2001 to 2004 saw more change than in all the previous changes.

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FLORISTIC CHANGE DURING EARLY PRIMARY SUCCESSION ON LAVA, MOUNT ETNA, SICILY

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ABSTRACT

We investigated the degree to which vegetation becomes more similar during primary succession and asked whether the age of a lava site alone determines species composition on otherwise similar sites or if site-specific factors are more important. The study was confined to lava flows found between 1,000 and 1,180 m on the south side of Mount Etna, Italy that formed from 1892 to 1169 or earlier. Ground layer cover was measured at 15 exposed sites and 12 sites under shrubs, using ten 1-m² quadrats in five plots at each site. Changes in species richness, cover, diversity, dominance, and similarity were only loosely related to lava age regardless of whether plots were exposed or in an understory. These measures did change predictably when compared to the degree of site development measured by vegetation cover. Analysis by nonmetric multidimensional scaling ordered vegetation by their degree of development, not along an age gradient. The presence of leguminous shrubs altered species composition and thus succession trajectories. Variable initial surface morphology, landscape factors, historical conditions, and random events have affected both species establishment rates and trajectories. Deterministic processes (e.g. competition) have not smothered the initial heterogeneity, nor have they after over 800 years forced understory development to a common terminus. Evidence for convergence (e.g. increased similarity within plots with increasing age) was obtained only if sites were arrayed by their developmental, not calendar, age. Thus, using developmental age may overcome some of the intrinsic pitfalls of the chronosequence approach when assessing vegetation dynamics.

KEYWORDS: chronosequence, convergence, primary succession, similarity, trajectory, volcanoes.

ABBREVIATIONS: ANOVA=analysis of variance; CV=coefficient of variation; DCA=detrended correspondence analy-

sis; GF=growth-form; GPS=global positioning system; HC=half-change; NMS=nonmetric multidimensional scaling; PS=percent similarity.

NOMENCLATURE: Pignatti (1982).

INTRODUCTION

The mechanisms that guide the assembly of species are complex (KEDDY, 1992; WALKER & DEL MORAL, 2003). During primary succession, landscape context and chance produce mosaics (DEL MORAL, 1998), whose variation declines over time (RYDIN & BORGEGÅRD, 1991; DEL MORAL & JONES, 2002). The relationship between composition and environmental factors usually strengthens to improve predictability (WILSON *et al.*, 1995). However, neither reduced heterogeneity nor stronger deterministic control of patterns ensures that trajectories will converge.

The traditional view of succession (CLEMENTS, 1916; BRAUN-BLANQUET, 1964; FACELLI & D'ANGELA, 1990) is that all trajectories converge to a single association. This view assumes that biotic interactions are intense and can override initial variations (MUELLER-DOMBOIS, 2000) and was demonstrated on Icelandic lavas by BJARNASON (1991). The alternative view is that mosaics persist due to priority effects and species traits (e.g. RAMENSKY, 1924; GLEASON, 1939; WHITTAKER, 1974; YOUNG *et al.*, 2001). This "assembly" view asserts that species accumulate and emphasizes contingency and priority (EGLER, 1954; DRAKE, 1990; DEL MORAL *et al.*, 1995; HONNAY *et al.*, 2001; DEL MORAL *et al.*, 2005). Multiple trajectories are common on glacier forelands (MATHEWS, 1992; FASTIE, 1995), slack dunes (ADEMA *et al.*, 2002), sand dunes (LICHTER, 2000), riparian sites (BAKER & Walford, 1995), disturbed forests (MC EUEN & CURRAN, 2004; SVENING & WRIGHT, 2005) and volcanoes (WHITTAKER & JONES, 1994; TAGAWA, 2005). There is a developing consensus, particularly among restoration ecologists, that community assembly is often stochastic and

can lead to alternative stable vegetation types (FATTORINI & HALLE, 2004; TEMPERTON & ZIRR, 2004; YOUNG *et al.* 2005).

Convergence can be recognized if sample similarity increases with age, but chronosequence methods may confound site and stochastic effects with effects due to age. Though chronosequence methods must be employed in long trajectories (DEL MORAL & GRISHIN, 1999), the underlying assumption that all sites were initially identical has rarely been tested. Here we explore the relationship between time and development on a small part of Mount Etna, Sicily to explore the relationship between age and vegetation development.

We sampled a ~832 yr chronosequence on lavas of Mount Etna to explore community assembly. Poli Marchese suggested (POLI, 1965, 1970, 1971; POLI & GRILLO, 1975; POLI *et al.*, 1995; POLI MARCHESE & GRILLO, 2000a) that convergence was likely at the plant-sociological class level after 1200 yr, but that rates varied with surface morphology, microclimate, and dispersal (cf. MAKANA & THOMAS, 2004). Poli Marchese has described how many early stages become a few shrub stages, and ultimately woodland associations in the class *Quercetea ilicis*.

We explored ground layer composition on substrates of different ages and contrasted variation in exposed sites with understory vegetation. We sought evidence for convergence by examining similarity changes along the chronosequence. Fundamental to the application of the chronosequence approach is that these assumptions are true: a) differences on the site are due solely to the age of the site; b) differences during establishment (e.g. weather patterns) are unimportant; c) landscape effects are minimal; and d) dispersal effects are similar at each stage. It is becoming clear that if these assumptions are not valid, the interpretations of succession can be in error (JACKSON *et al.*, 1988). Further, local substrate variation and constraints on plant growth can cause succession trajectories to develop at significantly different rates (ELLIS, 2004), compromising the use of

Tab. 1 - Site age, location and general vegetation. Date is the year of the documented flow. Coordinates are for the most distant sites.

Date	Elevation (m)	Latitude-N	Longitude-E	Vegetation Type
<i>Exposed Sites</i>				
1892	1010 to 1020	37°38' 48.3"	014°59' 57.4" to	Herb field-Stressed
		37°38' 49.4"	015°00' 03.9"	
1780	1130 to 1150	37°39' 33.6"	014°57' 55.8" to	Herb field
		37°39' 35.8"	014°58' 00.0"	
1636	1110 to 1160	37°39' 42.0"	015°01' 30.1" to	Herb field
		37°39' 49.8"	015°01' 34.5"	
1536A	1050 to 1075	37°39' 08.7"	014°58' 38.0" to	Herb field-interior of flow
		37°39' 15.0"	014°58' 43.5"	
1536B	1060 to 1065	37°39' 05.6"	014°58' 35.4" to	Herb field-edge of flow
		37°39' 09.4"	014°58' 37.9"	
<i>Shrub Sites</i>				
1886	990 to 1020	37°38' 47.7"	015°00' 11.6" to	Genista aetnensis
		37°38' 54.6"	015°00' 38.5"	
1766	1060	37°39' 24.3"	015°01' 12.4"	Genista & Spartium junceum
1636	1140 to 1170	37°39' 47.3"	015°01' 30.6" to	Genista & Spartium
		37°39' 51.1"	015°01' 36.2"	
1537	980 to 990	37°38' 48.3"	015°00' 42.9" to	Genista & Spartium
		37°38' 52.5"	015°00' 43.8"	
<1169	1050 to 1080	37°39' 05.6" to	014°58' 35.2" to	Quercus ilex
		37°39' 12.4"	014°58' 40.2"	

space-for-time substitutions.

METHODS

STUDY AREA

Mount Etna dominates north eastern Sicily. This volcano reaches 3350 m a.s.l. Chronic eruptions, from the summit and from many fissures, have occurred since A.D. 500. We conducted this study on its south slope between 1,000 and 1,180 m elevation during May 2001, the height of the growing season. Pastures, orchards, and quarries

affect this zone on very old substrates. Selected lavas date from 1169 (or earlier), 1536, 1537, 1634-1638, 1766, 1780, 1886, and 1892, and were largely free from such disturbances. Younger lavas (1910 and 1983) were common in the study area, but they lacked significant vascular plant vegetation. All sites were on *a'a* lava (POLI, 1970), which fractures to facilitate succession. The nearest weather station is in Nicolosi (698 m), where the mean annual precipitation of 111 cm, occurs primarily during autumn and winter. The mean temperature is 14.3 °C.

The vegetation samples were do-

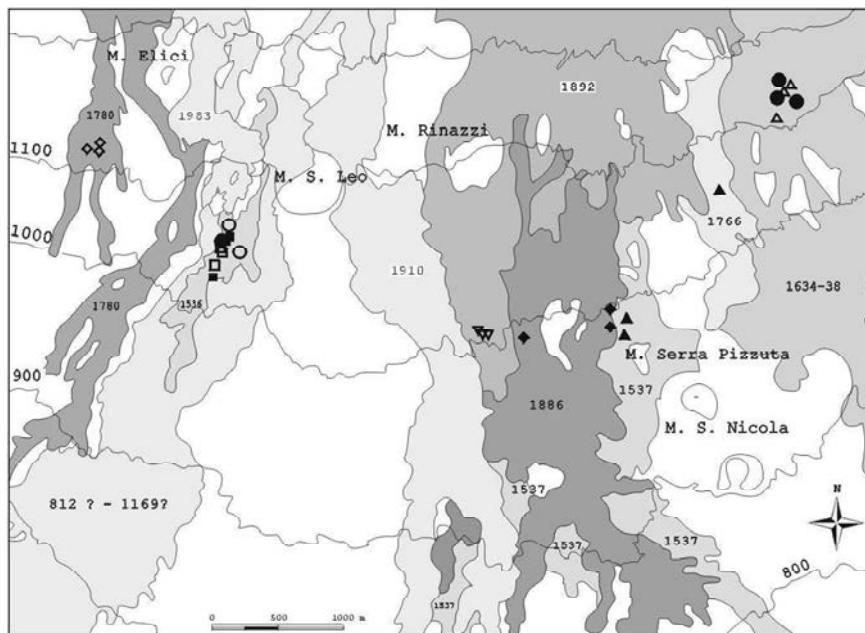


Fig. 1 - Locations of study sites. Key to symbols: ∇ =exposed-1892; \diamond =exposed-1780;
 \triangle =exposed-1636; \circ =exposed-1536A; \square =exposed-1536B; \blacklozenge =understory-1886;
 \blacktriangledown =understory-1766; \bullet =understory-1636; \blacktriangle =understory-1537; \blacksquare =understory-1196

minated either by tall shrubs, henceforth called shrub sites, or by ground layer species, henceforth called exposed sites (Tab. 1). Latitude and longitude were determined by GPS, and plotted on a topographic map, from which elevations were determined (Fig. 1).

There is a vegetation mosaic formed in response to lava age, surface morphology, microsites, and later disturbance (POLI MARCHESE & GRILLO, 2000b). *Stereocaulon vesuvianum* and other lichens and mosses colonized barren lavas that were formed since 1910. These species form soil that fills crevices and facilitate invading vascular plants. *Centranthus ruber* and *Rumex scutatus* are early vascular plant pioneers because they can establish in crevices.

The 1892 flow had a mosaic of cryptogams, with scattered annuals and perennial forbs confined to cracks. The 1886 flow supported a denser mosaic. The nitrogen-fixing shrubs *Genista aetnensis* and *Spartium junceum* had established sporadically. As these shrubs alter their surroundings, they may facilitate herb establishment. Lavas formed in 1780 were floristically similar to younger ones, with *Micromeria graeca* locally common. A flow deposited in 1766 sustained scattered *Genista* and *Spartium*. A complex array of flows was deposited from 1634 to 1638 (here termed "1636"). Diverse herbaceous vegetation was in close proximity to extensive areas dominated by *Genista* and *Spartium*. The 1537 flow extends beyond the 1886 flow, and shrubs dominated the sample plots. The 1536 flow, dominated by herbs, was in close proximity to vegetation dominated by *Quercus ilex* that had established on a flow from 1169 or earlier. Thus, after ~832 years, several distinct plant associations persist (POLI MARCHESI & GRILLO, 2000a), dominated by several deep-rooted species (cf. BORNKAMM, 1981) and annuals. Similar vegetation appeared to occupy lavas of quite different age.

SAMPLING METHOD

Nested sampling was used to partition variation and similarity at three scales (Tab. 2). The **site** was homogeneous with a known age and little disturbance. There were three **samples** per site, except that for understories, only one sample from 1766 and two samples from 1537 were obtained. Since there were few areas in the study area large enough to satisfy the selection criteria, sites were selected subjectively.

vely, but starting sample locations were determined by tossing a stake (i.e. it was haphazard). Samples of a site were separated by at least 50 m. Each sample had five **plots**, with four surrounding the initial plot within 10 to 30 m (determined randomly) at the four cardinal directions. The plant cover was estimated using ten 1-m² **quadrats** in each plot. Quadrats were divided into 25 squares to facilitate estimation. For exposed sites, quadrats were located in a predetermined pattern. Due to irregular and small shrub canopies, understories were sampled as follows. A shrub anchored a plot. One or two quadrats (0.5 by 2 m to fit under the canopy) were sampled. Understories were sampled in an expanding circle of shrubs until ten quadrats had been described. A second plot was established at least 30 m from the nearest sampled shrub. This procedure continued until five plots had been sampled. Sampling was based on shrubs, not microsite differences.

STATISTICAL METHODS

Sites were described using richness, the information theory [$H' = -\sum p_i \ln p_i$], and Simpson's Index complement [$D = 1 - \sum p_i^2$], each calculated at several scales. The mean number of species (richness) was determined for quadrats, plots, and samples.

We used nonmetric multiple dimensional scaling (NMS; MCCUNE & MEFFORD, 1999) to visualize relationships among plots and samples. Preliminary analysis showed both sets to be two-dimensional (cf. MCCUNE & GRACE, 2002). The final analysis was started from the best configuration, based on the least stress. Varimax rotation maximized the degree to which patterns were aligned with the axes.

Detrended correspondence analysis (DCA; MCCUNE & MEFFORD, 1999) was used to compare ground layer vegetation and to determine heterogeneity. The eigenvalues from DCA at each site and scale estimated overall variation. Species turnover (β diversity) along floristic gradients was estimated using half-changes in the floristic composition.

The relationships among quadrats of a plot, plots of a sample, and samples of a site were calculated by percent similarity ($PS = 200 \sum_{min}(X_{ik}, X_{jk}) / \sum(X_{ik} + X_{jk})$), where X = cover of species k in samples i, j). Calculations (KOVACH, 1999) used the percent cover (quadrats) or mean percent cover (plots and sample).

Tab. 2 - Sampling design.

Level	Sample Area	N	Total N	Selection criterion
Sites	Variable	10		Homogeneous; 950 to 1200 m
Exposed	Variable	5		Homogeneous; 950 to 1200 m
Understory	Variable	5		Homogeneous; 950 to 1200 m
Samples per site ¹	Variable; < 0.25 ha	3	27	Internally homogeneous
Plots/sample—exposed	about 300 m ²	5	75	10 - 50 m apart, random
Plots/sample—understory	< 0.10 ha	5	60	Clusters > 30 m from nearest plot
Quadrats/plot	1-m ²	10	1350	Fixed sampling position in plot

¹ Except 1 sample for 1766 understory and 2 samples for 1537 understory.

Structural features of plot vegetation were compared with one-way analysis of variance (ANOVA), followed by Bonferroni pair-wise comparisons of differences (ANALYTICAL SOFTWARE, 2000). Graphs were produced with Axum 7 (INSIGHTFUL CORPORATION, 2001).

RESULTS

Both exposed and understory vegetation occupied a chronosequence several centuries long. Exposed vegetation was sampled on sites initiated during episodes dated from 1536 to 1892. Understory vegetation was sampled on sites initiated from 1169 (or earlier) to 1886. Shrubs alter microclimate conditions to favor growth and development of a somewhat different suite of species than those that colonize bare lavas.

FLORISTICS

Therophytes (59%) and Hemicryptophytes (25.6%) dominated the sampled flora. The remaining vascular plants were Chamaephytes (7.7%), Geophytes (2.6%) and Phanerophytes (5.1%). Therophyte dominance results from the Mediterranean climate, the immature soil, and nearby human disturbances. Of the Therophytes, 20.5% were native xerophilous species common to exposed habitats (*Helianthemetea guttatae* class) and an additional 23.1% were ruderal-nitrophilous species (*Stellaria mediae* class) that spread on lava after human disturbances. The Hemicryptophytes and the Chamaephytes established in cracks on *a'a* lavas because they possess extensive root systems. Such species as *Rumex scutatus*, *Centranthus ruber*, and some N-fixing Phanerophytes (*Genista aetnensis* and *Spartium junceum*) are common the pioneers on Mount Etna, as are species of these plant functional types elsewhere (TSUYUZAKI, 1991). Once woody vegetation has established, forest species such as *Geranium robertianum* (*Quercio-Fagetea* class) can invade and domi-

nate. POLI MARCHESE & GRILLO (2000a) provided a detailed description of the successional dynamics of this vegetation and listed the life forms and community affiliations for each species.

Mean cover at ten sites is shown for species with > 1% cover in at least one plot (Tab. 3). *Rumex multifidus* dominated E1892 and E1536 sites, but was scarce in better-developed exposed lavas and also in the understory. *Bromus tectorum* was best developed in lavas with good vegetation development (Tab. 4). *Centranthus ruber* was common across all sites and ages, but was best developed on U1886, which has a rough surface to permit its establishment. This species and other perennials as *Rumex scutatus* form pockets of vegetation between blocks on the flow. Its absence beneath *Quercus* suggested that it can persist in a chronosequence until dense shade, deep tannin-rich litter and deeper soils are formed. Grasses, Asteraceae, annuals, and other small herbs dominated the lavas of E1780 and E1636. The lavas of E1536 were relatively barren, and were characterized by *Rumex multifidus*, *Isatis tinctoria*, and an assortment of annuals including *Aira cupaniana*. Species typical of exposed lavas were best developed in sites of intermediate age (1780 and 1636), but were sparse or absent from both younger and older lavas.

Understory vegetation was related floristically to adjacent exposed vegetation. Shrubs establish in cracks while the ground layer can establish on surfaces with or without cracks. As a result, the establishment of shrubs does not depend upon the establishment of herbs, so we should expect similarity between the understories and the exposed ground layers. However, the presence of shrubs clearly alters the microclimate, thus permitting species adapted to shade and more favorable conditions to expand at the expense of more stress-tolerant species. *Centranthus*, *Rumex scutatus*, *Isatis tinctoria*, *Geranium robertianum*, and grasses dominated site U1886. Many of these species were common on young, exposed lavas. *Bro-*

Tab. 3 - Mean cover of species with a mean cover > 1% in at least one plot. *Genista aetnensis*, *Spartium junceum* and *Quercus ilex* were excluded because canopies were uniformly high (80 to 99%). Species listed by in order of DCA Axis 1 (all plots). T=Therophytes; H=Hemicryptophytes, Ch=Chamaephytes, G=Geophytes, P=Phanerophyte. GF=growth-form.

Species	GF	Sample									
		Exposed Sites				Understory Sites					
		1892	1780	1636	1536A	1536B	1886	1766	1636	1537	1169
Taraxacum laevigatum	H	0	0.18	1.62	0	0	0.02	0	0	0	0
Petrorhagia velutina	T	0	0	1.31	0	0	0	0.02	0	0.03	0
Anthemis arvensis	T	0	0.28	15.2	0	0	0	0	1.79	0	0
Bromus tectorum	T	0.21	1.58	2.47	0	0	0	0	0.15	0	0
Hypochaeris glabra	T	0	0	4.09	0.01	0.02	0.03	0	1.02	0.62	0
Plantago bellardii	T	0	0	1.31	0	0	0	0	0.32	0	0
Trifolium arvense	T	0.67	1.24	12.00	0.01	1.17	0.01	0.02	0.25	3.48	0.42
Aira cupaniana	T	0.17	2.57	2.64	0.25	0.53	0.06	0	0.61	0.02	0
Vulpia ciliata	T	0.07	0	0.96	0	0.01	0	0	0	0.79	0.11
Rumex bucephalophorus	T	0	0.02	2.27	0	0.12	0.74	0.08	2.19	0.08	0.05
Centaura cyanus	T	0	0.73	0.09	0	0	0	0	0.06	0	0.12
Rumex multifidus	H	3.87	0.25	0.17	3.07	3.89	0.17	0.08	0.11	0.08	0
Poa bulbosa	H	2.36	1.23	2.04	0	0.81	0	0.52	4.19	3.78	0.70
Crupina crupinastrum	T	0	0.14	0.25	0.03	0.03	0.03	0.02	0.85	0.45	0
Rumex scutatus	H	0	3.80	0.67	0.08	0.01	4.19	0.72	0	0.62	0.07
Crepis leontodontoides	H	0.03	0.09	0.95	0	0	0.37	1.26	0.45	3.39	0
Centranthus ruber	Ch	7.2	2.69	1.06	0.81	3.27	12.1	0.02	1.45	3.20	0.12
Sedum rubens	T	1.15	0	0.42	0	0.06	0	0	0.06	0	0
Reichardia picroides	H	0	0.95	0	0	0	0.73	0	0	0.62	0
Biscutella didyma	T	0	0.11	0.03	0	0.01	0	0	0.61	0.98	0
Carlina corymbosa	H	0	0	0.29	0	0.01	0.29	0	0.35	2.17	0
Isatis tinctoria	H	0.97	1.55	0.47	0.18	0.86	6.45	7.0	9.00	4.33	0
Avena barbata	T	0	0.08	0.17	0.01	0	0.69	0.72	0.39	0.81	0
Bromus madritensis	T	0.45	2.15	1.32	0.09	2.3	15.5	27.3	4.73	6.83	0.01
Sedum tenuifolium	Ch	0.33	0	1.39	0	1.10	0	1.82	2.67	5.76	0
Vicia pseudocracca	T	0	0	0.03	0	0	0	0	0.96	1.71	0.17
Tragopogon crocifolius	H	0	0	0.03	0	0	0.08	0.26	0	1.05	0
Leopoldia comosa	G	0.02	0	0	0	0	0	0.14	0.10	0.78	0.13
Silene gallica	T	0	0	0.03	0	0.01	0	0	0.57	4.38	0
Briza maxima	T	0.04	0.40	0	0.02	0.02	3.41	4.64	0.01	5.78	0
Daucus carota	H	0	0	0	0	0	0.56	0.28	0	0.93	0
Cerastium semidecandrum	T	0	0.17	2.73	0.05	0.27	0.15	3.76	0.69	0.65	0
Cynosurus echinatus	T	0	0.03	0.03	0	0	0.65	3.20	0	2.74	0
Galium aparine	T	0	0.11	0	0	0	0	6.48	1.15	3.69	0.62
Geranium robertianum	T	0	0	0	0	0	17.37	13.7	2.47	9.94	2.80
Geranium molle	T	0.01	0.02	0.41	0	0.01	0.02	0	0.01	0	2.06
Rubia peregrina	P	0	0.07	0	0.15	0	0	0	0	0	2.71
Micromeria graeca	Ch	0	0	0.02	0	0.07	0.89	0	4.05	3.69	13.8
Hedera helix	P	0	0	0	0	0	0	0	0	0	2.83

Tab. 4 - Richness and cover in ground layer communities. All quadrats are included in calculations, even those without vascular plants. Date is the year of the lava flow; N is the number of quadrats with vascular plants of 150 sampled; parentheses give the size of the sample unit. There were five plots per sample of a site.

Site	Date	N	Richness (species per unit)			Cover (%)	
			Quadrat (m ²)	Plot (300m ²)	Sample (< 1 ha)	Site (~3 ha)	Plots (300 m ²)
Exposed	1892	107	1.0 ^a	6.5 ^a	12.3 ^a	19	5.8 ^a
	1780	135	5.8 ^e	17.6 ^c	24.7 ^{ab}	35	27.9 ^c
	1636	150	13.0 ^d	26.1 ^d	37.7 ^b	49	62.2 ^d
	1536A	113	2.3 ^b	13.5 ^{bc}	22.7 ^a	31	17.9 ^b
	1536B	115	2.2 ^b	10.4 ^b	16.7 ^a	31	18.7 ^b
Understory	1886	150	7.0 ^b	13.8 ^b	21.0 ^b	34	76.0 ^c
	1766	50	9.7 ^e	17.6 ^{bc}	28 ^b	28	77.7 ^c
	1636	150	9.8 ^c	19.8 ^c	34.7 ^b	52	57.1 ^b
	1537	100	14.8 ^d	24.3 ^d	35.5 ^b	43	75.1 ^c
	1169	75	2.7 ^a	5.5 ^a	12.3 ^a	23	16.2 ^a

Note: exposed and understory values were analyzed separately; superscripts indicate common membership in groups determined after significant ANOVA ($P<0.01$) by Bonferroni tests ($P<0.05$).

mus madritensis, *Geranium robertianum*, *Briza maxima*, *Isatis*, *Cerastium semidecandrum*, *Crepis leontodontoides*, and *Galium aparine* dominated U1766. U1636 was diverse, and contained *Centranthus*, *R. bucephalophorus*,

Isatis, *Poa bulbosa*, *Sedum tenuifolium*, *Geranium robertianum*, and *Micromeria*, a species common in all older understories. U1537, which was located on a flow that was partially covered by the lava of 1886, had a sparse canopy, with grasses, *Centranthus*, *Isatis*, several common forbs such as *Crepis leontodontoides*, *Sedum tenuifolium*, *Silene gallica*, *Galium aparine*, and *Geranium robertianum*. This composition suggested some disturbance and little suppression by shade. The vegetation under *Quercus* (U1169) was distinct from the other sites and included species from the class *Querco-Fagetea* such as *Hedera helix*, *Geranium molle*, *G. robertianum*, and scattered legumes. Common native species included *Micromeria* and *Rubia peregrina*, a species from the class *Quercetea ilicis*.

STRUCTURE

Plots were analyzed by linear regression of plot age with the structural feature in question: species richness, percent cover, information theory diversity (H'), and the reciprocal of Simpson's index (D). Patterns in richness were similar at each scale, so only plot values were analyzed by regression. Site richness (total number of species) was not linearly related to age in either exposed or understory plots (Tab. 4). Richness peaked in the intermediate site (1636) and was lower in younger and older sites. The pattern was similar in understory sites. Understories were richer in species in young sites, and in lavas from 1537, but low beneath *Quercus* (1169). There were significant differences between substrates at each scale, but the differences were not related to substrate age. Plot richness displayed a strong quadratic relationship to age ($r^2 = 0.64$; $P < 0.0001$). There were twice as many species per plot in samples that were 100 years younger. Richness beneath the sparse crowns of *Genista* and *Spartium* increased significantly with age at each scale. If *Quercus* samples are excluded, there is a significant linear increase in plot richness with age ($r^2 = 0.65$; $P < 0.0001$). The relationship including *Quercus* is quadratic ($r^2 = 0.76$; $P < 0.0001$). *Quercus* samples had low richness at each scale and were floristically distinct from other communities (Tab. 3).

Vegetation cover in exposed sites was not linearly related to site age (Tab. 4). Percent cover demonstrated a significant quadratic relationship ($r^2 = 0.61$; $P < 0.0001$). Cover of the understories

was similar to each other, except for those beneath *Quercus*, which date from 1169 or earlier. The quadratic relationship among all understory cover was strong ($r^2 = 0.72$; $P < 0.0001$), but excluding 1169 lavas eliminated any significant relationship.

H' changed significantly on both exposed and understory plots at each scale (Fig. 2). Quadrats of E1892 had significantly lower H' than most older sites because many quadrats had only one species. The highest H' values on exposed lavas at each scale were deposited in 1780 and in 1636. The lowest H' was on E1536, perhaps due to adverse surface conditions. Only the quadratic regression was significant ($r^2 = 0.59$; $P < 0.0001$). Understory H' increased with age ($r^2 = 0.29$; $P < 0.0001$), but the dense canopy of the 1169 plots reduced H' dramatically.

Dominance changed significantly in both exposed and understory vegetation (Fig. 3). At the quadrat level, exposed sites increased in D between 1892 and 1636, but the 1536 samples were less diverse. At the plot level, exposed lavas differed significantly, but the linear regression was poor ($r^2 = 0.08$; $P < 0.02$). The quadratic relationship predicted D based on age to a much greater degree ($r^2 = 0.34$; $P < 0.0001$) demonstrating that structural changes are not related primarily to lava age. The understories were relatively similar, but the quadratic regression was significant ($r^2 = 0.57$; $P < 0.0001$). When *Quercus* plots were excluded, there was a linear relationship of D with age ($r^2 = 0.45$; $P < 0.0001$).

COMMUNITY PATTERNS-NMS

The 24 samples (*Quercus* samples excluded) were analyzed by NMS to clarify the floristic pattern. Samples were composed of the mean of 50 quadrats (10 in 5 plots). The observed stress of 9.7 (instability < 0.06) provided a useable analysis.

The floristic pattern on exposed samples was poorly related to site age (NMS-2; Fig. 4). The pattern was significantly different from random and any inferences would be robust (stress < 9.5 instability < 0.07). Exposed plots were distinct from understory plots. The floristic gradient, which describes patterns of accumulating species richness and cover, is not correlated to substrate age for either exposed or understory plots. Within each group, there was a correlation between the ordination and the degree of plot development.

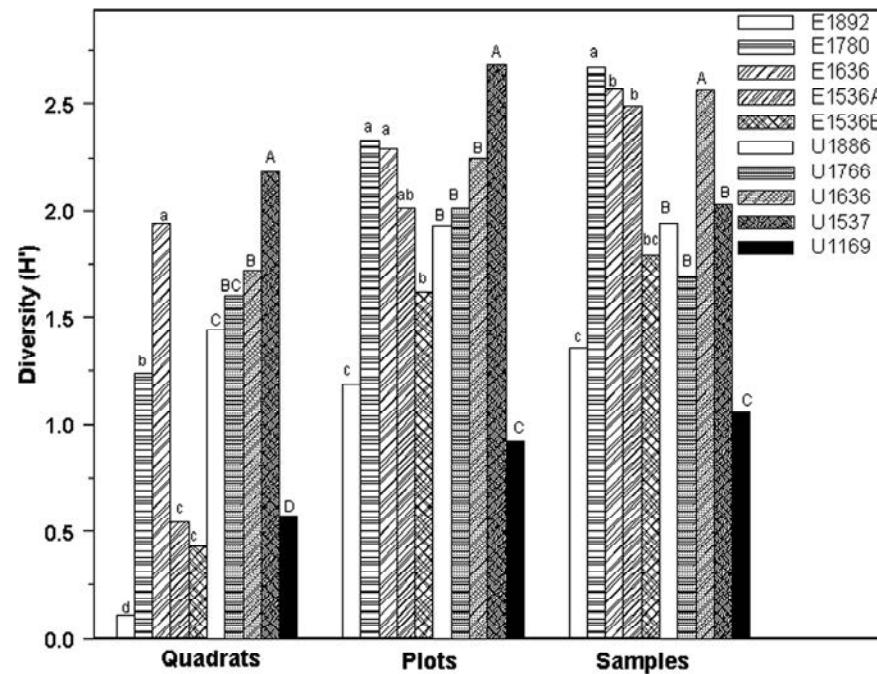


Fig. 2 - Vegetation diversity (H') on nine young lava sites. "Quadrats" is the mean value for each quadrat (from 75 to 150) at a site; "plots" are the mean value for plots at a site; "sample" the mean value for each sample at a site. Values were analyzed by one-way ANOVA, with exposed and understory vegetation analyzed separately. At each level, letters over the bars indicate group membership as determined by Bonferroni comparisons ($P < 0.05$).

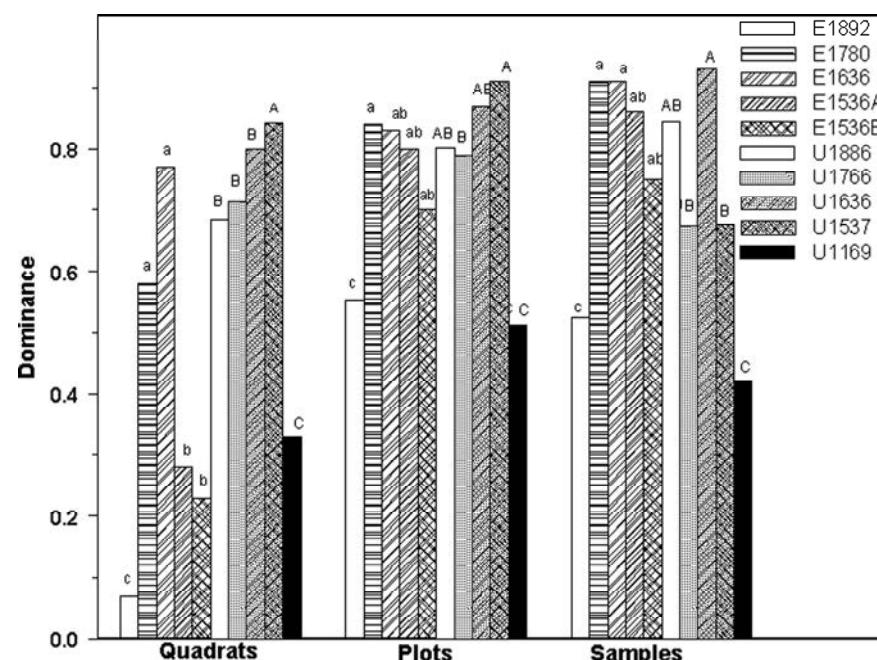


Fig. 3 - The complement of Simpson's index (D) on nine young lava sites. Analysis described in Fig. 2.

TURNOVER

Turnover is the floristic variation between samples and is termed β -diversity. We examined turnover at the plot scale with DCA because this method artfully measures floristic variation. Turnover was estimated by half-changes (HC) in DCA scores of the ordination (Tab. 5) when 120 plots were analyzed (excluding U1169). If sites were more homogeneous with age, then turnover should be reduced with time, and

the variation among plots of a sample, measured by standard deviations of the DCA scores, should decline.

The first DCA axis revealed no trends of HC with age or between exposed and understory plots. Understory plots also showed little pattern. Here, turnover was influenced by factors other than age, in particular the surface morphology. If sites were arranged by the degree of vegetation development, then exposed sites demonstrated a decline in variation with time.

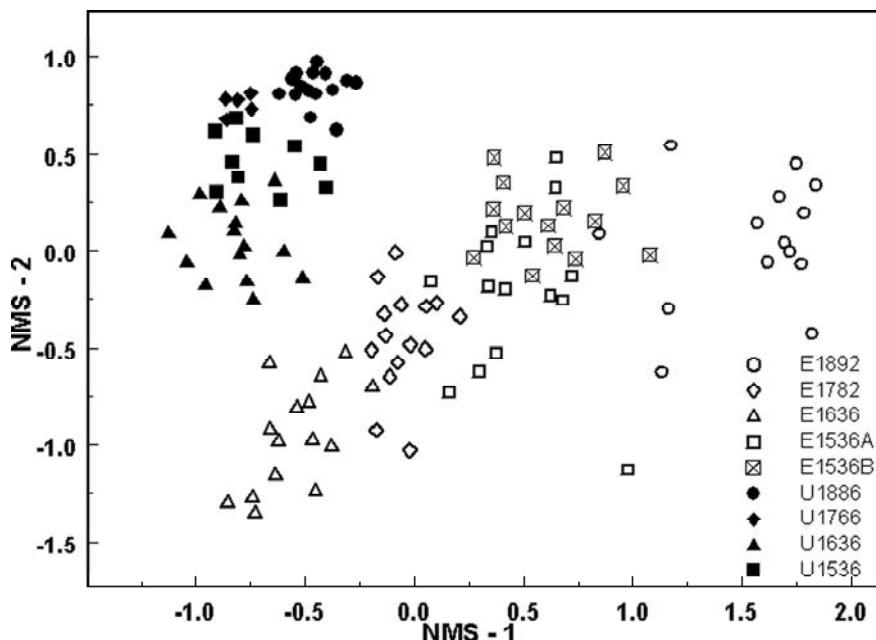


Fig. 4 - Nonmetric multidimensional scaling (NMS) ordination of 120 plots from 8 sites. U 1169 was excluded because it was too distinctive.

Tab. 5 - Turnover (HC) in ground layer vegetation and the variation in DCA scores when plots were examined in a single data set (U1169 excluded). SD is the variation of the sample DCA scores of the site.

Site	Half-Change (HC)		Variation (SD)	
	DCA - 1	DCA - 2	DCA - 1	DCA - 2
Exposed (N=15)				
1892	0.47	1.21	15.7	41.9
1780	1.44	0.58	32.3	17.5
1636	1.17	0.62	36.2	15.0
1536A	1.26	1.30	37.8	32.9
1536B	0.68	0.94	17.1	30.6
Understory				
1886	0.99	0.58	28.8	18.4
1766	0.31	0.31	11.9	11.6
1636	0.91	1.11	31.1	30.6
1537	1.15	0.47	39.8	14.7

Tab. 6 - Turnover estimated by floristic similarity among understory and among exposed samples.

	Similarity (%)			
Exposed Sites →	E 1892	E 1780	E 1636	E 1536A
Exposed Sites ↓				
E 1780	11.8 ^{ab}	—		
E 1636	3.6 ^a	31.0 ^{cd}	—	
E 1536 A	41.0 ^d	36.7 ^{cd}	18.2 ^b	—
E 1536 B	38.2 ^{de}	29.6 ^c	13.3 ^{ab}	51.5 ^e
Understory Sites →	U 1886	U 1766	U 1636	U 1537
Understory Sites ↓				
U 1766	57.5 ^d	—		
U 1636	31.2 ^{bc}	34.2 ^{bcd}	—	
U 1537	44.0 ^{cd}	55.5 ^{cd}	44.3 ^{cd}	—
U 1169	7.9 ^a	10.7 ^{ab}	22.3 ^{ab}	21.9 ^{ab}

Note: Comparisons were made among all understory sites and among exposed sites (ANOVA, P<0.05) followed by Bonferroni comparisons; values with the same superscript are within the same group.

Turnover also was estimated by similarity among plots. The samples of a site were compared with each of the samples of the comparison sites and analyzed by ANOVA. There was significant turnover in response to age and canopy (Tab. 6). PS in exposed sites ranged from 3.6% to 51.5%, indicating large turnover. There were no trends of similarity with age among exposed plots. Similarity declined regularly if sites were arrayed by structure. For example, the youngest site (E1892) was most similar to the oldest sites (E1536A, B) because the development of these old sites was least.

Understory similarities were always lowest when compared to U1169. There were no clear patterns between understory similarity and their age differential. The similarity of other understories to U1169 increased with site age, suggesting that understory turnover tends towards composition found under denser canopies. Species such as *Micromeria*, *Geranium robertianum*, *Galium aparine*, *Poa* and *Sedum tenuifolium* were common beneath *Quercus* and denser *Genista* and *Spartium* canopies.

WITHIN-SITE HETEROGENEITY

As a site matures, species invade, expand, and interact. An initially heterogeneous site should become less variable because as biomass increases, microsite variation is subdued. We measured heterogeneity using DCA of the individual sites and floristic similarity within sites at three scales.

The ground layer vegetation was explored to examine floristic variation (Tab. 7). The eigenvalues shown for E1892 and E1536-A are arbitrary because so many quadrats had no species in common. The eigenvalues of exposed sites were least at intermediate ages and highest in youngest and oldest sites. This variation is correlated to vegetation development, not substrate age. HC (turnover) was reduced slightly at the quadrat level, but at plot and sample levels HC was minimal at intermediate ages. Understory vegetation variation increased with plot age, as did HC, at each scale. Rather than becoming more homogeneous, each there is evidence for greater differentiation within a site. The low values in U1766 are due in part to the lower sample size. Exposed vegetation generally expressed greater variation at a given scale than did the understories of a comparable age. The exception was quadrats in 1636, where

the understory vegetation was slightly more variable than the exposed sites.

We determined percent similarity (PS) among all quadrats of a site, among 10 quadrats in each of the plots in a site, and among the five plots in each sample at a site (Fig. 5). The PS of exposed sites differed significantly with site age at each scale (ANOVA, $P << 0.001$). However, in no case was there a simple relationship between substrate age and community similarity, due primarily to surface effects. PS at exposed sites was lower than that of the understory at comparably aged sites, except in 1636, where the understory values were lower. Shrubs permitted higher PS than in exposed sites at each scale, presumably by creating a more homogeneous environment. Though PS among understory plots differed significantly, there was no particular pattern. *Quercus* plots were the least similar, but at smaller scales, these old sites were comparable to other sites. Over this chronosequence, variation within a site remains more important than effects that could create homogeneity.

CANOPY EFFECTS

Shrubs strongly affected species composition and thus altered the trajectory of succession. We compared the five exposed sites to the five understory sites (Tab. 8). The youngest understory was most similar to older exposed sites, while the youngest exposed sites had very little in common with any understory. Exposed and understory vegetation had limited similarity. The presence of a dense evergreen canopy markedly altered the species understory composition, such that its highest similarity was to that of the adjacent E1536A site. U1169 does not appear to be the “target” to which all trajectories are currently aimed. Intermediate stages do occur in the general area, but not within the immediate area sampled (POLI MARCHESE & GRILLO, 2000a).

DISCUSSION

The focus of this study was to determine if, during succession on young lavas, vegetation converges. In a relatively confined geographic area, can the chronosequence approach be used to assess this question? Alternatively, do even minor differences in site qualities and location lead to persistent vegetation differences?

Measures of vegetation structure

Tab. 7 - Summary of DCA of individual sites on the first axis at three scales. Eigenvalue estimates variance, HC is the number of half-changes on the gradient. Shrub plots were analyzed without shrubs.

Date	Quadrats (n=75-150)		Plots (n=15)		Samples (n=3)	
	Eigenvalue	HC	Eigenvalue	HC	Eigenvalue	HC
Exposed						
1892	0.99	A	0.54	2.16	0.21	1.05
1780	0.45	3.40	0.18	1.60	0.11	0.73
1636	0.34	2.64	0.27	1.99	0.14	0.81
1536-A	0.99	A	0.36	2.41	0.22	0.98
1536-B	0.85	1.92	0.25	1.77	0.16	0.95
Site Age	Quadrats (n=50-150)		Plots (n=5-15)		Samples (n=1-3)	
Understory						
1886	0.36	2.60	0.21	1.41	0.11	0.72
1766	0.27	1.95	0.12	0.8	---	---
1636	0.40	2.82	0.31	2.15	0.24	1.12
1537	0.37	3.11	0.28	1.66	---	---
1169	0.84	3.18	0.89	3.54	0.58	2.15

Note: A=values could not be calculated due to low species richness in many quadrats and the number of times quadrats had no species in common.

changed dramatically among the exposed sites, but changes were not linearly related to age. Species accumulated over time at different rates, leading to a complex mosaic of similar vegetation on substrates of different ages. Two examples are the similarity between exposed vegetation on lavas of 1892 and 1536, and the similarities among understory vegetation on lavas of 1766 and 1537. In contrast, vegetation of nearly the same age may differ strongly, even aside from the low similarities among the samples of a site (Fig. 5). For example, the lava of 1636 sustains both well-developed exposed vegetation and

shrub-dominated vegetation. The lava of 1892 lacked shrubs, while that of 1886 had a significant shrub population. The effect of a canopy is to accelerate the development of the understory and to permit a more rapid accumulation of vegetation cover.

Observations of young lavas suggest that species in this chronosequence invade sporadically and individualistically. They establish episodically, influenced strongly by stochastic and contingent factors and by variations in soil depth, surface texture and morphology.

Priority effects (BELYEAL & LANCASTER, 1999) may alter trajectories. Whi-

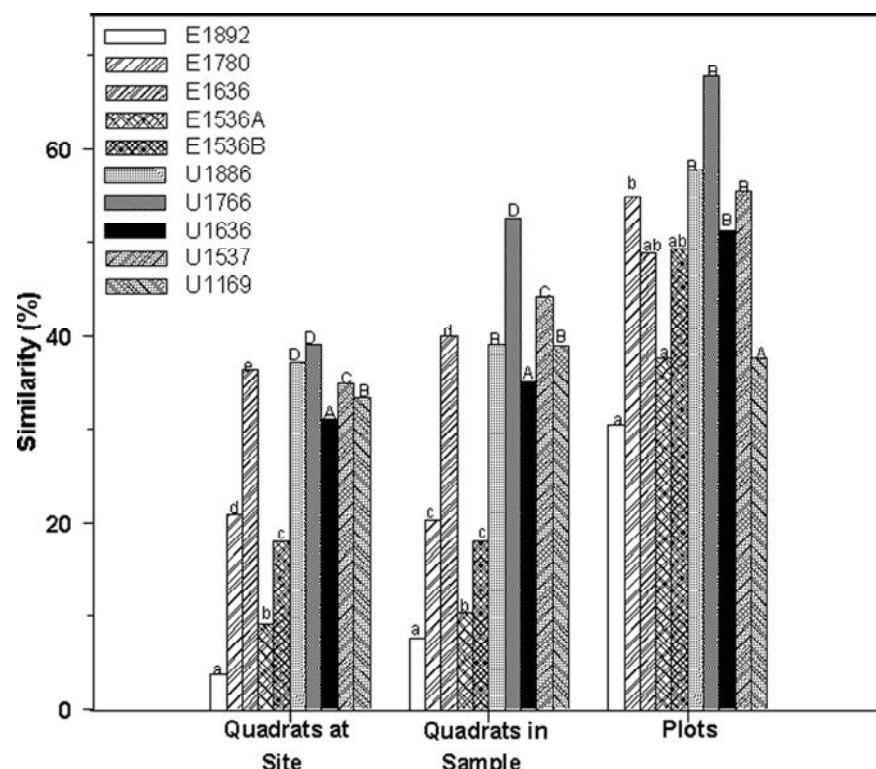


Fig. 5 - Percent similarity at three scales. Quadrats at site = mean pair-wise comparisons among all quadrats (75 to 150) in one site; Quadrats in site = the mean of pair-wise comparisons of quadrats within each sample; Plots = the mean similarity among the plots at a site. Statistics are described in caption for Fig. 2.

Tab. 8 - Floristic similarity (percent) of ground layer vegetation samples: exposed sites vs. understorey sites. Values are the mean of the nine pair-wise comparisons among the three samples of one site and the three samples of the comparison site.

		Similarity (%)				
Understory Sites → Exposed Sites ↓		U1886	U1766	U1636	U1537	U1169
E 1892 (n=3)	(n=3)	(n=1)	(n=3)	(n=2)	(n=3)	
E 1892 (n=3)	4.32 ^{ab}	2.3 ^a	4.75 ^{ab}	2.75 ^a	0.85 ^a	
E 1780 (n=3)	25.8 ^g	12.2 ^{bcd}	23.7 ^{fg}	19.3 ^{efg}	7.81 ^{abc}	
E 1636 (n=3)	8.0 ^{bcd}	11.8 ^{bcd}	24.7 ^g	19.4 ^{efg}	7.59 ^{abc}	
E 1536 A (n=3)	17.1 ^{efg}	11.9 ^{bcd}	24.8 ^g	17.4 ^{efg}	12.1 ^{bcd}	
E 1536 B (n=3)	25.8 ^g	5.8 ^{ab}	20.1 ^{efg}	15.6 ^{def}	4.75 ^{ab}	

Note: Comparisons were made between all understory sites and all exposed sites (ANOVA, P<0.05) followed by Bonferroni comparisons; values with the same superscript are not different.

le the *Quercus* plots sampled in this study showed no evidence of having once supported *Genista* or *Spartium*, other nearby sites at lower elevations have *Q. ilex* that has invaded these shrubs, and which sustains a more diverse understorey. It is quite possible that the *Quercus* studied here did invade shrubs that long ago disappeared. Therefore, while species accumulate and structure develops through time, the process proceeds at different rates on different lavas and is affected by many factors. As noted by FASTIE (1995) in relationship to succession at Glacier Bay, the presence or absence of a legume can substantially alter the subsequent succession (cf. DEL MORAL & ROZZELL, 2005).

Species turnover clearly occurred on exposed sites. Many species that were initially sparse in E1892 sites were common on older substrates. The presence of shrubs, whether established prior to, simultaneous with, or after ground layer, has altered the herb layer, but different dominants occurred in different plots of a site. The composition of shrub understorey appears less variable when assessed by NMS (Fig. 4). Shrubs reduce options available to understorey species and enhance local homogeneity. However, variation at the sample scale remains similar to that of exposed sites. Variation patterns provide no evidence for convergence on any but the smallest scale. One small area might develop homogeneity under shrubs, but substantial between-sample variation persisted even in the oldest sites. Shrubs increased the homogeneity of understorey vegetation and changed species composition. Shrubs increased shade and soil organic matter and altered the competitive balance among understorey species. Overstorey dominance may be the principal mechanism by which convergence to a single association oc-

curs (GLENN-LEWIN & VAN DER MAAREL, 1992). However, for the process to be completed, initial effects due to landscape (cf. DEL MORAL & LACHER, 2005), persistent of initial colonizers, and chance (cf. DEL MORAL & ECKERT, 2005) must be extinguished. To the extent that such confounding factors remain, convergence cannot occur, even if homogeneity is increasing (WALKER & DEL MORAL, 2003).

Turnover (HC) in exposed plots declined with vegetation development on DCA-2, but not with lava age. The presence of shrubs tended to increase, not decrease understorey variation. The understorey beneath *Quercus* was even more variable at these scales, and was so distinct that we did not analyze these samples along with other plots. The rate of succession appears to vary on each lava flow, leading to nonlinear changes in turnover with age.

There is little evidence for convergence in this chronosequence if one uses chronological age. However, if we apply the concept of developmental age, there are some indications of partial convergence. Similarity among quadrats at a site, within a sample, and, to a lesser degree within plots, increased with developmental age (Fig. 5), but understorey vegetation demonstrated no trend. We found no evidence for floristic convergence at the level of a sample.

Similarity between exposed sites declines not with their age differential, but with differences in development. For example, E1892 is most similar to E1536A, which is the sample most similar to it in cover and measures of dominance (Tab. 6). The PS of U1886 to other understoreys declines not with age but with structure. These results suggest that within this small area, species composition will tend to develop along somewhat similar trajectories.

The rate of vegetation development on young lavas of Mount Etna has been fitful. Sites of the same age can differ subsequently due to surface characteristics, nature and proximity to pools of potential colonists, and contingent factors. The chance establishment of large herbs (e.g. *Centranthus* or *Isatis*) or tall shrubs (e.g. *Spartium*) alters the chronosequence. As a result, each site experiences a unique vegetation trajectory. Given the importance of legumes and of landscape effects, we believe that while convergence among dominants (e.g. *Quercus*) may be expected, understorey differences will persist. Early in the chronosequence, microsites diverge under the influence of different pioneers, and it is only later that there is the potential for even partial convergence. Because *Quercus ilex* and *Q. pubescens* (s.l.) are both long-lived species capable of exerting strong influences in the understorey, it is likely that heterogeneity within a site will decline. Increasing similarity and reduced overall variation reflected by NMS support this assumption. However, because *Quercus* individuals, even within a small area, may establish at different times under varied circumstances, variation between samples may remain high (as it did in this study).

The situation on the lower south slope of Mount Etna suggests a hypothesis that can be tested over a long period using a modified chronosequence concept. Proper comparisons are not between samples based on their calendar age, but on their relative age, determined by measures of vegetation development. Completely deterministic succession is unlikely to occur because the effects of early, often stochastic or contingent events persist indefinitely. During a long chronosequence new factors are introduced that affect young sites that never influenced older ones. For example, disturbances due to roads, quarries, and pastures alter the landscape; new species that potentially can alter growing conditions are transported to the site; and climate patterns shift. However, there are some deterministic processes that do mute heterogeneity, limit the species capable of persisting, and can promote convergence. Legumes (e.g. *Lupinus*, *Vicia*) alter soil nitrogen, while tall vegetation modifies the site to favor mesophytic species. The diversity and abundance of annuals are reduced in favor of persistent herbaceous perennials.

What we observed on Mount Etna is that several communities assemble during the first few centuries on similar

substrates. Each is the result of unique combinations of variable substrate morphology, landscape factors, competitive interactions, and stochastic processes. Collectively the vegetation forms a mosaic. At a given site, the vegetation becomes more homogeneous over time, but the rate of change is variable, controlled primarily by substrate factors that do not strongly correlate with age. The oldest exposed lava supports vegetation similar to that of the youngest because it has decomposed more slowly. Once established, species can fill open space (hence the importance of priority effects.) Increasing homogeneity can produce convergence. Even initially similar sites can develop distinct patterns (e.g. the two 1636 samples). Eventually, canopy shrubs and small trees may exert strong dominance on the understory, but within the span of this study, their understories remained variable. The understories of *Quercus* vegetation, dominated by persistent species, remain captive to their histories. While the development of a canopy spurs species turnover, it does not necessarily produce convergence. Vegetation development on the young lavas of Mount Etna combines assembly with succession, but succession processes have yet to manifest strongly. This Mediterranean climate prolongs colonization, so that a longer chronosequence is required to provide a better assessment of the degree of convergence on this volcano.

ACKNOWLEDGEMENTS

We thank Maria Grillo for plant identification and translations. RDM is particularly grateful to the students of the Ecology Section, University of Catania for their valuable assistance and help in the field.

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ASSOCIAZIONI ALGALI DEI CORSI D'ACQUA DELL'APPENNINO CENTRALE

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ABSTRACT

Some algal associations found in the last decades in the central Apennine watercourses are listed and briefly discussed. They are reported with their original denominations, even though they are not in accordance in many cases with the international nomenclatural Code. Among these, *Ceratoneieto-Hydruretum rivulare*, *Chantransieto-Phormidietum incrassans* and *Diatometo-Meridionetum rivulare* require cold, fast flowing and well oxygenated waters. Thus they lie strictly in the upper stretch of the rivers. *Diatometo vulgaris-Melosiretum variantis*, *Cymbelletun ventricosae* and *Phormidietum membranaceum* follow the preceding associations along the hydrographic basin of the Apennine watercourses. *Cladophoretum glomeratae*, *Vauclerietum rheobenthicum* and *Ulothrichtum zonatae* have a remarkable ecological plasticity and occur either upstream or downstream, but above all in the middle stretch. All these associations request a basic pH and running waters. *Oedogonieto-Heterocontetum*, on the contrary, was found in a slightly acid environment and calm waters, with a very richness in species.

KEYWORDS: algal associations, watercourses, central Apennine.

RIASSUNTO

Vengono elencate e brevemente commentate alcune associazioni algali rinvenute nei corsi d'acqua dell'Appennino centrale. Esse vengono riportate con le loro denominazioni originali, anche se spesso non in accordo con le norme del Codice internazionale di nomenclatura. Tra queste, *Ceratoneieto-Hydruretum rivulare*, *Chantransieto-Phormidietum incrassans* e *Diatometo-Meridionetum rivulare* esigono acque fredde veloci e ben ossigenate, pertanto sono rigorosamente legate al tratto superiore, torrentizio, dei corsi d'acqua centro-appenninici. *Diatometo vulgaris-Melosiretum variantis*, *Cym-*

bellelun ventricosae e *Phormidietum membranaceum* seguono immediatamente le precedenti associazioni lungo il bacino idrografico di questi fiumi. *Cladophoretum glomeratae*, *Vauclerietum rheobenthicum* e *Ulothrichtum zonatae* possiedono una notevole plasticità ecologica e si trovano sia nel corso superiore che inferiore dei corsi d'acqua, ma soprattutto in quello intermedio. Tutte queste associazioni richiedono un pH basico ed acque correnti. *Oedogonieto-Heterocontetum*, invece, è stato trovato in acque tranquille ed a pH leggermente acido con una notevole ricchezza in specie.

INTRODUZIONE

Sulla scia del fervore scaturito all'inizio del XX secolo per lo studio delle associazioni vegetali a seguito della pubblicazione di Braun-Blanquet (1928) che poneva le basi per lo studio della vegetazione terrestre, numerose associazioni algali sono state descritte anche per le acque correnti, ad opera soprattutto di MARGALEF (1948, 1949) e SYMOENS (1957). Alcune di queste associazioni sono state trovate anche nei corsi d'acqua dell'Appennino centrale e verranno qui elencate e brevemente commentate.

Questi corsi d'acqua, generalizzando al massimo, possono essere suddivisi, nella maggior parte dei casi, in tre tratti principali: superiore, medio ed inferiore, lungo i quali la pressione antropica aumenta gradualmente fino a diventare importante nel tratto terminale.

Il tratto superiore, o montano, si trova al di sopra dei 500 m di quota ed include la zona delle sorgenti, dei ruscelli e dei torrenti, questi ultimi con acque veloci, tumultuose e bene ossigenate a causa dell'elevato dislivello; la temperatura si mantiene piuttosto bassa in tutte le stagioni (8-12 °C); l'alveo è ricoperto da massi, pietre e talvolta da roccia madre in posto.

Il tratto medio, o collinare, inizia dai 500 m s.l.m. e termina intorno ai 100 m s.l.m.; lungo questo tratto i

torrenti aumentano via via di dimensioni mentre la velocità della corrente si attenua; anche gli aspetti granulometrici dell'alveo cambiano: pietre, ciottoli e ghiaia grossolana ricoprono il fondo.

Il tratto inferiore, o pianiziale, si sviluppa al di sotto dei 100 m s.l.m. e qui il corso d'acqua scorre ormai lentamente sopra i propri depositi alluvionali; ghiaia sempre più fine, sabbia e limo ricoprono ora il letto del fiume.

I fiumi centro-appenninici hanno una lunghezza media di 80-100 km e si gettano per la maggior parte nel Mare Adriatico; alcuni, come il torrente Ussita ed il fiume Nera fanno parte invece del bacino idrofico del Tevere. Tutti scorrono in prevalenza su terreni carbonatici ed il pH è sempre alcalino, per lo più compreso tra 7,5 e 8,5.

Fa eccezione alla tipologia suddetta il Fosso Mergani di Pian Grande di Castelluccio di Norcia (Perugia), a 1300 m di quota, con un pH leggermente acido ed acque calme o poco fluenti.

LE ASSOCIAZIONI ALGALI

Le associazioni algali riscontrate nei corsi d'acqua centro-appenninici vengono qui riassunte e riproposte nelle loro denominazioni originali, anche se queste spesso non rispondono alle norme del Codice fitosociologico di nomenclatura internazionale. Per alcune proposte di inquadramento delle associazioni algali in unità sistematiche superiori si rimanda a SYMOENS (1951) e MARGALEF (1958, 1960). I corsi d'acqua in cui queste associazioni sono state espressamente segnalate (Tab. 1) sono i seguenti: fiume Potenza (DELL'UOMO, 1970), torrente Ussita (DELL'UOMO e CICCOTTI, 1977), fiume Nera (CORTINI PEDROTTI e DELL'UOMO, 1977; DELL'UOMO, 1982a), fosso Mergani (DELL'UOMO, 1979, 1982b), fiume Menotre (DELL'UOMO, 1982c). Tuttavia si può dire fin d'ora che esse, rispetto a queste segnalazioni, sono molto più ampiamente diffuse nei corsi d'acqua appenninici.

Tab. 1 - Alcune associazioni algali rinvenute nei corsi d'acqua dell'Appennino centrale.

Associazioni algali

Ceratoneieto-Hydruretum rivulare
 Diatometo-Meridionetum rivulare
 Chantransieto-Phormidietum incrustans
 Phormidietum membranaceum
 Cymbelletum ventricosae
 Diatometo vulgaris-Melosiretum variantis
 Cladophoretum glomeratae
 Vaucherietum rheobenthicum
 Ulothricetum zonatae
 Oedogonieto-Heterocontetum

Fiumi in cui sono state segnalate

Ussita - Nera - Menotre
 Ussita - Nera - Potenza - Menotre
 Ussita - Nera
 Ussita - Nera - Menotre
 Ussita - Nera - Potenza - Menotre
 Potenza - Menotre
 Ussita - Nera - Potenza - Menotre
 Ussita - Nera - Potenza - Menotre
 Ussita - Nera - Potenza - Menotre
 Fosso Mergani

CERATONEIETO-HYDRURETUM RIVULARE
MARGALEF 1948

Descritta inizialmente per i corsi d'acqua pirenaici della Cerdaña (MARGALEF, 1948), questa associazione è stata rinvenuta in alcuni torrenti montani dell'Appennino umbro-marchigiano, dove si sviluppa sulle pietre in piena

corrente. Specie caratteristica e quantitativamente dominante è *Hydrurus foetidus* (Vill.) Trèv., una crisoficea ad organizzazione palmelloide i cui talli macroscopici, spesso molto voluminosi e di colore giallo pallido, sono irregolarmente ramificati ed estremamente polimorfi. È questo un organismo rigorosamente stenotermo d'acqua fredda

che non sopporta, se non per breve tempo, temperature superiori a 12 °C. I talli di *Hydrurus* sono ricoperti da una miriade di frustuli della diatomea *Ceratoneis arcus* (Ehrenb.) Kützing [nome considerato ora valido: *Fragilaria arcus* (Ehrenb.) Cleve], altra specie caratteristica dell'associazione. Tra le specie compagne si possono ricordare le seguenti Diatomee: *Achnanthes lanceolata* (Bréb.) Grunow, *Amphora montana* Krasske, *A. ovalis* (Kütz.) Kützing, *Cocconeis placentula* Ehrenb., *Navicula radiosa* Kützing, *N. tripunctata* (O.F. Müller) Bory, *Neidium ampliatum* (Ehrenb.) Krammer e *Ulnaria ulna* (Nitz.) Compère. Alcune delle specie citate sono rappresentate in Fig. 1.

DIATOMETO-MERIDIONETUM RIVULARE
MARGALEF 1949

Altra associazione algale che si sviluppa nel tratto montano dei corsi d'acqua appenninici, ma che al contrario della precedente, qualitativamente piuttosto povera di specie, possiede una notevole ricchezza floristica dovuta soprattutto alle Diatomee. Essa si presenta in forma di flocculi e grovigli di filamenti di colore bruno-giallastro, dapprima attaccati alle pietre sommerse poi liberi tra le idrofite fanerogamiche (*Nasturtium officinale* R. Br., *Veronica beccabunga* L., *V. anagallis-aquatica* L., *Apium nodiflorum* (L.) Lag., *Petasites hybridus* (L.) Gaertner ed altre. Specie caratteristiche dell'associazione sono *Diatoma hyemalis* (Roth) Heiberg, *Diatoma mesodon* (Ehrenb.) Kützing e *Meridion circulare* (Grev.) Agardh; le prime due formano lunghe colonie filamentose, la terza eleganti colonie circolari. Tra le specie compagne: *Campylodiscus hybernicus* Ehrenb., *Caloneis alpestris* (Grun.) Cleve, *Cocconeis euglypta* Ehrenb., *Gomphonema angustum* Agardh, *G. olivaceum* (Hornem.) Bréb. e *Navicula radiosa* Kützing.

DIATOMETO VULGARIS-MELOSIRETUM VARIANTIS
SYMOENS 1954

Specie caratteristiche dell'associazione sono due Diatomee che prediligono acque moderatamente fresche ed ossigenate: *Diatoma vulgaris* Bory e *Melosira varians* Agardh. La prima forma colonie zigzaganti con le cellule aderiscono le une alle altre solo per un angolo del frustulo, la seconda lunghe colonie cilindriche. Entrambe danno luogo a flocculi sulle pietre sommerse o

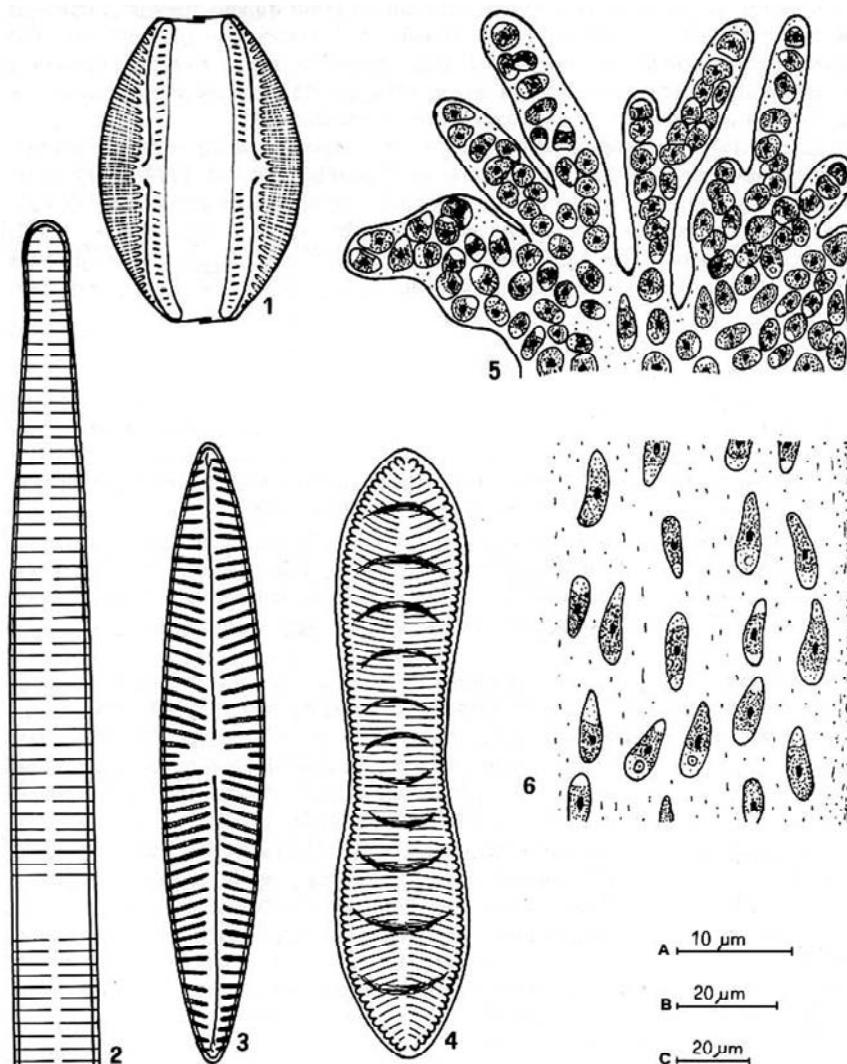


Fig. 1 - Alcune alghe dell'associazione *Ceratoneieto-Hydruretum rivulare* disegnate alla camera lucida (da DELL'UOMO, 1982a): 1) *Amphora ovalis* (Kütz.) Kützing (scala A); 2) *Ulnaria ulna* (Nitz.) Compère (scala A); 3) *Navicula tripunctata* (O.F. Müller) Bory (scala A); 4) *Cymatopleura solea* (Bréb.) W. Smith (scala B); 5-6. *Hydrurus foetidus* (Vill.) Trèv., parte apicale e cellule centrali di un tallo (scala C).

a masserelle filamentose tra i cauli di piante acquatiche. Numerose altre Diatomee accompagnano l'associazione, tra cui: *Navicula viridula* (Kütz.) Ehrenb., *Surirella minuta* Brébisson, *Gyrosigma attenuatum* (Kütz.) Rabenh., *Navicula capitatoradiata* Germain, *Nitzschia dissipata* (Kütz.) Grunow, *N. sigmoidea* (Nitz.) W.M. Smith.

Lungo il corso del fiume questa comunità si sviluppa un po' più a valle delle precedenti perché meno esigente, o più tollerante, nei riguardi delle condizioni ambientali.

CHANTRANSIETO-PHORMIDIETUM INCRUSTANS SYMOENS 1957

Phormidium incrustatum (Näg.) Gomont è un'alga azzurra filamentosa con guaina molto sottile che ha la capacità di incrostarsi di carbonato di calcio dando così luogo alla formazione di tufo calcareo. Anche *Chantransia*, studio filamentoso strisciante sul substrato che si ritrova in diverse alghe rosse d'acqua corrente, ha questa capacità. Entrambe sono caratteristiche dell'associazione e accompagnate da poche altre specie, tra cui *Cymatopleura elliptica* (Bréb.) W. Smith, *Hantzschia amphyoxys* (Ehrenb.) Grunow, *Surirella spiralis* Kützing, *Cymbella helvetica* Kützing e *C. lanceolata* Agardh, tutte Diatomee.

Questa associazione, molto meno diffusa delle precedenti, è stata rinvenuta nell'alto corso del fiume Nera (bacino del Tevere), ma osservata anche (DELL'UOMO, dati inediti) nella gola del fiume Fiastrone (bacino del Chienti), a valle della diga.

Interessanti fenomeni di formazione di tufo calcareo dovuti all'azione di alghe che hanno la proprietà di precipitare carbonato di calcio, a partire dal bicarbonato in soluzione, sono stati descritti anche da FRITSCH (1949) in alcuni corsi d'acqua britannici.

PHORMIDIETUM MEMBRANACEUM FJERDING-STAD 1950

Feltri sulle pietre sommerse, sovente molto spessi e di colore blu scuro, costituiscono questa associazione, che risulta dall'intima unione dei filamenti di varie specie del genere *Phormidium* (Cyanophyceae): *Ph. autumnale* (Agardh) Gomont, *Ph. favosum* (Bory) Gomont, *Ph. subfuscum* Kützing e *Ph. retzii* (Agardh) Gomont. Il primo di questi è dominante e sempre presente, gli altri partecipano in proporzioni minori alla

formazione dei feltri e mai tutti insieme. Poche e rappresentate da sole Diatomee le specie compagne, alcune delle quali già elencate in precedenza. L'area di distribuzione di questa comunità algale lungo i fiumi appenninici a volte si sovrappone a volte si trova un po' più in basso rispetto a quella delle precedenti associazioni.

CYMBELLETUM VENTRICOSAE SYMOENS 1957

Si tratta di un'associazione pressoché monospecifica a *Cymbella ventricosa* Kützing [nome considerato ora valido: *Encyonema minutum* (Hilse) D.G. Mann]. Si sviluppa negli anfratti delle pietre in piena corrente, sulle quali forma sottili rivestimenti di colore bruno-verdastro, ma anche tra i cespi di muschi acquatici come *Brachythecium rivulare* Bruck et al., *Rhynchostegium riparioides* (Hedw.) Cardot, *Fontinalis antipyretica* Hedw., ecc. Alcuni di questi formano, a loro volta, un'associazione muscinale, *Platyhypnidietum riparioidis* Gams 1927, riscontrata da CORTINI PEDROTTI (1970) lungo il corso del fiume Potenza e dallo stesso autore (1982) anche nell'alto corso del fiume Nera.

CLADOPHORETUM GLOMERATAE MARGALEF 1949

Specie caratteristica e nettamente dominante è *Cladophora glomerata* (L.) Kützing un'alga verde che forma vistosi cespugli, lunghi anche più di un metro, attaccati alle pietre dell'alveo fluviale. All'interno della massa dei filamenti di *Cladophora*, abbondantemente ramificati e pettinati dalla corrente, trovano rifugio numerose Diatomee, tra cui *Cymatopleura solea* (Bréb.) W. Smith, *Navicula cryptocephala* Kützing, *Gyrosigma acuminatum* (Kütz.) Rabenh., *Nitzschia dubia* W.M. Smith e *Pinnularia brebissonii* (Kütz.) Rabenh. In particolare, i filamenti dell'alga verde sono spesso ricoperti da un numero incredibile di frustuli di *Coccineis pediculus* Ehrenb. che ne possono alterare addirittura la fisionomia. Questa associazione possiede una notevole plasticità ecologica per cui la si ritrova lungo tutto il corso d'acqua, anche se con uno sviluppo più rigoglioso nel tratto medio.

VAUCHERIETUM RHEOBENTHICUM

SYMOENS (1957) descrive due as-

sociazioni, *Vaucherietum rheobenthicum diatomatosum vulgaris* e *Vaucherietum rheobenthicum diatomatosum hiemalis*, rispettivamente per le acque correnti calcaree e non calcaree della regione delle Ardenne. Sotto il nome *Vaucherietum rheobenthicum*, non ulteriormente specificato, si vuole qui intendere una associazione presente nei fiumi appenninici, costituita da varie specie del genere *Vaucheria* (Xanthophyceae), che forma caratteristici feltri di aspetto vellutato, compatte e di colore verde-giallastro, sulle pietre ed altri substrati sommersi. Le specie possono essere di volta in volta diverse, *V. geminata* (Vauch.) De Candolle, o *V. sessilis* (Vauch.) De Candolle, oppure *V. dillwynii* (Weber et Mohr) Agardh, ma il corteggio flogistico, costituito soprattutto da Diatomee, è in ogni caso molto simile: *Amphora ovalis*, *A. pediculus* (Kütz.) Grunow, *Diatoma vulgaris*, *Cymatopleura solea*, *Navicula lanceolata* (Agardh) Ehrenb., *N. tripunctata*, *Nitzschia palea* (Kütz.) W. Smith e molte altre. L'associazione a *Vaucheria* è molto frequente, soprattutto nel tratto medio, dei corsi d'acqua centro-appenninici.

ULOTHRICETUM ZONATAE SYMOENS 1957

Specie dominante è l'alga verde *Ulothrix zonata* Kützing i cui lunghi e grossi filamenti sono fissati quando sono giovani alle pietre sommerse e accompagnati da varie Diatomee, mentre da adulti si staccano e si ritrovano in forma di flocculi filamentosi tra le idrofite fanerogamiche. È proprio in questo secondo caso che la comunità algale si arricchisce di altre specie filamentose come *Ulothrix aequalis* Kützing, *U. tenuissima* Kützing, *U. terrima* (Kütz.) Kützing e la xantoficea *Tribonema viride* Pascher.

OEDOGONIETO-HETEROCONTETUM MARGALEF 1958

È questa l'unica delle associazioni qui riportate che non si sviluppa in piena corrente ed in acque a reazione alcalina, ma in ambienti lenti o astatici e con un pH da neutro a leggermente acido. Alcune delle specie che la costituiscono, ad iniziare da quelle caratteristiche, sono le seguenti: *Oedogonium pratense* Transeau, *Oe. tapeinosporum* Wittr., *Oe. crispum* fo. *granulosum* (Nordst.) Hirn, *Tribonema affine* West, *T. viride* Pascher, *T. elegans* Pascher, *Spirogyra pratensis* Transeau, *Micro-*

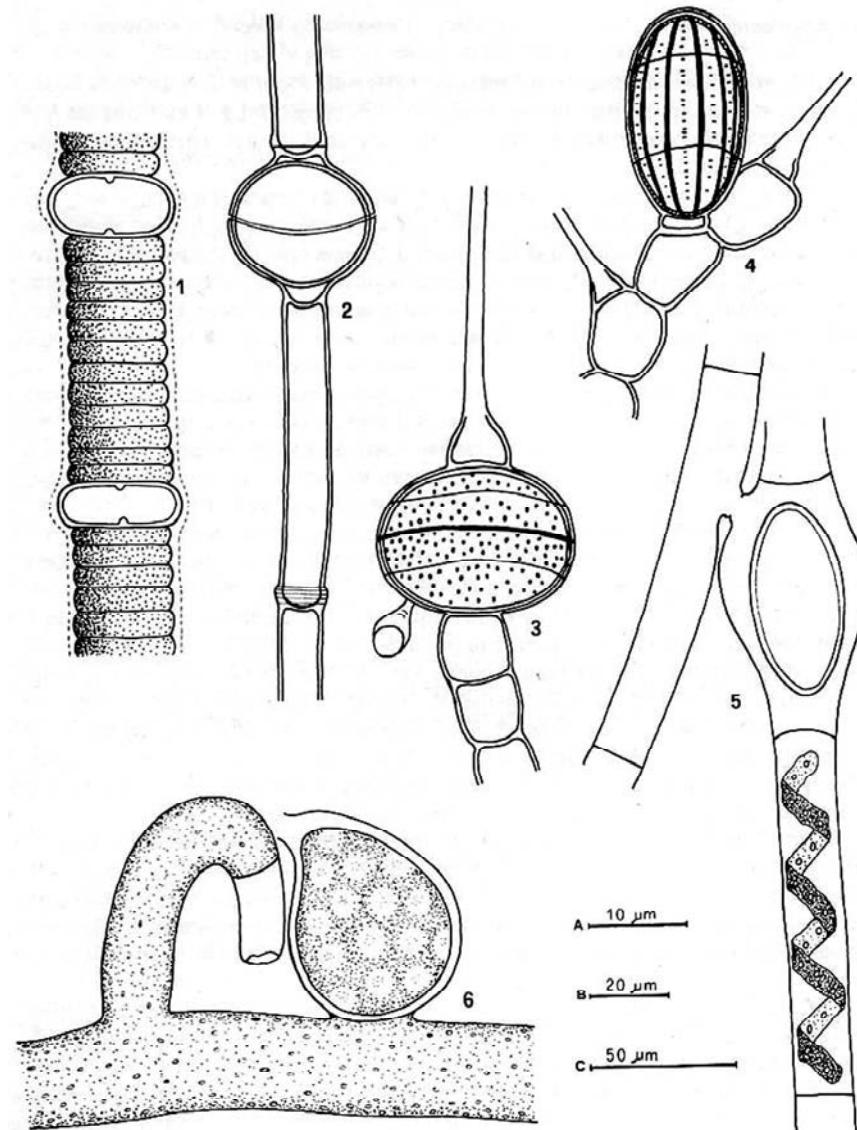


Fig. 2 - Specie caratteristiche e specie compagne dell'associazione *Oedogonieto-Heterocontetum* disegnate alla camera lucida (da DELL'UOMO, 1982b): 1) *Nodularia spumigena* Mertens (scala A); 2) *Oedogonium pratense* Transeau (scala B), *Bulbochaete intermedia* De Bary (scala B); 4) *Bulbochaete repanda* Wittr. (scala B); 5) *Spirogyra pratensis* Transeau (scala B); 6) *Vaucheria repens* Hassall (scala C).

spora amena var. *gracilis* (Wille) De Toni, *M. floccosa* (Vaucher) Thuret, *M. stagnorum* (Kütz.) Lagerh., *Bulbochaete intermedia* De Bary, *B. repanda* Wittr., *Gloeocheate wittrockiana* Lagerh., *Vaucheria repens* Hassall, *Ophiocytium capitatum* Wolle, *Characiopsis closteriana* Dell'Uomo. Si tratta sia di alghe verdi che di Xanthophyceae, cui si aggiungono alcune Cyanophyceae, come *Nodularia spumigena* Mertens e varie Diatomee, tra cui *Amphipleura pellucida* Kützing, *Pinnularia viridis* (Nitz.) Ehrenb., *Eunotia praerupta* Ehrenb., ecc. È inoltre presente anche una componente tico-planctonica con *Phacus orbicularis* Hüb., *Trachelomonas hispida* (Perty) Stein em. Defl., *Dinobryon sertularia* Ehrenb., *Pandorina morum* Bory, *Eudorina elegans* Ehrenb., *Botryococcus brunii* Kützing, *Peridinium cinctum*

(Müller) Ehrenb., ecc. Alcune delle specie citate sono rappresentate in Fig. 2.

Questa associazione è stata rinvenuta esclusivamente nel Fosso Mergani, a Pian Grande di Castelluccio di Norcia (Perugia), alla quota di 1300 m s.l.m. in acque a pH leggermente acido.

Nello stesso Fosso Mergani PEDROTTI (1969) ha segnalato *Nitella syncarpa* (Thui.) Chev. var. *capitata* (Nees) Kütz. (alge Caracee).

CONSIDERAZIONI CONCLUSIVE

Alcune delle associazioni elencate e brevemente commentate sono strettamente localizzate nel tratto superiore dei corsi d'acqua centro-appenninici in quanto richiedono acque fredde, veloci e bene ossigenate. Inoltre le loro specie caratteristiche sono estremamente sen-

sibili all'inquinamento organico e minerale ed anche alla eccessiva presenza di nutrienti nel corpo idrico (forme stenoterme, reofile, ossifile, xenosapobie, alofobe e tipiche di ambienti ipotrofici). Esse sono:

- *Ceratoneieto-Hydrurometum rivulare*
- *Diatometo-Meridionetum rivulare*
- *Chantransieto-Phormidietum incrassans*

Altre associazioni, le cui specie dominanti sono più tolleranti e si adattano a condizioni ambientali meno rigorose, seguono le precedenti lungo il bacino idrografico dei fiumi:

- *Cymbelletum ventricosae*
- *Diatometo vulgaris-Melosiretum varians*

Phormidietum membranaceum

Altre ancora possiedono una notevole plasticità ecologica e vengono rinvenute lungo tutto il corso dei fiumi, dal tratto torrentizio a quello in vicinanza della foce; tuttavia esse presentano il maggiore rigoglio nel tratto medio, dove trovano le condizioni ambientali più idonee al loro sviluppo:

- *Cladophoretum glomeratae*
- *Vaucherietum rheobenthicum*
- *Ulothricetum zonatae*

Tutte richiedono comunque acque correnti ed a reazione alcalina. Fa eccezione, a quelle sopra elencate, l'associazione *Oedogonieto-Heterocontetum* che è stata rinvenuta in acque tranquille ed a pH leggermente acido. Essa presenta, inoltre, una elevata ricchezza in specie, sia filamentose che unicellulari, con una buona presenza anche di forme tico-planctoniche.

Nella Tab. 1 sono stati riportati solo i fiumi in cui le associazioni sono state effettivamente segnalate in precedenti lavori. Tuttavia, osservazioni successive consentono di affermare che esse sono in gran parte comuni a molti altri fiumi appenninici, nei quali manifestano una simile distribuzione longitudinale lungo i vari bacini idrografici. Tale distribuzione, tuttavia, è fortemente influenzata dalle caratteristiche idrografiche, idrologiche e granulometriche presenti localmente.

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CONCEPT OF THE POPULATION STRUCTURE OF COMMUNITIES: PLANT DEMOGRAPHY AND PHYTOSOCIOLOGY

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ABSTRACT

The paper presents a discussion of community theories from the point of view of phytosociology and plant demography. The formation, development and decline of various floristical compositions were analysed as the effects of demographic population processes. Because they are decisive for the stability of, and changes in, the size of populations forming an ecological assemblage, i.e. a community, it is suggested that these processes are decisive for the structure and dynamics of communities. Much attention was paid to the evolutionary strategies of species forming the community, particularly to various life history traits.

KEYWORDS: community concepts, mechanisms, plant coexistence, plant demography.

CONCEPTS OF THE PLANT COMMUNITY: ALTERNATIVE OR COMPLEMENTARY?

Major differences in concepts of plant community result from the adoption of holistic or reductionistic philosophies, which entails certain methodological consequences. Studies adopting the reductionistic approach focus on individuals, and the formulated regularities are transposed on the higher levels. In the holistic approach, studies are conducted at the level of biological organisation, e.g. community, ecosystem, etc.

The community theory assumes the presence of a pronounced discontinuity between the formed species compositions, which provides a sufficient background to distinguish community types and establish community classification, as they demonstrate repeatability under certain biogeographical and ecological conditions. In contrast to the individualistic concept, which assumes that species compositions are unique in nature and thus there are no grounds for their classification, the community the-

ory considers them as distinct and repeatable under certain ecological conditions.

The following trends have been marked out recently in the community theory:

- shift of the gravity centre from the holistic point of view to the reductionistic, particularly in the investigation of plant convergence mechanisms;
- questioning the predictability of direction in community (vegetation) changes;
- search for mechanisms shaping comparable or distinct floristic compositions under identical or varying conditions.

In the second half of the 20th century the discussion on the repeatability and uniqueness of floristic compositions in nature and the legitimacy of establishing systems for phytosociological classification of communities was reopened. The revival of this discussion was stimulated in the second half of the 20th century when a new discipline - plant demography - was distinguished in botany. Its intense development in the 1960s-1980s contributed to a deeper knowledge of the biology and ecology of species coexisting in one habitat (HARPER, 1977). These results inspired scientists to formulate new concepts explaining the mechanisms based on which characteristic systems - plant communities - are formed. A number of theories and models have been proposed to explain this process. All concepts trying to explain species coexistence on a particular site premise that the species bank of a given natural site is the result of evolution, the history of a region and ecological conditions. Here are a few examples:

- niche theory proposes that differences in environmental conditions from place to place favour different combinations of species (TILMAN, 1988);
- the non-equilibrium concept assumes that the environment changes over time; disturbances favour less competitive species and thus the coexistence of species with different competitive abilities (PICKETT, 1980);
- the concept of a balanced competition

states that competitive abilities are considered to converge under natural selection with the net effect of a reciprocal balancing of competitive abilities for resources which are contested for (GRUBB, 1977).

Adoption of the concept of competition and niche being the primary mechanisms for plant convergence resulted in the treatment of a community as a system of reciprocal species interactions (CRAWLEY, 1986; CANULLO & FALIŃSKA, 2003). The axiom that the coexistence of organisms results in their reciprocal interaction has been adopted in ecology. Cooperation between plants can be analysed through cause and effect relations or through studying structural relations. Yet there is a reason for which no community is fully replete with species and individuals, nor is the space fully populated. How many species are able to coexist on a given site and why is a question that has still not been answered.

The comparison of the effects of reciprocal interaction between many species has identified at least three coexistence models:

- stable species coexistence;
- unstable equilibrium between species;
- domination of one species and elimination of another.

As plant population ecology has developed, more and more attention has been paid to research on the mechanisms responsible for species compositions than to the formulation of new community classification systems. Attempts have been made to verify the phytosociology hypothesis on repeatable community patterns present in nature which can be ordered and classified, as well as the hypothesis on plant demography, which states that each plant composition is unique and requires separate description (DIERSCHKE, 1994; PIGNATTI, 1995).

Therefore, it is worth recalling the theoretical background from which these two different standpoints on community definition originate. It has been assumed in phytosociology that similar biogeographical, ecological and historical conditions cause the formation of

species compositions of characteristic properties - phytocenoses (communities) (BURROWS, 1990; DIERSCHKE, 1994; CRISTEA *et al.*, 2004). This concept provided a background for the definition of a plant community as *a repeatable and distinguishable combination of species characterised by a complicated structure*.

Studies on plant communities in many world regions and under various ecological conditions (FALIŃSKI, 1986; FALIŃSKI & PEDROTTI, 1990; KWIAŁTOWSKA, 1994) have contributed to the development of phytosociology and the establishment of classification systems which adopt different criteria (RODWELL, 1991; MATUSZKIEWICZ, 2001). Almost in parallel Anglo-Saxon ecology has been developing, which propose that each species composition is unique and thus communities are characterised by many variable and distinct features (WHITE, 1985). This in consequence makes impossible the creation of a consistent system based on precisely defined criteria for community classification. At that time the community was defined as:

a discrete unit in nature which is the result of population coexistence formed during evolution (PIANKA, 1981)

or as

a set of populations present on the same site, and integrated to some degree by competition, complementarity and dependence (GRUBB, 1977).

The community definition by GRIME (1979) is the closest to plant demography:

a combination of many plant species that compete with each other and modify their own environment.

INDIVIDUAL, POPULATION, COMMUNITY

An interesting attempt to merge study results from two disciplines - plant demography and phytosociology - was presented in a monograph on the population structure of vegetation (WHITE, 1985). It presents an overview of theories explaining the processes which occur at the level of individuals, populations and communities, and its major message is the thesis that the nature of vegetation (communities) is the net result of features describing individuals of species forming floristic compositions under specified ecological and geographical conditions. This explains why, under the same conditions, the formed species combinations are not always identical, because interactions

between individuals are variable and often unpredictable. Because of advances in plant ecology, the community is often defined as *a specific ecological assemblage of species populations* (FALIŃSKA, 1991, 2002). In contemporary ecology an increasing number of experimental studies are focused on explaining the mechanisms responsible for species coexistence and the consequences of their coexistence on the same site (CRAWLEY, 1986; CANULLO & FALIŃSKA, 2003).

Although there are indisputable correlations between the spatial and chronological distribution of species and biotic and abiotic environmental conditions, the formation of a certain floristic composition - a community that can be classified based on phytosociological criteria - is not always possible to explain. In such cases it is suggested that cross-population and inter-population interactions are, apart from habitat conditions, the final factor decisive for the formation of a specified community. Such conclusions can be made based on the finding that none of the species takes full advantage of its physiological and ecological amplitude when colonizing available environments. The number of communities in nature is considerably lower than could be expected based on the bank of species in a given region of nature, even if ecological conditions are favourable. Therefore, it has been suggested that an understanding of species and the spatial structure of communities requires an understanding of demographic processes in plant populations, as they are decisive for their size and spatial relationships between individuals characterised by contradistinctive life history features and, consequently, the nature of the community. Such an assumption entails the need to extend studies on communities with life strategies of species that form diversified floristical compositions. This means that individual features of neighbour plants are significantly decisive for quantitative and spatial relationships between populations forming a specific community and, as a result, for the floristic composition (HARPER, 1980). The objective of plant ecology is to investigate mechanisms that form various communities and which result from physiological amplitude, the life history of individuals (STEARNS, 1992), as well as from the sociology history of species, because in their coexistence it is important not only **where** but also with **whom** the species can establish an *ecological assemblage*.

British scientists have proposed a

new view of the community, contrasting with the view of the Central-European school of phytosociology, based on the hierarchical system of units. This results from the discussion on the search for answers to the following questions:

- are the formed species compositions repeatable or random assemblages?
- are the communities unstructured and variable combinations of many organisms?
- or are they integrated groups of coexisting species characterised by inherent, repeatable structures under the same conditions?

Regardless of the adopted concept of plant community, it has been concluded that the possibility of finding many and diversified species on the same site and at the same time results from the initially similar ecological amplitude of plants and the individualistic reaction of species. However, their further coexistence is determined by heterogeneous interactions which depend on the evolutionary strategy of species (GRIME, 1979). These are life history traits of neighbours that finally decide the quantitative and spatial relationships between the populations of species forming a specific community, as well as its structure and dynamics. Generally, research on communities is the field of phytosociology, vegetation science - **which studies processes describing the models of species composition observed in nature**.

This is the continental European point of view, which differs to some extent from the British one, formulated by WHITE (1985): **vegetation science is sociology plus plant demography**.

The search for various models of floristic compositions, i.e. diversified communities, was facilitated by studies on:

- reaction of species to living conditions;
- interaction between species: positive (facilitating) and negative (eliminating);
- random events - at the level of environment and population;
- life strategies of species.

Controversial ideas on the repeatability and uniqueness of communities in nature have led to the creation of a synthetic community concept:

species compositions are partly stochastic and partly determined by the environment.

There is a view that vegetation science should be based on a reductionistic methodology which would enable the explanation of ecological processes at a higher hierarchical le-

vel (vegetation) and which would consider interactions at a lower level (individuals). The vegetation theory would then have to address in a clear fashion the reciprocal interactions between individuals and their environment, and specify the role of these processes in the formation of species compositions. WHITE (1985) formulated this in the following manner: the nature of vegetation is determined by the life history of species forming the vegetation on a given site and at a

given time.

It has been observed recently that the understanding of the structure and dynamics of populations is possible through the understanding of demographic population processes, which is the key to understanding mechanisms decisive for characteristic species combinations (HARPER, 1977). In such an approach it is assumed that the number of individuals, their distribution in space, and colonization pattern by populations in the area occupied by a commu-

nity are decisive for the role of the species in the community (Fig. 1). These features establish the relationships between individuals representing different species and their environment, and form the population structure of communities. Whether the community is considered a repeatable integrated system or not, the opinion that the combined knowledge of the diversification of vegetation and the demography of plant communities allows for a more detailed explanation of the key point for species

Carex cespitosa

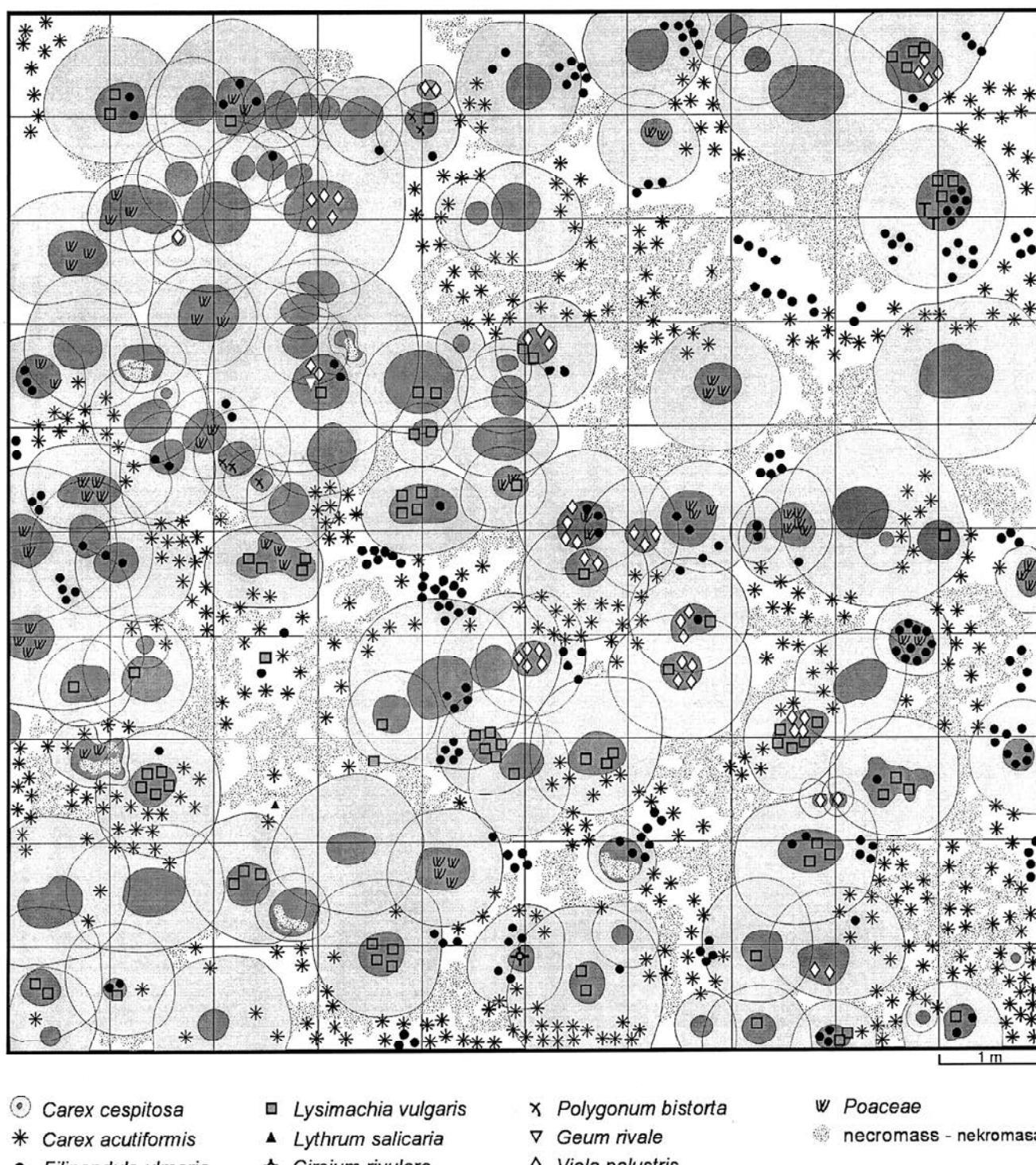
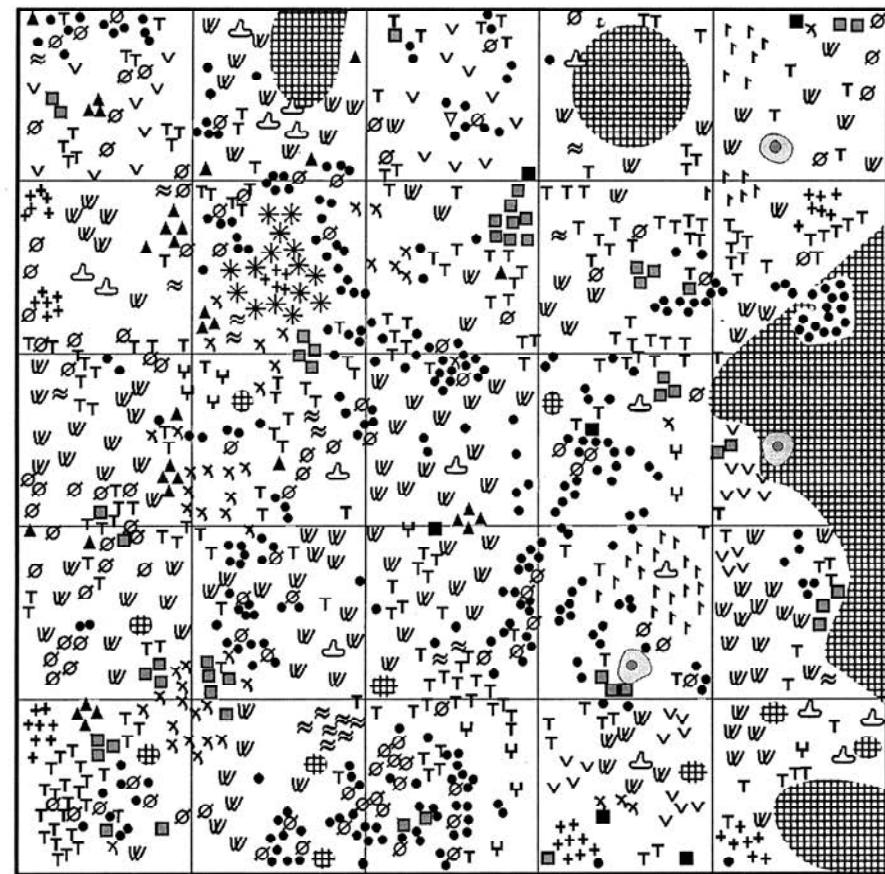
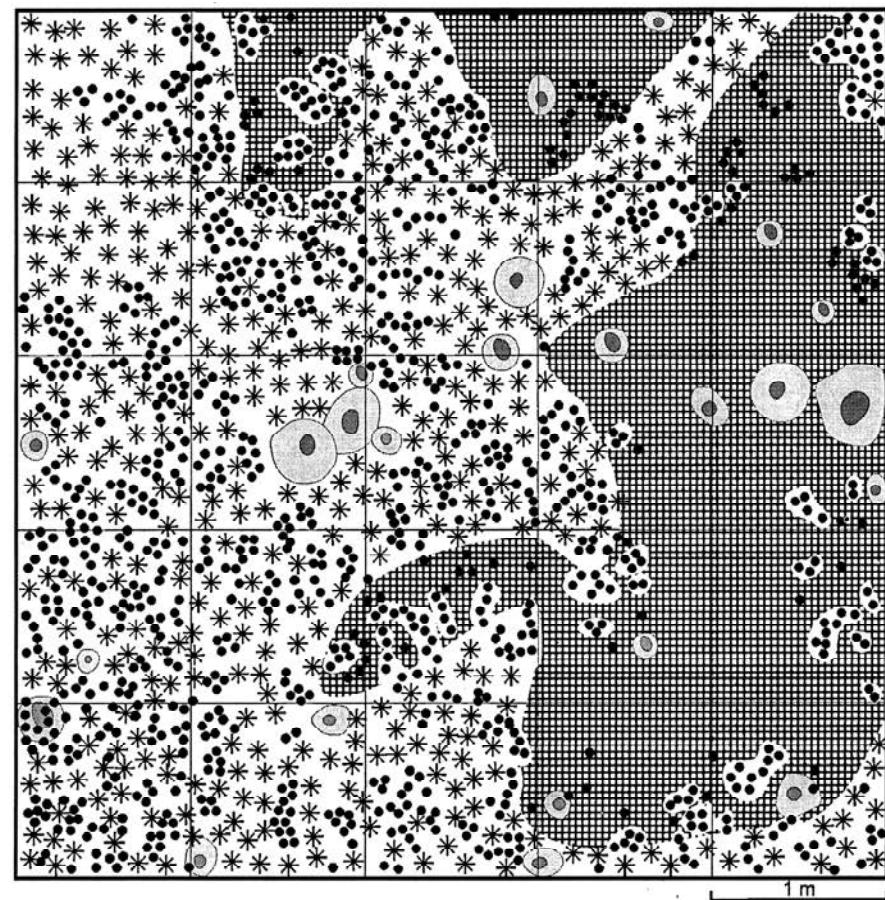


Fig. 1 - Relation between spatial distribution of tussocks and necromass and other species in long-term persistent patch of sedges (100 m²) on a meadow abandoned for 30 years (from FALINKA, 2003).

1980



1985



- | | | | | |
|------------------------------|-----------------------------|------------------------------|-----------------------------|----------------------------|
| Δ <i>Lychnis flos-cuculi</i> | ▽ <i>Geum rivale</i> | ∨ <i>Juncus effusus</i> | + <i>Caltha palustris</i> | * <i>Carex acutiformis</i> |
| ♦ <i>Cirsium rivulare</i> | ≈ <i>Myosotis palustris</i> | ● <i>Filipendula ulmaria</i> | ↑ <i>Scirpus sylvaticus</i> | ○ <i>Carex cespitosa</i> |
| ∅ <i>Cirsium palustre</i> | ⊟ <i>Galium palustre</i> | ■ <i>Lysimachia vulgaris</i> | ✗ <i>Polygonum bistorta</i> | ₩ <i>Poaceae</i> |
| ⊣ <i>Ranunculus acris</i> | ↑ <i>Comarum palustre</i> | ▲ <i>Lythrum salicaria</i> | ◊ <i>Viola palustris</i> | ⊗ <i>Salix cinerea</i> |

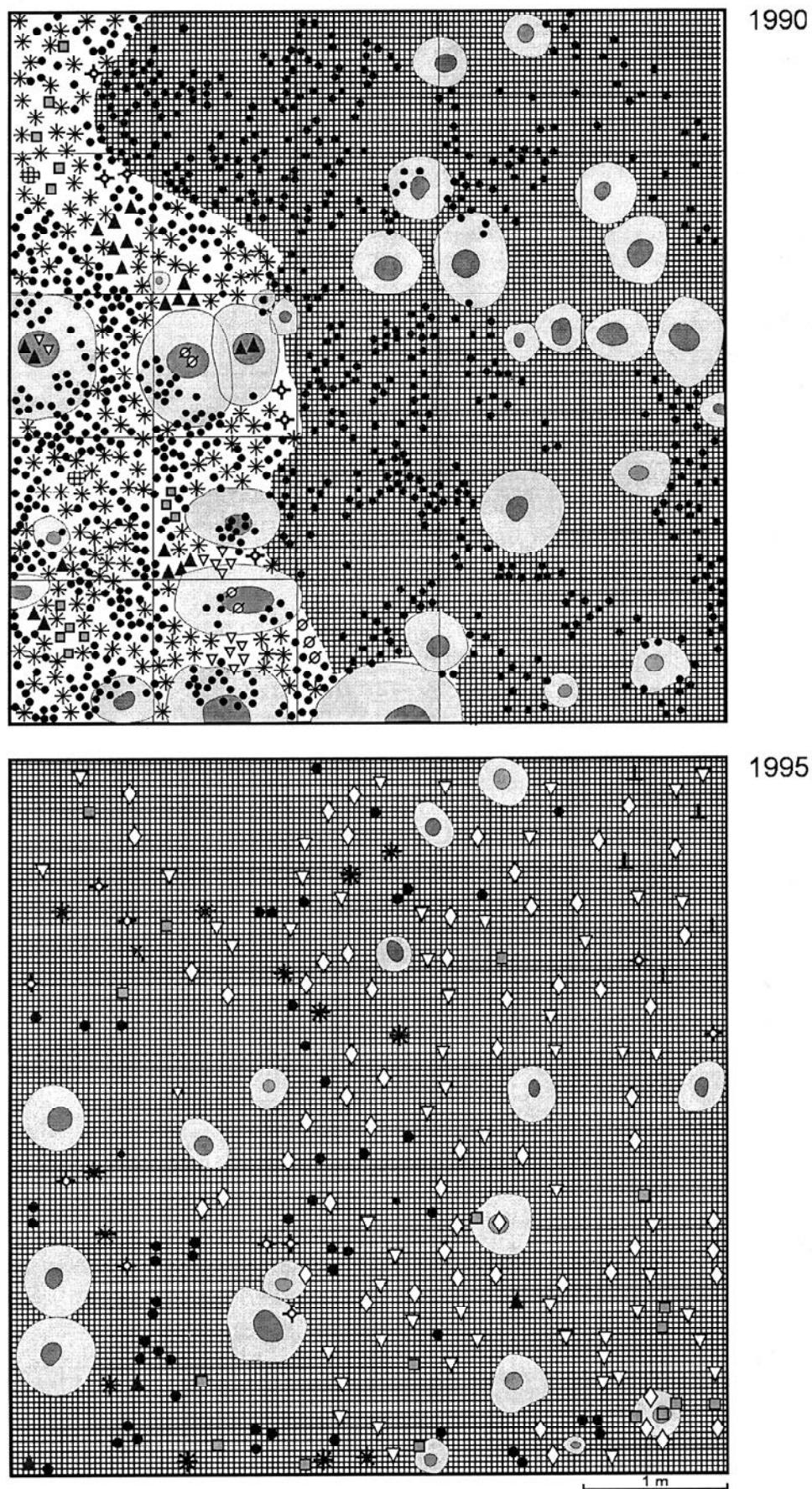


Fig. 2 - Changes in the species composition of *Cirsietum rivularis* community on abandoned meadows since 1975. Development of willow brushwood; on the left the permanent quadrats for the years 1980 and 1985; on the right for the years 1990 and 1995 (from FALIŃSKA, 2003).

convergence - their share in the community, spatial relationships and dynamics through time - is becoming more popular (Fig. 2). Major mechanisms forming specific species combinations

are considered to be:

- selective effect of abiotic factors;
- competition between species colonizing the same site;
- evolutionary strategies of species.

EFFECTS OF DEMOGRAPHIC PROCESSES IN POPULATIONS VS. SHARE OF SPECIES IN COMMUNITIES

Individual species are represented

in a community by a varying number of individuals, and their number is described by a slight skew distribution. As a rule, communities are formed by the lowest number of the most numerous species, but the majority of individuals belongs to this group in a phytocenosis. Phytosociology studies have demonstrated that the floristical diversity of

communities has a repeatable structure, quantifiable features of which include: number of species, number of individuals in a population, floristical diversity coefficients, coefficients describing the dominant species or, conversely, coefficients of the uniform distribution of species populations. According to plant demography, these features result

from relations between two population processes in each of the community components - fertility and mortality. Life history traits(STEARNS, 1992), such as longevity, fertility and persistence determine population processes (HARPER, 1977) which affect the stability or instability in population size of various natures - fluctuations, increase or de-

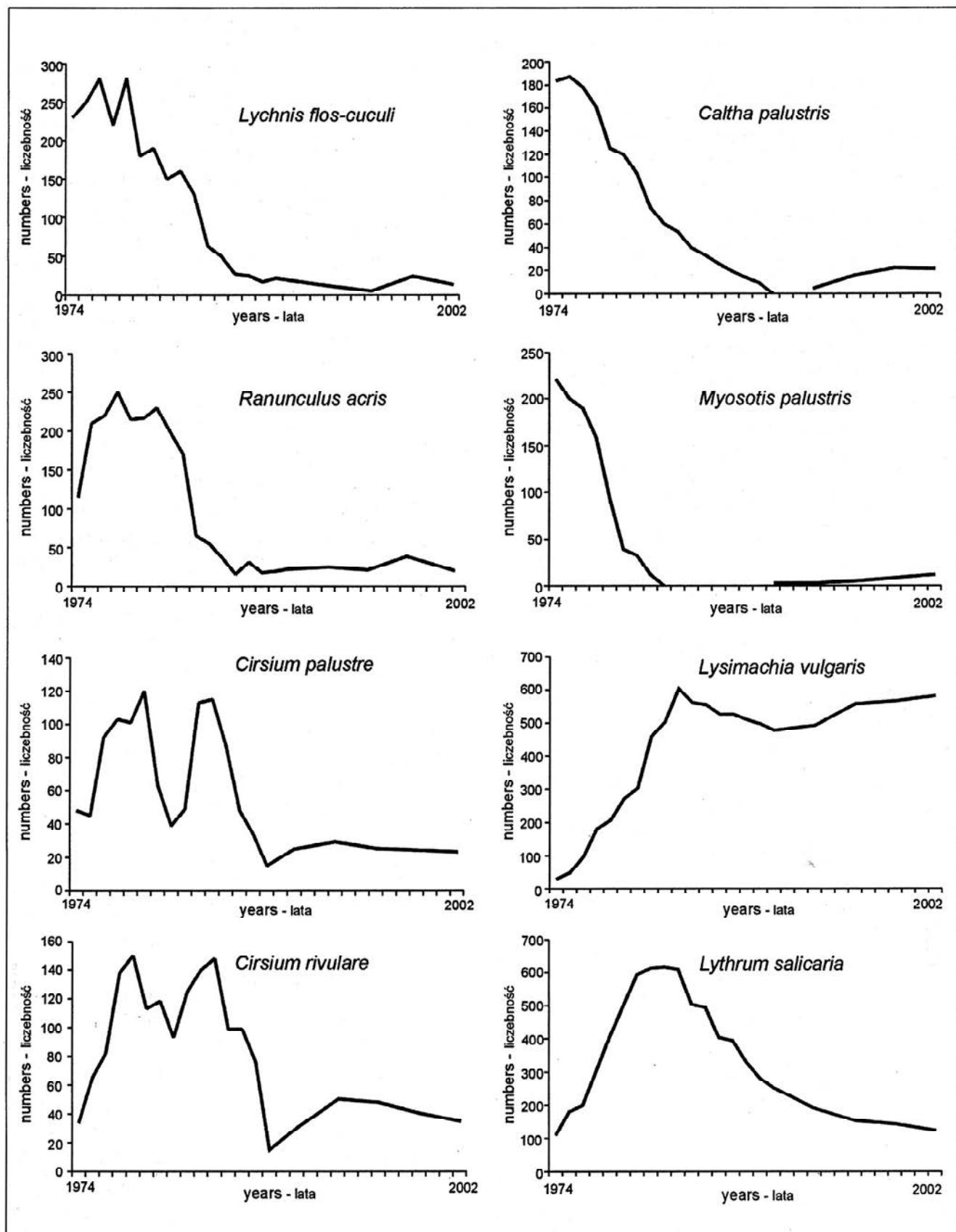


Fig. 3 - Patterns of changes in population abundance during succession on abandoned meadows (*Cirsietum rivularis*) (from FALIŃSKA, 2003).



Photo II-1. Range Reski in Narewka River Valley.



Photo II-2. Sedge swamp in the contact of bog alder forest.



Photo II-4. Isolated fragment of flood plain forest.



Photo II-3. Herb layer in bog alder forest.



Photo II-5. Young ash-alder flood plain forest developed during secondary succession.

Fig. 4 - Abandoned meadows in the contact with primaeval forest in the Białowieża National Park (photo J.B. Faliński).

crease (Fig. 3). Therefore, they decide on the presence and role of a species in a community, or change in species composition (Fig. 2).

A number of identified demographic features of plants support the population concept of community structure:

- populations of the same species are characterised in different communities by various numbers of individuals, spatial structure and dynamics;
- variation in population may result from the modification of life history traits or may have an ecotypic nature;
- physiological and ecological amplitudes of species most frequently do not overlap;
- none of the species colonizes the entire site, which would have been potentially colonized in view of the habitat, climate and geographical limit; the dispersal potential of a species faces an obstacle, namely the same potential of other plants able to exist under the same ecological conditions.

Therefore, comparable floristic compositions are not always formed under comparable ecological conditions and vice versa. This view is even more authenticated by the changes in vegetation that occur in response to anthropogenic activity disturbing the species structure in communities and thus making their classification difficult according to known phytosociology models (Fig. 4).

DOES A PHYTOSOCIOLOGICAL RELEVÉ REFLECT THE RESULTS OF DEMOGRAPHIC PROCESSES IN VEGETATION?

In contrast to the individualistic concept, which assumes that species compositions are unique in nature and thus there are no grounds for their classification, the phytosociology concept assumes the community is distinct and repeatable under specified ecological conditions. The population concept of vegetation structure suggests that in nature the population traits, especially the life history traits of individuals, are decisive for vegetation diversity. WHITE (1985) concluded that vegetation structure and dynamics depend on the features of the individuals from different species forming it, particularly their architecture, growth patterns, phenology and reproductive strategies. The question of whether communities are mere assemblages of organisms in a location or whether they are tightly linked and structured groups of interacting species

is still debatable (HARPER, 1977; SILVERTOWN, 1982).

Regardless of the adopted concept (community, continuum) it has been more and more frequently concluded that the possibility of finding many and diversified species on the same site initially results from their ecological amplitude (individualistic reaction of species). However, their further coexistence is determined by various interactions between individuals that depend on their life history, and which correspond with demographic processes in populations, like fertility, mortality and population size. Despite the differences in community concepts, in the basic method for phytosociological studies, it is a phytosociological relevé based on a floristical criterion, information such as relationships between species is expresses by "degrees of presence", i.e. the population size, and between individuals - by "sociability degree", i.e. life history traits and demographic processes. Therefore, these two concepts are complementary in certain situations.

HARPER (1981) suggested that the plant community concept, based on neighbour interactions which are mechanisms for species coexistence, is a challenge yet to be faced by ecology. However, experimental studies based on this concept have so far been limited to communities formed by a few species. For communities with a complicated and complex structure this concept has to be extended, especially with precise experimental methods.

Summarizing, the description of vegetation is more exhaustive if it contains more information on species life history, diversification of populations formed by the same species in various communities and, when characterising species role (share, frequency) in the community, such parameters as changes in size and spatial structure of populations which establish an ecological assemblage - the community.

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APPLICAZIONE DEL METODO FITOSOCIOLOGICO PER LA DEFINIZIONE DEI CRITERI GESTIONALI DI HABITAT FORESTALI DELL'ALL. I ALLA DIRETTIVA 92/43/CEE

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ABSTRACT

The 92/43/EEC Habitat Directive offered the opportunity to combine phytosociological knowledge and practical management of many natural and half-natural habitats. The presented case-studies, focused on some central-Italy *Quercus frainetto* and *Q. virgiliiana* communities, show the need of an interdisciplinary approach in the management of forest habitats in order to safeguard their floristic and vegetational peculiarity. Forestry techniques, together with a phytosociological approach, can represent the proper tool to “restore or maintain the natural habitats and species of Community interest at a favourable conservation status”.

KEYWORDS: 92/43/EEC Habitat Directive, forest vegetation, 91M0, management, *Quercus frainetto*, *Quercus virgiliiana*, forestry, phytosociology.

INTRODUZIONE

Gli studi della vegetazione basati sul metodo fitosociologico di BRAUN-BLANQUET (1928, 1951, 1964), fondatore della Scuola di Zurigo-Montpellier, hanno così fortemente caratterizzato l’Europa negli ultimi cento anni (un secolo fa è stato definito per la prima volta il termine ‘associazione’) tanto che i modelli sintassonomici proposti sono serviti da strumento per la definizione della Carta delle vegetazione naturale potenziale d’Europa (BOHN *et al.*, 2003) e degli habitat di interesse comunitario riportati nella Direttiva 92/43/CEE (EUROPEAN COMMISSION, 2007).

Con l’applicazione di tale Direttiva il metodo fitosociologico in Italia e anche in Umbria esce dal mondo accademico ed entra di diritto in quello delle discipline applicate e delle professioni. Ciò ha determinato un aumento della popolarità e del numero degli esperti, non sempre a vantaggio di una coerente interpretazione della Direttiva stessa. A tale scopo, la Società Botanica Italiana e la Società Italiana di Fitossociologia (ora Società Italiana di Scienza delle

vegetazione) hanno approntato il Manuale interpretativo *on-line* (BIONDI *et al.*, 2009; <http://vnr.unipg.it/habitat/>).

Un altro campo in cui il metodo fitosociologico si è dovuto confrontare con il mondo delle professioni è rappresentato dalla risoluzione pratica dei problemi relativi alla redazione di piani di gestione finalizzati alla tutela di specie ed habitat di rilevanza comunitaria. In questa fase applicativa si è posta con urgenza la necessità di formulare procedure chiare, in termini di risultati attesi, nella gestione sostenibile degli ecosistemi, forestali e non, che coniughino finalità produttive e obiettivi di conservazione.

I casi di studio presentati descrivono la necessità del confronto delle informazioni sintassonomiche necessarie per l’interpretazione degli habitat forestali con informazioni ecologiche spesso carenti, soprattutto se gli habitat considerati sono caratterizzati da alcune specie forestali poco comuni, quali *Q. frainetto*, o addirittura poco chiare dal punto di vista tassonomico, quali *Q. virgiliiana* e *Q. dalechampi*, oppure costantemente neglette nelle tradizionali attività di selvicoltura (*Fraxinus ornus*, *Acer* sp. pl., *Sorbus* sp. pl., ecc.). È chiaro che il rapporto attuale dei valori di copertura e abbondanza delle specie presenti in un bosco è il risultato anche della storia selviculturale di quel sito: un piano gestionale non corretto potrà alterare per molto tempo (secoli) le caratteristiche floristico-strutturali di una fitocenosi forestale, anche nel caso in cui questa venga lasciata a naturale evoluzione.

Ciò è vero in particolare per diverse formazioni forestali a dominanza di alcune specie quercine quali il farnetto e la quercia virgiliiana, oggetto del presente studio. Dal punto di vista gestionale, tali entità presentano dei comportamenti che le differenziano notevolmente dalle altre querce caducifoglie dell’Italia centrale; in particolare, rispetto al cerro o alla roverella, vi sono notevoli differenze per quanto riguarda il grado di eliofilia, la capacità pollonifera, la capacità germinativa, l’accrescimento ipsometrico giovanile. Tali

differenze, unitamente alla diversa composizione vegetazionale delle formazioni in esame, fanno ritenere inadeguate per queste cenosi le tecniche culturali impiegate per i boschi di cerro o di roverella. A tale proposito si esaminano alcuni casi esemplificativi sottoposti a diverse tipologie sperimentali di gestione selviculturale.

CASI DI STUDIO

I casi di studio qui proposti (Fig. 1) si riferiscono a due cenosi forestali con distribuzione localizzata nei territori preappenninici occidentali dell’Umbria. Tali aree si caratterizzano per la bassa quota e la compresenza di tipologie di vegetazione ecologicamente e biogeograficamente molto differentiate che, spesso, trovano il limite dell’areale proprio in quest’area, conferendo interessanti combinazioni floristiche e fitoceanotiche alle stazioni interessate. All’origine di tale particolarità è l’esistenza in questi territori di un’area di transizione climatica tra la Regione temperata e quella mediterranea; importante direttrice biogeografica è inoltre quella che va dai territori W e NW-Europei a quelli sud-orientali dell’Europa. Le due tipologie fitocenotiche prese in esame sono i boschi a dominanza di farnetto (*Maloflorentinae-Quercofrainetto* sigmetum), profondamente influenzati nella composizione floristica dalla componente balcanica e SE-Europea (BIONDI *et al.*, 2001), e quelli a dominanza di quercia virgiliiana (*Asplenio-Querco cerridis* sigmetum var. *a Quercus virgiliiana*) che presentano al loro interno un discreto contingente di entità a carattere subatlantico e centro-europeo (GIGANTE *et al.*, 2007a, 2008). La loro distribuzione in Umbria è molto ristretta; le stazioni di presenza sono state inserite nella Rete di Siti Natura 2000 (IT5210020, IT5210028, IT5210033, IT5210077).

INQUADRAMENTO VEGETAZIONALE

Fitocenosi a dominanza di *Quercus frai-*

netto (*Malo florentinae-Quercetum frainetto* Biondi, Gigante, Pignattelli e Venanzoni 2001).

Q. frainetto è specie rara a livello regionale e di grande interesse fitogeografico. È inclusa nella Lista Rossa Regionale con la categoria VU (vulnerabile) (CONTI *et al.*, 1997) nonché tutelata dalle Leggi Regionali 28/01 (Tabella "A") e 27/00 (P.U.T., All. A). Si tratta di una specie a distribuzione SE-Europea che trova in Umbria e Toscana il proprio limite nord-occidentale di areale; è legata ad habitat di pianura e di versante dolcemente acclive, su suoli moderatamente freschi e acidi. Le formazioni prese in considerazione sono state riferite all'associazione *Malo florentinae-Quercetum frainetto* ed inquadrate nell'alleanza *Teucrio siculi-Quercion cerridis* Ubaldi 1988 nomen conserv. prop. Filesi, Di Pietro e Blasi 2004 (BIONDI *et al.*, 2001, 2002). Si tratta di censi miste caducifoglie a dominanza di cerro e farnetto legate a morfologie pianegianti o dolcemente acclivi, con inclinazione media pari a circa 5° (BIONDI *et al.*, 2001). L'associazione presenta determinismo edafico e sopperisce alla carenza idrica derivante dal contesto

climatico submediterraneo grazie alla presenza di suoli profondi e ricchi di argilla. Questi boschi rappresentano la testa della serie umbra submesomediterranea acidofila del farnetto *Malo florentinae-Querco frainetto* sigmetum (VENANZONI *et al.*, 2010). Le formazioni a dominanza di *Q. frainetto* sono state riferite all'Habitat 91M0 "Foreste pannoniche-balcaniche di cerro e rovere" (GIGANTE *et al.*, 2007b). La loro distribuzione nel contesto nazionale e regionale è molto ristretta; in Umbria le uniche località di rinvenimento sono Collestrada, Colombella, S. Biagio della Valle, Giove, Montecastrilli.

Fitocenosi a dominanza di *Quercus virgiliiana* (*Asplenio-Quercetum cerridis* Ubaldi, Zanotti, Puppi, Speranza e Corbetta ex Ubaldi 1995 var. a *Quercus virgiliiana*).

Il secondo caso di studio è rappresentato dalle censi forestali a dominanza di *Quercus virgiliiana*, entità affine al gruppo di *Q. pubescens*, taxon complesso e non del tutto noto, di volta in volta interpretato come macrospecie o come gruppo di specie interfertili, distinguibili sulla base di caratteri

talora ambigui e molto variabili. Con riferimento a recenti proposte che combinano i più validi caratteri morfologici con l'ecologia delle singole specie, l'entità *Q. virgiliiana* è stata identificata sulla base della classificazione proposta da BRULLO *et al.* (1999).

Le analisi svolte si riferiscono alle formazioni planiziali presenti nella Piana di Ferretto in Umbria, ad ovest del Lago Trasimeno (VENANZONI *et al.*, 2005; GIGANTE *et al.*, 2007a). Dal punto di vista geo-pedologico, l'area è coperta da sedimenti Villafranchiani sui quali si sviluppano suoli lisciati, decarbonatati, caratterizzati da falda superficiale temporanea. Benché a forte vocazione agricola, l'area è di particolare rilevanza dal punto di vista naturalistico ed ospita al suo interno il SIC IT5210020. Le formazioni forestali in esame sono caratterizzate da un elevato grado di frammentazione in relazione all'intenso utilizzo antropico; si tratta spesso di parcelli di modeste dimensioni, a diretto contatto con le aree agricole.

Sulla base di recenti indagini fitosociologiche la vegetazione viene riferita all'associazione *Asplenio-Quercetum cerridis* per la quale viene identificata una variante a *Quercus virgiliiana*, in corso di approfondimento (GIGANTE *et al.*, 2007a, 2008); l'inquadramento sintassonomico fa riferimento anche in questo caso all'alleanza *Teucrio siculi-Quercion cerridis*. Questi boschi rappresentano la Testa della Serie preappenninica umbra submesomediterranea acidofila edafa-mesofila planiziale della quercia virgiliiana (*Asplenio-Querco cerridis* sigmetum var. a *Quercus virgiliiana*). Vengono riferiti all'Habitat 91M0; la loro distribuzione nel contesto nazionale e regionale è molto ristretta.

Entrambe le tipologie forestali considerate presentano un elevato grado di vulnerabilità verso numerose minacce, alcune delle quali direttamente derivanti da un'attività gestionale poco appropriata. Tra queste possono essere menzionate: la dimensione troppo ridotta delle parcelli forestali, con conseguente isolamento della specie dominante e vulnerabilità ad attacchi parassitari e malattie; l'attività di ceduazione con turni troppo ravvicinati; la semplificazione strutturale del bosco con omogeneizzazione delle classi di età ed eliminazione della componente arbustiva; l'omogeneizzazione e l'impoverimento floristico dello strato arboreo a causa del taglio delle essenze non economicamente interessanti; l'eccessiva vicinanza delle aree agricole, con sot-



Fig. 1 - Localizzazione delle aree di studio.

trazione di spazi e persistenza di disturbo; l'accumulo di sostanze azotate provenienti dalle aree agricole adiacenti, con alterazione delle caratteristiche dei suoli; la scarsa presenza delle formazioni di mantello in quanto la lavorazione agricola si spinge spesso fino alla base degli alberi; la conseguente ingressione di specie nitrofile e ruderali.

ASPECTI GESTIONALI

Nel sito di Ferretto (bosco di proprietà pubblica) *Q. virgiliiana* è presente insieme a un'elevata percentuale di resinose introdotte con piantagioni di conifere effettuati all'inizio del XX secolo (in particolare con *Pinus pinaster*), spesso con l'obiettivo di svolgere attività vivaistica in bosco, per la produzione di piante ornamentali.

Il trattamento applicato è classificabile come 'fustaia sopra ceduo': negli ultimi decenni questi boschi sono stati gestiti ceduando le latifoglie e rilasciando quasi totalmente le conifere; solo sporadicamente sono stati rilasciati esemplari di quercia come matricine. Tale modalità di trattamento ha portato inevitabilmente a favorire il pino marittimo rispetto alla quercia virgiliana, diventando molto spesso la specie prevalente.

Nel bosco in esame l'ultimo intervento era stato effettuato circa 30 anni fa e la struttura verticale si presentava tendenzialmente monoplana, con i polloni che avevano raggiunto lo strato

delle piante di alto fusto. La percentuale di conifere risultava notevole, pari a circa il 55% dell'area basimetrica. Molti piante di pino marittimo presentavano evidenti problemi di stabilità ed erano presenti numerose piante schiantate.

Nel sito di San Biagio della Valle (bosco di proprietà privata), nel bosco a prevalenza di *Q. frainetto*, il trattamento applicato dall'inizio del XX secolo può essere riferito al 'ceduo composto', con il rilascio di un elevato numero di matricine (circa 400 a ettaro) di più classi cronologiche. Questo trattamento era motivato dal fatto che il bosco costituiva una riserva di caccia e pertanto venivano salvaguardate le piante più grandi e con chioma più espansa. Negli ultimi decenni sono stati effettuati interventi più moderati, paragonabili a diradamenti di media intensità, che hanno portato a uno strato di fustaia di origine mista con copertura pari a circa il 70% e a uno strato dominato di ricacci e rinnovazione da seme.

Nella selezione delle piante da rilasciare sono stati privilegiati gli individui di migliore forma e pertanto lo strato della fustaia presenta una percentuale molto maggiore di *Q. cerris* rispetto allo strato dei polloni e della rinnovazione.

Nel bosco in esame l'ultimo intervento era stato effettuato circa 15 anni fa e la struttura verticale si presentava tendenzialmente stratificata, con abbondante rinnovazione di *Q. frainetto*, anche affermata. La distribuzione diametrica delle piante mostra un andamento

assimilabile a una fustaia disetaneiforme, sebbene non vi siano piante di dimensioni particolarmente elevate (Fig. 2), e l'area basimetrica complessiva risulta moderata (circa 20 mq/ha).

Le modalità di trattamento applicate hanno portato a una diminuzione progressiva della capacità di rigenerazione agamica del farnetto, a un aumento del cerro nello strato dominante e a una scarsa diffusione delle specie sporediche minori (in particolare *Sorbus domestica* e *S. torminalis*, molto frequenti in zone limitrofe non sottoposte a intervento).

Nel sito di Collestrada (bosco di proprietà pubblica) è presente una fustaia transitoria a prevalenza di *Q. frainetto* e *Q. cerris*. L'ultima utilizzazione del ceduo risale a circa 45 anni fa; nel 2002-2003 a seguito di interventi finanziati per il miglioramento del bosco sono stati effettuati tagli di avviamento a fustaia con modalità d'intervento omogenee su tutta la superficie, senza tener conto dell'elevata diversità microstazionale presente e delle fitocenosi interessate dal taglio. L'intervento ha favorito gli individui di migliore forma e quindi il cerro rispetto al farnetto: le piante morte sono state sempre eliminate, lo strato arbustivo è stato tagliato completamente e specie d'importanza minore quali l'orniello e il sorbo, quasi del tutto eliminate dallo strato arboreo dominante. Sono stati improvvisamente interrotti i processi di rigenerazione del bosco (FALINSKI e PEDROTTI, 1990) che a distanza di decenni dall'ultimo

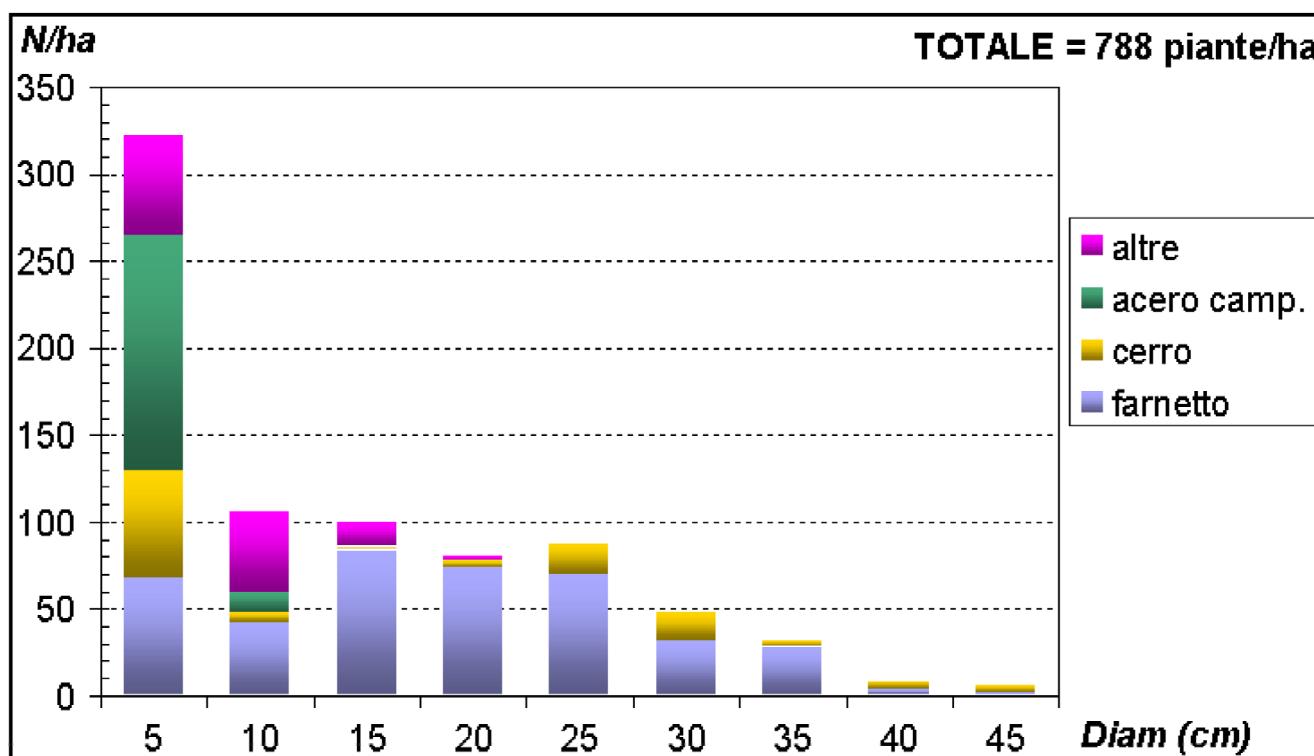


Fig. 2 - Distribuzione diametrica nell'area di San Biagio della Valle, con indicazione della composizione specifica.

taglio cominciavano ad avere effetti positivi.

L'intervento effettuato ha quindi portato a una diminuzione della diversità specifica e strutturale, favorendo in tutte le fitocenosi il cerro rispetto al farnetto. Ciò nonostante, risulta presente un'abbondante rinnovazione in fase di affermazione, prevalentemente di farnetto e orniello.

PROPOSTE GESTIONALI

Allo scopo di individuare modalità colturali più idonee per *Q. virginiana* e *Q. frainetto* e soprattutto per garantire la conservazione degli habitat ai sensi della Dir. 92/43 CEE, in particolare del 91M0, sono stati effettuati degli interventi a carattere sperimentale/dimostrativo nei boschi di Scopeti e San Biagio. Nel bosco di Collestrada non sono stati effettuati interventi, considerato il brevissimo intervallo di tempo intercorso dal taglio di avviamento, ma sono stati proposti gli indirizzi gestionali per il futuro.

Nel sito di Ferretto, in loc. Scopeti, è stato effettuato un diradamento localizzato e puntuale che interviene sul piano dominante (FRATEGIANI *et al.*, 2006). Gli obiettivi dell'intervento erano:

- garantire condizioni favorevoli alla rinnovazione ed affermazione delle specie autoctone;
- favorire la graduale sostituzione delle conifere.

L'intervento è stato effettuato su una superficie di circa 2 ettari con un prelievo pari a circa il 15% dell'area basimetrica; il 97% delle piante tagliate erano di *Pinus pinaster*. Lo strato arbustivo è stato tagliato solo nelle zone necessarie per l'abbattimento e l'esbosco del materiale (circa il 20% della superficie complessiva).

L'intervento ha agito su:

- nuclei di piante che ostacolavano l'affermazione della rinnovazione di latifoglie;
- nuclei di piante situati in zone in cui favorire l'insediamento di nuova rinnovazione;
- piante instabili che rappresentano un rischio diretto per la stabilità del popolamento.

Nel sito di San Biagio è stato effettuato un diradamento localizzato e puntuale che interviene sul piano dominante e prevalentemente sulle piante di *Q. cerris*. Gli obiettivi dell'intervento erano:

- favorire la diversificazione strutturale;
- favorire i nuclei di rinnovazione pre-

senti;

- favorire le specie sporadiche (sorbi, olmi, aceri);
- favorire il farnetto rispetto al cerro;
- aumentare la necromassa presente.

L'intervento è stato effettuato su una superficie di 16,6 ettari in 5 anni, con un prelievo pari a circa il 5% della dendromassa totale. Lo strato arbustivo è stato tagliato solo nelle zone necessarie per l'abbattimento e l'esbosco del materiale (circa il 15% della superficie complessiva).

L'intervento ha agito su:

- nuclei di piante che ostacolavano l'affermazione della rinnovazione di latifoglie
- nuclei di piante situate in zone in cui si intende favorire l'insediamento di nuova rinnovazione.

Le fitocenosi forestali di Collestrada rivestono una notevole importanza scientifico-ecologica e anche didattica; già da tempo gli Autori svolgono ricerche e attività di insegnamento in queste formazioni. La ricerca scientifica è essenziale viste le limitate conoscenze sulle dinamiche evolutive, sulle peculiarità ecologiche e sulla gestione selvicolturale dei boschi di farnetto in Italia centrale; gli aspetti didattici rivestono particolare rilevanza in vista di un potenziale turismo naturalistico da valorizzare e incentivare anche nelle aree SIC.

La relativa abbondanza nella produzione di seme, la minore eliofilia e la minore capacità pollonifera del farnetto rispetto ad altre querce decidue italiane, unite alla presenza relativamente diffusa di rosacee arboree all'interno di questi boschi, fa supporre una particolare vocazione di queste formazioni a una gestione selvicolturale che si ispiri ai concetti della selvicoltura "naturalistica", con particolare riferimento ai principi enunciati dall'associazione "Pro Silva Europa" e indicati come esempio dalla Commissione Europea per la gestione dei boschi di interesse comunitario.

Per i boschi di farnetto di Collestrada si propone quindi una gestione mirata ad approfondire le conoscenze su queste formazioni, attraverso l'istituzione di una foresta sperimentale, prevedendo zone a evoluzione naturale e zone da sottoporre a interventi riconducibili alla selvicoltura "naturalistica".

CONCLUSIONI

Tutti i boschi esaminati sono sottoposti a gestione attiva, sebbene con modalità completamente differenti, di-

mostrando un interesse economico ancora presente nell'utilizzazione forestale. In considerazione della necessità di garantire allo stesso tempo le attività umane e la conservazione degli habitat, si ritiene indispensabile individuare modalità gestionali che tengano in maggiore considerazione le peculiarità delle due specie in esame e delle strutture ecosistemiche a loro associate.

La scarsa disponibilità di conoscenze di carattere ecologico e selvicolturale relative a *Q. frainetto* e *Q. virginiana* hanno portato da sempre all'applicazione di una *selvicoltura per approssimazione*, considerando le due specie equivalenti a quelle a loro ecologicamente più affini: il farnetto è stato considerato equivalente al cerro, la virginiana alla roverella.

Questa politica gestionale si rivela assolutamente sbagliata, andando nel tempo a favorire le due specie similari rispetto a quelle più rare e che la normativa vigente (e la coscienza ecologica di ognuno di noi) ci obbliga a tutelare.

Per tale motivo si ritiene di particolare importanza l'analisi della tipologia fitosociologica e del contesto ecologico correlato (clima, suolo, morfologia, ecc.), proponendo per tale scopo:

- la realizzazione di una rete di aree sperimentali sull'ecologia e sulla gestione di *Quercus frainetto* in Italia centrale;

- la realizzazione di una indagine specifica sulla diffusione di *Quercus virginiana* in Italia centrale e sulle modalità gestionali applicate.

La presenza dei SIC aumenta le opportunità e le necessità di istituire piani di continuo monitoraggio, particolarmente importanti in tipi forestali con diffusione limitatissima.

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THE WARM-TEMPERATE RICHNESS ZONE IN COASTAL DUNE VEGETATION OF CONTINENTAL EAST SIDES (NORTHERN HEMISPHERE)

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ABSTRACT

This paper compares east-coastal dune vegetation in the Northern Hemisphere, in particular between Japan and eastern North America. Both regions extend north-south over about 3000 km of coastline, and their floras have been compared since the time of Asa Gray. The first phytosociological classifications of coastal vegetation were reported in Europe by BRAUN-BLANQUET and TÜXEN (1943), and Japanese coastal vegetation was studied phytosociologically by OHBA *et al.* (1973). Ammophilete arenariae Braun-Blanquet & Tüxen 1943 is the main class in the Northern Hemisphere, but it is quite fragmented in eastern North America and is more complex in Japan. Temperate forest composition is similar around the Northern Hemisphere at the genus level, but coastal dune vegetation can be very different. Dune vegetation in southern temperate areas is quite different from northern areas, and it may overlap, also with subtropical-tropical dune vegetation, creating a region of higher diversity, at least for the main dune species.

KEYWORDS: relevé data, Japanese dune vegetation, vegetation zonation, warm-temperate zone, Eastern North American Vegetation Survey.

INTRODUCTION

Coastal sand-dune vegetation is unique vegetation occurring under severe environmental constraints such as salt spray, frequent strong wind, and sand movement. Substrate stability is especially important for vegetation on dunes and beaches, which are also quite dry environments physiologically, as is described by BARBOUR *et al.* (1985). In tropical and subtropical areas, low-energy coastlines generally have mangroves while high-energy coastlines have sandy beaches, with cosmopolitan scrub (e.g. *Scaevola*) and colonizers (e.g. *Ipomoea pes-caprae*). As frost appears northward, the mangroves give way to salt marshes and the beaches tend to

have higher dunes behind them, carrying dune grasses and dune scrub in the warm-temperate zone. Salt marshes extend northward well into boreal latitudes.

Eastern sides of continents show similar climatic and vegetation zonation in the Northern Hemisphere (Box, 1995), with many common plant genera. Similarities between the vegetation and taxa of East Asia and eastern North America have been known since the time of GRAY (1846), if not earlier, and have been studied in some detail (e.g. GRAHAM, 1972; BOUFORD & SPONGBERG, 1983; Box, 1988), albeit less so along the coasts. Japan, including the Ryukyu Islands, is located along the eastern rim of the Eurasian mainland and corresponds latitudinally to the region in eastern North America from southern Québec to the Florida Keys. This similarity in zonation means that one might compare coastal East Asia and eastern North America and expect to find similar patterns not only in the structure of dune vegetation and plant communities, but also in plant taxa and species richness. The latitudinal zonation of coastal vegetation is somewhat decoupled from that further inland, however, and is generally shifted somewhat toward the poles, since winter temperatures are moderated along the coasts.

Dune vegetation in the temperate zone is characterized by particular species of Gramineae and Cyperaceae, which typically grow on small mounds and fix potentially mobile dunes with their well developed root systems. Other species, such as Convolvulaceae (*Calystegia* and/or *Ipomoea*) and Compositae (*Ixeris*), fix the sand by creeping along the ground and rooting at the nodes. Dune and other coastal vegetation has been studied in various parts of the world, but usually only locally (e.g. SUZUKI, 1979; SUZUKI & FUJIWARA, 2001; HAYASAKA & FUJIWARA, 2006; DA SILVA *et al.*, 2008). Major studies in Japan include that by OHBA *et al.* (1973), a study of longshore seed distribution by NAKANISHI (2010), and syntheses of coastal vegetation in the "Vegetation of

Japan" series (MIYAWAKI, ed., 1980-1989). Study of coastal vegetation in eastern North America began earlier, and major studies include many by OOSTING (1945, 1954), a compendium of seaside plants by DUNCAN & DUNCAN (1987), a short coastal synthesis by CHRISTENSEN (1988), and a synthesis of dune vegetation by COOPER (1975). Only DOING (1985) seems to have attempted a broader global synthesis of dune vegetation.

A first approximation of latitudinal coastal zonation is suggested by maps of inland zonation. The ecoregion map by BAILEY (1990), for example, shows five along the east coast from maritime Québec to south Florida and four along the Pacific coast of Japan (Ryukyu Islands not shown). Some regions carry the same type name and number in corresponding locations in the two regions. There is also a clear tendency for the coastal grasses, sedges, and scrub taxa to segregate into distinctly northern and distinctly southern species in the temperate and tropical zones, with an overlap region in the middle. Where is this "middle"? Using relevé data from both regions, this paper develops the idea that the overlap occurs primarily in what corresponds to the warm-temperate zone and that this zone has the richest coastal dune vegetation, at least in terms of co-occurring major dune species. Analysis involves comparison of latitudinal and other patterns in the coastal vegetation of the two regions, looking in particular at which major species occur together, how far north subtropical/tropical species extend, and how far south the northern species extend. If there is an identifiable overlap zone, on the two continental east sides, where is it located?

DATA AND METHODOLOGY

Relevés of coastal dune vegetation were made, in Japan, from northern Hokkaido through all the Ryukyu Islands and, in North America, from maritime Québec to south Florida. The Japanese data were collected during the

exhaustive inventory (1980s), directed by Prof. Akira Miyawaki and funded by Monbushō (the Japanese Ministry of Science, Education and Culture), that culminated in the ten-volume "Vegetation of Japan" series, which includes maps and phytosociological summary tables with each volume (MIYAWAKI, ed., 1980-1989).

The data for eastern North America come from the so-called Eastern North American Vegetation Survey (ENAVS, 1988-1990), which was also directed by Miyawaki and funded by Monbushō in order to gather data for comparison with parallel geographic situations in Japan (MIYAWAKI *et al.*, 1994). Field itineraries focused on na-

tural vegetation, are shown in Box (1994), and collected about 1400 relevés in total, nearly 300 for coastal vegetation and about 160 for coastal sand dunes and related sandy substrates (littoral, berms, beaches). Coastal vegetation in eastern North America was sampled most along the St. Lawrence estuary and on the ocean coastlines of Nova

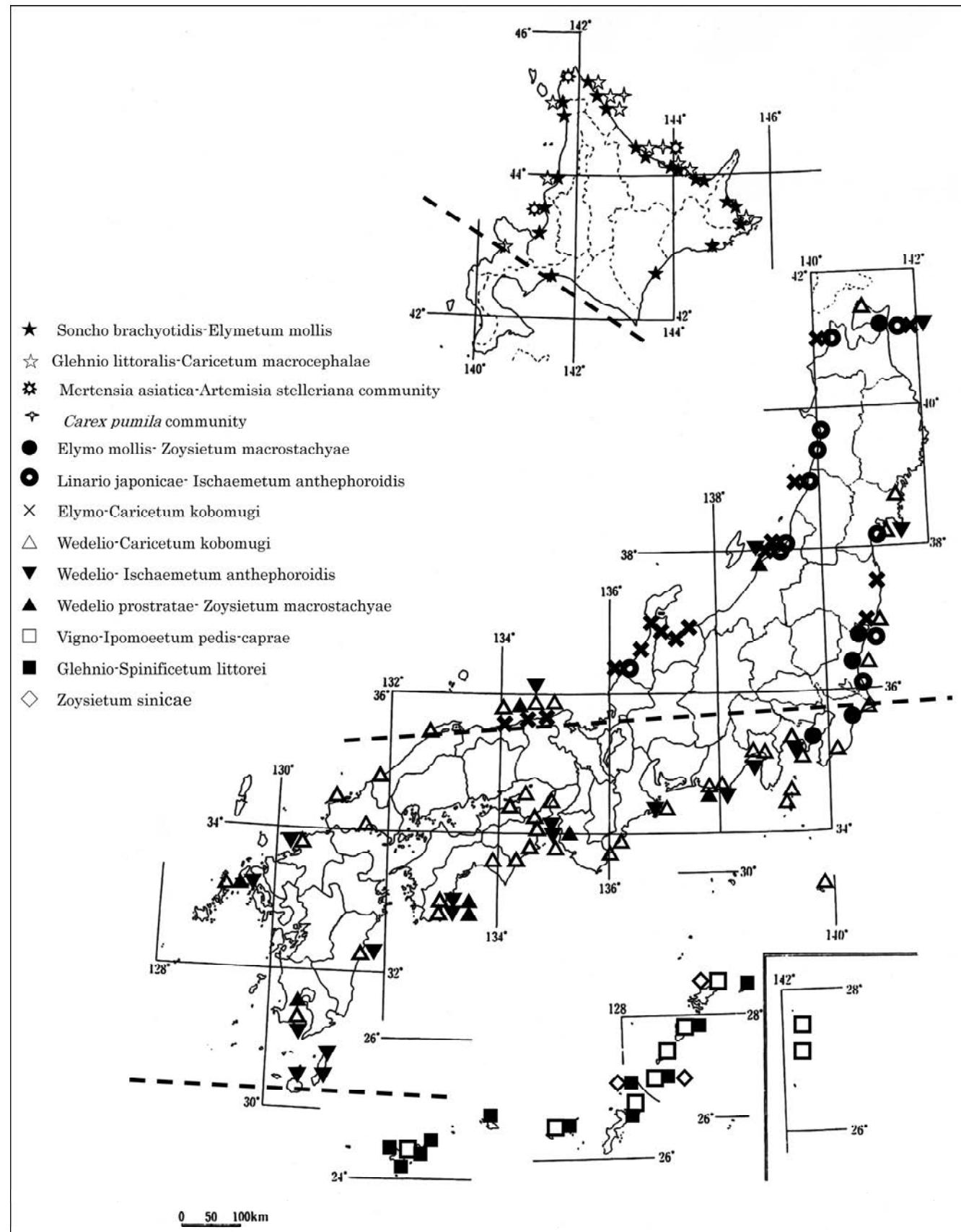


Fig. 1 - Japan map with presence locations of different associations.

Scotia, Cape Cod, Long Island, North Carolina, Georgia, and both sides of the Florida peninsula, including the Gulf of Mexico coast of western Florida.

The relevés were recorded by traditional Braun-Blanquet methodology, using cover and sociability scales of 1–5, as described by FUJIWARA (1987). Each relevé was recorded on a form that included the species data, date and relevé number, layer heights and cover amounts, location, elevation, slope and aspect, relevé size, personnel, and verbal descriptions of vegetation type. The Japanese data were synthesized with Microsoft Excel, using standard phytosociological methods and table-work. The ENAVS data were computerized in 1989–1991 by the second author, including standardized topography and substrate information that was recorded for each site (see Box & FUJIWARA, in this volume). A raw table for the ENAVS coastal data was produced by RAWTAB-BLR (Box, unpublished), and phytosociological summary tables were produced by the first and third authors, by standard table-work methodology.

RESULTS

Communities of coastal dune-meadow vegetation and sampling locations in Japan, on both the Pacific and Japan Sea sides, are shown in Fig. 1. The most important plants in northern coastal dune meadows are generally *Elymus mollis*, *Carex macrocephala* and other sedges, and *Zoysia macrostachya*, along with *Artemisia stelleriana* in Hokkaido. In the south *Zoysia sinica* and *Spinifex* become important, along with *Ipomoea pes-caprae*. Fig. 1 suggests several distinct sectors: subtropical and northernmost sectors that are quite distinct and from which association ranges generally do not extend toward each other; a region of northern Honshu and southernmost Hokkaido with northern communities but also some occurrences of species and communities from further south; a counterpart in southern Honshu, Shikoku and Kyushu, with southern communities but some effects from the subtropical sector further south; and finally a main overlap region (about 41–36° N), from Kanto (the region around Tokyo Bay) to northernmost Honshu, in which some northern and warm-temperate taxa and communities overlap. Vegetation zonation along the coastline was described phytosociologically by OHBA *et al.* (1973). Foredune vegetation exposed to salt spray is mainly Cakiletea maritimae with *Salsola ko-*

marowii and *Atriplex gmelinii*. Meadow vegetation, including *Calystegia soldanella*, *Ixeris repens*, *Carex kobomugi* (on convex dunes), *Carex pumila* (on concave dunes) and *Glehnia littoralis*, occurs on the first mobile dunes. Behind these dunes, *Ischaemum anthiphoroides* occurs on stable dunes. Scrub communities are not covered in this report, but wind-stunted scrub does occur, involving species such as *Vitex rotundifolia* (Honshu), *Rosa rugosa* (northern Japan), and *Scaevola* (southern islands). The most important dune-meadow communities are summarized, phytosociologically, in Tab. 1.

Tab. 1 shows a clear difference between Yakushima (off southern Kyushu) and the Amami Islands, with their tropical and subtropical species such as *Ipomoea pes-caprae*, *Vigna marina*, *Spinifex littoreus* and *Zoysia sinica*. These species characterize tropical associations. On the other hand, characteristic species of Glehnietea littoralis occur northward until Hokkaido. OHBA *et al.* (1973) recognized two classes in coastal meadow vegetation in Japan. Northern vegetation is described as belonging to a Honckenyo mayoris-Elymetea Tüxen 1966 and southern and middle Japan as belonging to a Glehnietea littoralis Ohba, Miyawaki et Tüxen 1973. In the summarizing Tab. 1, though, there is no clear difference between these two classes. Coastal meadow vegetation is classified into associations very simply, but European and Japanese species groups cannot be separated in northern Japan. A clear boundary is shown in Fig. 1, at about 30° N, between Yakushima and the Amami Islands. This also represents the northern limit of subtropical species, but forest species extend northward to around 38° N (FUJIWARA, 1986), which corresponds to the southern limit of the northern communities. These northern and southern communities overlap between 36° and 42° N, especially at 36–38° N. This middle area represents the northern part of the warm-temperate zone in Japan, where warm-temperate deciduous *Quercus* forest can be found as secondary forests of potential natural evergreen laurel forests.

The distributions of some important dune and beach elements in North America are shown in Fig. 2, from the on-line USDA Plant Database (USDA, 2010). *Elymus* is also an important dune-grass genus in eastern North America, especially in the north, but then *Ammodophila breviligulata* and especially *Uniola paniculata* appear further south, stabilize the dunes, and dominate the

southern dune vegetation. Species richness increases in foredune lees and includes species less tolerant of salt spray than is *Uniola*, such as *Panicum* subsp. (especially *P. amarum*), *Andropogon scoparius*, *Distichlis spicata*, *Cenchrus tribuloides*, and various forbs, some of which also occur in inland areas (cf OOSTING & BILLINGS, 1942; OOSTING, 1945; BOYCE, 1954). Wind-stunted scrub also occurs in protected swales, involving *Iva imbricata*, *Baccharis halimifolia*, *Myrica cerifera*, *Ilex vomitoria*, *Juniperus virginiana*, and *Quercus virginiana*. WELLS (1939) referred to the maritime forest (*Quercus*, *Pinus*, etc.) behind the foredunes as the “salt-spray climax”, and BOYCE (1954) described the entire complex as the salt-spray community.

Coastal vegetation types have been classified phytosociologically on the west coast of North America (PEINADO *et al.*, 2009) but not on the east coast. One can, however, find general indications of communities and zonation in KNAPP (1965), BARBOUR *et al.* (1985), DUNCAN & DUNCAN (1987), and CHRISTENSEN (1988), and in JOHNSON & BARBOUR (1990) for Florida. Based on the small total number of relevés available from the ENAVS data-base, an initial phytosociological summary table for coastal dune vegetation in eastern North America was constructed and is shown as Tab. 2. The dune-meadow vegetation is simpler in eastern North America than in Japan. There are not so many common species and even subtropical Florida has *Uniola paniculata*.

Finally, an attempt is made in Tab. 3 to compare the zonation in the two regions and to show the overlap region, which has the greatest richness in coastal dune species and communities. This overlap region appears to represent most of the warm-temperate climatic zone (inland and generally), both in Japan and in eastern North America.

Elymus mollis occurs in both regions, but the community composition is different. Ranges of northern species come down to about 30° N in both countries. Japan, however, is composed of separated islands, so tropical species stop in the subtropical zone and subtropical communities have no temperate species. Along the continuous coastline of eastern North America, on the other hand, there are no clear climatic or vegetation boundaries. So there is a significant temperate overlap region, and species may extend over more than one zone, such as *Uniola paniculata* in both the warm-temperate and subtropi-

Tab. I - Coastal sand-dune vegetation in Japan. 1-3) *Sonchus brachyotis*-*Elymus fum mollis*; 4-5) *Glehnia littoralis*-*Caricetum macrocephalae*; 6) *Mertensia asiatica*-*Artemisia stelleriana* community; 7) *Carex pumila* community; 8-12) *Elymo mollis*-*Zoysietum macrostachyae*; 13-17) *Linaria japonicae*-*Ischaemum antephoroidis*; 18-23) *Elymo-Caricetum kobomugi*; 26-33) *Wedelio-Caricetum kobomugi*; 34-41) *Wedelio-Ishaemum antephoroidis*; 42-45) *Wedelio prostratae*-*Zoysietum macrostachyae*; 45-55) *Vigno-Ipomoeaeum pedis-caprae*; 56-59) *Glehnio-Spinifex eum littorei*; 60) *Zoysietum sinicæ*.

Serial number	Number of relevés	Characteristic and differential species of ass.
1	2	<i>Carex macrocephala</i>
9	25	<i>Mertensia asiatica</i>
	47	<i>Zoysia macrostachya</i>
	13	<i>Ischaemum antiphorooides</i>
	8	<i>Carex kobomugi</i>
	5	
	5	
	8	
	5	
	16	
	10	
	11	
	4	
	11	
	6	
	8	
	16	
	18	
	6	
	8	
	12	
	3	
	14	
	32	
	8	
	6	
	5	
	7	
	52	
	30	

Characteristic and differential species of ass.

Local species

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Characteristic species of ass. and differential species of subunits

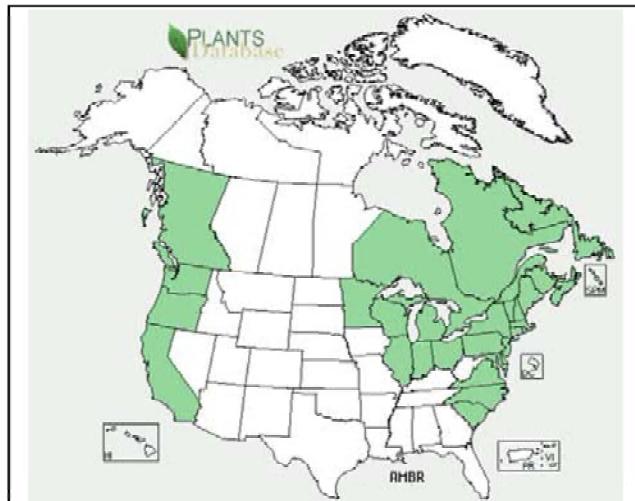
<i>Ipomoea pes-caprae</i>	<i>Vigna marina</i>
<i>Cassytha filiformis</i>	<i>Canavalia lineata</i>
<i>Spinifex littoreus</i>	<i>Thurea involuta</i>
<i>Philocerurus wrightii</i>	<i>Maytenus diversifolia</i>
	<i>Lepturus repens</i>

• 6

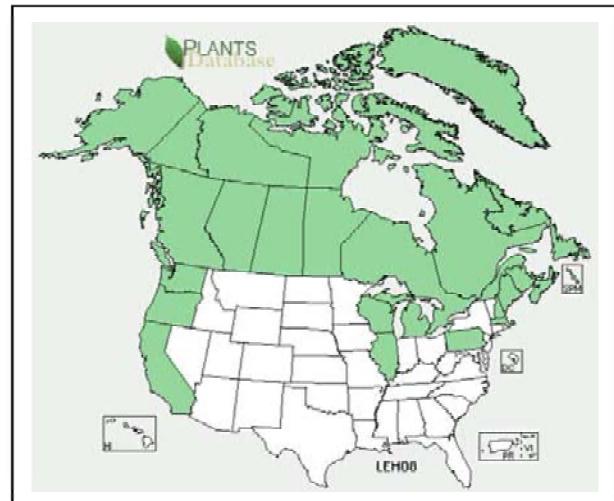
Tab. 1 - (continuation).

Serial number	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60				
Number of relevés	35	5	12	6	6	7	7	5	8	8	5	25	4	7	8	5	15	6	9	5	11	11	3	6	5	4	2	3						
Characteristic and differential species of ass.																																		
Carex macrocephala				
Mertensia asiatica				
Zoysia macrostachya				
Ischaemum antenniferoides				
Carex kobomugi				
Local species																																		
Elymus mollis	r			
Artemisia stelleriana			
Linaria japonica	r			
Festuca rubra			
Arabis stelleri var. japonica			
Wedelia prostrata	II	III			
Species of <i>Glehnia littoralis</i>																																		
Calystegia soldanella	IV	III	IV	III	III	II	V	IV	III	·	I	IV	2	III	V	III	II	I	·	I	·	·	·	3	·	·	·	1	·	·				
Glehnia littoralis	II	I	·	I	·	III	·	I	IV	IV	·	III	·	III	1	·	·	·	·	·	·	·	·	1	·	·	·	1	·	·				
Ixeris repens	III	II	·	·	·	V	III	III	·	II	I	III	·	II	I	·	·	·	·	·	·	·	·	1	·	·	1	·	·	·				
Carex pumila	+	·	·	·	1	1	·	1	II	·	I	II	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·				
Lathyrus japonicus	+	·	1	1	·	·	1	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	1	·	·	·				
Characteristic species of ass. and differential species of subunits																																		
Ipomoea pes-caprae	IV	III	IV	III	III	II	V	IV	III	·	I	IV	2	III	V	III	II	I	·	1	·	2	·	·	·	·	·	·	·	·	·			
Vigna marina	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·				
Cassytha filiformis	V	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II	·	·	II	·	·	III	V	·	1	1	·	·				
Canavalia lineata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	V	V	3	·	·	·	·	·	·	·	·	·	·				
Spinifex littoreus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·				
Thaumea involuta	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	V	V	IV	·	·	·	·	·	·	·	·	·	·				
Phloxurus wrightii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2	·	·	2	·	·	·				
Maytenus diversifolia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2	·	·	2	·	·	·				
Lepturus repens	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	·	+	·	·	1	·	·	·	·	·	2	·	·				
Zoysia sinica	·	·	·	·	·	·	·	·	·	·	II	·	·	·	·	·	·	1	·	·	1	II	·	1	3	·	3	·	·	·				
Other species																																		
Oenothera laciniata	+	III	·	IV	1	·	II	IV	·	1	I	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·			
Vitex rotundifolia	·	III	·	1	1	·	·	·	·	·	·	·	·	·	·	·	·	III	II	·	·	·	·	·	·	·	·	·	·	·	·	·		
Artemisia capillaris	r	1	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	3	V	1	·	·	·	·	·	·	·	·	·	·	·	·	·	
Rosa rugosa	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	
Messerschmidia sibirica	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·		
Cynodon dactylon	+	·	III	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·		
Raphanus sativus var. raphanistrum	·	·	·	·	·	·	1	·	·	1	·	·	·	·	·	·	·	V	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	
Euphorbia atropurpurea	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	III	·	1	·	·	·	·	1	1	1	2	2	2	2	2	2	2
etc.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	

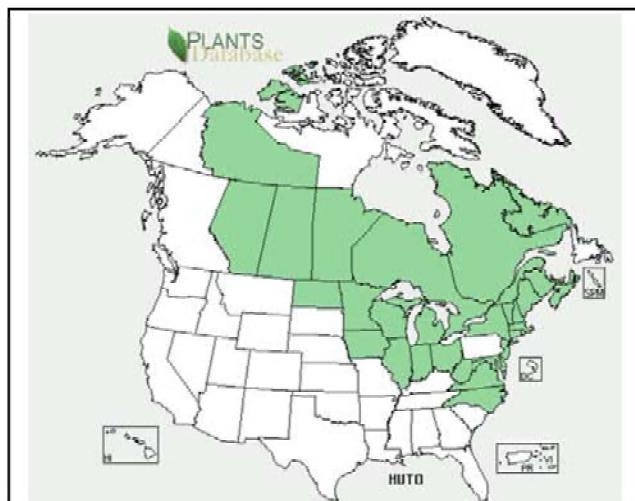
References of Serial Number 1-7, 18: Vegetation of Japan (V.J.) vol. 9 (Hokkaido); 8-11, 16, 17, 19-21, 26, 36, 42; V.J. 8 (Tohoku); 12, 13, 15, 31, 34; V.J. 7 (Kanto); 14, 22, 25, 37, 42; V.J. 6 (Chubu); 23, 30; V.J. 4 (Chugoku); 24, 41, 42; V.J. 5 (Kinki); 27-29, 32, 35, 43-45; V.J. 2 (Kyushu); 38, 42; V.J. 3 (Shikoku); 40; V.J. 1 (Yakushima); 46-60; V.J. 10 (Okinawa & Ogasawara).



AMMOPHILA BREVILIGULATA



ELYMUS MOLLIS



HUDSONIA TOMENTOSA



PANICUM AMARUM



BORRERIA FRUTESCENS



UNIOLA PANICULATA

Fig. 2 - Distribution of some main dune plants in eastern North America (from Plants Database, USDA).

cal zones.

CONCLUSIONS

The vegetation of coastal dune meadows has characteristic species and composes unique vegetation types in the warm-temperate zones of Japan and eastern North America. Generally the eastern sides of continents are seen as similar (e.g. GRAY, 1846; MIYAWAKI *et al.*, 1994), and quite different from west sides. In warm-temperate regions there are unique vegetation types, such as warm-temperate deciduous forests, and dune vegetation is also different. The northern parts of the warm-temperate zone, in particular, show overlapping vegetation types, which are thus a little richer than the more northern and southern regions.

Northern regions of both countries have the same circumpolar dune species, such as *Elymus mollis*, but the species composition of the communities is different (Tabs. 1 & 2). *Calystegia soldanella* occurs all over Japan, in North Carolina and Virginia of eastern North America and on the west coast of North America. It is a unique species in dune vegetation, corresponding to *Ipomoea pes-caprae* of the same family. *Lathyrus japonicus* occurs in Japan, northern Canada and the Great lakes area, Washington and Oregon, on Pacific islands, and in Germany, southern Sweden and around the Baltic Sea (DOING, 1985). The unusually extensive native range of *Lathyrus japonicus* is explained by the long-term viability of its seeds while floating in sea water and drifting perhaps worldwide. Germination occurs when the hard outer seed coat is abraded by waves on sand and gravel. Even with this wide range of *Lathyrus japonicus*, however, the species composition of communities is determined locally. In the ENAVS data, *Lathyrus japonicus* was recorded only at Chappaquoit in Massachusetts.

Tab. 2 - Synoptic table of dune vegetation in eastern North America: 1) *Panicum amarum* community; 2) *Borrichia frutescens* community; 3) *Uniola paniculata*-*Ipomoea pes-caprae* community; 4) *Hydrocotyle bonariensis*-*Uniola paniculata* community; 5) *Cakile constricta* community; 6) *Sporobolus virginicus* community; 7) *Schizachyrium littorale* community; 8) *Uniola paniculata* community; 9) *Uniola paniculata*-*Ammophila breviligulata* community; 10) *Ammophiletum breviligulatae*; 11) *Elymus virginicus* community; 12) *Elymus mollis* community; 13) *Elymus arenarius* community; 14) *Hudsonietum tomentosi*; 15) *Carex mackenziei* community; 16) *Honckenya peploides* community.

Community number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Number of relevés	2	2	6	9	7	4	2	14	5	24	1	2	3	7	1	1
Panicum amarum	2	I
Ipomoea pes-caprae	.	V	.	I
Borrichia frutescens	1	2	III	II
Cakile constricta	V	.	.	+
Sporobolus virginicus	4
Hydrocotyle bonariensis	.	.	I	V	III	3
Ipomoea stolonifera	.	.	III	III	.	1
Schizachyrium littorale	2	+
Uniola paniculata	1	1	III	V	III	2	2	V	V	r
Ammophila breviligulata	1	.	V	V	.	.	.	I	.	.	.
Elymus virginicus	.	.	.	I	.	.	I	.	r	1
Elymus mollis	2
Elymus arenarius	3
Ligusticum scoticum	2
Polygonum convolvulus	1	3
Agropyron trachycaulum	1	3
Hudsonia tomentosa	V
Polygonella articula	III
Carex mackenziei	2	1
Honckenya peploides

Other species

Cakile edentula	I	II	II	.	1	1
Iva frutescens	2	I	II
etc.

It has been suggested that coastal vegetation in Japan belongs to the same vegetation class as in Europe (OHBA *et al.*, 1973), but Japanese dune-meadow vegetation can be summarized in a separate Glehnietea littoralis, characterized by *Glehnia littoralis*, *Ixeris repens*, *Carex pumila* and including *Calystegia soldanella* and *Lathyrus japonicus* (Tab. 1). This suggests that the warm-temperate zone may produce unique vegetation types in each region and that these should be in phytosociologically distinct classes. There are similarities and differences in the zonation patterns in Japan and eastern North America, cau-

sed to some extent by the ranges of circumpolar species in the north and by land-mass continuity versus the island character of Japan. The richest vegetation region is in the warm-temperate zone. The vegetation units of eastern North America need further scrutiny.

LOCATION OF RELEVES

Tab. 1 - Location in Serial Number: 1) Shari Beach, Estuary of Teshio River, Tomakomai city & Notsukesaki Cape in Hokkaido; 2) Notoriko Lake, Ishikari-machi (Ishikarihama Beach etc.),

Tab. 3 - Distribution and Vegetation Richness of Sand-Dune Meadows in Japan and Eastern North America.

Latitude	24-30°N	30-42°N (40°N ENAm)		42(40 ENAm)-50°N
		30-35°N	35-42°N	
Japan	<ul style="list-style-type: none"> • Vigno-Ipomoecetum pes-caprae • Glehnia-Spinifecetum littoralis • Zoysietum sinicae 	<ul style="list-style-type: none"> • Wedelio-Ischaemetum anthephoroidis • Wedelio-Carcetum kobomugi • Wedelio prostratae-Zoysietum macrostachiae 	<ul style="list-style-type: none"> • Elymo-mollis-Zoysietum macrostachiae • Linario japonicae-Ischaemetum anthephoroidis 	<ul style="list-style-type: none"> • Elymo-Carcicetum kobomugi • Soncho brachyotidis-Elymetum mollis • Glehnia littoralis-Carcetum macrocephala • Carex pumila comm. • Mertensia asiatica-Artemisia stelleriana comm.
ENAm	<ul style="list-style-type: none"> • Uniola paniculata comm. • Hydrocotyle bonariensis-Uniola paniculata comm. • Panicum amarum comm. • Uniola-Ipomoea pes-caprae comm. • Cakile constricta comm. 	<ul style="list-style-type: none"> • Borrichia frutescens comm. • Uniola paniculata-Ammophila breviligulata comm. • Sporobolus virginicus comm. • Schizachyrium littorale comm. 	<ul style="list-style-type: none"> • Elymus virginicus comm. • Ammophiletum breviligulatae 	<ul style="list-style-type: none"> • Elymus mollis comm. • Elymus arenarius comm. • Honckenya peploides comm. • Carex mackenziei comm. • Hudsonietum tomentosi
Florida		Georgia, North Carolina, Virginia		Long Isl., Massach., Québec

Hamatonnibetsu-machi (Benia-Genseikaen), Shibetsu-machi, Koshimizu-machi, Shari Beach, Ikuka Beach, Saruhutsu-mura (Shineshinko), Tomakomai City, Toyokoro-mura, Nemuro City (Shunkunitai), Hamamasu-mura, Oumu-machi, Rumoi City, Obira-machi in Hokkaido; 3) Akkeshi-machi, Abashiri City (Notoriko Lake etc.), Benia-Genseikaen, Yumigahama Beach, Mienotaki Beach, Minehama Beach, Shari Beach, Koshimizu-genseikaen, Saruhutsu-mura (Shineshinko), Toyotomi-machi, Horonobe-machi, Tokoro-machi, Tomakomai City, Nemuro City (Shunkunitai), Oumu-machi, Okoppe-machi in Hokkaido; 4) Hamamasu-mura, Yumigahama Beach, Nakahama Beach, Obira-machi, Toyotomi-machi, Okoppe-machi, Nemuro City (Shunkunitai), Tokoro-machi; in Hokkaido; 5) Tokoro-machi, Notoriko Lake, Benia-genseikaen, Saruhutsu-mura (Shineshinko) in Hokkaido; 6) Hamatonbetu-machi, Okoppe-machi in Hokkaido; 7) Rumoi City, Obira-machi, Okoppe-machi, Wakkanai City, Hamamasu-mura in Hokkaido; 8-11) Shimokita Peninsula in Pref. Aomori; 12) Takahagi City & Katsuta City in Pref. Ibaraki, Kujukuri-machi & Futtsu City in Pref. Chiba; 13) Takahagi City & Kashima County in Pref. Ibaraki; 14) Kaga City Katano-kaigan), Shiunji-machi Fujizukahama, Muramatsu-hama, Nakamurahama & Arai-hama), in Pref. Ishikawa; 15) Sendaiwan Bay in Pref. Miyagi; 16) Shimokita Peninsula in Pref. Aomori; 17) Tsugaru Peninsula in Pref. Aomori, Sakata City in Pref. Yamagata, Akita City & Yuri County in Pref. Akit, Sendai City in Pref. Miyagi; 18) Hamamasu-mura, Horobobe-machi & Tomakomai City in Hokkaido; 19) Tsugaru and Shimokita Peninsula in Pref. Aomori, Sakata City in Pref. Yamagata, Haranomachi City, Iwaki City & Souma City in Pref. Fukushima; 20) Shimokita Peninsula in Pref. Aomori; 21) Sakata City in Pref. Yamagata; 22) Shiunji-machi (Fujidukahama, Nakamurahama, Matsuhama), Nakajo-machi (Arai-hama), Iwafune County (Kurosaki) in Pref. Niigata, Toyama City (Iwasehama) in Pref. Toyama, Mattou City in Pref. Ishikawa; 23) Ketaka-machi in Pref. Tottori; 24) Hama-saka-machi & Kumihama-machi in Pref. Hyogo, Mihamo-machi (Shichirimihama) & Kumano City in Pref. Mie; 25) Fuji City, Asaba-machi, Shimoda City, Shizu City (Mihono-matsubara), Hamaoka-machi (Hamaoka dune) & Omaezaki-machi in Pref. Shizuoka, Shiunji-machi (Muramatsu-hama, Fujitukahama, Nakamurahama) in Pref. Niigata, Nyu-

zen-machi, Himi City & Toyama City (Iwasehama) in Pref. Toyama, Kanazawa City, Mattou City, Hakui City & Kaga City in Pref. Ishikawa; 26) Sendaiwan Bay in Pref. Miyagi; 27) Fukuoka City in Pref. Fukuoka & Miyazaki Beach in Pref. Miyazaki; 28) Satsuma Peninsula in Pref. Kagoshima; 29) Pref. Miyazaki; 30) Yuya-machi & Hikari City in Pref. Yamaguchi, Masuda City, Koryo-machi & Taisya-machi in Pref. Shimane, Tottori City (Hakuto Beach, Tottori Dune), Iwami County & Ketaka-machi in Pref. Tottori, Naruto City, Matsushige-machi, Nakagawa-machi, Mugi-machi & Anan City in Pref. Tokushima, Takamatsu City in Pref. Kagawa, Toyo-machi, Nakamura City & Tosashimizi City in Pref. Kohchi, Iwaki City in Pref. Fukushima, Sendai City, Motoyoshi-machi in Pref. Miyagi, Ooma-machi in Pref. Aomori; 31) Tokai-mura, Takahagi City, Kitaibaraki City in Pref. Ibaraki, Kouzushima Island, Nijima Island & Hachijo Island in Pref. Tokyo, Shonan Beach in Pref. Kanagawa, Wada-machi & Asahi City in Pref. Chiba; 32) Western Kyushu; 33) Shonan Beach in Pref. Kanagawa; 34) Shonan Beach in Pref. Kanagawa; 35) Satsuma Peninsula in Pref. Kagoshima; 36) Sendaiwan Bay, Naruse-machi, Sendai City in Pref. Miyagi, Shimokita Peninsula in Pref. Aomori; 37) Shiunji-machi (Matsu-hama, Fujituka-hama) in Pref. Niigata, Hamaoka-machi (Hamaoka dune), Fuji City in Pref. Shizuoka; 38) Nakagawa-machi, Anan City in Pref. Tokushima, Nakamura City & Tosashimizu City in Pref. Kohchi; 39) Fukuoka City in Pref. Fukuoka, Pref. Miyazaki, Western Kyushu; 40) Kamiyaku-machi, Minamitane-machi & Nishinoomote-machi in Pref. Kagoshima; 41) Kumihama-machi in Pref. Hyogo, Ise City (Gozamisaki) in Pref. Mie; 42) Hama-saka-machi, kumihama-machi & Nandan-machi in Pref. Hyogo, Nakamura City, Kochi City (Suzure dune) in Pref. Kochi, Shodojima Island in Pref. Kagawa, Hiwasa-machi & Anan City in Pref. Tokushima, Hamaoka-machi (Hamaoka dune) in Pref. Shizuoka, Shiunji-machi in Pref. Niigata; 43) Genkai in Pref. Saga, Satsuma Peninsula in Pref. Kagoshima; 44) Western Kyushu; 45) Genkai in Pref. Saga; 46) Yoron & Okinoerabu Islands in Pref. Kagoshima; 47) Yoron Island in Pref. Kagoshima, Okinawa & Iriomote Islands in Pref. Okinawa; 48) Tokunoshima, Okinoerabu & Yoron Islands in Pref. Kagoshima, Kumejima (Ifu Beach), Ikona & Okinawa (Okuma Beach) Islands in Pref. Okinawa; 49) Yoron & Amami-ohshima Islands in Pref. Kagoshima,

Iriomote Island in Pref. Okinawa; 50) Iriomote Island; 51) Ogasawara Islands (Hahajima, Anesima, Nishinoshima, Kitanoshima, Kitaioujima Islands) in Pref. Tokyo; 52) Ogasawara Islands (Ioujima & Chichijima Islands) in Pref. Tokyo; 53-54) Iwo-jima Islands in Pref. Tokyo; 55) Tokuno-shima Island in Pref. Kagoshima, Okinawa Island (Okuma beach) in Pref. Okinawa; 56) Tokunoshima Island in Pref. Kagoshima, Ishigaki, Hateruma, Iheya Islands in Pref. Okinawa; 57) Yoron, Kikai Islands in Pref. Kagoshima, Iriomote & Okinawa Islands in Pref. Okinawa; 58) Ishigaki, Shiniji & Kume Islands in Pref. Okinawa; 59) Taketomi Island in Pref. Okinawa; 60) Yoron & Okinoerabu Islands in Pref. Kagoshima, Iheya Island in Pref. Okinawa.

Tab. 2 - Locations of communities: 1) Key Biscayne (Fl); 2) St. Simons Bridge (Ga); 3) Key Biscayne (Fl), Nags Head (NC); 4) Grayton Beach (Fl), St. Augustine Rd. AIA (Fl); 5) Grayton Beach (Fl); 6) Jekyll Isl. (Ga), St. Augustine Rd. AIA (Fl); 7) Bogue Island, Ft. Macon (NC); 8) Grayton Beach (Fl), Key Biscayne (Fl), Bogue Island, Ft. Macon (NC), Back Bay NWR (Va); 9) Nags Head (NC); 10) Jekyll Isl. (Ga), Back Bay NWR (Va), Lloyd Harbor (Long Isl.), Baie St. Paul (Quebec); 11) Nags Head (NC); 12-13) Baie St. Paul (Quebec); 14-15) Chappaquoit (Massac); 16) Forillon National Park (Quebec).

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SCALES AND DIVERSITY RESPONSES TO MANAGEMENT IN BEECH COPPIES OF CENTRAL APENNINES (MARCHES, ITALY): FROM FLORISTIC RELEVÉS TO FUNCTIONAL GROUPS

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ABSTRACT

Species number changes refer to only one among basic aspects of biodiversity. Exploring the functionality of diversity patterns allows discover ecological processes acting in the background. In present study, we examined the vascular plant diversity responses to different intensity levels of forest management on beech coppices in a functional aspect at different spatial scales. The forest patch, intermediate between stand (plot) and landscape scales, was examined. We applied probabilistic sampling in four beech forests (two with still active coppice management and two with abandoned management) at the Monti Sibillini (Apennines, Central Italy). Floristic data were collected for vascular plants, according to standardized Braun-Blanquet method. Relevés were performed in 83 plots (20-22 on each site), sized 20x20 m. Species were grouped into Social Behaviour Types (SBT) to reveal the functionality of responses to management. Our results, based on accumulation models, show that a significant reduction of species in the abandoned patches is to be expected. Surprisingly the species pool of forest specialists is poorer in abandoned coppices respect to active ones. Regarding the forest generalists SBT, the number of pooled species is similar for both management intensity levels on forest patch scale. It proved to be an unforeseen result that the pool of non-forest species does not differ respect to management. Marginal species have a minor importance in abandoned coppices. Richness of gap species doesn't change with management intensity. On higher spatial scale than stand level, impoverished pool of forest specialist and marginal species can be interpreted as a result of competitive exclusion process initially acting in maturing, closed-canopy abandoned beech coppices. The distinct relations of species groups to various spatial scales highlight the importance of including scales on diversity studies, since plot level results would lead to misleading conclusions respect to land management and planning. With

regard to the latter, the forest patch level proved to be an important scale, and functional aspects showed to be a relevant aspect to evaluate changes in plant diversity.

KEYWORDS: forest patches, Social Behaviour Types, spatial scale, vascular plants, accumulation curves.

RIASSUNTO

Le variazioni del numero delle specie sono soltanto uno degli aspetti della biodiversità. Esplorare i modelli di diversità dal punto di vista funzionale può consentire di comprendere i processi ecologici sottesi. Il presente lavoro riguarda le risposte della diversità biologica delle specie vascolari all'intensità del disturbo dovuto alla gestione selvicolturale nei cedui di faggio, secondo alcuni aspetti funzionali legati alla scala. In particolare, si è esaminato il comportamento dei dataset a livello di singola faggeta, una scala intermedia tra popolamento (o plot) e unità di paesaggio. Si è costruito un disegno sperimentale campionario su quattro distinti frammenti di faggeta (due gestiti a ceduo e due soggetti all'abbandono delle pratiche selviculturali), nel complesso dei Monti Sibillini (Appennino centrale). I dati floristici sulle specie vascolari sono stati raccolti adottando il metodo di Braun-Blanquet in forma standardizzata. I rilevamenti sono stati effettuati in 83 plot (20x20 m) equiripartiti tra le 4 aree di studio. Le specie sono state raggruppate in gruppi cenologici (Social Behaviour Types, SBT) per evidenziare le risposte funzionali all'intensità gestionale. I risultati, basati sui modelli d'accumulo, hanno evidenziato una riduzione significativa del numero di specie alla scala del singolo bosco di faggio. Sorprendentemente, il gruppo delle specialiste di faggeta è costituito da un minor numero di specie nei cedui abbandonati. Considerando il gruppo delle specie generaliste di ambienti forestali, invece, la ricchezza specifica è del tutto simile nei frammenti di faggeta cedua e in quelli non più gestiti. Un risultato inatteso è costituito dal fatto che il pool di specie non forestali è sostanzialmente identico nelle due tipologie gestionali. Il gruppo delle specie marginali ha una importanza ridotta, specialmente nei cedui di faggio abbandonati, mentre la ricchezza specifica del gruppo delle chiarie non varia con l'intensità della gestione selviculturale. La riduzione delle specie appartenenti ai gruppi delle specie specialiste della faggeta e delle specie marginali nei cedui abbandonati, può essere interpretato come il frutto di processi di competizione esclusiva che si instaurano a seguito della omogenea chiusura della volta arborea che si viene a creare nelle prime fasi di rigenerazione. Le diverse relazioni dei gruppi funzionali alle diverse scale sottolinea l'importanza di tale fattore nello studio della diversità biologica, dato che i risultati a livello di singolo popolamento (rappresentato da ciascun rilevamento) potrebbe portare a conclusioni fuorvianti nel campo della gestione e pianificazione territoriale. Il livello intermedio delle unità boschive in un paesaggio forestale frammentato, si dimostra una scala di analisi molto rilevante, e gli aspetti funzionali associati alla diversità tassonomica costituiscono un aspetto determinante per la corretta valutazione ed interpretazione dei cambiamenti nella diversità vegetale.

INTRODUCTION

It is widely known, also considering the floristic compartment *per se*, that forest management affects diversity, so that plant diversity assessment plays an increasing role within management-oriented programmes and studies (ROBERTS & GILLIAM, 1995; VOLIN & BUONGIORNO, 1996; RUBIO *et al.*, 1999).

Braun-Blanquet's relevés can be a good source of floristic datasets, providing that problems associated with sampling are solved (MUCINA *et al.*, 2000; GRABHERR *et al.*, 2003; PODANI, 2006). The lists of species obtained by standardized field relevés can be directly used

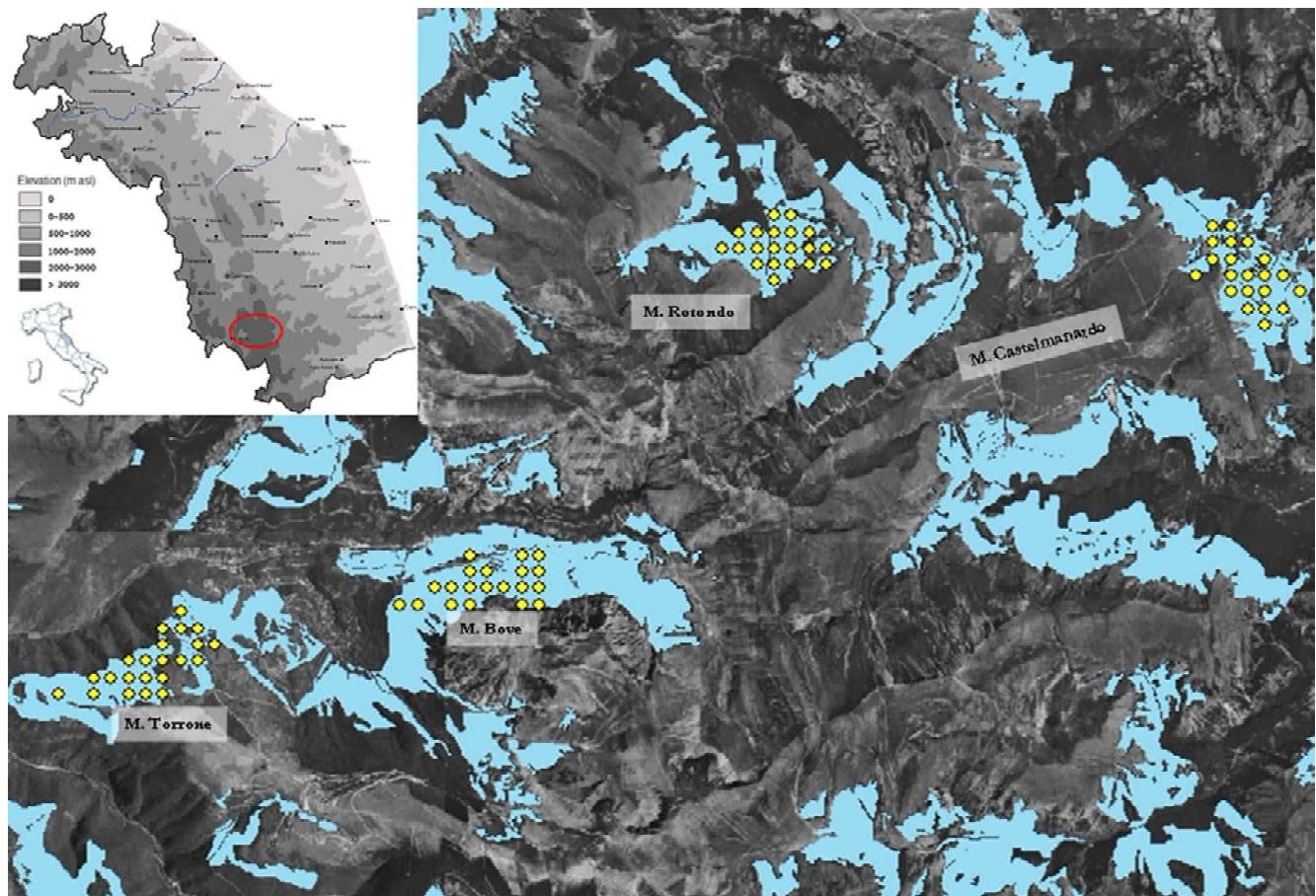


Fig. 1 - Sampling design applied in the Beech forest patches of the study area near Bolognola and Ussita.

for diversity assessments (ex.: in forest monitoring, cf. ALLEGRENI *et al.*, 2009).

Using ecological groups of species in diversity analyses can highlight mechanisms behind simple species number differences, as it is recommended by BARBIER *et al.* (2008) in their review. Grouping species based on their social behaviour (SBT, see BORHIDI, 1995) gives the possibility to investigate how habitat preference spectrum is changing in space and time (BARTHA *et al.*, 2008).

Coppicing was a traditional way of forests management in Europe (PETTERKEN, 1981). The basis of this management type lies in the vegetative re-sprouting ability of tree species after cutting. In the coppice-with-standards method, some selected trees (so called "standards") remain in the stand avoiding cutting.

In Italy, about 4 million ha of forests were managed in this way (CIANCIO *et al.*, 2006). In Central-Apennines the mountain beech (*Fagus sylvatica* L.) woodlands were mostly coppiced until the last century (PAVARI, 1999).

In the last decades, in parallel to socio-economic changes (e.g. countryside abandonment: see ANTROP, 2004; AGNOLETTI, 2007) this traditional management is declining (BARBERO *et al.*, 1990; EVANS & BARKHAM, 1992; COPPINI & HERMANIN, 2007). Abandonment

of coppicing implies in general a natural conversion into high forest management. This altered management induces changes in abiotic parameters like soil-nutrient availability, soil-water patterns and microclimate (HÖLSCHER *et al.*, 2001; CUMMINGS & COOK, 1992; CHEN *et al.*, 1999). In background of species compositional changes stays frequently the modification of light conditions, as indicated in several studies from beech forests (THOMSEN *et al.*, 2005; STANDOVÁR *et al.*, 2006; NAAF & WULF, 2007; BARBIER *et al.*, 2008). Based on Ellemberg values analyses (GARADNAI *et al.*, unpublished), nutrient availability and temperature discriminate active beech coppices and abandoned coppices better than light availability and soil-moisture. The changed physical environment affects the structural features (see MONTES *et al.*, 2004; VAN CALSTER *et al.*, 2007, 2008) and modifies diversity of previously coppiced forests (MASON & MACDONALD, 2002; GONDARD & ROMANE, 2005).

During maturation of a coppiced forest the overall diversity of plants often decrease (DEBUSSCHE *et al.*, 2001; MASON & MACDONALD, 2002; DECOCQ *et al.*, 2004; GONDARD & ROMANE, 2005; BARTHA *et al.*, 2008). In functional point of view, the first phase of recovery is mainly dominated by disturbance tol-

erant species, while only a reduced number of true forest species can be found which are generally shade tolerant (NAGAIKE *et al.*, 2003; DECOCQ *et al.*, 2004).

BARTHA *et al.* (2008) investigated changes in plant diversity and some functional aspect using chronosequence approach on similar beech coppices in the Monti Sibillini (central-Apennines, Italy) as present paper does. They used the SBT (Social Behaviour Types) categorization system to group species, at the plot level. They found a consistent increase of non-forest species and a decrease of beech forest specialists in young, recently managed beech coppice stands compared to the late regenerative phases. The existence of a specialist species pool even in early stages after cutting (in spite of their minor importance), makes the Authors suggesting the importance of heterogeneity at the above-plot level and land-use in maintaining the species pool of the area. Forest generalist species have the same importance at all stages of coppice regeneration on limestone bedrock.

Species diversity depends considerably on spatial scale (PODANI *et al.*, 1993; CRAWLEY & HARRAL, 2001) also. Diversity studies concern usually large (landscape - km²) or small (plot - m²) scales (BROCKWAY, 1998; CHIARUCCI *et al.*, 2008; BARTHA *et al.*, 2008) and in-

between scales could remain unexplored. Combining functional richness comparisons on plot- and on broader spatial scales (GOTELLI & COLWELL, 2001; CHIARUCCI & BONINI, 2005; CHIARUCCI *et al.*, 2008), it makes possible to answer diversity-scale relationships questions.

The objective of the present paper was to fill knowledge gaps considering spatial diversity relations by comparing the functional diversity of coppiced and abandoned beech forest patches at different spatial scales in the central-Apennines.

MATERIALS AND METHODS

STUDY SITE

Our study site is located in central Apennines, in the “Monti Sibillini” National Park (Marches, Italy). The area belongs to a meso-temperate climatic zone of the low and high mountain belt, where mean annual precipitation is ranging from 1,100 to 1,400 mm and mean annual temperatures vary between 8 and 12 °C (BIONDI & BALDONI, 1995). The bedrock of the selected sites is mainly Mesozoic and Tertiary limestone. The soil (belonging to Skeleti-Calcaric Phaeozems and Calcareous Leptosols groups) are weakly structured, shallow, with a low water holding capacity. They have medium-high content of carbonates (10-40%) loamy texture with a remarkable amount of organic matter and pH ranging from neutral to sub-alkaline (ASSAM, 2006). The forest vegetation of the area is mainly composed of beech forest communities belonging to *Cardamino kitaibelii-Fagetum sylvaticae* and *Lathyrus veneti-Fagetum sylvaticae* associations (following BIONDI *et al.*, 2002).

SAMPLING DESIGN

We applied several criteria to select sites differing only in current management regime, namely the contrasting options “active coppicing” and “abandoned coppice”. IPLA (2001) management characterization was used, which were given for all forest stands in Marche Region. To control for differences in forest characteristics other than management regime we selected beech forest patches on limestone bedrock in the bioclimatic “warm” *Fagus* forests zone (800-1,000 m to 1,500 m a.s.l., as proposed in Central Apennines by PIOVESAN *et al.*, 2005a), on NW-N-NE fa-

Tab. 1 - Application of Chao, Jackknife1, and Bootstrap richness estimators with their standard errors (se), based on total number of species to compare the species pool of abandoned and coppiced Beech forests patches. The relative upper and lower confidence limits never overlap, thus the differences were considered as significant.

	Species	chao	chao.se	Jackknife1	Jackknife1.se	bootstrap	boot.se
Abandoned	20	24.0000	5.29150	23.9000	2.398437	21.8286	1.370229
Coppiced	39	44.7857	5.04434	47.7907	3.246498	43.5070	2.066733
Abandoned upper estimate		34.3714		28.6009		24.5142	
Coppiced lower estimate		34.8988		41.4276		39.4562	

cing slopes, with minimum continuous cover of 80 ha. Selection was carried out using ArcGIS 9.2. Four sites were chosen: two still active and two abandoned coppices near Ussita and Bolognola villages (at both territories an active coppice-abandoned coppice pair).

To represent the floristic composition and structural attributes of each forest patch, sampling plots were placed regularly in a 200 m grid pattern in the N-W-S-E direction. This distance was chosen to sample the highest level of heterogeneity, thus avoiding overrepresentation of single management units which are usually between 0.5-2 ha in the study area (CANULLO *et al.*, 2009). The digital grid was positioned on the selected sites randomly (Fig. 1). In order to represent the forest patch scale, at least 20 plots sized 20x20 m were placed in each site, each on a grid-cell. The coordinates of the NE corner of each plot were assigned in GIS. Each point was located in the field using GPS (Garmin Vista Etrex). To minimize edge effects, plots were placed at a minimum distance of 20 m from roads or forest edges in a random direction. Plots falling into non-*Fagus* facies were placed elsewhere only in the case of positive findings respect to the 20 m buffer threshold, otherwise they were rejected.

In the plots, vascular plant species were assessed by a standardized phytosociological method (Braun-Blanquet scale), and the output were used to obtain species density data at 400 m² (field surveys June to August 2008).

STATISTICAL ANALYSIS

Species were classified into Social Behaviour Types (SBT). Grouping species into SBT types is based on their common habitat preference: this categorization takes into account the similar phytocoenological role of species (BORHIDI, 1995; NAGAIKE *et al.*, 2003.), as determined by regional synecology and their actual role in the local floras (assigned from PIGNATTI, 1982, 1998; PIGNATTI *et al.*, 2004; BALLELLI *et al.*, 2005).

The functional groups named SBTs

were defined as follows (see Appendix):

SBT1 - Beech forest specialist species;
SBT2 - Forest generalist species;
SBT3 - Non-forest species (preferring open habitat communities);
SBT4 - Marginal species (exotics, weeds, members of ruderal and agricultural plant communities);
SBT5 - Gap species (linked to forest edges and gaps).

At forested landscape scale pooled richness of SBTs were compared using species accumulation curves (GOTHELLI & COLWELL, 2001), and the “exact method for combining plots” (UGLAND *et al.*, 2003, COLWELL *et al.*, 2004, KINTDT *et al.*, 2006).

By means of three richness estimators’ applications (Chao, Jackknife1, Bootstrap), the difference of the compared species pool was tested: when at least two of the used estimators resulted in overlapping of confidence interval at the end of the curve, the observed asymptotical difference was rejected as not significant.

RESULTS

Considering the accumulation values with the three estimators, based on the total number of species, the observed differences appeared to be significant between abandoned and coppiced Beech forest patches (Tab. 1).

SOCIAL BEHAVIOUR TYPES

Around 300 vascular plant species were found in the 83 plot during the field survey (on overall 3.3 hectares surveyed).

Considering the forest patch scale, at our sampling effort, the species pool of forests still actively managed seems to contain more specialist (SBT1) species than the abandoned one, and based on 43 plots still could not reach an asymptotic accumulation curve. For abandoned forests, 40 sampling unit proved to be enough to explore the total richness of specialist species at forest patch scale (Fig. 2).

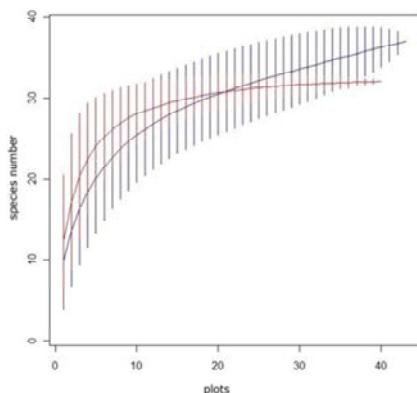


Fig. 2 - Species accumulation curve for beech forest specialist species (SBT1), with envelops of confidence intervals. Species pools are different. Vertical lines are confidence intervals for the number of plots on the x axis. Blue line = coppiced forest, red line = abandoned forest.

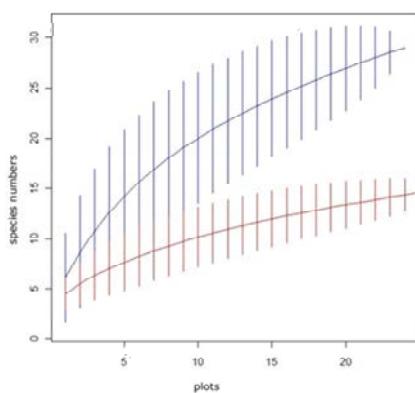


Fig. 5 - Species accumulation curve for marginal species (SBT4), with overlap of confidence intervals (at the end of the curve) at less than 2 of the 3 considered richness estimators. Species pools are different. Vertical lines are confidence intervals for the number of plots on the x axis. Blue line = coppiced forest, red line = abandoned forest.

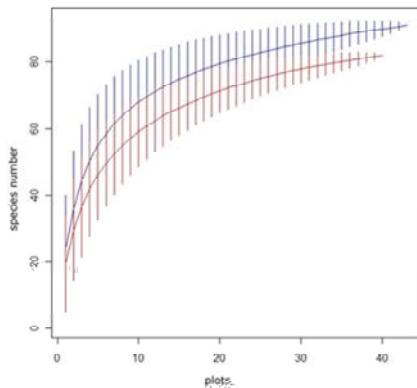


Fig. 3 - Species accumulation curve for forest generalist species (SBT2), with overlap of confidence intervals (at the end of the curve) at more than 1 of the 3 considered richness estimators. Species pools are not different. Vertical lines are confidence intervals for the number of plots on the x axis. Blue line = coppiced forest, red line = abandoned forest.

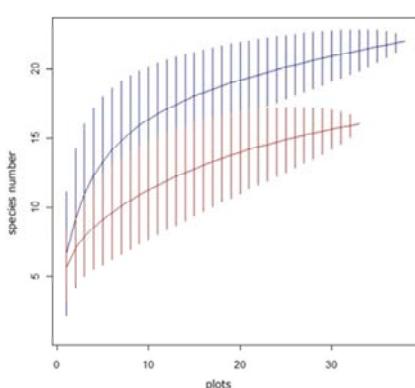


Fig. 6 - Species accumulation curve for gap species (SBT5), with overlap of confidence intervals (at the end of the curve) at more than 1 of the 3 considered richness estimators. Species pools are not different. Vertical lines are confidence intervals for the number of plots on the x axis. Blue line = coppiced forest, red line = abandoned forest.

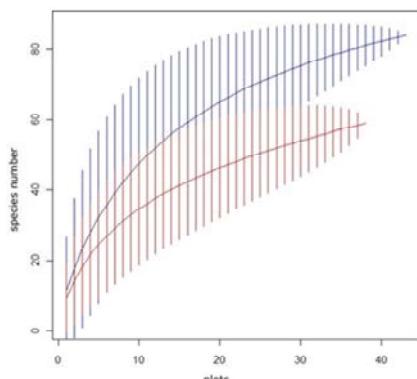


Fig. 4 - Species accumulation curve for non-forest species (SBT3), with overlap of confidence intervals (at the end of the curve) at more than 1 of the 3 considered richness estimators. Species pools are not different. Vertical lines are confidence intervals for the number of plots on the x axis. Blue line = coppiced forest, red line = abandoned forest.

Generalist species (SBT2) tend to similar richness estimation at both forest types; the sampling effort was not enough to catch the total richness of this functional group (Fig. 3).

The coppiced forests do not contain more non-forest species (SBT3) compared to abandoned ones (Fig. 4).

Considering marginal species (SBT4), accumulation curves show a clear distinction between the two silvicultural systems, which becomes obvious even at lower sampling effort (Fig. 5).

Distinction of gap species pools (SBT5) between the observed forest patches is not significant (Fig. 6).

In diversity studies, considering ecological character of species allows a better understanding of mechanisms resulting changes in species diversity (BARBIER *et al.*, 2008).

At the forest patch scale, abandoned study areas are expected to show more beech forest specialists (SBT1) than coppiced ones. This result seems not to support the finding of other studies reporting decrease of forest specialist plant species in forests after silvicultural treatments (NAGAIKE *et al.*, 2003; DECOCQ *et al.*, 2004); similarly, BARTHA *et al.* (2008) found linear positive regression for SBT1 species with coppice age. These Authors carried out their studies at the plot scale, which can explain their different findings (figures at lower scales in Fig. 2 are consistent with that results). BARTHA *et al.* (2008) also emphasized a remnant of SBT1 functional group even at young stages; to explain that phenomenon, they assumed the landscape heterogeneity can play an important role in that. Our sampling design, with the regular grid of sampling units, was constructed just to explore this spatial heterogeneity at an intermediate (forest patch) spatial scale, and the results emphasize that even the active coppiced patch maintains a species pool of specialists. Abandoned forest patches permit around 30 specialist species to coexist in maturing beech coppices; this number proved to be the maximum potential threshold, as suggested by the asymptotic accumulation curve. With the closure of beech forests canopy, the competitive exclusion ability of the *Fagus sylvatica* (PIOVESAN *et al.*, 2005b) strongly determines the number of coexisting species in the understory. As for the total pool of beech forest specialist species (SBT1), 6 species are missing completely from abandoned coppices. Among them there are trees (*Acer monspessulanum*, *Carpinus betulus*, *Sorbus aucuparia*), shrubs (*Ribes multiflorum*, *Ribes alpinum*), and *Adoxa moschatellina*. Negative effect of canopy cover on woody richness was found by ESTEVAN *et al.* (2007) in beech dominated forests of NE-Spain. Not trivial, but as our results indicate, active coppices can maintain a higher richness of beech forest specialist species at patch scale, because species distribution is not restricted by the closed canopy, and local extinction (at plot or stand scale) can be buffered in the case of larger continuous forests areas. The structural and spatial heterogeneity of coppiced forest patches, in facts, originates from the co-occurrence, at the landscape level, of different regeneration

DISCUSSION

ve stages. This allows the coexistence of more species than expected at the plot scale.

For generalist forest species (SBT2), the richness doesn't predict management, and their species pool seems to have the same magnitude. This is to be expected given the wider range of habitats in which they can occur in the region.

Surprisingly, the non-forest species (SBT3) are not characteristic of coppiced forest patches respect to abandoned ones. Again, the reason for discrepancy with previous studies is to be found in the scale of analysis. For example, BARTHA *et al.* (2008) found 5–10 times differences in richness of that group along forest age classes, but they compared single plots at distinct regeneration phases: species were filtered from the functional point of view. In our study, we describe the diversity status of a forest patch as a whole unit, and since it contains management units with different regeneration phases, the data of the sampling plots were buffered. Moreover, we selected at least 80 ha continuous forest stands, to minimize the influence of external non-forested ecosystems (like grasslands), but we could not avoid the effect of little internal open areas inside the forest patch. It seems therefore to be the case, that results are scale dependent, as it is well known and documented in the landscape ecology literature (CRAWLEY *et al.*, 2001; ANDERSON *et al.*, 2004; DAVIES *et al.*, 2005; BEEVER *et al.*, 2006).

Considering marginal species (SBT4), they are represented by few species in both forest patch types. The small proportion of weeds and exotics to overall richness indicates a good and semi-natural status of coppiced woods in the Beech belt of Sibillini Mountains. However, management results in a bigger pool of that species at the forest patch scale respect to abandoned coppices.

There is no difference between forests management as gap species richness (SBT5). Since short time passed from the abandonment of management considering natural beech forest dynamic cycles (RADEMACHER *et al.*, 2004), the formation of natural gaps is still missing from both forest types. This can explain the equally small contribution of this species' group to the total species pool.

CONCLUSION

Species diversity depends consi-

derably on spatial scale (PODANI *et al.*, 1993) since different factors influence species richness at different scales (CRAWLEY & HARRAL, 2001). At the minor spatial scales species density proved to be an important descriptor, while on wider scales (e.g. landscape scale) the species pool seems to be determinative as demonstrated by BARTHA & IRTZÉS (2001). Such species coexist in the forested landscape mosaic of stand ages determined by management, and by natural disturbance in the case of abandoned forest. The latter is not as frequent as the former. Therefore, it seems that the selective pressure of the closed canopy *Fagus* forest excludes more species than in the coppiced case, and even some species that are thought to be forest-type specialists should be considered as forest generalists. However, this cannot be detected considering only plot scale analyses. Similarly, the lack of management select out the marginal species from the abandoned coppices on the forest patch scale, but the proportional contribution to plot level richness remain on the same level as in active coppices.

The marginalization of forest areas in the Apennines calls for conservation action plans sustaining the considerable species diversity heritage. Maintenance of diversity is an important criterion of forest management. Statements about the effect of forest management on diversity should always define the spatial scale they concern. Conclusions drawn from investigations considering only plot-level data might be misleading, even if the study is at the scale of a single sylvicultural action (say: cutting). Our results emphasize that forest patch scale proved to be an important level for considering the plant diversity status, preferably representing the ecological unit to which a management plan should be referred.

APPENDIX

SBT1 SPECIES

- Abies alba* Miller
- Acer campestre* L.
- Acer monspessulanum* L.
- Acer obtusatum* W. et K.
- Acer platanoides* L.
- Acer pseudoplatanus* L.
- Actaea spicata* L.
- Adenostyles australis* (Ten.) Nyman
- Adoxa moschatellina* L.
- Allium ursinum* L.
- Aremonia agrimonoides* (L.) DC.
- Cardamine bulbifera* (L.) Crantz

- Cardamine enneaphyllos* (L.) Crantz
- Cardamine heptaphylla* (Vill.) O. E. Schulz
- Carpinus betulus* L.
- Cephalanthera damasonium* (Miller) Druce
- Fagus sylvatica* L.
- Fraxinus excelsior* L.
- Galium odoratum* (L.) Scop.
- Hordelymus europaeus* (L.) Harz
- Laburnum alpinum* (Miller) Berchtold et Presl
- Luzula sylvatica* (Hudson) Gaudin
- Mercurialis perennis* L.
- Orthilia secunda* (L.) House
- Polystichum aculeatum* (L.) Roth
- Polystichum setiferum* (Forsskal) Woynar
- Prenanthes purpurea* L.
- Ribes alpinum* L.
- Ribes multiflorum* Kit.
- Ruscus hypoglossum* L.
- Sanicula europaea* L.
- Senecio fuchsii* Gmelin
- Sorbus aucuparia* L.
- Taxus baccata* L.
- Viola reichenbachiana* Jordan ex Boreau

SBT2 SPECIES

- Aegopodium podagraria* L.
- Agropyron caninum* (L.) Beauv.
- Aquilegia vulgaris* L.
- Asarum europaeum* L.
- Asperula laevigata* L.
- Asplenium adiantum-nigrum* L.
- Astragalus glycyphyllos* L.
- Brachypodium sylvaticum* (Hudson) Beauv.
- Campanula persicifolia* L.
- Campanula trachelium* L.
- Carex digitata* L.
- Carex flacca* Schreber
- Carex sylvatica* Hudson
- Castanea sativa* Miller
- Cephalanthera longifolia* (Hudson) Fritsch
- Cephalanthera rubra* (L.) L. C. Rich.
- Ceterach officinarum* DC.
- Clematis vitalba* L.
- Clinopodium vulgare* L.
- Cornus mas* L.
- Corylus avellana* L.
- Crataegus oxyacantha* L.
- Cruciata glabra* (L.) Ehrend.
- Cyclamen hederifolium* Aiton
- Daphne laureola* L.
- Dianthus monspessulanus* L.
- Digitalis micrantha* Roth
- Doronicum columnae* Ten.
- Dryopteris filix-mas* (L.) Schott
- Epipactis helleborine* (L.) Crantz
- Euonymus europaeus* L.
- Euonymus latifolius* (L.) Miller

<i>Euonymus verrucosus</i> Scop.	<i>Viola riviniana</i> Rchb.	<i>Leontodon hispidus</i> L.
<i>Euphorbia amygdaloides</i> L.	SBT3 SPECIES	<i>Leucanthemum vulgare</i> Lam.
<i>Euphorbia dulcis</i> L.		<i>Lilium bulbiferum</i> L. ssp. <i>croceum</i>
<i>Festuca heterophylla</i> Lam.	<i>Achillea millefolium</i> L.	(Chaix) Baker
<i>Fragaria vesca</i> L.	<i>Acinos alpinus</i> (L.) Moench	<i>Lilium martagon</i> L.
<i>Fraxinus ornus</i> L.	<i>Agrostis tenuis</i> Sibth.	<i>Lolium perenne</i> L.
<i>Galium corrudifolium</i> Vill.	<i>Ajuga reptans</i> L.	<i>Lotus corniculatus</i> L.
<i>Geranium robertianum</i> L.	<i>Amelanchier ovalis</i> Medicus	<i>Medicago lupulina</i> L.
<i>Geum urbanum</i> L.	<i>Anthemis tinctoria</i> L.	<i>Minuartia verna</i> (L.) Hiern
<i>Hedera helix</i> L.	<i>Arabis alpina</i> L. ssp. <i>caucasica</i> (Wil-	<i>Orchis maculata</i> L.
<i>Helleborus bocconeii</i> Ten.	ld.) Briq.	<i>Origanum vulgare</i> L.
<i>Hepatica nobilis</i> Miller	<i>Arabis collina</i> Ten.	<i>Peucedanum carvifolia</i> Vill.
<i>Hieracium sylvaticum</i> (L.) L.	<i>Arabis hirsuta</i> (L.) Scop.	<i>Phleum alpinum</i> L.
<i>Hypericum montanum</i> L.	<i>Arabis sagittata</i> (Bertol.) DC.	<i>Picris hieracioides</i> L.
<i>Ilex aquifolium</i> L.	<i>Arctium nemorosum</i> Lej. et Court.	<i>Poa molinieri</i> Balbis
<i>Laburnum anagyroides</i> Medicus	<i>Arctostaphylos uva-ursi</i> (L.) Sprengel	<i>Poa pratensis</i> L.
<i>Lamiastrum galeobdolon</i> (L.) Ehrend.	<i>Arenaria serpyllifolia</i> L.	<i>Primula veris</i> L.
et Polatschek	<i>Asperula purpurea</i> (L.) Ehrend.	<i>Pteridium aquilinum</i> (L.) Kuhn
<i>Lamium garganicum</i> L.	<i>Astragalus danicus</i> Retz.	<i>Ptilostemon strictus</i> (Ten.) Greuter
<i>Lapsana communis</i> L.	<i>Brachypodium rupestre</i> (Host) R. et S.	<i>Ranunculus bulbosus</i> L.
<i>Lathyrus venetus</i> (Miller) Wohlf.	<i>Calamagrostis varia</i> (Schrader) Host	<i>Rhamnus alpinus</i> L.
<i>Lathyrus vernus</i> (L.) Bernh.	<i>Campanula apennina</i> Podlech	<i>Rhinanthus alectorolophus</i> (Scop.) Pol-
<i>Listera ovata</i> (L.) R.Br.	<i>Campanula glomerata</i> L.	lich
<i>Lonicera caprifolium</i> L.	<i>Carduus carlinaefolius</i> Lam.	<i>Rosa pendulina</i> L.
<i>Lonicera xylosteum</i> L.	<i>Carex hallerana</i> Asso	<i>Rosa pimpinellifolia</i> L.
<i>Lunaria rediviva</i> L.	<i>Carex macrolepis</i> DC.	<i>Rubus hirtus</i> W. et K.
<i>Luzula forsteri</i> (Sm.) DC.	<i>Centaurea ambigua</i> Guss.	<i>Sambucus ebulus</i> L.
<i>Malus sylvestris</i> Miller	<i>Centaurea bracteata</i> Scop.	<i>Sanguisorba minor</i> Scop.
<i>Melampyrum italicum</i> (Beauverd) Soo	<i>Centaurea triumfetti</i> All.	<i>Scabiosa columbaria</i> L.
<i>Melica uniflora</i> Retz.	<i>Cerastium tomentosum</i> L.	<i>Scrophularia canina</i> L.
<i>Melittis melissophyllum</i> L.	<i>Clematis recta</i> L.	<i>Sedum album</i> L.
<i>Milium effusum</i> L.	<i>Cnidium silaifolium</i> (Jacq.) Simonkai	<i>Sedum rupestre</i> L.
<i>Moehringia muscosa</i> L.	<i>Convallaria majalis</i> L.	<i>Sesleria nitida</i> Ten.
<i>Moehringia trinervia</i> (L.) Clairv.	<i>Cotoneaster integerrimus</i> Medicus	<i>Sesleria tenuifolia</i> Schrader
<i>Monotropa hypopitys</i> L.	<i>Cotoneaster nebrodensis</i> (Guss.) C.	<i>Silene italicica</i> (L.) Pers.
<i>Mycelis muralis</i> (L.) Dumort.	Koch	<i>Stachys officinalis</i> (L.) Trevisan
<i>Neottia nidus-avis</i> (L.) L. C. Rich.	<i>Cruciata laevipes</i> Opiz	<i>Stachys tympaea</i> Hausskn.
<i>Ostrya carpinifolia</i> Scop.	<i>Cytisus sessilifolius</i> L.	<i>Tanacetum corymbosum</i> (L.) Sch.-Bip.
<i>Peucedanum austriacum</i> (Jacq.) Koch	<i>Dactylis glomerata</i> L.	<i>Teucrium chamaedrys</i> L.
<i>Platanthera bifolia</i> (L.) Rchb.	<i>Daphne oleoides</i> Schreber	<i>Thalictrum minus</i> L.
<i>Poa nemoralis</i> L.	<i>Daucus carota</i> L.	<i>Trifolium campestre</i> Schreber
<i>Polygonatum multiflorum</i> (L.) All.	<i>Epilobium montanum</i> L.	<i>Trifolium ochroleucum</i> Hudson
<i>Polypodium interjectum</i> Shivas	<i>Epipactis atropurpurea</i> Rafin.	<i>Trifolium pratense</i> L.
<i>Polypodium vulgare</i> L.	<i>Eryngium amethystinum</i> L.	<i>Trifolium repens</i> L.
<i>Polystichum lonchitis</i> (L.) Roth	<i>Eupatorium cannabinum</i> L.	<i>Valeriana montana</i> L.
<i>Primula vulgaris</i> Hudson	<i>Euphorbia cyparissias</i> L.	<i>Veratrum nigrum</i> L.
<i>Pulmonaria vallarsae</i> Kerner	<i>Falllopia dumetorum</i> (L.) Holub	
<i>Quercus cerris</i> L.	<i>Festuca circummediterranea</i> Patzke	SBT4 SPECIES
<i>Quercus pubescens</i> Willd.	<i>Festuca dimorpha</i> Guss.	<i>Arctium minus</i> (Hill) Bernh.
<i>Ranunculus lanuginosus</i> L.	<i>Galeopsis angustifolia</i> Ehrh.	<i>Asplenium trichomanes</i> L.
<i>Ranunculus nemorosus</i> DC.	<i>Galium mollugo</i> L.	<i>Campanula rapunculus</i> L.
<i>Rosa arvensis</i> Hudson	<i>Gentiana dinarica</i> Beck	<i>Chelidonium majus</i> L.
<i>Rubus caesius</i> L.	<i>Graffia golaka</i> (Hacq.) Rchb.	<i>Cirsium arvense</i> (L.) Scop.
<i>Salvia glutinosa</i> L.	<i>Gymnadenia conopsea</i> (L.) R. Br.	<i>Convolvulus arvensis</i> L.
<i>Sambucus nigra</i> L.	<i>Helianthemum canum</i> (L.) Baumg.	<i>Geranium molle</i> L.
<i>Saxifraga rotundifolia</i> L.	<i>Helianthemum nummularium</i> (L.) Mil-	<i>Geranium pyrenaicum</i> Burm. f.
<i>Scutellaria columnae</i> All.	ler	<i>Heracleum sphondylium</i> L.
<i>Solidago virgaurea</i> L.	<i>Hieracium pilosella</i> L.	<i>Lactuca saligna</i> L.
<i>Sorbus domestica</i> L.	<i>Hypericum perforatum</i> L.	<i>Leucanthemum pallens</i> (Gay) DC.
<i>Stellaria holostea</i> L.	<i>Inula conyzoides</i> DC.	<i>Linaria purpurea</i> (L.) Miller
<i>Tamus communis</i> L.	<i>Juniperus communis</i> L.	<i>Picea excelsa</i> (Lam.) Link
<i>Tilia platyphyllos</i> Scop.	<i>Juniperus oxycedrus</i> L.	<i>Pinus nigra</i> Arnold
<i>Ulmus glabra</i> Hudson	<i>Koeleria macrantha</i> (Ledeb.) Sprengel	<i>Pinus sylvestris</i> L.
<i>Veronica officinalis</i> L.	<i>Laserpitium latifolium</i> L.	<i>Plantago lanceolata</i> L.
<i>Viburnum lantana</i> L.	<i>Laserpitium siler</i> L.	
<i>Viola alba</i> Besser	<i>Lathyrus sylvestris</i> L.	

- Plantago major* L.
Potentilla reptans L.
Prunus avium L.
Seseli tommasinii Rchb. f.
Silene dioica (L.) Clairv.
Silene vulgaris (Moench) Gärcke
Stellaria media (L.) Vill.
Tanacetum parthenium (L.) Sch.-Bip.
Taraxacum officinale Weber (aggregato)
Urtica dioica L.
Veronica hederifolia L.

SBT5 SPECIES

- Alliaria petiolata* (Bieb.) Cavara et Grande
Anagallis arvensis L.
Arabis brassica (Leers) Rauschert
Arabis turrita L.
Atropa belladonna L.
Bromus ramosus Hudson
Cardamine graeca L.
Chaerophyllum hirsutum L.
Cornus sanguinea L.
Coronilla emerus L.
Crataegus monogyna Jacq.
Helleborus foetidus L.
Lamium maculatum L.
Peucedanum verticillare (L.) Koch
Populus nigra L.
Populus tremula L.
Potentilla micrantha Ramond
Prunus mahaleb L.
Prunus spinosa L.
Rosa canina L. sensu Bouleng.
Rubus idaeus L.
Salix caprea L.
Sorbus aria (L.) Crantz
Vincetoxicum hirundinaria Medicus

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RÉPARTITION GÉOGRAPHIQUE ET ÉCOLOGIQUE DE *CLAYTONIA CAROLINIANA* VAR. *CAROLINIANA* DANS LES COMMUNAUTÉS VÉGÉTALES DU QUÉBEC-LABRADOR, AU CANADA

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ABSTRACT

Claytonia caroliniana Michx. var. *caroliniana* (Portulacaceae) was systematically sampled to record its distribution within a grid system, its frequency and its ecology in the plant communities of Quebec-Labrador. The data obtained from the main Eastern-Canadian herbaria or specifically collected *in situ* show that this is a very frequent taxon south of the 50th parallel, but extremely less frequent north of this line. Its present area in Quebec-Labrador extends from the Magdalen Islands to the border of Ontario and from the United States to Manowin island, near Sept-Îles, where it reaches its most northern limit. Its vertical distribution is bi-altitudinal with a clear preference for the plains and the hills. The species is linked to gentle slopes and to two main deposit types: stony till and fine-textured deposits. It grows mainly on brunisols, podzols and gleysols, moderately to imperfectly drained, and covered by acid moder or mull humus. It is found typically in sugar-maple forests but also occurs in balsam-fir communities and in about twenty other types of vegetation. Gregarious and exclusively linked to the low herbaceous layer, *C. caroliniana* is present in the maple and fir great domains and at the subalpine level. Its flowering period stretches, according to its domain, from the end of April to the end of July. Soon afterwards, seed setting follows. This taxon is to be sought after towards west and north and along the streams coming from the mountains where it is present. The grid mapping system was found well adapted to the study of the distribution of taxa which frequency is to be determined.

KEYWORDS: *Claytonia caroliniana*, distribution, ecology, phenology, frequency.

RÉSUMÉ

Le *Claytonia caroliniana* Michx. var. *caroliniana* (Portulacaceae) a fait

l'objet d'un échantillonnage systématique visant à déterminer sa répartition en réseau, sa fréquence et son écologie dans les communautés végétales du Québec-Labrador. Les données provenant des principaux herbiers de l'Est du Canada et de récoltes effectuées expressément montrent qu'il s'agit d'un taxon très fréquent au sud du 50^e parallèle, mais extrêmement peu fréquent au nord de cette limite. Son aire actuelle, dans ce territoire, s'étend des Îles-de-la-Madeleine à la frontière de l'Ontario et de la frontière des États-Unis à l'île Manowin, près de Sept-Îles, où il atteint son point le plus septentrional. Sa répartition verticale est bi-modale, avec une nette préférence pour la plaine et les collines. *C. caroliniana* est lié aux faibles pentes et à deux types principaux de dépôt: le till pierreux et les dépôts à texture fine. Il croît surtout sur des brunisols, podzols et gleysoirs, moyennement à imparfaitement drainés et recouverts des humus moder ou mull acides. C'est un taxon des érablières sucrières qui transgresse dans les sapinières baumières et une vingtaine d'autres groupements. Gréginaire et exclusivement limité à la strate herbacée basse, il est présent dans les grands domaines de l'érablière et de la sapinière, et à l'étage subalpin. Sa floraison va, selon les domaines, de la fin d'avril à la fin de juillet. Elle est suivie, peu de temps après, par la fructification. Le taxon est à rechercher vers l'ouest et le nord, et le long des cours d'eau qui descendent des montagnes où il est présent. Quant à la cartographie en réseau, elle se prête à l'étude de la répartition des taxons dont on veut déterminer le degré de fréquence.

INTRODUCTION

Le *Claytonia caroliniana* Michx. var. *caroliniana* (Portulacaceae) possède en Amérique du Nord une aire de répartition très vaste. On le trouve de l'est du Manitoba à Terre-Neuve et, vers le sud, jusqu'aux montagnes du Tennessee et de la Caroline du Nord (BRAUN, 1937; ROLAND et SMITH, 1969;

ROUSSEAU, 1974; BOUCHARD *et al.*, 1990; ROULEAU et LAMOUREUX, 1992). BRAUN (1937) le qualifie de taxon des Grands-Lacs, alors que DANSEREAU (1957) l'inclut parmi les espèces appalachiennes. Selon DOYON et LAVOIE (1966) et ROUSSEAU (1974), il serait à classer parmi les éléments de la région Grands-Lacs-Saint-Laurent, telle que définie par DANSEREAU (1957) et ROWE (1959).

Au Québec, le *Claytonia caroliniana* atteint la limite nord de son aire sur l'île Manowin près de Sept-Îles, sur la côte nord du golfe du Saint-Laurent (ROUSSEAU, 1974). Cependant, jusqu'en 1940, à l'exception de cette donnée basée sur une récolte de SAINT-CYR (1886a, 1886b), il a été rapporté surtout de la partie méridionale de la province (ROUSSEAU, 1974) et plus particulièrement des érablières sucrières (ordre des *Aceretalia sacchari* Gr. 1966) dont il était considéré comme l'une des espèces caractéristiques (DANSEREAU, 1943; GRANDTNER, 1966). La découverte subséquente de nouvelles populations (Duparquet, Abitibi-Ouest: EMPAIN et ROUSSEAU, 1940; prairie subalpine, mont Logan: GERVAIS, 1964; forêt d'orme et d'aulne, lac Témiscamingue: DOYON et LAVOIE, 1966; sapinière baumière, lac Chicobi: GAUDREAU, 1972 et érablière bâtarde, parc national Forillon, Gaspésie: GRANDTNER et ROUSSEAU, 1975) indiquait une aire de distribution et une amplitude écologique beaucoup plus vastes, comme Raymond le prédisait dès 1949. Ce taxon, loin de se limiter à l'érablière, s'étend sur plusieurs domaines et grands domaines climatiques et sur une grande variété de milieux (GERVAIS et GRANDTNER, 1981).

Compte tenu de ces nouvelles données et du fait que malgré les travaux de ROUSSEAU (1974) et de GERVAIS et GRANDTNER (1981), la géographie et l'écologie de *C. caroliniana* au Québec-Labrador demeuraient imprécises, nous avons décidé d'entreprendre une étude systématique de sa répartition géographique actuelle et une analyse des données écologiques et phénologiques pouvant l'expliquer.

Tableau 1 - Échelle exponentielle de fréquence relative d'un taxon.

%	Fréquence	Coefficient
< 1	extrêmement peu fréquent	+
1-3	très peu fréquent	1
3-7	peu fréquent	2
7-15	fréquent	3
15-40	très fréquent	4
40 - 100	extrêmement fréquent	5

MATÉRIEL ET MÉTHODE

INVENTAIRE ET RÉCOLTES

Un inventaire des spécimens a d'abord été effectué dans les herbiers canadiens suivants dont les abréviations sont selon HOLMGREN *et al.* (1990): CAN, DAO, MT, MTJB, MTMG, QEF, QFA, QFBE, QMP, QPAR, QUE, SCFQ, SFS, ULF, UQAM, UQAR, UQTR. L'herbier du Collège d'enseignement général et professionnel de Rimouski (COLR) et celui du Collège

d'enseignement général et professionnel de Sainte-Foy (COLSF) ont aussi été consultés. La présence de la claytonie a été pointée sur la carte générale des feuillets au 50000^e du système topographique fédéral du Canada et les renseignements écologiques transférés dans une base de données.

Cet inventaire a été complété, entre 1984 et 1991, par une exploration méthodique du territoire des 129 feuillets additionnels restés vides, enclavés ou limitrophes, représentant une superficie approximative de 129.000 km².

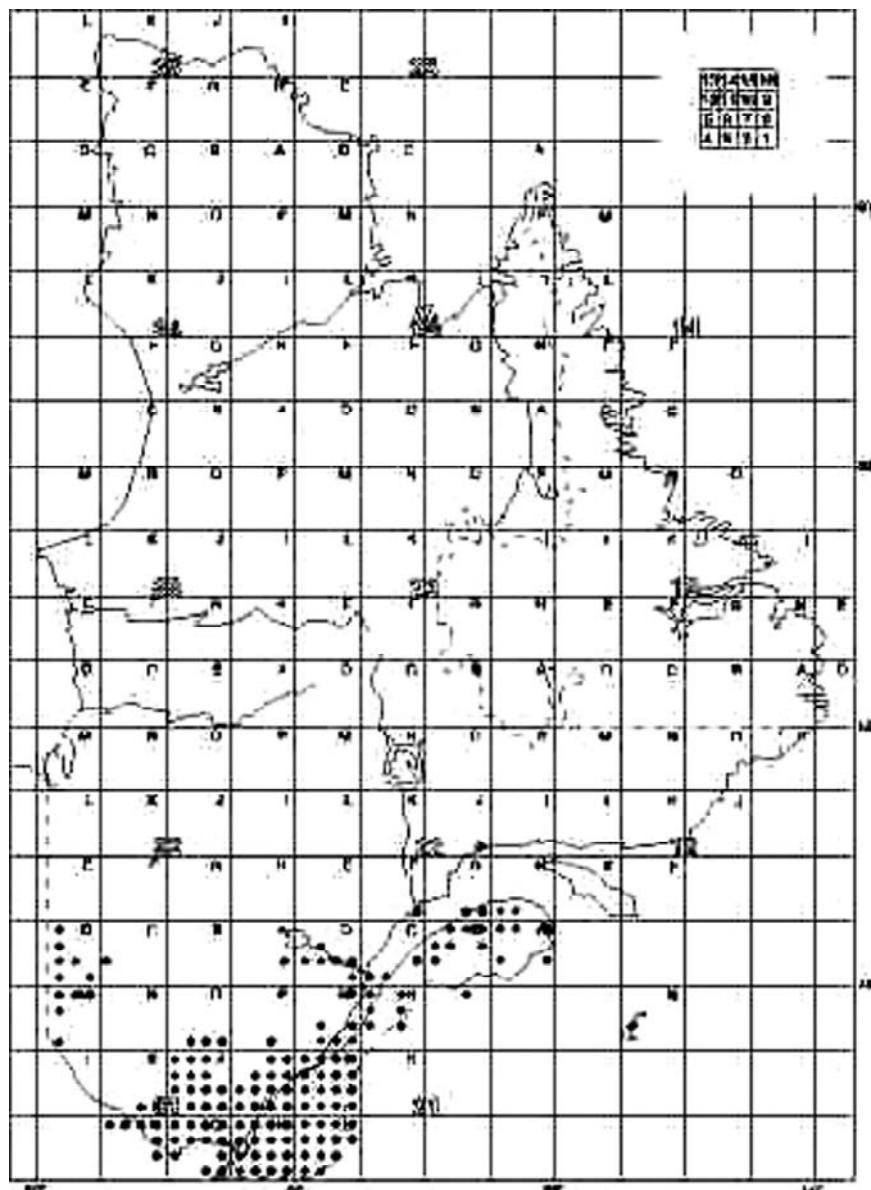


Fig. 1 - Répartition géographique de *Claytonia caroliniana* var. *caroliniana* au Québec-Labrador. Le carré isolé, en haut à droite, indique le mode de numérotation et l'ordre des feuillets cartographiques.

Cette exploration a été effectuée principalement par le premier auteur, aidé d'une équipe de quelques botanistes et de nombreux membres de l'Ordre des ingénieurs forestiers du Québec coordonnés par Rosaire Jean (voir les Remerciements). À chaque première découverte de la claytonie, trois spécimens ont été récoltés et une fiche de terrain a été établie. Elle comprenait le numéro de la carte, une description sommaire du groupement végétal, le numéro de l'échantillon du sol, l'humidité du sol (humide, moyennement sec, sec), la date et le nom du récolteur. L'échantillon du sol était prélevé près du corme et, après séchage à l'air libre, a servi notamment à la détermination du pH. Les spécimens récoltés ont été déposés à l'herbier QEF, aujourd'hui incorporé à l'herbier QFA.

Pour un certain nombre de spécimens, des fiches plus complètes ont été rédigées. L'étude a pu donc finalement porter sur les paramètres suivants: latitude, longitude, altitude, pente, exposition, dépôt, sol, drainage (ramené à une échelle de 5 classes: 1-rapide, 2-bon, 3-moyen, 4-imparfait, 5-mauvais), humus, réaction (pH), groupement végétal, strate, abondance-dominance (selon l'échelle de BRAUN-BLANQUET, 1932, légèrement modifiée par GRANDNER, 1974), sociabilité (selon les mêmes auteurs), domaine climacique (au sens de GRANDNER, 1966), date de floraison et date de fructification.

CARTOGRAPHIE ET FRÉQUENCE

La méthode employée était celle de la cartographie en réseau qui consiste, selon DELVOSALLE (1975) et GÉHU (1984), à représenter graphiquement la présence d'un taxon dans une surface de référence (maille). La surface de référence ou maille, fournie par la trame du réseau, correspondait, dans ce cas-ci, à un feuillet de la carte au 50000^e du système canadien national de référence cartographique. Les mailles étaient rectangulaires, mesuraient environ 37x28 km et couvraient une superficie approximative de 1.000 km².

La présence de la claytonie à l'intérieur de chaque maille était indiquée par un point. Pour permettre l'utilisation des points de la même dimension sur tout le territoire du Québec-Labrador, la projection cartographique a été modifiée afin d'obtenir partout des surfaces carrées uniformes. Seuls les spécimens présents dans un herbier ont servi à la cartographie.

En ce qui concerne la fréquence

absolue de la claytonie, celle-ci correspond au nombre de surfaces de référence (mailles ou feuillets cartographiques au 50000^e) du réseau, pour lesquelles existe au moins un spécimen d'herbier. La fréquence relative, elle, est exprimée en pourcentage du nombre de mailles comprenant le taxon, par rapport au total des mailles du Québec-Labrador (2154) ou encore d'une portion de ce territoire (p. ex. du Québec-Labrador méridional (473), du Québec-Labrador septentrional (1681), d'un domaine climacique, d'une région écologique, etc.). Une échelle exponentielle universelle de fréquence relative a permis ensuite de la qualifier comme indiqué au Tableau 1.

ANALYSE DES DONNÉES

L'analyse écologique a porté sur les données disponibles concernant les 814 spécimens relevés dans les herbiers ou récoltés au cours de l'exploration. Malheureusement, les informations sur les fiches de récolte existantes dans les herbiers sont, la plupart du temps, très rudimentaires. À toute fin pratique, seules les récoltes effectuées pour les herbiers QEF, ULF et celui du Bureau d'aménagement de l'Est du Québec incorporé dans UQAR, contiennent, de façon plus systématique, en plus du lieu, le numéro de la carte, les coordonnées géographiques et les données concernant l'altitude, la pente, l'exposition, le dépôt (roche-mère), le sol, l'humidité (drainage), l'humus, le pH, le groupement végétal, la description du spécimen, la strate, l'abondance-dominante et la sociabilité. Dans quelques cas, la mention du numéro de relevé écologique correspondant et l'observation du spécimen d'herbier ont permis la déduction des renseignements concernant les facteurs précités ou encore la date et le degré d'avancement de la floraison et de la fructification. Au total, le nombre de données utilisables ne dépassait cependant pas 20% de tous les spécimens considérés ce qui a réduit le nombre de mesures entre 42 et 159, à l'exception du groupement végétal et de la floraison où ils atteignaient respectivement 503 et 645 observations.

RÉSULTATS ET DISCUSSION

RÉPARTITION GÉOGRAPHIQUE

L'inventaire effectué dans les herbiers a permis de pointer la présence de la claytonie dans 121 feuillets ou 5,6%

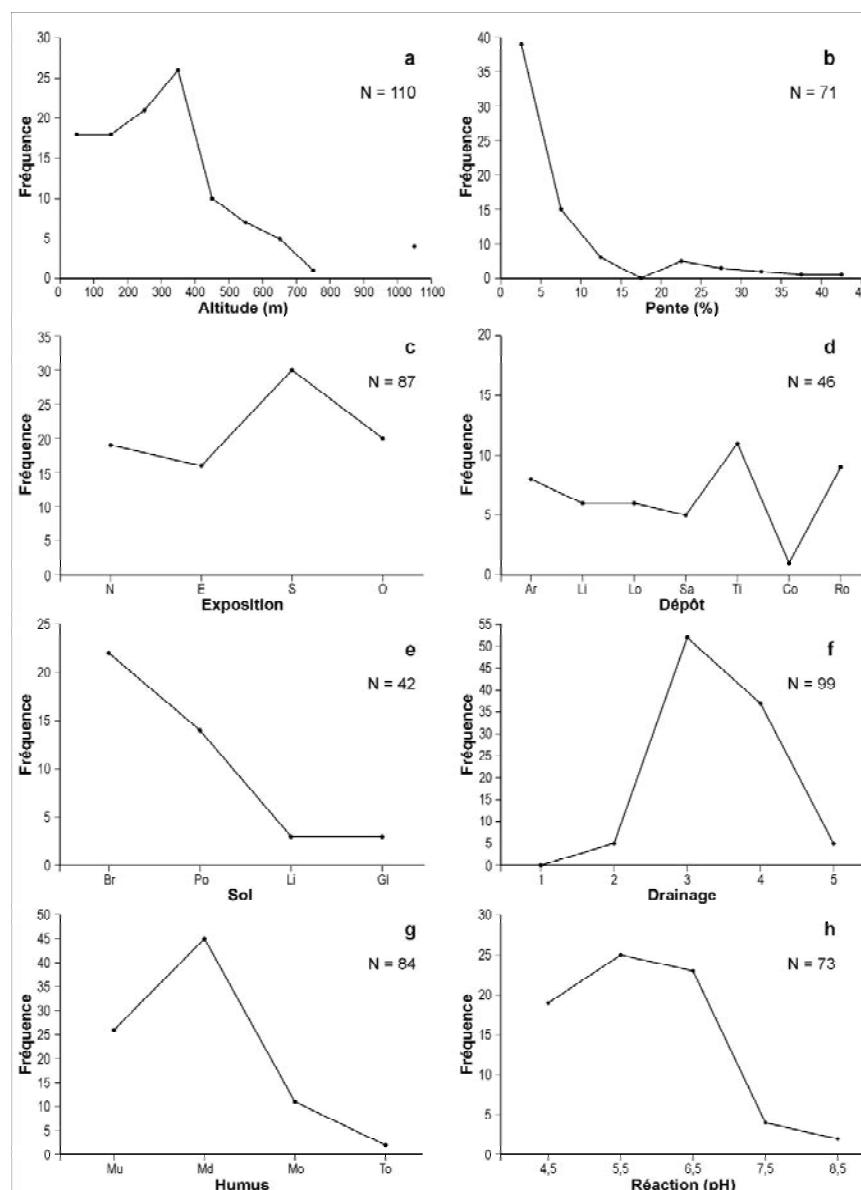


Fig. 2 - Fréquence de *Claytonia caroliniana* var. *caroliniana* en fonction de quelques facteurs physiques, au Québec-Labrador. a. Altitude, b. Pente, c. Exposition (N-nord, E-est, S-sud, O-ouest), d. Dépôt (Ar-argile, Li-limon, Lo-loam, Sa-sable, Ti-till, Co-colluvion, Ro-roc), e. Sol (Br-brunisol, Po-podzol, Li-lithosol, Gl-gleyisol), f. Drainage (1-rapide, 2-bon, 3-moyen, 4-imparfait, 5-mauvais), g. Humus (Mu-mull, Md-moder, Mo-mor, To-tourbe), h. Réaction.

des 2154 feuillets que compte Québec-Labrador (Fig. 1). Ces feuillets étaient situés surtout dans le centre-sud du Québec, sur le pourtour de la Gaspésie et au Saguenay-Lac-Saint-Jean. Bien que la comparaison avec les cartes de ROUSSEAU (1974), de DOYLE *et al.* (1984) et de DOYLE et DOYLE (1998) soit difficile à cause de la méthode que ceux-ci ont utilisé, la claytonie présentait déjà, après cet inventaire, une aire de répartition beaucoup plus vaste couvrant tout le centre-sud du Québec, la Gaspésie, d'où elle était absente sur les cartes de DOYLE *et al.* (1984) et de DOYLE et DOYLE (1988), et les Îles-de-la-Madeleine, où elle n'a pas encore été cartographiée malgré une vieille récolte à l'Île d'Entrée faite par HYATT *et al.*, rapportée par DAVIS (1966). Il subsistait,

toutefois, de vastes régions à l'ouest et au centre-sud du Québec, ainsi qu'à l'intérieur de la Gaspésie où sa présence restait souvent purement littéraire (Abitibi) ou franchement inconnue.

La prospection sur le terrain qui a suivi, a permis d'ajouter 28 nouveaux feuillets portant le nombre de mailles avec claytonie à 149 au total, ou 6,9% de tous les feuillets du Québec-Labrador, ce qui en fait un taxon peu fréquent dans l'ensemble de ce territoire. Cependant, lorsqu'on considère sa fréquence au sud du 50^e parallèle seulement, celle-ci atteint, avec les 148 présences-feuilles, 31,3%, faisant de la claytonie un taxon très fréquent au Québec-Labrador méridional. À l'opposé, au nord du 50^e parallèle, la claytonie est présente dans un seul feuillet, ce qui représente

seulement 0,06%, et en fait un taxon extrêmement peu fréquent au Québec-Labrador septentrional, selon l'échelle du Tableau 1.

Au total, les plus importantes additions cartographiques se trouvent aux Îles-de-la-Madeleine (1) et en Abitibi-Témiscamingue (10). Elles étendent la limite de l'aire québécoise de répartition cartographiée du taxon vers l'est et confirment sa présence en Abitibi-Témiscamingue. Cette aire va désormais des Îles-de-la-Madeleine (61°52' long. O) à la frontière de l'Ontario (79°26' long. O) et de la frontière des États-Unis (45°00' lat. N) à l'île Manowin, près de Sept-Îles (50°05' lat. N), où se trouve la localité la plus nordique sur le continent. Les additions complètent également l'aire de répartition notamment sur la Côte-Nord (Baie-Comeau), au

sud-ouest du Québec et à l'intérieur de la péninsule gaspésienne.

CARACTÉRISTIQUES ÉCOLOGIQUES

ALTITUDE. La claytonie de Caroline typique possède, au Québec-Labrador, une répartition verticale bi-modale (Fig. 2a). Des 110 récoltes (13,5%) dont l'altitude est connue, 106 occupent des stations de plaine et de collines (entre 15 et 700 m d'altitude) et 4 des stations subalpines (entre 1.000 et 1.090 m d'altitude). Le maximum de sa fréquence (26 présences) est atteint vers 350 m, alors que la station possédant la plus haute altitude (1.090 m) se trouve au mont Logan, en Gaspésie, où elle a déjà été signalée par GERVAIS (1964) et GERVAIS et GRANDTNER (1981, 1990).

PENTE. Le degré d'inclinaison de la pente est connu dans le cas de 71 récoltes (8,7%). La claytonie semble liée surtout aux pentes très faibles (0-5°) et faibles (5-10°), bien qu'on puisse la trouver, exceptionnellement, jusqu'à une inclinaison de 45° (Fig. 2b). GERVAIS et GRANDTNER (1981, 1990) l'ont signalée sur des pentes de 4-5° et 25° respectivement, voire, au pied du mont Logan, sur une pente de 60°. Dans le secteur étudié par MERCIER *et al.* (1990), la pente variait entre 8 et 29%.

EXPOSITION. Les 87 récoltes (10,7%) pour lesquelles l'exposition était déterminée, occupent les pentes orientées vers tous les points cardinaux (Fig. 2c). Toutefois, l'exposition sud est la plus fréquente et celle de l'est la moins fréquente.

DÉPÔT. Quarante-quatre récoltes, ou 5,4%, possèdent la mention du type de dépôt. La majorité d'entre elles ont été faites sur du till, fréquemment pierreux, suivi du roc, puis des textures fines (argile, limon, loam) (Fig. 2d). DOYON et LAVOIE (1966) et GERVAIS et GRANDTNER (1961, 1990) signalent des substrats similaires (loam argileux, loam sableux et till). MERCIER *et al.* (1990) rapportent surtout le till (principalement mince) et, une seule fois, un dépôt fluvio-glaciaire. Par contre, la claytonie semble éviter l'instabilité d'une colluvion, où elle a été récoltée une seule fois.

SOL. Des 42 récoltes (5,1%) dont le type de sol soit connu, plus de la moitié (22) provenait d'un brunisol, 14 d'un podzol et 3 d'un lithosol et gleysol respectivement (Fig. 2e). Parmi les catégories inférieures à l'ordre, le brunisol dystrique dégradé se classe en tête de liste (14), suivi par le podzol humo-ferrique (9). GERVAIS et GRANDTNER (1981, 1990) et MERCIER *et al.* (1990) rapportent la claytonie sur des sols analogues (brunisols mélanique, sombre et dystrique, podzol humo-ferrique) et sur régosol.

DRAINAGE. La classe de drainage du sol, appelée parfois humidité, existe pour 99 ou 12,2%, de récoltes examinées. La Fig. 2f montre que la claytonie se trouve le plus fréquemment sur les sols moyennement et imparfaitement drainés (classes 3 et 4). Par contre, celle-ci n'a pas été récoltée, ou la classe de drainage n'a pas été notée, dans les stations à drainage rapide (classe 1) et très rarement dans les stations à drainage bon (classe 2) et mauvais (classe 5). Ce qui nous permet de qualifier la claytonie

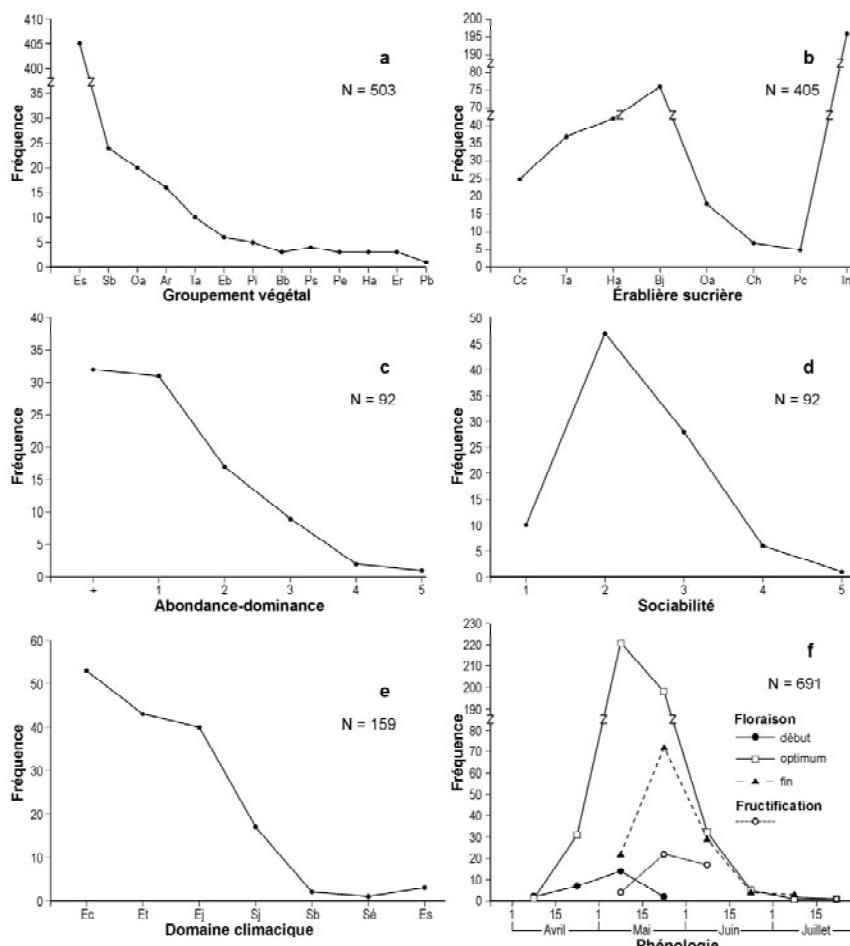


Fig. 3 - Fréquence de *Claytonia caroliniana* var. *caroliniana* en fonction de quelques facteurs biologiques, au Québec-Labrador. a. Groupement végétal (Es-érablières sucrières, Sb-sapinières baumières et bétulaie jaune, Oa-ormaie américaine et frênaie noire, Araulnaie rugueuse, Ta-tremblaines américaines et peupleraie baumière, Eb-érablière bâtarde, Pi-pinèdes blanche et rouge et chênaie rouge, Bb-bétulaies blanches, Ps-prairies subalpines, Pe-prairie secondaire, Ha-hêtraie américaine, Er-érablière rouge, Pb-pessière blanche), b. Érablière sucrière (Cc-à caryer cordiforme, Ta-à tilleul américain, Ha-à hêtre américain, Bj-à bouleau jaune, Oa-à orme américain, Ch-à chêne rouge, Pc-à pruche canadienne, Indéterminée), c. Abondance-dominance (+: <1% de recouvrement, 1: 1-5%, 2: 5-25%, 3: 25-50%, 4: 50-75%, 5: 75-100%), d. Sociabilité (1-croissance isolée, 2-en touffe, 3-en petite colonie, 4-en grande colonie, 5-en très grande colonie), e. Domaine climatique (Ec-érablière à caryer cordiforme, Et-érablière à tilleul américain, Ej-érablière à bouleau jaune, Sj-sapinière à bouleau jaune, Sb-sapinière à bouleau blanc, Sé-sapinière à épinette blanche, Es-étage subalpin), f. Phénologie.

d'espèce mésophile à subhygrophile. Ces résultats correspondent bien aux données rapportées par GERVAIS et GRANDTNER (1981, 1990) et par MERCIER *et al.* (1990), bien qu'au mont Logan le drainage indiqué par GERVAIS et GRANDTNER (1981, 1990) a été plus souvent imparfait, une fois même, mauvais.

HUMUS. La Fig. 2g montre que la très grande majorité de 84 spécimens, ou 10,3% des spécimens examinés, pour lesquels le type d'humus a été déterminé, poussaient sur l'humus moyenement ou bien décomposé (moder et mull). La présence de la claytonie était beaucoup plus rare sur l'humus brut (mor) et, particulièrement, sur la tourbe. Dans ce dernier cas, il s'agissait exclusivement de tourbe mésique. GERVAIS et GRANDTNER (1981, 1990) et MERCIER *et al.* (1990) la signalent sur les mêmes types d'humus (moder et mull), bien qu'au mont Logan plus fréquemment sur mor. Par ailleurs, GRANDTNER l'avait qualifiée d'espèce indicatrice de moder (1990-1991).

RÉACTION. Les données sur le pH du sol existent pour 73 spécimens (9,0%). La Fig. 2h illustre le caractère acidophile de la claytonie dont le maximum de fréquence se situe entre les pH 4,5 et 6,5 (min. 4,0 et max. 8,0). Les valeurs de pH rapportées par GERVAIS et GRANDTNER (1981, 1990) et par MERCIER *et al.* (1990) (4,1-6,7) se situent entre ces deux derniers extrêmes.

GROUPEMENT VÉGÉTAL. C'est l'une des caractéristiques les plus fréquemment notées, étant disponible pour 503, ou 61,8% des spécimens examinés. La claytonie apparaît sur la Fig. 3a, sans aucun doute, comme une espèce des érablières sucrières (ordre des *Aceretalia sacchari* Gr. 1996), dont elle a été considérée, par ailleurs, comme l'une des espèces caractéristiques (DANSEREAU, 1943; GRANDTNER, 1966). Cependant, elle est également présente, bien qu'à un moindre degré, dans les sapinières baumières (ordre des *Abietetalia balsameae* Gr. 1990-1991), surtout à bouleau jaune, et dans les groupements végétaux aux sols riches mais imparfaitement drainés (ordre des *Ulmetalia americana* Gr. 1990-1991, comme l'orme américaine, la frênaie noire, l'aulnaie rugueuse, etc.) où elle a déjà été signalée par DOYON et LAVOIE (1966). En examinant la Fig. 2b, on constate, si l'on exclut les érablières non déterminées, que sa plus grande fréquence se trouve dans l'érablière à bouleau jaune,

suivie par l'érablière à hêtre. C'est le cas aussi à la montagne de Stoneham (MERCIER *et al.*, 1990). Elle est, cependant, également fréquente dans les érablières dites riches (alliance de l'*Acerion sacchari* Gr. 1966), c'est-à-dire à tilleul américain et à caryer cordiforme, comme rapporté par GERVAIS et GRANDTNER (1981). Quant à sa fréquence dans les prairies subalpines, où elle a déjà été signalée par GERVAIS et GRANDTNER (1981, 1990), elle est comparativement beaucoup plus faible (Fig. 3a). Les autres groupements, non signalés dans la littérature, dans lesquels la claytonie a également été récoltée sont les suivants: les sapinières (à thuya occidental, à bouleau blanc, à épinette blanche), les tremblaies (à érable sucrier, à frêne noir, à bouleau blanc, à aulne rugueux), la peupleraie baumière, l'érablière rouge à frêne noir, la pinède blanche à bouleau blanc, la pinède rouge plantée, la chênaie rouge, les bétulaires blanches (à érable sucrier, à sapin baumier), la hêtraie américaine, la pessière blanche et les prairies secondaires. GERVAIS et GRANDTNER (1990) l'avaient également signalé, au mont Logan, dans une pessière blanche rabougrie.

STRATE. La claytonie fait uniquement partie de la strate herbacée basse (0-60 cm de hauteur) comme noté sur 92 étiquettes de récolte, ou 11,3% des spécimens examinés.

ABONDANCE-DOMINANCE. La fréquence de la claytonie en fonction du coefficient d'abondance-dominance est représentée à la Fig. 3c. Celle-ci montre que sa fréquence diminue à mesure que le coefficient d'abondance-dominance augmente. Les maxima sont atteints dans les classes + et 1, c'est-à-dire entre <1 et 5% de recouvrement de la place-échantillon et le minimum dans la classe 5 représentant 75 à 100% de recouvrement.

SOCIABILITÉ. Il s'agit d'une espèce grégaire (Fig. 3d). La majorité (47 des 92), ou 11,3%, des spécimens dont l'étiquette contient cette donnée, forment des touffes (classe 2) et 29 forment des petites colonies (classe 3). Le reste est réparti entre le mode de croissance isolé, en grandes colonies et en très grandes colonies (classes 1, 4 et 5).

DOMAINE CLIMACIQUE. La claytonie est une espèce du grand domaine de l'érablière au sens de GRANDTNER (1990-1991). En effet, 136 des 159 spécimens pour lesquels cette information a pu être déduite, y ont été récoltés. Elle

déborde toutefois, dans 20 cas, dans le grand domaine de la sapinière (au sens du même auteur), puis réapparaît, 3 fois, à l'étage subalpin. Pour ce qui est des différents domaines climaciques, la Fig. 3e montre que sa fréquence diminue du sud au nord pour réaugmenter, très légèrement, à l'étage subalpin.

DONNÉES PHÉNOLOGIQUES

FLORAISON. Les renseignements sur la floraison proviennent principalement de l'observation de 645 spécimens d'herbier représentant 79,2% des spécimens examinés. La Fig. 3f représente la fréquence du début, de l'optimum et de la fin de ce phénomène. Elle montre que le début de la floraison de la claytonie s'étend de la première quinzaine du mois d'avril (domaine de l'érablière à caryer cordiforme) à la dernière quinzaine du mois de mai (domaine de la sapinière à bouleau jaune) avec le maximum situé dans la première quinzaine de mai. Ce début est sans doute plus tardif à l'étage subalpin où il arrive, probablement, dans la deuxième quinzaine de juin. L'optimum de floraison suit de près le début et s'étend, dans le même sens, de la deuxième quinzaine d'avril à la deuxième quinzaine de juillet, avec un fort maximum de fréquence à la mi-mai. La date la plus tardive de l'optimum de la floraison connue jusqu'à présent, est celle du 24 juillet. Elle a été observée dans un ravin ombragé du mont Logan, à 1 050 m d'altitude. Quant à la fin de la floraison, elle a été notée entre le début de mai et la mi-juillet, avec un maximum à la fin de mai, bien qu'il soit fort probable qu'à l'étage subalpin, la claytonie finisse de fleurir à la fin de juillet seulement. Deux études seulement traitent de ce phénomène au Québec-Labrador. VÉZINA et GRANDTNER (1965) situent le début, l'optimum et la fin de la floraison de la claytonie dans une érablière à tilleul américain au 5, 16 et 27 mai respectivement en la mettant en rapport avec la feuillaison des arbres, la température de l'air et la radiation solaire. Dans une deuxième étude, réalisée dans une érablière à bouleau jaune, GRANDTNER et GERVAIS (1985) placent le début et la fin de la floraison au 1^{er} mai et au 14 juin respectivement.

FRUCTIFICATION. La fréquence de la fructification suit un patron semblable à celui de la floraison, bien qu'avec un décalage d'une quinzaine de jours (Fig. 3f). Elle débute au commencement de mai pour se terminer à la fin de juillet.

Son maximum est atteint dans la deuxième quinzaine de mai et le phénomène se termine sans doute vers la fin de juillet, voire au début d'août seulement, à l'étage subalpin. Selon VÉZINA et GRANDTNER (1965) le début, l'optimum et la fin de la fructification se produisent dans une érablière à tilleul américain les 17 et 25 mai et 9 juin respectivement, alors que dans une érablière à bouleau jaune, plus nordique, le phénomène débute à la fin de mai, pour se terminer à la mi-juin (GRANDTNER et GERVAIS, 1985).

En conclusion, la claytonie de Caroline typique est un taxon très fréquent au Québec-Labrador méridional, mais extrêmement peu fréquent, selon l'échelle du Tableau 1, dans la portion septentrionale de ce territoire. La nouvelle carte en réseau montre son aire actuelle nettement agrandie. Celle-ci va désormais des îles-de-la-Madeleine à la frontière de l'Ontario et de la frontière des États-Unis à l'Île Manowin, près de Sept-Îles, où se trouve sa localité la plus nordique sur le continent. Elle complète aussi, substantiellement, cette aire notamment en Abitibi-Témiscamingue, dans le sud-ouest du Québec, sur la Côte-Nord et à l'intérieur de la Gaspésie. Sa répartition verticale est bi-polaire, avec une nette prédominance pour la plaine et les collines, l'autre portion, isolée, étant à l'étage subalpin du mont Logan. Elle est liée aux faibles pentes de toutes les expositions, mais particulièrement à l'exposition sud et à deux catégories de dépôts: le till pierreux et les dépôts à texture fine. Ses préférences édaphiques vont aux brunisols, podzols et gleysols moyennement à imparfaitement drainés, recouverts des humus moder et mull acides. C'est, sans aucun doute, un taxon caractéristique des érablières. Cependant, il est aussi présent dans les sapinières et dans une série de groupements végétaux aux sols riches et imparfaitement drainés, ainsi que dans une vingtaine d'autres groupements mentionnés pour la première fois. Grégaire, il est exclusivement limité à la strate herbacée basse des grands domaines de l'érablière et de la sapinière, ainsi qu'à l'étage subalpin. Sa fréquence diminue dans le même sens. Il en est de même de ses dates de floraison et de fructification, légèrement décalées dans le temps, qui s'étendent, selon les domaines, de la fin d'avril à la fin de juillet, voire au début d'août. C'est un taxon à rechercher vers l'ouest, vers le nord et le long des cours d'eau qui descendent des montagnes où il est présent et, notamment, ceux du mont

Logan.

Enfin, la cartographie en réseau, utilisée pour la première fois au Québec, pourrait être appliquée à l'étude de la répartition et de la fréquence d'autres taxons.

REMERCIEMENTS

Les auteurs remercient Rosaire Jean qui a coordonné les travaux de prospection et les personnes suivantes qui y ont pris part: D. Audet, Gaétan Auger, François Baril, René Barry, Henriot Beaudet, A. Beausoleil, Réjean Bégin, Yves Bergeron, Serge Bernard, Doris Bibeau, Jacques Bibeau, Marcel Blondeau, Elisabeth Bossert, Bernard Bouchard, Pacôme Boucher, Jean-Pierre Bourassa, Jacques Bournival, Maurice Carignan, Jean-Louis Caron, Denis Chabot, Marie Cliche, Michèle Desjardins, Pierre Desrochers, R.V. Dixon, Francine Dorion, Renaud Dostie, Adrien Dubé, Madeleine Dumais, Danièle Fabri, Luc Filion, Gilles Fortier, Sylvain Fortin, Marcel Fraser, Alain Gaudreau, Normand Gendron, Paul Gilbert, Jean-Marc Hardy, Daniel Huard, Guy Huot, Jean-Marie Johnston, Guy Laflamme, Yoland Laflamme, Marie-Claude Lambert, Luc Lapointe, Roger Larivière, Diane Larose, Herman Lavoie, Philippe Lebreux, Gérald Lebrun, Martin J. Lechowicz, Raymond Lord, Luc Magneau, Lucie Maillette, Denise Marquis, Jacques Martel, Renée Martial, Roger Masson, Normand Morin, Pierre Morin, A.W. Morris, Pierre Morisset, Thomas Morrisette, Charles Neveu, Jean-Pierre Otis, Denis Ouellet, François Pelletier, Jeannot Pelletier, Jean-Pierre Pelletier, Serge Pinard, J.R. Pitre, Francine Plante, Pierre Robitaille, Félix Roy, Jocelyn Roy, André Sabourin, Germain Savard, Jacques Sormany, Robert St-Amour, Paul Saint-Laurent, André St-Pierre, Daniel Tanguay, Bernard Tremblay, Richard Tremblay, Gino Trudel, Pierre Viens, Alfred Vietinghoff et Normand Villeneuve. Ils remercient également Yves Lachance pour le graphisme, Lyse Sanfaçon et Paule Delisle pour le traitement de texte.

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IL RUOLO DELLA FITOSOCIOLOGIA NELLE RICERCHE INTERDISCIPLINARI

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ABSTRACT

The utility of the phytosociology to facilitate interdisciplinary approach and connect the results obtained by various scientific branches between them is discussed. Some examples of application of the knowledge of the flora and vegetation on different levels of deepening during the evaluating the quality of urban environment are illustrated. Also proposed is the possibility to define the phytoallergenic potential of urban biotopes through the control of the allergenicity of plant associations.

KEYWORDS: Phytosociology, Interdisciplinary research, Urban ecosystem, Central Italy.

RIASSUNTO

Viene discussa l'utilità di ricerche fitosociologiche per agevolare l'approccio multidisciplinare e collegare tra loro i risultati ottenuti da altre branche delle scienze. Vengono illustrati esempi applicativi delle conoscenze sulla flora e vegetazione a diversi livelli di approfondimento nella valutazione della qualità dell'ambiente urbano. Tramite la valutazione dell'allergenicità delle associazioni vegetali viene proposto il controllo del potenziale fitoallergenico nei biotopi urbani.

INTRODUZIONE

L'inizio della fitosociologia come disciplina scientifica, avvenuto nel secolo scorso con il metodo di BRAUN-BLANQUET (1928) e dei suoi collaboratori della scuola Zurigo-Montpellier, è stato seguito dalla pubblicazione di contributi riguardanti la vegetazione di diverse parti d'Europa (BRAUN-BLANQUET e TÜXEN, 1943; BRAUN-BLANQUET *et al.*, 1952; OBERDORFER, 1957-1992, ecc.). Caratterizzato da un notevole entusiasmo scientifico, il periodo iniziale ha dato luogo a numerose ricerche fitosociologiche aumentando velocemente le

conoscenze locali e globali sulla vegetazione. Sono stati pubblicati anche diversi contributi teorici o quelli rivolti all'interpretazione ed elaborazione dei dati (WESTHOFF VANDER MAAREL, 1973; ORLOCI, 1978; GÉHU, 1980, ed altri). Con l'applicazione dei programmi computerizzati è stato infine facilitato il lavoro base sulle tabelle fitosociologiche ed agevolata una più rapida comparazione dei risultati.

Il progressivo aumento delle conoscenze fitosociologiche non è invece stato seguito da un adeguato uso di queste informazioni per scopi applicativi e pratici. Sono infatti ancora pochi i contributi che riguardano i rapporti tra la fitosociologia ed altre discipline scientifiche. Si intende perciò discutere questa possibilità illustrando alcuni esempi riguardanti l'ambiente urbano dell'Italia centrale.

A causa della crescita della popolazione urbana mondiale si assiste attualmente al fenomeno della dissipazione insediativa urbana ("urban sprawl", GOTTMAN e HARPER, 1967). Un continuo avanzamento delle aree urbanizzate a scapito di quelle naturali e semi-naturali è diventato ormai un fenomeno globale. Dominato dalle attività umane ed influenzato dalle interazioni tra le condizioni ecologiche, gli abitanti e le specie vegetali ed animali, il territorio di una città diventa sempre di più complesso ed eterogeneo. Attratte favorevolmente da questo ambiente, diverse piante ed animali si insediano qui sempre più numerosi, causando la globalizzazione della flora e della fauna. In una città si intrecciano in un forte legame i fattori ecologici e quelli antropici, urbanistici e storici. Lo studio dell'ecosistema urbano richiede perciò un approccio interdisciplinare e l'utilizzo di diversi metodi di ricerca a seconda di ognuna delle discipline che trattano i molteplici problemi presenti nelle città.

ACQUISIZIONE DEI DATI

Una continua frammentazione dello spazio urbano, in relazione alle vicende storiche e culturali della popola-

zione umana, porta alla formazione di un mosaico di numerose aree parziali diverse tra loro, che vengono indicate come macro-, meso- e microbiotopi (HRUSKA, 2006). I biotopi urbani ospitano, oltre agli abitanti, una componente vegetale ed animale caratteristica, a sua volta costituitasi in numerose comunità. Attirate dalle condizioni ambientali dei singoli biotopi, quest'ultime si sviluppano in determinate zone urbane. Differiscono tra loro per la struttura e la dinamica, l'età e la collocazione nello spazio urbano. Siccome si tratta di un ecosistema complesso, ovvero un sincosistema, diventa importante, in base alle problematiche riscontrate, definire il livello di approfondimento ed indicare la scala usata durante lo studio. Questo facilita la comparazione dei dati tra diverse discipline scientifiche. Iniziando per esempio le ricerche fitosociologiche al livello del macrobiotopo e verificando i risultati ottenuti al livello meso e microecologico si può mettere in relazione la componente biotica (uomo compreso) con lo spazio urbano. Viene così agevolata l'interpretazione finale dello studio complessivo in una determinata superficie urbana con specifico riferimento alla qualità della vita della popolazione umana.

ESEMPI

VALUTAZIONE DELLA QUALITÀ DELL'ECOSISTEMA URBANO

Il territorio urbano viene influenzato da diversi fattori: ecologici, antropici, urbanistici, sociologici, storici ed altri. Questi portano nel corso dei secoli alla formazione di superfici simili tra loro, presenti in varie città italiane, nonostante le differenze geografiche e culturali tra queste. Le peculiari condizioni ecologiche di ognuna di queste aree influenzano l'insediamento di una particolare flora e vegetazione. Le mura di cinta, le aree calpestate, i rudereti, le aree ombreggiate dei parchi e dei boschetti urbani, le sponde dei canali e dei corsi d'acqua sono i biotopi più frequenti nelle città italiane. Utilizzando le

Tab. 1 - Valutazione di alcune caratteristiche parziali dei biotopi urbani dell'Italia centrale tramite i dati fitosociologici.

Biotope	Unità fitosociologica	Posizione (zona urbana)	Urbanizz. (livello)	Età biotopo (classe)	Rarità (grado)	I.A. alleanza
Terreni calpestati	Polycarpion tetraphylli Rivas Martínez 1975	1	10	5	4	3,7
Mura	Parietario judaicæ Segal 1969	1	9	5	5	5,9
Orti	Diplotaxidion erucoidis Braun-Blanquet 1936	3	8	1	1	4,1
Margini delle strade e dei marciapiedi	Chenopodion muralis Braun-Blanquet 1936	2,3	7	1,2	1	5,7
	Dauco-Melilotion Görs 1966	2,3	6	1,2	1	5,6
	Convolvulo-Agropyrrion repentis Görs 1966	2,3	6	1,2	1	6,1
	Ornithogalo-Leopoldion Hruska 1995	2,3	6	1,2	1	2,9
	Pastinacion sativae urentis Hruska 1995	2,3	6	1,2	1	4,7
Incolti aridi	Arction lappae R. Tüxen 1937	2,3	5	2,3	1	4,5
Incolti ombreggiati	Silybo-Urticion Sissingh 1950	2,3	5	2,3	2	4,4
	Convolvulion sepium R. Tüxen 1950	2,3	4	2,3	2	4,9
	Aegopodium podagrariae R. Tüxen 1967	2,3	4	2,3	2	5,1
Sponde dei corsi d'acqua e dei canali artificiali	Galio-Alliarion (Oberd. 1957) Lohmeyer et Oberd. in Oberd. et al. 1967	2,3	4	2,3	2	5,4
	Bidention tripartitae Nordhagen 1940	3	3	3	3	4,1

I-A = indice allergenico *sensu* HRUSKA, 2003.

conoscenze sulla flora e vegetazione urbana si può controllare la qualità di questo ambiente. Per abbreviare i tempi e i costi necessari per ottenere i dati complessivi sulla flora urbana, per gli ecosistemi urbani dell'Italia centrale è stata effettuata la valutazione della qualità dell'ambiente elaborando gli elenchi parziali della flora. Questi sono basati sul valore diagnostico dei gruppi di piante caratteristiche dei biotopi urbani (HRUSKA, 2000). Essi permettono di individuare piuttosto velocemente i biotopi predominanti su una superficie urbana. Tramite la valenza fitosociologica di questi gruppi vengono individuate le associazioni vegetali presenti. Queste indicano, tramite la loro composizione floristica, determinate condizioni ecologiche e per ragioni di praticità possono essere riunite in categorie sistematiche superiori (Tab. 1). Viene studiata la loro dinamica all'interno e verso l'esterno della città in relazione all'uso dello spazio e all'età del singolo biotopo. Il lavoro prosegue individuando varie qualità parziali dei biotopi urbani come per esempio il livello di urbanizzazione, l'età e la rarità di un biotopo, l'allergenicità della flora presente, la naturalità, il valore paesaggistico, la continuità storica, la vulnerabilità, il "verde urbano" ornamentale e coltivato, ed altro. La valutazione di ognuna delle caratteristiche prese in considerazione viene effettuata mediante appropriate scale numeriche (HRUSKA, 1997).

Il giudizio complessivo sulla qualità di un determinato ambiente urbano si esprime prendendo in considerazione il maggior numero possibile delle caratteristiche parziali. I risultati ottenuti da questo approccio possono essere rappresentati tramite la cartografia computerizzata. La superficie urbana in questo caso viene suddivisa in varie zone in base all'indice della qualità dell'ambiente urbano (UEI = urban environmental quality index, HRUSKA, 2000).

Coinvolgendo gli studiosi di varie discipline scientifiche possono essere approfonditi diversi aspetti come quelli legati alla salute dell'uomo, alla conservazione e protezione dei biotopi caratteristici, al recupero delle aree degradate, all'educazione naturalistica degli abitanti, al valore ricreativo delle superfici "verdi", all'impianto ed alla gestione dei parchi e quant'altro.

VALUTAZIONE DEL POTENZIALE FITOALLERGENICO URBANO

Il progressivo aumento delle manifestazioni allergiche nella popolazione umana rende urgenti le ricerche sulla presenza, distribuzione e fenologia delle piante che producono pollini allergenici. Questi provocano nell'organismo umano un insieme di manifestazioni allergiche, tra le quali la più conosciuta è quella denominata "febbre del fieno". Sono numerose le allergofite che fanno parte della flora urbana spontanea come per esempio le *Urticaceae* (*Parietaria judaica* L., *P. lusitanica* L., *Urtica dioica* L., *U. urens* L. ed altre). I granelli pollinici microscopici fortemente allergenici di queste piante penetrano facilmente nell'apparato respiratorio umano. Ad aumentare l'allergenicità dell'ambiente urbano si aggiungono i pollini di vari alberi e arbusti coltivati per scopi ornamentali come *Cupressus sempervirens* L., *Pinus* sp. pl., *Corylus avellana* L. ed altre. Gli effetti causati dai pollini allergenici vengono ultimamente molto accentuati dalle interazioni tra questi e gli inquinanti atmosferici o addirittura tra pollini e determinati alimenti. Le persone che soffrono di allergopatie vengono a contatto con notevoli quantità di polline allergenico, sia quello trasportato dal vento dagli ecosistemi circostanti, ma soprattutto con quello prodotto all'interno della stessa città. Diventa indispensabile perciò in-

dividuare le allergofite urbane fortemente allergeniche ed indicare le zone urbane a rischio per la permanenza dei soggetti allergici a determinati pollini.

Dal punto di vista pratico, il controllo della flora allergenica si può effettuare mediante l'indice allergenico o I.A. (HRUSKA, 2003). Questo indice integra le caratteristiche biologiche ed ecologiche delle singole specie, tenendo contemporaneamente conto sia dello sviluppo della pianta in determinate aree urbane che dell'effetto allergenico del suo polline sull'uomo. Il risultato finale, espresso tramite un valore numerico che può variare da 1 a 10 in ordine crescente di allergenicità, raggruppa le allergofite in: poco allergeniche, moderatamente, fortemente allergeniche. L'indice può essere calcolato per una sola pianta, per una associazione vegetale o per altre unità fitosociologiche, in base al livello di approfondimento che ci si propone di ottenere. Può addirittura essere usato per esprimere l'allergenicità di un biotopo, di un'intera zona urbana o di un quartiere.

Ogni singolo biotopo urbano possiede una caratteristica flora allergenica. Alcune tipologie architettoniche particolari delle città italiane come le mura di cinta, agevolano l'insediamento e lo sviluppo delle allergofite, in particolar modo di quelle disperse dai venti. Le mura urbane ospitano infatti alcune *Urticacee* fortemente allergeniche caratteristiche di questo ambiente, come *Parietaria judaica* e *P. lusitanica*. Nella Tab. 1 vengono indicate le alleanze fitosociologiche più importanti nei biotopi delle città dell'Italia centrale. Il controllo del loro potenziale fitoallergenico tramite l'indice allergenico ha rilevato una notevole allergenicità proveniente dalle mura di cinta e dalle scarpate stradali. L'allergenicità delle scarpate e dei margini stradali è causata dall'abbondante presenza di diverse *Graminacee* e *Composite* di prati, pa-

Tab. 2 - Relazione tra dati fitosociologici, fenologici ed ecologici durante la valutazione dell'allergenicità causata dai pollini sui margini delle scarpate stradali e dei marciapiedi delle Marche (Italia centrale).

Associazione	Periodo fenantesico dell'associazione	Indice allergenico dell'associazione
Poo compressae-Tussilaginetum R. Tüxen 1931	febbraio	2,2
Ornithogalo umbellati-Muscarietum atlanticum Hruska 1995	febbraio/marzo	2,4
Lepidio drabae-Agropyretum repens T. Müller et Görs 1969	marzo	2,8
Diplotaxidi tenuifoliae-Agropyretum repens Philippi in T. Müller et Görs 1969	aprile/maggio	5,7
Echio-Melilotetum R. Tüxen 1947	maggio/giugno	6,1
Poo compressae-Anthemidetum tinctoriae T. Müller et Görs 1969	giugno	6,2
Achilleo collinae-Agropyretum repens Hruska 1995	luglio/agosto	5,7
Echio italicici-Pastinacetum urens Hruska 1995	agosto/settembre	5,1
Aggr. ad Artemisia verlotiorum Hruska 1995	settembre//ottobre	5,4

scoli ed aree ecotonali. Tramite i rilievi fitosociologici vengono individuate le associazioni che si sviluppano in queste aree. Lo studio della loro dinamica spaziale e temporale e le osservazioni fenologiche permettono di indicare il periodo di fenatesi delle specie con polline allergenico e il momento della massima produzione di questo. Mediante l'indice allergenico viene espresso il potenziale fitoallergenico di ognuna delle associazioni. Esso rappresenta il valore medio dell'allergenicità di tutte le allergofite riscontrate nella composizione floristica dell'associazione (Tab. 2).

Il passaggio dallo studio autoecologico a quello sinecologico, dalla pianta all'associazione vegetale, permette di indicare con più precisione la pericolosità di un'area urbana. Le osservazioni fenologiche indicano il periodo dell'anno con la massima produzione del polline allergenico. Da uno studio effettuato sulle scarpate stradali delle Marche, tra tutte le associazioni riscontrate, risultano maggiormente allergiche quelle che si sviluppano tra i mesi di aprile e giugno (*Diplotaxidi-Agropyretum*, *Echio-Melilotetum*, *Poo-Anthemidetum tinctoriae*; Tab. 1). I dati epidemiologici raccolti dalle unità sanitarie e dai laboratori privati della città di Macerata nelle Marche (TELLONI e HRUSKA, 1997) hanno rilevato il numero più elevato di casi di allergopatie nel mese di maggio, in concomitanza con i massimi fenatesici delle suddette associazioni vegetali. I risultati di queste ricerche possono essere usati dai medici allergologi per effettuare una tempestiva terapia preventiva dei soggetti allergici.

CONCLUSIONI

A causa di un progressivo aumento delle superfici urbane diventa sempre più necessario indicare sia la qualità dell'ambiente di una città che i rapporti

tra gli abitanti, le condizioni ecologiche nonché la flora e la fauna che essa ospita. Si tratta di interazioni piuttosto complesse che per essere chiarite hanno bisogno di ricerche interdisciplinari. La valutazione della qualità dell'ambiente urbano tramite gruppi caratteristici di piante, presenti nei biotopi urbani in relazione al livello di urbanizzazione e ad altre caratteristiche parziali, permette di ottenere informazioni sulla situazione realmente presente in una città. I dati ottenuti su diverse scale spaziali collegano ecologia, fenologia, aerobiologia, epidemiologia, immunologia ed altre discipline scientifiche. Una valutazione interdisciplinare della qualità dell'ambiente urbano può individuare anche le cause dell'aumento dei casi di allergopatie nelle città. Le ricerche aerobiologiche partono dal riconoscimento, nell'aria, della presenza e dell'abbondanza del polline allergenico delle singole specie vegetali. Il contatto diretto delle persone allergiche con determinati pollini avviene invece spesso all'interno dello spazio urbano. Risulta molto utile conoscere la struttura di una determinata associazione o di gruppi di associazioni per individuare il maggior numero possibile di piante con polline allergenico. L'effetto finale dell'allergopatia, espresso mediante le reazioni allergiche dell'organismo umano, può essere provocato da vari pollini che nella diagnosi classica vengono di solito trascurati attribuendo la causa a quello più conosciuto. L'allontanamento dei soggetti sensibili dalle zone con maggiore concentrazione di determinati pollini allergenici e la terapia farmacologica preventiva portano alla diminuzione delle manifestazioni cliniche. L'uso dei dati fitosociologici durante l'impostazione delle ricerche immunologiche sugli allergeni potrebbe indirizzare lo studio verso le piante ancora poco conosciute dal punto di vista allergenico al fine di produrre farmaci adatti

ad una efficace terapia preventiva delle persone allergiche.

Il rapporto tra la fitosociologia ed altre discipline scientifiche in relazione ai diversi livelli di approfondimento dimostra che, riunendo differenti approcci, possono essere effettuati corretti interventi gestionali in questo complesso ambiente. La pianificazione del territorio, il recupero delle aree degradate, il restauro del paesaggio urbano, l'impatto sociale e pedagogico del verde urbano, sono solamente alcuni aspetti che possono avvalersi delle conoscenze sulla presenza e distribuzione delle unità fitosociologiche in città.

La gestione dell'ambiente urbano tramite l'approccio interdisciplinare contribuisce a prevenire la semplificazione qualitativa e la monotonia ecologica delle aree fortemente urbanizzate, inconvenienti che si sono già verificati in diverse metropoli del mondo. L'ecosistema urbano italiano rappresenta un ambiente di alto valore storico, culturale e paesaggistico, il quale per la sua unicità ed irreperibilità merita di essere protetto e gestito su basi scientifiche.

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LES DAYAS A *PISTACIA ATLANTICA* DESF. D'ALGERIE

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ABSTRACT

The main object of the authors is to present the *Pistacia atlantica* community of Algeria. The floristic composition of this forest is analysed. Using phytosociological method adapted to plant community of arid and Saharan land, this study describes three new syntaxa. The *Pistacia atlantica* community is submitted to important damages by most populations which explain the regression of its current distribution area.

KEYWORDS: *Pistacia atlantica*, dayas, structure, syntaxonomy, Algeria.

INTRODUCTION

Si le paysage végétal majeur qui caractérise le mieux les confins saharo-méditerranéens algériens est sans conteste la steppe, l'un de leurs traits floristiques remarquables reste la présence des ultimes représentants d'une végétation méditerranéenne à base de *Pistacia atlantica* Desf. (pistachier de l'Atlas ou bétoum). Cette végétation colonise un habitat exceptionnel désigné localement par le terme de «dayas». Celles-ci correspondent à des dépressions fermées à fond plat, grossièrement circulaires et relativement vastes (d'une dizaine à plusieurs centaines de mètre de diamètre). Localisées de part et d'autre de l'Atlas saharien, les dayas sont particulièrement concentrées dans la «région des dayas», vaste périmètre de près de 30.000 km² situé à la limite méridionale absolue de la région méditerranéenne. Les auteurs ont mené une série d'observations avec pour objectifs d'identifier le cortège floristique des dayas et d'en analyser la structure.

CONTEXTE ECOLOGIQUE

Grâce à la conjonction de facteurs mésologiques favorables, les dayas se distinguent par un contexte écologique remarquable caractérisé par:

- un cadre physique homogène sur les plans géomorphologique, édaphique et



Figure 1
● localisation des sites

Fig. 1 - Localisation des dayas étudiées.

climatique: la daya est une zone de concentration des eaux de ruissellement, de décantation de diverses particules en suspension et d'accumulation. À une telle localisation correspond un sol profond (jusqu'à une dizaine de mètres) à texture limono-argileuse. Avec des moyennes annuelles de 50 à 300 mm de pluie et des températures élevées ($39,6^{\circ}\text{C} < M < 44,1^{\circ}\text{C}$ pour les mois les plus chauds), les dayas se répartissent dans deux types de bioclimat, aride et saharien. Cependant, au-delà de la quantité, la régularité et la distribution saisonnière de la pluviosité déterminent la richesse floristique des dayas et la dynamique des communautés végétales «temporaires» à base de thérophytes;

- un cadre phytogéographique exceptionnel: les dayas à pistachier de l'Atlas représentent de remarquables irradiations phytogéographiques méditerranéennes au sein des vastes étendues prédésertiques;
- enfin un cadre socio-économique centré sur l'exploitation des ressources pastorales associées à des pratiques agricoles plus ou moins élaborées, avec mise en culture céréalière des fonds des dayas.

MATERIEL ET MÉTHODES

Compte tenu de l'objectif envisa-

gé, quatre dayas ont été retenues selon un gradient phytogéographique (Fig. 1): deux sont situées au sein du domaine maghrébin-steppique qui constitue la limite méridionale absolue de la Région méditerranéenne (une daya au nord de Aïn-Ben-Khelil dans le secteur des hautes plaines steppiques, relevés A1 à A3; la daya Bentoumi au sud-est de Messaad dans le secteur de l'Atlas saharien, rel. D1 à D3). La troisième (daya Zyania à 55 km au sud de Laghouat; rel. L1 à L4) est située dans le Sahara septentrional au sein même de la «région des dayas». La quatrième (daya Oum-Chegag, à 75 km au nord-ouest de Béchar; rel. B1 à B4) est localisée dans le domaine saharo-méditerranéen spécifique au Sahara nord-occidental algérien. L'analyse, l'identification et la caractérisation des communautés végétales ont été conduites selon les principes de la méthode phytosociologique «sigmatiste», avec une technique d'échantillonnage et d'analyse des données floristiques adaptée aux végétations des milieux aride et saharien (KAABÈCHE, 1990) et basée sur l'analyse de la structure et de la composition floristique des communautés végétales (KAABÈCHE, 1998). La finesse de cette première approche ne peut que s'ouvrir sur la méthode phytosociologique synusiale (GILLET *et al.*, 1991; DE FOUCault, 1993) qui nous

a donc semblé la plus appropriée dans le contexte écologique des dayas et la mieux à même de décrire la végétation colonisant ce type d'habitat. La nomenclature suit la *Flore pratique du Maroc*, du moins pour les deux volumes parus (FENNANE *et al.*, 1999, 2007); les taxons non traités par ceux-ci sont nommés selon la flore du Sahara (OZENDA, 2004).

RÉSULTATS ET DISCUSSION

STRUCTURE

L'élément le plus remarquable des dayas est sans conteste le bétoum qui constitue, dans un contexte prédésertique asylvatique, des «forêts parcs». De souche méditerranéenne, cette espèce se présente, dans les dayas, sous divers ports: phanérophyte avec des individus imposants (les plus beaux, observés dans la daya Oum Chegag, ont une taille impressionnante: plus de 1 m de diamètre pour le tronc et une dizaine de mètres pour le houppier), mais également nanophanérohyte lorsque de jeunes pistachiers cohabitent intimement avec des éléments arbustifs. Il y a lieu d'observer que cette «cohabitation» favorise le développement de relations interspécifiques privilégiées: la germination des graines de bétoum, la survie des plantules et l'accroissement des jeunes plants dépendent étroitement de la présence de *Ziziphus lotus*. En effet, celui-ci assure deux fonctions vitales pour le pistachier:

- une fonction édificatrice: par sa forme buissonnante, il constitue un obstacle sur la trajectoire de diverses particules aussi bien sableuses que limono-argileuses transportées par le vent; ainsi, au fur et à mesure de son développement, le jujubier édifie un biotope particulièrement riche, connu localement par

le terme de nébkas (nébkhas) et au sein duquel la semence du bétoum trouve les conditions indispensables à sa germination et à sa survie jusqu'au stade plantule;

- une fonction protectrice: les jeunes plants de bétoum ne peuvent assurer leur survie que grâce à la protection des buissons épineux de jujubier (*Rhus tridentata*) et *Retama retam* assurent la même fonction dans la daya d'Oum Chegag; aussi, les seules possibilités de régénération du bétoum n'existent-elles qu'au sein des buissons où les jeunes plants sont assurés d'une protection efficace face aux herbivores.

Le maintien et la conservation de cette essence forestière sont, à l'heure actuelle, intégralement liés à cette double fonction. Cet aspect est d'autant plus remarquable que nulle part ailleurs dans l'ensemble du territoire algérien le bétoum ne constitue de telles formations. En effet, l'aire de répartition de cette essence englobe de nombreuses localités en Algérie (MONJAUZE, 1965) depuis les maquis telliens, où il se trouve ça et là en individus isolés, jusqu'au Sahara où il ne subsiste qu'à l'état de relique dans le massif de l'Ahaggar.

COMPOSITION FLORISTIQUE ET SYNTAXONOMIE

L'analyse de l'ensemble spécifique (seuls les taxons ayant une fréquence supérieure à 2 ont été reportés dans le Tableau 1), tout en montrant une extrême hétérogénéité floristique, permet de distinguer diverses combinaisons floristiques remarquables.

La synusie arborescente se limite à l'heure actuelle strictement à *Pistacia atlantica*. La synusie arbustive et sarmenteuse lianescente (Tableau 2) montre, sur la base de neuf relevés où elle est

réalisée, une combinaison de *Zizyphus lotus*, *Rhus tripartita*, *Asparagus stipularis*, *A. acutifolius*, *Launaea arbore-scens*, *Zilla spinosa* subsp. *macroptera*, *Ephedra fragilis*, qu'accompagnent de jeunes *Pistacia atlantica*; elle se rattache aux *Ziziphos loti-Rhoetea oxyacanthae* de Foucault 1993 et aux *Warionio saharae-Withanietalia frustescens* de Foucault 1993, sans correspondre encore clairement à une alliance et une association précises (DEFOUCAULT, 1993; KAABÈCHE *et al.*, 2010).

La synusie basse vivace, caractérisée par des chaméphytes et des hémicryoptophytes, montre une différenciation en deux syntaxons originaux (Tableau 3):

- l'*Ononido platycladae-Coronilletum pomelii* ass. nov hoc loco (Tableau 3: rel. B1 à B4; *typus nominis*: rel. B2), plus proche du centre des dayas, donc sur des sols plus profonds et plus longuement gorgés d'eau;

- le *Teucrio campanulati-Pulicarietum crispae* ass. nov hoc loco (Tableau 3: rel. L1 à L4, D1 à D3 et A1; *typus nominis*: rel. L1); sur la périphérie des dayas, sur sols peu profonds et moins humides; avec *Stipa parviflora*, les relevés A2 et A3 pourraient n'être que des relevés fragmentaires du présent syntaxon; il se rattache aux *Pergulario tomentosae-Pulicarietalia crispae* Quézel 1965 et peut-être à l'*Antirrhino ramosissimi-Zillion macropterae* Quézel 1965

La présence d'un élément à caractère saisonnier et éminemment fugace est représentative de pelouses à thérophytes spécifiques aux dépressions et cuvettes sablonneuses à caractère non nitrophile. Les relevés réalisés sont probablement incomplets. Sur la base des données rassemblées ici, cet élément peut être scindé en deux ensembles:

- l'un (relevés B1 à B3, L1, L2) à

Tableau 1 - Synusies arborescentes et arbustives des dayas à *Pistacia atlantica*.

Tableau 2 - Synusies vivaces basses des dayas à *Pistacia atlantica*.

Relevés	B1	B2	B3	B4	L1	L2	L3	L4	D1	D2	D3	A1	A2	A3
Recouvrement global (%)	50	50	50	50	25	25	50	50	25	50	50	25	50	75
Ononido - Coronilletum pomelii														
Coronilla juncea subsp. pomelii	11	21	+	+
Ononis angustissima subsp. polyclada	+	21	+	1+
Salvia verbenaca subsp. pseudo-jaminiana	+	+	+	+
Helianthemum lippii var. intricatum	11	21	+	+
Catananche coerulea	+	1+	+
Haplophyllum vermiculare	+	+	+	.	+
Astragalus gombiformis	.	+	+
Euphorbia guyoniana	.	+	+
Marrubium deserti	+	.	+
Antirrhinum ramosissimum	+	.	.	+
Erodium glaucophyllum	+	.	+
Centaurea omphalotricha	+	.	+
Trichodesma calcarata	+	.	+
Centaurea furfuracea	+	.	.	+
Centaurea maroccana	+	.	+
Teucrio - Pulicarietum crispae														
Pulicaria crispae	32	11	1+	.	+	.	+	+	.	.
Pulicaria laciniata	1+	+	+	+	+	+
Teucrium campanulatum	+	11	+	+	.	+	+	.	.	.
Scorzonera undulata	+	+	.	+	+	+	+	+	.	.
Stipa parviflora	+	+	.	.	+	+	+	+	+	+
Autres taxons														
Anvillea radiata	+	11	+	.	1+	+	.	+	1+	.	.	+	+	+
Aristida obtusa	+	+	.	+	+	+	+	+	.	.
Atractylis babelii	+	21	+	.	1+	.	+	.	.	+
Salvia verbenaca subsp. verbenaca	+	1+	.	+	1+	.	.	+	1+
Asteriscus graveolens	.	+	+	+	+	+
Carduncellus duvauxii	+	1+	.	+	+	.	.	+
Morettia canescens	.	+	+
Chrysanthemum deserticolum	+	+

Tableau III - Synusies thérophytiques des dayas à *Pistacia atlantica*.

Relevés	B1	B2	B3	L1	L2	B4	L4	L3	D1	D2	D3	A1	A2	A3
Recouvrement global (%)	50	50	50	25	25	50	50	50	25	50	50	25	50	75
Haplophyllum tuberculatum														
Astragalus crenatus	+	+	+	.	+
Euphorbia retusa	+	.	+	+	+
Reseda villosa	+	1+	.	+
Erucaria erucarioidea	+	+	.	+
Moricandia foleyi	.	+	+	+
Kickxia aegyptiaca	+	.	+	+
Aristida adscencionis	+	+	.	+	.	+	+	+
Neurada procumbens	.	+	.	+	+	+	+	+	+	.
Linaria peltieri	+	+	.	+	.	+
Anethum graveolens	11	22	11	.	.	+
Malva parviflora	+	+	+	+	+	+	.	+
Scabiosa arenaria	+	.	+	+	+	+	+	+	+
Chrysanthemum fuscatum	+	.	+	+	+	11	11	+
Lonchophora capiomontiana	+	+	.	+	+	+	+	+	+
Anacyclus cyrtolepidioides	.	.	.	+	.	.	+	+	+	+	+	+	+	+
Hedysarum spinosissimum	+	+	+	+	+	+	+	+
Astragalus hamosus	+	.	+	.	+	+	+	+	+	+
Autres taxons														
Stipa capensis	.	.	+	+	.	.	+	+	.	+	+	+	+	+
Astericus pygmaeus	+	.	.	+	+	+	+	+	.	+	+	+	+	.
Pseuderucaria teretifolia	+	+	+	+	.	.	+	+	.	.	+	.	.	.
Limonium lobatum	.	.	.	+	.	.	+	.	+	.	+	+	+	+
Muricaria prostrata	.	.	.	+	+	.	+	.	+	+	.	+	+	.
Astragalus sinaicus	+	.	+	.	+	.	.	+	+	.
Erodium glaucophyllum	+	.	+	.	.	+	.	+	.	+
Reseda arabica	.	.	+	.	+	.	+	.	+

Reseda villosa, *Erucaria erucariooides*, *Moricandia foleyi*, *Euphorbia retusa*, *Astragalus crenatus*, *Aristida adscensionis*, *Linaria peltieri*, *Anethum graveolens*;

- le second (relevés D1 à D3, A1 à A3) à *Malva parviflora*, *Hedysarum spinosissimum*, *Scabiosa arenaria*, *Chrysanthemum fuscatum*, *Lonchophora capiomontiana*, *Anacyclus cyrtolepidioides*, *Astragalus hamosus*, ce qui n'empêche pas l'existence de relevés de passage (B4, L4, L3) entre ces deux ensembles. On peut les rapprocher de la classe des *Notoceretea bicornis* Nègre 1956 emend. de Foucault 1993, sans pouvoir les rattacher à des unités inférieures, sauf peut-être le second à rapprocher du *Lonchophorion capiomontiana* Kaabèche 1990, spécifique au domaine maghrébin steppique à bioclimat aride relevant de la région phytogéographique méditerranéenne.

Au sein des quatre dayas, l'altération anthropogène de la végétation initiale est nettement prononcée dans les relevés proches de leur centre (B4, L4, D3) et dans les relevés A1, A2 et A3 originaires de la daya de Aïn Ben Khellil qui est excessivement anthropisée. Au sein de ces relevés, on note un apport conséquent de taxons (*Bromus madritensis*, *B. rubens*, *Hypicum littorale*, *H. pendulum*, *H. procumbens*, *Papaver hybridum*, *Reseda decursiva*) associés aux communautés sétigères et aux pelouses thérophytiques subnitrophiles.

L'infiltration d'éléments saharo-arabiques particulièrement adaptés au contexte des confins saharo-méditerranéens est également remarquable. Ces végétaux répandus au Sahara septentrional et nord-occidental sur substrats rocaillieux constituent le fond floristique majeur de la steppe à *Hammada scoparia* relevant des *Gymnocarpo-Arthropytetalia scoparii* Kaabèche 1990. En s'infiltrant dans les dayas, ces éléments bénéficient des potentialités de leur contexte édaphique très favorable à leur développement.

Ainsi, sur le plan phytosociologique, l'analyse conduit à reconnaître au sein des dayas une mosaïque de diverses communautés, la plus remarquable étant représentée par la végétation ligneuse enclavée aux confins saharo-méditerranéens. Du fait de leur structure, les dayas offrent, aux périodes favorables, «le couvert» à toutes ces communautés prédésertiques qui vivent habituellement au voisinage de leurs conditions écologiques extrêmes. Cette situation contribue évidemment, au niveau de la composition floristique globa-

le, à estomper les discontinuités floristiques entre les communautés citées et même, au premier abord, à les homogénéiser. Elle permet aussi d'expliquer l'absence de statut phytosociologique effectif reconnu aux espèces annuelles par l'approche «globaliste» (prise en compte de la totalité des espèces inventoriées quel que soit leur type biologique) de la quasi-totalité des travaux relatifs à la végétation steppique et saharienne d'Algérie. En effet, à défaut d'un statut précis, les auteurs de ces travaux considèrent l'inclusion de ces thérophytes dans le lot des «espèces compagnes de haute fréquence» comme la solution la plus commode.

CONCLUSION

Si le contexte écologique peut expliquer le mode d'organisation spatiale en phytocénose mosaïquée des communautés végétales des dayas, leur physionomie est le résultat de pressions anthropiques soutenues depuis plus d'un siècle et demi. De nombreux écrits témoignent de l'ancienneté de ces pratiques (E.G. Paris 1867 in MONJAUZE, 1982), ce qui explique la régression et la fragmentation de l'aire de répartition actuelle du bétoum en Algérie, alors que, selon ces écrits, la végétation des dayas était reconnue comme «la forêt du Sahara». De par leur position phytogéographique, aux confins saharo-méditerranéens dans un contexte écologique asylvatique, les dayas constituent un habitat écologique exceptionnellement riche, jouissant d'une biodiversité de qualité remarquable. Cette richesse leur confère un statut de conservatoire naturel *in situ* de valeur patrimoniale mondiale; aussi, leur protection représente-t-elle un enjeu majeur en vue de la conservation de la biodiversité et de son utilisation dans le cadre du développement durable de cette région.

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DER WALD DER INSEL VILM (NORDDEUTSCHLAND)

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ABSTRACT

Vilm is a small Isle located near Rügen at the Southern coast of the Baltic Sea in Germany. The moraine and coastal landscape was formed by glaciers of the last glacial period 13,000 BP and by the development of the Baltic Sea since 6,000 years. With the occurrence of nearly all morphological coastal forms and ecosystems as well as forest development stages it represents a typical part of the NE-German coastal landscape. But with the diversity of biotopes at the small area of 94 ha and with high degree of naturalness it is a unique phenomenon of natural coastal landscape in North Germany. As medieval pilgrim site, as isle with long nature conservation tradition, as pain-

ters island in the 19th and 20th century and as location of the International Nature Conservation Academy Vilm is an isle with special importance for cultural history also. The article summarizes the forest history and the main forest types. The name "Vilm" is of Slavic origin and means "elm" (*Ulmus*). In the 12th century the forest cover changed from *Ulmus-Tilia-Quercus* mixed deciduous forests to beech dominated forests. The only one timber exploitation is documented in the early 16th century. Since that time the forests are in natural development without forestry, but used as pasture woodland until the 20th century. The following forest types can be distinguished: a) Ancient Beech forest (*Asperulo-Fagion*), typical climax forest of the Northern Central European

lowland, about 250-300 years old beeches, high degree of naturalness; b) former pasture woodland with ancient oak trees (about 400 years) in regeneration to natural forests, characterized by a very rich flowering spring aspect; c) succession stages at different former pasture grassland and agricultural fields. The Isle of Vilm is protected by law since 1936. The forests are without any use for many decades and today one of the core zones of the biosphere reserve SE-Rügen. A declaration to the first National Natural Monument (IUCN Cat. III) of Germany is in preparation.

KEYWORDS: Insel Vilm, *Melico-Fagetum*, virgin forests, regeneration, nature protection.



Abb. 1 - Die Wälder auf der Insel Vilm sind seit Menschengedenken allein von der Natur geformt.

EINLEITUNG

Im Mai 2001 fand an der Internationalen Naturschutzakademie Insel ein Workshop zur „*Anwendung und Auswertung der Karte der natürlichen Vegetation Europas*“ statt, an dem Experten aus 18 Ländern Europas teilnahmen (BOHN *et al.*, 2005). Prof. Franco Pedrotti aus Camerino referierte über „*Erhaltungszustand der natürlichen Vegetation und deren Repräsentanz in Schutzgebietssystemen in Italien*“ (PEDROTTI, 2005). Er war von den alten Bäumen, von der Urwüchsigkeit des Waldes auf der kleinen Insel Vilm tief beeindruckt und so fasziniert, dass er mir sagte „*Du musst für meine Zeitschrift Braun-Blanquetia über diesen Wald schreiben*“. Ich versprach es ihm, kann dieses Versprechen aber erst jetzt, neun Jahre später, einlösen.

Im Juni 2002 führte Prof. Pedrotti eine Woche lang eine internationale Exkursion durch Mittel- und Süd-Italien, die unvergessliche Eindrücke großartiger Landschaften und der Vielfalt mediterraner Pflanzenwelt vermittelte. Ich hatte das Glück, daran teilnehmen zu können und widme diesen Beitrag über den Wald der Insel Vilm meinem Freund Franco Pedrotti in dankba-

rer Erinnerung an diese eindrucksvolle Exkursion.

Seit zweihundert Jahren kommen Künstler, Forscher und Naturfreunde auf die kleine Insel im Rügischen Bodden, um die „kräftige Urnatur des Nordens“, wie es der universale Naturforscher, Arzt und Maler Carl Gustav Carus (1789-1869) in Erinnerung an seinen Besuch der Insel im Jahre 1819 ausdrückte, und insbesondere den Wald zu erleben, einen Wald, der seit Menschengedenken nicht durch Axt und Säge sondern allein durch die Natur geformt wurde (Abb. 1).

Der erste Eindruck des Waldes mag manchen Besucher verunsichern. Es empfängt ihn ein scheinbares Chaos, das Angst auszulösen vermag, menschliche Urangst vor Wildnis. Das Nebeneinander von alten und jungen, dicken und dünnen, lebenden und toten Bäumen verschiedener Arten, von abgebrochenen Kronen und modernden Stämmen, von kreuz und quer liegendem Totholz, von aufstrebendem Jungwuchs stellen das gewohnte Waldbild „aufgeräumter“ Forsten auf den Kopf.

Doch wer sich mit wachen Sinnen auf die Waldwildnis von Vilm einlässt, der erfährt eine unglaubliche Faszination, dem offenbart sich etwas vom urei-

gensten Wesen und der Dynamik des Waldes. Der erlebt den zyklischen Wechsel der Jahreszeiten, den ewigen Kreislauf von Werden und Vergehen - der erkennt auch menschenhafte Züge in den bizarren Gestalten mancher Bäume. Ein Hauch von Erhabenheit umweht Jahrhunderte alte Baumriesen, deren Lebensspanne die des Menschen um ein Vielfaches übertrifft. Wir tauchen ein gleichsam in einen Raum von Andacht und Stille, empfinden ein Leuchten in den Bäumen, das die Seele schwingen lässt. Manch einer wähnt sich in einen Märchenwald entrückt, meint Zauberstäfelchen zu schauen und erahnt die Wesenheiten der Bäume. Es gibt nur wenige Orte in Deutschland, an denen Wald so elementar erlebbar ist wie auf Vilm (Abb. 2).

DIE INSEL VILM

Die Insel Vilm ist ein Kleinod norddeutscher Küstenlandschaft (Abb. 3). Sie liegt im Rügen-Greifswalder Bodden, einem Randgewässer der Ostsee, nahe der großen Insel Rügen im Lande Mecklenburg-Vorpommern ganz im Nordosten von Deutschland. Sie ist Teil der Moränen- und Küstenlandschaft der



Abb. 2 - Auf Vilm ist Naturwald elementar erlebbar, 300jährige Buche.

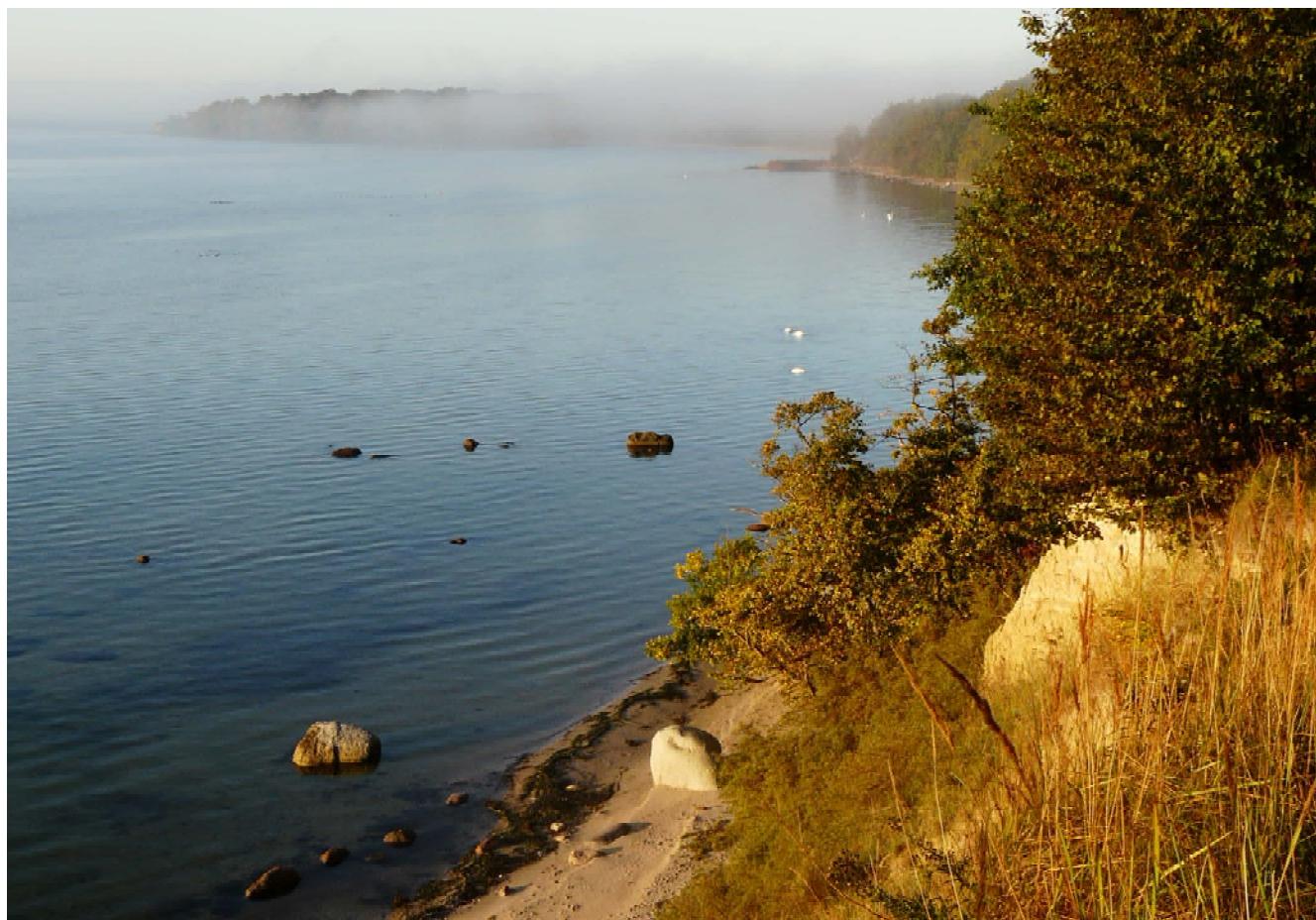


Abb. 3 - Kleinod norddeutscher Küstenlandschaft.



Abb. 4 - „Urnatur des Nordens“ (C. G. Carus, 1819).

Insel Rügen, die vor 13.000 Jahren von den letzten Gletschervorstößen der jüngsten Eiszeit in Mitteleuropa geprägt wurde und seit 6.000 Jahren eng mit der Entwicklungsgeschichte der jungen Ostsee verbunden ist.

Sie besteht aus drei eiszeitlichen Moränenkernen (Großer Vilm, Mittel-Vilm, Kleiner Vilm), die durch holozäne Nehrungsbildungen miteinander verbunden sind. Vilm stellt somit einerseits einen typischen und repräsentativen Ausschnitt der Küstenlandschaften an der südlichen Ostseeküste dar, indem hier nahezu alle Küstenformen und küstendynamischen Prozesse mit den entsprechenden Ökosystemen vorkommen. Sie stellt auch einen typischen und repräsentativen Ausschnitt südbaltischer Buchenwaldlandschaft dar. Andererseits ist die Insel mit der Kombination der verschiedenen Küstenformen auf kleinem Raum (die Landfläche umfasst nur 94 ha) wie ein Modell der südlichen Ostseeküste und in ihrer weitgehenden Naturbelassenheit ein einzigartiges Kleinod norddeutscher Jungmoränen- und Küstenlandschaft. Der Wald reicht bis an seine natürlichen Grenzen in den Dünen des Mittel-Vilm, an den Kliffkanten der Moränenkerne und an der Hochwassergrenze des Strand-

des. Maler und Fotografen begeistern sich bis heute an bizarren Baumgestalten, Waldwildnis und unverbauter Küste.

Hinzu kommt eine ungewöhnliche kulturhistorische Bedeutung als mittelalterlicher Kapellen- und Wallfahrtssort, als Ort einer der frühesten privaten Naturschutzinitiativen in Deutschland, als Malerinsel, an deren Beispiel sich die Geschichte der Landschaftsmalerei in Deutschland seit Caspar David Friedrich (1774-1840) dokumentieren lässt (PRECHOCKI, 1995). und nicht zuletzt als Sitz der Internationalen Naturschutzaademie des Bundesamtes für Naturschutz, die im Ergebnis der Wende in der DDR und der Vereinigung Deutschlands vor 20 Jahren gegründet wurde und sich seither zu einer Arbeits- und Tagungsstätte mit nationaler und internationaler Ausstrahlung entwickelt hat. Naturschützer aus vielen Ländern der Welt tauschen hier Erfahrungen aus, lernen voneinander, suchen nach Lösungen für brennende Fragen des Naturschutzes in unserer Zeit (SUCCOW, JESCHKE, KNAPP, 2001). Die Inselnatur in ihrer Eigenart, Schönheit und Unverschrtheit bestätigt und motiviert Menschen, sich für den Schutz der Natur einzusetzen. Mit je einer täglichen öffentlichen Führung von April bis Oktober trägt die Insel zum Bildungsauftrag des Biosphärenreservates SO-Rügen bei und vermittelt Menschen aus den verschiedenen Bevölkerungskreisen Begegnung mit einem Stück „Urnatur des Nordens“ (Abb. 4).

GESCHICHTE DER INSEL UND DES WALDES

Funde mesolithischer Artefakte belegen, dass die vor etwa 6.000 Jahren infolge des Meeresspiegelanstiegs der Ostsee entstandene Insel Menschen der Mittleren Steinzeit günstige Lebensbedingungen bot. Sie lebten von Jagd, Fischfang und den Früchten des Waldes, der die Insel schon damals bedeckte. Die vor etwa 5.000 Jahren einwandernden neolithischen Ackerbauern leiteten den Wandel der Waldwildnis zur Kulturlandschaft auf Rügen ein. Davon zeugen die Megalithgräber der Jungsteinzeit, von denen Anfang des 19. Jahrhunderts auf Rügen noch über 230 kartiert wurden und heute nur etwa 55 übrig geblieben sind. Die Reste eines zerstörten Megalithgrabes sind auch auf Vilm erhalten. Der Lindenwald mit Eiche und Ulme dürfte in der Jungstein-



Abb. 5 - Platz der mittelalterlichen Kapelle.

zeit (3.000-1.800 v. Chr.) und anschließenden Bronzezeit (1.800-600 v. Chr.) durch Viehweide aufgelichtet und mit kleinen Äckern durchsetzt gewesen sein. Spätestens in der Völkerwanderungszeit (250-600 n. Chr.) konnte der Wald regenerieren und als im 7. Jh. slawische Volksstämme in den nur noch dünn besiedelten Raum von Rügen einwanderten, hatte der Wald einen großen Teil früherer Kulturlandschaft zurückeroberet. Dies trifft auch auf Vilm zu.

Der Name „Vilm“ leitet sich vom slawischen „ilumu“ ab und bedeutet Ulme (lat. *Ulmus*, engl. elm, russ.ilm). Der Name ist ein Hinweis darauf, dass zur Zeit slawischer Besiedlung (7.-12. Jahrhundert) die Ulme offenbar eine auffallende Rolle im Waldkleid der Insel gespielt haben muß. Dies wird durch vegetationsgeschichtliche Befunde bestätigt. Die Buche gelangte auf Rügen erst im 12. Jahrhundert zur Vorherrschaft, bis dahin beherrschten Lindenmischwälder mit Eiche und Ulme (*Tilia cordata*, *Quercus robur*, *Ulmus glabra*) die natürliche Waldvegetation (LANGE, JESCHKE, KNAPP, 1986).

Die Insel wird erstmals im Jahre 1249 urkundlich erwähnt als Besitz des Hauses Putbus. Ein Jahrhundert später wurde auf der Insel eine Kapelle gestiftet. Drei Mönche des Zisterzienserklosters Eldena, das 1199 am Südufer des Greifswalder Boddens gegründet worden war, werden 1336 als einzige Bewohner der Insel erwähnt. 1396 erhalten vier Einsiedler die Erlaubnis, die wüste Kapelle wieder herzurichten und auf der Insel zu leben. Nach deren Tod verfiel die Kapelle erneut, sie wurde erst 1490 erneuert und 1494 durch den dänischen Bischof von Røskilde geweiht. Sie war einige Jahrzehnte ein Wallfahrtsort, wurde nach der Reformation in Pommern (1534) aufgegeben und verfiel (Abb. 5).

1527 verkaufte die Besitzerin der Insel das vom Sturm geworfene Holz auf zehn Jahre an zwei Stralsunder Kaufleute mit der Maßgabe, mindestens sechzig alte „Hegebäume“ stehen zu lassen. Sie erhielten auch die Erlaubnis sechs Rinder und sechs Pferde zu halten. Die Kühe dienten der Selbstversorgung der Walddarbeiter, die Pferde zum Transport des geschlagenen Holzes. Der jüngst aufgefundene Rest eines Glasschmelzofens legt den Schluss nahe, dass ein großer Teil des Holzes zu Holzkohle verarbeitet und vor Ort zur Glashgewinnung verbrannt worden ist. Dies war der letzte und wahrscheinlich überhaupt der einzige große Holzeinschlag auf der Insel. 150 Jahre später hat sich

der Wald offenbar regeneriert, wie die schwedische Matrikelkarte von 1695 dokumentiert (Abb. 6).

Nach der Reformation (in Pommern und auf Rügen 1534) ist die Kapelle verfallen und die Insel für lange Zeit unbewohnt gewesen, doch im 18. Jahrhundert wurde Jungvieh zur Sommerweide auf die Insel gebracht, 1767 wird ein Gehöft mit fünf Bewohnern erwähnt. Das um 1810 entstandene Gemälde „Landschaft mit Regenbogen“ von Caspar David Friedrich zeigt die Insel mit Wald bedeckt und Johann Jacob Grumbke (1771-1849) erwähnt in einer erstmals 1805 erschienenen Reisebeschreibung „mächtige Buchen und Eichen heben sich hier aus mutigem Unterholz..., Eichen von wirklich ungeheurem Wuchs“ (GRÜMBKE, 1988). In einem 1845 erschienenen Beitrag über die Flora der Insel Rügen werden auf dem Kleinen Vilm besonders statliche Bäume des Bergahorns (*Acer pseudoplatanus*) erwähnt. Als stärkster Baum wird von HAAS (1924) eine Rotbuche von fast 6m Stammumfang und über 35 m Höhe angegeben (Abb. 7).

Nachdem die Insel im Verlauf des 19. Jahrhunderts zu einem beliebten Ausflugsziel insbesondere für Maler geworden war, wurde 1886 ein Logierhaus auf der Insel errichtet und dank

reger Nachfrage 1914 erweitert. 1960 wurden alle Gebäude abgerissen und auf der Ackerfläche eine Ferienhausiedlung gebaut, die bis 1989 als Gästehaus der DDR-Regierung genutzt wurde. 1990 wurde die Internationale Naturschutzakademie Insel Vilm drei Tage nach der Wiedervereinigung Deutschlands durch den damaligen Bundesumweltminister Prof. Klaus Töpfer eingeweiht.

WALDTYPEN UND WALDDYNAMIK

Die Insel ist auch heute zum größten Teil mit Wald bedeckt. Die urwaldartigen Bestände auf dem Großen Vilm gehören zu den eindrucksvollsten Waldbeständen des norddeutschen Tieflandes. Sie blieben seit Menschengedenken von forstlichen Nutzungen verschont und sind seit vielen Jahrzehnten ganz ihrer natürlichen Dynamik überlassen. Der Wald der Insel Vilm setzt sich zusammen aus:

- a) Buchen-„Urwald“;
- b) ehemaligem Eichen-Hudewald;
- c) Sukzessionsstadien (Pionierwald, Zwischenwald) auf Schwemmland der Haken und Nehrungen, sowie
- d) Sukzessionstadien auf ehemaligen



Abb. 6 - Der Vilm auf der Schwedischen Matrikelkarte von 1696.

Äckern und ehemaligen Weiderasen auf dem Moränenkern des Großen Vilm.

Buchenwälder sind die natürliche Klimax-Vegetation des nordostdeutschen Tieflandes. Auf basenreichen, nährstoffkräftigen Jungmoränenstandorten ist der zu den Waldmeister-Buchenwäldern (*Asperulo-Fagion*) gehörende Perlgras-Buchenwald (*Melico-Fagetum*) die vorherrschende Waldform. Er stellt auch auf Moränenstandorten auf Vilm die natürliche Vegetation dar. Über 250jährige Buchen gewaltiger Dimension bilden die Baumschicht in Beständen der Altersphase, die an mehreren Stellen in die Zerfallsphase übergegangen ist. Umstürzende und umbrechende Baumriesen haben Lücken in das geschlossene Kronendach gerissen, so dass Licht auf den Waldboden dringt. Zwischen dem rasch von Pilzen und Käfern besiedelten Totholz erscheint

schlagartig Lichtungsvegetation aus *Urtica dioica*, *Rubus idaeus*, *Lonicera periclymenum*. Auf Rohboden umgestürzter Wurzelsteller keimen vereinzelt *Betula pendula*, *Salix caprea*, *Sambucus niger*. Die Lücken werden jedoch rasch von dicht aufwachsenden jungen Bäumen von *Fagus sylvatica* oder *Acer pseudoplatanus* geschlossen. Auf mittleren bis kräftigen Standorten verjüngt sich die Buche direkt und sehr konkurrenzstark, auf reicherem Standorten bleibt sie zunächst dem üppig aufschießenden Berg-Ahorn unterlegen, der eine Zwischenwaldphase von 150 bis 200 Jahren bilden kann, bevor im nächsten Zyklus sich die Buche wieder durchsetzt.

Der Frühjahrsaspekt des Perlgras-Buchenwaldes ist durch einen dichten Teppich blühender *Anemone nemorosa* ausgezeichnet, gefolgt von *Galium odoratum* und *Holosteum umbellatum* sowie

frühsommerlichem Grün der *Melica uniflora*.

Auf ärmeren Standorten nahe der Küste, wo die Bodenreifung infolge von Laubverwehung durch den Wind gehemmt wird, kommt Schattenblümchen-Buchenwald (*Majantheo-Fagetum*) mit *Majanthemum bifolium*, *Vaccinium myrtillus*, *Avenella flexuosa* vor, dessen Regenerationszyklus eine Lichtungsphase mit *Pteridium aquilinum* und Pionierphase mit *Sorbus aucuparia* einschließt.

An konsolidierten Steilufern reicht der Buchenwald bis an seine natürlichen Grenzen am Strand. In sonnigen Lagen kommen am Steilufer auch *Sorbus torminalis*, *Ulmus campestris* sowie *Vincetoxicum hirundinaria* vor.

Ehemaliger Eichen-Hudewald wird einerseits durch mehrhundertjährige Eichen (*Quercus robur*) und einzelne alte Buchen (*Fagus sylvatica*) gekennzeichnet, es sind Relikte des ehemals parkartig gelichteten Hudewaldes. Andererseits bilden jüngere Hainbuche (*Carpinus betulus*), Berg-Ulme (*Ulmus glabra*) und vor allem Berg-Ahorn (*Acer pseudoplatanus*) ein Zwischenwaldstadium im Regenerationsprozeß zum Klimawald. Sie sind seit Beendigung der Beweidung in den Lücken des Hudewaldes aufgewachsen. So zeigt sich heute ein in Teilen reliktärer und in anderen Teilen progressiver zweischichtiger, sehr ungleichaltriger Bestand mit hohem Anteil stehenden und liegenden Totholzes. Der ehemals durch Waldweide genutzte Bestand ist seit vielen Jahrzehnten in der Entwicklung zum Naturwald, doch dauert es mindestens einen Waldregenerationszyklus, bis die Spuren früherer Nutzung nicht mehr kenntlich sind. Die Eiche verjüngt sich hier praktisch nicht. Auch die Zeit der Hainbuche scheint vorüber, hingegen sind *Acer platanoides* und vor allem *Acer pseudoplatanus* im Vordringen. Auch kommen junge Buchen vor.

Der Frühjahrsaspekt vor dem Laubaustrieb der Bäume ist besonders reich entfaltet. *Anemone nemorosa*, *A. ranunculoides*, *Corydalis cava*, *C. intermedia*, *Gagea lutea*, *Ficaria verna*, bilden einen bunt gewebten Blütenteppich, stellenweise dominiert *Allium ursinum* und seltener kommt auch *Hepaticanobilis* vor. Im Mai beherrschen *Stellaria holostea* und *Galeobdolon luteum* die Krautschicht und dann bestimmen Nitrophyten wie *Alliaria petiolata*, *Urtica dioica*, *Galium aparine* das phänologische Bild dieses Waldes.

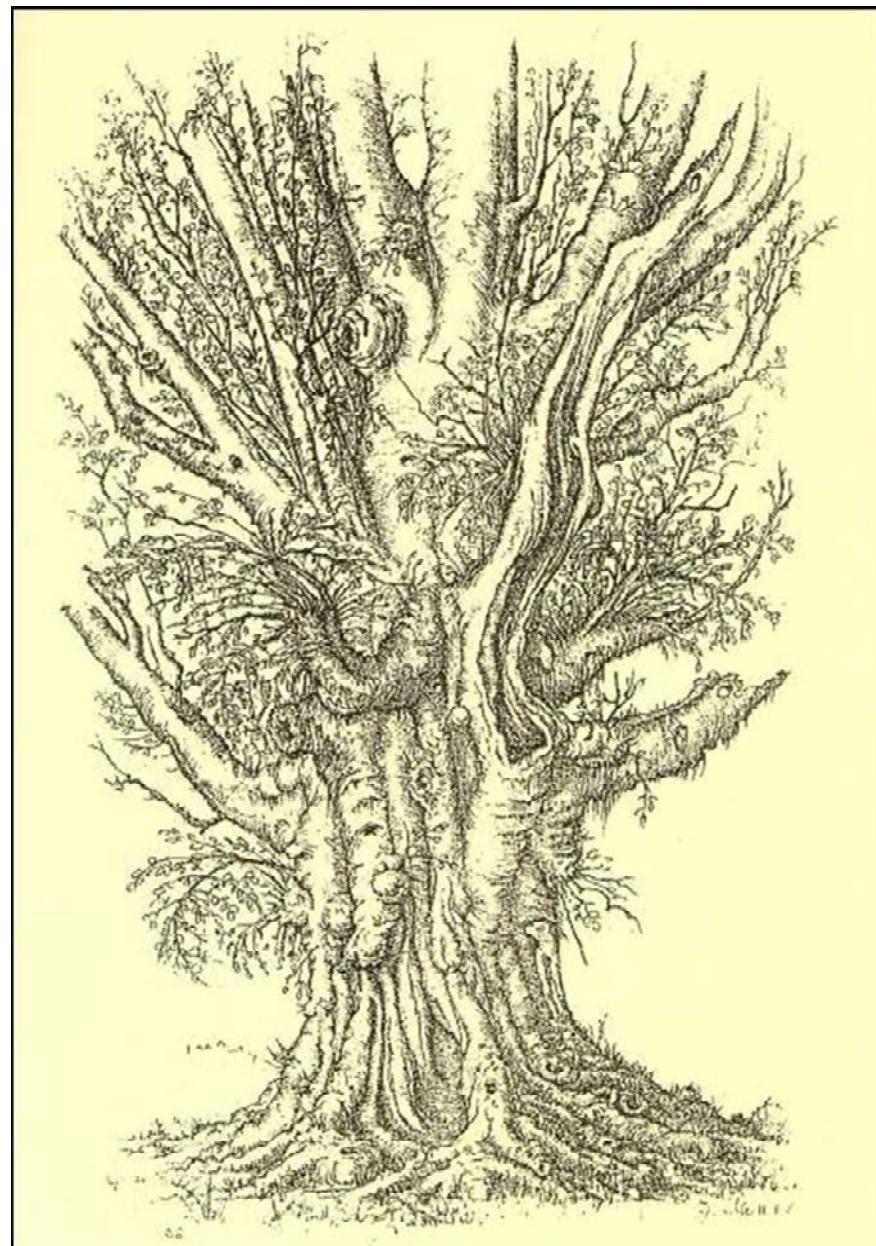


Abb. 7 - Die „Zwölfpastorbeche“ auf Vilm (Joachim Daerr, 1935).

Auf nährstoffschwachen Sand-

standorten des Großen Hakens auf dem Nordteil der Insel und auf der kleinen Nehrung des MittelVilms, haben sich ehemals locker mit Büschen bewachsende halboffene Weidelandschaften zu dichten Pioniergebüsch aus *Prunus spinosa*, *Rosa canina*, *R. rubiginosa*, *Crataegus monogyna*, *Rhamnus cathartica*, *Pyrus communis*, *Malus sylvestris* entwickelt. Besonders auffallend ist der hohe Anteil von *Pyrus communis* in den Pionierwaldbeständen in den Dünen des Mittel-Vilm. Einzelne Eichen und Birken leiten über zum **Birken-Eichen-Zwischenwaldstadium**, in dem *Quercus robur* die vorherrschende Baumart darstellt, oft malerisch überrankt von *Lonicera periclymenum*. In Lücken entfaltet sich zunächst der Adlerfarn (*Pteridium aquilinum*) stark, bevor die weitere Waldentwicklung im Schutz von Totholz durch *Sorbus aucuparia* eingeleitet wird.

Ein Teil der ehemaligen Ackerflächen am Rande der Siedlung unterliegt seit Beendigung des Ackerbaus einer eigenständigen Waldentwicklung, die über ein Pionierstadium mit *Betula pendula*, *Carpinus betulus*, *Populus tremula* heute zu einem bunt gemischten Zwischenwald aus *Carpinus betulus*, *Acer pseudoplatanus* geführt hat. Auf ehemaligen Weiderasen wird die Waldregeneration durch Sträucher (*Rosa canina*, *R. rubiginosa*, *Crataegus monogyna* u.a.) eingeleitet. Ohne Beweidung und Mahd wäre auch im Siedlungsgebiet zwischen den Häusern eine Pionierwaldphase entwickelt.

NATURSCHUTZ

Vilm hat eine zweihundertjährige Naturschutztradition. Die Rettung des Waldes auf Vilm durch den Fürsten Wilhelm Malte zu Putbus vor der Abholzung durch napoleonische Besatzungsstruppen um 1810 ist eine der frühesten Naturschutzinitiativen in Deutschland. „Als die Insel Rügen im Anfang des 19. Jahrhunderts von den Franzosen besetzt war, beabsichtigten diese, die Insel Vilm abzuholzen und das Holz verkaufen zu lassen. Nur mit großer Mühe gelang es damals dem Fürsten zu Putbus, das drohende Unheil vom Vilm abzuwenden“ (VON HAAS, 1924, S. 41). Und weiter heißt es „...jetzt wird der Wald auf dem Vilm schon seit Jahren in forstwirtschaftlicher Hinsicht nicht bearbeitet und ausgenutzt, sondern er bleibt in seinem natürlichen und urwüchsigen Zustand erhalten“. Diese Behandlung des Waldes hat sich einmal aus seiner insularen Lage ergeben, die eine

Verwertung des Holzes infolge der Schwierigkeiten des Abfahrens... erschwerte oder auch völlig unmöglich machte. Sodann aber hatten die Besitzer der Insel auch aus Pietät für die fast durchweg wahre Naturdenkmale darstellenden Bäume die Axt vom Vilm ferngehalten. Dieses Verfahren ist, nach den Beständen zu urteilen, augenscheinlich schon seit 200 Jahren geübt worden (VON HAAS, 1924, S. 15 f.).

Nachdem die Insel Vilm bereits 1910 durch eine private Anordnung des Fürsten Wilhelm zu Putbus unter Naturschutz gestellt worden war, erfolgte 1936 die offizielle Erklärung zum Naturschutzgebiet durch den Regierungspräsidenten von Pommern. Die „Verordnung über das Naturschutzgebiet «Insel Vilm» im Rügen-Greifswalder Bodden, Kreis Rügen“ wurde am 5. Dezember 1936 im Amtsblatt der Preußischen Regierung in Stettin veröffentlicht. Darin heißt es u.a. „Die «Insel Vilm» im Rügen-Greifswalder Bodden, Kreis Rügen, wird mit dem Tage der Bekanntgabe dieser Verordnung in das Reichsnaturschutzbuch eingetragen und damit unter den Schutz des Reichsnaturschutzgesetzes gestellt“ (Verordnung, 1936).

Der Status als Naturschutzgebiet (NSG) bleibt in der DDR bestehen. In amtlichen Behandlungsrichtlinien von 1967 und 1970 wird festgeschrieben, dass der Wald keiner forstlichen Bewirtschaftung unterliegt. 1990 wird mit dem Nationalparkprogramm der DDR der südöstliche Teil der Insel Rügen zum Biosphärenreservat erklärt. Das NSG Insel Vilm wird Teil des Biosphärenreservates. Die gesamte Insel mit Ausnahme des Siedlungsbereiches wird als Kernzone festgeschrieben und ganz der natürlichen Entwicklung überlassen.

Derzeit wird vom zuständigen Ministerium des Landes Mecklenburg-Vorpommern die Erklärung zu einem «Nationalen Naturmonument» vorbereitet (KNAPP, 2010). Diese Kategorie wurde in Deutschland erst 2009 mit einer Novelle des Bundesnaturschutzgesetzes eingeführt, sie entspricht der IUCN-Kategorie III (Natural Monument). Die Insel Vilm wird das erste Nationale Naturmonument in Deutschland.

Nur wenige Orte im dicht besiedelten Mitteleuropa vermögen ein so reines Naturerleben zu vermitteln wie der Vilm. Jahrhundertlang von zerstörerischen Eingriffen verschont ist diese Insel prädestiniert als Ort des Nachdenkens über den Umgang von uns Menschen mit der Natur. Mit der Inter-

nationalen Naturschutzakademie hat die Insel Vilm eine Bestimmung erhalten, die der kulturhistorischen Bedeutung gerecht wird und auch die weitere ungestörte Entwicklung der Inselnatur gewährleistet.

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DYNAMIQUE DE LA VÉGÉTATION DANS UN COMPLEXE FORESTIER DES ALPES DU SUD: DÉTERMINISME HISTORICO-ÉCOLOGIQUE

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ABSTRACT

In the Southern French Alps, the pastoral activity decreases unrelentingly enhancing post-cultural successions. Thus recent forest often undeveloped while old growth associated with traditional uses of mountain is present. The watershed of the “Petit-Buëch” (Hautes-Alpes, 57 km²), a French hot-spot of endemism and biodiversity and included in a Natura 2000 site, has been studied the effect of tenure status on the wooded vegetation dynamics. According to a stratified sampling design, 78 relevés were conducted in recent forests and ancient forests. The floristic composition of these two groups differs according to the continuity of the forested stage. Constraint and unconstraint Ordinations of plant communities has also highlight the flora associated with these ancient forests. This study highlights the importance of taking into account historical factors in understanding the dynamics of forest vegetation in the Alps and to better prioritize future conservation of these forests.

KEYWORDS: vegetation dynamism, Southern French Alps, ancient forests, recent forests, forest plant communities, forests conservation.

RÉSUMÉ

Dans l’arc alpin, l’activité pastorale a diminué inexorablement. Les successions post-culturales ont édifiées des forêts récentes souvent non aménagées tandis que subsistée des forêts anciennes associées aux usages traditionnels des populations montagnardes. Le bassin versant du “Petit Buëch” (Hautes-Alpes, 57 km²) haut lieu de l’endémisme français inscrit dans un site Natura 2000 a servi de base à l’analyse de l’effet de l’ancienneté de l’état boisé sur la dynamique de la végétation forestière. Selon un plan d’échantillonnage stratifié complexe, 78 relevés ont été réalisés dans les forêts récentes et les forêts anciennes. La composition floristique de ces groupements diffère selon

l’ancienneté de l’état boisé. L’ordination et la classification des groupements végétaux a permis de mettre également en évidence la flore associée à ces forêts anciennes. Ces travaux mettent en évidence l’importance de la prise en compte des facteurs historiques dans la compréhension de la dynamique de la végétation forestière dans l’arc alpin et de mieux prioriser les futures mesures de conservation de ces forêts.

INTRODUCTION

La structure et la composition de la végétation forestière sont sous le double déterminisme des conditions édapho-climatiques et de la gestion forestière (DECOCQ *et al.*, 2005). Les principaux facteurs de structuration des communautés forestières sont d’abord à rechercher dans les niveaux de disponibilité en ressources trophiques et hydriques mais aussi dans le régime de perturbations lié aux modes d’exploitation des forêts.

Cependant l’ancienneté de l’état boisé est maintenant largement reconnue comme un facteur déterminant le tapis herbacé des communautés forestières (PETERKEN et GAME, 1984; WULF, 1997). La flore associée aux forêts anciennes est largement étudiée en Europe tempérée (DAMBRINE *et al.*, 2007; DUPOUY *et al.*, 2002; HERMY *et al.*, 1999; SCIAMA *et al.*, 2009), mais rarement dans un contexte montagnard sous influence méditerranéenne. Grâce à l’existence de documents cartographiques (cadastre napoléonien) nécessaires à l’identification précise des anciens modes d’occupation du sol, il est actuellement possible de caractériser à la fois les types d’utilisation (futaie, taillis, landes...) mais également la période d’utilisation.

Dans les Hautes-Alpes, un bassin versant, haut-lieu de l’endémisme français et inscrit dans un site Natura 2000, la végétation forestière a été analysée selon leurs anciens modes d’occupation du sol, la continuité de cette utilisation en tenant compte à la fois de la géologie et du déficit hydrique

climatique.

L’objectif est d’analyser la structuration de la végétation forestière et ses principaux facteurs d’organisation, puis de démontrer le rôle de l’ancien mode d’occupation du sol, notamment l’ancienneté de l’état boisé sur la composition floristique.

MATERIEL ET METHODES

CARACTÉRISTIQUES DU SITE D’ÉTUDE

Le bassin versant du Petit-Buëch se situe dans le département des Hautes-Alpes (05) à environ dix kilomètres au Nord-Ouest de Gap (Fig. 1). Cet ensemble, que le cours du Petit-Buëch entaille globalement du Nord au Sud, est vaste de 57,3 km². La végétation repose essentiellement sur les formations du Malm (Jurassique supérieur) et du Néocomien (Crétacé inférieur), et s’inscrit dans la partie méridionale du massif du Dévoluy. Ces substratum sont souvent masqués par des formations superficielles qui représentent 31% des formations géologiques de la zone. Les contrastes thermiques, liés à de fortes pentes, ont en effet favorisé le développement d’importantes zones d’écoulement (19% de la superficie totale).

Le bassin versant reçoit, en moyenne, 1.138 ± 66 mm d’eau par an pour une tranche altitudinale comprise entre 1.050 m et 2.709 m. Le régime pluviométrique du bassin versant est à tendance méditerranéen.

L’angle de Gams permet d’individualiser trois zones à l’échelle de l’arc alpin (OZENDA, 1985). Une zone dite externe où l’angle est inférieur à 40°, puis une zone intermédiaire comprise entre 40 et 50°, enfin une zone intraalpine avec un angle supérieur à 50°. Avec un angle de Gams supérieur à 50°, la majorité du bassin versant du Petit Buëch est en zone intraalpine. Son corollaire est une dynamique de végétation favorable au mélèze et au pin à crochets (Fig. 2).

La température moyenne annuelle est de $5,9 \pm 1,0$ °C, avec un minima mensuel de $-2,3 \pm 0,8$ °C en janvier et un

maxima mensuel moyen de $15,2 \pm 1,0$ °C.

Le rayonnement solaire global permet d'estimer le bilan radiatif. Celui-ci est une donnée fondamentale à l'échelle des topoclimats montagnards (CHOI-

SNEL, 1986). Ce sont essentiellement l'exposition et la pente qui modèlent le bilan radiatif. Celui-ci est, en grande partie, responsable du déterminisme de la répartition des formations végétales. Les valeurs annuelles cumulées, pour le

bassin versant, oscillent entre 215 W.m^{-2} et 3.125 W.m^{-2} . La valeur moyenne est de $2.075 \pm 498 \text{ W.m}^{-2}$ (MARAGE, 2004).

Les composantes climatiques concourent à décrire le climat local du bassin versant comme sous influence méditerranéenne par des températures élevées dans les fonds de vallon; des variations intersaisonnieres avec un maximum en automne et une sécheresse estivale marquée. Cependant, des minima hivernaux négatifs et une hauteur de précipitations importante, placent, sans ambiguïté, ce site dans le climat montagnard, à l'interface entre la zone intermédiaire et intraalpine. Le site d'étude se situe réellement au carrefour bioclimatique entre les Alpes internes et intermédiaires.

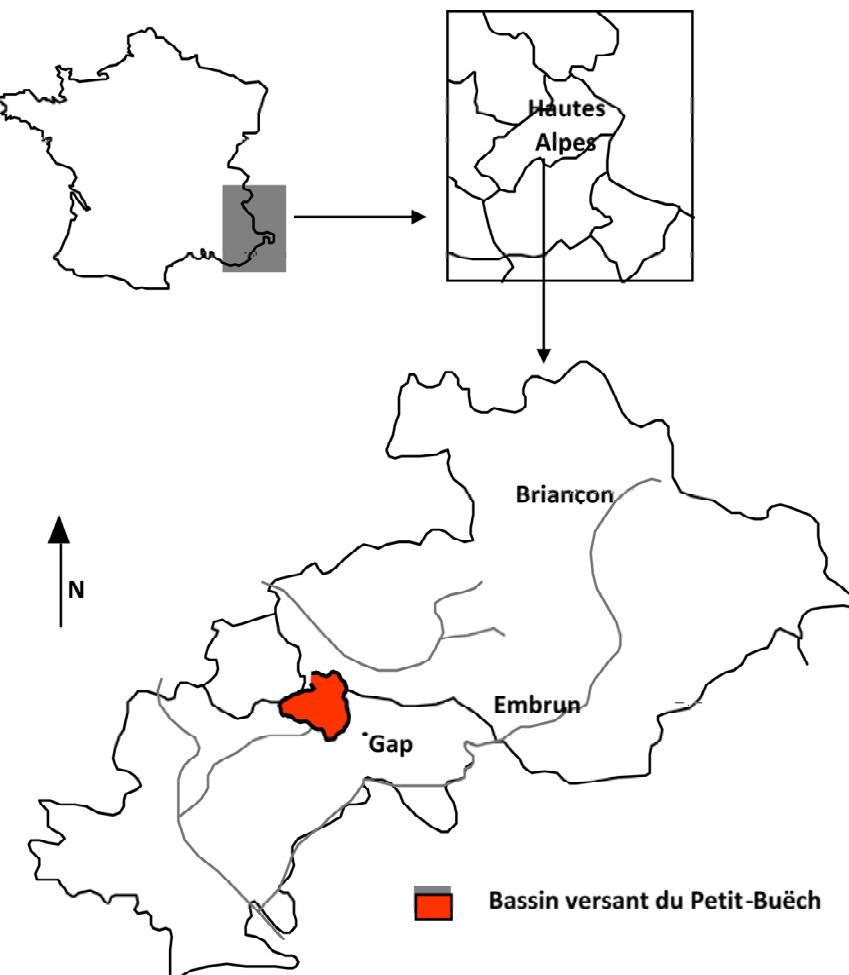


Fig. 1 - Localisation géographique du bassin versant du Petit-Buëch (France - Hautes-Alpes).

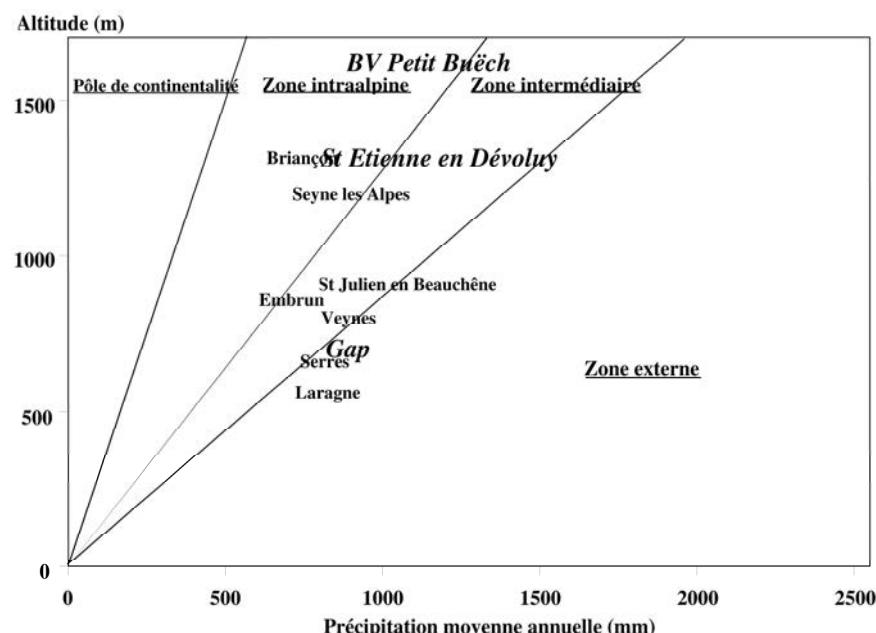


Fig. 2 - Position du bassin versant du Petit Buëch et de quelques postes météorologiques des Hautes Alpes selon les zones définies par l'angle de Gams (valeurs extraites de PETETIN, 1994).

LA VÉGÉTATION ET LE CADRE PHYTOGÉOGRAPHIQUE

Des herborisations de l'abbé Chaix, aux découvertes et travaux récents sur de nouveaux taxons comme le Cotoneaster de Rabou (*Cotoneaster raboudensis*) (FLINCK *et al.*, 1998), la vallée du Petit-Buëch ne manquèrent pas d'attirer l'attention de nombreux botanistes (ALLEIZETTE (D'), 1931; BRAUN-BLANQUET, 1926; CHAS, 1994; VIDAL, 1979). Ce haut lieu de l'endémisme français est d'ailleurs inscrit dans le réseau Natura 2000 n. FR9301511 DEVOLUY-DURBON-CHARANCE.

Ce bassin versant est inscrit, selon OZENDA (1985), dans les Alpes intermédiaires. Or, d'après les données climatiques calculées, ce site est un carrefour bioclimatique entre zone intermédiaire et intraalpine (Fig. 2). La caractérisation phytogéographique des Alpes intermédiaires suscite encore de nombreux problèmes de définitions (GAULTIER, 1989; OBERLINKELS *et al.*, 1990). Elle est souvent définie par défaut, faute de cortèges floristiques propres. Ces cortèges floristiques se caractérisent par l'absence de l'*Helianthemo-Aphyllanthion* et du *Rosmarinion*, la présence du *Lavandulo-Genistion* et du *Buxo-Quercenion pubescens* (OZENDA, 1985; GAULTIER, 1989). A l'étage montagnard, la hêtre-sapinière à *Trochiscanthes nodiflorus* (*Geranio-Fagenion*) prend le relais des hêtraies de l'*Eu-Fagenion*, confinant l'épicéa à une représentation sporadique dans le bassin de Seynes-les-Alpes plus au Sud.

Si ce schéma peut être reconduit dans son ensemble pour le bassin versant du Petit Buëch, il faut noter l'absence du Buis (*Buxus sempervirens* L.) dans la chênaie pubescente et ses

Tableau 1 - Principaux syntaxons forestiers du bassin versant du Petit Buëch regroupés par complexes d'habitats (code Corine Biotopes).

Complexes d'habitats	Dénomination
Complexes forestiers:	
Buxo sempervirens-Quercenion pubescens (Zólyomi et Jakucs 1960) Rivas Martinez 1972 (CB 41.71)	Chênaie pubescente à Buis
Cephalanthero rubrae-Fagion sylvaticae (Tüxen in Tüxen et Oberdorfer 1958) Bouillet et Rameau all. nov. hoc loco (CB 41.16)	Hétraie à Céphalanthère
Geranion nodosii-Fagion sylvaticae (Gentile 1974) Ubaldi et Speranza 1985 (CB 43.174)	Hétraie-sapinière à Trochischantes
Tilio platyphyllo-Acerion pseudoplatanii Klits 1955 (CB 41.41)	Erable-Frênaie
Rhododendro ferruginei-Abietion albae Rameau suball. nov. hoc loco (CB 42.1332)	Sapinière à Rhododendron
Ericion carneae Rübel ex Grabherr, Greimpler et Mucina in Grabherr et Mucina 1993 (CR 42.422)	Pineraié de montagne xérophile
Complexes d'écotones:	
Geranion sanguinei Tüxen in Th. Müller 1962 (CB 34.41)	Lisière xéro-thermophile
Trifolio medi-Geranienion sanguinei van Gils et Gilissen 1976 (CB 34.42)	Listière mésophile
Adenostylion alliariae Braun-Blanquet 1926 (CB 37.81)	Mégaphorbiaie à Adénostyle
Berberidion vulgaris Géhu, de Foucault et Delelis 1983 (CB 31.8123)	Fruticée à Cotoneaster et Amélanchier
Berberido vulgaris-Juniperion sabinae Theurillat in Theurillat, Aeschimann, Küpfer et Spichiger 1995 (CB 31.432 et 31.8125)	Fruticée intra-alpine à Générvier sabine
Corylo avellanae-Populinion tremulae (Braun-Blanquet ex Theurillat, Aeschimann, Küpfer et Spichiger 1995 (CB 31.81, CB 41.39 ou CB 41.D1)	Boisement post-cultural intra-alpin
Juniperion nanae Braun-Blanquet in Braun-Blanquet, Süssingh et Vlieger 1939 (CB 31.43 et CB 31.47)	Lande à Générvier nain

groupements de dégradation alors qu'il est présent dans la vallée du Buëch toute proche (PIGEON, 1990). Est-ce un effet anthropique lié à l'exploitation ou comme le suggèrent plutôt LENOBLÉ et BROUER (1945), un effet paléoclimatique lié à l'extension maximale du glacier durancien? (LENOBLÉ et BROUER, 1945). A l'étage montagnard, la présence des communautés du *Berberido-Juniperion sabinae* et du *Corylo-Populinum* marque le caractère intraalpin de ce site. Dans les cortèges du *Geranio-Fagion*, l'*If* (*Taxus baccata*) est souvent présent alors qu'il n'est pas mentionné dans le *Trièves-Beaumont* (PETETIN, 1994), dans la vallée du Buëch (PIGEON, 1990), ou dans les Alpes de Haute-Provence (DARRACQ, 1992). Enfin, à l'étage subalpin, le pin cembro (*Pinus cembra*) est absent ou sporadique, mais il aurait pu former le climax climatique avec le mélèze, avant les premiers défrichements (THINON, 1995).

Ainsi le bassin versant du Petit Buëch est une mosaïque d'habitats regroupés en complexes. Le Tableau 1 indique les principaux syntaxons forestiers observés. La nomenclature phytosociologique suit celle du prodrome des végétations de France (BARDAT *et al.*, 2004). Pour chaque syntaxon, le code Corine Biotope (RAMEAU *et al.*, 1997), inscrit entre parenthèses, correspond à l'habitat élémentaire observé dans le site.

Les nombreux travaux sur la végétation des Alpes intermédiaires (GAULTIER, 1989; OBERLINKELS *et al.*, 1990; PIGEON 1990; DARRACQ, 1992; RAMEAU, 1992; VARESE, 1993; PETETIN, 1994) nous permettent de tracer les principales chronoséquences¹ selon les étages bioclimatiques (Fig. 3). Ces trajectoires sont très proches de celles rencontrées dans les Préalpes septentrionales. La continuité géographique avec les Préalpes du Nord semble favoriser les échanges floristiques e. g. la

présence de *Primula auricula* dans le Dévoluy (CHAS, 1994).

LES PRATIQUES FORESTIÈRES ANCIENNES ET ACTUELLES

Les premiers indices de l'occupation humaine du bassin versant remontent à l'époque gallo-romaine. Un pont romain, dont la chronologie est indéterminée, enjambe le cours du Petit Buëch en contre-bas du village de Rabou. Il faut attendre le XI^e siècle pour que soit fait mention des massifs forestiers du Chapitre et du Tavanet. Deux communautés villageoises, Rabou et Chaudun, s'établissent dans la vallée du Petit Buëch, Chaudun en tête de pont du Chapitre de Gap. Les communautés ecclésiastiques, la Chartreuse de Berthaud et le Chapitre de Gap sont en effet détentrices d'un patrimoine forestier important qu'elles souhaitent préserver. À Chaudun, les biens communaux représentent les landes, la montagne pour pâturage et trois bois: le bois de la Ville, bois rond et bois du petit plaine. Il semble que les habitants de Rabou et de Chaudun, ont une grande liberté quant à la gestion et à l'usage de leurs bois par l'absence de véritable pouvoir coercitif. En règle générale, les forêts de la vallée sont concédées moyennant le paiement d'un cens récitatif ou réputé «libre ou de plain usage». La gestion est confiée à la communauté, donc tend vers un réel droit de propriété (GIMBERT, 2001). Les essarts et défrichements sont présents mais sont réfutés par les deux communautés villageoises. Le charbonnage est une activité signalée surtout à l'Ufernet et Loubet. De nombreuses traces sont encore bien visibles dans ces bois, mais également dans le bois de Donnes, avec parfois l'existence de véritables murs de soutènement.

Des impératifs sociaux opposés vont conditionner la physionomie des peuplements. Les bois ecclésiastiques privilégièrent le sapin au détriment du hêtre. La commission de réformation des Eaux et Forêts note l'existence de

mélèzes à Chaudun et de pins à Rabou. Les procès verbaux des commissaires réformateurs du XVIII^e siècle, témoignent de la constance des surfaces boisées et d'une réelle volonté de gestion, nonobstant que la situation géographique de ces bois semble être une des raisons principales de leur bonne conservation. A l'opposé, les communautés villageoises exercent une pression plus importante *via* un affouage anarchique et un pâturage tant ovin que caprin.

Les premiers aménagements forestiers du XIX^e siècle entérineront ce constat. La dichotomie des préoccupations sociales entre ecclésiastiques et villageois de cette vallée vient confirmer les travaux de (DUBOIS, 1991) qui exprime qu'une part du déterminisme des écosystèmes montagnards provient de l'intrication des processus socio-économiques et écologiques, montrant: «*combien la composante naturelle des paysages étalés selon les versants de la montagne, doit aux partis économiques décidés par les habitants ou les administrations en fonction des besoins ou des idéaux des sociétés qu'ils expriment*». Après la révolution, de nombreuses coupes sont effectuées dans les différents massifs de la vallée. Le câble est employé dès 1930 pour le transport des billes. Le flottage du bois sur le Petit Buëch prend fin en 1950, période de ses dernières utilisations.

Actuellement, les différents massifs soit communales soit domaniales font l'objet d'aménagements forestiers et sont gérés par l'Office national des forêts.

STRATÉGIE ET PLAN D'ÉCHANTILLONNAGE

Quatre classes de données géoréférencées ont été retenues. La première concerne un gradient écologique indirect, ici le substrat géologique avec deux modalités: perméable (calcaire compact du Jurassique supérieur) et peu perméable (calcaire et marno-calcaire du Crétacé) (Tableau 2). La seconde

¹ Succession des unités fonctionnelles sur un territoire défini BRAVARD, AMOROS, PAUTOU (1986).

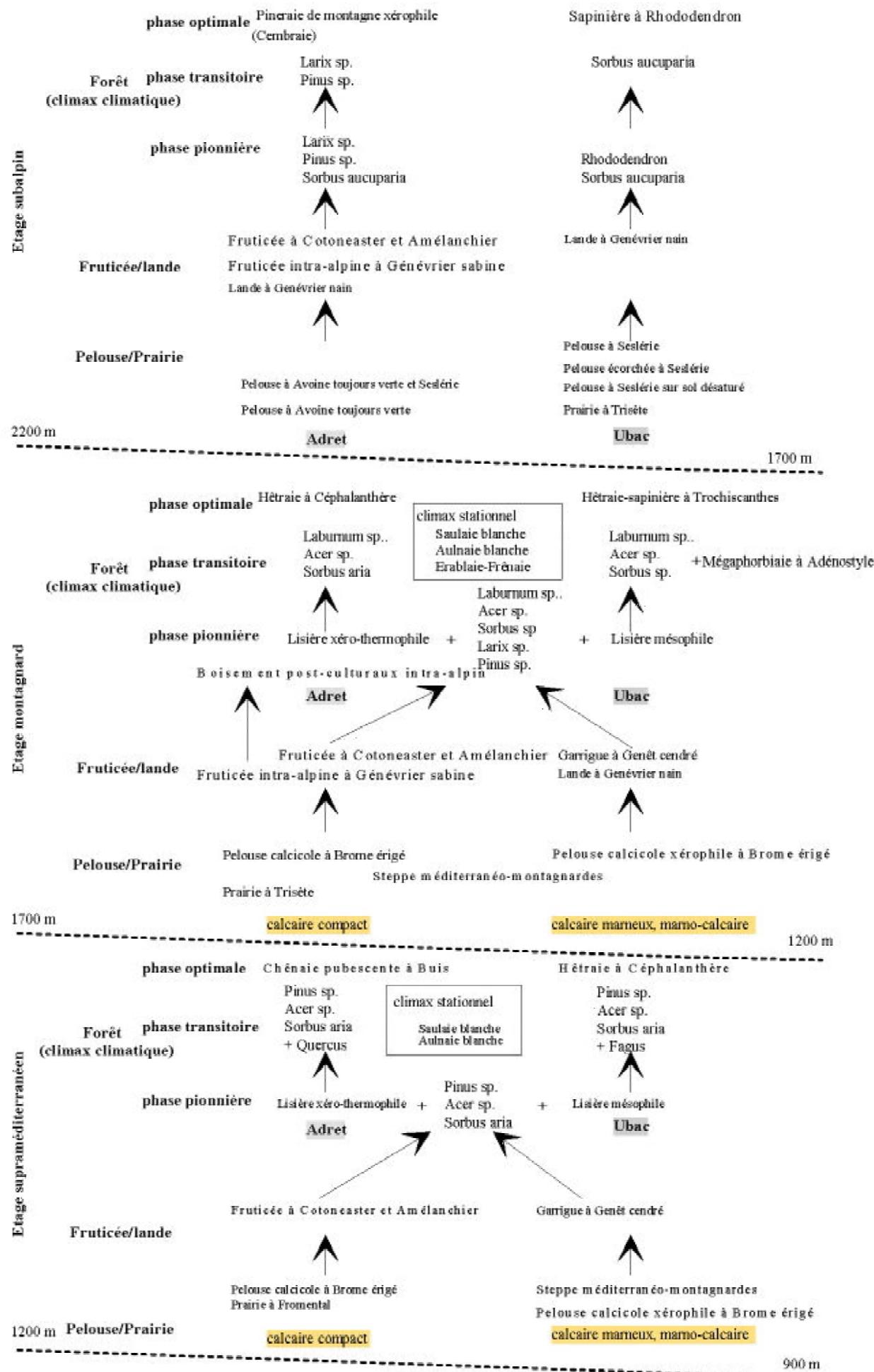


Fig. 3 - Principales chronoséquences par étages bioclimatiques dans le bassin versant du Petit Buëch.

traite d'un gradient direct, le bilan hydrique climatique avec trois modalités. Celui-ci a fait l'objet d'une modélisation basée sur le modèle AURELHY de Météo-France (BENICHOU et LE BRETON, 1987). Le mode de gestion actuelle a été extrait des plans d'aménagement forestier actuel (LAMOISSON, 2000). Il se décompose en 2 modalités, respectivement, des parcelles non gérées (mise en réserve) et des parcelles exploitées. Enfin, la quatrième classe regroupe l'ancien mode d'occupation du sol d'après le cadastre napoléonien de 1808 et les stades phisyonomiques (pelouses, fruticée, forêts) déterminés respectivement d'après les orthophotographies de 1948, 1971 et 1993. Une table de critères a ensuite été établie pour définir les stades dynamiques. La continuité historique des pratiques forestières est alors connue. Ce facteur historique de la végétation présente 4 modalités (Tableau 2).

Le croisement sous SIG de ces différentes couches d'information a donc permis de stratifier le plan d'échantillonnage en unités fonctionnelles où les communautés végétales ont subi la même histoire d'occupation du sol, la même pression sélective et les mêmes contraintes abiotiques. Nous avons également choisi de travailler dans une tranche altitudinale qui englobe les étages bioclimatiques montagnards et la base du subalpin, soit entre 1.200 et 1.850m, toutes expositions confondues.

Un tirage aléatoire de 4 polygones par condition a été réalisé. Une grille de points a été installée sur chacun des polygones retenus. Un tirage aléatoire d'un point par grille a été réalisé. 42 placettes sont localisées dans des forêts anciennes (modalités a. et b., Tab. 2) contre 36 pour les forêts récentes (modalités c. et d., Tab. 2).

Les placettes ont été localisées au moyen d'un GPS (Trimble Geoexplorer 3). Un inventaire exhaustif des spermatophytes selon la méthode phytosociologique de BRAUN-BLANQUET (1932) a été réalisé durant la période de végétation sur une surface de 400 m².

ANALYSE DES DONNÉES

L'Analyse factorielle des Correspondances (AFC) a été utilisée pour rechercher la structure du tableau floristique. Cette analyse est optimale en raison de la structure de la matrice espèces-relevés et des propriétés de modélisation de la succession des espèces sur un gradient écologique. La recherche de la signification des axes factoriels a été réalisée par régression

Tableau 2 - Modalités des facteurs historico-écologiques du plan d'échantillonnage.

Variables géoréférencées	Modalités	Fréquence (%)
Facteurs écologiques:		
1. Substrat géologique (LITHO)	a. Perméable b. Peu perméable	53,8 46,2
2. Déficit Hydrique Cumulé (DHCU)	a. faible (< -198 mm) b. modéré (-198 et -330 mm) c. fort (> -330 mm)	29,5 43,6 26,9
Facteurs historique de gestion:		
3. Gestion actuelle (GEST)	a. non-gérée (réserve) b. exploitée	41 59
4. Ancien usage (AMOS)	a. Haute-Futaie, Futaie b. Taillis c. Landes d. Labours et pâturages	37,2 17,9 28,2 16,7

multiple pas à pas et par les valeurs indicatrices pondérées de Landolt (LANDOLT, 1977) pour la lumière, l'azote, l'humidité et l'acidité, selon la formule:

$$V_i = \sum_{i=1}^n \frac{(v_i y_i)}{y_i}$$

Avec y_i , l'abondance/dominance de l'espèce i dans le relevé et v_i la valeur indicatrice de l'espèce.

La Classification Ascendante Hiérarchique (CAH), par le critère de l'inertie (Méthode de Ward) a été employée, après AFC, pour rechercher la typologie des relevés et la typologie des espèces.

Des analyses canoniques des correspondances (ACC) ont été réalisées dans le but de quantifier les relations entre les facteurs du plan d'échantillonnage (Tableau 2) et la composition floristique (i.e. 185 espèces x 78 relevés). Cette procédure permet d'étudier de manière simultané les relations complexes entre les espèces et entre les espèces et leur environnement (ØKLAND, 1996; TER BRAAK, 1987). Le principe général de l'ACC est de contraindre l'ordination des axes factoriels par la combinaison linéaire des variables environnementales (LEBRETON *et al.*, 1991). Dans notre étude, les influences propres ou combinées des facteurs écologiques (i.e. LITHO et DHCU) et des facteurs historiques de gestion (i.e. GEST et AMOS) ont été analysées par des ACC partielles (ØKLAND, 1999; ØKLAND et EILERTSEN, 1994; SABATIER *et al.*, 1989; TER BRAAK, 1987). Cette procédure permet d'éliminer d'un plan d'échantillonnage un facteur prédominant qui masquerait l'effet de facteurs secondaires plus influents (YOCOZ et CHESSEL, 1988). Différentes combinaisons de facteurs ont été réalisées (Tableau 2) de façon à ventiler la variance de manière séparée ou additives (CHESSEL, 1997; SABATIER *et al.*, 1989). Les

ACC restent des méthodes robustes à condition que le nombre de facteurs et leurs combinaisons ne dépassent pas 10% du nombre de relevés (PRODON et LEBRETON, 1994).

Les effets de chaque facteur ou leurs combinaisons ont été testés au moyen de simulation de Monte-Carlo à raison de 2000 permutations. De plus, le rapport de l'inertie totale de chaque ACC sur l'inertie totale de l'analyse factorielle peut-être considéré comme un coefficient de corrélation multiple (MCR, en %) (SABATIER *et al.*, 1989). Ce coefficient permet d'évaluer le pourcentage de variation de la composition floristique expliquée par un facteur ou leurs combinaisons (LEBRETON *et al.*, 1991). Le rapport entre l'inertie totale de l'ACC et le nombre de facteurs, noté I/F, a également été calculé afin de comparer le pouvoir explicatif des facteurs ou de leurs combinaisons.

L'ensemble de ces analyses multivariées a été réalisée en trois étapes: 1) analyse de l'effet des facteurs écologiques (LITHO, DHCU) et leurs combinaisons; 2) analyse de l'effet des facteurs historiques de gestion (GEST et AMOS); 3) analyse de l'effet de la combinaison des facteurs écologiques et historiques, afin d'obtenir le meilleur modèle de prédiction de la composition floristique. Toutes les analyses ont été réalisées avec le logiciel ADE-4 (THIOLOUSE *et al.*, 1997).

Enfin, des tests du χ^2 ont été réalisés pour comparer la flore des forêts anciennes et des forêts récentes.

RESULTATS

UNE FLORE FORESTIÈRE TRÈS RICHE ET DIVERSIFIÉE

La flore des complexes forestiers et des écotones du bassin versant du Petit Buëch est très riche. 330 espèces y

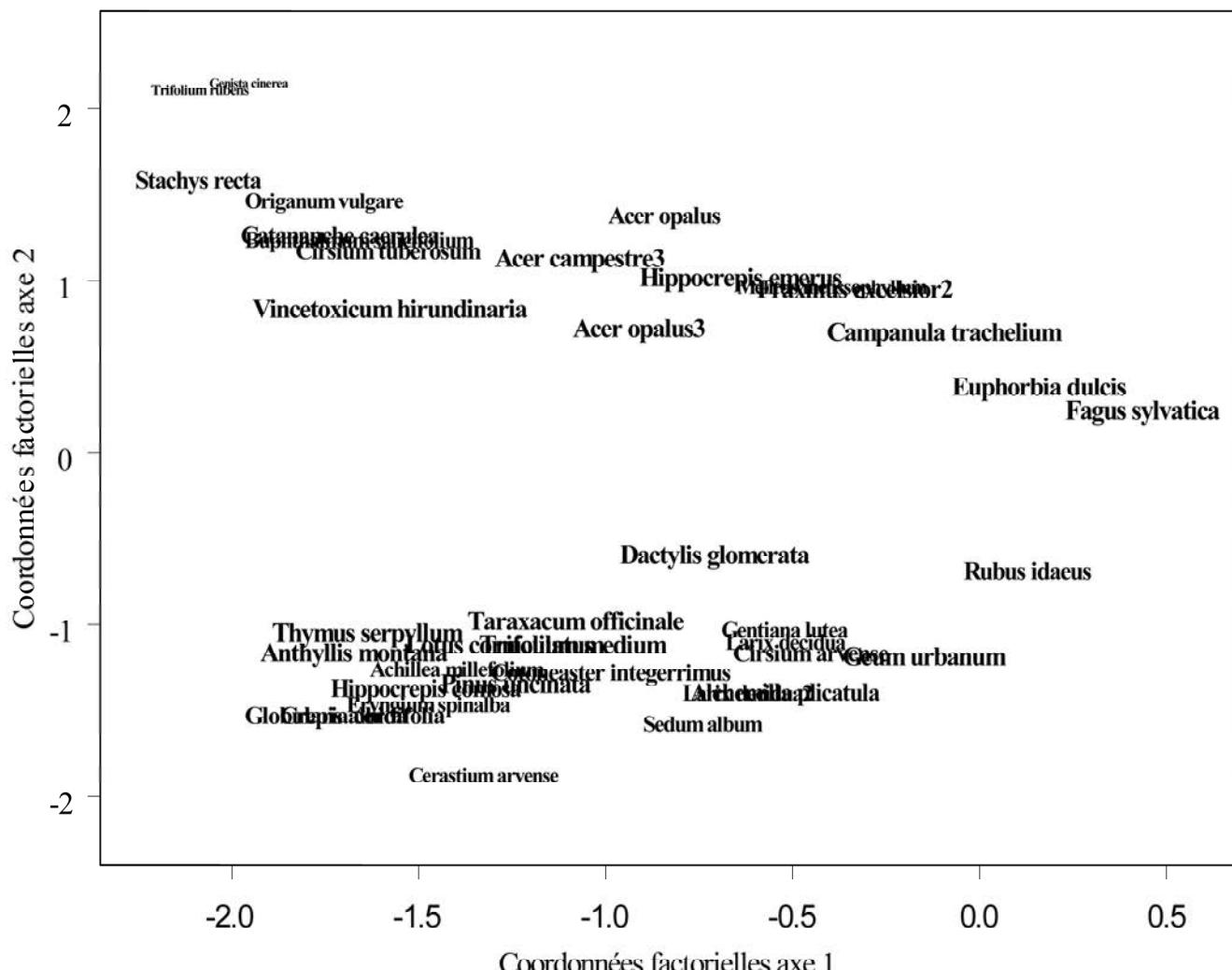


Fig. 4a - Ordination des espèces des complexes forestiers dans le plan factoriel 1-2 de l'AFC; en gras: espèces dont le $\cos^2 > 0,3$.

Tableau 3 - Résultats de la régression multiple pas à pas entre coordonnées des relevés des complexes forestiers de l'axe 1de l'AFC et les variables écologiques.

Term	Coeff. regression	SE	t-values	p-values
Intercept	4.779	1.362	3.50	0.000
cover arbo	0.015	0.001	8.96	0.000
rad3	-0.005	0.000	-7.32	0.000
prec6	-0.059	0.016	-3.63	0.000

Tableau 4 - Résultats de la régression multiple pas à pas entre coordonnées des relevés des complexes forestiers de l'axe 2 de l'AFC et les variables écologiques.

Term	Coef. regression	SE	t-values	p -values
Intercept	3,326	0,448	7,41	0,000
alt	-0,002	0,000	-7,36	0,000

ont été identifiées, appartenant à 59 familles, dont 4 sont représentées par plus de 20 espèces. Il s'agit des Asteraceae (41), Fabaceae (29), Poaceae (26) et des Apiaceae (22). Parmi les espèces à haute valeur patrimoniale, signalons la présence *Epipogium aphyllum*, *Asperula taurina*, pour les complexes forestiers et *Eryngium spinalba* pour les complexes d'écotones, toutes protégées à l'échelle nationale.

Le tapis herbacé des communautés forestières est dominé par le Prénanthe pourpre (*Prenanthes purpurea*), l'Aspérule odorante (*Galium odoratum*) et le Gaillet aristé (*Galium aristatum*). Ces trois espèces sont des espèces caractéristiques des forêts neutrophiles de l'étage montagnard. *Galium aristatum*, espèce des cortèges continentaux sous influence méditerranéenne, marque le caractère thermophile des communautés étudiées.

ÉTALONNAGE DES GRADIENTS ÉCOLOGIQUES

L’AFC de référence a été réalisée sur une matrice en absence/présence de 185 espèces par 78 relevés, après élimination des espèces présentes dans moins de 5 relevés (Figs. 4a, 4b et 4c). Les deux premiers axes factoriels expliquent 19% de l’inertie totale du nuage de points.

L'axe 1 (corrélation canonique = 0,73) oppose, du côté négatif, des espèces héliophiles mésophiles à thermophiles (*Helleborus foetidus*, *Trifolium rubens*, *Stachys recta*, *Phyteuma*,

orbiculare) et les espèces pionnières (*Amelanchier ovalis*, *Acer* sp. plur., *Larix decidua*, *Pinus* sp. plur.), et du côté négatif des espèces sciaphiles et neutrophiles (*Galium odoratum*, *Cardamine heptaphylla*, *Polygonatum verticillatum*, *Galium aristatum*, *Calamintha grandiflora*) et des dryades (*Abies alba*, *Fagus sylvatica*). L'axe 1 s'éta-lonne sur un gradient successionnel des lisières mésophiles et xéro-thermophiles, en passant par les boisements post-culturaux vers les hêtraies calcicoles et hêtraies-sapinières neutrophiles ($r^2 = 0,73$). Ce gradient successionnel est également une fonction linéaire du bilan radiatif (rad3, radiation solaire global du mois de mars) et hydrique (prec6, précipitations moyenne du mois de juin) (Tableau 3).

Le Tableau 3 présente les termes linéaires de la régression multiple pas à pas et leur niveau de signification pour l'axe 1.

L'axe 2 (corrélation canonique = 0,48) oppose du côté négatif, les espèces alticoles (*Gentiana lutea*, *Cotoneaster integrerrimus*, *Rumex arifolius*) et les espèces ligneuses pionnières (*Larix de-*

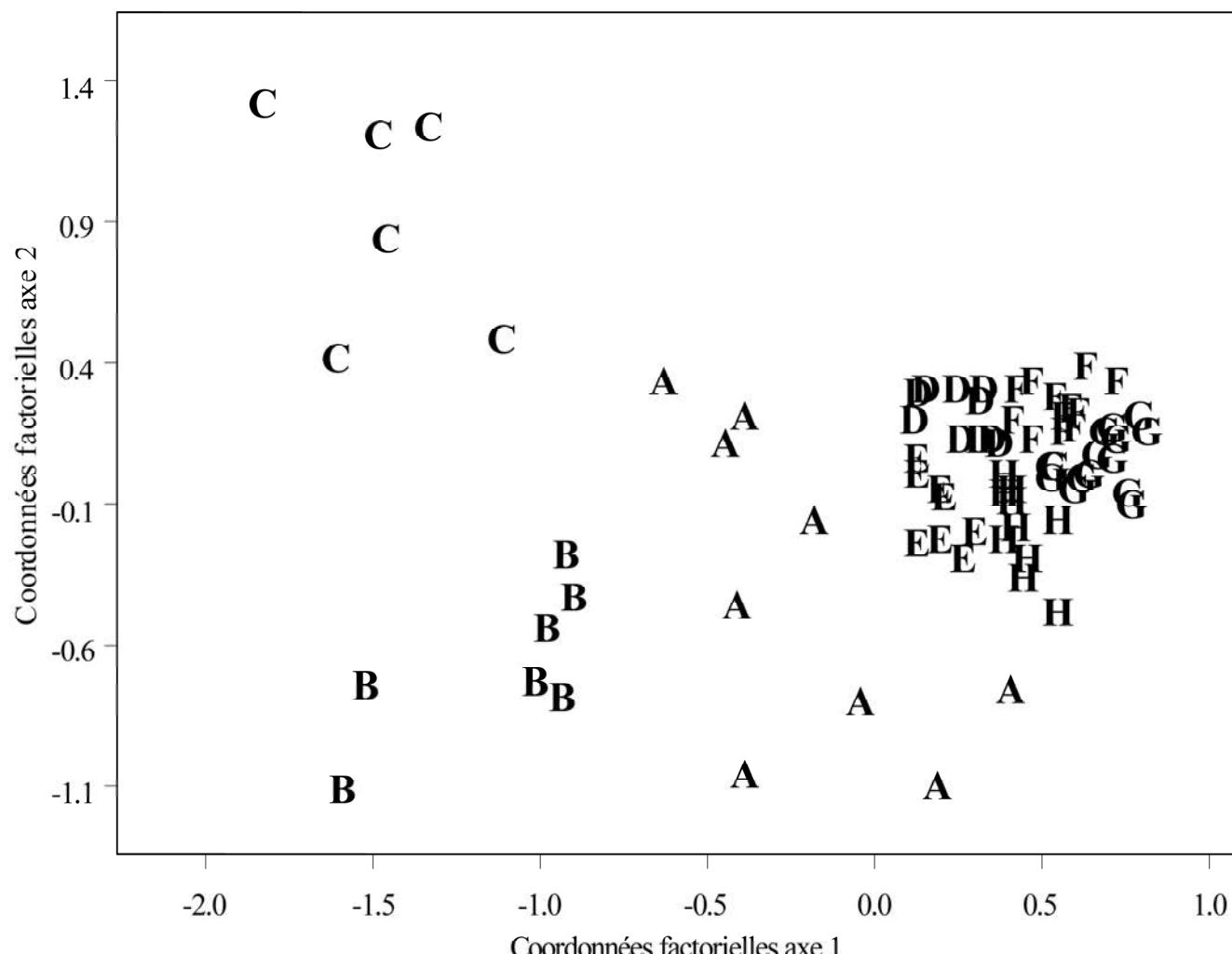


Fig. 4b - Ordination des espèces des complexes forestiers dans le plan factoriel 1-2 de l'ADF; ordination des relevés d'après CAH dans le plan factoriel 1-2 de l'ADF.

cidua, *Pinus uncinata*), aux espèces de l'étage supraméditerranéen (*Melittis melissophyllum*, *Tanacetum corymbosum*) et les espèces ligneuses qui l'accompagnent (*Hippocratea emerus*, *Acer opalus*). Le Tableau 4 présente les termes linéaires de la régression multiple pas à pas et leur niveau de signification pour l'axe 2. Seule l'altitude (alt) est corrélée à l'axe 2, avec un $r^2 = 0,41$ (Tableau 4). Seule la valeur indicatrice moyenne de la température est en relation avec les coordonnées factorielles de l'axe 2 ($F_{1,76} = 8,76$, $P = 0,004$, $r^2 = 0,10$). Cette relation confirme le positionnement des espèces subalpines du côté négatif de l'axe 2.

CLASSIFICATION DES SYNTAXONS FORESTIERS

La CAH a permis de classer les relevés, d'après les indices de niveaux d'agrégation, en 8 types de formations (Fig. 4b), caractérisées à la fois par les facteurs écologiques et la dynamique successionnelle.

Un premier groupe est composé de

Tableau 5 - Ventilation de la variance issue des analyses canoniques des correspondances totales et partielles.

	<i>I</i>	<i>F</i>	<i>I/F</i>	MCR (%)	<i>p</i>
<i>(1) Effet des facteurs écologiques</i>					
GEOL		0,0916	2	0,045	2,20
DHCUM		0,1739	3	0,057	4,17
Effet multiplicatif : GEOL X DHCUM		0,4082	6	0,068	9,80
<i>(2) Effet des facteurs historiques</i>					
GEST		0,093	2	0,046	2,23
AMOS		0,4242	4	0,106	10,20
Effet multiplicatif : GEST X AMOS		0,6745	8	0,084	16,20
<i>(3) Effet multiplicatif : facteurs historico-écologiques</i>					
DHCUM x AMOS		0,9958	12	0,083	23,90

I est l'inertie totale de l'ACC, *F* est le nombre de facteurs (i.e. le nombre de modalité par facteur), MCR est le coefficient de corrélation multiple qui permet de mesurer la qualité du modèle (en % de variance totale expliquée), il est calculé par le rapport entre l'inertie totale d'une ACC sur l'inertie totale de l'ADF. Cette dernière est égale à 4,168; *p* est le niveau de signification selon le test de Monte-Carlo avec 2000 permutations; *, $p < 0,05$, **, $p < 0,01$ et ***, $p < 0,001$.

forêts en voie de constitution, principalement à l'étage subalpin. La CAH permet de distinguer, d'une part des formations hygroclines (*Heracleum sphondylium*, *Ranunculus platanifolius*, *Chrysanthemum hirsutum*) et altoiles (*Leucanthemum ircutianum*, *Alchemilla plicatula*, *Gentiana lutea*) à base de mélè-

Tableau 6 - Liste des espèces significativement inféodées aux forêts anciennes dans le bassin versant du Petit Buëch (fréquence > 3% ; Test χ^2 , $P < 0,05$).

DHCU	faible	modéré	fort
Pulsatilla alpina		Melica uniflora	Hepatica nobilis
Aconitum lycoctonum subsp. vulparia		Erythronium latifolius	
Actaea spicata		Galium aristatum	
Asperula taurina		Galium odoratum	
Dryopteris filix-mas		Hieracium murorum	
Euphorbia amygdaloides		Lathyrus vernus	
Lonicera alpigena		Lilium martagon	
Polygonatum verticillatum		Prenanthes purpurea	
		Sanicula europaea	
		Trochiscanthes nodiflora	
		Viola reichenbachiana	

ze (type A) et d'autre part, des formations xérophiles (*Coronilla minima*, *Linum suffruticosum* subsp. *appressum*, *Silene otites*, *Globularia cordifolia*) à base de Pin à crochet (type B). Leur rattachement phytosociologique est complexe puisqu'une part des cortèges floristiques peut être rattachée aux pelouses subalpines et aux mégaphorbia-

ies de l'*Adenostylium alliariae*.

Le type C est constitué par des formations xérophiles rattachées au *Geranion sanguinei* (*Laserpitium gallicum*, *Pimpinella saxifraga*, *Trifolium rubens*, *Thalictrum minus*, *Vincetoxicum hirundinaria*) et des formations associées au *Lavandulo-Genistion* (*Buphthalmum salicifolium*, *Catanan-*

che caerulea, *Genista cinerea*). Ce type peut être rattaché aux chênaies pubescente à Buis (*Buxo sempervirens-Quercenion pubescens*). L'absence du Buis (*Buxus sempervirens* L.) dans ce type de formation est vraisemblablement due à un effet paléoclimatique lié à l'extension maximale du glacier durancien comme le confirme l'examen des formations quaternaires (GIDON et MONJUVENT, 1969).

Le type D est rattaché aux hêtraies à Céphalanthère (*Cephalanthero rubrae-Fagion*). Il est composé des formations xérophiles du *Geranion sanguinei* et d'un groupe d'espèces mésoxérophiles (*Daphne mezereum*, *Laserpitium latifolium*, *Lonicera nigra*, *Rubus saxatilis*). Depuis l'arrêt des exploitations, le niveau de maturation sylvigénétique a progressivement augmenté avec l'apparition du sapin en sous-étage.

Les types suivants se rattachent tous aux hêtraies-sapinières à Troschiscanthes (*Geranio nodosi-Fagenion*).

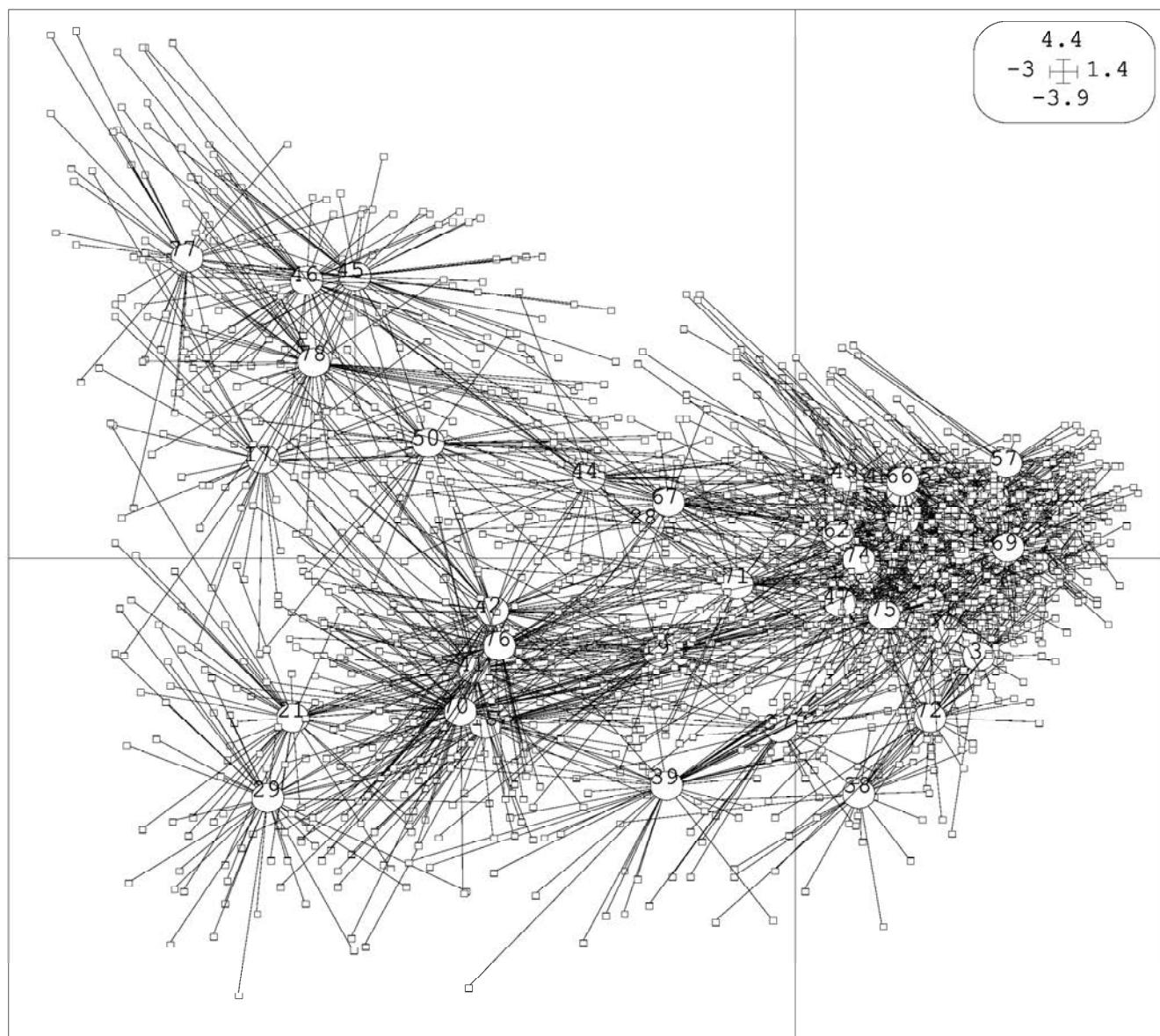


Fig. 4c - Ordination des espèces des complexes forestiers dans le plan factoriel 1-2 de l'AFC; amplitude écologique des espèces des complexes forestiers dans le plan factoriel 1-2.

Ils sont caractérisés par des groupements neutrophiles constitués de *Calamintha grandiflora*, *Euonymus latifolius*, *Geranium nodosum*, *Trochiscanthes nodiflora*, *Veronica urticifolia*.

Le type H se distingue par la présence de quelques espèces des formations alticoles des types A et B (*Geum urbanum*, *Gentiana lutea*).

Le type E constitue la phase pionnière des hêtraies-sapinières. Il est constitué des formations du *Trifolio-Geranion* (*Primula veris*, *Hieracium lachenalii*) et de l'*Adenostylium alliariae* (*Knautia dipsacifolia*, *Rumex arifolius*, *Senecio ovatus* subsp. *ovatus*). La strate arborecente est composée du Cytise des Alpes (*Laburnum alpinum*), des érables (*Acer pseudoplatanus*, *A. platanoides*) et du frêne (*Fraxinus excelsior*). La maturation sylvigénétique de cette phase est assurée par la régénération du sapin et du hêtre sous le couvert. Les types G et F constituent la phase de maturité des hêtraies-sapinières. Les cortèges floristiques du type F sont constitués d'espèces plus hygroclines (*Dryopteris filix-mas*, *Actaea spicata*) et hygrosciaphiles (*Chaerophyllum hirsutum*) que celles du type G.

Le plan factoriel 1-2 présente une convergence vers les formations du *Geranio nodosi-Fagenion*, climax climatique de la zone étudiée (RAMEAU, 1992). Cette convergence s'accompagne d'une réduction de l'amplitude écologique des espèces, comme le montre la Fig. 4c.

COMPOSITION FLORISTIQUE ET L'ANCIENNETÉ DE L'ÉTAT BOISÉ

EFFETS DES FACTEURS ÉCOLOGIQUES

Les forêts anciennes se cantonnent dans les zones où le bilan radiatif est le plus faible (Tableau 3). Les valeurs indicatrices pondérées de Landolt pour la lumière et l'humidité sont significativement corrélées aux coordonnées factorielles de l'axe 1. Les coefficients moyens d'humidité sont une fonction croissante des coordonnées factorielles ($F_{1,76} = 314,2$, $p = 0$, $r^2 = 0,80$), confirmant le rôle du bilan radiatif dans la structuration des communautés forestières. Les coefficients moyens d'héliophilie sont, en revanche, une fonction décroissante des coordonnées factorielles ($F_{1,76} = 241,2$, $p = 0$, $r^2 = 0,76$), confirmant l'étalonnage de l'axe sur un gradient de fermeture de la canopée.

Du côté négatif de l'axe 1 correspondent les formations d'écotones associées aux forêts récentes, alors que du

côté positif ce sont les hêtraies et hêtraies-sapinières des forêts anciennes.

L'influence de la géologie (GEOL) sur les phytocénoses était de 2,2%, et l'inertie de ce facteur était égale à 0,091, significatif à $p < 0,01$, tandis que celle associée au déficit hydrique cumulé (DHCU) était égale à 4,17%, significatif à $p < 0,001$ (Tableau 5). L'influence combinée des facteurs écologiques a permis d'expliquer 9,8% de l'inertie totale et paraît insuffisant pour permettre la prédiction de la composition floristique de ces complexes forestiers.

EFFETS DES FACTEURS HISTORIQUES

Les effets combinés de la gestion actuelle (GEST) et de l'ancien mode d'occupation du sol (AMOS) étaient les facteurs déterminants de la structure et de la composition du tapis herbacé de ces complexes forestiers, avec une inertie totale (0,6745), une inertie par facteur (0,084) et un MCR (16,2%) élevées, significatif à $p < 0,001$ (Tableau 5). Ainsi, la composition du tapis herbacé devrait être largement prédictible grâce à ces facteurs historiques.

EFFET MULTIPLICATIF DES FACTEURS HISTORICO-ÉCOLOGIQUES

Les résultats ont montré que 23,9% de la variance était expliquée par l'effet multiplicatif des facteurs historico-écologiques. L'ordination des espèces par cette ACC multiplicative est très proche de celle obtenue par l'AFC de référence (Fig. 4a). Ainsi, cela semblait indiquer que les forêts anciennes issues du traitement en futaie ont permis la persistance d'une flore spécifique. 20 espèces sont strictement inféodées à ces forêts. L'autécologie des espèces liées à ces forêts anciennes est également conforme au gradient de déficit hydrique cumulé. Les espèces hygrosciaphiles (*Actaea spicata*, *Asperula taurina*...) sont liées à des zones de faible déficit hydrique. Les espèces mésophiles (*Gallium odoratum*, *Prenanthes purpurea*...) sont significativement présentes dans les zones de déficit hydrique modéré, et enfin *Hepatica nobilis*, espèce thermophile, est lié aux zones de fort déficit hydrique.

DISCUSSION

EFFET DES FACTEURS ÉCOLOGIQUES

Le bilan radiatif semble être le

premier facteur écologique déterminant la présence des forêts du *Geranio nodosi-Fagenion* dans le bassin versant du Petit-Buëch. Nous corroborons ainsi les résultats acquis sur la position aux expositions nord, nord-est des forêts du *Geranio-Fagenion* (OZENDA, 1985; OBERLINKELS *et al.*, 1990; PIGEON, 1990; RAMEAU, 1992; PETETIN, 1994). Ces radiations sont particulièrement importantes en zone montagnarde, car elles déterminent la vitesse de la fonte des neiges (KIENAST *et al.*, 1998). Fonction parabolique de l'exposition, leur niveau est maximal aux expositions sud, sud-est. Ces radiations conditionnent vraisemblablement l'installation des groupements thermophiles et xérophiles observés. Ces résultats corroborent les caractères généraux des forêts relevant du *Cephalanthero-Fagion* (BENSETTITI *et al.*, 2001).

L'altitude est indirectement reliée au bilan radiatif par l'intermédiaire de la température. Les courbes de réponse ajustées indiquent un optimun pour ce facteur vers 1.550 m, avec une amplitude variant de 1.200 m à 1.800 m (MARGARE, 2004). Ces résultats sont en accord avec les études régionales menées dans les Alpes du Nord (PETETIN, 1994) et les Alpes intermédiaires (PIGEON, 1990). Le bilan hydrique intervient également dans le déterminisme des forêts du *Geranio-Fagenion*, par l'intermédiaire des précipitations mensuelles moyennes du mois de juillet. Avec l'ETP, les précipitations mensuelles sont les termes principaux du calcul du bilan hydrique climatique. Toute augmentation des précipitations concourt à une réduction du bilan hydrique climatique.

Cependant, comme l'indiquent les résultats des ACC partielles, les facteurs écologiques seuls ne permettent pas d'expliquer la variation de la composition floristique de ces complexes forestiers. Les effets combinés de la géologie (GEOL) et du déficit hydrique cumulé (DHCU) n'expliquent que 9,8% de l'inertie totale de l'AFC.

EFFET DE L'ANCIENNETÉ DE L'ÉTAT BOISÉ ET DE L'ANCIEN MODE D'OCCUPATION DU SOL

La convergence des communautés vers le climax climatique (Fig. 4c) a déjà été signalé, tant dans les successions secondaires (CHRISTENSEN et PEET, 1984) que dans les successions primaires (LICHTER, 1998). Ce processus semble être attribuable à la diminution de l'hétérogénéité spatiale et par voie de conséquence à celle du nombre de ni-

ches écologiques disponibles. Il pourrait également s'interpréter comme la conséquence des facteurs historiques de gestion, comme le suggèrent nos résultats, car l'effet combiné des facteurs historiques expliquent près de 16% de la composition du tapis herbacé des complexes forestiers étudiés. Dans le détail, les formations secondaires à Mélèze (type A) sont présentes sur l'ensemble du gradient de déficit hydrique cumulé, avec un net préferendum pour les déficits hydriques faibles. Ces formations sont majoritaires dans les zones actuellement pâturées, et sont issues d'anciens pâturages ou d'anciennes landes. Les formations secondaires à Pin à crochets (type B) dominent dans les zones non pâturées actuellement à fort déficit hydrique cumulé sur substrat perméable. Elles dérivent essentiellement d'anciens pâturages ou de landes. Les formations du *Quercion pubescens* (type C) dérivent exclusivement d'anciennes landes. Elles sont majoritaires dans les zones pâturées à déficit hydrique modéré, toujours sur les substrats imperméables. Les formations du *Geranio-Fagenion* des types F, G et H de forêts récentes dérivent toutes d'anciens pâturages ou d'anciennes zones de labour. Ceci tend à montrer que la reconstitution du cortège floristique de ces formations climaciques a pu s'opérer en l'espace de 200 ans.

Cependant comme semble le suggérer de nombreux travaux sur les banques de graines du sol (MARAGE *et al.*, 2006; PLUE *et al.*, 2008; PLUE *et al.*, 2010), le poids de l'ancien mode d'occupation du sol dicte, en partie, la dynamique des communautés végétales. Elles pourraient aussi signifier que la banque de graines du sol est d'autant plus similaire que les antécédents culturels sont communs. Quelques espèces inféodées aux milieux pastoraux telles que *Cerastium arvense* subsp. *strictum*, *Picris hieracioides*, *Trifolium pratense*, ont été détectées dans la banque de graines de forêts récentes, renforçant le rôle de mémoire séminale, témoin des anciens modes d'occupation du sol (MARAGE *et al.*, 2006). Dans les stades forestiers, la banque de graines est essentiellement composée d'espèces pionnières issues des premiers stades de la succession. *Epilobium* sp., *Rubus idaeus*, *Sambucus racemosa* sont présentes dans la banque de graines du sol des forêts anciennes étudiées, alors qu'elles sont absentes des relevés des types F, G et H. Ces espèces, appartenant aux groupements des trouées (*Epilobietea angustifolii*), se sont maintenues grâce à une persistance et une viabilité étendue de

leurs semences. Cependant, quelques espèces sciaphiles telles que *Calamintha grandiflora*, *Luzula nivea* et *Viola reichenbachiana* sont également présentes dans la banque de graines. Leur recrutement doit passer par le remaniement de la litière par de grands mammifères, ici *Sus scrofa* et *Ovis gmelini musimon*, donc une modification des micro-sites de germination, plutôt que par l'ouverture de la canopée comme l'ont montrés JANKOWSKA-BLASZCZUK et GRUBB (1997) pour d'autres espèces sciaphiles de forêts primaires. La banque de graines du sol de ces forêts anciennes constitue donc le témoin des variations temporelles cycliques de ces écosystèmes.

La flore associée à ces dernières est difficilement comparable avec d'autres études car peu d'études similaires sont disponibles. Cependant, SCIAMA *et al.* (2009) ont étudié la végétation des forêts récentes et anciennes dans le Jura français (SCIAMA *et al.*, 2009). Parmi les espèces inféodées aux forêts anciennes, *Euphorbia amygdaloides*, *Galium odoratum*, *Lathyrus vernus*, *Lilium martagon*, *Viola reichenbachiana* et *Melica uniflora* sont des espèces que nous retrouvons également significativement inféodées aux forêts anciennes étudiées (Tableau 6). Ces espèces semblent être de bons indicateurs de l'ancienneté de l'état boisé et de traitements en futaie depuis de longues dates dans des forêts neutrophiles montagnardes relavant des *Fagetalia*. La composition floristique de ces forêts ayant eu un passé agro-pastoral semble donc de celle des forêts récentes issues d'anciens usages agricoles. D'autres travaux seraient utiles pour confirmer ces résultats et une prise en compte des traits d'histoire de vie nécessaire pour dégager des similitudes fonctionnelles comme le montrent de nombreux travaux dans les forêts tempérées (BORCHSENIUS *et al.*, 2004; HERMY *et al.*, 1999; SCIAMA *et al.*, 2009; VERHEYEN et HERMY, 2001).

Enfin, notre étude semble minorer l'effet de la gestion actuelle sur la structure et la composition du tapis herbacé de ces forêts. Ce facteur (GEST) à deux modalités ne reflète pas réellement le régime de perturbations inhérent aux différents modes de traitements sylvicoles actuelles pratiqués dans ce bassin versant. L'influence du régime de perturbation des coupes forestières semble être un paramètre clé conditionnant la structuration des communautés forestières comme l'indiquent (DECOCQ *et al.*, 2004), influence qu'il conviendrait de prendre en compte dans de futures travaux.

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LA CONTRIBUTION DU PROFESSEUR JEAN-MARIE GÉHU À LA CONNAISSANCE SYNTAXONOMIQUE ET SYNSYSTEMATIQUE DES COMMUNAUTÉS VÉGÉTALES EN ALGÉRIE

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ABSTRACT

This article is published to honour the important contribution of Professor Jean-Marie Géhu to the knowledge of the plant communities and the development of a typology of habitats in Algeria. By this choice of topic, the authors wish to pay a tribute to the support which Professor Géhu gave to Algerian researchers, over many years, by welcoming them to the Centre Régional de Phytosociologie de Bailleul, by participating in various phytosociological meetings and to draft jointly articles which were published in numerous journals including the *Documents phytosociologiques* giving a real boost to both the production of articles and to the emergence of young Algerian phytosociologists. We present a synthesis of all the vegetation units which were the subject of observations in the field and published works.

KEYWORDS: plant communities, Algé-

ria, syntaxonomy.

RÉSUMÉ

Cet article est rédigé en l'honneur du Professeur Jean-Marie Géhu pour son importante contribution à la connaissance des communautés végétales et la mise en place d'une typologie des habitats en Algérie. Par le choix de ce thème, les auteurs désirent rendre un hommage au soutien que le Professeur Géhu n'a pas manqué d'accorder aux chercheurs algériens, durant de longues années, en les recevant au niveau du Centre Régional de Phytosociologie de Bailleul, de participer aux différents Colloques phytosociologiques et de rédiger conjointement des articles publiés dans de nombreuses revues, dont les *Documents phytosociologiques*. Ceci a donné une véritable impulsion à la phytosociologie par la production d'articles et à l'émergence de jeunes phytosociologues algériens. Nous présentons

une synthèse de tous les groupements végétaux qui ont fait l'objet d'observations sur le terrain et des travaux publiés par Jean-Marie Géhu pendant cette période.

LES RÉGIONS ÉTUDIÉES

Les observations phytosociologiques ont concerné divers sous-secteurs phytogéographiques de l'Algérie Nord-orientale, à savoir le sous-secteur de la petite Kabylie [K2], celui de la Numidie (ou annabi) [K3], du Tell constantinois [C1], du littoral algérois [A1], des hautes plaines steppiques constantinoises [H2], du bassin du Hodna [Hd], et enfin le sous-secteur oriental du Sahara septentrional (Biskra) [SN2] (Fig. 1).

Ce n'est assurément pas par hasard qu'en 1991 que Jean-Marie Géhu et des chercheurs algériens inaugurent une série de travaux au niveau du «*microhot-spot*» de la petite Kabylie [K2], localisé au NE algérien, qui aboutissent à la

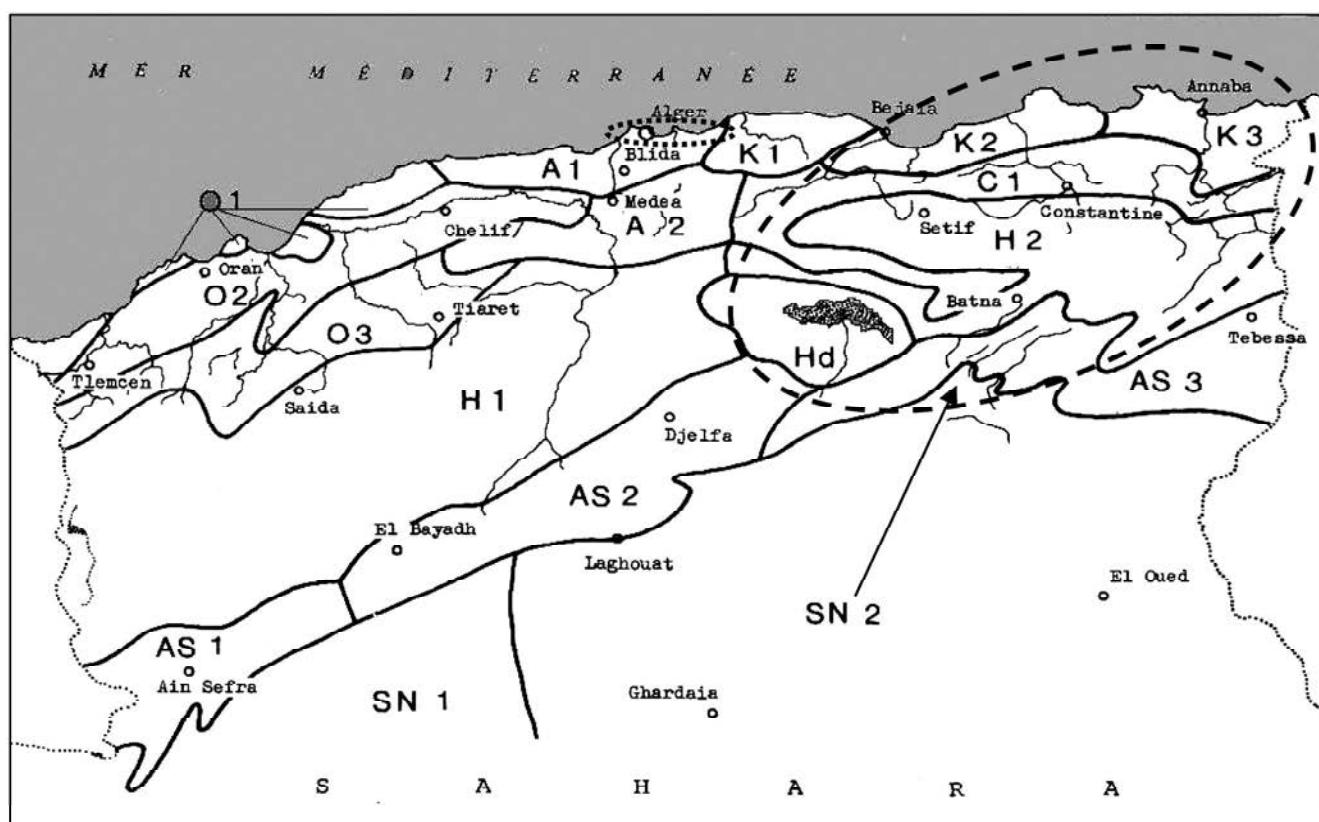


Fig. 1 - Les régions concernées par les études phytosociologiques (sous-secteurs phytogéographiques de QUEZEL et SANTA, 1962).

description d'une centaine de syntaxons pendant la période 1992-1998. Une quarantaine est totalement inédite et une trentaine d'associations végétales déjà identifiées ailleurs dans le bassin méditerranéen ou en Europe occidentale sont reconnues pour la première fois en Algérie. Enfin, une trentaine de groupements végétaux nouveaux sont interprétés et insérés dans le synsystème phytosociologique, mais pour lesquels il est nécessaire d'apporter de nouveaux matériaux pour une analyse plus fine. Ils mettent ainsi en évidence une grande variété phytocoenotique du NE algérien, et sont parfois d'une exceptionnelle originalité, liée à la grande diversité d'habitats et des paysages.

Nous rappelons très brièvement ces groupements végétaux, en mettant en exergue les nouvelles unités décrites pour l'Algérie.

SYNTAXONS NOUVELLEMENT IDENTIFIÉS ET DÉCRITS POUR L'ALGÉRIE

Pas moins de 32 classes sur les 43 que compte au total le synsystème phytosociologique en Algérie, ont été étudiées soit 15 classes mentionnées pour la première fois s'inscrivant dans une dizaine de grands types d'habitats. Il nous paraît ainsi plus intéressant de rappeler l'œuvre du Professeur Géhu et de ses collaborateurs (M. Kaabèche et R. Gharzouli, pour le NE algérien; N. Sadki, pour le littoral algérois), en suivant un fil directeur celui du système écologique des classes de végétations d'Algérie, qui d'ailleurs a été mis en place grâce à Géhu *et al.* (1998), après un premier synopsis sur les groupements forestiers et préforestiers de l'Algérie (MEDDOUR et GÉHU, 1998). C'est dire l'importante contribution du Professeur Géhu, qui a mis en place une première typologie des habitats naturels, dans ce domaine jusqu'alors inconnu en Algérie. Ceci a permis le développement de nombreux aspects pratiques et appliqués de la phytosociologie sigmatiste en réponse à une demande sociale importante.

In fine, il faut signaler l'application de la phytosociologie paysagère caténale (géosymphtosociologie) pour la première fois en Algérie, avec quelques géosynrelevés (à Jijel et Chott el Hodna). Un exemple d'adaptation qualitative de la symphytosociologie, nous est également proposé dans un tableau résumant les phytocoeno-complexes des lacs d'El Kala (GÉHU *et al.*, 1994c).

LES VÉGÉTATIONS AQUATIQUES

Quatre classes ont été formellement identifiées, celles de la végétation aquatique des eaux douces des *Lemnetea minoris* (R. Tüxen 1955) Schwabe et R. Tüxen 1981 et des *Potametea pectinati* Tüxen et Preising 1942 ex Oberdorfer 1957; de la végétation lacustre, fontinale et palustre des *Littorelletea uniflorae* Braun-Blanquet et R. Tüxen 1943 et des *Montio fontanae-Cardaminetea amarae* Braun-Blanquet et R. Tüxen 1943. Parmi lesquelles de très nombreuses nouvelles associations sont décrites, essentiellement localisées au sein des «lacs» de la région d'El Kala [K3]. Citons: *Wolffio arrhizae-Ricciocarpetum natantis* Géhu, Kaabèche et Gharzouli 1994; *Myriophyllo spicati-Potametum nodosi* Géhu, Kaabèche et Gharzouli 1994; *Zannichellio palustris-Myriophylletum alterniflori* Géhu, Kaabèche et Gharzouli 1994; *Wolffio arrhizae-Utricularietum neglectae* Géhu, Kaabèche et Gharzouli 1994; *Echino-doro ranunculoidis-Paspalitetum distichi* Géhu, Kaabèche et Gharzouli 1994; *Helosciado inundati-Utricularietum exoletae* Géhu, Kaabèche et Gharzouli 1994; *Nymphaeetum albae*, exceptionnel en Algérie, *Nupharretum lutei*, encore plus rarissime et désormais détruit, *Ranunculetum laterifolio-aquatalis* Géhu, Kaabèche et Gharzouli 1994; *Cerastio atlantici-Ranunculetum hederacei* Géhu, Kaabèche et Gharzouli 1993, ces deux dernières communautés aquatiques sont décrites du Tell constantinois [C1].

LES VÉGÉTATIONS DES ROSELIÈRES ET GRANDES CARIÇAIRES

Il s'agit bien entendu de la classe des *Phragmiti australis-Magnocaricea elatae* Klika in Klika et Novak 1941 qui s'est également avérée riche en syntaxons nouveaux, rencontrés principalement à El Kala [K3], mais aussi à Bejaia [K2] et à Sétif [C1]: *Equiseto ramosissimae-Cladietum marisci* Géhu, Kaabèche et Gharzouli 1992; *Cladio marisci-Thelypteridetum interruptae* Géhu, Kaabèche et Gharzouli 1994; *Alismomichaleti-Sparganietum neglecti* Géhu, Kaabèche et Gharzouli 1994; *Panicetum repens* Géhu, Kaabèche et Gharzouli 1994; *Alismo michaleti-Helosciadietum nodiflori* Géhu, Kaabèche et Gharzouli 1994; *Alismo michaleti-Typhaetum angustifoliae* Géhu, Kaabèche et Gharzouli 1994 et *Alismo michaleti-Nasturtietum officinalis* Géhu, Kaabèche et Gharzouli 1994.

LES VÉGÉTATIONS PIONNIÈRES À DOMINANTE THEROPHYTIQUE SUR SUBSTRAT DÉNUDÉ OU BOULEVÈRSE

Les classes de ce type de végétation pionnière et éphémère, identifiées en Algérie par de nouveaux syntaxons, dans la région d'El Kala [K3], sont les *Bidentetea tripartitae* R. Tüxen, Lohm. et Preising 1956 (classe exceptionnelle pour l'Algérie et citée pour la première fois), *Isoëto durieui-Juncetea bufonii* Braun-Blanquet et R. Tüxen 1943; *Ranunculo scelerati-Polygonetum hydropiperidis* Géhu, Kaabèche et Gharzouli 1994; *Laurentio michelii-Isolepidetum cernui* Géhu, Kaabèche et Gharzouli 1992; *Laurentio bicoloris-Fimbrystigidetum squarrosae* Géhu, Kaabèche et Gharzouli 1994; *Crypsio aculeatae-Cressetum cretiae* Géhu, Kaabèche et Gharzouli 1993 et *Saginetea maritimae* Westoff, V. Leeuw. et Adriani 1961 em. Géhu et Biondi 1986, avec l'association à *Spergularia diandra* et *Sphenopus divaricatus* Kaabèche, Gharzouli et Géhu 1995, colonisant les bords des dépressions salées du [H2].

LES VÉGÉTATIONS PIONNIÈRES VIVACES DES DUNES MARITIMES, DES DUNES CONTINENTALES ET ERGS SAHARIENS

Domaine de prédilection du Professeur Géhu, la classe des *Euphorbio paraliadis-Ammophilettea arundinaceae* Braun-Blanquet et R. Tüxen 1943 em. J.-M. et J. Géhu 1988, a retenu toute son attention aussi bien dans la région de Bejaia/Jijel [K2], qu'à El Kala [K3] et sur le littoral algérois [A1]. Bien que cette unité supérieure ait été relativement bien étudiée auparavant, cependant, l'ensemble des groupements végétaux a été redéfini avec une vision plus territoriale spécialement sur la côte algéroise. Des syntaxons inédits sont décrits, comme: *Loto cretici-Elymetum farcti* Géhu et Sadki 1995; *Scrophulario caninae-Crucianelletum maritimae* Géhu et Sadki 1995 et le groupement à *Otanthus maritimus* et *Spartina juncea* Géhu et Sadki 1995. La découverte de deux associations à *Echinophora spinosa*, sur le cordon dunaire de Jijel, le plus humide d'Algérie: *Echinophoro spinosae-Elymetum farcti* Géhu 1987 et *Echinophoro spinosae-Ammophiletum arundinaceae* (Braun-Blanquet 1921) Géhu, Rivas-Martínez et Tüxen 1974 représentant des «exclaves européennes» exceptionnelles pour l'ensemble du littoral maghrébin (GÉHU et

al., 1992).

Lors d'investigations dans la région de Biskra [SN1] et au Chott el Hodna [Hd], une nouvelle classe saharienne est proposée, pour réunir les végétations des dunes saharo-arabiques, le *Calligo comosi-Aristidetea pungentis* Kaabèche, Gharzouli et Géhu 1994. Dans cette classe de végétation halopsammophile, deux nouvelles associations s'insèrent dans une alliance inédite *l'Aristidion pungentis* Géhu, Kaabèche et Gharzouli 1993; *Anaboso oropediori-Aristidetum pungentis* Géhu, Kaabèche et Gharzouli 1993 et *Rhamtherio suaveolentis-Anabasidetum oropediori* Géhu, Kaabèche et Gharzouli 1993.

LES VÉGÉTATIONS PRAIRIALES

Ce type de végétation vivace, très peu étendu et peu connu en Algérie, le *Molinio caeruleae-Arrhenatheretea elatioris* R. Tüxen 1937, s'est avéré pourtant riche en syntaxons décrits pour la première fois, essentiellement dans la région des lacs d'El Kala [K3] et du constantinois [C1]: *Echinodoro ranunculoides-Paspaletem distichi* Géhu, Kaabèche et Gharzouli 1993; *Helosciadio crassipedis-Paspaletem distichi* Géhu, Kaabèche et Gharzouli 1994; *Eryngio barrelieri-Caricetum divisae* Géhu, Kaabèche et Gharzouli 1994; *Senecioni giganteae-Scrophularietum sambucinae* Kaabèche, Gharzouli et Géhu 1995 (type de mégaphorbiaie rare en Algérie).

LES VÉGÉTATIONS FRUTESCENTES DES SANSOUIRES ET SOLS SALES CONTINENTAUX

L'analyse de la classe des *Salicornietea fruticosae* Tüxen et Oberdorfer 1958, dans la région du Chott el Hodna [Hd] et de la sebkha Melloul [H2], a permis l'identification de deux syntaxons inédits: *Halocnemetum strobilacei* Géhu, Kaabèche et Gharzouli 1993 et *Suaedetum brevifoliae* Kaabèche, Gharzouli et Géhu 1995 et pour la classe *Pegano harmalaee-Salsoletea vermiculatae* Braun-Blanquet et O. de Bolos 1957, à caractère anthropozoogène, plusieurs groupements végétaux originaux ont été décrits par GÉHU *et al.* (1994a), du Sahara septentrional [SN2] (groupement à *Salsola vermiculata* et *Atriplex halimus*) et des plaines du Hodna (ziziphaires des groupements à *Salsola vermiculata* et *Ziziphus lotus* et à *Lycium afrum* et *Ziziphus lotus*).

LES VÉGÉTATIONS NITROPHILES VIVACES DES FRICHES OU MEGAPHORBIAIES

Ce type de végétation quasiment méconnu auparavant en Algérie, appartenant plus spécialement aux *Artemisietea vulgaris* Lohmeyer, Preising et R. Tüxen in R. Tüxen 1950 et *Onopordetia acanthii* Braun-Blanquet (1962) 1964, a été mis en évidence sur la corniche kabyle [K2] et dans l'oued Rhumel [C1], avec en particulier des associations inédites: *Sylibo mariani-Onopordetum arenarii* Géhu, Kaabèche et Gharzouli 1994, groupement à *Parietaria officinalis* et *Urtica dioica* Géhu, Kaabèche et Gharzouli 1992 et *Cirsium scabri* Géhu, Kaabèche et Gharzouli 1994.

LES VÉGÉTATIONS DEMAQUIS ET GARRIGUES

Ce sont surtout les maquis juxtalitoriaux des *Cisto ladaniferi-Lavanduletea stoechadis* Braun-Blanquet (1940) 1952, qui ont été étudiés par GÉHU *et al.*, (1994c), avec la définition d'un nouveau groupement à *Calicotome villosa* et *Halimium halimifolium*, à El Kala. La nouveauté vient ici surtout de la première mention en Algérie de la classe des génistaines et rétamaies pionnières ibéro-maghrébines, les *Cytisetea scopario-striati* Rivas-Martínez 1974, pour les rétamaies du littoral oriental kabyle-annabi [K2, K3].

LES VÉGÉTATIONS PIONNIÈRES FORESTIÈRES PALUSTRES OU RIVULAIRES

A côté de la végétation arbustive du *Nerio oleandri-Tamaricetea africanae* Braun-Blanquet et O. de Bolos 1957, où une nouvelle association a été décrite, *Nerio oleandri-Tamaricetum africanae* Géhu, Kaabèche et Gharzouli 1994, il faut surtout rappeler la mise en évidence d'une classe médio-européenne «insolite» en Algérie, les *Alnetea glutinosae* Braun-Blanquet et R. Tüxen 1943, sur sols fangeux et tourbeux, regroupant deux syntaxons originaux d'El Kala: *Rusco hypophylli-Alnetum glutinosae* Géhu, Kaabèche et Gharzouli 1994 et *Rusco hypophylli-Salicetum atrocinereae* Géhu, Kaabèche et Gharzouli 1994 pour lesquels Géhu a appelé à d'urgentes mesures conservatoires.

LES VÉGÉTATIONS FORESTIÈRES

ET PREFORESTIÈRES

Pour les forêts riveraines non marécageuses des *Querco roboris-Fagetea sylvatica* Braun-Blanquet et Vlieger 1937 (plus exactement des *Populetalia albae* Braun-Blanquet 1931), deux nouveaux groupements ont été définis au niveau de l'oued Bou Sellam [C1]: gr. à *Fraxinus angustifolia* et *Ulmus campestris* et gr. à *Salix alba* et *Fraxinus angustifolia* Géhu, Kaabèche et Gharzouli 1994.

Les maquis littoraux des *Quercetea ilicis* Braun-Blanquet (1936) 1947 (alliances de l'*Oleo-Ceratonion siliquae* Braun-Blanquet 1936 em. Rivas-Martínez 1975 et du *Juniperion turbinatae* Rivas-Martínez 1975), du littoral algérois et kabyle-annabi, ont retenu toute l'attention du Professeur Géhu, qui accorda à leur description une place particulière (GÉHU *et al.*, 1992, 1994a; GÉHU et SADKI, 1995). En premier, l'*Ephedro fragilis-Pistacietum lentisci* (Géhu *et al.* 1992) Géhu et Sadki 1995 et l'*Ephedro fragilis-Juniperetum turbinatae* (Zaffran 1960) Géhu et Sadki 1995 ont été redéfinis dans la remarquable synthèse phytosociologique et synchorologique sur le littoral algérois, et un nouveau syntaxon de pré-maquais (*Chamaeropo humilis-Artemisietum arborescentis* Géhu et Sadki 1995) a été individualisé à Tipaza [A1]. Ensuite, une place privilégiée a été réservée au maquis à *Euphorbia dendroides*, étudié pour la première fois dans toutes ses stations algériennes (GÉHU *et al.*, 1992, 1994a; KAABÈCHE *et al.*, 1998, 2000), qui répond à un syntaxon original (*Bupleurofruticosi-Euphorbiatum dendroidis* Géhu, Kaabèche et Gharzouli 1992), géosynvicariant de ses homologues nord-méditerranéens des *Oleo-Euphorbieta dendroidis*. Enfin, première mention pour l'Algérie du *Periplocion angustifoliae* Rivas-Martínez 1975, avec un groupement inédit à *Periploca laevigata* et *Ziziphus lotus* (GÉHU *et al.*, 1994a).

A l'issue de plusieurs études et investigations sur le terrain, le professeur Géhu a permis d'identifier une centaine de syntaxons nouveaux ou revisités dans le sysystème phytosociologique algérien. Il est indéniable qu'il a fourni une matrice de base et une structure solide du sysystème avec la rigueur qu'on lui connaît.

OBSERVATIONS INÉDITES DANS LE DOMAINE DE LA DIVERSITÉ FLORISTIQUE

Sur le plan de la diversité floristi-

que, les découvertes de nouveaux taxons (*Salicornia emerici*, *Sarcocornia fruticosa* var. *deflexa* = *S. alpina*), de nouvelles stations de taxons et de redécouvertes d'autres raretés, qui n'ont pas été revues depuis leur description principes, mériteraient à elles seules de faire l'objet d'une synthèse originale. Nous pouvons citer le très bel exemple de la flore des zones humides d'El Kala, où 145 taxons ont été inventoriés au total (au niveau d'une quarantaine de communautés végétales), parmi lesquels 45 sont rares à très rares en Algérie, voire exclusifs de cette région (16 taxons). En outre, 5 espèces n'ont pas été signalées à El Kala auparavant et sont donc à rajouter à la flore locale: *Cicendia filiformis*, *Lemna gibba*, *Paspalum paspalodes*, *Plantago crassifolia* et *Zostera noltii* (= *Z. nana*). Ajoutons à cela, *Cotula coronopifolia*, «cité à El Kala par Battandier sans certitude» (QUEZEL et SANTA, 1963), qui n'est plus énigmatique, puisque recensé au niveau de quasiment tous les lacs d'El Kala, sans parler d'espèces ligneuses comme *Salix atrocinerea*, *Frangula alnus*... la liste est trop longue (voir GÉHU *et al.*, 1994a, 1994b). Le mérite n'en est que plus grand, puisqu'elles ont été identifiées dans la région d'El Kala, censée être parmi les régions les mieux connues d'Algérie!

ÉLABORATION D'UN THESAURUS BIBLIOGRAPHIQUE SUR LA VÉGÉTATION ET LA FLORE D'ALGERIE

Un autre mérite revient indéniablement au Professeur Géhu, c'est d'avoir montré tout l'intérêt d'un théaurus bibliographique sur l'étude de la végétation de notre pays, plus spécialement phytosociologique, en co-signant un article avec Sadki en 1993, publié dans *Excerpta Botanica, sectio B, sociologica*, recensant près de 200 références, à l'intention des jeunes chercheurs qu'il qualifia d'enthousiastes. Un autre catalogue plus exhaustif existe au Centre Régional de Phytosociologie de Bailleul.

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ON THE CLASSIFICATION OF IBERIAN AQUATIC VEGETATION

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ABSTRACT

About 50 associations have been recognised in aquatic Iberian vegetation. This paper examines the characteristics used to establish the higher rank syntaxa (alliances, orders and classes), as well as other features considered important in the occurrence and distribution of water-plant communities. It is suggested that in addition to plant life forms, water nutrient status and water regime currently used in syntaxonomical classifications, water Ca levels and climate should also be taken into account. This work also highlights the need to increase the knowledge of the ecology of this vegetation at the level of the Iberian Peninsula.

KEYWORDS: Aquatic macrophytes, Ceratophylletea, Iberian Peninsula, Lemnetea, Potametea.

INTRODUCTION

Vascular aquatic flora comprises plants which are specifically adapted to the water environment (SANTAMARÍA, 2002) in different ways (DEN HARTOG & SEGAL, 1964). Aquatic plant communities are often poor in vascular species in comparison to terrestrial communities, and one species is usually dominant (RODWELL, 1995). This fact often enables easy definition and identification of associations, and leads to a proliferation of high syntaxa (FEOLI & GERDOL, 1982).

Several characteristics have been considered in the syntaxonomical classification for grouping plant communities; among the most important are: plant life-form, water salinity, water regime (moving or still waters, period of flooding), and nutrient status of the water (BRAUN-BLANQUET & TÜXEN, 1943; DEN HARTOG & SEGAL, 1964; OBERDORFER, 1977; WIEGLEB, 1980; GÉHU & MERIAUX, 1983; RIVAS-MARTÍNEZ *et al.*, 2001). Iberian aquatic vegetation is constituted by two main types of water plant biotypes: those forming the Hydrophytia errantia as free flo-

ting plants, Lemnetea, Ceratophylletea and those forming the Hydrophytia radicantia as rooted plants - Potametea, Ruppietea - (RIVAS-MARTÍNEZ, 1973). Amphibious growth-forms are also a part of hydrophytic communities (Litorelletea, Isoëto-Nanojuncetea).

Based on a review of the literature and my own experience in the field, the aim of this work is to answer the following questions: a) does the criteria used for syntaxonomical classification reflect the main ecological factors involved in the performance and distribution of hydrophytic communities? b) can we still expect to describe any new associations in the Iberian Peninsula?

CHARACTERISTICS ON WHICH SYNTAXONOMICAL CLASSIFICATIONS ARE BASED

LIFE FORMS

Aquatic plants provide a particular architecture and important structural component to freshwater habitats (DEN HARTOG, 1982). Based on plant/substrate relationships and plant growth form, DEN HARTOG & SEGAL (1964) proposed 11 biotypes which have been widely used in the characterisation of syntaxonomical higher units in the Iberian Peninsula (RIVAS-MARTÍNEZ, 1973; NAVARRO *et al.*, 2001; RIVAS-MARTÍNEZ *et al.*, 2001; PÉREZ LATORRE *et al.*, 2002; MELENDO *et al.*, 2003; MOLINA & SARDINEIRO, 2008). Water plant communities can be formed by a dominant or even a single biotype, or can show a structural complexity derived from the co-existence of two or more biotypes (DEN HARTOG, 1982). Biotypes separate certain classes such as Lemnetea, Potametea and Litorelletea from each other, but not others such Potametea and Ruppietea.

SALINITY LEVELS

The number of aquatic plants that occur in brackish and saline habitats gradually decreases with increasing sa-

linity, when they are reduced to a few taxa of certain families (SANTAMARÍA, 2002). Vegetation occurring in permanent or ephemeral coastal and inland brackish and saline wetlands consists of rooted and submerged macrophytes which are stress-tolerant and can grow with very different salinity levels and flooding periods (VERHOEVEN, 1979; VERHOEVEN, 1980; CURCÓ, 1996). This vegetation has been placed by some authors in the Ruppietea class (DEN HARTOG & SEGAL, 1964; OBERDORFER, 1977; MUCINA, 1997; RIVAS-MARTÍNEZ *et al.*, 2001).

NUTRIENT LEVELS

Nutrient status is known to affect the composition of aquatic vegetation. The trophic characteristic ranges from dystrophic to eutrophic waters, and has usually been reflected in syntaxonomical schemes. Dystrophic and oligotrophic water bodies host communities of small nymphaeids - Luronio-Potametalia - (DEN HARTOG & SEGAL, 1964). Mesotrophic water bodies are home to the highest number of biotypes and plant communities - Potametalia, Lemnalia. It is worth noting that cultural eutrophication involving widespread fertilisation with phosphorous and nitrogen has led to a change - due to replacement or disappearance - in aquatic flora and vegetation (HAURY & MULLER, 1991; LACHAVANNE *et al.*, 1992; LUMBRERAS *et al.*, 2009; own observations).

WATER REGIME

Water flow is a natural disturbance which enables a wide heterogeneity of fluvial habitats ranging from fast to slow-flowing, and a species selection (DAWSON, 1988). Very low flows allow the development of the characteristic still-water vegetation as found in ponds and lakes. In contrast, very high or turbulent flows preclude or restrict the development of aquatic vegetation. Seasonal water flooding allows the development of the characteristic vegetation

of temporary wetlands (Isoëto-Nanojuncetea, Littorelletea). Water regime (either still or flowing) has been used within batrachiid vegetation to distinguish still-water communities - Callitricho-Batrachion - and running-water communities - Ranunculion fluitantis - (RIVAS-MARTÍNEZ *et al.*, 2001). However, other alliances make no such distinction, e.g. Nymphaeion, which comprises nymphaeids and myriophyllids in still and moving waters (RODWELL, 1995).

CHARACTERISTICS OVERLOOKED IN SYNTAXONOMICAL CLASSIFICATIONS

CALCIUM

Soil Ca content is one of the main ecological factors for distinguishing plant and vegetation distribution in many types of terrestrial ecosystem. In European syntaxonomical classifications, several terrestrial vegetation types including certain grasslands and scrublands are grouped into calcareous or siliceous classes (MUCINA, 1997; RIVAS-MARTÍNEZ *et al.*, 2001). Specifically, in aquatic ecosystems, habitat differences in carbon availability related to water alkalinity and pH may result in marked differences in their aquatic flora (SANTAMARÍA, 2002). It has been demonstrated that Ca is a major factor in separating habitats in batrachiid communities (LUMBRERAS *et al.*, 2009). In spite of the above, no relevance has been given to this characteristic in aquatic syntaxonomical typology.

CLIMATE GRADIENT

The Western Iberian Peninsula has the highest richness in endemic aquatic plants in Europe and the Mediterranean area (COOK, 1983). Approximately two thirds of the Iberian Peninsula has a Mediterranean climate, characterised by summer drought, which influences the occurrence of ephemeral water bodies. In contrast, the remaining northern third has a Temperate climate which influences the permanent water bodies (RIVAS-MARTÍNEZ, 1987; ALONSO, 1987). This variety in the climate, in addition to the role of the Iberian Peninsula as a refugium in past glaciations and climatic oscillations, may help to explain its high diversity in aquatic vascular plants. Climatic factors have been shown to have limited effects on water-plant distributions, and are largely restricted to

the determination of major climatic disjunctions (SANTAMARÍA, 2002), although some aquatic species show a regional climatic segregation in Iberia (MOLINA, 2007). This feature should therefore be revised in building aquatic syntaxonomy.

THE SEARCH FOR A DEFINITIVE INVENTORY

A comprehensive revision of Iberian vegetation revealed 37 associations for Potametea, including Ceratophylletea, 9 for Lemnetea, and 6 for Ruppieteа (RIVAS-MARTÍNEZ *et al.*, 2001). Thus Iberian aquatic vegetation is composed of 52 aquatic associations, to which some amphibian associations of Littorelletea and Isoëto-Nanojuncetea should probably be added.

However, it is worth highlighting some considerations to be taken into account in order to reach a definitive Iberian inventory of aquatic associations. Firstly, there is a lack of information on water physical-chemical conditions for the majority of the associations. This information is particularly important in these habitats as they are formed by species-poor communities, sometimes in mixtures or intimate mosaics of dominant plants with few - if any - associates (RODWELL, 1995). Secondly, the syntaxonomical place of certain communities needs to be evaluated. This is the case, for example, of the *Polygonum amphibium* community (ARNÁIZ & MOLINA, 1986; BIURRUN, 1999), *Potamogeton polygonifolius* community and *Myriophyllum alterniflorum* community (NAVARRO *et al.*, 2001), among others. Thirdly, the role and occurrence of *Callitricho*-dominated associations widely cited as such in Europe (RODWELL, 1995) should also be revised, with only two associations recognised in the Iberian Peninsula (CIRUJANO *et al.*, 1986; PÉREZ LATORRE *et al.*, 1999). Finally, the latest taxonomical revisions of Iberian flora (CASTROVIEJO *et al.*, 1986-2010) should be taken into account and a new taxonomical revision of Iberian *Batrachium* species should be undertaken.

CONCLUSIONS

Current syntaxonomical classifications are mainly based on plant life forms, water nutrient status and water regime. However, gradients of water Ca - and consequently, of alkalinity and pH - and climate have been described as

being an important factor in the performance and distribution of aquatic vegetation. These factors should become part of the syntaxonomical schemes, as occurs in terrestrial vegetation.

Iberian aquatic vegetation requires a critical review of each association, including its ecology and distribution. For this purpose, more ecological information on its habitat is necessary.

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FRAXINO ANGUSTIFOLIAE-ULMETUM GLABRAE: AN ORIGINAL ENDEMIC AND EXTREMELY LOCALIZED FOREST FROM MAINLAND PORTUGAL

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ABSTRACT

The natural occurrence of *Ulmus glabra* in mainland Portugal has been recently recognized. These punctuated occurrences are peripheral and scattered from the main distribution area in the centre and north of Europe. *U. glabra* colonizes soils of heavy textures, relatively rich in bases, cool and frequently rocky on steep slopes (e.g. ravines, shadowy canyons), under supra to orotemperate, humid to hyperhumid bioclimates. This combination of ecological factors is rather unusual in mainland Portugal, however during an inventory excursion in the north of Portugal (Serra do Montemuro), in a small canyon of Balsemão river we detected a mesophilous/temporihygrophilous forest dominated by *U. glabra* and *Fraxinus angustifolia*. This forest is extremely localized occurring on Ordovician silty schists, under upper mesotemperate to supratemperate hyperhumid bioclimate. It probably corresponds to an interglacial refugium for the species. We ran an edaphoclimatic model within a geographical information system, in order to highlight other possible areas of occurrence for this forests and guide future efforts in finding it in mainland Portugal.

KEYWORDS: *Ulmus glabra*, *Fraxino angustifoliae-Ulmetum glabrae*, Serra do Montemuro, GIS analysis.

RIASSUNTO

È stata recentemente riconosciuta la presenza naturale di *Ulmus glabra* nel territorio del Portogallo continentale. Questa presenza puntuale è periferica e separata dal restante areale continuo del centro e nord Europa. *U. glabra* colonizza suoli di tessitura pesante, relativamente ricchi in basi, freschi e frequentemente rocciosi di versanti molto inclinati (per es. burroni, orridi ombrosi), con bioclima da supra a orotemperato, umido a iperumido. Questa com-

binazione di fattori ambientali è piuttosto rara in Portogallo, però durante un'escursione per eseguire rilevamenti floristici realizzata nel nord del Portogallo (Serra do Montemuro), in un piccolo canyon del fiume Balsemão, abbiamo individuato una foresta mesofilo-temporigrofila dominata da *U. glabra* e *Fraxinus angustifolia*. Questa foresta, molto limitata, si sviluppa su suoli derivati da scisti siltitici ordoviciani, con bioclima da meso a supratemperato, iperumido, e corrisponde molto probabilmente a un rifugio interglaciale di *U. glabra*. Si presenta un modello edafoclimatico realizzato con il GIS, in modo da poter individuare altre aree di presenza potenziale di questa comunità forestale e condurre future ricerche nel Portogallo continentale.

INTRODUCTION

The natural occurrence of *Ulmus glabra* Huds. in mainland Portugal has been long debated and dubious. BROTERO (1804), WILLKOMM & LANGE (1870) and COUTINHO (1939) considered the existence of only one species of the genus *Ulmus* in Portugal (today recognized as *Ulmus minor* Mill.). FRANCO (1971) did not refer *U. glabra* in mainland Portugal, not even as cultivated. NAVARRO & CASTROVIEJO (1995) considered the species cultivated in the Portuguese Estremadura (Lisbon region). However, the data available in the NATURHISTORISKA RIKSMUSEET (2004) indicate the punctuated occurrences in the Iberian Peninsula as spontaneous, which are peripheral and scattered from the main distribution area in the centre and north of Europe. In the rest of Europe, the species is found on soils of heavy textures, relatively rich in bases, cool and frequently rocky on steep slopes (e.g. ravines, shadowy canyons), under supra to orotemperate, humid to hyperhumid bioclimates (RIVAS-MARTÍNEZ *et al.*, 2002). The natural presence of this species in the north of Portugal has never been thoroughly studied.

Several paleopalynological studies refer the presence of *Ulmus* sp. in the Iberian Peninsula (RAMIL-REGO *et al.*, 1998; CARRIÓN GARCÍA *et al.*, 2000; MUÑOZ SOBRINO *et al.*, 2004; IRIARTE *et al.*, 2005; ALCALDE *et al.*, 2006). Particularly, RAMIL-REGO *et al.* (1998) studied several pollen sequences from the north of the Iberian Peninsula where *Ulmus* sp. was found frequently associated with Eurosiberian species and genera (e.g. *Quercus robur* type, *Corylus*, *Betula*, *Fagus*, *Castanea*). The *Ulmus* sp. pollen percentage maxima are generally associated to increases of these species, revealing moisture or moisture-cold climates. For that reason it is most probable that, in the northwest of the Peninsula, *Ulmus* sp. pollen corresponds in fact to *U. glabra* species. The same authors consider the presence of *U. glabra* in the northern Peninsula as a characteristic species of the sub-coastal mountains deciduous oak forests, occurring in the montane (>800 m; supratemperate) bioclimatic belt. Additionally, SVENNING *et al.* (2008) modelled the distribution of several tree species both for current climate and for the last glacial maximum (21,000 years ago). The model for the last glacial maximum showed the potential distribution of *U. glabra* in the north of the Iberian Peninsula.

U. glabra has been recently found by HONRADO (2003), MONTEIRO-HENRIQUES *et al.* (2005) and PORTELA-PEREIRA *et al.* (2008) in the centre and north of mainland Portugal, where systematic vegetation data collection occurred. Taking into account those paleopalynological and modelling studies, as well as the findings of the referred Portuguese authors we now accept the occurrence of *U. glabra* Huds. in mainland Portugal as natural.

The species appears mainly isolated, generally among stands of mature forests. Plant communities co-dominated by *U. glabra* were not known in mainland Portugal until an inventory excursion realized in 2005 in the Serra do Montemuro (centre-north of main-

Tab. 1 - *Fraxino angustifoliae-Ulmetum glabrae ass. nova.*

Relevé no.	6006	6008	6069	6070	6081	6082	6083
Taxa no.	24	11	18	15	31	22	19
Altitude (m)	779	768	810	853	818	783	783
Minimal area (m ²)	80	20	20	40	20	25	30
Aspect	NW	W	E	E	SE	N	N
Slope (grad)	30	30	10	50	60	50	50
Total coverage (%)	90	100	100	100	100	90	100
Order no.	1	2	3	4	5	6	7
Characteristic combination:							
<i>Ulmus glabra</i>	3	3	3	1	1	4	1
<i>Lonicera periclymenum</i> ssp. <i>hispanica</i>	1	2	3	1	2	+	1
<i>Polystichum setiferum</i>	2	2	+	1	2	3	
<i>Fraxinus angustifolia</i> ssp. <i>angustifolia</i>	.	.	+	5	4	2	5
<i>Rosa canina</i>	.	.	1	1	+	1	+
<i>Helleborus foetidus</i>	1	1	.	.	2	+	
<i>Tamus communis</i>	.	.	.	2	1	1	+
<i>Stellaria holostea</i>	1	3	3
<i>Crataegus monogyna</i>	.	.	.	1	.	2	+
<i>Crepis lampsanooides</i>	+	.	.	.	2	1	.
<i>Hedera hibernica</i>	2	+	1
<i>Euphorbia amygdaloides</i> ssp. <i>amygdaloides</i>	1	+	+
<i>Prunus avium</i>	2	1	.
<i>Polygonatum odoratum</i>	+	2
<i>Sambucus nigra</i> ssp. <i>nigra</i>	+	.	2
<i>Dryopteris dilatata</i>	+	1
<i>Quercus pyrenaica</i>	+	1	.
<i>Acer pseudoplatanus</i>	+	.	+
<i>Hyacinthoides hispanica</i>	+	.	+
<i>Silene latifolia</i>	+	.	+
<i>Viola riviniana</i>	+	.	.	.	+	.	.
<i>Asplenium onopteris</i>	1
<i>Corylus avellana</i>	.	1
<i>Laurus nobilis</i>	.	.	1
<i>Phyllitis scolopendrium</i> ssp. <i>scolopendrium</i>	1
<i>Athyrium filix-foemina</i>	.	+
<i>Castanea sativa</i>	.	.	+
<i>Fraxinus angustifolia</i> ssp. <i>angustifolia</i> (frut.)	+	.	.
<i>Teucrium scorodonia</i> ssp. <i>scorodonia</i>	+
Companion species:							
<i>Anthriscus sylvestris</i>	+	3	2	.	+	+	.
<i>Gallium aparine</i> ssp. <i>aparine</i>	2	.	+	.	+	+	+
<i>Rubus ulmifolius</i>	2	.	.	3	+	.	2
<i>Lamium maculatum</i>	2	.	1	.	+	+	+
<i>Geranium robertianum</i>	+	.	.	2	.	+	.
<i>Pteridium aquilinum</i> ssp. <i>aquilinum</i>	+	.	.	2	+	.	.
<i>Pentaglottis sempervirens</i>	1	.	+	.	+	.	.
<i>Geranium purpureum</i>	.	.	.	+	+	.	+
<i>Arrhenatherum elatius</i> ssp. <i>bulbosum</i>	.	.	.	2	1	.	.
<i>Rubus</i> sp.	1	1
<i>Arum italicum</i>	+	1
<i>Polypodium interjectum</i>	1	+
<i>Urtica dioica</i>	.	1	+
<i>Epilobium obscurum</i>	.	.	+	.	+	.	.
<i>Frangula alnus</i>	3	.	.
<i>Thapsia villosa</i>	.	.	.	1	.	.	.
<i>Agrostis stolonifera</i>	+	.	.
<i>Bidens aurea</i>	+	.
<i>Bidens frondosa</i>	+	.
<i>Chelidonium majus</i>	+
<i>Cytisus grandiflorus</i> ssp. <i>grandiflorus</i>	.	.	.	+	.	.	.
<i>Dactylis glomerata</i> ssp. <i>lusitanica</i>	+	.	.
<i>Digitalis purpurea</i> ssp. <i>purpurea</i>	+
<i>Eupatorium cannabinum</i> ssp. <i>cannabinum</i>	+
<i>Heracleum sphondylium</i>	.	.	+
<i>Linaria aeruginea</i> ssp. <i>aeruginea</i>	+	.	.
<i>Picris hieracioides</i> ssp. <i>longifolia</i>	+	.	.
<i>Poa trivialis</i> ssp. <i>trivialis</i>	.	.	+
<i>Saxifraga fragosoi</i>	+	.	.
<i>Sonchus asper</i> ssp. <i>asper</i>	.	.	+
<i>Urtica urens</i>	+
<i>Vicia angustifolia</i>	.	.	.	+	.	.	.
<i>Vicia sativa</i> ssp. <i>sativa</i>	+	.	.

land Portugal), where a mesophilous/temporihygrophilous forest dominated by *U. glabra* and *Fraxinus angustifolia* was found in a small canyon of Balsemão river, nearby Magueija (MONTEIRO-HENRIQUES, 2010). The result of that excursion is presented here, where we propose the first association co-dominated by *U. glabra* in Portugal.

In order to highlight other possible areas of occurrence of this forests and guide future efforts in finding it in mainland Portugal, we ran an edaphoclimatic model within a geographical information system.

The *Fraxino angustifoliae-Ulmetum glabrae* probably corresponds to an interglacial refugium for the species, the only one known in mainland Portugal, for now.

METHODS

The phytosociological relevés here presented followed Braun-Blanquet methodology (vide BRAUN-BLANQUET, 1932; MÜLLER-DOMBOIS & ELLENBERG, 1974; KENT & COKER, 1992): in each registered phytocoenosis, all the occurring plant taxa were recorded, moreover, synthetic minimal area (see MÜLLER-DOMBOIS & ELLENBERG, 1974; VAN DER MAAREL, 2005; MONTEIRO-HENRIQUES, 2010), slope, aspect (using a digital compass) and total vegetation cover (%) were estimated. A value of abundance-dominance was specified for each taxon, adopting Braun-Blanquet scale. Successional and zonation aspects presented here are discussed following the landscape sigmatist school terminology (GÉHU & RIVAS-MARTÍNEZ, 1981; RIVAS-MARTÍNEZ, 2005; RIVAS-MARTÍNEZ, 2007). Bioclimatic terminology follows RIVAS-MARTÍNEZ (2008).

For the modelling exercise, a geographic information system (GIS) was used (ArcMap™ 9.3 SP1) to highlight the combination of ecological factors where the *U. glabra*-dominated communities were found. Therefore, for the centre-north of mainland Portugal we selected areas with:

- 1) Slope greater than 10 grads (the smaller slope where the community was found);
- 2) Areas presenting upper mesotemperate to orotemperate thermotype;
- 3) Areas presenting humid to ultrahyperhumid ombrotype;
- 4) Rock types relatively rich in bases and capable of forming heavy textured soils, namely: schists from the Super-group Dúrico-Beirão, basic rocks (amphibolite, calc-schist, limestone etc.),

biotic granodiorites, shale-schists and silty shale-schists, among others.

In practice, this corresponds to a distribution model of the synhabitat of that community. The slope map was obtained within the used GIS using data from SRTM4 (CONSULTATIVE GROUP ON INTERNATIONAL AGRICULTURAL RESEARCH - CONSORTIUM FOR SPATIAL INFORMATION, 2008). Bioclimatologic maps were obtained as in MONTEIRO-HENRIQUES (2010) but for the most recent publication of Rivas-Martínez's World Bioclimatic Classification (RIVAS-MARTÍNEZ, 2008). Lithologic data was obtained from the Carta Geológica de Portugal Continental at 1:500,000 (INSTITUTO NACIONAL DE ENGENHARIA, TECNOLOGIA E INOVAÇÃO, 2007).

RESULTS

In Tab. 1 we present the phytosociological relevés realized on the communities co-dominated by *U. glabra* and *F. angustifolia*. For the typification of those forests we propose the new syntaxa *Fraxino angustifoliae-Ulmetum glabrae ass. nova hoc loco* (typus: relevé n. 06082), with the following characteristics:

DISTRIBUTION

The association is only known to occur on a small canyon of the Balsemão River valley, nearby Magueija.

SYNECOLOGY

Mesophilous to temporihygrophilous forest, supra to upper mesotemperate, hyperhumid, eooceanic. On deep soils derived in very steep slopes. In the visited locations the substratum corresponds to Ordovician silty schists.

CONTACTS

Climactic forest contacting categinally with *Galio broterianoi-Alnetum glutinosae scrophularietosum scorodoniae* hygrophilous forests. It also contacts with *Holcomollis-Quercetum pyrenaicae* mesophilous forests, which occurs on nearby granites.

DESCRIPTION

Deciduous mesoforest dominated by *U. glabra* and *F. angustifolia*. Prun-

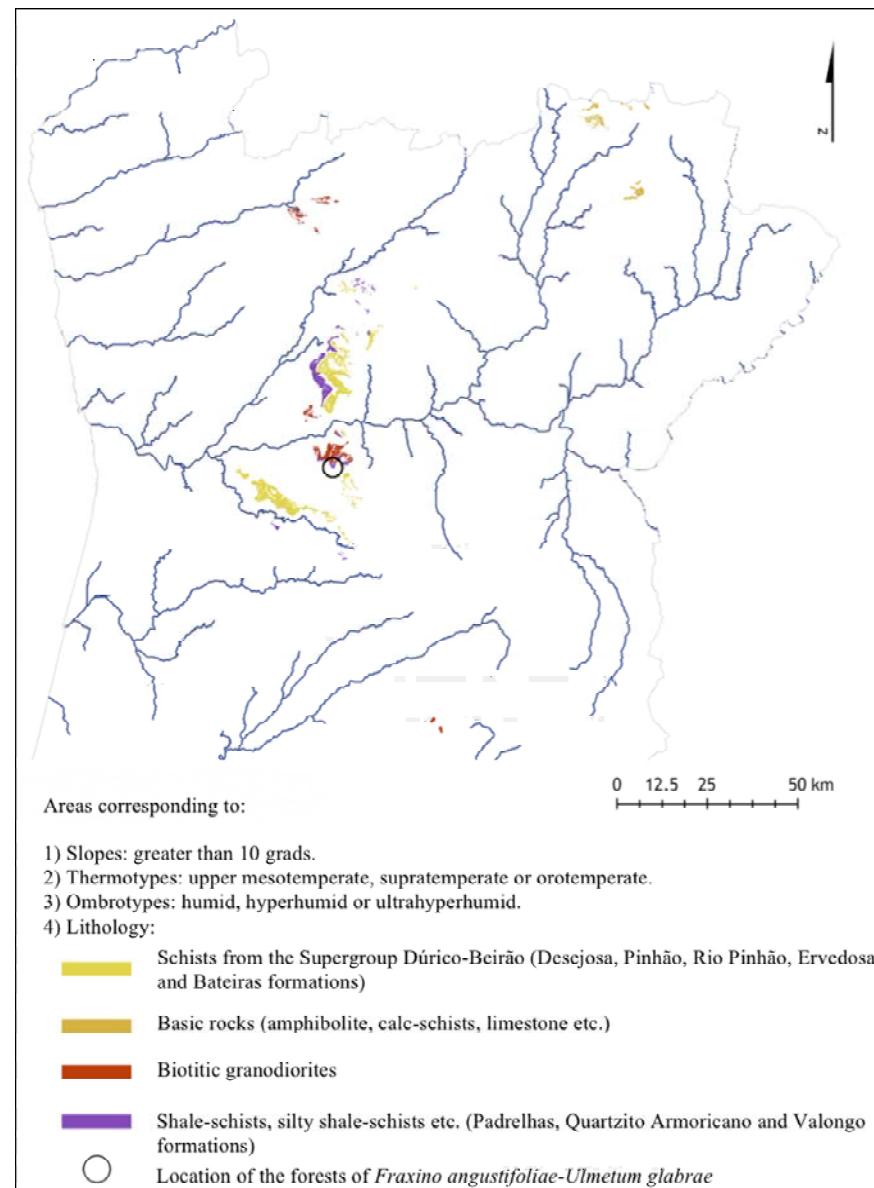


Fig. 1 - GIS model of the areas environmentally similar to those where *Fraxino angustifoliae-Ulmetum glabrae* was found.

nus avium, *Crataegus monogyna*, *Corylus avellana*, *Sambucus nigra*, *Laurus nobilis*, *Acer pseudoplatanus* occur in the underwood, together with nemoral species as *Polystichum setiferum*, *Helleborus foetidus*, *Stellaria holostea*, *Polygonatum odoratum*, *Crepis lampsanoides*, *Dryopteris dilatata*, *Omphalodes nitida*, *Phyllitis scolopendrium* subsp. *scolopendrium*, *Teucrium scorodonia* subsp. *scorodonia*, *Arum italicum*, *Viola riviniana*, *Athyrium filix-foemina*, among others and lianas like *Lonicera periclymenum* subsp. *hispanica*, *Rosa canina*, *Hedera hibernica*, *Tamus communis*, *Rubus ulmifolius* etc. (Tab. 1).

SYNTAXONOMY

Even if the forest dominated by *U. glabra* and *F. angustifolia* found nearby Magueija is extremely localized, we

propose its typification as an association due to the great consistency between the ecology of the found community and the other communities where the species is present in Europe. Therefore, we propose to place this association in the *Tilio-Acerion* Klika 1955 alliance, *Fagetalia sylvatica* Pawłowski in Pawłowski, Sokołowski et Wallisch 1928 order, from the *Querco-Fagetea* Braun-Blanquet et Vlieger in Vlieger 1937 class, mainly due to the synhabitat similarities to the Alpine and Pyrenean communities from steep slopes/ravines dominated by *U. glabra*, and also for the presence of *Crepis lampsanoides*, *Dryopteris dilatata*, *Euphorbia amygdaloides* subsp. *amygdaloides*, *Helleborus foetidus*, *Stellaria holostea*, *Prunus avium* and, of course, *U. glabra*.

Finally, the GIS analysis highlighted the areas environmentally similar to those where *Fraxino angustifoliae-*

Ulmetum glabrae was found, in the centre-north of mainland Portugal (Fig. 1). Those environmental characteristics resulted rather unusual in mainland Portugal, as the areas of potential occurrence correspond to small areas from the mountain ranges of Estrela, Montemuro, Marão-Alvão, Montalegre, Nogueira and Montesinho.

DISCUSSION

The recognition of the *Tilio-Acerion* alliance in mainland Portugal implies also the presence of the Natura 2000 priority “natural habitat” *9180 *Tilio-Acerion* forests of slopes, screes and ravines. These communities underwent regression due to Dutch elm disease (*Ophiostoma ulmi* and *Ophiostoma novo-ulmi*), nevertheless, many mature *U. glabra* trees still exist on the found stands. As *U. glabra* is intolerant to dryness, climate change represents also a threat to this community, as it exists on the southwestern boundary of the distribution of *U. glabra*, and also close to the boundary between Eurosiberian and Mediterranean region. Thus, monitoring and active protection measures are certainly justified.

According to the paleopalynological studies referred in the introduction, in particular the models implemented by SVENNING *et al.* (2008), we believe that it is highly probable that the very localized canyon of Balsemão river correspond to an interglacial refugium for *U. glabra*, giving it even more value for Nature Conservation.

APPENDIX

Tab. 1 - 1 Viseu: Lamego, Magueija, right margin of Balsemão River; 2 Viseu: Lamego, Magueija, Relampa; 3 Viseu: Lamego, Magueija, Magueija; 4, 5, 6 and 7 Viseu: Lamego, Magueija, between Reconcos bridge and Magueija.

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CARTA DEL PAESAGGIO VEGETALE DEL CASTELLO DI LANCIANO (FONDAZIONE MARIA SOFIA GIUSTINIANI BANDINI) MARCHE (ITALIA)

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ABSTRACT

A plant landscape map of a hilly territory of Umbria-Marches Apennines (Macerata Province, Marches Region) at the scale 1:12,000 has been carried out. The study area (Castello di Lanciano, former "Marchesato di Lanciano"), composed of four sub-areas whose surfaces range from 2 to 47 hectares, belong to Maria Sofia Giustiniani Bandini (Ma.So.Gi.Ba.) Foundation (acknowledged by D.P.R. 584/1982). The analysis of vegetation led to the identification of the following units: thermophilous and mesophilous deciduous woods with a dominance of *Quercus pubescens*; hygrophilous woods with a dominance of *Salix alba* and *Alnus glutinosa*; *Buxus sempervirens* shrub community; mesophilous haymeadows; dry pastures; herbaceous and woody cultivations; hedgerows. To highlight the evolution of plant landscape of the study area, the plant landscape map was compared with a cadastral map made in the mid-19th century. The main differences identified are related to land abandonment, which caused the spread of woods, and to the change of the agricultural management system, which led to the homogenization of rural landscape.

KEYWORDS: plant landscape, vegetation mapping, Lanciano castle, *Peucedano cervariae-Quercetum pubescantis*, *Aro italicici-Alnetum glutinosae*, *Salicetum albae*.

RIASSUNTO

In un'area collinare dell'Appennino Umbro-Marchigiano (Provincia di Macerata, Regione Marche) è stata realizzata una carta del paesaggio vegetale in scala 1:12.000. L'area di studio (Castello di Lanciano, anticamente "Marchesato di Lanciano"), composta da quattro sotto-aree le cui superfici variano tra 2 e 47 ettari, fa parte della Fondazione Maria Sofia Giustiniani Bandini (Ma.So.Gi.Ba.), riconosciuta con D.P.R. 584/1982. L'analisi della vegetazione

ha portato all'identificazione delle seguenti unità: boschi caducifogli termofili e mesofili di *Quercus pubescens*; boschi igrofili a dominanza di *Salix alba* e *Alnus glutinosa*; aggregamenti arbustivi a *Buxus sempervirens*; prati-pascoli mesofili; pascoli xericci; colture erbacee e arboree; alberate. Per mettere in evidenza l'evoluzione del paesaggio vegetale dell'area di studio, la carta del paesaggio vegetale è stata confrontata con una mappa catastale risalente alla metà del XIX secolo. Le principali dif-

ferenze individuate sono legate all'abbandono di alcune aree agricole, che ha determinato l'espansione dei boschi, e al cambiamento del sistema di gestione agricola, che ha portato all'omogeneizzazione del paesaggio rurale.

INTRODUZIONE E SCOPI DEL LAVORO

La presente ricerca si riferisce alla cartografia del paesaggio vegetale di

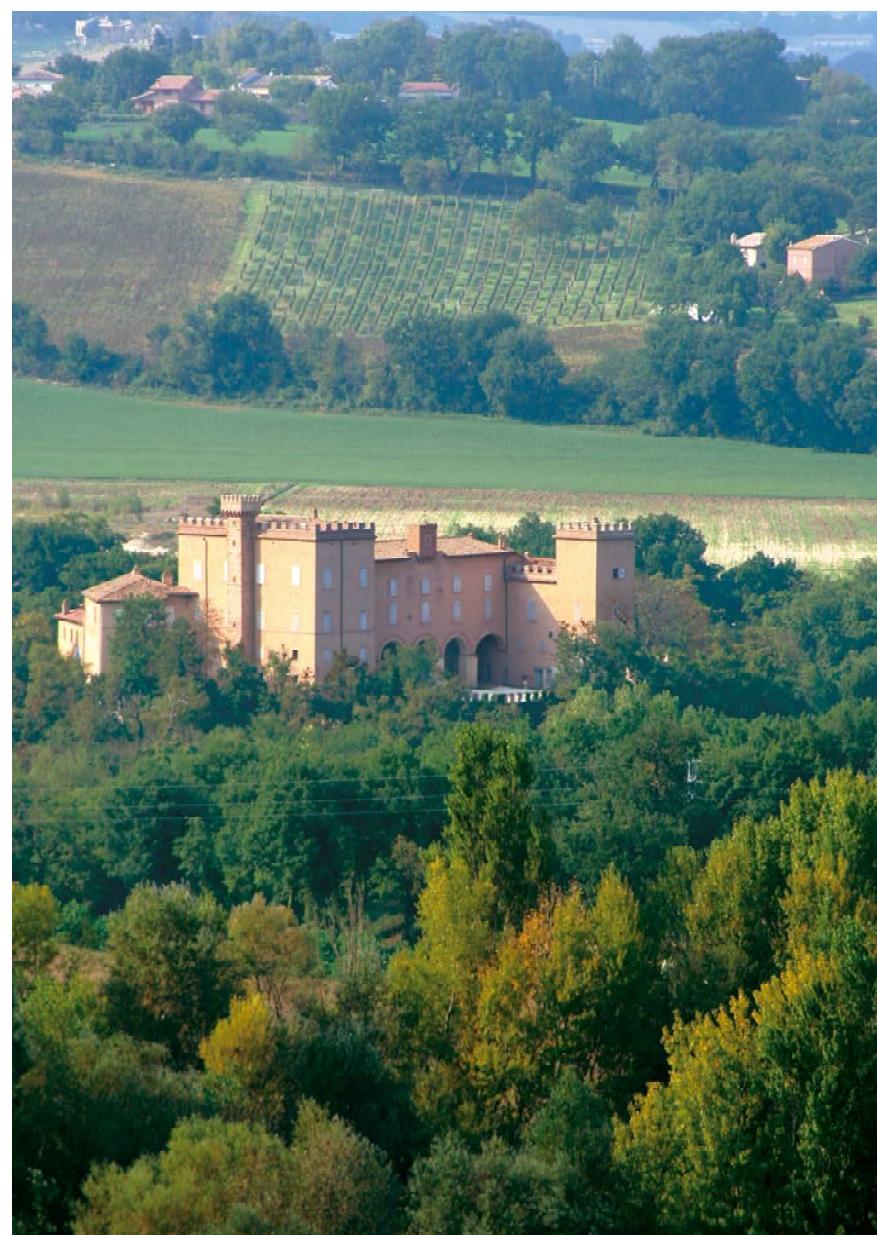


Fig. 1 - Il Castello di Lanciano.

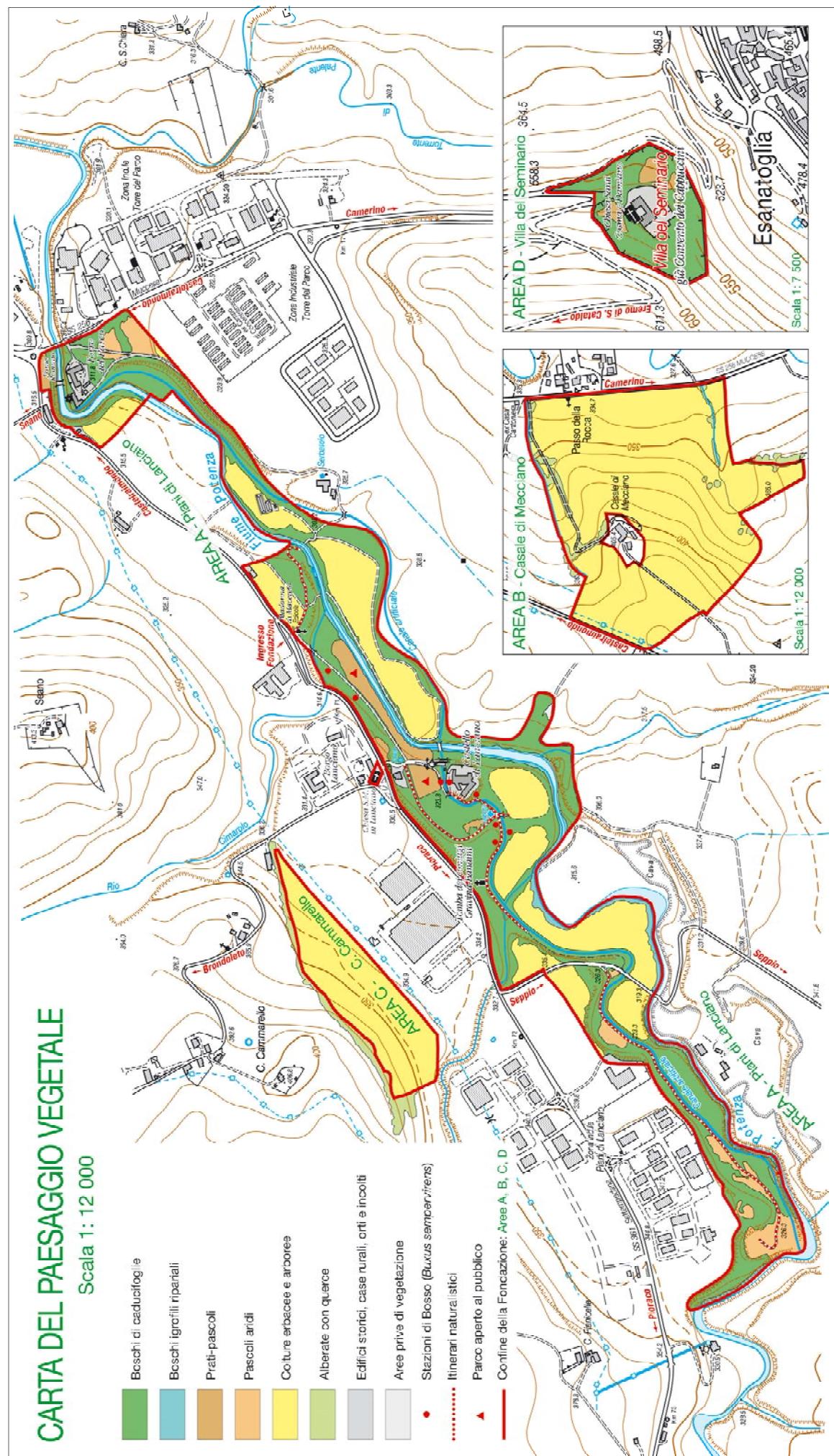


Fig. 2 - Carta del paesaggio vegetale del Castello di Lanciano (anticamente "Marchesato di Lancianò") e di tre aree contigue (Casale di Mecciano, C. Cammarello, Villa del Seminario) (da: ORE OMANDO e FALASCII, 2010).



Fig. 3 - Mappa Catastale del "Marchesato di Lanciano" (da: ORSAMANDO et al., 2010).

un'area collinare dell'Appennino Umbro-Marchigiano, che si estende su una superficie di 93 ettari, ripartita in quattro aree non molto distanti tra loro, che ricadono nel territorio della Provincia di Macerata. Tre di esse (area A, 47 ettari; area B, 26 ettari; area C, 18 ettari) appartengono ai Comuni di Castelraimondo, Camerino e Pioraco; una (area D, 2 ettari) si trova in Comune di Esanatoglia.

Le aree A, B e C (anticamente note come "Marchesato di Lanciano") sono state ereditate, con tutti i beni ambientali storico-artistici ad esso annessi (con atto testamentario della Principessa Maria Sofia Giustiniani Bandini), dagli Arcivescovi *pro tempore* dell'Arcidiocesi di Camerino-S. Severino Marche, che le gestiscono attraverso l'istituzione della Fondazione Maria Sofia Giustiniani Bandini (formalizzata con Decreto Arcivescovile del 16 novembre 1981 e riconosciuta a tutti gli effetti giuridici e civili con Decreto del Presidente della Repubblica Italiana del 3 giugno 1982, n. 584). Tra i beni storico-artistici, inseriti in un contesto paesaggistico naturale e agrario di notevole rilievo per la Regione Marche, risaltano il Castello di Lanciano (Fig. 1), nobilitato da straordinarie opere d'arte, e la Torre del Parco, detta anche Torre dei Bilancioni, eretta nel 1381-1382 da Giovanni da Varano, Signore di Camerino, e situata in prossimità di un antico ponte di probabile impianto romano.

L'area D, nelle carte geografiche indicata con il toponimo Convento dei Cappuccini e nota come Villa del Seminario, è entrata a far parte del patrimonio della Fondazione dal 1982, a seguito del trasferimento dal Seminario Arcidiocesano di Camerino.

Nel territorio della Fondazione i valori storico-botanici, relativi a specie e habitat, sono attestati dal materiale depositato nell'archivio della Fondazione, dove si conservano diverse centinaia di campioni di erbario, probabilmente attribuibili a Vincenzo Ottaviani (1790-1853) insigne micologo e botanico marchigiano del primo Ottocento (fondatore nel 1828 dell'Orto Botanico dell'Università di Camerino) e da numerose carte e mappe catastali che delineano i paesaggi dei secoli passati.

L'insieme di queste emergenze ci ha consentito di realizzare una serie di documenti cartografici contenenti informazioni botanico-ecologiche, utili non solo per una migliore descrizione dell'ambiente naturale, seminaturale e antropico del territorio della Fondazione e per il confronto delle tipologie paesaggistiche attuali con quelle del passato, ma anche per una più idonea utilizzazione e conservazione delle risorse esistenti.

Al termine di una serie di rilevamenti condotti, nell'arco di due anni, sulle comunità vegetali presenti e mai precedentemente osservate, è stato possibile realizzare due carte geobotaniche: una in scala 1:12.000, presentata in questo contributo (Fig. 2) e riprodotta sul quaderno *Beni ambientali e culturali della Fondazione Maria Sofia Giustiniani Bandini* (ORSOMANDO e FALASCHI, 2010) e una in scala 1:5.000, *Carta bionaturalistica con itinerari ed emergenze della Fondazione Maria Sofia Giustiniani Bandini* (ORSOMANDO et al., 2010), nella quale è inoltre riportata l'antica *Mappa Catastale del Marchesato di Lanciano*, risalente alla prima metà dell'800 (Fig. 3).

È stato inoltre possibile fare il con-

fronto fra il paesaggio rappresentato nell'antica mappa catastale e quello attuale raffigurato nella carta in scala 1:12.000, allo scopo di mettere in evidenza l'evoluzione subita dalle forme del paesaggio agrario nel territorio studiato.

L'AMBIENTE ABIOTICO

Le quattro aree studiate per realizzare i due documenti cartografici geobotanici a diversa scala topografica si distinguono per gli aspetti altitudinali, morfologici, idrografici, geologici e climatici di seguito descritti brevemente.

ALTIMETRIA - L'altitudine massima si raggiunge nell'area D con la quota di 558 m, segnata dalla Villa del Seminario, mentre nelle aree B e C le altezze oscillano tra 340 e 400 m. Nell'area A, che si contraddistingue per essere completamente semipianeggiante, si raggiungono le quote più basse comprese tra 310 e 330 m.

MORFOLOGIA - Mentre le aree C e D interessano parte dei rilievi basso-collinari con una morfologia piuttosto dolce e regolare, priva di tratti aspri o dirupati e l'area D si estende sul versante soleggiato del Monte Corsegno (la cui cima, fuori della proprietà della Fondazione, segna 998 m), l'area A, la maggiore, occupa buona parte dei primi terrazzi fluviali del Fiume Potenza.

IDROGRAFIA - Tre delle quattro aree (A, B, C) rientrano nella parte alta del bacino del Fiume Potenza; l'area D, invece, ricade nel tratto iniziale del bacino del Fiume Esino, uno dei corsi d'acqua che a livello regionale si distinguono per lunghezza ed elevata portata.

GEOLOGIA - Nel territorio delle quattro aree trovano esclusivo sviluppo le formazioni continentali di fondovalle del Neozoico e le formazioni marine del Cenozoico e Mesozoico che caratterizzano i rilievi collinari e basso-montani. Infatti i primi terrazzi, solcati dalle acque del Fiume Potenza e quelli immediatamente di ordine superiore (area A) sono prevalentemente costituiti da sedimenti alluvionali attuali e recenti (depositi di ghiaie e limi del Quaternario), i rilievi collinari (aree B e C) sono composti da molasse in banchi e strati con alternanze marnoso-arenacee e ar-



Fig. 4 - Veduta dal Castello di Lanciano dei boschi planiziari di querce caducifoglie (*Peucedano-Quercetum pubescens*). Sullo sfondo le altezze che circondano Castelraimondo.

gille del Terziario. Le formazioni più antiche (riferibili al Mesozoico), rappresentate da calcari di maiolica e calcari marnosi con noduli di selce, interessano la località Villa del Seminario di Esanatoglia (area D).

CLIMA - Le caratteristiche climatiche che contraddistinguono le quattro aree della Fondazione sono essenzialmente correlate alla presenza delle acque dei Fiumi Potenza ed Esino, alla posizione geografica e al regime delle piogge e delle temperature in funzione dell'altitudine. Sulla base di questi principi, dei valori delle precipitazioni medie annue attorno ai 1.000-1.100 mm (con massimi stagionali in autunno-inverno, per complessivi 640 mm di pioggia) e dei valori delle temperature medie, che oscillano attorno a 11-12 °C, il clima, a grandi linee, può essere rapportato a quello di tipo submediterraneo, come evidenziato dalla presenza di boschi a prevalenza di querce caducifoglie. Queste condizioni climatiche (che quasi mai determinano periodi di aridità estiva intensa e prolungata) riguardano maggiormente le aree A, B e C. L'area D, invece, si contraddistingue per essere una zona microclimatica con valori di termofilia e xerofilia più elevati, dovuti alla favorevole esposizione e alla presenza del substrato roccioso calcareo, come attestato dalla presenza del leccio.

L'AMBIENTE BIOTICO

STUDIO DELLA VEGETAZIONE

L'analisi dei tipi vegetazionali ai fini cartografico-paesaggistici non ha previsto la realizzazione di rilievi fitosociologici, ma si è limitata al riconoscimento dei tipi stessi sulla base degli elementi fisionomico-strutturali omogenei, supportati dalla presenza e dalla combinazione di specie indicatrici o caratteristiche di associazioni o unità sintassonomiche superiori, nominate (ove possibile) alla fine delle singole descrizioni.

In mancanza di specifici rilevamenti di campo, c'è da osservare che i *syntaxa* denominati non si riferiscono sempre ad un preciso inquadramento fitosociologico dei tipi cartografati, ma costituiscono un'accettabile approssimazione.

TIPI CARTOGRAFATI

Allo scopo di identificare i diversi

tipi paesaggistici, si è proceduto ad una serie di indagini preliminari, consistenti nella lettura dei fototipi mediante l'uso di ortofotocarte e di immagini satellitari, e una fase successiva finalizzata al riconoscimento e al controllo sul terreno delle tipologie fotorestituite. Per praticità, le tipologie scelte sono quelle più estese e facilmente riscontrabili sul terreno, non solo dagli addetti ai lavori, ma anche dagli appassionati della natura che a migliaia annualmente visitano i beni storico-artistici della Fondazione e percorrono i sentieri naturalistici presenti.

La rassegna dei tipi vegetazionali paesaggistici segue quella utilizzata nella legenda della carta alla scala 1:12.000.

BOSCHI CADUCIFOGLI - Si tratta di formazioni a prevalenza di *Quercus pubescens* s.l., con *Quercus cerris* e presenze di *Taxus baccata*, molto fitte, a tratti rinfoltite con conifere o intercalate a colture di pioppi ibridi, contraddistinte dalla presenza di querce secolari. Si dividono in aggruppamenti mesofili e termofili. I boschi mesofili ricoprono i terreni alluvionali profondi e umidi dei terrazzi fluviali del Fiume Potenza (area A) e rappresentano gli ultimi residui dell'originaria foresta planiziale che dalla Torre del Parco si estendeva fino ai pressi di Pioraco (Fig. 4). Nel sottobosco, comuni sono *Buglossoides purpureaerulea*, *Cyclamen repandum*, *C. hederifolium*, *Vinca major*, *Iris foetidissima* e *Ruscus aculeatus*. Quest'ultima specie è particolarmente diffusa nei boschi che sono stati sottoposti a tagli di sottobosco spinti o al pascolamento forzato. I boschi termofili sono sviluppati attorno alla Villa del Seminario (area D), sui versanti soleggiati scoscesi calcarei, con presenza di *Ostrya carpinifolia*, *Fraxinus ornus*, *Acer monspessulanum* e *Cytisophyllum sessilifolium*. Dal punto di vista fitosociologico la posizione dei boschi mesofili di roverella si può ricondurre all'associazione *Peucedano cervariae-Quercetum pubescantis* (ALLEGREZZA et al., 2002), mentre quelli termofili si possono inquadrare nella subassociazione *Scutellario columnae-Ostryetum carpinifoliae cytisitosum sessilifolii* (BONDI et al., 1989).

BOSCHI IGROFILI RIPARIALI - Riguardano esclusivamente le sponde del Fiume Potenza (Fig. 5) e sono caratterizzati dalla presenza di *Salix alba*, *Alnus glutinosa*, *Populus alba*, *Ulmus minor*; dalle rampicanti *Humulus lupulus*, *Solanum dulcamara* e negli spazi sabbiosi dei bordi del fiume da *Apium nodiflorum*, *Petasites hybridus*, *Carex pendula*, *Eupatorium cannabinum* ed *Equisetum telmateja*. Nello strato arbustivo sono frequenti gli arbusti *Cornus sanguinea*, *Ligustrum vulgare* e *Sambucus nigra*. Questi boschi si caratterizzano per essere sviluppati in una sottile fascia dove le specie arboree per lo più si alternano a nuclei o ad alberi isolati, associati a pioppi ibridi. Si tratta di vegetazione frammentata riferibile alle associazioni *Salicetum albae* e *Aro italicci-Alnetum glutinosae* (PEDROTTI e GAFTA, 1996).

PRATI-PASCOLI - Sono formazioni erbacee mesofile, sfalciate più volte l'anno, talvolta sottoposte al pascolo di ovini e caprini. Ricoprono le aree pianeggianti con suoli profondi e umidi che circondano in parte il Castello di Lanciano (Fig. 6). Si caratterizzano per la prevalenza di Graminacee, Ranunculacee e Composite e nel periodo primaverile-estivo si contraddistinguono per le copiose fioriture di *Ranunculus neapolitanus* (nelle zone più umide) e di *Bellis perennis* (nelle zone meno umide). Sicuramente l'utilizzazione di questi prati-pascoli costituisce un blocco all'evoluzione spontanea della vegetazione verso formazioni dinamicamente più stabili. Per quanto concerne l'inquadramento fitosociologico, sulla base del corteccia floristico, tali formazioni si possono riferire alla classe *Molinio-Arrhenatheretea*.

PASCOLI XERICI - Sono formazioni secondarie che occupano aree limitate, aride e soleggiate, a volte semirupostri, a dominanza dell'emicriptofita *Bromus erectus*. Si tratta di strutture erbacee aperte dove si sviluppano alcune camefite, tra cui *Helychrysum italicum*, *Artemisia alba* e l'emicriptofita scaposa *Globularia punctata*. Per la composizione floristica e le caratteristiche ecologiche, tali formazioni possono essere riferite all'alleanza *Phleo ambigui-Bromion erecti*.

COLTURE ERBACEE E ARBOREE - Questo tipo cartografico si riferisce prevalentemente a seminativi e coltivazioni a breve rotazione costituite da colture primaverili-estive (cereali), estivo-autunnali (mais e girasole) ed erbai polifitici. Qua e là si trovano filari di vigneti e piccoli noceti. Numerose sono le querce secolari isolate presenti nei campi o allineate a delimitare i vari appezzamenti.



Fig. 5 - Il Fiume Potenza, nel periodo estivo-autunnale, circondato dalla vegetazione igrofila ripariale (*Salicetum albae* e *Aro italic-Alnetum incanae*).

menti o i margini delle tortuose e strette strade rurali.

ALBERATE CON QUERCE - Si tratta di piccoli boschi a forma allungata, che si snodano lungo le strade di campagna, costituiti da alberi di *Quercus pubescens* s.l., per lo più secolari, contornati da siepi di *Prunus spinosa*, *Euonymus europaeus*, *Rosa canina* e *Lonicera caprifolium*.

STAZIONI DI *BUXUS SEMPERVIRENS* - All'interno dei boschi planiziari di querce, ai

piedi del Castello di Lanciano, ai bordi delle strade che attraversano gli stessi boschi e lungo i canali storici artificiali che portano acqua alla centrale idroelettrica di Lanciano, si trovano folte e rigogliose stazioni di *Buxus sempervirens*, con esemplari alti oltre 3 m, dai tronchi con diametro superiore a 30 cm.

Si tratta di formazioni monospecifiche, molto omogenee, sviluppate nell'area della piana di Lanciano (area A) in luoghi ombrosi e suoli umidi e profondi. In particolare, le stazioni di *Buxus sempervirens* presenti attorno al castello, vegetano in condizioni microclimatiche molto favorevoli e sono le

meglio conservate poiché saltuariamente curate dall'uomo.

LA CARTA STORICA DEL MARCHESATO DI LANCIANO

La mappa catastale del Marchesato di Lanciano (ALEFFI, 1986; PEDROTTI, 1990), riprodotta nella Fig. 2, fu realizzata dal Geometra Luigi Antinori di Camerino nel 1841 e rientra nella vasta opera di controllo fiscale operata nelle regioni dello Stato Pontificio dal secolo XVII in poi. In essa sono rappresentati in dettaglio numerosi elementi tipici del paesaggio collinare delle Marche (tipi di coltura, elementi naturali del paesaggio, insediamenti rurali), presenti attorno al castello omonimo. La mappa ci permette di esaminare le tecniche cartografiche di rappresentazione del paesaggio agli inizi del XIX secolo e, contemporaneamente, di rilevare le variazioni intervenute fra il paesaggio in essa raffigurato ed il paesaggio attuale (ALEFFI, 1988). Si tratta di un disegno a penna e acquerello a cinque colori per indicare le diverse destinazioni colturali. La mappa è divisa in due fasce. Nella fascia superiore è posta la rappresentazione della proprietà, sormontata da un cartiglio di colore azzurro, mentre in basso è disegnata la "Scala geometrica di ca. 100 Camerinesi". Il "Camerinese" rappresentava l'unità di misura in uso a quel tempo che corrispondeva a circa 1 metro. Nella fascia inferiore è posta la legenda, divisa in sei riquadri, con la descrizione dei tipi di terreno e di insediamento e la loro estensione in stara (1 stara = 539,11 m²). Nella mappa sono rappresentate dieci diverse destinazioni colturali, ciascuna raffigurata con un proprio simbolo. L'arativo alberato è rappresentato da uno stretto rigato rosa su cui sono disegnati degli alberi disposti in file regolari. L'arativo nudo (o seminativo) è rappresentato con un rigato stretto di colore rosa. Il gelseto indica la coltivazione del gelso, utilizzata per l'allevamento del baco da seta. Il pioppeto (o bidolletto), indicato con alcune file regolari di alberelli, la cui presenza fa supporre una sua coltivazione per utilizzarne il legno per lavori artigianali. Il sodivo, con la variante con querce, è rappresentato con un colore verde scuro e sta ad indicare i terreni incolti o mai lavorati. Il querceto è sicuramente la rappresentazione più suggestiva e artisticamente più riuscita poiché rende molto bene l'idea del bosco di roverella, tipico della fascia collinare, indicato nella legenda con i termini di selvato e querciato, secondo le

due principali utilizzazioni del bosco: il selvato era il bosco mantenuto "a selva", mentre il querceto era utilizzato dai contadini per la produzione della ghianda. Infine, il sodivo con cipresso e bosso doveva costituire sicuramente il parco vero e proprio annesso al castello, disegnato con piante ornamentali.

CONFRONTO TRA LA VEGETAZIONE ATTUALE E QUELLA DEL PASTATO

Il confronto fra il paesaggio rappresentato nell'antica mappa catastale e quello attuale raffigurato nella carta in scala 1:12.000 mette in evidenza l'evoluzione subita dalle forme del paesaggio agrario.

L'*arativo alberato*, che caratterizzava il paesaggio nell'antica rappresentazione, sia dal punto di vista qualitativo che quantitativo, scompare quasi totalmente, così com'è possibile osservare un po' dovunque nel paesaggio agricolo delle Marche, essendo sostituito da sistemi agrari a rotazione. Anche la coltura del gelso (*gelseto*) per l'allevamento del baco da seta, rappresentata nell'antica mappa e un tempo fiorente, oggi è caduta in disuso.

Si sviluppa al contrario il seminativo (*arativo nudo*), che rappresenta oggi, con il 50%, la pratica più comune nel territorio studiato.

Il saliceto (*veticetheto*) che formava, come la raffigurazione dell'antica mappa lascia intuire, boschetti sviluppati in corrispondenza delle anse del fiume, oggi appare ridotto ad una fascia ripariale rimaneggiata e frammentata.

È scomparso il pioppetto (*bidolletto*) come forma di piantagione, anch'esso sostituito dal seminativo nudo, che risulta limitato alla fascia ripariale del Fiume Potenza e a piccole superfici frammiste al bosco naturale (non cartografate per la limitata estensione).

Occorre invece rilevare che il bosco di querce ha incrementato sensibilmente la copertura totale, passando da una superficie di circa 9 ettari agli inizi dell'800, come si deduce dall'analisi dell'antica mappa catastale, ai quasi 30 ettari attuali (circa un terzo della superficie totale del territorio).

Il bosco si è sviluppato in maniera continua in corrispondenza dei terreni adiacenti al Fiume Potenza, un tempo occupati dal *sodivo* e dal *sodivo con quercie*; quindi in territori inculti e abbandonati da lungo tempo. In alcune aree esso è scomparso, in considerazione dei mutati interessi agricoli ed inseriativi della zona.

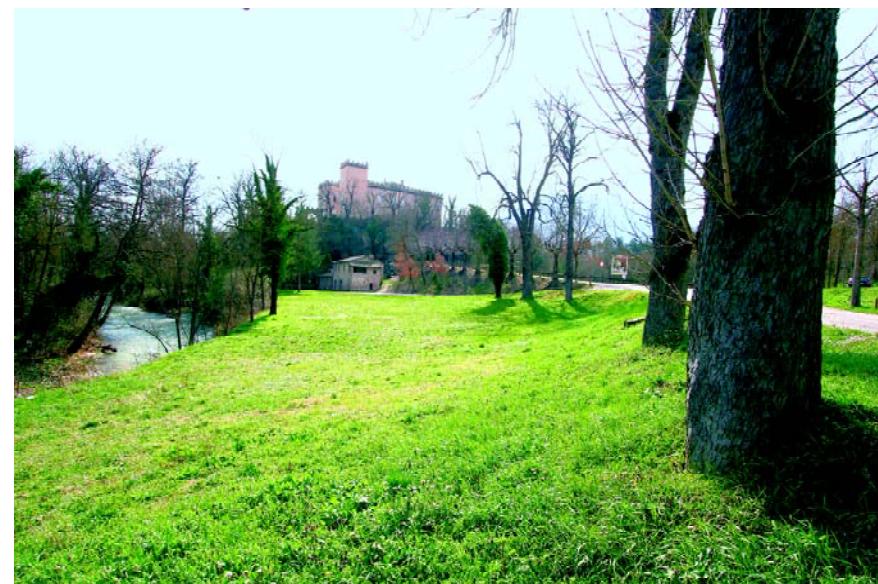


Fig. 6 - Prato-pascolo sottostante il Castello di Lanciano. Sulla sinistra un tratto del Fiume Potenza, sulla destra il viale alberato che sale al Castello.

Il querceto è rimasto inoltre lungo una stretta e pressoché continua fascia nella zona immediatamente retrostante il saliceto, poiché le colture, data l'acclività del terreno, non si sono spinte fin sulle rive del fiume.

Quanto al parco vero e proprio, sviluppato attorno al castello, sono scomparsi i cipressi, sostituiti dall'ippocastano e dal tasso. Si possono al contrario ammirare ancora siepi di bosso (*Buxus sempervirens*), per lo più rigogliosamente sviluppate ai piedi del castello.

Possiamo concludere che, mentre il paesaggio agrario si è modificato sensibilmente, semplificandosi e riducendosi sostanzialmente al solo seminativo, nudo ed in parte alberato, la vegetazione naturale, rappresentata dal bosco di querce, ha incrementato la sua copertura originale. Questo incremento va senz'altro messo in relazione con l'emergenza storica rappresentata dal castello e dalla proprietà ad esso annessa, che ha di fatto evitato una parcellizzazione del territorio in piccole proprietà, provvedendo perciò da un lato a proteggere il bosco e dall'altro a sviluppare l'agricoltura con forme sempre più specializzate in quelle zone dove già la pratica agricola era in atto. L'istituzione di una Fondazione ha accentuato tale tendenza, preoccupandosi di proteggere il bosco, sottraendolo alla ceduzione, e di sviluppare, nei terreni a vocazione agraria, nuove forme, anche sperimentali, di pratiche culturali.

Tuttavia la presenza, a ridosso dei confini del territorio della Fondazione, incentrato sull'imponente Castello di Lanciano, di cave per l'estrazione di ghiaia e di complessi industriali, realizzati in questi ultimi decenni senza alcun

rispetto del paesaggio vegetale e agrario, hanno provocato una modifica radicale dell'ambiente storico-naturale. Occorre pertanto realizzare una pianificazione che salvaguardi le attività economiche e tuteli i beni del patrimonio storico-naturale del territorio di Lanciano ritenuto un *unicum ambientale* non riscontrabile in nessun'altra località delle Marche.

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LES MARES TEMPORAIRES MÉDITERRANÉENNES: UN COMPLEXE D'HABITATS ÉLÉMENTAIRES. EXEMPLE DE LA CORSE

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ABSTRACT

In Corsica, Mediterranean temporary ponds (priority habitat 3170) are quite numerous at a low altitude. They are characterized by the alternation between a flooding phase and a dried up phase; they include many groups, to be classified into several syntaxonomic units: *Charion vulgaris* (*Charettalia hispidae*, *Charetea fragilis*) - *Ranunculion aquatilis* (*Potametalia pectinati*, *Potametea pectinati*) - *Littorellion uniflorae*, *Elodochalinion-Sparganion*, *Elocharition acicularis* (*Littorelletalia uniflorae*, *Littorelletea uniflorae*) - *Isoëtion durieui*, *Cicendion filiformis*, *Agrostion pourretii* (*Isoëtetalia durieui*, *Isoëto durieui-Juncetea bufonii*) - *Verbenion supinæ* (*Nanocyperetalia flavescentis*, *Isoëto durieui-Juncetea bufonii*).

Each group corresponding to an elementary habitat, temporary ponds are therefore complexes of habitats.

KEYWORDS: temporary ponds, Corsica, elementary habitat, priority habitat.

INTRODUCTION

Les mares temporaires "méditerranéennes" sont des écosystèmes occupant, dans la région méditerranéenne, des biotopes présentant, en cours d'année, une alternance d'inondation et d'assèchement. Il s'agit de dépressions endoréiques, de superficie et de profondeur très variables, inondées de la fin de l'automne à la fin du printemps par de l'eau douce oligotrophe (parfois mérotrophe) puis s'asséchant très fortement. Ces biotopes, présentant des espèces rares, ont attiré, depuis longtemps, l'attention des botanistes et phytosociologues (BRAUN-BLANQUET, 1936; MALCUIT, 1962; QUÉZEL et ZEVACO, 1964; BARBERO, 1965, 1967). Plusieurs taxons inféodés à ce biotope ont été inclus dans le Livre Rouge de la flore menacée de France (OLIVIERETAL., 1995) tandis qu'au niveau européen, les "mares temporaires méditerranéennes" sont considérées comme un habitat prioritaire (Code

Natura 2000: 3170) et menacé (GRILLAS et al., 2004).

La Corse montre un assez grand nombre de telles mares, d'origine variée. Leur végétation a fait l'objet de plusieurs études récentes (LORENZONI et PARADIS, 1997, 1998, 2000; PARADIS et al., 2002, 2008, 2009; PARADIS et POZZO DI BORGO, 2005), en suivant la méthodologie sigmatiste et en attribuant, pour définir les groupements et associations, une grande importance à la phytomasse des espèces, comme cela est recommandé par GÉHU (2000).

Cet article, en hommage au Professeur Jean-Marie Géhu, présente l'inclusion syntaxonomique des principaux groupements végétaux des mares temporaires corses, en tenant compte des particularités hydrologiques du biotope.

La nomenclature des taxons suit JEANMONOD et GAMISANS (2007).

PRÉSENTATION DES MARES TEMPORAIRES DE LA CORSE (PARADIS ET POZZO DI BORGO, 2007)

ORIGINE DES MARES TEMPORAIRES DE LA CORSE

La plupart des mares temporaires de la Corse ont une origine naturelle:

- mares situées sur d'anciennes plates-formes littorales d'abrasion, formées lors des divers hauts niveaux marins quaternaires (OTTMANN, 1958), contemporains des phases interglaciaires et situées entre 3-5 et 10 m environ au-dessus du niveau marin actuel (mares de la côte sud-occidentale et de la pointe du Cap Corse);
- mares localisées dans des dépressions d'origine tectonique, de nombreuses failles accidentant le socle granitique du sud de la Corse (mares de la Réserve naturelle des Tre Padule de Suartone, comprises entre 100 et 110 m d'altitude; mares du massif de Frasselli situées à des altitudes de 220, 200 et 130 mètres),
- mares de dépressions résultant d'une altération différentielle de septas granodioritiques au sein d'un monzogranite (mares temporaires des bergeries de

Padulaccia);

- mares des dépressions karstiques (poljés) accidentant le plateau calcaire de Bonifacio (mares de Padulu et de Musella);
- mares de dépressions au sein de terrasses alluvionnaires fluviatiles (mares des environs de Porto-Vecchio);
- mares cupulaires, très peu profondes, localisées dans des cavités de rochers granitiques (mares très peu nombreuses en Corse).

Quelques mares résultent d'activités humaines:

- mares éphémères dans des carrières d'extraction de roches granitiques;
- abreuvoirs créés en barrant des talwegs ou en creusant le lit mineur dans les basses vallées;
- trous formés par les tirs d'obus et de mortiers, lors de manœuvres militaires (cas de plusieurs petites mares du massif de Frasselli, au nord de Bonifacio).

PRINCIPALES MARES TEMPORAIRES DE LA CORSE (FIG. 1)

En 2008, il a été dénombré en Corse plus de 60 mares temporaires. Dans ce dénombrement, ne sont comprises ni les mares cupulaires, ni les très petites dépressions temporairement humides, visibles au sein des maquis et au bas des crêtes rocheuses du Cap Corse.

Sur la figure 1 ne sont représentées que les mares temporaires d'une superficie assez grande. On remarque que le plus grand nombre de mares temporaires se situe dans le sud de l'île, mais quelques unes sont aussi présentes à la pointe du Cap Corse et au nord-ouest, dans la région nommée Agriate.

CONTRAINTE DU BIOTOPE ET PERTURBATIONS SUBIES

Les végétaux peuplant les mares temporaires sont adaptés aux contraintes provoquées par les deux phases de cet écosystème: phase d'inondation et phase de forte sécheresse.

TEMPÉRATURES - En hiver et au début de printemps, les températures de l'eau

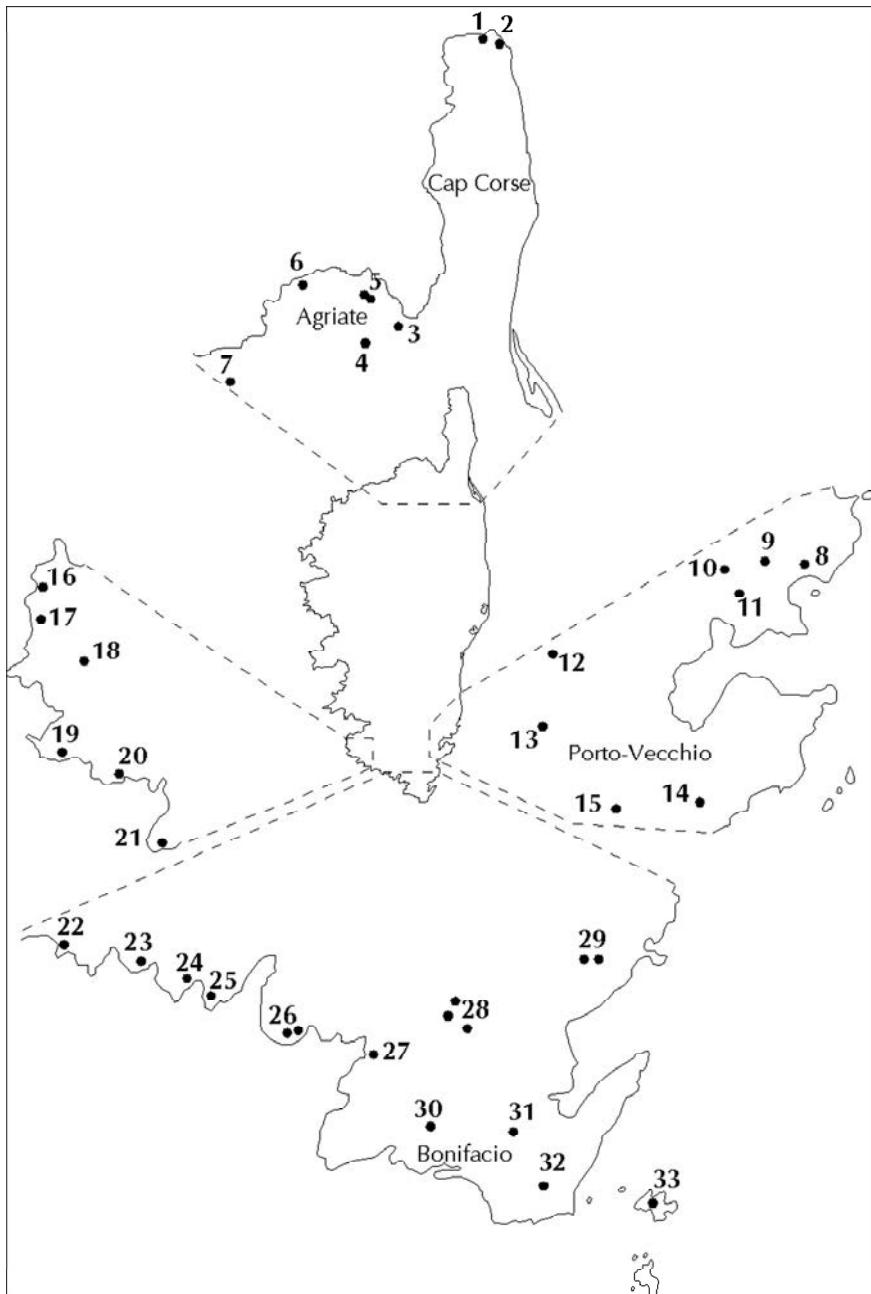


Fig. 1 - Carte schématique localisant les principales mares temporaires de la Corse.
Cap Corse: 1. Barcaggio; 2. Capandola (3 mares). Agriate: 3. champ de tir de Casta; 4. Capu Castincu; 5. Grottone et Chiuvina; 6. Taglia Carne; 7. Speloncato. Environs de Porto-Vecchio: 8. Arasu (2); 9. Mura dell'Unda; 10. Sant'Antonaccio; 11. Piobba; 12. Alzu di Gallina; 13. Muratello; 14. Padulellu; 15. Pietralba. Littoral du sud-ouest: 16. Canusellu; 17. Salina; 18. Padulaccia (6 mares); 19. Senetosa; 20. Cala di Barcaju; 21. Capu di Zivia. Sud de la Corse: 22. Tour d'Olmeto; 23. Arbitru; 24. Chevanu; 25. Capineru; 26. Punta di Ventilegne (2 mares); 27. Est du golfe de Ventilegne; 28. massif de Frasselli (12 mares); 29. Réserve naturelle des Tre Padule de Suartone (5 mares et ruisseaux temporaires); 30. Padulu et Ouest de Cavallo Morto; 31. Musella; 32. mares A et B sur le granite de Bonifacio; 33. île Cavallo.

sont basses et ne sont pas favorables à une croissance rapide. Cependant, plusieurs espèces (*Ranunculus peltatus*, *R. ophioglossifolius*, *Illecebrum verticillatum*, *Littorella uniflora*, *Isoëtes velata*...) commencent à croître en hiver, sous l'eau.

OLIGOTROPHIE - La pauvreté de l'eau et du substrat empêche la croissance des espèces compétitrices nécessitant un milieu riche. L'oligotrophie diminue la concurrence et est aussi une des raisons

de la petite taille de la plupart des espèces de ce biotope.

SÉCHERESSE - En été les mares étant très fortement asséchées, seuls les végétaux vivaces capables de puiser l'eau à une certaine profondeur peuvent encore croître. Les autres ont leur cycle de vie adapté à la phase asséchée, passant l'été en vie ralenti, soit à l'état de graines (cas des thérophytes comme *Illecebrum verticillatum* ou *Ranunculus revelierei*), soit à l'état de bulbes ou de rhizomes

dormants (cas des géophytes comme *Littorella uniflora*, *Isoëtes velata* ou *Pilularia minuta*).

PERTURBATIONS - En Corse, le pacage extensif de bovins s'est produit sur beaucoup de sites, dès la fin du printemps et tout au long de l'été. Ce pacage est favorable au maintien des géophytes et thérophytes de petite taille, en empêchant la colonisation des bordures des mares par des espèces de taille plus haute (*Schoenus nigricans*, *Juncus acutus*, *Scirpoïdes holoschoenus*, *Myrtus communis*, *Erica scoparia*, *Arbutus unedo*, *Pistacia lentiscus*, *Oenanthe lachenalii*, *Agrostis stolonifera*...) ou en entretenant une végétation en mosaïque. Par contre, une trop forte densité d'animaux peut être nocive pour les espèces rares, en provoquant des écrasements des jeunes pieds et une eutrophisation du milieu. Actuellement, la quantité de bovins paissant extensivement sur les mares temporaires s'est très fortement réduite, ce qui risque de favoriser, à l'avenir, un embroussaillage. Mais les sangliers (*Sus crofa* s.l.), de plus en plus nombreux, retournent le substrat à la recherche de bulbes et de rhizomes et limitent cet embroussaillage. Malheureusement ils détruisent beaucoup de géophytes.

Une autre perturbation est le tassement du substrat dû à l'homme, par les passages et les stationnements de véhicules. Cet impact, qui dépend du nombre de véhicules par jour au cours de l'été, se traduit par des dénudations qui empêchent les embroussaillements, ce qui a un effet positif car pouvant favoriser les petits géophytes et les thérophytes. Mais là où la densité de véhicules est très élevée, le tassement et la dénudation sont très nettement néfastes pour la végétation.

CARACTÈRES ADAPTATIFS DES ESPÈCES DES MARES TEMPORAIRES

NANISME - Beaucoup d'espèces des mares temporaires sont des végétaux de petite taille, qu'il s'agisse de géophytes à bulbes (*Isoëtes velata*, *Littorella uniflora*) ou à rhizomes (*Pilularia minuta*) ou de thérophytes (*Lythrum borysthenicum*, *Solenopsis laurentia*...). Ce nanisme est interprété comme dû à la pauvreté minérale du substrat et de l'eau, à la durée de la phase inondée et à la faible profondeur du substrat.

DISSÉMINATION DES SEMENCES PAR LES OISEAUX - Lors de la phase inondée, les sites étant visités par des oiseaux, en particulier des migrateurs, il est admis que la plupart des espèces de ces bioto-

pes sont ornithochores.

FLUCTUATION DES POPULATIONS ET BANQUES DE GRAINES - La taille des populations fluctue d'une année à l'autre. Ainsi, les années très pluvieuses, les petits thérophytiques et géophytes ont de très importantes populations. C'est l'inverse les années très sèches. De telles fluctuations sont une des caractéristiques des biocénoses de cet écosystème. Elles sont liées à l'existence, dans le substrat, de banques de graines dormantes, graines dont la longévité paraît être très longue.

POLYMORPHISME DE L'APPAREIL VÉGÉTATIF - Le port de la plupart des espèces varie en fonction du degré d'inondation. Par exemple, dans une dépression très peu longtemps humectée, *Illecebrum verticillatum* est très petit (de 1 à 5 cm de long) et ses entre-noeuds sont très courts (de moins de 1 mm). Au contraire, en pleine eau, il présente une tige non ramifiée, traversant tout le plan d'eau, à entre-noeuds très longs (de plus de 15 cm et pouvant dépasser 1 m) et une importante ramifications à la surface du plan d'eau, émettant de nombreuses tiges secondaires, flottantes et florifères, de 10 à 20 cm de long et à entre-noeuds courts, de moins de 1 cm. Un polymorphisme du même type existe chez d'autres espèces: *Alopecurus bulbosus*, *Cynodon dactylon*, *Lotus angustissimus* subsp. *suaveolens*, *Polypogon subspathaceus*.

PRINCIPALES ESPÈCES VÉGÉTALES DES MARES TEMPORAIRES DE LA CORSE (PN: espèce protégée au niveau national français; PR: espèce protégée au niveau régional corse):

Agrostis pourretii (Poaceae), *Alopecurus bulbosus* (Poaceae), *Anagallis arvensis* subsp. *parviflora* (Primulaceae), *Antinoria insularis* (Poaceae, PN), *Cicendia filiformis* (Gentianaceae), *Crassula vaillantii* (Crassulaceae), *Baldellia ranunculoides* (Alismataceae), *Callitricha brutia* (Callitrichaceae), *Elatine brochonii* (Elatinaceae, PN), *Elatine hydropiper* (Elatinaceae), *Elatine macropoda* (Elatinaceae), *Eleocharis acicularis* (Cyperaceae), *Eleocharis acicularis* (Cyperaceae), *Eleocharis multicaulis* (Cyperaceae), *Eleocharis palustris* (Cyperaceae), *Eleocharis uniglumis* (Cyperaceae), *Eryngium pusillum* (Apiaceae, PN), *Exaculum pusillum* (Gentianaceae), *Helosciadium crassipes* (Apiaceae), *Illecebrum verticillatum* (Caryophyllaceae), *Isoëtes durieu* (Isoëtaceae, PN), *Isoëtes histrix* (Isoëtaceae, PN), *Isoëtes velata* (Isoëtaceae, PN), *Juncus heterophyllus* (Juncaceae),

Juncus pygmaeus (Juncaceae), *Kickxia cirrhosa* (Caryophyllaceae, PN), *Kickxia commutata* (Caryophyllaceae, PN), *Littorella uniflora* (Plantaginaceae, PN), *Lotus angustissimus* subsp. *suaveolens* (Fabaceae), *Lotus conimbricensis* (Fabaceae), *Lythrum borysthenicum* (Lythraceae), *Lythrum hyssopifolium* (Lythraceae), *Lythrum juncinum* (Lythraceae), *Molinieriella minuta* (Poaceae, PN), *Mentha pulegium* (Lamiaceae), *Myosotis sicula* (Boraginaceae), *Myriophyllum alterniflorum* (Haloragaceae), *Narcissus serotinus* (Amaryllidaceae), *Oenanthe globulosa* (Apiaceae), *Pilularia minuta* (Marsileaceae, PN), *Plantago lanceolata* var. *timbali* (Plantaginaceae), *Polypogon maritimus* (Poaceae), *Polypogon subspathaceus* (Poaceae), *Prospero corsicum* (Liliaceae), *Pulicaria sicula* (Asteraceae), *Pulicaria vulgaris* (Asteraceae, PN), *Radiola linoides* (Linaceae), *Ranunculus ophioglossifolius* (Ranunculaceae, PN), *Ranunculus peltatus* (Ranunculaceae), *Ranunculus revelierei* (Ranunculaceae, PN), *Romulea revelierei* (Iridaceae, PR), *Schoenus nigricans* (Cyperaceae), *Solenopsis laurentia* (Campanulaceae), *Tolypella glomerata* (Charophytes), *Trifolium michelianum* (Fabaceae), *Triglochin bulbosa* subsp. *laxiflora* (Juncaginaceae, PN).

GROUPEMENTS VÉGÉTAUX DES MARES TEMPORAIRES

SUCCESSION CYCLIQUE DES GROUPEMENTS VÉGÉTAUX

Chaque mare temporaire est au cours d'une année, d'abord un plan d'eau (phase inondée) puis un biotope à sec. Au début de la phase d'assèchement, le substrat est très imbibé d'eau, puis devient de plus en plus sec. Aussi, au même endroit, se succèdent quatre types de groupements végétaux, très différents (CHEVASSUT, 1956; CHEVASSUT et QUÉZEL, 1956): groupements hydrophytiques, groupements hygrophytiques, groupements méso-hydrophytiques et groupements estivaux colonisant le substrat très asséché.

GROUPEMENTS HYDROPHYTIQUES, À ESPÈCES FLOTTANTES, CARACTÉRISANT LA PHASE D'INONDATION

Bien développés à la fin de l'hiver et dans la première partie du printemps, quand les mares sont totalement inondées, ces groupements appartiennent à deux classes phytosociologiques.

Chareta fragilis Fukarek ex Krausch 1964 (Herbiers enracinés de charophytes, pionniers des eaux calmes, douces à saumâtres, claires, oligotrophes à méso-eutrophes, formant des communautés pauci à monospécifiques).

Chareta hispidae Sauer ex Krausch 1964 (Communautés thérophytiques de characées).

Charion vulgaris (Krause ex Krause et Lang 1977) Krause 1981 (Communautés thérophytiques et éphémères des characées des eaux temporaires ou peu profondes).

Peuplement de *Tolypella glomerata*, très bien représenté en Corse quand l'inondation se produit dès la fin novembre (SOULIÉ-MÄRCHE, 2004).

Potametea pectinati Klika in Klika et Novák 1941 (Communautés macrophytiques, vivaces, généralement enracinées, des eaux douces ou faiblement subsaumâtres, oligomésotrophes à eutrophes).

Potametalia pectinati Koch 1926, *Ranunculion aquatilis* Passarge 1964 (Communautés d'hydrophytes de morphotypes batrachide et/ou myriophyllide, des eaux douces oligotrophes et méso-eutrophes, peu profondes et calmes).

Les associations et groupements (grt) suivants ont été mis en évidence:

- *Apietetum crassipedis* Paradis et Pozzo di Borgo 2005;
- grt à *Helosciadium crassipes*, *Ranunculus ophioglossifolius* et *Ranunculus peltatus*;

- *Myriophylletum alterniflori* Lemée 1937 em. Siss. 1943 *apietosum crassipedis* Paradis et Pozzo di Borgo 2005;

- grt à *Illecebrum verticillatum* forme flottante, grt à *Illecebrum verticillatum* et *Helosciadium crassipes*, grt à *Lotus angustissimus* subsp. *suaveolens* et *Galium elongatum*, peuplement de *Polypogon subspathaceus* à tiges flottantes, peuplement de *Lotus angustissimus* subsp. *suaveolens* à tiges flottantes.

GROUPEMENTS HYGROPHYTIQUES, À ESPÈCES AMPHIBIES, GÉOPHYTIQUES ET THÉROPHYTIQUES

Ces groupements hydrophiles, où dominent des géophytes nains, sont bien développés quand les mares sont moins inondées ou viennent de s'assécher, mais dont le substrat est très engorgé. Cela se produit le plus souvent dans la deuxième partie du printemps. De tels groupements appartiennent aux *Littorelletea uniflorae*.

Littorelletea uniflorae Braun-Blan-

quet et Tüxen ex Westhoff, Dijk et Passchier 1946 (Classe holactique, des végétations vivaces, rases, amphibiennes, pionnières des bordures de plans d'eau, oligotrophes à mésotrophes, stagnantes ou à cours très lents).

Littorellatelia uniflorae Koch 1926, *Littorellion uniflorae* Koch 1926 (Pelouses rases, amphibiennes, des bordures de lacs et de mares temporaires oligotrophes).

Littorella uniflora est présente dans une dizaine de mares du sud de la Corse. Une autre espèce caractéristique est *Isoëtes velata*, présent dans la plupart des mares temporaires corses.

Les associations et groupements (grt) suivants ont été mis en évidence:

- *Littorello uniflorae-Isoëtetum velatae* Paradis et Pozzo di Borgo 2005;

- grt à *Isoëtes velata*, grt à *Littorella uniflora*, grt à *Helosciadium crassipes*, *Isoëtes velata* et *Eleocharis palustris*, grt à *Helosciadium crassipes* et *Isoëtes velata*, grt mixte à *Eleocharis palustris*, *Helosciadium crassipes* et *Isoëtes velata*, grt mixte à *Cyperus longus*, *Helosciadium crassipes* et *Isoëtes velata*, grt à *Ranunculus ophioglossifolius* et *Isoëtes velata*.

Elodo palustris-Sparganion Braun-Blanquet et Tüxen ex Oberdorfer 1957 (Communautés des grèves sableuses ou tourbeuses d'étangs ou de zones humides oligotrophes à mésotrophes).

Baldellia ranunculoides et *Juncus heterophyllus* sont des caractéristiques de cette alliance et sont des espèces présentes dans de nombreuses mares temporaires corses.

Deux unités ont été mises en évidence:

- *Eleocharo palustris-Juncetum heterophylli* Paradis et Pozzo di Borgo 2005;
- groupement à *Eleocharis multicaulis* et *Littorella uniflora*.

Eleocharition acicularis Pietsch 1967 (Communautés amphibiennes des substrats limoneux ou argilo-limoneux, subissant des alternances d'inondation et d'assèchement).

En Corse, les groupements à *Eleocharis acicularis* ne sont connus que de deux mares temporaires, localisées sur le massif de Frasselli (PARADIS *et al.*, 2009).

GROUPEMENTS MÉSO-HYDROPHILES SURTOUT THÉROPHYTIQUES, SE DÉVELOPPANT DANS LA DEUXIÈME PARTIE DU PRINTEMPS, LORSQUE LE SUBSTRAT S'ASSÈCHE

Ces groupements se localisent:

- les années très pluvieuses, en bordure

des mares temporaires, c'est à dire à des niveaux topographiques moyen à supérieur, mais qui n'ont pas été recouverts par une forte épaisseur d'eau;

- les années où, par suite d'une faible pluviométrie hivernale, la phase d'inondation a été de courte durée, au sein même des mares asséchées.

Les principales espèces constitutives sont *Isoëtes hystrix*, *I. durieui*, *Myosotis sicula*, *Ranunculus revelierei* et *Cicendia filiformis*.

Isoëto durieui-Juncetea bufonii Braun-Blanquet et Tüxen ex Westhoff, Dijk et Passchier 1946 (Communautés riches en annuelles, hygrophiles à mésohygrophiles, des sols exondés ou humides, oligotrophes à méso-eutrophes).

Isoëtetalia durieui Braun-Blanquet 1936 (Communautés amphibiennes et hygrophiles, méditerranéennes et thermoméditerranéennes, sur des sols oligotrophes).

Isoëtion durieui Braun-Blanquet 1935, synonyme de *Isoëtion* Braun-Blanquet 1935, comprenant:

- groupements de bordure à *Isoëtes hystrix* et à *I. durieui*, sur un niveau topographique moyen;

- *Solenopsio laurentiae-Lythretum borysthениci* Paradis et Pozzo di Borgo 2005;

- groupement fini-printanier à *Lythrum borysthenum*.

Cicendion filiformis (Rivas Goday *in* Rivas Goday et Borja 1961) Braun-Blanquet 1967 (Communautés mésohygrophiles des niveaux topographiques moyen à supérieur).

De nombreuses unités ont été mises en évidence:

- *Bellido annuae-Cicendietum filiformis* de Foucault 1988, comprenant plusieurs sous-associations (*cicendietosum filiformis*, *plantaginetosum weldenii*, *scirpetosum cernui*, *juncetosum pygmaei*, *polypogonetosum subspathacei*, *solenopsietosum laurentiae*) (PARADIS et POZZO DI BORGO, 2005);

- *Junco pygmaei-Ranunculetum revelierei* Paradis et Pozzo di Borgo 2005;

- *Isoëto histicris-Radioletum linoidis* Chevassut et Quézel 1956 *anagallidetosum parviflorae* Paradis et Pozzo di Borgo 2005;

- groupement mixte à *Mentha pulegium* et thérophytes du *Cicendion*.

Agrostion pourretii Rivas-Godoy 1958 (Pelouses denses dominées par la graminée *Agrostis pourretii*, à son optimum de développement dans le dernier tiers du printemps, quand le substrat vient de s'assécher).

Dans les mares temporaires du sud de la Corse, ont été observés les groupements (grt) suivants:

- grt à *Agrostis pourretii*, grt à *Agrostis pourretii* et *Polypogon maritimus*, grt à

Agrostis pourretii et *Lotus angustissimus* subsp. *suaveolens*, grt à *Agrostis pourretii* et *Cynodon dactylon* (PARADIS *et al.*, 2002, 2008).

VÉGÉTATION ESTIVALE SUR LE SUBSTRAT TRÈS ASSÉCHÉ

À la fin du printemps et au cours de l'été, sur le substrat très sec du fond des mares temporaires, croissent quelques thérophytes (*Exaculum pusillum*, *Pulicaria sicula*) et quelques vivaces (*Mentha pulegium*, *Cynodon dactylon*).

A la fin de l'été et au début de l'automne, sur le substrat asséché de plusieurs mares corses croissent *Narcissus serotinus* et, sur de très rares sites, *Heliotropium supinum*, végétal habituellement eutrophe et qui, sur le substrat oligotrophe des mares temporaires à sec, est minuscule.

Isoëto durieui-Juncetea bufonii Braun-Blanquet et Tüxen ex Westhoff, Dijk et Passchier 1946.

Nanocyperetalia flavescens Klika 1935.

Alliance à préciser.

Menthopulegii-Exaculetum pusilli Paradis et Pozzo di Borgo 2005.

Menthopulegii-Pulicarietum siculae Paradis et Pozzo di Borgo 2005.

? *Verbenion supinae* Slavnic 1951.

Peuplement d'*Heliotropium supinum*.

CONCLUSION: IMPORTANCE DE L'ALTERNANCE DE PHASES INONDÉE ET ASSÉCHÉE

L'alternance de périodes d'inondation et d'assèchement est la caractéristique principale des mares temporaires méditerranéennes. Les variations de la hauteur d'eau et de la durée de la phase d'inondation conditionnent la structure phytosociologique (composition floristique, densité et taille des espèces, phénologie) des groupements des quatre types de végétation, décrits ci-dessus.

Le début de la période d'assèchement, coïncidant avec l'élévation de la température printanière, provoque, au même endroit, la coexistence (ou "superposition") de trois types d'espèces appartenant à des groupements différents et qui sont donc à des stades phénologiques différents: 1) espèces en fin de cycle (phase de sénescence), 2) espèces en pleine maturité et 3) espèces en début de cycle (phase de jeunesse).

Cette coexistence (ou superposition) d'espèces paraît être une des raisons des nombreuses divergences dans l'interprétation phytosociologique de

plusieurs groupements de ces biotopes (RIVAS GODAY, 1970; FOUCAULT, 1988; BRULLO et MINISSALE, 1998; PARADIS *et al.*, 2002; RIVAS-MARTÍNEZ *et al.*, 2002; BARDAT *et al.*, 2004).

GROUPEMENTS CORRESPONDANT À UNE ZONATION

La plupart des mares temporaires comprennent des ceintures de végétation, liées à des gradients de profondeur et de contenu hydrique du substrat. Ainsi, les trois mares de la Réserve naturelle des Tre Padule de Suartone montrent de l'extérieur vers le centre (LORENZONI et PARADIS, 2000):

- une ceinture de maquis, principalement à *Juniperus phoenicea* subsp. *turbinata*, *Myrtus communis* et *Erica scoparia*, classable dans le *Juniperion turbinatae* Rivas-Martínez 1975 corr. 1987 (*Pistacio lentisci-Rhamnetalia alaterni* Rivas-Martínez 1975, *Quercetea ilicis* Braun-Blanquet in Braun-Blanquet, Roussine et Nègre 1952) et isolant la mare temporaire du maquis qui colonise les rochers à l'extérieur de la mare;
- des ceintures de végétation vivace assez basse (à *Schoenus nigricans*, à *Eleocharis multicaulis* et à *E. uniglumis*), classables dans le *Molinio arundinaceae-Holoschoenion vulgaris* Braun-Blanquet ex Tchou 1948 (*Holoschoenetalia vulgaris* Braun-Blanquet ex Tchou 1948, *Molinio caeruleae-Juncetea acutiflori* Braun-Blanquet 1950) et en mosaïque, à la fin du printemps, avec des groupements du *Cicendion filiformis*;
- un peuplement d'hélophytes hydrophiles (*Eleocharis palustris*, *Glyceria fluitans*) classable dans les *Glycerio fluitantis-Nasturtietea officinalis* Géhu et Géhu-Franck 1987;
- les groupements de la mare temporaire proprement dite, qui subit en cours d'année l'alternance des communautés précédemment décrites (en 2.1).

CONCLUSIONS GÉNÉRALES

MENACES SUR LES MARES TEMPORAIRES MÉDITERRANÉENNES DE LA CORSE

Les mares temporaires sont des écosystèmes fragiles, pouvant totalement disparaître ou s'altérer.

DESTRUCTION PAR COMBLEMENT

De petites mares ont été détruites

par suite de comblements volontaires ou de drainage. Les Tre Paduli de Frasselli ont ainsi été plantées de vignes et drainées dans les années 1970. Après l'abandon de la vigne, l'habitat naturel s'est reconstitué, sauf aux endroits où des remblais avaient été réalisés.

Des sédimentations peuvent avoir lieu lorsque le maquis de la bordure des mares et les ceintures de végétation plus internes ont été détruits, à la suite d'incendies ou volontairement, lors de la construction de pistes par exemple. Le sol ainsi mis à nu est érodé par l'eau de pluie; les particules se déposent dans les bas-fonds et les comblent ou, tout au moins, recouvrent la végétation. La mare de Padulellu (Porto-Veccchio), présentant la seule station de l'espèce rarissime et protégée *Elatine brochonii* (LORENZONI et PARADIS, 1997), subit une telle sédimentation, qui met en danger sa biodiversité.

MODIFICATIONS DE L'ÉCOSYSTÈME

Une forte densité du bétail (vaches ou chevaux) apporte beaucoup d'excréments ce qui peut être une cause d'eutrophisation. Cela aurait pu se produire à la Padule Maggiore, mais depuis le classement en réserve naturelle, aucun bétail, à l'exception de quelques chèvres, ne fréquente le site.

On a précédemment signalé que les sangliers creusent fortement le substrat de toutes les mares, à la recherche de nourriture. Il est trop tôt pour se prononcer sur le bilan de ces creusements, mais ils paraissent dangereux pour les petits géophytes à bulbe.

De même, on a indiqué précédemment que les stationnements de véhicules trop nombreux peuvent être très nocifs pour les groupements végétaux. Ainsi, devant l'ampleur des dégâts causés par ces stationnements, la mare de Chevanu (au nord de Bonifacio) a fait l'objet en 2005 d'une mise en défens.

La destruction du maquis de bordure des mares et des ceintures de végétation plus internes (à *Schoenus nigricans*) rompt l'isolement des mares temporaires et les met en contact avec les chemins, les champs ou les espaces incendiés. Les mares sont alors exposées à une invasion par des végétaux possédant une bonne dispersion de leurs diaspores. En Corse, les végétaux envahisseurs les plus fréquents dans ces milieux sont *Dittrichia viscosa*, *D. graveolens*, *Cynodon dactylon*, *Sympyotrichum squamatum*, *Erigeron canadensis*, *E. bonariensis*, *E. sumatrensis*, *Heliotropium europaeum*, *Portulaca ole-*

racea et, dans quelques mares proches du littoral, *Cotula coronopifolia*. Des études ultérieures chercheront à mettre en évidence leur impact sur les groupements caractéristiques des mares temporaires.

REMARQUE SUR LA DÉFINITION DES MARES TEMPORAIRES MÉDITERRANÉENNES

Certains auteurs (BAGELLA *et al.*, 2007) proposent de ne retenir comme mares temporaires méditerranéennes que des dépressions superficielles, de quelques centimètres de profondeur et caractérisées par les groupements de l'*Isoëtion à Isoëtes durieui* et *I. hystrix*.

A notre avis, une telle conception traduit mal les caractéristiques de l'écosystème car:

- elle occulte le caractère "mare" de l'habitat 3170, les groupements à *Isoëtes durieui* et à *I. hystrix* se localisant à l'extérieur des mares temporaires proprement dites, dans la partie la moins longtemps inondée (PRELLI, 2001);
- elle ignore les groupements amphibiens des *Littorelletea uniflorae*.

De plus, de telles dépressions superficielles ne sont observables sur le terrain qu'en hiver et au début du printemps, quand la pluviométrie a été suffisante pour les inonder. En outre, il est impossible de les repérer sur les photographies aériennes, ce qui rend leur inventaire quasiment impossible.

De même, les Cahiers d'habitats Natura 2000 (2002) ne tiennent pas compte des communautés hydrophiles dans la définition des mares temporaires.

Dans notre conception, les mares temporaires ne peuvent pas être définies par des groupements appartenant à une seule alliance phytosociologique, comme l'*Isoëtion*. Ce sont des complexes d'habitats, car elles comprennent un grand nombre de groupements végétaux (cf. § 2.1), c'est à dire une multitude d'habitats élémentaires. Les groupements typiques de la phase d'inondation nécessitant une profondeur généralement supérieure à une vingtaine de centimètres, les dépressions de quelques centimètres de profondeur sont, à notre avis, à exclure des mares temporaires. Et à cause de l'alternance en cours d'année des phases d'inondation et de fort assèchement, les mares temporaires d'une profondeur d'au moins une vingtaine de centimètres se repèrent très bien sur le terrain aux diverses saisons. De plus, elles sont distinguables sur les photographies

aériennes qui, généralement, sont prises au mois de juin, c'est à dire au début de la phase asséchée. Aussi, "l'habitat" prioritaire 3170 nous paraît être facilement inventorable et pourra faire l'objet d'études comparatives entre les différentes régions du pourtour méditerranéen.

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ASSOCIAZIONI DELLA CLASSE LEMNETEA DELLA SELVA DI SAN ROSSORE (TOSCANA)

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ABSTRACT

In this contribution, the description and the occurrence of two associations: *Ricciocarpetum natantis* and *Ricciocarpetum fluitantis* are reported. The two association are located on the forest complex of San Rossore, to the mouth of the Arno river, in the Tuscany region. The two association could be localized on ditches, little channels and swamps depressions, that locally are called "lame" or "lagacce". Such two associations are found in the oligotrophic and phreatic waters, but the *Ricciocarpetum natantis* is more exigent respect to the *Ricciocarpetum fluitantis*.

KEYWORDS: *Ricciocarpetum natantis*, *Ricciocarpetum fluitantis*, San Rossore forest, Tuscany.

INTRODUZIONE

Scopo della presente nota è quello di segnalare le associazioni di idrofite natanti della classe *Lemnetea* presenti nella Selva di San Rossore (Toscana).

La Selva di San Rossore si estende in un'area pianeggiante di circa 5.000 ha situata fra i fiumi Arno e Serchio; tale zona è formata da un sistema di dune risalenti al quaternario, alle quali si alternano aree paludose, corsi d'acqua naturali e fossi artificiali.

La vegetazione forestale è formata dalle seguenti associazioni: *Viburno-Quercetum ilicis* (Braun-Blanquet 1936) Rivas Martínez 1975, presente sul "tombolo", che è la duna lungo l'attuale linea di costa del mare; *Hydrocotylo-Alnetum glutinosae* Gellini, Pedrotti e Venanzoni 1986, sviluppata nelle depressioni interdunali; *Fraxino-Quercetum roboris* Gellini, Pedrotti e Venanzoni 1986, sviluppata nella parte pianeggiante della Selva di San Rossore; *Carici remota-Fraxinetum oxycarpeae* Pedrotti (1970) 1992, nelle depressioni innondate che si trovano all'interno dell'associazione precedente; *Carici elatae-Fraxinetum oxycarpeae* Tomei et al. 2004, in depressioni più profonde e quindi con maggior ristagno di acqua rispetto a

quelle dove è sviluppata l'associazione precedente; *Populetum albae* Braun-Blanquet 1931, lungo i corsi d'acqua (GELLINI et al., 1986; TOMEI et al., 2004).

I boschi sono alternati da aree palustri con associazioni igrofile erbacee tra le quali le seguenti: *Schoeno-Erianthetum* Pignatti 1953, *Phragmitetum australis* (Gams 1922) Schmale 1939, *Eleocharitetum palustris* Schennikov 1919, *Caricetum elatae* Koch 1926, *Juncetum acuti* Molinier et Tallon 1970 (TOMEI et al., 2004).

LE IDROFITE NATANTI DI SAN ROSSORE

Negli ambienti umidi della Selva di San Rossore (canali, fossi, depressioni acquitrinose denominate "lame" o "lagacce", paludi, depressioni interdunali) sono presenti le seguenti specie di Idrofite natanti.

CORMOFITE

Azolla caroliniana Willd., San Rossore, 10 giugno 1984, non segnalata in precedenza a San Rossore; presente anche nella Macchia Lucchese e nel vicino Lago di Massaciuccoli (MONTELUCCI, 1964; TOMEI e GUAZZI, 1995);

Lemnaminor L., segnalata da CORTI (1955); nota anche per Viareggio, per la Macchia Lucchese e per il Lago di Massaciuccoli (MONTELUCCI, 1964; ARRIGONI, 1990; TOMEI e GUAZZI, 1995);

Lemna gibba L., segnalata da CORTI (1955); nota anche per la Macchia Lucchese e per il Lago di Massaciuccoli (MONTELUCCI, 1964; TOMEI e GUAZZI, 1995);

Lemna trisulca L., comune in varie località della Selva, 10 giugno 1984, non segnalata in precedenza a San Rossore; presente anche nella Macchia Lucchese e nel vicino Lago di Massaciuccoli (MONTELUCCI, 1964; TOMEI e GUAZZI, 1995);

Spirodela polyrhiza (L.) Schleid, segnalata da CORTI (1955); nota anche per la Macchia Lucchese e per il Lago di Massaciuccoli (MONTELUCCI, 1964; ARRIGONI, 1990; TOMEI e GUAZZI, 1995);

RIGONI, 1990; TOMEI e GUAZZI, 1995);

Wolffia arrhiza, presente in una lagaccia del bosco del Palazzetto, 10 giugno 1984, non segnalata in precedenza per San Rossore.

BRIOFITE

Chiloscyphus polyanthus Corda (cfr.), segnalata da CORTI (1955) al Palazzetto;

Riccia fluitans L., vasche del Palazzetto; in un canale fra il Viale del Gombo e le dune, alla sinistra entrando, lg. Carmela Cortini, 10 giugno 1984 (CAME), specie di nuova segnalazione per San Rossore. Tale specie è stata segnalata in precedenza per Porta (Montignoso) e per Forte dei Marmi e Fiumetto, località situate poco a nord di Viareggio (SANTARELLI, 1958; CORTINI PEDROTTI et al., 1991); in Italia è distribuita dalle regioni del nord fino alla Calabria, mentre manca in Sicilia e Sardegna (ALEFFI et al., 2008).

Ricciocarpos natans (L.) Corda, vasca ad *Hottonia palustris* al Paludetto, lg. Carmela Cortini, 10 giugno 1984 (CAME), specie di nuova segnalazione per San Rossore e conferma per l'intera regione Toscana; in precedenza tale specie in Toscana era stata segnalata soltanto per l'Orto botanico di Siena da A. Tassi nel 1901, ma non per un ambiente naturale (ALEFFI et al., 2008). In Italia *Ricciocarpos natans* è distribuito dalle regioni del nord fino all'Abruzzo (ALEFFI et al., 2008).

LE ASSOCIAZIONI DELLA CLASSE LEMNETEA

Nella Selva di San Rossore è stata rilevata la presenza delle seguenti associazioni della classe *Lemnetea*, qui tratte secondo il relativo inquadramento sintassonomico:

Lemnetea de Bolòs e Masclans 1955

Lemnetalia minoris de Bolòs e Masclans 1955

Lemnion minoris de Bolòs e Masclans 1955

Ricciocarpetum natantis Tüxen 1974

Tab. 1 - *Ricciocarpetum natantis* (ril. 1-8) e *Riccieturn fluitantis* (ril. 9-17).

Numero del rilievo	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Superficie del ril. (cmq)	800	800	800	800	800	900	900	900	400	400	800	800	800	800	400	1000	1000
Grado di ricoprimento %	60	60	90	80	100	100	90	80	80	60	100	95	70	50	95	100	100
Numero di specie per ril.	2	4	3	4	3	3	4	4	3	3	3	2	2	3	3	3	3
Ricciocarpos natans	3.3	1.1	4.4	3.3	5.5	5.5	4.4	3.3
Riccia fluitans	.	+	+	+	+	+	+	+	3.3	1.1	1.1	2.2	2.2	+2	+	1.1	+
Lemna minor	.	2.2	.	+	1.1	+	2.2	3.3	1.1	2.2	3.3	4.4	3.3
Lemna trisulca	+2	+	+	+	+	+	+	+	2.3	.	.	.	+2
Azolla caroliniana	+	1.2	+	3.4	.	.	.	2.2	.	.	.
Wollfia arrhiza	1.1	2.2	.

Riccieturn fluitantis Slavnic 1956

Nella Selva di San Rossore sono dunque presenti le due associazioni *Ricciocarpetum natantis* e *Riccieturn fluitantis*, ambedue di nuova segnalazione per tale località. Esse sono caratterizzate rispettivamente da *Ricciocarpos natans* e *Riccia fluitans*, cui si accompagnano poche altre specie (Tab. 1); da segnalare, in particolare, la presenza di *Wollfia arrhiza* in 2 rilievi di *Riccieturn fluitantis* eseguiti in una lagaccia del bosco del Palazzetto.

Nel *Ricciocarpetum natantis* sono state rinvenute da 2 a 4 specie, nel *Riccieturn fluitantis* da 2 a 3 specie. Queste associazioni sono sempre formate da un basso numero di specie, in quanto l'intera classe *Lemnetea* comprende soltanto 9-10 specie, fra specie caratteristiche delle diverse unità fitosociologiche e specie compagne.

Ambedue queste associazioni si sviluppano in acque oligotrofiche, nel caso di San Rossore si tratta prevalentemente di acque freatiche; considerando il gradiente dalle acque oligotrofiche a quelle eutrofiche, la prima associazione è il *Ricciocarpetum natantis*, alla quale segue il *Riccieturn fluitantis* e quindi le altre associazioni della classe *Lemnetea* caratterizzate dalle varie specie del genere *Lemna*.

Le due associazioni sono distribuite in tutta Europa, sempre in acque chiare di sorgenti e ruscelli da esse derivati, oppure acque freatiche come quelle che caratterizzano i boschi palustri, tra cui nella zona studiata l'*Hydrocotylo-Alnetum glutinosae*, ma anche il *Carici remotae-Alnetum glutinosae* e il *Carici elatae-Alnetum glutinosae*.

In base alle osservazioni di CORTI (1955), che segnala per il Fosso dell'Anguillara (San Rossore) *Lemna minor*, *Lemna gibba* e *Spirodela polyrhiza*, è facile presumere a San Rossore anche l'esistenza di altre associazioni della classe *Lemnetea*, che - tuttavia - nel 1984 non sono state osservate. Analoga considerazione vale per la Mac-

chia Lucchese, per la quale MONTELUCCI (1964) segnala *Lemna minor*, *Lemna trisulca*, *Lemna gibba*, *Spirodela polyrhiza* e *Salvinia natans* per i canali che intersecano una risaia a Massarosa, ove sicuramente formano una o più associazioni.

LOCALITÀ E DATA DEI RILIEVI

Tab. 1 - Selva di San Rossore, 10 giugno 1984.

BRIOFITE RACCOLTE DA CARMELA CORTINI NELLA SELVA PISANA DI S. ROSSORE

Viene qui riportato un elenco di Briofite raccolte da Carmela Cortini nella Selva di San Rossore il 10 giugno 1984; i campioni raccolti sono depositati nell'Erbario del Dipartimento di Botanica ed Ecologia dell'Università di Camerino (CAME). Questo elenco va ad aggiungersi a quello di CORTI (1955), rispetto al quale le specie segnate con * sono di nuova segnalazione per San Rossore.

- **Amblystegium riparium* (Hedw.) B.S.G.
- Anomodon viticulosus* (Hedw.) Hook et Taylor
- Calliergonella cuspidata* (Hedw.) Loeske
- **Drepanocladus aduncus* (Hedw.) Warnst., vasca ad *Hottonia palustris*, Paludetto
- Mnium hornum* Hedw., su un cespo di *Osmunda regalis*, Palazzetto
- **Neckera complanata* (Hedw.) Huebner
- **Riccia fluitans* L., vasche del Palazzetto; in un canale fra il Viale del Gombo e le dune, alla sinistra entrando
- **Ricciocarpos natans* (L.) Corda, vasca ad *Hottonia palustris*, Paludetto.

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NEOFITISMO E ASSOCIAZIONI VEGETALI

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ABSTRACT

This work examines the impact of Neophytes on plant associations of a given territory. In particular, it analyzes the presence and distribution in the Trentino-Alto Adige Region of two neophyte species (*Galinsoga parviflora* and *Galinsoga ciliata*) reported for the first time in 1920 and 1932 respectively. These species form the *Galinsogo-Portulacatum* and *Euphorbio-Galinsogetum ciliatae* associations, both of which grow in fields of potatoes and corn. The *Galinsogo-Portulacatum* association, which was the first to establish itself in Trentino-Alto Adige, has disappeared from some locations (such as the Val di Sole) because it has been progressively substituted by *Euphorbio-Galinsogetum ciliatae*, the development of which began a few decades later. Thus two neophyte associations have been substituted, a phenomenon that can be attributed to some biological and ecological characteristics of the two principal species, such as seed production, ease of seed distribution because of different pappus conformation, the different nitrophilous properties of the species, and substrate type.

KEYWORDS: Neophytism, *Galinsogo-Portulacatum*, *Euphorbio-Galinsogetum ciliatae*.

RIASSUNTO

Viene esaminata la presenza e la distribuzione nella Regione Trentino-Alto Adige di due specie di neofite (*Galinsoga parviflora* e *Galinsoga ciliata*) segnalate per la prima volta nel 1820 e nel 1932 rispettivamente. Tali specie formano le due associazioni *Galinsogo-Portulacatum* e *Euphorbio-Galinsogetum ciliatae*, ambedue sviluppate nei campi di patate e di mais. È stato osservato che il *Galinsogo-Portulacatum*, associazione insediata per prima nel Trentino-Alto Adige, è scomparso da alcune località (come la Val di Sole), in quanto è stato progressivamente sostituito dall'*Euphorbio-Galin-*

sogetum ciliatae, il cui sviluppo è iniziato alcuni decenni dopo. È quindi avvenuta la sostituzione di due associazioni di Neofite, fenomeno che si può attribuire ad alcune caratteristiche biologiche ed ecologiche delle due principali specie, come: produzione di semi, facilità di diffusione dei semi a causa della diversa conformazione del pappo, maggiore o minore nitrofilia delle due specie, tipo di substrato.

INTRODUZIONE

La presente nota ha lo scopo di esaminare l'impatto provocato sulle associazioni vegetali esistenti in un determinato territorio dall'introduzione e dalla successiva naturalizzazione di Neofite, fenomeno noto come Neofitosmo (FALIŃSKI, 1998b).

Le Neofite sono specie vegetali introdotte involontariamente dall'uomo dopo il 1500, anno di scoperta dell'America (GÉHU, 2006). Tali specie tendono ad espandere il loro areale geografico esponenzialmente, in quanto per un certo tempo non sono limitate da fattori ecologici come i fenomeni di competizione e le caratteristiche abiotiche e biotiche dell'ambiente (BROWN, 2003).

L'introduzione delle Neofite in nuovi areali produce effetti molto vasti sia sulla flora che sulla vegetazione. La proporzione fra le specie aliene e le specie autoctone è chiamata "livello di invasione" (CHYTRY *et al.*, 2009); tali Autori hanno realizzato una carta del "livello di invasione" dell'Europa, che nelle pianure e colline è superiore al 5%, come in tutta la pianura padana, mentre sulle catene montuose scende a meno dell'1%, come sulla catena delle Alpi e su quella dell'Appennino. Le specie alloctone, inoltre, producono un abbassamento del grado di naturalità della vegetazione, come è stato messo in evidenza per le due regioni Trentino-Alto Adige e Marche (MINGHETTI, 1999; BALLELLI e PEDROTTI, 2009), ove le Neofite sono oggi presenti in quasi tutti i tipi di vegetazione, sia erbacea che arbustiva ed arborea, ad esclusione del-

l'alta montagna.

Il tasso di Neofite presenti in un determinato territorio ha anche permesso di realizzare carte della "sinantropizzazione" della vegetazione, come la carta della Polonia di FALIŃSKI (1975 e 1998a) e del Trentino-Alto Adige di PEDROTTI e MINGHETTI (1997).

NEOFITE E VEGETAZIONE

Lo sviluppo e l'espansione delle Neofite nelle associazioni vegetali autoctone avviene secondo modalità diverse, individuate e descritte da FALIŃSKI (1998b), che ha messo in evidenza consecutive fasi di colonizzazione da parte delle specie aliene. Le Neofite provocano sempre modificazioni alla composizione floristica e alla struttura delle associazioni nelle quali si insiedano, sono cioè la causa di uno squilibrio biologico più o meno marcato, come: degenerazione delle associazioni vegetali per modifica della loro composizione floristica originaria, scomparsa di associazioni vegetali, formazione di nuove associazioni vegetali, "sinantropizzazione" della vegetazione, abbassamento del grado di naturalità della vegetazione.

Sulla base delle osservazioni eseguite nella Regione Trentino-Alto Adige, lo sviluppo e l'espansione delle Neofite avviene in prevalenza secondo le seguenti modalità:

- sviluppo di una o più specie di Neofite in determinate associazioni vegetali; a titolo di esempio viene citato il caso di *Parthenocissus quinquefolia* nelle ontanete appartenenti all'associazione *Stellario nemorum-Alnetum glutinosae* del Laghestel di Piné (PEDROTTI, 2004a);
- sviluppo di popolamenti monospecifici di una data specie in associazioni autoctone; è il caso di *Helianthus tuberosus* e *Solidago canadensis* nei molinieti dello *Junco-Molinietum* e negli arrenatereti del *Centaureo-Arrhenatheretum* in Valsugana (Trentino) (PEDROTTI, 2004b);
- sviluppo di una o più specie di Neofite al limite di altre associazioni vegetali, per esempio nardeti o arrenatereti, come

Tab. 1 - *Euphorbio-Galinsogetum ciliatae*.

	1	2	3	4	5	6	7	8	9	10	P
Numero del rilievo											
Superficie del ril. (mq)	10	8	20	10	9	8	10	20	20	10	r
Grado di ricoprimento %	95	90	90	100	100	90	100	100	95	95	e
Numero di specie per ril.	14	14	17	14	17	15	14	21	16	15	s
Galinsoga ciliata	3.3	3.3	3.3	3.3	4.4	1.1	4.4	2.2	3.3	3.3	10
Sp. caratt. All (<i>Spergulo-Oxalidion</i>) e Ord. (<i>Chenopodietalia albi</i>)											
Chenopodium album	1.1	2.2	1.1	1.1	1.1	1.1	1.1	+	1.1	+	10
Sonchus oleraceus	+	+	1.1	1.1	+	1.1	+	.	1.1	+	9
Capsella bursa-pastoris	+	+	.	.	+	+	+	+	+	+	8
Galinsoga parviflora	.	+	+	3.3	1.1	+	.	3.3	1.1	1.1	8
Setaria viridis	.	.	+	+	.	.	.	+	1.1	.	4
Amaranthus retroflexus	.	+	1.1	1.1	.	.	.	1.1	.	.	4
Lamium purpureum	+	+	.	+	.	.	3
Setaria glauca	.	.	+	+	.	.	.	+	.	.	3
Euphorbia helioscopia	.	.	+	.	+	.	.	+	.	.	3
Veronica persica	+	.	+	+	.	+	3
Solanum nigrum	+	+	.	.	2
Amaranthus silvestris	.	.	.	+	.	.	.	1.1	.	.	2
Portulaca oleracea	+	.	1.1	2
Panicum sanguinale	.	.	.	+	1
Geranium pusillum	+	1
Echinochloa crus-galli	+	1
Sp. caratt. Cl. (<i>Stellarietea mediae</i>)											
Stellaria media	+	1.1	+	.	1.1	+	1.1	+	.	+	8
Galeopsis tetrahit	2.2	1.1	.	+	1.1	.	1.1	+	.	1.1	7
Polygonum convolvulus	.	1.1	+	.	+	.	+	+	+	.	6
Polygonum aviculare	.	.	.	+	+	.	.	.	+	.	2
Matricaria chamomilla	.	+	1
Cirsium arvense	.	.	.	+	1
Viola tricolor	+	1
Anagallis arvensis var. coerulea	+	+	1
Sherardia arvensis	+	+	1
Specie compagne											
Convolvulus arvensis	+	+	2.2	+	.	2.2	+	1.1	+	1.1	9
Polygonum persicaria	+	1.1	.	+	1.1	+	1.1	+	+	1.1	9
Taraxacum officinale	+	.	+	+	+	+	+	.	.	.	6
Malva silvestris	.	+	+	.	+	+	+	.	.	.	5
Vicia cracca	+	.	+	.	.	+	3
Galium aparine	+	.	.	+	.	+	3
Equisetum arvense	.	+	+	.	.	+	.	.	+	.	2
Anchusa officinalis	.	.	+	.	.	+	.	.	+	.	2
Geranium rotundifolium	.	.	.	+	.	.	+	.	.	.	2
Mentha arvensis	+	.	.	.	+	.	2
Conyza canadensis	+	+	.	.	2
Urtica dioica	+	+	1
Artemisia vulgaris	.	.	+	.	.	+	1
Sisymbrium sophia	+	1
Rumex obtusifolius	+	1
Atriplex hastatus	+	1
Arenaria leptoclados	+	.	+	.	.	1
Oxalis corniculata	+	.	+	.	.	1
Lychnis alba	+	.	.	+	.	1
Erigeron annuus	+	.	+	.	.	1

è il caso di *Bromus inermis* in molte località del Trentino (PEDROTTI, 1987); nelle praterie delle Viotte del Monte Bondone, in particolare, la specie si addensa al bordo delle strade che attraversano le praterie (associazione *Scorzoneraria aristatae-Agrostetum tenuis*), formando un popolamento monospecifico denominato "Aggruppamento a *Bromus inermis*", che è stato anche cartografato sulla carta della vegetazione delle praterie in scala 1: 5.000 (PEDROTTI, 1996);

- sviluppo di una o più specie di Neofite in ambienti ruderali e nitrofili, lungo le strade, ecc., come *Senecio inaequidens*; - sviluppo di una o più specie di Neofite nelle colture agrarie, caso molto comune, con moltissimi esempi tra cui quelli di *Galinsoga parviflora* e di *G. ciliata*, di cui si parlerà più avanti; - sviluppo di una neofita in un'associazione vegetale preesistente, con neoformazione di una nuova associazione vegetale; è questo il caso della maggior parte delle associazioni infestanti nelle colture agrarie. Molto interessante è il caso dell'associazione *Juncetum macri* formata da *Juncus tenuis* (syn. *J. macer*), specie originaria dell'America del Nord ora comune in Trentino negli ambienti umidi, in particolare in zone calpestate di ambienti umidi e rive dei laghi, come il lago di Madrano e il Laghestel di Piné (PEDROTTI 1990, 2004a); in alcuni casi *Juncus tenuis* si è inserito in una precedente associazione dell'ordine *Plantagini-Prunelletalia* riferibile allo *Junco compressi-Trifolietum repens*, dando così luogo all'associazione *Juncetum macri* (PEDROTTI, 1995). *Juncus tenuis* è una specie tuttora in espansione in Trentino-Alto Adige; fino agli anni 1986-1991 non era ancora arrivata nella torbiera di Fiavé, ove è presente l'associazione *Junco compressi-Trifolietum repens* (CANULLO, PEDROTTI e VENANZONI, 1994).

IL CASO DI DUE SPECIE AMERICANE NELLA REGIONE TRENTO-ALTO ADIGE: *GALINSOGA PARVIFLORA* E *GALINSOGA CILIATA*

Galinsoga parviflora Cav. e *Galinsoga ciliata* (Rafin.) S.F. Blake [*Galinsoga quadriradiata* Ruiz. et Pavon] sono due Asteracee originarie dell'America del Sud che sono giunte nella Regione Trentino-Alto Adige in anni successivi nel corso del 1800 e del 1900.

In Trentino *Galinsoga parviflora* è stata segnalata per la prima volta in Valsugana, dove la pianta si era sviluppata in un orto di Ferdinando Paterno,

parroco a Tezze dal 1812 al 1852, da dove si diffuse nelle località circostanti (AMBROSI in HAUSMANN, 1851-1854; AMBROSI, 1857, 1864). In particolare, AMBROSI (1857) osserva che dopo il 1820 la specie, “emigrata dall’orto del rev. Sacerdote Paterno, si diffuse per la Valsugana, dove infesta ed ingombra i campi di Tezze, di Grigno, di Castelnovo, di Borgo, di Telve, ecc”. Ed inoltre aggiunge “Trovansi anco nei dintorni di Trento”.

Galinsoga ciliata è stata segnalata per la prima volta nella Regione Trentino-Alto Adige da Leo Treuenfels nel 1898 a Merano, secondo quanto riporta DALLA FIOR (1955a, 1955b); ma la prima segnalazione documentata è quella di BIASIONI (1932) a Trento. Nello stesso anno la specie era presente anche nell’orto della casa del prof. Giuseppe Dalla Fior, sita in via della Collina, e in uno dei cortili del castello del Buon Consiglio (DALLA FIOR, 1955b).

Oggi sia *Galinsoga parviflora* che *Galinsoga ciliata* sono diffuse in tutto il territorio regionale, prevalentemente come specie delle colture agricole e degli orti, ma anche in condizioni ruderali e nitrofile, ad esempio presso le case e lungo le strade dei paesi di montagna.

In America del sud, ove è autoctona, *Galinsoga parviflora* è stata rilevata con gradi di copertura compresi fra il 40 e il 60% nel “chaparral”, una formazione arbustiva di *Acacia macracantha* e *Prosopis laevigata* var. *andicola* delle valli mesotermiche della Bolivia (PEDROTTI et al., 1988).

LE ASSOCIAZIONI VEGETALIFORMATE DA *GALINSOGA PARVIFLORA* E *GALINSOGA CILIATA* NELLA REGIONE TRENTINO-ALTO ADIGE

Nel Trentino è stata segnalata l’associazione *Galinsogo-Portulacetum* Braun-Blanquet 1949 ex Pedrotti 1959, tipica delle colture estive di patata (*Solanum tuberosum*) e di mais (*Zea mays*), oltre che degli orti del piano montano, come la Val di Sole (PEDROTTI, 1959); tale associazione è stata osservata anche nelle colture di grano saraceno (*Fagopyrum esculentum*), ma in una forma impoverita rispetto a quella che si osserva nei campi di patate (PEDROTTI, 2005).

Galinsoga ciliata è, invece, la principale specie edificatrice dell’associazione *Euphorbio-Galinsogetum ciliatae* Passarge 1981, di cui vengono riportati alcuni rilievi nella Tab. 1, tutti provenienti dalla Val di Sole (Trentino); l’associazione è sviluppata negli orti presso le case. Tale associazione è

stata descritta per la Germania ed è segnalata anche per l’Austria nei campi di patate delle valli alpine (MUCINA et al., 1993).

Da notare che *Galinsoga ciliata* raggiunge sempre gradi di copertura molto elevati, ad eccezione di un rilievo, mentre *Galinsoga parviflora* partecipa con valori quasi sempre molto bassi, anche se in 2 rilievi si equivale a *Galinsoga ciliata* ed in uno la supera. Ne risulta che l’equilibrio fra le due specie non sembra essere ancora ben definito.

Nei rilievi della Tab. 1 non è stata mai rinvenuta *Euphorbia peplus*, specie diffusa in tutto il Trentino (BONAPACE, 1948) ed osservata anche in Val di Sole, ma non frequentemente. Presso una concimaia in Val di Rabbi, laterale della Val di Sole, è stato possibile effettuare un rilievo ove compare tale specie (Tab. 2); tale rilievo presenta una composizione floristica intermedia fra l’*Urtico urentis-Chenopodietum boni-henrici* e l’*Euphorbio-Galinsogetum ciliatae*, infatti si distingue dai rilievi della Tab. 1 per la presenza di specie tipicamente nitrofile come *Chenopodium bonus-henricus* e per l’ambiente nel quale si sviluppa.

Va rilevato che *Galinsoga ciliata* compare, peraltro, in altre associazioni di erbe infestanti, come risulta dalle analisi eseguite per la Cecoslovacchia da LOSOSOVA (2004), LOSOSOVA et al. (2006) e LOSOSOVA et GRULICH (2009), che la segnalano nelle seguenti alleanze: *Scleranthion annui*, *Oxalidion europeae*, *Caucalidion lappulae*, *Panico-Setarion*, *Veronico-Euphorbion*, *Eragrostion*; fra le alleanze elencate, prevale però nettamente nell’*Oxalidion europeae*, sinonimo di *Spergulo-Oxalidion*, l’alleanza alla quale viene attribuita l’associazione *Euphorbio-Galinsogetum ciliatae*.

La composizione floristica delle due associazioni *Galinsogo-Portulacetum* ed *Euphorbio-Galinsogetum ciliatae* è abbastanza diversa; nel *Galinsogo-Portulacetum* sono state trovate complessivamente 140 specie (PEDROTTI, 1959), mentre nell’*Euphorbio-Galinsogetum ciliatae* soltanto 46 specie (Tab. 1). Di conseguenza, anche il numero medio di specie per rilievo è molto differente nelle due associazioni, e precisamente 46 nella prima e soltanto 15,7 nella seconda. Le specie del *Galinsogo-Portulacetum* che mancano nell’*Euphorbio-Galinsogetum ciliatae* sono specie dell’alleanza *Panico-Setarion* (tra cui *Lamium amplexicaule*), dell’ordine *Chenopodiatalia albi* (tra cui *Erodium cicutarium* e *Fumaria offi-*

Tab. 2 - *Urtico urentis-Chenopodietum boni-henrici*.

Ril. n.	1
Superficie mq	6
N. specie per ril.	20
<i>Lamium album</i>	1.1
<i>Chenopodium bonus-henricus</i>	+
<i>Galinsoga ciliata</i>	3.3
<i>Urtica dioica</i>	1.2
<i>Galinsoga parviflora</i>	1.1
<i>Taraxacum officinale</i>	1.1
<i>Galeopsis tetrahit</i>	1.1
<i>Urtica urens</i>	+
<i>Sonchus asper</i>	+
<i>Geranium rotundifolium</i>	+
<i>Malva silvestris</i>	+
<i>Euphorbia peplus</i>	+
<i>Lychnis alba</i>	+
<i>Lamium purpureum</i>	+
<i>Galium aparine</i>	+
<i>Veronica persica</i>	+
<i>Sonchus oleraceus</i>	+
<i>Capsella bursa-pastoris</i>	+
<i>Euphorbia helioscopic</i>	+
<i>Chenopodium album</i>	+

cinalis) e della classe *Stellarietea mediae* (come *Myosotis arvensis* e *Linaria minor*). Fra le specie compagne, vanno segnalate *Silene cucubalus*, *Medicago lupulina* e *Trifolium repens*. Per contro, tutte le specie rinvenute nei rilievi di *Euphorbio-Galinsogetum ciliatae* sono presenti nel *Galinsogo-Portulacetum*, ad eccezione di *Galinsoga ciliata* e di poche specie sporadiche come *Sisymbrium sophia*. Questa differenza si può in parte spiegare con i due tipi di “habitat” occupati dalle due associazioni: campi di patate e di mais per il *Galinsogo-Portulacetum*, orti presso le case per l’*Euphorbio-Galinsogetum ciliatae*.

In base alle osservazioni eseguite nell'estate 2009, si può dire che in Val di Sole l'associazione *Galinsogo-Portulacetum* è praticamente scomparsa, in quanto oggi non si trovano più campi di patate e di grano saraceno ove l'associazione era sviluppata in passato.

Per contro, negli orti presso le case, ove in passato era pure sviluppata l'associazione *Galinsogo-Portulacetum*, essa è stata completamente sostituita dall'associazione *Euphorbio-Galinsogetum ciliatae*.

VARIAZIONI NELLA VEGETAZIONE INFESTANTE

Si fa qui riferimento alla vegeta-

Tab. 3 - Elenco di specie osservate nelle colture di patata da Francesco Ambrosi nel 1864.

Polygonum persicaria
Amaranthus retroflexus
Chenopodium album
Solanum nigrum
Setaria viridis
Digitaria sanguinalis
Panicum crus-galli
Bidens bipinnatus
Bidens tripartitus

zione infestante delle colture estive di patata e di mais.

AMBROSI (1864) riporta un elenco di piante che, prima dell'arrivo di *Galinsoga parviflora*, erano le abituali compagne delle colture di mais (Tab. 3); si tratta di specie cosmopolite o subcosmopolite (*Polygonum persicaria*, *Chenopodium album*, *Solanum nigrum*, *Setaria viridis*, *Digitaria sanguinalis* e *Panicum crus-galli*) e di due neofite (*Amaranthus retroflexus* e *Bidens bipinnatus*), a cui si aggiunge una specie eurasiatica (*Bidens tripartitus*). Queste specie formavano un'associazione di erbe infestanti oggi non più esistente, di cui sappiamo soltanto quello che ha scritto Francesco Ambrosi, associazione che potremo teoricamente denominare "*Polygonetum persicariae*"; esse sono tutte presenti nel *Galinsogo-Potentacum*, ad eccezione delle due specie di *Bidens*.

Con l'avvento di *Galinsoga parviflora*, si è formata verso la metà del 1800 l'associazione *Galinsogo-Potentacum*, la quale ora è scomparsa da molte località in quanto è venuto a mancare l'ambiente nel quale si sviluppava, cioè i campi di patate. Circa 100 anni dopo si è formata una nuova associazione, l'*Euphorbio-Galinsogetum ciliatae*, che è andata ad occupare l'unico ambiente disponibile, cioè le piccole aree degli orti presso le case, non trovandosi più campi di patate. Interessante, a tale riguardo, l'osservazione di DALLA FIOR (1955b): "fino ad oggi (1955) non m'è mai occorso di rinvenirla sulle prode o nell'interno dei campi di granoturco o di patate, dove domina invece la *Galinsoga parviflora*".

Il motivo della sostituzione delle due associazioni non è dovuto soltanto all'arrivo di nuove Neofite, ma anche alla loro capacità competitiva, nel caso qui presentato di *Galinsoga parviflora* e *Galinsoga ciliata*, dipendente da alcune caratteristiche biologiche delle due specie: produzione dei semi, conformazione del pappo, facilità di diffusione dei semi; altri motivi sono di ordine ecologico, relativamente alla maggiore

o minore nitrofilia ed eliofilia delle due specie e al tipo di ambiente, soprattutto campi oppure orti presso le case. Secondo GIACOMINI (1946) e DALLA FIOR (1955b) *Galinsoga parviflora* sarebbe più avvantaggiata, avendo un pappo più grande e a squamette più espanso e leggere, mentre *Galinsoga ciliata* sarebbe nelle condizioni più sfavorevoli per la piccolezza del pappo, che non ha un'azione efficace nella disseminazione appena un poco lontana. Va tuttavia rilevato che nella diffusione delle due specie intervengono attivamente anche gli altri fattori prima elencati, soprattutto quelli di carattere ecologico.

In effetti, nei primi anni di osservazione di *Galinsoga ciliata* in Italia sembrava che tale specie avesse un comportamento più contenuto rispetto a *Galinsoga parviflora*, essendo limitata ad aree ruderale e nitrofile e agli orti, ma successivamente c'è stato un cambiamento della dominanza, come è stato illustrato in precedenza.

In circa 190 anni si sono dunque susseguite 3 associazioni vegetali diverse, in conseguenza delle successive ondate di arrivo e sviluppo di nuove specie di Neofite e precisamente: "*Polygonetum persicariae*" fino al 1820, *Galinsogo-Potentacum* fino ad alcuni anni dopo il 1959, *Euphorbio-Galinsogetum ciliatae* negli anni successivi.

LOCALITÀ E DATA DEI RILIEVI

Tab. 1 - Val di Sole (Trentino occidentale), agosto 2009: 1 - Montes; 2 - Ortisé; 3 - Termenago; 4 - sotto Termenago; 5 - Peio; 6 - ; 7 - Celledizzo; 8 - Carciato; 9 - Bolentina; 10 - Presson.

Tab. 2 - Val di Sole, agosto 2009: 1 - Piazzola di Rabbi.

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APROXIMACIÓN GEOBOTÁNICA DEL BOSQUE TROPICAL SECO CADUCIFOLIO EN LA MICROCUENCA DEL RÍO SAN JOSÉ DE CHILÁ, MICHOCÁN, MEXICO

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ABSTRACT

It is indisputable that tropical forests harbour most current genetic resources and comprise innumerable environmental goods and services. Among tropical forests, the dry ones have been significantly less studied than wet ones. Yet geobotanical studies are practically nonexistent in this tropical dry forest (TDF). The present paper followed a geobotanical framework to distinguished, describe and map plant communities in a TDF of México, where 7 out 10 species are reckoned as endemic. Over 45 relevés were surveyed from April 2004 till October 2005. Data were analyzed via Twinspan, DCA and CCA in order to depict plant communities and detect governing attributes responsible of their distribution pattern. Results were tested for significance via Monte Carlo permutation, G and X² tests. Four communities were depicted and distribute differently across the landscape. *Heliocarpus occidentalis-Lysiloma acapulcensis* occupies mayor elevation on granites rocks; next to this, *Bursera heteresthes-Lonchocarpus hintoni* occurs at slightly lower elevations but on tubas and andesitic rocks. In contrast, *Caesalpinia platyloba-Cordia dodecandra* and *Cochlospermum vitifolium-Luehea candida* (dominating on tubas, granite and schist) distribute at low elevations. These four are comprised within a plant community group dominated by *Lysiloma divaricata-Cordia eleagnoides*. It is here concluded that elevation and lithology play a key role affecting evapotranspiration rates and therefore governing plant community distribution patterns at this TDF. The extent of this statement to explain other plant community patterns elsewhere is yet to be determined.

KEYWORDS: México, tropical dry forest, forest communities, communities mapping.

INTRODUCCIÓN

Marco conceptual

Los bosques tropicales constituyen

sobresalientes reservorios de biodiversidad a nivel mundial, además de proveer de múltiples bienes y servicios ambientales pese a lo cual su conocimiento y estado de conservación no siempre es el adecuado (TERBORGH, 1992; MARTÍNEZ-RAMOS, 1995; FAO, 2002; COSTANZA *et al.*, 1997). De acuerdo a GENTRY (1988) se acepta que existen en su seno dos grandes categorías: los húmedos siempre verdes o perennifolios (BTHP), cubriendo alrededor de un 52% de la superficie mundial de los bosques tropicales, y los secos, deciduos o caducifolios (BTSC), cuyo recubrimiento alcanza el 48% (MURPHY y LUGO, 1986). Los primeros han sido tema de estudio para numerosos investigadores y agencias de conservación por lo que el conocimiento sobre sus diferentes aspectos es amplio (GEIST y LAMBIN, 2001, 2002; SÁNCHEZ *et al.*, 2005a, 2005b). En contraste, los BTSC han concentrado menos interés, en especial en temas de corte sinecológico (GENTRY, 1988), con algunas excepciones limitadas a territorios específicos (DURÁN, 2004). De manera muy especial destaca la carencia de estudios geobotánicos que incluyan aspectos como composición, estructura, dinámica espacial y temporal, distribución, nomenclatura y sintaxonomía de sus comunidades.

Pese a la importancia de los BTSC como banco genético (GENTRY, 1982), se estima que cerca del 80% de su superficie original presenta un alto grado de perturbación (HOUGHTON *et al.*, 1991; SÁNCHEZ *et al.*, 2005a, 2005b). Los BTSC, a diferencia de los BTHP, no han sido utilizados en aspectos de manejo forestal y su principal uso deriva hacia su transformación agropecuaria (cultivos o pastizales), siempre que el suelo y/o el agua no sean factores limitantes (SÁNCHEZ *et al.*, 2005). Sin embargo, ambas formas de uso han probado ser de bajos rendimientos en el corto plazo y de drásticas consecuencias ambientales en el largo (LAMBIN *et al.*, 1997; FAO, 2002). Por contra, gran número de especies vegetales han sido, son y seguirán siendo plantas de interés etnobotánico que a pesar de conocerse

y utilizarse empíricamente, son poco mencionadas en las publicaciones de corte florístico y carecen, en muchos casos, de una estrategia de aprovechamiento comercial.

Proyectos de corte geobotánico han probado ser fundamentales para elaborar estrategias de manejo, conservación y restauración de la vegetación y sus hábitats (<http://ec.europa.eu/environment/nature/home.htm> y <http://www.schweizerbart.de/j/phytocoenologia>), lo que a su vez se refleja en mejores alternativas de calidad de vida para actores locales y por ende para amplios sectores sociales. Bajo el escenario anterior resulta prioritario llevar a cabo estudios de vegetación en BTSC que documenten aspectos sinecológicos en especial en países intertropicales como Brasil, Venezuela o México donde los BTCS aún son abundantes y paradójicamente confrontan elevadas tasas de deforestación. (www.maweb.org/documents/document.290.aspx.pdf; MILES *et al.*, 2006). En México, por ejemplo, las tendencias de pérdida rebasan los promedios mundiales (TREJO, 2000), y se ven favorecidas por la prevalencia de influencia antrópica en buena parte de su ámbito de distribución (SÁNCHEZ *et al.*, 2005a, 2005b), al margen de alguna figura de protección. Este tipo de vegetación está subrepresentado en el sistema de áreas protegidas de México conformando sólo 4% de su superficie, pese a ocupar el segundo lugar junto con el Bosque Tropical Subcaducifolio en cuanto a extensión a nivel nacional (MAS y PÉREZ-VEGA, 2005; PALACIO *et al.*, 2000).

Para profundizar en el conocimiento y variabilidad de los BTSC se considera importante y prioritario realizar estudios de tipo fitosociológico que pongan en contexto el valor intrínseco de este tipo de vegetación con el fin de respaldar políticas y estrategias que aseguren su mantenimiento. Antecedentes de trabajos elaborados a través de métodos fitosociológicos en BTSC son muy recientes, destacan los realizados en Bolivia y Brasil, donde el método fitosociológico ha sido de gran utilidad (KESSLER y BACH, 1999; BACH *et al.*,

1999) o México (HERNANDEZ-TORO, 2003). También se tienen diversos trabajos desarrollados en los piedemontes de los Andes (Orlando Rangel-Churro, Maximina Monasterio y Otto Huber comentario personal), para la Catinga Brasileña donde abundan condiciones similares de vegetación en términos fisionómicos y fenológicos pero de gran diferencia florística. Estos trabajos, aunque rigurosos, en su mayoría se han publicado en forma de tesis o en revistas de circulación local o regional.

El presente trabajo se centra en identificar las comunidades presentes en el BTSC estudiado, a través de la identificación y análisis de los atributos que mejor explican los patrones de su diferenciación. Para cada una de las comunidades reconocidas se abordan aspectos de su fisionomía, composición florística y ecología que repercuten en su diferenciación. Cabe aclarar que los trabajos de vegetación para la zona de estudio son inexistentes, a pesar de que el área alberga una fitodiversidad extraordinaria por lo que se ha reconocido como un refugio de un gran número de especies endémicas.

AREA DE ESTUDIO

La zona de estudio se localiza al suroeste del estado de Michoacán, en la vertiente septentrional de la Sierra Madre del Sur, e insertada dentro de la denominada Tierra Caliente, vertebrada por el río Tepalcatepec, de cuya cuenca forma parte (Fig. 1).

El área de estudio corresponde a la microcuenca del Río San José de Chila, ubicado en los municipios de Apatzingan y Aguililla. El área conforma una superficie aproximada de 570 km² del área total de la cuenca, cuya variación

altitudinal oscila entre 200 y 970 m.s.n.m donde se establece el BTSC y su transición hacia bosques de encino y pino.

pendientes de moderadas a altas.

CLIMA

La zona de estudio presenta una estación seca bien definida que abarca los meses de noviembre a mayo; el resto del año se corresponde con la época de lluvias, cuyo promedio de precipitación oscila entre 628 mm (198 m.s.n.m) a 1,061 mm (979 m.s.n.m.) Estas precipitaciones son de carácter torrencial e impredecible. Las temperaturas mensuales promedios máximos ocurren en el mes de mayo (42 °C); las temperaturas mensuales promedios mínimos se registran en los meses de invierno (24 °C). La disponibilidad de agua en la zona de estudio es escasa y restringida a la temporada de lluvias, lo que condiciona el desarrollo socioeconómico de la región.

Los climas según GARCIA (2004) van desde BS1(h')w(w)(i)g; BS0(h')w(w)(i)g; BS1(h')w(w)(i)gw'' y BS1(h')w(w)(e)g, todos estos climas corresponden a climas semiáridos (excepto BS0 es árido, el más seco de los secos), con temperaturas anuales encima 22° y el mes más frío sobre los 18°; con precipitación 10 veces mayor la cantidad de lluvia del mes más húmedo de la mitad caliente del año que en el más seco; y en los casos de las letras (i') con poca oscilación; (e) extremoso; g marcha de la temperatura tipo Ganges (el mes más calido se presenta antes del solsticio de verano) y w'' presencia de canícula. Otro clima que también se presenta en la zona de estudio es Aw1(w)ig; el cual corresponde a un clima cálido el más húmedo de los subhúmedos, isotermal (i) (oscilación menor 5°) y marcha de la temperatura tipo Ganges.

En cuanto a su adscripción bioclimática, y siguiendo el modelo global de RIVAS-MARTÍNEZ (2005) la cuenca estudiada tiene un bioclima Tropical Xérico con representación de los termotipos Infratropical y Termotropical, y con ombrotipos que oscilan entre el Semírido y el Seco.

PAISAJE VEGETAL

Son precisamente los BTSC de esta región, los que son reconocidos como un refugio de un gran número de especies endémicas, donde se estima que 7 de cada 10 son oriundas de México (MIRANDA, 1947; RZEDOWSKI, 1978, 1991). Es también el centro más importante de variedad de copales o papelil-

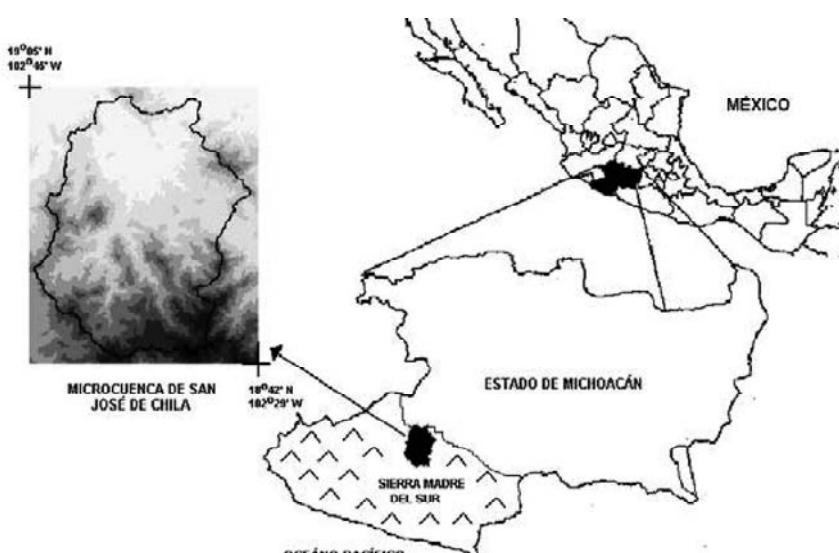


Fig. 1 - Localización del área de estudio.

los, que se cosechan con fines comerciales y para uso ritual (MARSHALL *et al.*, 2006).

El BTSC de la cuenca estudiada está representado fundamentalmente por las siguientes especies: *Lysiloma divaricata*, *Cordia elaeagnoides*, *Caesalpinia platyloba*, *Bursera coyucensis*, *Caesalpinia eriostachys*, *Erythroxylon rotundifolia*, *Tabebuia chrysanthia*, *Lonchocarpus caudatus*, *Randia laevigata* y *Cochlospermum vitifolium*. La estructura, composición y tipo de bosque permiten claramente relacionarlo con las *Hiemisilvas* indicadoras del Bioclima Tropical Xérico (PEINADO *et al.*, 2008). A medida que se sobrepasa la cota de 700 m aproximadamente, coincidiendo con pequeñas hoyas en la ladera, comienzan a establecerse diferentes especies de encinos como *Quercus glaucoides*, *Q. magnolifolia*, *Q. obtusa*, *Q. resinosa* y *Q. sororia*. A partir de los 1,000 m aproximadamente hacen su aparición los pinos (*Pinus spp.*).

METODOLOGÍA

LEVANTAMIENTO DE DATOS DE CAMPO

La presente investigación se llevó a cabo a través del método fitosociológico (WERTER, 1974; BRAUN-BLANQUET, 1979), basado en la realización de relevés y su posterior comparación y organización en tablas de vegetación (Tabla 1). La parte correspondiente al trabajo de campo fue efectuada durante un período de año y medio (abril 2004-octubre 2005).

Para la selección de los lugares de muestreo se llevó a cabo un trabajo previo en gabinete, a través de la utilización de un sistema de información geográfica en el cual se sobrepusieron cuatro capas de información: 1) Geología (GARDUÑO *et al.*, 1999); 2) Geomorfología (ORTIZ, 2000); 3) Vegetación (INEGI, 1980) y 4) Cobertura de una imagen SPOT (10 m resolución). Estos insu- mos permitieron verificar la heterogeneidad del paisaje en la zona de estudio para garantizar un reparto homogéneo del número de levantamientos entre los diferentes escenarios del paisaje; localizando las áreas mejor conservadas y tomando en cuenta la cercanía a vías de acceso.

Para seleccionar los lugares a inventariar se consideró por un lado el criterio de zonalidad y de vegetación climatófila de RIVAS-MARTÍNEZ (2007), y por otro el criterio de superficie florísticamente homogénea establecida en un área de 20x20 m (KENT y COKER,

Tabla 1 - Relevés de las comunidades.

Tabla 1 - (continuación).

1992).

Previamente a la realización de los relevés se llevó a cabo una intensa colecta florística en el ambiente del BTSC objeto de estudio, centrada en las especies representativas de los estratos subarbóreo y arbóreo (≥ 3 m) que incluyen diferentes subtipos de fanerófitos. Se desestimaron los estratos arbustivo y herbáceo por las dificultades de identificación de su flora durante el prolongado periodo de estiaje, lo que dilataría enormemente la obtención de resultados. Los ejemplares fueron determinados en laboratorio y sirvieron como referencia para la posterior identificación de las especies inventariadas en los relevés; en ocasiones se utilizaron los nombre vernáculos dados por los lugareños para establecer los vínculos de la identificación. En ellos, además de la composición florística, se obtuvieron los índices de cobertura de cada especie (BRAUN-BLANQUET, 1979) e información complementaria de altura y cobertura de los estratos. En la determinación de la flora se consultó herbarios en línea y el cotejo de ejemplares en el herbario de Instituto de Ecología, A.C. en Pátzcuaro - Michoacán (IEB). En este mismo centro fueron depositados los ejemplares colectados.

ANÁLISIS TABULAR Y ESTADÍSTICO

La información de campo conformó una base de datos tabular que permitió ser sometida a un análisis de especies indicadoras de dos vías (TWINSPAN, HILL, 1979). Se utilizaron tres niveles de corte con un mínimo de cinco especies y seis relevés para caracterizar con consistencia las comunidades propuestas. La baja dominancia específica y la alta diversidad dificultaron, hasta cierto grado, la obtención de "eigenvalues" altos. No obstante, la distribución elevacional, la información fisonómica y los atributos del escenario físico permitieron distinguir con un alto grado de confianza las comunidades florística y ecológicamente diferentes. Éstas se describen de manera formal en la sección de resultados.

La exploración de las variables del medio físico que mejor explican la distribución de los grupos florístico-ecológicos diferenciados previamente, se realizó a través del Análisis de Discriminación Canónica y Análisis de Correspondencia Canónica (TER BRAACK, C.U.F., 1986). Ambos resultados fueron sujetos a su significancia por medio de la prueba de permutaciones de Monte Carlo. Todo lo anterior se ejecutó en

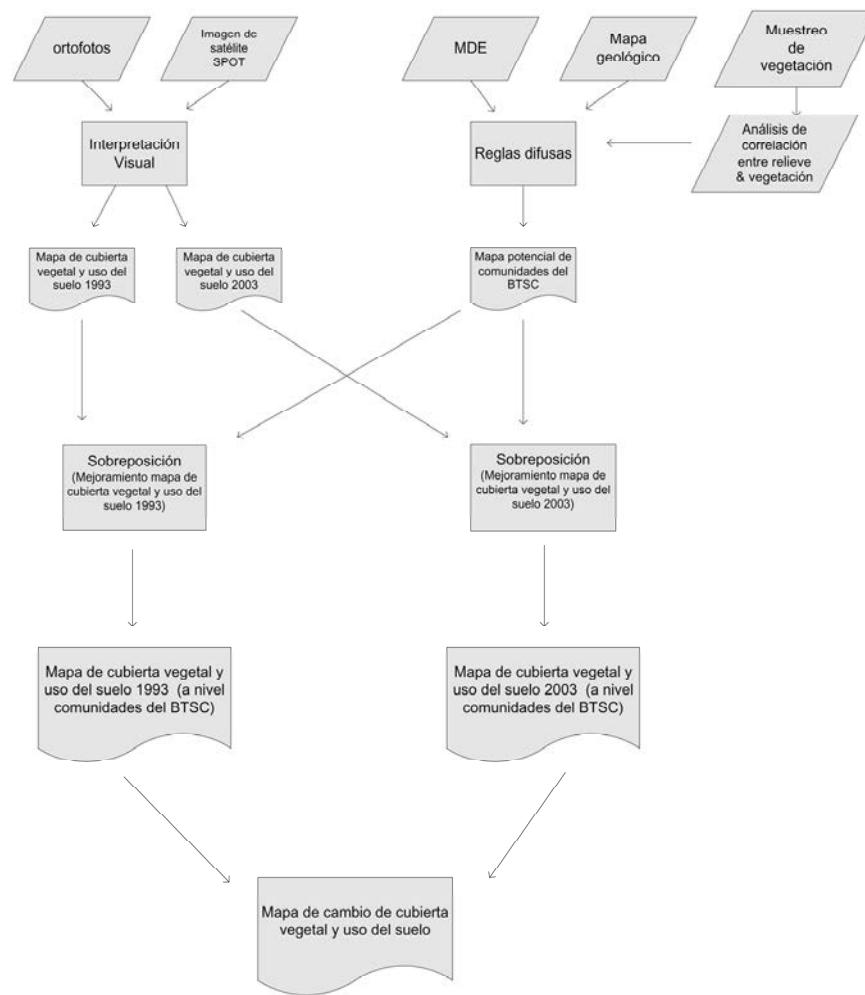


Fig. 2 - Diagrama que muestra el procedimiento metodológico para la generación del escenario de la distribución de la vegetación.

el programa PC-ORD (McCUNE y MEFORD, 1995). Los resultados obtenidos del análisis de ACC fueron comparados con pruebas de Chi² y G para comprobar diferencias entre valores observados y esperados.

ESCENARIOS DE DISTRIBUCIÓN DE LA CUBIERTA VEGETAL

Se llevó a cabo la interpretación de ortofotos e imágenes de satélite de donde se derivaron mapas de cubierta vegetal y uso del suelo para los años 1993 y 2002. La interpretación es un proceso híbrido que se realiza mediante la combinación entre clasificación digital y la interpretación visual en pantalla (GEOVIS software). La validez de la interpretación se corroboró con salidas a campo. La elaboración de un mapa de distribución potencial de las comunidades se basó en reglas de distribución utilizando atributos del relieve (litología, altitud, profundidad del suelo y porcentaje de arena) a través de un enfoque de conjuntos difusos (ZADEH, 1965; GOODCHILD, 1994). Estas reglas se elaboraron con base en el análisis de la frecuencia de las especies diagnósticas en función de los atributos del relieve. La elaboración del escenario de distribución de las comunidades vegetales y el análisis de dinámica de cambio se realizó en dos etapas. La primera incluyó la correspondencia de las clases de cobertura con cada una de las comunidades descritas. La segunda etapa se realizó mediante el cruce de mapas entre dos fechas (Fig. 2).

Una revisión detallada de cada una de las partes aquí descritas brevemente se encuentra en la disertación de PÉREZ-VEGA (2008).

RESULTADOS

LA VEGETACIÓN DE LA CUENCA DEL RÍO CHILA

El análisis tabular permitió distinguir cuatro comunidades que por sus características florísticas, fisonómicas, ecológicas y geofísicas difieren significativamente (Fig. 3, Cuadro 1). Estas comunidades se relacionan entre sí a través de un conjunto de especies de amplia distribución en la zona, aunque con valores de cobertura divergentes. En éste se incluyen como principales

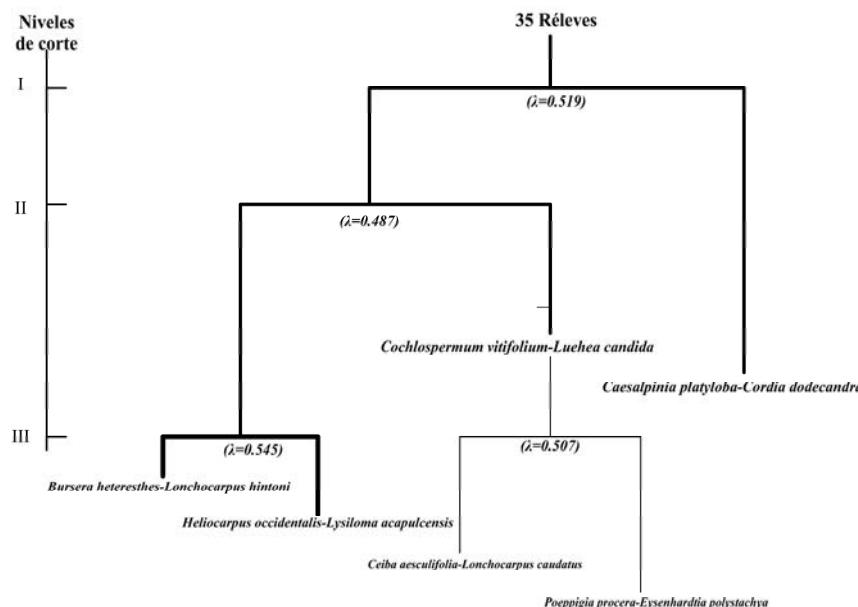


Fig. 3 - Dendrograma resultado del análisis en TWINSPAN. El Nivel de corte II y III ilustra las afinidades estadísticas (dadas entre los corchetes) entre las cuatro comunidades diferenciadas. Para la comunidad central el nivel III denota a las subcomunidades.

Lysiloma divaricata-Cordia eleagnoides	Comunidades	Subcomunidades
	<i>Bursera heteresthes-Lonchocarpus hintoni</i>	
	<i>Helicocarpus occidentalis-Lysiloma acapulcensis</i>	
	<i>Cochlospermum vitifolium-Luehea candida</i>	<i>Ceiba aesculifolia-Lonchocarpus caudatus</i> <i>Poepigia procera-Eysenhardtia polystachya</i>
	<i>Caesalpinia platyloba-Cordia dodecandra</i>	

Cuadro 1 - Sintaxonomía de la vegetación de la Cuenca de Chila, Michoacán, México.

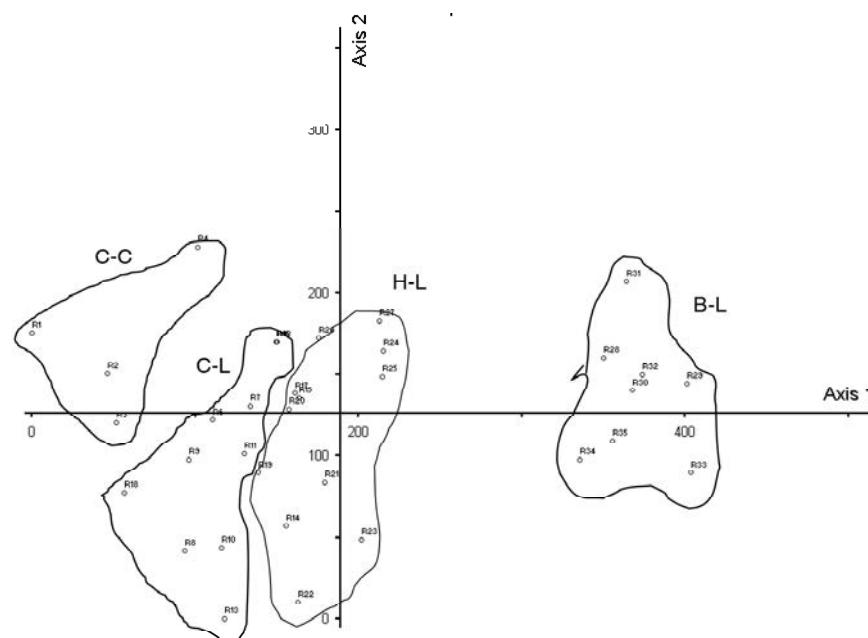


Fig. 4 - Ordenograma que denota la distribución de las comunidades y subcomunidades a lo largo de dos ejes. El I correlacionada con la elevación y el II con la tipología litológica.

elementos al tepemezquite (*Lysiloma divaricata*), el cueramo (*Cordia eleagnoides*) el crucillo (*Randia laevigata*) y la parotilla (*Poepigia procera*), mismas que podrían integrar a nivel de alianza provisional a las comunidades encontradas (*Lysiloma divaricata-Cordia eleagnoides*).

CORRELACIÓN ENTRE ATRIBUTOS Y COMUNIDADES

Los análisis canónicos arrojaron que las cuatro comunidades se distribuyen diferencialmente en el espacio de ordenación a lo largo del eje I ($\lambda=0.603$) y eje II ($\lambda=0.419$). El por-

centaje de varianza explicada para cada eje fue de 53 y 29 respectivamente. Los atributos con mayor correlación fueron: litología (toba ácida-brecha volcánica -0.937; granito -0.680; esquisto 0.770), altitud (0.635) y profundidad del suelo (0.558).

A lo largo del eje I se separan las cuatro comunidades en donde la de *Helicocarpus occidentalis-Lysiloma acapulcensis* (mayor altitud y sobre granitos acapulcensis) ocupan el extremo izquierdo del ordenograma (Fig. 4) y otra dominada por tobas y andesitas donde ocurre la comunidad de *Bursera heteresthes-Lonchocarpus hintoni*. La condición de menor altitud (derecha del ordenograma) la denota la comunidad de *Caesalpinia platyloba-Cordia dodecandra* para la cual la condición litológica fue menos determinante y por ende no se detectaron subcomunidades. La situación intermedia corresponde a *Cochlospermum vitifolium-Luehea candida*. Esta última comparte condiciones tanto de elevación como de un tipo de roca (toba ácida) con la de *Bursera heteresthes-Lonchocarpus hintoni*. No obstante, existe una clara diferencia entre las dos tanto en su componente florístico como fisonómica y se denota una subcomunidad favorecida por las rocas graníticas (*Poepigia procera-Eysenhardtia polystachya*) y otra por los esquistos (*Ceiba aesculifolia-Lonchocarpus caudatus*).

Los resultados obtenidos a través de la prueba de Monte Carlo mostraron significancia para ambos ejes y las pruebas de Chi² y de G confirmaron los resultados obtenidos en los análisis canónicos. La litología, la altitud y la profundidad del suelo tienen una influencia significativa sobre la distribución de las comunidades ($p= 0.05$).

Por otro lado sobre las variables catenales como curvatura, pendiente y exposición de la ladera, los resultados no mostraron ninguna influencia significativa entre estos y la distribución de la vegetación.

ESCENARIO DE DISTRIBUCIÓN DE LAS COMUNIDADES

El mapa de la Fig. 5 muestra el patrón de distribución de las cuatro comunidades descritas. Cabe mencionar que el polígono en blanco está predominantemente ocupado por planicies cubiertas con cultivos y pastizales. En cuanto a la dinámica del cambio de la cubierta vegetal, el análisis arrojó que la vegetación representada por las cuatro comunidades descritas se alteró en un

3.5 por ciento de la superficie original en un periodo de 10 años (1993-2002). La agricultura y el pastoreo se incrementaron en un 3.2 y 2.3 por ciento respectivamente. El resto de las cubiertas vegetales tanto naturales como antrópicas no presentaron porcentajes de cambio importantes.

DISCUSIÓN Y CONCLUSIONES

Un aspecto regularmente documentado a escalas globales y regionales es la relación entre la riqueza fitoespecífica y las condiciones ambientales. Investigaciones específicas han encontrado que la altitud, geología, características físicas y químicas de los suelos tienen una importante correlación en la distribución y riqueza de especies en los BTSC (HUSTON, 1980; OLIVEIRA FILO *et al.*, 1994, 1998; VELÁZQUEZ y CLEEF, 1994; BARBOUR y BILLINGS, 2000; PYKE, 2001; DEL BON *et al.*, 2002; VILLERS *et al.*, 2003; DURAN, 2004).

GENTRY (1988) encontró que la precipitación ejerce de forma general una fuerte influencia en la riqueza y distribución de especies en los bosques tropicales de diversas partes del mundo. Para México LOTT *et al.*, (1987) postula que dicho patrón no aplica y esto es apoyado por TREJO (1998) quien encuentra para muestreos próximos como factores como la evapotranspiración y el tipo de roca inciden sobre la distribución de las especies.

De la revisión de los estudios realizados anteriormente, es posible postular que existen factores que tienen un efecto regional y otros influyen de forma local en los patrones de distribución de la vegetación del BTSC. Así, el clima (distribución y valor de temperatura y precipitación) y la evapotranspiración resultan ser aspectos de importancia regional mientras las condiciones litológicas y las características físicas y químicas de las unidades morfoedáficas (relieve-suelo) influyen en el balance hídrico (disponibilidad de agua), lo cual afecta la distribución en los patrones de vegetación locales. El entendimiento y conjugación de ambos es necesario para la predicción de patrones de distribución en los BTSC.

El presente trabajo no siguió de forma ortodoxa el método fitosociológico (no se consideró el estrato herbáceo), pero permitió generar información rápida y precisa para una zona sin conocimientos anteriores.

Así, se distinguen por primera vez cuatro comunidades, tres de ellas bien diferenciadas en cuanto a la composi-

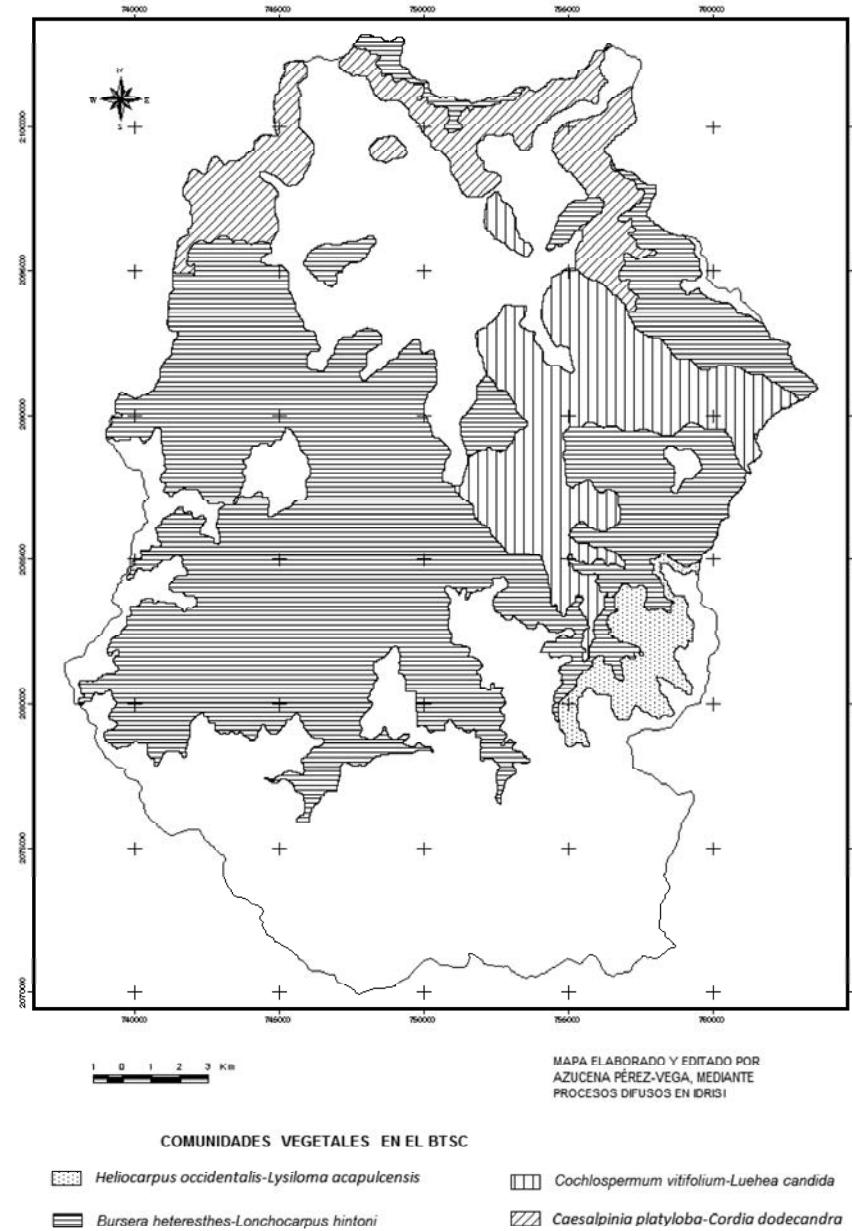


Fig. 5 - Escenario de la distribución de las comunidades de vegetación derivado del método de lógica difusa.

ción florística de las especies diagnósticas que la conforman. Las cuatro comunidades mostraron una estructura bien definida en cuanto a la altura arbórea de los individuos.

En el presente trabajo se concluye que los factores como: litología, altitud, profundidad del suelo ejercen una influencia significativa en la distribución de las comunidades, mientras que pendiente y curvatura no presentan una correlación significativa dentro del BTSC, porque la mayoría de los muestreos se hicieron sobre laderas con pendiente superiores a 20° y en donde predominaron formas rectas en planta. Los procesos como concentración de humedad y desarrollo del suelo, no presentan cambios sustanciales entre laderas de pendiente moderada a fuerte y con una forma recta a convexa, lo cual al mismo tiempo no expresen diferen-

cias en el establecimiento de especies. Ello no contradice la correlación encontrada entre profundidad del suelo, ligada al tipo de roca, y la distribución de especies. Por otro lado las superficies con pendientes suaves, vinculadas a piedemontes y planicies, se encuentran totalmente transformadas, y ocupadas por cultivos y pastizales por lo que no se pudo establecer su vínculo relacional con las comunidades vegetales originales. Sin embargo, un trabajo de RAWITSCHER (1948) reporta que, en una porción de vegetación conservada de Brasil que abarca también áreas de planicie, el BTSC sólo se distribuye en las superficies de laderas debido a la diferencia en el contenido de elementos nutritivos del suelo entre laderas y planicies.

En la zona de estudio la mayoría de los atributos pertenecientes estrictamen-

te al relieve (curvatura, pendiente, exposición de ladera), no tuvieron una relación importante con la distribución de las comunidades, a excepción del atributo de altitud como un factor local indirecto del clima. En nuestro caso la elevación juega un papel local ya que los rangos de distribución de una determinada especie pueden variar independientemente del factor altitudinal. Es, por ejemplo, el caso de *Cochlospermum vitifolium*, cuya presencia en la zona de estudio, se localiza de forma importante por arriba de los 600 m.s.n.m.m., mientras en las laderas expuestas al Océano Pacífico se encuentra con la misma frecuencia desde el nivel del mar, debido a la mayor humedad de dicha vertiente.

El presente trabajo concluye que son diferentes factores tales como: clima, litología, suelo (química y física), altitud, evapotranspiración, exposición al mar, entre los más estudiados, los que determinan condiciones de mayor o menor disponibilidad de humedad para las especies vegetales del BTSC, lo cual repercute en la conformación de los patrones de distribución de la misma.

Finalmente, resaltamos la importancia del estudio de los BTSC desde un punto de vista geoecológico utilizando información florística, ecológica y geoespacial para brindar mayor conocimiento del comportamiento y los procesos que afectan a este tipo de vegetación.

AGRADECIMIENTOS

La DGAPA-UNAM a través de los proyectos PAPIIT IN112803 e IN218510-3 aportó recursos para el desempeño de este estudio. De igual forma el proyecto apoyado por la AE-CID (A/023310/09) en su primera y segunda fases permitieron llevar a buen término el manuscrito presente.

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TROPISCHE REGENWÄLDER VON DAINTREE IN QUEENSLAND, AUSTRALIEN - WHERE THE RAINFOREST MEETS THE REEF

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ABSTRACT

Fossil records suggest that tropical northern Australia was dominated by a humid tropical environment supporting rainforest in the Early Paleogene. The increasing aridity of the continent from mid Miocene on, the prevalence of a cool climate during the Oligocene and the glacial cycles of the Pleistocene promoted the development of grassland and tropical savannas and the establishment of fires leading to the existence of fragmented patches of rainforest on geologically young sites especially in the eastern slopes of the Great Dividing Range in Queensland between Cooktown and Cairns. The region referred to as "The Daintree Rainforest" encompasses an area of approximately 1,200 square kilometres from the Daintree-River north to Cooktown and west to the Great Divide. It represents the largest block of tropical rainforest in Australia. This tropical rainforest is one of the most complex on earth. Its plant diversity and structural complexity is unrivalled on the Australian continent and represents the origins of the modern Australian flora. In the Daintree-region the climate and topography were ideal, so the area became a last remaining refuge for tropical rainforest, mangrove and coastal reef. Many species have survived with little change and even today their descendants retain many of their primitive characteristics - some dating back 110 million years, like *Davidsonia pruriens* (Davidsoniaceae) and the local endemic *Noahdendron nicholasii* (Hamamelidaceae), which only occurs in Noah-Creek, Daintree. One plant species in particular, the Ribbon wood (*Idiospermum australiense*, Idiospermaceae) is one of the rarest and most primitive of the flowering plants. Its discovery in the Cape Tribulation National Park in 1972 war arguably Queensland's most significant botanical find, greatly increasing scientists' awareness of just how ancient these forests really are. From a total of 19 primitive flowering plant families on Earth, 7 are represented in the Daintree region making the highest representa-

tion of these plants world wide. The landscape of Daintree is one of striking diversity including magnificent scenery, mountain ranges, fast-flowing streams and waterfalls, deep gorges and dense rainforests.

The vegetation of the area is the most diverse in Australia both floristically and structurally. There have been 4 different main rainforest types identified. From the tall forests of the coastal plains with massive curling liana growth and enormous buttress roots, through the middle altitude forests, to the montane forests and areas of heath-like growth that adorn the mountain tops. It is further interesting to note that the mangrove forest fringing the mouths of the creeks and rivers the Daintree area boast the highest species diversity of this habitat type in Australia.

KEYWORDS: Tropical Rainforests, Daintree, Structure, semideciduousness, living fossils, Mangroves.

ZUSAMMENFASSUNG

In dieser Studie beschreiben wir den geringen Anteil laubwerfender Arten im Kronendach der saisonalen tropischen Regenwälder von Daintree in Queensland im Verhältnis zur Saisonalität vom Klima, von Bodenbedingungen und von evolutiven Aspekten der Baumartenkomposition. Unfruchtbare und wechseltrockene Böden haben in der Evolution offensichtlich den immergrünen Habitus gefördert, es scheint, dass der Anteil laubwerfender Arten in diesen saisonalen Regenwäldern also nicht in erster Linie klimatisch bedingt ist, sondern eher evolutiv als eine Anpassung an die temporären Temperaturbedingungen, das Tageslicht und die Lichtmenge insgesamt während der Trockenzeit bei höherer Sonneneinstrahlung und die damit verbundenen Variationen im Niederschlag. Saisonale Niederschlagsvariationen begünstigen Laubfall; langjährige gleichbleibende Variabilitäten im Niederschlag dagegen begünstigen Immergrüne Gehölze. Die „primitiven“ Angiospermen im Dain-

tree-Gebiet sind allesamt immergrün – ein Hinweis darauf, dass Laubfall in verschiedenen Pflanzenfamilien unabhängig und zu verschiedenen Zeiten evolutiv entstanden ist. Eine methodologisch interdisziplinäre Studie über die räumliche Variabilität der Böden, ihres Alters und ihrer Fruchtbarkeit, der verschiedenen entsprechenden Regenwaldgesellschaften und deren paläökologischer Nachweis wäre ein sehr sinnvoller Test unserer Hypothesen zur Relation laubwerfender und immergrüner Regenwaldbäume in den Wäldern von Daintree. Das Daintree-Regenwaldgebiet ist seit 1988 in das Weltnaturerbe der UNESCO aufgenommen. Seine Gesamtfläche umfasst derzeit über 800 Hektar mit Regenwäldern, Mangroven und den Riffen. Hier finden wir die einmalige Kombination der natürlichen Verzahnung von tropischen Regenwäldern, weißen sandigen Stränden und Korallenriffen, die auf der Erde in dieser Form einzigartig sind. „Where the rainforest meets the reef“, so werben die Australier touristisch für dieses einmalige Gebiet.

EINLEITUNG

Tropische Regenwälder gibt es auf der Erde in drei großen Lebensräumen, wie es auch WHITMORE (1990), RICHARDS (1996) und MORLEY (2004) betonen. Zunächst sind hier die großen Regenwaldgebiete entlang des Äquators zwischen dem jeweils 5. Breitengrad nördlicher und südlicher Breite zu nennen, die durch die Innertropische Konvergenzzone (ITCZ) bestimmt sind (Abb. 1). In diesen Regionen haben das inneräquatorische Tageszeitenklima und das Fehlen ausgesprochener Jahreszeiten oder jeglicher Saisonalität die reichhaltigsten und höchstentwickelten inneräquatorialen Regenwälder hervorgebracht, besonders im Amazonasgebiet, im Kongobecken und im indomalaiischen Archipel in Südostasien sowie in Australien.

In Richtung der subtropischen Hochdruckgebiete gehen diese inneräquatorialen Regenwälder beiderseits des

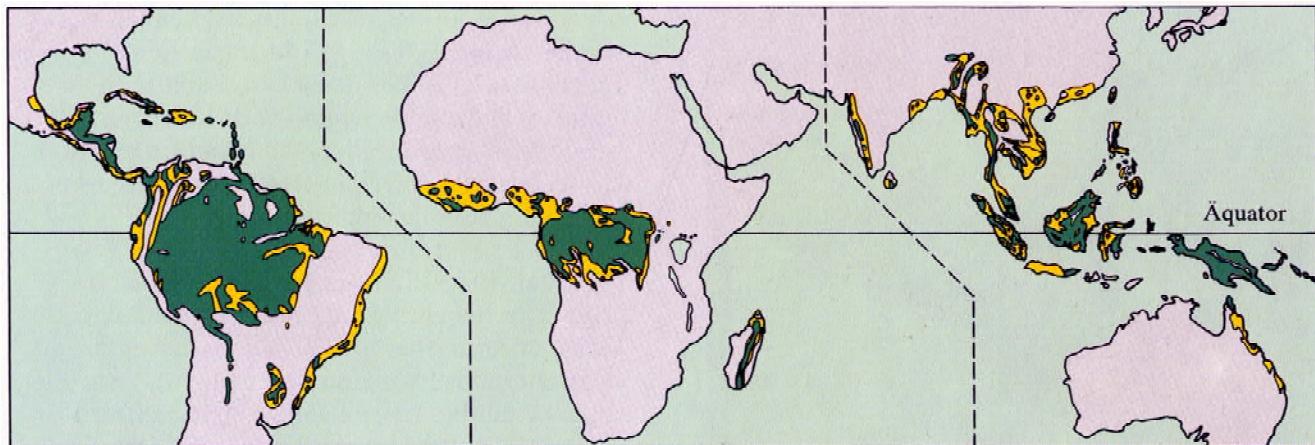


Abb. 1 - Verbreitung tropischer Regenwälder auf der Erde nach TERBORGH (1993).



Abb. 2 - Schematische Abfolge der Regenwälder vom Äquator zu den Wendekreisen.

Aquators in teilimmergrüne und regengrüne Wälder über, wie wir dies in Abb. 2 sehen und wie es ausführlich bei WALTER und BRECKLE (1999) sowie POTT (2005) beschrieben ist.

In Australien kommt tropischer Regenwald zusammenhängend nur an der Ostküste von Queensland zwischen 16° und 19° südlicher Breite bei 1500 bis 3000 Millimetern Jahresniederschlag vor. In Höhen über 500 Metern ist hier zudem ein artenärmer und dem tropischen Regenwald verwandter montaner Regenwald entwickelt. Nach Norden und Süden gibt es von hier aus gesehen in Australien nur noch Regenwaldfragmente in Schluchten und Tallagen; dazwischen wachsen immergrüne *Eucalyptus*-Wälder und spezielle Trockenwälder mit Eucalypten, Casuarinen und Akazien. Ein solches Vegetationsmosaik finden wir in Queensland nördlich von Cairns vor allem auf der Cape York-Halbinsel, wo Monsune und Passatwinde die hohen Niederschläge bedingen, welche durch Steigungsregen an Gebirgshängen der Great Dividing Range lokal noch verstärkt werden können. Wegen der Saisonalität solcher Regenfälle besitzen die dortigen Regenwälder auch relativ geringe Anteile laubwerfender Bäume - in Relation zu ihrer geographischen Lage -, und solche teilimmergrünen tropischen Regenwälder können hier nur unter ganz speziellen Klimabedingungen gedeihen,

wie wir dies nachfolgend am Beispiel der Regenwälder von Daintree genauer betrachten wollen (HÜPPE und POTT, 2007; HEISE-PAVLOV *et al.*, 2008).

DIE TROPISCHEN REGENWÄLDER VON DAINTREE

Die artenreichen Tieflagenregenwälder in Nordostaustralien nördlich von Cairns sind einmalig auf der Erde: Es gibt sie nur noch einigermaßen großflächig in den Küstenregionen nördlich des Daintree River am Cape Tribulation bis hinauf nach Cooktown am Eingang zur Cape York-Halbinsel östlich der Great Dividing Range, dem Gebirgszug, der den gesamten Osten Australiens vom Cape York bis zum Mt. Wellington bei Hobart in Tasmanien von Norden nach Süden durchzieht. Hier in der innertropischen Konvergenzzone Australiens kennt man keine Jahreszeiten, nur dort, wo sich Monsune und Passatwinde bemerkbar machen, sind zwischen den saisonalen Regenfällen kurze Trockenphasen in den Jahresgang eingeschaltet. Dementsprechend wachsen in der Great Dividing Range als tropische Wälder nur Tieflagenregenwälder und montane Regenwälder auf engstem Raum untereinander verflochten. Diese Regenwälder verändern sich je nach Einfluss der Niederschläge mit zunehmender Entfernung von den Wendekreisen zu subtropischen warm-temperaten und temperaten Regenwäldern. In Queensland finden wir solche südlich von Cairns bis in die Gegend von Frazer Island und bis nach Brisbane (BEADLE, 1981; BELL *et al.*, 1987; ADAM, 1992; GROVES, 2001).

Derartige immergrüne Regenwälder unterliegen dabei wegen der zunehmenden Saisonalität der Niederschläge einem besonderen phänologischen Wechsel: Sie verändern sich allmählich

mit zunehmender Entfernung von den Tropen zu teilimmergrünen, halb-laubwerfenden und zu laubwerfenden Wäldern, je nach Dauer und Intensität der Trockenzeit. Die einzigen saisonalen bis immergrünen tropischen Tieflagenwälder Australiens wachsen jedoch hier im Daintree-Gebiet von Queensland. Sie sind weltweit ein Unikat! Wir wollen uns fragen, was ihre Einzigartigkeit bedingt, welche Standortfaktoren dabei wirksam sind und welche Anpassungen ihre Pflanzenwelt an das dortige saisonale Klima entwickelt hat.

Im tropischen Klima der Daintree-Region herrscht normalerweise eine kurze Trockenphase; die Temperaturen variieren im Jahresgang um etwa 5 Grad Celsius mit monatlichen Maxima von 31,5 Grad Celsius im Süd-Sommer zwischen Dezember und Februar und winterlichen Höchsttemperaturen von 25,5 Grad Celsius in den Süd-Wintern im Juni und Juli. Die Niederschläge betragen - wie gesagt - im allgemeinen mehr als 3.000 Millimeter pro Jahr, wobei etwa 60 Prozent in der feuchten Sommersaison zwischen Dezember und März niedergehen mit monatlichen Spitzen von bis zu 550 Millimetern (HERBERT, 1960; FRANCIS, 1970; HOPKINS *et al.*, 1999). Von Juli bis Oktober fallen in der Regel dagegen nur etwa 90 Millimeter Niederschlag im Monat, was kurze saisonale „Trockenphasen“ zur Folge hat. Hohe Luftfeuchtigkeit setzt dann ein am Ende der Trockenzeit, wenn vor dem Regenbeginn die Temperaturen ansteigen, in einer Phase, welche die Australier als „*the wet*“ bezeichnen. Die vergleichsweise hohen Niederschlagssummen liegen dann am oberen Ende des globalen tropischen hydrologischen Spektrums insgesamt (KEAST, 1981; MEIER und FIGGIS, 1989; MACK und CORLETT, 2005) und sind vor Ort durch vier niederschlagsbringende Erscheinungen bedingt: Konvektion, Kon-

vergenz, Zyklone und die Orographie der Region mit ihren steilen Berggrücken und tief eingeschnittenen Tälern (Abb. 3).

Hier im Daintreegebiet verändert sich der Tieflagenregenwald über zahlreiche Stufen montaner Typen bis zum Bergregenwald, dem „Highland-Rain Forest“, wie es auch BEARD (1967), ASH (1988), BORCHERT *et al.* (2002), HUGHES (2003) und MORLEY (2004) beschreiben. Für unser Untersuchungsgebiet lassen sich somit folgende vier allgemeine Typen nach der Höhenlage differenzieren, die in den Abb. 4-7 dargestellt sind.

Die Abb. 4 bis 7 vermitteln allerdings nur einen groben Eindruck über diese Waldtypen. Insgesamt können nach TRACEY (1982) sogar dreizehn verschiedene Regenwaldtypen nach ihrem verschiedenartigen Aufbau und ihrer Struktur unterschieden werden, die nach Schichtung, Artenzusammensetzung, Höhenlage und insbesondere nach der Blattgröße charakteristischer Baumarten differenziert werden. Das macht eine Klassifikation sehr unübersichtlich und die hier vorgestellten vier Haupttypen reichen nach unserer Meinung für eine allgemeine Ansprache und Differenzierung der Regenwälder in Queensland jedoch aus.

MORLEY (2004) differenziert in seiner globalen Betrachtung der tropischen Regenwälder besonders diese Regenwälder entlang der Nordostküste von Queensland als spezielle saisonale Typen, ohne jedoch auf Details oder die floristische Differenzierung dieser Wälder genauer einzugehen. Deshalb wollen wir die Daintree-Regenwälder hier genauer betrachten und besonderen Augenmerk auf die Phänomene des Laubwechsels legen.

Zustand und Status solcher Immergrünen tropischen Regenwälder sind in der Literatur schon immer verschiedentlich beschrieben und interpretiert worden. WEBB (1978) sowie WEBB und KIKKAWA (1990) und WEBB und TRACEY (1994) bezeichnen beispielsweise noch solche Regenwälder als immergrün, wenn auch noch bis zu 25 Prozent ihrer Gehölzanteile aus laubwerfenden Arten bestehen. Grundsätzlich sind derartige immergrüne Regenwälder aber an Gebiete ohne jegliche Saisonalität gebunden. Hier in Queensland ist die Situation jedoch eine andere: Für Australiens tropische Monsungebiete haben BOWMAN und PRIOR (2005) verschiedene Saisonalitätsindices kalkuliert, - diese basieren auf Ausdauer und Verlauf der Relation von Trockenzeit zu Regenzeit -, und für unser Gebiet von

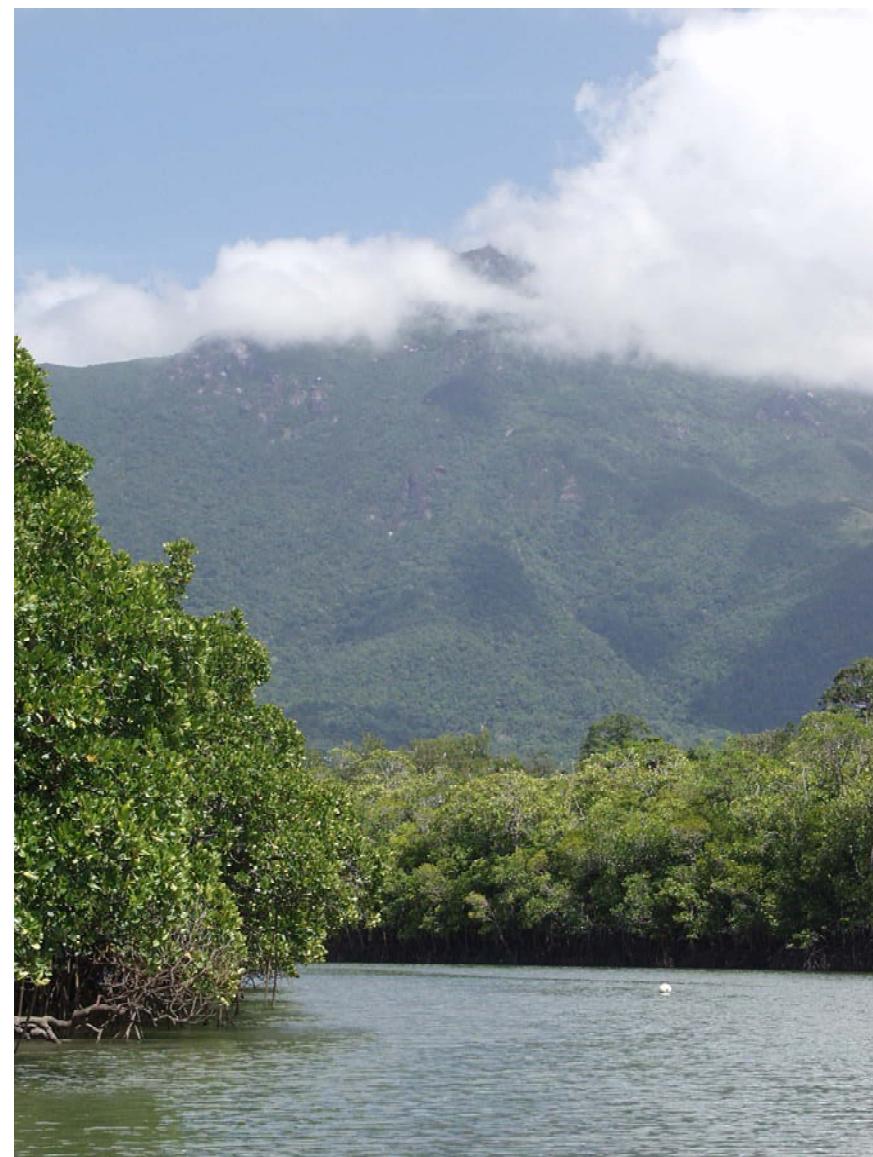


Abb. 3 - Steile Berggrücken und tief eingeschnittene Täler kennzeichnen die Ostabdachung der Dividing Range im Daintree-Regenwaldgebiet. Der Thornton-Peak bildet mit 1379 m die höchste Erhebung.

Daintree sind vor allem Trockenzeiten von über 3 Monaten Dauer sowie kurze intensive Monsunregenzeiten bezeichnend (vgl. auch BEARD, 1967; BEADLE, 1981; BOWMAN, 2000 und GIVNISH, 2002). Abbildung 8 zeigt die wichtigsten Klimadaten der Daintree-Region und es wird deutlich, dass der Saisonalitätsindex 0.676 beträgt bei einem Variationsindex langjähriger Niederschläge von 0.238.

DIE PHÄNOMENE „IMMERGRÜN“ UND „LAUBWERFEND“

Wie auch immer der Begriff „Immergrüner tropischer Regenwald“ genau zu verstehen ist, darüber herrscht noch immer keine absolut einheitliche Auffassung: Manche wollen diesen Begriff sehr eng fassen und ihn nur auf extreme Regenwaldgebiete mit mehr als 5.000 Millimetern Jahresniedersch-

lag angewendet wissen, andere zählen auch Gebiete mit kurzen Trockenzeiten dazu, wenden diesen Begriff also in einem weiteren Sinne an. Als entscheidende allgemein anerkannte Hauptbedingung für die Existenz eines Regenwaldes gilt jedoch das Regime gleichmäßig über das Jahr verteilter hoher Niederschläge bei gleichbleibenden hohen Temperaturen. Selbstverständlich müssen in diesem Zusammenhang noch weitere Gegebenheiten berücksichtigt werden, ansonsten bestünden weite Teile der Tropen nur aus einem Regenwaldtyp. Als Nebenfaktoren wären hier zu nennen: kürzer oder länger währende, wenn auch seltene Trockenperioden, verschiedene starke Hangneigungen mit entsprechender Bodenerosion, verschiedene Struktur und Zusammensetzung des Bodens, Höhenlage und Vorherrschen von Schwarz- oder Weißwasser.

Tropische Regenwälder sind ver-

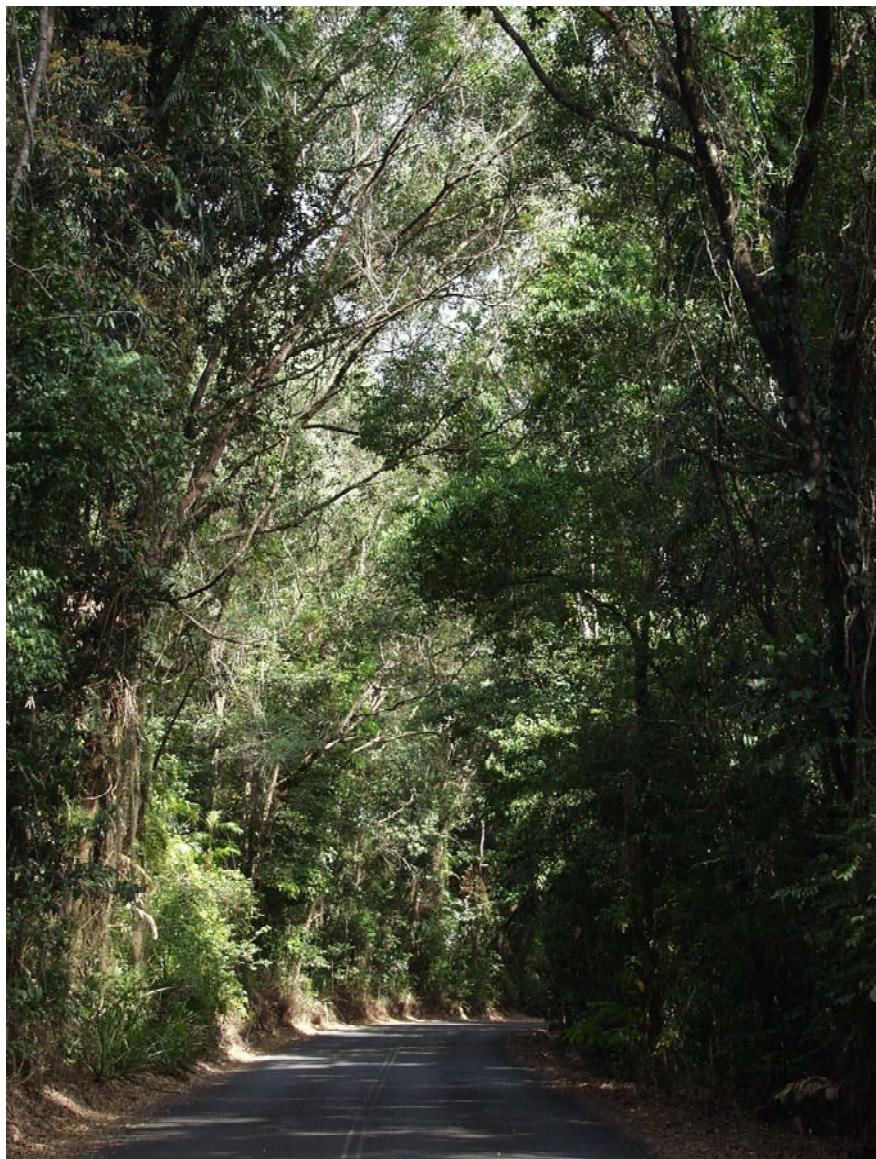


Abb. 4 - Lowland-Rainforest-Typ unter 400 m NN am Cape Tribulation.

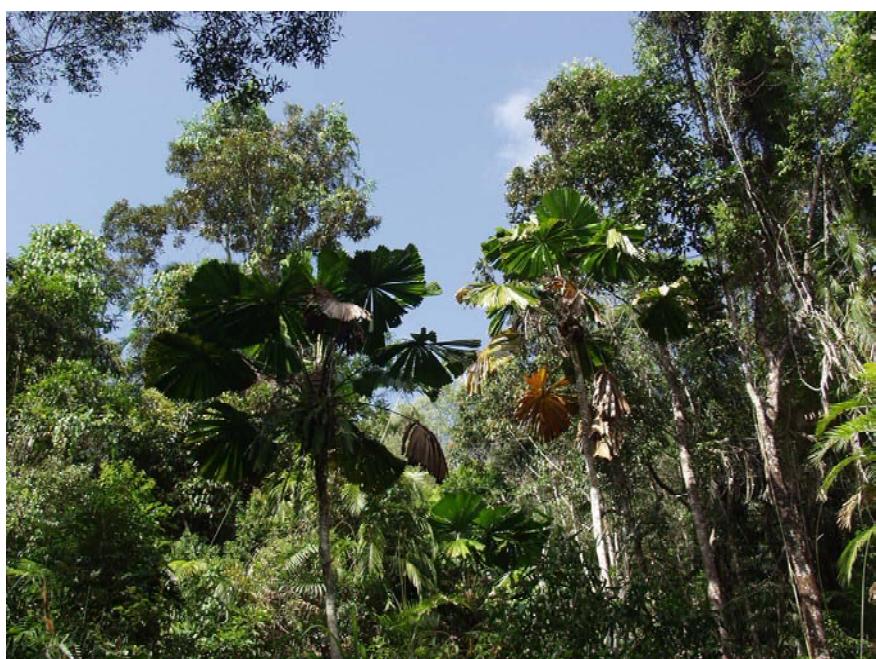


Abb. 5 - Upland Rainforest-Typ zwischen 400 und 1200 m NN mit *Licuala ramseyi* auf feuchten Böden.

breitet in Großklimaten mit einem Jahresmittel von ungefähr 24-28° Celsius. Im Gegensatz zu den gleichförmigen Temperaturen während des Jahres kommt es im Verlaufe eines Tages jedoch zu teilweise erheblichen Temperaturschwankungen. Mittlere tägliche Temperaturschwankungen können bis zu 12° Celsius betragen und die Differenzen zwischen absoluten Minima und Maxima können sogar 20° Celsius übersteigen. Das Mikroklima des tropischen Regenwaldes weicht deshalb erheblich vom oben geschilderten Großklima ab: Tägliche Temperatur- und Luftfeuchtigkeitsschwankungen weisen beispielsweise nur noch minimale Werte auf. Sie sind am Boden nahezu konstant, betragen 1-3° Celsius und nehmen mit steigender Höhe über dem Boden allerdings rasch zu. Für sehr dichte Regenwälder ist deshalb eine ständig wasser dampfgesättigte Luft am Boden charakteristisch (ADAM, 1992, 1994; CONDIT *et al.*, 2000; JOHNSON, 2005). Dies wirkt sich auch in den Daintree-Regenwäldern aus.

Das Phänomen „laubabwerfend“ kann für die Daintree-Regenwälder vor allem klimatisch begründet werden: Die ausgeprägte Saisonalität der Monsune und Passate mit einem Saisonalitätsindex von größer > 1 und einem Variationsindex langjähriger Niederschläge von > 0.3 (nach BOWMAN und PRIOR 2005) begründen offenbar diese Erscheinung. Das Phänomen „Immergrün“ in tropischen Regenwäldern mit einem Anteil von bis zu 25 Prozent laubabwerfender Bäume ist bedingt durch ein Klima ohne ausgeprägte Saisonalität, der Saisonalitätsindex liegt hier < 0.8 und zeigt gleichzeitig einen geringen Variationsindex langjähriger Niederschläge mit Werten von 0.1 bis 0.3. Der geringe Anteil immergrüner Arten und der hohe Anteil laubwerfender Arten im australischen Regenwaldgebiet, wie ihn die Tab. 1 aus unserem Untersuchungsgebiet von Daintree belegt, bezeugt dieses. Hier haben wir einen Saisonalitätsindex von > 1.0.

Von der geographischen Lage und der klimatischen Situation her könnte man indes aber einen höheren Anteil laubwerfender Arten im Daintree-Gebiet erwarten. Von den zahlreichen Baumarten des Gebietes gehören insgesamt 31 Vertreter zu den laubwerfenden, also teillimmergrünen Gehölzen, die anderen sind obligat immer grün. Die laubwerfenden Arten sind aber allesamt nur kurzfristig laubwerfend, also „*brevi-deciduous*“. Jetzt kann man nach den Gründen fragen für dieses Phänomen des viel höheren Anteils immergrüner

Arten im Daintree-Gebiet als erwartet: Es bieten sich insgesamt drei Hypothesen an, die wir kurz nennen wollen. Hypothese 1 wäre: Relativ hohe Niederschläge von durchschnittlich 85 Millimeter während der drei trockensten Monate sind dafür verantwortlich. Hypothese 2 wäre zu begründen mit extrem feuchten lokalen Bedingungen gerade an Berghängen und in Tallagen mit bis zu 65 Prozent Oberflächenabfluss der tropischen Regengüsse und extremer Auswaschung der Böden mit nachfolgender Nährstoffarmut (BENSON, 1993). Hypothese 3 begründet dieses Phänomen mit einer hohen Anzahl plesiomorpher Familien im Daintree-Gebiet. Wir wollen dies in Kapitel „Plesiomorphe Pflanzenfamilien“ weiter ausführen.

STRUKTUR DER DAINTREE-WÄLDER

Von den in den Abb. 4 bis 7 gezeigten Regenwaldtypen aus der Höhenabfolge der Dividing Range wollen wir nur den Tieflagen-Typ und den Bergregenwald eingehender beleuchten:

Die große Feuchtigkeit im Lowland-Rainforest, dem Tieflagen-Regenwald, auch nach mehreren regenlosen Tagen, ist besonders auf den starken nächtlichen Taufall zurückzuführen, der vom Kronendach der Bäume in die tiefen Schichten abtropft. Sehr wichtig für den ausgeglichenen Temperaturverlauf ist vor allem eine Abschwächung der Sonneneinstrahlung im Waldinneren. Oberste Schichten des Regenwaldes sind mit zahlreichen sehr hohen Emergenten aufgebaut (Abb. 7): Sie stehen über einem mehr oder weniger geschlossenen Kronendach. Lianen und Epiphyten siedeln sich vorzugsweise auf diesen höchsten Bäumen an. Eine wesentliche Abschwächung der Lichtintensität geht in der unteren geschlossenen Kronenschicht in 25 bis 40 Metern Höhe vor sich. Die Krautschicht und der Aufwuchs erlangen dort 3 bis 10 Meter Höhe. Die Erdoberfläche ist meist nur spärlich bewachsen. Die letztendlich noch auf den Boden auftreffende Lichtmenge beträgt ungefähr 0,1 bis 1 Prozent des Tageslichtes, eine eigentliche Bodenschicht fehlt daher meistens (WEBB *et al.*, 1976). Trotz solcher geringen Lichtintensitäten sind auch in den unteren Regionen des Regenwaldes nur noch speziell angepasste Pflanzen anzutreffen: So findet man *Selaginella*-Arten, oder Laub- und Lebtermose, die mit 0,2 Prozent des Tageslichtes auskommen. Des weiteren trifft



Abb. 6 - Mountain Rainforest-Typ zwischen 800 und 1200 m NN im Atherton Tableland.



Abb. 7 - Highland Rainforest-Typ von 1200 bis 1379 m NN am Thornton Peak mit Blick auf das Kronendach.

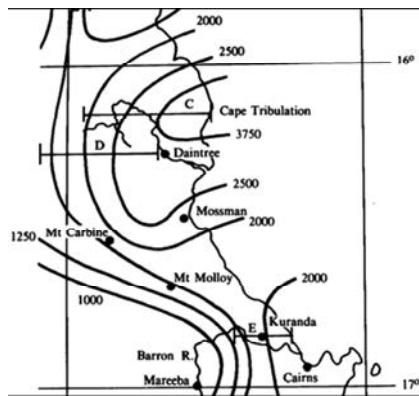


Abb. 8 - Jahresniederschläge an der Ostküste von Queensland (nach Tracey 1982).

Tab. 1 - Laubwerfende Bäume aus Angiospermen-Familien im Daintree River - Cape Tribulation-Gebiet (aus HEISE-PAVLOV et al., 2008).

Familie	Baumarten insgesamt	laubwerfend	% laubwerfende Arten
Apocynaceae	7	1	14.28
Boraginaceae	2	1	50.00
Combretaceae	5	5	100.00
Euphorbiaceae	33	1	3.03
Fabaceae	5	2	40.00
Lecythidaceae	1	1	100.00
Meliaceae	21	2	9.52
Mimosaceae	23	3	13.04
Moraceae	25	6	24.00
Rubiaceae	14	2	14.28
Sapotaceae	13	1	7.69
Solanaceae	3	1	33.33
Sterculiaceae	7	3	42.85
Urticaceae	2	1	50.00
Verbenaceae	10	1	10.00



Abb. 9 - Fluss im Regenwald von Mosman.

man auf Hymenophyllaceen und andere Farne, Lycopodiaceen mit 0,25-0,5 Prozent; selbst Vertreter der schattentoleranten Begoniaceae, Rubiaceae und Zingiberaceen kann man bei diesen Lichtintensitäten finden. Hohe Temperaturen, die intensive CO₂-Produktion und eine einseitige Auswaschung bestimmter basischer Verbindungen der Böden führen zur Anreicherung von Al₂O₃ und Eisen-III-oxiden (Fe₂O₃) im tieferen

Untergrund mit der charakteristischen ziegelroten Farbe vieler tropischer Böden als Roterde oder Latosole. Die angesichts des üppigen Wachstums überraschende Nährstoffarmut hängt hier mit den gesteigerten Abbauprozessen organischen Materials zusammen. Das feuchtwarme Klima fördert die Mineralisierung und bietet Pilzen, Bakterien, sowie anderen Mikroorganismen ideale Lebensbedingungen. Zu einer Humusanreicherung kommt es daher nicht. Aus solchen Gebieten abfließendes Wasser ist so mineralarm, dass seine Leitfähigkeit der von destilliertem Wasser entspricht und die ausgeschwemmten Humin- und Fulvosäuren erzeugen eine teeblaue Wasserfarbe solcher oligotrophen dunkel gefärbten Flüsse. Die Verweildauer pflanzlicher Nährstoffe im Boden verkürzt sich hier extrem, kaum freigesetzt, werden sie schon wieder aufgenommen und zur Bildung höher organisierter Strukturen herangezogen. Nährstoffarmut und üppige Vegetation sind daher kein Widerspruch, das sieht man besonders gut im Nationalpark von Mosman bei Daintree (Abb. 9).

Das gesamte Nährstoffpotential des Regenwaldes befindet sich deshalb

Kronen 30 bis 40 Meter, einzelne freistehende Exemplare der Emergenten bis 55 Meter, die darunterliegende mittlere Schicht wird 20 bis 30 Meter hoch (Abb. 10). Die untere Schicht, hauptsächlich aus Jungwuchs bestehend, wird im Mittel etwas über 10 Meter hoch. Ihre Kronen sind oft spindelförmig ausgebildet. Unter der Baumschicht wachsen, je nach Lichtbedingungen verschiedene Sträucher, hohe Kräuter und eine Bodenschicht aus Keimpflanzen, kleinen Kräutern, Moosen, Farnpflanzen und Moosfarne. Gegenüber anderen tropischen Nebelwäldern nehmen Lianen und Epiphyten hier im allgemeinen keine so dominierende Rolle ein; besonders die Epiphyten weisen im montanen Regenwald eine zehnmal größere Individuenzahl auf.

Im Daintree-Gebiet kann man beispielsweise auf einem Hektar mehr als 120 verschiedene Baumarten finden. Bestimmte morphologische Strukturen wiederholen sich und sind somit ein fester Bestandteil tropischer Vegetation. Es sollen hier nun einige charakteristische Merkmale tropischer Wälder erläutert werden:

Brettwurzelbildung entsteht durch einseitiges Wachstum der Wurzeloberfläche (im Boden setzt sie sich also nicht fort) und formt auf diese Weise »Bretter«, die bis zu 9 m am Stamm hinaufreichen und eben so weit, nach außen hin niedriger werdend, radial auslaufen können (Abb. 11). Verständlich werden diese sonderbaren Wurzelformen, wenn man die Sauerstoffarmut vieler tropischer Böden bedenkt. Eine niedrige Sauerstoff-Konzentration hemmt das Längenwachstum und fördert die Seitenwurzelbildung. Infolgedessen sind die Bäume durch die flachreichenden Wurzelsysteme nur mangels verankert und erreichen durch Brettwurzeln eine höhere Standfestigkeit. Dieser Effekt ist aber nur nebensächlich. Wichtigste Aufgabe jener oftmals gewaltigen Oberflächenvergrößerung scheint eine zusätzliche Sauerstoffversorgung der unteren Pflanzengewebe zu sein. Darauf deutet auch das gehäufte Vorkommen von Lentizellen in den unteren Stammbereichen hin (Abb. 12).

Luft- und Stelzwurzeln bilden sich aus der Sprossachse und stellen damit Adventivwurzeln dar. Besonders auffällig präsentieren solche Wurzeln bei der Gattung *Ficus* (Abb. 12). Je nach Hauptfunktion der sprossbürtigen Wurzeln werden diese mit entsprechenden Namen belegt: Atem-, Luft-, Stützwurzeln oder Stelzwurzeln gewährleisten der Pflanze neben ihrer Verankerung

in der lebenden Pflanzenmasse sowie in den geringen Mengen unzersetzter, toter Pflanzenbestandteile. Da die Wurzeln freiwerdende Nährstoffe sofort aufnehmen, gibt es vor Ort keine Nährstoffverluste und eine hohe Strukturvielfalt. Die tropischen „Upland-Rainforests“ - die montanen Regenwälder sind im allgemeinen dreistöckig aufgebaut: Im Schnitt erreicht die obere Baumschicht mit ihren schirmförmigen

ebenfalls die ausreichende Sauerstoffversorgung basalliegender Pflanzengewebe (Abb. 13 und 14), wie es auch besonders LÜPNITZ (2000, 2003) betont.

Luftwurzeln sind eine Eigenart vieler tropischer Epiphyten. Sie sorgen für eine gesicherte Wasser- und Nährstoffzufuhr und ermöglichen vielen Pflanzen dadurch die epiphytische Lebensweise und damit die Unabhängigkeit von humosen Substraten. Viele Orchideen, *Ficus*-Arten und Aronstabgewächse sind mit solchen Luftwurzeln ausgestattet.

Sehr charakteristisch für die Wälder um Daintree sind ferner Kauliflorie und Ramiflorie: Darunter versteht man die Ausbildung von Blüten und Früchten an verholzten Stämmen und Ästen. Eine Entwicklung der Blüten erfolgt aus ruhenden Knospen, welche plötzlich austreiben. Kauliflorie tritt fast nur bei Baumarten der unteren Schichten auf und wird daher als Anpassung an die in diesem Bereich häufige Fledermausbestäubung (Chiropterogamie) gedeutet. Ramiflorie zeigen auch die höherwüchsigen *Brachychiton*-Arten (Abb. 15). Ohne Tierbestäubung ließe sich eine gesicherte Samenbildung wohl kaum erreichen, bedenkt man die reiche Artenzahl der tropischen Wälder und den Abstand zwischen zwei Individuen der gleichen Art in einem Gebiet.

Durch eine frühzeitige Ausdifferenzierung entstehen oft langausgezogene Blattspitzen, die man als Träufelspitze bezeichnet. Sie sollen für eine beschleunigte Ableitung des Wasserfilms von der Blattoberfläche sorgen. Diese ökologische Funktion wird aber mehr und mehr in Frage gestellt, zumal Träufelspitzen gerade in den extremen Regenwäldern fehlen. Es handelt sich eher um eine von vielen Blattformen, die aufgrund der optimalen Lebensbedingungen der Tropen »toleriert« wird und im Laufe des langen Evolutionsprozesses bei vielen taxonomisch differenzierten Gattungen und Arten zu einer ähnlichen Blattgestalt geführt hat.

Unter dem Begriff Laubschüttung versteht man die plötzliche, oft innerhalb von ein bis zwei Tagen erfolgende Entfaltung eines Triebes mit Zweigen und Blättern (Abb. 16). Aufgrund des schnellen Streckungswachstums wird dieser Vorgang als Laubausschüttung bezeichnet. Er dient der schnellen Regeneration von Blättern. Da das Festigungsgewebe diesem raschen Wachstum nicht sogleich folgen kann, hängt der gesamte »ausgeschüttete« Spross schlaff herab und verleiht diesem ein scheinbar abgewinkeltes Aussehen. Die Triebe sind blassgrün bis rötlich. Nach

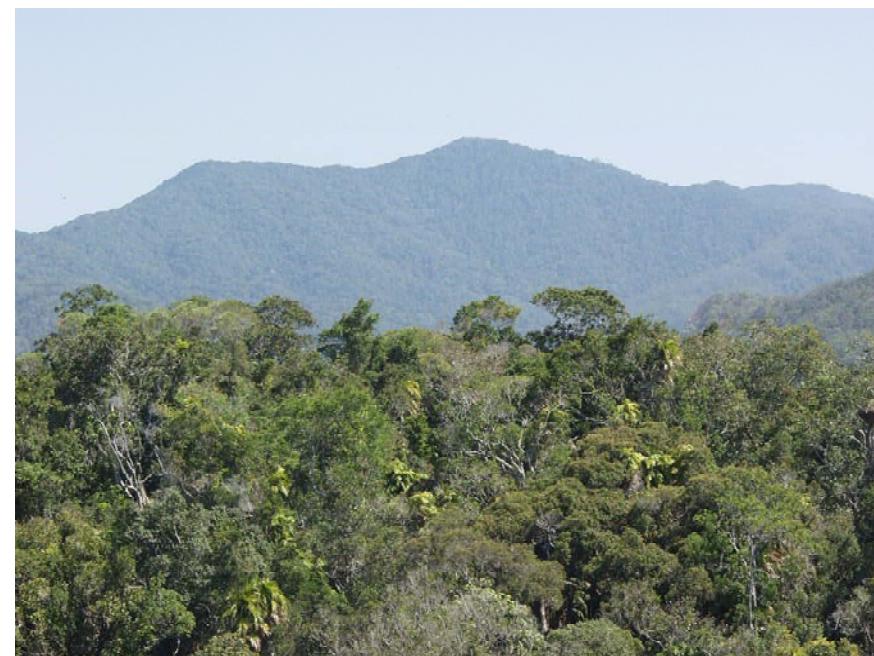


Abb. 10 - Struktur des Regenwaldes von Kurunda mit *Cerbera floribunda* (Apocynaceae), *Ficus pantoniiana* (Moraceae), *Agathis robusta*, *Araucaria cunninghamii* (beide Araucariaceae) und *Archontophoenix alexandrae* (Arecaceae) als Emergenten in der oberen Baumschicht.



Abb. 11 - Brettwurzel bei *Ficus pleurocarpa* (Moraceae).



Abb. 12 - Luftwurzeln bei *Ficus pleurocarpa* (Moraceae).

dem allmählichen Erstarken des Triebes nimmt das Flächenwachstum der Blätter zu, gleichzeitig bildet sich das Blattgrün aus. »Schüttellaub« ist schlecht gegen Verdunstung geschützt und daher nur im feuchten Klima anzutref-

fen; dieses Phänomen wird auch als Chamouflage gegen gefräßige monophage Pflanzenschädlinge gedeutet. Alle diese coevolutiven Anpassungen finden wir auch in den Regenwäldern von Daintree.

GESCHICHTE DER REGENWÄLDER VON DAINTREE

Wegen der früheren Landverbindung nach Papua-Neuguinea und des damit verbundenen intensiven Flore-



Abb. 13 - Wurzelschleier von *Ficus virens* (Moraceae) können mächtige vorhangartige Baumriesen bilden, die als „Curtain Fig“ bezeichnet werden.

naustausches mit diesem Raum zeigen die tropischen Regenwälder von Queensland allgemein mit 60 Prozent ihrer Arten enge pflanzengeographische Beziehungen zur indomalaiischen Paläo-

tropis und beherbergen - mehr als anderswo - zahlreiche evolutionsbiologisch „primitive“ Arten, von denen einige sogar noch mit Arten des Gondwanalandes identisch sind (KETO, 1989;

LÜPNITZ, 1998; WEBB und KIKKAWA, 1990; WEBB und TRACEY, 1994; MILLER et al., 2005). Gattungen wie *Orites*, *Lomatia*, *Oreocallis* oder *Agathis* geben ferner Hinweise auf die früheren



Abb. 14 - Nachdem die Würgefeige *Ficus pleurocarpa* (Moraceae) einen Trägerstamm umwurzelt hat und ihn zum Absterben brachte, bleibt im Lauf der Zeit nur noch ein Hohlraum übrig, der erneut weiteren Wurzeln Raum gibt.

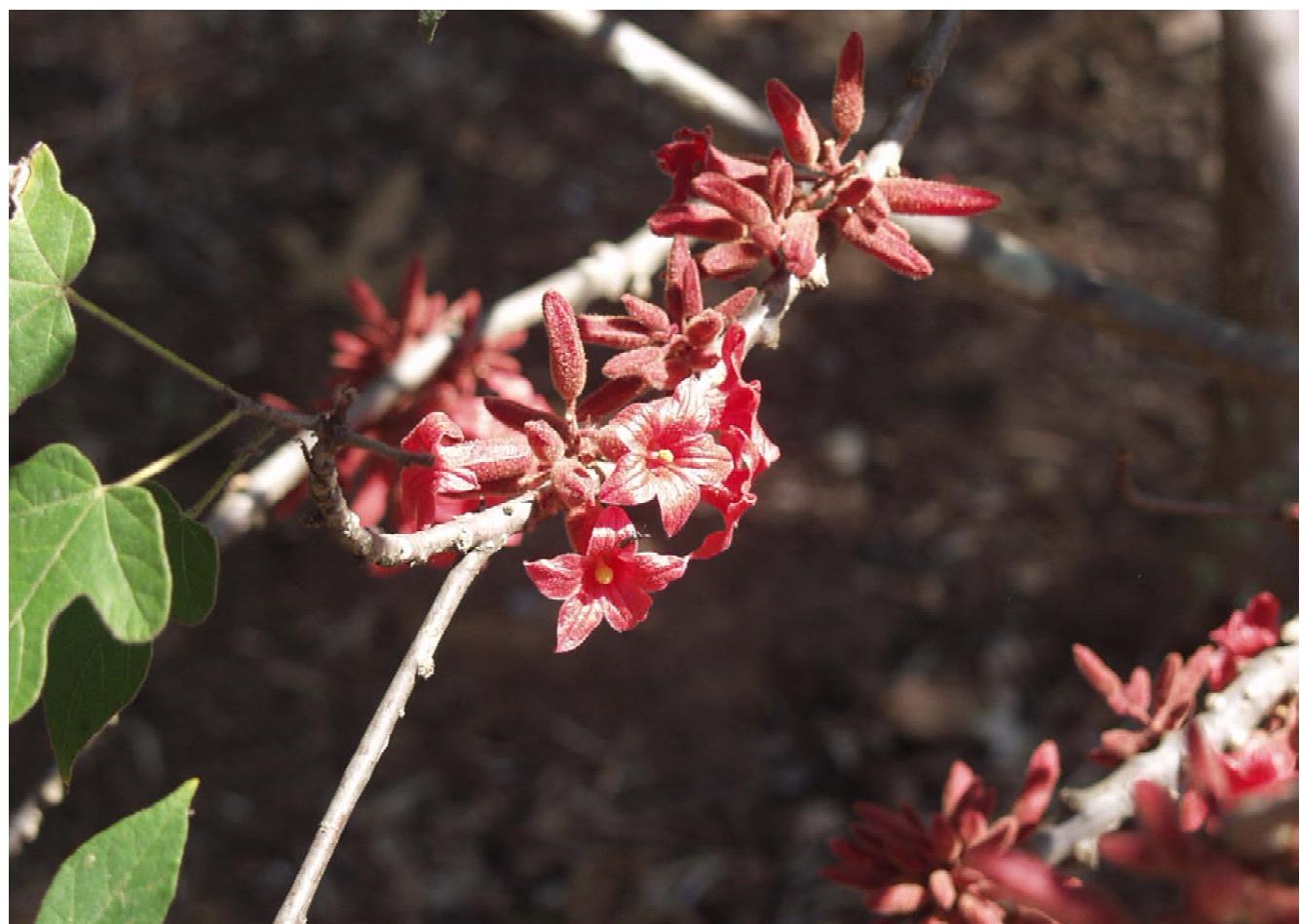


Abb. 15 - Ramiflorie bei *Brachychiton bidwillii* (Sterculiaceae).

Verbindungen mit Südamerika, Neukaledonien und Neuseeland im alten Kontinent von Gondwana.

Die letzte Epoche des Mesozoikums, die Kreidezeit, datieren wir ab 144 Millionen Jahre bis 65 Millionen Jahre vor heute; ihre Differenzierung in Ober- und Unterkreide erfolgt nach den wichtigen Leitfossilien unter anderem der Ammoniten, Muscheln und Foraminiferen. Umfangreiche Flachmeere müssen in dieser Zeit existiert haben, als sich Laurasia und Gondwana endgültig voneinander lösten und der Südatlantik sich bildete. Die Tethys wurde durch die beginnende Norddrift Indiens verschmälert und schließlich nachfolgend verdrängt. In der Pflanzenwelt gab es die wichtige evolutive Neuerung: Während am Beginn der unteren Kreidezeit noch die jurassischen Bärlappe, Farne und Gingkogewächse vorherrschten, traten am Ende der Unterkreide, in der Gault-Epoche ab etwa 110 Millionen, erstmals die Angiospermen auf und bildeten zusammen mit den schon existierenden Gymnospermen, beispielsweise den Araucariaceen, den Cycaden und den Baumfarne eine neue spezifisch gondwanische Flora. Dazu



Abb. 16 - Laubschütten ist eines der wichtigen Kennzeichen der Tropenwaldbäume. Da diese keine Knospen besitzen, bilden sich in kürzester Zeit beblätterte Triebe als Ganzes, deren Chlorophyllbiosynthese und Festigung erst später erfolgen. Die frisch „ausgeschütteten“ Sprosse hängen zunächst schlaff herab und sind auf Grund ihres hohen Carotinanteils gelblich bis rötlich gefärbt.



Abb. 17 - *Castanospermum australe* (Fabaceae) wächst in den Regenwäldern Australiens zu einem stattlichen Baum mit wickenartigen Blüten heran.



Abb. 18 - *Agathis robusta* (Araucariaceae) ist ein endemischer Baum in Queensland, der von nur zwei Lokalitäten derzeit bekannt ist. Eine südliche wächst auf Frazer-Island und in der Gegend von Maryborough und eine nördliche Population im Atherton Tableland westlich von Cairns.

gibt es eine umfangreiche Literatur z.B. bei ANDREWS (1916), AXELROD (1959, 1966), SMITH (1982), SMITH *et al.* (1994), CRANE (1985), CRANE *et al.* (1995), DILCHER (2001), DILCHER und CRANE

(1984), MARTIN (1978), RAVEN und AXELROD (1974), WALKER und CHEN (1987), WHITE (1989) sowie SOLTIS *et al.* (2000). Zahlreiche Angiospermen-Familien gelangten über die damals noch

zusammenhängenden Landmassen von Südamerika und der Antarktis auf den australischen Kontinent, wo sie noch heute mit charakteristischen Vertretern unter anderem am Aufbau der tropi-



Abb. 19 - *Ficus variegata* (Moraceae) als Beispiel einer laubabwerfenden Baumart, Cape Tribulation, Queensland.



Abb. 20 - Die kletternde Palme *Calamus moti* (Arecaceae) ist in den Regenwäldern Queenslands endemisch.

schen Regenwälder vertreten sind. Als Beispiele seien nach THORNE (1976) sowie WHIFFIN und HYLAND (1986) die Pflanzenfamilien der Rutaceae, die Lauraceae, Fabaceae, Epacridaceae, Styliadiaceae, Myrtaceae und Proteaceae an-

geführt.

Der nachfolgende Zerfall von Gondwana zwischen 115 und 40 Millionen Jahren vor heute führte zur Lage der Kontinente der Südhemisphäre in ihrer heutigen Position, mit den zuneh-

mend erweiterten Ozeanen dazwischen. Die Drift des australischen Kontinents weg von Gondwana erfolgte mit einer Nordwärtsbewegung bis 15° südlicher Breite. Konsequenzen sind die Endemiten und die Großdisjunktionen gond-



Abb. 21 - *Platycerium superbum* (Aspleniaceae) wächst auf Regenwaldbäumen ausschließlich in Queensland.

wanischer Florenelemente in Südamerika und im australisch-pazifischen Raum. Subtropische und tropische Regenwälder beherrschten während des Neogens bis etwa 1,8 Millionen Jahre vor heute den australischen Kontinent

und die Proteaceae, Myoporaceae, Mimosaceae und die Myrtaceae erfuhren in jener Zeit eine starke Ausbreitung. Erst im nachfolgenden Pleistozän kam es zur Austrocknung der Landmassen Australiens mit entsprechendem Rück-

gang der Regenwälder auf ihr heutiges Areal und auf Refugialstandorte, wie dies ausführlich bei KEMP (1981), AUDLEY-CHARLES (1987), CHEN (1988), WHITE (1989), KERSHAW *et al.* (2005) sowie POTT (2005) dargestellt ist.

Tab. 2 - Pflanzenfamilien und Anzahl ihrer Arten und Gattungen mit ausschließlich immergrünen Baumarten im Daintree-Cape Tribulation-Gebiet. Die phylogenetisch alten Familien sind kursiv hervorgehoben (aus HEISE-PAVLOV et al., 2008).

Familie	Artenzahl	Familie	Artenzahl	Familie	Artenzahl
Actinidiaceae	1	Erythroxylaceae	1	Oleaceae	5
Agavaceae	1	Eupomatiaceae	1	Pittosporaceae	4
Alangiaceae	1	Fabaceae	5	Proteaceae	18
Anacardiaceae	6	Flacourtiaceae	7	Rhamnaceae	5
Annonaceae	7	Grossulariaceae	2	Rhizophoraceae	1
Aquifoliaceae	1	Hammamelidaceae	3	Rosaceae	1
Araliaceae	7	Hernandiaceae	2	Rutaceae	29
Balanopaceae	1	Icacinaceae	4	Santalaceae	1
Bignoniaceae	1	Idiospermaceae	1	Sapindaceae	37
Burseraceae	3	Lauraceae	48	Simaroubaceae	1
Casuarinaceae	1	Loganiaceae	1	Symploceae	1
Celastraceae	7	Malvaceae	2	Theaceae	1
Clusiaceae	5	Melastomataceae	2	Tiliaceae	1
Coryncarpaceae	1	Monimiaceae	8	Thymelaeaceae	2
Cunoniaceae	5	Myristicaceae	1	Ulmaceae	5
Davidsoniaceae	1	Myrsinaceae	3	Violaceae	1
Dilleniaceae	1	Myrtaceae	69	Xanthophyllaceae	2
Ebenaceae	1	Nyctaginaceae	1		
Elaeocarpaceae	14	Ochnaceae	1		



Abb. 22 - Die kauliflore *Davidsonia pruriens* var. *jerseyana* (Davidsoniaceae) wächst natürlich, aber nicht sehr häufig, als endemischer Baum in den Regenwäldern Queenslands.

PLESIOMORPHE PFLANZENFAMILIEN

Die fast 1.200 am Waldaufbau Australiens beteiligten Blütenpflanzen repräsentieren heute zugleich 25 Prozent aller australischen Gattungen. Angesichts solcher Artenfülle werden hier nur einige Beispiele hervorgehoben: Dazu gehören die überaus attraktive *Oreocallis wickhamii*, das monotypische *Castanospermum australe* (Abb. 17), *Schefflera actinophylla* und weiter lan-

deinwärts *Agathis robusta* (Abb. 18). Von den übrigen zahlreichen Baumarten des Waldes sind einige Vertreter aus der Gattung *Ficus* besonders häufig (Abb. 19).

Detaillierte Angaben zum Thema der Paläoendemiten sind vor allem KERSHAW (1970), WILLIAMS (1979-1987), BEADLE (1981), JONES (1971), PEARSON (1992), WEBB und TRACEY (1994) sowie HYLAND et al. (2002) zu entnehmen. Die unteren Gehölzschichten der Wäl-

der werden von zahlreichen solcher Arten bestimmt, eine davon ist die Palme *Archontophoenix alexandrae*. Von den Lianen sind insbesondere *Calamus australis* und *Flagellaria indica* sowie einige Würgefeigen und Araceen hervorzuheben (Abb. 20). Zur Gruppe der Epiphyten gehören vor allem Flechten, Moose, Farne und Orchideen. Auffällig sind Humus und Wasser sammelnde Nest-Epiphyten (z. B. *Asplenium*-, *Cytharia*- und *Platycerium*-Arten) sowie Wasser speichernde Orchideen, etwa die seltene *Phalaenopsis amabilis* (Abb. 21). Allgemein lässt sich jedoch sagen, dass die tropischen Regenwälder Queenslands im Vergleich mit denjenigen Afrikas, Südamerikas und Südostasiens eher arm an Epiphyten sind. Ihre Bodenflora wird neben Baum sämlingen von zahlreichen Monokotylen, vor allem Zingiberaceae, Costaceae, Araceae und Orchidaceae, bestimmt. Ferner sind in den nordostaustralischen Regenwäldern über die Hälfte aller australischen Farn-Arten anzutreffen, wie es auch WALKER und CHEN (1987) und KETO (1989) betonen.

Die Wälder von Daintree besitzen obendrein eine unglaubliche Artenvielfalt: Allein im Daintree-River - Cape Tribulation-Gebiet konnten wir auf nur wenigen Hektaren Waldfläche insgesamt 517 verschiedene Baumarten feststellen. Diese gehören zu über 50 verschiedenen Pflanzenfamilien. Davon sind wiederum 25 Pflanzenfamilien australische Endemiten. Die wichtigsten Familien seien hier in der Tab. 2 aufgezählt:

LEBENDE FOSSILIEN

Die Daintree-Regenwälder sind zudem Zentren der Pflanzenevolution: Hier wachsen eine Reihe Archäoendemiten aus der Erdvergangenheit: Das Bärlappgewächs *Lycopodium squarrosum* verkörpert noch die Formen fossiler *Baragwanathia*, eines 450 Millionen Jahre alten Fossils, welches als eine der ältesten Landpflanzen der Erde gilt. Moosfarne und Baumfarne der Gattungen *Psilotum*, *Selaginella* und *Cyathea* repräsentieren noch die Steinkohlezeit des Karbon vor 350 bis 290 Millionen Jahren und Koniferen wie *Podocarpus* und *Prumnopitys* aus der Familie der Podocarpaceae sowie Cycadeen wie *Lepidozamia* und *Bowenia* ähneln noch immer ihren Vorfahren aus der Jurazeit vor 200 bis 140 Millionen Jahren. Dazu kommt eine hohe Zahl primitiver Angiospermen: Allein 7 von derzeit in Australien 19 bekannten Pflanzenfami-

lien dieser „alten“ Angiospermen wachsen im Gebiet. Das zeigt die Tab. 2. In den südamerikanischen Regenwäldern gibt es dagegen nur wenige „alte“ Angiospermen Familien. Diese Tatsache führte beispielsweise AXELROD (1959, 1966) sowie TAKHTAJAN (1969) zu dem Schluss, dass die Entwicklung der Angiospermen irgendwo in Asien oder in Austral-Asien stattgefunden haben muss, irgendwo zwischen Assuan und Fidschi, wie es auch WHITMORE 1981, RUSSEL und SMITH 1991 und MORLEY (2004) annehmen.

Besonders zu erwähnen sind in diesem Zusammenhang die seit über 110 Millionen Jahren nachgewiesenen „primitiven“ Angiospermen der Gattungen *Davidsonia*, *Noahdendron* und *Idiospermum*. Von der Baumgattung *Davidsonia* sind drei Regenwaldarten bekannt, von denen die kauliflore *Davidsonia pruriens* var. *jerseyana*, ein sehr dekorativer kleiner, schlanker, bis 10 Meter hoher Baum, auf die Wälder von Daintree beschränkt ist (Abb. 22). Dieser Baum ist sehr selten an seinen natürlichen Standorten, wegen seiner essbaren sauren Pflaumen werden *Davidsonia* aber auch in Plantagen kultiviert und ihre schmackhaften Früchte werden als „gourmet bushfood“ verkauft. Ihren Namen hat diese endemische Baumgattung nach DAVIDSON (1841-1923), einem Pionier des Zuckerrohranbaus in Queensland. *Davidsonia pruriens* ist eine Pionierpflanze in den Tieflagenregenwäldern und kann vom Meeressniveau bis auf eintausend Meter Meereshöhe in die montanen Wälder aufsteigen.

Die endemische Gattung *Noahdendron* ist sogar auf das Cape Tribulation-Gebiet beschränkt und man kennt nur die eine Art *N. nicholasi* entlang von kleinen Bächen, vor allem am Noah-Creek, dem sie auch ihren Namen verdankt (Abb. 23). Dort im Regenwald direkt an der Küste gibt es die weltweit einzige Population auf einer Fläche von 20 Hektar vom Strand bis in Höhen von maximal 100 Metern. Die Bäume von *Noahdendron nicholasi* werden etwa 10 Meter hoch, bilden also das untere Stratum der Tieflagenregenwälder. Dieser Baum wurde erst im Jahre 1981 entdeckt, er ist charakterisiert durch seine stark duftenden, rosafarbenen, bis sieben Zentimeter langen Blütentrauben mit hunderten von kleinen Einzelblüten, welche wiederum durch eingekrüllte Petalen in die Familie der Hamamelidaceae verweisen.

Auch *Idiospermum australiense* ist auf das Cape Tribulation-Gebiet beschränkt. Dieser alte, im Jahre 1972



Abb. 23 - Der kätzchenblütige Baum *Noahdendron nicholasi* (Hamamelidaceae) wurde erst 1981 im Noah-Creek von Daintree entdeckt.

wiederentdeckte Baum ist ebenfalls ein Relikt aus der Gondwanazeit und gilt als monotypischer Vertreter der Familie der Idiospermaceae. Der Begriff *Idiospermum* kommt von seiner merkwürdigen Frucht, welche Anlagen für vier oder sogar fünf Keimblätter besitzt. *Idiospermum australiense* erzeugt große Samen, die nur von wenigen Tieren verbreitet werden können. Eine Hypothese besagt, dass Vertreter der ausgestorbenen australischen Megafauna wichtige Verbreiter waren, die aber allesamt - mit Ausnahme der Cassowaries (Abb. 24) - ausgestorben sind. Diese Samen keimen nur nach endozoochorer Ausbreitung.

Idiospermum australiense gilt als eine der ursprünglichsten Blütenpflanzen, die nachweislich schon vor 110 Millionen Jahren schon existiert haben. Es ist ein immergrüner Baum von 20 bis

30 Metern Höhe mit quirlständig angeordneten 15 bis 20 Zentimeter langen Blättern und roten Blüten (Abb. 25). Die Früchte sind kugelförmig und zerfallen bei der Reife in vier Segmente und entlassen dann ihre Samen. Diese sind stark strychninhaltig und extrem giftig. Der Gattungsnname *Idiospermum* hängt damit zusammen und wird angeleitet vom griechischen „*Idio*“ - ungewöhnlich und „*spermum*“ - Samen. Das gilt auch für den Familiennamen der Idiospermaceae, welche in manchen botanischen Systematiken neuerdings jedoch erneut der Familie der Calycanthaceae unterstellt werden.

Nur das Ratten-Känguru (*Aepyprymnus rufescens*) ist heute noch in der Lage, die Samen von *Idiospermum* zu verbreiten, indem es sie vergräbt. Man nimmt an, dass ursprünglich die ausgestorbenen *Diprotodon*-Beutel-



Abb. 24 - Einer der faszinierenden, bis 2 Meter hohen flugunfähigen Vögel ist der südliche Cassowary (*Casuarius casuarius*), endemisch im Cape-Tribulation-Regenwald. Er frisst die großen Regenwaldfrüchte, vor allem die blaue Cassowary-Plum (*Cerbera floribunda*, Apocynaceae), die ihm die schöne Echt-Blaufärbung seiner Halsfedern garantiert und steuert damit die Ausbreitung der Fruchtbäume im Regenwald.



Abb. 25 - *Idiospermum australiense*, einzige Art der Gattung *Idiospermum* (Idiospermaceae), ist eine der primitivsten bekannten Blütenpflanzen der Erde, die seit mehr als 100 Millionen Jahren im Daintree-Regenwald lebt.

tiere und einige weitere inzwischen ausgestorbene australische Beuteltiere ebenfalls dazu in der Lage waren.

Idiospermum australiense wurde zuerst vom deutschen Botaniker Ludwig DIELS (1874-1945) als *Calycanthus australiense* im Jahre 1902 beschrieben. Danach wurde sie vergessen und galt als ausgestorben, bis sie im Jahre 1971 wiederentdeckt wurde, nachdem man ihre giftigen Samen in den Mägen verendeter Rinder identifiziert hatte. Der australische Botaniker BLAKE (1910-1973) hat diese Art aufgrund ihrer besonderen Anatomie und ihres Blütenaufbaus reklassifiziert und im Jahre 1972 neu beschrieben. Die Population in Daintree ist klein. Die Blüten von *Idiospermum* sind protogyn, einige Individuen sind andromonözisch, andere hermafroditisch. Die Blüten halten nur 10 bis 16 Tage, und während dieser Zeit differenzieren sich die Blütenorgane räumlich und zeitlich als männlich und als weiblich mit entsprechendem wechselndem Duft oder Blütenfarbwechsel. Dies lockt jeweils verschiedene Pollinatoren an, von denen besonders verschiedene Arthropoden, insgesamt beispielsweise mehr als 10 verschiedene Käferarten mit verschiedenen Formen von Eiablage, Larvalentwicklung und Nahrungsaufnahme in extremer Form als Bestäuber angepasst sind (WORBOYS und JACKES, 2005).

MANGROVEN

Bei den Mangroven handelt es sich um küstennahe Wälder, die durch die Gezeiten und über Flussmündungen regelmäßig von Salzwasser überflutet werden. Von der Landseite und über den Regen wird Süßwasser zugeführt. Der Salzgehalt der Mangroven ist daher sehr starken Schwankungen unterworfen. Die in diesem Lebensraum gediehenden Pflanzen, vor allem die Rhizophoraceae, haben in Anpassung an diese Verhältnisse im Laufe ihrer Evolution verschiedene Adaptionen entwickelt (ADAM, 1994; BRIDGEWATER, 1994).

Ebbe und Flut bewirken Wassersstandsschwankungen von mehreren Metern. Dem hierbei entstehenden mechanischen Druck müssen die Pflanzen ebenfalls standhalten. Mangroven wachsen ausschließlich in den Gezeitenzonen tropischer Meere. Ihre größte Ausdehnung erfahren diese Wälder an den Küsten, die vor hohem Seegang und starken Brechern geschützt sind. Dies ist der Fall an der pazifischen Ostküste Queenslands, der ja das riesige Barrier-Korallenriff vorgelagert ist.



Abb. 26 - Undurchdringliches Dickicht von Atem- und Stelzwurzeln bestimmt das Bild des Untergrundes der Mangrove im Daintree-Gebiet.



Abb. 27 - Die epiphytisch lebende *Myrmecodia beccari* (Rubiaceae) gehört zur myrmekophytischen Gattung *Myrmecodia*, die in Südostasien und in Australien beheimatet ist. Sie bildet eine Symbiose mit Pilzen und Ameisen auf Ästen von Bäumen der Mangrove.

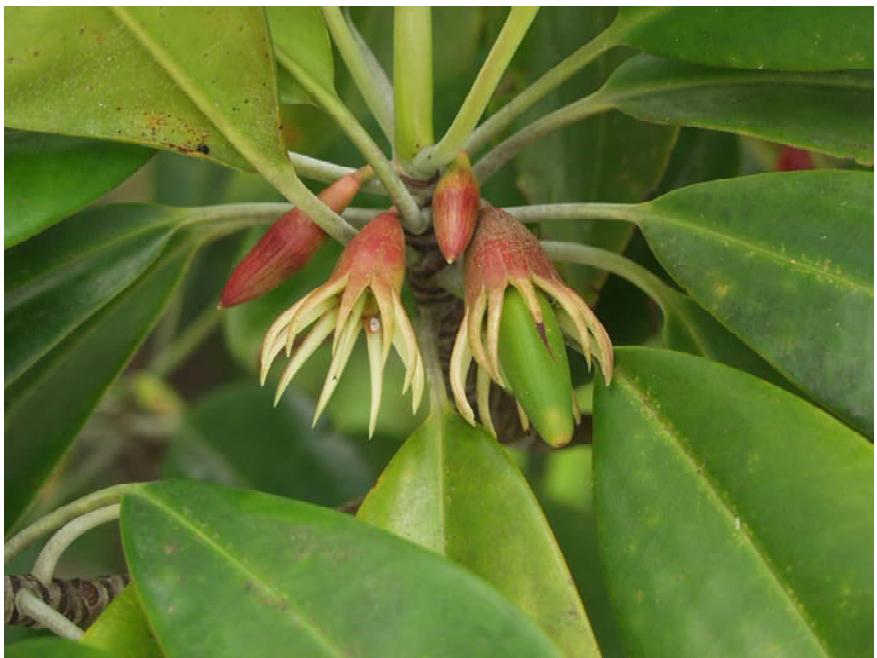


Abb. 28 - Bald nach der Befruchtung entwickelt sich bei *Bruguiera gymnorhiza* (Rhizophoraceae) ein lang auswachsendes Hypocotyl, das der Pflanze bei der Etablierung am Standort hilft.



Abb. 29 - *Rhizophora stylosa* (Rhizophoraceae).

Je weiter man an dieser Küste nach Norden reist, desto ausgeprägter und vielfältiger erscheint der grüne Gürtel der Mangroven, bis diese an der Mündung des Daintree River nördlich der Stadt Cairns ihre größte Ausdehnung erfahren (TOMLINSON, 1986).

Nördlich und südlich des Äquators erreichen Mangroven normalerweise ihre Verbreitungsgrenze am 32sten Breitengrad. Eine Ausnahme bildet *Avicennia marina*, eine widerstandsfähige niedrigwüchsige Pflanze, die auf der nördlichen Halbkugel auf der Sinai Halbinsel und auf der japanischen Insel Yakushima ihre am weitesten vorgezogenen Standorte erreicht und in Australien am 38sten Breitengrad im Staate Victoria den südlichsten Punkt (POTT, 2005). Dies ist wohl die härteste, anpassungsfähigste Mangrove, welche oft Pionier-Bestände bildet und mit wechselndem Salzgehalt des Standorts am besten zurecht kommt. An der australischen Pazifikküste wird diese Art mit einer Varietät geführt: *Avicennia marina* var. *australasica*. Es gibt noch eine Reihe anderer Arten, die alle in der Familie der Avicenniaceae zusammengefasst sind. Den größten Anteil an der Pflanzengemeinschaft der Mangroven haben jedoch die Rhizophoraceae, denen auch die stattlichsten Vertreter angehören, Bäume, bis 20 Meter hoch, der Gattung *Rhizophora* und *Bruguiera* (Abb. 26). Allen gemeinsam ist ihre große Anpassungsfähigkeit an ihren außergewöhnlichen Standort, die salzhaltigen Schlammzonen an Küsten und Flüssen. Salz- und Süßwasser sind sehr wechselnd miteinander gemischt, der Salzgehalt ist großen Schwankungen ausgesetzt. An extremen Standorten bilden sich Salzverkrustungen auf dem Schlamm und den Blättern der Pflanzen. Alle Mangroven bilden Wurzeln aus, die aus dem Schlamm herausragen, Pneumatophoren genannt, die die Fähigkeit haben, der Pflanze Luft zurückzuführen und sie im haltlosen Schlamm zu verankern. Dazu breiten sich die Wurzeln weit aus, in den kuriosesten Formen liegen sie dem weichen Untergrund auf. Eine weitere Form der Anpassung ist das Vorkeimen der Sämlinge an der Elternpflanze, die Pseudoviviparie. Erst der weit entwickelte Keimling löst sich von der Mutterpflanze. Er ist vorbereitet, im weichen Schlamm sofort Fuß zu fassen und ohne Unterbrechung sein Wachstum fortzusetzen. Gewiss schwimmen auch eine Menge dieser Keimlinge bei Flut davon, sinkt das Wasser wieder, werden entfernt liegende Teile der Küste besiedelt. So dehnt sich der Mangrove-Gür-



Abb. 30 - Cape Tribulation - where the rainforest meets the reef.

tel aus, landgewinnend und küstenbefestigend.

Im Mangrovenwald überall unter den Bäumen wächst der Mangrovenfarn *Acrostichum speciosum*, ein Vertreter der Familie der Arecaceae. Im Kronendach einiger Mangrove-Bäume hängen kopfüber spezielle Epiphyten, die Ameisen beherbergen: Die Blätter der *Myrmecodia beccarii* sind fleischig und ihre verdickten Stiele stachelig, knollenförmig aufgebläht. Das Innere dieser Knette ist ein Labyrinth von Gängen, in dem bestimmte Ameisen mit der Pflanze in Symbiose leben (Abb. 27; vgl. POTT und HÜPPE, 2007). Im Inneren der Mangrovenwälder erheben sich die baumartigen, hohen Pflanzen von *Bruguiera gymnorhiza* und *Bruguiera parviflora*. Die schönsten Mangroven sind sie wahrhaftig, mit ihren auffallenden roten Blüten (Abb. 28). Zwischen den blank glänzenden grünen Blättern erscheint auch die Rinde mancher Pflanzen rötlich. Diese beiden Arten stattlicher Mangroven kommen nicht nur im nördlichen Australien vor, sondern im ganzen indonesischen Archipel und Malaysia.

Die größte Mangrove in diesem Gebiet ist *Rhizophora stylosa* mit weit

ausgreifenden Stelzwurzeln und stark duftenden, gelblich-weißen Blüten (Abb. 29). Zugleich mit den Blüten hängen an jedem Zweig „Pfeile“ von Keimlingen, an dem großen Baum sind es sicher hunderte. Sie drohen jeden Augenblick in den Schlamm abzustürzen, wo sofort neues Leben beginnt. Stelzwurzeln bewirken eine größere Standfestigkeit der Pflanzen, die im Lebensraum Mangrove vor allem der Kraft der Wassermassen bei Ebbe und Flut standhalten müssen.

Bei Jungpflanzen kann man die wie Finger aus dem unteren Teil des Stammes herauswachsenden Wurzeln erkennen. Weitere Mangroven-Gattungen aus der Familie der Rhizophoraceae sind: *Bruguiera*, *Kandelia*, *Ceriops*. Die Rhizophoraceae sind pantropisch verbreitet. Weitere wichtige Mangrovenpflanzen sind *Sonneratia* (Sonneratiaceae) und *Avicennia* (Verbenaceae), die ebenfalls teilweise die oben besprochenen Anpassungen aufweisen. Im indomalaiischen Raum erreichen die Mangroven den größten Artenreichtum.

Die australischen Mangroven werden von ca. 50 verschiedenen Gehölzen aufgebaut und erweisen sich damit als vergleichsweise artenreich (ADAM,

1994; BRIDGEWATER, 1999). Von hochwüchsigen geschlossenen Beständen bis hin zu niedrigwüchsigen offenen Gebüschen sind alle Ausbildungsformen vertreten. Sie sind unter geeigneten Bedingungen gewöhnlich an den Küsten im Norden Australiens verbreitet, nehmen bezüglich ihrer Wuchshöhe, Artenzahl und Ausbreitung nach Süden hin allmählich ab und fehlen in Tasmanien gänzlich. Die markantesten Arten sind *Avicennia marina*, *Aegiceras corniculatum*, *Bruguiera gymnorhiza* und *Rhizophora mucronata*. In den besonders artenreichen Mangroven im Norden von Queensland lässt sich eine deutliche Zonierung erkennen. Landeinwärts oder seeseitig sind dann meist ganz spezielle Arten vorherrschend. Ferner gibt es landesweit zahlreiche Übergänge von Mangroven zu niedrigwüchsigen krautigen Wattgemeinschaften hinüber in die Unterwasserwelt des Great Barrier Reef. Hier hat sich eine erweitert einmalige Konstellation verschiedener typischer Ökosysteme auf engstem Raum benachbart herausgebildet: Die Inselwelt der Korallen, die Unterwasserwelt der Riffe, die Mangroven mit ihren langgestreckten Riffbögen und Flussmündungen bilden hier

ein einmaliges Ensemble von unübertrefflicher landschaftlicher Schönheit, wie es auch JONES (1971), DAVIES (1975) und LÜPNITZ (2003) betonen (Abb. 30).

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PINUS SYLVESTRIS HEIGHT AND RADIAL GROWTH STRATEGIES IN THE NINE PHYTO-SOCIOLOGICAL ASSOCIATIONS OF TRENTINO-ALTO ADIGE (NORTH-EASTERN ITALY)

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ABSTRACT

Scots pine height and radial growth are compared in nine *Pinus sylvestris* associations of north-eastern Italy (Trentino and Alto-Adige). Tree growth and growth dynamics are assessed using stem and tree-ring measurements in 31 Scots pine stands; on the whole 445 trees have been measured and 715 cores have been made and studied.

It has been possible to evaluate the growth of the pine in the different plant associations and the site fertility according to parameters, such as the stem volume calculated at a cambial age of 100 years (V_{100}), which are independent from the tree age.

It has been found that, among all associations, the lowest stem volume (mean $V_{100} = 82 \text{ dm}^3$ at 100 years) and consequently the lowest growth is reached in oligotrophic *Sphagnum* peat bogs, where *Vaccinio uliginosi-Pinetum sylvestris* develops. These sites are unproductive and their major interest is for vegetation preservation, due to the presence of rare plant species.

Growth is slightly better (179 dm^3) for *Molinio coeruleae- Pinetum sylvestris* in meso-eutrophic bogs on hydro-morphic flat soils, and for *Chamaecytiso purpurei-Pinetum sylvestris* (143 dm^3) in warm sites (extreme southern location) with soil erosion. Higher values are measured for *Antherico liliaginis-Pinetum sylvestris* (213 dm^3), established on dry eroded sites, and for *Salici eleagni-Pinetum sylvestris* (221 dm^3) on river shores with episodic alluvial events. Volume growth is 245 dm^3 for *Erico-Pinetum sylvestris*, a climax on dry southern carbonate slopes. The endemic *Astragalo vesicarii-Pinetum sylvestris* association in dry and xeric inner valleys shows higher stem volumes (292 dm^3), probably due to longer sunny periods, and a similar tree growth (298 dm^3) is found in the Gramineae-rich *Pinus* association (*Molinio litoralis-Pinetum sylvestris*), on marly slopes. Optimal growth values are found in mesophilous *Vaccinio vitis-ideae-Pinetum sylvestris* (470 dm^3), established on siliceous plateaux or gentle slopes fa-

cing north. Only the sites of the two latter associations can be taken into account for timber production.

As far as growth dynamics is concerned, four different patterns of yearly increase in basal area have been established: basal area growth curves show a plateau growth for both *Chamaecytiso purpurei-* and *Molinio coeruleae-Pinetum sylvestris*, almost no ageing effect for *Erico-*, *Molinio litoralis-*, and *Antherico liliaginis-Pinetum sylvestris*, a quick start before decrease (pioneer behaviour) for *Astragalo vesicarii-*, *Vaccinio vitis-ideae-*, and *Salici eleagni-Pinetum sylvestris*, and a linear stagnation for *Vaccinio uliginosi-Pinetum sylvestris*.

Therefore, *Pinus sylvestris* ecological plasticity enables this species to withstand a huge number of growth conditions by using different radial growth strategies, and leads to large variability in wood production (over a 1 to 5.75 scale according to phytosociology, and a 1-22 scale for individual stands). Furthermore these results suggest that growth tables for this conifer could be improved by including information of site vegetation.

KEYWORDS: *Pinus sylvestris*, dendroecology, forest typology, wood production, tree growth.

RIASSUNTO

È stato confrontato l'accrescimento radiale e verticale del pino silvestre in nove associazioni vegetali del Trentino-Alto Adige. Dallo studio, basato su 193 rilievi fitosociologici (in MINGHETTI, 2003), 31 rilievi dendrometrici, 445 piante misurate e 715 carote analizzate, è emerso che il pino silvestre assume modelli di crescita e di dinamica della crescita ben definiti e differenziati a seconda delle diverse condizioni ecologiche dove si trova a crescere.

Sulla base di indicatori di crescita indipendenti dall'età degli alberi, come il volume del tronco calcolato all'età cambiale di 100 anni (V_{100}), risulta che l'associazione tipica delle torbiere a sfa-

gni oligotrofiche (*Vaccinio uliginosi-Pinetum sylvestris*), mostra i minori valori in assoluto (media $V_{100} = 82 \text{ dm}^3$ all'età di 100 anni). La crescita degli alberi è migliore (179 dm^3) nel *Molinio coeruleae-Pinetum sylvestris*, associazione caratteristica nelle torbiere basse meso-eutrofiche, su suoli gleyformi, e nel *Chamaecytiso purpurei-Pinetum sylvestris* (143 dm^3), associazione pre-alpina di stazioni rupestri carbonatiche con suoli rendziniformi di erosione. Valori di crescita relativamente maggiori sono espressi dall'*Antherico liliaginis-Pinetum sylvestris* (213 dm^3), un'associazione delle ripide e soleggiate scarpate silicate su suoli aridi e soggetti a erosione, e dal *Salici eleagni-Pinetum sylvestris* (221 dm^3), una pineta dei greti carbonatici dei torrenti endoalpini soggetti a periodiche alluvioni. Un volume di 179 dm^3 si riscontra nell'*Erico-Pinetum sylvestris*, la classica pineta a erica endoalpina dei versanti calcarei e dolomitici esposti a sud, su suoli rendziniformi soggetti a rapido prosciugamento. L'*Astragalo vesicarii-Pinetum sylvestris*, associazione endemica delle aride valli endoalpine come la Val Venosta, mostra un volume del tronco leggermente superiore (292 dm^3), valore probabilmente da attribuire alla maggiore insolazione delle sue stazioni. Simili valori di crescita (298 dm^3) si riscontrano nel *Molinio litoralis-Pinetum sylvestris*, pineta ricca in graminacee su substrati argillosi, mentre i valori ottimali (470 dm^3) sono espressi dal *Vaccinio vitis-ideae-Pinetum sylvestris*, che si insedia in stazioni mesofile su substrati silicatici.

Per quanto riguarda la dinamica della crescita invece sono stati definiti quattro differenti modelli di accrescimento dello spessore degli anelli in funzione dell'età: le curve di incremento dell'area basale mostrano un plateau di crescita sia nel *Chamaecytiso purpurei-P.s.* sia nel *Molinio litoralis-P.s.*; non si notano invece variazioni nell'incremento dell'area basale in funzione dell'età nell'*Erico-, Molinio litoralis-* e *Antherico liliaginis-P.s.*, mentre l'*Astragalo vesicarii-*, il *Vaccinio vitis-ideae-* e il *Salici eleagni-P.s.* evidenziano

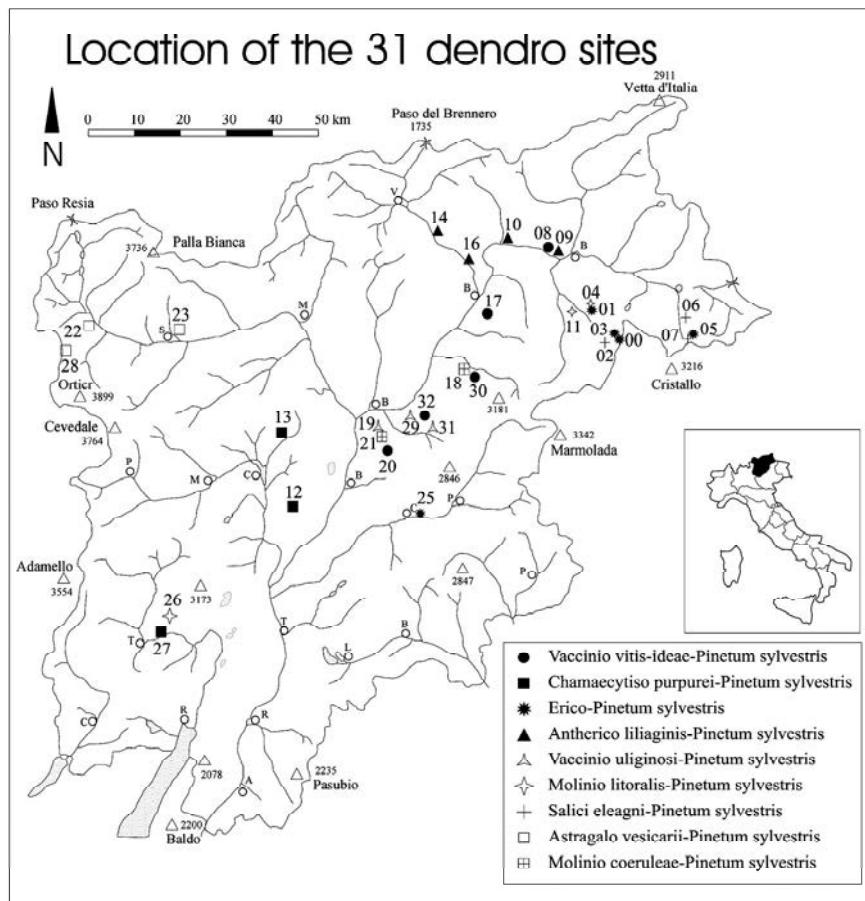


Fig. 1 - Location map of the 31 dendro-sites in the Trentino and Alto-Adige region (north eastern Italy) within 9 phyto-sociological associations.

una partenza rapida prima di una decrescita, andamento tipico delle piante pioniere; la pineta delle torbiere alte oligotrofiche, il *Vaccinio uliginosi-P.s.*, mostra invece una stagnazione lineare.

In definitiva, l'elevata plasticità ecologica del pino silvestre permette a questa specie di far fronte a una grande varietà di condizioni ecologiche adottando di volta in volta differenti strategie di crescita radiale e, di conseguenza, esprimendo una grande variabilità nella sua produzione in legno (una variabilità fino a 5,7 volte tra le diverse associazioni e fino a 22 volte se si confrontano invece le singole aree di campionamento). Questi risultati inoltre suggeriscono che le tabelle di crescita di questa conifera dovrebbero essere sempre corredate di informazioni ecologico-vegetazionali.

INTRODUCTION AND AIMS

Scots pine (*Pinus sylvestris* L.) is a rustic tree species that is able to grow over a large range of situations (MINGHETTI, 2003), with a vast distribution area that extends from Catalogna (Spain) to Siberia (Russia). It can face harsh growing conditions such as sandy xeric areas (GUILLET & LABERCHE, 1972), calcareous soils on steep slopes in dry

inner Alpine valleys (BARTOLI, 1966), sandy soils in Central Europe, marly slopes in Jura mountains, as well as acid bogs with *Sphagnum* (ELLENBERG, 1988).

This conifer produces wood of good quality (NEPVEU & BLACHON, 1989) and can colonize very different soils, especially sites unfavourable for other species, which explains its great value for foresters. Unfortunately, timber production is often reduced by the low fertility of sites where Scots pines usually grow. Most of the time, the better areas are colonized by species more resistant to inter-specific competition, except when Scots pine is temporarily established as a pioneer species on abandoned lands.

Thus, large variations in tree growth are expected due to the extreme ecological plasticity of Scots pine. However, up to now little is known about how site conditions influence Scots pine growth, although some results obtained in Finland have clearly underlined their importance (VANNINEN *et al.*, 1996).

The purpose of this study, carried out in Italy, is to investigate height and radial growth of *Pinus sylvestris* in different phytosociological associations, and to determine the relationships between growth and site conditions.

Our aim is: 1) to quantify wood production and to discover which are the most productive associations; 2) to compare tree growth strategies in very different situations.

MATERIAL AND METHODS

SITES AND SAMPLING

The study area was located in the Trentino-Alto Adige region, in north-eastern Italy. Phytosociological study of Scots pine forests has already been carried out there (MINGHETTI, 2003) using Braun-Blanquet classical methods, in forests where this species represents more than 80% of the trees. It covered the entire region and all growth conditions where *Pinus sylvestris* can be established. A vegetation matrix of 193 relevés totaling 334 different plant species (and 5,569 abundance/dominance coefficients) was analysed to establish a forest typology. Nine main phytosociological associations were distinguished, four on limestone soils and five on siliceous soils. Complete floristic lists were published by MINGHETTI (2003), with details on classification results and soil analyses.

In each of these nine associations, from 2 to 5 stands were sampled (depending on the extension of each association), with a total of 31 stands (Fig. 1, Tab. 1). The stand density, the development phase and the disturbance (natural or anthropic) history were similar and therefore comparisons were made possible. In particular we chose stands that have reached a stable mature phase without signs of recent human intervention.

In each site a complete soil analysis was carried out, with soil description, granulometry analysis, determination of soil pH at different depths, C, N, CO_3^- , Fe, Al, Si, and Mn measurements (in MINGHETTI, 2003). The dominant Scots pines of each site were measured using a Blume-Leiss dendrometer for tree height, and with a tape for stem circumference, including bark (CORONA, 1969). By dominant trees we mean the 4 largest trees ha^{-1} in a multi-layered or unevenaged stand. Increment cores were taken on those trees at 1.30 m above ground using a Pressler borer, with two cores per stem taken in opposite directions perpendicularly to the slope line. A total of 445 pines (mean value of 15 trees per stand) and 715 cores (mean value of 23.1 cores per stand) were studied. Ring widths were measured under a binocular microscope

Tab. 1 - Topography (altitude, slope, aspect), location and bedrock of the 31 dendro-sites.

N°	Dendro site	Forest typology	Altitude	Slope	N = 0, E = 90 °	GPS location		Bedrock		
			m.	deg	Aspect	deg	Latitude	Longitude		
0	Val di Tamores 2	Erica herbacea	*	1615	60	S	200	46° 38' 52"	12° 02' 19"	Limestone rocks
1	Val di Tamores 1	Erica herbacea	*	1367	40	SW	230	46° 40' 54"	11° 58' 07"	Dolomite scree
2	Alberi	Salix eleagnos	+	1416	20	SW	220	46° 39' 29"	12° 00' 02"	Torrential alluvial fan
3	Val di Tamores 3	Erica herbacea	*	1730	40	SW	230	46° 38' 54"	12° 01' 50"	Limestone scree
4	Val di Tamores	Molinia litoralis	◆	1231	35	SW	220	46° 41' 23"	11° 57' 12"	Marl
5	Val di Landro	Erica herbacea	*	1418	40	S	200	46° 38' 17"	12° 14' 27"	Limestone scree
6	Lago di Landro 1	Salix eleagnos	+	1414	0	flat	0	46° 38' 06"	12° 14' 09"	Peebles, gravel
7	Lago di Landro 2	Salix eleagnos	+	1201	0	flat	0	46° 38' 03"	12° 13' 58"	Peebles, gravel
8	Chines 1	Vaccinium vitis-ideae	●	1192	35	N	0	46° 48' 27"	11° 51' 30"	Crystalline schist
9	Chines 2	Antherico liliaginis	▲	1052	45	W	250	46° 48' 20"	11° 51' 04"	Crystalline schist
10	Vendoies	Antherico liliaginis	▲	910	40	S	180	46° 49' 09"	11° 44' 56"	Flaked granite
11	Piccolino	Molinia litoralis	◆	1239	38	SE	130	46° 40' 25"	11° 53' 44"	Marlous-limestone
12	Vervó	Chamaecytisus purpureus	■	924	35	S	180	46° 18' 33"	11° 07' 39"	Dolomite
13	Brez	Chamaecytisus purpureus	■	963	40	SE	130	46° 25' 14"	11° 05' 54"	Flaked dolomite
14	Maules	Antherico liliaginis	▲	823	40	SSW	220	46° 50' 20"	11° 31' 58"	Blocks
16	Aicha	Antherico liliaginis	▲	800	35	SSW	220	46° 46' 48"	11° 38' 00"	Granite
17	Val di Eores	Vaccinium vitis-ideae	●	1343	10	NW	320	46° 40' 29"	11° 40' 00"	Schist
18	Passo Pinei 1	Molinia coerulea	申	1357	5	SE	130	46° 34' 48"	11° 37' 35"	Ryholithe
19	Totes Moos	Vaccinium uliginosum	**	1524	0	flat	0	46° 26' 58"	11° 22' 50"	Ryholithe
20	Nova Ponente 1	Vaccinium vitis-ideae	●	1400	10	NW	310	46° 25' 12"	11° 24' 17"	Ryholithe
21	Nova Ponente 2	Molinia coerulea	申	1387	0	flat	0	46° 25' 14"	11° 24' 18"	Ryholithe
22	Monte Chiaro	Astragalus vesicarius	□	1398	30	ESE	120	46° 39' 12"	10° 33' 35"	Crystalline schist
23	Paces	Astragalus vesicarius	□	1396	45	S	180	46° 38' 09"	10° 48' 50"	Crystalline schist
25	Tésero	Erica herbacea	*	1201	25	SSE	140	46° 17' 29"	11° 31' 58"	Dolomitic alluvial fan
26	Piné	Molinia litoralis	◆	1414	40	SSE	160	46° 05' 42"	10° 48' 07"	Marl
27	Monte Amolo	Chamaecytisus purpureus	■	812	45	SE	120	46° 02' 53"	10° 45' 02"	Dolomite
28	Prato Allo Stelvi	Astragalus vesicarius	□	1399	50	SSE	150	46° 36' 40"	10° 33' 56"	Crystalline schist
29	Tschigger Moos	Vaccinium uliginosum	**	1330	0	flat	0	46° 27' 39"	11° 27' 36"	Ryholithe
30	Passo Pinei 2	Vaccinium vitis-ideae	●	1387	10	N	0	46° 34' 52"	11° 37' 27"	Porphyry blocks
31	Landschnerier	Vaccinium uliginosum	**	1320	0	flat	0	46° 27' 42"	11° 28' 45"	Ryholithe
32	Tschigger Moos	Vaccinium vitis-ideae	●	1330	0	flat	0	46° 27' 39"	11° 27' 36"	Ryholithe

(magnified by 12 to 50 times) and cross-dated with classical dendroecological techniques (SCHUELLER & ROLLAND, 1994).

MEASUREMENTS AND FORMULAE

For each tree the stem volume was calculated using TABACCHI & TOSI (1992) equations, based on *Pinus sylvestris* diameter and height values measured in 151 forests growing in northern Italy (altitudes from 380 m to 1,820 m), and including the Trentino and Alto-Adige areas:

$$\text{Stem volume (in dm}^3\text{)} = A + B \times D^2 \times H + C \times D^2 \times H^2$$

with $A=2.8459$, $B=4.1776 \times 10^{-2}$, $C=-2.4970 \times 10^{-4}$, $D=\text{diameter at } 1.30 \text{ m}$ (in cm) and $H=\text{tree height (in m)}$ (a, b, and c values published by TABACCHI & TOSI, 1992).

The mean dominant tree height, diameter and volume were calculated for each site. Similarly, mean values were obtained for each phytosociological group by averaging several dendro-sites.

Site comparisons are only practicable when the same tree age is used everywhere, for instance at 100 years. We also computed the stem radius at 100 years (R_{100}) by adding up the 100

first ring-width values (from stem centre). Tree height at 100 years (i.e. site index H_{100}) was derived from a height growth model based on a Chapman-Richards equation (similar to those obtained for Spruce trees by Brandini *et al.* 1994), in the form:

$$H(\text{age}) = B_1 \times [1 - \exp(-B_2 \times \text{Age})]^{B_3}$$

with $B_1=13.87983$, $B_2=0.03474$, and $B_3=1.536154$. (B coefficients adjusted with our data set). Tree volumes at 100 years (V_{100}) were finally obtained using TABACCHI & TOSI (1992) equation $V_{100}=A+B \times D_{100}^2 \times H_{100}+C \times D_{100}^2 \times H_{100}^2$.

In each stand, all ring-widths formed on different trees at the same cambial age (but at different years) were averaged to compute the mean ring-width growth curve as a function of tree age. Then these values were added together to give the radial growth curve of the whole stand (SCHUELLER & ROLLAND 1994). For a given forest, the mean ring-width $\langle C_k \rangle$ as a function of cambial age (k) was given by:

$$\langle C_k \rangle = \frac{\sum_{j=1}^{N_k} C_{jk}}{N_k}$$

, by averaging all Scots pine rings at every given cambial age. Here, C_{jk} stan-

ds for the ring-width (expressed in 0.01 mm) formed by the tree number j when it was k years old. Thus, k ranges from 1 (at pith) to Age_j (under bark) for this tree j. N_k is the number of trees that reach this age k.

Furthermore, the mean radius $\langle R_k \rangle$ as a function of cambial age was calculated by:

$$\langle R_k \rangle = \sum_{i=1}^{i=k} \langle C_i \rangle$$

, by cumulating the successive mean ring-widths (from pith until a given age k). This value (hereafter called "radial growth") does not include bark. Because of geometrical effects (circular rings get larger), the mean ring-width $\langle C_k \rangle$ decreases after a few years. That is why a better estimation of the amount of wood formed each year was given by the area comprised between two successive rings, $dS_k = (S_k - S_{k-1})$ with $S_k = \pi \cdot R_k^2$. This value dS_k is hereafter called "yearly increase in basal area". The yearly increase in tree height was not analysed here. In a first step, these calculations were achieved for each of the 31 individual stands, and then by gathering trees of different locations to characterize tree growth of all stands that belong to the same phytosociological group.

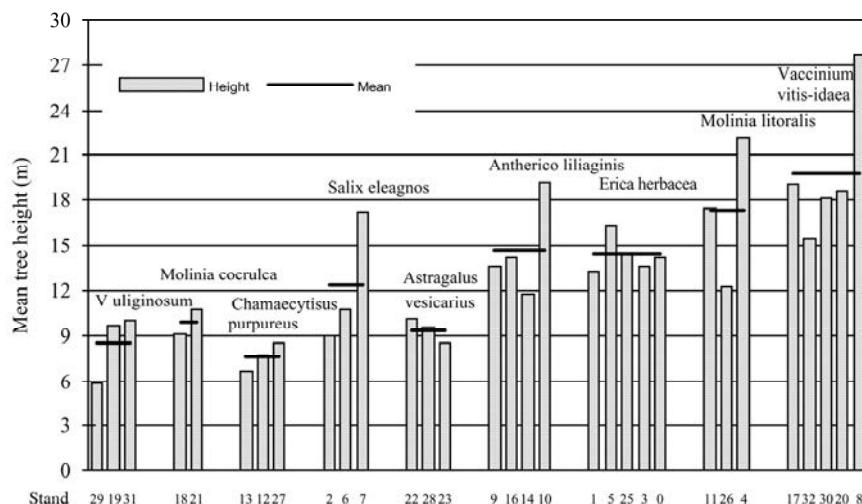


Fig. 2 - Mean dominant tree height (in m.) for 31 *Pinus sylvestris* stands divided into 9 phytosociological groups, and average values (horizontal lines) for each group.

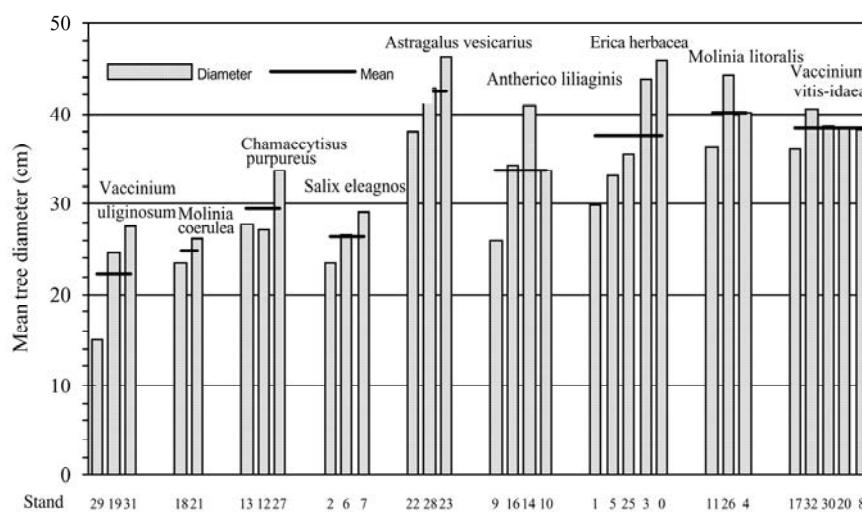


Fig. 3 - Mean dominant tree diameter (in cm; with bark and at a height of 1,30 m) for 31 *Pinus sylvestris* stands divided into 9 phytosociological groups, and average values (horizontal lines) for each group.

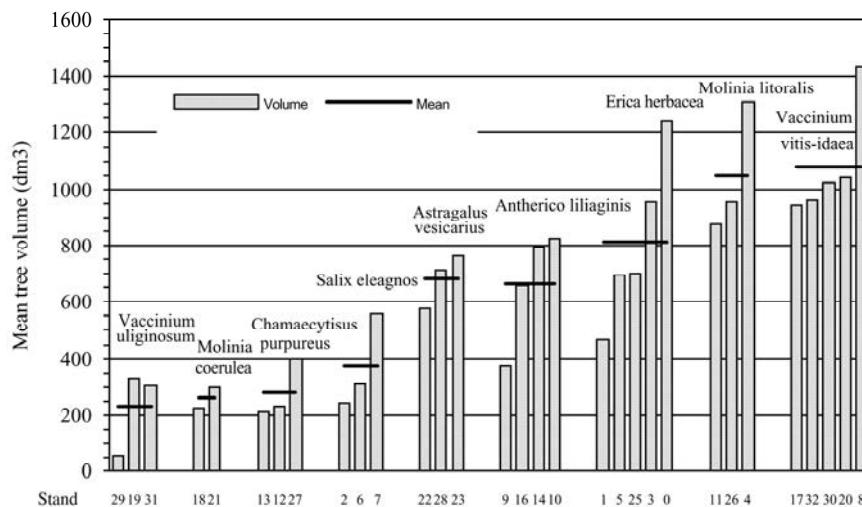


Fig. 4 - Mean dominant tree volume (whole stem, in dm³) calculated for 31 *Pinus sylvestris* stands according to 9 phytosociological groups using H and D measurements. Average values (horizontal lines) for each group.

3. RESULTS

3.1. PHYTO-SOCIOLOGICAL ASSOCIATIONS

Pinus sylvestris L. grows over a large range of conditions (AGOSTINI,

1955) which explains the considerable variations in the floristic relevés observed here (MINGHETTI, 2003), as well as already reported in France (BARTOLI, 1966) or in Spain (PAUSAS, 1994). In the Trentino-Alto Adige region, nine main

floristic associations were distinguished (MINGHETTI, 2003):

- On carbonate bedrocks:

1a) The *Erico-Pinetum sylvestris* Braun-Blanquet in Braun-Blanquet *et al.* 1939 is the inner alpine Spring Heath-Pine forest and represents the most characteristic association on carbonate bedrocks. Its floristic structure shows a clear basiphilous character: besides *Erica herbacea*, the most frequent species are *Coronila vaginalis*, *Polygala chamaebuxus*, *Gymnadenia odoratissima* and *Carex alba*. This association colonizes southern steep slopes (30°), especially on dolomite bedrock and hard limestone, from 1,000 to 1,600~1,700 m. The typical soil is a colluvial rendzina (Rendosol and Dolomitosol after AFES, 1995, or Calcaric Phaeozems according to FAO classification, 1990): it is superficial, with basic pH, rich in carbonate and shows rapid drainage;

1b) The *Carex humilis Pinus* forest forms a sub-association (*Erico-Pinetum sylvestris caricicetosum humilis* Minghetti 2003) during pioneer phases;

2) The *Chamaecytiso purpurei-Pinetum sylvestris* (Aichinger) Minghetti 2003 is the south-alpine Spring Heath-Pine forest that grows in the southern part of Trentino, in a less continental climate than *Erico-P.s*. It contains some broadleaf species, like *Fraxinus ornus*, *Ostrya carpinifolia*, and other south-alpine or Illyrian species, like *Chamaecytiso purpureus*, *Asperula purpurea* and *Cotinus coggygria*, not to be found in the inner Alps. This association develops on superficial calcareous soils with basic pH (Rendosols and Dolomitosols after AFES, 1995, or Calcaric Phaeozems according to the FAO classification of 1990) and in general with characteristics very similar to those of *Erico-P.s*;

3) The *Molinio litoralis-Pinetum sylvestris* Schmid ex Etter 1947 is located on marly slopes with many Graminaceae such as *Molinia arundinacea*, *Calamagrostis varia*, *Brachypodium rupestre*, *Brachypodium pinnatum* and Cyperacees like *Carex flacca*. The soils, belonging to the family of calcareous brown soils, are clayey, basic and rich in carbonate (Calcosols, according to AFES 1995, or Calcaric Pheozems according to FAO classification, 1990). They are repeatedly soaked with water although in the dry summer the topsoil may dry;

4) On fluvial and river shores, with episodic alluviation processes, the water balance is strongly contrasted with alternating drought and flooded periods on the topsoil, whereas the water

reserve remains quite constant at lower depths. Deeply rooted hygrophilous species (such as various willow species and *Alnus incana*) co-occurred with superficially rooted drought-tolerant species. Scots pine is there a temporary pioneer species and forms the *Salici eleagni-Pinetum sylvestris* Oberdorfer 1957 sub-association *ericetosum herbaceae*. It ranges from 1,300 to 1,500 m a.s.l. and is characterized by *Salix eleagnos*, *S. purpurea*, *S. glabra*, *Calamagrostis epigejos*, *C. pseudophragmites*, *Hieracium staticifolium*, *H. florentinum*, and by *Salix nigricans* and *Pinus mugo*. The soils of this association are very young and undeveloped, gravely, very poor in fine particles and carbonate-rich. They belong mainly to Fluvisols (Fluviosols, after AFES 1995, or Calcari-leptic Fluvisols, after FAO classification, 1990).

- On siliceous bedrocks, five other associations were distinguished:

5) The most extended association on this type of substrate is *Antherico liliaginis-Pinetum sylvestris* Mayer ex Minighetti 2003, which is characterised by the presence of *Carex humilis* in the herb layer, together with *Silene rupestris*, *Veronica officinalis*, *Polypodium vulgare*, *Campanula rotundifolia*, *Anthericum liliago*, mosses such as *Rhytidium rugosum* and *Hypnum cupressiforme*, and several *Sedum* and *Sempervivum* species. *Antherico liliaginis-Pinetum sylvestris* colonises steep slopes facing south where strong soil erosion and important colluvial processes are present. The soils, which may belong to colluvial soils or to acid brown soils (Colluviosols and Alocrisols after AFES 1995; Eutric or Dystric Regosols, and Dystric Cambiosols according to FAO classification, 1990), are sandy and continuously remixed by colluvial processes and therefore are young and undeveloped. They are oligosaturated and pH varies from weak acid to acid;

6) In the undergrowth of *Vaccinio vitis-ideae-Pinetum sylvestris* Mayer et Hoffmann 1969 *Vaccinium myrtillus*, *V. vitis-idaea*, *Pyrola media*, *Avenella flexuosa* and *Rhododendron ferrugineum* dominate. This association develops at an altitude comprised between 800 and 1,600 m a.s.l., on plateau and north facing slopes made of granite, quartzite, and rhyolite. The soil is of a podzolic type (Podzosols ocriques and Alocrisols ocreux, after AFES 1995; Haplic or Cambic Podzols and Spodo-Dystric Cambisols after FAO, 1990), highly developed, from acid to very acid and desaturated;

7) The *Astragalo vesicarii-Pinetum syl-*

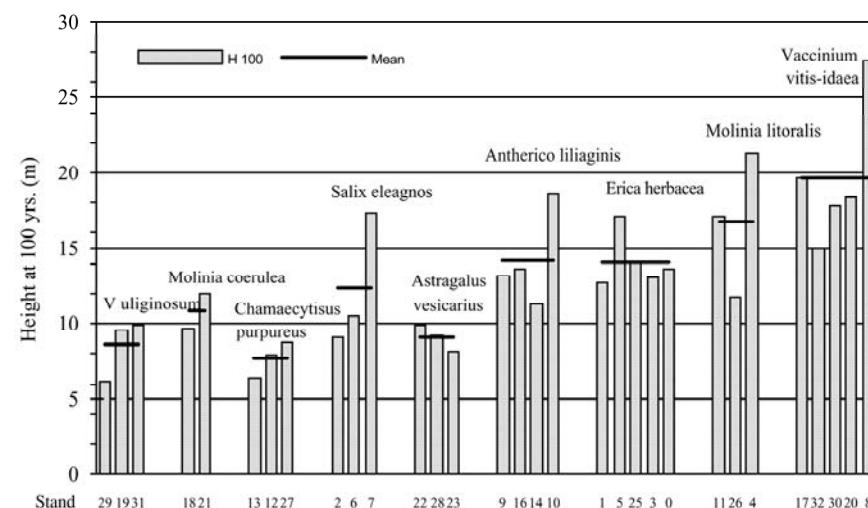


Fig. 5 - Mean dominant tree height (in m) at 100 years (H_{100}) for 31 *Pinus sylvestris* stands divided into 9 phytosociological groups, and average values (horizontal lines) for each group.

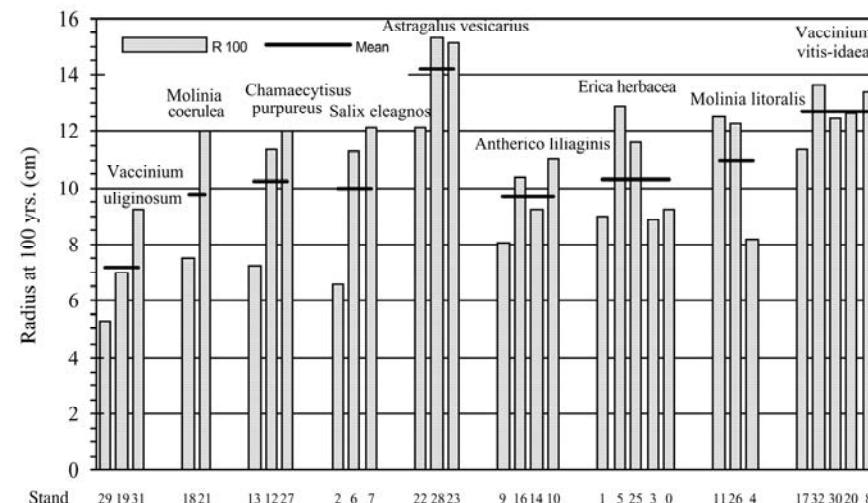


Fig. 6 - Mean dominant tree radius at 100 years (R_{100}) (in cm; without bark and at a height of 1.30 m) for 31 *Pinus sylvestris* stands divided into 9 phytosociological groups, and average values (horizontal lines) for each group.

vestris Braun-Blanquet 1961 can be found in the dry areas of the Venosta valley, where average rainfalls do not reach 500 mm in a year, and it is characterized by more or less endemic species of inner alpine dry valleys such as *Astragalus vesicarius* ssp. *pastellianus* and *Oxytropis halleri* ssp. *velutina*. This association develops between 1,000 to 1,600 m a.s.l., on 20-40° slopes on mica-schist bedrocks. The soils (saturated Colluviosols after AFES 1995, or Eutric Regosols after FAO, 1990) are weakly acid superficially and neutral-basic in depth;

8) The *Vaccinio uliginosi-Pinetum sylvestris* Kleist 1929 can be found in oligotrophic peat bogs with *Sphagnum* and *Vaccinium uliginosum*, *V. oxycoccos*, *Eriophorum vaginatum*, *Carex pauciflora*, *Polytrichum strictum*, *Drosera rotundifolia* and *Andromeda polifolia*. It is established in only a few sites from 1,300 to 1,600 m a.s.l., on Histosols sphagnofibrillaires (AFES, 1995) or

Fibric Histosols (FAO, 1990) with acid peat;

9) The *Molinio coeruleae-Pinetum sylvestris* (Hofman) Passarge 1978 - Minighetti et Pedrotti 1999 develops in meso-eutrophic peat bogs and other wet sites on hydromorphic flat soils. Reductisols stagniques and histosols mesiques eutrophes (AFES, 1995) are typical soils, (or Eutric Gleysols and Eutric Histosols according to FAO classification, 1990) and show a slightly acid pH. The understorey is characterized by *Molinia coerulea*, *Carex fusca*, *Carex canescens*, *Cirsium palustre*, and *Succisa pratensis*.

DENDROMETRICAL RESULTS

For all pine stands (31 sites), the average dominant tree height is 13.3 ± 4.7 m, with extreme values ranging from 5.9 m to 27.6 meters, (Fig. 2). The average value for the dominant tree

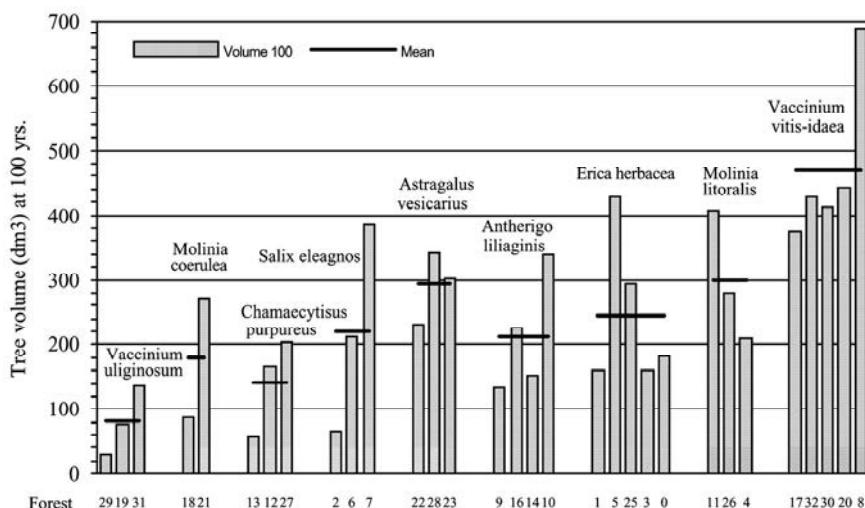


Fig. 7 - Mean tree volume (in dm^3) at 100 years (V_{100}) calculated for 31 *Pinus sylvestris* stands according to 9 phytosociological groups using H_{100} and R_{100} values. Average values (horizontal lines) for each group.

Mean ring width as a function of cambial age (0.01mm/year)

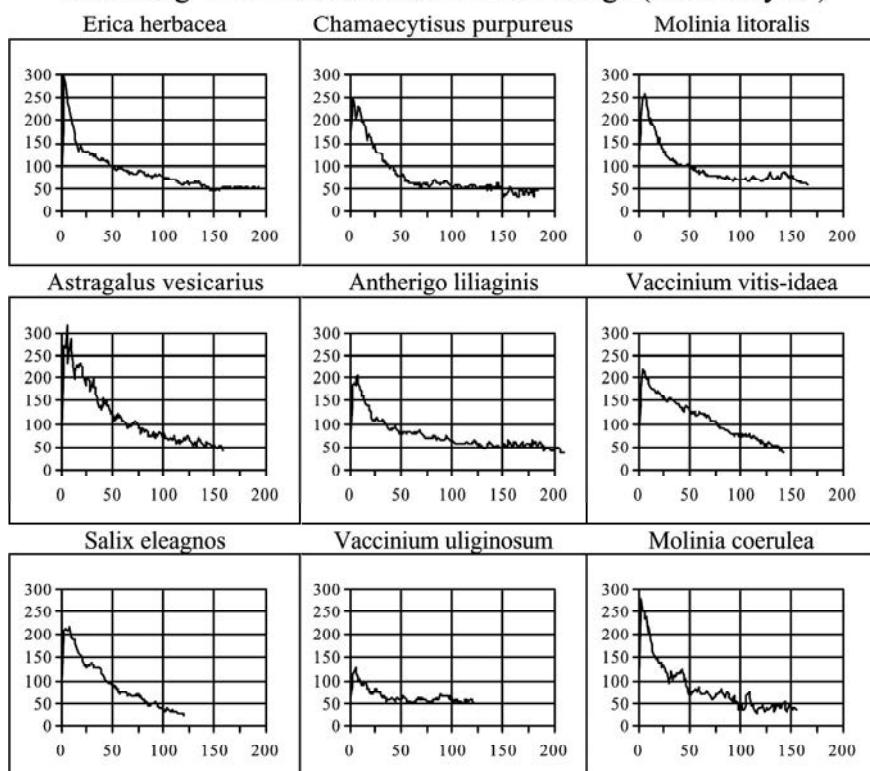


Fig. 8 - Mean tree-ring width (expressed in 0.01 mm) as a function of cambial age for all Scots pines of the same phytosociological group.

diameter is 33.8 ± 7.75 cm, with extreme values ranging from 14.9 cm to 46.2 cm (Fig. 3). The average stem volume is $659.8 \pm 360.0 \text{ dm}^3$, with extreme values ranging from 58.1 dm^3 to $1,428.9 \text{ dm}^3$ (Fig. 4).

HEIGHT, DIAMETER, AND VOLUME GROWTH

Height and volume of the dominant trees are measurements commonly used by foresters as indicators of tree growth. This method is not always reliable, because height and volume are also affected by tree age, but is largely

used and is adopted in this chapter.

More reliable comparisons are presented in the following chapters on the basis of tree volume and height calculated at the 100-years threshold.

As expected, the lowest dominant tree height values are observed in the two kinds of bogs; in the *Vaccinio uliginosi-Pinetum sylvestris* (8.5 m) and in the *Molinia coerulea-P.s.* stands (9.9 m) (Fig. 2). Similarly, tree height growth appears strongly reduced in the *Chamaecytiso purpurei-Pinetum sylvestris*, with a mean tree height of 7.6 m only, as well as in the *Astragalo vesicarii-P.s.* (9.4 m in average). Comparatively, hei-

ght growth appears to be better in the *Salici eleagni-Pinetum sylvestris* (12.3 m), along riverbeds deposit on bare soils. The larger variability is probably associated with soil depth and water supply differences within sites.

The last four phytosociological associations appear more valuable for timber production, since both the *Antherigo liliaginis-P.s.* and the *Erico-Pinetum sylvestris* are characterized by moderately high growth values (14.7 m and 14.9 m respectively). The highest trees are found in the *Molinio litoralis-Pinetum sylvestris* (17.2 m), established on marly slopes and more especially in the *Vaccinio vitis-idae-Pinetum sylvestris* that appears to be the optimum for Scots pine height growth in that region (19.8 m in average, with values up to 27.6 m).

In addition to height growth, radial growth was also examined, despite the fact that stem diameter is more influenced by tree age compared to dominant tree height values (Fig. 3). The most striking result is the opposition between height and radial growth for the *Astragalo vesicarii-Pinetum sylvestris*. In this particular association, pine vertical growth is poor, but it is largely compensated by a sharply enhanced radial growth. The largest stems are found here, with a mean diameter of 42.4 cm that even exceeds those measured in the optimal growth conditions (42.1 cm in the *Molinio litoralis-P.s.* and 38.3 cm in the *Vaccinio vitis-idae-P.s.*).

Tree volume is calculated using TABACCHI & TOSI (1992) equations based on diameter and height measurements. This parameter is a direct estimation of wood production, and therefore provides valuable information for site comparisons (Fig. 4). Five growth levels are distinguished:

- 1) Extremely low wood production has been recorded in both *Vaccinio uliginos-Pinetum sylvestris* and *Molinio coeruleae-P.s.* associations, which correspond with unproductive sites (respectively 229 and 262 dm^3). Hence the major interest of such forest types, unsuitable for timber production, is for vegetation preservation due to the presence of rare plant species.
- 2) Very low wood production is observed in the *Chamaecytiso purpurei-P.s.* and the *Salici eleagni-P.s.* (respectively 280 and 370 dm^3), both with poor interest for wood production. In the later one, Scots pine plays an important part for soil formation and impedes erosion processes.
- 3) Intermediate growth values were measured in the *Astragalo vesicarii-*

P.s. and in the *Antherigo liliaginii-P.s.* (respectively 685 and 661 dm³). The former is characterized by short but large stems, whereas the second one presents tree shapes more suitable for timber production.

4) Moderately productive sites are located in the *Erico-Pinetum sylvestris* (811 dm³).

5) Highly productive sites are located in both the *Molinio litoralis-P.s.* and in the *Vaccinio vitis-ideae-P.s.*, with tree volumes of 1,046 and 1,078 dm³ respectively. In the later case, *Pinus sylvestris* often competes with *Picea abies*, whereas Spruce is virtually absent in the *Molinio litoralis-P.s.*

COMPARISONS AT 100 YEARS

Since the Scots pines do not have exactly the same ages in the different stands, tree growth was also analysed at a given cambial age (100 years). This technique allows one to eliminate the influence of age on tree growth analysis. The results obtained for tree height at 100 years (H_{100}) (Fig. 5) appear to be highly consistent with those previously obtained with dominant tree height H_{dom} (Fig. 2), despite the effect of age heterogeneity observed for H_{dom} . These two values show a strong correlation (H_{dom} and H_{100} : $r = 0.991$ $n = 32$), confirming that dominant tree height is an efficient predictor of site fertility (PARDÉ & BOUCHON, 1988). It does not depend on tree age, but levels off when trees are old. Moreover, the height growth threshold only depends on site fertility.

Contrarily, tree radius at 100 years (R_{100}) obtained with ring-widths (Fig. 6) differs from results obtained with stem diameter measurements (Fig. 3) due to both age influence and bark width. As already observed with the height values, the use of the tree volume at 100 years (V_{100}) (Fig. 7) was found more efficient to compare inter-site production than the use of the tree volume (V) of dominant pines (Fig. 4). Considerations about comparisons at 100 years are made in the discussions and in the conclusions of this paper.

GROWTH DYNAMICS

Some previous studies about conifer growth (PETITCOLAS *et al.*, 1997) had revealed that roughly similar values in tree volumes could in fact hinder important differences in tree growth patterns. For instance, *Pinus cembra* and *Pinus uncinata* strongly differ in their

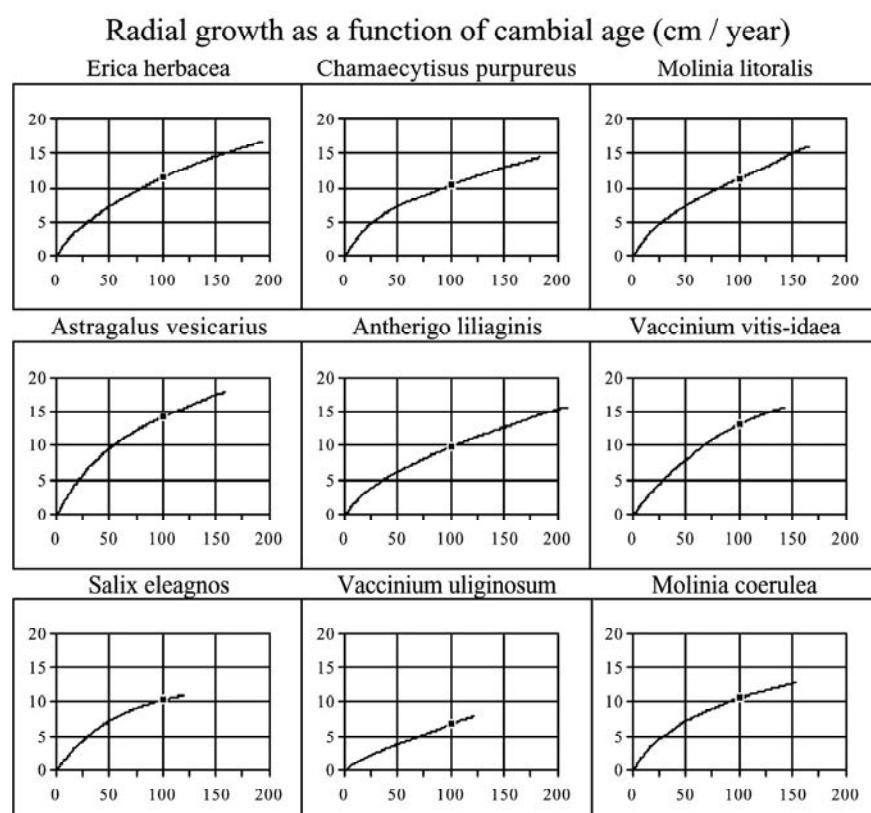


Fig. 9 - Mean tree radius (in cm) as a function of cambial age for all Scots pines of the same phytosociological group (derived from ring-width measurements, without bark). The squares indicate the value at 100 years.

juvenile phase of ring formation, even when they grow in the same stand. For that reason we have also investigated here the dynamism of ring formation with cambial age (i.e. the age of the tree when the ring was formed).

MEAN RING-WIDTH AS A FUNCTION OF CAMBIAL AGE

Ring-widths variation with cambial age usually show an optimum when trees are quite young, followed by a gradual decrease for most pioneer species such as pines (BRÄKER, 1981; SCHUELLER & ROLLAND, 1994; PETITCOLAS *et al.*, 1997). In all stands the tree's largest ring was formed at an age ranging from 3 to 10 years (Fig. 8). For all pines, regardless of site, this maximum ring-width reaches 2.21 mm at 4 years old. Striking differences appear among the nine phytosociological groups. The stands characterized by *Astragalus vesicarius* show the highest peak (3.15 mm), above stands with *Erica herbacea* (2.94 mm). On the contrary, in *Vaccinium uliginosum* stands the largest rings only reach 1.26 mm.

Another sharp contrast is visible among the different kinds of forest: most types show, after the initial phase, an exponential decline of ring width with increasing age, whereas the *Vacci-*

nio vitis-idaeae-P.s. differs by a quite linear decline, which is therefore slower.

The mean ring-width at 100 years is 0.66 mm for all trees and ranges from 0.37 mm in *Salix eleagnos* stands to 0.75 mm in *Vaccinium vitis-idaea* stands.

DYNAMICS OF RADIAL GROWTH

Such variations in ring formation patterns according to forest typology lead to important differences in radial growth curves (Fig. 9). The nine main radial growth curves are given here, to provide a guideline to foresters. Note that radial growth patterns in *Vaccinium uliginosum* stands were quite weak and linear, whereas the highest non-linearity was observed in *Astragalus vesicarius* stands.

YEARLY INCREASE IN BASAL AREA

The curves of increase in basal area appear to be a highly efficient indicator for the understanding of the differences in stand growth dynamism. Four main patterns were distinguished in these growth patterns (Fig. 10).

Type A, that includes the *Chamaecytiso purpurei-Pinetum sylvestris* and the *Molinio coeruleae-P.s.* is charac-

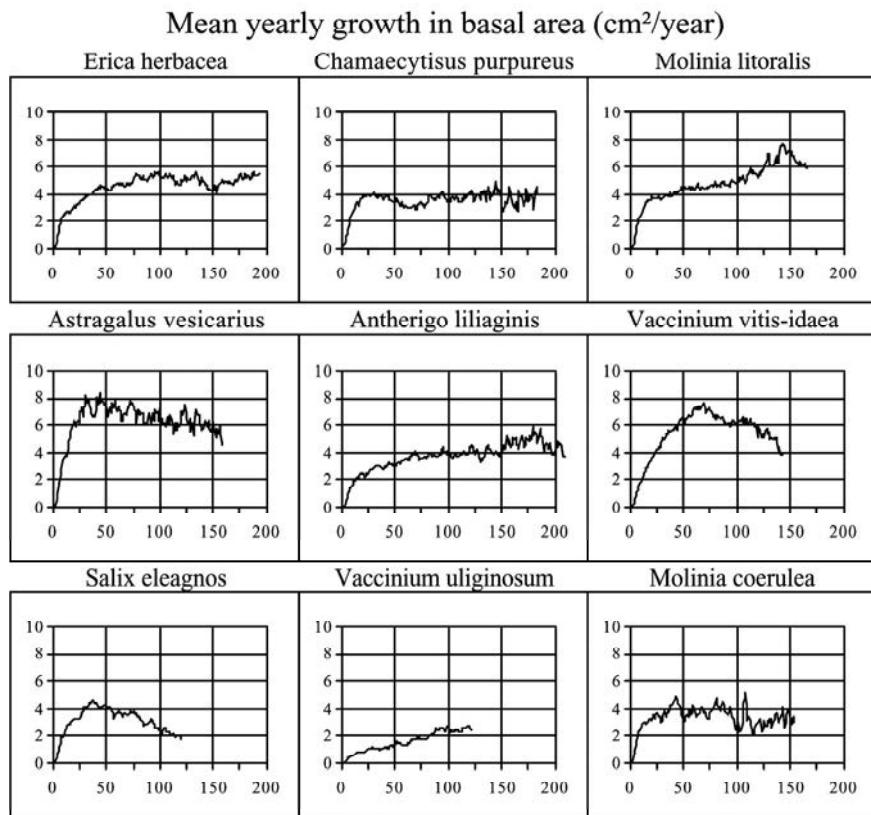


Fig. 10 - Mean increase in basal area ($\text{cm}^2 / \text{year}$) as a function of cambial age for all Scots pines of the same phytosociological group (derived from ring-width measurements, without bark).

rized by a rapid increase extending during the 25 first years of tree growth, followed by a roughly constant plateau (about $3.5 \text{ cm}^2/\text{year}$ and $3.0 \text{ cm}^2/\text{year}$ respectively).

Type B, with 3 types of forests (*Erico-Pinetum sylvestris*, *Molinio litoralis-P.s.*, and *Antherico liliaginensis-P.s.*) does not show such a leveling off, but on the contrary presents a continuous yearly growth increase in basal area with tree age. In such a case, tree senescence seems to be delayed, and Scots pine remains able to form more and more wood as they get older.

Type C, with *Astragalo vesicarii-P.s.*, *Vaccinio vitis-idaeae-P.s.* and *Salici eleagni-P.s.* types, shows a maximum in basal area yearly increment followed by a decline. Thus, the maximums are reached at 38 years for the *Salix* type ($4.59 \text{ cm}^2/\text{year}$), at 44 years for the *Astragalus* type ($8.3 \text{ cm}^2/\text{year}$), and at 68 years for the *Vaccinium* type ($7.61 \text{ cm}^2/\text{year}$).

Type D, for *Vaccinio uliginosi-P.s.* is characterized by a slow and linear trend with a continuous increase.

DISCUSSION

In Italy, pure Scots pine forests grow in the whole of the alpine area, especially in the inner valleys (PIGNAT-

TI, 1988). *Pinus sylvestris* is abundant in the Centro-oriental area of the Alps (in Trentino and Alto-Adige, and in some parts of the Lombardian Alps) and, to a lesser extent, in the western part (Piemonte) (TABACCHI & TOSI, 1992). According to the national forest survey (Inventario Forestale Nazionale), pine species cover 228,600 ha in Italy (TABACCHI & TOSI, 1992). As in neighbouring countries (DÉCOURT, 1965; OTTORINI & NYS, 1981a-b; VANNIÈRE, 1984; OFFICE NATIONAL FORÊTS, 1994; CLUZEAU *et al.*, 1998), several growth tables (CASTELLANI, 1970) were established in Italy for Scots pine wood production: for Valle di Susa (QUAGLINO *et al.*, 1987), for Trentino-Alto Adige (CORONA & FERRARA, 1987), as well as for whole of Northern Italy (TABACCHI & TOSI, 1992).

Nevertheless, at our knowledge this study is the first one that takes into account the part played by site variability (described by forest phytosociology) on pine growth in Italy, and that points out different ring-width growth patterns.

Our sampling strategy covered the entire ecological range of *Pinus sylvestris* in the Trentino-Alto Adige region; thus, allowing us to quantify the plasticity of that species. From stand to stand, the variations of the dendrometrical measurements are particularly high, since a 3.1 times variability in dominant tree

diameter is reported here (Fig. 3), whereas the values of dominant tree height vary up to 4.7 times (Fig. 2); this gives rise to considerable variation in stem volume, over a 1 to 24.6 scale (Fig. 4). Regardless of the influence of ageing, results at a cambial age of 100 years (more valuable for site comparisons) lead to similar conclusions. Thus, stem diameter D_{100} (without bark) falls between 10.6 and 30.6 cm (variations over a 2.9 times interval), tree height H_{100} varies from 6.2 to 27.4 meters (showing a 4.4 times change), and volume V_{100} falls between 30.7 and 688.6 dm^3 (i.e. its variations cover a 22.4 times interval). Such extreme high variability in tree growth clearly underlines the extreme range of growth conditions that *Pinus sylvestris* can tolerate.

Very small height growth (H_{100} less than 10 m) is reported in the two kind of bog communities (*Vaccinio uliginosi-Pinetum sylvestris* and *Molinio coeruleae-P.s.*), due to the particularly unfavourable growth conditions, characterized by insufficient drainage that causes root asphyxia (KAUNISTO & TUKEVA, 1986). Meso-eutrophic conditions in bogs on hydromorphic flat soils (with *Molinia coerulea*) lead to a slightly enhanced tree growth compared to more oligotrophic conditions encompassed by pines in the acid peat bogs with *Sphagnum* (+ 20% in height growth H_{100} , and + 54% for V_{100}). These findings are consistent with KAUNISTO (1987) results in peat sites, where P and K fertilisation enhanced *Pinus sylvestris* height growth.

Surprisingly, the lowest height growth is not recorded in bog sites, but in the *Chamaecytiso purpurei-Pinetum sylvestris* ($H_{100} = 7.7 \text{ m}$). However, larger diameters partly compensate this phenomenon. Volume growth there, is intermediate between the two bog types. Moreover, this association is the only one where some stands are infected by mistletoe (*Viscum album*). This is especially the case of stands at lower altitudes (mean altitude 852 m for the 6 infected sites, versus 948 m for the 27 uninfected stands of the same association where floristic relevés were done), facing S and SW, on lower slopes (24.2° versus 33.1°), and characterized by a higher shrub cover (41% versus 29%). Such mistletoe infection may be considered as an indication of tree water stress. This is corroborated by the extreme location of this association, developed in the southern part of Trentino with many thermophilous deciduous species such as *Fraxinus ornus*, *Ostrya carpinifolia*, and *Quercus pubescens*.

(in the extreme sites).

Poor growth is found in the *Astragalo vesicarii-P.s.*, due to the extreme climatic factors of the dry inner valleys. In fact, the climate of Val Venosta, that represents the distribution centre of this association, is characterized by low rainfall amounts and high temperature contrasts. For instance, yearly rainfall equals 473 mm/year in Silandro (at 706 m), whereas the evapotranspiration is 664 mm/year (GAFTA & PEDROTTI, 1996). However, this endemic association reveals an unusual behaviour pattern compared to all other Scots pine forests. Although height growth is particularly low ($H_{100} = 9.9$ m), stem diameters are the largest ($D_{100} = 28.4$ cm) compared to results reported in all other stands, even in the most productive ones. Consequently, tree volume ($V_{100} = 292 \text{ dm}^3$) is high, despite a tree shape characterized by an extremely low H/D ratio, unfavourable for timber production. Such tree form may be due to the presence of a genetically different ecotype of *Pinus sylvestris* there, as already reported by ANTONOROLLI *et al.* (1985) in the Emilia-Romagna Appenines, and generally accepted for this species (ZOLLER, 1981).

The *Molinio litoralis-Pinetum sylvestris* and the *Vaccinio vitis-idaeae-Pinetum sylvestris* appear to be the best phytosociological types for Scots pine growth. This species is therefore able to develop with high wood production on marly calcareous soils as well as on acid soils (schistes and rhyolites), regardless soil chemistry.

Such large ability of Scots pine to colonize different kinds of substrates appears to be associated with differences in ring formation patterns. Unfortunately, until now, such phenomenon have only received little attention. The maximum ring-width is found at very young cambial tree age, that is in agreement with the pioneer behaviour of *Pinus sylvestris*. This species is therefore characterized by rapid early growth. Moreover, four main patterns of radial growth curves are distinguished in our study. The slow linear increase in basal area with cambial age (in the *Vaccinio uliginosi-P.s.*) may be interpreted as a survival strategy of trees facing soil flooding, and therefore requiring many years for root establishment. Such a feature is also visible for the pines established in the *Molinio litoralis-P.s.*, also growing on flooded soil, and for the *Antherico liliuginis-P.s.* sites with continuous soil erosion. On the other hand, pioneer behaviour of pines may be inferred from the growth curve reported in the *Astragalo vesicarii-P.s.*, with a

quick start during the juvenile phase. Canopy closure may be responsible for basal area growth decline after 68 years in the *Vaccinio vitis-idaeae-P.s.*, due to the competition of *Picea abies* and *Larix decidua*.

CONCLUSIONS

As hypothesized, Scots pine wood production shows considerable variations depending on the phyto-sociological groups. By increasing order, the stem volume at 100 years (without bark) (V_{100}) reaches only 82 dm^3 in the *Vaccinio uliginosi-Pinetum sylvestris*, 143 dm^3 in the *Chamaecytiso purpurei-P.s.*, and 179 dm^3 in the *Molinia coerulea-P.s.*. Such extremely low pine growth seems to be caused by insufficient drainage in both *Vaccinio uliginos-P.s.* and *Molinio coerulea-P.s.*, leading to root asphyxia and aggravated by soil oligotrophy. Contrarily, in the *Chamaecytiso purpurei-P.s.*, soil erosion processes seem responsible for such poor tree vigour, by reducing soil water storage capacity (pines are confined in extreme sites). Intermediate values are found for the *Antherico liliuginis-P.s.* (213 dm^3), for the *Salici eleagni-P.s.* (221 dm^3), and for the *Erico-Pinetum sylvestris* (245 dm^3). The large variability in the *Salici eleagni-P.s.* is probably associated with differences in soil water table depths according to the sites. Higher values were measured in both the *Astragalo vesicarii-P.s.* (292 dm^3) and the *Molinio litoralis-P.s.* (298 dm^3). In the former group, a high sunshine duration in the Val Venosta inner valley may be responsible for better photosynthesis, in spite of high thermic contrast that leads to water stress. Contrarily, the later group seems favoured by marly soils that provide sufficiently high water reserve. Timber production reaches its top in the *Vaccinio vitis-idaeae-P.s.* (470 dm^3), where shade species such as Norway Spruce are able to establish, and probably eliminate pioneer Scots pines.

These values cover a 5.75 time variation among the phyto-sociological group, whereas values for individual stands (that range from 31 to 689 dm^3) cover a 22-time interval.

Our results clearly point out and quantify the part played by site conditions for Scots pine growth, a species with an extreme ecological plasticity. Thus, growth tables for this conifer could be improved by including information of site vegetation.

Moreover, important differences

according to the phytosociology are demonstrated here in the radial growth strategies, since four ring-width patterns are distinguished:

- Both *Chamaecytiso purpurei-P.s.* and *Molinio coerulea-P.s.* show "plateau growth";
- The *Erico-Pinetum sylvestris*, *Molinio litoralis-P.s.* and *Antherico liliuginis-P.s.* show "no ageing effect";
- The *Astragalo vesicarii-P.s.*, *Vaccinio vitis-idaeae-P.s.* and *Salici eleagni-P.s.* are characterized by "pioneer behaviour" (i.e. a quick start followed by a decrease);
- In acid bogs, (*Vaccinio uliginosi-P.s.*) a "linear stagnation" is observed.

Such unexpected results indicate that, even though *Pinus sylvestris* can survive in a huge number of various growth conditions, this species behaves specifically in each of its phyto-sociological associations.

ACKNOWLEDGEMENTS

This research was supported by the Centro di Ecologia Alpina (Viotte del Monte Bondone, I-38040 Trento). We also thank prof. R. Michalet (Bordeaux, France) and prof. F. Pedrotti (Camerino, Italy) for their support.

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QUELQUES ASSOCIATIONS INÉDITES DES *TRIFOLIO MEDII-GERANIETEA SANGUINEI* DES VALLÉES INTERNES DES ALPES OCCIDENTALES

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ABSTRACT

Preliminary study of the *Trifolio medii-Geranietea sanguinei* Müller 1962 vegetations in the inner valleys of the western Alps. Description of three new associations and of an original vegetal group.

KEYWORDS: *Trifolio medii-Geranietea sanguinei*, western Alps.

RÉSUMÉ

Étude préliminaire des végétations des *Trifolio medii-Geranietea sanguinei* Müller 1962 des vallées internes des Alpes occidentales. Description de trois associations nouvelles et d'un groupe-ment végétal inédit.

INTRODUCTION

La classe des *Trifolio medii-Geranietea sanguinei* Müller 1962 est encore peu étudiée dans les Alpes occidentales, notamment pour ce qui concerne la partie française. Nous avons, à l'occasion de nombreux séjours, constaté que ces groupements sont bien représentés dans l'ensemble des Alpes occidentales, depuis le lac Léman jusqu'aux Alpes-Maritimes, mais qu'ils restent à décrire pour l'essentiel. Notre propos se limitera aux vallées internes, réputées pour leur végétation xérothermophile à caractère steppique.

La végétation des vallées internes des Alpes occidentales, du moins celle des milieux thermoxérophiles, est bien connue depuis les travaux de BRAUN-BLANQUET (1961) et de SCHWABE et KRATOCHWIL (2004). BRAUN-BLANQUET n'a pas abordé l'étude des ourlets, mal identifiés à son époque. Les groupements des *Trifolio medii-Geranietea sanguinei* Müller 1962 sont cependant présents dans ces différentes vallées (VAN ALTHUIS *et al.*, 1977, SCHWABE et KRATOCHWIL, 2004). Il s'agit le plus souvent d'ourlets extensifs, en nappe, développés au détriment des pelouses et des prairies suite à leur abandon. Mais on

trouve également quelques ourlets primaires développés au niveau de lisières forestières stabilisées depuis longtemps.

Les secteurs prospectés sont les vallées internes des Alpes françaises (Tarentaise, Maurienne, Briançonnais, Embrunais, Ubaye) et italiennes (Val d'Aoste).

Les quarante relevés phytosociologiques réalisés entre 1983 et 2009 ont été traités par les méthodes numériques (AFC, CAH). Les détails de ces analyses ne sont pas présentés ici. Les traitements numériques ont permis d'identifier cinq syntaxons différents :

- *Lathyro heterophylli-Vicietum onobrychiodis ass. nova*, ourlet extensif xérophile très répandu.
- *Lilio crocei-Laserpitietum sileri ass. nova*, ourlet xérophile, sur pentes raides.
- *Digitalo grandiflorae-Trifolietum medii ass. nova*, ourlet extensif mésophile très commun.
- Groupement à *Vicia cracca* subsp. *incana* et *Melampyrum nemorosum*, ourlet mésophile des versants exposés au nord.
- Groupement à *Trifolium rubens* et *Origanum vulgare*, ourlet en nappe dynamique.

Seuls les quatre premiers syntaxons sont étudiés dans le cadre de cet article. Ils appartiennent tous à la classe des *Trifolio medii-Geranietea sanguinei* Müller 1962 et à l'ordre des *Origanetalia vulgaris* Müller 1962 (DE FOUCALUT *et al.*, 1983, THEURILLAT *et al.*, 1995, BARDAT *et al.*, 2004). Le *Lathyro heterophylli-Vicietum onobrychiodis*, le *Lilio crocei-Laserpitietum sileri* et le groupement à *Trifolium rubens* et *Origanum vulgare* se rangent dans le *Geranion sanguinei* Tüxen in Müller 1962. Le *Digitalo grandiflorae-Trifolietum medii* et le groupement à *Vicia cracca* subsp. *incana* et *Melampyrum nemorosum* appartiennent au *Trifolion medii* Müller 1962.

D'autres groupements, très mésophiles, à *Vicia sylvatica* et *Knautia dipsacifolia*, ont été notés à plusieurs reprises. Leurs relevés, très différents de ceux des syntaxons précédents, n'ont pas été intégrés aux analyses. Ils ne seront pas étudiés ici.

Il existe d'autres associations qui

restent à décrire, notamment dans le sud des Alpes françaises, dont un groupement très particulier, présent dans le Haut-Var, qui contient *Geranium sanguineum*, *Trifolium alpestre*, *Cnidium silaifolium*, *Inula bifrons*, *Pedicularis comosa* (ROYER, 2000). Il en est de même pour les syntaxons très originaux des Alpes-Maritimes.

Les groupements des *Trifolio medii-Geranietea sanguinei* Müller 1962 des vallées internes alpines se distinguent assez nettement d'un point de vue floristique des autres groupements des *Trifolio medii-Geranietea sanguinei* Müller 1962 d'Europe occidentale par l'absence ou la rareté d'un certain nombre d'espèces caractéristiques à différents degrés et par la présence d'espèces originales. Les principales espèces absentes ou très raréfierées dans les syntaxons des vallées internes sont *Anthericum ramosum* (nomenclature d'après *Flora alpina*, AESCHIMANN *et al.*, 2004), *Aster amellus*, *Bupleurum falcatum*, *Inula conyzoides*, *Lathyrus niger*, *Melampyrum cristatum*, *Melittis melissophyllum*, *Peucedanum cervaria*, *Seseli libanotis*, *Tanacetum corymbosum*, *Viola hirta*, et pour le *Trifolion medii*, *Agromonia eupatoria* et *Lathyrus sylvestris*. Il faut noter que la plupart de ces espèces existent dans les syntaxons des *Trifolio medii-Geranietea sanguinei* Müller 1962 des Préalpes nord-occidentales (VAN ALTHUIS *et al.*, 1977). Les espèces particulières aux syntaxons des vallées internes sont surtout *Vicia onobrychiodes* (également présente dans les ourlets du Massif Central), *Lathyrus heterophyllus*, *Asphodelus albus*, *Verbascum thapsus* subsp. *montanum*, *Centaurea triumfettii*, *Lilium bulbiferum* subsp. *croceum*, *Pulmonaria picta*, *Vicia cracca* subsp. *incana*, *Campanula medium* (cette dernière également présente dans les syntaxons préalpins).

LATHYRO HETEROPHYLLI-VICIE-TUM ONOBRYCHIODIS ASS. NOVA HOC LOCO

Le Tableau 1 donne la composition floristique de cette association.

Tableau 1 - *Lathyro heterophylli*-*Vicietum onobrychioidis* ass. nova hoc loco.

Tableau 1 - (continuation).

	1	2	3	4	5	6	7	8	9	10	11	12	13
Numéro du relevé	90	90	95	85	80	95	90	95	100	90	90	95	90
Recouvrement (%)													
Exposition Pente (degrés)	3 E	10 E	10 W	10 S	10 W	5 S	5 W	10 SW	20 E	5 S	10 E	30 S	10 E
Altitude (m)	1200	1480	1680	1720	1700	1880	1720	1650	1780	1150	1740	1250	1920
Onobrychis viciifolia	+	.	+
Lathyrus tuberosus	+	+
Trifolium ochroleucon	+	+
Potentilla rupestris	.	1.1	1.1
Fourraea alpina	.	1.1	+
Sanguisorba minor	.	.	+	+
Galium verum	.	.	+	+
Arrhenatherum elatius	.	.	+	1.1	.	.
Vicia sepium	.	.	+	1.1
Trifolium pratense	.	.	.	+	+	.
Senecio doronicum	+	1.1
Rubus idaeus	1.2	.	+
Poa nemoralis	1.1	1.1
Veronica chamaedrys	+	.	.	.	+
Galium boreale	.	.	1.2
Gentiana lutea	.	.	.	2.2
Pteridium aquilinum	2.3	.	.
Calamagrostis varia	2.2	.
Hieracium prenanthoides	2.2	.
Accidentelles	3	2	1	5	3	3	3	3	6	1	0	3	8

Holotype: relevé 6, Maurin (Ubaye), vers le village, pentes exposées au sud, ourlet extensif.

Cette association est très répandue dans l'ensemble des vallées internes des Alpes occidentales. Elle se développe entre 1.200 et 1.900 mètres d'altitude, sur des pentes exposées à l'ouest, au sud et à l'est, jamais au nord. Il s'agit le plus souvent d'un ourlet extensif, en nappe, qui envahit les pelouses du *Stipetum capillatae-Poion carniolicae* Braun-Blanquet 1961 au contact des fruticées, à partir des îlots de brachypode (*Brachypodium rupestre*). La combinaison floristique caractéristique est constituée par *Vicia cracca* subsp. *tenuifolia*, *Vicia onobrychoides*, *Lathyrus heterophyllus*, *Trifolium alpestre* et *Laserpitium latifolium*. Les espèces dominantes sont *Brachypodium rupestre*, *Vicia onobrychoides*, *Vicia cracca* subsp. *tenuifolia* et *Laserpitium latifolium*.

Le *Lathyro heterophylli-Vicietum onobrychoidis* est le vicariant méridional des associations dominées par *Vicia cracca* subsp. *tenuifolia* comme le *Campanulo bononiensis-Vicietum tenuifoliae* d'Allemagne et d'Autriche (MUCINA et KOLBECK, 1993) et le *Coronillo variae-Vicietum tenuifoliae* de Bourgogne (ROYER et RAMEAU, 1983). Il est également apparenté au «*Trifolio medii-Laserpitietum latifoliae* VAN GILS et GILISSEN 1976» décrit du Valais et des Préalpes nord-occidentales (VAN GILS et KAY-

SERS, 1977; VAN ALTHUIS *et al.*, 1977). Il s'agit dans les deux cas d'ourlets en nappe succédant à des prés de fauche ou à des pelouses pâturées. Il est par contre bien différent du *Trifolio medii-Laserpitietum latifoliae* van Gils et Gilissen 1976 du Tyrol, qui se range dans le *Trifolion medii* Müller 1962 (MUCINA et KOLBECK, 1993).

Les relevés 9 à 13 se rapportent à une sous-association particulière, *digitalatosum grandiflorae* subass. nov. hoc loco, différenciée notamment par *Digitalis grandiflora* et *Geranium sanguineum* (holotype: relevé 11). Les relevés 12 et 13, dépourvus de *Vicia cracca* subsp. *tenuifolia* et de *Vicia onobrychoides*, rappellent le *Geranio sanguinei-Trifolietum alpestris* Müller 1962; ils proviennent d'ourlets subprimaires développés au contact de bosquets anciens. C'est peut-être une autre association ou une forme particulière du *Geranio sanguinei-Trifolietum alpestris* Müller 1963. Ce dernier est signalé dans les Préalpes aux environs de Grenoble (VAN ALTHUIS *et al.*, 1977), mais il pourrait s'agir d'une association originale (DE FOUCAUT *et al.*, 1983).

LILIO CROCEI-LASERPITIETUM SILERIS ASS. NOVA HOC LOCO

Le Tableau 2 donne la composition floristique de cette association.
Holotype: relevé 3, vallée de Champor-

cher (Val d'Aoste), juillet 2009, versant raide en pied de falaise.

Cette association est plus rare que la précédente. Les relevés proviennent de la Maurienne et du Val d'Aoste. Mais nous avons constaté sa présence également en Tarentaise, en Ubaye et dans le Briançonnais. Nous ne l'avons rencontrée que sur des pentes exposées au sud et à l'est, souvent assez raides et à une altitude supérieure à celle de la précédente (1.900 à 2.300 mètres). Cet ourlet se rencontre dans des conditions souvent subprimaires, au contact de fruticées. La combinaison floristique caractéristique est constituée par *Laserpitium siler*, *Lilium bulbiferum* subsp. *croceum*, *Centaurea triumfettii*, *Paradisea liliastrum* et *Asphodelus albus*. Les espèces dominantes sont *Brachypodium rupestre*, *Laserpitium siler* et *Laserpitium latifolium*.

Le *Lilio crocei-Laserpitietum sileris* présente quelques affinités avec le *Trifolio medii-Laserpitietum latifoliae* VAN GILS et GILISSEN 1976 du Tyrol (MUCINA et KOLBECK, 1993), qui est cependant plus mésophile. Il pourrait s'agir d'un vicariant occidental.

DIGITALO GRANDIFLORAE-TRIFO- LIETUM MEDII ASS. NOVA HOC LOCO

Le Tableau 3 (relevés 1 à 7) donne

Tableau 2 - *Lilio crocei-Laserpitietum sileris ass. nova hoc loco.*

	1	2	3	4	5
Numéro du relevé					
Recouvrement (%)	90	95	90	90	95
Exposition Pente (degrés)	20 S	10 E	30 S	30 S	30 S
Altitude (m)	2300	1920	1940	1950	1950
Combinaison caractéristique					
<i>Laserpitium siler</i>	3.2	2.1	2.2	3.3	3.3
<i>Lilium bulbiferum</i> subsp. <i>croceum</i>	.	+	1.2	1.1	1.1
<i>Centaurea triumfettii</i>	1.1	.	+	1.1	.
<i>Paradisea liliastrum</i>	.	.	1.2	1.1	+
<i>Asphodelus albus</i>	.	.	+	.	1.2
Caractéristiques de classe et unités inférieures					
<i>Brachypodium rupestre</i>	3.3	3.4	3.2	3.3	1.1
<i>Laserpitium latifolium</i>	2.1	2.2	2.2	2.3	1.2
<i>Silene nutans</i>	1.2	1.1	1.1	1.1	+
<i>Galium mollugo</i>	1.1	1.1	1.2	1.1	.
<i>Polygonatum odoratum</i>	+	.	1.1	1.1	.
<i>Geranium sanguinum</i>	.	.	+	1.1	+
<i>Vicia cracca</i> subsp. <i>tenuifolia</i>	1.1	1.1	.	.	.
<i>Peucedanum oreoselinum</i>	2.2	1.1	.	.	.
<i>Poa angustifolia</i>	.	1.1	.	1.1	.
<i>Verbascum lychnitis</i>	.	1.1	.	.	+
<i>Thalictrum minus</i>	.	.	1.1	2.2	.
<i>Hypericum montanum</i>	.	.	+	+	.
<i>Vicia onobrychoides</i>	1.1
<i>Turritis glabra</i>	+
<i>Vincetoxicum hirundinaria</i>	1.2
<i>Verbascum thapsus</i> subsp. <i>montanum</i>	+
<i>Rosa spinosissima</i>	+
<i>Trifolium alpestre</i>	+
<i>Anthericum liliago</i>	+
<i>Thalictrum foetidum</i>	+
Autres espèces					
<i>Bromus erectus</i>	+	1.2	.	1.1	.
<i>Rosa canina</i>	.	1.1	+	+	.
<i>Fragaria vesca</i>	.	2.2	2.2	1.2	.
<i>Campanula spicata</i>	.	+	+	+	.
<i>Sesleria caerulea</i>	.	.	1.2	1.1	2.2
<i>Rumex scutatus</i>	+	1.1	.	.	.
<i>Rubus idaeus</i>	1.2	.	+	.	.
<i>Dactylis glomerata</i>	.	.	1.1	+	.
<i>Melica nutans</i>	.	.	1.2	+	.
<i>Gymnadenia conopsea</i>	.	.	+	1.1	.
<i>Trifolium montanum</i>	.	.	.	1.1	1.2
<i>Epilobium angustifolium</i>	1.2
<i>Pimpinella major</i>	.	.	2.1	.	.
<i>Potentilla rupestris</i>	.	.	+	.	.
<i>Melampyrum sylvaticum</i>	.	.	+	.	.
<i>Carex humilis</i>	1.2
<i>Gentiana lutea</i>	1.1
<i>Pulsatilla alpina</i>	1.1
Accidentelles	2	5	1	1	6

la composition floristique de cette association.

Holotype: relevé 6, Le Villard, Méribel (Tarentaise), juillet 2007, lisière de forêt.

Nos relevés proviennent de Tarentaise, du Briançonnais et de l'Ubaye, mais cette association est très répandue dans l'ensemble des vallées internes

des Alpes occidentales. Il est étonnant qu'elle ne soit pas décrite à l'heure actuelle. On la trouve sur des pentes essentiellement exposées au nord, au nord-ouest et au nord-est, jamais au sud, entre 1.200 et 1.600 mètres d'altitude. Il peut s'agir d'un ourlet extensif, en nappe qui envahit les pelouses du *Mesobromion erecti* (Braun-Blanquet

et Moor 1938) Oberdorfer 1957, à partir des îlots de brachypode, ou d'un ourlet mieux constitué, en lisière de forêt ou de bosquet. La combinaison floristique caractéristique est constituée par *Digitalis grandiflora*, *Gentiana lutea*, *Geranium sylvaticum*, *Trifolium medium*, *Campanula persicifolia*, avec, dans une certaine mesure, *Melampyrum nemorosum*. Les espèces dominantes sont *Brachypodium rupestre*, *Trifolium medium*, *Digitalis grandiflora*, parfois *Melampyrum nemorosum*. *Digitalis grandiflora* est souvent considérée comme une espèce des *Epilobetea angustifoliae* Tüxen et Preising ex Von Rochow 1951; dans les Alpes occidentales, comme dans le Jura, elle s'intègre bien aux groupements des *Trifolio medii-Geranietea sanguinei* Müller 1962.

Il existe dans les Préalpes nord-occidentales un groupement assez proche du *Digitalo grandiflorae-Trifolietum medii*, riche en *Trifolium medium*, *Melampyrum nemorosum*, *Geranium sanguineum*, mais dépourvu de *Digitalis grandiflora*, rapporté à tort au *Geranio sanguinei-Trifolietum medii* des côtes de Norvège (VAN ALTHUIS et al., 1977). Le *Trifolio medii-Melampyretum nemorosi* d'Allemagne et d'Autriche (MUCINA et KOLBECK, 1993) est également affine de notre association.

GROUPEMENT À *MELAMPYRUM NEMOROSUM* ET *VICIA SUBSP. INCANA*

Le Tableau 3 (relevés 8 à 10) donne la composition floristique de ce groupement dont nous ne possédons pas suffisamment de relevés pour l'élever au rang d'association.

Nos relevés proviennent exclusivement de l'Embrunais, où ce groupement semble fréquent. Nous ne l'avons pas observé ailleurs à l'heure actuelle, en dehors du Haut-Var où les relevés restent à faire (ROYER, 2000). On le trouve exclusivement sur des pentes exposées au nord, au nord-ouest et au nord-est, jamais au sud, entre 1.100 et 1.600 mètres d'altitude. Il s'agit souvent d'un ourlet bien constitué, en lisière de forêt ou de bosquet. La combinaison floristique caractéristique est constituée par *Melampyrum nemorosum*, *Calamagrostis varia*, *Pulmonaria picta*, *Laserpitium latifolium* et *Vicia cracca* subsp. *incana*. Les espèces dominantes sont *Brachypodium rupestre* et *Melampyrum nemorosum*. Notre groupement apparaît comme un vicariant méridional du *Trifolio medii-Me-*

Tableau 3 - *Digitalo grandiflorae-Trifolietum medii ass. nova hoc. loco et groupement à Melampyrum nemorosum.*

	1	2	3	4	5	6	7	8	9	10
Numéro du relevé										
Recouvrement (%)	90	100	85	90	90	90	85	90	90	80
Exposition Pente (degrés)	5 NE	10 N	10 NW	5 NE	15 E	2 W	20 N	5 NE	30 NE	5 N
Altitude (m)	1280	1290	1600	1320	1300	1540	1250	1250	1630	1150

Combinaisons caractéristiques

Digitalis grandiflora	1.1	+	1.1	2.2	2.2	3.2	1.2	.	.	.
Gentiana lutea	+	.	+	+	1.2	1.1	1.2	.	.	.
Geranium sylvaticum	1.1	.	1.1	1.1	1.2	2.1	1.1	.	.	.
Trifolium medium	1.2	+	1.1	2.2	2.3	+	1.2	1.2	.	.
Campanula persicifolia	1.1	1.1	1.1	.	.	2.2	.	+	+	.
Melampyrum nemorosum	2.2	.	.	3.3	3.3	.	.	3.3	3.3	2.3
Pulmonaria picta	.	1.2	+	+	.
Calamagrostis varia	1.2	+	1.2
Vicia cracca subsp. incana	1.1	+	+
Laserpitium latifolium	1.2	+	2.2

Caractéristiques de classe et unités inférieures

Brachypodium rupestre	3.3	3.3	2.3	+	2.2	3.3	2.2	1.2	.	3.3
Galium mollugo	1.1	1.1	1.2	1.2	1.1	.	1.2	.	.	+
Knautia dipsacifolia	.	1.1	.	.	1.1	1.1	+	.	.	.
Clinopodium vulgare	.	1.1	.	.	.	1.1	.	.	.	1.2
Lathyrus heterophyllus	.	.	1.2	2.2	+	1.1	1.1	.	.	.
Astragalus cicer	.	.	+	+	.	.	+	1.2	+	.
Silene nutans	+	.	1.1	.	.	1.1
Campanula rapunculoides	.	2.1	+	1.1	+	.
Viola hirta	1.1	+	.	+
Campanula rapunculus	1.1	1.1
Valeriana wallrothii	+	.	.	.	+
Vicia cracca subsp. tenuifolia	.	4.4	.	1.2
Vincetoxicum hirundinaria	.	+	1.1
Rosa spinosissima	.	1.2	1.2
Polygonatum odoratum	.	.	1.1	+	.	.
Astragalus glycyphyllos	.	.	+	.	+
Poa angustifolia	.	.	.	+	+
Securigera varia	.	.	.	+	.	1.2
Vicia onobrychoides	.	.	2.3
Trifolium alpestre	.	.	1.1
Verbascum thapsus subsp. montanum	.	.	+
Lathyrus latifolius	.	.	1.2
Verbascum lychnitis	2.1
Paeonia officinalis	1.1	.	.
Scorzonera hispanica	+	.
Tanacetum corymbosum	+	.
Bupleurum falcatum	1.1
Epipactis muelleri	1.1
Hypericum montanum	+
Digitalis lutea	2.2
Agrimonia eupatoria	1.1
Autres espèces										
Lathyrus pratensis	+	1.1	1.2	1.1	1.1	1.1	2.2	.	+	.
Vicia sepium	+	+	+	.	+	.	1.1	.	+	.
Knautia arvensis	+	+	.	+	.	1.1	1.1	.	.	.
Dactylis glomerata	.	.	+	+	1.1	+	1.1	.	1.1	+
Bromus erectus	2.2	.	.	+	.	1.1	+	.	.	.
Heracleum sphondylium	+	.	.	1.1	+	1.2
Primula veris subsp. columnae	+	+	+	1.1	.
Phyteuma spicatum	+	.	.	.	+	.	1.2	.	.	.
Luzula nivea	1.1	.	.	.	+	.	.	.	2.2	.
Cytisophyllum sessilifolium	.	1.1	1.1	.	2.2
Arrhenatherum elatius	.	+	.	+	1.1
Fragaria vesca	.	.	.	+	.	+	1.2	.	.	.

Tableau 3 - (continuation).

Numéro du relevé	1	2	3	4	5	6	7	8	9	10
Recouvrement (%)	90	100	85	90	90	90	85	90	90	80
Exposition Pente (degrés)	5 NE	10 N	10 NW	5 NE	15 E	2 W	20N	5 NE	30 NE	5 N
Altitude (m)	1280	1290	1600	1320	1300	1540	1250	1250	1630	1150
Potentilla rupestris	1.1	.	.	+
Crepis biennis	1.1	.	.	1.1
Chaerophyllum aureum	1.1	2.2	.	.	.
Campanula rhomboidalis	+	+	.	.	.
Salvia pratensis	.	+	+
Melica nutans	.	+	+	.	.
Veronica chamaedrys	.	+	+	.
Rubus idaeus	.	.	1.2	.	+
Epilobium angustifolium	.	.	+	+
Silene vulgaris	.	.	.	+	.	.	+	.	.	.
Luzula sieberi	.	.	.	+	.	.	+	.	.	.
Rumex acetosa	.	.	.	+	.	.	+	.	.	.
Hypericum perforatum	+	+
Campanula rotundifolia	+	+
Aquilegia vulgaris	+	+	.
Galium boreale	+	1.2	.
Ranunculus aduncus	1.1	1.1	.
Geranium nodosum	+	2.1	.
Euphorbia dulcis	+	1.1	.
Hepatica nobilis	+	+	.
Astrantia major	1.1	.	+
Accidentelles	2	4	2	5	5	3	5	4	8	6

lampyretum nemorosi d'Allemagne et d'Autriche (MUCINA et KOLBECK, 1993).

ORIGINE DES RELEVÉS, ESPÈCES ACCIDENTELLES

Tableau 1 - Origine des relevés, espèces accidentnelles: **1** Montagny, Le Villard (Tarentaise), août 2005, *Campanula bononiensis* +, *Ligustrum vulgare* 1.1, *Clematis vitalba* +; **2** Puy-Saint-Pierre (Briançonnais), juillet 1983, *Sorbus aria* +, *Carex pairae* +; **3** Le Lauzet (Briançonnais), juillet 2007, *Colchicum autumnale* +; **4** Villard d'Arènes, juillet 2007, *Colchicum autumnale* +, *Herculum sphondylium* +, *Verbascum nigrum* +, *Cerinthe minor* +, *Chærophylleum aureum* +; **5** Cogne, Lillaz (Val d'Aoste), juillet 2009, *Phyteuma betonicifolium* +, *Juniperus sabina* +, *Laserpitium halleri* +; **6** Maurin (Ubaye), juillet 2008, *Galium pumilum* +, *Phyteuma ovatum* +, *Orobanche caryophyllacea* +; **7** Cogne, Lillaz (Val d'Aoste), juillet 2009, *Campanula spicata* +, *Onobrychis montana* +, *Anchusa officinalis* +; **8** Cogne, Lillaz (Val d'Aoste), juillet 2009, *Rumex scutatus* +, *Knautia purpurea* +, *Melica transsilvanica* +; **9** Dormillouse (Briançonnais), juillet 1983, *Campanula trachelium* 1.1, *Geum urbanum* +, *Anthoxanthum odoratum* +, *Hieracium piloselloides* +,

Galium rubrum +, *Phyteuma scorzonellifolium* +; **10** Montagny, Le Villard (Tarentaise), août 2005, *Allium oleraceum* +; **11** Valloire (Maurienne), juillet 2007; **12** Bozel (Tarentaise), juillet 2009, *Campanula rotundifolia* 1.1, *Rubus canescens* 1.2, *Helleborus foetidus* +; **13** Abbaye de Laverq (Ubaye), juillet 2008, *Gentiana villosa* +, *Rosa pendulina* +, *Rubus saxatilis* 1.1, *Polygonum verticillatum* +, *Phyteuma michelii* +, *Aquilegia vulgaris* +, *Hypochoeris maculata* 1.1, *Trisetum flavescens* 1.1

Tableau 2 - Origine des relevés, espèces accidentnelles: **1** Cogne (Val d'Aoste), juillet 2009, vers le Pont Tchezen, *Hieracium villosum* +, *Hypericum perforatum* +; **2** Vallée de Champorcher (Val d'Aoste), juillet 2009, *Primula veris* subsp. *columnae* +, *Lotus corniculatus* +, *Geranium robertianum* +, *Achillea millefolium* +, *Ranunculus acris* +; **3** Vallée de Champorcher (Val d'Aoste), juillet 2009, *Festuca flavescens* +; **4** Vallée de Champorcher (Val d'Aoste), juillet 2009, *Scabiosa columbaria* +; **5** Mont-Cenis, carrière du Paradis (Maurienne), juillet 2004, *Centaurea scabiosa* +, *Rosa pendulina* +, *Stachys recta* +, *Astragalus penduliflorus* +, *Juniperus communis* subsp. *alpina* +, *Sorbus aria* +

accidentelles: **1** Méribel, Le Villard (Tarentaise), juillet 2007, *Lotus corniculatus* +, *Carex flacca* +; **2** Saint-Vincent-les-Forts (Ubaye), juillet 2008, *Lilium martagon* +, *Aegopodium podagraria* 1.2, *Fourraea alpina* 1.1, *Inula helvetica* +; **3** Puy-Saint-Vincent (Briançonnais), juillet 1994, *Silene flos-jovis* +, *Hieracium amplexicaule* +; **4** Méribel, Le Villard (Tarentaise), juillet 2007, *Sanguisorba minor* +, *Tragopogon pratensis* +, *Trifolium repens* 1.2, *Picris hieracioides* +, *Trifolium aureum* +; **5** Les Allues (Tarentaise), juillet 2009, *Aruncus dioicus* 1.1, *Agrostis capillaris* 1.2, *Corylus avellana* juv. 1.1, *Filipendula ulmaria* 1.1, *Equisetum arvense* +; **6** Méribel, Le Villard (Tarentaise), juillet 2007, *Galium pumilum* 2.2, *Helleborus foetidus* 1.1, *Acinos alpinus* +; **7** Méribel, Le Villard (Tarentaise), juillet 2007, *Campanula trachelium* 2.1, *Geum urbanum* +, *Hieracium murorum* +, *Vicia cracca* subsp. *cracca* 2.2, *Campanula medium* +; **8** Abbaye de Boscodon (Embrunais), juillet 1991, *Galium verum* +, *Mercurialis perennis* +, *Galium aristatum* +, *Salvia glutinosa* +; **9** Forêt de Saluces (Embrunais), juillet 1991, *Campanula glomerata* subsp. *farinosa* +, *Hypochoeris maculata* +, *Hieracium prenanthoides* 2.2, *Briza media* +, *Pulsatilla alpina* +, *Lathyrus linifolius* +, *Carex ferruginea* subsp. *tendae* 1.2, *Phyteuma orbiculare* 1.1; **10** Ab-

Tableau 3 - Origine des relevés, espèces

baye de Boscodon (Embrunais), juillet 1983, *Centaurea scabiosa* 1.1, *Carex humilis* 1.1, *Achillea millefolium* +, *Hieracium piloselloides* +, *Orobanche gracilis* +, *Buphthalmum salicifolium* 1.2.

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LA VEGETAZIONE DEL PARCO REGIONALE MARTURANUM (LAZIO SETTENTRIONALE, ITALIA CENTRALE): LINEAMENTI FITOSOCIOLOGICI E GENESI DEL PAESAGGIO VEGETALE

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ABSTRACT

The Marturanum Regional Park is a small protected area (1,240 hectares), however it is placed along the interface between two of the main lithological units of Lazio, hence featuring a high diversity of flora, vegetation and landscape. Further, it includes a small part of the Monti della Tolfa, a 30,000 hectares hilly range which features an exceptionally low population density. The Tolfa hills are a biodiversity hotspot of C-Italy and show a very distinctive landscape pattern. The present paper outlines a phytosociological classification and syntaxonomical discussion of the numerous plant communities found in the Marturanum Park. The present work describes also the different role of the natural constraints and of the historical and cultural processes that have led to the peculiar landscape patterns nowadays found in the area, and in particular to the differentiation between the two landscape systems of the pyroclastic flow and the Tolfa flysch.

KEYWORDS: Flysch, Landscape history, Lazio, Pyroclastic flow, Syntaxonomy.

INTRODUZIONE

Da alcuni anni il laboratorio di geobotanica dell'Università della Tuscia sta studiando, sotto vari aspetti, la flora e la vegetazione del Parco Regionale Marturanum (VT), un'area protetta di grandissimo interesse per l'elevata eterogeneità ambientale e l'alta diversità floristica (con presenza di numerose specie molto rare e minacciate) nonostante la sua estensione limitata (es. MAGRINI *et al.*, 2006; SCOPPOLA e FILIBECK, 2008b; FILIBECK e SCOPPOLA, in stampa). Il parco, inoltre, è adiacente al comprensorio dei Monti della Tolfa, un distretto collinare che costituisce uno degli *hotspots* di biodiversità nel Lazio (es. CONTOLI, 1977; BATTISTI e GIPPOLITI, 2004; FORNIZ, 2005), con cui condivide la peculiare storia del paesaggio e la bassissima densità di urbanizzazione, normalmente riscontrabile in Italia

solo a quote ben più elevate.

Nell'ambito di una convenzione con l'Ente gestore, è stata recentemente realizzata una carta della vegetazione del parco in scala 1:10.000 (SCOPPOLA e FILIBECK, 2008a). Gli aspetti fitosociologici delle comunità rilevate sono stati finora solo sinteticamente discussi in appendice ad un volume, di taglio prevalentemente divulgativo, sulla flora e la vegetazione del parco (SCOPPOLA e FILIBECK, 2008b).

Il presente lavoro, pertanto, si propone in primo luogo di esporre una dettagliata analisi floristica ed ecologica delle cenosi dell'area protetta, completa, in particolare, delle necessarie discussioni sintassonomiche. Inoltre, nella presente trattazione, la vegetazione viene analizzata nel quadro dell'evoluzione storica del peculiare *pattern* paesaggistico dell'Alto Lazio, nell'ambito di una più ampia linea di ricerca da poco intrapresa (cfr. FILIBECK e SCOPPOLA, in stampa) sull'area di interfaccia fra i due principali distretti geologici che caratterizzano il Lazio settentrionale, e che costituiscono due unità paesaggistiche sia in senso ecologico ("sistemi di paesaggio", *sensu* BLASI *et al.*, 2000) che sotto il profilo dei paesaggi culturali (*sensu* BASTIAN *et al.*, 2006). Ritenia-

mo, infatti, essenziale sperimentare percorsi di integrazione fra l'analisi vegetazionale e quella dei processi storico-sociali, per una migliore comprensione delle dinamiche evolutive e delle caratteristiche ecologiche dei paesaggi.

AREA DI STUDIO

Il Parco Regionale Marturanum si trova in provincia di Viterbo, nel comune di Barbarano Romano, in un'area collinare interposta fra i Monti della Tolfa e i rilievi che circondano il Lago di Vico (Fig. 1). Si estende per 1.240 ha; le quote sono comprese tra 180 e 550 m.

L'area protetta ricade nella fascia di transizione fra le regioni climatiche mediterranea e temperata; BLASI (1994) colloca il territorio del parco tra l'orizzonte "collinare subumido superiore/umido inferiore" e quello "mesomediterraneo subumido superiore/umido inferiore".

Il parco è, inoltre, ubicato a cavallo di un tratto della lunga linea di contatto litologico che divide la provincia di Viterbo in un distretto occidentale sedimentario (il comprensorio dei Monti della Tolfa e più a nord la Maremma Laziale) e in uno orientale vulcanico (i



Fig. 1 - Ubicazione dell'area di studio.

monti Vulsini, Cimini, Vicani e Sabatini e i relativi plateaux piroclastici) (cfr. ad es. ACCORDI *et al.*, 1988; DI FILIPPO, 1993). In particolare, il parco è diviso tra una porzione dove il substrato prevalente è il “Flysch della Tolfa” (successione torbiditica meso-cenozoica, formata da un’alternanza di calcari marnosi, calcareniti, argilliti e marne), e una costituita dal “Tufo Rosso a Scorie Nere Vicano” (colate piroclastiche pleistoceniche) (MADONNA, 2008).

La morfologia dei due settori è profondamente diversa. Quello costituito dal Flysch presenta colline arrotondate, incise da corsi d’acqua a carattere torrentizio, con greti sassosi al fondo di avvallamenti poco profondi. Il settore piroclastico, invece, è formato da ampi tavolati pianeggianti, bruscamente interrotti da profonde gole dalle pareti verticali, che ospitano corsi d’acqua permanenti.

Nella porzione sedimentaria (localmente nota come “Il Quarto”) la proprietà è pubblica, con uso civico di pascolo. Vi si pratica un intenso pascolo brado bovino ed equino; non vi sono centri abitati né case sparse. Sui tavolati del substrato vulcanico, invece, si ha una proprietà privata molto parcellizzata, e prevalgono le colture legnose ed orticole o si pratica il pascolo ovino. Qui è ubicato il paese di Barbarano e un certo numero di case sparse.

LE COMUNITÀ VEGETALI

IL SETTORE SEDIMENTARIO DEL PARCO

Boschi di cerro. Fra le tipologie forestali dell’area protetta, le cerrete costituiscono quella largamente prevalente per superficie. Sono comunità dominate da *Quercus cerris*¹, quasi sempre accompagnato da *Q. pubescens*. Si presentano degradati dall’eccessivo carico di pascolo, che ha portato alla scomparsa di molte specie erbacee del sottobosco e all’ingressione di specie prative o sinantropiche, nonché alla locale dominanza nel sottobosco di *Rubus ulmifolius* o *Paliurus spina-christi*.

Il secondo strato arboreo è formato generalmente da *Fraxinus ornus*, *Acer campestre*, *A. monspessulanum*; lo strato arbustivo ha come specie dominanti *Rosa sempervirens*, *Prunus spinosa*, *Rubus ulmifolius*, *Lonicera caprifolium*, *Crataegus monogyna*. Il carattere subacidofilo è sottolineato dalla presenza (con scarsa frequenza) di *Sorbus torminalis*, *Mespilus germanica*, *Malus flo-*

rentina. Le specie erbacee più comuni sono *Rubia peregrina*, *Tamus communis*, *Viola alba* subsp. *dehnhardtii*, *Bu-glossoides purpurocaerulea*.

Come accade in gran parte del più ampio territorio del Flysch della Tolfa, la composizione floristica è caratteristica per la mescolanza, apparentemente paradossale, di specie mesofile (*Anemone apennina*, *Lathyrus venetus*, *Melica uniflora*, *Oenanthe pimpinelloides*) e termoxerofile (*Smilax aspera*, *Rubia peregrina*, *Asparagus acutifolius*, *Clematis flammula*); si aggiunge, inoltre, il contingente delle erbacee più proprie dei querceti subacidofili, quali *Luzula forsteri*, *Cruciata glabra*, *Asperula laevigata*, *Echinops sibiricus*, *Aristolochia rotunda*, *Clinopodium vulgare*, *Lathyrus niger*.

I suoli (F. Biondi, com. pers.) si presentano debolmente acidi; l’orizzonte B si presenta ricco sia di argilla che di scheletro, garantendo quindi una buona disponibilità di acqua e avvantaggiando così il cerro nella competizione con le altre essenze, nonostante l’aridità estiva (infatti, da un lato lo scheletro favorisce la permeabilità a scapito dello scorrimento superficiale: dall’altro, l’acqua percolata viene intercettata e trattenuta dall’argilla, e per capillarità può poi risalire agli orizzonti sovrastanti).

La comunità va riferita all’alleanza *Teucrio siculi-Quercion cerridis*, come ridefinita da BLASI *et al.* (2004), cioè al syntaxon dei boschi subacidofili di cerro dell’Italia tirrenica centrale e meridionale, dal piano basale a quello submontano². Infatti, sebbene fra le specie caratteristiche dell’alleanza siano presenti, nei rilievi effettuati, solo *Echinops sibiricus*, *Malus florentina* e *Silene viridiflora*, sono tuttavia frequenti molte delle specie considerate da BLASI *et al.* (2004) come differenziali rispetto all’alleanza *Carpinion orientalis*: *Oenanthe pimpinelloides*, *Asperula laevigata*, *Ligustrum vulgare*, *Aristolochia*

rotunda, *Malus sylvestris*, *Lathyrus niger*, *Ranunculus lanuginosus*, *Mespilus germanica*, *Rumex sanguineus*, ecc.

Più complessa è la collocazione a livello di associazione. DI PIETRO *et al.* (2010) hanno attribuito i boschi di cerro rilevati su flysch nei vicini Monti della Tolfa a due distinti *syntaxa*. Una prima tipologia, definita dagli Autori più termofila, è stata riferita all’associazione *Rubio peregrinae-Quercetum cerridis*, già descritta in forma invalida da PIGNATTI E. e PIGNATTI S. (1968), e ridecritta sotto il profilo formale nonché ridefinita nella sua delimitazione ecologica e floristica dagli Autori sopra citati (peraltro, nella nuova combinazione caratteristica vengono incluse anche specie di scarsa indicazione cenologica, come *Hedera helix* e *Stachys officinalis*). Una seconda tabella, considerata più mesofila, viene riferita da DI PIETRO *et al.* (2010) all’associazione *Melico uniflorae-Quercetum cerridis*, già nota per i substrati flyschoidi della Toscana meridionale e spesso citata anche per i suoli piroclastici del Lazio settentrionale. Tuttavia, tale suddivisione in due associazioni distinte è stata basata su una cluster analysis operata su valori di copertura, scelta che appare scarsamente opportuna per comunità forestali fortemente disturbate dal pascolo e dagli interventi selviculturali, e pertanto con i rapporti quantitativi fra le specie influenzati da fattori contingenti e stocastici; più in generale, la ripartizione appare piuttosto arbitraria, basandosi essenzialmente sulla variazione (che mostra uno spettro continuo) del rapporto fra specie mesofile e termofile, giacché entrambi i pacchetti sono presenti in ambedue le associazioni. I primi risultati di studi ancora in corso da parte degli Autori della presente nota (Filibeck e Scoppola, dati ined.), volti ad una revisione complessiva delle cerrete su substrati flyschoidi dell’Italia centrale, e basati su un’estensiva utilizzazione di tecniche di analisi multivariata applicate ad un’interpretazione biogeografica ed ecologica, suggeriscono da un lato che le due tipologie proposte da DI PIETRO *et al.* (2010) non sono significativamente distinte né fra di loro né nei confronti delle cerrete del Parco Marturanum (che mostrano al loro interno un gradiente continuo fra i due “estremi”); dall’altro che l’intero gruppo costituito dai rilievi dei M. della Tolfa più quelli del Parco Marturanum è più affine ad altri *syntaxa*, quale l’*Asparago tenuifolii-Quercetum cerridis*, di quanto non sia simile alla tabella originale del *Melico-Querco-*

²Il nome di questo syntaxon ha subito complesse vicende nomenclaturali. Secondo DI PIETRO *et al.* (2010), anche il tentativo di BLASI *et al.* (2004) di recuperarlo come *nomen conservandum* non sarebbe ammисibile ai sensi dell’ICPN, e pertanto il nome valido da utilizzare sarebbe *Crataego laevigata-Quercion cerridis* Arrigoni 1997. Tuttavia, dato l’ampio utilizzo sinora effettuato del nome *Teucrio-Quercion* da parte dei fitosociologi italiani (specialmente a seguito della revisione di BLASI *et al.*, 2004) e la delimitazione originariamente diversa del *Crataego-Quercion*, e considerata l’esistenza di numerosi studi ancora in corso sui querceti dell’Italia centrale, abbiamo preferito utilizzare qui il nome più consolidato.

¹La nomenclatura segue CONTI *et al.* (2005).

Boschi di roverella. Nel settore sedimentario del parco, *Q. pubescens* assume la dominanza solo in occasione di alcuni affioramenti conglomeratici, dove però le cenosi si presentano come piccoli frammenti interposti fra i semi-nativi, oppure come boscaglie molto degradate. Sono comunque riferibili al *Carpinion orientalis*, e, almeno nel caso delle formazioni interpoderali, avvicinabili al *Roso sempervirentis-Quercetum pubescentis* per il corteggiaggio di specie sclerofille (*Phillyrea latifolia*, *Clematis flammula*, *Rosa sempervirens*, *Asparagus acutifolius*).

Boschi di Fraxinus oxycarpa. Nell'intero territorio del Flysch della Tolfa si rinvengono interessanti lembi non-ripariali di bosco a *Fraxinus angustifolia* subsp. *oxycarpa*, in corrispondenza di affioramenti argillosi con ristagno o scorrimento idrico (SPADA, 1977; DI PIETRO *et al.*, 2010). Nel parco, l'esempio di maggiore estensione si presenta come una frassinetta quasi pura, con composizione floristica molto alterata dalla concentrazione di bestiame al pascolo. Ospita, fra le specie più abbondanti: *Ulmus minor*, *Acer campestre*, *Ligustrum vulgare*, *Crataegus oxyacantha*, *Oenanthe pimpinelloides*, *Ranunculus ficaria* s.l., *R. lanuginosus*, *R. velutinus*, *Sympyton tuberosum* subsp. *angustifolia*, *Prunella vulgaris*. L'interpretazione fitosociologica di queste formazioni è difficile (cfr. BLASI e FRONDONI, 1998). Nella Riserva di Monte Rufeno, sempre nel Viterbese ma su flysch più arenaceo, i lembi a cerro e frassino delle nicchie di frana sono stati interpretati (SCOPPOLA e FILESI, 1995) come una subassociazione *fraxinetum oxycarpeae* della circostante cerreta dell'*Asperago tenuifolii-Quercetum cerridis*. In Toscana, in ambito pianiziere, i boschi di cerro e frassino sono stati descritti come *Fraxino oxycarpae-Quercetum cerridis* (FOGGI *et al.*, 2000) e molte delle specie caratteristiche si rinvengono anche nel nostro caso.

Boscaglie di aceri. Sono formazioni dinamicamente intermedie fra cespuglieto e bosco, molto caratteristiche dell'area studiata; sono fisionomicamente molto variabili, anche nell'ambito dello stesso nucleo: l'eterogeneità strutturale sembra essere una loro caratteristica costante ed intrinseca. Talvolta sono veri preboschi ad *Acer campestre*, *A. monspessulanum*, *Fraxinus ornus*, con presenza di querce; altre volte constano di un mosaico fra un cespuglieto sviluppato in altezza (*Pyrus amygdaliformis*, *Ulmus minor*, *Prunus spinosa*,

ecc.) e piccoli nuclei, o singoli individui, di *Quercus cerris* e *Q. pubescens*. In questo secondo caso, si può ipotizzare se siano evoluti a partire da un pascolo alberato. Secondo rilievi pedologici riportati da PORTOGHESI *et al.* (2008) per gli acereti dei Monti della Tolfa, la ricchezza di carbonato di calcio nel substrato è uno dei fattori che favoriscono l'instaurarsi di comunità ad *A. monspessulanum* dominante. Per la presenza di specie mediterranee (*Phillyrea latifolia*, *Smilax aspera*, ecc.), riferiamo gli stadi più evoluti al *Carpinion orientalis* (che ci sembra possa ragionevolmente costituire, in questi ambienti submediterranei, uno stadio seriale del *Teucrio siculi-Quercion cerridis*), e quelli arbustivi al *Pruno-Rubenion ulmifolii*.

Cespuglieti. I cespuglieti coprono vaste superfici del "Quarto", e sono molto caratteristici di tutta l'area del Flysch della Tolfa. La loro genesi è da ricollegarsi alla cessazione, avvenuta alcuni decenni fa, della pratica originariamente diffusa nei terreni di proprietà collettiva di alternare l'utilizzo a pascolo con colture cerealicole finalizzate a ripulire periodicamente il terreno (cfr. ZONGOLI, 2005). Attualmente le praterie si presentano quindi infiltrate da un articolatissimo mosaico di nuclei di cespuglieto e ampi arbusteti chiusi (SCOPPOLA e FILIBECK, 2008a); le specie dominanti sono quasi sempre spinose, per via della pressione del pascolo. La fisionomia è molto eterogenea, con rapporti fra le specie che variano in modo continuo. Su gran parte dell'area, le specie a maggiore copertura sono *Prunus spinosa* e *Crataegus monogyna*; elevata frequenza è raggiunta da *Rubus ulmifolius*, *Spartium junceum*, *Paliurus spina-christi*, *Ulmus minor*, *Pyrus amygdaliformis*, *Rosa* sp. pl., *Ligustrum vulgare*; le prime quattro di queste specie possono a loro volta assumere la dominanza o concorrervi. Fra le lianose e le erbacee sono frequenti *Rosa sempervirens*, *Lonicera etrusca*, *Rubia peregrina*, *Oenanthe pimpinelloides*. In condizioni più termoxerofile partecipano anche arbusti sempreverdi (*Phillyrea latifolia*, *Rhamnus alaternus* e raramente *Pistacia lentiscus*), senza però mai diventare dominanti.

Tutte queste comunità appartengono chiaramente al *Pruno-Rubenion ulmifolii*, come ridefinito per l'Italia da BLASI *et al.* (2002) e POLDINI *et al.* (2002), vale a dire il syntaxon più termofilo dei *Prunetalia spinosae*, formato da associazioni submediterranee a fisionomia decidua ma con significativa presenza

dielementi di *Quercetea ilicis*. A livello di associazione, proprio nell'area del parco è stato descritto il *Lonicero etruscae-Rosetum sempervirentis* (CUTINI *et al.*, 1996), di cui però rimane a nostro avviso da meglio chiarire la caratterizzazione specifica e l'applicabilità alle varie fisionomie presenti.

Sono diffuse nel parco, inoltre, peculiari comunità a dominanza di *Paliurus spina-christi*, talora quasi monofitiche (caratteristiche e ben note anche per il resto del Flysch della Tolfa, cfr. ad es. SPADA, 1977); contrariamente a quanto supposto in CUTINI *et al.* (1996) e in BLASI *et al.* (2002), non riteniamo che queste cenosi siano da interpretare come una variante edafo-igrofila dei cespuglieti a *Rosaceae*. Infatti, sebbene *Paliurus* mostri in tutta la Maremma Laziale una tolleranza ecologica che raggiunge anche situazioni più meso-igrofile rispetto agli altri arbusti spinosi (Filibek, dati ined.), le condizioni di elevata disponibilità idrica non sembrano costituire la condizione necessaria per lo sviluppo dei paliureti puri, che nel parco come altrove sono spesso svincolati da morfologie depresse. Riconoscimenti pedologiche mirate da noi effettuate nel parco (in coll. con F. Biondi, dati ined.) non hanno rilevato significative differenze rispetto ai pruno-crategeti in termini di materiale parentale, componente argillosa, tessitura e acidità. L'unica differenza osservata è la maggiore abbondanza in materiale organico. Appare, pertanto, probabile che *Paliurus* sia particolarmente competitivo in condizioni eutrofiche e blandamente ruderali, colonizzando quindi soprattutto terreni agricoli abbandonati o suoli recentemente deforestati, perciò più ricchi di humus (come appare confermato dal suo comportamento "infestante" nei boschi più pascolati, e dal fatto che la fascia disboscata pochi decenni fa per il passaggio di una linea elettrica attraverso uno dei boschi del parco è invasa da un paliureto). In questa stessa ottica va probabilmente spiegato il suo apparente comportamento "igrofilo", giacché le vallecole e i boschi ripari oltre che più umidi sono anche più ricchi in materia organica.

Praterie. Insieme ai cespuglieti, le praterie secondarie pascolate costituiscono l'aspetto più caratteristico dell'intero comprensorio del Flysch della Tolfa (cfr. LUCCHESE e PIGNATTI, 1990; FANELLI e MENEGONI, 1997). Come si è detto più sopra, fino agli anni '60 queste superfici venivano a rotazione utilizzate anche per coltivazioni cerealicole, mentre oggi ne sopravvive solo l'uso

come pascolo brado. La composizione floristica è altamente variabile, in funzione dell'elevatissima variabilità degli affioramenti dei termini che compongono il Flysch, della geomorfologia, della disponibilità idrica e della distribuzione del carico di bestiame. Particolarmente caratteristico e frequente è il pattern a mosaico strettamente interdigitato ad una scala di pochi metri tra lembi a composizione decisamente xerofila e lembi schiettamente meso-igrofili. Complessivamente, però, quasi tutte le tipologie sono accomunate da un gruppo di specie fra le quali particolarmente abbondanti risultano *Bromus hordeaceus*, *Lolium multiflorum*, *Cynodon dactylon*, *Malope malacoides*, *Coleostephus myconis*, *Trifolium campestre*, *T. scabrum*, *Bartsia trixago*, *Linen bienne*, *Scorpiurus muricatus* e *Sanguisorba minor* subsp. *balearica*.

Si possono distinguere almeno i seguenti aspetti:

- a) Tero-brometi. Comunità pioniere, basifile, termo-xerofile, con elevata diversità specifica (fino a 50-70 specie in 10-15mq!), a prevalenza di terofite (es. *Trachynia distachya*, *Triticum neglectum*, *Helianthemum salicifolium*, *Hippocratea biflora*, *Medicago minima*, *Geropogon glaber*, *Polygala monspeliaca*, ecc.), degli ambienti ad accentuata aridità edafica, come gli espluvi e le dorsali in cui affiorano i termini calcarei-marnosi o i conglomerati. Sono inquadrabili nel *Trachynion distachyae* ma con molte ingressioni di specie dei *Thero-Brometalia* e *Echio-Galactition*. I pascoli e inculti dei termini più argillosi, ma sempre su suoli sottili, si arricchiscono invece di *Onobrychis caput-galli*, *Pallenis spinosa*, *Blackstonia perfoliata*, *Astragalus hamosus*, *Hedypnois cretica*, *Medicago intertexta*, *Xeranthemum cylindraceum*, *Catananche lutea* e altre. Maggiori affinità floristiche ed ecologiche si hanno in questo caso con alcune comunità recentemente descritte per l'Umbria (in contesti più sian tropici), inquadrate nei *Thero-Brometalia* (GIGANTE e VENANZONI, 2007).
- b) Lande ad asfodelo. Sui pendii assolti degradati e sovrappascolati e più volte percorsi dal fuoco, le comunità erbacee sono riferibili all'*Echio-Galactition* (cfr. SCOPPOLA, 2000; GIGANTE e VENANZONI, 2007); queste entrano localmente in contatto con aspetti frammentari dei *Brachypodietalia phoenicoidis* caratterizzati da *Asphodelus ramosus*, *Foeniculum vulgare*, *Hyparrhenia hirta*, *Richardia picroides*.
- c) Prati mesofili. Su superfici pseudopianeggianti, con discreta disponibilità idrica almeno nei mesi autunnali e in-

vernali, prevale un cotico più chiuso e in genere rasato per l'intensa frequentazione del bestiame, con *Gaudinia fragilis*, *Dactylis glomerata*, *Phleum pratense*, *Elymus repens*, *Bellis perennis*, *Sulla coronaria*, *Achillea ageratum*, *Daucus carota*, *Trifolium resupinatum*, diverse orchidacee, ecc.; analoghe composizioni floristiche hanno i cotici di origine postcolturale, sensibilmente impoveriti se non sottoposti alla pressione del pascolo. Entrambi possono essere provvisoriamente inquadrati nell'*Inulo viscosae-Agropyrion repentis* (*Agropyretalia repentis*) per le discrete analogie floristiche ed ecologiche con alcune comunità di origine postcolturale segnalate per i territori pianeggianti e basso-collinari della valle del Fiume Paglia e della conca Ternana (cfr. SCOPPOLA, 1998; BIONDI et al., 2002, ecc.).

d) Prati meso-igrofili. Negli ambiti micro-geomorfologici con elevata disponibilità idrica (a causa di impluvi, scorrimento ipodermico, sorgenti stagionali legate a strati a franapoggio, ecc.) si può ulteriormente distinguere nel pascolo una componente di specie meso-igrofile quali *Ranunculus velutinus*, *Oenanthe globulosa*, *O. pimpinelloides*, *Briza minor*, *Prunella laciniata*, *Trifolium fragiferum*, *T. repens*, *Lotus tenuis*, *Cynosurus cristatus*, *Ononis spinosa* subsp. *antiquorum* e diverse orchidee fra cui la rara *Orchis laxiflora*; la comunità erbacea è qui spesso a mosaico con cespuglietti mesofili affini al *Pruno-Rubenion ulmifolii*. La stessa composizione floristica è stata rinvenuta, sempre su Flysch e nelle stesse condizioni geomorfologiche, anche nella vicina Riserva Naturale Monterano (FANELLI e MENEGONI, 1997), dove è stata descritta l'associazione *Gaudinio-Cynosuretum cristati* inquadrata nel *Ranunculion velutini* (*Trifolio-Hordeetalia*, *Molinio-Arrhenatheretea*), alleanza che però si riferisce a prati permanenti, sfalciati, di bacini carsici e pianure alluvionali su suoli periodicamente inondati (cfr. ad es. PEDROTTI, 1976; PEDROTTI et al., 1992; VENANZONI, 1992; PIRONE, 1997), in un contesto bioclimatico e biogeografico nettamente temperato. Poiché, però, tanto nel Parco Maturanum che nella Riserva Monterano si tratta, invece, di prati fortemente pascolati, in un contesto submediterraneo, in cui la presenza di specie mesofile è legata a particolari condizioni edafiche e microtopografiche (suolo argilloso, profondo, molto umido fino alla primavera inoltrata e poi secco in estate), preferiamo al momento considerare questa associazione come *incertae sedis*, con possibile affinità per gli

Holoschoenetalia vulgaris.

Vegetazione ripariale. I versanti più ripidi (perché impostati sui termini più calcarei del Flysch) delle vallecole incise dai torrenti ospitano frammentaria e discontinua vegetazione sclerofillica a *Quercus ilex* e *Phillyrea latifolia* (*Quercion ilicis* fragm.). La concentrazione, apparentemente paradossale (come già notato per il comprensorio Tolpetano da SPADA, 1977), degli elementi sempreverdi proprio negli ambienti potenzialmente più freschi (quando queste componenti sono invece assai rare nella vegetazione zonale circostante) è spiegabile con il fatto che proprio qui affiorano gli strati a maggior contenuto carbonatico. I versanti incisi in affioramenti prevalentemente argilosì presentano discontinua vegetazione ad *Arundo plinii* (*Inulo viscosae-Agropyrion repentis* fragm.). I versanti con microclima umido e ombreggiato e/o con suolo profondo, e gli ambiti di raccordo morfologico fra versante e fondo dell'impluvio, ospitano lembi di bosco mesofilo a dominanza di *Quercus cerris* e/o *Ostrya carpinifolia*, con *Acer campestre* e *Carpinus betulus*; caratteristico *Cornus mas* nello strato arbustivo, mentre la flora erbacea include tipicamente *Allium pendulinum*, *Anemone apennina*, *Lathyrus venetus*, *Melica uniflora*. Queste comunità si possono pertanto considerare affini al *Melico uniflorae-Quercetum cerridis*. I corsi d'acqua sono a carattere torrentizio, con greti ghiaiosi spesso asciutti. Le sponde ed i piccoli terrazzi ciottolosi del greto, lievemente rialzati, ospitano un interessante mosaico fra una discontinua vegetazione sub-xerofila ad *Acer monspessulanum*, *Cercis siliquastrum*, *Phillyrea latifolia* (aff. *Carpinion orientalis*), e frammenti di vegetazione peri-ripariale sub-igrofila a *Fraxinus angustifolia* subsp. *oxycarpa* e *Ulmus minor* (cfr. *Populin albae*). I greti ospitano singoli individui di *Salix purpurea* e *Tamarix africana* (*Salicion elaeagni* fragm.); la presenza di questa combinazione di specie nei saliceti pionieri del greto del Fiume Paglia ha permesso di segnalare una variante a *T. africana* del *Saponario-Salicetum purpureae* (SCOPPOLA, 1998).

IL SETTORE VULCANICO DEL PARCO

Toposequenza dei canyons piroclastici. Le gole dalle pareti verticali sono caratteristiche del paesaggio piroclastico: la loro genesi è legata alle particolari proprietà meccaniche del tufo

(scarsa durezza associata ad un'eccellente capacità di reggere forti penedenze). Esse ospitano, in uno spazio spesso ristrettissimo, una complessa sequenza catenale che si ripete piuttosto costante in tutti i morfotipi analoghi del Lazio settentrionale e della Toscana meridionale (cfr. ad es. ABBATE *et al.*, 1990; FANELLI e MENEGONI, 1999; VICIANI *et al.*, 2004). La sequenza completa si osserva solo nei canyons più larghi; le forre di dimensione modesta presentano solo alcune comunità, oppure vedono il mescolarsi in una stessa cenosi di elementi provenienti dalle varie fasce.

La toposequenza delle gole tufacee del parco può essere schematizzata come segue:

1) Cigli dei pianori in esposizione meridionale: ospitano fasce di macchia sclerofillica a copertura discontinua ed altezza inferiore a 2-3 metri. Prevalgono per copertura *Phillyrea latifolia* ed *Erica arborea*; frequenti *Quercus ilex*, *Rhamnus alaternus*, *Spartium junceum*, presenti anche *Arbutus unedo*, *Viburnum tinus*. Tra le erbacee, frequenti *Pulicaria odora*, *Asphodelus ramosus*, *Origanum vulgare*. La sintassonomia delle comunità sclerofilliche extrazonali del Lazio è notoriamente irrisolta, anche per la loro frammentarietà; in attesa di dati di dettaglio le riferiamo per il momento ad un generico *Quercion ilicis* s.l. sebbene un possibile riferimento possa essere l'*Erico-Arbutum*, associazione che riunisce macchie e stadi preforestali dinamicamente collegati a boschi termofili subacidofili (leccete e querceti caducifogli). I lembi di macchia dei cigli tufacei formano generalmente mosaico seriale con le garighe dominate da *Cistus salvifolius*, accompagnato da *Helichrysum italicum*, *Thymus longicaulis*, *Helianthemum nummularium* subsp. *obscurum*, *Reichardia picroides*, *Lupinus graecus*, *Teucrium chamaedrys*, *Anthoxanthum odoratum*. Anche in questo caso, siamo di fronte a formazioni extrazonali ed impoverite, che si possono riferire al *Cisto-Ericion*.

2) Cigli dei pianori in esposizione settentrionale: vi si riscontra una caratteristica fascia dominata da *Quercus pubescens* con *Fraxinus ornus*, del tutto priva di *Q. cerris*. Questa comunità manca nelle descrizioni della sequenza catenale delle forre di altre aree del Lazio piroclastico (cfr. i lavori più sopra citati); tuttavia, successivamente al rinvenimento nel Parco Marturanum, è stata da noi rilevata in analoga collocazione topografica anche in altre aree del Viterbese (Filibeck e Facioni, dati ined.):

ne è in corso lo studio sintassonomico. 3) Versanti rupestri e sfasciumi di frana: presentano frammentari nuclei a *Quercus ilex* e/o *Celtis australis*, floristicamente poveri e disturbati (aff. *Quercion ilicis* s.l.).

4) Terrazzi morfologici che interrompono i versanti: ospitano boschi mesofili di *Q. cerris*. Non sono stati ancora indagati in dettaglio; per la presenza di specie quali *Cornus mas*, *Melica uniflora*, *Euphorbia amygdaloides*, *Festuca heterophylla* ed *Allium pendulinum*, si possono preliminarmente riferire al *Melico uniflorae-Querchetum cerridis*.

5) Raccordo morfologico fra pareti e fondo della forra: presenta caratteristici boschi misti mesofili, ad elevata ricchezza di specie arboree (*Quercus cerris*, *Carpinus betulus*, *Corylus avellana*, *Ostrya carpinifolia*, *Fraxinus ornus*, *Acer opalus* subsp. *obtusatum*, *Castanea sativa*, *Fagus sylvatica*, *Ulmus glabra*). La dominanza è piuttosto variabile: nel vallone del Biedano, in un largo impluvio laterale con esposizione settentrionale, abbiamo rinvenuto anche un lembo di vera e propria faggeta extrazonale. In ogni caso, il sottobosco arbustivo ed erbaceo è ricco di specie proprie delle faggete termofile (*Adoxa moschatellina*, *Allium pendulinum*, *Corydalis cava*, *Daphne laureola*, *Euphorbia amygdaloides*, *Galanthus nivalis*, *Ilex aquifolium*, *Lathyrus venetus*, *Mercurialis perennis*, *Milium effusum*, *Sanicula europaea*, *Vinca minor*, ecc.); vanno perciò riferiti ai *Fagetalia sylvaticae*. Più controversa è la collocazione a livello di dettaglio di queste singolari cenosi, specifiche del paesaggio piroclastico: in passato è stato fatto frequentemente riferimento all'*Anemono-Fagetum sylvaticae* (ad es.: BLASI, 1992; ATTORRE *et al.*, 1997; SCOPPOLA e CAPORALI, 1998; FANELLI e MENEGONI, 1999), vale a dire all'associazione delle faggete termofile dell'Appennino meridionale (cfr. DI PIETRO *et al.*, 2004), tuttavia considerazioni di ordine biogeografico, floristico e fisionomico rendono oggi poco opportuna questa attribuzione per le forre dell'Alto Lazio (cfr. la discussione in DI PIETRO *et al.*, 2010 - anche se non riferita a comunità di forra). Il problema è meritevole di ulteriore studio, anche per il problema delle eventuali affinità verso le alleanze *Erythronio-Carpinion* e *Tilio-Acerion* s.l. (VICIANI *et al.*, 2004).

6) Il fondo della forra presenta frequentemente boscaglie a *Corylus avellana*; spesso insistono su antichi terrazzamenti (i valloni erano fortemente antropizzati fino agli anni '50), perciò almeno in parte sono interpretabili come derivanti

dall'inselvaticimento di colture. D'altra parte, il nocciolo è pianta spontanea e caratteristica degli ambienti di forra dell'Italia centrale, quindi queste coltivazioni potrebbero a loro volta essere state inizialmente ricavate a partire da cenosi spontanee. La flora erbacea è inquadrabile nei *Fagetalia*.

7) Sponde dei corsi d'acqua: ospitano formazioni ripariali, lineari, ad *Alnus glutinosa*; sono presenti nel sottobosco *Rubus caesius*, *Circaeaa lutetiana*, *Carpendula*, *C. remota*, *Lathraea squamaria*, *Stachys sylvatica*, ecc. La cenosi è molto caratteristica delle incisioni nei territori piroclastici del Lazio, osservabile anche in forre di modeste dimensioni. Appartiene all'*Alno-Ulmion*, e in particolare all'associazione *Circaeao lutetianae-Alnetum glutinosae* (BLASI e FRONDONI, 1998).

Vegetazione delle aree archeologiche. Le grandiose opere (tombe a tumulo, tombe rupestri, "vie cave"), realizzate in epoca etrusca grazie alle particolarissime proprietà meccaniche del tufo, hanno significativamente modificato la stessa geomorfologia di alcune forre e ripiani piroclastici. Di conseguenza, il mosaico catenale della vegetazione si presenta in parte differente da quello delle forre non modificate, con alcune comunità legate in modo caratteristico ai morfotipi artificiali.

Sulla sommità delle grandi tombe a tumulo, si insediano piccoli nuclei di boscaglia di *Quercus pubescens* (con sottobosco e orlo di *Osyris alba*, *Asparagus acutifolius*, *Cyclamen repandum*, ecc.), riconducibili al *Carpinion orientalis*. Nelle depressioni fra i tumuli e nelle "vie cave" poco profonde si insediano lembi di boscaglia mesofila di *Corylus avellana* con *Carpinus betulus* (con specie dei *Fagetalia sylvaticae*), mescolati a frammentari nuclei più xerofili e rupicolli di *Celtis australis* e/o *Ficus carica*. Le superfici litoidi umide e ombrose delle "vie cave" più profonde presentano sinusie di felci molto simili a quelle riscontrabili nei valloni naturali (*Phillytis scolopendrium*, *Polystichum setiferum*, *Dryopteris filix-mas*, *D. affinis* subsp. *borreri*, *Polypodium interjectum*, ecc.).

Boschi di cerro dei tavolati. I pianori tufacei sono in massima parte coltivati: le cerrete occupano limitate superfici, localizzate nella parte terminale dei tavolati e tutte recentemente utilizzate, pertanto di difficile inquadramento a livello di associazione. La composizione floristica, comunque, è riconducibile al *Teucrio siculi-Quercion cer-*

ridis; è però complessivamente più acidofila rispetto alle cerrete del settore flyschoide, e priva di gran parte del contingente più mediterraneo; può essere ricondotta al *Coronillo emeri-Quercetum cerridis* (cfr. ABBATE et al., 1990).

Cespuglieti. A differenza del settore flyschoide, nella porzione piroclastica del parco i cespuglieti decidui ospitano superfici modestissime. Sono nettamente dominati da *Prunus spinosa*; caratteristici, ma non molto frequenti, *Cytisus scoparius* e *Chamaecytisus hirsutus*.

Praterie. Le comunità erbacee del settore tufaceo del parco sono del tutto differenti da quelle del substrato sedimentario. La loro articolazione può essere schematizzata come segue (le praterie dei substrati piroclastici del Viterbese sono tuttora in corso di studio, per cui di taluni aspetti presentiamo solo un inquadramento provvisorio):

1) Sui litosuoli del ciglio dei pianori tufacei si incontrano pratelli floristicamente ben caratterizzati per la presenza delle acidofile *Tuberaria guttata*, *Aira elegans*, *Trifolium bocconeii*, *Rumex bucephalophorus*, *Plantago bellardii*, *Filago gallica*, *Tolpis umbellata*, *Hypochaeris glabra*, *Silene gallica*, *Lotus angustissimus*, inquadrati nell'*Helianthemion guttati*. Occupano modeste superfici e rappresentano un interessante esempio di cenosi pioniera. Il riferimento al *Moenchio-Tuberarietum guttatae*, descritto per altre località laziali (LUCCHESE e PIGNATTI, 1988; FANELLI, 2002) è al momento il più plausibile; gli autori presentano tuttavia una tabella piuttosto complessa in cui sono inclusi anche aspetti riconducibili ai *Poëtalia bulbosae*, peraltro riscontrati anche nel parco. È comunque riconoscibile una variante pioniera differenziata da *Helianthemum aegyptiacum*, *Linum trigynum*, *Galium divaricatum* e *Psilurus incurvus* intercalata a frammenti di gariga a *Fumana tymifolia*, *Helianthemum nummularium* subsp. *obscurum* e *Helychrysum italicum*.

2) Nei siti con esposizione meridionale, il mosaico seriale della vegetazione edafoxerofila prevede, tra i cisteti e i pratelli, vistosi popolamenti di *Lupinus graecus* e frammenti extrazonali di prateria di tipo substeppico di graminacee cespitose quali *Stipa pulcherrima*, *Cleistogenes serotina*, *Bothriochloa ischaemum*, *Melica transsilvanica*, che riferiamo provvisoriamente ai *Brachypodietalia phoenicoidis*.

3) Su alcuni pianori sfruttati per il pascolo ovino, il tuberarieto (qui di origi-

ne secondaria) si insedia in aree incolte o su terreni denudati arricchendosi di elementi termofili e lievemente nitrofili (*Aira* sp. pl., *Vulpia* sp. pl., *Briza maxima*, *Avena barbata*, *Trifolium campestre*, *T. angustifolium*, *Scorpiurus muricatus*, *Erodium* sp. pl., *Crepis neglecta*, *Muscari comosum*) dei *Thero-Brometalia* (al contrario dei precedenti, i prati e pratelli terofitici di quest'ordine sono legati a stazioni un po' più disturbate e includono specie subnitrofile: cfr. GIGANTE e VENANZONI, 2007).

4) Al contatto con oliveti e vigneti si riscontrano densi prati seminaturali ricchi di graminacee (terofite di grande taglia ed emicriptofite a ciclo breve), mantenuti con il pascolo ovino o lo sfalcio. Essi possono essere ascritti al *Vulpio ligusticae-Dasyppyretum villosi* (*Thero-Brometalia*) associazione già nota nell'area romana (FANELLI, 1998, 2002; CESCHIN et al., 2003) e osservata nel Viterbese (SCOPPOLA, 2000).

IL PAESAGGIO VEGETALE DEL PARCO: GENESI E TRASFORMAZIONI

La presenza di una linea di contatto litologico fra due substrati molto differenti (che danno luogo ad evoluzione morfologica e pedologica diversissima) all'interno della piccola superficie del parco, e pertanto nell'ambito di un unico contesto sia climatico che storico-umano, consente di isolare il ruolo del controllo litologico nei processi che portano alla differenziazione e "identità" dei paesaggi.

Sotto il profilo del paesaggio vegetale potenziale, i due settori si presentano costituiti da geosigmeti completamente distinti. Il distretto flyschoide presenta come vegetazione potenziale prevalente un querceto deciduo termofilo, sub-xerofilo e sub-acidofilo, a dominanza di *Q. cerris*, in contatto catenale con i boschi termo-igrofili a dominanza di *Fraxinus oxycarpa* in corrispondenza delle conche argillose, e con la sequenza della vegetazione ripariale, propria delle vallecole calcaree e dei greti ciottolosi, più sopradelineata (dalla fascia a *Carpinus betulus* a quella a *Tamarix africana*), in corrispondenza del reticolo idrografico. Il territorio piroclastico presenta anch'esso come vocazione potenziale, sui tavolati tufacei, un querceto deciduo a dominanza di cerro, ma con una composizione floristica più mesofila e acidofila; sui suoli più sottili verso il margine dei pianori, subentra la potenzialità per boschi di *Q. pubescens*; questi si trovano in conti-

nuità catenale con la vegetazione dei profondi canyon che interrompono i plateaux, a sua volta articolata in un complesso geosigmeto, che inizia dalle comunità sempreverdi extrazonali degli ambienti rupestri (è interessante rilevare come queste siano presenti solo nel settore tufaceo, a causa della maggiore articolazione geomorfologica qui presente, nonostante i termini calcarei del flysch costituiscano apparentemente un substrato più arido delle piroclastiti), passa per i querctei decidui mesofili dei terrazzi morfologici e per i boschi misti di fondo forra con faggio (e anch'essi pertanto extrazonali, ma in tutt'altra direzione!), e termina con la vegetazione ripariale che orla i corsi d'acqua permanenti.

A causa della relazione di tipo gerarchico che intercorre fra le differenti sorgenti di eterogeneità del paesaggio (O'NEILL et al., 1989; KLIJN e DE HAES, 1994; BLASI et al., 2000), anche l'intervento umano su questi due territori, per lo meno quello tradizionale, ha dovuto necessariamente operare entro le potenzialità e i limiti offerti dall'ambiente fisico e da quello vegetazionale, cosicché nel paesaggio reale alcune differenze fra i due settori sono state rafforzate dai processi antropici.

Il settore flyschoide del parco (loc. "Il Quarto") si presenta oggi coperto da un'alternanza di vaste estensioni di boschi, pascoli e cespuglieti di rosacee spinose; sono del tutto assenti le coltivazioni legnose, rari i seminativi, e del tutto mancanti le case sparse e i centri abitati. Questo pattern è generalizzabile all'intero distretto del Flysch della Tolfa, che si estende per oltre 30.000 ettari, quindi ben oltre la modesta estensione dell'area protetta. Sia la scarsità dell'urbanizzazione che l'estensione dei pascoli naturali raggiungono nel paesaggio del Flysch livelli inconsueti per le aree collinari italiane: ciò comporta la presenza di un'elevata diversità floristica (LUCCHESE e PIGNATTI, 1990; FORNIZ, 2005; MAGRINI et al., 2006; SCOPPOLA e FILIBECK, 2008b) come pure la sopravvivenza di numerose specie animali sensibili all'antropizzazione (ad es. il lupo, che ha sempre mantenuto qui una popolazione molto vitale) (BATTISTI e GIPPOLITI, 2004; FORNIZ, 2005).

La genesi di questo paesaggio può essere, nelle sue linee essenziali, ricondotta ai seguenti fattori ambientali ed umani. Il flysch dà luogo, soprattutto laddove affiorano i termini più calcarei, a suoli scarsamente produttivi per l'agricoltura pre-industrializzata a causa dell'elevata petrosità e della fertilità non ottimale; anche le intercalazioni di ar-

gilliti ("argille varicolori") erano difficilmente sfruttabili (cfr. POTENZA, 2005). Grandi superfici erano perciò più convenientemente lasciate a boschi cedui e pascoli. Fino agli anni '60, i seminativi (a frumento prevalente) erano comunque presenti, ma si concentravano soprattutto in situazioni pedo-litologiche intermedie, che davano luogo a suoli decarbonatati e con materiale più fino ma non eccessivamente argilloso, come ad es. i suoli colluviali (F. Biondi, com. verb.). È essenziale però considerare che gran parte del territorio flyschoide tollefano, compreso quello ricadente nel parco, era (ed è tuttora) di proprietà dei Comuni, che lo gestiscono per il tramite delle "Università Agrarie". Con questo nome si indicano istituzioni tipiche dei centri del Lazio settentrionale, di antica origine (alcune sono documentate già dal '500), con status di ente pubblico, nate originariamente come associazioni di categoria dei proprietari di bestiame, successivamente deputate alla gestione delle terre collettive (cfr. ad es. BARGIACCHI, 2005; CHIRICO, 2005). Il toponimo "Quarto" deriva dall'antico uso, nelle terre delle Università Agrarie, di dividere ogni anno il terreno in parcelle, per separare le aree a pascolo da quelle temporaneamente (uno o due anni) assegnate ai braccianti per coltivarle a grano (CECCARINI e BENASSI, 2005): quest'ultima utilizzazione veniva effettuata appunto ogni quattro anni (cfr. BORTOLOTTI, 1988). La consuetudine della "quarteria" sembra nascere come un compromesso fra i contrastanti interessi delle classi dei braccianti e degli allevatori (MORETTI, 1925; cfr. anche FINODI *et al.*, 2005). Le conseguenze sulla storia del paesaggio sono numerose. In primo luogo, essendo la quota di terreno temporanea, il coltivatore non aveva interesse a costruirvi edifici permanenti, né ad impiantarvi colture legnose. Anche la spietratura o l'introduzione di migliorie tecniche erano rese poco convenienti su terreni assegnati provvisoriamente (MORETTI, 1925). La resa dei terreni, quindi, era molto bassa: perciò con i cambiamenti socio-economici degli anni '60 questi seminativi furono i primi ad essere abbandonati. Il pascolo, peraltro, era di tipo brado (bovino ed equino), giacché la proprietà collettiva dei terreni rendeva poco praticabile costituire prati artificiali e altre forme di allevamento più intensive. D'altra parte, il temporaneo utilizzo a frumento aveva anche la funzione di ripulire periodicamente il pascolo, azzerando le dinamiche vegetazionali e la selezione negativa operata dal bestiame, impedendo così l'ince-

spugliamento delle praterie (cfr. ZONGOLI, 2005): la cessazione di questa consuetudine, unitamente al fatto che il pascolo brado continua invece ad essere tuttora praticato, ha portato alle vaste estensioni di cespugli spinosi, oggi così caratteristiche del paesaggio dell'intero flysch tollefano ma in effetti relativamente recenti. La presenza delle Università Agrarie ha, comunque, avuto un ruolo di forte resistenza alle trasformazioni del paesaggio, seppur in parte involontario.

Nel settore vulcanico del Viterbese, invece, è presente una fitta rete di centri abitati, favoriti dall'abbondanza di corsi d'acqua permanenti e dalla peculiare geomorfologia, che offre, ogni qualvolta si abbia la confluenza fra due gole, una "penisola" triangolare circondata su due lati da inespugnabili pareti verticali: questi siti così facilmente difendibili sono stati sfruttati per gli insediamenti permanenti fin da epoca preistorica (cfr. ad es. POTTER, 1985). Fino almeno all'Unità d'Italia, tuttavia, anche il distretto piroclastico dell'Alto Lazio era caratterizzato da ampie terre delle Università Agrarie e soprattutto da enormi latifondi di proprietà religiosa o privata, cosicché, mancando la piccola proprietà contadina, erano inconsistenti le case sparse (la struttura del paesaggio era la stessa del famoso "Deserto Apostolico" dei tavolati piroclastici della Campagna Romana) (cfr. ALMAGIA, 1966; BORTOLOTTI, 1988; CHIRICO, 2005). Le grandi proprietà erano basate su un'agricoltura a bassissima intensità, imperniata sul pascolo, soprattutto ovino, e sul frumento: il primo avveniva solo nel periodo autunnale ed invernale, nell'ambito della transumanza delle greggi e degli uomini dall'Appennino; il secondo, coltivato anche qui "a quarteria", richiedeva uomini quasi soltanto al momento del raccolto, reclutati tra gli abitanti dei paesi. I centri edificati rimanevano pertanto confinati al loro perimetro medievale sugli speroni tufacei. Relativamente rari erano l'ulivo e la vite, anche perché i latifondi erano in genere gestiti non direttamente dal proprietario ma dai "fittavoli", mercanti che prendevano in affitto dai nobili o dal clero intere tenute con contratti di circa 10 anni; per la brevità del contratto non avevano interesse né alle colture legnose né a migliorie o edificazioni, preferendo a loro volta subaffittare ai pastori o assoldare braccianti, per il tramite dei "capoccia" (caporali) (FINODI *et al.*, 2005).

Tuttavia, l'elevata fertilità dei suoli piroclastici (ricchi di microelementi, dotati di buona ritenzione idrica e gene-

ralmente pianeggianti) ha fatto sì che l'evoluzione recente del paesaggio subisse dinamiche diverse rispetto al settore flyschoide. Già originariamente, presso i centri abitati erano presenti piccole proprietà familiari, intensamente coltivate, chiuse all'accesso degli animali. Esse erano però insufficienti al sostentamento, cosicché gli usi civici sulle terre collettive o sui latifondi rappresentavano una risorsa determinante (CAFFIERO, 1983; FINODI *et al.*, 2005). Una serie di norme emanate a partire da metà '800, che restringevano di molto le servitù di uso civico che gravavano sui grandi proprietari, metterà in crisi questo pur stentato equilibrio economico; il conseguente disagio sfocerà fin dai primissimi anni del '900 in rivendicazioni e occupazioni dei braccianti sui latifondi del Lazio, finché nel 1920 un decreto ministeriale concederà decine di migliaia di ettari alle organizzazioni di contadini (CHIRICO, 2005). L'avvento del fascismo porterà poi ad un deciso passo indietro già dal 1923, ma dopo la caduta del regime nuove occupazioni da un lato e strategie politiche dei partiti al governo dall'altro condurranno nel 1950 alla c.d. "legge stralcio", cioè alla riforma agraria affidata all'Ente Maremma. Quest'ultimo evento produrrà cambiamenti notevolissimi nella struttura del paesaggio: gli espropri dell'Ente Maremma sui latifondi costituiscono il principale processo che nel dopoguerra ha portato, nell'Alto Lazio vulcanico, dalle grandi tenute indivise all'attuale frammentazione della proprietà. Un altro fattore rilevante fu l'assegnazione, da parte dei Comuni, di particelle coltivabili ricavate dai terreni delle Università Agrarie (FINODI, 2005). Tra il 1951 e il 1961, nella sola provincia di Viterbo, furono espropriati circa 33.000 ettari; essi vennero ridistribuiti in "poderi", di circa 11 ha ciascuno, in ognuno dei quali veniva costruita una casa colonica, ove la famiglia assegnataria doveva trasferirsi: venne così introdotto nel paesaggio l'insediamento sparso (un migliaio di case costruito nella provincia in meno di 10 anni), fino ad allora inesistente. Vennero costruiti centinaia di km di strade interpoderali; aree a pascolo o a vegetazione arbustiva furono messe a coltura con lavorazioni profonde e spietramenti; ad ogni podere venivano concessi un centinaio di olivi ed alcuni capi bovini; su richiesta del conduttore venivano impiantati anche vigneti (ENTE MAREMMA, 1955; FINODI, 2005). Furono, inoltre, assegnate le c.d. "quote", piccoli appezzamenti di 2-4 ha, concessi a scopo integrativo a famiglie che avevano già altri piccoli

Tab. 1 - Comparazione fra le % di copertura delle diverse classi di copertura del suolo (secondo la legenda CORINE Land Cover) nel settore sedimentario e tufaceo del Parco Marturanum. Elaborazione condotta sulla carta della vegetazione del parco (SCOPPOLA e FILIBECK, 2008a), che comprende anche una fascia contigua, per una superficie totale di 1.678 ha, di cui 1.137 ha su flysch (e conglomerati) e 541 ha su tufo. L'elevato valore % delle foreste su tufo nel parco non è del tutto rappresentativo del paesaggio piroclastico in generale, in quanto l'area protetta è stata istituita in un'area più boscata della media.

Codice CLC	Categoria di land cover	Flysch % area	Tufo % area
111	Insediamento residenziale continuo	0,00	1,10
112	Insediamento residenziale discontinuo	0,00	2,50
122	Aree stradali e ferroviarie	0,40	1,22
142	Aree ricreative e sportive	0,31	0,36
211	Seminativi non irrigui	1,73	17,00
221	Vigneti	0,00	0,89
222	Frutteti (incl. noccioli)	0,00	1,28
223	Oliveti	0,80	12,80
242	Sistemi particellari complessi	0,10	15,96
311	Boschi di latifoglie	41,28	36,87
321	Aree a pascolo naturale	30,16	6,70
322	Cespuglietti	24,01	3,32
324	Aree a vegetazione arborea e arbustiva in evoluzione	1,22	0,00

redditi e che avrebbero continuato a vivere nei paesi (ENTE MAREMMA, 1955). La necessità di ricavare quote e poderi per un numero più alto possibile di famiglie, a scopo politico (BARBERIS, 1979), indusse ad un frazionamento delle superfici che già all'epoca apparve in contrasto con le esigenze economiche ed agronomiche (INEA, 1955, p. 508; FINODI, 2005; e cfr. lo stesso ENTE MAREMMA, 1955, p. 60). Il frazionamento si è in seguito moltiplicato con la divisione ereditaria dei terreni, ed ha probabilmente incentivato un altro processo di trasformazione del paesaggio avvenuto a partire dagli anni '60: l'abbandono dell'agricoltura da parte di larghe fasce della popolazione che si trasferì a lavorare nell'industria nelle grandi città. Di conseguenza, il paesaggio dei grandi pascoli e dei centri compatti si trasformò, in parte, in un mosaico di piccoli poderi, punteggiati da case sparse, intersecati da un reticolo di strade e caratterizzati da colture legnose e dall'allevamento bovino intensivo. Poiché però gli espropri non interessarono la totalità delle superfici, rimasero, e permangono tuttora, grandi appezzamenti coltivati a seminativo e/o sfruttati per il pascolo ovino. Già prima di queste trasformazioni, comunque, i boschi erano stati relegati solo sulle ripide scarpate delle forre; anche i piccoli fondovalle pianeggianti dei *canyons* tufacei presso i centri abitati, oggi per lo più invasi da lussureggante vegetazione spontanea, erano in passato sfruttati per piccoli orti e per la coltura della canapa e il nocciolo (CECCARINI e BENASSI, 2005).

Il piccolo lembo di vulcaniti presente nel parco, pertanto, è caratterizzato da un mosaico paesistico del tutto contrastante con quello del Quarto: pianetti coltivati con piccole parcelle di noccioli, oliveti e vigneti, alternati a *plateaux* più ampi con seminativi o pascoli, e a boschi dall'andamento lineare che seguono rigorosamente le incisioni morfologiche.

La Tab. 1, che mostra i valori percentuali delle categorie di copertura del suolo nei due settori del parco, consente di cogliere a colpo d'occhio le differenze nell'identità dei due paesaggi.

CONCLUSIONI

L'area indagata presenta, oltre alla, già nota, elevata diversità della composizione floristica, anche una notevole diversità cenologica e paesistica. Molte delle comunità vegetali sono esclusive dei particolari substrati litologici qui presenti, e formano delle toposequenze legate agli speciali morfotipi (vallecole calcaree e conche argillose nel flysch; *canyons* e *plateaux* sul tufo).

Il paesaggio vegetale del Flysch della Tolfa ha mantenuto un *pattern* estremamente peculiare, e di grande importanza ai fini del sostentamento di specie floristiche e faunistiche di pregio, grazie al processo di resistenza alle trasformazioni implicitamente ma involontariamente operato dalle terre collettive. Sebbene alcuni aspetti oggi caratteristici di questo paesaggio (in particolare i vasti cespuglietti) siano in realtà molto recenti, esso costituisce un

mosaico paesistico del Lazio nord-occidentale, giacché il particolare tipo di formazione flyschoide che lo controlla è ristretta a questo territorio, come ristretti a questo territorio sono stati gli eventi storico-sociali che lo hanno modellato.

Il paesaggio piroclastico si estende su un'area più vasta, che va dalla Campagna Romana ad una piccola porzione della Toscana meridionale, ma è anch'esso molto ben caratterizzato sia sotto il profilo del mosaico vegetazionale che sotto quello dell'uso del suolo, sebbene sia stato in parte profondamente modificato dalla riforma agraria degli anni '50 del Novecento: anche qui, pertanto, alcune forme di uso del suolo (come l'olivicoltura) oggi percepite come "tradizionali" di questo territorio, hanno origine recentissima. Peraltro, nuove dinamiche del mercato agricolo (tra cui i contributi comunitari per l'olio di oliva) stanno ulteriormente favorendo l'estensione delle colture legnose rispetto a quella del tradizionale pascolo ovino.

Un cambiamento ancora più radicale del distretto piroclastico del Viterbese è però avvenuto negli ultimi 30 anni, con la forte aggressione del fenomeno dello *urban sprawl*: le dinamiche economiche, che rendono di accesso sempre più difficile il mercato immobiliare non solo della Capitale ma anche degli altri centri urbani, unitamente all'evoluzione dei costumi che tende a privilegiare uno stile di vita che possa godere di spazi aperti, hanno portato all'invasione dell'urbanizzazione diffusa di tipo residenziale (e non più agricolo!). Persino il paesaggio del Flysch, storicamente molto più "resistente" a tutti i fenomeni di trasformazione, comincia a mostrare segni di infiltrazione da parte dell'edilizia residenziale sparsa, così perdendo tra l'altro la sua caratteristica identità di paesaggio "disabitato". I due paesaggi, pertanto, fortemente identitari del territorio dell'Alto Lazio - anche a causa della lunga e sinuosa interfaccia fra di essi, che ne sottolinea le differenze percettive - e portatori delle tracce di una complessa storia sociale, richiederebbero una specifica tutela come mosaici paesistici in quanto tali (NAVEH, 1993; FILIBECK e SCOPPOLA, in stampa).

RINGRAZIAMENTI

Ricerca effettuata in parte nell'ambito della convenzione fra il Parco Regionale Marturanum e l'Università degli Studi della Tuscia, finalizzata alla

redazione della carta della vegetazione del parco. Gli AA. ringraziano: il direttore del parco, Stefano Celletti, e il personale di vigilanza dell'area protetta per l'assistenza fornita; Francesco A. Biondi per le informazioni di carattere pedologico; Elena Barchiesi, Edda Lattanzi, Sara Magrini e Francesca Surbera per la collaborazione in varie fasi della ricerca.

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Agropyretalia repentis Oberdorfer, Müller & Görs in Oberdorfer et al. 1967
Alno-Ulmion Braun-Blanquet & Tüxen ex Tchou 1948
Anemono-Fagetum (Gentile 1969) Brullo 1983
Asparago tenuifolii-Quercetum cerridis Scoppola et Filesi 1995
Asparago tenuifolii-Quercetum cerridis fraxinetosum oxycarpae Scoppola et Filesi 1995
Brachypodietalia phoenicoidis (Braun-Blanquet 1931) Molinier 1934
Carpinion orientalis Horvat 1958
Circaeo lutetianae-Alnetum glutinosae Blasi et Frondoni 1998
Cisto-Ericion Horvatí 1958
Coronillo emeri-Quercetum cerridis Blasi 1984
Crataego laevigatae-Quercion cerridis Arrigoni 1997
Echio plantaginei-Galactition tomentosae O. de Bolos et Molinier 1969
Erico arboreae-Arbutetum unedonis Allier et Lacoste 1980
Erythronio dentis-canis-Carpinion betuli Marincek in Wallnöfer, Mucina et Grass 1993
Fagetalia sylvaticae Pawłowski in Pawłowski et Wallisch 1928
Fraxino oxycarpae-Quercetum cerridis (Scoppola et Filesi 1995) Foggi, Selvi et Viciani in Foggi et al. 2000
Gaudinio-Cynosuretum cristati Fanelli et Menegoni 1997
Helianthemion guttati Braun-Blanquet in Braun-Blanquet, Molinier et Wagner 1940
Holoschoenetalia vulgaris Braun-Blanquet ex Tchou 1948
Inulo viscosae-Agropyrrion repantis Biondi et Allegrezza 1996
Lonicero etruscae-Rosetum sempervirentis Cutini, Fabozzi, Fortini, Armanini et Blasi 1996
Melico uniflorae-Quercetum cerridis Arrigoni in Arrigoni, Mazzanti et Ricceri 1990
Moenchio-Tuberarietum guttatae Lucchese et Pignatti 1988
Molinio-Arrhenatheretea Tüxen 1937
Poëtalia bulbosae Rivas-Goday et Ri-

vas-Martínez in Rivas-Goday et Ladero 1970
Populion albae Braun-Blanquet ex Tchou 1948
Prunetalia spinosae Tüxen 1952
Pruno-Rubenion ulmifolii Arnaiz et Lodi 1983
Quercetea ilicis Braun-Blanquet ex A. et O. de Bolos 1950
Quercion ilicis Braun-Blanquet ex Molinier 1934
Ranunculion velutini Pedrotti 1976
Roso sempervirentis-Quercetum pubescens Biondi 1986
Rubio peregrinae-Quercetum cerridis Di Pietro, Azella et Facioni 2010 (non Pignatti E. et Pignatti S. 1968, nom. inv.)
Salicion eleagni Aich. 1933
Saponario-Salicetum purpureae (Braun-Blanquet 1930) Tchou 1946
Teucrio siculi-Quercion cerridis Ubaldi (1988) 1995
Thero-Brometalia (Rivas-Goday et Rivas-Martínez ex Esteve 1973) O. de Bolos 1975
Tilio-Acerion Klika 1955
Trifolio-Hordeetalia Horvatí 1963
Vulpio ligusticae-Dasypyretum villosi Fanelli 1998

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LA PLACE OCCUPÉE PAR *VERBENA OFFICINALIS* L. DANS LES PHYTOCOENOSES HERBACÉES; OBSERVATIONS EFFECTUÉES EN PICARDIE ET DANS LE NORD DE LA FRANCE

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ABSTRACT

On the chalky soils of Picardie and northern France, *Verbena officinalis* is usually settled in the grassy lanes present in the fields and along the little roads. A phytosociological table describes that community, unrecognized in France, which takes place in the alliance called *Lolio perennis-Potentillion anserinae* Tüxen 1947.

KEYWORDS: *Verbena officinalis* communities, *Lolio perennis-Potentillion anserinae*, northern France.

PREAMBULE

Bien que la verveine officinale (*Verbena officinalis* L.) soit relativement répandue dans la France septentrionale (DELVOSALLE *et al.*, 2010), elle semble avoir peu retenu l'attention des phytosociologues. À l'issue d'observations poursuivies pendant une trentaine d'années, essentiellement en Picardie et dans le nord de la France, il s'avère que *V. officinalis* est plus qu'une rudérale assez banale et qu'elle occupe une place précise parmi les phytocénoses herbacées régionales. Les quelque quarante cinq relevés de végétation progressivement réalisés et rassemblés dans un tableau phytosociologique synthétique vont permettre de préciser celle-ci.

AUTOECOLOGIE DE *VERBENA OFFICINALIS*

V. officinalis est une plante héliophile, plutôt mésophile; comme elle recherche les substrats riches en bases, la craie blanche picarde lui convient particulièrement. Son implantation dans les formations herbacées occupant les chemins ruraux et les bermes routières révèle un caractère nitrotolérant, voire parfois nitrophile. *V. officinalis* supporte le piétinement et même le tassemement, ce qui explique sa présence dans les chemins et le fond des carrières. La localisation stationnelle des communautés dans lesquelles *V.*

officinalis était implanté est la suivante: chemins herbeux secs 18; bermes de «petites routes» 17; chemins herbeux plus frais 4; friches calcaires 2; fonds de carrières de craie 2; trottoir dans un village 1; non précisé 1.

ÉVOLUTION DES GROUPEMENTS A *VERBENA OFFICINALIS*

Dans l'ensemble les groupements herbacés dans lesquels *V. officinalis* est implanté offrent une certaine stabilité; des relevés similaires auraient pu être réalisés dans les mêmes sites à une vingtaine d'années d'intervalle. Toutefois, la destruction d'un certain nombre de bermes (de façon à élargir les voies) nuit au maintien de ces communautés. *V. officinalis* paraît mieux protégé dans les chemins herbeux qui sillonnent la campagne picarde.

QUELQUES DONNÉES PHYTOSOCIOLOGIQUES

A) Un certain nombre de travaux phytosociologiques mentionnent *V. officinalis*; rapportons ces données. OBERDORFER (1983) indique que *V. officinalis* est une caractéristique de l'*Agropyro-Rumicion* et qu'on l'observe également dans le *Polygonion* et l'*Arction*. Les informations tirées de l'ouvrage de WESTHOFF et DEN HELD (1969) et qui concernent les Pays-Bas sont précises; *V. officinalis* est susceptible d'être observé dans:

- le *Balloto nigrae-Chenopodietum* Tüxen 1931 (classe des *Artemisieta vulgaris*);
- le *Junco inflexi-Menthetum longifoliae* Lohmeyer 1953 (alliance de l'*Agropyro-Rumicion*);
- le *Lolio perennis-Cynosuretum cristati* (Braun-Blanquet et De Leeuw 1936) Tüxen 1937, plus précisément dans la sous-association *ononidetosum repens* Westhoff 1969, aux côtés de *Ononis repens*, *Eryngium campestre* et *Cichorium intybus* (alliance de l'*Arrhenatherion elatioris*);
- le *Bromo sterilis-Hordeetum muri-*

num Lohmeyer 1950 *apud* Oberdorfer 1957 (alliance du *Sisymbrium officinalis*).

Curieusement, ZONDERWIJK (1979), auteur d'un ouvrage de vulgarisation bien illustré concernant également les Pays-Bas, *De bonte Berm*, ne mentionne pas la verveine, pas plus que ne le fait SÝKORA (1982) dans une étude descriptive des communautés végétales du *Lolio perennis-Potentillion anserinae* de Belgique et du nord de la France.

V. officinalis n'est pas davantage cité dans le *Guide des végétations des zones humides de la région Nord-Pas de Calais* (CATTEAU *et al.*, 2009) mais figure par contre dans deux des dix-huit relevés de végétation décrivant les arrhenathéraies sèches marquées par une forte présence d'*Eryngium campestre* (WATTEZ, 1982; cf. infra). Mentionnons, pour mémoire que GUYOT (1942) signale la présence de la verveine dans certaines friches et pelouses en Picardie. La place occupée par *V. officinalis* dans les phytocénoses du Bassin parisien est évoquée par BOURNÉRIAS *et al.* (2001) qui notent sa présence dans les groupements suivants: les pelouses urbaines du *Polygono arenastri-Coronopodion squamati*, les lieux secs irrégulièrement piétinés du *Sisymbrium officinalis*, les friches héliophiles à Composées épineuses de l'*Onopordion acanthi*, les friches calcaro-sableuses après abandon des cultures du *Dauco carota-Melilotus albi*.

B) Le tableau joint (Tableau 1) synthétise 45 relevés originaux possédant en commun *V. officinalis*, *Plantago major* **m*¹, *Agrostis stolonifera* **s*., *Lolium perenne* que l'on peut répartir en deux syntaxons élémentaires:

- le premier, le mieux représenté (43 relevés) et le plus riche en taxons (en moyenne 20,7 par relevé), accueille des taxons des prairies pâturées sur sol tassé (*Phleum pratense*, *Potentilla reptans*...) et des taxons des pelouses et ourlets calcicoles locaux (*Medicago lupulina*, *Centaurea gr. nemoralis*...); on peut le

¹* Remplace *subsp.* et l'initiale est utilisée quand c'est la *subsp. type*. Par exemple, au lieu d'écrire *Plantago major* *subsp. major*, j'écris *Plantago major* **m*.

*Tableau 1 - Synthèse de la végétation à *Verbena officinalis* de Picardie et du nord de la France.*

Répartition générale des relevés par département - Somme: 33 relevés; Oise: 6 relevés; Pas-de-Calais: 4 relevés; Mayenne: 2 relevés.

Nombre de relevés	43	2
Nombre moyen de taxons	20,7	9
Combinaison floristique commune		
<i>Verbena officinalis</i>	V	2
<i>Lolium perenne</i>	V	
<i>Plantago major</i> *m.	IV	2
<i>Agrostis stolonifera</i> *s.	IV	2
Syntaxon 1		
<i>Phleum pratense</i> s.l.	IV	
<i>Potentilla reptans</i>	IV	
<i>Centaurea gr. nemoralis</i>	IV	
<i>Arrhenatherum elatius</i> *e.	IV	1
<i>Daucus carota</i> *c.	III	
<i>Medicago lupulina</i>	III	
<i>Odontites vernus</i> *serotinus	III	
<i>Artemisia vulgaris</i>	III	
<i>Trifolium pratense</i> *p.	III	
<i>Origanum vulgare</i>	II	
<i>Crepis capillaris</i>	II	
<i>Agrimonia eupatoria</i>	II	
<i>Lotus corniculatus</i> *c.	II	
<i>Brachypodium pinnatum</i>	II	
<i>Knautia arvensis</i>	II	
<i>Pimpinella saxifraga</i>	II	
<i>Reseda lutea</i>	II	
<i>Convolvulus arvensis</i>	II	
<i>Linaria vulgaris</i>	II	
<i>Galium mollugo</i> *m.	II	
<i>Potentilla anserina</i>	II	1
<i>Festuca gr. rubra</i>	II	
<i>Pastinaca sativa</i>	II	
<i>Poa trivialis</i> *t.	II	1
<i>Heracleum sphondylium</i> *s.	II	
<i>Vicia sativa</i>	II	
Syntaxon 2		
<i>Eupatorium cannabinum</i> *c.	2	
<i>Angelica sylvestris</i> *s.	2	
Agrostietea stol. + Arrhenatheretea el.		
<i>Trifolium repens</i> *r.	IV	2
<i>Dactylis glomerata</i> *g.	IV	
<i>Achillea millefolium</i> *m.	IV	
<i>Plantago lanceolata</i> *l.	IV	
<i>Ranunculus repens</i>	II	1
Autres taxons		
<i>Cirsium arvense</i>	III	1
<i>Hypericum perforatum</i>	III	
<i>Rubus</i> sp.	II	
<i>Rumex obtusifolius</i>	II	
<i>Silene alba</i>	II	
<i>Urtica dioica</i> *d.	II	
<i>Polygonum aviculare</i>	I	1

Taxons accidentels dans le syntaxon 1 - *Glechoma hederacea* I, *Elytrigia repens* I, *Ononis repens* I, *Senecio jacobaea* I, *Holcus lanatus* I, *Melilotus officinalis* I, *Trisetum flavescens* I, *Medicago sativa* I, *Scabiosa columbaria* +, *Centaurea scabiosa* +, *Carex hirta* +, *Trifolium fragiferum* +, *Bupleurum falcatum* +, *Prunella vulgaris* +, *Rumex crispus* +, *R. conglomeratus* +, *Hypochaeris radicata* r, *Leontodon autumnalis* r.

rapprocher du *Prunello vulgaris-Potentilletum reptantis* Eliáš 1978 (ELIÁŠ, 1978: 376), qui serait alors nouveau pour la France à notre connaissance; ce syntaxon se range dans le *Lolio perennis-Potentillion anserinae* Tüxen 1947,

les *Potentillo anserinae-Polygonetalia avicularis* Tüxen 1947 et les *Agrostietea stoloniferae* Oberdorfer 1983 selon le système de BARDAT *et al.* (2004);

- le second est nettement plus rare (2 relevés) et plus pauvres en taxons (9 par relevé en moyenne), différencié par *Eupatorium cannabinum* et *Angelica sylvestris*, sur substrat plus hygrophile. C) La verveine officinale a également été rencontrée dans d'autres groupements végétaux comme l'indiquent les relevés isolés suivants:

- une arrhenathéraie littorale sur une digue herbeuse au Cap-Hornu (Saint-Valéry-sur-Somme, Somme), sur 8 m², 100% *Verbena officinalis* 3, *Arrhenatherum elatius* 4, *Dactylis glomerata* 2, *Bromus hordeaceus* +, *Lolium perenne* 1, *Trifolium repens* 2, *T. pratense* 1, *T. fragiferum* +, *Cirsium vulgare* 1, *Daucus carota* 1, *Plantago lanceolata* 1, *Convolvulus arvensis* 1, *Eryngium campestre* +, *Agrimonia eupatoria* 1, *Picris hieracioides* 1, *Artemisia vulgaris* +;

- une friche de hautes herbes, Dommiers (Oise), 3 m²; 90%

Verbena officinalis 3, *Dipsacus sylvestris* 3, *Artemisia vulgaris* 2, *Glechoma hederacea* 2, *Echium vulgare* 1, *Achillea millefolium* 1, *Rumex conglomeratus* +, *Origanum vulgare* 1, *Arrhenatherum elatius* 1, *Dactylis glomerata* 1, *Agrostis stolonifera* 2, *Phleum pratense* +;

- un chemin caillouteux dans le «ried» alsacien, lors de la session de la SBF (07/2000), 6 m², 95% *Verbena officinalis* 4, *Potentilla anserina* 3, *Plantago major* 2, *Polygonum aviculare* 1, *Artemisia vulgaris* +, *Agrostis stolonifera* 2, *Agropyron repens* 1, *Lolium perenne* 1, *Phragmites australis* 2, *Equisetum arvense* 1, *Vicia cracca* 1, *Urtica dioica* 2, *Cirsium arvense* +, *Sisymbrium officinale* +, *Calystegia sepium* +, *Rubus* sp. 1.

USAGES

Bien que son nom spécifique laisse supposer que *V. officinalis* soit une plante usitée en médecine et en pharmacie, il faut reconnaître que son utilisation actuelle en tant que plante médicinale est désormais très limitée. La verveine officinale était traditionnellement considérée comme efficace contre les fièvres et les céphalées, également comme sédatrice. La drogue (c'est-à-dire les sommités fleuris) a conservé un certain usage en phytothérapie comme stomachique, diurétique et surtout expectorante (sous forme de gargarismes); en

usage externe, *V. officinalis* serait efficace dans le traitement des ulcères (BÉZANGER *et al.*, 1975). Selon BONNIER, la verveine aurait joué autrefois un rôle important en sorcellerie, ce qui expliquerait l'un des noms vernaculaires qui lui sont parfois attribués, à savoir «l'herbe aux enchantements».

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FORMATIONEN UND HÖHENSTUFEN DER VEGETATION DES NATURSCHUTZGEBIETES YUNWUSHAN (AUTONOME REGION NINGXIA, VR CHINA)

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ABSTRACT

In the nature reserve Yunwushan (Autonomous Region Ningxia, PR China), which is protected by law since 1982, large areas of rather natural steppe vegetation exist. Besides the steppe vegetation, shrub communities and humid meadows grow in Yunwushan. In total six formations of vegetation are represented: semi desert steppe, dry steppe, humid meadow, mesophytic deciduous shrub, xerophytic deciduous shrub and open thorny shrub. Amongst these formations, the dry steppe shows the greatest variation. Here five subformations are detectable: *Stipa grandis* steppe, *Stipa bungeana* steppe, dwarf shrub steppe, semi shrub steppe and *Convolvulus ammannii* steppe. The three types of feather grass steppe are characteristic of different altitudinal belts: in the lower regions of the 1,600 to 1,900 m above sea level the *Stipa bungeana* steppe dominates. Between 1,900 to 2,100 m the *Stipa grandis* steppe is the prevailing type and the highest peaks of the area are covered by the *Stipa tianshanica* var. *gobica* steppe. Remarkably *Stipa bungeana* steppe and *Stipa grandis* steppe, which clearly represent different steppe types, by severe and long lasting overgrazing are transformed to *Convolvulus ammannii*-steppe, both.

RÉSUMÉ

Dans la région Yunwushan (Région Autonome de Ningxia, République

que populaire de Chine), qui a été déclarée réserve naturelle en 1982, des grandes surfaces couvertes d'une végétation des steppes relativement intacte existent encore. Sur des sites spéciaux, on rencontre des groupements de broussailles et des prés humides. Au total, 6 formations peuvent être différencierées: steppe semi désertique, steppe aride, prairie humide, broussailles mésophytes à feuilles caduques, broussailles xérophytes à feuilles caduques ainsi que brousse épineuse ouverte. La steppe aride est la plus différencierée, avec cinq sub-formations existant dans la région: steppe à *Stipa grandis*, steppe à *Stipa bungeana*, steppe à arbustes nains, steppe semi-arbustive et steppe à *Convolvulus ammannii*. Trois types de steppe dominés par *Stipa* caractérisent chacun une différente altitude: de 1.600 à 1.900 m au dessus du niveau de la mer domine la steppe à *Stipa bungeana*, de 1.900 à 2.100 m la steppe à *Stipa grandis* et dans les zones les plus élevées la steppe semi désertique à *Stipa tianshanica* var. *gobica*. Il est remarquable que la steppe à *Stipa bungeana* et la steppe à *Stipa grandis*, floristiquement et physiognomiquement nettement différentes, dégénèrent toutes les deux vers la steppe à *Convolvulus ammannii* sous l'effet d'un surpâturage extrême.

ZUSAMMENFASSUNG

Im Gebiet Yunwushan (Autonome Region Ningxia, VR China), das 1982 unter Naturschutz gestellt wurde,

existieren großflächige Bestände relativ naturnaher Steppenvegetation. Neben der eigentlichen Steppenvegetation finden sich an Sonderstandorten Gebüschesellschaften und Feuchtwiesen. Insgesamt sind 6 Formationen unterscheidbar: Halbwüstensteppe, Trockensteppe, Feuchtwiese, mesophytisches laubabwerfendes Gebüsch, xerophytisches laubabwerfendes Gebüsch sowie offener Dornbusch. Am stärksten differenziert ist die Trockensteppe, von der im Gebiet fünf Subformationen existieren: *Stipa grandis*-Steppe, *Stipa bungeana*-Steppe, Zwerstrauch-Steppe, Halbstrauch-Steppe und *Convolvulus ammannii*-Steppe. Drei von Federgräsern dominierte Steppentypen sind für unterschiedliche Höhenstufen bezeichnend: von ca. 1.600 bis 1.900 m ü.M. herrscht die *Stipa bungeana*-Steppe vor, in 1.900 bis 2.100 m ü.M. dominiert die *Stipa grandis*-Steppe und für die höchsten Lagen ist eine Halbwüstensteppe mit *Stipa tianshanica* var. *gobica*-Steppe bezeichnend. Bemerkenswert ist, dass *Stipa bungeana*-Steppe und *Stipa grandis*-Steppe, die floristisch und physiognomisch deutlich voneinander verschiedenen Formationen bilden, bei extremer Überbeweidung beide zur *Convolvulus ammannii*-Formation degenerieren.

EINLEITUNG

Überbeweidung und als Folge davon Bodenerosion stellen in allen Trockenwäldern der Erde ein großes ökologisches und ökonomisches Problem dar

云雾山自然保护区地处中国宁夏回族自治区南部黄土高原区，设立于 1982 年。研究表明：该地区分布有连续成片，近自然状态针茅(*Stipa* ssp.)草原群落。除针茅草原优势群落外，在局部特殊的生境中，分布有灌丛和湿生草甸群落。半荒漠草原，干草原，湿生草甸，中生阔叶落叶灌丛，旱生阔叶落叶灌丛及有刺灌丛等 6 个植物群系在自然保护区内较为常见。其中，干草原群系可进一步划分为：大针茅(*Stipa grandis*)草原，本氏针茅(*Stipa bungeana*)草原，矮灌丛草原，半灌木草原和银灰旋花(*Convolvulus ammannii*)草原等 5 个亚群系。在垂直分布上，海拔 1600-1900 m 之间以本氏针茅为优势种；1900-2100 m 之间为大针茅；山顶海拔最高处则以戈壁针茅(*Stipa tianshanica* var. *gobica*)为绝对优势种。研究还表明：大针茅草原亚群系与本氏针茅草原亚群系在自然状态下，其植物区系组成及外貌具有明显区分，但在极度放牧条件下，它们均退化演替为银灰旋花(*Convolvulus ammannii*)草原亚群系。

关键词：针茅草原群系 垂直分布 云雾山 中国宁夏

(U.N.E.P. 1982/1992, THAMPAPILLAI und ANDERSON, 1994). Man schätzt, dass global 8,8 Miliarden Tonnen Boden der weidebedingten Erosion unterliegen (STOCKING, 1987; ZHU et LIU, 1989; ZHU und WANG, 1990; F.A.O., 1995/1996/1997).

Im Gebiet der chinesischen Steppen spielt die Weidewirtschaft seit Jahrhunderten eine große Rolle (LI, 1988; WU, 1998). Vegetation und Landschaft sind hiervon nicht unbeeinflusst geblieben. Seit den 50er Jahren sind Landschaft und Vegetation in Nord- und Westchina aufgrund von Überbeweidung und landwirtschaftlichem Missmanagement extrem beeinträchtigt. 80% der 224 Mio. Hektar nutzbarer Weideflächen in dieser Region haben unter Überbeweidung zu leiden, 41,8% davon sind stark degradiert (ZHONG et al., 1988; XU und CHEN, 1997; WU, 1998; CAO und YANG, 1999). Nach Studien von XU und ZHANG (1999), YANG (1988), ZHANG (1997) und SHAN et al. (1997) ist die Tragfähigkeit des Graslandes in Nord- und Westchina bereits um 56% überschritten und die Pflanzenproduktivität der Steppen seit den 50er Jahren um 34,5% reduziert. Die Trockensteppe, die im autonomen Gebiet Ningxia Hui mit knapp 60% der Gesamtfläche der dominierende Vegetationstyp ist (GAO et al., 1986; GUO et al., 1988), wurde in den letzten 30 Jahren extrem degradiert, wobei wiederum Überbeweidung, landwirtschaftliche Missnutzung (beides zurückgehend auf das exponentielle Wachstum der Bevölkerung) sowie landwirtschaftspolitische Fehlentscheidungen als Ursachen anzuführen sind. Zur Zeit existiert im gesamten Gebiet von Ningxia nur ein einziger Bereich, in dem gut erhaltene

Steppenvegetation großflächig anzutreffen ist: das Naturschutzgebiet "Yunwushan" (im weiteren Text NSG genannt). Im Folgenden wird die Vegetation dieses aus vegetationskundlicher und naturschutzfachlicher Sicht sehr bedeutenden Gebietes vorgestellt.

eine hohe Einstrahlung zu verzeichnen (jährlich um 521,25 kJ/cm²). Als Folge der nur wenig durch Wolkenbildung gestörten, kräftigen täglichen Einstrahlung und der ungehinderten nächtlichen Ausstrahlung entstehen große Temperaturgegensätze zwischen Tag und Nacht sowie Sommer und Winter. Die Schwankung der Monatsmitteltemperatur liegt im NSG zwischen -8,6 °C und +18,2 °C, als absolute minimale und maximale Temperaturen wurden -28,2 °C und +33,8 °C gemessen.

Frostfrei ist es im NSG von Anfang Mai bis Mitte September, in den übrigen Monaten gibt es ca. 220 bis 240 Frosttage. Die 210 bis 230 Tage dauernde Vegetationsperiode beginnt gegen Ende März mit einem durch das Blühen zahlreicher einjähriger Arten und einiger Geophyten deutlich ausgeprägten Frühlingsaspekt. Die übrigen Arten der Trockensteppen blühen erst in der anschließenden Sommerzeit. Im Laufe des Oktobers endet die Vegetationsperiode.

Das NSG liegt im westlichen Bereich der ostasiatischen Monsunregen. Die Regenperiode beginnt Ende April, erreicht im Juli, August und September mit 65% des Jahresniederschlages ihren Höhepunkt und ist gegen Ende Oktober beendet. Die Niederschläge fallen von Dezember bis Februar als Schnee, sonst abwechselnd als Regen oder Schnee, im Hochsommer nicht selten auch als Hagel und Gewitterregen. Die jährliche Niederschlagsmenge im NSG beträgt 424,5 mm.

Geringe Niederschlagsmengen und starke Verdunstung bewirken eine hohe Aridität und ein deutlich kontinentales Klima. Nach den Messdaten von 1993 bis 1998 beträgt die potentielle Verdunstung im NSG 1.684,4 mm, das heißt ca. viermal soviel wie die Jahresniederschlagsmenge. Da der Boden im Sommer relativ feucht und die Luft viel wärmer als in den anderen Jahreszeiten ist, entfallen 44 bis 50% der jährlichen Evaporationsmenge auf den Sommer, 4 bis 8% auf den Winter, 31 bis 33% auf den Frühling und 15 bis 17% auf den Herbst. Nach KÖPPEN (1931) gehört das Gebiet zur Steppenklimazone (BS).

Im Winter herrschen großräumige Winde aus Nord und Nordwest mit eisigen, trockenen Luftmassen vor, im Sommer wehen sie hauptsächlich aus entgegengesetzter Richtung (Süden und Südosten) und bringen feuchtwarme Luftmassen mit. In den übrigen Jahreszeiten kommen die Winde aus wechselnden Richtungen. Die durchschnittliche Windgeschwindigkeit ist im Sommer und Herbst (9,7 km/h) deutlich

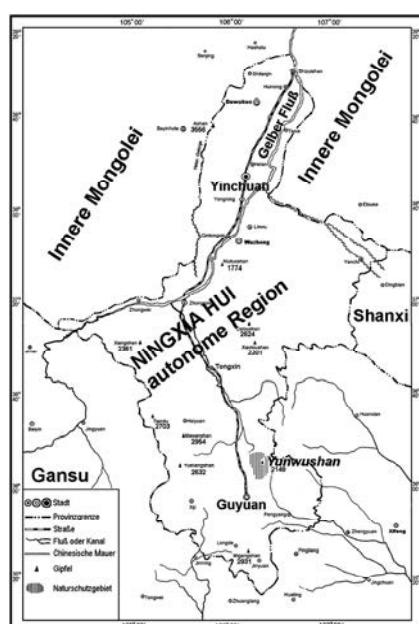


Abb. 1 - Lage des Untersuchungsgebietes.

KLIMA

Im Untersuchungsgebiet herrscht ein leicht vom pazifischen Sommermonsun beeinflusstes, typisches Kontinentalklima der nördlichen Hemisphäre. Der Sommer ist relativ feucht und warm, der Winter ziemlich kalt, trocken und windig.

Da das Untersuchungsgebiet im Löbhochland Zentral-Chinas liegt, ist

niedriger als im Winter und Frühling (13,6 km/h).

GESTEINE UND BÖDEN

Das NSG, dessen Geologie und Schichtenfolge von verschiedenen Autoren ausführlich beschrieben wurden (AMT FÜR BODENSCHÄTZUNG NINGXIA, 1976; ZHU, 1989), gehört zum westlichen Teil des Nord-Shanxischen Lößplateaus. Aufgrund langjähriger Bodenerosion ist die Landschaft durch Lößhügel mit schmalen Tälern und stellenweise emporragenden Bergen charakterisiert. Über einem Kalkstein- und Rotsandsteinbasement liegt eine 5 bis 60 m mächtige Lößschicht. Die Böden sind direkte Entwicklungsprodukte der darunter liegenden Lößschicht. Im NSG gibt es zwei verschiedene Bodentypen, nämlich basenreichen Kastanozem und Gebirgs-Phaeozem.

Der weit verbreitete zonale Bodentyp ist ein basenreiches Kastanozem mit einem ausgeprägten Ah1/Ah2/C-Profil. Der Ah1-Horizont ist ca. 20 cm mächtig, braun bis dunkelbraun, schwach humos, feinsandig, schluffig, sehr gut durchwurzelbar, besitzt ein krümeliges Gefüge, hat einen pH-Wert von 8,4 und enthält 2,8% organische Substanz. Der Ah2-Horizont von 20 bis 50 cm ist leicht bis mittel braun gefärbt, besteht aus grobschluffigem Lehm, ist gut durchwurzelbar und zeigt mittlere Verschlämmbarkeit. Der C-Horizont bis 120 cm ist hellgelb gefärbt und lößlehmig; ab 90 cm kommen weiße Ausblühungen von Calciumcarbonat (CaCO_3) vor.

Ab etwa 2.000 m ü.M. ist ein Gebirgs-Phaeozem entwickelt. Seine horizontale Gliederung ist ähnlich wie die des Kastanozems. Der obere Horizont (A) ist ca. 25 cm tief, graubraun, mittel humos, feinsandig und grobschluffig, sehr gut durchwurzelbar und krümelig. Er hat 3,5% organische Substanz und einen pH-Wert von durchschnittlich 8,2. Der mittlere Horizont (B) ist bis 70 cm tief, graubraun bis hell graubraun, feinsandig und grobschluffig sowie leicht verschlämbar. Der C-Horizont hat eine hell gelbe Farbe, ist lößlehmig und enthält ab 70 cm weiße Ausblühungen von Calciumcarbonat (CaCO_3).

METHODEN

Die Zusammensetzung der Flora des Untersuchungsgebietes wurde in den Jahren 1998 und 1999 in mehreren, z.T. mehrwöchigen, Aufenthalten ermittelt.

Die Vegetationskarte gibt den Zustand im Jahre 1999 wieder.

Die Gliederung der Vegetation erfolgte nach physiognomischen Merkmalen unter Berücksichtigung dominanter Arten. Als Grundlage diente die allgemeine Darstellung von GAO *et al.* (1986). Diese Autoren gliedern die Vegetation des Untersuchungsgebietes physiognomisch in Gebüsche- und Steppenvegetation, wobei letztere in die Subformationen Feuchtwiese, Trockensteppe und Halbwüstensteppe unterteilt wird. Die Nomenklatur der Pflanzenarten folgt MA und LIU (1986, 1988).

ERGEBNISSE

FLORISTISCHE ZUSAMMENSETZUNG DER VEGETATION

Im Rahmen der vorliegenden Arbeit wurden in den Jahren 1998 und 1999 insgesamt 184 Pflanzenarten als Bestandteil der spontanen Vegetation des NSG identifiziert, die zu 50 Familien und 131 Gattungen gehören. Die dominierenden Familien sind (der Einstufung von WU und WANG, 1983, folgend) *Asteraceae* (37 Arten), *Poaceae* (21), *Rosaceae* (18), *Fabaceae* (17) und *Lamiaceae* (11). Floristisch gesehen sind die mongolischen Steppenelemente (*Stipa grandis*, *Thymus mongolicum*, *Artemisia frigida*, *Potentilla bifurca*, *Agropyron cristatum*, *Cleistogenes squarrosa*, *Achnatherum splendens*, *Koeleria cristata*, *Ephedra sinica*) und die zentralasiatischen und ostasiatischen Steppenelemente (*Stipa bungeana*, *Artemisia sacrorum*, *Potentilla chinensis*, *Lespedeza davurica*, *Bothriochloa ischaemum*, *Artemisia giraldii*) im NSG dominierend, aber auch nordchinesische Elemente (*Ulmus pumila*, *Ostryopsis davidiana*) kommen nicht selten vor.

Gemäß der ökomorphologischen Charakterisierung der Flora von Ningxia (MA und LIU, 1986, 1988) sind 74% der Pflanzenarten des Untersuchungsgebietes als xerophytisch oder xero-mesophytisch einzustufen und 26% als mesophytisch oder meso-xerophytisch.

Hinsichtlich der Lebensformen herrschen in den großflächig verbreiteten Grasfluren Hemikryptophyten vor (Abb. 2). Mit weitem Abstand folgen etwa gleichrangig Chamaephyten und Therophyten. Dagegen beschränken sich höherwüchsige Phanerophyten (> 2 m) auf Sonderstandorte mit besserer Wasserversorgung, gehören also zur extrazonalen Vegetation. In den von ihnen gebildeten Gebüschen dominieren

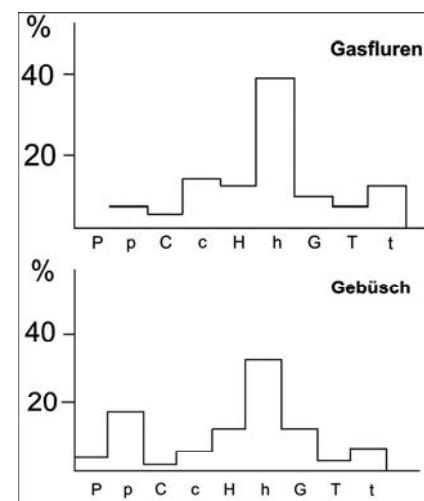


Abb. 2 - Lebensformspektren der Grasfluren und Gebüsche im Naturschutzgebiet Yunwushan (erstellt nach einer kombinierten Artenliste aus den Jahren 1998 und 1999). X = makro; x = nano.

ebenfalls die Hemikryptophyten, hier mit deutlichem Abstand vor den Geophyten. Bäume sind im NSG sehr selten.

VEGETATIONSGLIEDERUNG NACH PHYSIOGNOMISCHEN MERKMALEN UND DOMINANTEN ARTEN

Im Allgemeinen hat die Vegetation des NSG aufgrund ihrer großräumigen Klima- und Bodenmerkmale den Charakter einer Trockensteppe. Zwerg- und Halbsträucher bilden dabei eine eigene Formationsunterklasse. Dagegen gehören Gebüsche zur extrazonalen Vegetation. In Anlehnung an GAO *et al.* (1986) wurden im NSG physiognomisch sechs Formationen unterschieden:

- Halbwüstensteppe (4.2.1)
- Trockensteppe (4.2.2)
- Feuchtwiese (4.2.3)
- mesophytisches laubabwerfendes Gebüsch (4.2.4)
- xerophytisches laubabwerfendes Gebüsch (4.2.5)
- offener Dornbusch (4.2.6).

Abb. 3 gibt die Verbreitung dieser Einheiten im NSG wieder, wobei die Trockensteppe durch fünf Subformationen repräsentiert wird (s. 4.2.2). Es zeigt sich, dass der größte Teil der Fläche von den verschiedenen Subformationen der Trockensteppe bedeckt ist. Nur auf topographischen Sonderstandorten und in größerer Meereshöhe findet man Gebüsche und Halbwüstensteppen.

FORMATION HALBWÜSTENSTEPPE

Die Halbwüstensteppe ist im NSG

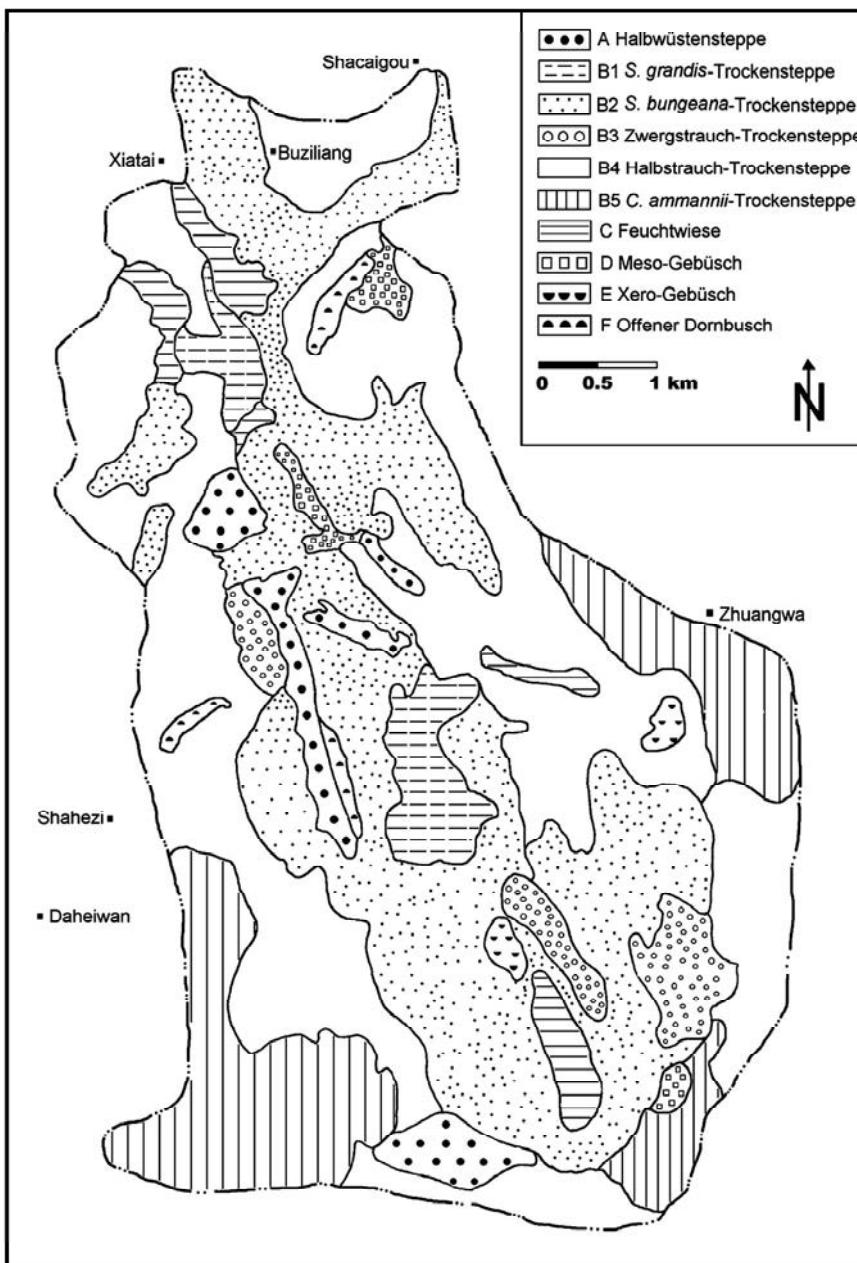


Abb. 3 - Vegetationskarte des NSG Yunwushan (Kartierung: XIE, 1999).

auf mikroklimatisch ungünstige, windexponierte Bergkuppen mit schlechten Bodenbedingungen beschränkt. Gelegentlich kommt diese Formation auch auf extrem warmen, trockenen Standorten um die Dörfer vor. Sie setzt sich aus niedrigen, mehrjährigen, trocken- und kälteresistenten Horstgräsern und Kräutern zusammen. Zu den dominierenden Arten gehören *Stipa tianschanica* var. *gobica* sowie an ruderализierteren Orten *Peganum harmala* var. *multisecta*. Die Pflanzendecke bleibt häufig offen.

FORMATION TROCKENSTEPPE

Die im NSG weit verbreitete Trockensteppe repräsentiert die charakteristische zonale Vegetation des Gebietes. In Abhängigkeit von Höhenlage, Bodenbedingungen, Relief und Beweidungsintensität sind fünf Subformationen

unterscheidbar:

- *Stipa grandis*-Steppe
- *Stipa bungeana*-Steppe
- Zwergstrauch-Steppe
- Halbstrauch-Steppe
- *Convolvulus ammannii*-Steppe.

Die *Stipa grandis*-Subformation der Trockensteppe ist im NSG nur auf flachen Bergabhängen mit günstigen Bodenbedingungen und relativ guter Wasserversorgung oberhalb 1900 m ü.M. zu finden. Das dominierende Horstgras *Stipa grandis*, eine in den mongolischen Steppen weit verbreitete Art, beansprucht ein relativ kühles Klima. Die typische *Stipa grandis*-Steppe bildet oft sehr dichte Pflanzenbestände mit hohem Deckungsgrad. Deshalb zählt diese Subformation zu den wertvollsten Weideflächen (XIE und WIRTIG, 2007).

Die *Stipa bungeana*-Subformation der Trockensteppe ist der dominierende zonale Vegetationstyp. Sie ist auf

Bergabhängen und Bergkuppen überall dort anzutreffen, wo die ökologischen Bedingungen in jeder Hinsicht der allgemeinen geographischen Situation des Gebietes entsprechen, bildet also die klimatische Klimax-Gesellschaft des NSG. Wegen der langen Beweidungsgeschichte der Region ist diese Subformation heutzutage außerhalb des NSG nicht mehr vorhanden.

Nur auf windexponierten Bergkanten oder in Kammlagen der mittleren Höhenstufe findet man eine Zwergstrauch-Subformation, in der *Caragana*-Arten (*C. maximoviczana* und *C. jubata*) dominieren. Es handelt sich hierbei um Standorte, in denen die Schneedecke im Winter stark verblasen wird, so dass sich oft eine außergewöhnliche Kombination von Kälte und Trockenheit ergibt.

Flächen, auf denen seit langen Jahren eine extreme Dauerbeweidung stattfindet, sind von einer Halbstrauch-Subformation mit verschiedenen *Artemisia*-Arten und *Thymus mongolicum* bedeckt. Stellenweise bestimmt diese Subformation den landschaftlichen Aspekt des NSG. Innerhalb dieser Subformation sind je nach Standortbedingungen und dominierenden Arten noch einige Untereinheiten niederen Ranges zu unterscheiden, wobei die äußere Erscheinung der Subformation allerdings ziemlich einheitlich ist.

In der nach *Convolvulus ammannii* benannten Subformation treten die für die Trockensteppe charakteristischen Arten *Stipa bungeana* und *Stipa grandis* stark zurück. Stattdessen kommen tritt- und verbissfeste Arten (*Potentilla acaulis*, *Convolvulus ammannii*, *Stellera chamaejasme* usw.) und Einjährige (*Salsola collina*, *Artemisia scoparia* usw.) zur Vorherrschaft. Die Pflanzendecke ist oft lückig und die Bodenoberfläche daher flächenweise frei exponiert. Die *Convolvulus ammannii*-Steppe ist meistens um Dörfer und an Weidewegen verbreitet. Als Weidefläche ist diese Subformation nicht mehr nutzbar. Man findet sie als Endstufe der weidebedingten Degeneration sowohl der *Stipa grandis*- als auch der *Stipa bungeana*-Steppe (XIE et al., 2007).

FORMATION FEUCHTWIESE

In tief liegenden Schluchten sowie im Bereich der Wasserzuglinie an Bergabhängen ist die Wasserversorgung wesentlich besser als im übrigen Gebiet. Dementsprechend tragen diese Standorte eine niedrige, meist dicht geschlossene Wiesendecke, in der Seggen- und

Gramineen-Arten (*Carex lanceolata*, *Koeleria cristata*, *Cleistogenes squarrosa*) dominieren. Dazwischen findet sich eine Vielzahl kleinerer Kräuter (*Melissitus ruthenicus*, *Halerpestes hainanica*, *Leontopodium calocephalum*, *Anaphalis lactea*, *Taraxacum platypetidum*, *Potentilla anserina*, *Potentilla multicaulis*). Weil das Vieh oft nur auf solchen Standorten Wasser zum Trinken findet, leidet die Subformation ständig unter Überbeweidung.

FORMATION MESOPHYTISCHES LAUBABWERFENDES GEBÜSCH

Auf steilen, nordexponierten Bergabhängen, wo der Wasserhaushalt günstiger und die Fläche für das Vieh schwer erreichbar ist, wachsen dicht schließende Gehölzbestände aus mehreren mesophytischen Sträuchern (*Ostryopsis davidiana*, *Syringa oblata*, *Berberis amurensis*, *Lonicera microphylla*, *Cotoneaster multiflorus*, *Clematis montana*, *Crataegus kansuensis*). In dieser Formation ist meist eine Krautschicht gut entwickelt, in der viele Waldarten (*Galium aparine* var. *tenerum*, *Aster ageratoides*, *Clematis brevicaudata*, *Sedum aizoon*, *Stachys baicalensis*, *Delphinium grandiflorum*, *Senecio argunensis*) vertreten sind.

FORMATION XEROPHYTISCHES LAUBABWERFENDES GEBÜSCH

Anders als die mesophytische lässt die xerophytische laubabwerfende Gebüsche-Formation mit der mono-dominanten Art *Hippophaë rhamnoides* keine enge Standortbindung erkennen. Sie ist vereinzelt auf für Menschen und Tiere schwer erreichbaren, von Siedlungen entfernt gelegenen Flächen anzutreffen und bildet dicht schließende Gebüschebestände. In ihrer typischen Ausprägung wird diese Formation oft allein von *Hippophaë rhamnoides* gebildet, deren jüngere Blätter im Allgemeinen dicht von weißen Schüppchen bedeckt sind, so dass die Gesellschaft grau-weiß erscheint. Auch in geschlossenen Beständen existiert eine Krautschicht, die oft aus Ein- und Mehrjährigen (*Artemisia scoparia*, *Potentilla acaulis*, *Thermopsis lanceolata*, *Setaria viridis*) zusammengesetzt ist.

FORMATION OFFENER DORNBUSCH

Im NSG beschränkt sich die offene Dornbusch-Formation auf extrem

steinige Schluchttäler. Die dornigen Gebüscharten *Rubus phoeniculasus* und *Rosa bella* bilden auf solchen oft wiederholt überfluteten, flächenweise von groben Steinen bedeckten Sonderstandorten offene Gebüschebestände, in der keine charakteristische Krautschicht entwickelt ist.

HÖHENSTUFUNG DER VEGETATION IM NSG

VORBEMERKUNGEN

Da das NSG nur eine absolute Höhendifferenz von ca. 500 m umfasst, ist die Abstufung der Vegetation entlang dieses Gradienten weder eindrucksvoll noch leicht erkennbar.

Dazu kommen noch folgende weitere Gründe, die eine Höhenstufengliederung der Vegetation des NSG erschweren: Erstens ist die Landfläche im Lößgebiet Chinas aufgrund langanhaltender starker Bodenerosion durch stark erodierte Schluchtentäler tief eingeschnitten. Schmale, tiefe Täler durchziehen mosaikartig die Landoberfläche, wodurch die übliche Höhenabstufung des Temperaturfaktors an Bedeutung verliert und vom Wasserfaktor vielfältig überlagert wird. Teilweise sind steile

Hänge und wellige Hügel in der gleichen Höhenstufe ausgebildet. Dadurch ergeben sich bei gleicher Höhe erhebliche Unterschiede in den jeweiligen Temperatur- und Feuchtigkeitsverhältnissen, so dass lokal sogar eine Umkehr der Höhenstufenfolge der Vegetation feststellbar ist. Zweitens hat das NSG eine sehr lange Nutzungsgeschichte. Böden und Vegetation wurden ständig durch menschliche Tätigkeiten, besonders Beweidung (XIE et WITTIG, 2004) und Ackerbau, beeinflusst und verändert. Die aktuellen Pflanzengesellschaften im NSG sind deshalb eher mosaikartig als stufenweise verbreitet.

Trotz dieser Schwierigkeiten wurde versucht, eigene Vorstellungen zur Höhenstufung der Vegetation im NSG in einem vereinfachten Diagramm (Abb. 4) darzustellen. Dabei wurden auch lokale Aridität und Beweidungsintensität berücksichtigt, um mehrere Informationen über das gemeinsame Einwirken der ökologischen und anthropogenen Faktoren auf die räumliche Verbreitung der Vegetation einzubringen.

VEGETATIONSSTUFEN

Wie aus Abb. 4 ersichtlich, erstreckt

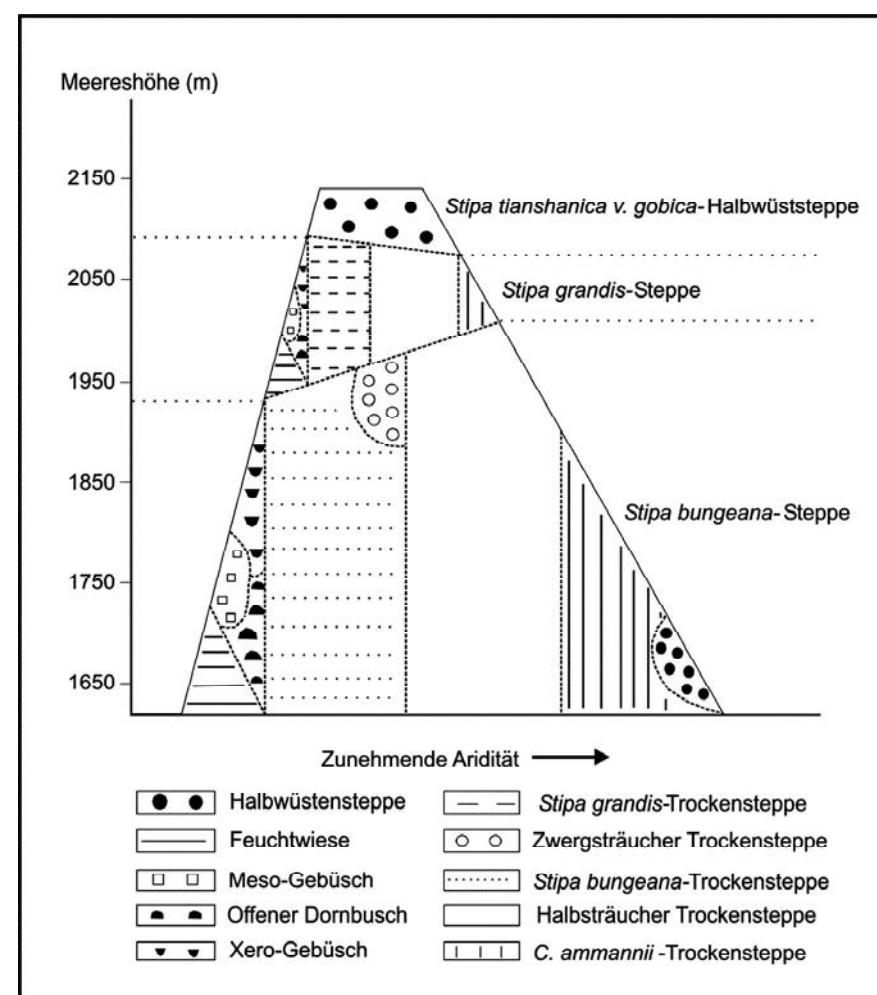


Abb. 4 - Höhenstufen der Vegetation des NSG Yunwushan in 1999.

ckt sich die Obergrenze der geschlossenen Vegetation des NSG bis zum Berggipfel Yunwushan (2.148 m), wobei auf Bergkuppen stellenweise allerdings auch offene Pflanzengesellschaften existieren. Die in Abb. 4 verwendeten Vegetationseinheiten wurden von der physiognomischen Gliederung übernommen. Die Vegetation im NSG lässt sich sowohl nach Klimabedingungen als auch nach pflanzenphysiognomischen Merkmalen in drei Höhenstufen gliedern.

Die Obergrenze der unteren Stufe liegt bei etwa 1.900 m, wobei, je nach den lokalen Wärme- und Feuchtigkeitsverhältnissen sowie nach der Intensität der Beweidung, Abweichungen, insbesondere nach oben, sind möglich.

In der unteren Stufe herrscht die zonale Trockensteppenvegetation mit *Stipa bungeana* vor, wobei in Abhängigkeit von der Beweidung verschiedene Untertypen ausgebildet sind. Die typische *Stipa*-Steppen-Formation gehört zu den wichtigsten zonalen Pflanzenformationen im semi-ariden Gebiet der gemäßigten Zonen. Neben typischer *Stipa*-Steppenvegetation ist die Halbstrauch-Steppe mit mehreren *Artemisia*-Arten der flächenmäßig am weitesten verbreitete Vegetationstyp in dieser Höhenstufe, wobei Letztere als Ersatzgesellschaft der typischen Steppengesellschaft bei intensiver Beweidung betrachtet werden kann.

Auf überbeweideten Flächen dieser Höhenstufe herrscht die *Convolvulus ammannii*-Steppe vor. Sie bildet eine niedrige Vegetationsdecke mit relativ tritt- und, verbissresistenten Pflanzenarten. Die Zergstrauch-Trockensteppe kommt in dieser Höhenstufe nur auf sonnenexponierten Standorten vor. Außerdem sind einige Gebüschesgesellschaften und Feuchtwiesen auf Sonderstandorten nicht selten.

In der Höhenlage zwischen etwa 1.900 m bis 2.100 m (mittlere Stufe) ist die Topographie des NSG mehr durch wellige bis ebene Flächen des Lößplateaus charakterisiert. Die Wärme- und Feuchtigkeitsverhältnisse sowie die Bodenbedingungen sind für die Vegetationsentwicklung relativ günstig. Hier kommt die Trockensteppenvegetation mit *Stipa grandis* vor, die für den östlichen Teil der mongolischen Steppen charakteristisch ist, im NSG also eine extrazonale Gesellschaft darstellt. Genau wie in der unteren Stufe wird auch in der mittleren die natürlicherweise bezeichnende Gesellschaft (hier also die *Stipa grandis*-Steppe) weidebedingt durch verschiedene Halbstrauch-Step-

pengesellschaften und schließlich durch die *Convolvulus ammannii*-Steppe ersetzt.

Die wenigen Berggipfel und -rücken des NSG, die sich höher als 2.100 m über den Meeresspiegel erheben, sind ständig dem Wind und der Sonne frei ausgesetzt. Daher weichen dort die lokalen Klimafaktoren und die Bodenbedingungen deutlich von denjenigen der unteren Höhenstufen ab. Die Bodenschicht erreicht im Allgemeinen weniger als 40 cm Tiefe. Teilweise liegt das Gestein frei an der Oberfläche. Aus diesen sehr ungünstigen Standortbedingungen, insbesondere den Temperatur- und Feuchtigkeitsverhältnissen, resultiert in dieser Höhenstufe des NSG eine Halbwüstenvegetation. Die dort dominierende Horstgrasart *Stipa tianshanica* var. *gobica* hat ihr Hauptverbreitungsgebiet in den Halbwüstensteppen Nordwest-Chinas.

Außer in den höchsten Lagen des NSG existieren Halbwüstensteppengesellschaften manchmal auch auf steilen, sonnenexponierten Hängen sowie in verlassenen Siedlungen der niedrigeren Höhenstufen.

DISKUSSION UND SCHLUSSFOLGERUNGEN

Die Unterschutzstellung war im Falle des Untersuchungsgebietes offensichtlich erfolgreich: Nach, bei Abschluss der Geländearbeiten für die vorliegende Arbeit, 18 Jahren Schutz hat sich die Vegetation im Kernbereich des Gebietes schnell erholt, wobei teilweise wieder stabile und naturnahe Stadien erreicht wurden.

In einer ansonsten weitgehend übernutzten Agrarlandschaft besitzt das NSG daher sowohl aus der Sicht des Naturschutzes als auch der Wissenschaft große Bedeutung.

Wie auch aus benachbarten Regionen beschrieben (z.B. MA *et al.*, 1990; XIAO *et al.*, 1995) und für weite Bereiche der zentralasiatischen Steppen typisch (s. KARAMYSHEVA und KHRAMTSOV, 1995), dominieren im Untersuchungsgebiet die Federgrassteppen. Mit zunehmender Beweidung kommen *Artemisia*-Arten zu Vorherrschaft. Auch dieses Phänomen wurde aus Nachbarregionen dokumentiert (z.B. ZHANG und SKARPE, 1995, 1996; PEER *et al.*, 2001). In der Mehrzahl der bisher vorliegenden Untersuchungen werden die *Artemisia*-Gesellschaften allerdings als Endstadium der weidebedingten Degeneration angesehen (z.B. LI B., 1988; LI Y., 1994; POISSONET und LI, 1990). Die

vorliegende Untersuchung zeigt jedoch, dass dies nicht der Fall ist, sondern dass eine weitergehende Degradation zu einem besonderen Vegetationstyp, der *Convolvulus ammannii*-Steppe, führt. Bemerkenswerterweise ist diese Gesellschaft sowohl das weidebedingte erste Degenerationsstadium sowohl der *Stipa bungeana*- als auch der *Stipa grandis*-Steppe.

Die Höhenstufung im Untersuchungsgebiet spiegelt die großflächigen Wuchsgeschiebe der zentralasiatischen Regionen wider: Offensichtlich entspricht das Oroklima der niedrigeren Regionen des NSG dem zentralasiatischen Großklima, das der mittleren Regionen (*Stipa grandis*-Steppe) dem Großklima der mongolischen Florenregion, und das der höchsten Stellen des NSG (*Stipa tianshanica*-Steppe) dem der Halbwüstensteppen Nordchinas.

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