15

THE VEGETATION OF GEORGIA
(CAUCASUS)

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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 connaisances.

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.

BRAUN-BLANQUETIA

RECUEIL DE TRAVAUX DE GÉOBOTANIQUE
REVIEW OF GEOBOTANICAL MONOGRAPHS

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J. BRAUN-BLANQUET, 1954
Drawn form a photograph by Françoise M. Dansereau

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*Dedicated to Carmela Cortini and
Franco Pedrotti*

the Author

INTRODUCTION

Georgia – an ancient Christian country – occupies the central and south-western parts of Caucasia – an isthmus between the Black and the Caspian Sea. In the west, it is contiguous to the Black Sea, in the east to the intermountain depression of the River Mtkvari (= Kura) in the Caspian Lowlands (the Transcaucasian Depression), the northern border follows the high mountain tops of the Greater Caucasus, the southern one crosses the Minor Caucasus (in the eastern part) and separates the Minor Caucasus from the adjacent mountain ranges of north-eastern Asia Minor. Politically, Georgia borders on the Russian Federation (to the north), Azerbaijan (to the east), Turkey (to the south-west) and Armenia (to the south-east). The borders have changed several times during the history of Georgia, especially in the earlier stages of the formation of the Georgian nation.

Kavkasioni, i. e. the Greater Caucasus range, rises up to 4605 m (Mt. Ushba, highest mountain within Georgia) and 5633 m s. m. (Mt. Elbrus, in the Russian Federation) i. e. over 1000 m above the eternal snow-line. Mountain passes at an altitude of 2200-3000 m s. m. were used as trade-routes from the earliest times. In the mountains of Kavkasioni permanent settlements are found up to an altitude of 2500 m s. m. Though the Minor (or Lesser) Caucasus mountains reach an altitude of 3304 m s. m., there are no glaciers and no eternal snow.

The natural conditions of the so-called intermontane lowlands of Georgia, consisting of the Colchic Lowlands (adjacent to the Black Sea, in West Georgia) and the foothills between Kavkasioni (in the north) and the Minor Caucasus (in the south-west), including the Mtkvari Valley (= Kura valley, in East Georgia), were favourable for settlement and mixed farming.

In the east, Colchic Lowlands are surrounded by the Imeretian Elevation which connects the Greater Caucasus with the Minor Caucasus. The highest part of it, the Surami range, divides the country into two major natural geographical regions: Eastern and Western Georgia, the first having been called Iberia and the latter Colchis by ancient Greek and Roman writers.

Diversity of climate and relief of Georgia has been highly important for its economic development since the early stages of human activities. Numerous rivers (more than 25.000), which promoted intensive agriculture, eliminated the need for irrigation systems, having proved so essential in the economy of the Ancient East (Egypt, Babylon). Besides, these rivers served as trade-routes. Due to their rapid current, the rivers were used for transportation of timber (especially in Colchis).

Georgia is rich in various mineral resources. In the mountains of Georgia copper was extracted, essential for non-ferrous metallurgy, which by that time reached a high level of development. Rich iron deposits prompted the progress of ferrous metallurgy. Magnetic sands along the Black Sea were of particular importance. Rivers, containing gold dust, were known during the Greek Epoch.

Vakhushti Bagrationi, the prominent Georgian historian and geographer of the 18th century, distinguished two botanical and agricultural zones within Georgia: the mountainous and the lowland one. Since the Neolithic Revolution, these two zones represented one closely integrated system. The lowlands were characterized by rich harvest of grain crops, vineyards and orchards. In the mountainous areas the harvest of grain crops was much poorer, vineyards and orchards were absent.

Georgia covers an area of 69.500 km². The population is 5.5 million (2/3 of them being Georgians). The Georgians call themselves "kartveli" (sing.) and "kartvelebi" (pl.), hence the name of the country in Georgian language is "Sakartvelo". The Georgian language belongs to the group of Kartvelian languages, included in the family of Iberian-Caucasian languages. It is suggested that the Georgian language is related to Anterior-Asian languages, the Basque language (the Basque nation is living in Spain, in the northern part of the Iberain peninsula, close to the Pyrenees), connections to the Indo-European languages, however, are uncertain. Written Georgian dates back to the 3rd century B.C. (to the reign of king Parnavaz).

Christianity, adopted as the official religion in 337 A. D., promoted the unification of Georgia and the development of written Georgian language.

In ancient times, Georgian tribes were known as skillful farmers, cattle-breeders and metallurgists. Various archaeological discoveries, as well as ancient oriental and Georgian manuscripts testify to an early economical, social and cultural development of the Georgian people. According to these data, the leading branches of economy of the country must have been: 1) agriculture (field crop cultivation, vine making, horticulture, vegetable growing, etc.); 2) cattle breeding; 3) domestic craft (weaving, wood work, blacksmith work, textile production, pottery, ceramics, etc.). Georgians developed plough-land cultivation, various forms of irrigation (especially in the mountain areas) aiming to increase crop capacity of natural grasslands (2 and 3 harvests per season). Of 16 species of wheat 11 are represented in Georgia.

Ancient Georgian manuscripts and special medical books ("Karabadini") contain information on various herbs. The first serious scientific information concerning the vegetation of Georgia was given by Vakhushti Bagrationi (18th century). According to several historical sources and notes of foreign travellers, the plants from different parts of Georgia and from other countries were cultivated in the park of Georgian kings in Legvta Khevi (now Botanical Garden of Tbilisi). In the 18th century, foreign scientists became interested in the extreme diversity of Georgian vegetation and flora. In 1852, on the basis of rich collections of Caucasian plants, the Caucasian Museum was founded. In the beginning of the 20th century, all the branches of botanical science (anatomy, physiology, taxonomy, floristics, phytosociology, etc.) started to develop in Georgia. The Institute of Botany, which belongs to the Academy of Sciences, was opened in 1933. Long-standing expeditions to different parts of the Caucasus and of Georgia, as well as monographic studies of separate taxa served as a basis for the 8-volume "Flora of Georgia". In 1971, the first volume of the totally revised second edition of "Flora of Georgia" appeared (11 volumes have already been published so far). Later, it was decided to publish "The Vegetation of Georgia" under the editorship of the present author (NAKHUTSRISHVILI, 1990, 1991). Only two volumes of this work have been published till now (DOLUKHANOV: "Forest Vegetation of Georgia", Part I, 1990, and SHATILOVA and RANISHVILI "Materials on the History of Flora and Vegetation of Georgia", 1991); several volumes are in print. Until its complete publication, the author of the present book decided to characterize briefly the main types of vegetation of Georgia and to publish it in English. This present publication bears a special purpose: During the 75-year period of isolation of the USSR and of Georgia in particular, it was not so easy for foreign scientists to get adequately acquainted with the interesting plant life of Georgia and to compare the Caucasian flora and plant communities with those of other countries.

Historico-Geographical Regions of Georgia
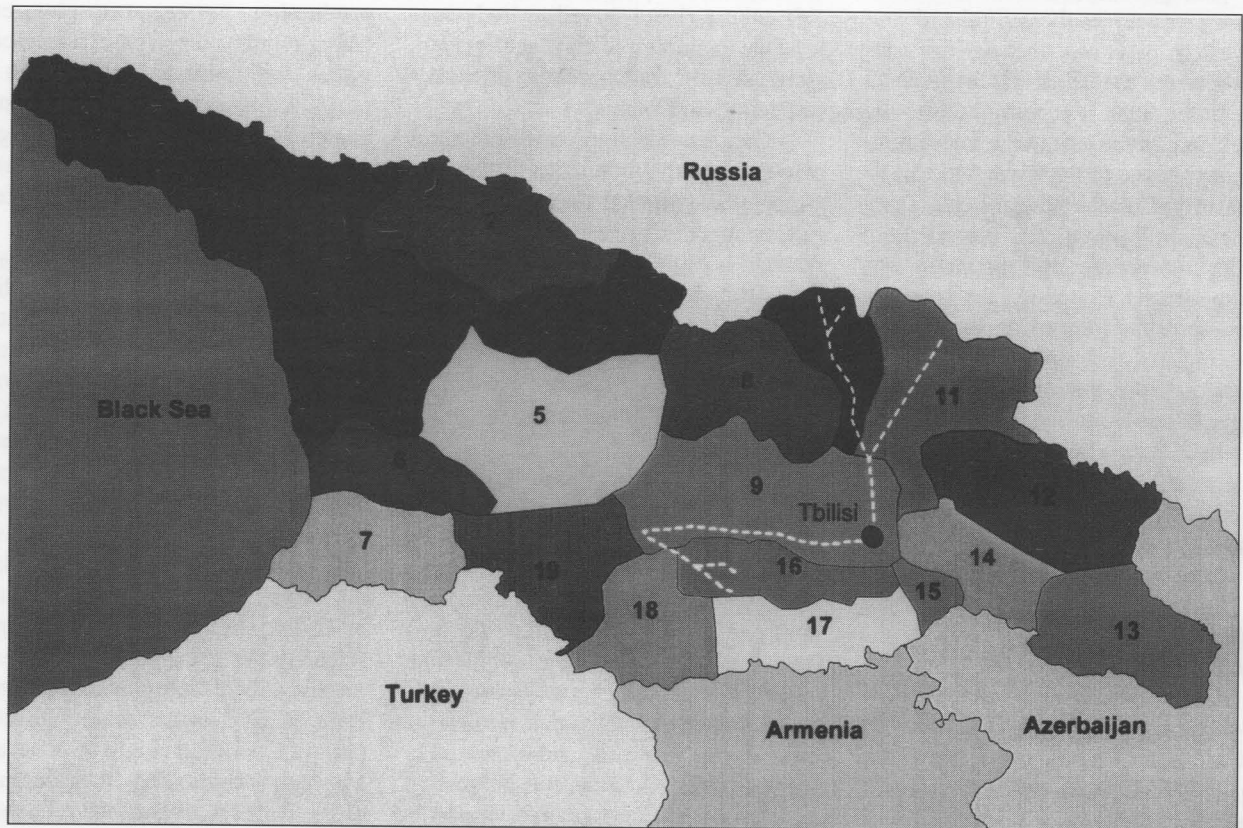
1.	Abkhazeti	11.	Tush-Pshav-Khevsureti
2.	Svaneti	12.	Kakheti
3.	Racha-Lechkhumi	13.	Kiziki
4.	Samegrelo	14.	Gare Kakheti
5.	Imereti	15.	Gardabani
6.	Guria	16.	Trialeti
7.	Adjara	17.	Kvemo Kartli
8.	Shiga Kartli	18.	Javakheti
9.	Kartli	19.	Meskheti
10.	Mtiuleti		

Today, Georgian botanists are glad to be able to collaborate with scientists from many other countries.

1. ENVIRONMENTAL CONDITIONS

Georgia occupies an interesting geobotanical position as a part of Caucasia – the region which links Europe with Asia. The country is characterized by rather contrasting natural conditions which account for the extremely high degree of divergence of plant communities within this comparatively small area. The landscape of the country includes different types of desert and semi-desert vegetation mainly in the eastern parts of Georgia, luxuriant Colchic forests of moist, almost subtropical climate in the west, and high-mountain plant communities in the north and in the south.

The complex orographic structure of Georgia and its geographical position account for the geographical and ecological isolation of certain plant communities, which has resulted in a high ratio of local endemism (particularly endemics of the Greater Caucasus Range and of the Colchis) and of a variety of species of different phytochorological groups, like Iberian and Anterior-Asian group, etc.). The flora of the country includes about 4.200 species of wild flowering-plant species, and over 8500 species of spore-bearing ones (75 pteridophytes, about 800 mosses, 600 lichens, 5000 fungi, 2000 algae).

1.1 Orography

Geologically, the territory of Georgia belongs to the Alpine System of Eurasia. Its geological and geomorphological structure reveals a great genetic diversity, as a result of tectonic, volcanic, petrological, gravitational, erosional and other processes.

Structurally, the area can be divided into the following major landforms:
1) The range of the Greater Caucasus (Kavkasioni);
2) the Georgian Intermontane Area (between the Greater and the Minor Caucasus);
3) the Mountain System of the Minor Caucasus (Meskheti-Trialetian Range), including the South Georgian Volcanic Upland.

Georgia comprises the southern side of the middle part of the Kavkasioni as well as the north-western parts of the Transcaucasian Depression, the Minor Caucasus, i. e. the Transcaucasian Uplan.

Altitudes in Georgia vary considerably from the sea level (at the Black Sea) to some of the highest peaks of the Greater Caucasus, reaching 4695 m (Mt. Ushba), 5068 m (in the Shkhara massif), and 5047 m s. m. (Mt. Kazbegi, Kazbek). From the geological point of view, this area consists, mainly, of Meso- to Cenozoic deposits. Ancient Precambrian and Paleozoic formations are poorly represented and of secondary importance.

1.2 Climate

The climate is one of extremes. It is possible to distinguish several climatic zones from the humid, almost subtropical climate to the climate of permanent snows and glaciers. Such a considerable range of climatic conditions is caused both by the orographic structure and the presence of the Black Sea and the Caspian Sea. The Black Sea and high mountain ranges of the Greater Caucasus are the most important orographic factors determining the climate of Georgia by preventing the invasion of cold air masses from the north. The climate of the country has been formed by the air masses blowing from sea, as well as by the latitudinal position between southern Russia and the Inner-Anatolian mountains system.

The highest mean annual temperature amounts to 15° C (Sukhumi in Abkhazia, on the Black Sea coast), the lowest in the Kavkasioni Ridge (altitude 5000 m). The warmest winter (5-7° C, in January) is in Colchis (West Georgia, on the Black Sea coast).

Annual precipitations in Georgia range from over 4500 to 400 mm or less. Increase of altitude e.g. in Svaneti (north-western Georgia) and Javakheti (south-western Georgia) is paralleled by reduction of precipitation, while in other districts (Kazbegi region, Kakheti, etc.) the amount of rainfall increases with elevation. The highest amounts of precipitation occur at the following altitudes: from 300-500 m to 3500 m s. m. in Western Georgia, and from 1200 to 3500 m in the eastern part of the country.

The climatic conditions of several districts of Georgia are demonstrated diagrammatically (fig. 1). Notwithstanding the short distance between these districts (40 km between Batumi and Bakhmaro, 380 km between Batumi and Shiraki, 155 km between Shiraki and Kazbegi), their climatic conditions are noticeably different.

1.3 Soils

There is a great diversity of soil types in Georgia. The following soil provinces can be distinguished:

1) the soil province of Western Georgia;
2) the soil province of Eastern Georgia;
3) the soil province of Southern Georgia.

The main types of soil are allocated in accordance with the altitudinal zones. In the Western Georgia soil province (between the Black Sea and Likhi Mts.) it is possible to distinguish the bog and podzolic soil zone in the lowlands, the krasnozem and zheltozem zone in the hilly piedmonts, the zone of mountain-forest and the mountain-meadow soils.

The soil province of Eastern Georgia comprises the plains, piedmonts and mountain massifs, situated eastwards from Likhi mountain range. Chestnut soils, chernozems, brown humic-sulphates, saline soils of steppes and semi-deserts, as well as intermediate forest-steppe and mountain-meadow soils occur in this province.

The Southern Georgia soil province includes Javakheti, Tsalka-Dmanisi and Erusheti uplands, the hollow of Akhaltsikhe, etc. A considerable part of this area is covered both with the mountain chernozems (which are formed at altitudes from 1200-2200 m) and meadow chernozem-like soils. In highlands they are replaced by mountain-meadow soils. Besides, the alluvial soils, redzinas, brown as well as the meadow-brown soils occur here, with the predominance of brown forest type of soil in the mountain forest belt.

2. HISTORY OF FLORA AND VEGETATION

The history of flora and especially the vegetation of Georgia is very complicated and, despite the intensive paleobotanical researches of the recent past, still needs to be studied.

The earliest records of fossil flora stem from the Paleozoic. Species of *Lepidodendron* (large trees reaching a height of nearly 40 m), *Sigillaria* (high plants with erect stems and characteristic rhizophore system-stigmarias), Asterocalamites were determined from the Lower and Middle Carboniferous deposition of the Khrami crystalline massif (South Georgia). From the same period are also known Cordaitales – a group with anatomic structures (tracheids, well-developed pith) very similar to that of conifers (SHATILOVA & RAMISHVILI, 1990).

In the Early Jurassic, almost the entire territory of Georgia was covered by sea, except for Khrami, Loki and Dzirula ancient massifs.
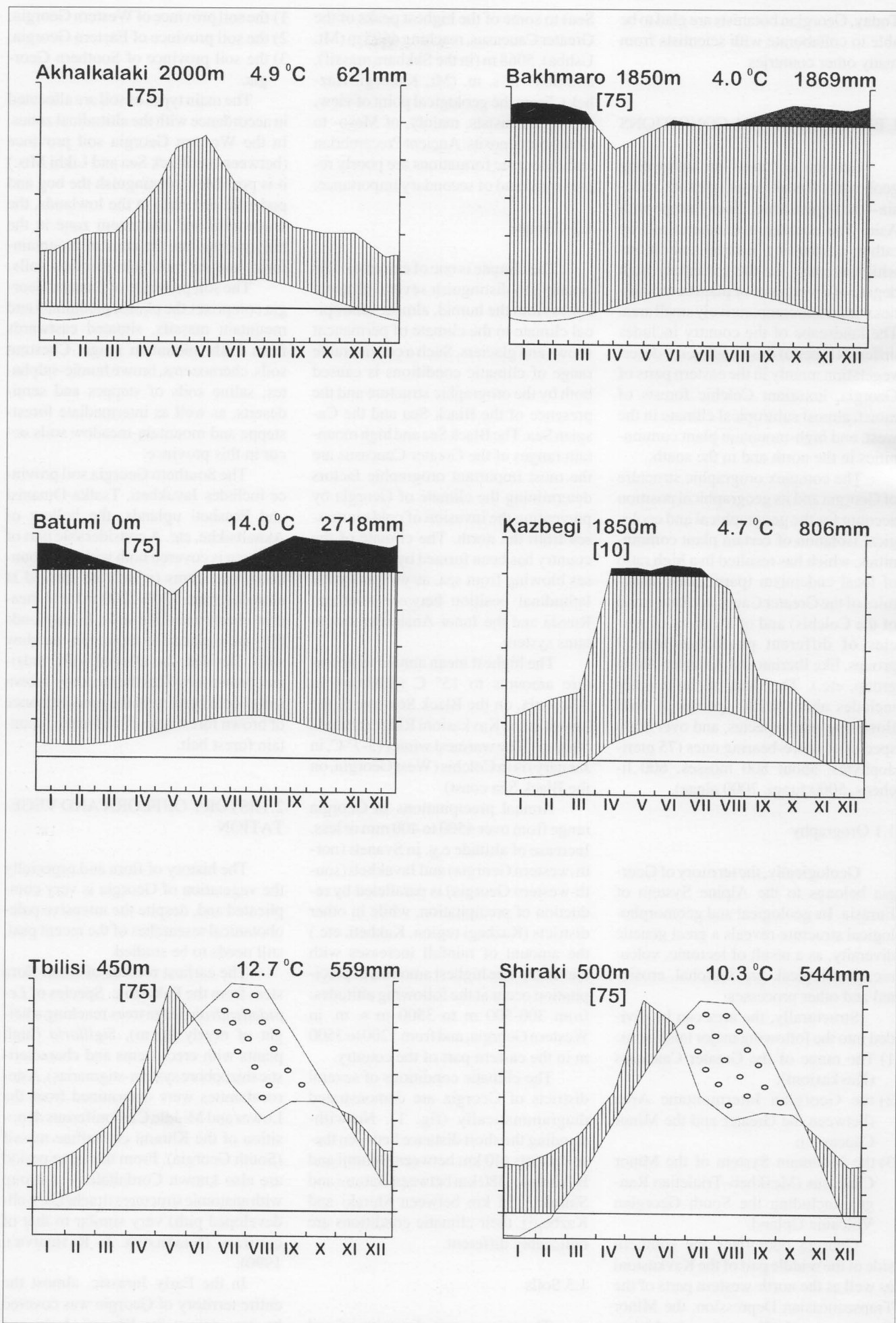
The climate of this period was

Fig. 1 — Climadiagrams of several regions of Georgia.

warm-temperate. Water temperature in the sea reached 23-24° C, but in the Late Toarcian it decreased considerably (7-15° C). From the Early Jurassic deposits, Calamitales are of special interest with the only species *Neocalamites hoerensis*. The above mentioned period was characterized by the wide-spread occurrence of equisetoides, which were restricted to marshes as nowadays (SVANIDZE, 1972; JASAMANOV, 1985).

Pteridophytes were represented by 25 taxa. Microfossils found belong mainly to the genera of *Cladophlebis* (Osmundaceae). At the same time *Gingko* was represented by 2 species – *G. mziae* (specific for Georgia) and *G. huttonii*. The species *Sphlenobaiera spectabilis* and *Phoenicopsis* ex gr. *angustifolia* also belong to Gingkoaceae. In the Early Jurassic a considerable group was formed by Bennettitales, the ancestors of the flowering plants (according to the viewpoint of several botanists) *Eucommidites troedssonii* (gymnosperms pollen) and many other plants were present in the same period too.

In the Bajocian (Middle Jurassic) the entire territory of Georgia was under the sea; by the end of it, first the eastern part and afterwards (in Bathonian) the whole territory have emerged. The appearance of freshwater basins was characteristic for that period, as well as the process of peat accumulation (KAKHADZE, 1947). The Early Jurassic flora is much richer than that of the Early Jurassic. To day nearly 175 plants species are known. Among them 55 species are ferns, (*Coniopteris,* Cyatheaceae, Osmundaceae, Gleicheniaceae). The other characteristic components were representatives of *Paracycas* (Cycadaceae) and *Ptilophyllum* (Bennettitaceae) etc. The climate of the Middle Jurassic seemed to have been tropical; the representatives of Cycadales and Gingkoales were dominant in woodlands (KARASHVILI, 1977; SVANIDZE, 1972).

In the Late Jurassic the territory of Georgia was covered by sea, except the Svaneti Elevation, as well as that of southern parts.

By the beginning of the Late Jurassic a great number of ferns, Ginkgoales, Cycadales and Bennettitales had extincted with the occurrence of an arid zone in Eurasia (from Spain to central China). *Brachyphyllum* and *Pagiophyllum* occupied a dominant position. As indicated by the prevalence of *Classopollis,* the Cheirolepidaceaea increased considerably.

The occurrence of remnants of new species *Angiopteris iberica* (Marattiaceae) in the Late Jurassic fossiliferous deposits is of great importance. It undermines the opinion, that these archais living ferns disappeared from the floras of the Northern Hemisphere after the Middle Jurassic.

According to VAKHRAMEEV (1988), the Late Jurassic paleofloristic province of the Caucasus was a part of the Euro-Sinian region.

The flora of the above-mentioned province could be characterized by the presence of occasional equisetoides, a few ferns, Ginkoales, the absence of *Czekanowskia* and the predominance of Cycadales, Bennettitales, as well as *Pachypteris, Sagenopteris, Pagiophyllum.*

The Tertiary

In the Paleocene and Eocene on the territory of the Caucasus a long island was formed as a basis of the further mountain range. According to AVAKOV (1989) in the Eocene the dominant position was occupied by the Angiosperms, representatives of evergreen Fagaceae and *Myrica*.

At the same time the process of migration of the Boreal cold-resistant plants, which had begun previously in the Cretaceous, resumed at the end of the Eocene.

At the Eocene/Oligocene boundary, the folded structure of the Alpine system began to form in the Mediterranean orogenetic band. It comprised the (geosynclinal) regions of the Southern Slope of the Greater Caucasus range and Ajara-Trialeti, the main part of today Georgia. Uplift caused a change in the climatic conditions; the latter determined the character of the vegetation: the number of conifers increased and warm-temperate plants became more numerous (SHATILOVA & RAMISHVILI, 1990).

During the Oligocene, the Caucasus was a small island surrounded by vast basin with scattered islands, where the tropical flora of the Poltava type (palms, laurels, etc.) was well developed. In the Oligocene deposits remnants of conifers were found, indicating the penetration of northern taxa into the Caucasus.

The Oligocene plant world was greatly influenced by Arcto-Tertiary or Turgay flora, formed in the Eastern and Northern parts of modern Asia. Representatives of this flora, especially Pinaceae, penetrated into the Caucasus. Many botanists consider that migration of the Turgay elements became more intensive after the Turgay Strait had become dry by the end of the Oligocene.

According to GROSSHEIM (1946) Turgay migrants began to change and gave rise to the ancient mesophytic forest flora, called Mediterranean-Turgay flora by this author.

During the Early Miocene the Caucasus island started to expand. Fossil assemblages from different part of Georgia, especially from Eastern Georgia, confirm the subtropical nature of the Miocene flora with the predominance of evergreen woody plants, accompanied by the deciduous *Castanea* sp., as well as by conifers of northern origin (*Pinus* sp.).

The following plants have been known since the Early deposits of Kartli (East Georgia): *Quercus neriifolia, Myrica lignitum, Laurophyllum primigenium,* species of *Apocynophillum*. Of the 46 taxa two are pteridophytes and gymnosperms. The dominant position is occupied by angiosperms, among them the predominance of Myricaceae, Juglandaceae and Lauraceae shoud be noted. Evegreen Fagaceae, Lauraceae and other thermophilous plants, contributing to the formation of moist-subtropical forests in the Paleogene, adapted to the reduced humidity of the Early Miocene (DJAPARIDZE, 1981).

In the Middle Miocene plants of warm and dry climate participated in sclerophyllous formations. *Myrica* species covered river banks. Sclerophyllous plants were represented by the species of *Myrica, Callistemophyllum, Acacia, Quercus* (*Q. drymeja*). Several species of Lauraceae, *Sapindus, Smilax* and *Magnolia* formed moist-subtropical forests (AVAKOV, 1979).

It is possible to suggest that an altitudinal differentiation of vegetation already existed in the Middle Miocene. Coastal and low mountainous areas were covered by evergreen Fagaceae, arborescent ferns, *Hymenophyllum*, etc. The next altitudinal belt was occupied by mesophilous deciduous forests of *Platanus, Comptonia, Juglans, Pterocarya*, accompanied by *Cathaya, Keteleeria* and etc. Cold-resistant plants occured even higher; mention should be made of species of *Betula, Fagus, Acer, Tilia, Ulmus* (SHATILOVA & RAMISHVILI, 1990).

During the Sarmatian (Upper Miocene) the Caucasian island, known in the literature as Jephetis was situated close to Iranian and Central Asian land. This encouraged the immigration of xerophilous elements into the Caucasus. It is suggested that the forestless formations of xerophytic plant communities were widely distributed during the Upper Miocene. According to GROSSHEIM (1946), *Pelargonium endlicherianum,* the fern *Ceterach*, etc., are relics of the ancient xerophytic flora of this period.

The close position of Jephethis to the Iranian mainland, separated as a cape, caused division of the mesophytic Mediterranean-Turgay flora into Western and Eastern parts. In the West the Colchic flora began to form, while the Hyrcanian elements evolved in the eastern part. Both were of mesophytic nature. The analysis of the contemporary vegetation makes many botanists suggest the existence of a third xerophytic flora.

Based on the fossils, it is possible to build up a picture of the Sarmatian flora: evergreen *Magnolia dianae*, species of Lauraceae (*Cinnamomum, Laurophyllum primigenium, L. pseudoprinceps*, etc.), as well as the representatives of the Mediterranean-Turgay and Turgay deciduous flora, such as *Salix, Pyrus, Carpinus, Juglans, Ulmus*, etc. Conifers (*Pinus saturni, Sequoia langsdorfii*) and xerophytic species of *Myrica* have been known from the same age.

Kolakowsky pointed out that the richest Sarmatian floras occurred in Abkhazeti (Colchis). They were closely related to the southern subtropical and tropical floras (*Melastomites, Mastixia microphylla, Ventilago* etc.). The Sarmatian floras of Abkhazeti are very similar to Oligocene-Miocene European floras. These floras indicate the wide distribution of subtropical evergreen plants, mainly Lauraceae, such as *Ocotea, Persea, Aniba*, and many others and the deciduous arborescent plants of warm climate which survived until now only in Central and South America, partly in the Mediterranean area and in the South-Eastern Asia, Himalayas and China, where the relic forests of *Ulmus, Fagus, Quercus, Abies* and *Cryptomeria* are represented. These forests show also a great similarity to the vegetation, confined to mountainous Japan during the Miocene-Pliocene (KOLAKOWSKY, SHAKRYL, 1976).

The Tertiary-relic species of Colchic type, such as the species of *Buxus, Pterocarya*, etc. and the hemixerophytic Mediterranean plants: *Arbutus, Celtis, Smilax, Thelycrania* (*Cornus*), *Quercus*, have been found in the Sarmatian deposits of Abkhazia.

The territory of Eastern Georgia, where steppes and semi-deserts are distributed now, is considered to have been covered with both sclerophyllous and moist-subtropical forests.

In South Georgia the shrubs of subtropical and temperate climate dominated by Lauraceae, were represented by narrow-leafed xerophytic elements (CHELIDZE, 1970).

In the Meotian after the regression of the Mediterranean Sea, the strait separating the Jepethis from the southern mainland disappeared and the Caucasus became a peninsula. The formation of main folded systems reached the final point and the vegetational belts were formed. The Meotian macrofossils included *Cryptomeria japonica*, species of Lauraceae, *Salix coriacea, Myrica lignitum*. Ferns, especially *Dicksonia*, were represented by a large number of species. Palynological data attest to the fact that the following genera of conifers were present: *Abies, Picea, Tsuga* (5 species), *Cedrus*, as well as *Carya*, "*Castanopsis frutinervis*", (leaf of *Quercus*) representatives of Hamamelidaceae, (*Liquidambar*, etc.).

Judging from the composition of the fossiliferous deposits, in this period, coniferous and broad-leaved forests (*Taxodium, Cryptomeria, Magnolia*, species of Hamamelidaceae, etc.) with the species of *Quercus, Carya, Fagus, Castanea* and *Platanus* began to prevail.

Relatively dry habitats were occupied by following hemixerophytes: *Quercus drymeja, Pistacia miocenica, Sophora europaeus, Pyracantha coccinea*. At the same time the following plants began to crop up (present-day members of the Georgian flora): *Rhododendron caucasicum, Fagus orientalis, Zelkova crenata* (= *Z. carpinifolia*).

The fossil flora of Goderdzi pass (South-Western Georgia) was distinguished by the feature characteristic of Sarmatian flora (PURCELADZE, TSAGARELI, 1974; UZNADZE, TSAGARELI, 1979).

Taking into account fossil deposits of Colchis, mesophytic flora obviously prevailed here. Representatives of Annonaceae, Hamamelidaceae and Lauraceae are known from this period, which was characterized by warm maritime climate. Ferns, distributed in Georgia during the Pontian can now be found only in the tropics.

During the Pontian gymnosperms were widespread. Nowadays some of them occur in mountain forests of tropical and subtropical countries. In the beginning of the Pliocene *Pinus pithyusa* was widely distributed (RAMISHVILI, 1969).

Investigations carried out by KOLAKOWSKY (1964) in Kodori (Abkhazeti) point to the existence of lowland and low-mountain forests with *Myrica lignitum, Salix varians, Alnus subcordata*. Coastal lowlands were covered with forests of *Quercus kodorica* and *Carya denticulata*, while the riversides were occupied by species of *Liquidambar, Taxodium, Nyssa, Tectocarya lusstica, Ocotea*, evergreen Fagaceae like *Pasania, Castanopsis*, etc., which were cha-

racteristic of the subtropical forests of the Pontian. In the lower mountain zone considerable areas were populated by Lauraceae with tree ferns (*Cyathea, Alsophila, Dicksonia*).

In the lower mountain zone sclerophyllous formations were distributed with the elements of maquis. Pines occupied rocky habitats.

KOLAKOWSKY (1964) pointed out that an important change in the flora of warm-temperate climate took place during the Pontian. The mid-mountain belt was populated by *Fagus, Castanea, Acer, Tilia* species. The presence of conifers – *Gingko, Keteleeria*, ferns like *Polypodium*, etc., lianas like *Vitis betulifolia, Parthenocissus quinquefolia* becomes fairly possible.

Dark coniferous forests (with the species of *Abies, Tsuga, Picea, Cedrus*, etc.) occupied relatively higher altitudes.

On the territory of Western Georgia a great number of angiosperms has extincted since Pontian.

In Cimmeridian (Middle Pliocene) taxa of Araliaceae, as well as ferns were well represented. The dominant position was occupied by species of *Pteris* and *Polypodium*. According to KOLAKOWSKY & SHAKRYL (1978) forests of warm-temperate climate began to prevail in Cimmeridian; they were composited by the species of moist monsoon climate, now peculiar of the mountains of Eastern Asia and xerophytes, ecologically similar to the plants of xerophytic forests of the Mediterranean. Above in the warm-temperate forest zone hardwood and coniferous forests grew.

During the Akchagylian (Upper Pliocene), the most striking feature of the fossil floras is the absence of Poltava flora elements and evergreen plants. The following plants are known from this period: species of *Populus, Ostrya, Fagus, Zelkova, Tilia, Pyrus, Ligustrum, Salix, Prunus, Acer, Quercus, Pterocarya*, together with representatives of *Carex* and *Phragmites*. All these plants are members of the present-day flora of Georgia, though they have changed their habitats. For example, remains of *Fagus orientalis* and *Ostrya carpinifolia* have been found in Akchagylian deposits of Shiraki steppe. Due to increasing aridity these trees are no longer there.

According to GROSSHEIM (1948) the Akchagylian flora by its nature is closely connected with that of the Quaternary. To quote his words: "The period between Sarmatian and Akchagilian was the turning-point in the floristic history of the Caucasus; the tropical flora had

been replaced by that of temperate climate" (GROSSHEIM, 1948; 171). Broad-leaved forests were replaced by conifers, namely species of *Picea, Abies, Tsuga*. In general, during the late Pliocene the role of polydominant forests vegetation was reduced and, instead, the formation of communities with one or two dominant species was stimulated. These changes in the vegetation cover were probably provoked by the intensification of cold at the end of the Miocene and in the Pliocene.

The existence of a dry and hot climate between the cold periods encouraged the enrichment of the Caucasian flora with xerophytes. In Akchagylian time many recent Mediterranean plants penetrated into the present area from the west.

Therefore, in the Pliocene, the piedmonts and the lower mountain zone were clothed by subtropical forest vegetation. Forests of warm-temperate climate were situated higher up. Many species known from this period are still member of the modern forest flora. In the beginning of the Pliocene, within the territory of Western Georgia and adjacent areas (e.g. Turkey), a Colchic refuge was formed for many relics of mesophytic forest flora. This was a direct result of the warm and humid climate of this territory. The Colchic refuge was of great importance as one of the most stable "shelters" for relic species during the Late Pliocene and especially in the Pleistocene, including the Ice Ages. Many species, which continue to exist in Colchis died out many millions of years ago on the territory of West Eurasia. Members of the Colchis flora are such relics and/or neoendemics as *Betula medwedewii, Quercus pontica, Rhamnus imeretina, Hedera colchica, Pterocarya pterocarpa, Laurocerasus officinalis, Arctostaphylos caucasica, Rhododendron ponticum, Rh. ungernii, Rh. smirnowii*. At present, their relatives with a similar autecology have mainly survived in the mountains exposed to the summer monsoon in Eastern and South-Eastern Asia, in the Appalachians of North America, etc.; for instance, genus *Epigaea* is represented now by just 3 species, one of which is distributed in Japan, the second in North America and the last in Ajaria (Georgia) and Lazistan (N.Turkey).

Thus, having surveyed the Tertiary history of Georgian flora, we now come to the Pleistocene. During the Pleistocene, most of the termophilic elements extinct from the flora of Georgia. The role of cold-resistant plants considerably increased, at the same time vertical

shifts of vegetational belts appeared, especially during the glacial periods.

Another event, which have occurred during the Pleistocene is the development of boreal elements. Though the flora of Georgia was strongly influenced by the neighbouring floristical centres of Eastern Mediterranean and SW Asia (Near East, Anterior Asia), in process of autochthonous development provided a large number of endemic species, including present-day local endemics.

In the Early Chaudian (Early Pleistocene) deposits the highest taxonomical diversity and an abundance of Taxodiaceae and Cupressaceae could be observed: these families were manifested by the following genera: *"Athrotaxis"*, (= extinct Taxodiaceae), *Cryptomeria, Metasequoia, Sequoia, Sequoiadendron, Taxodium, Cupressus, Chamaecyparis, Libocedrus, Juniperus* (CHOCHIEVA, 1985).

The dominant position was occupied by *Abies nordmanniana, Tsuga diversifolia*, whereas *Abies alba, Cedrus* aff. *libani* and some other had extincted.

In the Chaudian flora Juglandaceae were represented by several genera: *Pterocarya, Carya, Juglans*, etc. Pollen of *Zelkova* was found in the Chaudian deposits of Georgia (SHATILOVA, MCHE-DLISHVILI, 1980).

The Chaudian pollen assemblages contain pollen of plants very closely allied to evergreen shrub *Fatis japonica*, which is now confined to the forests of Japan, as well as of that of Symplocos which is largely distributed in tropical areas. Obviously the prevailing types of vegetation in the Early Chaudian were monodominant forests of *Tsuga, Abies*, representatives of Taxodiaceae and *Fagus*. Lower mountain and piedmont belts were covered by the forests of *Juglans, Carpinus, Quercus, Zelkova* and also by subtropical species of *Magnolia, Fatsia, Symplocos*, etc.

The second half of the Chaudian was characterized by the predominance of *Picea-Abies* communities in almost all mountain belts, whereas the lower parts were covered with broad-leaved forests.

In the Middle Pleistocene (Old. Euxinian) taxonomical diversity of *Abies, Picea* and *Tsuga* was reduced. Members of the Taxodiaceae family prevailed in forests communities. Within the territory of Georgia only 6 out of 66 taxa, known from the Old Euxine have been extinct.

In Western Georgia the Old Euxinian deposits are covered by that of Uzunlarian. In this time ferns were re-

presented by those species which continue to exist in present-day Georgia. A dominant position in forests was occupied by widely spread *Abies nordmanniana, Picea orientalis* with the admixture of *Cedrus deodara, Tsuga diversifolia* and *T. shatilovae*. The Taxodiaceae family was represented by *Taxodium, Cryptomeria, Sequoia* and *Glyptostrobus*. Hardwood forests consisted by the following species which have become members of the modern Georgia flora: *Fagus orientalis, Castanea sativa, Carpinus caucasica*. It should be mentioned here that mesophytic species were substituted in East Georgia by those of *Pinus, Carpinus, Quercus*.

In the Late Pleistocene there were still a number of species which have disappeared from the territory of Georgia. Mention should be made of the representatives of Taxodiaceae, of *Cedrus deodara* and *Carya aquatica*. Other angiosperms were represented by species which are characteristic of modern Georgia flora (SHATILOVA, RAMISHVILI, 1990).

Man introduced considerable changes into the vegetational cover of Georgia. Forest destruction, development of secondary meadows cultivated lands are the result of human activities. At the same time the Georgian flora was enriched both by cultivars and adventive weeds.

3. ON THE ALTITUDINAL DIFFERENTIATION OF THE VEGETATION OF GEORGIA

Considerable difference between the climates of East and West Georgia determined the diversity of their vegetal landscapes, as well as the structure of altitudinal zonation.

The absence of arid and semi-arid vegetation belts is characteristic of West Georgia. It accounts for a more simple profile of altitudinal zonation here, which is represented by 5 main belts: forests (0-1900 m s. m.), subalpine (1900-2500 m), alpine (2500-3100 m), subnival (3100-3600 m), nival (above 3600 m).

In East Georgia, the altitudinal zonation is more complicated. One can observe here 6 main belts: deserts, dry steppes and arid light forests (150-600 m), forests (600-1900 m), subalpine (1900-2500 m), alpine (2500-3000 m), subnival (3000-3500 m), and nival (above 3500 m). The borderline between the semi-arid belt and that of forests varies considerably due to the climatic conditions and the exposure of slopes. Within the forest and subalpine belts of South-

Georgian Upland there are small areas occupied by semi-arid ecosystems with the prevalence of mountain-steppe vegetation.

Thus, almost all the altitudinal belts, characteristic of the Nemoral Zone of Northern Hemisphere, are represented in Georgia.

We would like to illustrate the differentiation of vegetation by vertical gradients in two strongly different parts of Georgia: the East and the West (the profiles are shown in fig. 2 and fig. 3a). In East Georgia, the vegetation of deserts, semi-deserts and hemi-xerophytic light forests is replaced by *Quercus iberica* forests with the admixture of *Carpinus orientalis* on southern slopes. At an altitude of 1300 m, there is a narrow zone of *Carpinus-Fagus* forest, which is substituted higher by that of *Quercus macranthera*. Comparatively dry meadows can be observed at an altitude of 2250-2300 m.

On the northern slopes, the situation is different. Above the hemi-xerophytic vegetation belt, there is a subzone of *Carpinus-Quercus* forest, higher up substituted by beech forest which occupies large areas from 600 m to 1800 m. *Acer trautvetteri* is a common associate of the dominant *Fagus orientalis*. Still higher up, these communities are replaced by a birch forest with tall herbaceous vegetation confined to glades. Above the timberline, all slopes are covered with *Rhododendron* scrub ("dekiani" is a native name of these communities, suggested for scientific use by Ketskhoveli) and carpet-like alpine meadows.

Beech forest is substituted by that of *Pinus kochiana* under more continental conditions (e.g. in Tusheti).

Unlike East Georgia, in the western part of the country, namely in South Colchis, forests begin to dominate from the sea level. The most characteristic species of these lowland forests are *Pterocarya pterocarpa, Alnus barbata, Pinus pithyusa* (in north-western Colchis), etc. Southern slopes are populated by the forests of *Quercus iberica, Qu. hartwissiana* and *Carpinus caucasica*. At 600-700 m, beech forests appear with admixture of *Abies nordmanniana*; spruce-fir forests (*Picea orientalis* and *Abies nordmanniana*) occur at 1200-1300 m. Near the timberline, *Picea orientalis* forests and that of *Betula medwedewii* are distributed. The alpine meadows occur higher up.

The oak forests are substituted by that of *Carpinus caucasica* and *Castanea sativa* on the northern slopes. Beech forests, situated higher up, form crook-

stem woods at the extreme altitudinal range of their distribution.

The second variant of altitudinal zonation in West Georgia (Svaneti) is also of particular interest. *Alnus barbata* forests populate the lowland area (see fig. 3b). The leading species of these communities is often accompanied by *Carpinus caucasica* and *Matteuccia struthiopteris*. At 600 m, beech forests begin to dominate; their undergrowth is represented by *Rhododendron ponticum*. At about 1300 m s. m., beech is usually accompanied by fir (*Abies nordmanniana*). The subalpine belt is characterized by the dominating position of *Acer trautvetteri* growing together with *Fagus orientalis*. The herbaceous vegetation is also characteristic of this belt. It should be noted that in several gorges the lower part of the subalpine belt is occupied by crook-stem beech forests, while the upper part is dominated by decumbent beech forests and *Rhododendron* scrub. On the southern slopes, lowland forests are substituted by those of oak, which are replaced by fir-spruce forests at about 1000 m; rocky habitats are covered by pine forests. Near the upper limit of forests, crook-stem beech forests occur. At 1850-2400 m, subalpine and alpine meadows appear.

4. ON THE CLASSIFICATION AND NOMENCLATURE OF PLANT COMMUNITIES

I find it necessary to make the reader acquainted with the principles and methods of plant community classification, used to recognize syntaxa given in this book.

In the former USSR, the main approach to the classification of vegetation units was based on the dominant species. The "Formation" (higher syntaxon) was defined by the dominant species in the layer. According to the former Soviet authors, an association includes plant communities with the same set of dominants in each layer (VASILEVICH, 1985). Communities with the same dominant species in the main layer and ecological-biomorphologically similar co-dominants or dominants of secondary layers belong to groups of associations.

The above-mentioned principle of classification is known also as an ecological and physiognomical approach. The names of the syntaxa used in this book are constructed according to the below instructions.

The names of associations may be constructed in two ways. The simplest

way is the following: the association is named after the names of the the dominant and the subdominant species of different layers connected by a hyphen (-) (e.g., "*Festuca varia-Carex meinshauseniana*"). While regarding the association which consists of two dominant species in one layer, the names of such species are connected by the sign "+" (e.g., "*Bromopsis variegata + Agrostis planifolia-Trifolium ambiguum*").

As mentioned above, there is also a second way of construction of association names. Concerning the association where the dominant species is accompanied by the subdominant one, the name of the association should be constructed in the following way: the genus name of the dominant taxon is used with the suffix "-*etum*", followed by the genus name of the subdominant with the suffix "-*osum*" or "-*etosum*" (e.g. "*Festucetum caricosum*"). When the association consists of two dominants in the main layer, its name is constructed as follows: "*Brometo-Agrostidetum trifoliosum*".

Names of groups of associations are constructed as follows: the genus name of the dominant taxa of the main layer has the suffix "-*eta*" followed by the genus name of the co-dominant or the dominant taxa of the secondary layer with the suffix "-*osa*" ("*Fageta rhododendrosa*"). In the case of formation the genus name of the dominant is used with the suffix "*eta*". An example is "*Fageta*". If we are dealing with the formation dominated dy two or more taxa, a compound noun is constructed using the same suffix "*eta*" ("*Pineto-Piceeta*", "*Festuceto-Bothriochloëta*").

Syntaxa with names constructed by the suffixes "-*etum*" or "-*eta*" mentioned in the present book, in many cases bear no syntaxonomic meaning.

5. THE VEGETATION OF SEMI-DESERTS[*], STEPPES AND ARID OPEN WOODLANDS

Semi-desert and steppe vegetation, as well as arid light forests, are confined mainly to the intermountain part of East Georgia, namely to the Inner Kartli and the Lower Kartli Lowlands and the Iori plateau.

These parts of Georgia enjoy a dry subtropical climate marked by cold winter and dry hot summer. The climate of Iori plateau is more continental. The

[*]According to some Caucasian botanists, the semi-deserts of Georgia are called "deserts".

mean annual temperature varies in inter-mountain area of East Georgia between 9 and 13° C, the mean monthly temperature in January between 1 and 4° C, in August between 20 and 25° C. Extreme minimum temperature falls to -20-25° C, and extreme maximum temperature amounts to 35-40° C. Annual precipitations range from 350 to 600 mm.

In the area under review, the common soil types are chestnut soils, chernozems and grey-brown soils.

5.1 Vegetation of Semi-Deserts and Steppes

Though typical desert vegetation is not represented in Georgia, it is remarkable that some fragments of it, namely solontchaks, can be found in the eastern part of the country (Lower Kartli Lowland, Tbilisi environs, Inner Kartli, Meskheti). GROSSHEIM (1948) points out that these fragments are predecessors of the semi-desert vegetation. The following species belonging to these communities should be mentioned:

Anabasis aphylla
Salsola ericoides
S. dendroides
S. glauca
Gamanthus pilosus
Suaeda microphylla
Petrosimonia brachiata
Aellenia glauca
Kalidium caspicum

Edificators of this desert vegetation are florogenetically connected with the Turan-Anterior Asian and Eastern Mediterranean floristical centres (SAKHOKIA, 1958).

The presence of ephemers and ephemeroids are characteristic for desert vegetation, including: *Poa bulbosa, Colpodium humile, Bromus japonicus, Eremopyrum orientale, Alyssum desertorum, Helianthemum salicifolium,* etc. The above mentioned plants should not be regarded as xerophytes because their short duration is connected with the vernal and autumnal vegetation period. In general, these plants are mostly of mesic nature.

The above communities are characterized by the presence of species of bryophytes (*Tortula* sp.*, Barbula* sp.), lichens (*Toninia caeruleonigricans, Collema tenax,* etc.) and algae (species of *Nostoc,* etc.).

Fragments of desert communities dominated by *Nitraria schoeberi* occur in Inner Kartli, Kakheti and Meskheti. Some variants of erosional-desert vegetation are to be found in the Iori plateau (Kakheti, East Georgia) (E. SOKHADZE & M. SOKHADZE, 1991). Vegetation is very
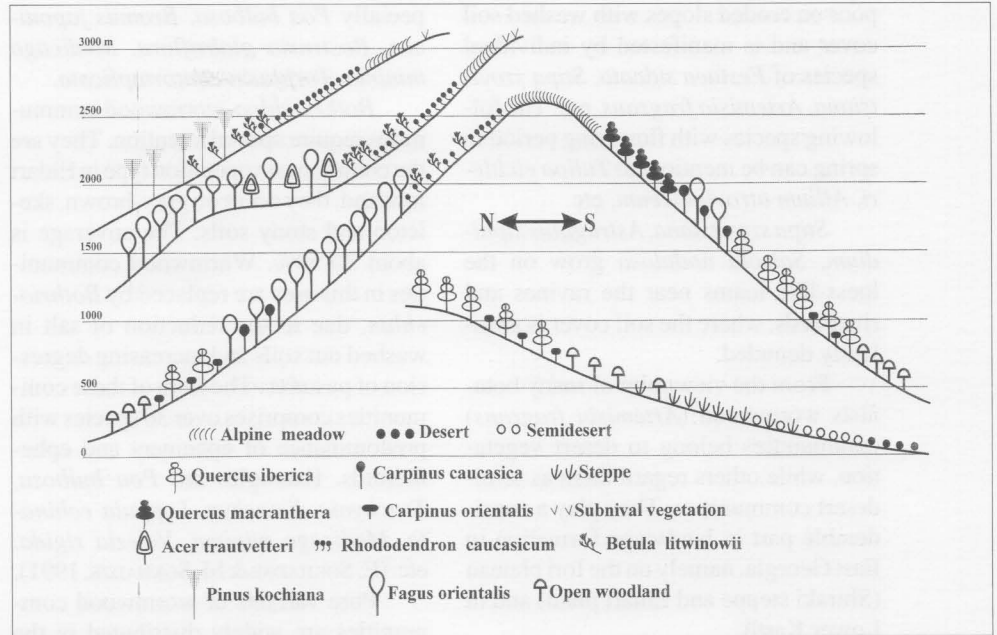

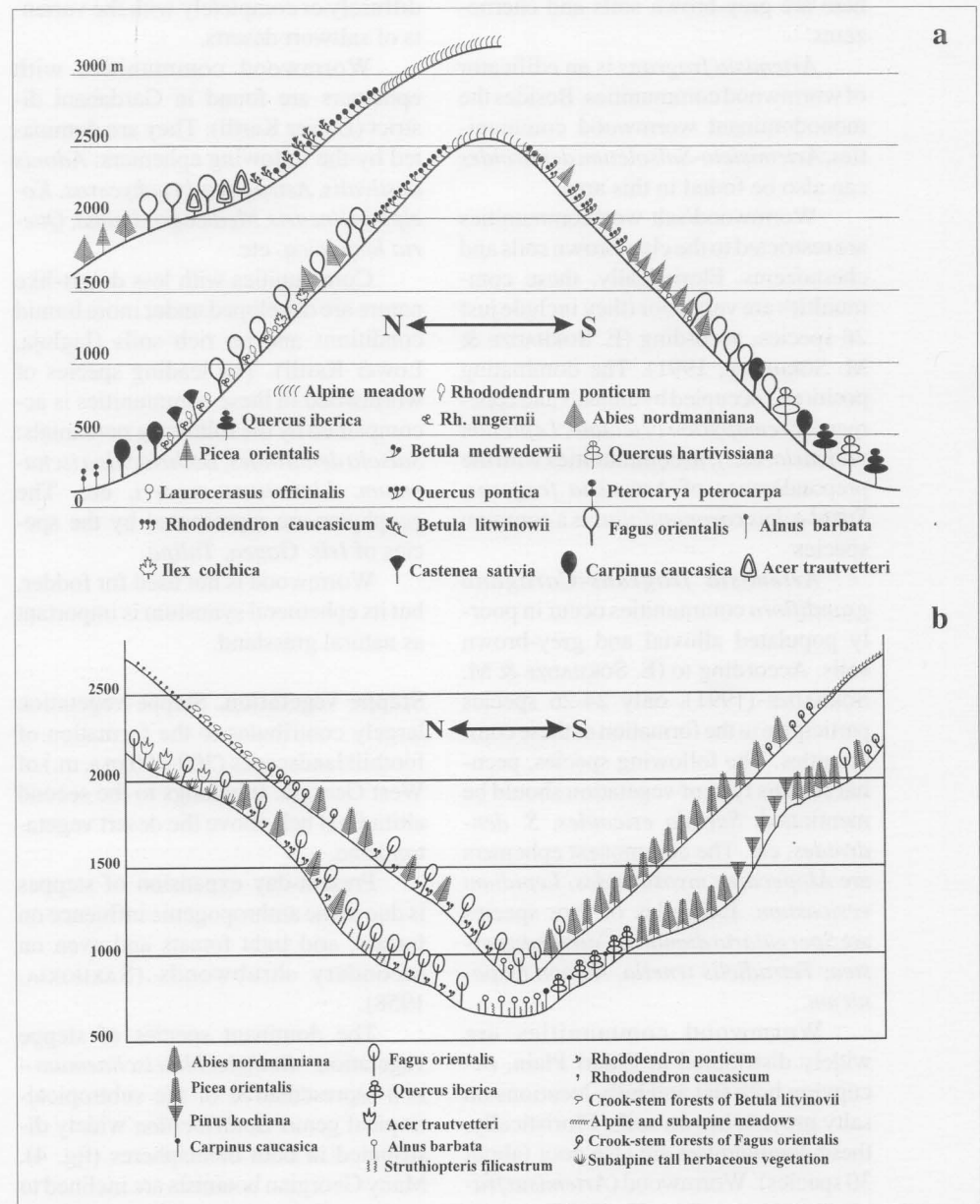Fig. 2 — The regularities of vertical distribution of vegetation in the East Georgia.

Fig. 3 — The regularities of vertical distribution of vegetation in Colchis (a - Ajara, b - Svaneti).

poor on eroded slopes with washed soil cover and is manifested by individual species of *Festuca sulcata, Stipa szovitsiana, Artemisia fragrans,* etc. The following species with flowering period in spring can be mentioned: *Tulipa eichleri, Allium atroviolaceum,* etc.

Stipa szovitsiana, Astragalus xiphidium, Salsola nodulosa grow on the loess-like loams near the ravines and river beds, where the soil cover is absolutely denuded.

From the viewpoint of many botanists wormwood (*Artemisia fragrans*) communities belong to desert vegetation, while others regard them as semidesert communities. They play a considerable part in landscape formation in East Georgia, namely on the Iori plateau (Shiraki steppe and Eldari plain) and in Lower Kartli.

The climate of Iori plateau is dry subtropical, the dominating soil types here are grey-brown soils and chernozems.

Artemisia fragrans is an edificator of wormwood communities. Besides the monodominant wormwood communities, *Artemisieto-Salsoletum dendroides* can also be found in this area.

Wormwood/salt-wort communities are restricted to the clay-brown soils and chernozems. Floristically, these communities are very poor (they include just 26 species, according (E. SOKHADZE & M. SOKHADZE, 1991). The dominating position is occupied by annuals and ephemers (*Eremopyrum orientale, Lepidium vesicaria,* etc.); in communities with the preponderance of *Artemisia fragrans, Stizolophus coronopifolius* is a common species.

Artemisia fragrans-Caragana grandiflora communities occur in poorly populated alluvial and grey-brown soils. According to (E. SOKHADZE & M. SOKHADZE (1991), only 24-26 species participate in the formation of these communities. The following species, peculiar for this type of vegetation should be mentioned: *Salsola ericoides, S. dendroides,* etc. The commonest ephemers are *Alopecurus myosuroides, Lepidium vesicarium.* Examples of rare species are *Spergularia diandra, Calendula persica, Tetradiclis tenella, Aizoon hispanicum.*

Wormwood communities are widely distributed in Eldari Plain, occupying both flat and hilly locations on salty greyish-brown soils. Floristically, these communities are also poor (about 30 species). Wormwood (*Artemisia fragrans*) is characterized by wide ecological amplitude. The coenotypes of these communities are mainly ephemers, es-

pecially *Poa bulbosa, Bromus japonicus, Rostraria glabriflora, Medicago minima, Torularia contortuplicata.*

Bothriochloa-wormwood communities require special attention. They are the commonest vegetation type in Eldari lowland, they occur on grey-brown, skeleton and stony soils. The coverage is about 30-50%. Wormwood communities in this area are replaced by *Bothriochloa,* due to the reduction of salt in washed out soils and increasing degression of pastures. The flora of these communities comprises over 30 species with predominance of ephemers and ephemeroids. Examples are *Poa bulbosa, Trachynia distachya, Lappula echinata, Medicago minima, Velezia rigida,* etc. (E. SOKHADZE & M. SOKHADZE, 1991).

Pure variants of wormwood communities are widely distributed in the Caucasus, namely Georgia, but there also occur intermediate types, mixed diffusely or completely with the variants of saltwort deserts.

Wormwood communities with ephemers are found in Gardabani district (Lower Kartli). They are dominated by the following ephemers: *Adonis aestivalis, Astragalus brachyceras, Koelpinia linearis, Medicago minima, Queria hispanica,* etc.

Communities with less desert-like nature are developed under more humid conditions and on rich soils (Iagluja, Lower Kartli). The leading species of wormwood in these communities is accompanied by the following perennials: *Salsola dendroides, Bothriochloa ischaemum, Limonium meyeri,* etc. The geophytes are represented by the species of *Iris, Gagea, Tulipa.*

Wormwood is not used for fodder, but its ephemeral synusium is important as natural grassland.

Steppe vegetation. Steppe vegetation largely contributes to the formation of foothill landscapes (300-700 m s. m.) of West Georgia. It belongs to the second altitudinal belt above the desert vegetaton zone.

Present-day expansion of steppes is due to the anthropogenic influence on forests, arid light forests and even on secondary shrubwoods (SAKHOKIA, 1958).

The dominant species of steppe vegetation – *Bothriochloa ischaemum* – is a representative of the subtropicaltropical genus *Bothriochloa* widely distributed in both hemispheres (fig. 4). Many Georgian botanists are inclined to attribute *Bothriochloa* to semi-steppes. Typologically, they are very diverse. Among the commonest communities the

following can be mentioned:
Glycyrrhizieto (G. glabra)-Bothriochloëta
Bothriochloëta xeroherbosa
Bothriochloëta ephemerosa
Festuceta-Bothriochloëta
Bothriochloëta pratoherbosa
Stipeto-Bothriochloëta

Bothriochloa communities mainly occur on chestnut soils and are rare on chernozems.

Glycyrrhizieto-Bothriochloëta. These communities are mostly distributed in lowland areas (500-600 m s. m.). The above communities are rather rich floristically, e.g. in an area of 100 m² the average number of species is 65 (E. SOKHADZE & M. SOKHADZE, 1991). Besides the edificator and sub-edificator, the following species should be mentioned: *Koeleria cristata, Phleum phleoides, Medicago caerulea, Bromus japonicus, Trifolium campestre, Vicia angustifolia, Crucianella angustifolia, Arabidopsis thaliana, Androsace elongata.*

Bothriochloa communities with xerophytes are restricted to slopes of eastern and western exposures; they occur mainly on thin chestnut soils (600-700 m s. m.). The following herbs play an essential part in these communities: *Teucrium chamaedrys, Galium verum, Picris strigosa, Scorzonera biebersteinii, Inula britannica, Aster ibericus, Stachys atherocalyx.* Among *Fabaceae* species a mention should be made of *Onobrychis kachetica, O. cyri, Astragalus brachycarpus.* An example of the commonest species is *Festuca sulcata.*

The early vernal vegetation is dominated by the following ephemers and ephemeroids: *Arabidopsis thaliana, Anthemis candidissima, Crocus adamii, Merendera trigyna, Muscari caucasicum, Gagea commutata.* These communities include endemics of Georgia and Caucasus, such as: *Polygala transcaucasica, Aster ibericus, Cephalaria media, Thymus tiflisiensis,* etc. The following species are to be found in *Glycyrrhizieto-Bothriochloëtum varioherbosum:*

Bothriochloa ischaemum
Bromus japonicus
Dactylis glomerata
Festuca sulcata
Koeleria gracilis
Melica transsilvanica
Phleum phleoides
Stipa capillata
Trisetum pratense
Carex bordzilowskii
Glycyrrhiza glabra
Medicago caerulea
Trifolium arvense

Achillea nobilis
T. campestre
Allium pseudoflavum
Vicia angustifolia
Crepis marschallii
V. hirsuta
Bellevalia wilhelmsii
V. tetrasperma
Crucianella angustifolia
Daucus carota
Dianthus inamoenus
Echinops sphaerocephalus
Eryngium campestre
Falcaria vulgaris
Galium verum
Gladiolus italicus
Hieracium pilosella
Linum corymbulosum
Muscari caucasicum
Ornithogalum ponticum
Picris strigosa
Polygala transcaucasica
Potentilla recta
Tragopogon graminifolium
Rumex tuberosa
T. tuberosus
Turritis (Arabis) glabra
Phlomis pungens
Xeranthemum squarrosum
Ph. tuberosa
Ranunculus illyricus

Bothriochloëta ephemerosa. These communities are confined to stony southern slopes of chestnut soils. The following ephemers can be mentioned: *Alyssum campestre, Callipeltis cuccularis, Sideritis montana, Meniocus linifolius, Ziziphora capitata, Trigonella spicata.* Examples of geophytes are *Juno caucasica, Allium atroviolaceum,* etc.

The less xeric variants of *Bothriochloa* communities are *Bothriochloëta pratoherbosa*, which populate depressions and dells with chernozem-like soils. Besides the leading species of *Bothriochloa*, the following plants can be found: *Agropyron cristatum, A. pectinatum, Elytrigia (Agropyron) repens* var. *glaucescens*.

Festuceto-Bothriochloëta. These communities are restricted to the slopes of hills. Associate of *Bothriochloa* is *Festuca sulcata*. Fragments of these communities have remained only in Lower Kartli (Iagluja).

Stipa-Bothriochloa coenoses are also found in the above-mentioned area; they are restricted to the northern mountain slopes, ridges, stony habitats. Most of the soils in these areas are grey-brown, thin, skeleton and saltless.

The leading species of these communities are accompanied by shrubs like *Paliurus spina-christi, Rhamnus pallasii,* etc. Herbs are represented by steppe

Fig. 4 — *Paliureto-Bothriochloëta* in the environs of Tbilisi (*Photo Ketzkhoveli*).

elements. Examples are *Stipa* spp., *Onobrychis* spp., *Phleum phleoides*. The number of ephemeroids is relatively small. The following list of species mentions members of *Bothriochloëta varioherbosa*:
Stipa lessingiana
Bothriochloa ischaemum
S. capillata
Festuca sulcata
S. pulcherrima
Koeleria macrantha
Phleum phleoides
Cleistogenes bulgarica
Medicago coerulea
Astragalus brachycarpus
Inula germanica
Stachys iberica
Galium verum
Thalictrum minus
Leontodon asperrimum
Filipendula vulgaris
Thymus tiflisiensis
Potentilla recta
Picris strigosa
Veronica multifida
Pimpinella aromatica
Bilacunaria caspia
Tragopogon pusillus
Seseli grandivittatum
Campanula hohenackeri
Cephalaria media
Crucianella angustifolia
Xeranthemum squarrosum
Trigonella spicata
Linum corymbulosum
Bromus japonicus
L. nodiflorum

According to SAKHOKIA (1958), *Bothriochloa* communities and their edificators are closely related to savannas florogenetically, rhythmologically and by the character of soding; though it is not the case, when the above communities get compared with the typical *Stipa* steppes. This opinion is confirmed by the fact that *Bothriochloa* communities are combined with arid light forests, which, in the past, had zonal significance in the Caucasus. The same author has proposed the term "savannoid vegetation" for the complex of *Bothriochloa* communities and arid light forests.

Typical steppe vegetation is illustrated by the comunities of *Stipa* (*S. tirsa, S. lessingiana, S. pulcherrima, S. capillata*). Participation of the above communities in landscape formation is insignificant. *Stipa* communities are of secondary origin. They favour the areas which have previously been occupied by mesic mountain forests, shrubwoods and herbaceous vegetation. Very often in the ridges of mountain ranges, *Bothriochloa* steppe becomes replaced by the communities of *Stipa*, including more xeric species, such as *S. pulcherrima, S. lessingiana, S. pontica*, and *S. capillata*. These communities are characterized by the presence of the following xeric species: *Seseli grandivittatum, Teucrium chamaedrys, T. polium, Thymus tiflisiensis, Scorzonera eriosperma, Psephellus carthalinicus,* and *Carex bordzilowskii.*

Stipa tirsa and its communities are confined to thick chernozems with a higher amount of moisture in soil. *S. tirsa* is known as a soding plant. Communities of *S. tirsa* are to be found in Gareji steppe. The associates of the dominant *Stipa* are *Glycyrrhiza glabra, Medicago caerulea, Koeleria cristata*.

Drier habitats are occupied by *Stipa joannis* and *S. lessingiana*. The plant

communities, which the above-mentioned species enter as the leading ones, do not include *Stipa tirsa*. Chernozems and grey-brown soils, mostly calcareous, are typical for this area. Slightly destroyed communities, restricted to the northern slopes, are characterized by the presence of *Dianthus subulosus*, and *Pyrethrum corymbosum*; among other associates is *Bothriochloa ischaemum*. Under the influence of intense animal grazing *Bothriochloa* becomes a co-edificator of the species of *Stipa*, whereas the community gets floristically poorer.

In rocky areas, such as the vicinity of David Gareja Church, the communities are dominated by the species of *Bothriochloa*, *Festuca*, etc., while *Stipa lessingiana* is not found here (E. SOKHADZE & M. SOKHADZE, 1991). Forb steppes (with *Stipa tirsa*) are rather rich in species; besides the representatives of *Stipa*, various forbs participate in the composition of this community.

It should be pointed out, that mountain steppes are peculiar only for South Georgia. Their altitudinal distribution ranges from 1800 to 2500 m s. m. They occur on leached chernozems. Mountain steppes are represented by that of *Festuca-Stipa* and meadow steppes.

Festuceto (*F. sulcata*)-*Stipeta* (*S. capillaris*). These are developed on flat grounds and southern slopes. They are characterized by high presence of *Dactylis glomerata, Stipa tirsa, Phleum phleoides, Trifolium alpestre, Medicago dzhavakhetica*, etc. Geophytes are exemplified by species of *Gagea, Muscari*, etc.

Meadow steppes are situated on the northern slopes. *Stipa tirsa* is an edificator of these communities. Tall dense herbage with a large amount of species is typical for this variant of steppes; a mention should be made of the high presence of dicots (*Betonica macrantha, Aster ibericus*, etc.). Besides, geophytes are well developed here.

Difference of opinion has arisen upon the issue of a possible connexion between the northern plain steppes (South Russia) and those of the Transcaucasian mountains.

GROSSHEIM (1948) indicates that South Russian and Transcaucasian mountain steppes, being separated from each other nowadays, have formed an integral steppe massif in the past. The formation of the above massif was connected to the process of peneplainization of the Caucasus during more or less xerothermic periods. The uplifting of the Greater Caucasus caused separation of the steppe massif from its northern part; it has been preserved under more or less favourable conditions in mountainous areas. Probably, the above mentioned events account for the great floristic and phytocoenotic similarity between the steppes of South Russia and those of the Transcaucasian highlands.

5.2 Arid Open Woodlands

Xeric (arid) open woodlands favour foothills and plains under the dry climatic conditions of East Georgia among steppe and desert vegetation. These communities are provided by the xerophytic woody plants on the background of drought-resistant grass cover (fig. 5).

The arboreal components of open woodlands or "light forests" (a term used by some Caucasian botanists) never make dense stands. In Georgia, these forests are well developed on the territory between the Alazani and the Iori river valleys, near the place Vashlovani, which holds an area of 5000 hectares.

The following types of communities of open woodland can be distinguished: pistache-woodlands, juniper open woodlands, communities dominated by species of *Pyrus* and *Celtis*.

Pistacia mutica communities occur on cinnamon-coloured and chernozem-like soils. These plant communities belong to West-Iranian type. The undergrowth of these open woodlands is represented by the following shrubs: *Paliurus spina-christi, Rhamnus pallasii, Cotinus coggygria, Cerasus incana, Lonicera iberica, Pyrus salicifolia, Amygdalus georgica* (fig. 6), *A. nairica, Colutea orientalis, Caragana grandiflora, Ephedra procera, Juniperus foetidissima, Punica granatum, Rhus coriaria*. The ground layer is made of xerophytic species; it is rather rich in species (*Bothriochloa ischaemum, Festuca sulcata*, species of *Stipa*, etc.). One can distinguish within the pistache-woodland the communities with: *Bothriochloa, Stipa, Stipa-Salsola*.

It is also possible to find pure Pistacia-woodlands and the pistache-woodlands with the admixture of single trees and shrubs (*Ulmus carpinifolia, Celtis caucasica, Pyrus salicifolia*, etc.).

Open woodland-communities of *Pyrus salicifolia, P. georgica*, etc. are formed by the xeric species of pear, which join the sections *Xeropyrenia* and *Argyromalon*.

From the coenoic point of view, the commonest types of the above-mentioned woodlands are the communities with shrubs and steppe elements (KETSKHOVELI, 1960).

Juniperus open woodlands occur on mountainous areas, in the environs of Mtskheta, and on the steep northern slopes of scraped mountain ranges of Vashlovani. In both places, the edificators of forests are *Juniperus foetidissima* (East-Mediterranean species) and *J. polycarpos* (species of Asia Anterior). In Vashlovani they are accompanied by *Pistacia mutica* (fig.7).

Besides the above mentioned species, the Caucasian *J. oblonga* and the East-Mediterranean *J. rufescens* occur here as undergrowth.

It should be noted, that Juniper open woodlands frequently substitute the post-forest vegetation.

Open woodlands occur on grey-cinnamon soils. The climate in the area of their distribution varies between dry subtropical and warm temperate with not very hot summer season. The amount of annual precipitation is 550 mm in Vashlovani. In the environs of Mtskheta, the climate is more warm temperate with hot summer and the amount of precipitation equals to 900 mm p. a. (SAKHOKIA, 1958).

Open woodlands of *Celtis caucasica* hold rather small areas. Usually, solitary plants or groups of plants of *Celtis caucasica* can be found.

Many Caucasian botanists regard open woodlands as savannas and savannoid vegetation. GROSSHEIM is of another opinion. To quote his words: "Savanna is a community of summer-dormant plants, whereas open woodlands are characterized by winter-dormant plants, to say nothing of the diverse floristic basis of these communities" (GROSSHEIM, 1948: 68). Open woodland is an independent vegetational type; its analogue can be encountered in California, in the Cape Region, in Australia. We share the opinion of the Caucasian botanists, that arid open woodlands physiognomically and phytocoenologically are very similar to those of savannas; thus, the term "savannoid vegetation" seems quite reasonable in respect of these communities.

5.3 Hemixerophytic Shrubwoods

Interzonal drought-resistant shrubwoods occur almost in every mountain belt, except in the highlands. In the geobotanical literature, different terms are applied to this type of vegetation, for example, "thorny shrubwoods", "shibliak", etc.

Many authors consider the above communities to be analogues of the Mediterranean shibliak. This affinity confirmed by Rikli - an eminent specialist of the Mediterranean vegetation.

About 25-30 species contribute to the formation of shibliak. Mediterranean shibliak consists of 13 species, including 5 edificators: *Paliurus spinachristi, Berberis vulgaris, Cotinus coggygria, Punica granatum* and *Carpinus orientalis.*

Communities dominated by the Christ's thorn are the commonest ones in the area under review; a mention should be made of *Paliureto-Bothriochloëta, Spiraeeto* (*S. hypericifolia*)-*Paliureta,* as well as hemixerophytic mixed-shrub shibliak with *Paliurus spinachristi, Crataegus orientalis, Lonicera iberica,* etc.

The most xeric variant of shibliak is confined to mother rocks and stony slopes (*Rhamnus pallasii, Caragana grandiflora, Atraphaxis spinosa, Ephedra procera*).

Within this certain area, the following types of shibliak are distinguished: 1) primary shibliak, restricted to slopes and steppe dell belts, as well as to beams, ancient detrital cones and naked rock outcrops; 2) the remnants of open woodland dominated by *Pyrus* and *Pistacia*; 3) secondary shibliak, the origin of which is connected with the destruction of forests (SAKHOKIA, 1958).

In East Georgia, phrygana, the second type of hemixerophytic Mediterranean vegetation, is distributed. In order to outline the difference between the Caucasian phrygana and the true Mediterranean one, many botanists define it by the term "phryganoid vegetation" (fig. 8). In the classical sense, phrygana is regarded as a community dominated by dwarf xeromorphic shrubs and subshrubs with an admixture of therophytes and geophytes. In the Caucasus and particularly in Georgia, it is often found among the xeric mountain vegetation.

Among its coenological formations, the following should be noted:
1) Tragacanthic communities, dominated by thorny *Astragalus* species (*Astragalus caucasicus, A. microcephalus,* etc.) and species of *Acantholimon* (*A. lepturoides,* etc.);
2) tomillares, low shrub and semi-shrub formations with the dominance of *Thymus tiflisiensis* (and other species of *Thymus*), *Salvia garedzhii,* etc.

6. FOREST VEGETATION OF GEORGIA

Forest is the prevailing type of vegetation in Georgia. The forest area makes up 36.7% of the country's total land area.
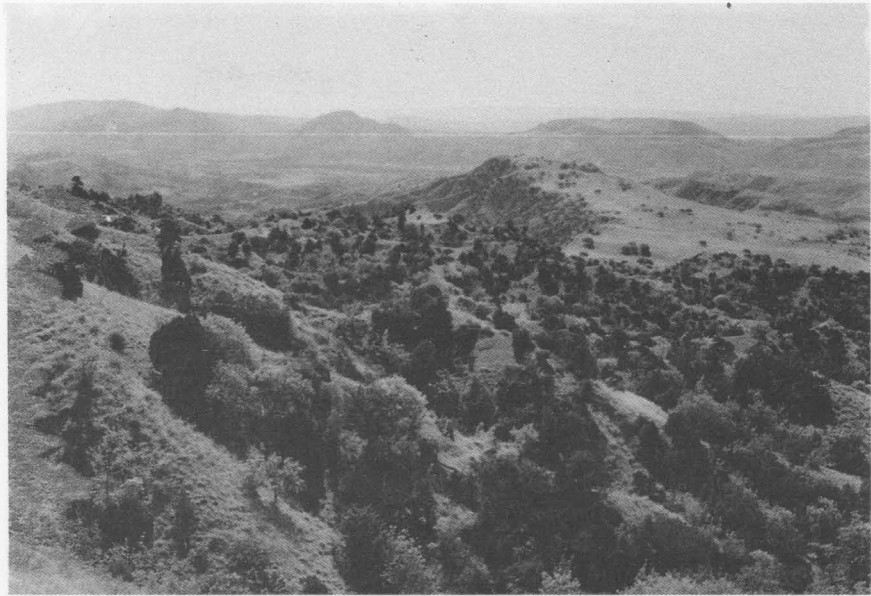
During the Holocene, when the cli-

Fig. 5 — Open woodlands in Vashlovani reservation (East Georgia).

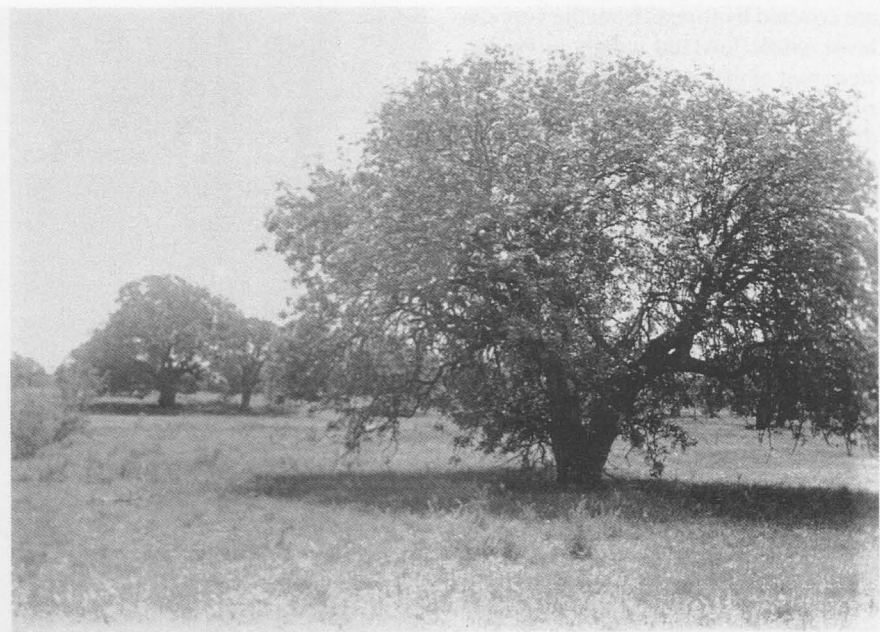Fig. 6 — Thickets of *Amygdalus georgica* (Kakheti, East Georgia) (*Photo Ketskhoveli*).

Fig. 7 — *Pistacia mutica* in Vashlovani reservation (East Georgia).

Fig. 8 — Phriganoid vegetation (Photo M. Sakhokia).

matic conditions were similar to those of nowadays, the entire territory of Georgia was occupied by forests. Very surprisingly, today beech (*Fagus orientalis*) occupies a dominating position, namely 51% of the total forest area. The following species are further dominants of Georgian forests: *Abies nordmanniana* (10% of the forest-coverage). *Quercus iberica* and other representatives of *Quercus* (3.3%), *Picea orientalis* (6.3%), *Pinus kochiana* (3.6%), *Alnus barbata* (3%), *Castanea sativa* (2.1%), *Betula litwinowi* and other *Betula* species (ca. 2%). Negligible areas are covered by *Carpinus caucasica, Tilia begoniifolia, Acer platanoides, A. trautvetteri, Fraxinus excelsior,* etc. (DOLUKHANOV, 1989).

As it was pointed out, the plains and mountain slopes in West Georgia are covered by forests from the very sea level, while lowland woods in the eastern part of the country are peculiar for riversides. At the same time, the plateau of Javakheti Upland (South Georgia) is absolutely devoid of forests.

6.1 Lowland Hardwood Forests

In the Caucasus, including Georgia, the lowland forests are spread on swamps, flood plains and in the lowlands, where local irrigatione conditions or groundwaters stimulate the development of forest vegetation (GROSSHEIM, 1948).

Swamp forests occupy the Colchic Lowland with its mainly damp and poorly drained soils. The leading species of this community is *Alnus barbata*. The above forests are floristically rather rich about 160 species can be found. The number of exclusive species is negligible; among them *Matteuccia struthiop-*

teris. Alnus forests with *Buxus colchica* are rather rare; near the upper range of distribution, *Alnus* forest with tall herbs (*Telekia speciosa, Heracleum ponticum*) is developed. Due to the extreme swampy conditions, alder becomes dwarfed and provides large hillocks, on which the following plants are developed: *Smilax excelsa* (climbing on alder), *Iris pseudacorus, Leucojum aestivum, Oenanthe abchasica,* etc. (KOLAKOWSKY, 1961).

Riparian or flood forests are to be met on river banks in both woody and woodless regions. In riparian forests of East Georgia, as well as in Colchis, *Pterocarya pterocarpa* is a typical species. Besides, these communities are characterized by presence of *Quercus pedunculiflora* (= *Qu. longipes*), *Po-*

pulus alba, Elaeagnus angustifolia, Tamarix ramosissima, T. hohenackeri, Hippophaë rhamnoides, etc.

Among the lianas climbing on these trees are the following: *Vitis sylvestris, Periploca graeca, Cynanchum acutum, Solanum persicum,* etc.

Lowland forests are characteristic of Kakheti, the East Georgia district, where the annual precipitation amounts to 900 mm p. a. These forests are dominated by *Quercus pedunculiflora* with the admixture of *Acer velutinum, Tilia caucasica, Fraxinus excelsior, Pyrus caucasica.* Frequently occurring as underwood in these communities are: *Crataegus pentagyna, Mespilus germanica,* etc. The following lianas are also present here: *Hedera pastuchowii, H. helix, Vitis sylvestris, Clematis vitalba, Smilax excelsa.* According to Grossheim, these forests reflect the vegetation of the Hyrcanian territory which is the refuge area of Tertiary flora in the Caucasus.

6.2 Lowland Coniferous Forests

These communities are demonstrated by *Pinus pityusa* forests (fig. 9).

The area of distribution of *Pinus pityusa* occupies almost the whole eastern coast of the Black Sea from Mussera (southwards from Bichvinta/Pitsunda cape) to Anapa (Ukraine). This relic species is closely related to the Mediterranean *P. halepensis*, to the Crimean *P. stankevichi* and to the east-Transcaucasian *P. eldarica*. In Bichvinta it forms high-trunk pine forests, where almost all the trees are of the same age; this community holds an area of 200 hectares and is considered to be of secondary origin,

Fig. 9 — Pinus pityusa in Abkhazeti (West Georgia) (Photo Dolukhanov).

due to the elevation of the sea coast and the exposure of sandy-pebble deposites of Bichvinta cape. Undergrowth of this forest is illustrated by *Cistus creticus, Ruscus ponticus, Rhododendron luteum* and *Mespilus germanica*. The following types of these communities are to be distinguished: *Pinus pityusa* forest with *Carpinus orientalis*, mixed pine-broad-leaved forest, Pitsunda pine forests of coastal area, etc. (TUMAJANOV, 1980).

A mention should be made of *Pinus eldarica*, which is confined to the Eilar-Ougi mountain range near the Georgian/Azerbaijan frontier (fig. 10).

The distribution range of Eldari pine includes the Mtkvari-Araxian desert and mountain-steppe province of the Afro-Asian desert region. The floristic complex of Eldari pine communities is greatly influenced by paleogeographical peculiarities of the present-day distribution area of *Pinus eldarica*. The associates of Eldari pine are the plants of arid open woodlands.

6.3 Mountain Forests

In the mountains of Georgia, within the forest belt, three sub-zones can be outlined: low mountain, mid-mountain and high-mountain (from 500 to 1900 m s. m.). Polydominance is one of the most striking features of mountain forests (except beech woods). Timberline today varies in altitude between 2200 and 2750 m, but almost everywhere it has been lowered by man. In the western part of the Greater Caucasus the upper limit of woody vegetation is decreased to 350-400 m, whereas in central and eastern parts – to 500-600 m (fig. 11). The same situation is in the Minor Caucasus. Due to the impact of anthropogenic factors, the forest vegetation of the Kazbegi region (eastern part of the Central Caucasus) has almost completely been destroyed.

Below, we try to characterize the main formations of forest vegetation of Georgia.

6.3.1 Beech Woods

Beech woods of the Caucasus and particularly Georgia, are dominated by the ancient east Mediterranean species of the Oriental beech *Fagus orientalis*. Its distribution range comprises Mountainous Crimea, the Greater and Minor Caucasus, Pontian Mountains and the Caspian sector of Iran.

The lower limit of beech forests ranges from sea level (Colchis) to 1000 m s. m., sometimes rising to 1200-1300 m (under the most arid conditions). The

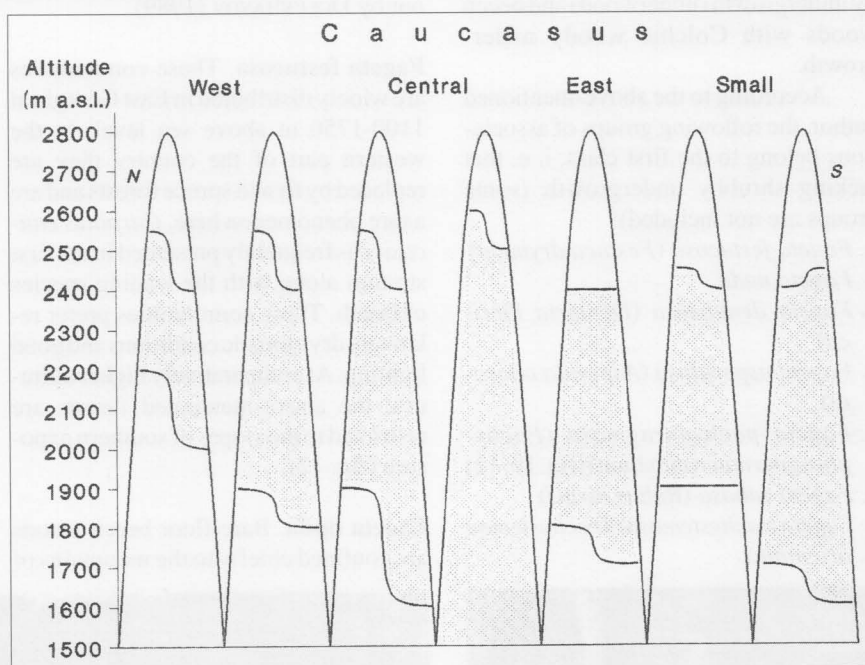Fig. 10 — *Pinus eldarica* (Eilar-Ougi, Azerbaijan) (*Photo Nakhutsrishvili*).

Fig. 11 — The upper limits of forests in several parts of the Caucasus (potential boundary above the dotted line, the present day boundary - lower the dotted line).

upper limit varies in altitude between 1400 m and 2000-2200 m, and this is the most constant boundary of their altitudinal distribution, which usually depends on the humidity of climate. This accounts for the fluctuations of the upper limit of beech woods in different districts of Georgia. For instance, in moist Colchis, the scope of distribution varies from sea level to 2200-2380 m, whereas in the eastern part of the country (Alazani basin) the lower limit of beech forests comes to approximately 350-400 m. In Trialeti mountains (southern Georgia) beech woods appear at an altitude of 800-900 m above sea level.

According to DOLUKHANOV (1989), the upper limit of the vertical distribution of beech depends on temperature regime and the amount of winter precipitation, protecting young beech trees from frosts, while the lower boundary depends on air humidity. Beech is the most shade-enduring plant among the deciduous woody species of Georgia.

One of the most characteristic species of the beech woods is *Carpinus caucasica*. Under the continental climatic conditions, beech forests are replaced by hornbeam forest communities. In Colchis, *Castanea sativa* is a common associate of beech woods. Among the other species accompanying *Fagus orientalis* are: *Quercus iberica, Qu. macranthera, Fraxinus excelsior, Ulmus elliptica, Acer platanoides, A. laetum, Tilia caucasica, T. cordata, Sorbus caucasigena*, etc. Examples of species present

exclusively in Colchic beech forests are *Vaccinium arctostaphylos, Viburnum orientale, Trachystemon orientale.* All these species are the local endemics of Colchis. Although in the majority of cases the dominant position in forests is occupied by beech, it frequently is a constituent of the formation of beech-fir, beech-chestnut and beech-spruce forest communities.

In the mountains populated by coniferous forests (1200-2000 m), beech woods have partially been extinct. Pure beech forests are not replaced by coniferous woods.

Beech woods occur on brown forest acid soils (dry and fresh forest types) and brown forest pseudopodzols (moist types of forest). DOLUKHANOV (1989) differentiates two classes of associations in the beech woods of Georgia: beech woods without a developed woody undergrowth (underwood) and beech woods with Colchic woody undergrowth.

According to the above-mentioned author, the following groups of associations belong to the first class, i. e. that lacking shrubby undergrowth (some groups are not included):
1. *Fageta festucosa (Festuca drymeja)*
2. *Fageta nuda*
3. *Fageta dentariosa (Dentaria iberica)*
4. *Fageta asperulosa (Asperula odorata)*
5. *Fageta pachyphragmosa (Pachyphragma macrophyllum)* (fig. 10, 11)
6. *Fageta rubosa (Rubus hirtus)*
7. *Fageta trachystemosa (Trachystemon orientale)*
8. *Fageta filicosa (Dryopteris filix-mas, D. pseudomas,* etc.)
9. *Fageta luzulosa (Luzula sylvatica)*

Among beech woods with Colchic woody undergrowth the following may be mentioned:
1. *Fageta rhododendrosa (Rhododendron ponticum, Rh. ungernii)*
2. *Fageta laurocerasosa (Laurocerasus officinalis)*
3. *Fageta ilicitosa (Ilex colchica)*
4. *Fageta ruscosa (Ruscus colchicus)*
5. *Fageta magnovacciniosa (Vaccinium arctostaphylos)*
6. *Fageta azaleoza (Rhododendron luteum)*
7. *Fageta viburnosa (Viburnum orientale)*

Below, we have attempted to give a brief description of some association groups of beech woods which is based on the results of investigations carried out by DOLUKHANOV (1989).

Fageta festucosa. These communities are widely distributed in East Georgia at 1100-1750 m above sea level. In the western part of the country they are replaced by fir and spruce forests and are a rare phenomenon here. *Carpinus caucasica* is frequently presented in the first stratum along with the leading species of beech. These communities prefer relatively dry climatic conditions and good lighting. At comparatively higher altitudes, the above-mentioned forests are restricted to the slopes of southern exposure (fig. 12).

Fageta nuda. Bare-floor beech woods are confined chiefly to the mountains of the Greater Caucasus. They are poorly represented in Colchis. Bare-floor beech woods lack shrubby undergrowth, but at the same time not a single herb is present in the undergrowth. These forests are distributed at an altitude varying from 500-600 to 1200 m, only rarely at 1400 m s. m. The fact that Transcaucasian bare-floor beech forests are distributed mostly in Georgia is of particular interest. They are restricted to the slopes of northern exposure. Bare-floor beech forest in Georgia occur on the soils characterized by poorly developed horizon of humus and belong to the subtype of brown forest pseudopodzolic soils with a strongly pronounced process of pseudopodzoliation (DOLUKHANOV & URUSHADZE, 1968). The Colchic variant of *Fageta nuda* reminds that of East Georgia (fig. 13). The main difference is in the presence of *Vaccinium arctostaphylos, Rhododendron luteum, Ilex colchica,* and *Laurocerasus officinalis* in the clearings of beech forests (although these species can rarely be found).

The origin of bare-floor beech forests is still under question.

Fageta asperulosa is a corresponding association to the west European beech woods with the same species (*Asperula odorata = Galium odoratum*) in the herbaceous undergrowth. But these Caucasian and European beech forest communities vary by their floristic composition and their process of succession; based on this difference, DOLUKHANOV is inclined to regard the Caucasian communities as a separate group *Fageta asperulosa caucasica*. The woody undergrowth

Fig. 12 — Fageta festucosa in Lagodekhi reservation (East Georgia) (*Photo Dolukhanov*).

Fig. 13 — Fageta nuda in Lagodekhi reservation (East Georgia).

is missing here except for a small amount of *Ilex colchica*.

Beech forests with *Galium* (*Asperula*) *odoratum* are to be found in comparatively moist habitats, on well-drained brown forest soils. They are situated on the slopes of medium steepness of the northern exposure; their altitudinal distribution ranges from 1100 to 1550 m.

Fageta pachyphragmosa. These communities require moist temperate conditions. The regeneration is rather high in these beech woods. The subdominant *Pachyphragma macrophyllum* belongs to an ancient, local endemic monotypic genus of Colchic stock. These beech woods are characterized by the admixture of such arboreal species as *Acer velutinum, A. pseudoplatanus, Tilia begoniifolia, Fraxinus excelsior,* sometimes *Abies nordmanniana. Ulmus glabra* (*U. elliptica*) was an associate of beech until the second half of 20th century. The woody undergrowth consists of *Sambucus nigra* and *Corylus avellana*, although the latter is often absent. The herbaceous field layer is well developed.

Typical forests of this group are met at the altitudes from 500 m to 1000-1100 m.

Fageta pachyphragmosa are well represented in Lagodekhi Reservation (East Georgia), where it is protected from destruction. The upper limit of such communities reaches 1820 m in the mountains of Upper Svaneti (Dolukhanov, 1989).

Fageta rubosa. These forests are confined to the middle parts of the forest belt; they are commonest among the moist beech woods of Georgia. These forests are characterized by a relatively high regeneration and dominance of *Rubus hirtus* (sect. *Glandulosi*) in the undergrowth. In Georgia, the area of distribution of *Fageta rubosa* comprises the southern slopes of the Greater Caucasus mountain system. The above communities are less characteristic of the Minor Caucasus. Typical *Fageta rubosa* are met on northern slopes at 1100-1600 m.

Fageta trachystemosa are characteristic for West Georgia. *Trachystemon orientale* is a relic species of Colchic stock. Under the moist climatic conditions it reveals a high synecological amplitude from the sea level up to the alpine zone (700-1200 m). In these forests, *Corylus* and *Sambucus nigra* are solitary, and the semi-prostrate *Viburnum orientale*, as well as other Colchic plants are to be found.

Fageta filicosa. These communities develop under moist conditions. One can find a stratum of large ferns, manifested by *Dryopteris filix-max, Athyrium filix-femina, Matteuccia struthiopteris,* etc., in this type of forest. It must be stated that natural regeneration is suppressed in the above-mentioned communities. Beech woods with ferns are widely distributed in West Georgia, whereas in the east of the country under relatively dry conditions, these forests are restricted to the upper parts of the forest belt. The floristic diversity is the most striking feature of beech forests with ferns (fig. 14, 15a, 15b).

Fageta luzulosa are typical only for upper parts of the forest belt of Svaneti (western part of the Greater Caucasus). Woody undergrowth consists of *Vaccinium arctostaphylos* with rather abundant *Laurocerasus officinalis, Rhododendron luteum, Viburnum orientale*. Herbaceous vegetation is sufficiently developed. Beech forests with Colchic undergrowth are of considerable interest because of to the absence of their analogues within the territory of West Eurasia. The Colchic undergrowth is rather dense and is constituted of semi-prostrate evergreen and partially deciduous shrubs. Floristic composition of the above undergrowth is related florogenetically to the relic complex of semi-prostrate plants, which represent subalpine crook-stem forests of Colchis. These plants require wet climatic conditions and equal distribution of precipitation during the year.

Fageta rhododendrosa unites two different associations of beech woods with *Rhododendron ponticum* and those with *Rh. ungernii.*

The first association is one of the commonests in Colchis. It can be found almost everywhere in West Georgia, while in the eastern part of the country it is quite rare. Under the moist climatic conditions (in districts with the annual precipitation over 1400-2000 mm) it is distributed from the sea level to 1950 and even to 2100-2200 m. The most favourable conditions are provided at the altitude of 1000 to 1300-1500 m above sea level.

Beech forests with *Rhododendron ungernii* (*Rh. ungernii* is a relic local endemic of Colchis) are typical for districts with a very high amount of precipitation (3000 mm p.a.). They are to be found at an altitude of 1200-2000 m. Under very moist climatic conditions they descend to 800, sometimes to 600 m s. m.
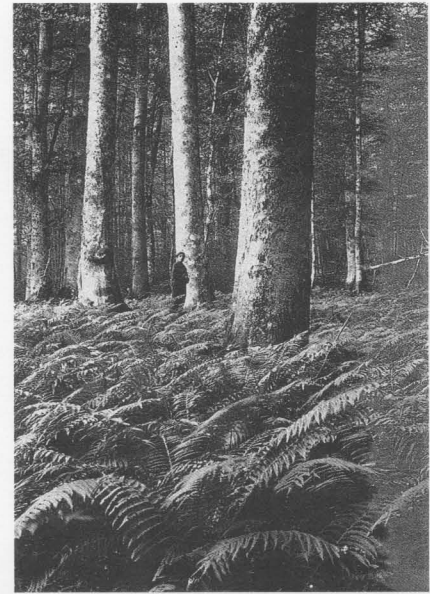

Fig. 14 — Fageta struthiopteridosa.

Fig. 15 — Mixed-brood-leaved forest in Lagodekhi reservation: A - with *Dryopteris pseudo mas*, B - with *Hedera pastuchowii* (*Photo Dolukhanov*).

Fageta laurocerasosa. These communities extend from the sea level up to 2250 m. Typical beech woods with *Laurocerasus* are distributed from 700 to 2000 m. Their vertical distribution depends on the humidity of climate. *Laurocerasus officinalis, Rhododendron ungernii*, require winter precipitation to protect them from frost. Unlike *Fageta rhododendrosa*, beech forests with *Laurocerasus* are well developed on limestones, and under the moist climatic conditions they are situated on the southern slopes with abundant sunlight. These communities occupy also some gorges of East Georgia.

Fageta ilicitosa. These communities extend from 500 up to approximately 2000 m, but they are most common from 1000 up to 1800 m. They occupy a larger distribution range than beech woods with *Rhododendron* and they almost coincide with that of *Fageta laurocerasosa*. Beech woods with *Ilex* are typical for Colchis, though in some localities they penetrate into East Georgia. It must be noted, that *Ilex colchica* is more shade-enduring, than *Ilex aquifolium*.

Fageta magnovacciniosa comprises the most common associations of West Georgia. In East Georgia these communities are rare. In the west, they are very common from 900 up to 2150 m above sea level. They never grow below 500 m. *Vaccinium arctostaphylos* is a relic endemic species of Colchis closely allied to the plants distributed nowadays in Japan and Maccaronesia (Madeira Island). That species is rather shade-enduring and is connected with beech woods.

Typical beech-woods with *Vaccinium arctostaphylos* can be found in the areas where precipitation amount does not exceed 1400-1500 mm p.a.

Fageta azaleosa associations prefer both moist and relatively dry climate. On the mountains of West Georgia they extend from 800 up to 1500 m above sea level, in the areas with precipitation amount of 1200-2000 mm p.a. Beech-woods with *Rhododendron luteum* of the upper part of forest belts extend to 1900 m. These beech-woods in East Georgia are situated on prominent mountain slopes from 1000 to 1700 m above sea level (Aragvi river basin, Upper Alazani and Iori rivers).

Fageta viburnosa associations are characterized by a narrow synecological distribution range. *Viburnum orientale* is a local endemic of Colchis; mainly, it forms undergrowth in beech-woods, but it can also be found in fir forests. Beech-woods with *Viburnum orientale* occupy moist ecotopes of Colchis, though they can also be met in East Georgia (Aragvi river basin and Upper Alazani). The above mentioned communities extend on the northern slopes of 900-1900 m above sea level. Typical beech-woods with *Viburnum orientale* are developed in a middle forest belt of West Georgia (1100-1600 m). These communities are peculiar for the presence of blackberry (*Rubus hirtus* group), as well as of *Hedera colchica, Trachystemon orientale* and *Dentaria bulbifera*. In the upper forest belt (above 1700 m) beech-woods with *Viburnum orientale* are spread only in West Georgia.

6.3.2 Dark Coniferous Forests

In Georgia, 5-6% of the entire forest area is occupied by coniferous forests (forests dominated by spruce) (5,6%) and fir (10%). Excluding beech-woods, dark coniferous forests are most abundantly developed in Georgia.

Fir forests are dominated by the Caucasian fir, *Abies nordmanniana*, whereas the Caucasian spruce, *Picea orientalis,* is a leading species in spruce forests. Caucasian fir (belonging to sect. *Abies*) is closely allied to *Abies bornmuelleriana*, which inhabits northern Anatolia. *Picea orientalis* belongs to sect. *Omorika*; as a typical species of this section, *P. omorika* occurs on rocky limestones of South-West Serbia.

In these forests, the dominant species of fir and spruce are associated with oriental beech. *Pinus kochiana* is more frequent in spruce forests than in fir communities (fig. 16).

Dark coniferous forests are widely distributed in Western Georgia and in the western part of East Georgia. These forests never form a continuous belt, though their development is connected with the definite altitudinal-climatic zone, which extends from 1000 m up to 2000 m s. m. Dark coniferous forests represent the commonest type of vegetation between 1400 and 1900 m.

Dark coniferous forests of Georgia and of the Caucasus, in general, are quite different from those of the taiga. Some typical representatives of taiga vegetation, such as larch, boreal species of spruce and fir, though unavailable in the Caucasus, can be found in West Europe (DOLUKHANOV, 1989).

The distribution area of oriental beech covers that of *Picea orientalis* (fig. 17, 18) and *Abies nordmanniana*, while the distribution area of Caucasian fir coincides with that of the Cuacasian spruce. However, due to the factor of moisture necessary for *Abies nordmanniana*, fir is missing in the most continental parts of its area. In East Georgia spruce penetrates into the area of upper parts of the river Didi Liakhvi and of the Aragvi gorge (in the Greater Caucasus). *Picea orientalis* occupies northern slopes of the Minor Caucasus up to Tedzami basin; it is also scattered around the districts of Tbilisi (upper reaches of r. Vera). In dark coniferous forests of East Georgia the role of spruce is reduced.

Abies/Picea forests occur on crystalline schists and rocky soils.

In fir dominated forests, *Fagus orientalis* is a common species.

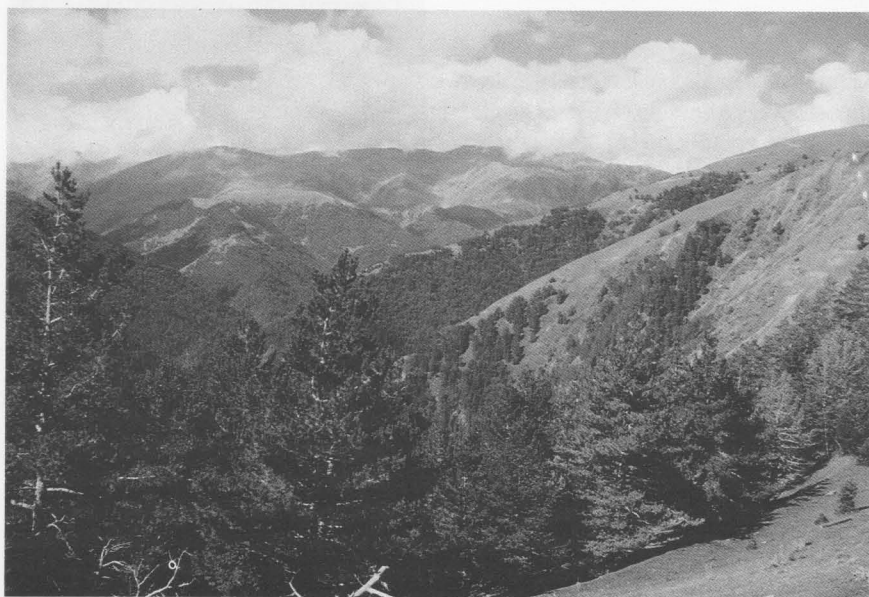Although dark coniferous forests are very rich in endemic and relic spe-

Fig. 16 — Pinus kochiana forest in the high mountains of Tusheti (East Georgia) (*Photo Shanshiashvili*).

cies, no exclusive species is to be found here.

Reduction of temperature during some of the Pleistocene periods promoted maximal development and wide distribution of dark coniferous forests. According to DOLUKHANOV (1949), their further decline is due to fir and dark beetles. From the view point of KO-LAKOWSKY (1961), this phenomenon is due to the natural process of substitution of dark coniferous forests in Colchis by broad-leaved ones, namely beech woods, caused by the changes of climate during the Quaternary.

Floristic composition of fir and beech forests seems identical; boreal elements are more abundant in spruce forests.

DOLUKHANOV specifies two classes of associations of these forests on the basis of their undergrowth. The first class of dark coniferous forests is devoid of any developed woody undergrowth and includes the following groups of associations:

1) *Piceeta orientalis maculato-muscosa*
2) *Abieteta festucosa, Fageto-Abieteta festucosa, Piceeta-Abieteta festucosa, Piceeta festucosa*
3) *Piceeta sicca*
4) *Abieteta luzulosa*
5) *Piceeta nanoherbosa, Piceeta-Abieteta nanoherbosa, Abieteta nanoherbosa, Fageto-Abieteta trachystemosa*
6) *Fageto-Abieteta filicosa*
7) *Abieteta subalpina calamagrostidosa*
8) *Abieteta subalpina heteroherbosa*
9) *Abieteta rariherbosa*

Dark coniferous forests with Colchic undergrowth belong to the second class and include the following groups of associations:

1) *Piceeta rhododendrosa, Piceeta-Abieteta rhododendrosa, Abieteta rhododendrosa, Fageto-Abieteta rhododendrosa*
2) *Piceeta laurocerasosa, Piceeta-Abieteta laurocerasosa, Abieteta laurocerasosa, Fageto-Abieteta laurocerasosa*
3) *Piceeta ilicitosa, Piceeta-Abieteta ilicitosa, Abieteta ilicitosa, Fageto-Abieteta ilicitosa*
4) *Piceeta-Abieteta magnovacciniosa, Abieteta magnovacciniosa, Fageto-Abieteta magnovacciniosa*
5) *Abieteta viburnosa, Fageto-Abieteta viburnosa*

Piceeta orientalis maculato-muscosa. Associations of this group are characteristic for spruce and pine forests. They extend from 1100 to 2100 m s. m. The

Fig. 17 — *Picea orientalis* in Svaneti (West Georgia) (*Photo Dolukhanov*).

Fig. 18 — Derivatives of fir forests and groves of *Rhododendron luteum* in Lechkhumi (West Georgia) (*Photo Dolukhanov*).

characteristic and constant species is *Goodyera repens*. Within well developed bryophytes in these forests the following may be mentioned: *Hylocomium splendens, Pleurozium schreberi*, etc. The appearence of these forests as well as the floristic composition of bryophytes is very similar to those of Eurasia boreal zone. Mossy spruce forests are well represented in the western part of East Georgia and in Colchis.

Dark coniferous forests with *Festuca*. The predominance of *Festuca drymeja* in the herbaceous undergrowth is characteristic for fir, fir-spruce and beech-fir forests. The altitudinal distribution of these forests ranges from 900 to 2100 m. The above-mentioned communities are characterized by the presence of following species: *Dryopteris filix-mas, Oxalis acetosella, Sanicula europaea, Viola reichenbachiana*.

Piceeta sicca. These communities are spread only in East Georgia at 1000-1500 m. They occur on poor skeletal soils of steep and sunny slopes. *Picea orientalis* is associated here with pine and Georgian oak (*Quercus iberica*). The ground layer is rather poor in species (*Poa nemoralis, Brachypodium sylvaticum, Oxalis acetosella*, etc.).

Abieteta luzulosa (*Luzula sylvatica*). These forests are restricted to the mountains of Svaneti (West Georgia). They extend from 1600 to 2150 m. These communities populate almost all the slopes, though northern slopes are still more favourable for them. There is no woody undergrowth in these forests, although the ground layer is well developed.

Dark coniferous forests with dwarf herbs. These associations prefer moist climatic conditions; they extend from 1300 up to 2000 m nearly in all massifs of dark coniferous forests. The main components of these communities are dwarf herbs; grasses are rather poor in species. In East Georgia these communities are exemplified by spruce forests, in the west of the country, however, by fir, fir-spruce and beech-fir forests. Among the species characteristic for fir and spruce communities the following may be mentioned: *Oxalis acetosella, Sanicula europaea*, and *Galium rotundifolium*. Frequently occurring as underwood in spruce forests of West Georgia are *Vaccinium arctostaphylos* and *Daphne pontica*.

Piceeta trachystemosa. These communities occur chiefly in the mountains of

northern Colchis (900-1900 m s. m.) under slightly moist conditions. *Fagus orientalis* is a common associate of spruce in these forests; sometimes spruce is even replaced by beech. Underwood consists of scattered *Vaccinium arctostaphylos, Viburnum orientale, Ilex colchica*, and *Rhododendron ponticum*. The ground layer is characterized by the prevailance of *Trachystemon orientale*.

Fageto-Abieteta filicicosa. These communities occupy almost all massifs of fir forests of West Georgia. They belong to the middle and upper parts of dark coniferous forest zone and are characterized by the presence of large ferns: *Athyrium filix-femina, Dryopteris filix-mas, D. oreades, Oreopteris limbosperma, Matteuccia struthiopteris*, etc. Natural regeneration is not satisfactory (fig. 19).

Dark coniferous forests with Colchic undergrowth are not as widely distributed as those of beech. As it was pointed out above, they occupy the mountains of West Georgia.

A special attention should be paid to the series of dark coniferous forests with *Rhododendron ponticum*; spruce, fir and beech are arboreal components of these communities. *Rhododendron ponticum* is more abundant in beech-spruce forests. Such forests can be rarely met in East Georgia. Dark coniferous forests above 1900 m can be found only in the mountains with moist climate (DOLUKHANOV, 1989).

Natural regeneration is suppressed here. Dark coniferous forests with *Laurocerasus* are peculiar for the upper part of the dark coniferous forest belt. They are developed under moist climatic conditions, but, contrary to those with *Rhododendron ponticum*, they are restricted to the slopes of southern exposure; they also occur on limestones. Fir forests with *Laurocerasus* represent a very rare type of vegetation in East Georgia.

Laurocerasus officinalis is less shade-resistant than *Rhododendron ponticum*. That is why it is not typical for dense fir forests. In the underwood of dark coniferous forests, *Ilex colchica* can be frequently observed with *Laurocerasus*; in many cases the above-mentioned species occupies a dominant position and forms series of associations. Among these associations, restricted to the middle part of the forest zone (1200-1700 m), special attention is paid to *Picea* forests with *Ilex* and with *Fagus-Ilex. Vaccinium arctostaphylos* and *Ruscus colchicus* are rather rare in Georgia. *V. arctostaphylos* is very common in the second stratum of beech-fir forests from 1200 to 1900 m. The ground

vegetation is composed of *Festuca drymeja, Asperula (Galium) odorata, Oxalis acetosella, Dentaria bulbifera*, etc.

Associations of spruce-fir forests with *Vaccinium arctostaphylos* occur only in Svaneti. The less common group of associations is *Piceeta viburnosa*. These communities are confined to several parts of Svaneti and extreme western parts of Trialeti Mts. (fig. 20).

6.4 Mixed Broad-Leaved Forests of Colchis

These forest communities belong to the Euxinian broad-leaved forests; they are restricted to Colchis. Stands of these forests can be observed on the eastern slopes of the Ajara-Imeretian mountain range, in the north-western part of the Greater Caucasus, etc. Mixed forests of Colchis are extended from approximately 200 m up to 1000-2000 m, though in South Colchis they almost approach the sea level. These forests occur on podzolized zheltozems, as well as on mountain forest brown soils and krasnozems.

These forest communities are developed under moist climatic conditions with precipitation amount of 2500 mm p. a.

Mixed broad-leaved forests are very rich floristically; a considerable number of relic mesophytic species of the Caucasus occur here. These forests mostly cover moist gorges with uniform air humidity all year long. High air humidity of these gorges is caused by the peculiarities of atmospheric precipitation and moderate temperature regime, which keep the surface of the slopes cool. Owing to these favourable conditions, many representatives of the Tertiary flora continue to exist in Colchis. A vivid example of Tertiary relics is the poikilohydric fern, *Hymenophyllum tunbridgense*, restricted to one of the moist gorges of South Colchis. Mixed broad-leaved forests are characterized by the occurrance of 50 arboreal and 80 herbaceous species (KOLAKOWKY, 1961; SAKHOKIA, 1980). Major forest-building species include: Old-Mediterranean *Castanea sativa*, Old-East-Mediterranean *Fagus orientalis*, Colcho-Hyrcanian *Zelkova carpinifolia*, Colchic *Quercus imeretina*, Euxinian *Qu. hartwissiana*, south-Caucasian *Qu. iberica* and Minor Asia-Caucasian *Carpinus caucasica*. The arboreal associates of the above-mentioned species are Colchic-Hyrcanian *Acer laetum* and *Pterocarya pterocarpa*, Colchic *Ficus colchica* and *Salix alba* subsp. *micans*, Caucasian *Pyrus caucasica, Malus orientalis* and *Salix pantoseri-*

cea, as well as European *Acer platanoides, Fraxinus excelsior, Taxus baccata,* etc. Additionally, a mention should be made of *Tilia caucasica, Ulmus glabra, U. elliptica;* Mediterranean-East-Asian *Diospyros lotus,* etc. Mediterranean *Rhododendron ponticum, Ruscus ponticus, R. colchicus, Daphne pontica;* Colchic *Ilex colchica, Rhododendron ungernii, Epigaea gaultherioides* and *Buxus colchica* frequently occur as undergrowth in these communities. Among the deciduous plants of the Colchic undergrowth, relics occupy the dominant position; examples are Colchic *Vaccinium arctostaphylos, Staphylea colchica, Viburnum orientale, Euonymus leiophloea, Hypericum xylosteifolium;* Colchic-Caucasian *Rubus caucasicus;* Colchic-Hyrcanian *Crataegus microphylla,* etc.

The ground vegetation (field layer) is characterized by the presence of such ferns as *Matteuccia struthiopteris, Athyrium filix-femina,* etc. Epiphytic ferns are exemplified by *Polypodium serratum.* Moist rock crevices and stony sites are inhabited by *Phyllitis scolopendrium, Pteris cretica,* etc.

Lianes (vines), though typical for Colchis forests, never form thickets even in forest margins. The commonest lianas are: *Hedera colchica* and *Dioscorea caucasica* (both are Colchic endemics); *Tamus communis* and *Periploca graeca* (Mediterranean species); *Smilax excelsa* and *Clematis vitalba,* etc. As indicated before, Colchic forests include epiphytes. Epiphytic plants are manifested by lichens (*Usnea barbata*), mosses (Neckeraceae representatives) and ferns (fig. 20).

Of the main plant communities *Fagus-Castanea, Carpinus-Castanea, Carpinus-Fagus-Castanea* and *Alnus-Carpinus-Fagus-Castanea* forests should be mentioned. Among these communities, forests dominated by five and more species can be observed. An example is the community where the dominant position is occupied by *Castanea sativa, Fagus orientalis, Tilia caucasica, Carpinus caucasica, Alnus barbata* and *Taxus baccata.* In the ground vegetation (where developed) *Brachypodium sylvaticum* and the adventive grass *Oplismenus undulatifolius* are dominants. They are associated with *Cardamine impatiens* and *Oxalis corniculata.*

Quercus imeretina forests with *Carpinus caucasica* are spread on river terraces.

It should be stated, that Colchic river gorges are characterized by a considerable amount of heterogeneity of natural conditions. Forest communities

Fig. 19 — Floristic complexes with predominance of *Fagus orientalis* (Svaneti, West Georgia) (*Photo Dolukhanov*).

Fig. 20 — Lowland forests of Colchis (*Photo Shanshiashvili*).

with *Buxus colchica* as undergrowth are typical for limestone regions, while in non-limestone areas forest undergrowth is composed of *Rhododendron ponticum, Rh. ungernii*, etc.

According to KOLAKOWSKY, these moist gorges covered by protective heavy snow in winter, have prevented Tertiary flora remnants from destruction, which overwhelmed the similar vegetation of exposed slopes.

The term "Shkeriani" is usually applied to define thickets of evergreen shrubs and even creeping trees. GOLITSIN (1939) attributes this term to a whole complex of evergreen shrubs, including *Epigaea gaultherioides, Ilex colchica* and also to deciduous *Betula medwedewii, Quercus pontica, Vaccinium arctostaphylos, Viburnum orientale*. According to KOLAKOWSKY, "Shkeriani" should be referred to the formation of shrubs, developed below the forest canopy and which now build up the second stratum. Mainly, the components of "Shkeriani" are the derivatives of forest vegetation, and such plants as *Epigaea gaultherioides, Ilex colchica, Betula medwedewii* should be excluded from its composition.

Destruction of Colchic forests in the lower part of the forest belt is the effect of man's agricultural activities; these areas, made subject to intensive farming, are manifested by the following cultivated plants: *Citrus* species, tea, tung tree, tobacco, maize, etc.

These areas are populated by many adventive plants like *Baccharis halimifolia* (North American), *Paspalum paspaloides* (pantropical), *Andropogon virginicus*, etc.

6.5 Pine Forests

Mountain pine forests of Georgia are dominated by *Pinus kochiana* which belongs to *P. sylvestris* group. The distribution area of *P. kochiana* comprises the Caucasus, Crimea and the northern Asia Minor up to the western part of the Pontic Mts. TUMAJANOV (1980) indicates that *P. kochiana* forests are to be found in all forest regions of moist temperate climate throughout the Euxinian phytogeographical province.

Main massifs hold by the above-mentioned forests, are situated on the mountains of the Greater Caucasus. In Georgia, pine forests cover negligable areas. In the eastern part of the country, these forests are distributed over the Mtkvari (= Kura) river basin, eastwards from Tbilisi and in Tusheti. In West Georgia they usually occur on stony and rocky slopes, where they cannot be re-

placed either by dark coniferous woods or by broad-leaved forest communities (DOLUKHANOV, 1992).

DOLUKHANOV (1992) noticed an interesting exception, specific for the pine forests of Georgia. In some parts of East Georgia, namely in the depth of Tushetis and Pirikitis Alazani river gorges, pine forests typical for stony and rocky slopes, also occur in habitats with a developed soil cover. These biotopes are favourable not only for pine but also for such forest-building trees as spruce and beech. Nevertheless, in the gorges, mentioned earlier, spruce and beech are absent and the climax communities of pine forests are formed instead. Dolukhanov explains this phenomenon by the orographic and geographic isolation of these gorges. Due to historical circumstances, only pine has been preserved in these sites; it escaped being replaced by beech and spruce only because their seeds never got to this area.

Mountain pine forests extend from 700 up to about 2400 m a. s. l. The most favourable conditions for pine forests are provided at an altitude of 1000-2200 m. In several parts, pines have been recorded at 2500-2600 m (TUMAJANOV, 1980).

P. kochiana grows on both limestone and acid magmatic rocks.

Following DOLUKHANOV (1992), the distribution of *P. kochiana* is controlled by phytogeographical conditions, while the influence of climate is less important. Occurrence of climax communities of pine forests on stony and rocky slopes accounts for their floristic composition, which is rich in endemic species.

Within the pine forests of Georgia, the following groups can be outlined: climax communities of the above forests and temporal-derivative pine forests.

Pine is well known as a pioneer tree to occupy the naked stony substrata, morain and fluvioglacial drifts. In Transcaucasia and particularly in Georgia, development of pine forests is subject to the impact of climatic fluctuations and activities of man (DOLUKHANOV, 1992).

The climax pine forests of Tusheti are very diverse, despite the fact that they occupy a limited area. They occur on substrata different by the character of weathering, as well as by the peculiarities of the lithological composition of the rocks (TUMAJANOV, 1938; DOLUKHANOV, 1992).

DOLUKHANOV (1992) differentiates the following categories of mountain pine forests:

1) Caucasian mountain pine forests of relatively dry ecotopes;
2) Caucasian mountain pine forests of

moderate-moist ecotopes;
3) Caucasian mountain pine forests of swampy habitats;
4) Caucasian mountain pine forests occurring on stony screes and rock streams.

6.5.1 Caucasian Mountain Pine Forests restricted to Rocky Slopes

Mountain pine forests of relatively dry ecotopes can be found almost everywhere within the distribution area of *Pinus kochiana*. They occur on skeletal and poorly-developed soils of prominent southward slopes. These pine forests are characterized by rich and diverse ground vegetation.

From the viewpoint of DOLUKHANOV, several groups of associations can be distinguished within this forest type. Our aim is to give a short description of some of them.

Pine forests with sparse herbaceous undergrowth are confined to prominent southern exposure. Availability of scattered herbs in the undergrowth is due to the washout of soils and destruction of ground vegetation. Pine forests of dry habitats with xerophytic herbs in the undergrowth are usually the climax communities which occupy northern slopes of Trialeti Mts, Meskheti, etc. The second stratum of these forests consists of *Quercus iberica* (below 1500 m), *Qu. macranthera* (above 1500 m) and species of *Acer*. Species dominant in the herbaceous undergrowth include *Carex buschiorum, Poa nemoralis, Brachypodium sylvaticum, Sesleria anatolica*, etc. Particular interest arise pine forests with tragacanthic species of *Astragalus* and those with *Juniperus* (*J. oblonga, J. hemisphaerica*) as undergrowth, frequent at 1900-2000 m s. m. Northern slopes of Trialeti Mts. are inhabited by pine forests with *Chamaecytisus caucasicus*, whereas those with *Ch. hirsutissimus* are restricted to mountainous Abkhazeti. In Ajara, the undergrowth of pine forests is dominated by *Cistus salviifolius*.

It is pertinent to note that Caucasian mountain-steppe pine forests and mountain meadow-steppe *P. kochiana* communities belong to the above-mentioned ecological type; they participate in generating park-like landscapes on the background of mountain meadow-steppe vegetation (usually in distant parts of the the Javakheti Upland plateau). The communities mentioned earlier are characterized by rather dense ground vegetation, extremely rich floristically. These forests occur at the altitude between 1700 and 2400 m. These communities

are also observed in Turkey.

Caucasian mountain pine forests of moderatly moist ecotopes are characterized by the admixture of spruce, as well as *Betula litwinowii, Abies nordmanniana, Sorbus caucasigena, Fagus orientalis, Fraxinus excelsior,* etc.

The undergrowth, though diverse, is poorly developed.

According to TUMAJANOV (1938), the above-mentioned pine forests can be divided into the following series: 1) *Hylocomiosa,* including *Pineta myrtillosa, Pineta oxalidosa, Pineta vacciniosa,* and 2) *Composita* with *Pineta rhododendrosa, Pineta mixtofruticosa, Pinetum azaleosum* and *Pinetum tiliosum* communities.

As indicated above, these pine forests are examples of climax communities. The series *Hylocomiosa* deserves special interest. These communities are dominated by representatives of the typical Taiga florogenetical complex. They populate steep slopes of northern exposure. The above forests can only be found in Tusheti.

Aside from these types of pine forests, MAKHATADZE *et alii* (1987) outlines the following communities: *Pinetum siccum, Pinetum cytisosum, Pinetum calamagrostidosum, Pinetum prasinosum,* etc. Oak-pine forests are attributed to a special group of forests; they are confined to lower parts of the pine forest belt (in East Georgia they occur at 800-1100 m. a. s. l., whereas in Ajara they descend to 300 m).

6.6 Oak Forests

From the coenotical and floristical points of view, the oak forests are among the richest forests of Georgia. According to DOLUKHANOV (1992), in prehistoric times, the area covered by oak trees was twice as large as it is today. These forests have also suffered from agricultural activities of man.

Oak forests which escaped destruction, are characterized by unsatisfactory regeneration and usually develope on poor soils.

In Georgia, the most abundant oak forests are those dominated by *Quercus iberica,* which is closely related to the widespread European *Qu. petraea.* The distribution area of *Qu. macranthera* is more limited. Broad-leaved forests of Colchis are characterized by the admixture of *Qu. hartwissiana.* Alluvial plains of the valley of river Mtkvari (= Kura) are covered by *Qu. pedunculiflora* forests; this species is very close to *Qu. robur,* in the lowlands of West Georgia this species becomes replaced by *Qu.*

imeretina. Remnants of *Qu. dschorochensis* communities, which were widely distributed in the past, have survived in Ajara. The characteristic species of crook-stem forest is *Qu. pontica* an ancient relic of the Colchic flora. This species can be found only within the creeping crook-stem forests.

Forests of Georgian oak (*Qu. iberica*)

The distribution area of these forests involves almost the entire territory of Transcaucasia, Daghestan and partly Chechnya-Ingushetia.

As it was pointed out, the south-Transcaucasian species *Qu. iberica* displays close taxonomical connections with *Qu. petraea,* though they are seperated ecologically and phytosociologically.

Qu. iberica is typical for eastern and south-eastern semi-arid parts of Transcaucasia; although, it can be encountered also in the Black Sea coastal area of Georgia. Even extreme conditions provided in the areas where the above oak forests come into contact with steppe and mountain-xerophytic vegetation, do not hinder their development. *Qu. iberica* forests extend from sea level up to 1500 and even 1800 m (in Svaneti).

Being very sensitive to excessive soil moisture and bad drainage, Georgian oak avoids alluvial plains.

Due to the fact that Georgian oak requires much light, in the areas favourable for the developement of beechwoods, populations of oak are replaced by more shade-enduring ones of beech.

Unlike in Europe, in Georgia *Fagus orientalis* and *Qu. iberica* are never found to grow together.

Of the arboreal components of *Qu. iberica* forests the following should be mentioned: *Carpinus caucasica, C. orientalis, Acer laetum, Sorbus torminalis, Zelkova carpinifolia.*

Depending on the degree of anthropogenic succession, derivatives of oak forests are illustrated by *Carpinus caucasica* forests and shibliak vegetation consisting of *Carpinus orientalis, Cornus mas, Cotinus coggygria, Swida (Cornus) australis, Crataegus pentagyna, Spiraea hypericifolia* and *Paliurus spina-christi.* At the last stages, shibliak is substituted by *Bothriochloa ischaemum.* Very often, meadows occupy the areas once covered with oak forests.

Taking into account that *Qu. iberica* forests were replaced in many areas by beech-woods, dark coniferous forests, etc., and that a considerable part of the above *Quercus* forests was destroyed by man, many associations of these fo-

rests have disappeared by now. Therefore, we assume that oak forests were well developed on the foothills and in the low mountain zone where competition between oak and beech, spruce, chestnut trees, etc. was impossible (DOLUKHANOV, 1992).

Oak forests are very rich floristically, owing to the illumination under the canopy and the heterogeneity of the physico-geographical conditions within the distribution area of Georgian oak. *Qu. iberica* forests are confined to rocky sites which promote enrichment of their floristical composition. In limestone regions many local endemics penetrate into the undergrowth of these forests (DOLUKHANOV, 1992).

DOLUKHANOV specifies the following variants (sub-formations) of *Qu. iberica* forest communities:
1) monodominant forests,
2) *Carpinus orientalis-Quercus iberica* forests,
3) *Carpinus caucasica-Quercus iberica* forests.

Today *Carpinus orientalis-Quercus iberica* forests are confined to the lower parts of the forest belt and occupy the largest area.

Carpinus caucasica-Quercus iberica communities occur on fertile and moist soils at relatively high altitudes. Monodominant forest communities are represented by forests with well-developed undergrowth as well as by those with no undergrowth. The same author specifies by convention the following ecologically different series within monodominant oak forests:
1) hemi-xerophytic,
2) xero-mesophytic.

Hemi-xerophytic oak forests develop under the driest conditions, regarding forest vegetation. In prehistoric times, these forests were widely distributed in semi-arid districts of East Georgia. Due to the impact of anthropogenic factors, these forests have always been subject to destruction.

As to the forest maintainance and timbering, regeneration in the above-mentioned forests is unsatisfactory.

Different associations of oak forests include *Quercetum iberici multifruticosum siccum* and the communities of oak forests with *Cotinus coggygria.*

It is suggested that in the past, oak forests included the following species as undergrowth: *Spiraea hypericifolia, Pyracantha coccinea, Juniperus oblonga.* Georgian oak forests with *Sesleria anatolica* and with *Psoralea bituminosa* are widespread in Abkhazeti.

It should be pointed out, that *Iberica-Quercetum genistosum* can be obser-

ved in east Transcaucasia (with *Genista transcaucasica*) as well as in Northern Colchis (*G. kolakowski, G. abchasica*).

Xerophytic *Qu. iberica* forests without woody undergrowth are characterized by presence of rich herbaceous ground vegetation. Associations of these forests have been united by Do-LUKHANOV (1992) into the Iberica-Querceta multiherbosa transcaucasica group. This group involves typical oak forests with forbs, *Qu. iberica* communities with various herbs and grasses, and *Qu. iberica* forests with various herbs and sedges.

Qu. iberica forests with various herbs are confined to river gorges of Pshavis Aragvi, Mtiuletis Aragvi, Gujaretis Tskhali and Nedzviskhevi; these forests extend from 830 up to 1460 m s. m.

Of the arboreal components of these forests the following should be mentioned: *Carpinus orientalis, C. caucasica, Sorbus torminalis, Acer laetum, Picea orientalis, Abies nordmanniana, Chamaecytisus caucasica, Lonicera caucasica*, and *Mespilus germanica*. Composition of the herbaceous undergrowth includes: *Clinopodium vulgare, Veronica peduncularis, Polygonatum glaberrimum, Campanula rapunculoides, Dactylis glomerata*, etc.

The commonest association of *Qu. iberica* forests with grasses is the one with various herbs and *Brachypodium sylvaticum*.

Qu. iberica forest with various herbs and *Carex buschiorum* is the typical representative of Georgian oak forests with sedges.

The group of associations of oak forests with *Epimedium* chiefly occurs on seaside mountains of Abkhazeti. The presence of *Epimedium colchicum* and *Hypericum xylosteifolium* as constant species is typical for these communities. *Dioscorea caucasica* is a constant species of oak forests restricted to limestone regions of West Georgia. The common species include *Sesleria anatolica, Trachystemon orientale, Ruscus ponticus, Carex transsilvanica, Dorycnium graecum*. Less common species are manifested by *Iris colchica, Dianthus imereticus, Hypochaeris radiata, Psoralea bituminosa, Aristolochia steupii, A. iberica, Primula sibthorpi, Veronica peduncularis, Helleborus abchasicus*, etc. These forests are inhibited by such Colchic shrubs as *Rhododendron luteum, Rh. ponticum, Vaccinium arctostaphylos*. Undergrowth of the forests confined to the cape of Bichvinta (Pitsunda) involves *Erica arborea*. Examples of common lianas are *Lonicera*

caprifolium and *Smilax excelsa*. Right at the seashores, *Arbutus andrachne* occurs as an arboreal component of oak forests. The following associations may be regarded as typical for the given group: *Quercetum hypericoso-epimedio-sum, Quercetum ericosum, Quercetum dioscoreoso-epimediosum, Quercetum multiherbosum-ibericum*.

Qu. iberica forests with developed woody undergrowth are characterized by the presence of dense thickets of shrubs and sparse undergrowth. The following associations belong to the above-mentioned first type of oak forests: *Querceta azaleosa (Rhododendron luteum), Querceta rhododendrosa (Rh. ponticum), Querceta staphyleosa (Staphylea colchica* is caracteristic of West Georgia, whereas *S. pinnata* is of East Georgia). According to DOLUKHA-NOV (1992), the second type of these forests involve too many variants to make them subject for any classification.

Qu. iberica forests with Carpinus orientalis.

These communities are widespread in East Georgia. Under the driest conditions they extend from 600 to 1000 m s. m., while in humid districts of West Georgia from 350 up to 700-800 m. MAKHATADZE (1987) regards these forests as the variants of complex oak forests. At lower altitudes the above communities are restricted to northern slopes, whereas at higher altitudes to southern ones. They can also be found in limestone regions of Abkhazeti and Samegrelo. In East Georgia they occur on different rocks. DOLUKHANOV (1992) distinguishes three main associations detectable in the oak forests with *C. orientalis*:

1) *Carpineto-Quercetum xerocaricosum (Carex buschiorum),*
2) *Carpineto-Quercetum poosum (Poa nemoralis),*
3) *Carpineto-Quercetum brachypodiosum (Brachypodium sylvaticum).*

The associations of oak forests with *Epimedium* are typical for West Georgia. In addition the following associations should be mentioned: *Carpineto-Querceta ruscosa (Ruscus colchicus), Carpineto-Querceta azaleosa (Rhododendron luteum), Carpineto-Querceta cotinosa (Cotinus coggygria).*

Carpineto-Querceta sesleriosum (Sesleria anatolica) and *Carpineto-Querceta xerobrachypodiosum (Brachypodium sylvaticum)* favour the driest climatic conditions.

Carpinus caucasica-Quercus iberica forests.

These forests occupy transition

zones between oak forests and those of beech. The second stratum is composed of *Carpinus caucasica*, which is a shade-enduring tree. Very little information is available on the typology of the above-mentioned forests because of the poor state of remnants of the climax communities. DOLUKHANOV (1992) indicates that *Carpinus-Quercus* forests with *Festuca drymeja* are abundant in East Georgia. Examples of typical species of these forests are *Cornus mas, Corylus avellana, Thelycrania (Cornus) australis. Carpinus caucasica-Quercus iberica* forests with *Rhododendron luteum* are common in West Georgia.

Qu. macranthera forests.

These forests are dominated by *Qu. macranthera* (sect. *Macrantherae*) which is known as highland oak". The distribution area of these species comprises the eastern parts of the Greater Caucasus (including both northern and southern macroslopes), the Minor Caucasus and mountains of Talysh. It is also found in West Caucasus (Svaneti). *Qu. macranthera* forests are developed in north-eastern Turkey and in northern Iran (Elburz Mts.).

These forests are confined to mid-mountain, high-mountain and subalpine zones; they are developed under relatively dry conditions at an altitude between 1450 and 2400 m s. m. (in some places at 2600-2700 m). The most favourable conditions for *Qu. macranthera* are provided at an altitude of 1450-1600 m near the upper limit of its distribution. Due to the aggravation of the process of regeneration, caused by overgrazing and other factors, highland oak started to form open woodlands and even crook-stem forests (SAKHOKIA, 1980; DOLUKHANOV, 1992).

Qu. macranthera forests grow on mountain forest brown soils; close to timberline they occur on mountain forest-meadow brown soils and those of meadow-steppe.

Qu. macranthera forms both mixed and monodominant forests. Birch-oak open woodlands (*Qu. macranthera* is accompanied by *Betula litwinowii*) and those of *Sorbus-Betula-Quercus (Sorbus caucasigena)* and *Acer-Quercus (Acer trautvetteri)* are developed in subalpine and high-mountain belts. Constant species of these forests are manifested by *Carpinus caucasica* and *Fraxinus excelsior*; less characteristic species are *Fagus orientalis*, species of *Tilia. Spiraea hypericifolia, Lonicera caucasica, Berberis iberica, Cotoneaster racemiflora*, etc. frequently occur as underwood in these communities.

Common oak forests are those with:
1) Forbs (*Polygonatum verticillatum, Silene wallichiana, Chaerophyllum aureum,* etc.);
2) forbs and ferns (*Dryopteris filix-mas*);
3) subalpine tall herbaceous vegetation (*Senecio platyphylloides, Cephalaria gigantea, Grossheimia macrocephala, Telekia speciosa*);
4) *Calamagrostis arundinacea, Phleum phleoides, Dactylis glomerata.*

Qu. macranthera forests with tall herbaceous vegetation are in contact with the vegetation of timberless volcanic uplands of South Georgia. Contact zones are of dry and cold climate; oak forests developed here bear the following names: "oak forests with sheep's fescue [*Festuca ovina* group]", steppe oak forests with forbs and grasses, oak forests with sedges (DOLUKHANOV, 1992). The herbaceous ground vegetation is exhibited by the following species: *Carex buschiorum, Festuca valesiaca, Achillea biserrata,* etc.

Monodominant forests of *Qu. macranthera* occur exclusively on steep southward slopes with poor skeletal soil. On the more fertile and moist soils *Qu. macranthera* communities are replaced by hornbeam-oak forests (DOLUKHANOV, 1992).

Qu. pedunculiflora forests. These forests occupy river valleys. *Qu. pedunculiflora* (*Qu. longipes*), closely allied to the European species *Qu. robur,* is an endemic species of Transcaucasia. It frequently occurs as arboreal component of oligo- and polydominant forests. *Qu. pedunculiflora* is often accompanied by *Carpinus caucasica,* and also by *Ulmus carpinifolia, Acer campestre, A. platanoides, A. velutinum, Tilia begonifolia,* and sometimes by *Fagus orientalis.* Under moist conditions, *Pterocarya pterocarpa* appears as admixture to these forests.

In past times the above forests covered vast areas in East Georgia, whereas today only few remnants of these, once luxuriant forests, can be found (DOLUKHANOV, 1992). Main massifs of these forests are situated in the valley of the river Alazani (Kakheti).

The following lianas are typical for *Qu. pedunculiflora* forests: *Smilax excelsa, Periploca graeca, Clematis vitalba, Vitis vinifera* and *Hedera helix.*

Qu. imeretina forests. *Quercus imeretina,* endemic species of West Georgia, is related to *Qu. pedunculiflora.* Distribution area of *Qu. imeretina,* which once was well developed in West Georgia and occupied relatively dry areas on the right bank of river Rioni, has reduced under the impact of anthropogenic factors (cutting for timber, destruction of forests for arable land, etc.).

Qu. imeretina forms both monodominant and mixed forests with *Carpinus caucasica, Zelkova carpinifolia, Fraxinus excelsior, Pterocarya pterocarpa, Alnus barbata.* DOLUKHANOV (1992) outlines the following groups of *Qu. imeretina* forest types of Georgia:
1) Moist oak forests with *Smilax excelsa,*
2) fresh oak forests with *Rhododendron luteum,*
3) dry oak forests with *Carpinus orientalis,*
4) dry oak forests with *Ruscus colchicus,*
5) dry oak forests with *Hypericum xylosteifolium,*
6) dry oak forests with *Zelkova carpinifolia.*

Qu. dschorochensis forests. *Qu. dschorochensis* forests are restricted to the south-western part of Ajara. Outside Georgia they occur in Chorokhi (Coruh) valley (Turkey). The remnants of these forests have survived only on sunny and dry rocky slopes (DOLUKHANOV, 1992).

Qu. hartwissiana forests. Contrary to other Caucasian oaks, *Qu. hartwissiana* has never formed monodominant forests. Today it participates in the formation of oligo- and polydominant forests of West Transcaucasia; it frequently occurs as a characteristic component of mixed forests of Colchis. *Qu. hartwissiana* grows on rich moist soils. It populates foothills and low-mountain zone up to 1200 m. The above-mentioned oak is often accompanied by *Zelkova carpinifolia.*

6.7 Hornbeam Forests

Carpinus caucasica is widely distributed throughout the Caucasus; it prefers fertile soils with good drainage.

These thermophilous species appear as dominants of the second stratum, forming hornbeam-beech and hornbeam-oak forests. *C. caucasica* is a usual component of polydominant forests. It should be underlined, that Caucasian hornbeam is adaptive to various conditions of biogeocoenotical environment (SHELYAG-SOSONKO, DIDUKH, 1980; DOLUKHANOV, 1992).

Hornbeam forests are very diverse phytosociologically. DOLUKHANOV distinguishes the following two classes in hornbeam forests: *C. caucasica* forests with Colchic undergrowth and those without Colchic undergrowth. The first class involves the following communities:
1) *C. caucasica* forests with *Poa angustifolia,*
2) *C. caucasica* forests with *Festuca drymeia,*
3) *C. caucasica* forests with forbs,
4) *C. caucasica* forests with *Trachystemon orientalis.*

Hornbeam forests with Colchic undergrowth are abundant in lower parts of the forest zone, where they are not replaced by beech-woods and dark coniferous forests (DOLUKHANOV, 1992). The above-mentioned forests include the following associations:
1) *C. caucasica* forests with *Rhododendron luteum,*
2) *C. caucasica* forests with *Vaccinium arctostaphylos,*
3) *C. caucasica* forests with *Rhododendron ponticum,*
4) *C. caucasica* forests with *Laurocerasus officinalis.*

Hornbeam communities with *Rh. luteum* are characteristic of West Georgia, though they can also be met in East Georgia (Kakheti and Aragvi river basin).

C. caucasica forests with *Vaccinium arctostaphylos* occur in West Georgia (Abkhazeti, Upper Svaneti, Guria, fig. 52) between 900 and 1750 m, whereas those with *Rh. ponticum* are restricted to northern slopes of the lower part of the forest zone of non-limestone regions of West Georgia; they extend from 100 up to 800 m.

Hornbeam forests with *Laurocerasus officinalis* occupy steep stony northern slopes of West Georgia at 300-800 m. They occur on both calcareous and non-calcareous soils.

6.8 Sweet-Chestnut Forests

Castanea sativa forests are developed in both West and East Georgia, but to the west of the country they occupy larger areas. In some localities pure stands of *C. sativa* can be found, but mainly sweet-chestnut occurs as a component of oligodominant beech-sweet-chestnut and hornbeam-beech-sweet-chestnut forests. In prehistoric times, the distribution area of *C. sativa* noticeably exceeded the present one.

Sweet-chestnut forests are chiefly restricted to shady slops. In West Georgia they extend from 100 up to 900-1000 m s. m.; approximately the absolute upper limit of *C. sativa* is situated at 1400-1450 m. In East Georgia (Kakhetis Kavkasioni) the lower limit of sweet-chestnut forests is about 400-500 m, and the

upper 1350-1380 m (DOLUKHANOV, 1992). *C. sativa* forests occur on yellow-brown soils (URUSHADZE, 1987). Though sweet-chestnut generally avoids calcareous soils, it can be found on limestone substratum in several localities in Georgia as well.

The forests of *C. sativa* are made subject to cutting in many regions. Besides, the bad state of *C. sativa* populations can be accounted by the impact of parasitic fungi. DOLUKHANOV (1992) considers that sweet-chestnut forests of Georgia still need to be adequately studied. He outlines the main association groups of *C. sativa* forests:

1) Sweet-chestnut forests with *Trachystemon orientalis*; these communities found in West Georgia, are represented mostly by beech-sweet-chestnut and hornbeam-beech-sweet-chestnut forests.
2) *C. sativa* forests with ferns (*Dryopteris filix-mas*). These communities occupy stony localities. Here sweet-chestnut is accompanied by *Alnus barbata, Ulmus carpinifolia, Acer laetum, Fagus orientalis, Carpinus caucasica.*
3) *C. sativa* forests with forbs (*Sanicula europaea, Galium (Asperula) odoratum, Festuca montana, Paris incompleta, Polygonatum polyanthemum*). These communities are typical for West Georgia. *Hedera helix* is a common liana here.
4) *C. sativa* forests with *Rhododendron luteum*. These communities are widespread in West Georgia. They occupy several localities in mountainous Kakheti.
5) *C. sativa* forests with *Vaccinium arctostaphylos*. These forests are abundant in Abkhazeti. Their arboreal components are represented by *Fagus orientalis* and rarely by *Carpinus caucasica.*

6) *C. sativa* forests with *Rhododendron ponticum.* They are confined to the mountains of West Georgia. Sweet-chestnut is accompanied by beech and especially by hornbeam (*Carpinus caucasica*). *Rh. ponticum* extends up to 3–4 m here (fig. 21).
7) *C. sativa* forests with *Laurocerasus officinalis*. Contrary to the communities with *Rh. ponticum*, these forests are rarely found. They are characterized by the admixture of *Rh. ponticum* to the dense thickets of *Laurocerasus officinalis*. These communities are confined to West Georgia.

6.9 Forests with *Zelkova carpinifolia*

Zelkova carpinifolia is a relic of the Arcto-Tertiary flora. The present-day distribution area of this species involves the refuges of Lenkoran (Azerbaijan) and Colchis; *Z. carpinifolia* sometimes occurs in Kakheti (East Georgia) and Karabakh (Armenia).

Monodominant forests of *Zelkova* are rarely found; usually it forms mixed communities with oak species (*Qu. imeretina, Qu. iberica, Qu. hartwissiana, Carpinus caucasica* and *C. orientalis*).

In many areas in Transcaucasia the upper limit of *Z. carpinifolia* varies in altitudes between 1200 and 1700 m s. m., whereas in Georgia it lies at 750 m. In West Georgia, *Zelkova* is chiefly confined to plains; very often it is met in forest margins and exposed locations. In Kakheti *Z. carpinifolia* occupies all slopes, excluding northern ones. This species occurs on both thin and rich soils, but avoids saline soils. In West Georgia *Zelkova* forests grow on alluvial-skeleton, sandy and clayey-sandy soils, whereas in Kakheti they are found on both deep brown and thin skeletal soils.

In West Georgia *Zelkova*-hornbeam-oak forests are well preserved. To

the east of the country, *Zelkova* forests are represented by *Z. carpinifolia-Carpinus orientalis* communities (SHARASHIDZE, 1967)

According to SHARASHIDZE, in West Georgia, *Z. carpinifolia* participates in generating the following associations: *Zelkoveto-Querceta* (*Qu. imeretina*) *hypericosa* (*H. inodorum*), *Zelkoveto-Querceta ruscosa* (*R. colchicus*), *Zelkoveto-Querceta brachypodiosa* (*Brachypodium sylvaticum*), *Zelkoveto-Querceta rhododendrosa* (*Rh. luteum*), *Zelkoveto-Querceta juncosa* (*J. effusus*), *Zelkoveto-Querceto carpinosa* (*C. orientalis*).

The following associations are typical for East Georgia: *Paliureto* (*Paliurus spina-christii*)-*Zelkoveta astragalosa* (*A. brachycarpus*), *Zelkoveto-Carpineta* (*C. caucasica*), *Zelkoveto-Crataegeta* (*C. pentagyna*) *geraniosa* (*G. palustre*), *Juglandeto-Zelkoveta clinopodiosa* (*Calamintha clinopodium*).

6.10 Forests with Yew (*Taxus baccata*)

Taxus baccata was once widely spread in Georgia. Forests with considerable admixture of the yew are preserved in Batsara Reserve (East Georgia). It occupies fresh moist soils, developed on carboniferous rocks. Within the territory of the reservation the yew extends from 900 up to 1350 m; in some locations it is registered to have reached 1500 m. In Colchis, the lower limit of *T. baccata* discends to the sea level, whereas in East Georgia the yew never comes down to 700 m. Below the dense canopy, *T. baccata* grows slowly and under the abundant sunlight it is characterized by stag headedness (DOLUKHANOV, 1992).

6.11 Forests with *Buxus colchica*

B. colchica is closely related to *B. sempervirens*, which is widely distributed throughout the southern sector of West Europe and Mediterranean. *Buxus colchica* is confined to West Georgia, especially to the limestone regions of Abkhazeti, Samegrelo, Racha-Lechkhumi. In East Georgia it has been cultivated since pagan times.

B. colchica extends from sea level up to 1300 m. It is an arboreal component of scattered forests of hornbeam and other broad-leaved trees. Cochic box, highly valued for timber, undergoes intensive cutting.

Fig. 21 — Castanea sativa forest with *Rhododendron ponticum* (*Photo Dolukhanov*).

The flora of the forests with *B. colchica* which occupy limestone slopes is very rich in local endemics and Mediterranean species. These forests involve such constant species, as *Ruscus ponticus, Hedera helix, Asplenium adiantum-nigrum, Carex divulsa, C. transsilvanica, Cyclamen abchasicum, Veronica peduncularis* and *V. persica* (DOLUKHANOV, 1992).

6.12 Forests with Maples (*Acer velutinum* and *A. laetum*)

Acer velutinum is a typical representative of Hyrcanian (Azerbaijan) forests. In Georgia it occurs only in the valley of river Alazani. The upper limit of *A. velutinum* amounts to 1000 m. *A. laetum* is confined to West Georgia and extends from sea level up to 1400-1600 m (higher it is replaced by *A. trautvetteri*). In East Georgia, *A. laetum* is restricted to moist mountain forests. Both maples occur in beech-woods and mixed forests.

7. NEAR-TIMBERLINE-VEGETATION

In the Caucasus and, particularly, in Georgia, the upper limit of forests is lowered (fig. 10). Straight-trunk forests of dense stands have definite climatic limits in their vertical distribution. Climate above this upper boundary noticeably varies: summer temperature falls with the increase of precipitation, slopes receive abundant solar radiation with the prevalence of ultraviolet refraction, etc.

Low forests composed of the species of *Abies, Pinus, Picea, Fagus* occur on relatively dry and sunny slopes above the forest belt, whereas subalpine crook-stem forests (*Betula litwinowii, Sorbus aucuparia*) are developed under moist conditions. Low forests have become very thin, due to the fatal effect of even slight anthropogenic influence. Continuous low forests, which have probably existed before, are unavailable in present-day Georgia.

Main forest communities of Georgia which reached the subalpine belt, involve the forests of spruce, pine, beech, fir and oak (*Qu. macranthera*).

As it was pointed out, dark coniferous forests extend to the altitude of 2100-2200 m on prominent slopes. According to DOLUKHANOV (1992), the upper limit of pine forests does not surpass the level of the 11-C°-isotherms of the warmest month, and that of low forests: 10.5 C°. Under moist climatic conditions, the above-mentioned forests are rarely found at altitudes higher than 2150 m, whereas in continental areas (Tusheti) they reach 2400 m s. m. (fig. 16).

Crook-stem forests of *Fagus orientalis* extend to 2300 m in some areas; at the same time vertical limits of these communities are located at 2350-2570 m in the moist mountains of South Colchis. It should be noted that beech does not occur under more continental conditions above 2200 m, and it never surpasses the level of 11-C°-isotherms of the warmest month. Vertical distribution of *Quercus macranthera* attract particular interest. Under dry climatic conditions *Qu. macranthera* occupies higher altitudes, than in areas with moist climate. The upper limit of its vertical distribution varies between 2100 and 2350 m.

Betula litwinowii, closely related to *B. pubescens,* is one of the most characteristic and common species of subalpine crook-stem forests of the Caucasus. Its upper distribution limit does not exceed the level of the 11-C°-isotherms of August, while in the areas where it is unprotected by snow coat, the 9.5-C°-isotherms. The common associate of the above-mentioned species is *Sorbus aucuparia* (fig. 23-26).

The Colchic endemics *Betula medwedewii, B. megrelica* and *Quercus pontica* are less frost-resistant, but they are well adapted to cold and moist subalpine summer. As components of crook-stem forests they reach 2300-2700 m, whereas under more continental conditions their upper limit is lower. DOLUKHANOV ascribes this dependence of upper limits on continentality of climate to the specific features of each species (fig. 22).

Open woodlands, low forests and crook-stem forests are very diverse and floristically rich. In the subalpine belt these communities are restricted to prominent slopes; they are rarely found at altitudes higher than 2150 m. Fir and spruce forests lose their productivity with the increase of altitude. Under the impact of anthropogenic factors, pine forests and those of *Quercus macranthera* have almost everywhere and quite irregularly retreated from their natural upper boundaries.

The upper limit of straight-trunk beech forests is situated at about 2050-2100 m (rarely at higher altitudes). At altitudes higher than approximately 2200-2300 m, beech forests are represented by dwarf semi-creeping formations; trees are pressed to the ground under the snow mass and lower parts of their trunks are rooted. The fact, that due to the increase of altitude, trunks of beech become dwarfed, arises special interest. Crook-stem forests of *Fagus orientalis* are characteristic of Colchis (fig. 23, 24). Several creeping, vegetative-migratory representatives of undergrowth (*Vaccinium arctostaphylos, Ilex colchica, Laurocerasus officinalis, Ruscus colchica,* and rare *Rhododendron ponticum*) grow under the canopy of these above-mentioned forests.

In the areas with less contrasting conditions, crook-stem forests of beech are in contact with *Sorbus-Betula* forests as well as with thickets of such Colchic endemics as *Rhamnus imeretina, Corylus colchica, Sorbus subfusca,* and the species of *Salix* distributed in high-

Fig. 22 — Subalpine crook-stem forest of *Betula medwedewii* (Bakhmaro, West Georgia) (*Photo Dolukhanov*).

Fig. 23 — Subalpine crook-stem forest of beech (Bakhmaro, West Georgia) (*Photo Dolukhanov*).

Fig. 24 — Subalpine crook-stem forest of beech (Abkhazeti, West Georgia) (*Photo Dolukhanov*).

the Minor Caucasus). The distribution area of another Caucasian birch, *B. raddeana,* includes Tusheti mountains and the upper parts of the rivers Didi Liakhvi, Aragvi and Tergi river basin. In Georgia, *B. raddeana* extends up to 225 m. In the lower sector of the subalpine belt *B. litwinowii* is found along with *Acer trautvetteri, Salix caprea, Padus avium,* etc. In Colchis *B. litwinowii* is accompanied by *Sorbus subfusca, Rhamnus imeretina, Ribes biebersteinii,* and *Rubus buschii.*

Rhododendron caucasicum, an endemic of the Caucasus, is a characteristic species of crook-stem forests of birch (fig. 26).

It is specific that birch forests with *Rhododendron* are characterized by presence of representatives of the flora of taiga. Examples are *Huperzia selago, Lycopodium annotinum, L. clavatum, Diphasiastrum (Lycopodium) alpinum, Gymnocarpium dryopteris, Cystopteris montana, Listera cordata, Deschampsia (Avenella) flexuosa, Orthilia secunda, Pyrola minor, Vaccinium vitis-idaea. Vaccinium myrtillus* and *Oxalis acetosella* are the exclusive species of these communities. *Vaccinium uliginosum* can be found, within the Caucasus, only in South Colchis.

Bryophytes growing in the abovementioned forests, are very diverse and peculiar for coenotic variability. These communities are rather rich in species (over 600) (DOLUKHANOV, 1992).

KVACHAKIDZE (1979), outlines 15 associations of birch forests situated on the southern slope of the Greater Caucasus. These associations may be united into the following 5 groups, such as:

1) birch forests with evergreen undergrowth,
2) birch forests with summergreen undergrowth,
3) birch forests with tall herbs,
4) birch forests with forbs,
5) birch forests with grasses.

West Georgia (especially South Colchis) is characterized by subalpine vegetation, which is unavailable in any other areas of West Eurasia (KOLAKOWSKY, 1980; DOLUKHANOV, 1992). Only creeping and semi-creeping woody plants grow in this subalpine belt, and among them, there are light-demanding and shade-bearing trees. Light-demanders are exemplified by *Betula medwedewii, B. megrelica, Quercus pontica, Rhamnus imeretina, Sorbus subfusca* and *Corylus colchica* (fig. 27, 28).

Crook-stem forests of *Quercus pontica* and *Betula medwedewii* emerge from under the snow cover only in June. Vegetative reproduction is typical for

lands. Low forests of *F. orientalis,* unavailable today, might have existed before.

Crook-stem forests of *Betula litwinowii* are the most typical communities of subalpine belt. This endemic species of the Caucasus is closely related to *B. pubescens.*

Under relatively continental climatic conditions, the lower limit of *B. litwinowii* comes to approximately 2000 m s. m., and the upper boundary varies between 2400-2600 m. At the same time, *B. litwinowii* occurs also at lower altitudes; it comes down by moraines, screes, rocky slopes, etc. Although *B. litwinowii*

is a light consumer, it occupies the slopes of northern exposure to secure protection by snow cover in winter (fig. 25).

The specific feature of *B. litwinowii* low forests is that they occur exclusively on dry mountains of East Georgia. Today these communities are almost completely destroyed.

Crook-stem forests of *B. litwinowii* contrary to beech communities are rarely monodominant: the constant species of these communities is *Sorbus aucuparia.* This species is represented in the Caucasus by the following two races (microspecies): *S. caucasigena* (in the Greater Caucasus) and *S. boissieri* (in

these species (DOLUKHANOV, 1956, 1992).

The following shade-enduring plants frequently occur as underwood in the creeping crook-stem forests: *Rhododendron ponticum, Laurocerasus officinalis, Ruscus colchicus, Ilex colchica.*

At present, relatives of the species forming crook-stem forests and Colchic undergrowth have mainly survived in the mountains exposed to the summer monsoon in eastern and south-eastern Asia, in the Appalachians of North America and on Maccaronesia. Thus, the Colchic refuge is isolated from the other centres of these floristic elements. This leads to the suggestion that the corresponding endemic species of the subalpine belt of Colchis belong to the relics of a rather remote past (DOLUKHANOV, 1956, 1966).

8. HIGH-MOUNTAIN VEGETATION

High-mountain vegetation (from the viewpoint of botany) comprises the area situated above the climatic limit of dense forests. They are characterized by specific environmental conditions: high solar radiation, high ratio of ultra-violet radiation, low temperature, intensive pressure of water vapour, etc.

One of the most pronounced peculiarities of high-mountains is the diversity of habitats within even a very small area.

All the altitudinal belts characteristic of the Nemoral Zone of temperate climate are represented in the high-mountains of Georgia. The following altitudinal zones can be observed here: subalpine (from 1800-1900 up to 2400-2500 m), alpine (from 2400-2500 up to 2960-3000 m), subnival (from 2400-3000 up to 3600-3750 m) and nival (above 3700 m s. m.).

The majority of Caucasian botanists regarded the high-mountain flora of the region to consist chiefly of the Boreal and Arcto-Alpine elements, which penetrated into this area during the Pleistocene; at the same time they presumed that only some high-mountain species were of autochthonous origin, genetically close to those of the low-mountain zones.

Later, it was stated that the most typical representatives of the Caucasian high-mountain flora are of autochthonous origin (FEDOROV, 1952; KHARADZE, 1960). According to these scholars, the high-mountain flora of today, being based on a Tertiary nucleus, developed during the Quaternary, in an autochthonous way.

According to KHARADZE (1960),
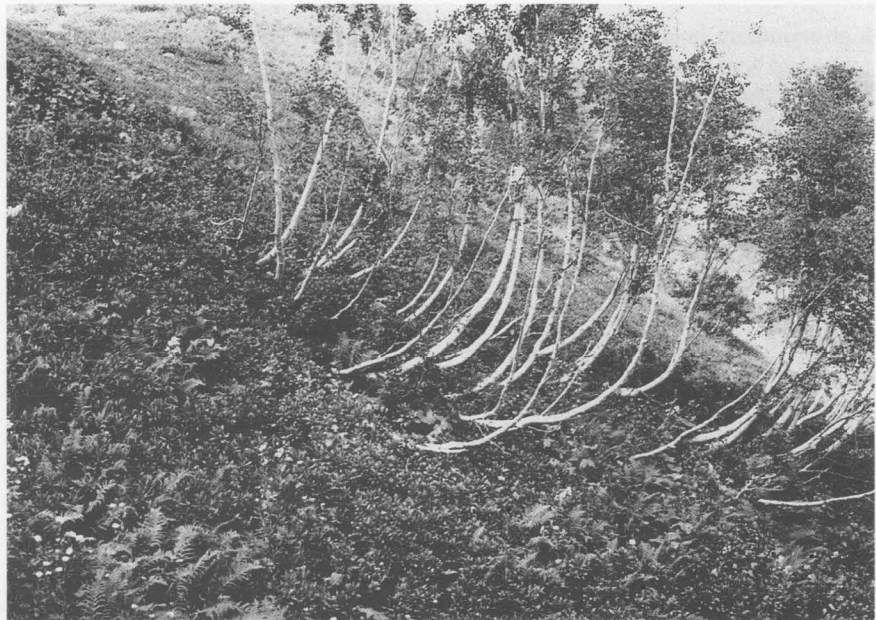
Fig. 25 — Subalpine crook-stem forest of *Betula litwinowii* (Abkhazeti, West Georgia) (*Photo Dolukhanov*).

Fig. 26 — *Rhododendron caucasicum* (Ajara, West Georgia) (*Photo Dolukhanov*).

Fig. 27 — Subalpine crook-stem forest of *Quercus pontica* (Ajara) (*Photo Dolukhanov*).

high-mountain landscapes of the Caucasus had been formed before the Pleistocene. The above-mentioned scholar does not share the opinion that the origin of high-mountain flora of the Caucasus is connected with the Late Quaternary. The high-mountain flora of the Caucasus is composed of ancient mesic and xeric elements.

In his analysis of the Caucasian endemism, GROSSHEIM (1936) indicates that the area of the Greater Caucasus, where the "processing" of migrated boreal and Anterior Asian elements took place, is of special significance.

KHARADZE (1960) outlines the following species which have penetrated to the Central Caucasus from Daghestan: *Stipa daghestanica, Thymus daghestanicus, Heliotropium styligerum*, etc. The same scholar suggests that the limestone mountain massifs of the North Caucasus participated in the formation of the pre-Pleistocene xerophytic flora. The example of such mountains is the limestone Rocky Mountain Range. Autochthonous hemixerophytic elements are well represented in the areas of the Central Caucasus from the mid-mountain zone to high-mountains.

Among the distant relations of the Caucasian oreoxerophytic flora its connections with those of the Mediterranean and Anterior Asian should be mentioned. Ancient connections with the Mediterranean flora have been found in the following genera: *Astragalus, Nepeta, Scabiosa, Symphyandra, Edraianthus*. The Late Pliocene is the period of the most ancient migrations from Anterior Asia (= Asia Minor) to the Caucasus. Penetration of these elements into the Caucasus is attributed to the xeric periods of Pleistocene and also of Holocene (GROSSHEIM, 1936; KHARADZE, 1960).

Autochthonous oreoxerophytic species of the Caucasus reveal ancient connections with those of the Anterior Asian flora. Examples are *Salvia canescens, S. daghestanica, Betonica nivea*, species of *Silene, Astragalus, Scutellaria, Ziziphora*, etc.

Members of the autochthonous high-mountain flora of the Caucasus are regarded as xerophytic elements of the humid flora of the same region (KHARADZE, 1960).

According to KHARADZE (1960), there have been two stages of formation of the Caucasian high-mountain elements. First, in the Miocene-Pliocene, more thermophilous elements had been formed, and after, in the Pliocene-Pleistocene the organisms fully changed in the direction of cryophytization. From the Upper Miocene to the Upper Pliocene, even the most elevated parts of the Greater Caucasus were populated by the representatives of thermophilous flora.

The most conservative palaeoendemics of the Caucasian high-mountains have remained in the mid-mountains and peripheries of the mountain glaciations. In the Alps and Carpathians, as well as in the Caucasus, the extreme mountain ranges served as refuges for the pre-glacial ancient endemic flora (KHARADZE, 1960). Both progressive and conservative palaeoendemics can be found in the Caucasian high-mountains. Conservative palaeoendemics are exemplified by *Sredinskya grandis, Campanula mirabilis, C. ossetica, Edraianthus owerinianus, Symphyandra lezgina*. Progressive palaeoendemics include such species, as *Charesia akinfiewii, Petrocoma hoefftiana* and *Symphyandra pendula*.

Apart from the above-mentioned plants, high-mountains of the Caucasus are populated by the following species:
1) endemo-vicariants of the Miocene-Pliocene differentiation (*Gypsophila imbricata, Arabis sachokiana, Scabiosa gumbetica, Campanula kolenatiana*);
2) endemo-vicariants with disjunctive distribution areas (*Ranunculus helenae, Hypericum nummularioides*);
3) progressive palaeoendemics and highly specialized species of eucryophytic complexes (*Pseudovesicaria digitata, Trigonocaryum involucratum, Pseudobetckea caucasica*);
4) endemo-vicariants of the Upper Pliocene differentiation (*Ranunculus lojkae, Cerastium undulatifolium, Cerastium kazbek, Senecio karjaginii*).

High-mountains of the Caucasus and Georgia in particular, display a great variety of life forms, which can be accounted for by their evolution under different climatic conditions, relief dissection, and also by the situation of the Caucasus at the junction of contrasting physico-geographical regions. Table 1 represents the classification of life forms, formulated by LARCHER and NAKCHUTSRISHVILI (unpublished data).

8.1 Subalpine Vegetation

The subalpine belt involves the areas which are situated above the dense forests up to the lower limit of the prevailing alpine grassland. Thus, the vegetation of the subalpine belt includes not only shrubwoods but also thin crookstem forests. The subalpine belt manifests remarkably high floristical and phytocoenotical diversity, stimulated by the following relatively optimal climatic conditions:
1) low daily temperature variations;
2) high air humidity;
3) rich soils;
4) not so high (as in alpine and subnival belts) solar radiation.

Due to the climatic conditions, the lower boundary of the subalpine belt varies in altitude between 2350 and 2500 m. In eastern and partially in central parts of the Greater Caucasus the upper limit attains 2450-2500 m s. m.

Subalpine vegetation is well deve-

Fig. 28 — Subalpine dwarf woody-shrub plant with many coumpound species (*Abies nordmanniana, Fagus orientalis, Betula litwinowii, Sorbus subfusca, Rhododendron caucasicum*) (*Photo Dolukhanov*).

Table 1 – Life forms (in a broad sense) of the high-mountain plants.

Morphological types:
1) Woody plants:
Straight-trunk-trees: *Acer trautvetteri, Pinus kochiana, Quercus macranthera.*
Crook-stem forest trees: *Betula litwinowii, Betula medwedewii, Quercus pontica.*
Shrubs: *Rhododendron caucasicum, Juniperus hemisphaerica, Rhamnus depressa.*
Subshrubs: *Artemisia splendens, Thymus nummilarius, Helianthemum buschii.*
Dwarf subshrubs: *Daphne glomerata, Vaccinium myrtillus, Vaccinium vitis-idaea, Empetrum hermaphroditum.*
Prostrate shrubs: *Salix kazbekensis, Juniperus sabina, Dryas caucasica.*
Cushion-shaped shrubs: *Astragalus denudatus.*

2) Herbaceous plants:
Plants with upright shoots - *Centaurea cheiranthifolia, Aconitum nasutum, Campanula lactiflora* (= *Gadelia lactiflora*).
Rosette plants: *Taraxacum stevenii, Chamaesciadium acaule, Plantago caucasica.*
Prostrate plants - *Veronica minuta, Minuartia aizoides, Astragalus captiosus, Trigonocaryum involucratum.*
Megaphytes - *Heracleum sosnowskyi, Telekia speciosa, Campanula lactiflora.*
Cushion-shaped plants - *Minuartia inamoena, Saxifraga moschata, Draba bryoides.*
Creeping plants - *Cuscuta epithymum, Convolvulus lineatus, Vicia grossheimii.*

Types based on relations of the perennating buds to the soil level:
Phanerophytes:
1) Macrophanerophytes: *Acer trautvetteri, Sorbus caucasigena, Betula litwinowii, Quercus macranthera.*
2) Nanophanerophytes: *Rhododendron caucasicum, Juniperus hemisphaerica, Rhamnus depressa.*
Chamaephytes: *Vaccinium myrtillus, Daphne glomerata, Dryas caucasica*
Hemicryptophytes: *Bromopsis variegata, Festuca varia, Betonica macrantha*
Cryptophytes (e.g. geophytes, hydrophytes): *Fritillaria lutea, Lilium georgicum, Hippuris vulgaris.*
Therophytes: All species of *Euphrasia, Rhinanthus minor, Gentianella caucasea, Lomatogonium carinthiacum.*

Phenorhythmotypes
1) Evergreen plants:
Continuously foliated plants: *Rhododendron caucasicum, Daphne glomerata, Saxifraga juniperifolia*
Summer-winter-green plants: *Festuca varia, Carex meinshauseniana, Alchemilla sericata*
2) Vernal-summer-green plants: *Rhododendron luteum, Betonica macrantha, Aconitum nasutum, Geranium ibericum.*
3) Plants with short vegetative period: *Fritillaria lutea, Galanthus caucasicus, Gagea glacialis.*

loped in the Caucasus, whereas in the Alps and Carpathians the typical subalpine meadows and tall herbs are comparatively poorly represented; at the same time elfin woodlands become substituted by low grass meadows.

Some botanists regard the subalpine belt as a part of the alpine zone. In the 19th and the beginning of the 20th centuries, subalpine meadows were considered to be of secondary origin.

Later it was stated, that the above-mentioned meadows are examples of climax communities.

In treeless areas of South Georgian Upland, mountain steppes compete with alpine meadows. It is evident that the subalpine belt is not represented in these regions.

The following types of vegetation are well developed in the subalpine belt of the Caucasus and Georgia, in particular:
1) crook-stem forests (see ch. 6);
2) elfin woodlands (see ch. 6);
3) subalpine tall herbaceous vegetation;
4) subalpine meadows.

In several regions of Georgia, subalpine the belt is characterized by the occurrence of oreoxerophytic vegetation, as well as meadow steppes and steppes.

8.1.1 Subalpine Tall Herbaceous Vegetation

Unlike many other mountain systems (Alps, Rocky Mts, Pamir, Himalaya, etc.), tall herbaceous vegetation is well represented in the subalpine belt of the Caucasus. Here it is confined to the lower part of the subalpine zone. Tall herbaceous vegetation is developed under the following favourable environmental conditions:
a) optimal air and soil temperature;
b) negligible daily fluctuations of temperature;
c) high air humidity;
d) solar radiation;
e) rich soils, etc.

Tall herbaceous vegetation is com-

posed of tall (3-4 m) herbs, chiefly dicots. They are characterized by rosetteless shoots, short top roots and rhizomes. Stratification is not pronounced within the tall herbaceous communities. According to GAGNIDZE (1974, 1977), the total number of species occurring in subalpine tall herbaceous vegetation amounts to 90, while their floro-coenotic complex includes only 70 species (table 2). A turning point in the composition of the floral-coenotic complex of tall herbaceous vegetation has commenced as early as Middle Pliocene. During subsequent periods, areas with tall herbaceous vegetation underwent reduction and even lost some individual components. According to GAGNIDZE, regularities of the present-day altitudinal distribution of the components of tall herbaceous vegetation of the Caucasus and the final formation of the corresponding floro-coenotical complex are related to the Pleistocene and Holocene (fig. 29a, 29b; 30a).

DOLUKHANOV *et alii* (1946) indica-

Fig. 29a — Subalpine tall herbaceous vegetation (*Heracleum sosnowskyi*, Kazbegi, 2200 m).
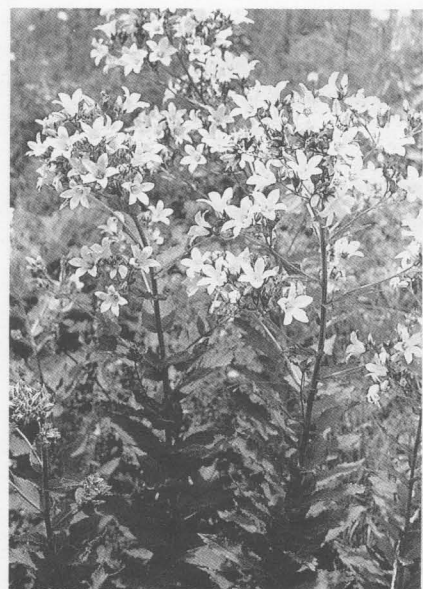

Fig. 29b — *Gadelia lactiflora* (Svaneti, West Georgia) (*Photo Dolukhanov*).

Fig. 30a — *Lilium monadelphum* (Ermani, East Georgia) (*Photo Dolukhanov*).

Table 2 — Tall herbaceous vegetation (Hochstaudenflur) (by GAGNIDZE, 1974).

Aconitum nasutum	*Doronicum macrophyllum*
A. orientale	*Euphorbia macroceras*
A. adzharica	*Gadelia lactiflora*
A. pachyptera	*Geranium kemulariae*
A. tatianae	*Grossheimia ossica*
Anthriscus nemorosa	*Heracleum aconitifolium*
Cephalaria gigantea	*H. asperum*
C. procera	*H. circassicum*
	H. colchicum
Cicerbita bourgaei	*H. cyclocarpum*
Campanula latifolia	*H. grossheimii*
	H. mantegazzianum
	H. ponticum
Chaerophyllum maculatum	*H. sosnowskyi*
	H. trachyloma
	H. wilhelmsii
Cicerbita deltoidea	*Inula magnifica*
C. macrophylla	*Knautia montana*
C. olgae	*Ligusticum alatum*
C. petiolata	*L. arafoe*
C. prenanthoides	*L. physospermifolium*
Cirsium aggregatum	*Lilium armenum*
C. albowianum	*L. georgicum*
C. buschianum	*L. kesselringianum*
C. czerkessicum	*L. monadelphum*
C. gagnidzei	*L. szovitsianum*
C. hypoleucum	*Milium effusum*
C. kuznetsowianum	*M. schmidtianum*
C. oblongifolium	*Petasites albus*
C. svaneticum	*Prenanthes abietina*
C. sychnosanthum	*Pyrethrum microphyllum*
Delphinium bracteosum	*Senecio cladobotrys*
D. buschianum	*S. othonnae*
D. dasycarpum	*S. platyphylloides*
D. dzavakhischvilii	*S. pojarkovae*
D. fedorovii	*S. propinquus*
D. flexuosum	*S. rhombifolius*
D. ironorum	*S. similiflorus*
D. mari	*S. subfloccosus*
D. megalanthum	*Telekia speciosa*
D. osseticum	*Valeriana alliariifolia,*
D. prokhanovii	*V. colchica*
D. pyramidatum	*V. tiliifolia*
D. speciosum	*Veratrum lobelianum*
D. tamarae	*Xanthogalum purpurascens*

te 3 groups of associations with the following leading species:
1) *Heracleum mantegazzianum, H. grossheimi, H. sosnowskyi* , etc. (fig. 30b);
2) *Senecio platyphyllus, Inula grandiflora*, etc.;
3) *Rumex alpinus, Senecio othonae*, etc.
  According to PANJUTIN (1934), the following associations are known from the north-western Colchis (Abkhazeti):
1) *Inuletum* (*Inula magnifica*),
2) *Telekietum* (*Telekia speciosa*),
3) *Aconitetum* (*Aconitum orientale*),
4) *Cicerbitetum* (*Cicerbita burgaei, C. cacaliaefolia*),
5) *Symphytetum* (*Symphytum asperum*),

6) *Heracleetum mantegazziani*.
  The same author attributes *Anthriscetum* and *Campanuletum* to intermediate associations. Weedy tall herbaceous vegetation should be divided into the following 7 associations, such as:
1) *Delphinietum pyramidati*,
2) *Senecietum platyphylli*,
3) *Senecietum chlorocomos*,
4) *Cirsietum obvullati*,
5) *Anthriscetum nemorosi*,
6) *Heracleetum asperi*,
7) *Pteridietum tauricumi*.
  We distinguish 6 formations of tall herbaceous vegetation, as well as several groups and association classes, characteristic of the subalpine belt of Lago-

characteristic feature of underground organs of subnival and nival is their shallow rooting (about 15-20 cm) which protects them from cold lower layers (opposite data were obtained in the Alps (KÖRNER, 1988). Even the longest underground organs at a certain level of depth (20-30 cm) begin to grow in horizontal direction (GAMTSEMLIDZE & NAKHUTSRISHVILI, 1984).

8.3.5 Reproductive Buds

Buds of herbaceous plants may be bare (without special bud scales), protected (with spacial bud scales), and proleptic (with bud scales which in autumn begin to burst and new shoots leave their shells).

According to GAMTSEMLIDZE (1979), in the subnival belt in sever winter conditions reproductive buds are covered by the residues of dead parts of plants and sheathes of dead leaves (*Jurinella subacaulis, Symphyoloma graveolens*). But sometimes they occur in the surface layer of soil (*Lamium tomentosum, Cerastium polymorphum*) or deep in soil (*Delphinium caucasicum*). Perennating buds of *Saxifraga sibirica* are covered by rosette-forming nodules which are partly in soil.

Reproductive buds of such wintergreen plants like *Saxifraga exarata, S. ruprechtiana* are protected by frame green leaves. A bud covering of plants which have protected proleptic buds is formed by solid bud scales and dead old leaves (*Scrophularia minima, Senecio karjaginii*).

It is characteristic that many subnival plants have stipules fitted closely to the base of stem and protect reproductive buds from damage (*Alchemilla sericea*).

Along with these adaptations for safe wintering of subnival plants snow cover protection is very important for reproductive buds. According to the data the biggest group of investigated plants is with bare buds (40%), then the group with proleptic buds (35%) and the smallest group is with protected buds (25%).

The point is, what determines such a great amount of plants with bare reproductive buds in the subnival belt. There are a number of opinions on this problem. According to SEREBRIAKOV (1961; 1992): "The absence of bud scales in arctic and alpine plants is connected with fact that their scales are remetamorphosed into green assimilative leaves, which usually hibernate under the protection of a snow cover and partly under the protection of a cover of moss. One of the factors for the remetamor-

phosis of bud scales into green leaves in Tundra zone and high-mountain alpine belts was a considerable shortening of a vegetation period. Plants get an opportunity to extend the period of photosynthetic activity through remetomorphosis". SAVILE (1972) explains unprotection of reproductive buds with scales by the fact that hard scales hinder rapid spring development and hence, the plants are unable to adapt to short arctic vegetation period.

By the state of the next year shoot in reproductive buds at the end of the vegetation period, subnival plants could be divided into two groups: 1) plants with completely formed shoots in buds including not only vegetative organs but also inflorescenses and single flowers (fig. 42); 2) plants in the buds of which only the vegetative part of a shoot is formed, the inflorescence and flower germs appearing during the next vegetation period.

As much as 68 species out of 78 investigated subnival plants (88 %) posess generative shoots in reproductive buds which are born in the year before flowering (group 1) and only 10 species in the year of flowering (group 2).

According to the degree of flower development in reproductive buds the first group can be devided into 3 subgroups:
1) next year flowers of reproductive buds are completely formed: sepales, a corolla, stamens, a pistil are developed (fig. 42) (*Primula bayernii, Scrophularia minima*);
2) next year flowers of productive buds are formed incompletely: sepales, petales, stamens are developed completely, the pistil is unformed (fig. 43) (*Saxifraga sibirica, Potentilla gelida, Alchemilla sericea, A. chlorosericea, Draba siliquosa, Jurinella subacaulis*);
3) inflorescenses and flowers of reproductive buds are not differentiated or start defferentiating (fig. 44) (*Senecio karjaginii, S. taraxacifolium, Tripleurospermum subnivale, Alopecurus glacialis, Delphinium caucasicum, Erigeron uniflorus*).

Profound studies of the subnival belt in the Tyrolean Alps (MOSER, 1968; LARCHER, 1980; ZACHUBER, 1975), showed that flower differentiation in buds still continues except *Cerastium uniflorum*, in which flower emergence begins only 4-6 month prior to flowering and their opening is different in various species. For instance this period lasts 11 months in *Saxifraga oppositifolia*, 12-18 months in *Primula glutinosa* and *Saxifraga bryoides* and 24-26 mon-
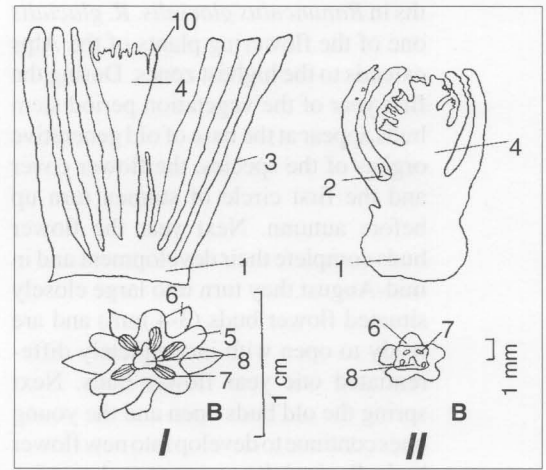

Fig. 42 — Reproductive buds of *Primula bayernii* (1), *Scrophularia minima* (2), where next year flowers developed completely (GAMTSEMLIDZE, 1979). A-reproductive bud sectional view, B-flower complete differentiation, 1-perennating reproductive bud, 2-axillary vegetative bud, 3-vegetative shoot, 4-inflorescence, 5petale, 6-sepale, 7-stamen, 8-pistil, 9-flower knobs, 10-covering leaves.
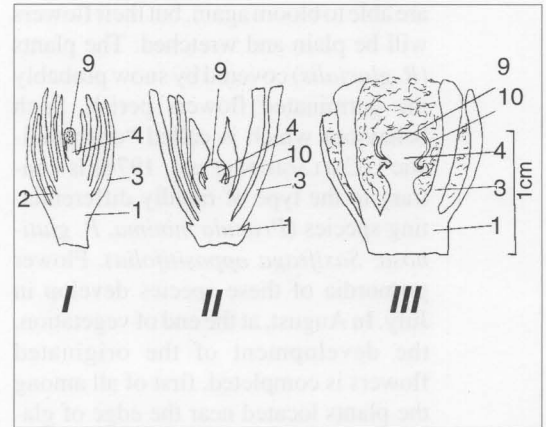

Fig. 43 — Reproductive bud section of *Alchemilla sericea* (1) and *Potentilla gelida* (2) where next year flowers developed incompletely. Designations are the same as in fig. 42.
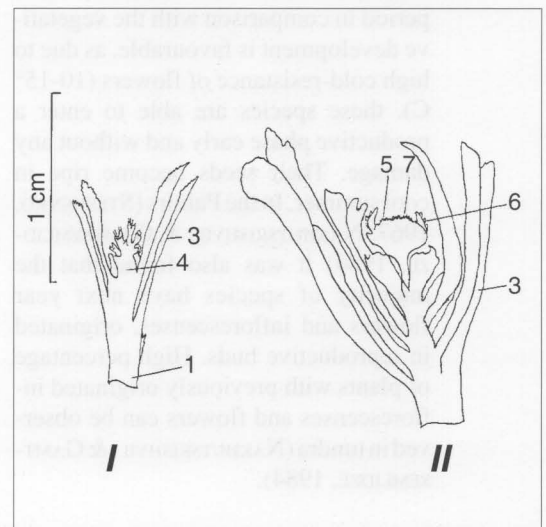

Fig. 44 — Reproductive byd section *Alopecurus glacialis* (1), *Senecio taraxacifolius* (2), *S. karjaginii* (3), where inflorescences and flowers have no differentiation sigus ands only about to start differentiating. Designations are the same as in fig. 42.

Table 4 – Hordeeta in Kazbegi.

Height (m s. m.)	1850
Exposition	S
Slope (°)	5
Cover (%)	100
Hordeum violaceum	5
Bromopsis riparia	2
B. variegata	2
Phleum pratense	2
Ph. phleoides	1
Agrostis planifolia	2
A. tenuis	2
Poa pratensis	4
Festuca pratensis	3
Koeleria gracilis	1
Tragopogon reticulatus	2
Rumex acetosa	1
Trifolium ambiguum	3
Myosotis alpestris	2
Rhinanthus minor	+
Lotus caucasicus	+
Pastinaca armena	2
Galium verum	1
Vicia grossheimii	2
Silene vulgaris	1
Trifolium fontanum	2
Ranunculus elegans	2
Seseli transcaucasica	4
Myosotis sylvatica	2
Cuscuta europaea	+
Anthriscus nemorosa	3
Alchemilla retinervis	2
Veronica gentianoides	2
Taraxacum confusum	2
Potentilla recta	+
Draba hispida	+
Leontodon hispidus	2
Pedicularis chroorryncha	2
Carum carvi	2
Euphrasia hirtella	+
Alchemilla sericata	1
Verbascum blattaria	+
Campanula trautvetteri	+
Polygonum alpinum	+
Cerastium arvense	+
Vicia alpestris	+

Variegated fescue Festuca varia (F. woronowii) meadows occupy huge slopes of subalpine belt, where they form the first stage of succession. Under the influence of intensive grazing, *Calamagrostis arundinacea* communities become replaced by those of variegated fescue, but after grazing is forbidden, demutation of *Festuca* coenoses can be observed. *F. varia* forms large bunches; interspaces are populated by grasses (*Helictotrichon asiaticum, H. pubescens, Agrostis planifolia*), sedges (*Carex meinshauseniana*) and forbs (*Betonica macrantha, Polygonum carneum*, etc.) (table 5; 7).

On wet slopes, *Festuca* communi-

Table 5 – List of *Festuca varia* communities (by KIMERIDZE, 1965).

Festuca varia + Calamagrostis arundinacea
Festuca varia + Calamagrostis arundinacea + Agrostis planifolia
Festuca varia + Calamagrostis arundinacea + Deschampsia flexuosa
Festuca varia + Poa iberica
Festuca varia + Festuca rubra + Poa iberica
Festuca varia + Festuca rubra + Calamagrostis arundinacea
Festuca varia + Calamagrostis arundinacea + Festuca ovina
Festuca varia + Poa iberica + Festuca ovina
Festuca varia + Calamagrostis arundinacea + Bromopsis variegata
Festuca varia + Festuca djimilensis + Calamagrostis arundinacea
Festuca varia + Festuca djimilensis
Festuca varia + Festuca rubra + Poa longifolia
Festuca varia + Festuca rubra
Festuca varia + Poa longifolia + Bromopsis variegata
Festuca varia + Bromopsis variegata + Festuca ovina
Festuca varia + Bromopsis variegata
Festuca varia + Alopecurus gracialis

Festuca varia-Festuca supina + Deschampsia flexuosa
Festuca varia-Festuca supina
Festuca varia-Koeleria caucasica
Festuca varia-Festuca ovina

Festuca varia + Bromopsis riparia
Festuca varia + Stipa pulcherrima
Festuca varia-Festuca sulcata

Festuca varia + Calamagrostis arundinacea - Betonica macrantha
Festuca varia - Betonica macrantha + Agrostis planifolia
Festuca varia - Agrostis planifolia - Trifolium canescens
Festuca varia - Alchemilla pyenotricha - Agrostis planifolia
Festuca varia - Geranium gymnocaulon - Agrostis planifolia
Festuca varia - Nardus stricta + Betonica macrantha
Festuca varia + Calamagrostis arundinacea - Alchemilla stellulata
Festuca varia + Calamagrostis arundinacea - Alchemilla sericata
Festuca varia + Bromopsis variegata - Betonica macrantha
Festuca varia - Deschampsia flexuosa - Alchemilla retinermis
Festuca varia + Calamagrostis arundinacea - Thymus nummularius
Festuca varia + Bromopsis variegata - Alchemilla caucasica
Festuca varia + Festuca ovina - Alchemilla caucasica
Festuca varia + Festuca ovina - Thymus caucasicus

Festuca varia + Anemone fasciculata
Festuca varia + Anemone fasciculata + Geranium ibericum
Festuca varia + Betonica macrantha + Geranium ibericum
Festuca varia + Geranium renardii + Betonica macrantha
Festuca varia + Geranium ibericum
Festuca varia + Geranium renardii
Festuca varia + Betonica macrantha
Festuca varia + Betonica macrantha - Trifolium canescens
Festuca varia - Geranium gymnocaulon
Festuca varia + Scabiosa caucasica

Festuca varia - Trifolium canescens + Trifolium ambiguum
Festuca varia - Trifolium ambiguum
Festuca varia - Trifolium canescens
Festuca varia - Trifolium ambiguum + Leontodon hispidus

Festuca varia - Alchemilla sericata - Betonica macrantha
Festuca varia - Alchemilla caucasica + Trifolium ambiguum
Festuca varia - Alchemilla retinervis
Festuca varia - Alchemilla pycnotricha
Festuca varia - Alchemilla grossheimii
Festuca varia - Alchemilla sericea
Festuca varia - Alchemilla caucasica
Festuca varia - Alchemilla sp. - Dianthus raddeanus

Table 5 (continued)

Festuca varia - Alchemilla sericata

Festuca varia + Calamagrostis arundinacea - Carex meinshauseniana
Festuca varia + Calamagrostis arundinacea - Carex tristis
Festuca varia + Bromopsis variegata - Carex meinshauseniana
Festuca varia + Festuca rubra + Carex meinshauseniana
Festuca varia - Poa caucasica + Carex meinshauseniana
Festuca varia + Bromopsis variegata - Carex tristis
Festuca varia + Bromopsis variegata - Kobresia schoenoides
Festuca varia + Bromopsis variegata - Carex huetiana

Festuca varia - Deschampsia flexuosa + Carex tristis
Festuca varia - Festuca supina + Carex meinshauseniana
Festuca varia - Festuca supina - Carex tristis
Festuca varia - Carex tristis + Festuca ovina

Festuca varia - Carex medwedewii + Carex huetiana
Festuca varia - Carex medwedewii
Festuca varia - Carex meinshauseniana + Carex medwedewii
Festuca varia - Carex meinshauseniana
Festuca varia - Carex tristis
Festuca varia - Carex huetiana

Festuca varia - Carex buschiorum + Festuca ovina
Festuca varia - Carex buschiorum
Festuca varia - Carex humilis + Festuca sulcata
Festuca varia - Carex humilis

Festucetum variae purum subalpinum
Festucetum variae purum alpinum

Festuca varia - Alchemilla rigida + Carum caucasicum
Festuca varia - Carum carvi + Campanula biebersteiniana + Taraxacum confusum
Festuca varia - Taraxacum steveni - Campanula biebersteiniana + Sibbaldia semiglabra
Festuca varia - Alchemilla retinervis + Sibbaldia semiglabra
Festuca varia - Plantago saxatilis + Campanula biebersteiniana
Festuca varia-Plantago saxatilis+Campanula biebersteiniana+Pedicularis chroorhyncha
Festuca varia - Sibbaldia parviflora - Polytrichum juniperinum
Festuca varia - Sibbaldia parviflora + Alchemilla caucasica + Carum caucasicum
Festuca varia - Trifolium polyphyllum + Thalictrum alpinum + Carum caucasicum

Festuca varia - Kobresia capilliformis
Festuca varia - Kobresia capilliformis + Alchemilla caucasica
Festuca varia - Kobresia schoenoides + Carex tristis
Festuca varia - Kobresia schoenoides

Festuca varia - Kobresia persica - Alchemilla caucasica

Festuca varia - Thymus nummularius
Festuca varia - Carex buschiorum - Thymus caucasicus
Festuca varia - Thymus caucasicus
Festuca varia - Thymus caucasicus + Thymus collinus - Psephellus dealbatus
Festuca varia - Thymus collinus

Festuca varia - Vaccinium myrtillus
Festuca varia + Calamagrostis arundinacea - Vaccinium myrtillus

Festuca varia - Daphne glomerata

Festuca varia + Salix caprea - Deschampsia flexuosa
Festuca varia - Salix arbuscula
Festuca varia + Rhododendron caucasicum
Festuca varia + Rhododendron caucasicum + Juniperus hemisphaerica
Festuca varia + Juniperus hemisphaerica

ties are richer than those which occur on dry ones.

JAROSHENKO (1942) and GEIDEMAN (1932) attributed variegated fescue meadows to steppe communities, while BUSCH (1935) and MAGAKIAN (1941) regarded them as typical meadows. Later Jaroshenko suggested, that *Festucetum variae* is a relic steppe, formed during the xerothermal period, and that since then, due to the further increase of climate humidity, the above-mentioned communities have been subject to the process of prairification. This opinion is shared by Grossheim.

Variegated fescue meadows are well-spread throughout the Caucasus. Though in South Georgian Uplands, unlike the Greater Caucasus, these communities occur on grazed areas of northern slopes.

Variegated fescue meadows include such widespread association as *Festucetum caricosum* (*Carex meinshauseniana*).

Festuca ovina meadows are confined to southern slopes. They are of a relatively simple structure (low herbage, low coverage percent, small number of coenoses). *Koeleria albovii, Bromopsis riparia, Agrostis tenuis, Carex buschiorum, Pulsatilla violacea, Thymus collinus* are the main components of these communities.

The driest eroded slopes of the subalpine belt are covered with communities dominated by *Bromopsis riparia, Festuca valesiaca, Koeleria albovii*, etc. They grow on thin, cobble and skeletal soils.

According to TUMAJANOV (1980), forb-grass meadows observed in park forests of *Qu. macranthera* in the eastern part of Kavkasioni, are steppificated. The following species are typical for these meadows: *Brachypodium pinnatum, Bromopsis riparia, Carex buschiorum* and *Onobrychis biebersteinii*.

Forb and grass-forb Meadows:

Meadows of this group are abundant in the areas with moist temperate climate. Florogenetically, these communities are connected with the upper forest belt: they occur in thin park forests. It must be noted, that due to the dominant position of chionophytes, these meadows can rarely be found in the mountain massifs with a complex relief. Meadows with *Woronowia speciosa* (= *Geum speciosum*) arise particular interest. They are very common in the western part of Kavkasioni (limestone-built mountains of Colchis). Usually,

these communities populate the slopes with a sharply defined karst relief. *Woronowia speciosa* coenoses with a considerable admixture of *Carex pontica* occupy the same area.

Woronowia communities present the first stage of succession on karst funnels. Vital activity of *W. speciosa* results in the formation of soil, on which the other meadow elements start to crop up. *Woronowia* meadows are likely to have been more abundant in Colchis before. Due to the influence of grazing, in many areas, *W. speciosa* communities became substituted by those of *Nardus* and alpine carpet-like meadows.

Meadows of *Trollius patulus* are very common in forest margins, thin park forests and elongated cavities. *Ranunculus caucasicus* frequently occurs in these communities as a subdominant. Pure *Ranunculus* meadows have been formed under the influence of overgrazing.

Geranieta gymnocauloni (*Geranium gymnocaulon*) communities are confined chiefly to the alpine belt of the western part of the Greater Caucasus, though they also come down to the subalpine belt.

The distribution area of *Geranium platypetalum* meadows comprises Kavkasioni (= Greater Caucasus) and the Minor (Lesser) Caucasus. They are unavailable in South Colchis. These communities occur on stony substratum of moraines. With the development of soil cover, *G. platypetalum* communities are being replaced by other communities.

Forest margins, mountain slopes of medium steepness and flat areas are inhabited by *Geranium ibericum*, although as subdominant this species more frequently occurs in *Calamagrostideta, Inuleta, Rhododendreta*, etc.

Inuleta orientalis coenoses are represented by pure thickets of *Inula*. It is very common in the high-mountains of the Caucasus. The following communities are characterized by predominance of this species: *Inuletum geraniosum* (*Geranium ibericum*), *Inuletum betonicetosum* (*Betonica macrantha*).

In the western part of the Greater Caucasus, communities of *Inula grandiflora* usually occur on negative landforms where they replace tall herbs (KOLAKOWSKY, 1961). *Astrania pontica* coenoses occupy screes and cobble substratum in limestone mountain ranges of Colchis (Abkhazeti).

Of the forb meadows, which are very rich in species, *Scabiosa caucasica* should be noted. These communities include such plants as *Helictotrichon pubescens, Inula orientalis, Agrostis planifolia, Betonica macrantha*, etc.

These meadows are very common in the Minor Caucasus.

Betoniceta (*Betonica macrantha*) is a typical variant of subalpine meadows. It is well represented in the central and eastern parts of Kavkasioni and the Minor Caucasus; the above-mentioned communities are rarely found in the western part of the Greater Caucasus.

Anemoneta (*Anemone fasciculata*) frequently populate slopes with optimal moisture and flat sites (fig. 31). Slopes exposed to sunlight and cobble sites are occupied by communities of hemixerophytic *Hedysarum caucasicum*.

Subalpine meadows of *Veratrum lobelianum* are abundant in western and partly Central Kavkasioni (Greater Caucasus), as well as in the Minor Caucasus. *Veratrum lobelianum* is a poisonous pasture weed, usually rejected by animals; it is developed on the forb (*Trollius patulus, Ranunculus caucasicus*, etc.) meadows (fig. 30).

Pulsatilleta (*Pulsatilla violacea*). These communities, typical for negligible areas, are confined to the slopes of northern exposure. *P. violacea* is frequently associated with hemixerophitic grasses (*Festuca ovina, Koeleria albovii*) and *Carex buschiorum* (table 6).

Pulsatilleta (*Pulsatilla aurea*): These communities are very common in northwestern Colchis. The distribution area of *P. albana* is more expansive.

Geranieto (*Geranium gymnocaulon*) - **Woronowieta** (*Woronowia speciosa*), **Geranieto-Inuleta** (*Inula magnifica*) illustrate subalpine mixed forb meadows, which often consist of 2-3 species and are found in Colchis. Pure forb communities are formed by *Euphorbia oblongifolia, E. scripta*, etc. Grass-forb meadows display high coenotical and floristic diversity. According to KOLAKOVSKY (1961), the following species are very abundant in the above-mentioned meadows of Colchis: *Aquilegia olympica, Psephellus abchasicus, Kemulariella caucasica, Senecio aurantiacus*, etc.

Grossheimia polyphylla (*Asteraceae*) is a typical component of grass-forb meadows which are confined to the Minor Caucasus and partly to western Kavkasioni (fig. 32).

The following plants frequently occur in subalpine grass-forb of the Caucasus: *Centaurea fischeri, C. cheiranthifolia, Vicia alpestris, Lotus caucasicus, Veronica gentianoides, Trifolium ambiguum, Leontodon hispidus, Ranunculus oreophilus*, etc.

Communities dominated by *Polygonum carneum* are worthy of notice; their area of distribution involves Kavkasioni and southern uplands. These meadows are of particular importance as natural grasslands. Under the influence of overgrazing, forb and grass-forb meadows become replaced by more resistant communities of compact-tussock grasses.

Astragaleta is characteristic of subalpi-

Fig. 31 — High-mountain landscape (*Anemonetum*) in Tskra-tskharo 2100 m (East Georgia) (*Photo Dolukhanov*).

ne belt of the Central Caucasus and especially of Kazbegi region; these communities, formed by endemic *Astragalus captiosus*, occupy stony and pebble substratum.

8.1.3 Tragacanthic Vegetation

On the northern slopes of Kavkasioni, tragacanthic vegetation is sporadically distributed in dry inter-mountain vallies and hollows (IVANISHVILI, 1973).

Caucasian tragacanthic vegetation is a version of Asia Anterior mountain-xerophytic vegetation; these communities are very rare in the Mediterranean mountains.

Astragaleta denudati (*Astragalus denudatus*) in Khevi (Central Caucasus) is restricted to the lower part of subalpine belt. These communities alternate with steppe-like meadows and saxicolous groupings; they occupy areas once populated by pine forests. In Daghestan (Eastern Caucasus) the above-mentioned coenoses can also be met in alpine belt; some individuals of *Astragalus aureus* penetrate even into the subnival zone (up to 3150 m; PRIMA, 1974).

Tragacanthic communities are dominated by plants, characterized by spiny cushion-like form. These communities also include the following plants:
1) Dwarf subshrubs (species of *Artemisia, Thymus, Scutellaria*);
2) mountain steppe grasses (*Elytrigia gracillimum, Bromopsis riparia, Stipa tirsa*, etc.);
3) *Carex buschiorum*;
4) hemixerophytic shrubs (*Juniperus hemisphaerica, J. sabina, Rhamnus tortuosa*).

The flora, formed on rocks has been enriched with lithophytes and chasmophytes, which involve many local endemics (IVANISHVILI, 1973).

The following is a concise list of species characteristic of one of tragacanthic communities:
Astragalus denudatus
Berberis vulgaris
Juniperus hemisphaerica
Spiraea hypericifolia
Ephedra procera
Artemisia chamaemelifolia
Artemisia marschalliana
Artemisia splendens
Scutellaria leptostegia
Agropyron gracillimum
Bromopsis riparia
Festuca sulcata
Koeleria cristata
Melica transsilvanica
Stipa caucasica
Stipa tirsa

Alopecurus vaginatus
Carex buschiorum
Oxytropis cyanea
Allium albidum
Allium ruprechtii
Asperula albovii
Astragalus kazbeki
Campanula hohenackeri
Dianthus cretaceus
Onosma armeniaca
Myosotis arvense

8.1.4 Microclimate and Energy Balance

A characteristic feature of high mountain ecosystems is their considerable variability within a relatively small area. As a result of particularly harsh climatic conditions (especially directed ones, like solar radiation and wind) and the relief of the high-mountains, a mosaic of various microhabitats emerges.

The microclimate and energetic

Table 6 — *Pulsatilleta* in Kazbegi	
Height (m s. m.)	2050
Exposition	S
Slope (°)	35
Cover (%)	90
Festuca rupicola	5
Carex buschiorum	4
Bromopsis veriegata	2
Agrostis tenuis	2
Koeleria cristata	2
Koeleria caucasica	2
Bupleurum polyphyllum	2
Plantago caucasica	3
Pulsatilla violacea	4
Anthyllis variegata	2
Potentilla crantzii	2
Trifolium ambiguum	1
Ranunculus oreophilus	2
Selaginella selaginoides	1
Leontodon hispidus	2
Silene ruprechtii	1
Cerastium arvense	2
Veronica gentianoides	2
Thymus nummularius	2
Alchemilla sericata	2
Ranunculus acutilobus	1
Campanula collina	2
Euphrasia hirtella	1
Lotus caucasicus	1
Minuartia oreina	1
Ranunculus buhsei	+
Astragalus captiosus	+
Minuartia circassica	+
Pedicularis chroorrhyncha	+
Rhinanthus minor	+
Thesium procumbens	+
Campanula bellidifolia	+
Gentiana aquatica	+

Fig. 32 — *Grossheimia polyphylla* (Svaneti, West Georgia) (*Photo Dolukhanov*).

conditions of phytocoenoses have been studied (by the method of CERNUSCA, 1976) on the following objects, selected for this purpose:

- *Hordeeta*: (1850 m s. m.) The meadow represents the *Hordeum violaceum-Poa pratensis-Anthriscus nemorosa* community with a very rich composition, including up to 70 species (table 4).

- *Festuceta*: (2000 m s. m.) The pasture meadow occupies extremely slanting and rocky slopes of a south-western exposure. The *Festuca varia-Carex meinshauseniana* community is widespread in the subalpine and alpine belts of the Central Greater Caucasus (table 7).

- *Deschampsietea*: (1750 m s. m.) These hay meadows are found on well-moistened habitats. Dominating species are *Deschampsia cespitosa* and *Equisetum palustre*, with regular occurrence of *Phragmites australis* (table 8).

- *Pulsatilleta*: (2050 m s. m.) Is part of an intensively grazed vast pasture. This is *Pulsatilla violacea-Festuca rupicola-Carex buschiorum* community (table 6).

- *Dryeta*: (2050 m s. m.) The community is found on an extremely slanted north-western slope. As a result of intensive grazing, the substrate is characterized as "step" relief. The dominants are *Dryas caucasica, Lerchenfeldia flexuosa* and *Daphne glomerata* (table 11).

- *Heracleeta*: (2200 m s. m.) This tall herbaceous phytocoenosis is found on gently slanting northern slopes, in a hi-

Table 7 – Festuceta variae in Kasbegi

Height (m s. m.)	2000
Exposition	NW
Slope (°)	45
Cover (%)	100

Carex meinshauseniana	4
Agrostis plantifolia	2
Bromopsis variegata	2
Festuca varia	5
Helictotrichon pubescens	2
Calamagrostis arundinacea	2
Poa longifolia	2
Anthoxanthum odoratum	2
Polygonum carneum	3
Vicia alpestris	3
Campanula collina	2
Alchemilla sericata	2
Trifolium ambiguum	1
Primula amoena	1
Betonica macrantha	2
Inula orientalis	2
Pedicularis chroorryncha	2
Silene ruprechtii	1
Ranunculus oreophilus	2
Ranunculus caucasicus	1
Pyrethrum roseum	2
Cuscuta europaea	+
Minuartia circassica	2
Minuartia imbricata	2
Scabiosa caucasica	2
Cirsium obvallatum	1
Trifolium trichocephalum	1
Myosotis alpestris	1
Polygala alpicola	1
Leontodon hispidus	2
Thymus nummularius	2
Lotus caucasicus	1
Anemone fasciculata	2
Alchemilla retinervis	2
Rhinanthus minor	1
Cerastium purpurascens	1
Carum alpinum	+
Centaurea cheiranthifolia	+
Coeloglossum viride	+
Cruciata glabra	+
Gentiana septemfida	+
Polygonum alpinum	+
Selaginella helvetica	+
Viola odorata	+

ghly humid substrate. Dominating species, *Heracleum sosnowskyi*, grows 2.4 m in height. The remaining 7 species are rather scarce.

- *Kobresieta*: (2175 m s. m.) Is found on gently slanting north-western slopes. The dominants are *Kobresia capilliformis*, *C. persica* and *Carex meinshauseniana* (table 8a; fig. 33).

- *Rhododendreta*: (2200 m s. m.) Is found on steep north-western slopes. It is *Rhododendron caucasicum* and *Vaccinium myrtillus* community. The former is more developed (table 8b).

Analysis of the canopy structure and spatial orientation of leaves; microclimatic characteristics, profiles of soil, canopy and air temperature and humidi-

Table 8 – Deschampsieta in Kasbegi

Height (m s. m.)	1750
Exposition	W
Slope (°)	3
Cover (%)	80

Deschampsia cespitosa	5
Phragmites australis	4
Festuca arundinacea	2
Festuca pratensis	2
Agrostis planifolia	2
Phleum pratense	2
Carex aequivoca	3
Ranunculus elegans	3
Ranunculus buhsei	2
Rhinanthus minor	2
Cerastium arvense	2
Cerastium caespitosum	2
Linium catharticum	1
Trifolium fontanum	1
Equisetum palustre	4
Trifolium ambiguum	1
Leontodon hispidus	1
Lotus caucasicus	2
Cuscuta europaea	+
Euphrasia hirtella	+
Plantago caucasica	+
Trifolium repens	+
Vicia grossheimii	+
Carum carvi	+
Cruciata glabra	+
Ligularia sibirica	1
Seseli transcaucasica	+
Ranunculus acutilobus	+
Cirsium simplex	2
Geranium ruprechtii	+
Trifolium repens	+

Table 8a – Kobresieta in Kazbegi

Height (m s.m.)	2150
Exposition	N
Fall (°)	5
Cover (%)	90

Kobresia capilliformis	5
Kobresia persica	4
Carex buschiorum	2
Trifolium ambiguum	2
Trifolium repens	2
Trifolium fontanum	1
Trifolium canescens	1
Agrostis planifolia	1
Helictotrichon asiaticum	2
Bromopsis variegata	1
Lotus caucasicus	2
Polygonum viviparum	2
Antennaria caucasica	2
Campanula biebersteiniana	2
Leontodon danubialis	+
Taraxacum confusum	2
Plantago caucasica	2
Minuartia circassica	2
Minuartia oriena	2
Cerastium purpurascens	2
Draba hispida	1
Draba repens	1
Cirsium pugnax	+
Gnaphalium supinum	+
Thesium alpinum	+

ty, falling and reflected radiation, net radiation, soil and convective heat flows and evapotranspiration have been made on the previously measured sites, which are described above.

As a result of this investigation of the structure of phytomass, the incident angle and the spatial orientation of leaves, 3 types of canopy have been relieved (TAPPEINER *et alii*, 1989);
1) Canopy with uniform leaf orientation (on different slopes), the phytomass concentrated in the lower parts of canopy.
2) Canopy with uniform distribution of phytomass in hight and with basically erectophile leaf orientation in all canopy layers.
3) Canopy with a "storey" distribution of the phytomass and mainly planophile leaf orientation. Individual plant species are dominant.

Dryeta, Pulsatilleta and *Kobresieta* can be attributed to the first type of canopy. The basic layer of radiation exchange in these phytocoenoses is close to the ground. The second type involves *Festucetum* and *Deschampsieta* with low absorption of radiation, observable in the upper layers of the phytocoenosis and almost linear absorption of radiation in the lower part of the canopy. *Hordeetum, Heracleetum* and *Rhododendretum* communities, which belong to the third type, reveal absolutely different strategy of adaptation to radiation. The bulk of the biomass and the assimilative ingredients are accumulated in the upper layers of the canopy, thus providing maximum utilisation of the PhAR by their assimilating organs.

As shown in table 9, intensively grazed phytocoenoses are the least utilizers of falling PhAR (*Hordeetum* pasture; *Pulsatilletum*; *Kobresietum*).

Measurements of vertical temperature profiles prove that irregularities between the temperature of the canopy and that of surrounding air are being smoothed. Regarding the energy balance of these phytocoenoses, a similar (post-grazing) tendency of utilisation of the absorbed solar energy into heat exchange and transpiration is evident. On all pastures, the ratio of evapotranspiration (20-40%) in the net radiation is reduced, while the ratio of convective and soil heat flows considerably grows. fig. 34 demonstrates the canopy structure, PhAR absorption and the energetic pattern of *Hordeetum* both in preserve and on pasture. All these obvious modifications (often irreversible) have been caused by strong human impact.

Every high-mountain phytocoeno-

sis in its natural development, acquires a special strategy of adaptation to environmental conditions, expressed in a definite spatial canopy structure (leaf orientation, distribution of LAI, etc.), which provokes a specific course of radiation energetic processes within the canopy. Heavy exploitation of the phytocoenoses (extensive haymaking, grazing) may stimulate irreversible processes, destroying habitual organisation of the canopy, leading to alterations in the direction of successive processes and moreover, arise dangerous erosion processes in the complex high-mountain relief. Therefore, exploitation of community should be subject to time limitation so as to prevent any such consequences and also to preserve the unique originality of high-mountain ecosystems.

8.1.5 Water Relations

An integral part of investigations into plant ecology is the study of the most important indicator of the vital activity of plants water relations. Water relations in the high-mountain plants of the Central Caucasus have been subject to intensive and long-term observations since the beginning of 1960s. Results of the analysis have been published in Georgia and abroad. However, the purpose of our further investigations is not only to expand the spectrum of the areas studied, but also to reconsider certain problems of water relations in highmountain vegetation in view of availability of highly sensitive and compact field measuring devices and owing to new conceptions in plant ecology.

Our investigations confined the thesis that the indices of water relations in plants, i.e. water contents in leaves, xylem water potential and leaf transpiration, studied in order to determine their characteristic features, present three interrelated and complementary physiolo-

Fig. 33 — *Kobresietum,* Kazbegi, 2150 m (East Georgia).

Table 9 – Distribution of Photosynthetically Active Radiation (PhAR) in different plant communities (Tappeiner, Cernusca, Nakhutsrishvili, 1990).

Community	Recorded Radiation	Albedo	Photosynthesizing parts of plants (leaves, green shoots, etc.)	Non-photosynthesizing parts of plants (trigs, dead matter, etc.)	Soil
	%	%	%	%	%
Hordeeta (*H. violaceum*)	100	5	84	10	1
Festuceta (*F. varia*)	100	4	30	65	1
Deschampsieta (*D. caespitosa*)	100	5	84	5	6
Festuceta (*F. ovina*)	100	7	53	14	26
Dryeta (*D. caucasica*)	100	7	65	25	3
Heracleeta (*H. sosnowskyi*)	100	5	88	7	0
Rhododendreta (*Rh. caucasicum*)	100	3	92	5	0

Table 8b – *Rhododendreta* in Kazbegi

Height (m s. m.)	2200
Exposition	N
Fall (°)	25
Cover (%)	100
Rhododendron caucasicum	5
Vaccinium myrtillus	3
Vaccinium vitis-idaea	2
Calamagrostis arundinacea	2
Pyrola minor	1
Agrostis planifolia	2
Anemone fasciculata	1
Geranium ibericum	1
Empetrum hermaphroditum	2
Luzula spicata	+
Carex tristis	+
Nardus stricta	+
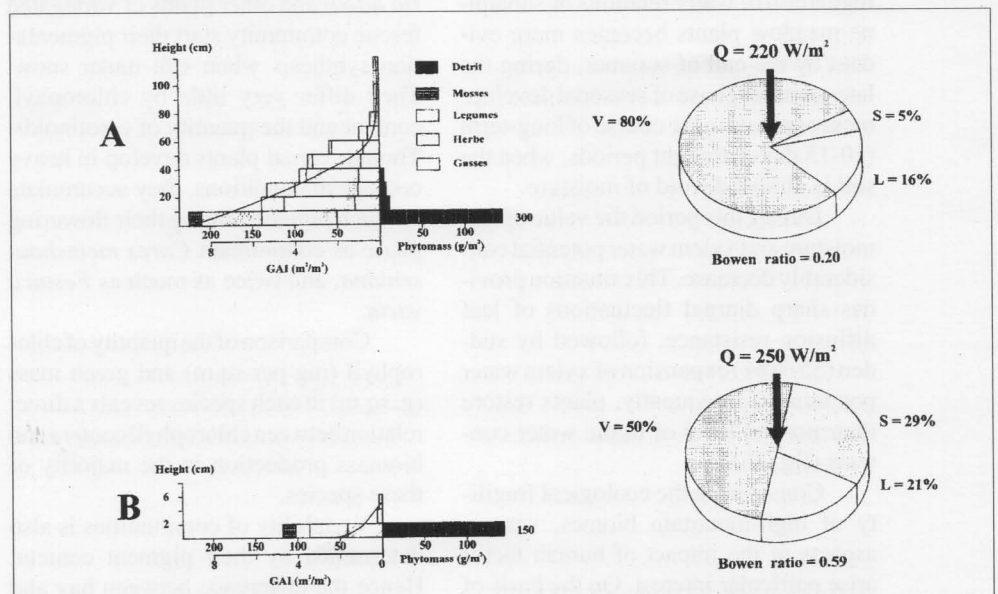
Fig. 34 — Canopy structure and energy budget in *Hordeetum* community. (Q - global radiation; V - evapotranspiration; L - convectional heat; S - soil heat; A - preserve; B - pasture).

gical parameters, giving an accurate picture of the water relations in plants. The determination of the diffusion resistance of leaves allowed us to judge of the function of stomatal apparatus in this vital process. In order to obtain structural characteristics of water relation, we had to study various anatomical and morphological peculiarities of leaves; for ecological purposes – the phytoclimate and other environmental factors, controlling water relations. The soil moisture has also been carefully examined.

Particular attention was paid to the analysis of regulation mechanisms of the water relations in high-mountain meadow plants. By recent observations even in the subalpine belt of the Central Caucasus, where hydrothermal conditions are most favourable, water evaporation in plants is frequently magnified according to the considerable rise of air temperature and PhAR in the afternoon. Consequently, water contents and xylem water potential noticeably diminish. These conditions stimulate leaf diffusion resistance, hence normal water supply is quickly restored (fig. 35). It should be noted, that physiological regulation by transpiration is expressed rather differently in species of various ecological groups and life forms.

Stomatal regulation of water exchange in plants of the subnival belt of the Central Caucasus is much more pronounced. Due to extreme ecological conditions, plants of this belt sharply diminish water release in the afternoon (88-97%) reducing transpiration to insignificant values as a result of intensification of leaf diffusion resistance.

However, the most important part of the stomata apparatus of leaves in the regulation of water relations of subalpine meadow plants becomes more evident by the end of summer, during the late-summer phase of seasonal development of plants in the course of long-term (10-15 days) drought periods, when the soil is almost devoid of moisture.

During this period the value of leaf moisture and xylem water potential considerably decrease. This situation provides sharp diurnal fluctuations of leaf diffusion resistance, followed by sudden (55-70%) expansion of xylem water potential. Consequently, plants restore their normal level of tissue water contents (fig. 36).

Considering the ecological fragility of high-mountain biomes, various aspects of the impact of human factor arise particular interest. On the basis of studies on the effect of grass-mowing and grazing on water exchange in high-mountain plants, the most favourable exploitation regime applicable to subalpine meadows has been determined, i.e. a systematic, regular (2-3 times per year) grass-mowing. Grazing or complete reservation, which cause gradual reduction of the green phytomass, seem inexpedient.

8.1.6 Pigment Content

Content of chlorophyll and carotinoid pigments in leaves of more than 100 species of the Central Caucasus plants has been subject to analysis in various habitat conditions at the altitudes of 1800-3000 m. The pigment content and distribution in different layers of phytocoenoses has been carefully studied. Chlorophyll content in leaves was determined spectrophotometrically.

By their chlorophyll and carotinoid content, the examined species clearly differ from each other as to their habitat and phytocoenoses, so within a single phytocoenosis. Results of our investigations are illustrated here by the variegated fescue community, found in moderately humid habitats of the north-western slope exposure (1950 m s. m.).

We selected 20 most typical species out of 60 plant species from this phytocoenosis, for close observation during the flowering phase.

Low chlorophyll content (2.66 mg g of dry mass) is typical for the dominant edificator *Festuca varia*, and the maximum (11.8 mg) – for *Vicia alpestris*. The low content of chlorophyll in dominant species can be accounted for by almost erectophyile orientation of leaves, unshaded by other plants.

Spring-flowering plants (*Anemone fasciculata, Primula amoena, Fritillaria lutea*) and other plants of variegated fescue community start their pigmentation synthesis when still under snow. They differ very little by chlorophyll content and the quantity of carotinoids. Though vernal plants develop in heavy ecological conditions, they accumulate as much pigment during their flowering phase as codominant *Carex meinshauseniana*, and twice as much as *Festuca varia*.

Comparison of the quantity of chlorophyll (mg per sq.m) and green mass (g. sq.m) in each species reveals a direct relation between chlorophyll content and biomass production in the majority of these species.

Variability of communities is also determined by their pigment content. Hence the difference between hay and pasture meadows.

Allocation of pigments depends on the height of phytocoenosis, e.g. pigment measurement in every 10 cm layer of the stand (herb-barley meadow) shows that max. amount of pigments (5.75 mg) is accumulated in the 50-60 cm layer and min. (1.00 mg) - in the first (90-100 cm) stand layer.

Consequently, the content of pigments in high-mountain phytocoenoses depends on the complexity of vegetation community structure, which in its turn predetermines the microclimate of the given phytocoenosis. Further, pigment content displays specific variety as a genetic property, in terms of plant species.

8.1.7 CO_2-Gas Exchange in Plants

Materials and Methods

Investigations were carried out in 13 different and most characteristic habitats of the Central and Minor Caucasus. 61 species of flowering plants have been studied for this purpose.

CO_2-gas exchange of intact plant leaves proceeded in under field conditions with infrared gas analyser techniques. The studies were conducted in the open system according to the universally accepted procedure (ABDALADZE, 1994).

Plant CO_2-Gas Exchange in Different Communities

Most intensive CO_2-assimilation in plants is observed in *Hordeetum* (moderate moist meadow) communities. In *Pulsatilletum* (dry meadow) and *Deschampsietum* (moist meadow) communities, the intensity of photosynthesis is slightly lower, whereas in *Rhododendron* communities it is considerably suppressed. CO_2-gas exchange in plants in the communities *Festucetum* (except *Festuca varia*) on dry south-western mountain side is strongly depressed. Particularly, net-photosynthesis midday depression frequency, duration and capacity are substantially increased and net-primary productivity-decreased.

CO_2-gas exchange in *Festuca varia* (tussock grass with rigid and rollied in peinomorphic leaves) is very steady: net-photosynthesis midday depression frequency is extremely low (5-8%), as well as the coefficient of variation of CO_2-gas exchange (22-25%). It should be noted, that all parameters in this species display an amazingly constant character on moderately moist slope, on relatively dry slope and at the upper boundary of distribution area of these species (3000 m s. m.), where *Festuca*

varia is not a dominant species and is represented by isolated specimen.

The CO$_2$-gas exchange character in *Festuca varia* can be considered as the ecophysiological basis of increased biological activity of this "powerfull" dominant, that promotes (particularly in the anthropogenic conditions) its intrusion into different coenoses – "capture" and "holding" of various territories.

Succulent species *Sedum oppositifolium* and *Sempervivum pumilum* are highly adapted to extreme temperature relations of their microhabitats. These succulents assimilate CO$_2$ by the CAM pathway, which is the most economical way of adaptation for their CO$_2$-gas exchange.

C$_3$-type of carbon assimilation is typical for *Saxifraga juniperifolia* and *Sedum gracile*.

The obtained data shows that in winter, the evergreen shrub *Rhododendron caucasicum* blocks maximally the interaction with environment and entirely restricts metabolic processes. Net-photosynthesis is not detectable. Dark respiration rate is extremely low (0.2-0.5 mmol CO$_2$/m^2. s). In winter this species undergoes "deep resting" period.

Contrary to evergreen shrubs, summer-wintergreen herbs (*Plantago lanceolata, Phleum pratense, Trifolium alpestre, Carex sylvatica*) in winter are capable of CO$_2$ uptake. During thaw the diurnal balance of CO$_2$-gas exchange, is usually positive. Maximum values of net-photosynthesis on the plots free from snow reach 5.4-9.5 (mmol CO$_2$/m^2. s (37-50% of vernal maximum). Under the snow cover CO$_2$ uptake is possible only for a short period of time (1-3 h a day).

Maximum Net-Photosynthesis

High net-photosynthesis maximum values show: the legumes – *Trifolium ambiguum, Trifolium fontanum, Vicia grossheimii*, etc. (17-20 mmol CO$_2$/m^2. s), *Ranunculus oreophilus, Pulsatilla violacea, Leontodon hispidus, Alchemilla sericata, Geranium gymnocaulon, Sibbaldia semiglabra* (18-22 mmol CO$_2$/ m^2. s). The grasses (*Agrostis planifolia, Hordeum violaceum, Bromopsis riparia, Nardus stricta, Festuca rupicola, Festuca varia*, etc.) show moderate values (10-15 mmol CO$_2$/m^2. s). Low maximums are characterized by C$_3$ succulents, *Rhododendron caucasicum, Parnassia palustris* and the sedges (4.5-10 mmol CO$_2$/m^2. s).

Dark Respiration
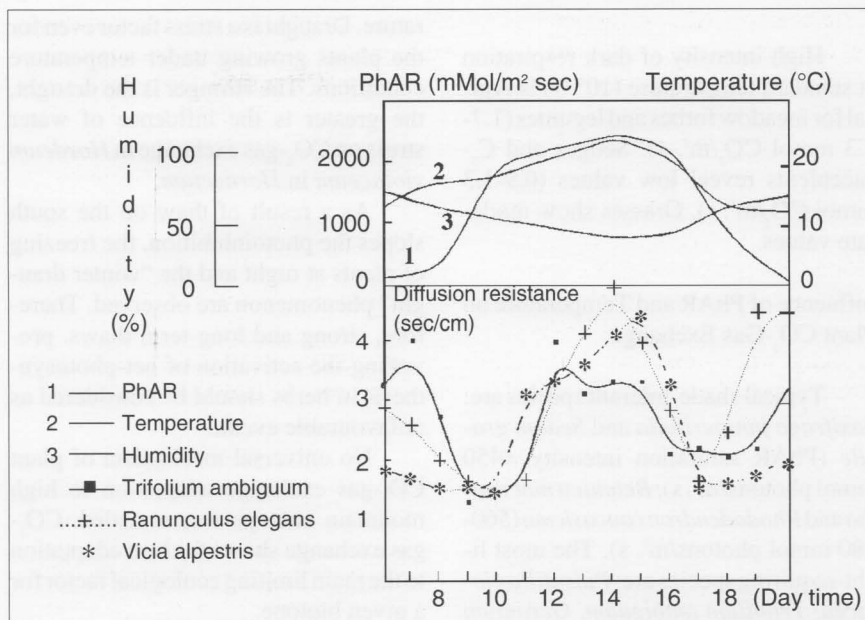
Fig. 35 — Diurnal course of leaf diffusion resistance of subalpine plants (Diffusion resistance of leaves was measured by a field ventilation air diffusion porometer, KÖRNER, CERNUSCA, 1976) (SANADIRADZE, 1986).
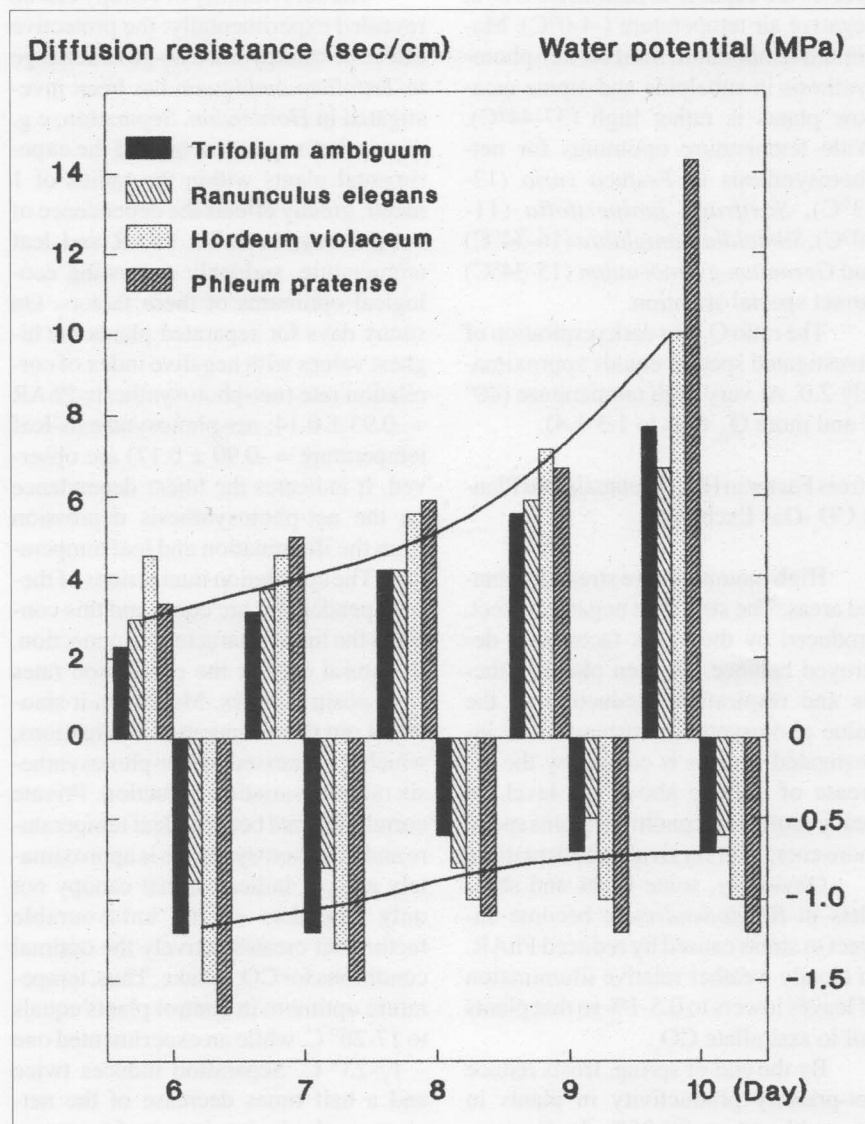
Fig. 36 — Oscillation of plant water potential and diffusion resistance under tense hydrothermal conditions (6-10 august 1985) (the water potential of xylem was investigated in a pressur chamber, KÖRNER *et alii*, 1978) (SANADIRADZE, 1986).

High intensity of dark respiration at standard temperature (10° C) is typical for meadow forbes and legumes (1.7-2.3 mmol CO_2/m^2. s). Sedges and C_3-succulents reveal low values (0.9-1.3 mmol CO_2/m^2. s). Grasses show moderate values.

Influence of PhAR and Temperature on Plant CO_2-Gas Exchange

Typical shade-tolerant species are: *Saxifraga juniperifolia* and *Sedum gracile* (PhAR saturation intensity =450 mmol photons/m^2. s), *Betonica macrantha* and *Rhododendron caucasicum* (560-580 mmol photons/m^2. s). The most light-requiring species are: *Pulsatilla violacea, Trifolium ambiguum, Geranium gymnocaulon, Sibbaldia semiglabra* and some others (1000-1500 mmol photons/m^2. s; 42-48% from full PhAR).

The majority of the investigated species are capable to assimilate CO_2 at negative air temperature (-4-0°C). Maximum temperature limit for net-photosynthesis in subalpine and alpine meadow plants is rather high (37-44°C). Wide temperature optimums for net-photosynthesis in *Festuca varia* (12-13°C), *Saxifraga juniperifolia* (11-30°C), *Sibbaldia semiglabra* (16-34°C) and *Geranium gymnocaulon* (15-34°C) attract special attention.

The ratio Q_{10} for dark respiration of investigated species equals approximately 2.0. At very high temperature (40° C and more Q_{10} falls to 1.3-1.4).

Stress Factor in High Mountain and Plants CO_2-Gas Exchange

High mountains are stress dominated areas. The strongest negative effect, produced by the stress factor is a destroyed balance between photosynthesis and respiration. Reduction of the value photosynthesis/respiration in investigated species is caused by the increase of altitude above sea level. In heavy ecological conditions plants spend more energy on survival and adaptation.

Obviously, some herbs and shrublets in *Rhododendretum* become subject to stress caused by reduced PhAR. In cloudy weather relative illumination of leaves lowers to 0.5-1% so that plants fail to assimilate CO_2.

By the end of spring, frosts reduce net-primary productivity in plants in *Agrostidetum* on 80-85%. In *Festucetum* (dry south-western slope) in all investigated species, except *Festuca varia*, net-primary productivity decreases for 11-35%, because of high air tempe-

rature. Draught is a stress factor even for the plants growing under temperature conditions. The stronger is the draught, the greater is the influence of water stress on CO_2-gas exchange in *Hordeum violaceum* in *Hordeetum*.

As a result of thaw on the south slopes the photoinhibition, the freezing of plants at night and the "winter draught" phenomenon are observed. Therefore, strong and long-term thaws, provoking the activation of net-photosynthesis in herbs should be considered as unfavourable event.

No universal mechanism of plant CO_2-gas exchange adaptation to high mountain ecotope was revealed. CO_2-gas exchange shows the best adaptation to the main limiting ecological factor for a given biotope.

Phytocoenotic Effect on Plant CO_2-Gas Exchange

The survivability of canopy can be revealed experimentally: the protective effect of canopy on CO_2-gas exchange in *Trifolium ambiguum* has been investigated in *Hordeetum*. Separation, e.g. removal of vegetation around the experimental plants within the radius of 1 meter, greatly effects the dependence of net-photosynthesis on PhAR and leaf temperature, suddenly narrowing ecological optimums of these factors. On sunny days for separated plants the highest values with negative index of correlation rate (net-photosynthesis-PhAR = -0.93 ± 0.14; net-photosynthesis-leaf temperature = -0.90 ± 0.17) are observed. It indicates the linear dependence on the net-photosynthesis depression from the illumination and leaf temperature. The correlation interactions of these dependencies are equal and this confirms the linear character of connection. In natural canopy the correlation rates have positive index. Moreover, it smoothed out the temperature fluctuations, which is expressed by net-photosynthesis ratio of variation reduction. Private correlation rate between leaf temperature and net-photosynthesis is approximately zero. It indicates, that canopy not only smoothes up the unfavourable factors but creates actively the optimal conditions for CO_2 uptake. Thus, temperature optimum in control plants equals to 17-26° C, while an experimented one – 17-23° C. Separation induces twice and a half times decrease of the net-photosynthesis maximums frequency. It also demonstrates the ability of vegetation cover to support favourable conditions temperature, air humidity, PhAR.

This effect is directed against stress

factors of the environment for support of optimal CO_2-gas exchange balance and is probably the result of a cooperative functioning of plants formed in the process of a long-standing joint evolution.

Anthropogenic Influence of Plant CO_2-Gas Exchange

Our investigations have been carried out in *Hordeetum* in the pasture, the hay and preserved plots. On intensively grazed meadow CO_2-gas exchange of plants is destabilised. Here, net-photosynthesis strong midday depressions are observed rather clearly (depression rate = 54-59%). On preserved and hay meadows net-photosynthesis reduction at depressions does not exceed 38-45%, whereas on pastures it is 78-81%. On pastures, net-primary productivity and diurnal balance of CO_2-gas exchange are substantially depressed.

On hay meadows (once a year) optimal CO_2-gas exchange balance was observed.

8.1.8 Life Activity of High-Mountain Plants in Winter

Life activity of high-mountain plants in winter has been studied in the upper-forest and subalpine belts of the Minor Caucasus. Our objective was to examine the strategies of hibernation of summer-winter-green meadow, herbaceous and evergreen shrub plants.

On the basis of the obtained data, winter evergreen shrubs usually hinder any interactions with the environment and entirely restrict metabolic processes. Therefore, leaf and air temperatures virtually remain immutable, water content in leaves slightly changes (1-2%) compared to autumn, stomata are closed, transpiration and net-photosynthesis are imperceptible, respiration rate is extremely low. In profound dormancy, resistance of shrubs against various stress factors is much higher. Safe hibernation depends on snow protection, which prevents plants from desiccation and dehydration.

Contrary to evergreen shrubs, summer-winter green herbaceous species are capable of vital activity at ever favourable opportunity in winter, particularly during thaw.

In free of snow areas, leaf temperature of the hibernating species amounts to high values on clear days, exceeding air temperature by 5.0-9.3° C. Diurnal dynamics of water content, xylem water potential, transpiration intensities and net-photosynthesis are displayed rather clearly. During thaw the diurnal balance

of CO_2-gas exchange is usually positive, whereas maximum intensity of the net-photosynthesis attains 37-50% of vernal maxima. CO_2 assimilation under snow cover becomes possible only for a short period.

8.2 Alpine Vegetation

The alpine belt in the Caucasus extends from 2400-2500 up to 2900-3000 m s. m. It is characterized by the dominance of short grass meadows; carpet-like alpine meadows, alternating with *Rhododendron caucasicum* thickets and rock-scree vegetation are also well developed here.

8.2.1 Alpine Meadows

Alpine meadows occupy vast areas in Georgia. They are valuable natural grasslands. These communities mainly occur on mountain wetlands. Within the alpine meadows, it is possible to distinguish firm-bunch and sedge meadows, forb meadows and those dominated by tussock grasses and forbs. These groups of formations are typical for all geographical variants of the mountain-meadow vegetation of the Caucasus. The occurrence of local endemics is one of the floristic peculiarities of the above-mentioned communities.Information on the syntaxa of high-mountain vegetation, including that of alpine belt is available in table 10. *Festuceta variae, F. supinae, Nardeta strictae, Cariceta tristis, Kobresieta capilliformis* and *K. persicae* are the major formations of firm-bunch meadows.

Festuceta variae (F. woronowii). These communities are confined to steep slopes of southern exposure. Most frequently they occur in the eastern part of Kavkasioni (Greater Caucasus).

Variegated fescue meadows are widespread in subalpine belt; they occupy areas, once populated by crook-stem forests, *Rhododendron* thickets and *Nardus* communities (KIMERIDZE, 1965).

Nardeta. Nardus communities are very abundant throughout the Caucasus; they are restricted to the slopes of all exposures. Though due to the overgrazing, the secondary *Nardus* communities prevail here. Mixed communities of *Nardeto-Festucetum variae* can be found in the central and eastern parts of the Greater Caucasus. Under the influence of pasturing hygrophytic *Nardus* communities have developed on swampy depressions of alpine belt.
Cariceta tristis. These coenoses are very

Table 10 — The phytosociological classification of the vegetation of alpine belt of Upper Svaneti (SAKHOKIA, KHARADZE, DOLUKHANOV *et alii*, 1942).

Communities

1.1. *Sibbaldia parviflora + Carum meifolium*

2.1. *Sibbaldietum mixtoherbosum*
2.2. *Sibbaldia semiglabra + Geranium gymnocaulon*
2.3. *S. semiglabra + Festuca supina*
2.4. *S. semiglabra + Taraxacum stevenii*
2.5. *S. semiglabra + Ranunculus svaneticus*
2.6. *S. semiglabra + Pedicularis condensata*
2.7. *Sibbaldietum lichenoso - muscosum*
2.8. *Sibbaldia semiglabra + Campanula biebersteiniana*
2.9. *S. semiglabra + Ranunculus svaneticus + Gnaphalium supinum*
2.10. *S. semiglabra + Gnaphalium supinum*
2.11. *S. semiglabra + Carex micropodioides + Festuca supina*

3.1. *Ranunculetum svanetici typicum*
3.2. *Ranunculus svaneticus + Gnaphalium supinum*
3.3. *R. svaneticus + Corydalis conorrhiza + Taraxacum stevenii*
3.4. *R. svaneticus + Pedicularis crassirostris*

4.1. *Caretum caucasici*
4.2. *Carum caucasicum + Trifolium ambiguum*
4.3. *C. caucasicum + Festuca supina*

5.1. *Minuartia colchica + Carum caucasicum*
5.2. *Minuartia aizoides + Campanula biebersteiniana*
5.3. *Plantago saxatilis + Festuca supina + Minuartia aizoides*
5.4. *Antennaria caucasica + Campanula saxifraga*
5.5. *Taraxacum stevenii + Gnaphalium supinum*
5.6. *Anthemis rudolphiana + Sibbaldia semiglabra*
5.7. *Festuca supina + Campanula saxifraga*
5.8. *Antennarietum caucasicae*
5.9. *Plantago saxatilis + Festuca supina*
5.10. *Antennaria caucasica + Alchemilla caucasica*
5.11. *Festuca supina + Chamaesciadium acaule + Plantago saxatilis*

6.1. *Alchemilletum caucasicae*
6.2. *Alchemilla caucasica + Antennaria caucasica + Festuca supina*

7.1. *Calamagrostis arundinacea + Betonica macrantha*
7.2. *Trollieto - Calamagrostidetum mixtoherbosum*
7.3. *Calamagrostidetum mixtoherbosum*
7.4. *Calamagrostis arundinacea + Anemone fasciculata*

8.1. *Deschampsieto - Calamagrostidetum mixtograminosum*
8.2. *Brometo - Calamagrostidetum mixtograminosum*
8.3. *Calamagrostis arundinacea + Trisetum pratense*

9.1. *Festuca djimilensis + Vaccinium myrtillus*
9.2. *Festuca djimilensis + Inula orientalis + Trollius caucasicus*

10.1. *Trifolieto - Brometum mixtoherbosum*
10.2. *Careto - Brometum mixtoherbosum*

11.1. *Trisetum pratense + Euphorbia abchasica + Polygonum carneum*

12.1. *Festuca djimilensis + Calamagrostis arundinacea + Geranium platypetalum + Vaccinium myrtillus*
12.2. *Calamagrostidetum arund. mixtograminoso - mixtoherbosum*
12.3. *Calamagrostidetum glaucae mixtograminoso - mixtoherbosum*
12.4. *Calamagrostis arundinacea + Festuca djimilensis + Anemone fasciculata + Betonica macrantha*
12.5. *Poetum longifoliae mixtoherbosum*

13.1. *Agrostis capillaris + Trifolium canescens*

14.1. *Trollius caucasicus + Geranium gymnocaulon*

15.1. *Anemone fasciculata + Betonica macrantha*

16.1. *Alchemilla tredecimbola + Valeriana colchica*
16.2. *Alchemilletum tredecimlobae mixtoherbosum*

17.1. *Geranium typicum*
17.2. *Geranium gymnocaulon + Calamagrostis arundinacea*

18.1. *Geranium gymnocaulon + Carex aequivoca + Phleum alpinum + Anthoxantum odoratum + Carum meifolium*
18.2. *Geranium gymnocaulon + Festuca supina + Senecio taraxacifolium + Aster caucasicus + Primula amoena*
18.3. *Triseto - Graminetum mixtoherbosum*

19.1. *Geranium gymnocaulon + Anemone fasciculata + Betonica macrantha*
19.2. *Geranium gymnocaulon mixtoherbosum*
19.3. *Geranium gymnocaulon + Trollius caucasicus + Anemone fasciculata*
19.4. *Geranium gymnocaulon + Sibbaldia semiglabra*
19.5. *Geranium gymnocaulon + Campanula biebersteiniana*
19.6. *Geranium gymnocaulon + Trollius caucasicus*
19.7. *Geranium gymnocaulon + Alchemilla sp.*

20.1. *Heracleetum (Heracleum aff. umbonatum Boiss.)*
20.2. *Ligusticetum alatae*

21.1. *Aconitum nasutum + Cephalaria gigantea + Heracleum aff. umbonatum*
21.2. *Senecio platyphyllus + Inula orientalis*

22.1. *Athyrium alpestris*

23.1. *Senecio platyphyllus + Rumex alpinus*

24.1. *Festucetum variae typicum*

25.1. *Festuca varia + Calamagrostis arundinacea*
25.2. *Festuca varia + Deschampsia flexuosa*

26.1. *Festuca varia + Alchemilla sp. div.*
26.2. *Festuca variae mixtoherbosum*

27.1. *Nardus stricta + Agrostis capillaris*
27.2. *Nardus stricta + Sibbaldia parviflora*
27.3. *Nardus stricta + Carum meifolium*
27.4. *Nardus stricta + Alchemilla sp. + Trifolium ambiguum*
27.5. *Nardus stricta + Plantago saxatilis*

28.1. *Carex meinshauseniana + Anthemis rudolphiana*
28.2. *Caricetum typicum*

29.1. *Festuca supina + Carex meinshauseniana*

30.1. *Festuca ruprechtii + Geranium renardii*

31.1. *Deschampsia flexuosa + Geranium renardii*

32.1. *Deschampsia flexuosa + Festuca supina + Anthemis rudolphiana*

33.1. *Deschampsia flexuosa + Anthemis rudolphiana + Campanula saxifraga*

34.1. *Kobresieta schoenoides*

35.1. *Carex dacica + Primula auriculata*
35.2. *Carex dacica + Primula auriculata + Trifolium ambiguum*

36.1. *Alchemilla tredecimbola + Deschampsia caespitosa*

37.1. *Rhododendronetum typicum*

38.1. *Rhododendron caucasicum + Chamaenerium angustifolium*
38.2. *Rhododendron caucasicum + Geranium gymnocaulon*
38.3. *Rhododendron caucasicum + Athirium alpestre*

39.1. *Rhododendron caucasicum + Vaccinium myrtillus + Deschampsia flexuosa*

abundant in the high-mountains of the Caucasus. Usually they inhibit prominent slopes exposed to winter winds. *Carex tristis* participates in the formation of sedge-fescue association *(Festuca supina-Carex tristis)*. The most typical communities are such, as: *Cariceto-Alchemilleta (Alchemilla caucasica)* and *Cariceto-Kobresieta (Kobresia capilliformis)*.

Kobresia capilliformis. These communities like those of *K. persica* are found chiefly in the central and eastern parts of Kavkasioni and the southern upland of Georgia. They cover mountai ridges and prominent slopes. Coenoses, with Middle Asian-Himalayan *Kobresia capilliformis*, are very common in Georgia; the above-mentioned communities occur on marl-like shales and limestones of the Central Caucasus. Within variegated fescue meadows *Kobresieta schoenoidis* occur on stony localities.

Festuceta djimilensis. It belongs to the tussock grass-forb meadows, which have penetrated into the alpine belt from subalpine zone; *Festuceta djimilensis* is typical for both cobble and wet substratum (mostly in the western part of Kavkasioni).

Bromus communities *(Bromopsieta variegati)*, which enter the same group, are restricted to the southern slopes of alpine belt. In the high-mountains of Colchis, dry meadows occur on limestones; these meadows are formed by *Sesleria anatolica*, a grass with creeping rhizome.

Geranieta (G. gymnocaulon). These communities of forb meadows of alpine belt, are distributed in the western part of Kavkasioni. According to DOLUKHANOV (1946), *Geranium* communities extend from the low-alpine subzone to the upper limits of dense vegetation; these meadows merge into the subnival belt. They occur on mountain-meadow skeletal soils.

8.2.2 Carpet-Like Alpine Meadows

Carpet-like alpine meadows are a diverse group of formations. They occur in the upper part of the alpine belt. These coenoses are to be found among large stones.

The term "carpet-like alpine meadows" proposed by GREBENSHCHIKOV (1965) coincides with "Dicotylen-Teppiche" of ELLENBERG (1996). Alpine carpet-like meadows are composed of the following low rosetted and caespito-

se plants: *Campanula biebersteiniana, Carum caucasicum, Veronica gentianoides, Gnaphalium supinum, Pedicularis crassirostris, P. armena, Poa alpina, Taraxacum stevenii, T. crepidiforme, Sibbaldia semiglabra,* etc.

These communities include such grasses as *Poa alpina, Phleum alpinum, Festuca supina,* etc.

Carpet-like alpine meadows differ from true meadows by their floristic composition and ecological peculiarities. Due to the lasting snow cover, they are characterized by short vegetative period. Herbage of the above-mentioned meadows does not exceed 3-4 cm. 80% of phytomass is accumulated in a 0-1 cm layer. As noted above, the carpet's sod belongs to the forb-type sod-forming. The typical carpet's sod has a two-layer structure. The main mass of the individual sod is concentrated in the upper layer (5-6 cm). The lower layer consists of separate deep roots (20-25 cm). Alpine carpet-like meadows are distinguished by large and brightly coloured flowers and inflorescences.

Some authors suggest to consider alpine carpet-like meadows as Nanoherbeta, which belong to eumesophytic meadows.

Besides the climax carpet-like alpine meadows, secondary carpets, enriched by meadow elements (especially *Alchemilla* species), occupy considerable areas. Development of these secondary carpets is caused by overgrazing.

Sibbaldia semiglabra communities as well as those of *S. parviflora* are of particular interest. Pure *Sibbaldia* communities are very poor floristically.

These secondary communities occupy the most exploited pastures. Endemic carpet-like alpine meadows with *Ranunculus helenae* occur on limestone substratum in Colchis. Moist sites are occupied by carpets of *Carum caucasicum*. Pure stands of the above-mentioned plant are quite rare; usually it associates with *Taraxacum stevenii, Campanula biebersteiniana, Plantago saxatilis, Minuartia aizoides,* etc. Carpet-like communities which are developed around the snow spots and at the edges of glaciers, include the following species: *Ranunculus oreophilus* var. *pumilus, R. baidarae, Primula algida, Gentiana djimilensis (= G. pyrenaica), G. angulosa, G. nivalis, Minuartia aizoides* and *Cerastium cerastoides*.Of the plants growing at the banks of brooks, the following may be mentioned: *Pedicularis crassirostris, P. nordmanniana, Primula auriculata, Poa alpina,* etc.

8.2.3 Alpine Shrub

Steep northern slopes of alpine belt are inhibited by *Rhododendron caucasicum* thickets ("dekiani" in Georgian). *Rhododendron* communities occur even at an altitude of 1700-1800 m. According to KOLAKOVSKY (1961), at greater altitudes *Rh. caucasicum* is restricted to cirques and valleys, which are characterized by high humidity and profound snow, protecting it from frost. The same scholar, attributes the present-day distribution of *Rh. caucasicum* in alpine belt to the lowering of upper forest margins, to which it has been confined before.

Rhododendron thickets occur on brownish-cinnamon bog soils, which are very rich in humus (usually skeletal) (fig. 37).

Subshrub communities, formed by *Dryas caucasica* (table 11) arise much interest. They favour cold stony slopes of northern exposure. In Colchis, *Dryas* communities are restricted to limestone rocks, rocky mountain ridges and stony slopes of northern exposure (KOLAKOVSKY, 1961).

Distribution area of elfin woods of *Juniperus hemisphaerica* and *J. sabina* extends throughout Kavkasioni. In Colchis, the fragments of *Juniperus* communities (fig. 38) rarely intermingle with *Rhododendron* thickets. Juniper coenoses with *Woronowia speciosa (= Geum speciosum)* occupy limestone mountains (KOLAKOVSKY, 1961).

Chionophilic communities of *Daphne glomerata* are very characteristic of Kavkasioni. Coenoses of *D. albowiana* and *D. woronowii* are abundant in Colchis. It should be noted, that *D. woronowii* communities occur on limestones.

8.2.4 Alpine Saxicolous Plants

Of the saxicolous plants of alpine belt the following should be outlined: *Campanula mirabilis, C. dzaaku, Arenaria lychnidea, Draba bryoides, Albowiodoxa elegans, Symphyandra armena,* etc. The screes are occupied by *Heracleum calcareum, Campanula schistosa, Athyrium alpestre, Anthemis sosnowskyana, Barbarea minor,* etc.

8.2.5 Ecological Characteristics of Alpine Communities

Ecological characteristics of *Nardetum strictae* and *Caricetum tristis* are presented bellow (fig. 39). These communities are typical representatives of alpine vegetation of the Caucasus. They are confined to the central part of the

Fig. 37 — Rhododendron caucasicum and *Betula litwinowii* near the upper limit of crook-stem forest (Kazbegi, East Georgia) *(Photo Abdaladze).*

| *Table 11 — Dryeta* in Kazbegi	
Height (m s. m.)	2050
Exposition	NW
Fall (°)	50
Cover (%)	100
Deschampsia flexuosa	3
Anthoxanthum odoratum	3
Carex meinshausaniana	3
Agrostis planifolia	2
Bromopsis variegata	2
Helictotrichon asiaticus	2
Nardus stricta	1
Poa alpina	1
Festuca supina	2
Daphne glomerata	2
Vaccinium vitis-idaea	1
Dryas caucasica	4
Carum caucasicum	3
Minuartia circassica	1
Trifolium ambiguum	2
Trifolium trichocephalum	1
Vicia alpestris	1
Primula amoena	1
Alchemilla sericata	1
Ranunculus caucasicus	1
Viola somchetica	1
Leontodon hispidus	1
Anemone fasciculata	1
Carum alpinum	1
Gentianella caucasica	1
Polygonum viviparum	2
Campanula collina	1
Betonica macrantha	1
Plantago caucasica	2
Selaginella selaginoides	1
Selaginella helvetica	1
Leontodon danubialis	1
Polygala alpicola	1
Polygonum carneum	1
Cirsium obvallatum	1
Ranunculus acutilobus	1
Cruciata laevipes	1
Pyrethrum roseum	1
Ranunculus oreophilus	2
Cirsium simplex	+
Parnassia palustris	+
Silene ruprechtii	+
Rhinanthus minor	+
Cirsium pugnax	+
Taraxacum confusum	+
Cerastium purpurascens	+
Minuartia imbricata	+
Scabiosa caucasica	+
Inula orientalis	+
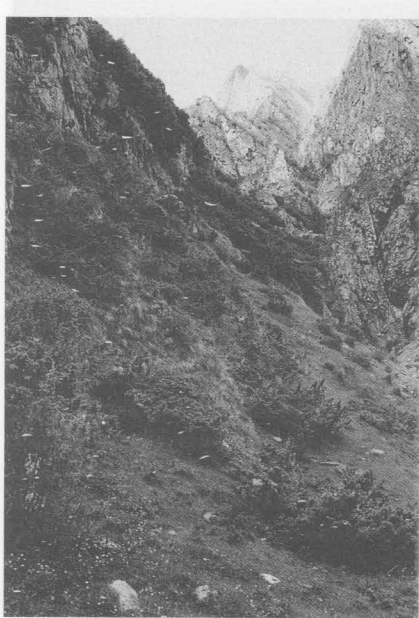
Fig. 38 — Juniperus hemisphaerica community (Kazbegi, East Georgia).

Greater Caucasus (Kazbegi region, 2650 m).

Soils

Mother rocks of this area are of volcanic origin. Soils, formed by volcanic ash, are becoming andosols or Andept (the term proposed by North American pedologists). Soils populated by the abore-mentioned communities have A-B-C profile. Transition to A-C soils can be observed at greater altitudes. Soil pH of A layer is very acid, sandy loam and pierced through with roots. It appears that water content in phytocoenosis accounts for the changes of soil color; thus, when lacking water, the colour of soil becomes lighter.

The content of organic water (17-20%) is rather high in A layer of both phytocoenoses. However, at an altitude of 1970 m, the same index is 14%.

Temperature Regime

On sunny days the herbages of both phytocoenoses undergo overheating. In *Caricetum* the lower layers and soil surface represent the "active surface" of conductive heat exchange. For example, the mean diurnal temperature of soil surface is 9,4° C higher than that of the air at the height of 2 m, and it is 10,5° C higher – at 1 m.

When studying microclimate and energy balance, we have applied the methods of CERNUSCA (1976).

Maximum temperature of soil surface is 29° C, more than that of the air at the height of 2 m.

In *Nardetum* the overheating of herbage is less than in *Caricetum*. Solar radiation is allocated over more expansive biomass, which accounts for less overheating. Maximum overheating is observed in the lower 3 cm layer of phytocoenosis. In this layer of herbage, the average diurnal temperature is 6,7° C higher and maximum temperature is 19,4° C higher than that of air at the altitude of 2 m. In *Nardetum* on soil surface the temperature reaches its maximum meaning 2 hours later, than at 3 cm higher above soil. This must be provided by a rather thick layer of detritus over the soil, which is characterized by low heat conductivity.

The temperature of leaves is very important for photosynthesis, respiration and transpiration. By the peculiarities of temperature of leaves, both phytocoenoses are of two-layer structure: in lower warm layers of herbage (*Caricetum* 0-1 cm, *Nardetum* 0-5 cm) the temperature of leaves is below the air temperature. In *Nardetum* at the height of 0,5 cm leaves are cooled off on average 1.3° C during the day, and in *Nardetum* at the height of 4 cm – on 2,6° C. Under the influence of wind, intensive convective heat exchange takes place in the upper layer of phytocoenosis. The temperature of leaves here almost equals with that of the air. On the average, the temperature of leaves in *Nardetum* (height –3 cm) exceed that of the air just by 0,1° C daily.

Air humidity, especially water vapour pressure gradients between leaves and their environment are very essential factors for many ecosystems.

The lack of water vapour cpeassure at different height levels from the surface of soil distinguishes two layers of phytocoenosis structure. In *Caricetum tristis* the layer above 1 cm is strongly influenced by wind and dry air; during the one hour (between 1.00 and 2.00 a.m.) the water vapour deficit amounts to 37,6 mbar at the height of 3 cm,

Fig. 39 — The regularity of the vertical distribution of high-mountain vegetation in Kazbegi region:

1. Subnival vegetation (*Tripleurospermum subnivale, Scrophularia minima, Nepeta supina,* etc.);
2. *Festuca supina - Carex tristis - Cobresia capilliformis*
3. *Cobresia capilliformis - C. persica - Polygonum viviparum*
4. *Bromopsis variegata-Agrostis tenuis-Scabiosa caucasica-Trifolium alpestre*
5. *Hordeum violaceum-Poa pratensis-Anthriscus nemorosa-Heracleum asperum*
6. *Festuca varia-Carex meinshauseniana*
7. *Dryas caucasica-Deschampsia flexuosa*
8. *Sibbaldia semiglabra-Taraxacum stevenii*
9. *Rhododendron caucasicum*
10. *Festuca supina-Carex tristis*

whereas at 1 cm above the surface of soil water pressure deficit is only 17,2 mbar.

Solar Radiation Regime

On sunny days, daily global radiation equals to 562 cal. cm^{-2}. In *Caricetum tristis* 21.9% of this amount is reflected by leaves, while in *Nardetum* only 19.2%. The value of albedo of *Caricetum tristis* coincides with that of *Caricetum curvulae*; these communities occur in Hohe Tauern (Cernusca, 1976). In *Caricetum* 358 cal. cm^{-2} is absorbed in the form of radiation balance, while in *Nardetum* 338 cal. cm^{-2}. For *Caricetum curvulae* in the Hohe Tauern Mts. (Austrian Alps) the radiation balance makes up 66% of global radiation.

In good weather, 44% of absorbed solar energy (radiation balance) in *Caricetum* is spent on evapotranspiration, 40.7% on air heating and 15.3% on soil heat flow, correspondingly, in *Nardetum* it is 62.5%, 28.7% and 8.8%.

Consequently, the soil heat flow in *Caricetum* is twice as much as in *Nardetum*. It can be accounted for by the fact, that a large amount of radiation is being absorbed in the lowest layers of phytocoenosis (0-0,5 cm) and in the soil surface. Whereas, in *Nardetum* radiation is absorbed in the upper layers. Besides, *Nardetum* has a rather dense layer of detritus, which retains the soil heat flow.

Results of the analysis confirm the conclusions based on the studies of dwarf shrub heaths in Patscherkofel (Tyrol, Cernusca, 1976) and alpine heaths in Hohe Tauern Mts. Obviously, the structure of phytocoenosis (orientation of leaves, shape, height of plants) and exposure have a great impact on the microclimate and energy balance of high-mountain ecosystems. Both of the studied phytocoenoses are of two-layer structure. The upper dry and relatively cool layers are more influenced by wind. The lower warm and moist layers are characterized by negligible wind speed. At the same time, we have found out that the structure of phytocoenosis, microclimate and energy balance of *Caricetum tristis* in the Caucasus is similar to those of *Caricetum curvulae* in Hohe Tauern.

Leaf Diffusion Resistance

Water Potential

Alpine plants of the Caucasus are characterized by higher value of stomatal conductance than those of Alps (Körner, 1977). Absence of stomata closing tendency, which is more pronounced in *Nardetum*, indicates at good water supply of both phytocoenosis. The values of stomatal conductance and water potential of leaves of *Carex tristis* seems to change in the opposite direction.

Extremely low values of maximum diffusion resistance speak of sufficient water supply and moist growth conditions of the plants, which occur in the alpine belt of Georgia.

8.3 Subnival Vegetation

The subnival belt is well represented in the Caucasus. It is situated between the belt of alpine meadows and that of firm fields at the altitude from 2900-3000 up to 3500-3700 m s. m.

In the Greater Caucasus, lower limit of the above-mentioned belt varies in altitude between 2900 and 3100 m, increasing from west to east. Due to the low position of eternal snow line (about 2800 m) in the western part of the Greater Caucasus, boundaries of subnival belt, represented here fragmentally, are not subject to classification.

8.3.1 Life Conditions in Subnival Belt

Subnival belt of the Caucasus is characterized by moist climate with short cold summer and long severe winter. On the basis of the data of observations by the meteorological station, situated at 3656 m s. m. (Kazbegi), the subnival belt can be characterized by the following figures: mean annual temperature 6,10° C, mean temperature of January -15° C, mean temperature of the warmest months (July-August) -10° C; extreme maximum +16° C; extreme minimum -42° C. annual amount of precipitation is 1074 mm, mean annual wind speed 6.4 m/sec.

The role of temperature as a limiting factor becomes more important; excessive solar radiation raises the temperature of soil surface and of boundary air layer, daily temperature fluctuations and evapotranspiration also increase. The role of wind as an ecological factor should be particularly emphasized, as the character of distribution of plants and communities in subnival and nival belts in many respects is dependent on the direction and strength of wind.

According to Larcher (1980), wind direction in high-mountains determines great differences in habitats, water and temperature relations of plants and soil. In respect of the observations produced by the same scholar, rocks, ridges and mountain-sides exposed to wind are less intensively warmed up by sun rays than the elongated cavities and ditches, protected from wind. The efficiency of CO_2 assimilation amounts with the altitude.

The pattern of plant microgrouping distribution, temperature and water relations of habitats, the phenological rhythm type of plants in subnival and especially nival belts are also predetermined by snow cover. In high-mountains some species of plants (chionophobes) are well adapted to low temperatures and others (chionophiles) have low frost resistance (Larcher defined characteristic properties of high-mountain biomes of diverse globe zones, including subnival and nival belts of the Caucasus, is a great variety of ecological niches within even small territories. Metabolism and plant growth in the extreme conditions of high-mountains are mainly governed by characteristic properties of microclimate of these niches.

Another unfavourable environmental factor affecting the growth of plants at high altitudes, is the ultraviolet radiation. However, due to the high concentration of carotinoids and flavonoids, these plants are well adapted to this factor (Caldwell, 1968).

Physical and geographical conditions of the subnival belt of the Caucasus are particularly extreme, but due to life strategy adaptations, for some plants, typical for this belt, such living conditions are quite optimal.

In connection with the absence of terrains with more or less mature soil, almost all the plants of subnival ecosystems are rock and talus plants. Very high percentage of endemic, including also narrow-endemic species are prominent. Some of them fall into mono- or oligotype genera (*Pseudobetckea, Symphyoloma, Pseudovesicaria, Didymophysa, Trigonocaryum, Eunomia, Vavilovia*).

Severe climatic conditions dictate strict reglementation of population variability of every species, which has its own life strategy, habitat, favourable to development of individuals in every population, often scattered at considerable distances create quite often favourable conditions for the development of another one. In this connection, competition between populations of different species often seems to be masked or even eliminated by positive effect of different plant coexistence.

Besides the peculiarities of climate, a lithologic composition of waste mantle and the degree of differences between high mountain conditions and the conditions similar to ones in edaphic and climatic respects, have a great impact on floristic composition of species, closely related to either rock, in the

majority of cases have narrow area, whereas among the species indifferent to lithologic base of waste mantle, one can find fewer endemic species; the species with wide distribution predominate (DOLUKHANOV, 1969).

A large amount of endemic species, which are typical representatives of subnival flora and even endemic genera, present enough grounds to suggest the existence of a suitable floristic complex, within the region, with analogues of high-mountain landscapes, in the geological past, far beyond the Pleistocene (KHARADZE, 1965).

In the extreme high-mountain conditions life activity of plants is mainly governed by the temperature of boundary air layer.

According to the represented tautochrones (fig. 40) high air temperature during the daytime (from 12.00-13.00 to 16.00-17.00) is observed at 0-10 cm above the soil surface. Temperature of the soil surface runs to high values, but at the depth of 10-20 cm it remains relatively low during the whole day. In the morning, the soil surface temperature is almost always negative.

8.3.2 Flora

Extreme environmental conditions appear in the subnival zone of the Caucasus. Nevertheless, more than 300 species occur here, among them plants which are typical for alpine and sometimes for subalpine belts (table 12). Only 109 species are characteristic for the subnival zone (KHARADZE, 1965). Location of upper boundary of flowering plants distribution depends on the level of continental climate and on highness of mountain. For example in the highest region of the Caucasus (Svaneti, Elbrus, Kazbegi) flowering plants reach 3900-3950 m s. m., while in continental Dagestan (East Caucasus) (PRIMA, 1974) and in mountain Aragatz (Minor Caucasus) (VOSKANJAN, 1976) they occur correspondingly at 3600-4000 m. At 3950 m (Central Caucasus) appears *Cerastium kazbek* and at 4000 m (Mt. Aragatz, Minor Caucasus) *Draba araratica*. The

following typical subnival species are found at 3600-3800 m s. m.: *Saxifraga moschata, S. exarata, S. flagellaris, S. sibirica, Tripleurospermum subnivale, Colpodium versicolor, Alopecurus dasyanthus, Draba supranivalis, Veronica minuta, V. telephiifolia, Senecio karjagini, Cerastium pseudokasbek, Pseudovesicaria digitata.*

A number of endemic species and genera occur in the subnival zone: monotypic genera – *Pseudovesicaria* (Brassicaceae), *Symphyoloma* (Apiaceae), *Pseudobetckea* (Valerianaceae).

From Caucasian-Asia Anterior genera there are found oligotypic *Coluteocarpus, Didymophysa* and *Eunomia* (Brassicaceae), *Vavilovia* (Fabaceae). They are mainly distributed in high mountains of the Minor Caucasus and Asia Anterior. Almost missing are Cyperaceae and shrubby plants. The same phenomenon is observed in polar deserts (ALEXANDROVA, 1983) the composition of the flora with respect to the soils is different. On the volcanic rocks of Keli Plateau has been established flora somehow different from one of mergel slates. High percentage of caucasian endemics are connected with mergel slates (DOLUKHANOV, 1969). Especially are distinguished limestone-built rocks of Western Caucasus where a number of local endemics appear.

8.3.3 Vegetation

Under subnival vegetation we consider the vegetation of a certain altitudinal zone placed between alpine low herbaceous meadows and snow line. Distribution of contagious vegetation is limited and open groups dominate mainly.

The following types of vegetation of the subnival zone are noticed.

1) Open groups are formed by one population or by few species of flowering plants, which are not contiguous to each other either by overground or by underground parts. Only biotope and environmental conditions are common for them.

2) Nanocoenosis or ultramicrocoenosis is dominated by individuals of vascular plants sprinking with turfs of certain plants or lichens. Plants contact with underground and overground parts. Nanocoenoses are spread in patches.

3) Fragments of turfy alpine meadows established by grasses and alpine carpets formed by various herbaceous plants. Fragments of alpine meadows have broad ecological amplitude, whereas "carpets" are found only at the snow edges. Overground and un-
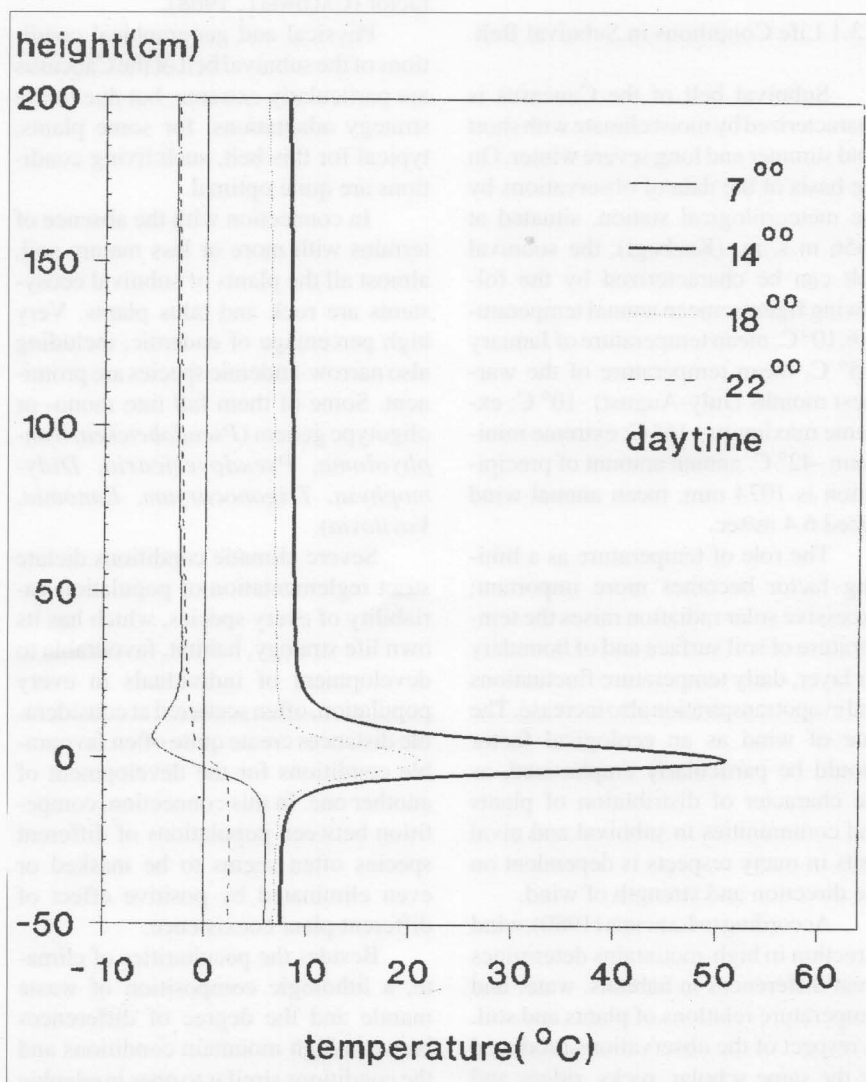
Fig. 40 — Temperature tautochrones of soil and air temperature in the subnival belt (3500 m a.s.l.).

derground relationship between plants is well presented.

Large amount of mosses and lichens occur in all types of vegetation. Mosses: *Bryum* sp., *Dicranum elongatum, Dicranoweisia crispula, Pohlia elongata, Pogonatum nanum, Tortella tortuosa, Tortula muralis,* etc.

Lichens: *Thamnolia vermicularis, Hypogimnia encausta, Cetraria islandica, C. nivalis, Parmelia vagans, Umbilicaria virginis, Placolecanora melanophthalma, P. rubina, P. murilis, Stereocaulon alpinum, Caloplaca elegans, Umbilicaria cylindrica, Lecidea atrobrunea, Rhizocarpon geographicum,* etc.

Species from open groups are presented in all biotopes of subnival zone with the exception of snow edges. For example on instable screes there occur: *Cerastium kazbek, Delphinium caucasicum*; on weekly moving: *Veronica minuta, V. telephiifolia, Scrophularia minima, Lamium tomentosum*; on fixed screes: *Aetheopappus caucasicus, Symphyoloma graveolens, Jurinella subacaulis, Minuartia inamoena*; on rocks: *Primula bayernii, Draba bryoides, Saxifraga moschata, S. exarata.* All these plants are chionophobes or hemichionophobes and are different from each other by living form. Espalier plants are: *Veronica minuta, V. telephiifolia*; acaulescent rosette plants: *Scrophularia minima, Symphyoloma graveolens, Aetheopappus caucasicus*; cushions: *Minuartia inamoena, M. trautvetteriana, Saxifraga moschata, S. exarata, Draba bryoides.*

Almost all above-mentioned plants are typical representatives of the subnival zone and are well adapted to the extreme environmental conditions.

Nanocoenoses are spread in patches through the whole subnival zone of the Caucasus. Their dimensions sometimes are 15-20 cm². Number of plant rarely exceeds 4-5 species (tab. 13). Nevertheless different aged populations are found there: sprouts, juvenils, immature and generative individuals with the whole seasonal cycle (NAKHUTSRISHVILI, 1974; NAKHUTSRISHVILI, GAMTSEMLIDZE, 1984). Subnival and alpine species are attended in all nanocoenoses which give possibility to alpine plants for successful survival and expansion of area.

Nanocoenoses are presented almost in all biotopes of subnival zone especially in the schistous substrate.

They often reach great altitudes, for example in the Mamisoni Pass nanocoenoses decrease only from 3600 m s. m. (tab. 14).

The floristic composition of nano-

Table 12 — List of plants growing in the subnival belt of the Caucasus.

Aetheopappus caucasicus	*Minuartia colchica*
Alchemilla chlorosericea	*Minuartia inamoena*
Alchemilla sericea	*Murbekiella huetii* (= *Phryne huetii*)
Allium szovitsii	*Muscari paradoxum*
Alopecurus armenus	*Nepeta alaghezi*
Alopecurus dasyanthus	*Nepeta supina*
Alopecurus vaginatus	*Omalotheca supina* (= *Gnaphalium supinum*)
Androsace raddeana	*Oxyria dygina* (= *O. elatior*)
Anemone anatolica	*Oxytropis meyeri*
Anthemis iberica	*Pedicularis armena*
Anthemis rudolphiana var. *subglabrescens*	*Pedicularis crassirostris*
Anthoxanthum alpinum	*Phleum alpinum*
Apterigia pumila (= *Thlaspi pumilum*)	*Poa alpina*
Arabis farinacea	*Poa araratica*
Arabis kazbegi	*Poa caucasica*
Arenaria lychnidea	*Potentilla crantzii*
Astragalus alpinus	*Potentilla gelida*
Astragalus gezelgarensis	*Potentilla bertramii* (*Potentilla raddeana*)
Astragalus vavilovii	*Potentilla seidlitziana*
Campanula aucheri	*Potentilla subpalmata*
Campanula tridentata	*Primula bayernii*
Carex tristis	*Pseudobetkea caucasica*
Carum caucasicum	*Pseudovesicaria digitata*
Chaerophyllum humile	*Pulsatilla albana*
Cerastium cerastoides (= *Dichodon cerastoides*)	*Pyrethrum aromaticum*
Cerastium araraticum	*Ranunculus aragazii*
Cerastium kasbek	*Ranunculus arachnoideus*
Cerastium multiflorum	*Ranunculus brachylobus*
Cerastium polymorphum	*Ranunculus dzhavakheticus*
Cerastium pseudokasbek	*Ranunculus lojkae*
Cerastium svanicum	*Ranunculus oreophilus* var. *pumilum*
Cerastium undulatifolium	*Ranunculus svaneticus*
Charesia akinfievii	*Saxifraga hirculus*
Cheilanthes persica	*Saxifraga juniperifolia*
Kobresia shoenoides	*Saxifraga exarata*
Colpodium araraticum	*Saxifraga fragellaris*
Colpodium colchicum	*Saxifraga moschata*
Colpodium versicolor	*Saxifraga pseudolaevis*
Corydalis alpestris	*Saxifraga pontica*
Corydalis conorhiza	*Saxifraga ruprechtiana*
Delphinium caucasicum	*Saxifraga scleropoda* var. *nivalis*
Dentaria microphylla	*Saxifraga sibirica*
Didimophysa aucheri	*Scropularia minima*
Draba araratica	*Sedum armenum*
Draba supranivalis	*Sedum tenellum*
Epilobium anagallidifolium	*Senecio taraxacifolius*
Erigeron venustus	*Senecio karjaginii*
Erigeron unilforus	*Senecio sosnowskyi*
Erysimum gelidum	*Sesleria anatolica*
Euphorbia kemulariae	*Silene humilis*
Eunomia rotundifolia	*Silene pygmanea*
Festuca chalcophaea	*Symphyoloma graveolens*
Festuca supina	*Sibbaldia semiglabra*
Gentiana dechiana	*Trisetum spicatum*
Gentiana pyrenaica	*Taraxacum stevenii*
Gagea glacialis	*Taraxacum porphyranthum*
Gagea sulfurea	*Taraxacum tenuisectum*
Galium coronatum (= *Cruciata coronata*)	*Trigonocaryum involucratum*
Galium elbrussicum (= *Cruciata elbrussica*)	*Tripleurospermum subnivale*
Galium sosnowskyi (= *Cruciata sosnowskyi*)	*Valeriana daghestanica*
Hedysarum armenum	*Valeriana saxicola*
Heracleum schelkovnikovii	*Vavilovia formosa*
Hypericum nummularioides	*Veronica bogosensis*
Jurinea filicifolia	*Veronica minuta*
Jurinea moschus	*Veronica schistosa*
Jurinella subacaulis	*Veronica telephiifolia* subsp. *glareosa*
Lamium tomentosum	*Veronica tumadzhanovii*
Luzula spicata	*Viola minuta*
Minuartia aizoides	*Ziziphora puschkinii* (= *Z. subnivalis*)
Minuartia brotherana (*M. ruprechtiana*)	

Table 13 — Nanocoenoses of the subnival belt (the Mamisoni Pass in the Central Caucasus)

Screes of southern slopes of 5-7°

Potentilla crantzii - Poa alpina - Symphyoloma graveolens
Poa alpina - Minuartia aizoides - Alchemilla sericea - Anthemis sosnowskyana
Alchemilla sericea - Poa alpina - Anthemis sosnowskyana
Minuartia inamoena - Poa alpina - Symphyoloma graveolens - Anthemis sosnowskyana - Taraxacum stevenii - Veronica gentianoides
Minuartia aizoides - Poa alpina - Symphyoloma graveolens
Arenaria lychnidea - Anthemis sosnowskyana
Minuartia inaomena - Campanula saxifraga - Potentilla gelida
Minuartia inamoena - Minuartia aizoides - Saxifraga exarata - Poa alpina
Minuartia inamoena - Saxifraga exarata - Symphyoloma graveolens - Anthemis sosnowskyana - Poa alpina - Taraxacum stevenii
Arenaria lychnidea - Campanula biebersteiniana - Saxifraga exarata - Taraxacum stevenii

Scree biotope of western exposure (10°) at 3200 m
Jurinella subacaulis - Saxifraga sibirica
Alopecurus glacialis - Tripleurospermum subnivale - Erigeron uniflorus
Alopecurus glacialis - Tripleurospermum subnivale
Alopecurus glacialis - Sedum tenellum
Poa alpina - Tripleurospermum subnivale - Draba supranivalis
Alopecurus glacialis - Saxifraga moschata
Eunomia rotundifolia - turf of mosses and lichenes

Mergel slates of western exposure at 3300 m
Saxifraga moschata - Tripleurospermum subnivale

3350 m Stony-scree biotope (Mt. Elbrus)
Potentilla gelida - Carum caucasicum
Potentilla gelida - Minuartia trautvetteriana - Saxifraga flagellaris - Veronica minuta
Minuartia trautvetteriana - Veronica telephiifolia
Tripleurospermum subnivale - Carum caucasicum - Cerastium cerastoides - Veronica telephiifolia - Senecio karjagini
Tripleurospermum subnivale - Veronica telephiifolia - Senecio karjaginii - Saxifraga flagellaris - Cerastium cerastoides - Anthoxanthum alpinum
Potentilla gelida - Minuartia trautvetteriana - Veronica telephiifolia - Saxifraga flagellaris

Table 14 — Basic nanocoenoses of the subnival belt of the Mamisoni Pass by the altitudinal gradient.

3000 m
Alchemilla sericea - Poa alpina - Sibbaldia semiglabra
Saxifraga moschata - Alchemilla sericea - Minuartia aizoides
Festuca supina - Campanula biebersteiniana - Carum caucasicum - Alchemilla sericea

3200 m
Alopecurus dasyanthus - Saxifraga moschata - Minuartia inamoena
Tripleurospermum subnivale - Scrophularia minima - Delphinium caucasicum
Alopecurus dasyanthus - Tripleurospermum subnivale - Erigeron uniflorus
Alopecurus dasyanthus - Sedum tenellum
Taraxacum stevenii - Campanula biebersteiniana - Carum caucasicum

3300 m
Saxifraga moschata - Tripleurospermum subnivale - Alopecurus dasyanthus
Alopecurus glacialis - Cerastium polymorphum
Erigeron uniflorus - Lamium tomentosum - Potentilla gelida

3400 m
Delphinium caucasicum - Saxifraga moschata - Lamium tomentosum
Tripleurospermum subnivale - Colpodium versicolor - Ziziphora puschkinii
Eunomia rotundifolia - Tripleurospermum subnivale
Saxifraga moschata - Cerastium cerastoides

3500 m
Saxifraga moschata - Eunomia rotundifolia - Senecio karjaginii

3600 m
Saxifraga moschata - Cerastium kazbek

coenoses occurring on the same relief is very alike.

To asses the homogeneity of vegetation in horizontal structure frequency diagrams were made up by the method of Raunkiaer (BRAUN-BLANQUET, 1964). Three sections of the Mamisoni Pass and one section placed at the foot of Mt. Elbrus were explored. Was used a circle (diameter 35,6 cm) restricting circle 1/100 m² of area 50 times. In brief, this method states that the vegetation of any surface is floristically homogeneous when the classes of higher frequency in the diagrams contain more number of species and the classes of lower frequency, accordingly, contain less number of species and vice versa (NAKHUTSRISHVILI, 1998).

The first section is located at 2950 m on the western slope of 5-7. General cover is 30-40%. From typical subnivale species here occur: *Aetheopappus caucasicus, Symphyoloma graveolens, Jurinella subacaulis* etc. Mainly are dominated species from alpine zone. Homogeneity of vegetation is low. The following plants have the greatest frequency: *Minuartia oreina, Veronica gentianoides, Anthemis sosnowskyana*.

Second section is situated on southern slope of 5-60 at 3000 m. Cover is 30-40%. Here appear subnival species: *Aetheopappus caucasicus, Silene marcowiczii, Symphyoloma graveolens*. However, still dominate species from alpine zone. Homogeneity is low as well. Greatest frequency is observed for *Minuartia oreina* and for *Aetheopappus caucasicus* and *Campanula saxifraga*.

The third section is placed on western slope of 5-70 at 3100 m. Cover of vegetation is 20-30%.

There occur subnival species: *Alchemilla sericea, Saxifraga moschata, Symphyoloma graveolens*. Nevertheless, presence of alpine plants prevail over subnival ones. Homogeneity is low.

Fourth section is located at the foot of Mt. Elbrus (3350 m). Mesorelief is plane, strongly stoned. With the subnivale species – *Minuartia trautvetteriana, Saxifraga flagellaris, Veronica minuta* – there appear typical alpine plants: *Carum caucasicum, Poa alpina, Cerastium cerastoides*. The following species have the high frequency: *Carum caucasicum, Veronica minuta, Potentilla gelida, Minuartia trautvetteriana, Saxifraga flagellaris*. Consequently, a little more homogeneity is characteristic for subnival zone especially on the transitional places from alpine and subnival belt.

Fragments of turfy meadows and alpine carpets are well developed in

subnival belt. ELLENBERG (1986) calls these fragments "Rasenstücke" and he considers that they are typical primary alpine meadows. REISIGL and PITSCHMANN (1958) call the above-mentioned fragments "Pionierrasen" and the zone of their distribution "Pionierrasenstufe". ELLENBERG accounts them as a formed and stabile climax association and refuses their farther development because of strongly restricted habitat. Composition of species very often remains to be stabile for the years.

Festuca varia, Festuca supina, Nardus stricta and other grasses form fragments of alpine meadows. Below is a list of some species appearing on the southern slope of 12-15° at 3100 m (the Mamisoni Pass).

1. *Festuca varia*
Carex tristis
Poa alpina
Potentilla crantzii
Anthemis sosnowskyana
Campanula biebersteiniana
Anemone speciosa
2. *Festuca varia*
Alchemilla sericea
Betonica macrantha
Poa alpina
Carex tristis
Anthemis sosnowskyana
Polygonum carneum
Taraxacum stevenii
Leontodon hispidus
3. *Festuca varia*
Poa alpina
Anthemis sosnowskiana
Aster alpinum
Veronica gentianoides
Campanula collina
4. *Festuca varia*
F. supina
Alchemilla caucasica
Carex tristis
Minuartia oreina
Veronica gentianoides
Polygonum carneum
Leontodon hispidus
5. *Festuca supina*
Minuartia oreina
Poa alpina
Anthemis sosnowskyana
Campanula saxifraga
Taraxacum stevenii

One can notice that the species of alpine meadows dominate but there appear plants from alpine carpets – *Taraxacum stevenii, Campanula biebersteiniana*, from scree habitats – *Anthemis sosnowskyana* and typical subnival landscapes – *Alchemilla sericea*. As in nanocoenoses fragments are formed by a small number of species, however here they occur in a large amount rather than in nanocoenoses. In more extreme envi-

ronmental conditions are established fragments dominated by *Kobresia schoenoides* and *Carex tristis* appearing mainly on windy slopes of subnival zone and by alpine species – *Campanula biebersteiniana, Gnaphalium supinum, Taraxacum stevenii, Poa alpina*, etc.

Fragments of alpine carpets or "Dikotylen-Teppiche" by ELLENBERG (1996) are established on moist places especially where snowbeds remain for the long time. On snow free places plants occur in better temperature conditions. There dominate espalier (*Minuartia aizoides, Sibbaldia semiglabra*) and rosette life forms (*Taraxacum stevenii, Plantago saxatilis*, etc.).

Below is a list of species collected at 3250 m on the southern slope of the Mamisoni Pass:
Poa alpina
Carex medwedewii
Minuartia aizoides
Sibbaldia semiglabra
Taraxacum stevenii
Luzula pseudosudetica
Campanula biebersteiniana
Carum caucasicum
Saxifraga flagellaris
Mosses:
Dicranum elongatum
Pohlia elongata
Pogonatum nanum
Tortella tortuosa
Lichenes:
Thamnolia vermicularis
Cetraria islandica
C. nivalis
Parmelia vagans, etc.

Vegetation of alpine carpets often develops between large stones and screes, where stones keep snowbeds and on snow free places as well. Stones protect plants from strong winds and after heating give them supplementary warmth (ALEXANDROVA, 1983; NAKHUTSRISHVILI etc., 1990). Below is a list of species occurring among stones in the subnival zone of Mt. Elbrus at 3350 m s. m.: *Minuartia aizoides, Carum caucasicum, Campanula biebersteiniana, Saxifraga flagellaris, Potentilla gelida, Draba siliquosa, Veronica minuta, Alchemilla chlorosericea, Festuca supina, Senecio karjaginii*.

Fragments of alpine carpets and turfy meadows as well are distinguished from real alpine meadows and carpets by appearing of species of subnival zone such as: *Veronica minuta, Saxifraga flagellaris, Senecio karjaginii*, etc.

At the 3100-3350 m one can notice such extrazonal phenomenon as appearing of *Salix kasbekensis* (= *S. arbuscula*) on morains, slopes in the Truso canyon and in the Mamisoni Pass. We

consider that it is a result of local foehns, when temperature increases while relative moisture decreases.

8.3.4 Life Forms

In the process of a long evolution, subnival plants have developed, along with metabolic and biochemical adaptive mechanisms, pronounced morphological qualities aiding in maximum warmth consumption, water loss prevention, protection against wind, drying up and withering caused by high temperatures of substratum surface. There are many plants with widely spread vegetative shoots (*Symphyoloma graveolens, Pseudovesicaria digitata, Scrophularia minima*) in this belt. There are also many plants with shoots creeping along the ground (*Veronica telephiifolia var. glareosa, Lamium tomentosum, Tripleurospermum subnivale*). Trailing and widely spread shoots of plant should be undoubtedly regarded as a form of adaptation to several environmental conditions, in particular, as a response to overheating of the substratum and to strong winds.

Dense-cushion plants (*Saxifraga subverticillata, S. ruprechtiana, S. moschata, Draba bryoides*) and loose-cushion plants (*Minuartia brotherana, M. inamoena*) are typical for the high-mountains of the Caucasus (NAKHUTSRISHVILI & GAMTSEMLIDZE, 1984). Plant propagation ability is of special importance in the subnival belt with a thinned plant cover. This undoubtedly depends on the individual mobility of one or another species. 28 out of 91 investigated species were qualified as vegetative immobile (*Symphyoloma graveolens, Scrophularia minima, Jurinella subacaulis*) (fig. 41). The other 63 species are vegetative mobile (*Minuartia inamoena, Veronica minuta, Cerastium polymorphum*). Few species belong to the type of vegetative highly mobile species, such as the plants with slight horizontal mobility. Perhaps this regularity can be accounted by severity of these ecotopes and the corresponding high degree of insufficiency in vegetative mobility of species.

Two groups of plants can be singled out in accordance with the nature of leaf downiness. The first group includes plants with undowny leaves (45 species): *Phryne huetii, Corydalis emanueli, Viola minuta*. In the second group are plants with downy leaves (46 species): *Alchemilla sericea, Aetheopappus caucasicus, Lamium tomentosum, Cerastium kazbek*. Downiness of plants protects them from strong solar radiation and from sever overheating of leaves.

Among the plants with undowny leaves there are species with succulent or semi-succulent types of leaves. For example, *Eunomia rotundifolia, Pseudovesicaria digitata, Tripleurospermum subnivale* and all species of *Saxifraga*, as well as the species with twisted leaves (*Festuca supina, Trisetum buschianum, Arenaria lychnidea*).

83 species of investigated subnival plants of the Central Caucasus appeared herbaceous. The other 8 species (*Sibbaldia parviflora, Ziziphora puschkinii*) are semi-shrubs (fig. 41).

There are 81 species of polycarpics among the investigated plants, the other 10 species are monocarpics. The latter can be subdivided into perennial and biennial plants (fig. 41). According to the data presented by GAMTSEMLIDZE (1977), monocarpic annual plants are unavailable in the subnival belt, although some monocarpic plants of this belt (*Draba siliquosa, Senecio sosnowskyi*) behave as annual monocarpic plants.

According to Raunkiaer classification, hemicryptophytes prevail in the subnival belt (fig. 41).

Rhizome, taproot and rhizome-taproot plants are the most prevalent biomorphes in the subnival belt. There are much less mat-forming plants here. Tuberiferous plants are rarely found. Almost all the plants of this belt are characterized by intensive branching of underground organs near the surface of substratum.

Thus the subnival and nival belts are specified quite a large variety of life forms, notwithstanding their poor floristic composition; almost every species displays an independent life form. The variety of the life forms of plants, scattered on rocks, mounds and glaciers, enables them to use completely different ecological niches within a very restricted territory.

The most typical features of life forms of subnival belt plants are the following:
1) out-spread, prostrate and cushion-shaped forms of the growth;
2) miniaturization;
3) not deeply penetrating into the ground downiness organs and widely branched near the substratum surface.

The out-spread and prostrated growth forms of the these plants promote:
a) maximum warmth consumption from the substratum surface warmed-up in sunny weather.
b) wind protection.
c) hibernating under snow cover which sometimes is not very thick.

Cushion-shaped plants form their microhabitat due to intensive orthotropic branching and spherical position of leaves and, thus, regulating the temperature relations and physiological processes under sever conditions of the belt.

Miniaturized life form "a very characteristic feature of humid alpine plants" is one of the important adaptive qualities for hibernating under a snow cover.

Downiness and succulence of leaves favour plant adaptation to the subnival and nival ecotopes with instable water relations protecting the stomatal apparatus from stress influence of wind and dry air, and establish an equalized water vapour concentration between leaves and the air around them (LARCHER, 1975; CERNUSCA, 1976; KÖRNER, 1977). Besides leaf succulence ensures diurnal Crassulacean Acid Metabolism (CAM-plants), which under sharp temperature changes and in dry periods results in CO_2 uptake by plants at night.

Underground organs widely branched near a substratum surface provide active water absorbtion in the morning as soon as the soil begins to thaw. Another
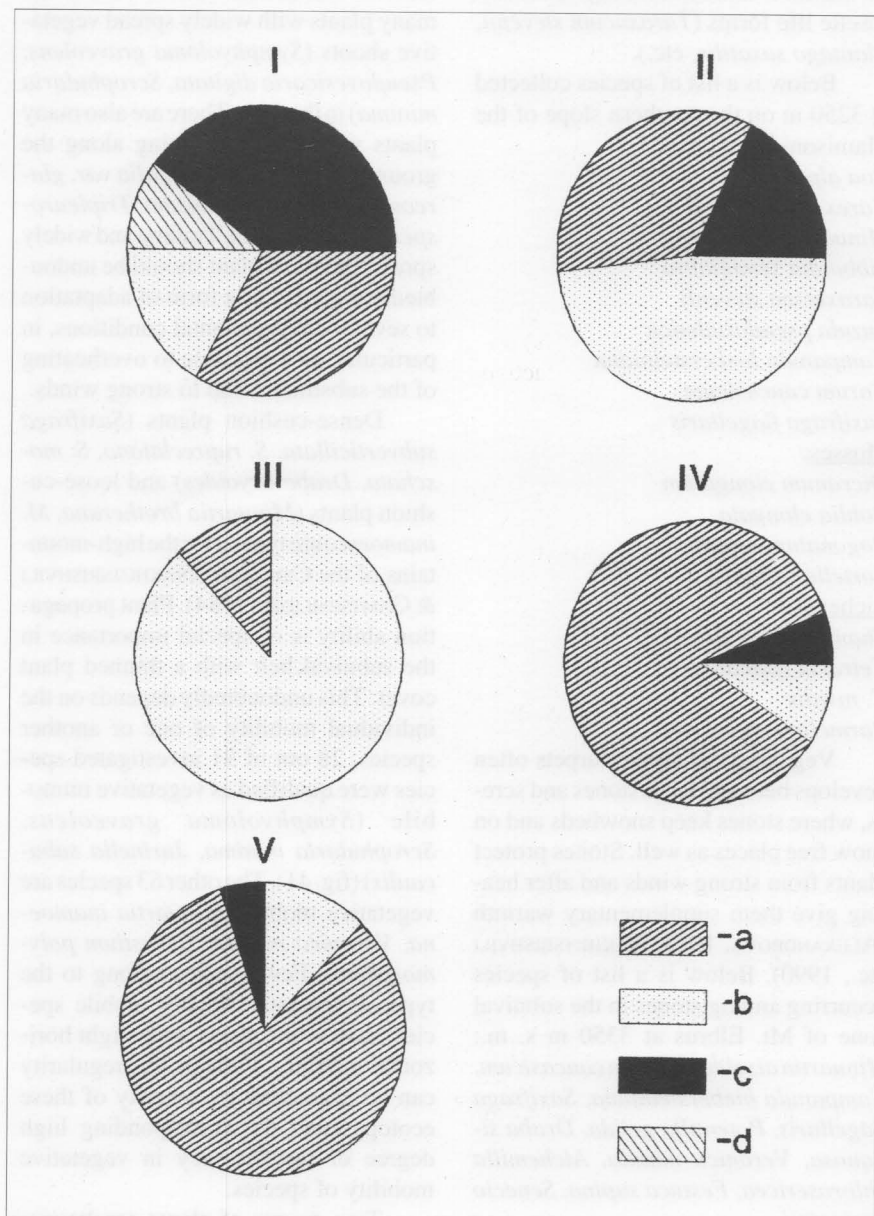
Fig. 41 — Subnival plants comparison with respect to the ecological-biomorphological indices:
I - with respect to the way of specimen mobility; a - vegetative-immovable; b - vegetative-poor-mobile type; c - vegetative-moderately-mobile type; d - vegetative-intensive-mobile type;
II - with respect to the character of leaf downiness: a - plant leaves with downiness on both side; b - plants with undowny leaves; c - plants with leaves the upper which is smooth and the other one is downy.
III - with respect to shoot lignification; a - dwarf semishrubs; b - herbaceous plants. IV - with respect to life lenght; a - polycarpics; b - perennial monocarps; c - biennial monocarps;
V - with respect to the type of plant reproductive bud distribution in unfavourable life period; a - hemicryptophytes; b - chamephytes; c - geophytes (NAKHUTSRISHVILI, GAMTSEMLIDZE, 1984).

characteristic feature of underground organs of subnival and nival is their shallow rooting (about 15-20 cm) which protects them from cold lower layers (opposite data were obtained in the Alps (KÖRNER, 1988). Even the longest underground organs at a certain level of depth (20-30 cm) begin to grow in horizontal direction (GAMTSEMLIDZE & NAKHUTSRISHVILI, 1984).

8.3.5 Reproductive Buds

Buds of herbaceous plants may be bare (without special bud scales), protected (with spacial bud scales), and proleptic (with bud scales which in autumn begin to burst and new shoots leave their shells).

According to GAMTSEMLIDZE (1979), in the subnival belt in sever winter conditions reproductive buds are covered by the residues of dead parts of plants and sheaths of dead leaves (*Jurinella subacaulis, Symphyoloma graveolens*). But sometimes they occur in the surface layer of soil (*Lamium tomentosum, Cerastium polymorphum*) or deep in soil (*Delphinium caucasicum*). Perennating buds of *Saxifraga sibirica* are covered by rosette-forming nodules which are partly in soil.

Reproductive buds of such wintergreen plants like *Saxifraga exarata, S. ruprechtiana* are protected by frame green leaves. A bud covering of plants which have protected proleptic buds is formed by solid bud scales and dead old leaves (*Scrophularia minima, Senecio karjaginii*).

It is characteristic that many subnival plants have stipules fitted closely to the base of stem and protect reproductive buds from damage (*Alchemilla sericea*).

Along with these adaptations for safe wintering of subnival plants snow cover protection is very important for reproductive buds. According to the data the biggest group of investigated plants is with bare buds (40%), then the group with proleptic buds (35%) and the smallest group is with protected buds (25%).

The point is, what determines such a great amount of plants with bare reproductive buds in the subnival belt. There are a number of opinions on this problem. According to SEREBRIAKOV (1961; 1992): "The absence of bud scales in arctic and alpine plants is connected with fact that their scales are remetamorphosed into green assimilative leaves, which usually hibernate under the protection of a snow cover and partly under the protection of a cover of moss. One of the factors for the remetamor-

phosis of bud scales into green leaves in Tundra zone and high-mountain alpine belts was a considerable shortening of a vegetation period. Plants get an opportunity to extend the period of photosynthetic activity through remetomorphosis". SAVILE (1972) explains unprotection of reproductive buds with scales by the fact that hard scales hinder rapid spring development and hence, the plants are unable to adapt to short arctic vegetation period.

By the state of the next year shoot in reproductive buds at the end of the vegetation period, subnival plants could be divided into two groups: 1) plants with completely formed shoots in buds including not only vegetative organs but also inflorescenses and single flowers (fig. 42); 2) plants in the buds of which only the vegetative part of a shoot is formed, the inflorescence and flower germs appearing during the next vegetation period.

As much as 68 species out of 78 investigated subnival plants (88 %) possess generative shoots in reproductive buds which are born in the year before flowering (group 1) and only 10 species in the year of flowering (group 2).

According to the degree of flower development in reproductive buds the first group can be devided into 3 subgroups:
1) next year flowers of reproductive buds are completely formed: sepales, a corolla, stamens, a pistil are developed (fig. 42) (*Primula bayernii, Scrophularia minima*);
2) next year flowers of productive buds are formed incompletely: sepales, petales, stamens are developed completely, the pistil is unformed (fig. 43) (*Saxifraga sibirica, Potentilla gelida, Alchemilla sericea, A. chlorosericea, Draba siliquosa, Jurinella subacaulis*);
3) inflorescenses and flowers of reproductive buds are not differentiated or start defferentiating (fig. 44) (*Senecio karjaginii, S. taraxacifolium, Tripleurospermum subnivale, Alopecurus glacialis, Delphinium caucasicum, Erigeron uniflorus*).

Profound studies of the subnival belt in the Tyrolean Alps (MOSER, 1968; LARCHER, 1980; ZACHUBER, 1975), showed that flower differentiation in buds still continues except *Cerastium uniflorum*, in which flower emergence begins only 4-6 month prior to flowering and their opening is different in various species. For instance this period lasts 11 months in *Saxifraga oppositifolia*, 12-18 months in *Primula glutinosa* and *Saxifraga bryoides* and 24-26 mon-

Fig. 42 — Reproductive buds of *Primula bayernii* (1), *Scrophularia minima* (2), where next year flowers developed completely (GAMTSEMLIDZE, 1979). A-reproductive bud sectional view, B-flower complete differentiation, 1-perennating reproductive bud, 2-axillary vegetative bud, 3-vegetative shoot, 4-inflorescence, 5petale, 6-sepale, 7-stamen, 8-pistil, 9-flower knobs, 10-covering leaves.
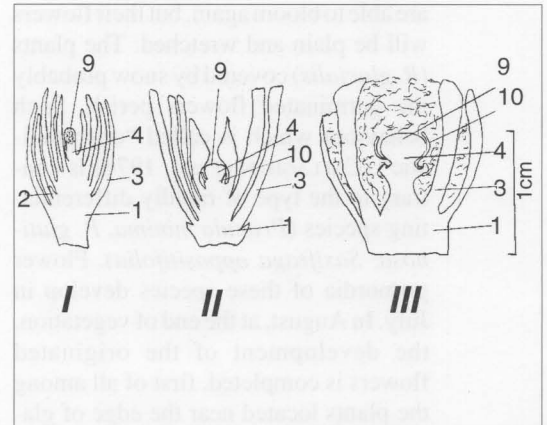

Fig. 43 — Reproductive bud section of *Alchemilla sericea* (1) and *Potentilla gelida* (2) where next year flowers developed incompletely. Designations are the same as in fig. 42.
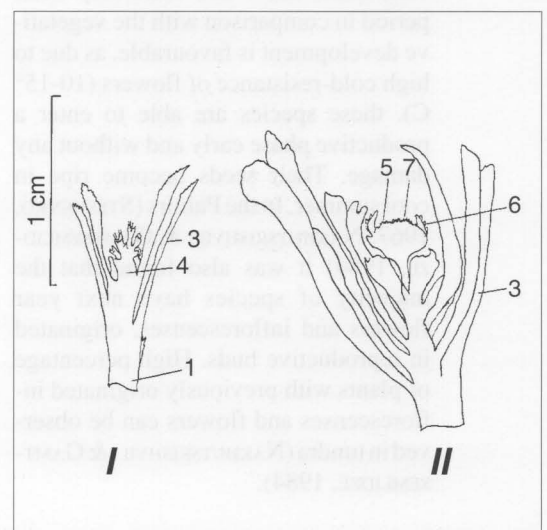

Fig. 44 — Reproductive byd section *Alopecurus glacialis* (1), *Senecio taraxacifolius* (2), *S. karjaginii* (3), where inflorescences and flowers have no differentiation sigus ands only about to start differentiating. Designations are the same as in fig. 42.

ths in *Ranunculus glacialis. R. glacialis* one of the flowering plants of the Alps extends to the highest zones. During the first year of the vegetation period stem buds appear at the base of old generative organs of the species, the flower cover and the first circle of stumen turn up before autumn. Next year the flower buds complete their development and in mid-August they turn into large closely situated flower buds (3-4 mm) and are ready to open with incompletely differentiated one year flower buds. Next spring the old buds open and the young ones continue to develop into new flower buds. *R. glacialis*, owing to such a periodical development of flowers retains the ability to flower every year in unfavourable conditions of vegetation.

Further development of flower buds of the plants, which are under snow cover during the whole summer stops for a while or at least slows down. Next year after the snow melts, these plants are able to bloom again, but their flowers will be plain and wretched. The plants (*R. glacialis*) covered by snow probably the germinated flowers perish. Such behaviour which is called "opportunistic" (CALLAGHAN *et alii*, 1976) is contrary to the type of rapidly differentiating species (*Primula minima, P. glutinosa, Saxifraga oppositifolia*). Flower primordia of these species develop in July. In August, at the end of vegetation, the development of the originated flowers is completed, first of all among the plants located near the edge of glaciers. *S. oppositifolia* flowers immediately after the snow melting and just before the growth of vegetative parts begins. Under the conditions of habitat with much snow and extremely short period in comparison with the vegetative development is favourable, as due to high cold-resistance of flowers (10-15° C), these species are able to enter a productive phase early and without any damage. Their seeds become ripe in cool summer. In the Pamirs (STESHENKO, 1967; NAKHUTSRISHVILI & GAMTSEMLIDZE, 1984) it was also found that the majority of species have next year flowers and inflorescenses, originated in reproductive buds. High percentage of plants with previously originated inflorescenses and flowers can be observed in tundra (NAKHUTSRISHVILI & GAMTSEMLIDZE, 1984).

8.3.6 Phenorhythmotypes

Phenorhythmotypes of the plants can be distinguished on the base of their phenological adaptation to environmental peculiarities. Taking into considera-

tion a period favourable for vegetation in typical habitats, they can be distinguished by the behaviour of vegetative plants, that is, by the beginning and process of germination, by formation of leaves, their ageing, yellowing and defoliation, by the growth, germination and hibernation of buds (BORISOVA, 1972; LARCHER, NAKHUTSRISHVILI, 1982).

Below we give the phenorhythmotype classification of subnival plants.

A. Plants with continuous leafing
1) Evergreen plants: *Saxifraga ruprechtiana, S. scleropoda, S. exarata*
2) Summer-wintergreen plants:

   Obligate summer-wintergreen plants: *Draba bryoides, Veronica minuta, Sedum tenellum, Saxifraga flagellaris, Antennaria caucasica*

   Facultative summer-wintergreen plants: *Potentilla gelida, Viola minuta, Senecio karjaginii, Alopecurus glacialis, A. dasyanthus, Alchemilla sericea, Sibbaldia semiglabra, Ziziphora puschkinii, Tripleurospermum subnivale, Colpodium versicolor, Cerastium kazbek.*

B. Plants with periodical leafing
Summergreen plants with winter dormancy: *Scrophularia minima, Jurinella subacaulis, Phryne huetii, Chaerophillum humile, Valeriana saxicola, Silene marcowiczii, Minuartia inamoena, Anthemis sosnowskyana, Erigeron uniflorus, Delphinium caucasicum, Lamium tomentosum, Cerastium polymorphum, Symphyoloma graveolens, Aetheopappus caucasicus, Nepeta supina.*

2) Spring and early summergreen plants with the late summer-winter dormancy: *Corydalis alpestris, C. emanueli, Draba supranivalis, Primula bayernii, Arabis kazbegii.*

3) Late summergreen and autumn plants with summer-winter dormancy: *Crocus scharojanii, C. suworowianus.* Among these groups summergreen plants with winter dormancy have the most widespreding (46.9%), then come facultative summer-wintergreen (23.4%), and spring-early summer-green with late summer-winter dormancy (9.4%), the obligate summer-wintergreen (9.4%), evergreen plants (7.8%) and late summergreen-autumn (3.1%) with summer-winter dormancy.

8.3.7 Temperature of Plants

Under extreme conditions of high-mountains the temperature of plants is one of the most important indicators of their life activity since it presents the

true background for physiological processes when the amount of effective air temperature is small (GORISHINA, 1979; KÖRNER & LARCHER, 1988).

Mountain plants show high leaf temperature and they should be included into the group of supratemperature plants (according to Lange) which probably have high protoplasmic resistance. Such plants are identified as high temperature species (according to KREEB, 1974).

In the subnival belt of the Caucasus a very distinct surface temperature differentiation of species in accordance with surface temperature of plant organs is observed. Such species as *Potentilla gelida* (fig. 45), *Veronica minuta, Alopecurus dasyanthus, Jurinella subacaulis*, have especially high temperature (29-30° C). Leaf position of these plants in relation to the substratum is planophylic. All these species are spread to the upper line of flower plants. In comparison with other species *Potentilla gelida* is specified by the highest temperature in the West Pamirs, at the altitude of 4750 m above sea level, as well as in the Caucasus (unpublished data by GAMTSEMLIDZE & CHKHIKVADZE). Difference of leaf- air temperatures around the investigated plants amounts to 12-16° C and 21-25° C.

Leaves of *Saxifraga moschata, S. kolenatina*, semisucculent *Tripleurospermum subnivale* and leaves of plants with intensive downiness – *Anthemis sosnowskyana, Aetheopappus caucasicus* – warm-up relatively less. The lowest leaf temperature (23-25°C) is recorded in coshion-plants – *Sibbaldia semiglabra, Minuartia inamoena.*

Plants with a high temperature of leaves also have the high temperature of flowers. In the investigated plants, except cushion, ones the temperature of flowers at noon is always lower than that of leaves. Very low temperatures of leaf surface (-4-6°C) were registered early in the morning at great heights, when the plants turned into icicles. However, these plants thaw very slowly as they were shadowed by huge-boulders (otherwise they would have died). Temperature of leaves reached 28° C and by 18-19°C exceeded that of air. Subnival plants with prostrated and outstretched leaves over the substratum surface have to protect themselves against overheating when the temperature of leaves is much lower than that of substratum promoting normal water regulation and photosynthesis.

8.3.8 Structure of the Photosynthesic

Apparatus

Structural adaptations related to photosynthetic activity play essential role in the adaptation of plants to habitat conditios, providing great ecological plasticity of the photosynthetic apparatus (GORISHINA *et alii*, 1985).

Among the investigated plants there are species with rather thin dorsiventral lamellate leaves (*Oxyria elatior, Saxifraga sibirica*), as well as with the isopalissade ones (*Astragalus kazbegi*) with the centric leaves of similar ones (*Arenaria lychnidea, Tripleurospermum subnivale*), sometimes without clear differentiation of mesophyll between palissade and spongy tissues (*Ziziphora puschkinii*). The leaf structure of some species has distinct features of succulence. Leaf structure type is not closely connected with habitat conditions and shape of mesophyll cells. For instance, *O. elatior, S. sibirica* have narrow and elongated cells of palissade tissue, *S. juniperifolia*, has shorter and more rounded ones. As a rule, the cells of spongy tissue are round, the composition of the tissue beimg dense without big intercellural spaces. The cells of palissade tissue are packed very tight.

The investigated species are characterized by well-developed plastid apparatus. The mesophyll cells are filled densely with numerous chloroplasts, with their total volume being 10-30% of the cell volume. The value of surface density of chloroplasts in leaves reaches 100 000–120 000/cm^2 accordingly the total surface chloroplasts is large. These peculiarities of the plastid apparatus are typical of the plants growing in habitats exposed to bright light. Such heliophilous plants grow in arid deserts, sea side littorals, deciduous forests in early spring as well as some in subalpine grasslands of the Caucasus. The values of the same indices in shade-requiring mesophytes are by an order more (GORISHINA *et alii*, 1985). Chloroplasts are usually small (*O. elatior* excluded) with very low chlorophyll content. This fact enables us to assume the presence of an ultrastructure with poorly developed system typical for the plants growing in the habitats exposed to bright-saturation. Chlorophyll content per unit of area and dry mass of the leaf is also not high (1.5-4 mg/dm^2 and 0.5-1.5 mg/g accordingly).

Light-requireness – "xerophilous" peculiarities of plants which can be called the "oreophytes", are expressed in different ways. They are best manifested in subnival oroxerophytes which inhabit rocks and talus and growing under the influence of substratum dryness

and overheating. However, microhabitat conditions can be quite different even in these places. For example, the indices of plastid apparatus of *Saxifraga juniperifolia*, preferring more oversdaded and damp crevices, as a whole are mesophilous (small volume of chloroplasts in the cell and leaf, high concentration of chlorophyl in the chloroplast). The change reactions, e.g. under extreme conditions one of the orophil properties of the inner structure of leaves in plants, growing at the edges of a glacier or in hollows are expressed to a lesser digree. Only *Veronica telephiifolia* var. *glareosa*, having perrenial green leaves and showing the trophorhythmotype of obligate-summer-winter-green stands by itself (LARCHER & NAKHUTSRISHVILI, 1982).

It was stated that the photosynthetical apparatus has considerable plasticity, manifested in the variability of leaf size and the indices of inner structure-surface density of chloroplasts etc. (fig. 46). When the surface of a leaf varies in 3.5-4 times, the total reserve of plastids in the leaf varies in a more or less degree (1.5-2 times), as such diminution of the size of a leaf partially compensated by a considerable increase of the number of chloroplasts per unit of the leaf surface. That is to say, the plants growing in extreme conditions lose the reserve of chloroplasts in their leaves in a less degree in comperison with the loss of an assimilative surface that is important for the preservation of photosynthetic abilities of leaves. Chlorophyll content in

chloroplasts differs substencially depending on a microhabitat (fig. 47): both its total mass and concentration are slightly higher in species, growing in canopy.

8.3.9 CO$_2$-Gas Exchange

In extreme conditions of high-mountains in the Caucasus the assimilative period of anthophytes is short (60–90 days). However, even during this time the assimilation period can be interrupted by frost or draught. Plant species respond to such extreme ecological conditions by different CO$_2$-gas exchange reactions, e.g. under the extreme con-

Fig. 45 — Temperature and water potential; (in Mpa indicated by dotted line) indices of *Potentilla gelida* from the Caucasus (3500 m a.s.1.) and Pamirs (4750 m).
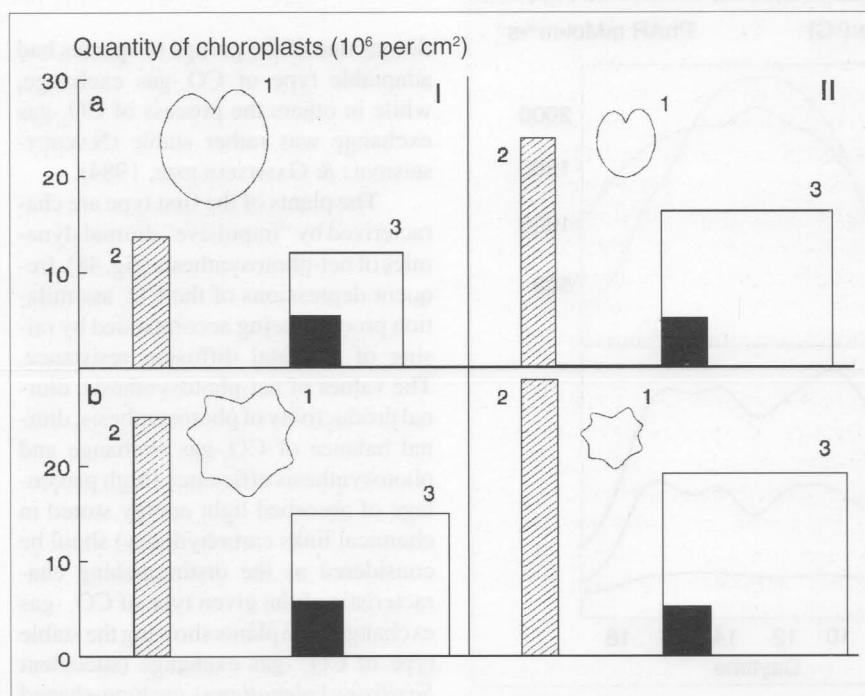
Fig. 46 — Change of leaf characteristic *Oxyria elatior* (a) and *Saxifraga sibirica* (b) in various ecological microniches of the subnival belt: I - with herbage fragments; II - on bare rocks; 1 - leaf area; 2 - number of chloroplasts on cm leaf area; 3 - total surface of chloroplasts (big square) in a unite of leaf area (black square) (GORISHINA *et alii*, 1985).
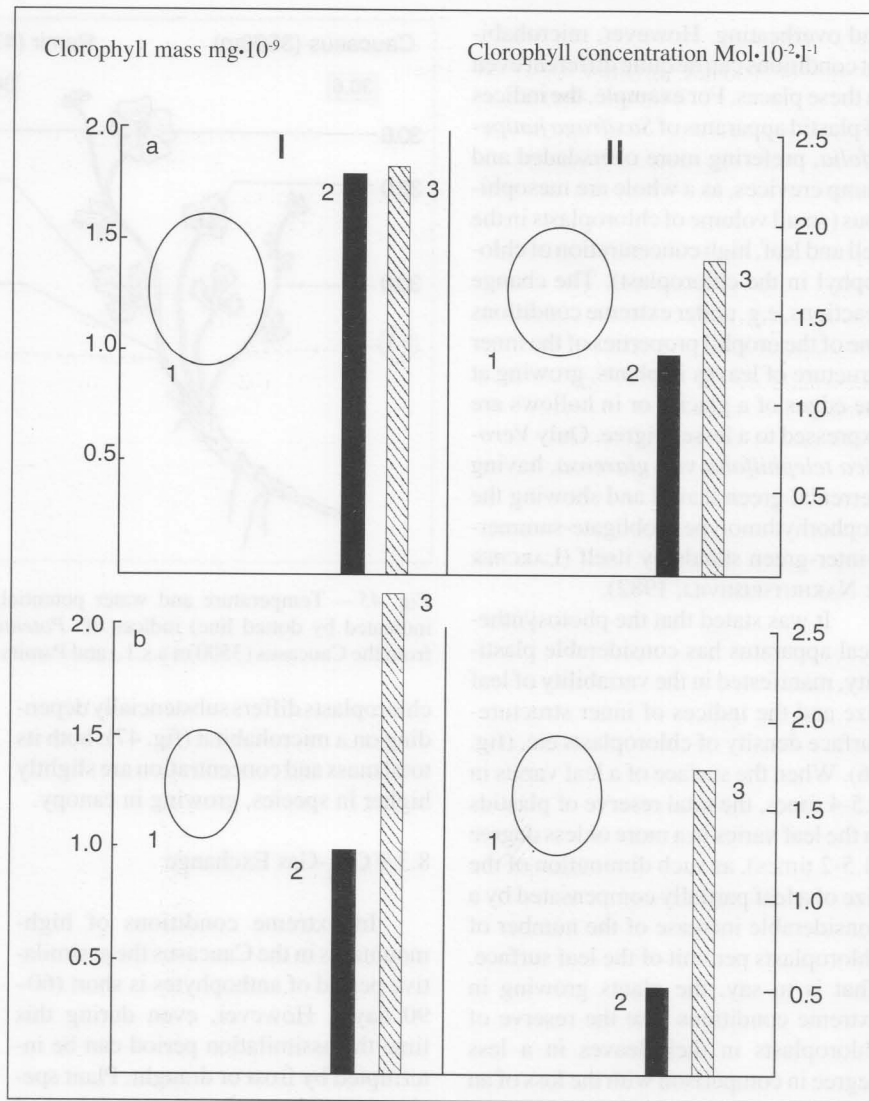
Fig. 47 — Plant chloroplasts in different ecological microniches: 1 - chloroplast projection; 2 - mass; 3 - chlorophyll molar concentration in chloroplasts. The other conventional signs see fig. 46 (GORISHINA *et alii*, 1985).
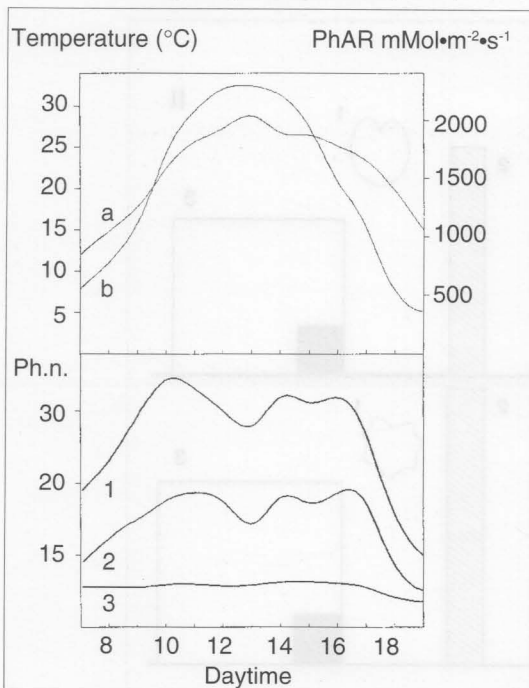

Fig. 48 — Daily course of air temperature (a), PhAR (b) and net-photosynthesis (mgCO$_2$ dm^{-2}h^{-1}) in *Arenaria lychnidea* (1), *Aetheopappus caucasicus* (2) and *Saxifraga kolenatiana* (3) in the subnival belt (3000 m) (ABDALADZE, 1990).

ditions one of the groups of species had adaptable type of CO$_2$-gas exchange, while in others the process of CO$_2$-gas exchange was rather stable (NAKHUTSRISHVILI & GAMTSEMLIDZE, 1984).

The plants of the first type are characterized by "impulsive" diurnal dynamics of net-photosynthesis (fig. 48), frequent depressions of the CO$_2$ assimilation process, being accompanied by raising of stomatal diffusion resistance. The values of net-photosynthesis, diurnal productivity of photosynthesis, diurnal balance of CO$_2$-gas exchange and photosynthesis efficiency (high percentage of absorbed light energy stored in chemical links carbohydrates) shoul be considered as the distinguishing characteristic of the given type of CO$_2$ -gas exchange. The plants showing the stable type of CO$_2$ -gas exchange (succulent *Saxifraga kolenatiana*), cushion-shaped (*Minuartia inamoena*) are characterized by absolutely opposite indices (table 15).

Subnival plants, as well as other mountain plants (LARCHER, 1984) are characterized by a very high net-photosynthesis. It should be noted that plants which are not distinguished by high intensity of photosynthesis (e.g. *Saxifraga kolenatiana*) demonstrate their economy by way of moderate use of assimilants that is displays in very low intensity of dark respiration (fig. 49).

Subnival plants are also characterized by wide temperature optimum of net-photosynthesis and well developed repair ability of assimilative apparatus (MOSER, 1973; NAKHUTSRISHVILI & GAMTSEMLIDZE, 1984; ABDALADZE, 1994).

8.3.10 Diffusion Resistance of Leaves

"Xeromorphic" structure as well as trailing and cushion forms of plant growing promote stomatal apparatus regulation in the extreme conditions of high-mountains (LARCHER, 1975; CERNUSCA, 1976; KÖRNER, 1978).

As is generally known, the higher the altitude the higher diffusive conductivity and duration of stomatal openings gaping. The main reason of this is lower pressure (KÖRNER, 1978; KÖRNER & MAYER, 1980), responsible for the high level of plant evaporation at high altitudes.

Stomata diffusion resistance in the water relations and CO$_2$ -gas exchange regulation of plants perform a very important function in the conditions of the subnival belt, where plants are isolated from each other and experience the impact of heavy dryness and heating of substratum. Diffusion conductivity in the majority of investigated subnival plants is rather high (1.5-1.7 cm s^{-1}).

As shown in figure 50, the highest level of conductivity of leaves with sharp fluctuations is observed in *Veronica minuta, Tripleurospermum subnivale, Senecio karjaginii* and *Potentilla gelida*. The *Saxifraga* species are characterized by low conductivity of leaves. No wonder that the values observed in this species (*Alopecurus dasyanthus*) are so small because of the ability of grasses to reduce the conductivity of water (KÖRNER, 1978; KÖRNER & SCHUBERT, 1978).

Majority of subnival plants are characterized by sharp diurnal water conductivity fluctuations. For example very often in the afternoon when high temperatures of substratum surface (50° C and over), high levels of solar radiation (PhAR may extend up to 2400-2450 micromol m^{-2}s^{-1}) and in this respect the encreased leaf temperatures (up to 30° C) occur, heavy depressions of water conductivity are observed. These depressions in defferent plants are manife-

sted in defferent degrees.

Usually water conductivity in *Tripleurospermum subnivale* and *Veronica minuta* at noon compared to morning hours falls by 88-96% (fig. 50). Low midday deviations can be noticed in *Saxifraga* species, especially in *S. sibirica,* which at very high altitudes grows only under boulders. Almost flat curve of diurnal water conductivity was displayed by cushion-plants, e.g. *Sibbaldia semiglabra*, a dwarf semishrub. However at high altitudes in unclosed communities average diurnal conductivity of leaves falls.

Average values of total deffusion resistance of leaves in the subnival belt of the Elbrus (3500 m a.s.l.) at low wind velocity. Table 16 shows data on total water deffusion resistance (rt). So called leaf boundary layer resistance is very important for transpiration. Its share in investigated species except *Tripleurospermum subnivale* as compared to subalpine grasses is smaller than the share of stomatal resistance (rl). Thus in extreme life conditions (especially in the plants growing in open places exposed to strong winds) stomatal play the most vital role in water relations of plants.

Plants growing in severe life conditions of high-mountains acquire reactivity potential after being exposed to extreme temperature (SEMIKHATOVA, 1965; LARCHER, 1980; ZALENSKIY, 1982). This has been confirmed by the results obtained in the course of observations of diffusion resistance of stomata in morning hours, i.e. after the impact of negative temperature of air (-2.5°C), of substratum surface (-1.6° C) and of leaf (-3.0° C). In all species after sunrise (630-1010 micromol m^{-2}s^{-1}) and with the increase of air temperature (10° C) and substratum temperature (5.0° C) leaf conductivity amounts up to 0.75-1.15 sm s^{-1}. Trailing plants, such as *Veronica minuta, Tripleurospermum subnivale* and the grass *Alopecurus dasyanthus* actively respond to the solar radiation and rise of temperature. Whereas *Senecio karjaginii* (plant with erect stalk and equally distributed leaves) reacts less actively and its leaf conductivity stays below 0.21 sm s^{-1} (NAKHUTSRISHVILI *et alii*, 1990).

8.3.11 Leaf Water Potential of Plants

Plants of subnival belt posess high transpiration and water potential values (NAKHUTSRISHVILI *et alii*, 1990). The question is wether water balance becomes equalized in the extreme conditions of high mountains. LARCHER (1983) considers that water potential reflects any

Table 15 — CO_2-gas exchange of plants in the subnival belt of the Mamisoni Pass at the altitude of 3000 m s. m. (from ABDALADZE, 1990).

Species	Maximum net photosynthesis mg CO_2 dm^{-2} h^{-1}	Diurnal productivity mgCO$_2$ dm^{-2} per day	Daily balance of CO_2-gas exchange mg CO_2 md^{-2} 24h	Photosynthesis efficiency %
Saxifraga kolenatiana	6,3	50	38	4,2
Arenaria lychnidea	42	277	230	20
Aetheopappus caucasicus	20	125	86	11
Alchemilla sericea	23	136	102	10
Minuartia inamoena	6,5	55	-	-
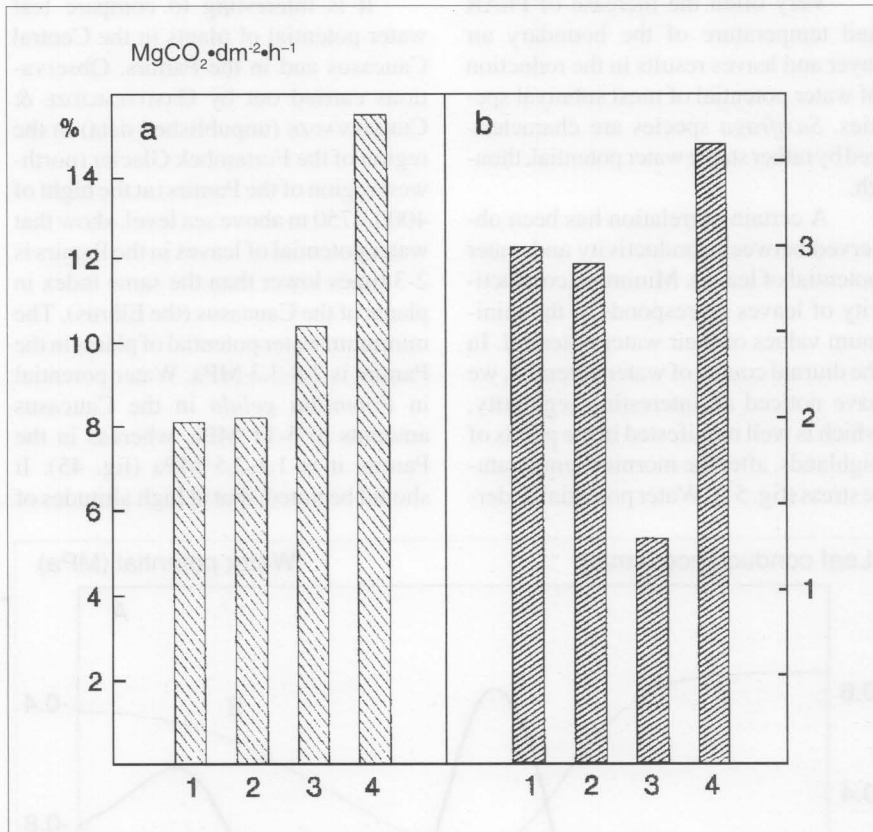
Fig. 49 — Economical coefficient of photosynthesis (a) and dark respiration (b) of plants in the subnival belt (3000 m): 1 - *Aetheopappus caucasicus*; 2 - *Alchemilla sericea*; 3 - *Saxifraga kolenatiana*; 4 - *Arenaria lychnidea* (ABDALADZE, 1990).
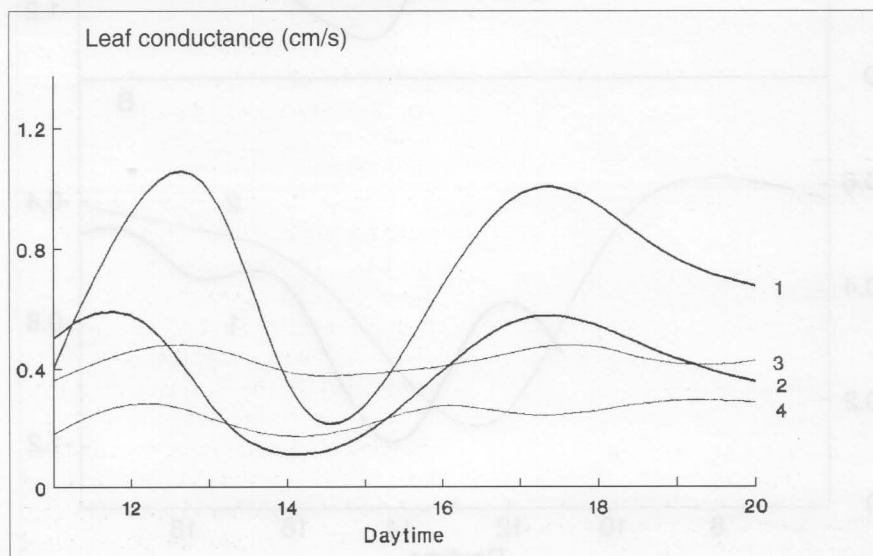
Fig. 50 — Leaf conductivity of subnival plants (3500 m a.s.l.) 1 - *Veronica minuta*; 2 - *Tripleurospermum subnivale*: 3 - *Saxifraga exarata*; 4 - *S. sibirica* (NAKHUTSRISHVILI *et alii*, 1990).

Table 16 — Average values of the total diffusion resistance of the leaves of plants in the subnival belt of the Elbrus (3500 m) at low wind velocity

Species	r_t	r_1	r_a
Veronica minuta	5.38	3.11	2.26
Tripleurospermum subnivale	3.6	1.52	1.50
Alopecurus dasyanthus	7.30	5.75	1.54

alterations in water balance as its tension immediately provokes loss of turgor and subsiquent growth of water potential.

Very often the increase of PhAR and temperature of the boundary air layer and leaves results in the reduction of water potential of most subnival species. *Saxifraga* species are characterized by rather stable water potential, though.

A certain correlation has been observed between conductivity and water potential of leaves. Minimum conductivity of leaves corresponds to the minimum values of their water potential. In the diurnal course of water potential, we have noticed an interesting regularity, which is well manifested in the plants of highlands, after the morning temperature stress (fig. 51). Water potential under-

goes gradual reduction until quite low values at noon. It restores in the second half of the day, due to the growth of diffusion resistance.

It is interesting to compare leaf water potential of plants in the Central Caucasus and in the Pamirs. Observations carried out by GAMTSEMLIDZE & CHKHIKVADZE (unpublished data) in the region of the Fortambek Glacier (northwest region of the Pamirs) at the hight of 4000-4750 m above sea level, show that water potential of leaves in the Pamirs is 2-3 times lower than the same index in plants of the Caucasus (the Elbrus). The minimum water potential of plants in the Pamirs is 2.8-3.3 MPa. Water potential in *Potentilla gelida* in the Caucasus amounts to 5-11 MPa, whereas in the Pamirs it is 1.1-2.5 MPa (fig. 45). It should be noted, that at high altitudes of

the Pamirs (4750 m) water potential of leaves, which is rather low, can still reduce to 3.0 MPa, e.g. in *Waldheimia glabra*.

8.3.12 Discussion and Conclusions

Subnival and nival ecosystems (viz. microecosystems) scattered among rocks and mounds, consist of a small number of anthophyte species. Thanks to adaptation they can survive in severe life conditions. High-mountain inhabitants obtain the quality to resist such factors as low temperature and frosts during the vegetation period, warmed-up substratum, hurricane wind and besides, low carbon dioxide content and the pressure of water vapour in the air. These plants have a short vegetation period and a great deal of chionophiles stay under a thick snow cover during 18 months.

Apparently, evolution of plants here, in contrast to the alpine and subalpine belts is aimed at the selection of species with high resistance against heavy physical conditions; here competition seems to be less important for the selection of species.

Severe climatic and edaphic conditions have a strong impact on the structure of plant cover. Vertical structure of plant groupings in the subnival and nival belts is characterized by the absence of stratum differentiation and unclosed horizontal structure. Unlike other altitudinal belts root systems here are closed only in case of penetration by one plant into the tufts of another, which leads to the formation of micro-and ultramicro-groupings.

Subnival belt displays a great variety of life forms, despite a restricted number of species; in extreme life conditions almost every species demonstrates an individual life form with its typical ecophysiological reaction to environmental changes. Probably, this accounts for the fact that various species of plants individually adapt to their existance within the same ecotope.

Analysis of life forms of plants of this belt revealed the prevalence of widely prostrate and cushion-plants with downy and semisucculent leaves. The subnival belt is also characterized by vegetative-movable plants, which form clumps and patches. They provide the security of widely represented rock-talus ecotopes. According to the Raunkiaer system the most frequent life forms here are illustrated by hemicryptophytes and chamaephytes. These life forms were caused by the adaptation of plants to the subnival ecotopes, which are subject to the impact of day-night temperature fluc-
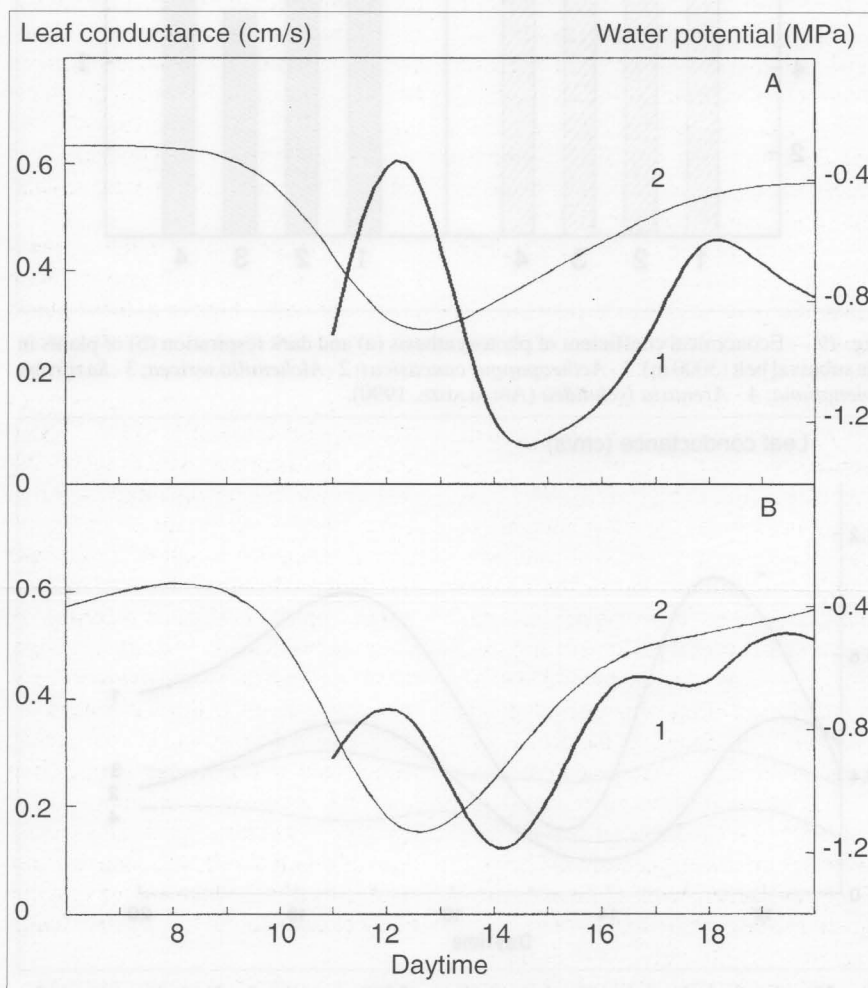
Fig. 51 — Relations between leaf conductance (1) and water potential (2). A - *Senecio karjaginii*; B - *Potentilla gelida* (NAKHUTSRISHVILI *et alii*, 1990).

tuations and strong wind, the latter is of particular importance.

High-mountain biomes are very rich in diverse life forms, especially the mountains of the torrid zone. Every mountain system and every altitudinal belt involves specific life forms which are typical only for them. For example, mountains of the torrid zone are characterized by rosette-like megaphytes, large bunches of tussock grasses, downy and thorn plants; in aried high mountain regions prevail cushion and prostrate dwarf semishrubs and shrubby plants. Humid high-mountain regions of temperate zones represent trailing shrubs and dense turf plants, small delicate grass species, and cushion-shaped, rosette-like, trailing and prostrate herbaceous plants wich dominate in the extreme conditions of the subnival and nival belts. In alpine tundra the prevalent life forms are shrubs and small shrubs. In general, humid high-mountain regions of temperature and high latitude zones are characterized by tiny life forms as compared to the tropical and arid (low latitude) mountains (NAKHUTSRISHVILI, 1981).

Plants growing at high altitudes of both tropical and temperate zones are characterized by "xeromorphism" particularly by strong downiness, succulence, twisting of leaf, its thickening and substitution by thorn, etc. (NAKHUT-SRISHVILI, 1974; LARCHER, 1975). These properties were regarded as a reaction of plants to water deficiency or poor mineral nutrition. The recent data advised by LARCHER (1975) suggest that small preasure of water vapour and the state of stomata along with other factors, determine the "xeromorphism" of plants. Water deficiency, caused by freezing of soil is observed in different high-mountain biomes (Alps, Andes, Caucasus, etc.) occurring only at night or in the morning. During the rest of time, plants absorb water from soil.

KÖRNER (1978) and KÖRNER & MAYER (1980) observed that the degree of stomatal opening is subject to the effect of dry air of high-mountain regions; various species react to dry winds (foehns) differently. Any increasing of the resistance of leaf boundary layer through their downiness, succulence, twisting protects the stomatal apparatus from strong influence of dry air and wind and establish aequilized concentration of water vapour of leaf and its environmental water. As a result of the scientific observation conducted by CERNUSCA (1976) it was found that the analogous effect was observed in the plants which have cushion and trailing growth

forms. According to LARCHER (1975) the ecological benefit of so called xeromorphic structure of high-mountain plants is in the levelling of air humidity fluctuations and, thus in maintaining (through the system of stomatal apparatus) the diffusion resistance of carbon dioxide gas and water at a comparatively optimum level.

Generative tissue, reproductive buds in particular, has decisive significance for plant adaptation to severe environmental conditions. Subnival plants are mainly characterized by bare and proleptic opening buds. Only a small number of species have closed ones. The majority of subnival plants have perennating reproductive buds in which flowers and inflorescences appear beforehand, that is one of the essential signs of adaptation of these plants to a very short period of vegetation.

The analysis of plants distribution in their habitat with different thickness of snow cover showed (NAKHUTSRISHVILI & GAMTSEMLIDZE, 1984) that the number of species considerably increased from the minimum snow zone to the maximum one. The least number of species accounted for the maximum snow zone. Unlike other altitude belts in the subnival belt, there are the least number of chionophobous plants. In this belt as well as in tundra so called greenhouse effect is apparent in spring. It must be mentioned that in such "greenhouse" the vegetation period begins about two weeks earlier in comparison with one in the conditions of an open biotope.

The beginning of plant vegetation depends mainly on the periods of snow cover disappearance and so fluctuations have especially pronounced character at the beginning of it. Mass vegetation of plants in the subnival belt is observed only from the end of June till the end of September and the beginning of October (depends on snow fall). The first flowering species appear in the only in the second ten-day period of June reaching their culmination in the second half of July. The flowering period in the given belt is observed for a rather long time, that lasts till the second half of September. During this period plants can hardly be found in the alpine and often in the lower subalpine belt.

Even the smallest territories of the subnival belt of the Greater Caucasus were rich in various phenorhythmotypes. Both, evergreen with summer-wintergreen species can be found there. Summergreen plants with winter dormancy were the prevailing phenorhythmotype of the subnival belt. Then comes facultative summer-wintergreen plants.

We came to the conclusion that plants growing at the highest altitudes were presented by high-temperature species which could survive in extreme conditions. Leaf temperature in sunny weather rises on average, than the ambient temperature and falls by the same degrees below the temperature of substratum surface over which leaves and shoots of subnival plants prostrate. The transpiration favours the hydrothermal regulation of plants not only in steppes and deserts but also in subnival conditions. In differentiation of plants in respect of temperature of their organs, the architectonics of plants, particularly the pattern of the position of their leaves in relation to the sun rays and highly warmed-up substratum is of high decisive importance. On the basis of example it is possible to consider the plants of cushion-shaped life form which is widely distributed almost in every biome with extreme conditions. According to our investigation the plants of such life form as opposed to many species are not overwarmed and at noon in sunny weather their leaf temperature is always optimal. Probably, such homeostasis is due to a ultramicrohabitat created by a specific form of growth of these plants. Their temperature conditions become favourable for active water exchange and carbon assimilation. The same function can be carried out by turf. Some of the plants not typical for the subnival belt and without such adaptive mechanisms, turn yellow and wither form intensive solar radiation in August.

Tolerance limits as to the temperature stress in the most subnival and nival plants are rather high, e.g. these plants may be due to their recover ability, leave the stress very quickly in spite of the fact that during a day leaf temperature varies from -2, -50° C to +30°, +34° C. Specifically, diffusion resistant of leaves decreases, water exchange and assimilation activity of plants are restored.

Temperature conditions of plants and their environment have a large extent an impact of diffusion resistance of leaves. Almost all the species investigated were found to be sensitive to stomata regulation. Plant with erect stocks are subject to winter influence to a greater degree and during a day period their stomatal conductivity varies. As it is apparent, basically in extreme conditions of subnival belt, diffusion resistance of leaves has to perform the function of water balance and CO_2 -gas exchange of plants.

As a whole a water relations of subnival plants is well regulated although the cases of considerable rise of water

low level, considerable reduction of water content in leaves and water potential, elevation of osmotic pressure and water conductivity reduction are observed in many species. That is why all the subnival plants which have been investigated, except succulents, are included in the group with hydrolabile species and at the same time, with euryhydrous (NAKHUTSRISHVILI & GAMTSEMLIDZE, 1984).

It is quite natural that peculiarities of water relations has an influence on carbon exchange of plants. For instance, the plants with low water content and high degree of water shortage are characterized by low intensity of photosynthesis. Midday depression of photosynthesis often observed at noon are mainly the result of increased diffusion resistance of leaves caused trees environmental conditions. Night frosts and midday depressions are the factors which limit day and seasonal course of photosynthesis. However, due to the recover ability of plants, their assimilation activity is restored rapidly after temperature stresses.

One of the most important strategies of plant survival in unfavourable conditions of high-mountains is a high temperature optimum of net-photosynthesis. On the basis of our work we concluded that a short period of assimilation in extreme high-mountain conditions may be sufficient for a considerable carbon accumulation.

Thus, there are species with absolutely different mechanisms of adaptation to the habitat conditions within small territories, they are micro and ultramicrogroupings.

During a long period of evolution, high-mountain plants have acquired ability to survive and reproduct in extreme conditions. The principal mechanism of plant adaptation are the following:

Growing species via the medium of both combined and individual distribution of plants among rock, talus and glaciers.

Formation of various specialized forms of growing resulted in the protection against the impact of unfavourable habitat conditions.

Completion of seasonal development cycle of plants in a short period of vegetation.

Early origination of almost all plant organs including all parts of flowers in reproductive buds.

Final formation of leaves after more favourable ecological conditions coming.

High leaf resistance to sharp daily fluctuations of temperature.

High temperature of leaves with their thermoregulation capacity, which assure active assimilation activity and water exchange of plants.

Regulation of physiological processes which manifest itself due to diffusion resistance of leaves.

High temperature optimum for photosynthesis.

High level of photosynthesis in the period between unfavourable weather conditions and low dark respiration in plants with poor photosynthetic activity resulting in economical expenditure of assimilants.

Well developed recover capacity in plants after stress impact.

The tendency to leaf succulence formation for optimum keeping of water balance and assimilation activity.

Long under-snow-cover stay of plants due to considerable accumulation of organic matter reserve in underground organs.

The variety of life forms, pheno- and trophorhythmotypes within the strongly limited territory demonstrating the species ability to occupy and develop their ecological niche.

In the conclusion we find it necessary to describe some distinctive characteristics of plants growing in extreme conditions of high-mountain regions of the Caucasus.

There are small or no such plants as bushes, dwarf shrubs, representative of sedge family in the subnival and nival ecosystems as opposed to alpine meadows having common border line with them. In such conditions root systems are closed very seldom and territory of unclosed vegetation cover; polygonal nature of relief that is the most characteristic property of the alpine belt-is hardly marked. As the altitude increases the activity of species decreases. In the subnival and especially nival belts the species activity are not enough or inactive (e.g. *Cerastium kazbek*).

It must be outlined that the analogous regularity has been revealed by ALEKSANDROVA (1983) as related to polar desert. This geobotanical region as well as the subnival and nival belts is characterized by small number of flowering plants, the absence of bushes and representatives of sedge family, the uncloseness of vegetation cover of species activity and etc.

When passing from the alpine belt to the subnival sharp changes of plant growth form is observed (cushion plants and prostrate ones predominate). In extreme conditions of high-mountain regions the species with "xeromorphic" features hold a dominating position as

opposed to mesophilous plants which are typical for the alpine belt.

Subnival and nival belt plants unlike the species of alpine belt are characterized by peculiar rhythmological features and physiological processes. For instance, they differ from each other by impulsive and peaked curves of efflorescence and two pronounced maxima of flowering. Diversity of aspects of ultramicrogroupings and aggregations is observed in the subnival belt even in the late summer phase of plant development while in the subalpine and alpine belts only some flower species. (NAKHUTSRISHVILI & GAMTSEMLIDZE , 1984). Aspects change in vegetative groupings is expressed neither in extreme conditions of polar deserts nor in the nival belt (ALEKSANDROVA, 1983). Interrelations of physiological processes with environmental factors is more tense in subnival plants than e.g. in alpine or subalpine plants in the conditions of closed grass cover. In the first case, in spite of high species ability to adapt to the unfavourable conditions, strong overheating of assimilative surface of plants, photosynthesis depression and sharp increasing of leaf diffusion resistance are often observed.

Unlike the alpine belt, plant ecological stress in the subnival and nival belts becomes heavier due to the absence of closed vegetation cover (basically grass sods) promoting the development of various homeostatic mechanisms.

The species growing in the subnival and nival belts in the period of their formation experienced the climatic stresses caused both by sharp fall of temperature and its rise. Undoubtedly, these plants were witnesses of the period of volcanic activities when they had to adapt themselves to the existence conditions of extreme with high concentration of carbon dioxide gas, mobile and highly warmed-up substratum, etc.

Only such high adaptation ability of these plants to comparatively big number of external factors helps them to survive in conditions of extreme press. The plants adapted to such wide range of changing ecological conditions are the representatives of the most ancient flora of high-mountain regions of the Caucasus.

9. THE HYDROPHYTIC VEGETATION (by KIMERIDZE, 1992)

Bog vegetation is a typical component of phytolandscapes of Georgia. It covers an area of approximately 200 hectares. Bogs are very common on *Colchic Lowland and South-Georgian*

Volcanic Upland, populating chiefly lowlands and subalpine belt, whereas in mid-mountain and alpine zone they are rare. The commonest bogs in Georgia are eutrophic, of which mesotrophic and oligotrophic formation occupy limited area. Under the special conditions of subalpine belt of the Greater Caucasus oligotrophic pit bogs are developed on crusts of weathering of different rocks.

Vertical distribution of *Sphagnum* bogs in West Georgia comprises all altitudinal belts from sea level to the subalpine zone; *Sphagnum* bogs are very rare in alpine belt with its severe climatic conditions. These bogs are not to be found at the altitudes below 2000 m in East Georgia due to the aridity of climate of this region.

Distribution area of *Sphagnum* bogs (meso-oligotrophic types) involves western parts of the Greater and Minor Caucasus, where they occur in the zone of *Picea-Abies* forests and mesic beechwoods. The following obligatory helophytes are characteristic of West Georgia: *Scheuchzeria palustris, Carex flava, Viola palustris, Cardamine seidlitziana, Heracleum apiifolium, Sredinskya grandis, Rhynchospora alba, Drosera rotundifolia, D. intermedia* and *D. anglica.*

Bog vegetation of Georgia is similar to that of North Eurasia, though one cannot find here many characteristic components of northern peat bogs. *Sphagnum* bogs in Colchic Lowland and Ajara Mts. are characterized by the presence of such relic species as *Rhododendron ponticum, Rh. luteum, Vaccinium arctostaphylos, Frangula alnus, Osmunda regalis,* etc. This type of vegetation is rich in species with disjunctive and wide area of distribution. It is moderately manifested as endemics of Georgia and the Caucasus (8%). Among the abovementioned endemics the following should be mentioned: *Hibiscus ponticus, Heracleum apiifolium, Rhynchospora caucasica, Scirpus colchicus, Sredinskya grandis, Carex szovitsii, Cardamine seidlitziana, Primula luteola, P. lazica, Oenanthe abchazica, Pycreus colchicus* and *Swertia iberica.*

Hydric tall herbaceous vegetation occurs mainly on lowlands and Volcanic Upland of the South Georgia. Its upper limit here is 2000 m. One of the most common formations of this group is *Phragmiteta australis. Typheta* is considered to belong to the above-mentioned group. It is dominated by *Typha latifolia, T. angustifolia* or *T. laxmanii. Schoenoplecteta* with its phytocoenoses dominated by *Schoenoplectus lacustris* or *S. tabernaemontani* attracts a special attention.

Cladieta marisci is populated on the lowlands and foothills of the Caucasus. The dominant *Cladium mariscus* is a thermophilous relic species; its upper limit lies at an altitude of 800 m.

Glycerieta arundinaceae and *Digraphieta arundinaceae* manifest rare formations of hydric tall herbaceous bog vegetation.

In Georgia the hydric low herbaceous bog vegetation extends from sea level up to 2300 m. In general it occupies a negligible area. *Equiseteta*, which is dominated by *Equisetum heleocharis, E. palustris* and *E. ramosissimum* species, is confined to lowlands and low mountain zone.

Hippuris vulgaris is one of rare obligatory helophytes.

Sparganieta is one of the most common formations of hydric low herbaceous vegetation. The monodominant phytocoenoses of this formation are dominated by *Sparganium polyedrum* or *S. simplex.*

Butometa umbellati, according to the published data, occupies limited areas in Georgia. In mountains it is represented just by one association – *Butometum umbellati.*

Cariceta dichoandrae, Cariceta acutiformis, Cariceta elatae, Cariceta caespitosae, Cariceta wilnicae and *Magnojunceta. Cariceta elatae* is rare in Georgia, as well as *Cariceta caespitosae*, which is spread in South Georgian Volcanic Upland and Ajara Mts. *Cariceta wilnicae* is confined to Javakheti Upland; it extends from 2000 to 2100 m

Magnojunceta differ from abovementioned *Carex* communities; it is dominated by *Juncus effusus* or *J. inflexus.*

Eutrophic bog vegetation including herbs with short rhizomes is very common for the subalpine belt of Georgia and the Caucasus; at the same time some formations are also characteristic of the alpine zone, for example *Cariceta daciae* (*Cariceta transcaucasicae*).

Cariceta kotschyana are typical for alpine belt of the Greater Caucasus; they extend from 2000 up to 2900 m s. m.

Blysmeta compressi are spread in the mountains of Georgia; the dominant species here is *Blysmus compressus.* The species of *Sphagnum* are not present among the coenoses of this formation.

Eumesotrophic bog vegetation, including herbs with short rhizomes, is also characteristic of subalpine belt. It plays an important role in the process of accumulation. The typical representative of this formation is *Cariceta canescentis.* Moss synusium is dominated by *Calliergon stramineum* and *C. gigan-*

teum, rarely by *C. richardsonii* and *C. cordifolium.*

Cariceta inflatae, which are confined to the subalpine belt are a typical syntaxon of eumesotrophic bog vegetation of Georgia.

Cariceta lasiocarpae are a typical formation of peat bog vegetation. *Carex lasiocarpa*, distributed in Holarctis, bears an important function in the process of peat accumulation. *Cariceta lasiocarpae* are very abundant in North Eurasia and North America.

Cariceta chordorrhizae are widespread in North Eurasia, while it is rarely found in the Caucasus. The leading species *Carex chordorrhiza* is an obligatory helophyte.

Cariceta songoricae are very rare in the Caucasus; their distribution area involves marl schists and limestones of Kavkasioni.

Menyantheta trifoliae occupy mountain bog surfaces; their upper limit is situated at the altitude of 2250 m.

Molinieta litoralis are restricted to the Colchic Lowland and is an important component of peat bog phyto-landscape.

Mesotrophic herbaceous bog vegetation is mainly distributed in West Georgia from sea level up to the subalpine belt. It participates in the process of peat accumulation. Formations of this group include *Scheuchzerieta palustrae*, a rare component in the vegetation of the Caucasus. It occurs only in Svaneti (West Georgia), at 1700-2100 m.

Cariceta limosae are a typical representative of mesotrophic herbaceous bog vegetation. The dominant *Carex limosa* is an obligatory helophyte developed on peat bog surface.

Cariceta irriguae extend from 1750 to 2400 m in the mountains of Georgia.

Eriophoreta vaginati are a typical formation of mesotrophic herbaceous bog vegetation; they are widely distributed in the taiga zone of Eurasia and occupy a limited area in Georgia and the Caucasus.

Rhynchosporeta caucasici are another interesting formation of the above-mentioned vegetation; they are typical for Colchic peat bogs.

Mesotrophic *Sphagnum* bogs mostly occur in the mountains of West Georgia.

The area of distribution of *Sphagnum* bogs comprises lowland and mountainous parts of West Georgia. Peat accumulation here is limited provided for the unfavourable physico-geographical conditions. In western part of Kavkasioni *Sphagneta magellanici* are confined to the upper limit of *Picea/Abies*

forests. A frequent component of meso-oligotrophic bog vegetation is *Sphagnetum magellanici cariosum*. Its moss synusium is characterized by a high presence of *Sphagnum angustifolium* and *S. amblyphyllum*.

Typologically, *Sphagneta palustris* are one of the most interesting formations of oligotrophic *Sphagnum* bog vegetation. They play an important part in the vegetal landscapes of Colchic Lowland. Their moss synusium is dominated by *Sphagnum palustre*. Frequent associates of dominant species are *Sphagnum apiculatum, S. papillosum, S.contrale, S. amblyphyllum*, etc.

Sphagnetum palustris caricoso-moliniosum occupies a vast area in Colchic Lowland. Herbaceous synusium is dominated by *Molinia litoralis* and *Carex lasiocarpa*, rarely by *Carex acutiformis*.

Sphagnetum palustris scheuchzeriosum extends from 1700 up to 2100 m, while *Sphagnetum palustris rhynchosporosum albae* occupies areas above 1500 m. These communities are distributed in West Georgia.

Sphagneta angustifolii are considered to belong to the group of formations of oligotrophic *Sphagnum* bogs. They extend from 1600 up to 2000 m and in some parts even to 2500 m.

The distribution area of *Sphagneta imbricati* is situated in the southern part of Colchic Lowland. *Sphagnetum imbricati moliniosum litoralis* belongs to the commonest coenoses. The above-mentioned communities involve the following constant species: *Molinia litoralis, Carex lasiocarpa, Rhynchospora caucasica, Drosera rotundifolia, Osmunda regalis*, etc.

Sphagneta fusci, characteristic of Eurasia and North America, occur in the Caucasus and Georgia, in particular. The dominant *Sphagnum fuscum* is a rare component of the Caucasian moss flora. Another example of rare communities is *Sphagneta acutifolii*.

Bog vegetation with arboreal components occupy considerable areas in the lowlands of West Georgia, whereas they are poorly represented in the mountains. *Alnus glutinosa* plays an important part in the communities distributed in lowland; its frequent associate in mountains is *Alnus incana*.

The *Alnus glutinosa-A. incana-Frangula alnus-Phragmites australis* complex covers the surfaces of several bogs in the mountains of West Georgia.

Bog vegetation with shrubs is very rare in Georgia. Mainly it extends on the mountains between 1700 and 2000 m.

These communities can be illustrated by *Saliceta varioherbosa* and *Saliceta herboso-sphagnosa*.

Aquatic vegetation of Georgia is also worth of a brief account. This type of vegetation still needs to be researched though.

According to KOLAKOWSKY (1961), *Lemna* groupings occur on stagnant waters, ditches and pools of Colchic Lowland. Typical plants of this grouping are *Lemna minor, Spirodela polyrhiza, Salvinia natans*.

Hydrocharis grouping consists of plants, which occur on still waters and among the thickets of tall aquatic herbs. 2 ecological types can be outlined within this grouping. The first type is manifested by *Ruppia* grouping, which occurs in water bodies along the coast and island salt lakes. This grouping consists of *Ruppia spiralis, R. maritima, Zostera marina*, etc. The second ecological type is represented by freshwater plants, such as *Potamogeton lucens, P. natans, P. crispus, Myriophyllum spicatum, Nymphaea candida, Nuphar luteum* and *Trapa colchica*. The rare groupings of *Utricularia vulgaris* and *Aldrovanda vesiculosa* are to be found in lakes Bebe-Syr and Anishkhara (Abkhazeti).

Mid-mountain aquatic vegetation of West Georgia is floristically very poor. *Callitriche verna* is the only typical aquatic plant of the alpine zone of Georgia.

10. SYNANTHROPIC VEGETATION

The synanthropic vegetation involves three large groups: 1) segetal plant communities of cultivated habitats; 2) ruderal vegetation formed by plants growing in the vicinity of dwellings, roadsides, disturbed lands etc.; and 3) pastoral groupings of pasture weeds.

10.1. Segetal Vegetation

The segetal plant communities of Georgia are extremely diverse floristically and ecologically and should be tentatively specified into the following five groups.

Grain crops

The segetal communities of grain crops are very rich in species. Over 700 species grow in corn, wheat and barley fields. Examples of the most troublesome weeds are *Avena ludoviciana, Lolium rigidum, Secale cereale, Sinapis arvensis, Rumex crispus, Convolvulus arvensis, Setaria pumila* and *Agrostemma githago*.

Corn fields in Georgia are manifested by *Setaria viridis, Amaranthus retroflexus, Cynodon dactylon* and especially by *Sorghum halepense*.

In montane areas of the Caucasus and Georgia, in particular, floristic composition of segetal communities is enriched by the plants, which frequently occur on mountain slopes. Of these plants the following may be mentioned: *Bunias orientalis, Vaccaria hispanica, Melampyrum arvense* and *Bifora radians*.

Cultivated subtropical plants

In West Georgia large areas are occupied by tea plantations. It should be noted that these plantations provided 95% of the tea produced in the former USSR.

Paspalum digitaria (North America native), *Digitaria sanguinalis, Calystegia sepium, Rumex crispus, Pteridium tauricum, Conyza canadensis*, etc., are the main weeds of these tea plantations. Weeds of the above-mentioned group include a number of annuals with the flowering period in spring, such as *Vicia tetrasperma, V. angustifolia, Vulpia myuros, Bromus japonicus, Stellaria media*, etc.

Segetal flora of the areas under tung tree, laurel and citrus fruit resembles tea plantations *Sorghum halepense, Echinochloa crus-galli, Setaria glauca, S. viridis, Cichorium intybus*, etc., frequently occur on theses plantations.

Orchards and vineyards

Viniculture and fruit growing are the leading branches of agriculture of Georgia. Large orchards with various fruit trees and vineyards have spread all over the country. Their diverse flora counts over 400 species. Common segetals can be manifested by *Cynodon dactylon, Setaria glauca, Convolvulus arvensis, Lavatera thuringiaca, Tragopogon graminifolius, Urtica dioica, Malva sylvestris,* etc.

Vegetable gardens

This group is involves not only common segetal weeds but also plants growing on rich, fertilised soils. Examples of the above-mentioned plants are *Sonchus asper, S. oleraceus, Chenopodium album, Amaranthus retroflexus, A. lividus, Portulaca oleracea, Cynodon dactylon*, etc.

Rice fields

In rice fields of West Georgia most of weeds are hygrophytes and hydrophytes. High presence of adventive weeds native to South-Eastern Asia and Mediterranean is a peculiar feature of the segetal flora of rice fields.

The following noxious weeds of rice fields should be mentioned: *Echinochloa crus-galli, Cyperus difformis* and *Cyperus glomeratus.*

10.2. Ruderal Vegetation

Communities enclosed in the group of ruderal vegetation differ by their habitat and composition.

Roadside communities are formed by plants resistant to trampling down. Common plants of roadsides include *Cynodon dactylon, Sclerochloa dura, Eleusine indica, Eragrostis pilosa, E. minor,* etc.

The following species occur on soils rich in organics: *Solanum persicum, Hyoscyamus niger, Conium maculatum, Datura stramonium, Solanum nigrum, Phytolacca americana,* etc.

It must be noted that these communities, along with ruderals include also weeds growing in vegetable gardens, such as the species of *Amaranthus, Conyza canadensis, Ambrosia artemisiifolia, Xanthium strumarium* and *Anchusa italica.*

Many plants recognised as ruderals are used in medicine (e.g. *Datura stramonium, Hyoscyamus niger,* etc.).

10.3. Vegetation of Pastures

Pastures, whether they consist of natural grasslands, hay fields, which have been used for grazing, or the land, which is too poor or otherwise unfit for anything but grazing, frequently include certain weeds associated with them. Many of the commonest pasture weeds are unpalatable, distasteful or even poisonous to stock plants. Others have spines, thorns or modifications unfavoured by stock.

In Georgia summer pastures are richer in weeds than winter ones. Majority of pasture weeds are not dominants of communities, but in overgrazed areas some of them form independent communities, such as *Veratrum lobelianum* and *Rumex alpinus.*

The following plants frequently occur in lowland semi-desert pastures: *Adonis aestivalis, Cynanchum acutum, Hirschfeldia incana, Xanthium strumarium,* etc.

Summer pastures of subalpine belts are characterized by the presence of *Cirsium arvense, C. incanum, Veratrum lobelianum, Daphne glomerata, Ranunculus caucasicus, R. oreophilus,* etc. In subalpine belt poisonous *Aconitum nasutum* and *A. orientale* are also to be found.

11. CULTIVATED FLORA (by MENABDE, 1961)

Formation of cultivated flora is constitutionally interconnected with human activities. It makes an integral part of the material culture of mankind. The most ancient memorials of human activities date back to the Palaeolithic. The earliest traces of agriculture in Georgia belong to the Mesolithic period. Among the monuments of this era are stone tools – pestles and graters. Archaeological findings of charred remains of wheat, barley, millet and flax seeds, as well as of agricultural utensils such as grain-grates, sickles, etc., confirm the diversity of the cultivated flora of Neolithic and particularly of the Eneolithic period.

Eneolithic culture of Georgia, which can be traced back to the third millennium B.C., was mainly represented by agriculture and cattle-breeding. Fruit gathering was also widely practised. Among the remains of the late Eneolithic and early Bronze Ages, such fruit of wild plants as chestnut (*Castanea*), beech (*Fagus*), oak (*Quercus*) and hazelnut (*Corylus*) have been discovered side by side with cultivated plants in the burial mounds of West Georgia.

Agriculture of ancient Georgia is best illustrated by the monuments of the early Bronze Age (second millennium B.C.). Many kinds of wheat were domesticated during that period; barley, millett, flax and vine were subject to cultivation. In the late Bronze Era (10-7 centuries B.C.), in the State of Urartu in Transcaucasia almost all branches of agriculture were well developed; cultivation of cereals, leguminous plants, horticulture, viticulture, fodder-grass cultivation (especially for horse food) and cattle-breeding. By that time irrigation had already been well organized.

Cultivation of many plants in ancient Georgia was mentioned in the works of writers of that time. Xenophon (the 5th century B.C.) speaks of two kinds of wheat cultivated in Colchis.

Wheat is one of the oldest domesticated plants in the world. Archeological discoveries prove that Karthvelis (Georgians) started to cultivate wheat more than five thousand years ago. During these millennia Karthveli farmers created many species and varieties of wheat.

The initial roots of some wheat species dating back to the Eneolith and Bronze eras (*Triticum macha, T. palaeocolchicum*) are being preserved in the agriculture of present-day Georgia. Such species of wheat as the so-called Zanduri, incomparable among world wheats for their qualities and immunity against diseases, are the products of labour of Kartveli farmers. So far, modern selection has failed to breed a kind of wheat with the properties of Zanduri.

By means of phylogenetic research, a basic variety of wheat species in the agriculture of Georgia has been revealed. Some of these species bear evolutionarily close affinity to wild wheat species, or have retained some of their features. The wheats Maha (*T. macha*), Colchic spelt (*T. paleocolchicum*), Zanduri (*T. timopheevi, T. zhukowskyi*) are unique plants, which are still being cultivated and which still retain the basic features of wild wheat.

Because of very brittle ears, harvesting of such species as Maha and Colchic spelt proceeds in two stages: first by means of two loosely bound sticks (so called shnakvi) you throw the ears into baskets and then cut the straw. The species Maha is the living relict of primary agriculture, which have been cultivated by man since the prehistoric era (Eneolith-Bronze). Another unique monument of the prehistoric culture is Zanduri wheat species. Species generating Zanduri population have nothing to do either with wild or cultivated species of Asia Minor, though they reveal genetic affinity with the species growing on the modern territories of Armenia and Azerbaijan.

On the whole the following cultivated species of wheat have been recorded in the fields of Georgia: *T. monococcum* (monograin), *T. dicoccum, T. timopheevi, T. zhukowskyi, T. paleocolchicum* (all spelts), *T. durum, T. carthlicum, T. turgidum, T. polonicum* (all hard wheats) and *T. aestivum, T. compactum, T. macha* (all soft wheats).

Georgian endemics are: *T. paleocolchicum, T. timopheevi, T. zhukovskyi, T. macha* and *T. carthlicum.* Only *T. carthlicum* has penetrated into the agriculture of neighbouring countries.

At present, maize, wheat, and barley are the principal cereals in Georgia. The first one, maize, absolutely predominates in West Georgia, while the second one, wheat, is mainly cultivated in the fields of East Georgia and in small quantities is available in foothill and mountain districts (Javakheti, Kazbegi), the greater part of acreage is hold under barley (about 85%). Winter wheat crops are encountered from the littoral or Black

Sea in the West (near the town of Gagra) to the high-mountain agricultural zone (up to 2 000 m s. m.) Spring wheat crops are spread everywhere but they prevail over winter crops only above 1500–1800 m.

The most widespread (and therefore the most important one at present) are three species: 1) soft wheat (*T. aestivum*), 2) Karthlian wheat (*T. carthlicum*) and 3) hard wheat (*T. durum*). The rest of the species occupy small areas.

Soft wheats are the leaders in the cereal economy of the country. Many centuries of popular selection resulted in a great number of local varieties, some of which (e.g. Dolis-puri) have retained their considerable part in national economy.

Karthlian wheat Dika (*T. carthlicum*) mainly occurs in the mountain agricultural belt within 1000–2300 m s. m. Popular varieties are sown, and partly those of modern pureline section. Hard wheat crops extend in the lower agricultural belt from 800–900 m. Its acreage can be found mainly in East Georgia.

On the Black Sea coast (in the vicinity of Gagra) small tracts of so-called English wheat (*T. turgidum*) have been preserved until now.

At present, production of wheat crops is mainly represented by selection and selectionally improved varieties, and more seldom by more popular selection varieties.

On the basis of phylogenetical research, it was ascertained that the principal specific variety of wheat has been preserved only in the agriculture of Georgia and has never even surpassed the boundaries of the land of wheat crop originators, so that primary species of crops close to wild species are known only here and used only by Georgian people.

The idea is that the creation of primary species of cultivated plants is genetically connected with the natural conditions of some geographical regions, where only useful plants of the wild flora make primordial source of popular selection. It has already been stated that Asia Anterior (including Transcaucasia) is the only region of habitation of wild wheats. Therefore, it is natural to presume that the culturation of wheat is the result of creative activities of civilized people of Asia Anterior. Archeological materials and botanico-genetical analysis of modern wheats composition give enouph grounds to attribute wheat culturation to Khetto-Iberian group of people.

Natural conditions for wheat do-

mestication did exist only in that region.

All the aforesaid underlines the primordial character of a Georgian wheat cultivation. The Georgian nidus by origin and formation of wheat species diversity is a consequence of a long process of popular selection, the main roots of which are genetically connected with the pre-historic activity of Hetto-Sumeret peoples, living on the territory of Asia-Anterior – the region of habitats of wild wheat.

The creative process of Georgian popular selection is not limited by the above-stated. The collective work of Georgian cultivators manifests itself by the cultivation of grape vine. At present there are over 400 varieties with Georgian appellations. Versatility and antiquity of the culture is confirmed not only by the existance of numerous sorts, but by data of Eneolithic culture as well. In the times of the existence of the state of Urartu wine-making as well as viticulture was highly developed. Georgian popular grape sorts – Saperavi, Rkatzhiteli, etc. –enjoy in our days the same unsurpassed fame, which in its turn points to the long process of selection of high-grade grape varieties.

Georgia is likewise the home of many fruit plants. Many species of wild fruit-trees (*Malus, Pyrus, Prunus*) have undoubtedly served as the principle components in the origin of cultured plants like apple, pear, and plum-trees.

It has been proved by the investigation of Georgian scientists that the Georgian apple sort Khomarduli is the initial variety for the so-called English and French paradise-apples widely diffused in European countries.

Ancient agricultural crops were formed exclusively on the basis of the utilization and cognition of aboriginal useful wild plants. In this way, primary independent nidi of agriculture arose. In the subsequent period of the cultural development and intercourse of peoples those primary agricultural groups were mutually enriched with imported plants. It has been ascertained from historical sources that in ancient Georgia the introduction of useful foreign plants was organized on a large scale.It is obvious that the presence of the *Citrus* type of agriculture production created in Georgia from representatives of foreign subtropical plants indicates a great interchange carried on between the peoples inhabiting lands with different ecologo-geographical conditions. Many of these plants, no doubt passed through a number of "replantation" points to the way from their initial habitation to their new home in Georgia. These points played a

certain part in acclimatization and selection.

Gardens of royal and feudal families of ancient Georgia played a major role in the introduction of foreign plants, in particular Citrus, decorative and other useful ones.

At present, numerous representatives of foreign vegetation – the tea-bush, the tangerine-tree, subtropical fruit-trees and technical and decorative plants, etc., are important (and in some regions the chief) objects of agricultural production.

რეზიუმე

საქართველოს ფიზიკურ-გეოგრაფიული პირობების
მრავალფეროვნებამ, მძიემ დანაწევრებულმა რელიეფმა,
ვერტიკალური სართულების კონტრასტულობამ, ხხვადახხვა
გენეზისის ფიტოლანდშაფტების საზდვარზე მისმა მდებარეობამ
განაპირობეს ამ ქვეყნის მცენარეული სამყაროს
განსაკუთრებული სიმდიდრე და ნაირსახეობა. შედარებით
ცირე ტერიტორიაზე საქართველოში განვითარებულია
ერთმანეთისაგან სრულიად განსხვავებული ეკოსისტემები,
ალახავლეთ საქართველოს ნახევრად უდაბნოთი და
დასავლეთ საქართველოს სუბტროპიკული კლიმატის კოლხური
ტყეებით დაწყებული და მეჯნქარისახრა მცენარეულობით
გამთავრებული.

კავკასიის რელიეფის მკვეთრმა დანაწევრებამ და მთების
თავისებურმა სტრუქტურამ განაპირობეს ფიტოცენოზების და
ცალკეული სახეობის გეოგრაფიული და ეკოლოგიური
იზოლაცია და ამასთან დაკავშირებით ენდემიზმის მაღალი
დონე.

საქართველოს ტერიტორიაზე გავრცელებულია ჭურჭლოვან
მცენარეთა 5000-მდე სახეობა; მათ შორის ~ 1500-მდე
ენდემურია.

ეოცენში საქართველოში გავრცელებული მცენარეების
მსგავსი სახეობების დღეს წარმოადგენილია
ინდოეთ-ავსტრალიაში მარადმწვანი ხეების, ხისმაკჯარი
გვიმრების, პალმების და სხვათა სახით.

ვცცა მიოცენში ეტყეო აგცილების გავალვაკამმდე
მცენარეულობა კავკასიაში ფართოდ იყო განვითარებული.
პლიოცენის დასაწყისში ხმელეთის იმ ნაწილზე, სადაც დღეს
დასავლეთ საქართვა და შავიზღვისპირეთის მოსახლეორე
ტერიტორია მდებარეობს, გაბატონებული იყო შედარებით
თბილი და ნოტიო კლიმატი. ამ პირობებში აქ
ჩამოყალიბდა უძველესი მეზოფილური ტყის ფლორის
კოლხეთის რეფუგიუმი. ამ რეფუგიუმმა ხლიოცენის მთელ
ხერიოდში და განსაკუთრებით კი მეოთხეული ხერიოდის
დიდი გამყინვარების ეპოქაში გადამწყვეტი ფუნქცია შეასრულა
რელიქტური სახეობების გადარჩენაში.

დასავლეთ საქართველოში არ არის ქსეროფილური
მცენარეულობის ეტყეო სარტეული. მეზოფილური ტყის
მცენარეულობა აქ განვითარებულია ზღვის სანაპიროდან
სუბალპურ სართულამდე. ამასთან დაკავშირებით საქართველოს
ამ ნაწილში მცენარეულობის ვერტიკალური პროფილი
უფრო მარტივია, ვიდრე აღმოსავლეთ საქართველოში,
კერძოდ, აქ წარმოდგენილია ტყის სართეული (1900 მ-მდე),
ხუბალპური (1900-2400 მ-მდე), ალპური (2400-2900 მ.), და
ხუბნივალური და ნივალური სართეული (> 2900 მ.).
აღმოსავლეთ საქართველოს მცენარეულობის ვერტიკალური
გავრცელების პროფილი უფრო რთულია. აქ კარგადაა
დიფერენცირებული 6 ხხვადახხვა სართეული ნახევარადუდაბნოს,
სტეპის და მშრალი ნათელი ტყის (150-600 მ.), ტყის
(600-1900 მ.), სუბალპური (1900-2500 მ.), ალპური
(2500-3000 მ.), ხუბნივალური (3000-3600 მ.) და ნივალური
(> 3600 მ.).

სამხრეთ საქართველოში, კერძოდ, ჯავახეთში, ტყის
სართეული არ არის განვითარებული. აქ გავრცელებულია
ძირითადად მაღალმთის სტეპები, კგრივკორდიანი ნახევრად
მშრალი მდელოები.

Zusammenfassung

Die Mannigfaltigkeit der physisch-geographischen Faktoren: die komplizierte Gliederung des Reliefs, die kontrastierenden Höhenstufen wie auch die Lage Georgiens an der Grenze von biogeographischen Großräumen verschiedener Genese bestimmen den Reichtum und die Vielfalt der Pflanzenwelt Georgiens. Auf einem verhältnismäßig kleinen Territorium entwickelten sich die verschiedenartigsten Pflanzengesellschaften, angefangen von Halbwüsten in den Ebenen und Hügeln im Osten über üppige Wälder unter feuchtem, fast subtropischem Klima im Vorgebirgsland der Kolchis bis zu der eigentümlichen kryophilen Hochgebirgsvegetation des Kleinen Kaukasus im Südwesten und insbesondere des Großen Kaukasus im Norden.

Die Gliederung des Reliefs und die Struktur der Gebirge bewirken ein hohes Maß an geographischer und ökologischer Isolation der regionalen Ökosysteme, was im hohen Grad des Endemismus (ungefähr 1500 Arten) seinen Niederschlag findet. Auf dem Territorium Georgiens trifft man gegen 5000 Arten wildwachsender und verwilderter Gefäßpflanzen.

Im Eozän unterschied sich die Flora sehr wesentlich von der gegenwärtigen. Die größte Ähnlichkeit mit jener hat heute aller Wahrscheinlichkeit nach die indisch-australische Flora mit ihren immergrünen Baumarten, Baumfarnen, Palmen u. a. Es wird angenommen, daß die waldlosen Formationen der trockenresistenten Vegetation im Kaukasus bereits im Miozän weit verbreitet waren. Bereits im Anfang des Pliozäns entsteht auf jenem Teil des Festlandes, wo jetzt Westgeorgien und einige angrenzende Territorien des Schwarzmeergebietes liegen, das kolchische Refugium mit Relikten einer älteren mesophilen Waldflora, begünstigt durch das dort herrschende verhältnismäßig warme und feuchte Klima. Das kolchische Refugium hat bei der Erhaltung reliktischer Arten im Lauf des Pliozäns eine große Rolle gespielt, und zwar besonders im Laufe des Quartärs einschließlich der Epochen der großen Vereisungen.

In Westgeorgien fehlt vollständig der waldlose Gürtel der Trockenvegetation, vielmehr sind sind Täler und Berghänge schon vom Meeresspiegel an mit Wäldern bedeckt. Deshalb ist die vertikale Stufung (Gürtelung) einfacher und durch vier Grundstufen darzustellen: Waldstufe (von der Küste bis zu 1900 m s. m.), subalpine (1900-2400 m), alpine (2400-2900 m), subnivale und nivale (2900 m) Stufe.

Im Ostgeorgien ist die vertikale Gürtelung komplizierter. Hier sind 6 Hauptstufen (Gürtel) ausgeprägt: der Gürtel der Halbwüsten, der trockenen Steppen und der trockenen Lichtwaldes (150-600 m s. m.), der Waldgürtel (600-1900 m), der subalpine (1900-2500 m), der alpine (2500-3000 m), der subnivale (3000-3600 m) und der nivale (3600 m s. m.) Gürtel. Innerhalb der Waldstufe und der subalpinen Stufe des südgeorgischen Hochlandes (Dschavacheti) entwickeln sich auch waldlose Vegetationstypen: Bergsteppen und Trockenwiesen.

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CONTENTS

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