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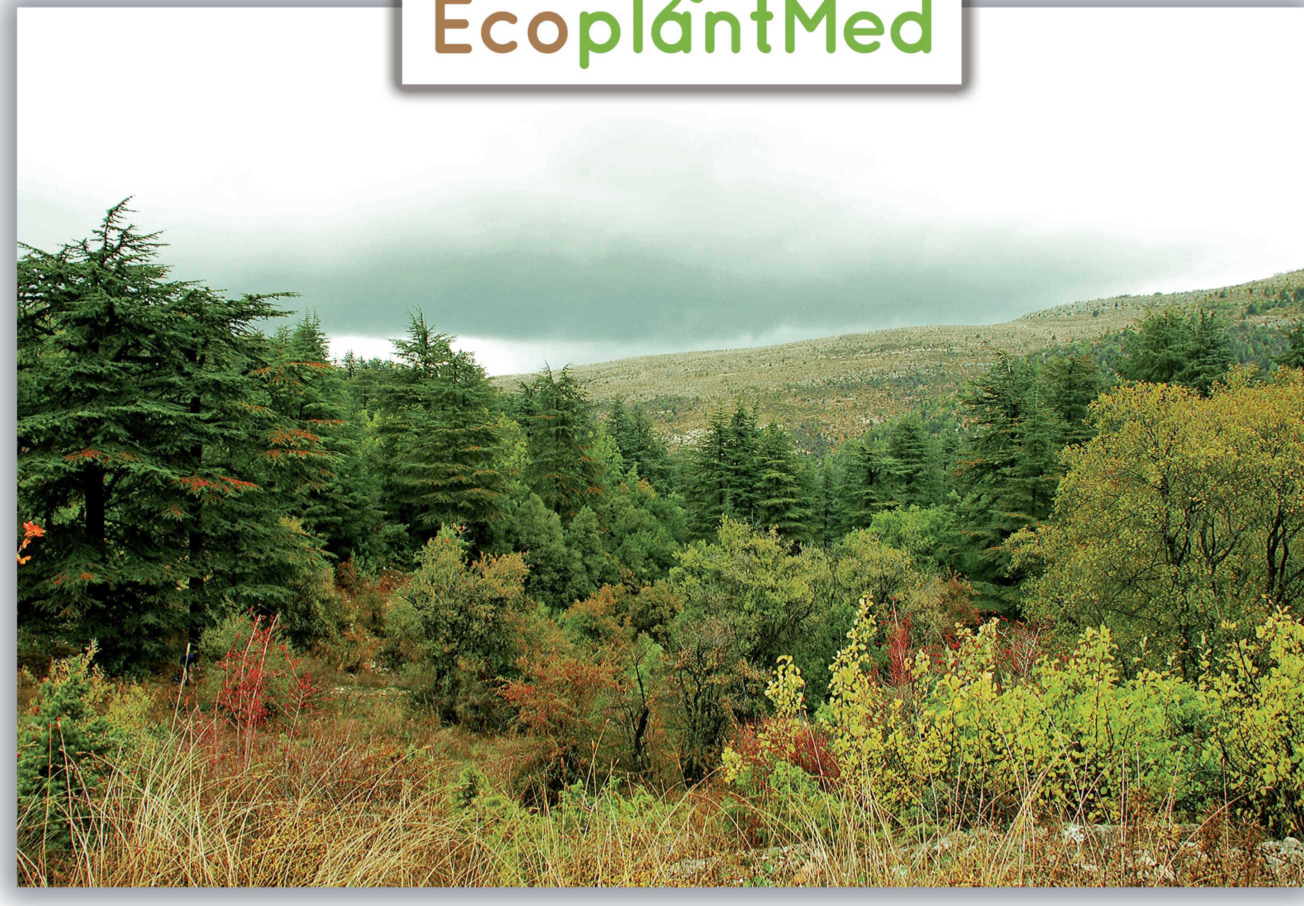

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Root adaptive management for improving plant quality and field performance under drought: experiences with native tree species from a South American Mediterranean-type ecosystem

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Abstract
Plant quality attributes have been widely studied for numerous tree species inhabiting the Mediterranean Basin, resulting in a positive impact on restoration success in degraded forest ecosystems. However, there has been less research on root morphological attributes, especially of native tree species in South American Mediterranean-type ecosystems, which are currently subject to unprecedented drought events and degradation. We summarize experiments examining the use of root adaptive management during the nursery and field stages for improving plant quality and seedling performance under water-limited conditions in central Chile. The first experiment (E-1) evaluated the effect of controlled-drought regimens on root development and seedling performance of two tree species (*Quillaja saponaria* and *Cryptocarya alba*) with contrasting root growth strategies. The E-1 results confirmed the importance of considering the root growth strategy as a criterion in the selection of species and watering decisions. The second experiment (E-2) assessed the effect of increasing fertilization doses in the nursery on *Q. saponaria* root morphology 1 year after planting seedlings in the field. The results showed that, as a result of nutrient deprivation, small plants with a greater stem diameter and lower shoot:root ratio contributed to improving water-stress resistance early during a drought period. The third experiment (E-3) determined the effect of different locations of fertilizer placement into the soil profile on rhizosphere salinity and root development of *Q. saponaria* seedlings. The E-3 results showed that fertilization practices in dryland areas require watering because this acts to control the increase in salinity in the rhizosphere and, consequently, avoids negatively impacting the root volume growth. Our findings could be useful for identifying the major gaps present in the production and establishment stages of native tress in Chile, and could address the latter through root adaptive management.

Key words: central Chile, dryland forest, nursery fertilization, seedling quality, root architecture.

Introduction

Mediterranean-type forest ecosystems around the world have a long history of land-use change and degradation (Fuentes *et al*., 1989; Vallejo *et al*., 2012; Cianfaglione *et al*., 2014; Vadell *et al*., 2016). In South America, the Mediterranean-type forest located in central Chile (30°–36°S) is the ecosystem with the highest native forest coverage loss in the region (including the Amazonian forest) following Spanish colonization in 1536, with 83% of the original cover lost (Salazar *et al*., 2016). Today, the remnants of the Chilean Mediterranean forest (sclerophyllous trees and shrubs species) cover an area of 473437 ha, representing only 3% of the total area of native forest in Chile (CONAF, 2011). In addition, the persistence of the current mega-drought has resulted in the deterioration of natural vegetation throughout central Chile (Garreaud, 2015), and represents a strong limitation to the seedling recruitment of most native tree and shrub species (Van de Wouw *et al*., 2011). In this context, active restoration in Chile has become a priority because of the magnitude of forest coverage loss and its impact on ecosystem services (Lara *et al*., 2009; Newton *et al*., 2012; Smith-Ramírez *et al*., 2015).

The increase in restoration and reforestation activities has generated an increase in the demand for native species, as well as for more information on nursery management and plantation practices (Santelices *et al*., 2011; Bannister *et al*., 2013). The most common native species used for the restoration of Chilean Mediterranean forest are *Acacia caven*, *Cryptocarya alba*, *Lithraea caustica*, *Maytenus boaria*, and *Quillaja saponaria* (Newton & Tejedor, 2011; Becerra *et al*., 2013). However, there is a lack of standardized management criteria and plant production protocols for use by local growers that would enable them to offer a product of certified quality. Currently, in Chile, the only rule in force (NCh Nº2957/2006) is voluntary, and establishes standards of genetic, physiological, and morphological quality only for major exotic tree species for industrial use (i.e., *Pinus radiata*, *Eucalyptus globulus*, and *Pseudotsuga menziesii*) (INN, 2006). Therefore, the poor technological development and scientific research around the quality of native plant species result in the provision of low-quality seedlings, with highly

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variable phenotypic traits (Quiroz *et al*., 2012) and low survival after outplanting during the first 2 years of establishment (Holmgren *et al*., 2006; Becerra *et al*., 2011).

Experiences in different Mediterranean-type climate ecosystems (central Chile, California, Southeast Spain, and Southwest Australia) recognize the importance of root morphological and functional traits of evergreen species for water stress resistance during severe drought periods (Giliberto & Estay, 1978; Canadell & Zedler, 1995; Padilla & Pugnaire, 2007; West *et al*., 2012). Therefore, given that the ability of seedlings to survive drought periods depends largely on the degree of development of the root system during nursery phase (Luis *et al*., 2009; Cuesta *et al*., 2010), nursery practices designed to promote root development could lead to plants that are able to exploit limited soil resources.

Nursery practices, such as nitrogen fertilization, are perhaps the most effective in producing changes in morphology and root biomass in Mediterranean tree species (Villar-Salvador *et al*., 2012; Oliet *et al*., 2013). A high nitrogen and/or phosphorus supply in nursery leads to the greater productive capacity of seedlings (i.e., larger plants and high foliar N concentration), thus helping to sustain the demand for resources used during the early growth of the root system, and to maintain a positive carbon balance during the initial phase of establishment under field conditions (Luis *et al*., 2009; Cuesta *et al*., 2010). However, the positive effect of high nutrient availability on seedling performance (Villar-Salvador *et al*., 2012) depends on the intensity and length of the dry season (Cortina *et al*., 2013). Under severe drought conditions (i.e., a drought period longer than 5 months), some morphological attributes become adverse for seedling performance, affecting the water balance as a consequence of a greater transpirational surface exposed to radiation, because of an increased shoot:root ratio and improved plant survival (Hernández *et al*., 2009; Cortina *et al*., 2013). Previous studies under Mediterranean conditions concluded that nutritional deficiency in the nursery promotes the development of xeromorphic traits, which favor drought avoidance and post-planting performance (Trubat *et al*., 2008; Cortina *et al*., 2013).

A better understanding of the interaction of fertilization and water availability during the transition from nursery to field is a key factor to correctly address the problem of root system quality of tree species destined for planting under highly stressful conditions, such as the Chilean Mediterranean region. To help fill the current knowledge gap, we investigated different approaches to root adaptive management based on nutritional and watering availability regimens during the nursery–field transition in native tree species growing under severe drought conditions in central Chile.

Material and Methods

Plant material

For the first experiment (E-1), the target species used were 2-year-old *Quillaja saponaria* (deep-rooted) and *Cryptocarya alba* (shallow-rooted) seedlings. By contrast, for the E-2 and E-3 experiments, only 2-year-old *Q. saponaria* seedlings were used. Both species are endemic to the Neotropics and are widely distributed throughout central Chile (30°–38° S); they are commonly used in the active restoration of degraded native forests, although with high heterogeneity in growth and survival. *Quillaja saponaria* is a shade-intolerant pioneer tree species that develops a strong tap root under natural conditions as one of its main strategies to survive long drought periods (Giliberto & Estay, 1978). By contrast, *C. alba* is a shade-tolerant late-successional species that grows in moist areas and develops shallow roots (Donoso, 1982).

The potting substrate comprised a mixture of loam soil, leaf mold, and compost at a ratio of 2:1:1. Seedlings were grown under 50% shade and a regular irrigation regimen to keep the soil permanently moist. Seedlings did not receive a nutritional supply (fertilization) while in the nursery.

Study site

For E-1, the plantation site was located at the experimental station of the Pontificia Universidad Católica de Chile (33º26'S, 71º01'W; altitude 195 m), Curacaví Valley, central Chile. For E-2 and E-3, the production and plantation sites were established in Quebrada de la Plata (33º29'S, 70º52'O; altitude 490 m), also located in central Chile (Fig. 1). Both study areas were located in a recently abandoned flat grazing area, near to piedmont. The climate of both study sites is Mediterranean, with a 6–8-month dry period and marked rainfall seasonality, with mean annual temperatures of 15°C, mean annual rainfall of 330 mm, and 67% relative humidity (Di Castri & Hajek, 1976) (Fig. 2).

Treatments and experimental design

E-1 was a completely randomized design with two treatments (watering regimes): either 2 L plant^{-1} week^{-1} (W+) or no watering (W-). Each treatment was applied to 48 replicates per species (96 plants in total per species).

E-2 had a nursery and field establishment stage. The nursery experiment (6 months) was a completely randomized design with four fertilization treatments. Each treatment was applied to 60 replicates (240 plants in total). Treatments comprised incremental doses of controlled-release fertilizer (CRFN): 0 (unfertilized), 3 (low), 6 (medium), and 12 g L^{-1} (high), equivalent to 0.00, 0.45, 0.90, and 1.80 g N L^{-1}, respectively. The CRFN used was Basacote® Plus (COMPO) 15N-

Fig. 1 - Location of the study area in central Chile (Mediterranean-type climate) (Photo: Juan F. Ovalle).

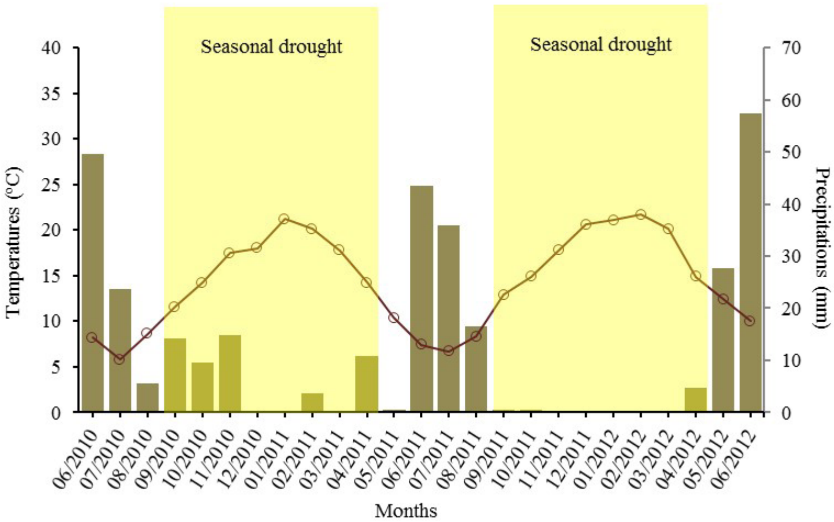

Fig. 2 - Mean monthly temperature (line) and Mean monthly precipitations (bars) during the period of field establishment (2010–2012) of three experiments (Source: Estación Meteorológica de Pirque, Región Metropolitana, Chile).

$8P_2O_5$-$12K_2O$ with a release period of 12 months. For the field establishment stage (12 months), half of the seedlings from each of the four nursery fertilization treatments were planted and watered with 2 L plant^{-1} week^{-1} (W+) and the other half were left unwatered (W-). These watering regimens corresponded to moderate and severe water stress, respectively, based on criteria commonly used in reforestation operations in Chile. The experimental design for the field establishment stage was a 4×2 factorial design (eight treatments). Each treatment had 15 replicates (120 plants in total) randomly assigned to each planting spot. The experimental and sampling units were an individual plant.

As in E-2, E-3 had a nursery and field establishment stage. The nursery experiment (6 months) was a completely randomized design with four treatments of depth of CRFN placement. Each treatment was applied to 60 replicates (240 plants in total). Treatments comprised a single dose of 6 g L^{-1} or 17.10 g plant^{-1} of CRFN (6-7 kg m^{-3} recommended by manufacturer) placed at a depth of 0 cm (top layer), 15 cm (middle layer), or 30 cm (bottom layer) in the container, and an unfertilized treatment (control). The CRFN was the same as used in the previous experiment. For the field establishment stage (12 months), half of the seedlings from each of the four nursery fertilization treatments were planted and watered with 2 L plant^{-1} week^{-1} (W+) and the other half were left unwatered (W-). The experimental design for the field phase was a 4×2 factorial design (eight treatments). Each treatment contained 15 replicates (120 plants in total) randomly assigned to each planting spot.

Measurements

For E-1, shoot height (cm) and collar diameter (mm) were evaluated periodically during two growth seasons between June 2010 to June 2012, in a random sample of 25 individuals selected from each treatment for each species. Survival (%) was evaluated three times per year for each treatment and species (n = 48). Twenty-four months after outplanting (June 2012), a random sample of 25 individuals of *Q. saponaria* from each treatment and five individuals of C. alba from each treatment was unearthed to analyze the effect of watering treatments on shoot height and collar diameter, shoot dry mass (g), root dry mass (g), shoot:root ratio (g g 1), root length (m), root volume (cm^3), root surface area (cm^2), and root diameter (mm). Roots of each species were separated from the substrate by applying abundant water at low pressure to avoid the loss of fine roots. Each plant was divided into shoot and roots by cutting up the cotyledon scar. Roots were grouped according to their diameter as fine (< 1 mm), medium (1–2 mm), or coarse (> 2 mm). The root morphological variables of each species were quantified using a high-resolution scanner (1200 DPI resolution, Epson Perfection V700 Scanner, USA) and image analysis software (WinRHIZO - Regent Instruments Inc., Quebec, Canada). Shoot and root dry mass were obtained by forced-air oven drying at 65°C until a constant weight was reached. The shoot:root ratio was estimated as the quotient between shoot dry mass and root dry mass.

For E-2 and E-3, shoot height, stem diameter, and survival were evaluated monthly. At the end of the establishment stage (April 2012), trees were unearthed (n = 12) to evaluate shoot and root morphological variables. All plant morphological variables were measured following the same protocol applied for E-1. For E-3, predawn xylem water potential (ΨW) (n = 5) was assessed every 2 months from July 2011 to April 2012. Measurements were carried out during predawn hours (0400 h–0700 h) using a Scholander pressure pump (Model 1000, PMS Instruments, Inc., Corvallis, OR, USA).

Data analysis

For E-1, differences among variables evaluated at the end of the field experiment for each species were detected using the Student's t-test (P <0.05). To analyze survival, the Chi-square test was applied based on the Kaplan–Meier method with a log-rank test (Mantel Cox).

For both E-2 and E-3, in the nursery and field establishment stages, simple linear correlation models (Pearson correlation) were applied to determine the relations among variables. Before testing, compliance of normality, homogeneity of variance, and linearity assumptions were verified. Differences among variables evaluated during the nursery stage were determined by a one-way ANOVA test (α = 0.05), and significant differences (P <0.05) were identified by a Tukey multiple comparison test (α = 0.05). All data obtained in the field establishment stages were subjected to a two-way ANOVA performed with the general linear ANOVA model (GLM), to evaluate fertilization doses (F), watering regimes (W), and fertilization doses x watering regimes interaction (F x W) effects. Treatments with significant differences (P <0.05) were identified by applying the Tukey multiple comparison test (α = 0.05). All statistical analyses of three experiments were carried out using the SPSS v 17.0 program (SPSS Inc., Chicago, IL, USA).

Results

Experiment 1: effects of controlled-drought regimens on root development

Significant effects of water availability treatments were seen in both *Q. saponaria* and *C. alba* in terms of total root length, root surface area, root volume, root diameter, thin root dry mass, shoot dry mass, and the shoot:root ratio at the end of second growing season (Table 1). We found that *Q. saponaria* (deep-rooted species) had high shoot growth and survival (> 95%) that occurred independently of water availability. However, the root growth (root surface area, root volume, and root diameter) improved under watering restrictions (Fig. 3). Meanwhile, *C. alba* (shallow-rooted species) had a better root growth (root dry mass, root length, and root surface area) (Fig. 3) and survival (70.8%) only when watered. With respect to total root dry mass, shallow-rooted species allocated more biomass to thin roots (41.9%) than did deep-rooted species (3.6%). The latter showed a marked capacity to allocate biomass to thick roots, which represented 89.3% of the total root dry mass.

Tab. 1 - (E-1) P-values of a set of morphological variables measured in deep-rooted (*Q. saponaria*) and shallow-rooted (*C. alba*) saplings under different water availability treatments (W+ and W-) during two growing seasons in the field (from June 2010 to June 2012). Results derived from Student's t-tests with significant differences at P < 0.05.

	Deep-rooted	Shallow-rooted
Variable	*P*-value	*P*-value
Shoot dry mas (g)	**0.001**	**< 0.001**
Shoot/root ratio (g g^{-1})	**0.042**	0.357
Total root dry mas (g)	0.055	**< 0.001**
Thin root dry mass (g)	**0.013**	**< 0.001**
Total root length (m)	**0.006**	**< 0.001**
Root surface area (cm^2)	**< 0.001**	**< 0.001**
Root volume (cm^3)	**< 0.001**	0.062
Root diameter (mm)	**< 0.001**	0.083

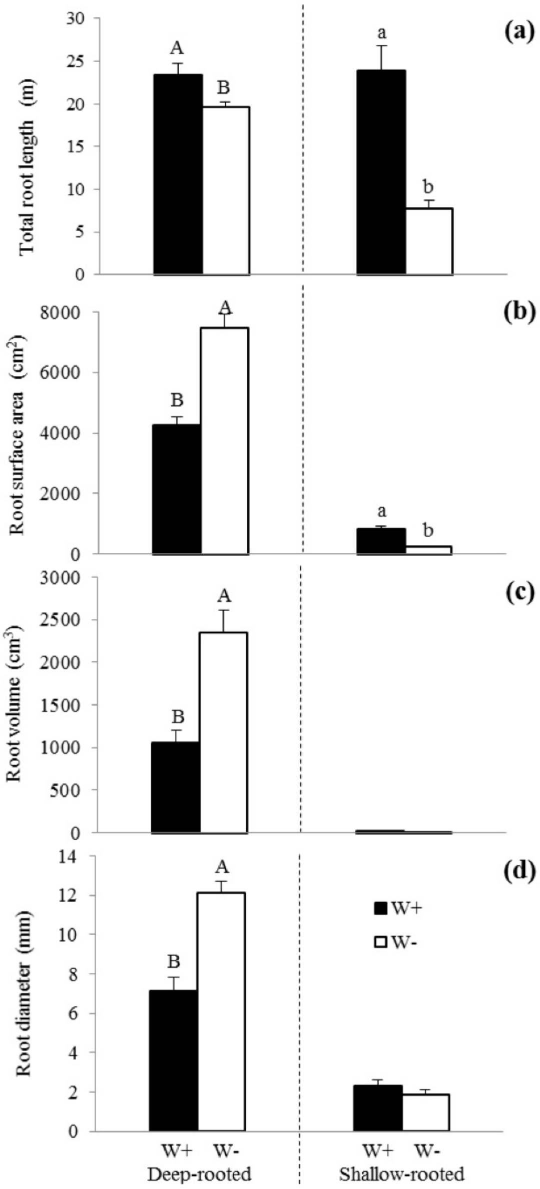

Fig. 3 - (E-1) Mean values ± SE of (a) total root length (m), (b) root surface area (cm^2), (c) root volume (cm^3), and (d) root diameter (mm) of deep-rooted and shallow-rooted saplings growing in the field under different water availability treatments (W+ and W-). Data were obtained at the end of the second growing season (June 2012). Means with different letters indicate significant differences at P < 0.05 (Student's t-test).

Experiment 2: effects of fertilization doses on root morphology

E-2 showed that the effect of CRFN dose on root morphological variables was highly dependent on the level of water stress. The medium dose of CRFN had a positive effect on the development of root attributes (Fig. 4); however, the W- treatment strongly limited root growth. For root volume, the unfertilized treatment and a high dose of CRFN had the significantly highest values, and similar results were reported in presence of W+ treatment (Fig. 4). Fine root volume represented approximately 50% of the total root volume, with a mean value of 6.32 cm^3 for all treatments. For medium and high doses with W+, fine root volume was significantly higher (8.61 ± 0.24 cm^3 and 8.45 ± 0.16 cm^3, respectively) than in the other treatments. In general, in small-type plants with greater stem diameters and low shoot:root ratios (0.5), nutrient deprivation contributed to improving the water-stress resistance during the early drought period. Shoot dry mass was significantly higher in all the treatments with the highest dose of CRFN in both W+ and W-, while no added water or fertilizer resulted in the lowest value (Fig. 5).

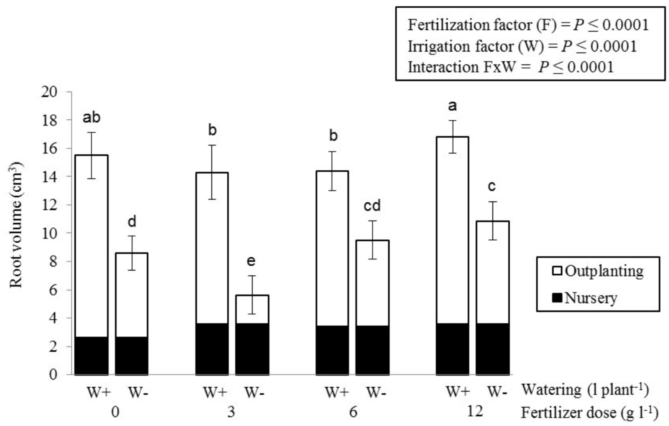

Fig. 4 - (E-2) Root volume of *Q. saponaria* seedlings grown under four CRFN doses and two watering regimes: 2 L $plant^{-1}$ $week^{-1}$ (W+) and no watered (W-). Mean values ± SE (n = 12) with different letters indicate significant differences at P < 0.05 (Tukey's HSD test).

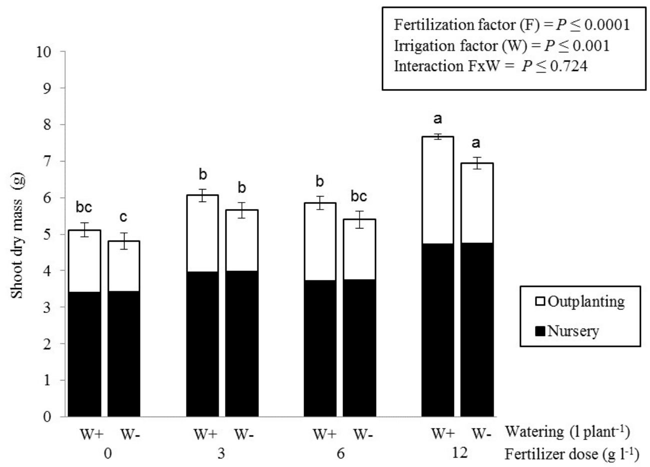

Fig. 5 - (E-2) Shoot dry mass of *Q. saponaria* seedlings grown under four CRFN doses and two watering regimes: 2 L $plant^{-1}$ $week^{-1}$ (W+) and no watered (W-). Mean values ± SE (n = 12) with different letters indicate significant differences at P < 0.05 (Tukey's HSD test).

Experiment 3: effects of localized nutrients supply on root morphology

E-3 showed that fertilization practices in drylands necessarily require watering because this acts to control the increase in salinity in the rhizosphere and, consequently, to avoid impairing root volume growth. For example, we found that, among all treatments, EC varied approximately in the range of 0.50–2.00 dS m^{-1}, and higher EC values were recorded in fertilized and non-watered seedlings. Under W+, CRFN location treatments (independent of placement depth) had significantly higher total root length compared with W-, whereas control treatments showed no differences for any of the watering regimes. With respect to the total root length by diameter class, fine or thin roots (30.56 ± 3.51 m, $P < 0.001$) and medium roots (4.76 ± 0.42 m; $P < 0.001$) were significantly greater in the middle layer/W+ treatment compared with thick roots (Fig. 6). The highest stem diameter increase (21.45 ± 1.23 mm) was found in the bottom layer/W+ treatment. A significant positive correlation (Pearson R = 0.72; $P < 0.001$) between stem diameter and root dry mass was found, which indicates that more than 50% root biomass variation was attributed to stem diameter increase. At the end of the dry season after outplanting (April 2012), plants in all treatments recorded a strong predawn Ψw (Fig. 7). The top layer treatment showed the highest predawn Ψw. The W+ regimen had a significantly higher predawn Ψw than the W- (Fig. 7). There was a rapid water status recovery in all treatments after the first rain. This response resulted in a strong predawn Ψw increase, from 0.91 to 1.59 MPa.

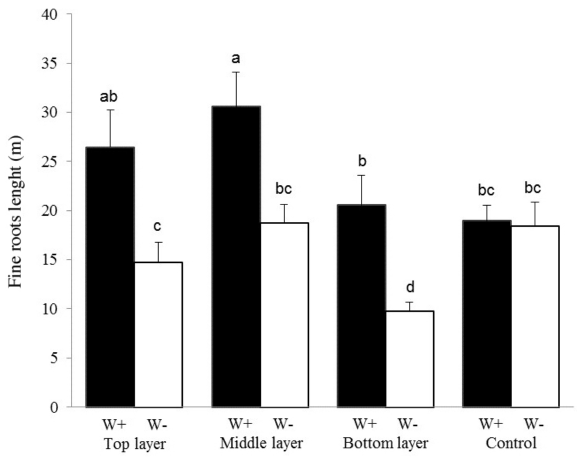

Fig. 6 - (E-3) Fine root length of *Q. saponaria* seedlings grown under four CRFN doses and two watering regimes: 2 L $plant^{-1}$ $week^{-1}$ (W+) and no watered (W-). Mean values ± SE (n = 12) with different letters indicate significant differences at $P < 0.05$ (Tukey's HSD test).

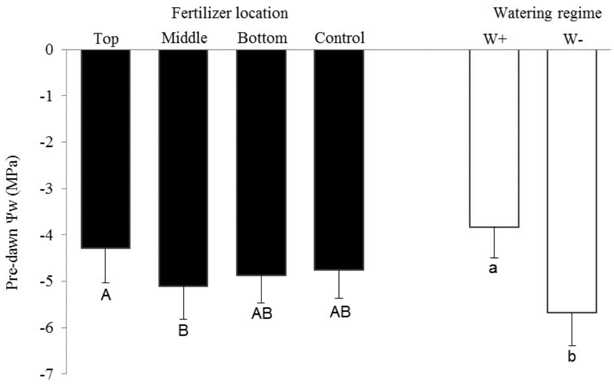

Fig. 7 - (E-3) Pre-dawn xylem water potential (pre-dawn Ψw, MPa) of *Q. saponaria* seedlings cultivated under different depths of CRFN placement (top layer, middle layer, bottom layer, control), and contrasting watering regimes (W+: 2 L $plant^{-1}$ $week^{-1}$; W-: unwatered). Data refer to final measurement of the dry season (April 2012) after first year outplanting. Each point represents the mean value ± SE (n = 5) and different letters indicate significant differences at P < 5% (Tukey's HSD test).

Discussion and conclusions

The experiments showed that nursery fertilization affected the root morphology of seedlings under different water availability regimens in the field; however, these effects did not affect seedling survival. In fact, seedling survival was particularity high in all three experiments, with an average range of 80–100% despite low precipitation during field establishment. The high survival reported strongly contrast with other revegetation experiences that recorded low survival rates (0–30%) for this species under similar drought conditions (Becerra *et al.*, 2011). To explain this high variability in survival outcomes, future studies should investigate the effects of variation in topography and the influence of early-morning haze from the coast, among others factors, on post-transplant performance.

With respect to E-1, clear differences were found in shoot and root growth in both species (*Q. saponaria* and *C. alba*), highlighting the different ecological requirements of each species and, therefore, the difference in their potential to adapt to drought conditions according to their rooting habit (Padilla & Pugnaire, 2007). For example, Peñuelas and Filella (2003) described in *Pinus nigra*, a deep-rooted Mediterranean species, high ΨW values in dry periods, in comparison to other shallower roots species. Another study reaffirmed the advantages of deep-rooted species (e.g., Pistacia lentiscus), with this species showing high ΨW values during dry periods, in comparison to other shallower roots species (Armas *et al.*, 2010). In native tree species of central Chile, Giliberto and Estay,

(1978) found a correlation between the water status of plants and rooting habits. Species such as Lithraea caustica and *Q. saponaria* had the highest and less variable ΨW during summer droughts. Therefore, our results confirmed the importance of considering the root growth strategy as a criterion in the selection of species and watering decisions.

E-2 showed that that low fertilizer dose (lower foliar N concentration) resulted in a lower shoot:root ratio, which led to a reduction in water loss through transpiration, thus achieving lower water stress during the summer drought (Cortina *et al*., 2013). This result confirmed the importance of promoting the development of xeromorphic traits by applying conservative fertilizer doses during the nursery phase, with the aim of improving water stress resistance. These results have a practical use because, in nurseries with low levels of technology (as in some developing countries), fertilization supplies are variable along the plant production stages, because doses are applied according visual criteria (e.g., plant vigor and/or foliage color) (Quiroz *et al*., 2012). This practice tends to overestimate the fertilization dose, which leads to an increased risk of toxicity in plants and root growth problems (Jacobs & Timmer, 2005). Moreover, high nutrient availability encourages greater imbalance in biomass allocation in species intended for environments that have a high water demand (Trubat *et al*., 2008).

E-3 showed the high sensitivity of the *Q. saponaria* root system to small changes in soil salinity. The greater proximity of the fertilizer to the active growing zone in the root plug (15–30 cm), operationally represented by fertilizer placement in the medium layer, had a positive influence post-planting on the root growth, and this effect was intensified by the watering supply treatment. In addition, greater water availability not only improved physiological responses, but was also highly effective in reducing salt concentration in the rhizosphere. The ecological impact of fertilizer placement in the medium layer could be associated with a greater deep rooting ability of *Q. saponaria* seedlings. This is one of the key adaptive morphological characteristics that could explain the high water stress resistance of some Mediterranean trees, such as *Q. saponaria* (Giliberto & Estay, 1978). By contrast, fertilizer placement in the bottom layer of the container was not suitable for root development because fertilizer-rich water accumulation resulted in a high salt concentration, negatively affecting the root volume (Drew, 1975) and, consequently, impacting soil nutrient uptake ability (Bernstein, 2013). In the current study, the highest average salt concentration values were obtained under conditions of water restriction; however, these cannot fully overcome the critical electric conductivity range (>2.50 dS m^{-1}), in which the plant begins to suffer toxicity (Timmer & Parton, 1984; Landis, 1989; Jacobs *et al*., 2003). However, we suggest that water supplements applied to fertilized seedlings contribute to decreasing root zone salinity and, consequently, improve root volume growth during early establishment under dry conditions.

The results of this set of experiments could be useful for identifying the major gaps present in the production and establishment stages of native tress in Chile, and could address the latter through root adaptive management. However, further research is needed into nursery cultural practices and field plantations to advance the standardization of plant-quality protocols for other evergreen tree species of degraded South American Mediterranean forests.

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