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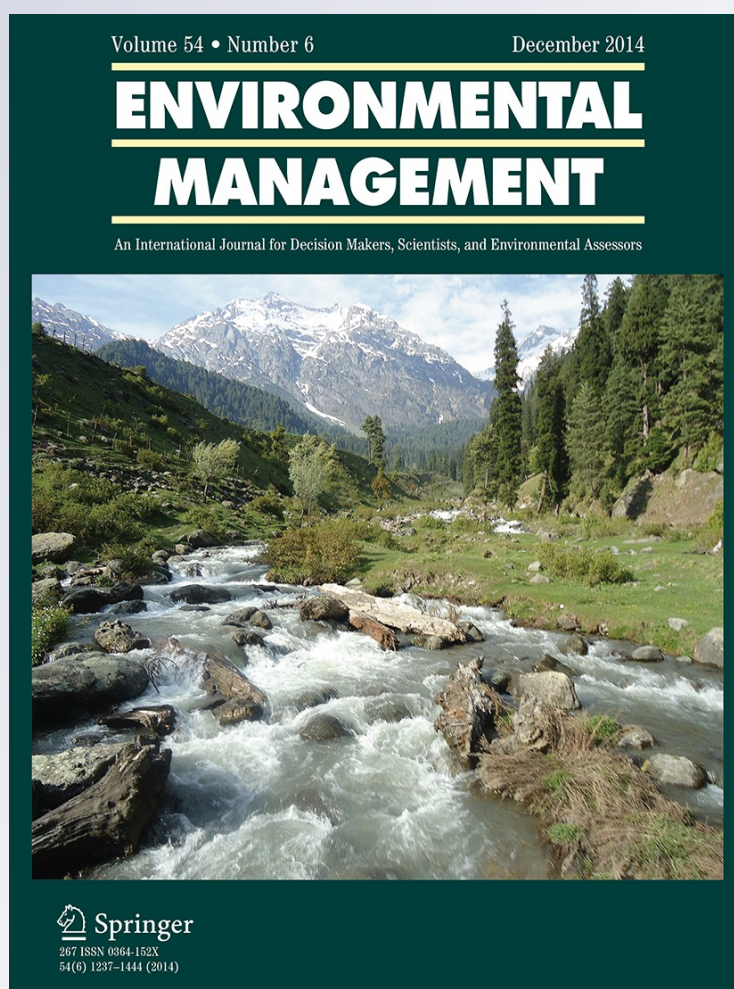
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Improving Survival and Growth of Planted *Austrocedrus chilensis* Seedlings in Disturbed Patagonian Forests of Argentina by Managing Understory Vegetation

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Abstract This study was aimed at determining, under field conditions, early interactions between planted cypress seedlings and their associated shrubs in a mesic area of Andean Patagonia and, in a nursery, the effects of increasing light availability on cypress performance when soil water was not a limiting factor. The field experiment was performed in a former cypress–coihue mixed forest (42°02'S, 71°33'W), which was replaced in the 1970s by a plantation of radiata pine. In 2005, 800 cypress seedlings were planted under maqui shrubs in a clear-cut area of the pine stand. In 2007, two treatments were set: no-competition treatment ([NCT] i.e., the surrounding aboveground biomass was removed) and competition treatment ([CT] i.e., without disturbance). The nursery experiment (42°55'S, 71°21'W) consisted of two groups: “shade” (grown under shade cloth) and “sun” (grown at full sun) cypress seedlings. After one growing season, seedling survival and stem growth (in height and diameter) were determined at both sites. Furthermore, the growth rate of leaves, stems, and roots was determined in the nursery. In the field experiment, height growth and survival in NCT were significantly greater than in CT, and a competition process occurred between cypress and surrounding shrubs. In the nursery, sun plants grew more in diameter and increased root weight more than shade plants. Results also showed that in mesic areas of Patagonia, decreasing competition and increasing light levels produced stouter seedlings better adapted to support harsh environmental

conditions. Therefore, the removal of protecting shrubs could be a good management practice to improve seedling establishment.

Keywords Cypress seedlings · Growth · Nursery · Restoration · Shrub removal

Introduction

Under natural conditions, plant community dynamics are affected by positive and negative interactions occurring among species (Silander and Pacala 1990). These interactions generally act simultaneously, and the resulting effects on the plant's fate may be complex and variable (Callaway and Walker 1997). This interaction complexity gradually increases from seed germination to early seedling development and then to establishment. When two species grow in close proximity and interact in some way, the end result of this interaction will depend not only on their intrinsic physiology and growing characteristics (Holmgren et al. 1997; Holzapfel and Mahall 1999; Maestre et al. 2003) but also on the macroclimatic conditions prevailing in their surrounding environment (Villalba et al. 1992). After germination and during the process of seedling development, gradual changes in the balance of interactions may occur, and the initial facilitation process exerted from one plant species to another may shift to competition (Pugnaire et al. 1996). Generally, the magnitude of these interactions will depend on the species involved and the environmental conditions that characterize the site in which each plant species thrives (Callaway 1995; Holmgren et al. 1997; Urretavizcaya et al. 2012). On some occasions, however, changes in macroenvironmental conditions could lead to different responses even considering the same interacting

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species (Urretavizcaya et al. 2012). In many semiarid, water-limited environments, shrubs can modify their surrounding microclimatic conditions (Tielböger and Kadmon 2000; Giladi et al. 2013; Urretavizcaya and Defossé 2013), thus generating positive effects (i.e., facilitation) for seed germination and early establishment of seedlings of other species (Chambers et al. 1999).

This appears to be the case for early seedling development of the tree *Austrocedrus chilensis* [(D. Don) Pic. Serm. and Bizzarri], which are grown in Andean Patagonia. This species, locally known as “cypress,” is an endemic conifer of the Andean temperate forests of Argentina and Chile. Cypress grows under a wide range of environmental conditions from xeric (approximately 400–700 mm/y) in the Andean piedmont, to mesic (approximately 700–1,000 mm/y) at medium altitudes, to humid (approximately 1,000–2,000 mm/y) sites at higher altitudes of the Andean cordillera (Dezzotti and Sancholuz 1991). Former studies showed that cypress seedling establishment in xeric sites may often be associated with the nursery syndrome induced by the presence of protecting shrubs (Kitzberger et al. 2000). In these sites, cypress seedlings only emerge under the presence of a protecting shrub, thus indicating a positive effect from the shrub to the emerging cypress seedling. This facilitation effect seems to be due to an attenuation of incoming radiation during the summer (preventing cypress desiccation) and a concomitant improvement in soil water status for cypress seedlings grown underneath the protecting shrub (Kitzberger et al. 2000). During the earlier stages of seedling growth in xeric sites, cypress survival is strongly conditioned by climatic variability mainly due to the amount and distribution of rains (Veblen et al. 1995; Villalba and Veblen 1997; Kitzberger et al. 2000). In mesic areas, instead, cypress establishment occurs in small and intermediate canopy gaps (Gobbi 1999) and in association with high herbaceous and shrub cover (Rovere 2000). The intensity of this positive association can also be related to the annual climatic variability and is more tangible during very dry summers (Kitzberger et al. 2000; Letourneau et al. 2004; Urretavizcaya and Defossé 2013).

However, other environmental factors may also influence the success of cypress seedling survival and establishment in Andean Patagonia. Strong westerly winds, snow fall, and grazing and trampling by native and non-native grazers may break or damage cypress shoots at the early stages of seedling development when their physical resistance (i.e., stability) to these disturbances is still low (Loguercio et al. 1999; Mitchell 2003). Cypress seedling stability may also be affected when surrounding conditions are drastically altered (i.e., elimination of neighboring plants). In this case and during the first years after plantation, a good indicator of seedling stability is given by the sturdiness ratio, which represents the quotient between stem height and diameter (Haase 2008). However, when

the surrounding conditions are not altered and once a cypress seedling becomes established, the former facilitation process may change to competition, and its growth, as happens with others species (Callaway 1995), may be limited by interference exerted by the surrounding shrub. In this case, the growth of cypress seedlings is somehow limited until they overcome this interference (Kitzberger et al. 2000; Letourneau 2006).

From the mid 1940s and up to the early 1990s, cypress forests in Patagonia were intensively used. Its wood has been extracted for lumber and house construction as well as to increase areas for sheep and cattle raising (Laclau 2002). Fire, either natural or anthropogenic, is another important disturbance that affected natural cypress forest dynamics (Kitzberger et al. 1997). Many times, these single or combined disturbances have deviated the course of natural succession, thus affecting cypress stand recovery. Furthermore, during the 1960s and 1970s, many logged or burned cypress forests were replaced by nonnative species of high growth potential. These species, mainly conifers of the genus *Pinus* (ponderosa pine, lodgepole pine, and radiata pine) or *Pseudotsuga* (Douglas fir), have generated invasion processes (Carpenter et al. 2004; Orellana 2007). The natural dynamics of adjacent pure cypress and/or mixed cypress and coihue [*Nothofagus dombeyi* (Mirb.) Oerst.] forests have been modified by these invasions (Simberloff et al. 2002; Pauchard et al. 2008), thus precluding their natural recovery. In these cases, active restoration practices (including sowing or planting key native species) appears to be the best strategy to allow recovering former community structural and functional characteristics (Clewell 2000).

With this in mind, several experiments were performed in the past with the objectives of determining the effects of different restoration practices on cypress stand recovery. In xeric sites, cypress seeds sown during wintertime under the protection of an established shrub showed higher seed emergence and seedling survival than those sown during the spring or grown unprotected (Urretavizcaya et al. 2012). Furthermore, early seedling survival was greater under the shading protection given by a shrub, thus confirming the previously reported observations for naturally grown cypress seedlings (Kitzberger et al. 2000). In mesic sites, however, information about cypress seedling responses to restoration experiments is still scarce. In this study, we hypothesized that in former mesic mixed cypress–coihue forests now occupied by conifer plantations, and after an acclimation period of at least 2 years, cypress seedlings planted under a shrub's protection will have improved survival and growth parameters if the adjacent shrubs are removed. Because soil water is not always a limiting factor in mesic sites during the growing season, increasing levels of incoming radiation (produced

by the removal of the shrub) will not produce the desiccating effects that it may generate in xeric sites. As a consequence, the decreased competition for soil water and greater incoming radiation will probably favor cypress seedling survival and growth compared with seedlings grown under root and light competition exerted by adjacent shrubs. In addition, it is expected that 1 year after shrub removal, the decrease of root and light competition will allow cypress seedlings to show better stability (*sensu* Hasse 2008) than those grown under root and light competition.

To test these hypotheses, we set up two experiments, one in the field (a mesic area) and the other in the nursery under controlled conditions. Specific objectives for the field experiment were as follows: (1) to assess early survival, growth, and stability of 4-year-old cypress seedlings (2 years after plantation) in response to the removal of adjacent shrubs and their comparison with undisturbed controls and (2) to determine the predominant interaction processes involved when adjacent shrubs are removed. For the nursery experiment, the main objective was to analyze the effects of an abrupt change in incoming radiation on aerial and root growth parameters while ensuring that soil water was not a limiting factor.

Up until some years ago, the main objectives of ecological studies for restoring former native cypress landscapes mainly focused on filling out some gaps of scientific information. The recent enactment (2009) of the native forest protection and conservation act of 2007 (Argentine Law 26.331), however, not only puts into value the ecosystem services that native forests offer in general but also provides economic incentives to promote their conservation or restoration through appropriate sustainable management practices based on sound science. Our study thus provides useful information to improve and adjust the current techniques to increase the success of seedling establishment for management purposes in cypress forest restoration plans on mesic areas of Andean Patagonia. The results may also be important to increase the general knowledge about the complex interactions among species when one or two limiting factors are experimentally altered.

Materials and Methods

The experiments were conducted in two different areas: an exotic plantation within a former mixed cypress–coihue forest in Lago Puelo, Chubut, and a nursery at the Patagonian Andes Forest Research and Extension Center (CIEFAP) in Esquel. Both areas are located in the northwest of Chubut province in Patagonia, Argentina.

Lago Puelo Experimental Site

The study site is located in an area called Parcela 20 (42°02'S, 71°33'W), which belongs to the Undersecretary of Forests of Chubut province. In this mesic area, the average annual precipitation is 920 mm (70 % of the annual precipitation falls during April to August followed by a dry period during the growing season, which occurs from September to March), whereas the mean annual temperature is 9.8 °C (period 1941 to 1979; Bustos and Rochi 1993). The study site was formerly a cypress–coihue mixed forest widely dominated by cypress trees in the medium to upper strata. Nearby measured stands showed that approximately 64 % of the total basal area and 71 % of trees density, respectively, belonged to cypress, whereas coihue presented more scattered trees dominating the upper strata. The understory vegetation was composed of the shrubs *laura* [*Schinus patagonicus* (Phil.) I. M. Johnst. ex Cabrera], which dominated the dryer microenvironments of those forests, and *maqui* [*Aristotelia chilensis* (Molina) Stuntz], which predominated in more humid areas (Manfredi et al. 1999; Todone 2005). During the early 1970 s, the site was clear cut and all cypress and coihue trees removed, but most understory vegetation was allowed to remain on the site. Right after the clear cut, the site was afforested with radiata pine (*Pinus radiata* D. Don). In 2005, when the afforestation was approximately 30 years old, and pine trees averaged 25 m in height, one stand comprising approximately 4 ha was clear cut in west-to-east strips (approximately 35 m wide and 125 to 175 long). The understory vegetation of these strips, which were mainly composed of shrubs and grasses, was dominated by *maqui* shrubs. *Maqui* is a Patagonian native wintergreen shrub that belongs to the *Elaeocarpaceae* family. It can reach up to 4 m in height and 35 cm in diameter in very good sites in the western slopes of the Andes in Chile (Avello Lorca et al. 2008), and in early development stages it branches near the ground (Muñoz and González 2006). In the study area and within the gaps produced by the cut strips, *maqui* presented a dense understory with plants reaching approximately 1.5 m height and presenting stems ≤ 5 –7 cm in diameter. In these gaps, 800 2-year-old cypress seedlings were planted under the protection of *maqui* shrubs at approximately 20–25 cm from each *maqui* stem base. The objective of planting cypress was to initiate the restoration process of the former cypress–coihue forest.

In September 2007 (at the beginning of the growing season in the Southern Hemisphere), in one of these strips, 74 cypress seedlings were randomly selected, and 34 of them were set to a no-competition treatment (NCT). This treatment involved the removal of all aboveground biomass of *maqui* shrubs in a radius of 50 cm around each cypress seedling. The other 40 selected seedlings and surrounding

vegetation remained undisturbed, and were set as the competition or control treatment (CT). After that, we measured seedling height and stem diameter (at 1 cm above ground level) in both the NCT and CT treatments. In May 2008 (the end of the growing season), seedling height, stem diameter, and survival was determined again for both the NCT and CT treatments. The sturdiness ratio (the quotient between height [mm] and diameter [mm]; Haase 2008) was calculated for each individual seedling in both the NCT and CT treatments.

To characterize the climatic conditions of the studied growing season (September to March), we used the temperature and precipitation data taken from the weather station belonging to the Fire Subcentral of the Undersecretary of Forests of Chubut, which is located 1.5 km away from the study site.

CIEFAP Nursery

The CIEFAP nursery is located in Esquel (42°55'S, 71°21'W), whose climatic characteristics (especially temperatures) are slightly lower than those registered in Lago Puelo. For this experiment, we used 3-year-old cypress seedlings. These seedlings were produced indoors using local seed sown in a common seedbed. Seedlings remained in that seedbed for 1 year and then were transplanted to individual pots of 900 cm³ each. The soil substratum of the pots was composed of organic topsoil of the area plus volcanic sand in a 3:1 proportion. Starting in 2005, all pots were placed outdoors for the other 2 years and received protection from a shade cloth (80 % shade) and were maintained irrigated at field capacity. In September 2007 (the beginning of the growing season), we selected 44 homogeneous cypress seedlings and measured their height and stem diameter. In October 2007, 10 of these seedlings were randomly selected, taken out of their pots, and their root system washed to eliminate soil particles or other soil debris. Afterward, these seedlings were morphologically characterized by measuring their height, stem diameter, and root length and then separated into biomass compartments of stems, leaves, and roots. These biomass compartments were oven-dried at 103 ± 2 °C to constant weight and weighed. The other 34 seedlings were separated into 2 groups of 17 individuals each. One group remained under the same previous conditions (hereafter “shade” seedlings), whereas the other group was placed without cover at full sun (0 % shade) (hereafter “sun” seedlings). At the end of the growing season, annual growth in height and stem diameter, total dry weight, and percentage of dry weight of leaves, stems, and roots of “shade” compared with “sun” seedlings were determined. Because the experiment was performed in Lago Puelo, we also calculated the sturdiness ratio for the nursery-grown cypress seedlings.

Statistical Analyses

For the field experiment, differences in height and diameter growth of NCT and CT seedlings, from initial values to the end of the first growing season, were evaluated through analysis of variance (ANOVA) for one factor (competition effect). In this case, we applied the Tukey–Kramer test because the data were unbalanced (Balzarini et al. 2008). To meet ANOVA assumptions, data for height growth were transformed by \sqrt{x} . Seedling survival between NCT and CT treatments was analyzed with the arcsine test (Sokal and Rohlf 1979), and the stability of NCT cypress seedlings, as compared with CT seedlings, was analyzed through analysis of variance (ANOVA) for one factor (time). The interaction balance was calculated by an index called the relative neighbor effect (RNE), which was proposed by Markham and Chanway (1996). The RNE determines the effect of surrounding shrubs regarding the better growing cypress seedlings and has a range from 1 to –1. This index is calculated as follows (Eq. 1):

$$\text{RNE} = \frac{\text{GRR} - \text{GRC}}{x}, \quad (1)$$

where growth rate removal (GRR) is the average growth rate of all NCT seedlings, and growth rate control (GRC) is the average growth rate of all CT seedlings. The denominator x corresponds to the greater value of either GRR or GRC. If the result of the equation gives a positive value, it indicates that a competition process is taking place, whereas a negative value indicates a facilitation process. To avoid confusion in interpretation, and as proposed by Callaway et al. (2002), we multiplied the resulting values by –1 so that positive values indicate that a facilitation process is occurring, whereas negative values indicate a competition effect.

For the nursery experiment, the annual growth in height and stem diameter, total dry weight, and percentage of leaves, stem, and root dry weight of shade compared with sun seedlings were evaluated through one-factor (light) ANOVA. To meet ANOVA assumptions, data for height growth were transformed by $\log_{10} x$. Percentage of dry weight per compartment (leaves, stem, and root) was calculated as the quotient between the dry weight average of each compartment and the average total dry weight multiplied by 100. The sturdiness ratio was analyzed as previously mentioned for the data from Lago Puelo.

Results

Environmental Conditions in Lago Puelo

Mean temperature for the 8-month studied period was 12.8 °C, a little bit lower than the historic mean for that

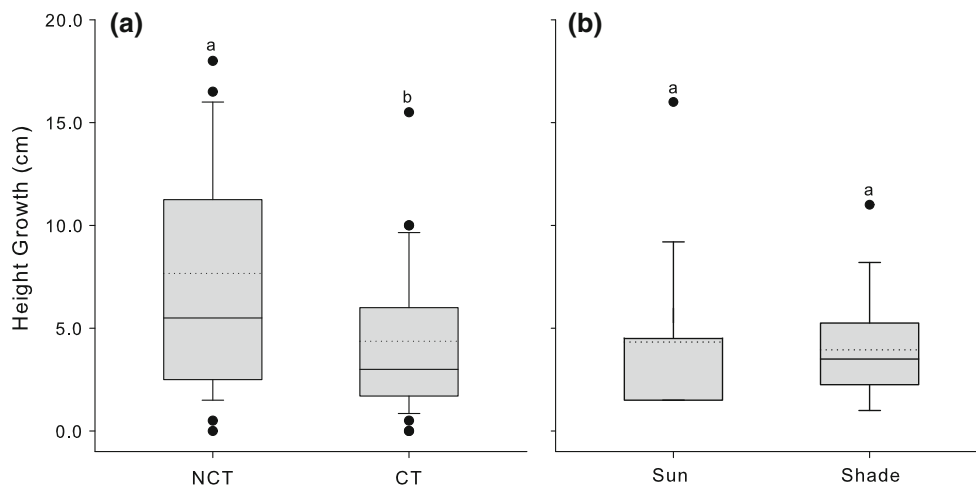


Fig. 1 Box plot representation of height growth for (a) NCT ($N = 34$) and CT ($N = 36$) in the Lago Puelo experimental site in Patagonia and (b) for sun ($N = 17$) and shade ($N = 17$) seedlings in the CIEFAP Nursery in Esquel. The bold line represents the median; the dotted line represents the mean; the box limits are the lower and

upper quartiles (25 and 75 %); the dotted points are the outliers; and the whiskers represent the minimum and maximum values. Different letters indicate statistically significant differences (ANOVA, $P \leq 0.05$)

period in the area ($13.4\text{ }^{\circ}\text{C}$). Cumulative precipitation for the same period was 133.4 mm, corresponding only to 61 % of the long-term average precipitation (216 mm) for the same period at that site. This indicates that although the experimental site could be considered as “mesic” according to its total annual precipitation, the low precipitation received during the study period should be carefully considered when drawing conclusions with respect to competition effects for soil water on each treatment.

Survival, Growth Parameters, and Interaction Balance

At the beginning of the growing season (i.e., initial conditions), average seedling stem height was 32.32 ± 1.32 cm, and the mean diameter was 3.44 ± 0.12 mm for all plants in Lago Puelo, whereas mean stem height and diameter for all seedlings in the nursery were 24.20 ± 0.85 cm and 3.24 ± 0.13 mm, respectively. At the end of the growing season and for seedlings of Lago Puelo, stem height growth ($P < 0.05$, Fig. 1a) and seedling survival ($P < 0.01$) were significantly greater for the NCT compared with the CT treatment, respectively. In the nursery, for instance, and although the stems of sun seedlings grew higher than those of shade seedlings, these differences were not statistically significant (Fig. 1b) In the nursery, both sun and shade seedlings showed 100 % survival at the end of the experiment.

In Lago Puelo, stem diameter growth showed greater absolute values in NCT compared with CT seedlings, although these were not significantly different (Fig. 2a). In the nursery, however, stem diameter growth was significantly greater for sun compared with shade seedlings ($P < 0.01$, Fig. 2b). The sturdiness ratio showed significant

differences from the beginning to the end of the season for NCT seedlings ($P < 0.05$), whereas for CT seedlings this value remained practically unchanged (Table 1). Meanwhile and for seedlings grown under full sun compared with shade plants in the nursery, sturdiness ratio values remained similar at the beginning and at the end of the season (Table 1). As a result, the RNE index was -0.43 for Lago Puelo-grown seedlings. This negative value indicates that a mid-intensity competition process occurred between cypress seedlings and the surrounding maqui shrubs at the end of this season.

At the beginning of the experiment in the nursery, dry weight of cypress seedlings per biomass compartments gave the following results: leaves 1.85 ± 0.18 g (45.4 %), stems 0.71 ± 0.07 g (17.5 %), and roots, 1.51 ± 0.17 g (37.1 %). These initial values gave an average total dry weight of 4.06 ± 0.35 g for every 3-year-old cypress seedling (Fig. 3a). At the end of the growing season, total dry weight of cypress seedlings presented significant differences compared with initial values ($P < 0.001$), although they did not present significant differences between shade and sun treatments (Fig. 3a). There were, however, differences in dry weight percentage for the different biomass compartments analyzed. Dry weight (in percentage) for leaves of shade plants was significantly greater ($P < 0.001$) than those of sun plants, whereas the reverse was true for root biomass percentage (dry weight of sun plants > shade plants) ($P < 0.01$) (Fig. 3b). Dry weight percentage of stems was similar for both sun and shade plants (Fig. 3b). Total dry weight of sun seedlings at the end of the season was on average 7.57 ± 0.42 g/plant, which represents an increment of 86 % in relation to initial values (4.06 g). However, total dry

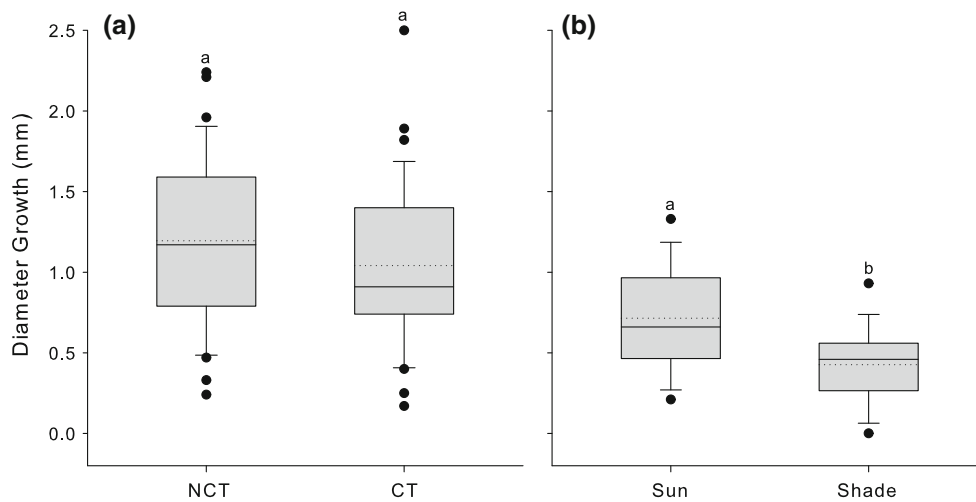


Fig. 2 Box plot representation of height growth for (a) NCT ($N = 34$) and CT ($N = 36$) in the Lago Puelo experimental site in Patagonia and (b) for sun ($N = 17$) and shade ($N = 17$) seedlings in the CIEFAP Nursery in Esquel. The bold line represents the median; the dotted line represents the mean; the box limits are the lower and

upper quartiles (25 % and 75 %); the dotted points are the outliers; and the whiskers represent the minimum and maximum values. Different letters indicate statistically significant differences (ANOVA, $P \leq 0.01$)

Table 1 Sturdiness ratio (± 1 SE) at the beginning (2007) and the end (2008) of the growing season for both the field and nursery experiments

Treatment/ years	Sturdiness ratio			
	Lago Puelo		Nursery	
	NCT	CT	Sun	Shade
2007	93.0 \pm 3.2a	97.0 \pm 4.0a	71.8 \pm 3.3a	72.8 \pm 2.2a
2008	84.6 \pm 2.6b	86.8 \pm 3.4a	68.9 \pm 2.4a	74.0 \pm 2.9a

Within the same column, different letters indicate statistically significant differences (ANOVA, $P \leq 0.05$)

weight of shade plants was 6.57 ± 0.42 g, thus representing 61 % of the initial values, respectively.

Discussion

In this study, we assessed (1) early survival, growth, and stability parameters as well as (2) main interactions that occurred when cypress seedlings, previously grown under field conditions in a mesic site, were abruptly freed from root and light competition exerted by adjacent shrubs. The study was completed by a nursery experiment in which similar cypress seedlings were subjected to a drastic increase in light availability, provided that soil water was not a limiting factor. As has been well established for xeric sites, cypress survival is strongly conditioned by climatic variability, and its early growth is favored by the presence of protecting shrubs (Veblen et al. 1995; Villalba and

Veblen 1997; Kitzberger et al. 2000). However, in mesic areas, such as the one in which this study was performed, cypress establishment generally occurs in small canopy gaps (Gobbi 1999) and in association with high herbaceous and shrub cover (Rovere 2000). In our study, we found that after removing competition (NCT group) from neighboring maqui shrubs, cypress seedlings rapidly responded to the new set of environmental conditions by increasing their survival and growth with respect to those grown under root and light competition (CT group). Although these greater survival and growth parameters may at first be attributed to increases in the availability of resources (mainly soil water and light), it is interesting to note that these positive responses were attained in an atypically dry growing season. In fact, environmental conditions at the field site during the 8-month growing season considered showed lower temperatures (5 %) and precipitation values (40 %) compared with the historical means. The lower precipitation values allowed us to consider this period as a “dry season” in the sense of Letourneau et al. (2004) and Zou et al. (2008). Under these very dry conditions, it would have been expected that soil water may have played a more important role as a limiting factor (Holmgren et al. 1997) for cypress seedlings than it really did. It should be pointed out, however, that in areas such as that of the study site, the amount of precipitation that reaches the soil surface, as well as the spatial and temporal distribution of water in the soil, may be highly influenced by the canopy of overgrowth vegetation (Huber and López 1993; Buduba 2006). It may be thought that in our mesic study site, the presence of nearby pines and other understory vegetation may have had

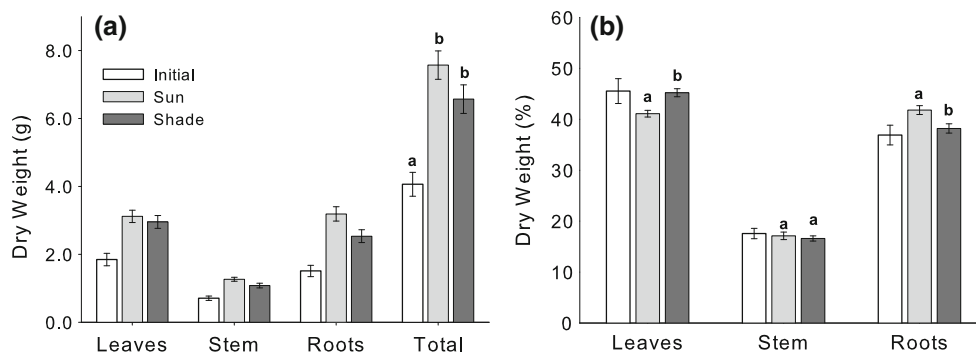


Fig. 3 Dry weight in grams (a) and in percentage (b) of cypress seedlings grown under different light conditions at the CIEFAP nursery in Esquel. Different letters indicate statistically significant differences (ANOVA, $P \leq 0.05$)

a great influence on attenuating peaks of extreme dryness in some years and water surplus in others.

In contrast, it seems that increases in light availability positively promoted NCT seedling growth performance compared with that of CT seedlings in the field. This was also corroborated in the nursery experiment, in which although sun and shade seedlings showed no differences in soil water availability, sun seedlings also presented better growth parameters. Both NCT seedlings in the field study and sun seedlings in the nursery showed greater growth in height and diameter compared with CT and shade seedlings, respectively. These findings not only support the hypothesis that cypress seedlings are sensitive to changes in light conditions (Letourneau 2006), they also reinforce the idea that these changes may occur in a short period of time after light exposure. Seedlings grown under the shade of a protecting shrub or a shading cloth may produce changes in their morphology and physiology, thus conditioning the availability of photosynthetic resources or the way these resources are assigned to either maintenance or structural growth (Mitchell 2003; Letourneau 2006). These responses may vary from morphological changes of newly produced leaves (increasing thickness, decreasing in size [Valladares et al. 2004]) to rapid acclimation to new light conditions because of the seedling's phenotypic plasticity (Letourneau 2006). These changes usually occur in other plants to compensate for the acquisition and assimilation of carbohydrates mainly due to limitations in light availability (Ericsson 1995). The acclimation process allows optimized seedling growth under the new shading conditions (McCook 1994) and may affect their future establishment. In contrast, seedlings that received greater light exposure in both the field and nursery experiments showed a decrease in sturdiness ratio, thus implying stouter seedlings with better stability (Haase 2008). This is an important factor to be considered, especially in cypress restoration plans in Patagonia, because the harsh environmental conditions require seedlings characteristics of high bend resistance to

wind and snow because at earlier stages of development, cypress physical resistance (i.e., stability) to these disturbances is particularly low (Loguercio et al. 1999; Mitchell 2003). If this trend is confirmed in subsequent stages of seedling development, it could be confirmed that sun seedlings are more “stable” than shade seedlings. This “stability” factor should be considered to assure success not only for cypress but also for seedlings of other species to be used in this or other ecosystem-sharing of a similar temperate Mediterranean climate.

The cypress seedling mortality detected only under maqui shrubs suggest that the shrubs could restrain the protection effect due to the competition for light, water, or both, thus increasing the possibility of death of the formerly protected plant as occurs in certain environments (e.g., temperate ecosystems in Mediterranean ecosystems in advanced successional stages [Valladares and Gianoli 2007]). It has been well established that nursery plants would generate an improvement in the microclimate (decrease of the soil temperature) as well as the soil structure (i.e., ameliorate the texture and increase organic matter) of protected seedlings (Franco and Nobel 1989; Puigdefábregas et al. 1999), but they did not necessarily increase water availability (Sala et al. 1989; Bellot et al. 2004). This null effect seems to be due to the water uptake and the rainfall intersection from nursery plants in detriment to protected seedlings. Nuñez et al. (2009) registered less water stress in summer on cypress regeneration under shrubs but no differences in spring. It should be pointed out, however, that Nuñez et al. (2009) worked in a xeric site and that our study was performed in a mesic site. These contrasting situations may suggest that for cypress seedling survival and early establishment, water availability may be more important than light availability in xeric sites, whereas the reverse could be true in mesic areas. This observation is based on the evidence presented in our study and considering that cypress is a drought-avoidant species, which exerts strong stomata control under water stress (Gyenge et al. 2005, 2007).

In the nursery, significantly greater increases in dry weight of root biomass were achieved by sun seedlings compared with shade seedlings. These differences in biomass allocation in the different seedling compartments could be attributed to a rapid acclimation of sun seedlings to greater light conditions and adequate levels of soil water for rapid root growth during the growing season. Shade seedlings, instead, may have been required to compensate for the lower irradiance by increasing resource allocation to photosynthetic tissues (i.e., leaves). This diminution of growth of the other two compartments (stems and roots) coincides with the results reported for the same species by Letourneau (2006) and for other species by Waring and Schlesinger (1985). The relative decrease in root biomass allocation due to increases in leaf biomass could also have negative consequences in terms of further plant development by decreasing the absorption capacity of water and/or nutrients (Letourneau 2006). That is why adaptations induced by shading conditions may be detrimental for some plants to survive under severe soil water stress (McCook 1994). This fact should be carefully considered when planning for restoration experiments.

The best growth parameters shown by NCT compared with CT seedlings are also corroborated by the RNE index values, which implied that 3 years after plantation, a competition process started to occur between cypress seedlings and the surrounding maqui shrub. This process indicates that the initial facilitation gradually changed to a competition situation that may persist until the tree overtops the shrub canopy. Holmgren et al. (1997) suggested that in mesic areas such as this, restrictions in light availability could be more detrimental for plant growth than the possible effect of competition for soil water. For that reason, the removal of protective shrubs 3 years after plantation appears as to be good intervention practice to improve cypress seedling establishment in restoration activities in Patagonia. These activities will gradually allow the change of exotic pine plantations to the natural cypress forests that once occupied the area.

The results of this study showed that changes in macroenvironmental and microenvironmental conditions are important factors to be considered in any restoration plan involving seedling plantation. It seems that in mesic areas such as this, and after a period of time to be determined for each species, the removal of the former protecting shrubs could be a good intervention practice to improve seedling establishment in restoration management. It should be stressed, however, that this study contemplated only one growing season after which shrub removal changed light conditions and soil water availability. Measurements during subsequent seasons will contribute to improve the knowledge about seedling response during other different growing stages. The results of this study cast light on the

interaction processes occurring right after an intervention process of liberating limited resources and represents a contribution to the field of restoration ecology in temperate Mediterranean ecosystems.

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References

- Avello Lorca M, Valladares Acosta R, Ordóñez Belmar JL (2008) Capacidad antioxidante de *Aristotelia chilensis* (Molina) Stuntz. Rev Cubana Plant Med 13(4):1–9
- Balzarini MG, Gonzalez L, Tablada M, Casanoves F, Di Rienzo JA, Robledo CW (2008) Infostat: manual del usuario. Editorial Brujas, Córdoba
- Bellot J, Maestre FT, Chirino E, Hernández N, de Urbina JO (2004) Afforestation with *Pinus halepensis* reduces native shrub performance in a Mediterranean semiarid area. Acta Oecol 25(1):7–15
- Buduba CG (2006) Modificaciones en el pH y contenido de materia orgánica en suelos del ecotono estepa/bosque andino patagónico por implantación de pino ponderosa. Doctoral thesis. Universidad Nacional de Buenos Aires, Buenos Aires.
- Bustos JC, Rocchi VC (1993) Caracterización termo-pluviométrica de veinte estaciones meteorológicas de Río Negro y Neuquén. Informe Técnico, INTA-EEA, Bariloche
- Callaway RM (1995) Positive interactions among plants. Bot Rev 61:309–349
- Callaway RM, Walker LR (1997) Competition and facilitation: A synthetic approach to interactions in plant communities. Ecology 78(7):1958–1965
- Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R et al (2002) Positive interactions among alpine plants increase with stress. Nature 417:844–848
- Carpenter FL, Nichols JD, Sandi E (2004) Early growth of native and exotic trees planted on degraded tropical pasture. For Ecol Manag 196:367–378
- Chambers JC, Vander Wall SB, Schupp EW (1999) Seed and seedling ecology of Piñon and Juniper species in the pygmy woodlands of Western North America. Bot Rev 65:1–38
- Clewell AF (2000) Restoration of natural capital [editorial]. Restor Ecol 8(1):1
- Dezzotti A, Sancholuz L (1991) Los bosques de *Austrocedrus chilensis* en Argentina: Ubicación, estructura y crecimiento. Bosque 12(2):43–52
- Ericsson T (1995) Growth and shoot: root ratio of seedlings in relation to nutrient availability. Plant Soil 168–169:205–214
- Franco A, Nobel P (1989) Effect of nurse plants on the microhabitat and growth of cacti. J Ecol 77:870–886
- Giladi I, Segoli M, Ungar ED (2013) Shrubs and herbaceous seed flow in a semi-arid landscape: Dual functioning of shrubs as trap and barrier. J Ecol 101:97–106
- Gobbi M (1999) *Austrocedrus chilensis* management: effects on microsites and regeneration. Int J Ecol Environ Sci 25:71–83
- Gyenge JE, Fernández ME, Dalla Salda G, Schlichter T (2005) Leaf and whole plant water relations of the Patagonian conifer *Austrocedrus chilensis* (D. Don) Pic. Serm. and Bizzarri: Implication on its drought resistance capacity. Ann For Sci 62:297–302

- Gyenge JE, Fernández ME, Schlichter T (2007) Influence of radiation and drought on gas exchange on *Austrocedrus chilensis* seedlings. *Bosque* 28:220–235
- Haase D (2008) Understanding forest seedling quality: Measurements and interpretation. *Tree Plant Notes* 52(2):24–30
- Holmgren M, Scheffer M, Huston MA (1997) The interplay of facilitation and competition in plant communities. *Ecology* 78(8):1966–1975
- Holzappel C, Mahall BE (1999) Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. *Ecology* 80(5):1747–1761
- Huber AJ, López D (1993) Cambios en el balance hídrico provocados por tala rasa de un rodal adulto de *Pinus radiata* (D. Don), Valdivia, Chile. *Bosque* 14(2):11–18
- Kitzberger T, Veblen TT, Villalba R (1997) Climatic influences on fire regimes along a rain forest-to-xeric woodland gradient in northern Patagonia, Argentina. *J Biogeogr* 24:35–47
- Kitzberger T, Steinaker DF, Veblen TT (2000) Effects of climatic variability on facilitation of tree establishment in northern Patagonia. *Ecology* 81(7):1914–1924
- Laclau P (2002) Evaluación financiera de bosques de ciprés de la cordillera (*Austrocedrus chilensis*). Fundación Vida Silvestre Argentina, Fundación Turner
- Letourneau FJ (2006) Estudio de las interacciones positivas y negativas sobre el crecimiento de *Austrocedrus chilensis* durante una etapa inicial de desarrollo, en un matorral sucesional méxico. Doctoral thesis. Universidad Nacional del Comahue, San Carlos de Bariloche, Argentina
- Letourneau FJ, Andenmatten E, Schlichter T (2004) Effect of climatic conditions and tree size on *Austrocedrus chilensis*–shrub interactions in northern Patagonia. *For Ecol Manag* 191:29–38
- Loguercio GA, Rajchenberg M, Rodríguez N, Pantaenius P (1999) Curso-Taller de actualización en silvicultura de los bosques de ciprés de la cordillera. CIEFAP, GTZ, El Bolsón, Argentina
- Maestre FT, Bautista S, Cortina J, Bladé C, Bellot J, Vallejo VR (2003) Bases ecológicas para la restauración de los espartales semiáridos degradados. *Revista Ecosistemas* 12 (1). www.revistaecosistemas.net/index.php/ecosistemas/article/view/333. Accessed: 27 May 2010
- Manfredi R, Urretavizcaya MF, Grosfeld J, Ramilo E, Caracotche S, Arosteguy C, et al. (1999) Plan Estratégico de Manejo de la Reserva Forestal Cuartel Lago Epuyén, Caracterización y Diagnóstico. CFI-CIEFAP-SNAP-DGByP. Esquel, Argentina
- Markham JH, Chanway CP (1996) Measuring plant neighbour effects. *Funct Ecol* 10(4):548–549
- McCook LJ (1994) Understanding ecological community succession: Causal models and theories, a review. *Vegetatio* 110:115–147
- Mitchell SJ (2003) Effects of mechanical stimulus, shade, and nitrogen fertilization on morphology and bending resistance in Douglas-fir seedlings. *Can J For Res* 33:1602–1609
- Muñoz A, González ME (2006) *Aristotelia chilensis* (Molina) Stuntz Familia: *Elaeocarpaceae*. In: Donoso Zegers C (ed) Las especies arbóreas de los bosques templados de Chile y Argentina. Autoecología. Marisa Cuneo Ediciones. Valdivia, pp 166–172
- Núñez CI, Raffaele E, Núñez M, Cuassolo F (2009) When do nurse plants stop nursing? Temporal changes in water stress levels in *Austrocedrus chilensis* growing within and outside shrubs. *J Veg Sci* 20:1064–1071
- Orellana IA (2007) Análisis de la sustentabilidad ambiental de las plantaciones con exóticas en Patagonia. In: EcoForestar—I Reunión sobre Forestación en la Patagonia, April 25–27, Esquel, Argentina, pp 403–406
- Pauchard A, Langdon B, Peña E (2008) Potencial invasivo de *Pseudotsuga menziesii* (Mirb.) Franco en Bosques nativos del centro-sur de Chile: Patrones y recomendaciones. In: Mujica R, Grosse H, Müller-Using B (eds) Bosques seminaturales, una opción para la rehabilitación de bosques nativos degradados. Instituto Forestal, Valdivia, pp 89–114
- Pugnaire FI, Haase P, Puigdefábregas P, Cueto M, Clark SC, Incoll LD (1996) Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semiarid environment in southeast Spain. *Oikos* 76:455–464
- Puigdefábregas J, Solé-Benet A, Gutiérrez L, Del Barrio G, Boer M (1999) Scales and processes of water and sediment redistribution in drylands: Results from the Rambla Honda field site in Southeast Spain. *Earth Sci Rev* 48:39–70
- Rovere A (2000) Condiciones ambientales de la regeneración del ciprés de la cordillera (*Austrocedrus chilensis*). *Bosque* 21(1):57–64
- Sala OE, Golluscio RA, Lauenroth WK, Soriano A (1989) Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* 81:501–505
- Silander JA, Pacala SW (1990) The application of plant population dynamics models to understanding plant competition. In: Grace JB, Tilman D (eds) Perspectives on plant competition. Academic press, San Diego, pp 67–91
- Simberloff D, Relva MA, Nuñez M (2002) Gringos en el bosque: Introduced tree invasion in a native *Nothofagus/Austrocedrus* forest. *Biol Invasions* 4:35–53
- Sokal RR, Rohlf FJ (1979) *Biometría. Principios y métodos estadísticos en la investigación biológica*. H Blume Ediciones, Madrid
- Tielbörger K, Kadmon R (2000) Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology* 81(6):1544–1553
- Todone F (2005) Plan de manejo de las forestaciones de la Provincia del Chubut en la Región del Noroeste. Dirección Gral. de Bosques y Parques
- Urretavizcaya MF, Defossé GE (2013) Effects of nurse shrubs and tree shelters on the survival and growth of two *Austrocedrus chilensis* seedling types in a forest restoration trial in semiarid Patagonia, Argentina. *Ann For Sci* 70(1):21–30
- Urretavizcaya MF, Defossé GE, Gonda HE (2012) Effect of sowing season, plant cover, and climatic variability on seedling emergence and survival in burned *Austrocedrus chilensis* forests. *Restor Ecol* 20(1):131–140
- Valladares F, Gianoli E (2007) How much ecology do we need to know to restore Mediterranean ecosystems? *Restor Ecol* 15:363–368
- Valladares F, Aranda I, Sánchez-Gómez D (2004) La luz como factor ecológico y evolutivo para las plantas y su interacción con el agua. In: Valladares F (ed) *Ecología del bosque mediterráneo en un mundo cambiante*. Ministerio de Medio Ambiente, EGRAF S.A, Madrid, pp 335–369
- Veblen TT, Kitzberger T, Burns BR, Rebertus AJ (1995) Perturbaciones y dinámica de regeneración en Bosques andinos del sur de Chile y Argentina. In: Armesto JJ, Villagrán C, Kalin Arroyo MT (eds) *Ecología de los Bosques Nativos de Chile*. Editorial Universitaria, Santiago, pp 169–198
- Villalba R, Veblen TT (1997) Regional patterns of tree population age structures in northern Patagonia: climatic and disturbance influences. *J Ecol* 85:113–124
- Villalba R, Holmes RL, Boninsegna JA (1992) Spatial patterns of climate and tree growth variations in Subtropical Northwestern, Argentina. *J Biogeogr* 19(6):631–649
- Waring RH, Schlesinger WH (1985) *Forest ecosystems. Concepts and management*. Academic press, New York
- Zou CB, Breshears DD, Newman BD, Wilcox BP, Gard MO, Rich PM (2008) Soil water dynamics under low- versus high-ponderosa pine tree density: Ecohydrological functioning and restoration implications. *Ecohydrology* 1:309–315