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# Light and Moisture Conditions Suitable for Establishing Andean Cypress and Coihue Beech Seedlings in Patagonia: A Nursery Approach

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Andean cypress and coihue beech are endemic species of the Patagonian Andean forests of Argentina. Both species grow in either pure or mixed stands. Some pure cypress stands are affected by a root disease called "mal del ciprés," reducing their possibilities of being managed for timber production. Coihue beech could be introduced in pure sick cypress stands to help recover their productive potential. However, knowledge is limited about how soil moisture and light may affect early establishment of seedlings of both species. In this study, we determined, under nursery conditions, how survival and growth of cypress and coihue beech seedlings are affected by the combined effects of different soil moisture and light conditions. Both species showed similar survival and growth responses and were susceptible to extreme drought. While similar survival percentages were shown between them, low light levels and higher adaptation to drought significantly delayed cypress seedling mortality compared with coihue beech. Low light and moisture levels negatively affect growth, while the highest growth was registered at intermediate and high levels of light and soil moisture. Although coihue beech seedlings grew faster than cypress, both have the potential for recovering cypress stands affected by "mal del ciprés."

**Keywords:** mixed forests, interaction, forest management, *Austrocedrus chilensis, Nothofagus dombeyi*

Light and soil moisture regimes are microenvironmental factors that greatly condition survival, growth, and regeneration patterns of forest species (Canham 1988, Kobe et al. 1995, Holmgren et al. 1997). Several field studies have found that the effects of light and water availability interact, sometimes combining in a very complex way (Valladares et al. 2004), in a great variety of site conditions. The identification of these effects is crucial to understand how they affect the establishment of several forest species (Aranda et al. 2004), and it is especially relevant in areas with seasonal water deficit or areas influenced by the effects of climate change (Peñuelas et al. 2004).

Several authors, using different and controversial models, have explained plants behavior as related to these factors. The "trade-off" model (Smith and Huston 1989), for example, points out that drought effects are more adverse to plants growing in the shade than for plants growing under full sun. Models dealing with "primary-limitation" (Canham et al. 1996) and "above-ground facilitation" (Holmgren 2000), suggest that the drought effect is less severe in plants that grow in shadow. The "interplay" model (Holmgren et al. 1997) predicts that fluctuations in soil water availability could change light effects, turning it in either beneficial or detrimental for

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plant growth. There is another model, identified as "independent-effects" (Nobel 1999, Sack and Grubb 2002), which proposes that drought and shadow effects are independent. The correct interpretation of these factors related to plant growth and distribution in their native environments will require detailed studies carried out under natural conditions. Under these conditions, however, the isolation of the effects of each individual factor is almost impossible (Sack and Grubb 2002, Valladares et al. 2004). This impossibility occurs mainly because of the occurrence of multiple successive or simultaneous stress factors, which often influence plant performance interactively, by affecting plant responses in an either positive or negative way (Niinements 2010).

Experiments carried out under controlled conditions allow for detecting interactions and separating the effects of each factor, making it possible to interpret their implications for survival and growth of the studied species (Valladares et al. 2004). These experiments have shown different results, especially those related to how interactions between light and soil moisture affect plant growth. No interaction was found for *Tilia cordata,* for example (Sack 2004), while it was evident for *Nothofagus pumilio* (Martínez Pastur et al. 2011). These results help speculate that for certain species and environmental conditions, the effect of one factor on survival or growth could overcome the effect of the other and could also overlap its interaction. To design management techniques to promote either natural or artificial regeneration in pure and mixed forest stands, it is essential to know the relationship between these two factors and their effects on plant survival and growth. Through different silvicultural systems (e.g., shelterwood or group selection methods), it is possible to manipulate light conditions and, indirectly, those related to soil moisture to favor or discourage the establishment of new plants and the liberation of advanced regeneration (Smith et al. 1997, Dezzotti et al. 2003). When a particular forest species lives across an environmental precipitation gradient, tree cover could be manipulated through silvicultural interventions, according to the response of the target species to different light levels (Oliver and Larson 1996).

Andean cypress (*Austrocedrus chilensis* [D. Don] Pic. Ser. et Bizzarri) and coihue beech (*Nothofagus dombeyi* [Mirb.] Oerst.) are both endemic trees to the Patagonian Andes forests in Argentina. These species grow in Patagonia in a narrow strip from 38° to 44° South latitude parallels. Although the natural distribution of cypress does not comprise a very large area (95,500 hectares, CIEFAP and MAyDS 2016), its ecological, productive, and scenic characteristics make it the most important native species in the northern Patagonian region of Argentina (Urretavizcaya and Defossé 2013). Coihue beech has its main distribution area West of the Andes in Chile, while in Argentinian Patagonia, it develops in mesic and humid environments, covering 245,500 hectares (CIEFAP and MAyDS 2016). Coihue beech also has very important ecological, productive, and scenic values. It possesses a good timber quality for house building and carpentry, although its wood is most appreciated for boat and dock construction (Hoffmann 1982). Both species grow in either pure or mixed stands, depending on their location on the marked East to West altitudinal and precipitation gradient that characterizes the eastern slope of Central Patagonian Andes in Argentina (Veblen and Lorenz 1987, Dezzotti and Sancholuz 1991).

The root disease "mal del ciprés" affects cypress natural forests in mesic and humid (more than 900 mm $yr^{-1}$) areas along its latitudinal distribution. "Mal del ciprés" is a complex disease in which *Phythophtora austrocedri* Gres. & E.M. Hansen (Pythiales, Peronosporomycetes, Straminipila) is usually present (Greslebin et al. 2007, Velez et al. 2014). The disease is also associated with site characteristics (mainly related to poor soil drainage conditions, La Manna and Rajchenberg 2004) and causes stand declining patterns and unpredictable mortality (Greslebin and Hansen 2007, Relva et al. 2009, Amoroso and Larson 2010a, 2010b). At present, there are no maps showing the total area affected by this disease. However, studies in representative areas of the four National Parks of the region that cover roughly 31,500 hectares showed that from 20 to 87 percent of cypress stands are already affected, the dry eastern part of cypress forests being less affected than western mesic or humid forests (Núñez et al. 2014). It has also been suggested that this disease has not yet reached its potential expansion area across the Andean landscape (La Manna et al. 2012).

## Management and Policy Implications

The outcomes of this nursery study are useful to determine optimal and limiting environmental conditions that may help promote or restrict seedling survival and growth on either sick pure cypress, degraded pure cypress, coihue beech, or mixed coihue-cypress stands in Patagonia. The ultimate goal is to find appropriate regeneration techniques aimed at restoring former ecological and productive functions of these deteriorated forests. The recovery and restoration techniques could involve either managing natural regeneration or seedling planting in the environmental precipitation gradient (xeric, from 500 to 700 mm $yr^{-1}$; mesic, from 700 to 1,000 mm $yr^{-1}$; and humid, > 1,000 mm $yr^{-1}$) in which both species grow. Our results show that medium levels of soil moisture (50–70 percent with respect to field capacity) and intermediate levels of light (46 percent relative to open sky) provide the best conditions for survival and maximize seasonal growth during early stages of seedling development for both species. These medium levels of soil moisture are normally found in the field in mesic areas, while adequate levels of light in these sites could be reached by planting seedlings of both species under intermediate cover (underneath a protecting shrub, by using artificial devices, or by managing overstory canopy cover). In xeric sites, planting would be recommendable when soil moisture at the end of the growing season does not fall below 5 percent. In these sites, however, seedlings must be more protected from radiation than those grown in mesic sites, and lower growing rates for both species will be expected. Field evidences also showed that in humid sites and in some particular mesic sites in which soil water is not limiting, seedling planting may not be necessary because natural regeneration is almost always present if livestock grazing or browsing is absent. However, for guaranteeing seedling establishment in these sites, intermediate to high light conditions should be provided through either management of canopy densities or by opening or expanding forest gaps. Because of the environmental gradient present in the distribution area of these species, shelterwood methods as a silvicultural management system should be used for promoting regeneration of both species in western, humid areas, when the goal is to obtain an even-age forest structure. Group selection systems should be used instead, when the goal is to attain uneven-age forest structure. In eastern mesic and xeric sites, the group selection system should be recommended. In these sites, however, the sizes of gap openings should be smaller and defined by considering the needs of solar radiation protection and the benefits of shade for allowing seedling survival during the seasonal summer drought. For acomplete success in establishing either species, it is advisable that seedling planting and natural regeneration be protected from domestic livestock browsing, at least during the early stages of seedling development.

Because of the disease, stand canopy is decreasing, changing microenvironmental conditions and limiting silvicultural possibilities of applying sustainable management on affected forests. Nevertheless, empirical observations of sick stands revealed that these microenvironmental changes produce the liberation of resources and trigger the process of natural regeneration of both cypress and coihue beech, providing the availability of nearby seed sources (Loguercio 1997, Amoroso and Larson 2010b, Amoroso et al. 2012). However, for this to occur grazing or browsing by large herbivores should be prevented in regeneration areas. This natural process suggests the possibility of converting pure, sick cypress stands into mixed cypress and coihue beech stands, augmenting forest management options, especially for sick cypress stands (Loguercio 1997, Loguercio et al. 2018). While mixed forest stands are more complex than pure stands, they are also more resilient, presenting alternatives for adaptive management schemes in a future scenario of climatic change (O'Hara and Ramage 2013).

Cypress and coihue beech are considered shade-intolerant species (Donoso 1981). Their light requirements, however, could vary during early stages of seedling development and depend on other environmental factors, mainly related to soil moisture availability. Studies on regeneration dynamics showed that coihue beech does not establish well under closed canopies (Veblen 1989, Veblen et al. 1995, Dezzotti 1996, Gobbi and Schlichter 1998), because of its low shadow tolerance (Müller-Using and Schlegel 1980, Dezzotti 1996, Amoroso and Larson 2010b). However, coihue beech can regenerate under mature forest stands if their understory is sparse (Pollmann and Veblen 2004), indicating a certain shadow tolerance. Coihue beech's affinity for sites with high light availability seems to be reduced in dry sites (Weinberg and Ramírez 2001) and in poorly drained soils (Soto et al. 2009, Donoso et al. 2013). Cypress, however, appears to be more shade tolerant (Veblen and Lorenz 1987, Veblen 1989, Kitzberger et al. 2000) and also more resistant to drought conditions than coihue beech (Veblen et al. 1996, Suárez and Kitzberger 2008, Scholz et al. 2014). Cypress establishment in xeric sites occurs in small closed canopy gaps or under protecting shrubs. This is so because during their first years after germination, cypress seedlings need some protection from excessive radiation and extreme temperatures (Loguercio 1997, Gobbi and Schlichter 1998, Rovere 2000, Urretavizcaya and Defossé 2013). In these xeric sites, cypress seedling survival appears to be more conditioned by high radiation and extreme temperatures than by soil moisture (Kitzberger et al. 2000, Letourneau et al. 2004, Gyenge et al. 2007). These evidences support the idea that both soil moisture and light play important roles in the survival of both species.

The combined effects of light and soil moisture conditions on the growth of cypress and coihue beech seedlings have scarcely been studied. The few available studies are restricted to light factor and consider one or the other species separately. These investigations showed that both species present their highest growth rates if exposed to intermediate light conditions and that this occurs either in the field (Gyenge et al. 2007, Donoso et al. 2013, Urretavizcaya and Defossé 2013) or under semicontrolled conditions at the nursery (Müller-Using and Schlegel 1980, Letourneau 2006).

The knowledge of the combined effects of light and soil moisture on seedling survival and growth is important to establish guidelines for planning regeneration of both species in pure and mixed forest stands and also to help recover cypress stands affected by "mal del ciprés." These guidelines should also consider the particular characteristics of the environmental gradient in which both species live. Moreover, global climatic change predicts the simultaneous modification of a series of environmental conditions and also changes in the severity of different stress factors (Niinemets 2010). These predictions may also be applicable to the Patagonian region inhabited by both species. For these reasons, this knowledge will be of great importance for assessing possible changes in the distribution of these species.

This study aimed at studying the combined effects of different light and soil moisture regimes on survival and initial growth of cypress and coihue beech seedlings. For this purpose, two experiments were settled under semicontrolled nursery conditions. The first one had the objective to determine seedling survival and initial growth of both species when exposed to the combined effects of two soil water conditions (e.g., field capacity and extremely dry) and three light regimes (e.g., high, medium and low). This experiment would allow setting the lower limit of survival of both species to extreme soil water conditions. The second one dealt with examining the combined effects of three soil water (e.g., high, medium, and low) and three light regimes (e.g., high, medium, and low),and determining which combination of these factors achieved the highest growth rates of seedlings of both species. Results of this study will provide basic information to improve traditional management of cypress and coihue forests for productive purposes. They are also important to help recover, or reconvert, sick cypress stands into productive single or mixed cypress-coihue beech forests.

## Material and Methods

This study was carried out under semicontrolled conditions at the nursery of the Patagonian Andes Forest Research and Extension Center (CIEFAP) in Esquel, Patagonia, Argentina (42°55'50.3"S, 71°21'51"W). The first experiment was established during the growing season 2014–15 and the second one during the 2015–16 growing season. The region in which both species naturally grow, as well as the nursery where the study was carried out, presents a Mediterranean climate, with cold and rainy winters and dry and warm summers (Defossé et al. 2015). We used daily (taken at the nursery) and historic mean monthly temperatures and precipitation data (from Esquel airport weather station, 15 kilometers apart from the nursery, provided by the National Meteorological Service of Argentina) as a reference to characterize, determine, and compare how the treatments (i.e., light and soil moisture) varied compared with the mean normal environmental conditions present in the region.

### Experimental Design

The factors under study were light, soil moisture, and species in a split plot design. Survival and growth of cypress and coihue beech seedlings were used as the response factor, while different levels of light and soil moisture were the treatment factors in both experiments (Table 1). Seedlings of each species were cultivated in the nursery and originated from seeds. For experiment one, we used four-year-old coihue beech and cypress seedlings, respectively. For experiment two, cypress and coihue beech seedlings used were three years and one year old, respectively. Differences in age or size of plants between experiments and species could not be avoided because of the lack of homogeneous batches with enough number of plants required for each experiment. This lack of homogeneity

**Table 1. Description of the experiments carried out during 2014–15 (experiment one) and 2015–2016 (experiment two) growing seasons.**

| | *Experiment one* | *Experiment two* |
|---|---|---|
| *Treatments* | Six treatments comprising three levels of light and two levels of moisture for the two species. Two repetitions | Nine treatments comprising three levels of light and three levels of moisture for the two species. Two repetitions |
| *Experimental design* | Split plot. First factor: level of light. Second factor: level of moisture and species. | Split plot. First factor: level of light and level of moisture. Second factor: species. |
| *Light levels* | Relative to open sky: 100 percent (High light, LA), 28 percent (Medium-low light, LM) and 8 percent (Low light, LB). | Relative to open sky: 95 percent (High light, LA), 46 percent (Intermediate light, LI) and 9 percent (Low light, LB). |
| *Soil moisture levels* | CC: 100–65 percent relative to field capacity (32–20 percent moisture). ES: stress, only initial irrigation to field capacity, no later irrigation throughout the experiment. | Relative to field capacity: R1: 100–80 percent (41–33 percent moisture), R2: 70–50 percent (29–21 percent moisture) and R3: 40–20 percent (16–8 percent moisture). |
| *Pot size* | 5 liters | 5 liters |
| *Seedlings age* | Cypress: 4 years<br>Coihue beech: 4 years | Cypress: 3 years<br>Coihue beech: 1 year |
| *Number of seedlings per experiment* | 114 per specie | 190 per specie |
| *Number of seedlings per treatment* | 16 per specie | 20 per specie |
| *Number of seedlings per cubicle* | 16 per species, half of each at the two moisture levels established (random). Each cubicle corresponds to a level of light. | 10 per species. Each cubicle corresponds to a level of light and a level of moisture. |
| *Number of cubicles* | 6 | 18 |
| *Duration of experiment* | 15 weeks | 16 weeks |
| *Response variables* | Survival (every week and final).<br>Absolute and relative increase in collar diameter, height and volume (final). | Survival (every week and final).<br>Absolute and relative increase in collar diameter, height and volume (final). |
| *Temperature and moisture monitoring* | 9 sensors of temperature and moisture of soil at 5 cm of depth, in stress level (ES) in each level of light. | 1 air temperature sensor at each light level. Since February, 6 soil moisture sensors at 5 cm depth at levels R2 and R3. |

among seedlings of each species necessitated calculating their relative growth to determine true differences in growth rhythm because of treatment effects independent from their initial size and age. Absolute increases were useful to know the growth rates of both species not only as affected by each factor or their combination but also as a precedent for further growth and productivity studies of both species.

Two weeks before starting each experiment, we transplanted individual seedlings of each species into five-liter pots containing a mixture of organic soil and volcanic sand in a 4:1 proportion. Coihue beech and cypress seedlings were then randomly set into specially designed 2 $m^3$ areas (cubicles). Light levels for these areas are shown in Table 1. Once a month, potted seedlings were randomly redistributed inside their cubicle to avoid the effects of any local condition that may affect the light and moisture conditions imposed by treatments. Each light level was defined as a percentage of Photosynthetic Active Radiation (PAR) received under a clear sky at noon and set as 100 percent light (Table 1). A Photosynthetic Photon Flux ceptometer, which integrates the flux of photons in a linear meter through 80 integrated sensors (Cavadevises Ceptometer Model BAR-RAD100), was used to measure light under clear sky. Incoming light inside each cubicle was determined by using a punctual sensor (Apogee Quatum meter Model MQ-200).

Soil moisture levels for each experiment were defined after determining the value of soil field capacity of the substratum used. Field capacity was determined then by using the classic method proposed by Richards (1965). This method roughly consists of the extraction of water from a saturated soil sample. The soil sample is put in a porous plate inside a special hermetic chamber and subjected to a pressure of 0.5 atm for about 72 hours. Then the sample is oven dried at 105°C to constant weight, and its moisture content is gravimetrically calculated (Richards 1965).

Before the beginning of the experiment, all pots containing seedlings of both species were irrigated to field capacity. We used a sample of pots per species (n = 12 and n = 18 for experiments one and two, respectively) to determine gravimetrically (with an Ohaus scale Model IS-45, capacity: 45 x 0.002 kg) the amount of water required to maintain the soil moisture values required by each treatment (Table 1). To keep plants from receiving direct precipitation that would interfere with the treatments, we used transparent nylon before the rainfall events, taking it out after cessation of the event in the case of experiment one. Throughout the duration of experiment two, we used a permanent nylon with 95 percent transmittance.

Light conditions for experiment one included three levels of light: 100 percent or clear sky, 28 percent or medium-low light, and 8 percent or low light (Table 1). These levels were achieved by using shadow cloth with 20 percent transmittance to reach medium-low light level and by superimposing two of these clothes for achieving 8 percent light. For experiment two, light levels were set as 95 percent or high light, 46 percent or intermediate light, and 9 percent or low light. We used a shadow cloth with 50 percent transmittance to attain the intermediate level of light (46 percent) and another with 20 percent transmittance in two layers to reach 9 percent light.

### Characterization of Cypress and Coihue Beech Seedlings

At the beginning of the experiment, seedlings were morphologically characterized by taking a random sample of 18 and 10 seedlings per species for experiments one and two, respectively. These characterizations consisted of measuring seedling collar diameter (CD), seedling height (H, from the collar at the stem base to its apex in cypress, and up to the apex of the dominant branch in coihue beech), and aboveground and belowground dry weight biomass (both oven dried to 103 ± 2°C for 48 hours). To separate roots from soil cores, the whole content of the pot was put into water for one day. Dirty water was discarded and replaced by clean water five or six times. Roots were then washed with running water in a 0.5 x 0.5 millimeter sieve to clean out fine roots containing soil particles and other small debris. Very small supernatant micro roots that may have passed through the sieve were collected from a water bucket installed underneath the sieve. All roots were then oven dried and weighed to the nearest 0.01 gram. At the beginning and end of both experiments, CD and H of all seedlings were measured identical to the method mentioned for seedlings characterization. We also determined seedling stem volume (VO) at the end of these experiments, assuming a cone-shaped stem for both species and using height (H) and collar diameter (CD) for its determination.

### Statistical Analyses

Differences among morphological characteristics of seedlings at the beginning of both experiments were analyzed using ANOVA techniques and the Tukey test to determine significant differences at $P \leq 0.05$. Changes in survival and growth (CD, H, and VO) at the end of both experiments were analyzed with linear mixed models, considering species, light, and soil moisture levels as fixed effects and the main plot (cubicles) as a random effect. Mean survival was analyzed considering treatments and repetitions. In these analyses, we used *p*-values and Bonferroni adjustments with a significance level of $P \leq 0.05$. When significance level was positive, means comparison was made by using the least significant difference (LSD) test with Bonferroni adjustment. We also verified that all data met the normality assumptions by using the Shapiro-Wilks test and that of homoscedasticity through residual analyses. We made corrections to these models when these assumptions were not met. A comparison of estimated models was made with the likelihood ratio test (LRT). In the case of significant interactions among factors, we performed the contrast among the different levels of one factor, with each level of the other factor to detect which one was significantly different.

Because of differences in initial size of seedlings within species, we analyzed both absolute and also relative growth increments. To determine significant differences among means of absolute increments in both experiments, we first explored the use of models with initial dimensions as covariates, but they did not improve the results obtained with the models without covariates. In experiment one, the analyses were only done for CC treatments because of the high mortality recorded at the stress level (ES) level.

All analyses were performed by using statistical software InfoStat (Di Renzo et al. 2017, www.infostat.com.ar). InfoStat implements an interface of the R platform (R Core Team 2017) for the estimation of mixed linear models through the Generalized Least Squares (gls) and Linear Mixed-Effects Models (lme) procedures of the library Nonlinear Mixed-Effects Models (nlme) (Pinheiro and Bates 2004, Di Renzo et al. 2017). The interface with R was written in Delphi®, and it depends on R-DCOM (Di Renzo et al. 2017).

## Results

### Experiment One

*Initial Morphological Characterization of Seedlings and Environmental Growth Conditions*

Even though seedlings of both species were of the same age, they presented dissimilar initial sizes, with exception of their aboveground and belowground biomass and VO (Table 2). Cypress seedlings were 3.8 centimeters taller than coihue beech seedlings but presented a lower CD.

The 2014–15 growing season was relatively hot and very dry. Maximum, mean, and minimum temperatures were 21.9°C, 14.2°C, and 7.7°C, respectively. These temperatures were 1.7°C, 0.7°C, and 1.3°C higher, respectively, than the long-term means. Accumulated precipitation during the same period was 87.8 percent lower than the long-term mean (10.6 millimeters versus 87 millimeters).

Pot soil temperature at 5 cm-soil depth reached a record of near 50°C during week 10 after setting the experiment (Figure S1). Maximum soil temperatures for seedlings grown at high light levels (LA) remained above the 35°C from week four and up to week 10. After this week, the temperature sensor LA stopped measuring this factor up to the end of the experiment because of a malfunction with the device. Minimum temperatures never reached values below 0°C in any light treatment. Mean soil temperatures fluctuated between 7° and 25°C along the studied period. Soil temperature in LA level showed an average of 4°C higher than in low light level (LB), while soil temperatures for the medium-low light was slightly higher than that of LB (Figure 1).

*Survival*

During the growing season in experiment one, survival showed significant interactions among light, soil moisture, and species ($P < 0.0001$). Through time, treatments under stress (ES) showed higher survival of cypress seedlings, and for the same light level, there was a delay in the initiation of mortality in cypress compared with coihue beech seedlings. In fact, 50 percent mortality under high light values was achieved in week seven after initiation of the experiment in coihue beech, while it began in week eight for cypress seedlings (Figure 1A). At the same time and for both species, a delay in the initiation of mortality was observed with lower light. As an example, for cypress in the ES level, 50 percent of mortality was reached during week eight for high light level, during week 12 for medium-low light, and in week 14 for low light (see Figure 1A).

The moisture levels at which mortality began was higher at high light levels compared with low light levels (Figure 2) for both coihue beech (9.7 percent versus 7.3 percent) and cypress (9.2 percent versus 6.9 percent). Similarly, 50 percent of mortality was achieved with high soil moisture levels at high light compared with low light

**Table 2. Morphological characters of coihue beech and cypress seedlings (mean and standard error) at the beginning of experiment one (n = 18 per species) and experiment two (n = 10 per species). Different lowercase letters indicate significant differences ($P \leq 0.05$).**

| *Parameter* | *Experiment one* | | *Experiment two* | |
|---|---|---|---|---|
| | *Cypress* | *Coihue beech* | *Cypress* | *Coihue beech* |
| *Collar diameter (mm)* | 3.3 (0.1) *b* | 4.3 (0.2) *a* | 3.6 (0.1) *a* | 3.0 (0.1) *b* |
| *Height (cm)* | 19.4 (0.9) *a* | 15.2 (1.3) *b* | 13.1 (0.5) *b* | 22.5 (1.5) *a* |
| *Volume (cm$^3$)* | 0.7 (0.1) *a* | 1.1 (0.2) *a* | 0.6 (0.03) *a* | 0.7 (0.1) *a* |
| *Aboveground biomass dry weight (g)* | 1.8 (0.2) *a* | 1.4 (0.2) *a* | 1.6 (0.2) *a* | 1.1 (0.1) *b* |
| *Belowground biomass dry weight (g)* | 1.5 (0.1) *a* | 1.9 (0.2) *a* | 1.6 (0.1) *a* | 0.8 (0.1) *b* |

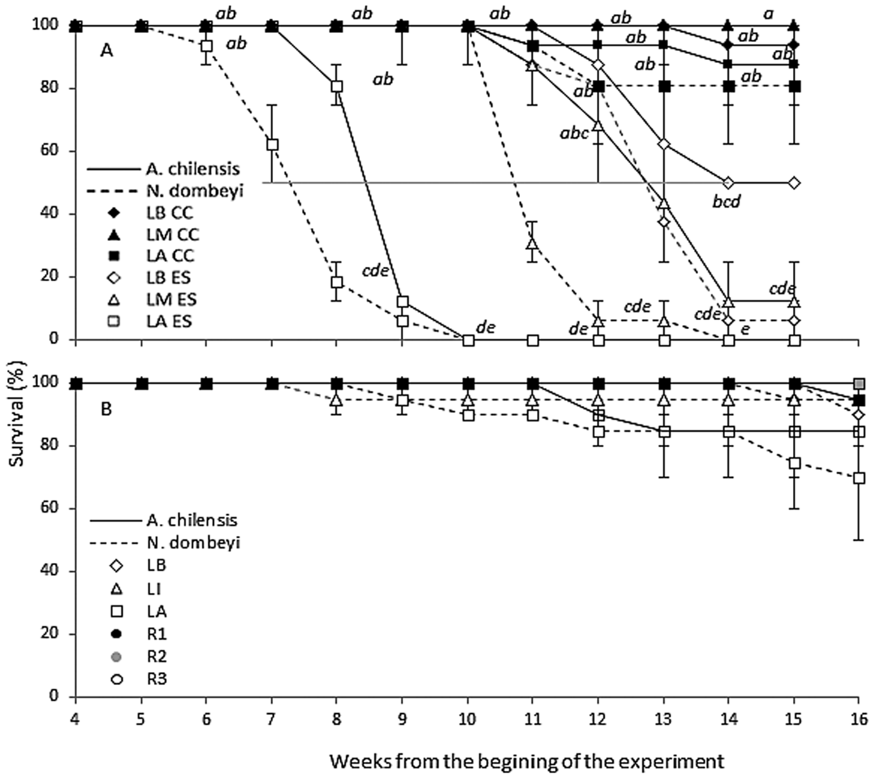


**Figure 1. Survival (percent) of coihue beech (*N. dombeyi*) and cypress (*A. chilensis*) seedlings as affected by different light and soil moisture conditions. A) 2014–15 growing season (experiment one). Light levels: percentage relative to open sky, 100 percent (LA), 28 percent (LM) and 8 percent (LB). Moisture levels: 65–100 percent relative to field capacity (CC) and without irrigation (ES). Different lowercase letters indicate significant differences ($P \leq 0.05$). The gray line indicates 50 percent survival. B) 2015–16 growing season (experiment two). Light: percentage relative to open sky, 95 percent (LA), 46 percent (LI), and 9 percent (LB). Moisture level: percentage relative to field capacity, 80–100 percent (R1), 50–70 percent (R2) and 20–40 percent (R3). Significant differences were not detected.**

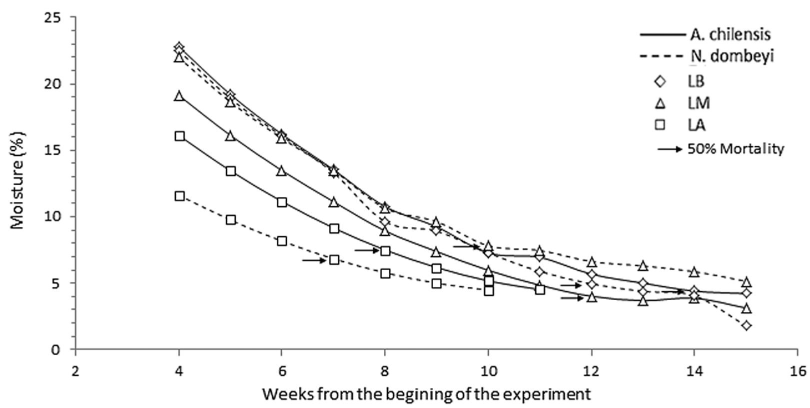


**Figure 2. Soil moisture evalution (percent) in ES level (without irrigation) during experiment one for cypress (*A. chilensis*) and coihue beech (*N. dombeyi*) as affected by different levels of light: percentages (percent) relative to open sky, 100 percent light (LA), 28 percent (LM), and 8 percent (LB).**

levels in coihue beech (6.8 percent versus 4.9 percent) and cypress (7.5 percent versus 4.4 percent).

For the same light level, a delay in mortality and a decrease in its magnitude were noticeable when soil moisture was at CC compared with ES. In CC treatments, mortality was initiated toward the end of the growing period (from week 10 onwards), and the differences between species and light levels were not significant. Survival at the end of the growing season was only affected by soil moisture, being significantly higher at CC compared with the ES treatment ($P < 0.0001$).

*Initial Growth*

As previously stated when discussing the statistical analyses, because of the high mortality at the ES level, we did not analyze the effects of soil moisture on CD, H, and VO. In the CC level, neither absolute nor relative growth parameters showed significant interaction effects between light and species, or of light considered alone. However, differences did exist between species in most cases (Table 3).

Absolute CD of both species was not significantly different (Table 3 and Figure 3A). Average growth in cypress was 1.2 mm

**Table 3. Bonferroni-corrected *p*-values for the effects of different light and soil moisture levels on absolute (AI) and relative (RI) increments in collar diameter, height, and volume of cypress and coihue beech at the end of experiment one and number of samples. Light: percent relative to open sky, 100 percent (LA), 28 percent (LM), and 8 percent (LB).**

| *Factor* | | *Collar diameter* | | *Height* | | *Volume* | |
|---|---|---|---|---|---|---|---|
| | | *AI (mm)* | *RI ( percent)* | *AI (cm)* | *RI ( percent)* | *AI (cm3)* | *RI ( percent)* |
| *Species* | | >0.9999 | **0.016** | **<0.0001** | **<0.0001** | **<0.0001** | 0.350 |
| *Light* | | 0.070 | 0.131 | 0.562 | 0.751 | 0.267 | 0.163 |
| *Light X Species* | | 0.136 | 0.525 | 0.990 | >0.9999 | 0.849 | >0.9999 |
| *Number of samples* | *Cypress* | 44 | | 43 | | 43 | |
| | *Coihue beech* | 42 | | 43 | | 40 | |

($_s$ = 0.1) and in coihue beech 1.3 mm ($_s$ = 0.1). Cypress, however, showed a higher relative increase in CD than coihue beech (Table 3 and Figure 3B). Regarding initial conditions, these numbers represented an increase of 44 percent ($_s$ = 4) and 31 percent ($_s$ = 3) for cypress and coihue beech, respectively.

Coihue beech grew more in height than cypress in either absolute or relative terms (Table 3 and Figure 3C, D). Absolute height increases were of 6.3 cm ($_s$ = 0.7) and 0.6 cm ($_s$ = 0.1) for coihue beech and cypress, respectively. The relative increment for coihue beech was 46 percent ($_s$ = 6), while cypress was only 4 percent ($_s$ = 1). Coihue beech also grew more in volume than cypress (Figure 3E, F). These differences, however, were only significant in terms of absolute volume growth (Table 3). On average, absolute coihue beech growth was 4.3 cm$^3$ ($_s$ = 0.4) and that of cypress was 2.0 cm$^3$ ($_s$ = 0.2). Relative volume growth increment was 173 percent ($_s$ = 22) for coihue beech and 124 percent ($_s$ = 12) for cypress, respectively.

Growth of surviving seedlings of the ES level was much lower compared with the CC levels and, in the case of cypress, similar among luminosity levels.

### Experiment Two

*Initial Morphological Characterization of Seedlings and Environmental Growth Conditions*

In this experiment, as expected, both cypress and coihue beech seedlings presented dissimilar initial sizes (Table 2), excepting that of the stem volume.

The 2015–16 growing season was hot and dry. Maximum, mean and minimum temperatures were 22.7°C, 14°C, and 8.6°C, respectively. These temperatures were 2.5°C, 0.5°C, and 2.2°C higher, respectively, as related to the long-term means. Accumulated precipitation during this period was 39.6 percent lower than the historical mean (52.5 versus 87 mm), except for February, which presented higher values (47.5 versus 17.9 mm). Air temperatures taken at different light levels showed very high values, reaching a maximum of 45°C during the sixth and eighth weeks after experiment initiation (Figure S2). On most days from week one to 14, maximum air temperatures under the different light treatments were over 30°C. The minimum temperature dropped below 0°C beginning in week 14 and lasting up to the end of the experiment.

*Survival*

Survival during and at the end of the growing season was similar for all treatments and species (Figure 1B). No significant differences were found among treatments (light, soil moisture, species and time) or their interactions. Survival at the end of the experiment was 98 percent for cypress and 94 percent for coihue beech (n = 180 per species).

*Initial Growth*

Absolute and relative increases in CD were affected by species, light, and soil moisture (Table 4). Coihue beech showed higher CD increments than cypress at all light levels, with absolute increases of 1.6 mm ($_s$ = 0.1) versus 0.8 mm ($_s$ = 0.03), respectively. For both species, CD relative and absolute growths were significantly higher at high and intermediate light values (Figure 4A, B). Mean absolute increases for high, intermediate, and low light values were 1.1 mm ($_s$ = 0.1), 0.9 mm ($_s$ = 0.04), and 0.2 mm ($_s$ = 0.02) for cypress and 2.0 mm ($_s$ = 0.1), 2.2 mm ($_s$ = 0.1), and 0.7 mm ($_s$ = 0.05) for coihue beech, respectively.

Relative collar diameter and absolute growths for both species were higher at R1 (100–80% percent relative to field capacity) and R2 (70–50% percent relative to field capacity) soil moisture levels compared with R3 (40–20% percent relative to field capacity) (Table 4 and Figure 4A, B). Absolute increases for R1, R2, and R3 were 1.2 mm ($_s$ = 0.1), 1.4 mm ($_s$ = 0.1), and 0.9 mm ($_s$ = 0.1), respectively, while the relative increments were 45 percent ($_s$ = 3), 49 percent ($_s$ = 3), and 32 percent ($_s$ = 3).

For absolute height increases, none of the interactions were significant. However, interactions were significant when the effects of light and species were considered in terms of relative height increments (Table 4). Absolute increment in height was significantly higher at intermediate (8.1 cm, $_s$ = 0.7) compared with low (4.9 cm, $_s$ = 0.5) and high (4.7 cm, $_s$ = 0.5) light levels. Both increments were significantly higher for coihue beech than for cypress (Figure 4C, D). Absolute and relative increases were 9.9 cm ($_s$ = 0.5) and 49 percent ($_s$ = 4) for coihue beech versus 2.1 cm ($_s$ = 0.2) and 16 percent ($_s$ = 1.2) for cypress, respectively.

When absolute increases in stem volume were considered, the interaction was only significant between light and species (Table 4). For relative increases in VO, significant differences were found between species and light levels. Both increments were higher for coihue beech than for cypress; the absolute and relative values were 5.3 cm$^3$ ($_s$ = 0.3) and 332 percent ($_s$ = 22) for coihue beech and 1.3 cm$^3$ ($_s$ = 0.1) and 84 percent ($_s$ = 5) for cypress (Figure 4E, F), respectively. Regarding light, absolute increments in VO in coihue beech were different in the three levels, higher for intermediate light (LI) (8.0 cm$^3$, $_s$ = 0.6), medium for LA (5.6 cm$^3$, $_s$ = 0.6), and lower for LB (2.2 cm$^3$, $_s$ = 0.2). In cypress, the VO increment at low light levels was the lowest (0.5 cm$^3$, $_s$ = 0.1) compared with the other two light levels (1.7 cm$^3$, $_s$ = 0.1 in LI and 1.6 cm$^3$, $_s$ = 0.1 in LA). Relative increment in VO was lower under low light values: 83 percent ($_s$ = 8) in LB, 288 percent ($_s$ = 26) in LI, and 252 percent ($_s$ = 23) in LA.

Absolute increases in stem volume were also different according to differences in soil moisture. The R2 treatment showed higher values compared with R1 and R3 (R2: 4.0 cm$^3$, $_s$ = 0.4; R1: 3.2 cm$^3$, $_s$ = 0.4, and R3: 2.3 cm$^3$, $_s$ = 0.3).

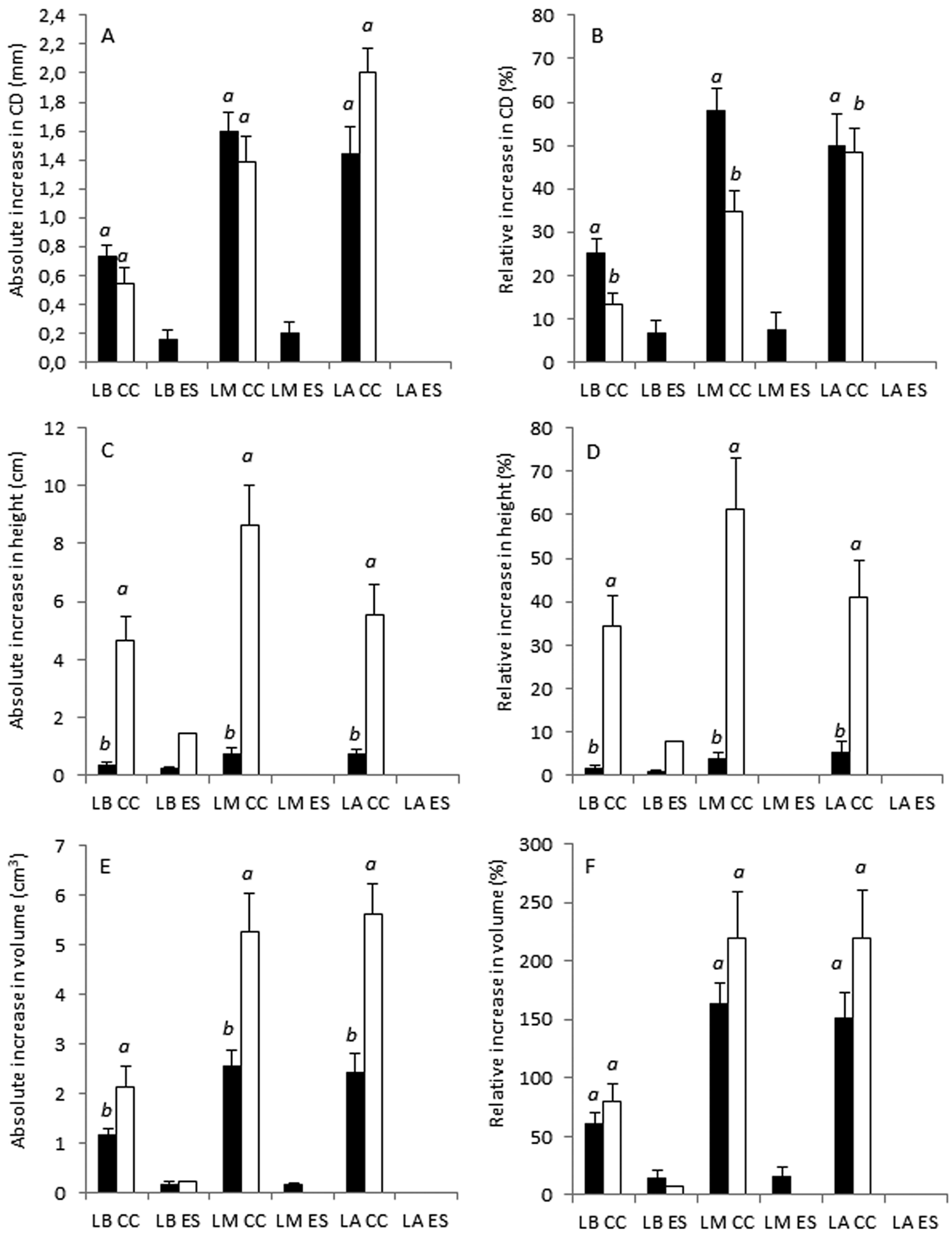


**Figure 3. Absolute (right) and relative (left) increments in seedling collar diameter (CD), seedling height (H) and stem volume (VO) per treatment at the end of experiment one for cypress (black bars) and coihue beech (white bars). Lines within bars represent the standard error. Light levels: percentage relative to open sky, 100 percent (LA), 28 percent (LM), and 8 percent (LB). Moisture levels: 65–100 percent relative to field capacity (CC) and without irrigation (ES). Different lowercase letters indicate significant differences (*P* ≤ 0.05).**

## Discussion

This study presents the results of two nursery experiments applied simultaneously to cypress and coihue beech seedlings, in which different light and soil moisture treatments affect their survival and growth. The different light and soil water treatments used in both experiments were chosen to mimic those normally occurring in the natural gradient of precipitation inhabited by either species. The outcomes of this study, however, should be carefully pondered before trying to generalize and expand them to what may happen under field conditions. The first aspect to be considered is that results were obtained under controlled conditions at the nursery and may not exactly replicate what might happen under field conditions. Under natural conditions, light and soil water interact with other factors in different ways and may result in somewhat different responses. However, semicontrolled conditions at the nursery had the advantage of isolating the effects of the studied factors and helping identify interactions between them (Valladares et al. 2004). These kinds of nursery studies, however, could provide valid evidence and consistent conclusions regarding the role of each of these factors in survival and growth of seedlings of the studied species.

The second aspect that may constrain generalization of these results is that each experiment only included one season of data. The time for seedlings to fully acclimate to the environmental conditions imposed may last longer than only one season. Nevertheless, the study as a whole had the advantage that both experiments were developed under contrasting weather conditions. The first experiment was carried out during an abnormally hot and dry season,

**Table 4. Bonferroni-corrected *p*-values for the effects of different light and soil moisture levels on absolute (AI) and relative (RI) increments in collar diameter, height, and volume of cypress and coihue beech at the end of experiment two and number of samples. Light: percent relative to open sky, 95 percent (LA), 46 percent (LI), and 9 percent (LB). Moisture: percent relative to field capacity, 80–100 percent (R1), 50–70 percent (R2), and 20–40 percent (R3). Ac: cypress. Nd: coihue beech.**

| *Factor* | *Collar diameter* | | *Height* | | *Volume* | |
|---|---|---|---|---|---|---|
| | *AI (mm)* | *RI (percent)* | *AI (cm)* | *RI (percent)* | *AI (cm3)* | *RI (percent)* |
| *Species* | | | **<0.0001** | **<0.0001** | | **<0.0001** |
| *Light* | | | **0.033** | 0.101 | | **<0.0001** |
| *LA vs LI* | | | **0.009** | | | >0.9999 |
| *LA vs LB* | | | >0.9999 | | | **<0.0001** |
| *LI vs LB* | | | **0.008** | | | **<0.0001** |
| *Moisture* | **0.004** | **0.006** | >0.9999 | >0.9999 | **0.0247** | 0.082 |
| *R1 vs R2* | 0.303 | 0.694 | | | 0.187 | |
| *R1 vs R3* | **0.005** | **0.005** | | | 0.075 | |
| *R2 vs R3* | **0.0005** | **0.001** | | | **0.003** | |
| *Light X Species* | **0.039** | **0.028** | >0.9999 | >0.9999 | **<0.0001** | 0.723 |
| *Ac LA vs LI* | 0.184 | 0.078 | | | >0.9999 | |
| *Ac LA vs LB* | **<0.0001** | **<0.0001** | | | **<0.0001** | |
| *Ac LI vs LB* | **<0.0001** | **<0.0001** | | | **<0.0001** | |
| *Nd LA vs LI* | 0.263 | 0.711 | | | **0.002** | |
| *Nd LA vs LB* | **<0.0001** | **<0.0001** | | | **<0.0001** | |
| *Nd LI vs LB* | **<0.0001** | **<0.0001** | | | **<0.0001** | |
| *LA Ac vs Nd* | **<0.0001** | **<0.0001** | | | **<0.0001** | |
| *LI Ac vs Nd* | **<0.0001** | **<0.0001** | | | **<0.0001** | |
| *LB Ac vs Nd* | **<0.0001** | **<0.0001** | | | **<0.0001** | |
| *Light X Moisture* | >0.9999 | >0.9999 | >0.9999 | >0.9999 | 0.871 | >0.9999 |
| *Moisture X Species* | >0.9999 | >0.9999 | >0.9999 | >0.9999 | 0.543 | >0.9999 |
| *Light X Species X Moisture* | >0.9999 | >0.9999 | >0.9999 | >0.9999 | >0.9999 | >0.9999 |

| *Number of samples* | *Species* | | *Light* | | | | | | *Moisture* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *LB* | | *LI* | | *LA* | | | | |
| | *Ac* | *Nd* | *Ac* | *Nd* | *Ac* | *Nd* | *Ac* | *Nd* | *R1* | *R2* | *R3* |
| *Collar diameter* | 173 | 170 | 58 | 57 | 59 | 59 | 56 | 54 | 119 | 118 | 106 |
| *Height* | 172 | 168 | 114 | | 119 | | 107 | | | | |
| *Volume* | 170 | 168 | 56 | 57 | 59 | 59 | 55 | 52 | 119 | 117 | 102 |

exposing plants into high atmospheric demands. This situation explored the limit of survival under drought conditions in only one season. The second experiment was carried out under more relatively normal weather conditions.

### Effects of Soil Moisture and Light on Seedling Survival

During the first experiment, low soil water moisture and high temperatures imposed stress on seedlings of both species, reducing their growth rates and producing high mortality at the end of the experiment. There was, however, a significant difference regarding the time seedlings both species began to die. While coihue beech started to show mortality five weeks after the experiment initiation, for cypress seedlings, this process started at seventh week after setting the experiment (see Figure 1A). This behavior may be related to differences in the physiological mechanisms of both species. To avoid soil water stress, cypress closes its stomata in response to high evaporative demands (Gyenge et al. 2007), which allows the plant to keep some water in its tissues. As it has also been stated for other species, this strategy may imply the risk of photo inhibition or cell tissue damage because of overheating (Gyenge et al. 2007). Under similar low soil water and high evaporative demands, coihue beech seedlings have not shown this strategy (Scholz et al. 2014), instead increasing their stomatal conductance (Read and Hill 1985, Zúñiga et al. 2006, Jiménez-Castillo et al. 2011). The high vulnerability of leaves to cavitation results in coihue beech dehydration, followed by abscission. Because of a water deficit, this process occurs if the hydraulic potential diminishes, and it may also lead to carbon starvation (Scholz et al. 2014). The strong hydraulic segmentation of coihue beech precludes this species from having an adaptive mechanism to help survive severe droughts (Scholz et al. 2014). Besides the extremely low soil moisture, high soil temperatures detected in the high light (LA) treatment of experiment one may have produced overheating at the level of stem collar for both species, thus accelerating seedling mortality compared with lower light levels of the other treatments (Figure S1). Seedling mortality as a consequence of soil overheating has also been reported in other studies dealing with cypress (Gyenge et al. 2007) and other species (Kolb and Robberecht 1996).

Under a soil moisture deficit, the threshold for seedling survival of both species varied according to the levels of light received (Figure 1A). At low soil moisture levels, seedlings growing at low light levels could endure more than those growing at high light levels. As it has been well established, shade may generate an improvement in the hydric conditions of individual seedlings by reducing the water vapor pressure deficit between the seedlings and the air contained in their surrounding microenvironment (Geiger 1965, Larcher 1983, Callaway 2007).

The high mortality experienced by seedlings at the end of experiment one for both species greatly contrasts with those achieved in experiment two. In the second experiment, survival was generally above 70 percent; the lower soil moisture treatments were the ones which presented higher mortality rates (Figure 1B). These values also showed that coihue beech had slightly higher mortality levels than cypress, although these differences were not statistically significant.

Results of both experiments showed that in general different soil moisture and light treatments affected survival and growth of cypress and coihue beech seedlings in a similar way. For both species, a decrease

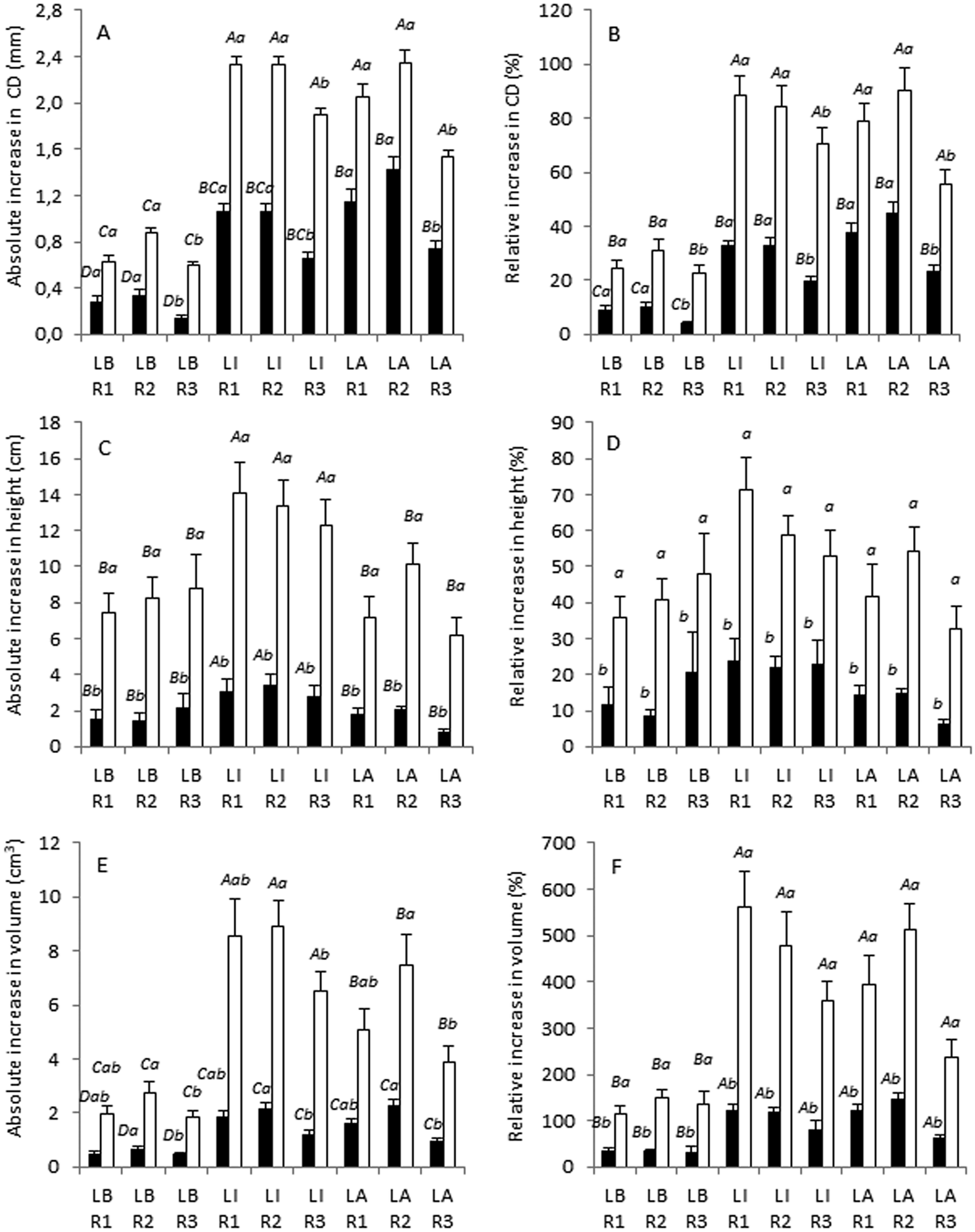


**Figure 4. Absolute (left) and relative (right) increase in seedling collar diameter (CD), seedling height (H), and seedling volume (VO) at the end of experiment two for cypress (black bars) and coihue beech (white bars). Lines within bars represent the standard error. Light: percentagerelative to open sky, 95 percent (LA), 46 percent (LI), and 9 percent (LB). Moisture level: percentage frelative to field capacity, 80–100 percent (R1), 50–70 percent (R2) and 20–40 percent (R3). Different letters indicate significant differences ($P \leq 0.05$): at AI and RI increase in CD and AI in VO, uppercase correspond to Light X Species interaction effect and lowercase to moisture effect; at AI in H and RI in VO, uppercase correspond to light effect and lowercase to species effect.**

of soil moisture along the growing season below a threshold of 8 percent of its water content (< 20 percent of its field capacity) triggered the process of seedling mortality. It is then reasonable to set 8 percent of soil water content (or 20 percent of its field capacity) as the lowest soil moisture limit for cypress and coihue beech seedling survival.

Light affinity of cypress and coihue beech can change according to soil moisture status, as it has been cited for other species (Valladares et al. 2004). The difficulty of coihue beech regenerating under a closed canopy has been attributed to its high light affinity, but results of our study showed that this species can survive well under light levels as low as 8 percent, if soil moisture is not limiting. Coihue beech seedlings' survival at high light levels was restricted by extreme water deficit. Cypress seedlings showed similar trends to coihue beech, although in terms of survival, they appear to be more tolerant to the negative effects of the factors studied. The lower drought resistance of coihue beech seedlings compared with cypress, as indicated by several authors (Veblen et al. 1996, Suárez and Kitzberger 2008, Scholz et al. 2014), has been corroborated in our study because coihue beech seedlings showed earlier mortality compared with cypress when both were exposed to equal levels of light in the ES treatment. Under these conditions, seedling survival at the end of the growing season was almost nil for both species, which coincides with the results obtained in other studies carried out independently for cypress (Rovere 2000) and coihue beech (Weinberger and Ramirez 2001).

Cypress and coihue beech survival was relatively high (>70 percent) when soil moisture was above 8 percent (or 20–25 percent of its field capacity) and was independent of light conditions if values were higher than 8 percent as related to clear sky. This value is slightly higher than the 5 percent of light availability proposed as the threshold value for *Nothofagus* spp. grown in Chile (Grosse Werner 1988). As already mentioned under limited soil moisture conditions and low light levels, cypress showed higher survival than coihue beech, coinciding with other studies, which stated that cypress is more tolerant to shadow than coihue beech (Veblen and Lorenz 1987, Veblen 1989, Kitzberger et al. 2000).

### Effects of Soil Moisture and Light on Seedling Growth

At the end of the first growing season and when soil water was not a limiting factor, coihue beech grew more than cypress. These results agree with those of other studies at different stages of plant development, such as seedlings (Pafundi et al. 2016), saplings (Loguercio 2005), or mature trees (Veblen and Lorenz 1987, Loguercio 1997). In our study, only CD presented different results in both experiments. These results may have been influenced by the lower relative root growth achieved by four-year-old coihue beech seedlings in comparison with that registered by one-year-old seedlings. In general, seedling growth values in our study were similar to those reported by Letourneau (2006) and Pafundi et al. (2014) for cypress and by Müller-Using and Schlegel (1980) for coihue beech—all of them conducted at the nursery with similar light levels as our study.

When soil water was not a limiting factor, light appears as the determining growth factor for both species. Under low light levels, CD and VO growth was low compared with LI and LA treatments (Figure 4). Height growth, in turn, was slightly higher under intermediate light compared with the other light treatments, although differences were not significant. Similar results were reported for cypress (Gyenge et al. 2007, Urretavizcaya and Defossé 2013) and also for coihue beech seedlings (Weinberg and Ramirez 2001, Donoso et al. 2013) both growing under field conditions. Our nursery study, by corroborating the results of these field results, provides more supporting evidences to understand how light influences early seedling establishment under field conditions. However, it should be considered that the development of both species in the field may change their light requirements as they age from seedlings to adult plants during their different stages of ontogeny. Once seedlings are established, however, their needs for protection starts to diminish, and they may need increasing light levels to continue developing and reach the canopy. To explore and elucidate this question, further specific studies will be required.

Soil moisture affected growth of both species in a similar way. As expected, CD growth was lower under low soil moisture levels, while there was not a clear trend when height growth was considered. This indicates that soil moisture may be a factor influencing height growth only in case of extreme water deficit. Conversely, these results also suggest that continual high levels of soil moisture do not produce higher growth in these species, coinciding what was found for *Nothofagus pumilio* (2011). This limitation in further seedling growth could be explained by considering that an excess of soil water may produce an inadequate soil aeration that affects roots development, reducing the growth of aboveground organs (Sun et al. 1995, Martinez Pastur et al. 2011).

## Conclusions

Under the soil moisture and light treatments evaluated in this study, the results at the end of both experiments appear to initially support the model of independent effects, similar to what occurs with other woody species (Sack and Gubb 2002, Löf et al. 2005). This could be because no interaction effects were detected between the factors evaluated and survival and growth of seedlings of both species. Nevertheless, during the progressive increase of water deficit along the season in experiment one, a facilitating effect of shadow in seedling survival was observed (Holmgren 2000). Although it later disappeared, this facilitating effect may somewhat contradict the independent effects model. Seedlings responses of both species showed subtle changes to the factors studied along the season, from the beginning and up to the end of the experiments. These changes constitute clear evidence of the difficulties of ascribing plant responses to the factors studied to one or another of the proposed structured models that try to explain plants behavior. In our study, it seems that a combination of the "independent" and "facilitation" models better explains cypress and coihue beech seedlings behavior as affected by different light and soil moisture conditions.

Based on our results, and to make sound recommendations for providing adequate conditions for survival and growth of these species, we recommend complementing this study with field experiments. These experiments should evaluate not only survival and growth of planted seedlings in humid and xeric sites but also growth of natural regeneration of both species under similar light conditions as those imposed in our nursery study. It is also recommended that the experiments be conducted within exclosures to isolate grazing and browsing effects of exotic animals (e.g., sheep, cattle and horses) that may interfere with the treatments. The complementation of nursery and field studies could provide solid evidences for forest managers designing strategies not only for recovering or restoring sick cypress stands but also for the promotion of better growth conditions for coihue beech. Our nursery study also suggests that manipulation of light conditions could be useful to establish one or the other species separately. However, the promotion of both species to create mixed cypress-coihue forest is encouraged. Mixed forests are more resilient to the expected climatic change and have proven to provide better ecological services (Scherer-Lorenzen et al. 2010, Kolstrom et al. 2011) and productive goods (Jactel et al. 2009) compared with pure forest stands. The final goal should be to produce healthy and productive cypress and coihue beech forest stands, contributing to restore their former ecological and scenic characteristics. The achievement of this goal will help satisfy the increasing demand of wood in Patagonia, also contributing to the economic development of the region.

## Supplementary Materials

Supplementary data are available at *Forest Science* online.

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