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Effects of Post-Fire Plant Cover in the Performance of Two Cordilleran Cypress (*Austrocedrus chilensis*) Seedling Stocktypes Planted in Burned Forests of Northeastern Patagonia, Argentina

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Abstract Cordilleran cypress (*Austrocedrus chilensis* [D. Don] Pic. Serm. et Bizarri) forests occupy 140,000 ha along a sharp environmental gradient of central Andean-Patagonia in Argentina. Every summer, about 3200 ha of these forests are affected by wildfires, taking thereafter long time to recover. To accelerate forest recovery, we determined in xeric and mesic cypress stands burned 5 and 2 year before whether survival and growth of two planted cypress seedling stocktypes are affected by plant cover and contrasting precipitation conditions. Two experiments were conducted on each site, involving 100 replicates of two seedling stocktypes, having each significantly different morphological attributes. The experiments comprised a dry and humid growing season on each site. Both stocktypes performed similarly within stands, but differently between stands. In the xeric stand, plant cover had neutral effects on seedling survival, favored seedling height growth in the dry season, and was negative on collar diameter and stem growth. In the mesic site, high plant cover favored survival and height growth, but was inconsequential for collar diameter and stem growth. In this short-term post-fire period, and independent of precipitation received during both seasons (dry or humid), plant cover appears as playing a facilitative role, having neutral or even positive effects on

survival and growth of planted seedlings. During the early post-fire successional stages, and besides seedling stocktype, there was a synergistic balance between light and soil moisture that seems to benefit planted seedling performance in burned cypress forests, and especially in mesic sites.

Keywords Temperate forests · Post-fire forest restoration · Ciprés de la cordillera · Facilitation · Morphological attributes · Seedlings survival and growth

Introduction

In the eastern slopes of the Andes in northwestern Patagonia, Argentina, forests of *Austrocedrus chilensis* [D. Don] Pic. Serm. et Bizarri (locally known as cordilleran cypress, or simply cypress from now on) cover about 140,000 ha (CIEFAP and MAyDS 2016). These forests occur on a wide variety of sites along a 60 km -East to West- narrow strip located between 37° 08' 09" and 43° 43' 57"S. This narrow strip comprises one of the most extreme precipitation gradients of the world, increasing from 400 mm yr⁻¹ at the eastern steppe, to nearly 2000–3000 mm yr⁻¹ going west toward higher altitudes on the Andes. On humid sites, cypress grows in mixed stands associated with *Nothofagus dombeyi* (Mirb.) Oerst. (locally named as coihue). In mesic areas at mid-elevations, cypress grows in either mixed or pure stands, while in xeric areas it grows in isolation or forming small patches of scattered trees (Dezzotti and Sancholuz 1991).

In xeric sites, cypress seedling establishment has often been associated to the presence of protecting shrubs, indicating a positive (i.e. facilitation) effect from the shrub to the emerging seedling (Kitzberger et al. 2000). This facilitation effect seems to act by moderating either low temperature during the winter or high radiation levels during

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the summer. During this dry season, the low radiation levels received around the microenvironment of seedlings grown underneath of protecting shrubs, appear to improve also their soil water status (Veblen et al. 1995; Villalba and Veblen 1997; Kitzberger et al. 2000). This positive association has been shown to be more tangible during very dry summers (Kitzberger et al. 2000; Letourneau et al. 2004; Urretavizcaya and Defossé 2013). 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).

Since long ago, cypress forest dynamics in Patagonia have been affected by natural (wildfires) and human disturbances such as logging, grazing, and arson fires. Data collected from 2001 to 2011 revealed that in northern Patagonia, an average of 3226 ha of cypress and associated forest types are yearly affected by wild or arson fires (SAyDS 2013). This fire-affected area represents 2.4 % of the total cypress forests, considering pure as well as mixed stands. Severe fires cause high cypress damage and mortality, since the species has a very thin bark and is unable to sprout (Veblen et al. 1995). Cypress reproduces strictly by seed, has a transient seed bank (Urretavizcaya and Defossé 2004), and its seed dispersal is restrained to a few meters around the mother tree (Veblen et al. 1995). Further seedling establishment is conditioned by site conditions and especially by the chance of seeds of finding “safe sites” [sensu Harper (1977)] where they can germinate and grow. These “safe sites” appear to be more abundant in humid and mesic sites than in xeric areas (Kitzberger et al. 2000). Wildland fires, along with other disturbances such as logging, grazing, exotic pine plantations, and urbanization of wildland urban interfaces, have resulted in fragmentation and depauperation of these forests.

In order to restore cypress forest landscapes, different actions have been taken. While natural regeneration has proven to take long time and render unpredictable results, some active restoration practices have shown promising results. So far, the role of nurse shrubs in facilitating cypress seed germination and early seedling establishment seems to be important in burned xeric sites (Kitzberger et al. 2000; Urretavizcaya et al. 2012). However, the potential protecting effect of post-fire vegetation on different planted cypress stocktypes has not been yet assessed.

In active restoration projects involving seedlings planting, seedling quality is one of the key components for their successful performance. This quality may be defined as “the attributes necessary for a seedling to survive and grow after out-planting” (Duryea 1985). Various quality assessment methods, based on morphological and physiological attributes, have been developed and tested to predict seedlings field performance (Folk and Grossnickle 1997; Landis and Dumroese 2006; Palacios et al. 2009). Morphological plant

attributes influence seedlings' ability to survive after being planted in a forest restoration site, because plants susceptibility to drought-induced mortality may be due to their hydraulic architecture (Grossnickle 2012). Cultural practices that alter seedling morphological characteristics in the nursery (i.e. hydraulic architecture), can thus modify their susceptibility to planting stress (i.e. water stress). That is why morphological attributes such as bigger seedling stem diameter and root system size may confer, in general, higher chances of survival. In container-produced seedlings, the relation between seedling height (cm) and its collar diameter (mm), known as sturdiness ratio (Hasse 2007), appears as one of the most relevant attribute for determining seedlings performance (Génére and Garriou 1999). The balance between seedling shoot and root system, and seedling overall size, needs to be adjusted in relation to the environmental conditions prevailing at the potential forest restoration site (Grossnickle 2012). The relation shoot-to-root balance may define seedlings drought avoidance potential. Different studies have shown that the survival of container-grown seedlings may be higher with lower shoot to root ratio (S/R) under droughty field conditions (Owston et al. 1992; Mexal 2012).

In nurseries of western Patagonia, the main cypress seedling production systems involve the use of different types of containers. Some containers may be simple polyethylene bags (in which Type B seedlings are produced), while others are plastic tray containers (producing Plug seedlings), that may or may not use fertilization in the production process. There is a combination, however, in which seedlings are produced in plastic trays and fertilized, and after a year are transplanted into polyethylene bags. The performance of nursery grown cypress seedlings by using these types of production systems are so recent that there are still no conclusive results (Oudkerk et al. 2003; Contardi and Gonda 2012). For this reason, there is a need in Patagonia to determine which of the morphologic parameters for cypress seedlings optimize their field response, particularly with regard to seedling proportion, or balance of shoot-to-root equilibrium and sturdiness, under different environmental conditions. For example in semiarid environments, the dry weight of shoot-to-root and the sturdiness ratio seem to play an important role in seedling survival (Urretavizcaya and Defossé 2013). A better understanding of the interactions occurring after seedling outplanting and during the early stages of establishment in different environments may provide useful information for developing tools to be applied in ecosystem restoration (Brooker et al. 2008).

To cast light on these issues, two cypress planting experiments were carried out in north-western Patagonia. The objective of these experiments were to determine, during two markedly different growing seasons (dry and humid), the effects of post-fire cover on survival and growth of two cypress seedling stocktypes (representative of the

regional production), established in two burned sites, one mesic and the other xeric.

Methods

Study Sites

Two burned cypress stands with different environmental and vegetational characteristics were selected to establish cypress seedling planting experiments in 2001. Prior to the occurrence of both fire events, the structure of the stands was typical of those located in the South-central range of cypress natural distribution in northwestern Patagonia. One study site was located near the town of Trevelin, Chubut province (43° 12' 57"S, 71° 31' 15"W), while the other one was placed close to the city of El Bolsón, Río Negro province (41° 59' 02"S, 71° 33' 20"W), both in Patagonia, Argentina. The Trevelin stand had burned in 1996, while the El Bolsón stand had burned in 1999. The origin of both fires was accidental and they were very intense and highly severe. Understory vegetation burned down to ground level, and no overstory vegetation, including cypress trees, survived the fire on either site. Soil parent material was composed of volcanic ash on both study sites. While Trevelin stand presented a glaci-fluvial lithological discontinuity and an A horizon with silty-clay texture, El Bolsón stand showed a very deep top soil and an A horizon with loamy texture. Previous data showed that in both burned sites, OM at shallow soil horizons (0–10 cm soil depth) was higher at Trevelin site than at El Bolsón (Urretavizcaya 2010). This was probably due to the longer rest period after the fire in Trevelin than in El Bolsón. Soil moisture content, however, was lower at higher soil horizons (0–56 cm) of Trevelin site than at El Bolsón (Urretavizcaya et al. 2006).

The climate in both study sites is temperate. Mean annual temperature and precipitation are 8.2 °C and 684 mm in Trevelin (Arbuinés 1998), and 9.9 °C and 921 mm in Bolsón, respectively (Bustos and Rocchi 1993). These comprise a cold and rainy fall and winter (from April to September in the Southern Hemisphere), in which about 75 % of the annual precipitation fall, and below freezing temperatures occur. The remaining 25 % of precipitation falls during the warm and dry spring and summer seasons (De Fina 1972). Taking into consideration climatic and soil characteristics, Trevelin can be considered as a typical xeric site, and El Bolsón as a mesic site.

Plant Cover

Post-fire vegetation structure differed between sites. The stand located at Trevelin site had burned 5 years before establishing the first experiment, and presented 350 burned cypress snags per ha; these dead trees added up to

10 m² ha⁻¹ of basal area, providing 18.8 ± 4.3 % of overstory cover. Post-fire understory was dominated by the native shrubs *Schinus patagonicus* (Phil.) I. M. Johnst., *Diostea juncea* (Gillies ex Hook.) Miers, *Discaria trinervis* (ex Hook. and Arn.) Geim., and *Berberis heterophylla* Juss. There were also some grasses of the genera *Holcus*, *Stipa* and *Agrostis*. Understory cover was 85.5 ± 9.7 % (Urretavizcaya et al. 2006). The stand located at El Bolsón had burned 2 years before the experiment was set, and had 1540 burned cypress snags per ha; they added up to 25 m² ha⁻¹ of basal area, providing 39.0 ± 11.8 % of the overstory cover. In the understory, the most important post-fire species were the shrub *Aristotelia chilensis* (Molina) Stuntz, the herbs *Rumex acetosella* L., *Cardus nutans* L., *Phacelia secunda* J.F. Gmel., *Lactuca seruola* L., and *Galium* sp., and the non-native grasses *Holcus lanatus* L. and *Dactylis glomerata* L. Understory cover was 60.1 ± 6.1 %. From the fire events and till the establishment of the experiments, vegetation remained undisturbed on both sites.

Seedling Stocktypes Used in the Experiments

On each study site, we set one experiment involving two different seedling stocktypes per site. These stocktypes came from different nurseries of the region and represented variants of the cultivation methods mentioned before. Both stocktypes were produced from seeds of the South genetic provenance region, in which Trevelin site, is part of (Pastorino et al. 2015). Seedlings established were 100 Plug1 + 1 and 100 B1 + 2 in each site. Plug1 + 1 seedlings were grown and ferti-irrigated during the first growing season in Daspastic 4090 plastic trays in a greenhouse, where they were cultivated for about nine months (Enricci and Massone 2000). These trays have 519 cavities per square meter, and each of them holds 93 cm³ of growing media (composed of 50 % volcanic sand and 50 % of coco soil). Nutrients were supplied with irrigation as N-P-K, Peters[®] Starter 9:45:15 for 6 weeks; P. Excel 21:5:20 for 10 weeks, and P. Finisher 4:25:35 for 14 weeks. Seedlings were then transplanted the second year into polyethylene bags having 900 cm³ holding capacity each, and unfertilized. This represents a mixed system and it is widely used to produce cypress seedlings in the region. Seedlings B1 + 2 were produced in indoor beds, where they remained for the first growing season. During the following fall, they were transplanted into 900 cm³ polyethylene bags (B), remaining there for other two growing seasons. The substratum in the polyethylene bags consisted of a mixture of common topsoil (75 %) plus volcanic sand (25 %). After being transplanted, seedlings remained under artificial shade provided by a black cloth having 65 % of light transmittance. This seedling stocktype was neither fertilized before nor after being

transplanted to polyethylene bags. Both stocktypes did not present significant differences about their production costs.

Seedling Morphological Attributes

Prior to setting the experiments, seedling samples from each stocktype (30 for Plug1 + 1 and 32 for B1 + 2) were randomly chosen to determine differences in morphological attributes. Then, shoot height (SH, in cm) and stem collar diameter (SCD, 1 cm above the cotyledon insertion point, in mm) were measured. Shoot weight as well as root biomass, was computed to calculate the S/R by drying the sampling seedlings at 103 ± 2 °C to constant weight. The sturdiness ratio [SH (cm)/SCD (mm)], was also calculated. All morphological parameters differed between the two seedling stocktypes (Tukey test, Table 1).

Experimental Design

Both experiments had the same design, and the factors studied were plant cover and seedling stocktypes. The cover factor varied between 0 and 100 %, and the seedling stocktypes had two levels per experiment. The response variables were seedling survival and growth. Growth was measured in terms of yearly increases in SH and SCD. The sample unit was a single seedling; they were planted in a square pattern separated by 3 m one from another (3 by 3 meters), in rows containing 8 by 25 plants (Fig. 1). The trials were established in June, which coincides with the end of the fall and the beginning of the winter season in the Southern Hemisphere. Plantation was done manually by using a shovel, making 20 cm diameter by 30 cm deep holes. Seedlings plantation was carried out by the same crew composed of four laborers. No other site preparation was done, since post-fire cover was one of the factors to be evaluated. Total plant cover was measured with a Spherical convex-glass Densitometer Model A (Forestry Suppliers), located at the apex of each seedling. A single reading per seedling was registered, and for consistency, it was always taken facing north. Cover measurements were done for both years on December 18th and 19th in Trevelin and El Bolsón, respectively. This time matches with almost the end of the spring season in the study region, right after the regrowth of herbaceous and shrub vegetation and before the beginning of the dry season.

Precipitation During the Study Period

Precipitation data registered during the growing seasons in which the experiments were conducted (2001–02 and 2002–03) were compared with the long-term mean. Meteorological information was obtained from weather stations located nearby each study site. In the case of

Table 1 Morphological parameters determined for cypress seedling stocktypes prior to out planting each experiment (mean \pm one standard error)

Morphological parameters	Plug1 + 1	B1 + 2
Age (years)	2	3
Stem diameter (mm)	2.8 \pm 0.1 a	2.2 \pm 0.1 b
Stem height (cm)	13.5 \pm 0.3 a	8.8 \pm 0.3 b
Root system length (cm)	20.0 \pm 3.1 a	18.0 \pm 2.0 b
Shoot dry weight (g)	1.4 \pm 0.0 a	0.9 \pm 0.0 b
Root dry weight (g)	1.1 \pm 0.0 a	0.5 \pm 0.0 b
Total dry weight (g)	2.5 \pm 0.0 a	1.4 \pm 0.0 b
Shoot to root ratio	1.3 \pm 0.1 a	1.8 \pm 0.1 b
Sturdiness ratio	49.3 \pm 1.2 a	40.7 \pm 1.2 b
<i>n</i>	30	32

Different lower case letters indicate statistically significant differences in seedling characteristics between stocktypes ($p < 0.05$)

Trevelin, data were provided by the Trevelin Station of the Chubut Province Fire Department, located 13 km away from the study site. For El Bolsón, data were supplied by one of the Río Negro province Water Department stations, located 2 km apart from the study site. Annual precipitation differed at least by plus or minus 45 % in relation to the historical mean on both sites for the years the experiments were run. For Trevelin, these records were 49 % lower for the 2001–2002, and 105 % higher for the 2002–2003 growing periods as compared to the historical mean. For El Bolsón site, instead, these records were 60 % lower for the 2001–2002, and 58 % higher for the 2002–2003 growing periods as compared to the historical mean. These values showed similar precipitation trends during the seasons analyzed between the two sites.

Analyses

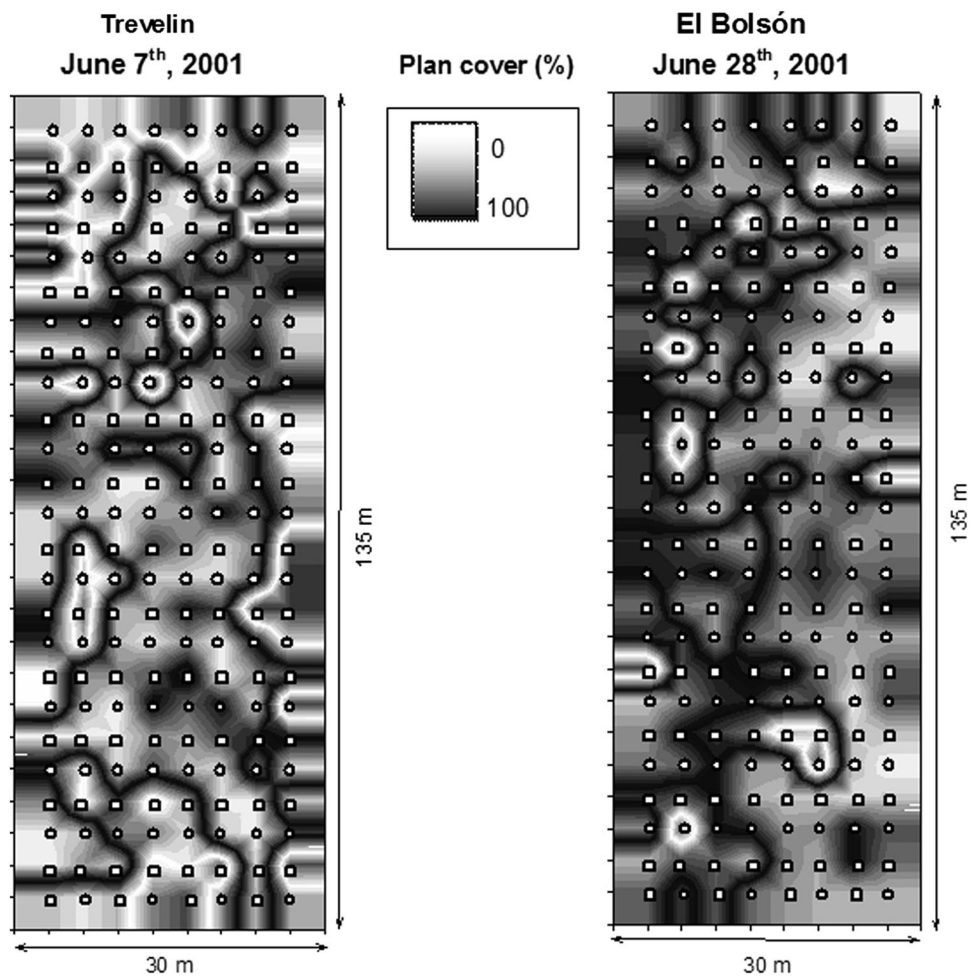
Independence of sampling units

Based on post-fire vegetation heterogeneity present in both sites before setting the experiments, we assumed that treatments were randomly assigned to sampling units. However, to test if seedlings located one next to another tended to be under the same shading condition, we carried out the Runs test for each experiment (Siegel 1957). Based on this, we did not find evidence to reject the hypothesis that seedlings of the same row had the chance of being under different shading conditions (TR $p = 0.20$; EB $p = 0.48$).

Data collection

The same measurements were taken for the two experiments. Right after planting, we measured all seedlings height (SH) and SCD. At the end of the first growing

Fig. 1 Contour 3D graph of the two experiments showing site name, outplanting date, seedling stocktype, as well as plant cover (Plug 1 + 1: ○- B1 + 2: □). In this graph, data was interpolated and plant cover percentage increase with darkness



season, we computed survival and measured SH. At the end of the second growing season, besides survival and SH, we also measured SCD.

Survival and growth analyses

To determine if survival differed among different treatments, we applied logistic regression, a suitable procedure for binary response variables. The adjusted model [1] was:

$$\text{logit } P(x) = \alpha + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2 \tag{1}$$

where *logit* is the logarithm of the odds ratio $\text{logit } P(x) = \ln \left[\frac{p}{(1-p)} \right]$; α is the constant; β_1 , β_2 and β_3 are the regression coefficients associated to the regression variables X_1 (stocktypes), X_2 (plant cover), and $X_1 X_2$ (their interaction) (Kleinbaum and Klein 2002). The predicting model for this *logit* function is its inverse [2], and it is called logistic function:

$$P = \frac{e^{\alpha + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2}}{1 + e^{\alpha + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2}} \tag{2}$$

The *P* value obtained is the proportion or estimated probability of survival of cypress seedlings.

To determine if SH, SCD, and stem growth differed among treatments, we ran an analysis of covariance. Seedling stocktype was considered a categorical factor, plant cover was treated as covariate, and planting line was included in the model as a random factor. However, we first determined if slopes of regression lines were different, by testing the interaction between the covariate plant cover and the stocktypes factor. Growth in height for the first and second year was analyzed separately. For the first year, height growth resulted as the difference in height registered at the end of this year and the initial value taken right after out planting. For the second year, growth in height resulted as the difference in height registered at the end of the second season minus the height registered at the end of the first growing season. We also analyzed total growth in height, in SCD and in stem growth based on initial and final measurements (at the end of the second growing season). Stem growth was calculated as the difference in stem volume at the end of the studied period minus the same volume at the

beginning of that period. The stem volume was calculated (assuming all seedlings presented a cone-shaped stem), by measuring total cone height and its basal diameter.

Results

Seedling Survival and Annual Seedling Height Growth

None of the variable responses analyzed over the plantations showed significant interactions between plant cover and stocktypes. At Trevelin, results showed that at the end of the first and second growing seasons, neither seedling stocktypes nor plant cover had a significant effect on seedling survival (Table 2, Fig. 2). However, seedlings of both stocktypes grown under high cover grew more in terms of height than those grown under low cover during the first dry growing season, but not in the second humid season (Table 3, Fig. 2).

For the experiment established in El Bolsón, instead, both stocktypes improved their survival under high plant cover, at the end of either the first dry or the second humid growing seasons (Table 2, Fig. 3). Additionally, both stocktypes grew more in height under high cover during the first and second growing season as compared to seedling grown under low cover (Table 3, Fig. 3).

Total Seedling Growth

Along the whole experiment, total height growth in Trevelin increased with plant cover, while SCD decreased (Table 4, Fig. 4). However, considering stem growth, seedlings Plug1 + 1 increased in volume more than B1 + 2, and both showed lower growth rates as plant cover increased. In El Bolsón and after 2 years, height growth increased as cover increased, although stem diameter was not associated with plant cover. Similarly to what occurred in Trevelin, stem growth was higher for seedlings Plug1 + 1, but in this site it was not associated to plant cover (Table 4, Fig. 4).

Discussion

This study was carried out in two contrasting environments (one mesic and the other xeric), and during two consecutive years which presented markedly different precipitation conditions related to mean historical climatic values. This indicates that one growing season was very dry and the other very humid. In each site, post-fire plant cover had similar effects on both seedling stocktypes related to survival, growth in diameter, or height growth. After 2 years, however, the two seedling stocktypes presented differences related to stem growth. Bigger seedlings (Plug1 + 1), with

Table 2 Probabilities of seedling survival as affected by stocktypes, plant cover, and their interaction in both experimental sites

Time of monitoring	Response variables	TR	EB
End of first year	Stocktype	0.5815	0.9911
	Plant Cover	0.6529	0.0014
	Plant Cover* Stocktype	0.8234	0.4665
End of second year	Stocktype	0.1969	0.4832
	Plant Cover	0.7915	0.0007
	Plant Cover* Stocktype	0.2141	0.4971

Survival was determined at the end of the first and second growing seasons for both experiments (values in bold showed significant differences at $p < 0.05$)

TR Trevelin, EB El Bolsón

higher stem diameter and height, significantly increased their volume as compared to smaller (B1 + 2) seedlings.

In Trevelin (the xeric site), the balance of plant cover effect on seedling survival was neutral for either the first or the second year. Considering that at the mesic site survival was improved with plant cover, Trevelin results may seem to be contradictory. However, this can be explained by the fact that in xeric sites, facilitation may not occur during abnormally dry or wet years, as it was the case with the two growing seasons while the experiments were carried out. In xeric sites, different studies (Bertness and Callaway 1994; Holmgren et al. 1997; Callaway 2007) suggested that the net effects of competitive and facilitative interactions vary along spatial and temporal gradients of abiotic stresses. Net facilitative effects of nurse plants may only become apparent during climatically sub-optimal years. Seabloom and van der Valk (2003) demonstrated that in xeric environments, survival would be low, even under the protection of nurse shrubs. Extremely low or high environmental stressing conditions appear to prevent facilitation (Brooker et al. 2008). For example in xeric sites and during unfavorable periods, cypress seed germination and seedling establishment was almost nil in either nursed or unprotected sites (Kitzberger et al. 2000). In our study, although seedling survival was not associated with shrub cover during the unfavorable year, a 70 % survival was achieved during the first year after planting, diminishing to 56 % the following year.

In El Bolsón (the mesic site), at the end of the first dry and second humid growing seasons, survival of both stocktypes was benefitted by high plant cover. In this mesic site, shade can indirectly facilitate water relations of cypress by decreasing the vapor pressure difference between leaf and ambient air as it happens in other species (Maestre et al. 2009). Drought avoidance behavior through early stomatal closure could be the main mechanism used by cypress to survive under soil water deficits coupled with high

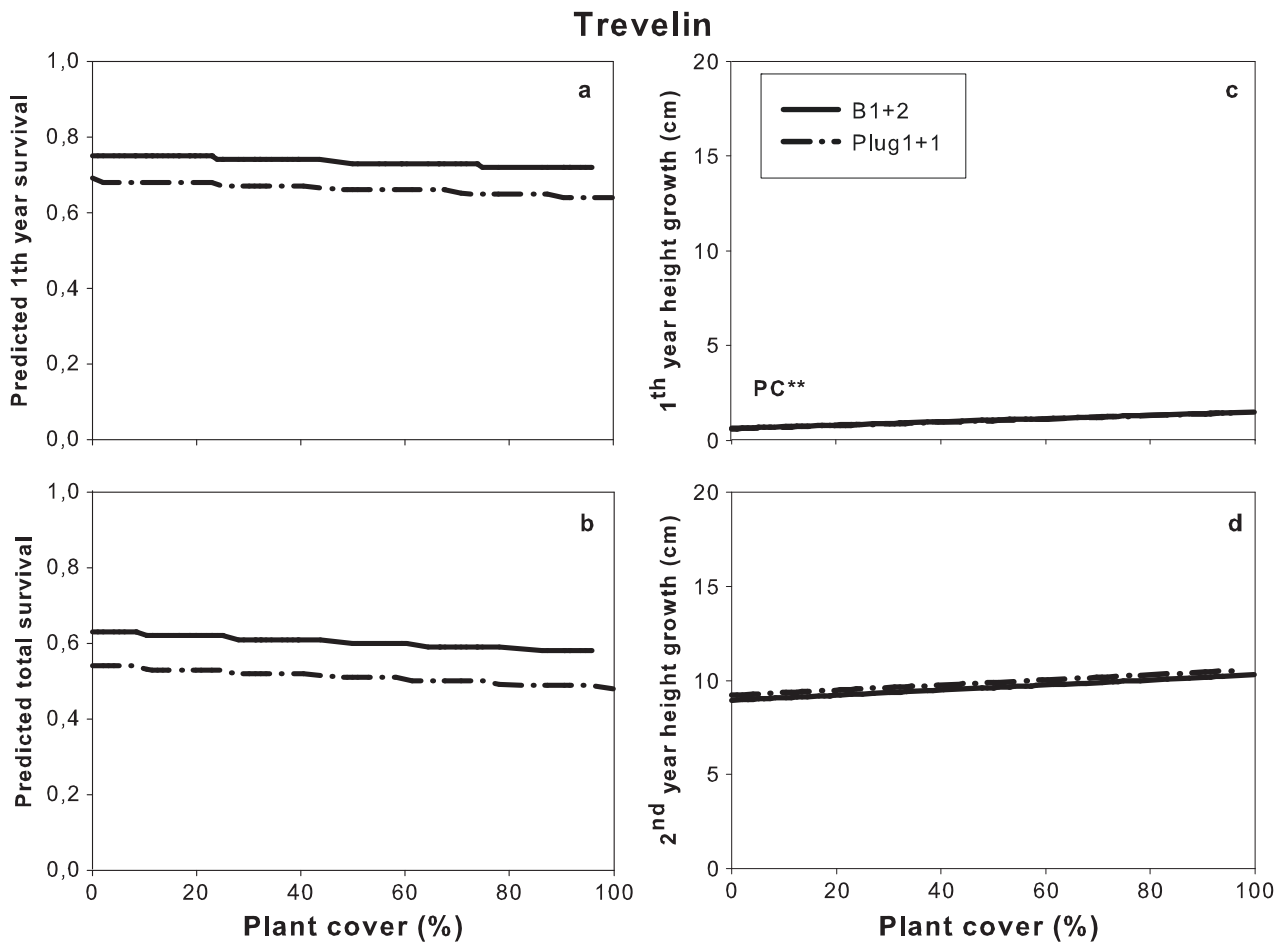


Fig. 2 Predicted survival and annual height growth as affected by plant cover and stocktypes at the end of the first (a, c) and second (b, d) growing seasons for the experiments established at Trevelin.

Significant factors are shown within each graph (PC: plant cover, * $p < 0.1$; ** $p < 0.05$; *** $p < 0.01$)

Table 3 Probability that seedling height growth at the end of the first and second growing season were associated to stocktypes and/or plant cover in both experimental sites

Response variable	Factors	TR	EB
First-year height growth	Stocktype	0.9044	0.1417
	Plant cover	0.0158	<0.0001
Second-year height growth	Stocktype	0.7689	0.9156
	Plant cover	0.3721	0.0155

Values in bold showed significant differences at $p < 0.10$

TR Trevelin, EB El Bolsón

evaporative demands (Gyenge et al. 2007). It also seems that in mesic sites and without water deficit, cypress seedlings may be associated to dense and short herbs and grasses. This association may indicate the absence of allelopathy and competition for water and nutrients between cypress seedlings and surrounding short herbaceous

vegetation, and may indicate a protective effects of these herbs on cypress seedlings (Gobbi 1999).

In the xeric site and contrary to what happened with survival, seedling height growth was facilitated by high cover values during the dry, unfavorable first growing season, but showed no significant differences between protected and unprotected seedlings during the following humid season. In El Bolsón, height growth of both stocktypes was higher under high plant cover than under low plant cover during the first dry, the second humid growing season, and during the whole study period. Holmgren (2000) found that in mesic sites like El Bolsón, growth rates tended to decrease with increasing photosynthetic active radiation (PAR) under dry conditions; carbon assimilation decreases under high light conditions, resulting in strong decrease in sapflow. Studies in other species with the same ecophysiological strategy as cypress, indicate that the risk of photoinhibition or cell damage due to over-heating is increased under this situation. For this reason, the shelter

El Bolsón

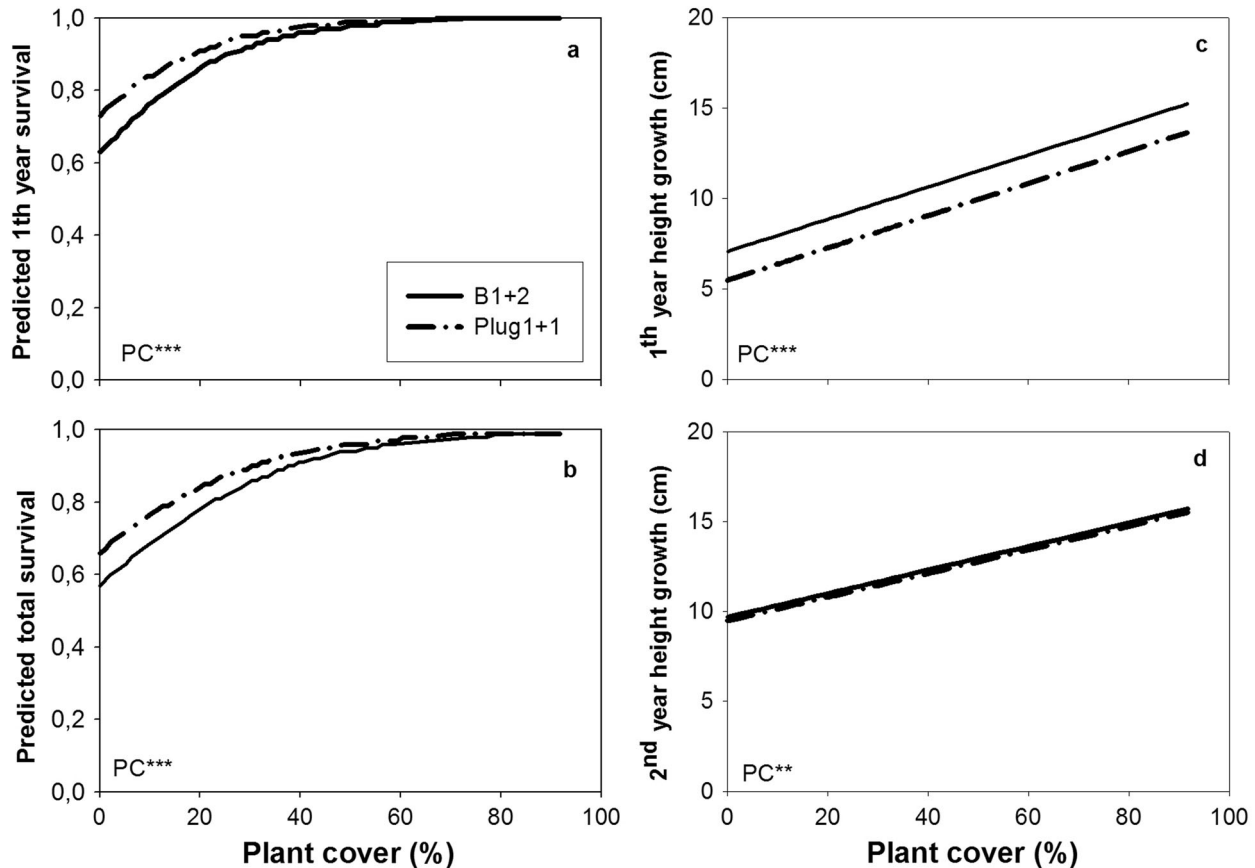


Fig. 3 Predicted survival and annual height growth as affected by plant cover and stocktypes at the end of the first (a, c) and second (b, d) growing seasons for the experiments established at El Bolsón.

Significant differences between factors are shown within each figure (ST: stocktype and PC: plant cover; * $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$)

Table 4 Probability that seedling height, stem diameter and stem growth at the end of the second growing season (2 years) were associated to stocktypes and/or plant cover study in both experimental sites

Response variable	Factors	TR	EB
Total height growth	Stocktype	0.6363	0.4948
	Plant cover	0.0834	0.0003
Total stem diameter growth	Stocktype	0.8693	0.1092
	Plant cover	<0.0001	0.7079
Total stem growth	Stocktype	0.0005	0.0016
	Plant cover	0.0618	0.3616

Values in bold showed significant differences at $p < 0.10$

TR Trevelin, EB El Bolsón

provided by shrubs or other plants is may be a possible way of avoiding these processes derived from excessive radiation (Gyenge et al. 2007). During the humid year, the facilitation effect was also positive on seedling height growth. Height growth was also noticeable for unprotected

seedlings, which grew more in this humid year than in the previous dry year (see Fig., 3c and d). At the end of the experiment, cypress seedlings increased their height growth under high cover at both sites, although it was higher under mesic conditions (see Fig. 4a and b). Root collar diameter and stem growth, instead, did not show the same association. In the xeric site, root collar diameter (Fig. 4c and d) and stem growth were lower at higher plant cover values, while in the mesic site they were similar (Fig. 4e and f). In a xeric site similar to Trevelin, this inverse association between collar diameter growth and plant cover was also reported for cypress seedlings by Dalla Salda and Schlichter (2005). In mesic sites, instead, this association appears to be not so clear. Letourneau (2006) reported that volume growth of cypress seedlings grown under shadow (protected by a nearby shrub) and full sun (unprotected) conditions during a dry, humid, and very humid years did not present a clear pattern associated to moisture conditions during the course of the growing seasons.

Without water limitations but with low light during the growing season, stem growth height and leaves elongation is

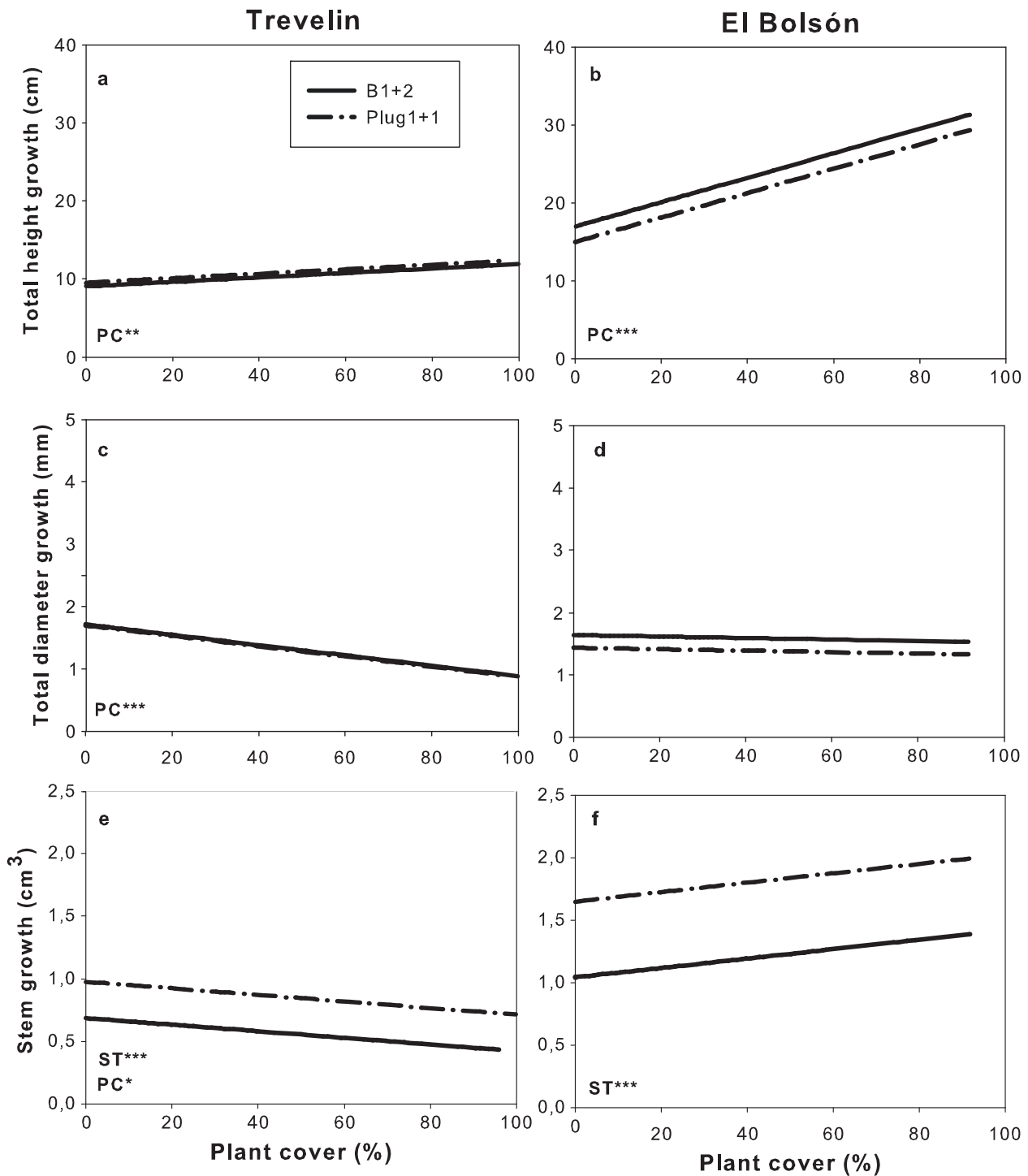


Fig. 4 Predicted total height growth (a, b), stem diameter (c, d), and stem growth (e, f) after 2 years, as affected by plant cover and stocktype for the experiments established at both experimental sites.

Significant differences between factors are shown within each figure (ST: stocktype and PC: plant cover; * $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$)

more noteworthy than the other growth parameters measured. This may be due to compensation mechanisms, by which the low irradiance levels produce an increment in photosynthetic tissues (Larcher 2003). The low levels of

photosynthetic active radiation (wavelengths from 400 to 700 nm) received could alter the proportion of total biomass that the plant invests in leaf production by concomitantly reducing root growth or seed production. This reduction in

received PAR may be compensated by increasing the photosynthetic area of leaves (Waring and Schlesinger 1985). This biomass partitions has been reported in other studies dealing with the same (Letourneau 2006; Pafundi et al. 2014) and other species (Waring and Schlesinger 1985). The 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).

The positive effects of shade on water relations and temperature may be counteracted by the negative effects of shade on light availability for many understory species (Callaway 2007). Interactions between the effects of shade and light as a resource, and temperatures and transpiration rates as a stress factor are unavoidable. Similarly and apart from the site conditions (xeric vs mesic), it could be speculated that differences found between sites could have been related not only to the specific aboveground cover, but also to the main predominant types of understory species present at each site, that is shrubs in Trevelin and herbs and grasses in El Bolsón. Several studies demonstrated that shrubs tend to compete more intensively for soil resources than graminous species (Petriřan et al. 2012).

Finally, results in the mesic site shown in our study coincided with those postulated by Holmgren et al. (1997). They took these potential trade-offs into account by modeling the relative importance of shade from a nurse plant as either a facilitative or a competitive effect, depending on the synergy between light and moisture in a plant's environment. Assuming that plant growth is a relatively simple product of light and moisture, and that soil moisture is affected by canopies to a greater degree in xeric environments than in mesic environments, they argued that plant growth will increase as light increases. However, Holmgren and Scheffer (2010), argued that the facilitation effects under moderate rather than under extreme conditions may be the rule rather than the exception.

Mediterranean environments are characterized not only by a water deficit during the growing season, but also by considerable fluctuations in annual distribution of rains and mean temperatures. This unpredictability in the occurrence of water stress and high temperature periods may thus greatly affect seedling performance (Valladares et al. 2004). For these reasons, it is highly probable that during the first or second season after planting, seedlings grown in Mediterranean environments may pass through an unfavorable dry and stressing growth period. That is why in forest restoration programs, the planting of seedlings with desirable attributes does not guarantee, per se, higher seedling survival rates. However, seedlings with desirable attributes increase their chances of survival when other factors, such

as care and manipulation in the nursery, transportation to the planting site, and the correct election of the planting season and plantation technique, are also taken into account (Palacios et al. 2009; Grossnickle 2012). In 2007, 4 years after the experiment was completed (2003), we remeasured seedlings on both sites and found that survival only decreased by 3 % in El Bolsón and by 9 % in Trevelin, and was similar considering both seedlings stocktypes. These results are a clear indication that in central Patagonia, and taking into consideration the proper care and manipulation from the nursery to the planting site, both B1 + 2 and Plug1 + 1 seedling stocktypes or with similar attributes, could be recommended for restoring fire damaged cypress forests. Additionally and in the short-term after a fire, the early successional herbs and shrub resprouts enhance survival and growth of planted seedlings, thus increasing the speed of recovery and the restoration possibilities of fire-affected temperate forests.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no competing interests.

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