Early performance of planted *Nothofagus dombeyi* and *Nothofagus alpina* in response to light availability and gap size in a high-graded forest in the south-central Andes of Chile

Respuesta temprana de plantaciones de *Nothofagus dombeyi* y *Nothofagus alpina* a la disponibilidad de luz y tamaño de claro en un bosque degradado en el centro sur de Los Andes de Chile

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SUMMARY

The Andes of south-central Chile (38 – 41° S) were once dominated by highly productive and valuable forests mainly dominated by *Nothofagus dombeyi* and *N. alpina*, but their exploitation led to extensive areas at present covered by high-graded stands. Although these tree species exhibit a light-demanding character and naturally grow in regions with severe winters, they show high mortality when planted in open areas with frequent spring frosts. The effect of light intensity and gap size on survival, size and form of *N. dombeyi* and *N. alpina* seedlings, planted in a high-graded stand, was analyzed. Direct and diffuse light (measured through hemispheric photographs) and effective gap area (range from 40 to 734 m^2) were estimated in 23 forest gaps, which were divided into small, medium and large for each species (12 gaps for *N. dombeyi* and 11 gaps for *N. alpina*). After two growing seasons, mean survival of *N. dombeyi* was > 95% and not significantly different among gap categories; in *N. alpina* there was complete survival in medium-sized gaps, which was significantly different from survival in the larger and smaller gaps. Growth of *Nothofagus dombeyi* significantly increased with gap size and light availability; a phenomenon which did not occur in *N. alpina*. *Nothofagus alpina* experienced a lower slenderness within larger gaps. This study suggests that rehabilitation of high-graded stands, based on plantations of genus *Nothofagus*, is an ecologically viable option although control of canopy and understory covers is required.

Key words: degradation, restoration, tree growth, survival, shade tolerance

RESUMEN

Los Andes del centro sur de Chile (38-41°S) estuvieron dominados por bosques altamente productivos y valiosos de (*Nothofagus dombeyi* y *N. alpina*, pero la explotación de estas especies llevaron a la existencia actual de grandes superficies cubiertas en el presente por bosques degradados. Aunque estas especies son demandantes de luz y naturalmente crecen en regiones con inviernos severos, ellas muestran altas tasas de mortalidad cuando son plantadas en zonas abiertas con heladas frecuentes de primavera. La luz difusa y directa (medida a través fotos hemisféricas) y el área efectiva de claros (rango de 40 a 734 m^2) se estimaron en 23 claros de bosque, los cuales fueron divididos en pequeños, medianos y grandes para cada especie (12 claros para *N. dombeyi* y 11 para *N. alpina*). Luego de dos temporadas de crecimiento, la sobrevivencia promedio de *N. dombeyi* fue > 95% y no significativamente diferente entre las categoría de claro estudiadas; en *N. alpina* hubo sobrevivencia completa en los claros de tamaño medio, lo que fue significativamente diferente a la sobrevivencia reportada en claros chicos y grandes. El tamaño de *N. dombeyi* fue significativamente mayor en claros más grandes y con aumentos en la disponibilidad de luz. Las plántulas de *Nothofagus alpina* no fueron afectadas en tamaño por la dimensión de los claros, pero experimentaron una menor esbeltez en claros grandes. Este estudio sugiere que la rehabilitación de bosques degradados, basada en plantaciones del género *Nothofagus,* es ecológicamente una opción viable aunque ello requiere control de la cobertura de copas y del sotobosque.

Palabras clave: degradación, restauración, crecimiento, sobrevivencia, tolerancia a la sombra.

INTRODUCTION

Degradation of natural forests due to exploitation is overshadowed by deforestation, in spite of being the major driver of losses of ecosystem goods and services, mainly in regions of the developing world (Nahuelhual *et al*. 2007). Particularly in old-growth forests, degradation is caused by high-grading which consists in the removal of the most commercially valuable trees, leaving a residual stand composed of poor timber quality individuals (Nyland 2006). This practice implies short-term economic benefits without any consideration of the diversity, regeneration and development of the growing stock left for the future forest. As a consequence, old-growth forests lose their original composition, structure and timber productivity, as well as many of the ecological services they once provided. In Chile, by the end of last century around 51 % of an area of 8.2 million hectares of second- and old-growth native forests had been exploited through high-grading; whereas only 5 to 25 % of harvested stands showed sustainable management (Lara *et al*. 1998, and references therein).

The Andes of south-central Chile (38-41°S) used to be covered by old-growth forests dominated by both, the shade-intolerant *Nothofagus dombeyi* ((Mirb.) Oerst.) and the shade-midtolerant *Nothofagus alpina* ((Phil.) Dim. *et* Mil.) (Donoso *et al.* 1986, 2006ab, Weinberger and Ramírez 2001). These early successional species form even-aged stands in sites where frequency of large-scale disturbances (*e.g.*, landslides, fires ignited following volcanic eruptions and massive tree fall due to windstorms) is shorter than life-span of these *Nothofagus* species, allowing these species to maintain their dominance in the landscape. In absence of such exogenous perturbations, late-successional, shade-tolerant trees tend to become established under the canopy and to successionally replace *Nothofagus* species (Veblen *et al.* 1980, 1996, Donoso *et al.* 1986, Donoso 1993). As a consequence of severe overexploitation, currently these highly commercially valuable forests have lost biomass, density and productivity; large *Nothofagus spp.* trees are almost absent and less valuable shade-tolerant trees are dominant (Donoso 1993). The understory is occupied by a thick and continuous cover of *Chusquea culeou* (E. Desv.); a bamboo that prevents tree regeneration (Lusk 2001, Muñoz and González 2009). Overall, these high-graded areas meet all the characteristics of degraded stands described by Nyland (2006).

Considering that it is urgent to implement strategies to reduce both processes of deforestation and degradation, it is essential to search for the best options to recover the productivity of current high-graded forests. This process has to be conducted with locally supported options that, in addition to augmenting the natural capital, will generate jobs and improve livelihoods and the quality of life of all in the economy (*sensu* Aronson *et al*. 2006). Planting *N. dombeyi* and *N. alpina* in these high-graded forests seems one interesting option. These *Nothofagus* species are naturally adapted to mild climates within temperate regions in Chile and Argentina (Donoso *et al.* 2006ab), and due to their rapid growth and good expected economic returns in open-field plantations (Donoso *et al*. 2011, and references therein), they have been introduced in other regions of similar climates, with the most successful experience being that in southwest England and Wales (Matthews *et al*. 1989). However, open-field plantations of these species on abandoned artificial pasturelands in the Andes of south-central Chile where severe spring frosts occur (> 650 m a.s.l.; Donoso *et al*. 2007, Soto *et al*. 2009) or in the west of England and Wales have had severe mortality or damage. Considering that partial shade from forest canopies can protect seedlings from frosts (Slot *et al*. 2005) and changes the intensity of direct and diffuse incident light (Norman *et al*. 1971), it might be possible to successfully plant *N. dombeyi* and *N. alpina* in high-graded forests. However, considering that the species are of low shade tolerance, the challenge is to find the proper combination of canopy protection and light availability for optimum performance of planted seedlings of *Nothofagus* species.

In this study we report the first experience with plantations under canopy gaps in high-graded forests in the Chilean Andes, where the aim is to rehabilitate *Nothofagus*-dominated forests that were once characteristic of this region. We evaluated the performance of *N. dombeyi* and *N. alpina* seedlings two years after being planted in small- and middle-sized gaps in a high-graded forest stand. We predict a higher survival and growth response to light avaiability and gap size of *N. dombeyi* due to its lower shade tolerance compared with *N. alpina* (Donoso *et al*. 2006ab). Hence, our main objective was to determine the relationship between gap size and light availability and the effects of these variables upon survival and growth of planted *N. dombeyi* and *N. alpina* seedlings in the south-central Andes of Chile.

METHODS

Study site. The study was carried out in a 10-ha high-graded forest that was harvested some 50 years ago in the San Pablo de Tregua experimental forest of the Universidad Austral of Chile in the Andes (39° 35' S, 72° 05' W; 650 m a.s.l.). The original old-growth forest likely had a structure similar to that reported for these type of Andean forests by Veblen *et al*. (1980) and Donoso *et al*. (1986) in their descriptions of pristine old-growth forests in the Province of Valdivia; i.e. forests with a basal area close to 100 m^2 ha^{-1} and an emergent tier of *Nothofagus* species (*N. dombeyi* and *N. alpina*) above a canopy of the more shade-tolerant species (*Laureliopsis philippiana* (Looser) Schodde., *Saxegothaea conspicua* Lindl. and *Dasyphyllum diacanthoides* (Less.) Cabr.). An inventory of three 1,000 m^2 plots in the high-graded forest stand used in this study (figure 1) shows large 20 - 25 m tall trees of *L. philippiana* and *S. conspicua* (species that had little commercial value by the time of harvest) and patchy distributed *N. alpina* trees of smaller diameters, which likely regenerated or remained (due to their small size by the time of harvest) following the cut. The stand is growing on a south to southwest facing slope. Its basal area is currently *ca.* 48 m^2 ha^{-1}. The low number of small trees even of the most shade-tolerant species is likely the result of the development of dense thickets of *C. culeou* in the understory that has prevented forest regeneration following forest degradation. In 2000 *C. culeou* had a synchronous death, hence by the time of implementing this study through plantations in the understory (October 2007), there was a large quantity of dead biomass of *C. culeou* and the new stems of *C. culeou* had on average 3 m in height (compared to the 6 - 9 m they can reach; Lusk 2001).

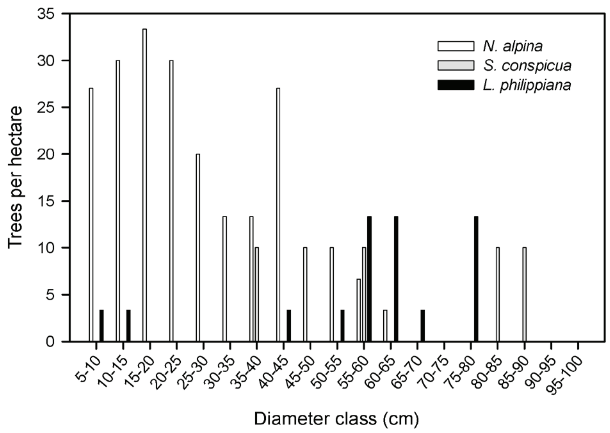

Figure 1. Diameter distribution of the high-graded mature forest stand in which *N. dombeyi* and *N. alpina* seedlings were planted in gaps of different sizes in the San Pablo de Tregua experimental forest.

Distribución diamétrica del rodal de bosque maduro degradado en el que plántulas de *N. dombeyi* y *N. alpina* fueron plantados en claros de distinto tamaño, predio San Pablo de Tregua.

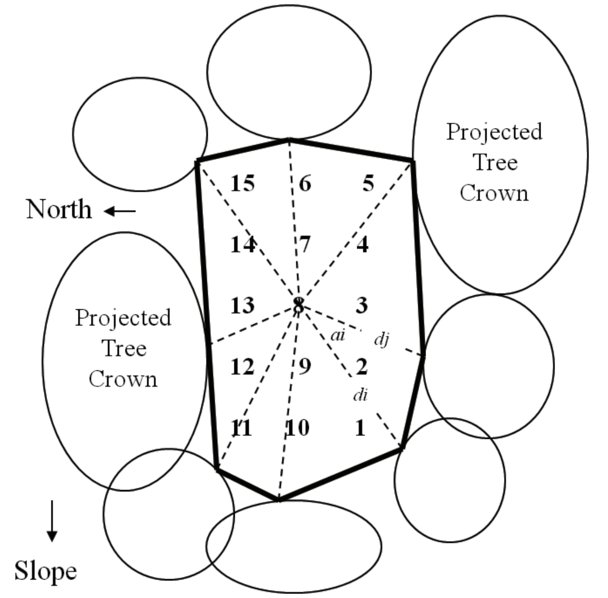

Figure 2. Schematic layout of gaps, crown projection of remnant trees (open circles), and the plantation of *N. dombeyi* and *N. alpina* in the gaps. The representation of polar coordinates (dashed lines) is shown for the predicted effective gap (*sensu* Runkle 1992). Spots from which photographs were taken to predict gap light transmission indices with the GLA (Gap Light Analyzer) were the center (seedling 8), the north edge (seedling 10), and the south edge (seedling 6) of the gaps. *di* is the distance from the center to each crown tree projected to the gap *i* (in m); *dj* is the distance from the center to the contiguous crown tree *j* (in m) and *ai* is the angle formed between both crown trees.

Esquema de los claros, proyección de copas de los árboles remanentes (círculos abiertos), y plantación de *N. dombeyi* y *N. alpina* en los claros. La representación de coordenadas polares (líneas discontinuas) se muestra para el área de claro efectivo (*sensu* Runkle 1992). Los puntos desde los cuales se tomaron las fotografías para predecir la transmisión de luz con el GLA (Gap Light Analyzer) fueron el centro (plántula 8), el borde norte (plántula 10), y el borde sur (plántula 6) de los claros. *di* es la distancia desde el centro de cada copa de árbol proyectada en el claro *i* (en m); *dj* es la distancia desde el centro de la copa del árbol contiguo *j* (en m) y *ai* es el ángulo formado entre las dos copas de los árboles.

Soils are derived from modern volcanic ashes (Acrudoxic hapludand), have a medium texture through the entire profile, with a pumice horizon over basaltic-andesitic rocks (CIREN 1999). This soil has a high water retention capacity (> 250 mm in 1 m depth) and total nitrogen content (0.97 ± 0.07 %), and a carbon/nitrogen relation of 11.6 ± 0.3 (Donoso *et al*. 2007). However, it also has a high phosphorus retention and aluminum levels due to the presence of alophan. The climate according to Köppen is coastal oceanic with a Mediterranean influence, with short and dry summers and humid winters. The annual precipitation, mostly rainfall, ranges between 3,863 and 4,849 mm (Oyarzún *et al*. 2011). Mean annual temperature is 11 °C, while the mean for the coldest month (August) is 5 °C and for the warmest (February) 16 °C. There are 30 - 50 annual frosts (minimum temperatures < 0 °C), concentrated from August through September (Soto *et al*. 2009).

Selection of gaps. We selected 23 gaps within the high-graded stand, which ranged in size from 40 to 734 m^2. In 12 of these gaps we planted *N. dombeyi* and in 11 we planted *N. alpina*; for further analyses we divided these gaps into size categories, which were named small (four for *N. dombeyi* and five for *N. alpina*), medium (five for *N. dombeyi* and three for *N. alpina*) and large (three for each species). Gap size was measured by taking the distance from the center of the gap to every vertical tree crown projection (effective gap; Runkle 1992); combining this with the compass direction of the line (azimuth from the center of the plot to the crown edges of each tree around the gap; figure 2). Equation 1 was used to calculate the effective area of gaps (Fajardo and de Graaf 2004).

$$\text{Gap area (m}^2) = \sum (0.5*di*(dj*\cos(90-ai))) \quad [1],$$

where *di* is the distance from the center to each crown tree projected to the gap *i* (in m); *dj* is the distance from the center to the contiguous crown tree *j* (in m); and *ai* is the angle formed between both crown trees (figure 2). Minimum gap size was similar for both species, but the mean and maximum gap sizes were larger for *N. dombeyi* (table 1).

Planting design. Seedlings were planted in gaps (an open area > 25 m^2 surrounded by trees (*sensu* Veblen 1985)). At the end of October 2007, we planted 15 one-year old containerized seedlings of *N. dombeyi* in each of the 12 gaps and the same number of *N. alpina* seedlings in each of the 11 gaps. These seedlings were planted inside each gap at a 2 by 3 m distance in a rectangular design (figure 2). Seedlings ranged in total height between 35 and 45 cm and in root-collar diameter between 3 and 4 mm. Seedlings were

Table 1. General characteristic of gaps planted with *N. dombeyi* and *N. alpina* in the San Pablo de Tregua experimental forest. Numbers in each cell (except for number of gaps) represent the mean ± the standard deviation plus the range, in parenthesis.

Características generales de los claros plantados con *N. dombeyi* and *N. alpina* en San Pablo de Tregua. Los números en cada celda (excepto para number of gaps) representan la media ± desviación estándar más el rango, en paréntesis.

Variable	*Nothofagus dombeyi*	*Nothofagus alpina*
Number of gaps	12	11
Gap size (m^2)	344.5 ± 228.6 (45.8-734.2)	274.3 ± 182.8 (42.9-484.9)
Small	124.6 ± 63.1 (45.8-184.6)	75.9 ± 22.4 (42.9-98.1)
Medium	327.1 ± 85.2 (223.9-440.3)	372.3 ± 56.6 (315.3-423.9)
Large	666.8 ± 116.6 (532.2-734.2)	474.5 ± 18.0 (453.7-484.9)
Canopy openness (%)	22.8 ± 6.9 (11.6-31.6)	19.5 ± 5.7 (12.4-30.8)
LAI (m^2 m^2)	1.8 ± 0.43 (1.3-2.6)	1.9 ± 0.31 (1.3-2.4)
Direct light transmission (mol m^2 d^{-1})	2.47 ± 1.47 (0.47-5.57)	1.71 ± 1.44 (0.13-5.46)
Diffuse light transmission (mol m^2 d^{-1})	4.53 ± 1.37 (2.32-6.20)	3.85 ± 1.12 (2.44-5.98)
Total light transmission (mol m^2 d^{-1})	6.97 ± 2.48 (3.23-11.28)	5.56 ± 2.27 (3.19-11.44)

produced with seeds collected from trees in the San Pablo de Tregua experimental forest. Seedlings' production followed the protocol described in Bustos *et al*. (2008).

Before planting, weeds (mostly *C. culeou*) in gaps were manually removed within 1-m wide strips in which seedlings were established. No seedlings were planted below tree crowns at the gap edges, and each seedling was measured for root-collar diameter (2 cm above the ground) and height following plantation. Two growing seasons after plantation, all live planted seedlings were recorded to calculate survival rates, and their root-collar diameter and total plant height was measured. The stem volume was later calculated from root-collar diameter and plant height using a cone formula [2]. The ratio between plant height and root-collar diameter was used to calculate the slenderness index, where lower values tend to reflect seedlings with a better biomass distribution and health (Bustos *et al.* 2008).

$$\text{Stem volume (cm}^3) = \pi * RCD^2 * TH/12 \quad [2]$$

where: RCD = root collar diameter (cm); TH = total height (cm) and π = constant.

Gap light availability. Gap light availability was estimated by hemispherical photographs, using a Coolpix 4500 digital camera (Nikon CO., Japan) with a FCE-8 fisheye lens that has a 182° field of view (Nikon CO., Japan). Three photographs per gap were taken at the apex of seedlings located in the center, north and south sides of the planted area (figure 2). Photographs were taken under homogeneous diffuse sky light conditions in March 5, 2009. The resulting photographs were analyzed for light transmission indices (daily total, direct and diffuse transmitted radiation through the canopy) and the percentage of canopy openness with the Gap Light Analyzer 2.0 software (GLA: Frazer *et al*. 1999). GLA local light environment input parameters were solar constant: 1,370 W m^{-2}, cloudiness index: 0.5, spectral fraction: 0.45, bean fraction: 0.85, clear sky transmission coefficient: 0.65 and standard overcast sky-regions brightness. Light transmission was, on average, higher in gaps planted with *N. dombeyi*. Canopy openness and leaf area index (LAI) were similar for both species (table 1).

Statistical analyses. Mean values per plot for canopy openness and daily total, direct and diffuse transmitted radiation through the canopy were used for analyses. Sample units corresponded to the mean of 15 measurements on 15 plants per gap, or less in case of some mortality. Second-order polynomial regression analyses were conducted to assess the relationship between gap size and canopy openness, and between gap size and daily total, direct and diffuse transmitted radiation through the canopy. Linear regression analyses were conducted to assess the relationship between light availability and size of *N. dombeyi* and *N. alpina* seedlings. Size and survival of seedlings of each species were evaluated in each gap. To evaluate the effect of gap size on seedling survival, survival percentage per gap was previously transformed with an arcsine square-root equation to meet normality. However, even so the data was not normally distributed and we used a non-parametric Kruzkal-Wallis (*H*-test) ANOVA and Dunn´s test for gap size separation when the *H*-test was significant ($P < 0.05$). To evaluate size, we used ANOVA and the Tukey test for *post hoc* analyses. Differences between treatments were considered significant at $P < 0.05$. For these statistical analyses we used the SigmaPlot 11.0 package.

RESULTS

Relationship between gap size and light availability. Canopy openness (R^2 = 57.2 %) and total radiation (R^2 = 49.4 %) increased with gap size (figures 3A and 3B; table 2). Howe-

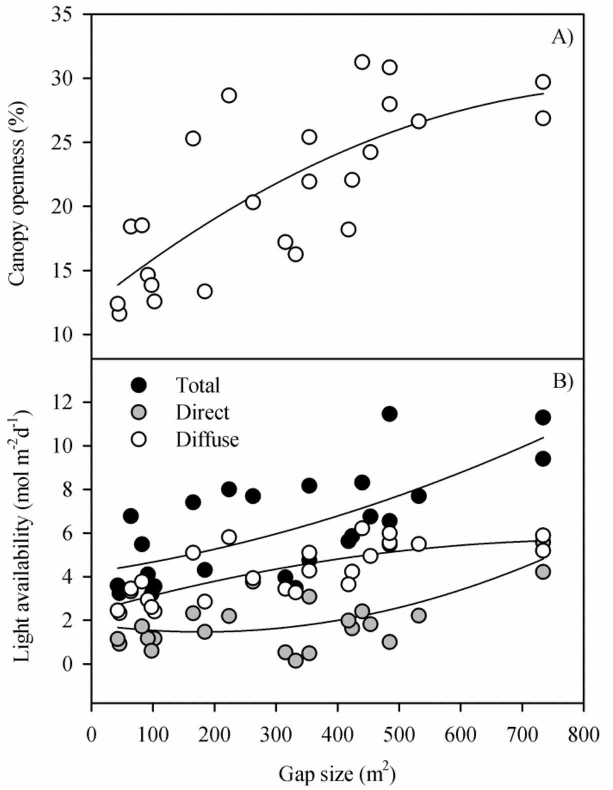

Figure 3. Relationships between gap size and light availability in a high-graded stand in the San Pablo de Tregua experimental forest. A) Second-order polynomial regression between canopy openness and gap size. B) Second-order polynomial regressions between total, direct and diffuse daily transmitted radiation and gap size.

Relaciones entre disponibilidad de luz y tamaño de claro en un bosque andino degradado. A) Regresión polinomial de segundo orden entre abertura de dosel y tamaño de claro. B) Regresión polinomial de segundo orden entre transmisión diaria de radiación directa y difusa y tamaño de claro.

ver, the best relationship was obtained between gap size and diffuse radiation (R^2 = 56.7 %), while the poorest was with direct radiation (R^2 = 38.3 %; figure 3B, table 2).

Effects of light availability upon the performance of seedlings. After two growing seasons, plant height of *N. dombeyi* significantly increased with total, direct and diffuse radiation (figure 4A). The increases in plant height were better explained by total (R^2 = 0.595; *P* = 0.003) and direct (R^2 = 0.508; *P* = 0.009) radiation than with diffuse radiation (R^2 = 0.405; *P* = 0.026). Plant height of *N. alpina* was not affected by total (R^2 = 0.0593; *P* = 0.471), direct (R^2 = 0.0231; *P* = 0.656) or diffuse (R^2 = 0.0485; *P* = 0.515) radiation (figure 4B). Root-collar diameter of *N. dombeyi* significantly increased with total (R^2 = 0.630; *P* = 0.002), direct (R^2 = 0.526; *P* = 0.008) and diffuse (R^2 = 0.432; *P* = 0.020) radiation (figure 4C). Conversely, root-collar diameter of *N. alpina* was not affected by total (R^2 = 0.217; *P* = 0.148), direct (R^2 = 0.0354; *P* = 0.580) or diffuse (R^2 = 0.271; *P* = 0.101) radiation (figure 4D).

Stem volume of *N. dombeyi* significantly increased with all types of available radiation. It was better explained by total (R^2 = 0.574; *P* = 0.004) and direct radiation (R^2 = 0.545; *P* = 0.006) than by diffuse radiation (R^2 = 0.342; *P* = 0.046; figure 5A). Stem volume of *N. alpina* was not affected by total (R^2 = 0.158; *P* = 0.226), direct (R^2 = 0.0274; *P* = 0.627) and diffuse radiation (R^2 = 0.192; *P* = 0.177; figure 5B). Slenderness of *N. dombeyi* seedlings was not significantly affected by radiation (figure 5C), but slenderness of *N. alpina* seedlings significantly decreased with diffuse radiation (R^2 = 0.393; *P* = 0.039; figure 5D).

Relationships between gap size and performance of seedlings. There were no significant differences in survival of *N. dombeyi* among gaps, but in *N. alpina* the medium-sized gaps had a significantly higher rate of survival than both the smaller and larger gaps (table 3). Plant height and root-collar diameter of *N. dombeyi* seedlings significantly increased with gap size (figure 6). Seedlings reached on average 85 cm in plant height in small gaps, and 150 cm in large gaps; in root-collar diameter seedlings had 7 mm in small gaps and 13 mm in large gaps. These differences in plant height and root-collar diameter also led to a significantly greater stem volume of seedlings in large gaps (290 cm^3 vs. 50 cm^3 in small gaps). The only variable not affected by gap size in *N. dombeyi* was slenderness (figure 6). On the contrary, plant height, root-collar diameter and volume of seedlings of *N. alpina* were not significantly affected by gap size, although root-collar diameter and stem volume showed an increasing growth trend with larger gaps (figure 6). However, *N. alpina* seedlings had a lower slenderness in large gaps.

Table 2. Summary of second-order polynomial regressions fitted for predicted canopy openness and for light partitioning as a function of gap size (m^2) in a high-graded stand in the San Pablo de Tregua experimental forest.

Resumen de regresiones polinomiales de segundo orden ajustadas para estimar apertura de copas y para partición de luz en función del tamaño de claro (m^2), en un bosque de San Pablo de Tregua.

Dependent variable	Equation	R^2	*P*-value
Canopy openness (%)	12.269 + 0.038(gap size) - 2.117(gap size^2)	0.572	< 0.0001
Total light (mol m^{-2} s^{-1})	4.200 + 4.112(gap size) + 5.845(gap size^2)	0.494	< 0.0001
Direct light (mol m^{-2} s^{-1})	1.814 – 3.891(gap size) + 1.085(gap size^2)	0.383	< 0.0001
Diffuse light (mol m^{-2} s^{-1})	2.383 + 7.976(gap size) - 4.815(gap size^2)	0.567	< 0.0001

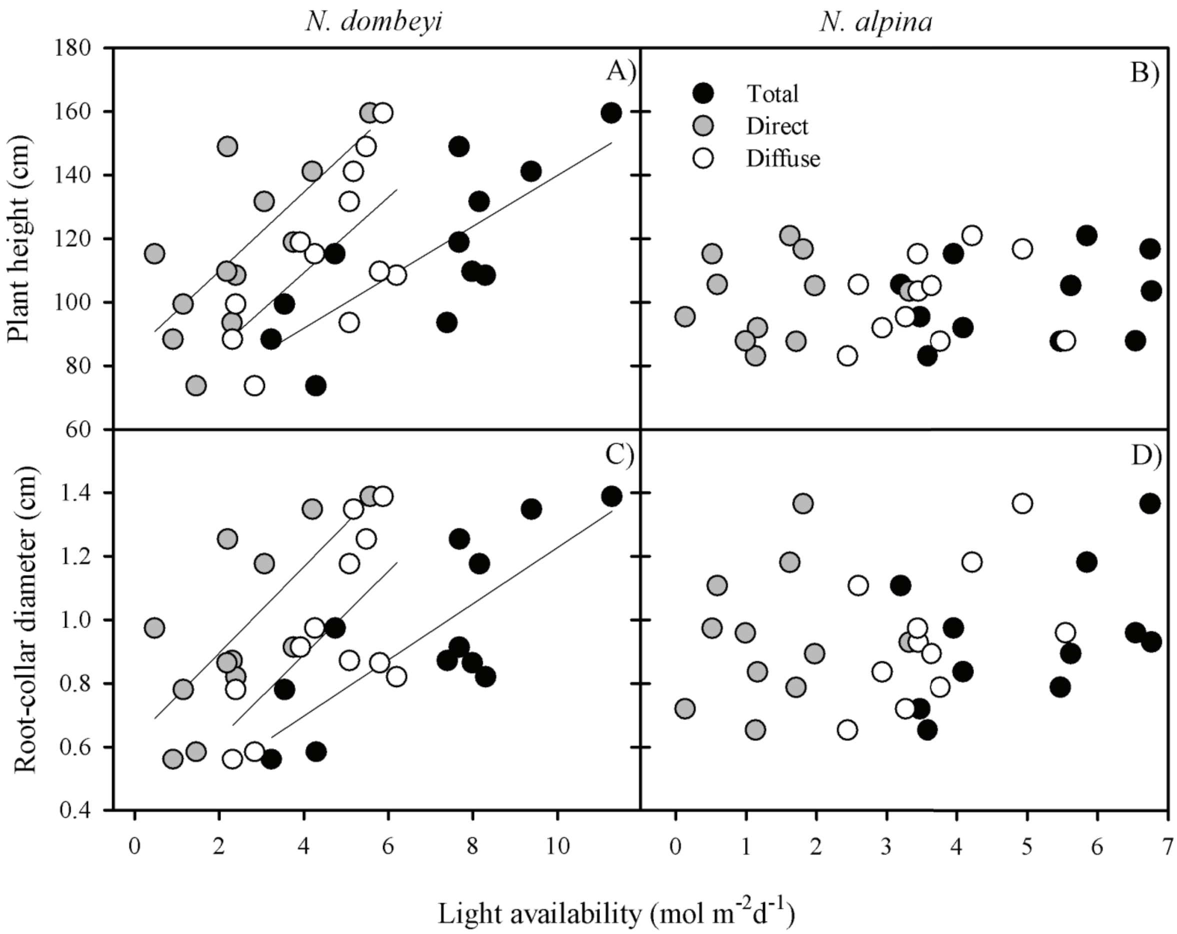

Figure 4. Relationships between light availability and plant height (PH) and root-collar diameter (RCD) of *N. dombeyi* and *N. alpina* seedlings planted in different gap sizes in an Andean high-graded mature forest (12 gaps for *N. dombeyi* and 11 gaps for *N. alpina*). Regressions among total, direct and diffuse daily transmitted radiation with PH and RCD were significant for *N. dombeyi* (A and C) but not for *N. alpina* (B and D). Lines for the relationships are only shown when coefficients of determination were significant.

Relación entre disponibilidad de luz y crecimiento en altura y diámetro de cuello de plántulas de *N. dombeyi* y *N. alpina* plantadas en claros de distinto tamaño en un bosque madura andino degradado. Las regresiones entre radiación diaria transmitida total, directa y difusa con altura total y diámetro de cuello fueron significativas para *N. dombeyi* (A y C) pero no para *N. alpina* (B y D). Las líneas para las relaciones solo se muestran cuando los coeficientes de determinación fueron significativos.

Table 3. Survival (mean % ± standard deviation) of seedlings, by species, in the study gaps as a function of gap size categories in a high-graded stand in the San Pablo de Tregua experimental forest.

Sobrevivencia (media % ± desviación estándar) de plántula, por especie, en los claros estudiados en función de las categorías de tamaño de claros en un bosque degradado en San Pablo de Tregua.

Gap size (m²)	*N. dombeyi*	n	*N. alpina*	n
Small	98.3 ± 3.3	4	96.0 b ± 3.6	4
Medium	94.7 ± 8.7	5	100.0 a ± 0	4
Large	94.5 ± 9.6	3	86.7 b ± 6.7	3
H-value	0.392ns		7.668*	

ns: nonsignificant, * $P < 0.05$

DISCUSSION

Differential responses of N. dombeyi *and* N. alpina *to light and gap size*. In the present study, canopy openness was only 10 - 15 % in the small gaps and 25 - 30 % in the large gaps, and the quantity of light transmitted to the apex of seedlings (affected also by the understory removal) ranged from 3.20 to 11.45 mol $m^{-2} d^{-1}$. These conditions were not ample enough to reflect any major effects of gap size on mortality of two-year old planted *N. dombeyi* and *N. alpina* seedlings (survival range from 84 to 100 %); although in medium-sized gaps the survival of *N. alpina* seedlings was significantly greater than in small and large gaps. Gap size did, however, significantly affect the size of *N. dombeyi* and the quality (slenderness) of *N. alpina* when light availability decreased within the range of gap sizes evaluated. These results support our prediction that *N. dombeyi* shows a higher growth responsiveness to light than

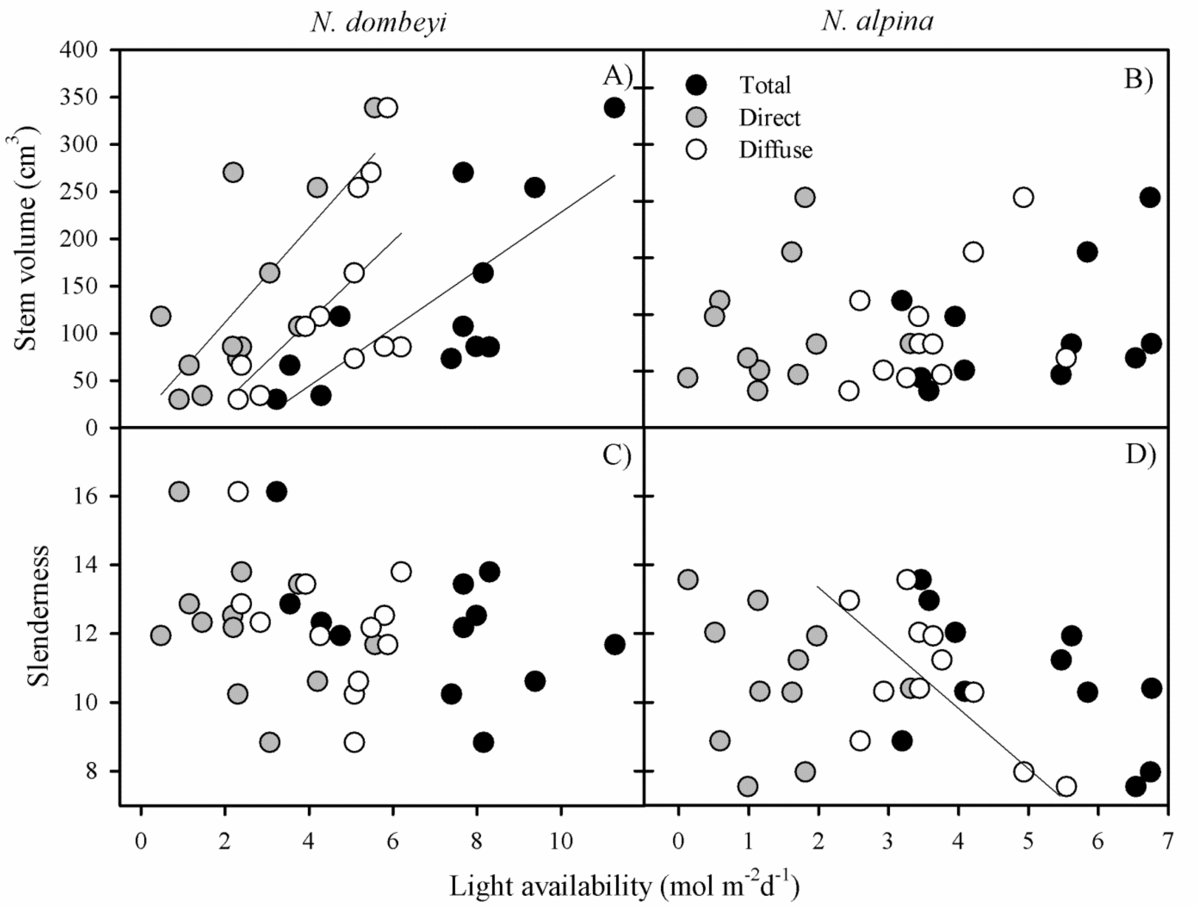

Figure 5. Relationships between light availability and stem volume (A and B) and slenderness (C and D) of *N. dombeyi* and *N. alpina* seedlings planted in different gap sizes in a high-graded stand in the San Pablo de Tregua experimental forest. Regressions among total, direct and diffuse daily transmitted radiation with stem volume for *N. dombeyi* (A), and between direct radiation and slenderness of *N. alpina* (D) were significant. Lines for the relationships are only shown only when coefficients of determination were significant.

Relaciones entre disponibilidad de luz y crecimiento en volumen (A y B) y esbeltez (C y D) para plántulas de *N. dombeyi* y *N. alpina* plantadas en distintos claros de bosque. Sólo la regresión entre radiación diaria transmitida con el volumen de *N. dombeyi* (A), y entre radiación directa y esbeltez para *N. alpina* (D) fueron significativas. Las líneas para las relaciones sólo se muestran para cuando los coeficientes de determinación fueron significativos.

N. alpina, and reflect the more shade intolerant character of *N. dombeyi* (Donoso *et al*. 2006ab).

The results indicate that after the two first growing seasons the performance of *N. dombeyi* and *N. alpina* was in general poor in the smallest gaps as reflected in size and/or quality of the seedlings. Seedlings of *N. dombeyi* performed better in larger gaps, and those of *N. alpina* in both medium-sized gaps (complete survival) and large gaps (bigger plants with significantly lower slenderness). These results support earlier suggestions that natural regeneration of *N. dombeyi* would respond better to larger gaps and that of *N. alpina* to relatively smaller gaps (Weinberger and Ramírez 2001). We have to consider, however, that the mean size of the large-gap category used for *N. alpina* had a rather small difference with that of the medium-gap category (only 102 m^2); hence, such small difference presents a limitation to interpret the effects of gap size upon the performance of *N. alpina*.

Comparison of growth with other plantations. Growth rates derived from the present study are lower than those reported in open field plantations established on abandoned pasturelands at lower elevations at the same latitude (Wienstroer *et al*. 2003, Donoso *et al*. 2011). However, they are higher than those reported for open-field plantations in the same experimental forest (Donoso *et al*. 2007). Yet, most important is the fact that the plantations in gaps evaluated in the present study had nearly complete survival, in contrast with the high mortality rates reported for plantations of these species in open fields at the same elevation described in this study after one growing season (53-79 % survival; Donoso *et al*. 2007) and two growing seasons (37 % survival; Soto *et al*. 2009). This finding is consistent with previous studies that show that shelter from neighboring vegetation (Álvarez and Lara 2008, Soto *et al*. 2009) or overstory vegetation (Grosse 1988) promotes a better performance of seedlings of these species, in spite

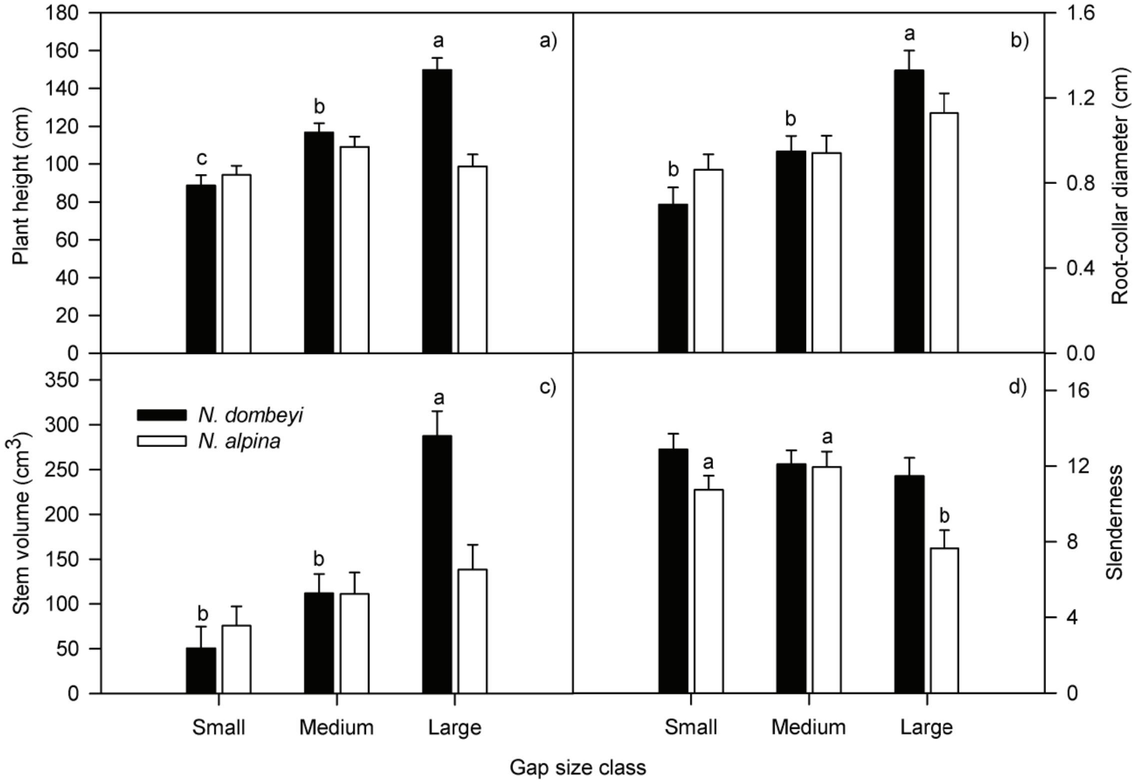

Figure 6. Size of planted *N. dombeyi* and *N. alpina* seedlings according to gap size categories in a high-graded stand in the San Pablo de Tregua experimental forest. Measured variables were A) Plant Height, B) Root-collar diameter, C) stem volume, and D) slenderness. Different letters on top of the bars (mean ± SD) indicate significant differences.

Respuestas en crecimiento de plántulas de *N. dombeyi* y *N. alpina* de acuerdo a categoría de tamaño de claros in en rodal estudiado. Las variables de crecimiento medidas fueron A) altura total (PH), B) diámetro de cuello (RCD), C) volumen, y D) esbeltez. Letras diferentes arriba de las barras (media ± DS) indican diferencias significativas.

of their high resistance to low temperatures (Reyes-Díaz *et al*. 2005). The interaction between coldness and high light in open conditions in the Andes may be the cause of severe photo-damage of seedlings (Huner *et al*. 1998), which eventually determines the productivity and growth of trees at high altitude sites (Slot *et al*. 2005).

An opportunity to restore high-graded forests. We aimed in this study to find a proper combination of canopy protection and light availability for optimum performance of planted seedlings of *Nothofagus* species that naturally have a pioneer behavior and low shade-tolerance. Within the range of gap sizes tested in this study, our results suggest that plantations of *N. dombeyi* and *N. alpina* perform better than plantations established on abandoned pasturelands (*i.e*. open-field conditions) and that smaller gaps seem more detrimental for *N. dombeyi*. Although our results are geographically limited, they suggest that there is a chance to restore current high-graded Andean forests in south-central Chile with *Nothofagus spp.* plantations in gaps within these forests. We believe that at least these preliminary results could also be expected in the transitional zone of the Mediterranean to temperate climates that occurs between 38° and 41° where similar forests of the Coihue-Raulí-Tepa forest type occur (Donoso *et al*. 1986). Within this region there are naturally variations in climate (differences in latitude, elevation and aspect) and soils that determine some changes in species composition, but *N. dombeyi* and *N. alpina* are always among the dominant species (Donoso *et al.* 1986). Studies similar to the one presented in this article should be conducted throughout the region, in order to evaluate variations in the performance of *Nothofagus spp.* plantations in high-graded forests according to the macroenvironment as affected additionally by the microenvironment, *i.e.* especially gap sizes.

Implications for practice. Successful plantations of species mid-tolerant or intolerant to shade under the canopy of degraded or managed forests (*e.g.* with shelterwood silvicultural methods) seem possible, and sometimes necessary, especially when thickets of bamboos impede for decades the growth of tree species (Lusk 2001). We show in the present study that planting *N. dombeyi* and *N. alpina* in gaps was not only possible but so far also successful as measured by survival and growth rates. Successful results of plantations with these two *Nothofagus* species in the understory was also proved in the south west peninsula of England; another region of mild temperate climate, where these species were planted after the third thinning applied in a conifer forests (page 178 in Matthews 1989). These experiences show that managers must pay special care in controlling the amount of shade to which planted trees are exposed, especially considering that shade increases with canopy expansion through time (Niinemets 2007). The effect of the understory is also of great relevance. *Nothofagus dombeyi* is unable to regenerate naturally in gaps smaller than 1,500 m^2 when there is a dense understory (Veblen 1985, Donoso 1993); nevertheless, where forests lack a thick understory (especially of *Chusquea sp.*), it is able to regenerate even under the closed canopy of old-growth forests (Pollmann and Veblen 2004). In the case of *N. alpina,* which can naturally regenerate in smaller gaps (Donoso 1993), the lack of competition in the understory also favors its growth (Donoso *et al*. 2006a). Overall, managers should most likely make decisions to rehabilitate or restore high-graded forest ecosystems based on the expected productivity and value of the future forest, which is a function of the species planted and their light requirements. In the case of this study it seems that restoration of the extensive areas of high-graded forests of the south-central Andes of Chile may be an attractive option considering the good growth and high value of *N. dombeyi* and *N. alpina,* in addition to their good reputation among landowners.

ACKNOWLEDGEMENTS

We thank the financial support from the FONDEF program (project D07I1034) of the Comisión Nacional de Investigación y Tecnología (CONICYT). RE Coopman thanks the Programa de Inserción Académica (PDA-24) of CONICYT.

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Recibido: 27.03.12
Aceptado: 02.08.12