Gayana Bot. 76(1): 12-23, 2019. ISSN 0016-5301
Original Article

Effects of solar radiation on regeneration patterns in a *Nothofagus dombeyi* (Mirb.) Oerst. old-growth forest in Chile's central-southern Andes

Efectos de la radiación solar sobre los patrones de la regeneración, en un bosque sobremaduro de *Nothofagus dombeyi* (Mirb.) Oerst. localizado en el centro-sur de los Andes, Chile

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ABSTRACT

Nothofagus species behave like early successional species that recolonize open sites after of regular and large-scale disturbances. This study analyzed the effects of light regimes on patterns of advanced regeneration dynamics, growth in diameter and height of *Nothofagus dombeyi* (Mirb.) Oerst. (Density of 240 trees ha^{-1}, basal area of 56.7 m^2 ha^{-1}). Systematic sampling every 50 m in three stands (7.5 ha) was used. At each point and with the same center, two concentric circular plots were established, 9.0 m and 1.8 m radius. For estimate solar radiation transmissivity in plots, a solariscope hemispheric photographic camera was used. Diameters at breast height and basal areas (BA), heights (H) were measured and then counted and measured *N. dombeyi* seedlings and saplings. 13 saplings of advanced regeneration were harvested from all gaps to obtain age (E), total height (TH), absolute radial growth (ARG), and absolute height growth (AHG). As results, solar radiation varied between 3 and 40%. ARG varied between 1.20 and 2.22 mm yr^{-1} and AHG between 0.15 and 0.43 m yr^{-1}. We found correlation for ARG and AHG with direct and global solar radiation transmissivity, but not with diffuse solar radiation transmissivity. The plant age and transmittance of direct and global solar radiation explains the increases in diameter and height. However, in our study stated that in the Andean region of south-central Chile, *N. dombeyi* stands is affected by small-scale disturbances. Therefore, transmissivity radiation solar inside the forest, explaining natural regeneration patterns and growth of *N. dombeyi*.

Keywords: Advanced regeneration, disturbance, solar radiation transmissivity.

RESUMEN

Las especies de *Nothofagus* se comportan como especies sucesionales tempranas que recolonizan sitios abiertos después de disturbios regulares y de gran escala. Este estudio analizó los efectos de los regímenes de luz, en los patrones de dinámica de regeneración avanzada, crecimiento en diámetro y altura de *Nothofagus dombeyi* (Mirb.) Oerst. (Densidad de 240 árboles ha^{-1}, área basal de 56,7 m^2 ha^{-1}). Se utilizó un muestreo sistemático cada 50 m en tres rodales (7,5 ha). En cada punto y con el mismo centro se establecieron dos parcelas circulares, 9,0 m y 1,8 m de radio. Se midió la transmisividad de la radiación solar con una cámara fotográfica hemisférica solariscope. Se midieron los diámetros a la altura del pecho, áreas basales (BA), alturas (H) y se contaron las plántulas y plantas de *N. dombeyi.* En los claros se cosecharon 13 plantas de la regeneración avanzada, para obtener la edad (E), la altura total (TH), el crecimiento radial absoluto (ARG) y el crecimiento absoluto en altura (AHG). La radiación solar varió entre 3 y 40%. ARG varió entre 1,20 y 2,22 mm año^{-1} y AHG entre 0,15 y 0,43 m año^{-1}. Se encontró correlación para ARG y AHG con transmisividad de radiación solar directa y global, pero no con transmisividad de radiación solar difusa. La edad de la planta y la transmitancia de la radiación solar directa y global explicaron los aumentos en diámetro y altura. Sin embargo, en nuestro estudio se indicó que en la región andina del centro-sur de Chile, los rodales de *N. dombeyi* se ven afectados por disturbios a pequeña escala. Por tanto, la radiación de transmisividad solar dentro del bosque explica los patrones de regeneración natural y el crecimiento de *N. dombeyi*.

Palabras clave: Disturbios, regeneración avanzada, transmisividad de la radiación solar.

INTRODUCTION

Silviculturalist have recognised the importance of natural disturbances in the development and maintenance of forest structures, functions and community dynamics (Attiwill 1994). Small-scale disturbances eliminate original vegetation, leaving open spaces in stands which represent canopy gaps (Parhizkar *et al*. 2011) and facilitate resources such as light, nutrients and water (Valladares & Niinemets, 2008). The temporary increase in light availability below the first canopy layer (Canham *et al.* 1990) varies at stand level more than for any other plant resource (Martens *et al*. 2000). The most important factors that explain this spatial variation in understory light levels are canopy shape, size, and distribution of neighbouring trees and local sky brightness distribution (Canham *et al*. 1999). Light is highly variable in time and space (Valladares & Guzmán 2006), as conditions change drastically over time and canopy gaps, essential for plant growth and survival, form (Canham *et al*. 1990; Hu & Zhu 2008; Kneeshaw & Bergeron 1998; Mountford *et al*. 2006). Therefore, light is a key factor affecting dynamics and succession of plant communities and the spectrum of species in forest ecosystems.

In central-southern Chile, *Nothofagus* species behave like early successional species that recolonize open sites after prior vegetation removal due to regular and large-scale disturbances such as landslides, material deposits from massive flooding or trees knocked down by strong winds (Veblen *et al*. 1996a). Without subsequent disturbances, later successional species tend to settle under the canopy, replacing shade-intolerant species such as *N. dombeyi* (Mirb.) Oerst., which is key to regeneration after large-scale disturbances (Veblen *et al*. 1996b). Every old-growth forest has certain characteristics, species, processes and interactions that rarely –or not at all– appearing younger forests. Old-growth forests belong to the natural diversity of life on Earth. It depends on our effort to conserve biological diversity from the scale of genes to ecosystems; it is important that we conserve old-growth in its natural spatial pattern, i.e., large, continuous expanses (Lapin 2005).

Nothofagus species have limited opportunities to recruit even in large canopy gaps (> 1,000 m^2) due to the release of advance regeneration of shade-tolerant trees and the vigorous proliferation of *Chusquea* spp. bamboos (Veblen *et al*. 1996a). Tree-fall gaps are larger and logs more abundant in old-growth *Nothofagus* spp. dominated stands (Schlegel & Donoso 2008), and these conditions can help *Nothofagus* spp. tree recruitment. *N. dombeyi* and *N. alpina* (Poepp. & Endl.) Oerst. can reach over 2 m in diameter at breast height (dbh) and above 50 m in height; both species can grow 10 to 30 m above the main canopy (Donoso & Lusk 2007; González *et al*. 2015). However, old-growth *Nothofagus* stands growing in the Andean region of south-central Chile are more affected by small-scale disturbances from *Chusquea culeou* (Desvaux.) bamboo thickets which suppress the regeneration of tree species and develop after canopy gaps formed. Depending on the abundance of *C. culeou* thickets, a biphasic pattern of positive feedback on the dynamics of regeneration of these forests has been suggested. In it, the first regeneration phase of *C. culeou* can give rise to a second phase of *N. dombeyi* regeneration (Lusk 2001). Winds and snow storms also remove overstory-trees individually or in smaller groups, resulting in small to medium-size canopy gaps that create a favourable environment for more shade-intolerant species. These species maximise their initial growth under higher light conditions, when is absent an aggressive colonizers *C. culeou* tickets since inhibit regeneration of tree species (Lusk 2001; Lusk & Del Pozo 2002). But can grow under different light regimes after episodes of bamboo dieback that provide the main opportunities for reestablishment of tall forest (Lusk 2001). Therefore, management of the stand light regime through silvicultural techniques is required to ensure better regeneration of this species (Sola *et al*. 2016). In our study, *N. dombeyi* in an old-growth forest stand could reach more than 2 m in dbh and above 50 m in height. Tree-falls of this size can create gaps larger than 700 m^2. Canopy gaps formation has been largely recognised as an important process with indifferent forest ecosystems. However, studies on temperate forests of the southern hemisphere are still lacking compared to tropical forests and northern hemisphere temperate forests (González *et al*. 2015).

We hypothesise that the regeneration is the response to small-scale disturbance, therefore the high spatial variability of all solar radiation transmissivity components inside the forest varies due to the different degrees of canopy openings, which alter light regimes in pure old-growth *N. dombeyi* stands, explaining natural regeneration patterns and growth. Thus, the study objectives are to analyse light regimes in patterns of regeneration dynamics and the effect these light regimes have on diameter and height growth of plants that compose stands of advanced regeneration.

METHODS

Study area

The study took place in three *N. dombeyi* old-growth forest stands near Yungay city, Biobío Region in central Chile (Fig. 1). All stands belong to *N. dombeyi* and *Saxegothea conspicua* Lindl. bioclimatic area called Andean Mediterranean temperate evergreen forests (Luebert & Pliskoff 2006). The stands are characterised by evergreen forest arboreal layers dominated by *N. dombeyi*, *S. conspicua*, *Podocarpus nubigena* Lindl., *Laureliopsis philippiana* (Looser) Schodde, and occasionally *Weinmannia trichosperma* Cav. species in the intermediate layers. However, in a state of old-growth, light conditions below the first canopy layer do often inhibit development of intermediate arboreal strata. The most characteristic geomorphological position of such a forest is in western mid-slopes of the Andes Mountains (Luebert & Pliskoff 2006). The climate is Mediterranean, with rainfall concentrated during winter and a dry summer lasting three to four months. Study area altitudes (600-1,500 m a.s.l.) correspond to an area with temperate Mediterranean climate as classified by Emberger (Del Pozo & Del Canto 1999). Average annual rainfall exceeds 1,400 mm, and ice and snowfall can cause disturbances in the native forest, while growing season lasts around three months due to low winter temperatures (Del Pozo & Del Canto 1999).

Soils originate from volcanic ash, most likely post glacial, resting on a non-related substrate comprising fluvial or glacio-fluvial materials that remain detected due to the depth at which they occur (Kühne *et al.* 2005). Soil is deep and medium-textured, generally silty loam within the first meter and silty clay loam at depths of 165 cm or more (Kühne *et al.* 2005).

Seedling and plant density measurements

Field work was carried out in 2015 during Chile's growing season from January to February. To measure density of saplings (lignified) and seedlings (non-lignified), systematic sampling was carried out in three old-growth *N. dombeyi* stands with a total area of 7.5 ha, a 240 trees ha^{-1} density, a basal area of 56.7 m^{2} ha^{-1} and 13 gaps of forest with an area between 45 and 300 m^{2}. The starting position for the systematic grid was determined randomly. With this information and a map of the study site, lines were drawn with a distance of 50 m in a parallel and perpendicular direction, giving rise to a network of 64 points for the three stands; at each point, two concentric circular plots with an only center of radius 9.0 m (large plot) and 1.8 m (regeneration plot) were established (Fig. 2). Within each large plot, adult tree diameter at breast height (dbh) was measured with a caliper in order to derive diameter distributions, basal areas (BA), and analyse their relationship with the occurring regeneration of *N. dombeyi*. In the regeneration plots, the saplings were height measured and counted along with all germinated and non-lignified seedlings of *N. dombeyi*.

Tree seedlings and saplings of *N. dombeyi* were counted and classified as: germinant and non-lignified < 0.05 m, and lignified > 0.051, $0.051 < 0.5$, $0.5 < 1$, $1 < 1.5$, $1.5 < 2$, and ≥ 2 m of height. Furthermore in 13 open canopy plots, it was harvested one species of the tallest, between 3.0 m to 5.0 m height, one per each plots of forest, to determine ARG, and a stem analysis was used. In each species a first cut was made to ground level and every 1.0 m until apex. Each disk was divided in four quadrants, where register the distance from the medulla until to each ring, considering the first distance in the ring the closest to the medulla. The average of the four quadrants, was considered as the absolute radial growth ARG stem analysis measurements were performed using a standing digital meter with an accuracy of 0.01 mm, for each distance of the rings to medulla. Total plant height and increases thereof were also analyzed obtain absolute height growth (AHG.)

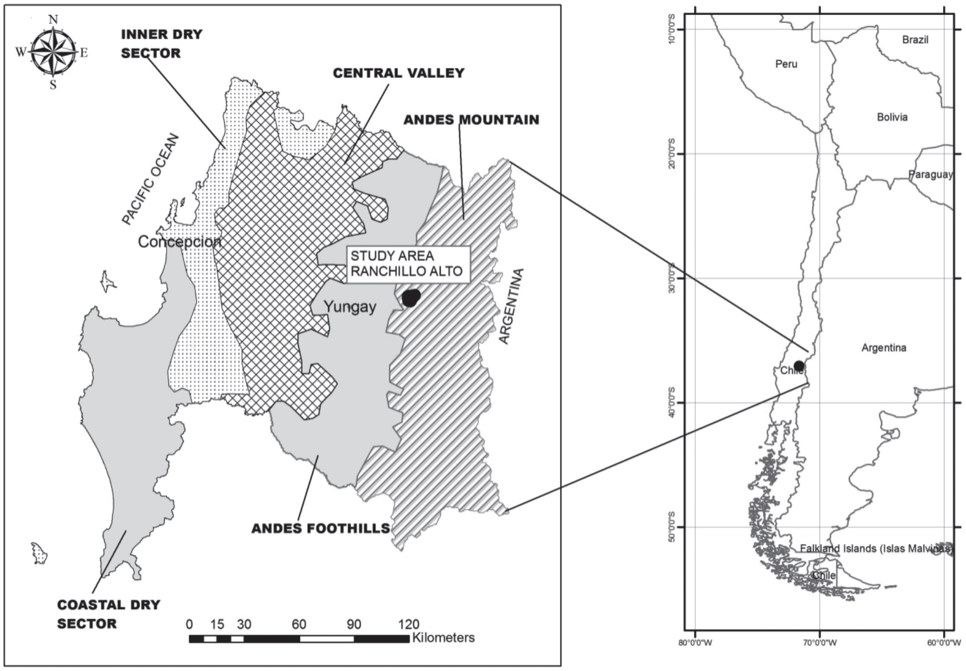

Figure 1. Orientation map of the study areain the Andes Mountains in the Biobío Region, Chile. / Mapa de orientación del área de estudio en la Cordillera de los Andes, Región del Biobío, Chile.

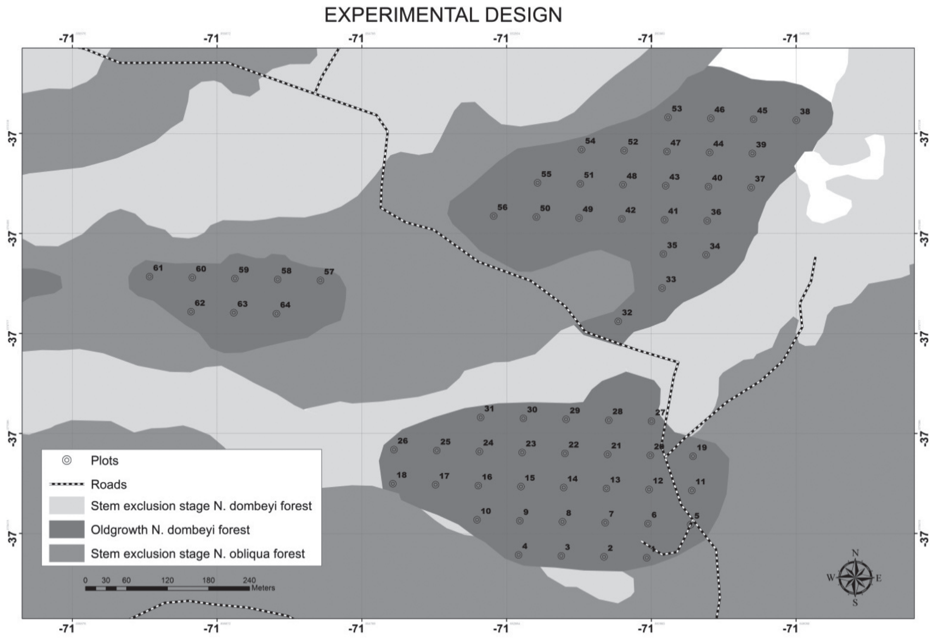

FIGURE 2. Map of the experimental design in the Andes Mountain in Chile's Biobío Region: numbers refer to plots; at each point, two concentric circular plots of radius of 9.0 m and 1.8 m (regeneration plot) were established, with a total of 64 points. / Mapa del diseño experimental en la Cordillera de los Andes en la Región del Biobío, Chile: los números se refieren a las parcelas. En cada punto se establecieron dos parcelas circulares concéntricas con un único centro de radio de 9,0 m y 1,8 m (parcela de regeneración), con un total de 64 puntos.

LIGHT MEASUREMENTS

Light conditions were measured in the center of each plot and solar radiation transmissivity was obtained for direct (Dir), diffuse (Dif) and global (GL) solar radiation by analysing hemispherical digital photos taken with a Solariscope camera (Behling SOL300, version 1.0). Photographs were taken during January 2015, two metres above ground when solar rays were vertical (between 11:00 and 15:00 h) (Vyncke 1969). Seven photographs were taken in each gap, resulting in 448 images as the best image per plot was visually selected, according to most accurate detection of canopy and sky.

STATISTICAL ANALYSIS

To analyse light regimes in patterns of regeneration it is necessary to explore using explanatory variables. By them, variables were correlated using Spearman's rank correlation coefficient to explore the relationship between varying densities of natural regeneration and solar radiation transmissivity, in AHG and ARG variable it was used Pearson rank correlation. To analyse the effect of light regimes have on diameter and height growth of plants, generalised linear regression models were used to evaluate natural regeneration density responses to Dir, Dif and GL variables. To detect significantes differences in variables, the Test Tukey, was used. Data and statistical analyses were performed using Statistica v.10 software, with significance values of $p < 0.05$.

RESULTS

SOLAR RADIATION TRANSMISSIVITY

Solar radiation transmissivity ranged from 3 to 39% with an average value of 13% (Fig. 3). Diffuse solar radiation transmissivity had an average value of 11%, ranging between 3 and 28%, while global radiation transmissivity reached an average of 12%, ranging from 4 to 31% (Fig. 3).The ranges of variation in solar radiation transmission, whether direct, diffuse or global, were closely related to the different opening levels of the canopy (Table 1). Mean values of 8.6, 9.6 and 9.4%, for Dir, Dif and GL solar radiation, respectively, represent a closed canopy, while mean values between 21.3 and 23.6% for Dir, Dif or GL solar radiation represent centre gaps (Table 1). However, no significant differences were detected for the border and centre gap, as Dir, Dif or GL solar radiation showed significant differences between gap centre and border centre or closed canopy (Table 1).

INFLUENCE OF SOLAR RADIATION ON REGENERATION DENSITY

Densities of natural regeneration for both seedlings and saplings varied widely within the forest between 0 and 14 plants m^{-2}. Highest densities emerged around the centre gap, varying between 0 and 3 seedlings m^{-2} and 5 and 13 saplings m^{-2}. In border gap densities, we recorded between 1 and 8 seedlings m^{-2} and 2 to 11 saplings m^{-2}. However, under closed canopy, 43% of the plots did not present sapling while 57% of the plots presented sapling, density varied between 0 and 8 plants m^{-2} (Fig. 4). As advanced regeneration for saplings (saplings density) showed no normal distributions. Seedling density did not correlate with any solar radiation component. However, sapling density related highly significantly to diffuse radiation ($p < 0.0001$) and global solar radiation ($p < 0.0031$) (Table 2).

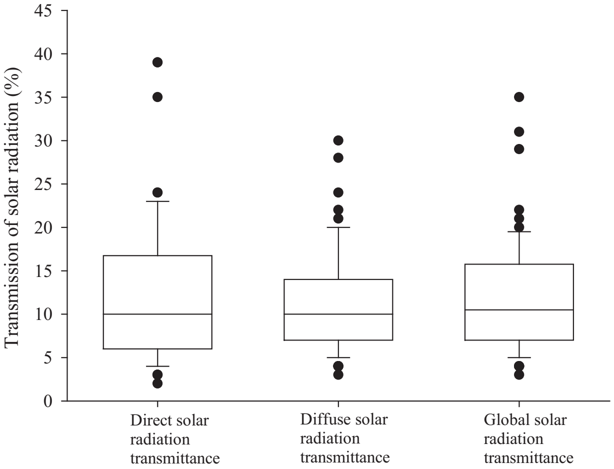

FIGURE 3. Solar transmittance at the 64 points of study: direct solar radiation, diffuse solar radiation, and global solar radiation in an old-growth forest of *N. dombeyi* in the Andean central-southern region of Chile. / Medición de la transmisividad solar en los 64 puntos de estudio: radiación solar directa, radiación solar difusa y radiación solar global en un bosque sobremaduro de *N. dombeyi* ubicado en la región andina centro-sur de Chile.

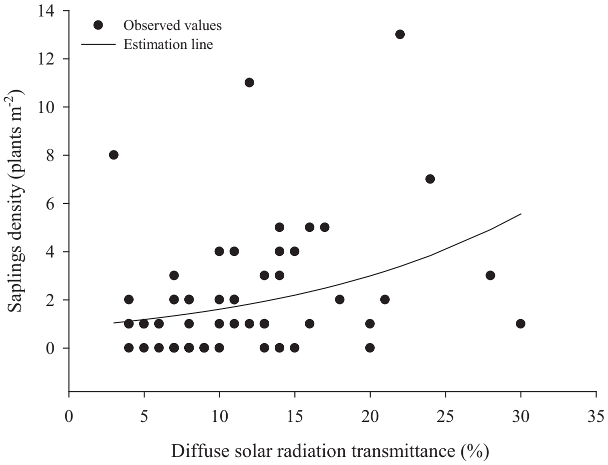

FIGURE 4. Poisson dispersion graphs howing the relationship between diffuse solar radiation transmittance and sapling density ($y=exp^{-0.1404+0.0619x}$; $R^2 = 0.26$; $p = 0.0001$) in an old-growth forest of *N. dombeyi* in Chile's central-southern Andean region. / Gráficos de dispersión de Poisson para la relación entre la transmisividad de la radiación solar difusa y la densidad de árboles jóvenes ($y=exp^{-0.1404+0.0619x}$; $R^2 = 0.26$, $p = 0.0001$) en un bosque sobremaduro de *N. dombeyi*, ubicado en la región andina del sur de Chile.

TABLE 1. Mean values of solar radiation transmittance in an old-growth forest of *N. dombeyi* in the central-southern Andean region of Chile. / Valores medios de la transmisividad de la radiación solar de un bosque sobremaduro de *N. dombeyi*, ubicado en la región andina centro-sur de Chile.

	PHOTO LOCATION IN THE PLOT		
VARIABLES	CENTRE GAP	BORDER GAP	CLOSED CANOPY
Dir	$23.6^{a} \pm 2.86$	$10.8^{b} \pm 3.08$	$8.6^{b} \pm 1.05$
Dif	$21.3^{a} \pm 1.72$	$10.0^{b} \pm 1.86$	$9.6^{b} \pm 0.64$
GL	$22.6^{a} \pm 2.17$	$10.3^{b} \pm 2.34$	$9.4^{b} \pm 0.80$

Note: Dir is direct solar radiation transmittance; Dif is diffuse solar radiation transmittance and GL is global solar radiation transmittance. Rows with different letters indicate significant differences at $p < 0.05$ (Tukey Test). / Nota: Dir es la Transmisividad de la radiación solar directa; Dif es Transmisividad de la radiacion solar difusa y GL es la Transmisividad de la radiación solar global. Las filas con letras distintas indican diferencias significativas en $p < 0,05$ (Tukey Test).

TABLE 2. Spearman's rank correlation matrix for transmittance of solar radiation and natural regeneration density in an old-growth forest of *N. dombeyi* in the central-southern Andean region of Chile. / Matriz de correlación de Spearman's para la transmisividad de la radiación solar y la densidad de la regeneración natural de un bosque sobremaduro de *N. dombeyi* ubicado en la región andina centro-sur de Chile.

VARIABLES	SED	SAD	DIR	DIF	GL
SED		0.50*			
SAD	0.50*			0.36*	0.27*
Dir				0.69*	0.95*
Dif		0.36*	0.69*		0.87*
GL		0.27*	0.95*	0.87*	

Note: SED is seedling density; SAD is saplings density; Dir is direct solar radiation transmittance; Dif is diffuse solar radiation transmittance and GL is global solar radiation transmittance. Symbol (*) the correlation is statistically significant ($p \leq 0.05$) ($n = 64$). / Nota: SED es densidad de plántulas; SAD es la densidad de plantas en un rodal de un bosque sobremaduro; Dir es la Transmisividad de la radiacion solar directa; Dif es la Transmisividad de la radiacion solar difusa y GL es la Transmisividad de la radiacion solar global. Símbolo (*) la correlación es estadísticamente significativa ($p < 0,05$) ($n = 64$).

Density of advanced regeneration of *N. dombeyi* increased with rising diffuse radiation (Fig. 4). Notably, under 3% in diffuse solar radiation transmittance regeneration does not occur and the maximum sapling regeneration density did not exceed 20% in diffuse solar radiation transmittance (Fig. 4). Considering the natural regeneration of seedlings and saplings, there was no correlation with the stand basal area (Table 2). Though the 0.051 to 0.5 m height classes in seedlings and saplings did not show a correlation with any solar radiation component, the remaining height classes showed at least one positive significant correlation (Table 3). Particularly sapling density regeneration showed a positive and significant correlation with diffuse and global solar radiation transmissivity (Table 3).

INFLUENCE OF SOLAR RADIATION ON RADIAL INCREASE AND PLANT HEIGHT

Advanced natural plant regeneration was observed on only 13 plots, which coincided with the borders or centres of canopy gaps in the stand. The average age of the tallest saplings (3-5 m in height) on the plot was 23 years (±7.1 SD) and ARG of plants varied between 1.20 and 2.22 mm year^{-1}, with an average increment of 1.52 mm year^{-1}. However, no correlation was observed between increasing radials and stand variables, such as basal area, total tree height and regeneration density. However, age presented a significant correlation ($p < 0.01$) but negative with ARG ($r = 0.6$) (Table 4). As global solar radiation transmissivity increased, ARG also increased (Fig. 5 and Table 4). Lowest ARG was observed when solar radiation transmissivity was at 5%, and highest when global solar radiation transmissivity values exceeded 35% (Fig. 5). Absolute height growth values (AHG) increased from 0.15 and 0.43 m year^{-1}, with an average of 0.22 m year^{-1} (Figs. 6 and 7). No correlation was observed between ARG and stands variables such as basal area or advanced regeneration species density. However, ARG and AHG presented a negative and significant correlation ($p < 0.05$) with age ($r = -0.71$). In addition, it showed a significant and positive correlation ($p < 0.05$) with the transmissivity of direct and global solar radiation ($r = 0.70$ for both) and a significant correlation ($p < 0.05$) with the transmissivity of diffuse radiation ($r = 0.51$; $p < 0.05$) (Table 3). Two regression models were constructed for AHG. Both models for transmissivity of direct and global radiation are explained by the proportion of variance for both models ($R^2 = 0.60$; $p < 0.01$ and $R^2 = 0.70$; $p < 0.01$) (Figs. 6 and 7). Height increase was influenced by the transmissivity of direct and global solar radiation.

TABLE 3. Spearman's rank correlation matrix for natural regeneration density according to height classes in relation to solar radiation transmittances in an old-growth forest of *N. dombeyi* in the central-southern Andean region of Chile. / Matriz de correlación de Spearman's para la densidad de la regeneración natural según las clases de altura en relación con la transmisividad de radiación solar en un bosque sobremaduro de *N. dombeyi* ubicado en la región andina centro-sur de Chile.

Height classes (m)	Dir	Dif	GL
seedling	-0.19	0.04	-0.11
saplings	0.14	0.36*	0.27*
0.051–0.5	-0.04	0.20	0.08
0.51–1.0	0.28*	0.38*	0.37*
1.1–1.5	0.17	0.36*	0.29*
1.51–2	0.19	0.34*	0.29*
>2	0.14	0.36*	0.28*

Note: Dir is direct solar radiation transmittance; Dif is diffuse solar radiation transmittance and GL is global solar radiation transmittance. Symbol (*) the correlation is statistically significant ($p \leq 0.05$) (n = 13). / Nota: Dir es la Transmisividad de la radiacion solar directa; Dif es la Transmisividad de la radiacion solar difusa y GL es la Transmisividad de la radiacion solar global. Símbolo (*) la correlación es estadísticamente significativa (p 0,05) (n = 13).

TABLE 4. Pearson rank correlation for absolute height growth (AHG) and absolute radial growth (ARG) and other measured variables in an old-growth forest of *N. dombeyi* in the central-southern Andean region of Chile. / Coeficiente de correlación de Pearson para el crecimiento de la altura absoluta (AHG) y el crecimiento radial absoluto (ARG) y otras variables medidas en un bosque sobremaduro de *N.dombeyi* ubicado en la región andina centro-sur de Chile.

VARIABLES	AHG	ARG
AHG		0.88*
ARG	0.88*	
E	-0.71*	-0.59*
Dir	0.70*	0.55
GL	0.70*	0.60*

Note: E is the age of the highest plant in the plot, Dir is direct solar radiation transmittance and Gl is global solar radiation. Symbol (*) the correlation is statistically significant ($p \leq 0.05$) (n = 13). / Nota: E es la edad de la planta más alta en la parcela, Dir es la Transmisividad de la radiacion solar directa y GL es la Transmisividad de la radiacion solar global. Símbolo (*) la correlación es estadísticamente significativa (p 0,05) (n = 13).

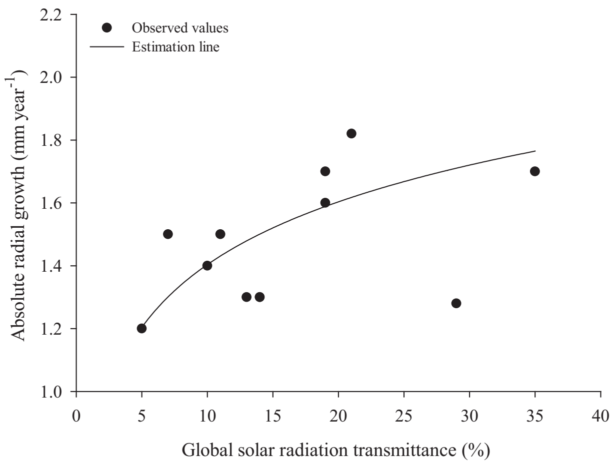

FIGURE 5. Scatter diagram for the relationship between global solar radiation transmittance and absolute radial growth (ARG = 0.7398 + 0.6638 * log10(x); $R^2 = 0.60$; $p = 0.031$) in an old-growth forest of *N. dombeyi* in the central-southern Andean region of Chile. / Diagramas de dispersión para la relación entre la transmisividad de la radiación solar global y el crecimiento radial absoluto (ARG = 0,7398 + 0,6638 * log10 (x), R^2 = 0,60; p = 0,031) en un bosque sobremaduro de *N. dombeyi* en el centro-sur región andina de Chile.

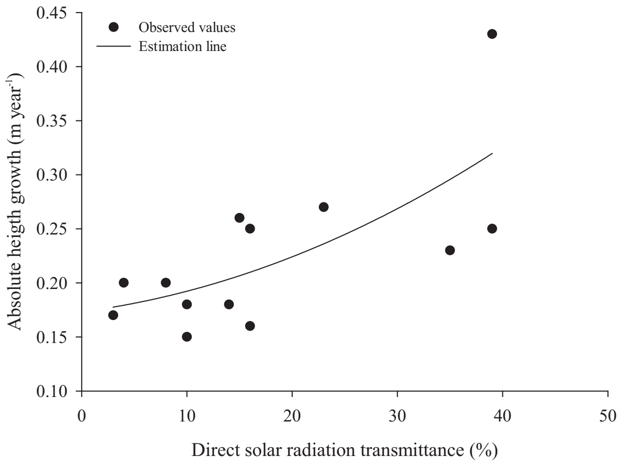

FIGURE 6. Scatter diagram showing the relationship between direct solar radiation transmittance (%) and absolute height growth (AHG = 0.1733 + 0.0013 * x + 6.3677e^{-5} * x^2; $R^2 = 0.69$, $p = 0.0081$) in an old-growth forest of *N. dombeyi* in the central-southern Andean region of Chile. / Diagramas de dispersión para la relación entre la transmisividad directa de la radiación solar (%) y el incremento absoluto de la altura (AHG = 0,1733 + 0,0013 * x + 6,3677e-^{5} * x^2; R^2 = 0,69, p = 0,0081) en un bosque sobremaduro de *N. dombeyi* ubicado en la región centro-meridional andina de Chile.

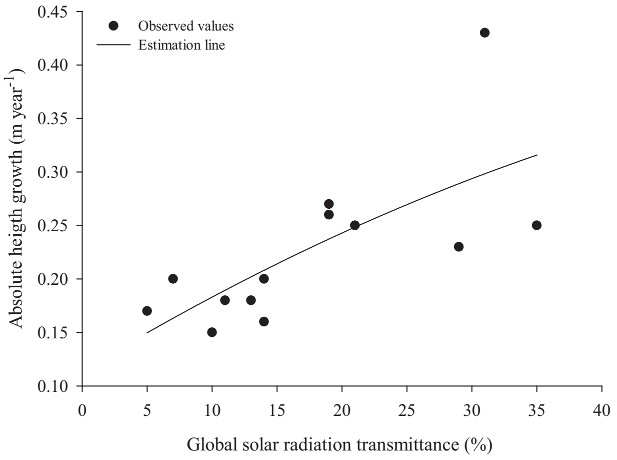

FIGURE 7. Scatter diagram for the relationship between global solar radiation transmittance (%) and absolute height growth (AHG = 0.1141 + 0.00073 * x – 4.5354e^{-5} * x^2; $R^2 = 0.703$; $p = 0.0073$) in an *N. dombeyi* old-growth forest in Chile's central-southern Andean region. / Diagramas de dispersión para la relación entre la transmisividad de la radiación solar global (%) y el crecimiento de la altura absoluta (AHG = 0,1141 + 0,00073 * x - 4,5354e^{-5} * x^2; R^2 = 0,703; p = 0,0073) en un bosque sobremaduro de *N. dombeyi* que crece en la región centro-meridional andina de Chile.

DISCUSSION

SOLAR TRANSMISSIVITY MEASUREMENTS AND DIFFERENTIATION OF GLOBAL, DIRECT AND DIFFUSE RADIATION COMPONENTS

Both intensity and direction of solar radiation transmissivity in forests are constantly changing due to daily and yearly movements of celestial bodies and the Earth in relation to the sun's position and cloud cover (Baldocchi & Collineau 1994). When tree canopies, shrubs or herbaceous strata at a particular site vary in size, shape and opacity, the transmissivity of solar radiation penetrating the canopy transforms, creating a wide variation of incoming light in the forest (Lieffers *et al*. 1999). In our stands showed high spatial variability for all transmissivity components of solar radiation inside forests (3 to 40%, Fig. 3), likely due to different degrees of canopy coverage caused by small-scale disturbance. In this sense, patterns of spatial solar radiation transmissivity observed in the study area are consistent with changes occurring in forests, particularly the presence of different gaps, canopies surface characteristics, and gap size and location (Parker *et al*. 2002). This has been proven through models (Hardy *et al*. 2004) showing that spatial changes in solar radiation transmissivity are due to the highly variable nature of light and canopy geometry, particularly discontinuous canopies, as seems to be the case for *N. dombeyi* old-growth forest stands. It is necessary to consider that sunfleck spectra are similar to direct solar radiation transmissivity (Leuchner *et al*. 2012), which can be physiologically important since plants use this solar radiation in photosynthesis (Dengel *et al*. 2015). In this sense, stands under forest understory conditions, leaves are at intermediate induction states for most of the day and the ability to utilize sunflecks may therefore be strongly influenced by the ability of leaves to maintain relatively high states of induction during long periods of low light (Chazdon & Pearcy 1986) and shade-tolerant species show that, particularly in low light, they are capable of efficient sunfleck utilization (Rijkers *et al*. 2000).

It is necessary to refer to the dominant solar environment of *N. dombeyi* old-growth forests, since it corresponds to the growth responses of temperate forests in a Mediterranean climate. It has been reported that this lighting can account for 15% of midday radiation coming through the canopy and 40% of the radiation below the shrub layer in deciduous leaf stands, representing between 14 and 41% of canopy transmittance for stands dominated by conifers (Canham *et al*. 1994); this also explains increases in diffuse light proportions under canopies (Dengel *et al*. 2015). Sunfleck spectra are similar to incident radiation (Leuchner *et al.* 2012) and could also function in areas with transiently higher temperatures, sometimes leading to physiological significance (Dengel *et al*. 2015), as in the case of the present study area. It is important to note that the transmissivity of diffuse solar radiation enhances terrestrial vegetation photosynthesis (Dengel *et al*. 2015), while the transmissivity of direct solar radiation can cause photosynthesis saturation in the upper canopy and possibly photoinhibition (Long *et al*. 1994).

The area under study has beenaffected to varying intensity and duration by recurring snowstorms and wind (Mitchell 2013), forming large gaps with a high proportion of surviving trees, creating gaps mosaics (Mitchell 2013). Wide crowns of *N. dombeyi* retain snow until damage occurs under snow weight pressure, but with more intense storms, a larger number of trees break or are uprooted, which opens the canopies, resulting in gaps, as Mitchell (2013) reported. Therefore, high spatial variability in solar radiation transmissivity due to these disturbances can satisfactorily explain structural changes and regeneration dynamics. High spatial variability in solar radiation transmissivity is directly related to small-scale disturbances, which is a characteristic of old-growth forests in the absence of fires (Gauthier *et al*. 2010), as is the case for the study area for which no fires have been reported over the last 50 years. Moreover, the wide age range of saplings harvested in the advanced regeneration observed in *N. dombeyi* gaps varies between 12 and 40 years; saplings are visibly related to the formation and development of various size of gaps in response to small-scale disturbances.

EFFECTS OF SOLAR RADIATION TRANSMISSIVITY ON NATURAL REGENERATION DENSITY, RADIAL INCREASE AND PLANT HEIGHT

The highest densities for advanced regeneration were observed in 13 plots from 64 total plots, with location at the edges or centres of stand gaps. However, sapling density showed low correlation with diffuse solar radiation transmissivity (R^2 = 0.26) (Fig. 4). Our results indicate until 30% of diffuse solar radiation transmissivity advanced sapling regeneration was highest (5 saplings m^{-2}), and with low levels of diffuse solar radiation transmissivity, under 5%, usually the density of advanced saplings was only 1 sapling m^{-2}, with exception in one plot with 8 saplings m^{-2} (Fig. 4). These results coincide with a study by Müller-Using (1973), who reported that for *N. dombeyi* regeneration density ranged from 0.08 to 0.8 plants m^{-2} with diffuse solar radiation transmissivity between 1.8 and 7%. The range of spatial regeneration variability was associated with diffuse solar radiation transmissivity between 3 and 40%, values which Collet & Chenost (2006) also reported for European beech (*Fagus sylvatica* L.).

In addition, our results are consistent with Saldaña & Lusk (2003), namely that available light explains most variation in advanced *N. dombeyi* regeneration density. Likewise, a controlled experiment found that the scarce regeneration of *N. dombeyi* under canopies of old-growth forests is at least partially attributable to higher light compensation points –but not shade– tolerant species. This is a typical characteristic of shade-intolerant species qualified as pioneers, such as *N. dombeyi* (Lusk & Del Pozo 2002). In this sense, site resources, especially water and nutrients in the soil, could be relevant to explain the density of advanced regeneration (Stancioiu & O'Hara 2006).

However, presence or absentia saplings under the canopy of old-growth forests are not only explained by the level of light at ground level, but also by different factors such as competition from herbaceous plants, bushes and overstory-trees as well as climatic extremes such as drought or frost (Pacala *et al*. 1994; Stancioiu & O'Hara 2006). Moreover, solar radiation transmissivity had no influence on the height of seedlings and saplings under the canopy for the height class shorter than 0.5 m (Table 3). This result is consistent with Promis *et al*. (2010) findings for *Nothofagus betuloides* (Mirb.) Oerst. and could be explained with low-height seedlings and saplings, high dependency on other site resources, especially water and nutrients in the soil (Aussenac 2000; Stancioiu & O'Hara 2006). Studies developed by Lusk (2004) and Ammer *et al*. (2008) found the same, indicating that size and age might affect plants' growth response to resource availability.

In contrast, both diffuse and global solar radiation transmissivity highly influenced height classes 1 < 1.5 m, possibly reflecting high competition for this resource, forcing saplings to invest more energy in height growth (Table 3) especially in old-growth forests where light is scarce. However, diffuse and global radiation considerably influence plants > 2 m (Table 3), due to competition for access to higher proportions of diffuse radiation under the canopy (Lieffers *et al*. 1999). Müller-Using and Schlegel (1981) found in a study controlling shade conditions that *N. dombeyi* height significantly increased with increasing light intensity. In the case of small gaps with a more or less closed cover, diffuse light total and daily carbon gain is linearly related to total daily PPFD. The proportion of total daily carbon gain during sunflecks ranged from 15 to 60% (Chazdon 1986; Peri *et al*. 2009), and consequently, may be important for the discovery of regeneration under shaded canopies in *Nothofagus* (Peri *et al*. 2009). Thus, direct light with higher energy levels, but lower occurrence during the day, stimulates photosynthetic processes leading to higher growth rates. In this respect, it has been reported that the effect of direct and global solar radiation transmissivity on height increment is relevant at levels above 20%, as in the case of *N. betuloides* (Lusk 2004). However, in large gaps, direct and global solar radiation transmissivity, produces an excess of light inhibits growths, due to high energy contents and can lead to the inhibition of photosynthesis if unavailable for long periods of the day (Dengel *et al*. 2015). In fact, high light levels in gaps in the Andes may be the cause of severe photoinhibition of *N. dombeyi* saplings (Donoso *et al*. 2013).

The largest increases in AHG occurred in the 15 to 23% range of direct and global solar radiation transmissivity (Figs. 6 and 7). Factors explaining AHG in the present study were also reported by Lusk (2004), Ammer *et al*. (2008), and Promis *et al*. (2010), who see transmissivity of direct and global solar radiation and age as a partial explanation of AHG ($R^2 = 0.7$; Figs. 6 and 7) because saplings also respond to other available site resources for growth. Therefore, maximum increases in growth do not correlate with the highest light level. An explanation is that competition in the advanced regeneration of *N. dombeyi* excludes other species from the understory; it could therefore be argued that ARG is much more sensitive to intraspecific competition than growth in height (Ammer *et al*. 2005). The observed AHG patterns suggest that advanced regeneration species compete mainly for light, simultaneously reducing total increases in biomass but increasing biomass in the stem area in terms of height at the expense of radial growth (Ammer *et al*. 2005).

Diaci *et al*. (2008) showed the relative importance of both diffuse and direct radiation transmissivity for the successful regeneration of *F. sylvatica* under canopy openings with diffuse radiation, which coincides with the findings in this study (Table 1). However, height classes ARG and AHG showed no correlation with diffuse solar radiation transmissivity, likely a response to competition for density and greater access to diffuse radiation under the canopy by light-demanding species (Lieffers *et al*. 1999).When competing for light, height growth is of prime importance due to mechanical stress, and therefore ARG and AHG are regulated by the local environment (Vanninen & Mäkelä 2000). In this study, the local microenvironment and site resources, such as water availability, were not analysed, but future studies should take these into account.

Silvicultural implications

The studied stands correspond to mono-specific old-growth evergreen *N. dombeyi* forests. As no universal definition for old-growth forests exists (Wirth *et al*. 2009), for this study, using a broader and more pragmatic approach, Shorohova *et al*. (2011) definition proved most suitable. They define old-growth forests as naturally regenerated forests with low human impact and dominated by trees that approach the end of their biological life cycle. This phase is interesting because it opens room for human intervention, such as forest rehabilitation or the practice of close-to-nature silviculture.

For old-growth *N. dombeyi* forests, it has been hypothesised that in the absence of large-scale disturbances, late successional species tend to settle under the canopy and replace early successional species; therefore, regeneration of these species would depend on disturbance frequency (Veblen *et al*. 1996b). However, this hypothesis does not apply to old-growth forests in this study, because old-growth canopy layers of *N. dombeyi* have been primarily affected by small-scale disturbances such as rain and snow pressure, giving rise to differently sized gaps that stimulate natural regeneration in absence of bamboo species such as *Chusquea culeou* (Lusk 2001). Wind also causes a variety of gap sizes that depend directly on the intensity and duration of storms, site heterogeneity and stand conditions. In this form, overstory gaps vary so much that it is difficult to distinguish between a medium gap with a low proportion of fallen trees and a mosaic of small gaps.

The old-growth *N. dombeyi* stands of this study contained mainly two features. First, the presence of single layered stands, since canopies are fully closed and a geometric extension of canopies largely prevents solar radiation transmissivity, especially diffuse radiation in the understory, which affects natural regeneration. The second condition was observed in gaps created by small-scale disturbances and consisting of saplings competing for light, since the trees in the upper canopy still reduce light availability in the lower canopy (Oliver & Larson 1996). Similar to the seedling and sapling regeneration of *N. betuloides* (Promis *et al*. 2010), regeneration in this study developed slowly in the understory, where saplings needed 20 to 40 years to reach a height of 5 m, without forming a consistent secondary tree layer. From this perspective, it is necessary to recommend a silvicultural system that ensures natural regeneration in an old-growth *N. dombeyi* forest. Silvicultural systems consider multiple and often conflicting management objectives. Due to the high economic and ecologic value of the species presented here, it is necessary to preserve attributes of this forest type (Bauhus *et al*. 2009). Thus, the group selection method constitutes an appropriate method to promote regeneration, given that trees are removed in small groups (Lindenmayer & Franklin 2002) and felling can continue at the border of the created gap. This method results in more or less “homogeneous” canopy gap patterns which allow for more resources, especially light, in areas lacking regeneration (Nyland 2002).

In the case of old-growth forests, no competition with *C. culeou* occurs and gaps are related to small areas on the forest floor where regeneration can develop over several years. However, the demand for light increases with age (Lieffers *et al*. 1999), making it necessary to expand existing gaps and create new ones to sustain the regeneration of new plants. These new gaps should imitate the collapse of old-growth trees, i.e. gaps should allow for enough light to stimulate regeneration; hence, cutting two to three trees of the overstory could prove useful, as it results in gaps with a diameter of around 30 m (0.07 ha), depending on stand density and tree size (Dezzotti & Sbrancia 2006). However, it is necessary to adjust silvicultural practices, particularly the level of canopy openings, to maintain species composition unaffected as a key indicator of sustainability at management unit scale (Sola *et al*. 2015). Likewise, it is necessary to analyse the impact on biodiversity related to this silvicultural regime. The existing gaps are large enough to introduce other tree species complementing the natural regeneration of shade tolerant *N. dombeyi*, such as *Laureliopsis philippiana* and *Podocarpus saligna* (D. Don), and *Nothofagus alpina*, which protects against excess lighting in the gap (Dezzotti 2008). Regarding gap size, Dezzotti & Sbrancia (2006) found an average *N. dombeyi* regeneration of 61.2 plants m^{-2} with observed gap sizes of 0.15 and 0.4 ha, demonstrating the effectiveness of this approach. These sizes suggest that gaps should have a maximum width of 40 to 60 m in wet temperate climates, preferably with winter rains. Under these weather conditions, gaps meet the objective of not creating central areas that are too large for the transmissivity of direct or global solar radiation or for natural regeneration defences against late frosts or desiccation (Dezzotti & Sbrancia 2006).

In this study, the range of the solar radiation transmissivity spectrum was lower, than wet temperate climate zones, expressed in a maximum transmissivity value of 40%. Therefore, gap sizes should be even smaller, in areas of Mediterranean climates, and this justifies that we propose a diameter of no more than 30 m for gaps and the study of enrichment techniques using shade-tolerant species.

CONCLUSION

In the case of old-growth *N. dombeyi* forest, recurrence of wind and snowstorms and the geometry of canopies cause the loss of individual trees if the storms are of low intensity. In cases of intense storms, the loss of a greater number of trees provides more and larger canopy openings. The age of higher plants varied between 12 and 40 years trying canopy opening at different times. It was estimated that the absolute radial increase of plants varied between 1.20 and 2.22 mm $year^{-1}$. However, the height classes, ARG and AHG did not correlate with the diffuse solar radiation transmissivity, but with the direct and global. Therefore, plant age and direct, and global transmittance of solar radiation through canopy openings explain the increases in diameter and height of saplings, and we recommend that local habitat and total sapling height of surrounding trees play a fundamental role in regulating competition in height growth for regeneration. Our findings suggest that single-tree or group-selection harvests should emulate the small-size gap disturbance as an important regeneration management for *N. dombeyi* old-growth forest.

ACKNOWLEDGEMENTS

The authors would like to thank the Chilean Project VRID 215.142.033-1.0 of the University of Concepción.

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Recibido: 14.06.2018
Aceptado: 26.09.2018