Sapling growth and crown expansion in canopy gaps of *Nothofagus pumilio* (lenga) forests in Chubut, Patagonia, Argentina

P. M. Lopez Bernal[1, 2, 3], *, G. E. Defosse[1, 2, 3], C. P. Quinteros[1, 2, 4] and J. O. Bava[1, 3]

[1] CIEFAP, Centro de Investigación y Extensión Forestal Andino Patagónico. Ruta 259 Km 4,
(CP 9200) Esquel, Chubut, Argentina
[2] CIEFAP-CONICET, Ruta 259 Km 4, (CP 9200) Esquel, Chubut, Argentina
[3] UNPSJB, Universidad Nacional de La Patagonia San Juan Bosco. Ruta Nacional 259 Km 4,
(CP 9200) Esquel, Chubut, Argentina
[4] SCTeIP, Secretaría de Ciencia Tecnología e Innovación Productiva, Provincia del Chubut, Argentina

Abstract

In the province of Chubut in Patagonia, Argentina, *Nothofagus pumilio* forests (locally known as lenga), are managed through selective cuts, which imply the opening of canopy gaps. This management scheme is carried out without taking into consideration the changes of sapling requirements through either a cutting cycle or the precipitation gradient in which these forests thrive. To analyze these changes, we inferred the facilitation-competition balance between the canopy and regeneration, studying the effects of precipitation levels, gap size and gap age on saplings growth in height on 45 canopy gaps artificially created between 1960 and 1993. Results showed that during the first 20 years since gap opening, growth of regeneration is determined by light availability in mesic sites and by water availability in xeric sites. However, differences due to precipitation levels gradually decrease over time. Moreover, in the period between 20 and 35 years after gap opening, in both mesic and xeric sites, growth is limited by light availability. This indicates that in xeric sites, sapling growth requirements shift from a water-dependent situation to a light-dependent situation. The average closing rate of gaps due to lateral growth of bordering trees is high enough so that within the proposed gap size range, gap healing can occur before regeneration reaches the upper stratum. Consequently, in mesic sites gap opening can be done by a single operation that generates gaps with diameters of approximately twice the average height of the canopy (D/H). While in xeric environments, lenga seedling establishment and initial growth require the cover of small gaps, but advanced regeneration requires bigger gaps to reach the canopy. For this reason, gaps should be opened in two stages: the first gaps should be opened with a D/H between 0.8 and 1, and after a cutting cycle of 35 years, these openings should be enlarged to a D/H between 1.5 and 2. The close relationship maintained between the new cohort and the upper strata require special considerations regarding the evolution of the balance between positive and negative interactions during development. Our work highlights the need to adjust management practices to these spatial and temporal variations to achieve an optimal growth along the entire production cycle.

Key words: regeneration; group selection; height growth; stem analysis.

Resumen

Crecimiento de renuevos y expansión de copas en claros del dosel de bosques de *Nothofagus pumilio* (lenga) en Chubut, Patagonia, Argentina

En la provincia del Chubut, Patagonia Argentina, los bosques de *Nothofagus pumilio* (lenga) son manejados mediante cortas de selección, que implican la apertura de claros en el dosel. Este esquema de manejo es implementado sin tener en cuenta los requerimientos de los renuevos a lo largo de todo el ciclo de cortas ni el gradiente de precipitaciones presente en su distribución. Para analizar estos aspectos estimamos el balance facilitación-competencia entre el dosel y la regeneración, considerando los efectos de los niveles de precipitación, el tamaño de los claros y la antigüedad de los mismos, en 45 claros creados artificialmente entre los años 1960 y 1993. Los resultados muestran que durante los primeros 20 años desde la apertura del claro, el crecimiento de la regeneración está determinado por la disponibilidad de luz en los sitios mésicos y por la disponibilidad de agua en los sitios xéricos. Sin embargo, la diferencias entre los distintos niveles de precipitación decrece gradualmente a lo largo del tiempo y entre los 20 a 35 años

luego de la apertura de los claros, tanto en los sitios mésicos como xéricos el factor limitante es la luz. Esto implica que en los sitios xéricos el crecimiento de los renuevos pasa de ser dependiente del agua a dependiente de la luz. Por otro lado, la tasa de cierre de los claros debida al crecimiento lateral de la copa de los árboles límite es lo suficientemente grande como para que pueda ocurrir el cierre antes de que los renuevos alcancen el estrato superior. Por lo tanto, en los sitios mésicos la apertura de los claros puede realizarse en una única operación que genere claros con un diámetro de aproximadamente el doble de la altura dominante del bosque (D/H ≈ 2). Por el contrario, en los sitios xéricos, el establecimiento y crecimiento inicial de los renuevos requiere la apertura de claros pequeños (D/H entre 0,8 y 1) que luego deberán ser ampliados para maximizar el crecimiento avanzado (D/H entre 1,5 y 2). La estrecha relación entre la regeneración y el dosel del bosque requiere la consideración de los posibles cambios en el balance entre los apsectos positivos y negativos de la misma a lo largo de todo su desarrollo. Nuestro trabajo resalta la necesidad de ajustar las prácticas de manejo a estas variaciones espaciales y temporales para alcanzar un desarrollo óptimo a lo largo del todo el ciclo productivo.

Palabras clave: regeneración; selección en grupos; crecimiento en altura; análisis fustal.

Introduction

The dynamics of canopy gaps, in which the fall of one or several trees that produces the gap is the main disturbance event, has been widely studied in different forests of the world (Runkle, 1985; White and Pickett, 1985; Pickett *et al.*, 1999). One characteristic of these gaps is that they could be either big enough as to freed the necessary resources for a new cohort to be established, or small enough so that the canopy of surrounding trees would exert a facilitation effect over the saplings grown in these gaps (Veblen, 1992). In the later case, regeneration of shade-tolerant species is promoted. This situation, which at the beginning could be considered favorable for the establishment of certain species, could vary during the course of time, due to two simultaneous events that promote the closeness of the gap. These events are the growth in height of the saplings, and the lateral growth of the bordering trees that conform the limits of the gap (Frelich, 2002).

In Andean Patagonia in Argentina, *Nothofagus pumilio* forests (locally known as lenga forests) develop over a wide distribution range, covering a great variety of ambient conditions and presenting different structures and regenerative dynamics. These dynamics are mainly associated to the frequency, magnitude, and severity of disturbances, and also to the productivity of the site (Donoso Z., 1995). In sites presenting summer water deficit (the northern area of its distribution in the provinces of Río Negro, Neuquén, and northern Chubut), lenga regeneration does not establish in areas in which vegetation cover is below 20% (Bava and Puig, 1992). In these sites, survival of lenga seedlings and saplings is frequently limited by the availability of water, and its establishment occurs in small gaps, product of tree fall that creates microsites showing low evapo-transpiration rates (Rusch, 1992; Heinemann *et al.*, 2000).

Recent studies have analyzed the effects of micro-environmental factors on lenga seedling establishment and growth. In general, they have determined that the shade generated by trees growing in the borders of the gaps, and the presence of fallen dead trees and other forest debris, could exert a facilitative effect on seedling establishment. This effect, however, has only been observed in dryer areas of lenga distribution (Heinemann *et al.*, 2000; Heinemann and Kitzberger, 2006). These authors concluded that in dry sites, seedling survival is positively correlated to water availability, while in more humid sites, survival is controlled by both water and light availability. However, the evolution of the relationship between forest canopy and regeneration in the gaps trough time is still not well understood. It is probable that at some point in time, when regeneration is growing, the balance between negative and positive interactions (facilitation-competition) could be altered, favoring competition over facilitation.

In the province of Chubut in northwestern Patagonia, lenga forests represent the main source of lumber for the forest industry. During the last decade, silvicultural practices based on sound science have been recommended, and forest management agencies have promoted the creation of an irregular forest through the adoption of selective cuts. These silvicultural practices imply the opening of gaps in which regeneration could satisfactorily establish (Coates and Burton, 1997; López Bernal *et al.*, 2003; Martinez Pastur *et al.*, 2007). This general recommendation, however, does not take into account the environmental variations along the precipitation gradient, and the different effects (facilitation/competition) they may have on establishment

and growth of lenga regeneration. This uncertainty generates some doubts about the optimum size the gaps should have along this gradient, and the cutting regime needed to maximize establishment and growth of the regeneration, to further improve lumber quality.

The knowledge of the balance of negative and positive interactions between the canopy and the regeneration through time would then be important to evaluate the convenience (or not) to increase the intensity of these interactions through the openness of small gaps, or to diminish them trough the openness of larger gaps. Knowing the changes of this balance through time, would also provide science evidence as to justify the decision for opening new small gaps and then to widen them, or perhaps make wider gaps at the beginning of the silvicultural treatment to allow trees to achieve their turn without more interventions.

The aim of this study was then to analyze changes in the facilitation - competition balance, inferred through the growth in height, between the canopy and regeneration in artificial gaps of lenga forests, during a cutting cycle of about 35 years. We tested the hypothesis that both the availability of resources (i.e. water) and the gap closure (due to the sapling growth and/or crown expansion) determines the balance between positive and negative effects from the forest canopy to regeneration strata. Thus, canopy-saplings interaction occurring in small gaps will be more favorable for regeneration in drier sites and during early stages of establishment. In more humid areas with higher productivity and / or in later stages of stand development, the balance will become increasingly negative for saplings due to increasing competition, and larger gaps, with lower levels of canopy-saplings interaction, will present the greatest growth.

Methods

Study area and experimental design

Measurements were performed on 45 lenga forest canopy gaps created during harvests conducted between 1960 and 1993 in the Andean region of northwestern Chubut province, Argentina (from the 42° 45' and 45° 00' South Latitude parallels and from the 71° 15' and 71° 50' West Longitude meridians) (Figure 1). These gaps were located at six sites having different levels of mean annual precipitation (MAP), and grouped into two classes: *xeric* sites (MAP: 900 ± 80 mm) and
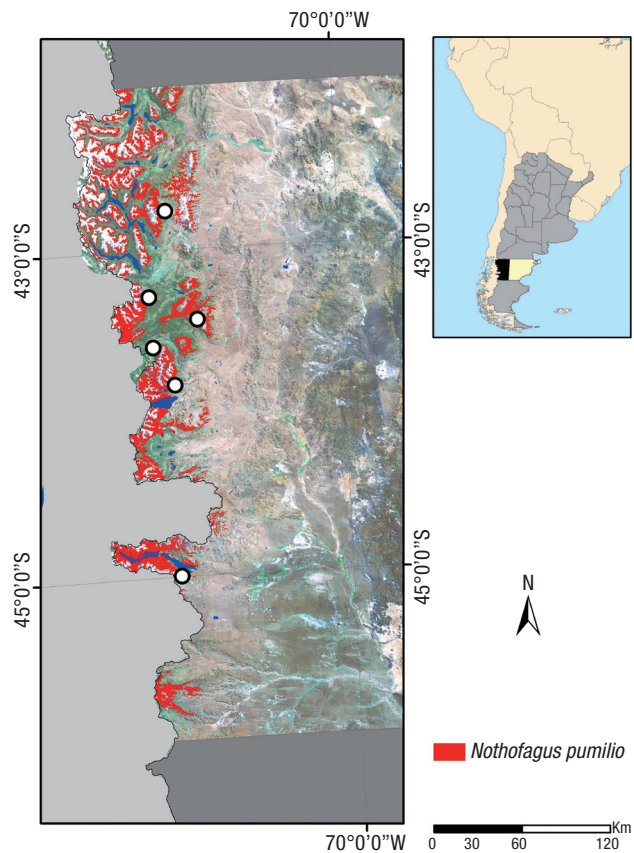
Figure 1. Study sites location (white circles).

mesic sites (MAP: 1,250 ± 60 mm). Precipitation levels were estimated based on the geographic longitude and the height above the sea level of each gap, using the equation [1] (adapted from Jobbágy *et al.*, 1995).

$$MAP = 534^{(-0.02231 \cdot (81.9 \cdot (72 - long) - 64))} + (hamsl - 663)/100 \cdot 37{,}5 \quad [1]$$

where MAP = mean annual precipitation; *long* = longitude; *hamsl* = height above mean sea level

At each site, we selected between 4 and 16 gaps (sampling units) of different sizes. The gaps selected had no signs of herbivore damage in dominant individual trees and were created by single cutting events. The sampling consisted of a split plot design, with the "gap size" factor nested in "precipitation". The gap size was defined as the ratio between the expanded gap diameter and the average height of the dominant bordering trees (D/H), a variable highly correlated with the incident radiation and soil moisture in the gap center (Lima, 2005; López Bernal *et al.*, 2010; Schliemann and Bockheim, 2011). Gaps were then divided into two size classes: small (D/H between 0.7 and 1.3) and large gaps (D/H between 1.3 and 2).

For the characterization of regeneration growth (in height) within each gap, 5 subplots of 4 m² were installed, one in the center of the gap and the others at every cardinal point at one-third of distance between the center and the gap edge (Figure 2). These subplots represented the central sector of gaps, where dominants saplings are most likely to occupy the upper canopy.

In each subplot, the tallest saplings were selected for some measurements, while complementary measurements were performed on the five tallest saplings of each gap whether or not they were growing within a subplot. This implied, thus, that six to ten dominant saplings were selected in each gap for growth measurement.

Sapling growth was measured in two ways: a) by measuring the last five growing units (GU) through distances between cataphylls scars, and b) by a stem analysis, where the tallest sapling of each gap was cut in ten equal length sections. From each sector, a slice was taken for ring counting and the data processed by the method proposed by Carmean (1972). This method has two assumptions: 1- that the intra-annual growth is constant and is totally or partially contained within each section, and 2- the slices were cut at the middle of each annual growth increment. The method uses different equations for the basal sector (equation [2]), intermediate sector (equation [3]), and the apical sector (equation [4]).

$$H_{ij} = h_i + \frac{j\left(h_{i+1} - h_i\right)}{\left[0.5 + \left(r_i - r_{i-1}\right)\right]} \quad [2]$$

$$H_{ij} = h_i + \frac{\left(h_{i+1} - h_i\right)}{\left[2\left(r_i - r_{i+1}\right)\right]} + \frac{\left(j-1\right)\left(h_{i+1} - h_i\right)}{\left(r_i - r_{i+1}\right)} \quad [3]$$

$$H_{ij} = h_i + \frac{\left(h_{i+1} - h_i\right)}{\left[2\left(r_i - r_{i+1} - 0.5\right)\right]} + \frac{\left(j-1\right)\left(h_{i+1} - h_i\right)}{\left(r_i - r_{i+1} - 0.5\right)} \quad [4]$$

where *Hij* is the total height at age *tij*; *tij* is the age of the tree associated with the *j*-th ring of the *i*-th slice; *hi* is the height at the *i*-th slice; *ri* is the number of rings in the *i*-th slice.

Gap closure through lateral crown growth

To determine if the gap size could have been significantly altered in the analyzed period, we estimated the gap closure rate by measuring the length of the last
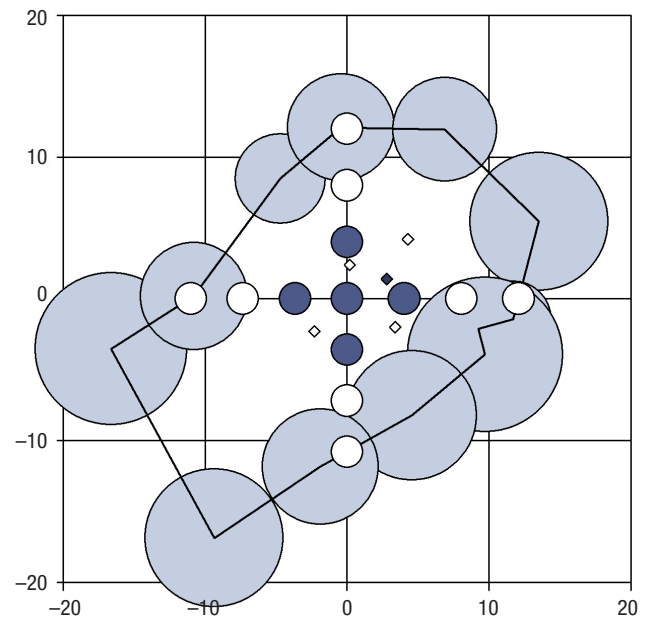
Figure 2. Gap scheme representing gap bordering trees (light gray circles), gap center regeneration subplots (dark gray circles), dominant saplings (diamonds) and the tallest sapling found on the gap (dark diamond).

four GU of the longest branches of each tree oriented to the gap center (*sensu* Trimble and Tryon, 1966). Additionally, this variable was associated with gap characteristics (i.e. size, MAP) and bordering tree characteristics (i.e. DBH, within gap position, etc.). We evaluated the lateral crown growth of 243 trees. The relative importance of each variable, including lineal transformations, was determined by a stepwise selection process (Schabenberger and Pierce, 2002).

The within-gap position (WGP) of each bordering tree was defined as a value from 0 to 100, where trees in the north edge of the gap, with the lowest level of direct incident radiation had the minimum value, and trees in the south, exposed to the highest direct incident radiation, received the maximum value.

Results

Saplings height increment

For gaps up to 20 years old, the analysis of variance for precipitation and the gap size on height growth showed no significant differences for main effects, while their interaction showed that the effect of gap size is different according to their location in xeric and

mesic sites, respectively (p = 0.012 and p = 0.032 at gaps of 10 and 20 years old, respectively) (Figure 3). For this reason, the interaction was studied by analyzing these effects separately. The growth in height of dominant saplings as a function of gap age found in mesic and xeric sites, and in small and big gaps is shown in figure 3 (a and b) and figure 4 (a to d). In mesic sites (i.e. greater than 1100 mm/year, figure 3 a and figure 4 a and c), either gap size had a positive effect on sapling height growth (p = 0.030 and p = 0.064 for gaps of 10 and 20, years old respectively). In xeric sites,

by contrast (i.e. lower than 1,100 mm / year, figure 3 b and figure 4 b and d), there were not significant differences due to the gap size, although there was a trend to lower growth in larger gaps. Similarly, we examined the effects of precipitation levels (mesic and xeric) considering the two gap sizes independently. In small gaps there was no difference between groups, while in large gaps, dominant saplings grew faster in mesic as compared to xeric sites, respectively (p = 0.014 and p = 0.038 for gaps of 10 and 20 years old, respectively).
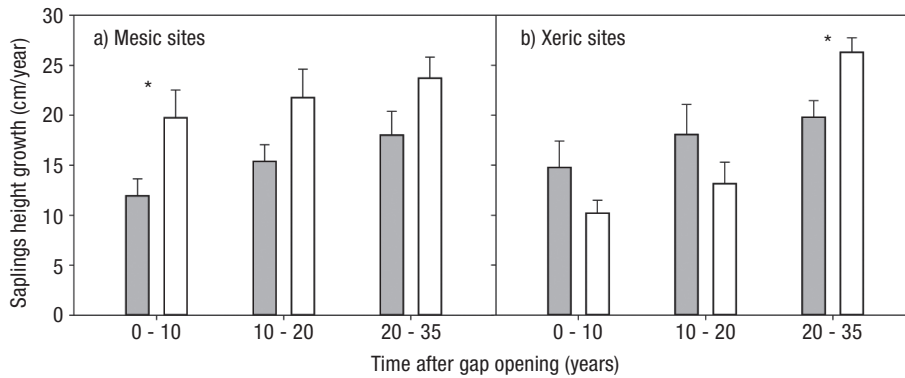
Figure 3. Mean annual increase in height (MAIh) for each precipitation level and gap size class (small gaps= gray bars, large gaps = white bars) along a 35 years cutting cycle. * Significant differences at a 0.05 level.
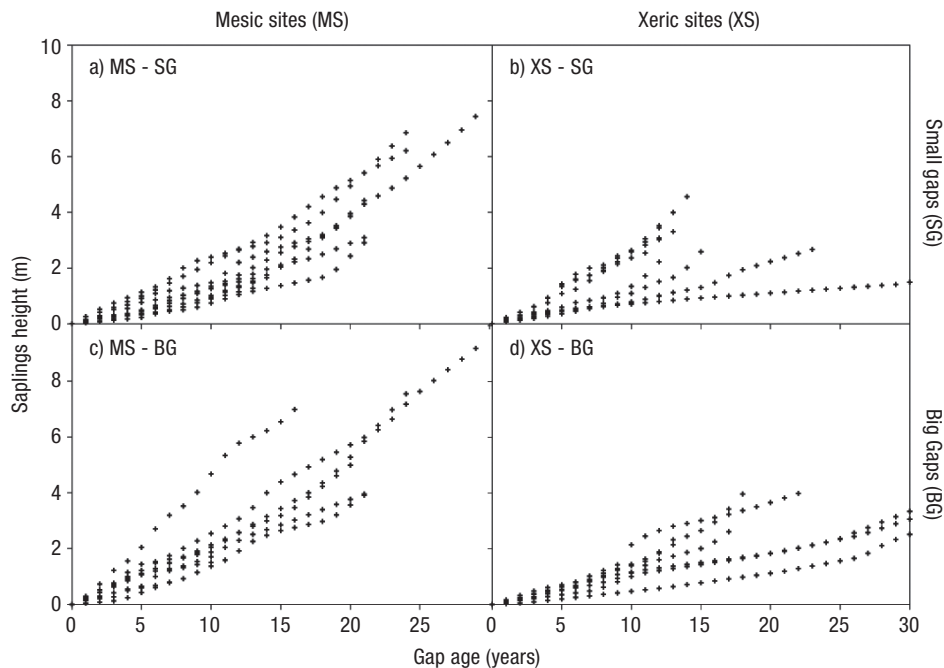
Figure 4. Height of dominant saplings in function of the gap age for each combination of precipitation levels and gap size.

Lateral crown growth of gap bordering trees

The average lateral crown growth (LCG) was 9.3 cm/year, with a standard deviation of 4.1 cm/year. Although relatively low for the three analyzed variables, a significant part of the observed variability was explained by either DBH of the bordering trees (p = 0.0027, η^2 = 0.07, Figure 5.a) and its "within-gap position" (WGP) (p = 0.030, η^2 = 0.024, Figure 5.b), being both variables negatively correlated. The gap size, by instance, was positively correlated (p = 0.02, η^2 = 0.23). In contrast, the precipitation level, put in the model as a continuous variable, showed no significant effect on lateral crown growth (p = 0.21). A regression analysis for these variables showed a low predictive model (Equation [5], R^2 = 0.079, SE = 3.45 cm year $^{-1}$) where the variable gap size was excluded by the stepwise selection process. Due to the weak correlation between the explanatory variables and the gap closure rate, long-term inferences were made by taking into account only the mean value and the dispersion measures.

$$LCG = 12.439 - 0.047 * DBH - 2.143 * WGP \quad [5]$$

Changes due to the gap closure

After a cutting cycle, the average lateral growth of bordering trees was high enough (about. 19 cm/year) as to produce the healing of the gap before regeneration reaches the upper stratum. The two mechanisms of gap healing (i. e. lateral crown growth of bordering trees and regeneration height growth), indicating the time needed to close the gaps of different sizes (ordinates) is shown in Figure 6. In general, larger gaps require more time for healing if lateral crown growth is considered, while less time is needed if the growth of regeneration is considered. Thus, the curves representing each mechanism are cut at the point corresponding to the gap size that allows regeneration to reach the canopy just before the crown growth of bordering trees prevents it. The time for gap healing could also be inferred by taking into consideration the two curves shown in this figure. The arrow ①, represents the development of a gap in a mesic stand, where it is feasible to open a gap with D/H between 1.5 and 2, favoring seedling installation and sapling development until their final height is achieved. Moreover, the ② and ③ arrows represent the development of a gap in a xeric stand. In these sites, it is necessary to open smaller gaps to ensure seedling establishment. However, after a 35 years cutting cycle, the gap should be enlarged to prevent its closure by the lateral growth of bordering trees. For example, considering a site with a rainfall level of 1300 mm/year and a dominant height of 21 m, it is necessary to open gaps with a D/H equal to, or greater than, 1.1, to ensure that 60 years later, the regeneration will reach the upper canopy.
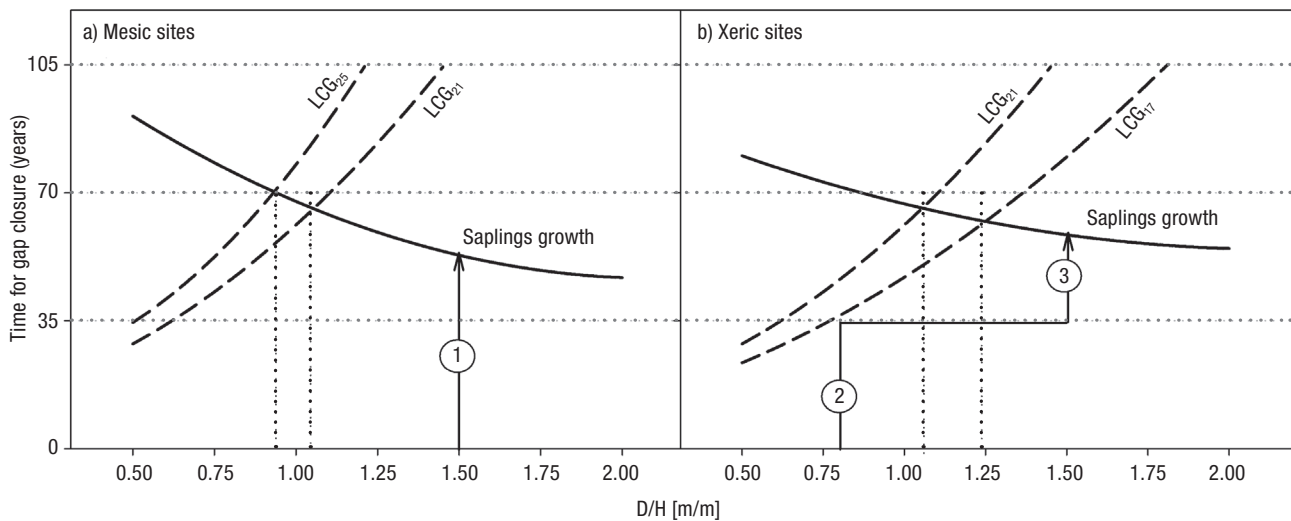
Discussion

Regeneration establishment and growth

In lenga forests, studies about the interactions between regeneration and upper adult strata have mainly been
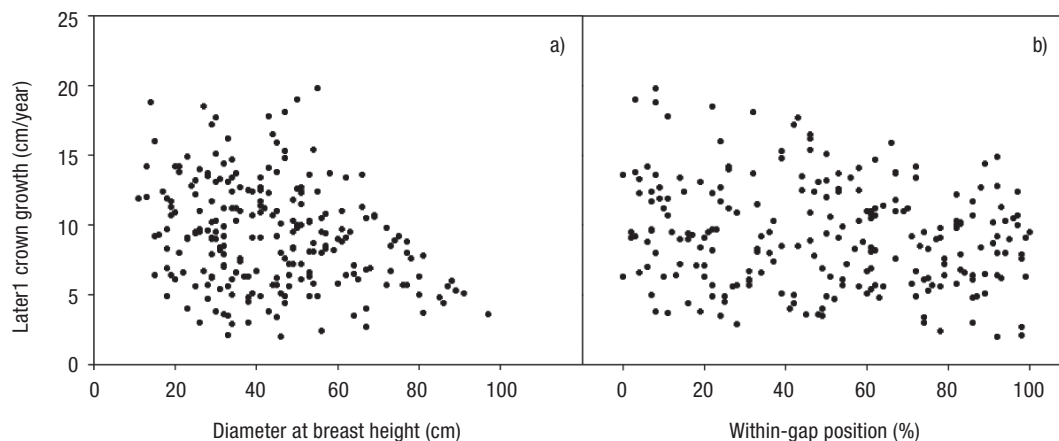
Figure 5. Lateral crown growth of trees bordering the gaps in function of their diameter at breast height (DBH) (a); and position within the gap (b).

Figure 6. Estimated time to gap healing through the regeneration height growth (solid lines) or the lateral crown growth of the bordering trees (dashed lines) by gap size (D/H) at sites with different dominant height (LCG$_{17, 21}$ & $_{25}$). For references of the arrows ①, ② and ③ see above.

concentrated in the processes occurring during the early development stages of seedlings and saplings (Rusch, 1992; Rechene, 1995; Heinemann *et al.*, 2000; Heinemann and Kitzberger, 2006). In our study, by contrast, we focused our attention to the changes occurring after these first stages of development have passed, and until saplings have reached the upper strata. The approach we used, however, was based on the effects of positive and negative interactions, and this allowed to make a global analysis of the whole process. In that sense, several studies in the northern area of distribution of lenga in Patagonia have concluded that the establishment of its regeneration is strongly dependent on the availability of water during the growing season. These studies showed that in the eastern and drier distribution sites, lenga regeneration is only installed on shaded microsites or where the presence of woody debris retains soil moisture for its use during the summer drought (Rusch, 1992; Rechene, 1995; Heinemann *et al.*, 2000; Heinemann and Kitzberger, 2006). Analyzing the microenvironment within the gap, Heinemann and Kitzberger (2006) found that the position of the sapling/seedling within it is a decisive factor for the recruitment of regeneration in drier sites, whereas in moist sites, the position does not seem to influence seedling survival. The same authors found that the initial growth of seedlings in the driest sites was greater in the shade, close to the gap border (i.e. the interaction balance is positive), while in moist sites it was higher in the center of the gap (i.e. the interaction balance is negative). They concluded that mois-

ture and light availability are the most important limiting factors for recruitment and early growth for sites with low and high levels of precipitation, respectively.

In general, our results agree with these studies, and corroborate the hypothesis that the balance of positive and negative interactions is altered during sapling development. During the first 20 years since the opening of the gaps, the regeneration growth is determined by light availability in mesic sites and the availability of water in xeric sites, with mean heights of about 22 cm/year and 15 cm/year for either sites, respectively (Figure 4). However, the difference due to the precipitation levels gradually decreases over time. Moreover, in the period between 20 and 35 years after gap opening, saplings in both mesic and xeric sites grew faster in larger gaps. This means that in the later sites, sapling growth shift from being water-dependent to light-dependent. A similar shift has already been reported for *Pinus strobus* and *P. resinosa* seedlings and saplings, under the cover of mature *Quercus rubra* trees (Kellman and Kading, 1992). These authors observed that facilitative effects of oak trees on juvenile pines continues up to 35 years after establishment and then the balance shifts to the negative effects of competition.

Gap closing rate

The lateral growth of crowns of the bordering trees puts a warning for making predictions about the growth

of saplings in gaps of different sizes, particularly in small gaps where these values represent a great proportional change. For example, if a gap is opened with a diameter equal to 0.7 times the dominant height, its size decreases 1.6% each year. After 35 years (i.e. a cutting cycle) the gap size will be reduced to less than a half. While there is no prior information about this process on lenga forests, for some species of the genus *Acer*, *Quercus*, *Juglans* and *Betula* grown in environmentally similar sites, their growth rates were similar, between 4 and 15 cm/year (Trimble and Tryon, 1966; Runkle, 1982; Runkle and Yetter, 1987).

Conclusions

The wide varieties of environments in which lenga forests develop produce significant differences in its structure and dynamics. This fact compels foresters to adapt their management practices to the prevailing local environmental conditions. Particularly in the Chubut province of Argentina, the rainfall gradient should be considered for gap size demarcation. If this system is chosen, the productive forests of this province could be divided in two classes, according to rainfall levels: i) Lenga forests grown in *Mesic sites* (i.e. western sites with rainfall above 1100 mm/year or more). In these sites, both the establishment of seedlings and the growth of advanced regeneration will depend on light availability, so the gap opening can be done by a single operation that generates gaps with diameters of approximately twice the average height of the canopy (D/H between 1,5 and 2); and ii) Lenga forests grown in *Xeric sites* (i.e. eastern sites with rainfall below 1,100 mm/year), where lenga seedling establishment and initial growth require the cover of small gaps, and advanced regeneration requires bigger gaps to reach the canopy. For these reasons and in xeric sites, gaps should be opened in two stages: the first gaps should be opened with a D/H between 0.8 and 1, and after a 35 years cutting cycle, these openings should be enlarged to a D/H between 1.5 and 2.

The sustainable forest management through low impact silvicultural methods presents a challenge to the forester, who must reconcile production goals with structure and dynamics of the natural forest. In this sense, the group selection system represents a practice adaptable to different situations and different species. However, the close relationship maintained between the new cohort and the upper strata require, during stand development, special considerations regarding the evolution of the balance between positive and negative interactions. Our work highlights the need to adjust management practices to these spatial and temporal variations, so that an optimal growth, along the entire production cycle, could be achieved.

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