Tree dynamics in canopy gaps in old-growth forests of *Nothofagus pumilio* in Southern Chile

Alex Fajardo[1,2,*] and Reitze de Graaf[1]

[1]*Forest Ecology and Management Group, Department of Environmental Sciences, Wageningen University, P.O. Box 342, 6700 AH Wageningen, The Netherlands;* [2]*Current address: School of Forestry, Science Complex 460, University of Montana, Missoula, MT 59812;* *Author for correspondence (fax: 01-406 243 6656; e-mail: afajardo@selway.umt.edu)*

Abstract

The gap dynamics of two *Nothofagus pumilio* (lenga) stands have been investigated. We evaluated and compared tree diameter distributions, spatial patterns, tree fall and gap characteristics and regeneration responses in gaps in two old-growth forests of *Nothofagus pumilio* in Southern Chile (Shangri-La: 36°60' S, 71°30' W; Reserva Coyhaique: 45°52' S, 72°00' W). In addition, we describe relationships between gap size and regeneration characteristics. We detected some differences in tree and sapling densities between sites. The causes of gap formation and the gap size distribution, mean gap area, and gap fraction were similar, but gap abundance was different at the two sites. The Reserva Coyhaique site had 15 gaps/ha compared to 10 gaps/ha for Shangri-La. Sizes of clumps of trees were within the range of sizes of canopy gaps at both sites. The density of saplings was higher in gaps than under closed forest at R. Coyhaique, but not at Shangri-La. We found that sapling densities were unrelated to gap size in both sites. The lower sapling density in gaps at Shangri-La might be explained by the presence of *Chusquea quila*, a competitive pioneer bamboo species. The height increment was related to gap size at Shangri-La, but not at R. Coyhaique. Gap size itself does not account for all the variation in recruitment performance in these Southern beech stands.

Introduction

In natural forests in which the frequency of large-scale, stand-replacing disturbance is low relative to the longevity of tree species, replacement of trees commonly occurs on a tree-by-tree basis through "gap dynamics" (Kimmins 1997). In many forests, gaps initiate a new regeneration cycle of overstory tree species. Newly available resources provide opportunities for seedling establishment or growth of already established advance regeneration, and these processes have been related to gap characteristics (Donoso 1993; Rebertus and Veblen 1993). For example, processes like germination, survival, and growth of juveniles of shade-tolerant and shade-intolerant tree species have been correlated, especially, with gap size (Whitmore 1989). However, gap size may not be a general feature related to establishment processes for all forests (Lawton and Putz 1988). The dilemma of whether or not gap characteristics, like size, can explain regeneration in natural forests needs to be resolved and should be linked as an ecological tool for management decisions, as well.

The genus *Nothofagus* occurs in Chile, Argentina, New Zealand, Australia, and New Guinea (Veblen et al. 1996*a*). They are located either at sites with environmental conditions restrictive for other tree species (high latitudes, high elevations, or edaphically sub-

optimal sites) or at more favourable sites with peri-
odic disturbances that vary in magnitude (Veblen and
Ashton 1978; Read and Hill 1985). The species of
this genus are considered shade-intolerant, and there-
fore they tend to be scarce or absent on mesic sites
with infrequent disturbances (Veblen et al. *in press*).
Nonetheless, in more frequently disturbed areas,
canopy gaps might be also important in establish-
ment, recruitment and growth of *Nothofagus* species
(Veblen 1985; Armesto et al. 1992; Donoso 1993;
Rebertus and Veblen 1993; Veblen et al. 1996*b*; Poll-
mann 2002). However, few studies have examined the
patterns of canopy gaps that characterize these forests
and the role of gaps in recruitment and growth of
trees. Additionally, little is known about changes in
gap dynamics across the broad latitudinal range of
some *Nothofagus* species (Rebertus and Veblen 1993;
Veblen et al., in press).

Nothofagus pumilio is the most prominent native
species for timber production in Chile, among the
species of this genus, and has been under continuous
management in the last decade (Uriarte and Grosse
1991; Arroyo et al. 1996). The specific requirements
for successful regeneration, however, are only partly
known. Such knowledge is needed to develop silvi-
cultural prescriptions for management of stands. This
study examines the effects of canopy gap size on the
structure and dynamics, and particularly, regenera-
tion, of two monodominant stands of *Nothofagus pu-
milio* in Southern Chile.

Methods

Study area

The study was conducted in two forests of *Nothofa-
gus pumilio* (Poepp. and Endl.) Krasser. (Marticorena
and Quezada 1985). *Nothofagus pumilio* (*Fagaceae*)
is a widespread deciduous, monoecious tree species
that occurs from 35° 35' to 55° 30'S and from near
sea level (at high latitude) to ca. 2000 m elevation in
Southern Chile and Argentina (Donoso 1993; Veblen
et al. 1996*c*). The first site, Shangri-La, is located at
the northern border of distribution of this species
(latitude 36° 60' S and longitude 71° 30' W, 1500 m
above sea level; Figure 1). Shangri-La site is in the
Ñuble province of Chile, which belongs to the Meso-
mediterranean belt with humid climatic conditions
(Amigo and Ramírez 1998). The aspect is southwest-
ern with a slope of 20 to 30%. The annual precipita-

tion is ca. 1800 mm and most of which falls as snow
from May to September (DGA 1999). The soils, de-
rived from andesitic rocks, are volcanic in origin.
Here the forest of *N. pumilio* is located ca. 100 m be-
low the timberline. The second site is located in a
protected area, Reserva Coyhaique (lat. 45° 52' S and
long. 72° 00' W, 900 m above sea level), in the Coy-
haique province, which belongs to the supratemper-
ate belt with humid climatic conditions (Amigo and
Ramírez 1998). The annual precipitation is ca. 1350
mm, again mainly as snow (Conama 1998). The as-
pect is south with a slope of 10%, and the stand is
located ca. 400 m below timberline. The soil is de-
rived from aeolian volcanic ash deposits.

Sampling

Sampling was restricted to areas without any history
of logging or recent stand-replacing natural disturb-
ance. Stand structure was determined from stem di-
ameter distributions, stem density and basal area; data
were collected using the point-centred quarter method
(Cottam and Curtis 1956). A master transect was
staked out more than 100 m from the forest edge (in
a randomly located manner and parallel to the forest
border) and eight 100 m transects were placed per-
pendicular to this master transect. Each transect was
spaced 30 m from its neighbour to avoid sampling of
the same area. Sample points were placed every 25 m
along each of the eight transects, resulting in five
points per transect and 40 sampling points per site.
The distance and diameter at breast height (dbh; 1.35
m) of the nearest live or dead standing tree ($>$ 5 cm
dbh) in each quarter was recorded. Saplings (stems
$\leq$ 5 cm dbh and $>$ 1.5 m tall) were sampled sepa-
rately by the same procedure described above. Sap-
ling and tree densities and basal area were scaled up
to one hectare. Dominant tree heights were estimated
from 5-10 trees per transect. Each sample point was
classified as lying under a gap, under a gap border (10
m from a gap border tree), or under closed forest. The
Mann-Whitney U-test by ranks was used to compare
structural variables (Sokal and Rohlf 1995).

In each stand all tree-fall gaps were measured
along the 8 transects to determine canopy gap and
expanded gap sizes. Only gaps from tree deaths were
considered; for example, gaps caused by rock
outcrops or swamp vegetation were not included. For
each gap-maker (tree whose mortality creates a gap;
Runkle 1981) we recorded type of damage (i.e., up-
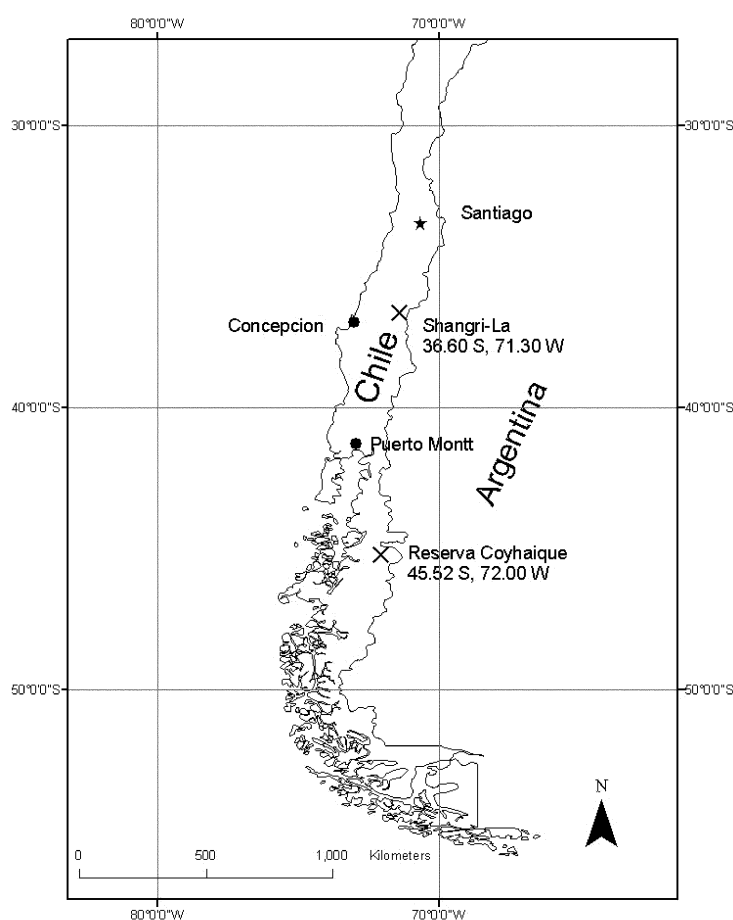rooted, dead standing, snapped trunks, or broken

Figure 1. Partial map of Chile, including the two locations (X); Shangri-La study site in Ñuble province, and Reserva Coyhaique study site in Coyhaique province (Patagonia).

branches). The compass direction and lengths of logs from snapped trunks and uprooted logs and the height of each fracture were recorded.

Canopy gap (or "developmental gap"; Lertzman et al. 1996) is defined as the vertical projection downward of any canopy opening in the forest that extends through the vegetation strata down to an average height of 2 m above ground (Brokaw 1982). Expanded gap is defined as the area formed by the canopy gap plus the adjacent area delimited by the stem bases of the canopy trees surrounding the canopy gap (Runkle 1982). We measured expanded gap area, as well as the canopy gap area because, at higher latitudes, sun angles are rarely near vertical. In such cases the microclimatic effects of openings in the canopy are frequently larger than and displaced from the direct vertical projection of the opening (Canham et al. 1990; Lertzman et al. 1996), even leading to a gap partitioning in species composition

(Poulson and Platt 1989), creating different microsites within the gap (Heinemann et al. 2000). The centre of each gap was located subjectively (roughly the geometrical centre). Size of the gap for both definitions was measured by taking the distance from the centre to every stem of the surrounding border trees and the distance to the crown projection as well, and combining this with the compass direction of the line (azimuth from the plot centre to each tree measured). The formula for the area of a gap then is:

$$\text{Area of a gap} = \sum_{g=\text{n}1}^{n} \left(0.5 * di * \left(dj * \cos\left(90 - ai\right)\right)\right)$$

(1)

Here di is the distance from the centre to the first randomly selected tree i; dj is the distance from the centre to the contiguous tree j, and ai is the angle

formed between both trees. A comparable approach is found in van der Meer (1995).

To calculate the total fraction of forest area under gaps (gap fraction) the line intercept sampling (LIS) method was used. Because transects are more likely to intercept a large gap than a small gap, each observation is adjusted by the size of the gap observed. The formula used to estimate gap fraction is:

Gap fraction

$$= (1/L)\sum_{j=1}^{n}(Aj/dj) \text{ Battles and Fahey } (1996) \quad (2)$$

In this formula L is the length of the line transect, n is the number of gaps found, Aj is the area measured of the jth gap found, and, dj is the "effective diameter" of the jth gap. For a convex shape (e.g. circle, ellipse), the effective diameter is $dj = P/\pi$, where P is equal to the actual perimeter. By the same procedure, gap abundance (gaps/ha) can be computed. In Equation 2, the area of the gap (Aj) must be replaced by 1, which represents the number of times a convex shape can be intercepted by a transect (Battles and Fahey 1996). We scaled our results to fraction of a hectare values:

$$\text{Gap abundance} = 10000 * (1/L) * \sum_{j=1}^{n}(1/dj) \quad (3)$$

Variance was estimated from the deviations between the overall mean and the gap fractions calculated for each transect. The contribution of each transect to the total variance was similar because each transect was the same length (c.f., de Vries 1986). The distinction between canopy and expanded gap was maintained to compare results with other studies. To test for site differences in gap fraction and gap abundance, Mann-Whitney U-test by ranks was computed using the means (Sokal and Rohlf 1995).

Regeneration and gap characteristics

All saplings in gaps were counted to assess regeneration. Five saplings (the tallest ones) from the centre of the gap were chosen for measuring the shoot length from the previous year (in cm), which was derived from the last bud scar, identifiable by short internodes (Puntieri et al. 1999). We assumed that each axis develops only one growth unit (each shoot portion ex-

tended during an interrupted time period; Hallé et al. 1978) in each spring-summer period, or one year. Den Ouden (1999) showed that this length is correlated with the height increment. The sapling density and the shoot length from the previous year were the dependent variables for two regression analyses (one for each variable), with canopy or expanded gap size as the independent variable (x) and sapling density or shoot length as the dependent variable (y).

Spatial dispersion

The spatial dispersion of trees was assessed in a 50×50 m plot at Shangri-La and in a 30×30 m plot in R. Coyhaique. Because the degree of clumping in the forest depends on tree development, the degree of dispersion was determined separately for trees ≤ 20 cm dbh and for trees > 20 cm dbh. We used Morisita's index to determine the departure from a random dispersion:

$$\text{Im} = q * \sum_{i=1}^{n}(ni*(ni-1))/(N*(N-1))$$
$$\text{Morisita } (1959) \quad (4)$$

Where Im is the Morisita's index, q is the number of quadrants into which the plot is divided, ni is the number of stems in the ith quadrant, and N is the total number of individuals in all q quadrants.

The value of Im equals 1 if trees are randomly distributed (random means the independent assortment of individuals into quadrants with an equal probability of each individual occurring in any quadrant). If individuals are clumped, meaning a high proportion of individuals concentrated into only a few of the quadrants, then Im is > 1; if the individuals are evenly distributed or hyperdispersed, then Im is < 1. Significance of departure from randomness of Im was assessed by the F-test of Morisita:

$$\chi^2 = \text{Im} * (N-1) + q - N$$
$$\text{Morisita } (1959) \quad (5)$$

If $\chi^2_{\text{calculated}} > \chi^2_{\text{(q-1; 0,05) Table}}$, the pattern is different from random,

If $\chi^2_{\text{calculated}} \leq \chi^2_{\text{(q-1; 0,05) Table}}$, the pattern is random.

For each plot (square plot) we recounted all of the trees, mapping them in Cartesian coordinates. From these data, it is possible to calculate the Morisita's in-
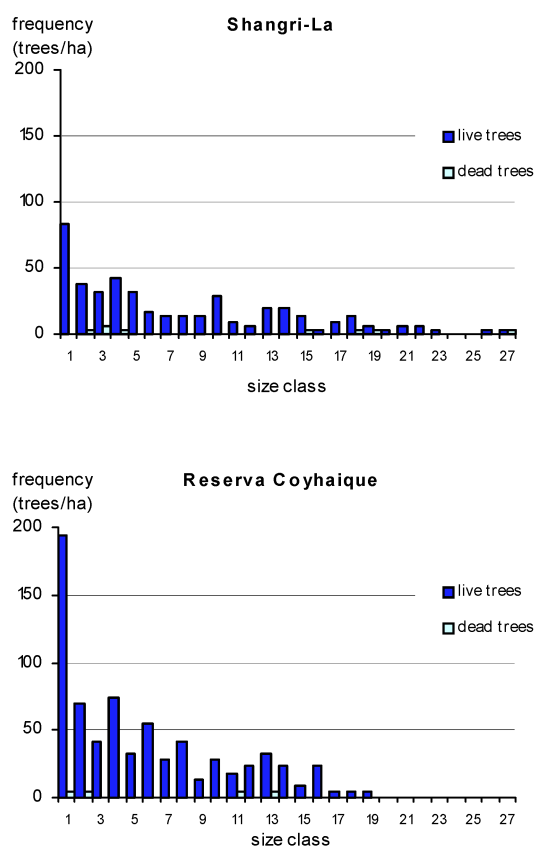
Table 1. Stand structural variables for Shangri-La and Reserva Coyhaique sites. The values correspond to the live trees, which constitutes over 95% of the total population. Means followed by the same letter were not significantly different ($P > 0.05$, Mann-Whitney U-test).

site	Density (trees/ ha)	Basal area (m^2/ha)	Den-sity (sapl./ ha)	Mean dbh (cm)	Max. dbh	Domi-nant height (m)
Shangri-La	499*a*	68.04*a*	318*a*	42.3	137	25.9
R. Coy-haique	782*b*	61.96*a*	691*b*	30.9	97	20.1

Table 2. Sapling density beneath the three conditions in the forest; in the gap, beneath canopy or on the gap border. Similar letters mean no significant difference among conditions on the site (Kruskal-Wallis, $P > 0.05$).

Site	Condition	n	Mean distance (m) (Std. Error)	Density (sapl./ ha)
Shangri-La	Closed forest	22	7.98 (1.11)	157*a*
	Gap border	7	5.93 (1.00)	284*a*
	Gap	11	7.43 (1.09)	181*a*
R. Coy-haique	Closed forest	17	7.78 (0.95)	165*a*
	Gap border	9	3.46 (0.59)	837*b*
	Gap	14	2.42 (0.43)	1708*b*

Figure 2. Tree size diagrams for Shangri-La and Reserva Coyhaique sites. The size classes used are for trees ≥ 5-cm dbh; each size class is 5 cm wide.

dex for different contiguous-quadrant sizes. These quadrant sizes were represented in 16 classes of size.

Results

Stand structure

Nothofagus pumilio was the only tree species found at the two sites. Both sites are located just below the timberline. Stands of *N. pumilio* at both sites had similar tree diameter distributions and basal area (Figure 2). No significant differences in diameter distributions were detected based on Kolmogorov-Smirnov goodness of fit procedure ($p > 0.05$; Sokal and Rohlf 1995), and no significant differences in total basal area of trees occurred at the two sites (Mann-Whitney U-test, $p > 0.05$). Nonetheless, adult tree and sapling densities were significantly lower at Shangri-La than at R. Coyhaique (Mann-Whitney U-test, $p < 0.05$; Table 1). No significant differences were found between densities of saplings growing under closed forest, gaps or gap borders at Shangri-La, based on the analysis of sapling abundance through the stand; however, the sapling density growing under closed forest was significantly lower than under gaps or gap borders in R. Coyhaique (Kruskal-Wallis, $p < 0.05$; Table 2).

Size and fraction of gaps in the forest

In general, the range of gap sizes was larger at Shangri-La than at R. Coyhaique (Figure 3). Canopy gaps ≤ 200 m^2 (Shangri-La) and ≤ 150 m^2 (R. Coyhaique) were most frequent, with a few very large canopy gaps present only at Shangri-La. We found no significant differences between the means of expanded and canopy gaps, or gap fractions when comparing both site. Gaps were significantly less abun-
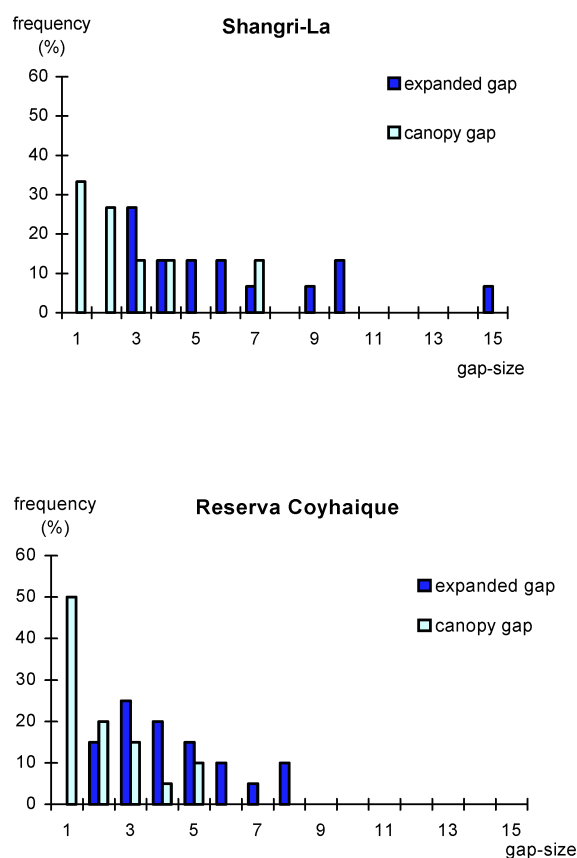
Figure 3. Diagrams of frequency of gap size distributions (n_1=15; n_2=20). Class sizes are in 50 m^2.

Table 3. Summaries of expanded and canopy gaps found in Shangri-La and R. Coyhaique study sites. The sampling was conducted through 8 100-m parallel transects at each site. Similar letters mean no significant difference among conditions on one site (Kruskal-Wallis, P > 0.05). Figures in parenthesis are standard deviations. For gap fraction and gap abundance the variance was calculated using the de Vries's formula (1986), when the sampling had more than one line.

	Shangri-La	R. Coyhaique
number of gaps	15	20
mean gap area (m^2)		
expanded	288.7a (173.0)	189.1a (92.2)
canopy	112.9a (95.1)	77.9a (64.9)
mean gap perimeter (m)		
expanded	67.1 (21.2)	58 (16.7)
canopy	42.6 (16.5)	39.9 (18.5)
gap fraction (% of forest)		
expanded	23.8a (14.3)	24.4a (19.1)
canopy	13.6a (9.7)	13.1a (9.9)
gap area range (m^2)		
expanded	125.5-744.1	60.2-394
canopy	20.9-312.1	6.1-228.9
gap abundance (#/ha)		
expanded	10a	15b

dant at Shangri-La (10 gaps/ha) than at R. Coyhaique (15 gaps/ha; p < 0.05; Table 3).

Spatial patterns

At both sites, *N. pumilio* displayed a clumped distribution for the younger cohorts and a random distribution for the older cohorts (assuming a positive correlation between age and diameter). Trees > 20 cm dbh were randomly dispersed, and trees ≤ 20 cm dbh were clumped (F-test of Morisita, p < 0.05; Figure 4). Maximum clustering occurred at plot size class 1 (quadrant size of 2.5×2.5 m; 6.25 m^2) at R. Coyhaique, and this clustering pattern continued until plot size class 13 (quadrant size of 15×15 m; 225 m^2). At Shangri-La, the maximal clustering began at plot size class 5 (quadrant size of 4.2×4.2 m; 17.6 m^2) and continued to plot size class 14 (16.7×16.7 m; 279 m^2); these values are also related to canopy gap sizes (20.9 to 312.1 m^2; see Table 3).

Tree fall characteristics

About 60% of the gaps in both sites involved the death of more than one tree (see Table 4). The total number of gap-makers was 30 and 35; the mean number of gap-makers per gap was 2 (s.e. 0.28) and 1.8 (s.e. 0.23), for Shangri-La and R. Coyhaique, respectively. The most common type of gap formation was by snapped and uprooted trees, accounting for 47% and 40% at Shangri-La, and 49% and 37% at R. Coyhaique, respectively. There were no differences detected in the proportion of tree-fall mode between sites, for snapped and uprooted trees (Mann-Whitney U-test, p > 0.05). Broken branches were infrequently detected. On the other hand, dead standing trees were present in 14% of the gaps at Shangri-La. The mean frequent direction of the tree falls was in accordance with the prevailing winds, e.g. southwest (240°) for Shangri-La and southeast (111°) for R. Coyhaique (Table 4).
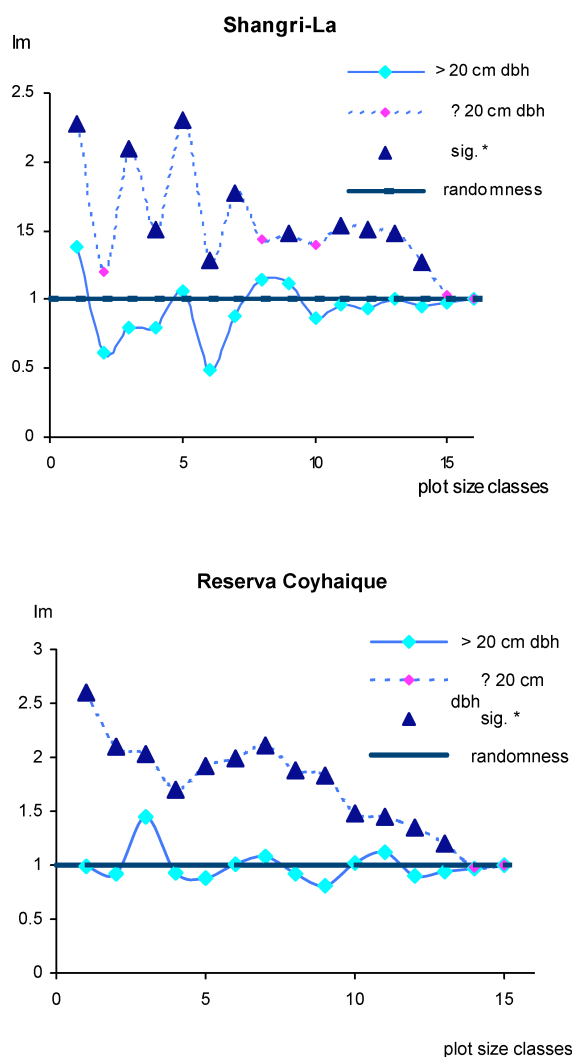
Shangri-La

legend:
- > 20 cm dbh
- ? 20 cm dbh
- sig. *
- randomness

Reserva Coyhaique

legend:
- > 20 cm dbh
- ? 20 cm dbh
- sig. *
- randomness

Figure 4. Morisita's index (Im) for Shangri-La and R. Coyhaique sites. These values indicate the departure from a randomly tree distribution at different quadrant sizes.

Gap and regeneration characteristics

The density of saplings was not significantly related to gap size, either for canopy or expanded gap areas (Table 5). Height increments (shoot lengths the previous year) were related to gap size at Shangri-La (canopy gap: $r^2 = 0.72$; expanded gap $r^2 = 0.69$). However, at R. Coyhaique, the height increment was not related to gap size.

Discussion and conclusions

Regeneration and structural patterns

The sapling densities under closed forest for both sites were similar, but density in gaps at R. Coyhaique was much greater than the values found at Shangri-La. We propose that low sapling density in gaps at Shangri-La results from competition with understory species, in this case a bamboo species, *Chusquea quila*. The distribution of this bamboo species coincides with the northern distribution of *N. pumilio* (Donoso 1993). *Chusquea quila* is not present in the southern forests (R. Coyhaique), possibly because it has less resistance to the lower temperatures and the longer periods of snow persistence (Veblen et al. 1979). Another possible explanation is differences in the altitudinal location of both sites. The stand at Shangri-La is closer to the timberline than R. Coyhaique, which might explain the lower density of sapling and adult trees. Cuevas (2000) states that the seedling emergence and density decrease with altitude both within the forest and into the alpine zone. The proximity to the timberline along with the presence of *Chusquea quila* might possibly result in lower rates of seedling establishment.

Gap fractions

The proportion of gaps was similar in forests at both sites, despite some structural (sapling and tree density) and gap abundance differences. However, the gap fraction for these stands tended to be larger than gap fractions found in other studies. The gap fraction values found in this study were 13.6% and 23.8% in Shangri-La, and 13.1% and 24.4% in R. Coyhaique, for canopy gap and expanded gap, respectively. Rebertus and Veblen (1993) had values of 11.6% for expanded gaps in forest of *N. pumilio* in Tierra del Fuego, and this is in accordance with other studies of *Nothofagus* forests in Chile (Veblen 1989). Runkle (1990) found values of 6.9 and 14.1% for canopy and expanded gaps, respectively, in *Acer-Fagus* forests in the United States. We found only one study with similar values, and this was conducted by Stewart et al. (1991) in *Nothofagus* forests of New Zealand; they had values of 8.4 and 22.2% of gap fraction for canopy and expanded gap, respectively. All the former studies used the Runkle's method (1982) for sampling gaps, which does not consider the size of each gap as a weighting factor (de Vries 1986; Battles

Table 4. Summary of tree-fall characteristics for Shangri-La and Reserva Coyhaique sites. Similar letters between sites mean no significant differences (p > 0.05) according to Mann-Whitney U-test by ranks.

Site	N° of gapmakers	density (gapm./gap)	Type of Treefall (%)				mean dbh	Orientation
			snapped	uprooted	Dead standing	Branch breakage		
Shangri-La	30	2.0	46.7*a*	40.0*a*	13.3*a*	0*a*	69.3	240°
Coyhaique	35	1.8	48.6*a*	37.1*a*	2.9*b*	11.4*b*	58.3	111°

*Similar letters between sites mean no significant differences, (p > 0.05) according to Mann-Whitney U-test by ranks.

Table 5. Outcomes from the regression analysis performed for Shangri-La and Reserva Coyhaique study sites, between sapling density variable and height increment (shoot lengths the previous year) with canopy and expanded gap sizes

Sapling density variable	R^2	Std. error	ANOVA		Last year's shoot length variable	R^2	Std. error	ANOVA	
			F	Sig.				F.	Sig.
Shangri-La									
Expanded gap	0.16	6.07	2.01	0.18	Expanded gap	0.69	3.76	19.85	0.002*
Canopy gap	0.12	6.19	1.51	0.25	Canopy gap	0.72	3.55	23.35	0.001*
R. Coyhaique									
Expanded gap	0.01	13.89	0.12	0.73	Expanded gap	0.07	4.93	1.36	0.26
Canopy gap	0.02	13.83	0.27	0.61	Canopy gap	0.11	4.82	2.23	0.15

*Means significance for the regression between the variable and sapling density or last year's shoot length.

and Fahey 1996). In this way the differences might be due to the methods used in the prior studies, which tend to under-represent smaller gaps (Rebertus and Veblen 1993; Battles et al. 1996).

Clumpiness in gaps

The spatial analysis conducted for these stands indicated episodic tree establishment in groups, as suggested by models of stand development (Peet and Christensen 1987). Although this study did not consider age analysis, the spatial pattern established for trees within a patch appeared to shift from a clumped to a random distribution with increases in size, probably due to self-thinning. This is in accordance with other studies conducted on tree spatial distributions (Peet and Christensen 1987; Mast and Veblen 1999; Woodall 2000).

The size of the patches can be expected to resemble the size of canopy gaps, especially at the establishment stage. The maximal Morisita's index values matched the range of canopy gap sizes at both sites. Williamson (1975) and Veblen et al. (1981) also found this relation for old-growth beech-maple, and

for *Nothofagus* forests, respectively, using the same spatial pattern analysis.

Tree falls

The most common type of gap formation was by snapped and uprooted trees, in both sites. Veblen (1985) in the South of Chile and Stewart et al. (1991) in New Zealand found similar results. However, in northern Patagonia uprooting was reported by Veblen (1989) to be more common than we found in our study. The uprooting high frequency can be explained in soil-depth terms, because this is one of the most important factors in the susceptibility, frequency, and magnitude of tree-falls (Everham and Brokaw 1996). Both sites have volcanic soils, which are relatively younger than soils of lower altitudes; these soils are shallow, and the rocky fragments occurred at about 20 cm depth (Schlegel et al. 1979). Root development of the trees remains superficial with these soil characteristics, and if the trees are in the foot zone of the hill, their susceptibility to the wind may increase.

Gap size and regeneration characteristics

In old-growth *Nothofagus* stands, the establishment of new regeneration and its growth are expected to be influenced by the availability of light resources in gaps (Donoso 1993; Rebertus and Veblen 1993; Veblen et al. 1996*c*). In this study, however, sapling density was unrelated to gap size at both sites. Stewart et al. (1991) found the same lack of relation between both variables in forests of *Nothofagus* in New Zealand. This lack of relationship between density and gap size might be explained by differences in ages of gaps and especially by differences in ages of regeneration occurring in the gaps. Gap closure by lateral branch expansion of surrounding trees has not been studied, but appears not to be rapid at the sites discussed. Mortality amongst saplings in a gap also remains as an uncertain development variable not studied yet.

Additionally, the presence of advance regeneration might be important in generating no relationship of regeneration with gap size. When one or more *N. pumilio* trees die and fall, forming a gap, advance regeneration, which survived under low light levels, renews growth. The density of the advance regeneration does not depend on the gap size because it was there before gap formation. Nonetheless, the growth rate of this advance regeneration might depend on gap size. Apparently, there is a perceived ability of *N. pumilio* to persist for some time in the understory and then display rapid growth after gap formation. There have been no studies that have measured density and growth of advance regeneration in *Nothofagus* stands, before or after gap formation. On the other hand, the gap size was correlated with the height increment in the site of Shangri-La; therefore, the shoot length from the previous year might be a useful parameter to evaluate the response of regeneration performance to the canopy opening. The fact that there was no relationship at R. Coyhaique might be a result of only small differences in light intensity within gaps (Canham et al. 1990).

Silvicultural implications

Our study identified a variable association between regeneration characteristics and gap size. This variable association needs to be taken into account in designing silvicultural systems. Gap size (influencing the amount of incident light) cannot be taken as a universal predictor for the performance of the new recruitment. So far, the coherence of many features of the gap environment with gap size has strongly tempted us to use gap size as an indicator of regeneration conditions, but Lawton and Putz (1988) have already pointed out the danger of succumbing to this simplistic assumption. At least, height of the forest around the gap, as well as the form (compact or long and narrow) have to be considered together with gap size, orientation on the path of the sun, and the microsite environmental variables: humidity and light within the gap (Heinemann et al. 2000). In a broader scale, factors like homogeneity of landscape, neighbourhood effects, and disturbance-regime severity, among others, should be taken into account as well (Frelich and Reich 1999). Additionally, this reflects the importance of understanding the variation of factors acting in different altitudes and latitudes (e.g. to develop site-specific knowledge; Kohm and Franklin, 1997): where a silvicultural system based on local observations, but applied outside the region of study can become ineffective and inconsistent.

References

Amigo J. and Ramírez C. 1998. A bioclimatic classification of Chile: woodland communities in the temperate zone. Plant Ecology 136: 9–26.

Armesto J.J., Casassa I. and Dollenz O. 1992. Age structure and dynamics of Patagonian beech forest in Torres del Paine National Park, Chile. Vegetatio 98: 13–22.

Arroyo M.T.K., Donoso C., Murua R.E., Pisano E.E., Schlatter R.P. and Serey I.A. 1996. Toward an ecologically sustainable forestry project. Universidad de Chile Press, Santiago, Chile.

Battles J.J. and Fahey T.J. 1996. Spruce decline as a disturbance event in the subalpine forests of the northeastern United States. Canadian Journal of Forest Research 26: 408–421.

Battles J.J., Dushoff J.G. and Fahey T.J. 1996. Line intersect sampling of forest canopy gaps. Forest Science 42(2): 131–138.

Brokaw N.V.L. 1982. The definition of treefall gap and its effect on measures in forest dynamics. Biotropica 14: 158–160.

Canham C.D., Denslow J.S., Platt W.J., Runkle J.R., Spies T.A. and White P.S. 1990. Light regimes beneath closed canopies and treefall gaps in temperate and tropical forests. Canadian Journal of Forest Research 20: 620–631.

Conama. 1998. Aysén Reserva de Vida. Texto de Apoyo para la Educación Ambiental Regional. I Edición. Santiago, Chile.

Cottam G. and Curtis J.T. 1956. The use of distance measures in phytosociological sampling. Ecology 37: 451–460.

Cuevas J.G. 2000. Tree recruitment at the *Nothosfagus pumilio* alpine timberline in Tierra del Fuego, Chile. Journal of Ecology 88: 840–855.

De Vries P.G. 1986. Sampling theory for forest inventory. Springer Verlag, Berlin.

Den Ouden J. 1999. Experimental Research in Ecology: Notes. Landbouwuniversiteit Wageningen, The Netherlands.

DGA (Dirección General de Aguas). 1999. Informe meteorológico, Termas de Chillán, Chillán, Chile.

Donoso C. 1993. Bosques templados de Chile y Argentina: Variación, estructura y dinámica. Tercera edición. Editorial Universitaria. Santiago de Chile.

Everham E.M. and Brokaw N.V.L. 1996. Forest damage and recovery from catastrophic wind. The Botanical Review 62(2): 113–185.

Frelich L.E. and Reich P.B. 1999. Neighborhood effects, disturbance severity, and community stability in forests. Ecosystems 2: 151–166.

Hallé F., Oldeman R.A.A. and Tomlinson P.B. 1978. Tropical trees and forests. An architectural analysis. Berlin: Springer.

Heinemann K., Kitzberger T., and Veblen T.T. 2000. Influences of gap microheterogeneity on the regeneration of *Nothosfagus pumilio* in a xeric old-growth forest of northwestern Patagonia, Argentina. Canadian Journal of Forest Research 30: 25–31.

Kimmins J.P. 1997. Forest ecology. A foundation for sustainable management. Second Edition. Prentice-Hall, New York.

Kohm K.A. and Franklin J.F. (eds), 1997. Creating a forestry for the 21st century. The science of ecosystem management. Island Press.

Lawton R.O. and Putz F.E. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. Ecology 69(3): 764–777.

Lertzman K.P., Sutherland G.D., Inselberg A. and Saunders S.C. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. Ecology 77(4): 1254–1270.

Marticorena C. and Quezada M. 1985. Catálogo de la flora vascular de Chile. Gayana 42: 1–157.

Mast J.N. and Veblen T.T. 1999. Tree spatial patterns and stand development along the pine-grassland ecotone in the Colorado Front Range. Canadian Journal of Forest Research 29: 575–584.

Morisita M. 1959. Measuring the dispersion of individuals and analysis of the distributional patterns. Memories of the Faculty of Science of Kyushu University. Series E, Biology 2: 215–235.

Peet R.K. and Christensen N.L. 1987. Competition and tree death. BioScience 37: 586–595.

Pollmann W. 2002. Effects of natural disturbance and selective logging on *Nothosfagus* forests in south-central Chile. Journal of Biogeography 29: 955–970.

Poulson T.L. and Platt W.J. 1989. Gap light regimes influence canopy tree diversity. Ecology 70(3): 553–555.

Puntieri J., Raffaele E., Martínez P., Barthélémy D. and Brion C. 1999. Morphological and architectural features of young *Nothosfagus pumilio* (Poepp. and Endl.) Krasser (Fagaceae). Botanical Journal of the Linnean Society 130: 395–410.

Read J. and Hill R.S. 1985. Photosynthetic response to light of Australian and Chilean species of *Nothosfagus* and their relevance to the rainforest dynamic. New Phytologist 101: 731–42.

Rebertus A.J. and Veblen T.T. 1993. Structure and tree-fall gap dynamics of old-growth *Nothosfagus* forests in Tierra del Fuego, Argentina. Journal of Vegetation Science 4: 461–654.

Runkle J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology 62: 1041–1051.

Runkle J.R. 1982. Patterns of disturbance in some old-growth mesic forests of the eastern North America. Ecology 63: 1533–1546.

Runkle J.R. 1990. Gap dynamics in an Ohio Acer-Fagus forest and speculations on the geography of disturbance. Canadian Journal of Forest Research 20: 632–641.

Schlegel F., Veblen T., Escobar B. 1979. Estudio ecológico de la estructura, composición, semillación y regeneración del bosque de lenga (*Nothosfagus pumilio*) XI Región. Informe de convenio n° 8. Universidad Austral de Chile, Valdivia, Chile.

Sokal R.R. and Rohlf F.J. 1995. Biometry. The principles and practice of statistics in biology research. Third edition. W.H. Freeman, New York.

Stewart G.H., Rose A.B. and Veblen T.T. 1991. Forest development in canopy gaps in old-growth beech (Nothofagus) forests, New Zealand. Journal of Vegetation Science 2: 679–690.

Uriarte A. and Grosse H. 1991. Los bosques de lenga. Una orientación para su manejo (recopilación bibliográfica). Instituto Forestal. Informe técnico 126. Concepción, Chile.

Van der Meer P.J. 1995. Canopy dynamics of a tropical rain forest in French Guiana. Thesis Landbouwuniversiteit Wageningen, The Netherlands.

Veblen T.T. 1985. Stand dynamics in Chilean *Nothosfagus* forests. In: Pickett S.T.A. and White P.S. (eds), The ecology of natural disturbances and patch dynamics. Academic Press, Orlando, FL.

Veblen T.T. 1989. Nothofagus regeneration in treefall gaps in northern Patagonia. Canadian Journal of Forest Research 19: 243–249.

Veblen T.T. and Ashton D.H. 1978. Catastrophic influences on the vegetation of the Valdivian Andes. Vegetatio 36: 149–67.

Veblen T.T., Veblen A.T. and Schlegel F.M. 1979. Understory patterns in mixed evergreen-deciduous *Nothosfagus* forests in Chile. Journal of Ecology 67: 809–823.

Veblen T.T., Donoso C., Schlegel F.M. and Escobar B. 1981. Forest dynamics in South-central Chile. Journal of Biogeography 8: 211–247.

Veblen T.T., Hill R.S., and Read J. 1996a. Introduction: Themes and concepts in the study of *Nothosfagus* forests. In: Veblen T.T., Hill R.S. and Read J. (eds), The ecology and biogeography of Nothofagus forests. Yale University Press, New Haven.

Veblen T.T., Donoso C., Kitzberger T. and Rebertus A.J. 1996b. Ecology of southern Chilean and Argentinean *Nothosfagus* forests. In: Veblen T.T., Hill R.S. and Read J. (eds), The ecology and biogeography of *Nothosfagus* forests. Yale University Press, New Haven.

Veblen T.T., Kitzberger T., Burns B.R., and Rebertus A.J. 1996c. Perturbaciones y regeneración en bosques andinos del sur de Chile y Argentina. Pp. 169-198. In: Armesto J.J., Arroyo M.K. and Villagrán C. (eds), Ecología del bosque nativo de Chile. Universidad de Chile Press, Santiago.

Veblen T.T., Kitzberger T. and Villalba R. Nuevos paradigmas en ecología y su influencia sobre el conocimiento de la dinámica de los bosques del sur de Argentina y Chile. In: Fragi J. and Brown A. (eds), Ecología y manejo de los bosques Argentinos (in press).

Whitmore T.C. 1989. Canopy gaps and the two major groups of forest of trees. Ecology 70(3): 536–538.

Williamson G.B. 1975. Pattern and seral composition in an old-growth beech-maple forest. Ecology 56: 727–731.

Woodall C.W. 2000. Growth and structural dynamics of uneven-aged ponderosa pine stands in eastern Montana. Ph.D. dissertation, University of Montana, Missoula.