

Disturbance and regeneration dynamics of an old-growth 1 North Patagonian rain forest in Chiloé Island, Chile

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Summary

1 Few studies have addressed the mechanisms of coexistence of shade-tolerant and intolerant tree species in the canopy of old-growth, lowland rain forests of southern South America. We explored the hypothesis that their forest dynamics result from frequent, single tree-fall gap episodes.

2 We analysed the disturbance regime and assessed the regeneration modes of shade-tolerant and intolerant canopy trees in a lowland, old growth North Patagonian rain forest in Chiloé Island (42° S) using dendroecological methods.

3 Dominant canopy trees were the shade-intolerant *Nothofagus nitida* (Fagaceae), *Drimys winteri* (Winteraceae) and the tolerant *Podocarpus nubigena* (Podocarpaceae). The oldest individuals, however, were represented by *Saxegothaea conspicua*, Podocarpaceae (shade tolerant > 498 years) and *Weinmannia trichosperma*, Cunnoniaceae (intolerant > 382 years). Shade-tolerant species have regenerated continuously for the past 400 years, but recruitment of shade-intolerant species has increased only in the past 50 years. These regeneration patterns suggest a lack of catastrophic disturbance, at least since 1650.

4 Analysis of tree radial growth patterns revealed frequent moderate releases of both shade-tolerant and intolerant tree species, consistent with frequent small-scale disturbances, such as individual tree-fall gaps. Increased releases, peaking in 1940 and followed by enhanced recruitment, may be a consequence of individual tree-falls induced by low-intensity windstorms or limited selective logging. Such disturbances have occurred for at least 250 years, but have had little overall effect on stand structure and canopy composition.

5 The replacement and coexistence of shade-tolerant and intolerant tree species in the canopy of this North Patagonian forest can be explained by frequent small-scale disturbances (i.e. gap-phase dynamics) and by the absence of large-scale natural or anthropogenic disturbances over the past four centuries.

Key-words: dendroecology, disturbance regimes, gap-phase dynamics, regeneration modes, shade-tolerance, species coexistence, temperate rain forest, tree-fall gaps

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2 Introduction

The role of disturbance in forest stand dynamics has been broadly studied because of its importance for the regeneration, coexistence and diversity of tree species (Henry & Swan 1974; Runkle 1982; Armesto & Pickett 1985; Pickett & White 1985; Foster 1988; Veblen 1992;

Runkle *et al.* 1995, 1997; Molino & Sabatier 2001). In addition, knowledge of disturbance regimes is critical for understanding the present and predicting the future composition of forests. Forest disturbance can be studied through long-term monitoring of permanent plots, but such data are currently unavailable for many forests. Given the lack of long-term data, the dendroecological approach (Fritts 1976; Schweingruber 1996), i.e. the analysis of tree radial growth and stand age structure, may be used to examine the disturbance regimes and

reconstruct the historical development of forest stands (Fritts & Swetnam 1989; Veblen 1992; Abrams & Orwig 1996). This technique provides a valuable tool to understand the year-to-year interplay of exogenous and endogenous factors that influence tree growth in a forest community (Schweingruber *et al.* 1990).

Disturbance regimes have had a major influence on forest structure and composition in temperate forests of southern South America (Veblen 1989; Veblen & Alaback 1996; Veblen *et al.* 1996). Andean temperate forests are periodically devastated by volcanism, landslides and mudflows triggered by earthquakes (Veblen & Ashton 1978; Veblen *et al.* 1981; Veblen 1985). These forests are often dominated by pioneer *Nothofagus* species (e.g. *N. dombeyi*) and shade-intolerant conifers such as *Fitzroya cupressoides* (Lara 1991; Donoso 1993; Donoso & Lara 1999). In contrast, lowland and mid-elevation coastal forests are dominated by evergreen, broad-leaved, shade-tolerant tree species, with a lower frequency or complete absence of *Nothofagus* and shade-intolerant conifers (Veblen *et al.* 1981; Donoso *et al.* 1984; Armesto & Figueroa 1987; Armesto & Fuentes 1988). This contrasting forest composition has been attributed to the lower frequency of large-scale disturbance and the prevalence of gap-phase dynamics in coastal forests (Veblen *et al.* 1981; Armesto & Fuentes 1988; Bustamante & Armesto 1995; Armesto *et al.* 1996). However, the dynamics associated with multiple gap episodes and low-intensity disturbances proposed for these forests has not been documented and dendroecological methods have rarely been used in mixed evergreen temperate rain forest (Roig 2000). In addition, old-growth stands suitable for study are becoming rare in human-dominated, lowland areas of southern South America. Old-growth North Patagonian rain forests are still found in rural areas of northern Chiloé Island (Veblen *et al.* 1983; Armesto *et al.* 1995). A mixture of shade-intolerant and shade-tolerant tree species dominates the canopy of these remnant, old-growth stands (Aravena *et al.* 2002), but no hypotheses have been advanced to explain this mixed canopy composition.

We examined the long-term regeneration dynamics of such stands to explore the hypothesis that frequent gap-creating tree-falls promote the coexistence of tree species with different degrees of shade tolerance. Our specific objectives are (i) to assess disturbance frequency from a tree-ring analysis of the main canopy species, and (ii) to analyse the regeneration modes (Veblen 1992) of shade-tolerant and intolerant canopy trees in relation to disturbance, using an intensive dendroecological analysis. The results are used to seek an explanation for the present structure and composition of this lowland forest.

Materials and methods

STUDY SITE

The study was conducted at Senda Darwin Biological Station in northern Chiloé Island, Chile (41°50' S),

about 20 km north of the city of Ancud. Fragments of both secondary and primary forests occur over rolling hills of low altitude (50–100 m a.s.l.) and are dispersed in a matrix of bogs, shrublands and artificial grasslands. The present landscape has been shaped by a history of widespread use of fire to clear land for pastures since the late 1800s followed by selective logging of remaining forest patches (Willson & Armesto 1996). Soils are generally thin (< 1 m), having originated from Pleistocene moraine fields and glacial outwash plains, and often have poor drainage (Denton *et al.* 1999; Carmona *et al.* 2002). The prevailing climate is wet-temperate with strong oceanic influence (Di Castri & Hajek 1976); rainfall occurs throughout the year, with an annual average of 2090 mm, and mean annual temperature is 12 °C. Mean maximum and minimum monthly temperatures are 16 °C (January) and 5 °C (July) (Aravena *et al.* 2002).

We studied a remnant stand of North Patagonian rain forest that has both conifers and angiosperms in the canopy. Floristically, this forest type is defined by the mixed dominance of *Podocarpus nubigena* (Podocarpaceae), *Drimys winteri* (Winteraceae) and *Nothofagus nitida* (Fagaceae) (Veblen *et al.* 1983; Armesto *et al.* 1995), with *Tepualia stipularis* and other Myrtaceous tree species common in the understorey. Epiphytes include filmy ferns (e.g. *Hymenophyllum* spp., *Hymenoglossum cruentum*) and angiosperms (e.g. Gesneriaceae and Bromeliaceae). Although no data exist on the specific area covered by North Patagonian forests, one of the main types of evergreen rain forest in southern South America, their geographical distribution (40–45° S) and altitudinal range (0–600 m) is extensive (Armesto *et al.* 1995). Data on floristic composition, tree regeneration, avian community structure, seed rain patterns, epiphytic cover and maximum tree ages indicate the stand is an old-growth forest (Willson *et al.* 1994; Smith-Ramirez *et al.* 1998; Armesto *et al.* 2001; Aravena *et al.* 2002; Carmona *et al.* 2002; Christie & Armesto 2003; Muñoz *et al.* 2003). Its structure and composition is similar to that described for both old-growth temperate rain forests elsewhere on Chiloé Island (Aravena 1991; Donoso *et al.* 1985, 1984; Veblen 1985; Lusk 1996a; Aravena *et al.* 2002) and coastal temperate rain forests on the mainland (Lusk 1995, 1996a, 1996b; Donoso 2002). No evidence of recent catastrophic disturbance, such as fire, or stand-scale timber extraction was detected. Although this stand is likely to reflect the history of North Patagonian old-growth forests in northern Chiloé Island, human impact, mainly small-scale tree removal, cannot be ruled out in such a populated rural area.

STRUCTURE AND FLORISTIC COMPOSITION

We selected 1 ha of the stand, at least 200 m away from any edge, to characterize its structure and floristic composition. We sampled two permanently marked plots, each 20 × 50 m, located at opposite ends of the delimited

Table 1 Density, dominance and relative importance for tree species in a North Patagonian rain forest in northern Chiloé Island, Chile (plots 1 and 2 added). To = shade-tolerant, In = shade-intolerant, It = intermediate (Figueroa & Lusk 2001; Aravena *et al.* 2002)

Species		Density (N ha ⁻¹)	Relative density (%)	Dominance (m ² ha ⁻¹)	Relative dominance (%)	Relative importance (RI) (%)
Main canopy species						
<i>Podocarpus nubigena</i>	To	490	18.8	16.1	22.4	41.2
<i>Nothofagus nitida</i>	In	155	5.9	17.5	24.3	30.2
<i>Drimys winteri</i>	In	385	14.8	5.2	7.2	21.9
<i>Weinmannia trichosperma</i>	In	25	1.0	13.8	19.1	20.1
<i>Saxegothaea conspicua</i>	To	35	1.3	2.1	2.8	4.2
<i>Laurehopsis philippiana</i>	To	15	0.6	0.7	0.9	1.5
Subcanopy and understorey species						
<i>Tepualia stipularis</i>	In	925	35.4	11.1	15.5	50.9
<i>Crinodendron hookerianum</i>	It	325	12.5	2.1	2.9	15.4
<i>Calchuyapaniculata</i>	It	140	5.4	0.7	0.9	6.3
<i>Amomyrtus luma</i>	To	90	3.4	0.7	0.9	4.4
<i>Gevuina avellana</i>	It	15	0.6	2.1	2.9	3.5
<i>Myrceugeniaparviflora</i>	To	10	0.4	0.0	0.0	0.4
Total		2610		72.0		

area. We identified all trees (stems > 1.3 m height and > 5 cm diameter at 1.3 m, d.b.h.) rooted within the plots and recorded their d.b.h. Stems were classified as alive (healthy), some branches dead, or standing dead. The relative importance (RI) of each tree species was calculated adding relative density (% of number of trees) to relative dominance (% of basal area) (Cottam & Curtis 1956). Saplings (stem > 1.3 m in height but < 5 cm d.b.h.) were counted and identified to species in a 500-m² subplot inside each permanent plot. Seedlings, *sensu lato* (stems < 1.3 m height), were identified to species and counted within 204-m² quadrats, located randomly within each 0.1-ha plot. We also constructed a vertical profile of the stand (Mueller-Dombois & Ellenberg 1974), including all trees present in a 5 m-wide transect along the longest side (50 m) of each permanent plot. We measured height, crown width (in two opposite directions) and the height of the first canopy branch for all trees in the transect. We classified species according to shade-tolerance (Table 1) following Aravena *et al.* (2002) and Figueroa & Lusk (2001). Nomenclature follows Marticorena & Rodriguez (1995) and Marticorena & Quezada (1985).

DENDROECOLOGICAL ANALYSIS

In winter 2000, we randomly located 10 400-m² plots within the large 1-ha plot, where we cored all stems of the main canopy trees (> 10 cm d.b.h.). In addition, we collected wedges of stems < 10 cm d.b.h. in 10 subplots of 10 m² distributed randomly within the 1-ha plot. Both wedges and cores were obtained at about 0.3 m from the base of the stem and were processed following the techniques outlined in Stokes & Smiley (1968). We obtained a total of 400 samples (cores and wedges) but 11.8% of them had rotten centres. Samples with less than 25% of the stem radii intact were discarded. Wedges and cores were used to assess stand age structure and analyse tree radial growth. Annual rings were counted

and visually cross-dated assigning a calendar year to each tree ring, according to the latest ring's date (Fritts 1976). For dating purposes, we followed Schulman's (1956) convention for the southern hemisphere, which assigns to each tree-ring the date in which radial growth started. The computer program COFECHA (Holmes 1983) was used to detect measurement and cross-dating errors. Annual growth increments were measured to the nearest 0.01 mm with an increment-measuring device and recorded in a computer. Minimum tree ages were estimated by counting tree-rings of each core. For cores where the pith was missing, the number of rings to the pith was estimated by the geometrical method of Duncan (1989). For complete cores of main canopy species, recruitment date was the year when the tree reached coring height, corrected according to Lara (1991).

Each sample was examined for releases in radial growth. Releases were analysed to search for evidence of canopy disturbances and used to infer stand dynamics. Based on studies of northern hemisphere forests (Lorimer & Frelich 1989; Veblen *et al.* 1991; Nowacki & Abrams 1997) and our analysis of radial growth of main canopy tree species, we defined a major release as > 100% increase in average radial growth lasting for at least 15 years and a moderate release as > 50% increase in average radial growth lasting for at least 15 years (Lorimer & Frelich 1989). We used these sustained release criteria (15 years) to eliminate short-term climatic pulses and gradual ring-width changes due to tree ageing, bole geometry and long-term climate shifts (Lorimer & Frelich 1989; Nowacki & Abrams 1997).

Results

STAND STRUCTURE

A total of 12 tree species were present (Table 1), of which the dominants were the conifer *P. nubigena* and the angiosperms *N. nitida*, *D. winteri* and *Weinmannia*

Table 2 Seedling (mean of 40 plots of 1 m²) ± standard error, and sapling (mean of 2 plots of 500 m²) density in a North Patagonian rain forest in northern Chiloé Island, Chile

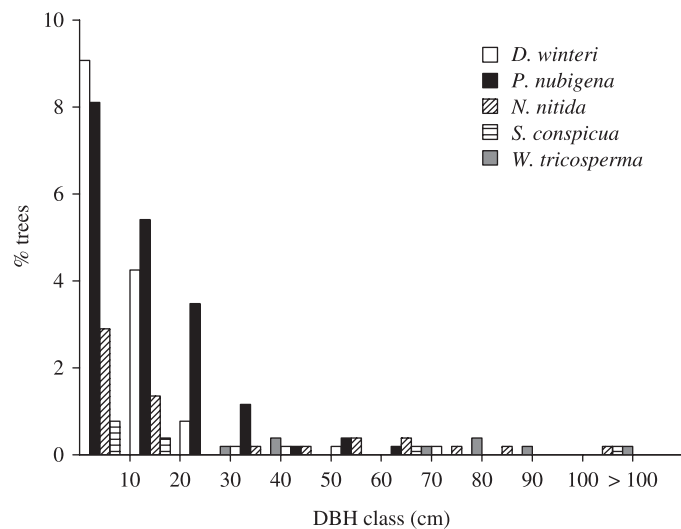
Species	Seedlings		Saplings	
	Density (N ha ⁻¹)	(%)	Density (N ha ⁻¹)	(%)
<i>Pseudopanax laetevirens</i>	175 500 ± 46763	46.8	0	0.0
<i>Drimys winteri</i>	74 250 ± 12278	19.8	470	12.2
<i>Amomyrtus luma</i>	65 250 ± 9289	17.4	1090	28.4
<i>Podocarpus nubigena</i>	29 750 ± 6144	7.9	520	13.5
<i>Caldcluvia paniculata</i>	8 750 ± 2846	2.3	1020	26.6
<i>Nothofagus nitida</i>	8 250 ± 2993	2.2	20	0.5
<i>Myrceugenia planipes</i>	7 000 ± 2824	1.9	360	9.4
<i>Saxegothea conspicua</i>	3 750 ± 1743	1.0	160	4.2
<i>Crinodendron hookerianum</i>	1 750 ± 869	0.5	190	4.9
<i>Laurehopsis philippiana</i>	750 ± 422	0.2	10	0.3
<i>Weinmannia trichosperma</i>	250 ± 250	0.1	0	0.0
<i>Tepualia stipularis</i>	0	0.0	260	6.8
Total	375 250		3840	

trichosperma (Cunoniaceae). *P. nubigena* contributed in terms of both number and size of trees. Both *N. nitida* and *W. trichosperma* were represented by a few, large individuals, and contributed much to stand basal area rather than density (Table 1), whereas *D. winteri* had few large trees and its RI resulted mostly from a high stem density. The only other canopy species, the *Saxegothea conspicua* (Podocarpaceae), had a comparatively low relative importance. The tree species with the highest density in the subcanopy was *Tepualia stipularis*, which has long, prostrate stems that reach up to 50 cm diameter, with many vertical vegetative stems sprouting, but rarely reach the canopy. The understory species *Crinodendron hookerianum* (Elaeocarpaceae) had a high stem density but, as all were < 15 cm d.b.h., a small basal area.

Pseudopanax laetevirens (Araliaceae) was the most abundant seedling (Table 2) but had no saplings or canopy trees within the stand. Propagules of this species come

from individuals growing hemi-epiphytically on large emergent trees and, although they show successful recruitment on the forest floor, they have low survival capacity in the understory. Main canopy species regeneration was numerically dominated by seedlings of *D. winteri* and subcanopy species by *Amomyrtus luma* (Myrtaceae) (Table 2). The other dominant species were present as seedlings or saplings, except *W. trichosperma*, which had almost no regeneration. *T. stipularis* lacked seedlings but this was compensated for by its profuse vegetative reproduction. Saplings were dominated by *A. luma* and *Caldcluvia paniculata* (Cunoniaceae), which together contributed > 50% of sapling density. One understory species, *Gevuina avellana* (Proteaceae), had no seedlings or saplings but was only represented by a small number of stems < 20 cm d.b.h. in this forest (cf. Tables 1 and 2).

The diameter-class distribution of canopy trees (Fig. 1) fitted a negative exponential function, typical of an

**Fig. 1** Diameter (d.b.h.) class distribution of canopy trees ($n = 518$) in a lowland, North Patagonian rain forest in northern Chiloé Island, Chile.

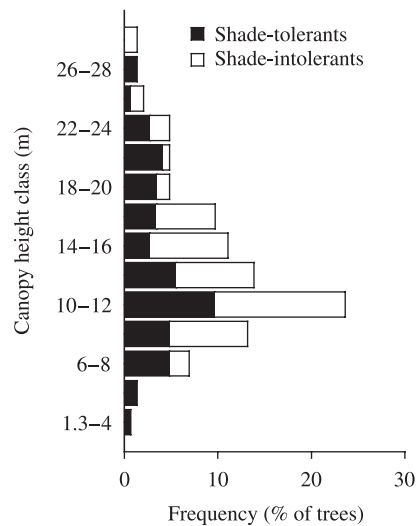


Fig. 2 Vertical distribution of shade-tolerant and intolerant tree species in a lowland, North Patagonian rain forest in northern Chiloé Island, Chile ($n = 144$).

uneven-aged stand. Large diameter classes (> 65 cm) were dominated by *N. nitida* and *W. trichosperma*, both of which are tall species that reach 27 m in height. Intermediate classes (25–55 cm d.b.h.) were dominated by *P. nubigena*. Two conifers (*P. nubigena* and *S. conspicua*) reached the canopy, with several emergent trees 26 m tall. *S. conspicua* had stems in two discrete d.b.h. classes, 65 cm and < 25 cm. The smaller d.b.h. classes in the stand (< 25 cm) were dominated by *D. winteri* and *P. nubigena* and together these accounted for most of the individuals under the canopy in the smallest diameter class (< 10 cm).

The stand vertical profile (Fig. 2) did not show evidence of stratification or layering, showing a continuous, unimodal distribution. Shade-tolerant and intolerant species contributed equally to the dominant height classes (> 20 m) and most of the tree species were distributed in a broad range of height classes. No differences were detected (Kruskal–Wallis $H = 0.098$, $P = 0.754$) in the vertical distribution of shade-tolerant and intolerant trees, except for the complete absence of shade-intolerant species below 6 m.

Table 3 Minimum tree age data for a north Patagonian rain forest in northern Chiloé Island, Chile. r^2 = correlation coefficient of DBH vs. age; * $P < 0.05$, ** $P < 0.0005$; n = number of trees sampled

Species	n	%*	Age range	Mean age	r^2	P
<i>Saxegothaea conspicua</i>	38	10.5	18–498	124	0.94	**
<i>Weinmannia trichosperma</i>	9	44.4	36–382	198	0.62	*
<i>Podocarpus nubigena</i>	100	3.0	11–236	85	0.73	**
<i>Drimys winteri</i>	127	0.0	7–87	33	0.87	**
<i>Nothofagus nitida</i>	45	15.6	17–169	54	0.53	**
Other species†	15	0.0	10–196	55	0.80	**
Total	334					

*Percentage incomplete cores (radii $< 75\%$).

†Includes *C. paniculata*, *L. philippiana*.

Age vs. diameter correlations were significant (Table 3) (see Donoso *et al.* 1984, 1985; Veblen 1985; Aravena *et al.* 2002, for similar data from other studies on Chiloé). However, *Nothofagus nitida* showed low r^2 values (0.53) because the large diameter trees often had rotten centres leading to underestimation of age. Thus, for most canopy tree species, d.b.h. distributions were roughly indicative of age structure. Age distributions (Fig. 3) confirmed that this stand had an uneven-age structure. The oldest trees in the stand were *S. conspicua* (at least 498 years) and *W. trichosperma* (382 years); both these ages cores were incomplete because of rotten tree centres and therefore underestimate the stand maximum age. Individuals of *P. nubigena*, *D. winteri* and *N. nitida* reached maximum (incomplete) ages of 236, 187 and 169 years, respectively (Table 3). *P. nubigena* was represented across all age classes < 250 years. *N. nitida* showed many individuals in the younger classes (< 50 years old) but it had a multimodal distribution with many older trees. *Drimys winteri* had a unimodal age distribution, with a mean age of 33 years. *W. trichosperma* was represented mainly by old trees, with a scattered age distribution. *S. conspicua* had several gaps in its age distribution. This conifer accumulated many saplings under the canopy, which survived for periods of up to 70 years; some, with d.b.h. < 10 cm, had a minimum age of 120 years.

TREE RADIAL GROWTH AND REGENERATION MODES

Regeneration of at least one of the main canopy species (Fig. 4) occurred in all intervals between 1770 and 1940, but an increase in recruitment of both shade-tolerant and intolerant species has occurred in the last 50 years. Shade-intolerant tree species, such as *D. winteri* and *N. nitida*, showed a sharp increase in recruitment since 1940, but only sporadic establishment prior to that decade (Fig. 4a). Considering their longevity (Lara 1991; Lusk 1999), the larger individuals of *N. nitida* and *D. winteri* with incomplete ages were probably recruited before 1850. *W. trichosperma* recruited mainly before 1750 and few individuals have become established during the last two centuries. On the other hand, shade-tolerant conifers (Fig. 4b), such as *P. nubigena* and *S. conspicua*, have recruited almost continuously.

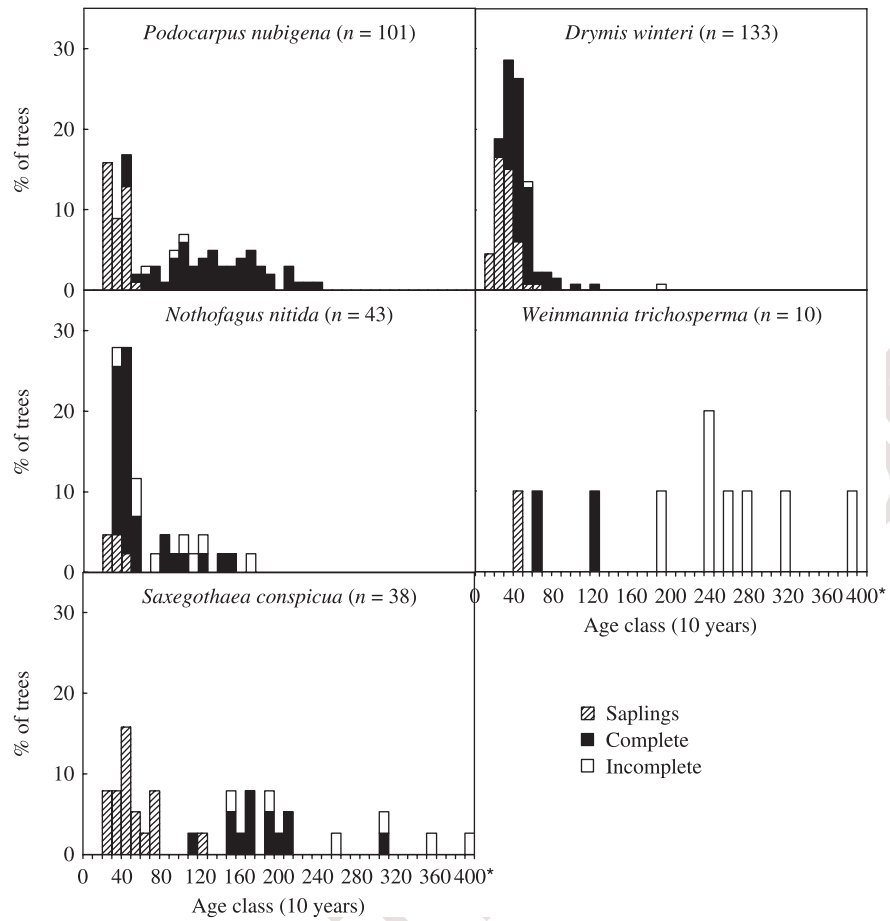


Fig. 3 Age class distribution (at 0.3 m above the ground) of saplings (individuals < 5 cm d.b.h.) and trees (d.b.h. > 5 cm) of main canopy tree species in a lowland, North Patagonian rain forest in northern Chiloé Island, Chile. *Indicates age > 400 year.

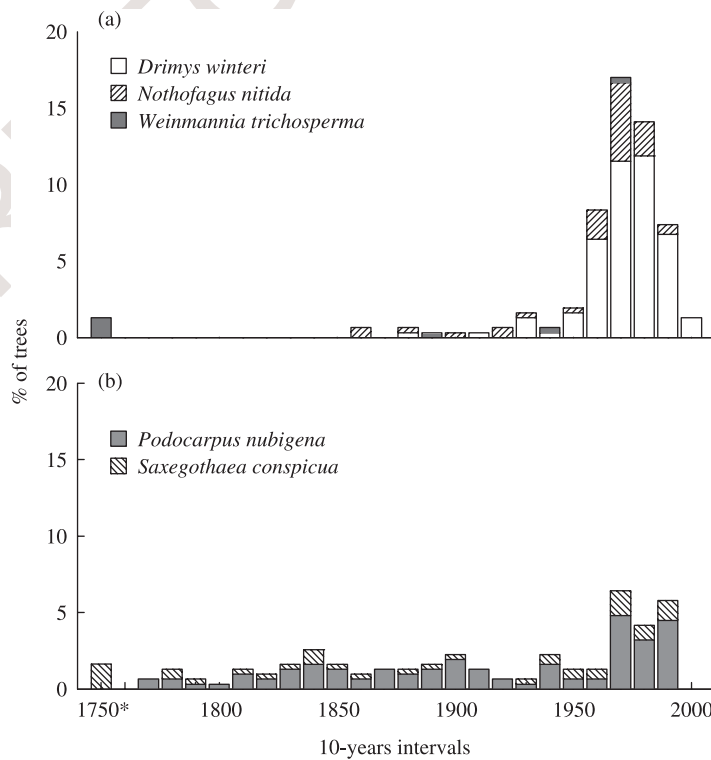


Fig. 4 Relative frequency of recruitment (n = 313) for shade-intolerant (a) and shade-tolerant (b) canopy tree species in a North Patagonian rain forest in northern Chiloé Island, Chile. Each bar represents the number of trees recruited for each decade. *Indicates that recruitment occurred before 1750.

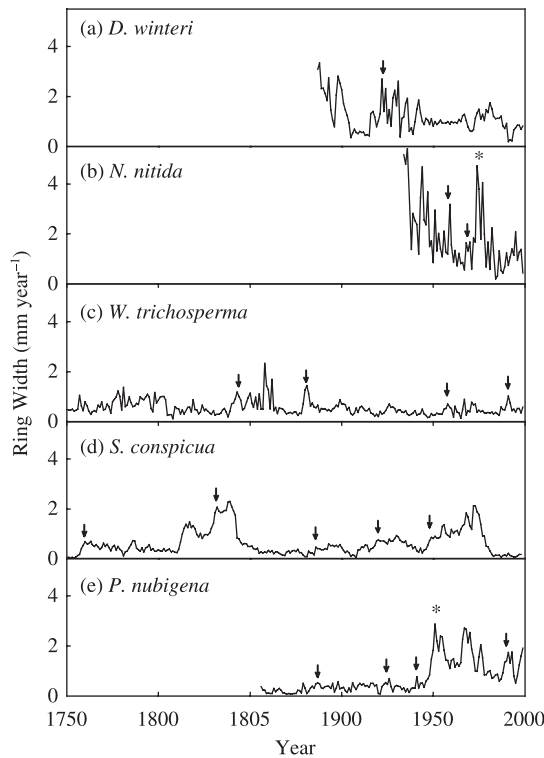


Fig. 5 Radial growth chronologies for selected trees of the five dominant species in a lowland, North Patagonian rain forest in northern Chiloé Island, Chile. Arrows indicate years of moderate releases, and asterisks show major releases (see text).

Radial growth patterns were characterized by numerous releases and suppressions, as illustrated by representative cores for the dominant species (Fig. 5). *Drimys winteri* and *N. nitida* had similar mean radial growth rate and release frequencies. Although maximum radial growth was slightly higher for *N. nitida* (Table 4), in both species high early growth was followed by a steep decline (Fig. 5a,b), a pattern typical of individuals originating in tree-fall gaps that gradually closed (Lorimer 1985; Abrams *et al.* 2001). The third shade-intolerant species, *W. Trichosperma*, had lower values for both mean tree-ring width and maximum growth and fairly constant ring width (Fig. 5c, Table 4). One of the shade-tolerants, *S. conspicua*, had the lowest mean tree-ring width (range 0.01–4 mm year⁻¹, Fig. 5d, Table 4), while the other, *Podocarpus nubigena*, often exhibited suppressed early growth, followed by abrupt releases (Fig. 5e), and both

had radial growth similar to the shade-intolerant *W. trichosperma* (Table 4).

For all species, we detected frequent releases during the past 250–400 years (Table 4) but these were more frequent for shade-tolerant species. These conifers, together with *W. trichosperma*, showed the highest growth release, reaching more than six times the average of the previous 15 years (Table 4). Nevertheless, moderate releases were more frequent than major ones, despite the fact that all species were capable of sustaining growth more than three times that in the previous 15 years. Releases were recorded in all decades for the past 250 years (Fig. 6), with pulses of higher frequency in 1780, 1840, 1870 and 1940. An abrupt increase in moderate releases occurred after 1930, affecting more than 15 trees (Fig. 6). More than half of the saplings of *N. nitida* and *D. winteri* were recruited during this period (Fig. 4a). After this peak, both releases and shade-intolerant recruitment showed a gradual decline until the present.

Discussion

STAND AGE AND STRUCTURE

Canopy composition, size distribution and vertical structure are indicative of a late successional status, with a fairly even mixture of shade-tolerant and intolerant tree species in the canopy. The similarity in vertical distributions among tree species with different shade tolerances suggests that both types can persist under the light conditions prevailing in the interior of this old-growth stand. Our vertical profile shows an absence of layering or stratification, because of the complex unimodal, height distribution of trees. This vertical structure may have important consequences for habitat creation, tree regeneration and growth in the forest (Parker & Brown 2000) and is consistent with a non-catastrophic disturbance regime.

Maximum tree ages of 300–500 years agree with canopy turnover rates estimated for southern temperate rain forests dominated by gap-phase dynamics (Veblen 1985; Stewart *et al.* 1991; Rebertus & Veblen 1993; Bustamante & Armesto 1995). However, tree ages in this North Patagonian forest are lower than those reported for other forests on Chiloé Island (Veblen 1985; Lusk 1996a), and upland coastal temperate rain forests on the

Table 4 Radial growth patterns for main canopy tree species in a north Patagonian rain forest in northern Chiloé Island, Chile. *n* = number of trees considered, SE = standard error of the mean. *Releases criterion following Lorimer & Frelith (1989). Maximum sustained release was calculated as the growth rate for the 15-year period following the release event, divided by the growth rate for the 15 years prior to release

	<i>D. winteri</i>	<i>N. nitida</i>	<i>W. trichosperma</i>	<i>S. conspicua</i>	<i>P. nubigena</i>
Number of trees	16	15	9	15	33
Mean radial growth (mm yr ⁻¹ ± SE)	1.2 ± 0.13	1.25 ± 0.14	0.59 ± 0.09	0.41 ± 0.03	0.57 ± 0.04
Maximum growth (mm yr ⁻¹)	5.8	7	3.5	4	2.9
Maximum sustained release	4.6	3.2	6.4	10	9.9
Number of moderate releases*	20	34	46	86	127
Number of major releases*	6	11	18	39	65

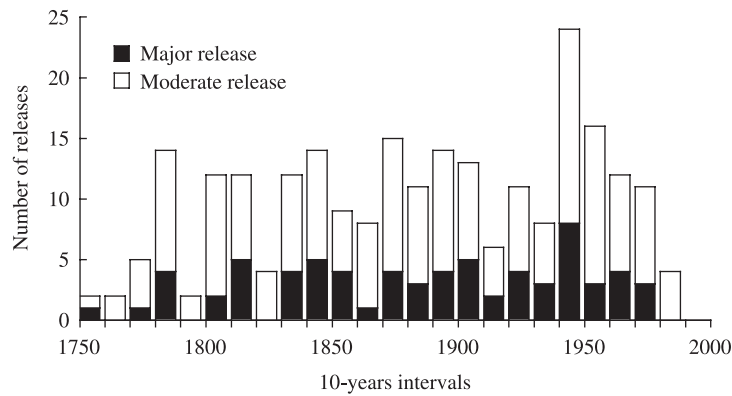


Fig. 6 Decadal distribution of major and moderate radial growth releases in 29 selected cores of dominant canopy trees in a lowland, North Patagonian rain forest in northern Chiloé Island, Chile.

mainland (Lusk 1996b, 1999). This difference may be an artifact because of the large number of tree cores with rotten centres in large d.b.h. classes. Nevertheless, minimum ages of emergent trees, size class distribution and overall age structure were all characteristic of old-growth, uneven-aged stands (Veblen 1985; Armesto & Figueroa 1987; Aravena *et al.* 2002).

DISTURBANCE REGIME AND REGENERATION DYNAMICS

The structure of this forest has been stable, i.e. unaffected by large-scale stand-disrupting disturbances, for at least 350 years. Stand age structure, the presence of shade-tolerant tree species in the canopy and their continuous regeneration, all point to the absence of allogenic coarse-scale disturbances, such as multiple tree-falls. This explains the low representation or absence of emergent pioneer, or light demanding, tree species adapted to regenerate in large clearings, such as other *Nothofagus* species (Veblen & Ashton 1978; Veblen & Alaback 1996; Veblen *et al.* 1996; Pollmann 2003), *E. cordifolia* (Donoso *et al.* 1984, 1985; Veblen & Alaback 1996) or *W. trichosperma* (Donoso 1993; Veblen & Alaback 1996; Lusk 1999). The increments in the number of releases in the 1940s, followed by enhanced recruitment in the 1960s suggest that, during this period, the canopy was affected by increased mortality probably due to natural processes. The potential effect of small-scale, selective logging, a traditional form of timber harvesting in Chiloé Island (Willson & Armesto 1996), may have caused some canopy opening since the mid-18th century, although comparable increments in release frequency were detected prior to this period of greater human impact (Fig. 6). In addition, accumulated basal area of this stand is typical of old-growth temperate rain forests free of anthropogenic impact, and several times higher than that of logged, second-growth stands (Donoso *et al.* 1985; Armesto & Figueroa 1987; Armesto & Fuentes 1988; Aravena 1991; Innes 1992; Donoso 1993; Donoso 2002).

Radial growth patterns of main canopy trees provide evidence for a high frequency of small-scale disturbances

(Figs 5 and 6). The low frequency of major growth releases supports a lack of massive disturbance, such as large-scale windthrow (Veblen 1985) and the fact that few releases occur in any one year, suggests that disturbances favoured a relatively small number of trees. Likewise, the predominance of moderate releases suggests the frequent occurrence of small rather than large canopy openings. Consequently, we interpreted the observed growth patterns as indicative of a regime dominated by repeated, small tree-fall gap episodes (Runkle 1985; Lorimer & Frelich 1989; Pollmann 2003). This result supports the hypothesis that gap-phase dynamics is the prevalent disturbance regime in low- to mid-altitude temperate rain forests in coastal areas (Veblen *et al.* 1981; Armesto & Figueroa 1987; Armesto & Fuentes 1988; Bustamante & Armesto 1995; Lusk 1996a).

Tree-fall gaps are important regeneration sites for both *N. nitida* and *D. winteri* in Chiloé Island forests (Armesto *et al.* 2001; Figueroa 2003). Regeneration modes and early radial growth of these two shade-intolerant tree species (Figs 4a and 5a,b) may explain their persistence in old-growth forests of Chiloé (cf. Aravena *et al.* 2002). Elsewhere, regeneration of these species is often associated with medium to large canopy openings (Donoso *et al.* 1984; Veblen 1985; Armesto *et al.* 1996; Veblen *et al.* 1996), but they appear to persist in this lowland forest independent of the occurrence of large gaps. Enhanced recruitment of shade-intolerant species in the 1960s (Fig. 4a) is related to increased disturbance frequency, as suggested by growth releases detected in the 1940s (Fig. 6). Evidence of fast early growth indicates that these shade-intolerant species can take advantage of opportunities provided by small tree-fall gaps. Comparable pulses in moderate releases in the past suggest that older individuals may have also been recruited after repeated small-scale disturbances.

In contrast, the regeneration modes of shade-tolerant *P. nubigena* and *S. conspicua* suggest that their regeneration success may be independent of tree-fall gap episodes. This is corroborated by the absence of fast early growth in these species. Their ability to survive under the canopy, in a suppressed condition, for up to a century, together with their rapid growth responses to canopy

openings (Figs 3 and 5d,e, Table 4), may allow these species to persist and reach the canopy despite the low frequency of disturbance. The current low representation and sporadic regeneration of the light-demanding emergent *W. trichosperma* reflects the infrequency of large disturbances in this forest (Donoso *et al.* 1984; Donoso *et al.* 1985; Veblen 1985; Donoso *et al.* 1993). The persistence of *W. trichosperma* in lowland forests can be explained by the 'long-lived pioneer syndrome', a trait combination of shade-intolerance, great longevity and relatively slow growth (Loehle 1988; Lusk 1999). Furthermore, large growth increases after disturbance accompanied by slow average radial growth under the canopy (Table 4), suggest that *W. trichosperma* has a similar growth strategy to that of shade-tolerant trees. It is possible, however, that some recruitment and mortality could be missed because of limitations inherent to our historical reconstruction (Lorimer 1985) and small sample size, as in the case of *W. trichosperma*. The small-scale disturbances that occur here increase the heterogeneity of the forest floor, producing a variety of microsites that favour the coexistence of tree species with different regeneration modes (Lusk 1995; Christie & Armesto 2003). Although several studies have documented how the regeneration and persistence of tree species in southern temperate forests depends on tree-fall gaps (Veblen 1985; Veblen *et al.* 1996; Pollmann 2003), natural disturbance regimes have not yet been incorporated into management protocols for natural or semi-natural areas (Grumbine 1994; Franklin *et al.* 2002). Future research should address the modification of disturbance regimes and gap-phase dynamics in fragmented North Patagonian forests in human-dominated landscapes. Dendroecological methods are valuable tools for such studies.

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