Journal of Biogeography (*J. Biogeogr.*) (2008) **35**, 1674–1687

ORIGINAL ARTICLE

Gap-phase dynamics and coexistence of a long-lived pioneer and shade-tolerant tree species in the canopy of an old-growth coastal temperate rain forest of Chiloé Island, Chile

Alvaro G. Gutiérrez[1,2]*, Juan Carlos Aravena[3], Natalia V. Carrasco-Farías[4], Duncan A. Christie[4], Mauricio Fuentes[5] and Juan J. Armesto[2,6]

[1]Department of Ecological Modelling, Helmholtz Centre for Environmental Research (UFZ), Leipzig, Germany [2]Instituto Milenio de Ecología y Biodiversidad (IEB), Facultad de Ciencias, Universidad de Chile, Santiago, Chile, [3]Centro de Estudios Cuaternarios (CEQUA), Universidad de Magallanes, Punta Arenas, Chile, [4]Laboratorio de Dendrocronología, Facultad de Ciencias Forestales, Universidad Austral de Chile, Valdivia, Chile [5]Sveriges lantbruksuniversitet SLU, Sweden and [6]Centre for Advanced Studies in Ecology and Biodiversity (CASEB), Pontificia Universidad Católica de Chile, Santiago, Chile

*Correspondence: Alvaro G. Gutiérrez, Department of Ecological Modelling, Helmholtz Centre for Environmental Research – UFZ, Permoser Straße 15, 04318 Leipzig, Germany.
E-mail: algutil@hotmail.com

SUMMARY

Aim A major question with regard to the ecology of temperate rain forests in south-central Chile is how pioneer and shade-tolerant tree species coexist in old-growth forests. We explored the correspondence between tree regeneration dynamics and life-history traits to explain the coexistence of these two functional types in stands apparently representing a non-equilibrium mixture.

Location This study was conducted in northern Chiloé Island, Chile (41.6° S, 73.9° W) in a temperate coastal rain forest with no evidence of stand disruption by human impact.

Methods We assessed stand structure by sampling all stems within two 50×20 m and four 5×100 m plots. A 600-m long transect, with 20 uniformly spaced sampling points, was used to quantify seedling and sapling densities, obtain increment cores, and randomly select 10 tree-fall gaps. We used tree-ring analysis to assess establishment periods and to relate the influences of disturbances to the regeneration dynamics of the main canopy species.

Results Canopy emergent tree species were the long-lived pioneer *Eucryphia cordifolia* and the shade-tolerant *Aextoxicon punctatum*. Shade-tolerant species such as *Laureliopsis philippiana* and several species of Myrtaceae occupied the main canopy. The stem diameter distribution for *E. cordifolia* was distinctly unimodal, while for *A. punctatum* it was multi-modal, with all age classes represented. Myrtaceae accounted for most of the small trees. Most tree seedlings and saplings occurred beneath canopy gaps. Based on tree-ring counts, the largest individuals of *A. punctatum* and *E. cordifolia* had minimum ages estimated to be > 350 years and > 286 years, respectively. Shade-tolerant Myrtaceae species and *L. philippiana* had shorter life spans (< 200 years). Most growth releases, regardless of tree species, were moderate and have occurred continuously since 1750.

Main conclusions We suggest that this coastal forest has remained largely free of stand-disrupting disturbances for at least 450 years, without substantial changes in canopy composition. Release patterns are consistent with this hypothesis and suggest that the disturbance regime is dominated by individual tree-fall gaps, with sporadic multiple tree falls. Long life spans, maximum height and differences in shade tolerance provide a basis for understanding the long-term coexistence of pioneer and shade-tolerant tree species in this coastal, old-growth rain forest, despite the rarity of major disturbances.

www.blackwellpublishing.com/jbi
doi:10.1111/j.1365-2699.2008.01908.x

Keywords

Chile, dendroecology, disturbance regime, regeneration modes, shade tolerance, temperate rain forest, tree life history, tree-fall gap dynamics, tree-species coexistence.

INTRODUCTION

The coexistence of tree species is often explained by shifts in species composition and dominance in response to local disturbance regimes. Such shifts are often associated with contrasting life-history traits of tree species (e.g. functional types) (Bazzaz, 1979; Noble & Slatyer, 1980). Because tree life cycles encompass diverse growth and developmental strategies over several centuries, different mechanisms of coexistence may operate on the various life-history stages (Nakashizuka, 2001). For example, responses to canopy gaps and understorey environments may differ between juvenile and adult trees (Veblen, 1986; Lusk & Smith, 1998). Such differences could be important for understanding the coexistence of tree species in the forest canopy. An unresolved question concerning the dynamics of southern temperate rain forests at coastal sites in Chile is the unexpected persistence of shade-intolerant tree species in old-growth forests (Lusk, 1999; Aravena *et al.*, 2002). Species-specific differences in patterns of tree regeneration (Christie & Armesto, 2003; Saldaña & Lusk, 2003), seed dispersal (Armesto & Rozzi, 1989; Armesto *et al.*, 2001) and longevity (Lusk, 1999) have all been recognized as relevant for explaining the canopy composition of old-growth southern temperate rain forests. However, the correspondence between disturbance regimes and species-specific life-history traits is not well understood (e.g. Loehle, 2000) and may explain the coexistence of tree species with markedly different shade tolerances in the canopy of these forests.

Temperate rain forests in southern South America are subjected to contrasting disturbance regimes. Andean forests occurring at mid and high elevation are subjected to repeated cycles of catastrophic disturbances (i.e. landslides, volcanism and fire), determining a stand-replacement regeneration mode (Veblen & Ashton, 1978; Veblen *et al.*, 1981) with a canopy dominated by pioneer *Nothofagus* species (e.g. *Nothofagus dombeyi*) (Veblen *et al.*, 1981). Conversely, in coastal-range and coastal-lowland forests of the same region (38–47° S), subjected to gap phase dynamics, the canopy is generally dominated by evergreen broad-leaved, shade-tolerant tree species (Veblen *et al.*, 1981; Donoso *et al.*, 1985; Veblen, 1985; Armesto & Figueroa, 1987; Armesto & Fuentes, 1988; Bustamante & Armesto, 1995) often lacking *Nothofagus* and other pioneer, shade-intolerant tree species. However, some old-growth temperate rain forest stands in coastal areas present a mixed canopy of pioneer, shade-intolerant trees (such as *Eucryphia cordifolia*) together with shade-tolerant tree species (Aravena *et al.*, 2002).

In the present work, we seek to understand the mechanisms explaining the long-term persistence of pioneer tree species (in particular, large individuals of *Eucryphia cordifolia*) in the canopy of an old-growth coastal rain forest in Chiloé Island, Chile (42° S). We examined the patterns of tree growth and recruitment of the main canopy species in this forest using a dendroecological reconstruction of long-term regeneration dynamics and historical disturbance regimes that prevail in this forest. Specifically, we addressed the following questions: (1) what is the predominant disturbance regime in this forest, (2) do canopy-emergent tree species differ in life spans and other important life-history traits related to regeneration strategies under the current disturbance regime, and (3) is there a correspondence between disturbance and species-specific life-history traits that may explain the coexistence of pioneer and shade-tolerant species in the canopy of this rain forest?

MATERIALS AND METHODS

Study site

The study was conducted in a coastal remnant of old-growth Valdivian rain forest in Guabún, 30 km north-west of Ancud, northern Chiloé Island, Chile (41.6° S, 73.9° W; Fig. 1). The landscape is a mosaic of patches of second-growth and old-growth forests over rolling hills of low altitude (50–100 m), dispersed in a matrix of anthropogenic grazing pastures. The present landscape has been shaped by a history of forest clearing through the use of fire and logging in the past half century, followed by occasional selective logging of the remaining forest patches (Willson & Armesto, 1996). Soils are generally deep (> 1 m), originating from Pleistocenic moraine fields and glacial outwash plains or coastal marine terraces (Denton, 1999). The prevailing climate is wet-temperate with a strong oceanic influence (Di Castri & Hajek, 1976), with rainfall throughout the year, but with less rainy summers (December–March). The nearest meteorological station in Punta Corona (41°47′ S, 73°52′ W, 48 m elevation, period 1911–2005) has an annual average rainfall of 2444 mm and a mean annual temperature of 10.8°C. Mean monthly maximum and minimum temperatures are 17.6°C (January) and 4.9°C (July), respectively.

Coastal forests are dominated by evergreen broad-leaved tree species, primarily the canopy emergents *E. cordifolia* (Eucryphiaceae) and *Aextoxicon punctatum* (Aextoxicaceae), reaching heights of > 25 m, and several species of Myrtaceae in the canopy and subcanopy (12–25 m). Tree trunks and branches are profusely covered with epiphytic ferns (e.g. *Hymenophyllum* spp., *Hymenoglosum cruentum*, *Polypodium feullei*) and several species of vascular epiphytes and climbers

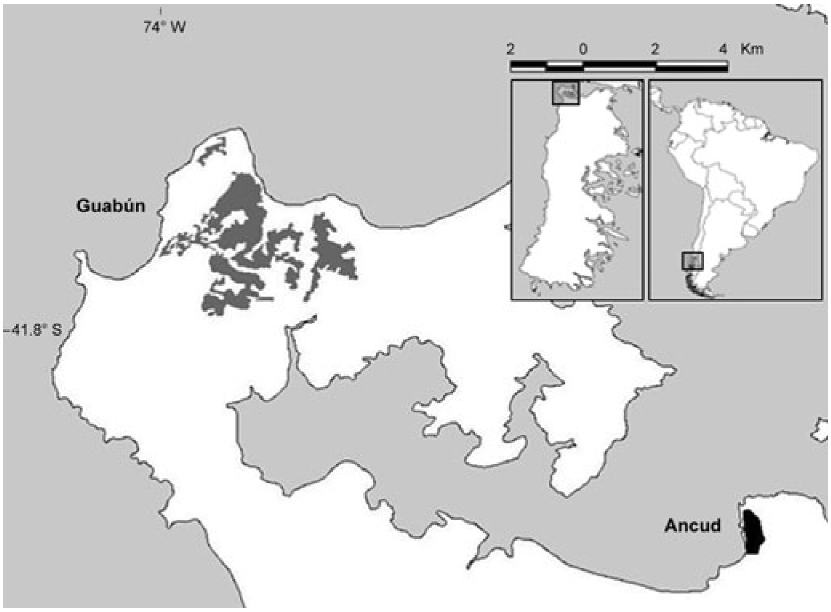

Figure 1 Location and extent of the coastal old-growth forest studied (shaded areas) in the Guabún Peninsula, northern Chiloé Island, Chile.

(e.g. species of Gesneriaceae and Bromeliaceae), including the hemi-epiphyte *Pseudopanax laetevirens* (Araliaceae). The stand selected for study has been free of fire or logging impacts for several centuries. *Chusquea* bamboos in this forest were confined to the forest edge and large canopy openings (> 1000 m^2). Because of intense clearing and logging of lowland coastal forests, including selective logging of *E. cordifolia* and *A. punctatum*, this forest is one of the last remnants of Valdivian coastal rain forest in northern Chiloé Island and resembles coastal rain forests in less accessible areas of Chiloé National Park (Armesto *et al.*, 1996) and coastal forests on the mainland (Smith-Ramírez, 2004) in both structure and floristic composition. Old-growth forests resembling the forest in Guabún have been described by Veblen (1985), Donoso *et al.* (1984, 1985), Armesto & Figueroa (1987) and Armesto *et al.* (1996) on Chiloé Island.

Field methods

Tree-species composition, age structure and regeneration

All sampling was conducted within an old-growth forest stand of about 200 ha. To sample a homogeneous area of this forest stand, our surveys were located > 100 m from any forest edge adjacent to the anthropogenic landscape matrix, and generally on gently sloping or relatively flat land. Canopy cover and old-growth forest structure were taken into account to define the environmental homogeneity of the studied stand. Because most spatial variability is generated by the presence of small tree-fall gaps (Armesto & Fuentes, 1988), sampling methods were designed to capture the structural and floristic composition presented in stands of this forest type (i.e. Donoso *et al.*, 1985; Veblen, 1985). To determine the stand structure and tree community composition, we randomly set up two 50 × 20 m plots, with an additional sampling of four 5 × 100 m strips, covering a total of 0.4 ha. Other studies in Chilean temperate rain forests have used similar sampled areas as representative of stand floristic composition and structure (Veblen *et al.*, 1977, 1980; Donoso *et al.*, 1985; Lusk, 1995). Our data, however, may not fully represent the structural heterogeneity at large spatial scales, which is associated with different disturbance histories and soil conditions (Lusk, 1996; Rüger *et al.*, 2007).

In each 50 × 20 m and 5 × 100 m plot, we identified and recorded the diameter at breast height (d.b.h.) of all adult trees (stems > 1.3 m tall and > 5 cm d.b.h.) rooted within the plot. Stems were classified as: (1) alive (healthy), (2) some branches dead, or (3) snags. Additionally, we utilized a 600-m long transect with 20 uniformly spaced (30-m apart) sampling points, to quantify seedling and sapling densities under closed canopy and within 10 randomly select tree-fall gaps (see below). The strip transect began at one arbitrarily selected point within the forest, far from any forest edge, and was run in a randomly selected compass direction. At each sampling point we identified and counted all tree seedlings (stems < 1.3 m in height) occurring within a 1 × 1 m plot, and all saplings (stems > 1.3 m in height but < 5 cm d.b.h.) occurring within a circular plot of radius 2 m. At each of the 20 sampling points, we obtained core samples of the nearest two to four adult trees (> 5 cm d.b.h.) within a distance of 10 m, using increment borers at a height of about 1.3 m from the trunk base. Additionally, we harvested cross sections from the two nearest saplings to each sampling point, one at ground level and the second one at 1.3 m above the ground to assess the minimum age of trees at breast height. Additional cores were obtained from the largest trees encountered along the strip transect, totalling four cores overall. We used both cores and cross sections to assess stand age structure, to analyse tree radial growth patterns, and to reconstruct the stand history.

Nomenclature for species names follows Marticorena & Quezada (1985) and Mabberley (1997).

Sampling under canopy gaps

We randomly selected 10 tree-fall gaps which intercepted the 600-m long strip transect or were located < 15 m away from this line. We defined canopy gaps as the area of the forest floor directly underneath a canopy opening produced by a single or a multiple tree fall (Runkle, 1992). In order to sample tree regeneration under canopy gaps produced by a single disturbance event, we sampled canopy gaps produced by single tree falls, as indicated by the presence of logs. Canopy gaps were defined as openings $< 1000\ \mathrm{m}^2$ that remained unfilled (tree regeneration > 2 m height, covering < 75% of the area under the gap; Brokaw, 1982). Canopy gap area was adjusted to an ellipsoid determined by the vertical projection of the canopy leaves of trees adjacent to the gap (Runkle, 1992). The expanded gap area was determined by the trunks of the edge trees (Runkle, 1992). Total gap area was determined by the sum of the gap area and the expanded gap area. Following Runkle (1992) we recorded for each gap its originating process (uprooting, snapping or standing dead trees), gap maker identity and gap maker stem diameter. To assess seedling densities within gaps, we set up four 1-m^2 quadrats in each of the 10 gaps, two in the centre of each gap and two in the expanded gap area. Saplings were counted within one circular plot of radius 2 m placed at the gap centre. The total area of all tree-fall gaps (individual tree-fall gaps and multiple tree-fall gaps $> 1000\ \mathrm{m}^2$) occurring along the transect divided by the strip-transect area (600 × 30 m) provided a rough estimate of the fraction of forest in gaps (Runkle, 1992). Gap ages were estimated by coring the trees bordering the gap and fallen gap makers, and from estimated ages of saplings growing on tree-fall mounds and nurse-logs.

Data analyses

Forest structure

The densities and basal areas of each tree species in the plots were added. Density of seedlings and saplings in areas under canopy gaps (gap centre + extended gaps) and under closed canopy were compared using the Kruskal–Wallis rank sum test. Because of possible confusion among seedling and sapling classes of *Amomyrtus luma*, *Amomyrtus meli* and *Luma apiculata*, their densities were combined in one group (Myrtaceae; Myrt) for the statistical analysis of regeneration. To provide a quantitative basis for comparing d.b.h. structures among tree species (Bailey & Dell, 1973), Weibull functions were fitted to the d.b.h. frequency distributions of tree species with > 20 sampled individuals > 5 cm d.b.h. Probability density functions were fitted to each diameter distribution using a maximum-likelihood algorithm (Cohen, 1965). Weibull distributions can accommodate a wide variety of shapes as indicated by the shape parameter, c. When $c \leq 1$, a descending monotonic distribution is indicated; when $c > 1$, the function is unimodal, either positively skewed ($1 < c < 3.6$), normal ($c = 3.6$), or negatively skewed ($c > 3.6$) (Lorimer & Krug, 1983). We use the shape parameter to compare the observed d.b.h. frequency distributions to models often assumed to represent a continuously regenerating population (Veblen, 1992).

Dendroecology

A total of 270 cores were obtained and processed following the techniques outlined by Stokes & Smiley (1968). We discarded cores ($n = 14$) with fewer than 25% of the stem radii intact. All discarded cores corresponded to *E. cordifolia* because of its greater tendency to have rotten tree centres with indistinguishable tree rings. Therefore, old trees (d.b.h. > 100 cm) of *E. cordifolia* may not be well represented in the age structure of this species. Because Myrtaceae tree species usually have extremely hard wood, i.e. $> 900\ \mathrm{kg\ m}^{-3}$ (Hall & Witte, 1998), few cores ($n = 4$) were obtained to estimate ages of the largest trees. Because increment cores were collected at 1.3 m above the ground, we considered the ages obtained as the minimum age of trees at breast height. Minimum tree ages were estimated by counting the annual tree rings in each core ($n = 256$). Rings were visually cross-dated using signature rings and assigning a calendar year according to the date of the latest ring (Stokes & Smiley, 1968). We assigned to each tree ring the date in which radial growth started (Schulman, 1956). For cores where the pith was missing and ring width geometry allowed us to correct ages, the number of rings to the pith was estimated following Duncan (1989). We used this method when ring width geometry implied an addition of < 15 rings. Cores where ring-width geometry would imply a larger correction were considered as incomplete ages. Ages obtained from cross sections, cores with pith and cores aged according to Duncan (1989) were considered as complete ages and were used to estimate recruitment dates. We defined recruitment date as the year when the tree reached coring height, corrected according to cross sections of saplings. Annual radial growth increments were measured to the nearest 0.01 mm with an increment-measuring device and recorded on a computer. We used the computer program COFECHA (Holmes, 1983) to detect measurement and cross-dating errors. After cross-dating, annual increments were standardized by dividing the measured growth by the average radial growth of the series. This standardization procedure facilitates detection of past disturbances because it preserves the growth trend, which can be due both to the stem geometry (i.e. the inherent growth trend) and to disturbance/competition (Veblen *et al.*, 1991) and allows for trees with different growth rates to be combined into a standardized mean chronology (Fritts, 1976). Tree-ring chronologies were produced for the canopy species with a sample size of > 15 trees (*A. punctatum* and *E. cordifolia*).

Each core sampled was examined for releases in radial growth. Releases provide evidence of enhanced tree radial growth presumably associated with canopy opening, and were used to make inferences about historical disturbance regimes and long-term stand dynamics. We defined a major release as an increment of > 100% in average radial growth lasting for at least 15 subsequent years and a moderate release as an increment > 50% in average radial growth lasting for at least 15 years afterwards (Lorimer & Frelich, 1989). To distinguish the effect of canopy disturbance from transient effects of climatic fluctuations on tree growth, we searched for sustained releases (15 years' enhanced growth) coinciding in several trees within the stand. This criterion ruled out short-term climatic pulses and gradual changes in ring width due to tree ageing, bole geometry and long-term climate shifts (Lorimer & Frelich, 1989; Nowacki & Abrams, 1997).

RESULTS

Tree-species composition and stand structure

A total of 14 evergreen, broad-leaved tree species made up the canopy of this old-growth forest (Table 1). Large individuals of *E cordifolia* and *A punctatum* occupied the emergent stratum (> 25 m tall). *Laureliopsis philippiana* together with several Myrtaceae species (including *A. luma*, *Myrceugenia planipes*, *Myrceugenia ovata* and *L. apiculata*) occupied the main canopy (20–25 m). A few large trees of *E. cordifolia* contributed disproportionately to the stand basal area (Table 1). *Laureliopsis philippiana* and *A. luma* contributed rather equally to forest structure in terms of both the density and basal area. Two species of *Myrceugenia*, *M. planipes* and *M. ovata*, had a high stem density in the forest, mainly in the subcanopy. Combining all species of Myrtaceae, they made up 47.5% of the stand tree density but < 30% of the basal area. Despite its uniform presence in the emergent and canopy layer, *A. punctatum* contributed only a small fraction of both density and stand basal area. Standing dead trees (snags) were common within the stand, accounting for 16% of total basal area (Table 1). Other tree species, such as *Drimys winteri* and *Rhaphithamnus spinosus*, were minor components of this old-growth forest.

Seedlings and saplings were numerically dominated by Myrtaceae tree species in this old-growth forest. Regeneration of *A. luma* was the most abundant (Table 2). *A. punctatum*, *L. philippiana* and *M. ovata* had lower densities of seedlings but they were well represented in the sapling size classes. Neither *Drimys winteri* nor *Pseudopanax laetevirens* had any saplings under the forest canopy or in gaps, although these tree species were present as seedlings. The hemi-epiphyte *P. laetevirens* was never found rooted to the ground (Table 1). In the plots, this tree typically adopted a hemi-epiphytic growth habit on large emergent trees of *E. cordifolia*.

The d.b.h. distributions of canopy trees in this forest presented the characteristic shape of an old-growth uneven-aged stand, which significantly departed from a negative exponential distribution (typical of actively growing stands) by the higher fraction of trees in the larger d.b.h. classes (Weibull $c = 1.13$). The largest-diameter classes (> 80 cm d.b.h., > 25 m tall trees) were numerically dominated (Fig. 2) by *E. cordifolia* (maximum recorded d.b.h. 243 cm) and *A. punctatum* (maximum d.b.h. 136 cm). The d.b.h. distribution of *E. cordifolia* was distinctly unimodal with a positive skew ($c = 2.48$; Fig. 2). Despite its importance as an emergent, *E. cordifolia* was poorly represented in the stand by stems < 30 cm d.b.h. In contrast, *D. winteri* had a unimodal d.b.h.

Table 1 Density, basal area, relative density and relative dominance (% of basal area) of tree species (stems > 5 cm d.b.h.) in the coastal temperate rain forest of Guabún, northern Chiloé Island, Chile.

Species	Abbrev.	Family	Density (No. ha^{-1})	Basal area (m^2 ha^{-1})	Relative density (%)	Relative dominance (%)
Eucryphia cordifolia	Euco	Eucryphiaceae	72	40.7	3.5	32.5
Amomyrtus luma	Amlu	Myrtaceae	425	18.7	20.7	15.0
Laureliopsis philippiana	Laph	Monimiaceae	432	13.7	21.0	11.0
Myrceugenia planipes	Mypl	Myrtaceae	290	7.4	14.1	5.9
Aextoxicon punctatum	Aepu	Aextoxicaceae	116	11.1	5.6	8.9
Myrceugenia ovata	Myov	Myrtaceae	160	3.2	7.8	2.5
Amomyrtus meli	Amme	Myrtaceae	58	5.2	2.8	4.2
Rhaphithamnus spinosus	Rhsp	Verbenaceae	123	0.9	6.0	0.7
Luma apiculata	Luap	Myrtaceae	43	2.4	2.1	1.9
Drimys winteri	Drwi	Winteraceae	36	1.4	1.8	1.1
Ovidia pillo-pillo	Ovpi	Thymeliaceae	40	0.1	1.9	0.1
Pseudopanax laetevirens	Psla	Araliaceae	0†	0.0	0.0	0.0
Other species*			120	0.2	5.8	0.2
Dead trees			140	20.3	6.8	16.2
Total			2055	125.2		

Abbrev.: species code name corresponding to the first two letters of each part of the binomial name.

*Includes: *Dashypyllum diacanthoides* and *Caldcluvia paniculada.*

†Found only as seedlings.

Table 2 Number of seedlings (mean ± standard error of n = 60 1-m^2 plots) and saplings (mean of 30 circular plots) in the coastal temperate rain forest of Guabún, northern Chiloé Island, Chile.

	Seedlings		Saplings	
Species	Density ± SE (No. ha^{-1})	Relative density (%)	Density ± SE (No. ha^{-1})	Relative density (%)
Eucryphia cordifolia	11,803 ± 4420	4.1	55 ± 55	1.7
Amomyrtus luma	129,016 ± 17,995	44.4	357 ± 109	10.9
Laureliosis philippiana	1967 ± 837	0.7	110 ± 86	3.4
Myrceugenia planipes	26,721 ± 4074	9.2	220 ± 67	6.7
Aextoxicon punctatum	10,000 ± 2024	3.4	604 ± 200	18.5
Myrceugenia ovata	3443 ± 1651	1.2	439 ± 183	13.4
Amomyrtus meli	74,426 ± 14,003	25.6	466 ± 192	14.3
Rhaphithamnus spinosus	27,213 ± 5063	9.4	357 ± 140	10.9
Luma apiculata	2951 ± 2628	1.0	439 ± 156	13.4
Drimys winteri	2295 ± 887	0.8	0	0.0
Ovidia pillo-pillo	328 ± 230	0.1	220 ± 152	6.7
Pseudopanax laetevirens	492 ± 364	0.2	0	0.0
Total	290,655		3265	

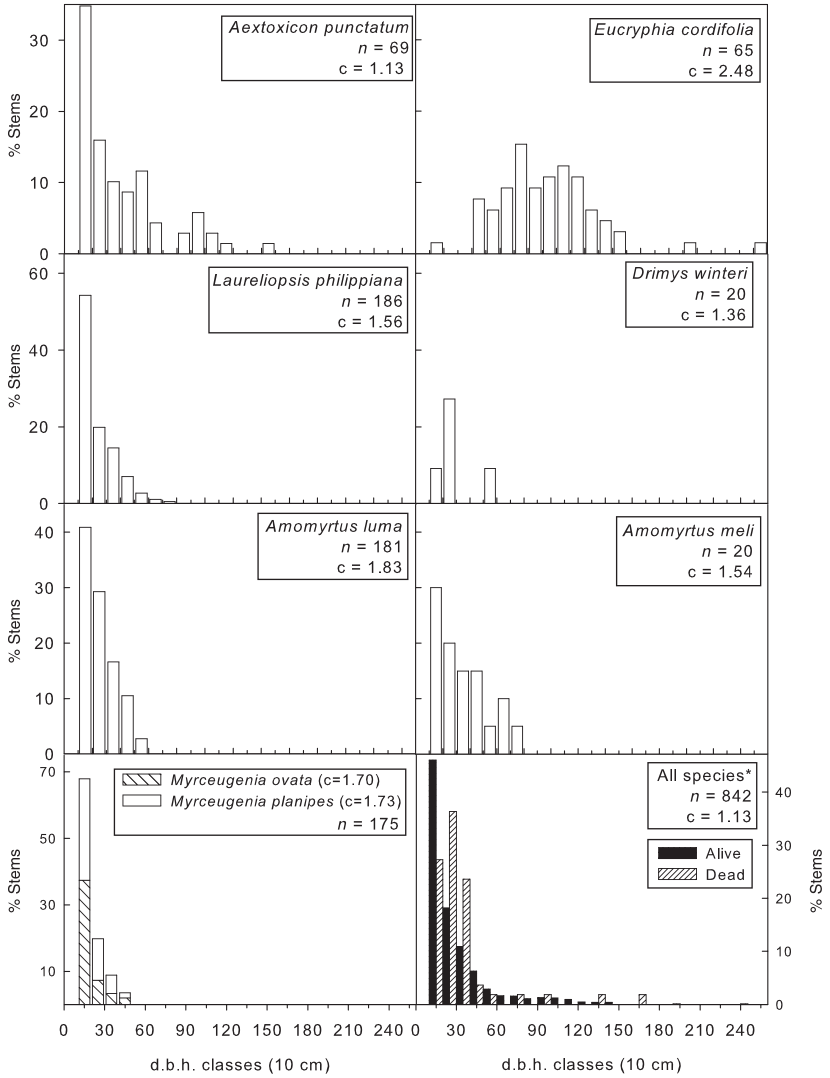

Figure 2 Diameter (d.b.h.) class distribution for the main canopy tree species (trees with d.b.h. > 5 cm; n > 20) in the coastal temperate rain forests of Guabún, in northern Chiloé Island, Chile. See details about Weibull shape parameter c in text. All species* includes all tree species listed in Table 1. Note different scales for the y-axes.

distribution (Weibull c = 1.36) dominated by small sized individuals (d.b.h. < 60 cm). *Aextoxicon punctatum* on the other hand was represented in the entire range of d.b.h. intervals < 60 cm, with a distinct secondary peak for d.b.h. > 70 cm (Weibull c = 1.13; Fig. 2). Intermediate size classes (30–70 cm d.b.h.) within this old-growth stand were almost entirely

Table 3 Characteristics of tree-fall gaps in the coastal temperate rain forest of Guabún, northern Chiloé Island, Chile. The total gap area is the sum of gap area plus expanded gap (see Materials and Methods for definitions).

Gap maker	Number of gaps	Gap maker stem diameter (cm)	Gap size range (m^2) Gap	 Expanded gap	 Total gap	Origin
Eucryphia cordifolia	5	30–111	31–137	261–350	291–476	Snapping, uprooting
Laureliopsis philippiana	2	53–75	53–104	136–159	212–239	Snapping
Aextoxicon punctatum	1	59	211.7	88.8	122.9	Uprooting
Amomyrtus luma	1	45	230.1	58.9	171.2	Snapping
Amomyrtus meli	1	78	292.1	184.5	107.6	Uprooting

dominated by Myrtaceae species and *L. philippiana* (Fig. 2), which had similar d.b.h. distributions (Weibull $c = 1.54–1.83$). Myrtaceae (four tree species combined) accounted for most individuals under the canopy in the smallest stem diameter classes (< 30 cm d.b.h.; 30% of all trees). Snags were more frequent in the smaller d.b.h. classes (< 40 cm, Fig. 2).

Regeneration in tree-fall gaps

Eucryphia cordifolia was the most frequent gap maker and produced the largest canopy gaps (Table 3). Most gap-makers had estimated trunk diameters > 50 cm. Including two large gaps recorded as > 1000 m^2, the total fraction of forest area in gaps was nearly 8%. Individual tree-fall gaps ranged in age between 31 and 115 years with an average age of 55 years, and ranged in size from 107–476 m^2, all of them formed by uprooting or snapping of canopy trees (Table 3). The total gap area for expanded gaps averaged 215.3 m^2 for all gaps sampled.

Most seedlings occurred under light-exposed canopy gaps, with much lower densities under closed canopies (Kruskal–Wallis $\chi^2 = 6.9$, d.f. = 1, $P < 0.01$; Fig. 3a). The combined density of seedlings of *A. luma*, *A. meli* and *L. apiculata* was significantly higher under tree-fall gaps than under the continuous forest canopy (Kruskal–Wallis $\chi^2 = 6.9$, d.f. = 1, $P < 0.01$; Fig. 3a). *Eucryphia cordifolia*, *R. spinosus* and *L. philippiana* had higher seedling densities under canopy gaps than under the shade (Kruskal–Wallis $\chi^2 = 6.3$, d.f. = 1, $P < 0.01$ for *E. cordifolia*; Kruskal–Wallis $\chi^2 = 5.2$, d.f. = 1, $P < 0.05$ for *L. philippiana*, Kruskal–Wallis $\chi^2 = 10.1$, d.f. = 1, $P < 0.01$ for *R. spinosus*). In this old-growth stand, saplings of *E. cordifolia* were not found under the closed canopy but they were present beneath gaps. *Ovidia pillo-pillo*, which is a tree species occurring mainly in secondary forests, and which was absent from old-growth forest canopy, had seedlings and saplings under canopy gaps only (Fig. 3). Saplings of *R. spinosus* were more abundant under tree-fall gaps than under the forest canopy (Kruskal–Wallis $\chi^2 = 11.7$, d.f. = 1, $P < 0.01$; Fig. 3b).

Tree age structures

Age structures were constructed for the four main canopy tree species, including the two emergents (Fig. 4). Age structures were also indicative of the old-growth condition of this forest, characterized by multi-aged cohorts (Fig. 4). The oldest tree recorded in the stand belonged to *A. punctatum* (minimum tree age > 350 years) followed by *E. cordifolia* (minimum tree age > 286 years) (Table 4). However, considering the maximum d.b.h. of *A. punctatum* (136 cm in this forest), the recorded minimum ages are likely to underestimate the age of

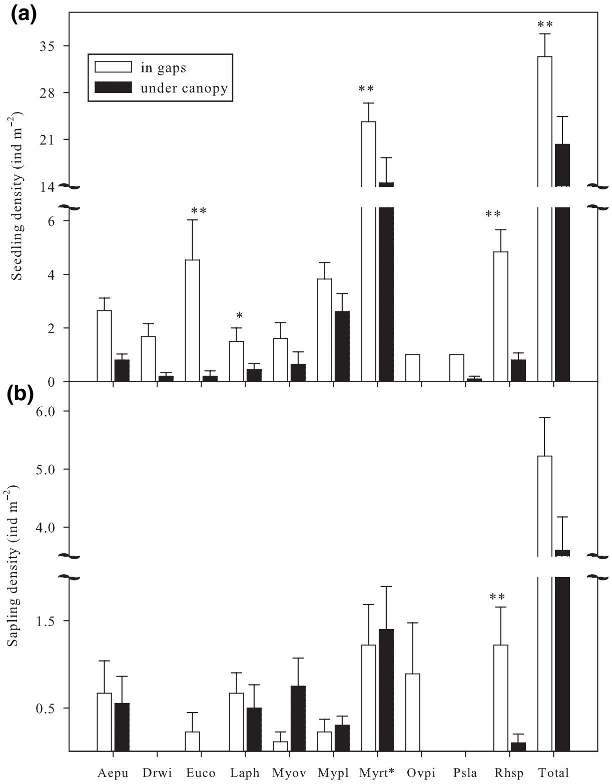

Figure 3 Mean seedling and sapling densities (individuals m^{-2}) recorded under the forest canopy ($n_{\text{seedling}} = n_{\text{sapling}} = 20$ plots) and within tree-fall gaps (gap centre + expanded gap) ($n_{\text{seedlings}} = 40$ plots; $n_{\text{saplings}} = 10$ plots) in Guabún, northern Chiloé Island, Chile. Abbreviations of species correspond to the first two letters of each part of the binomial name as listed in Table 1. Myrt* represents the pooled density of seedlings and saplings of *A. luma*, *A. meli* and *L. apiculata*. Significant differences in density of seedlings and saplings between closed and open habitats (Kruskal–Wallis test) are indicated: $^*P < 0.05$ and $^{**}P < 0.01$.

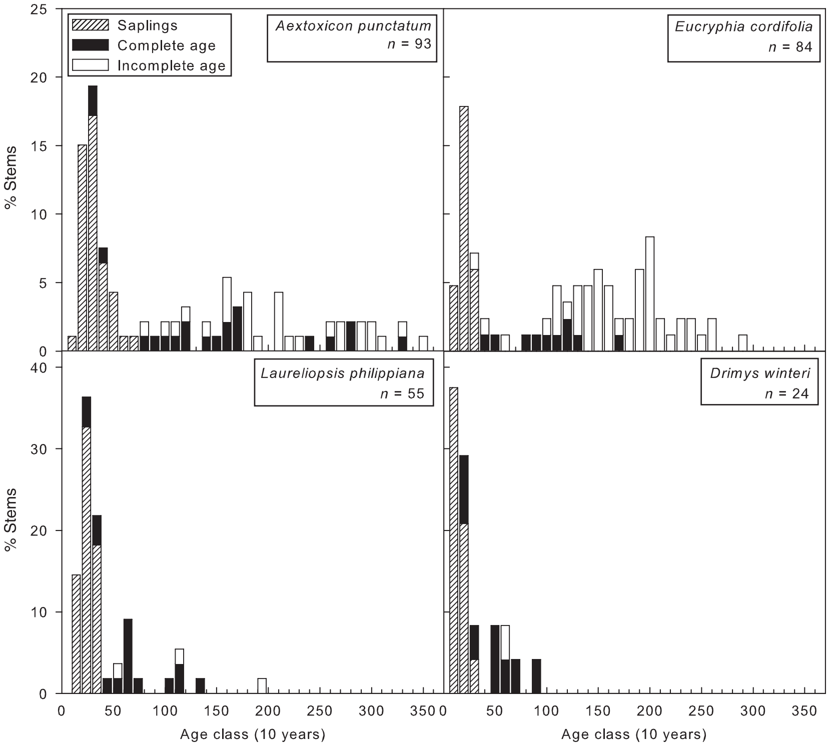

Figure 4 Age class distribution (at 0.3 m above the ground) of saplings (individuals < 5 cm d.b.h.) and adult trees (d.b.h. > 5 cm) in an old-growth coastal temperate rain forest, Guabún, northern Chiloé Island, Chile. Ages of saplings were obtained using cross sections. Complete ages were obtained from cores with pith and cores aged according to the method of Duncan (1989). Incomplete ages were obtained from cores where the pith was missing and ring width geometry did not allow a correction using Duncan (1989).

Table 4 Minimum ages and life-history traits of main canopy tree species in the coastal temperate rain forest of Guabún, northern Chiloé Island, Chile. The age at coring height (1.3 m) was obtained using cross sections from saplings, one at the ground level and the second one at 1.3 m above the ground.

Species	Shade tolerance	Mean age at coring height (years ± SD)	Minimum age range (years)*	Life span† (years)	Maximum height (m)‡	Maximum d.b.h. recorded (cm)§
Aextoxicon punctatum	To	16 ± 10 [19]	8–349 [93]	480	34	136*
Amomyrtus luma	To	–	–	200	22	137
Amomyrtus meli	Int	–	113 [1]	113*	26*	59
Drimys winteri	In	7 ± 3 [11]	5–89 [24]	280	22*	104
Eucryphia cordifolia	In	11 ± 3 [18]	8–286 [70]	650	38	243*
Laureliopsis philippiana	To	8 ± 6 [21]	6–187 [55]	657	34	121
Luma apiculata	Int	–	–	n.d.	23	84
Myrceugenia ovata	To	–	–	n.d.	22	44
Myrceugenia planipes	To	–	73–140 [3]	260	17	39

To, shade-tolerant; In, shade-intolerant; Int, intermediate (after Figueroa & Lusk, 2001; and authors' personal observations).

SD, standard deviation of the mean. Number of trees sampled is indicated in brackets [ ]. n.d. indicates no data available.

*Data from this study.

†Life span (or mean estimated maximum longevity) follows the literature (Lara, 1991; Lusk & Del Pozo, 2002; Pollmann & Veblen, 2004; Veblen, 1985).

‡Data from Parada *et al.* (2003).

§Gutiérrez *et al.*, unpublished data.

the oldest tree because the longest tree core obtained represented only 33% of the stem radius. Fig. 4 also shows that at least three trees more of *A. punctatum* had ages > 300 years (35–40% stem radii intact). These two canopy emergent tree species had numerous individuals established in the last 30 years, but they were well represented across all age intervals, showing uneven-aged structures (Fig. 4). The multi-modal age distribution of *E. cordifolia* indicated a distinctive recruitment pulse about 150–200 years ago. Other canopy trees, *A. meli*, *L. philippiana* and *M. planipes*, had life spans of about 100 years, whereas all *D. winteri* stems were younger than 90 years (Table 4). *Laureliopsis philippiana* and *D. winteri* had similar monotonically descending age distributions, with a large proportion of young individuals (Fig. 4).

Tree radial growth and regeneration modes

The number of radial growth releases recorded since 1670 differed among species (ANOVA $F_{3,152} = 101.9$, $P < 0.01$; Table 5). Radial growth patterns of the four canopy species analysed produced sustained releases to a level defined here as a major release (Table 5). However, release frequencies, indicative of synchronous growth releases among nearby trees within the stand, were much higher for moderate than for major releases (Table 5). A low frequency of synchronous major releases suggests that large tree-fall gaps are infrequent in this old-growth forest. This is supported by the fact that only moderate releases were detected in cores obtained from trees located along the edges of current tree-fall gaps (Fig. 5). Shade tolerant *A. punctatum* and *L. philippiana* had a greater frequency of moderate growth releases than *E. cordifolia* (Table 5).

Growth releases were compared for the oldest trees ($n = 44$, minimum age > 150 years; Fig. 6a) in the forest for every 10-year interval from 1750 to 1990. The number of growth releases fluctuated greatly, with higher frequencies recorded in 1790, 1840, 1890–1900, 1930 and 1970. Tree-fall gap dates coincident with release events were obtained for the period between 1940 and 1970 and for one tree-fall gap dated in the 1890s (Fig. 6b). The highest frequency of major releases in the entire period analysed was detected in the 1930s (coincident in eight trees).

The recruitment of canopy-dominant tree species was fairly constant over the past 300 years of forest history, except for an apparent gap in the number of trees established during the period 1920–50 (Fig. 6c). Lower establishment in the period between 1920 and 1950 was more noticeable for *E. cordifolia* and may be responsible for the two distinct cohorts of trees identified in the age structure of this species (Figs 4 & 6c). Radial growth of *A. punctatum* and *E. cordifolia* generally increased in contrasting periods during the recent history of the stand (Fig 6c) and both species presented a strong growth decline during the period 1870–1900, with similar levels of radial growth suppression.

DISCUSSION

Tree regeneration patterns

The long-term patterns of regeneration of tree species in this old-growth coastal rain forest suggest that most tree species responded to small canopy openings (Figueroa & Lusk, 2001). As in tropical forests (Schnitzer & Carson, 2001), individual tree-fall gaps < 300 m^2 in their expanded area were important sites for the regeneration of most tree species in the forest canopy (Fig. 3a). This lends support to the idea that tree-fall gaps play a major role in the maintenance of tree-species composition in the canopy of this temperate old-growth forest. Although the light requirements reported for seedlings of shade-tolerant *A. punctatum*, *L. philippiana* and Myrtaceae species are relatively lower than those of shade-intolerant tree species (Figueroa & Lusk, 2001), seedlings and saplings of both functional types were more frequently found in tree-fall gaps than under the continuous forest canopy. The regeneration of shade-tolerant tree species under canopy gaps (Fig. 3) suggests that they are able to respond to slight differences in understorey light levels, as has been shown in other temperate forests (Canham, 1989). This physiological plasticity is also supported by the fact that seed germination of shade-tolerant tree species in Chilean and other forests is relatively unresponsive to overstorey light conditions (Swaine & Whitmore, 1988; Figueroa & Lusk, 2001). Although both *E. cordifolia* and *D. winteri* are generally considered pioneer tree species, which regenerate more frequently in large openings (Donoso, 1993), in this coastal forest both species regenerate within small canopy openings. Shade-intolerant species may be restricted to small canopy gaps largely due to their higher light requirements for regeneration (Canham, 1989). *Drimys winteri* seems broadly tolerant to light conditions during the seedling and sapling stages (Figueroa & Lusk, 2001; Gutiérrez *et al.*, 2004; Chacón & Armesto, 2005). However, the regeneration pattern of *E. cordifolia* contrasts with the findings for lowland (but not coastal) Chiloé forests where the regeneration of this species appeared to depend on larger gaps (Donoso *et al.*, 1985; Veblen, 1985). The sprouting ability of *E. cordifolia* (Veblen

Table 5 Radial growth patterns for the main canopy tree species in the coastal temperate rain forest of Guabún, northern Chiloé Island, Chile. Major and moderate releases defined as in Lorimer & Frelich (1989).

	Aextoxicon punctatum	*Eucryphia cordifolia*	*Laureliopsis philippiana*	*Drimys winteri*
Number of trees	38	35	14	5
Mean radial growth (mm year^{-1}) ± SD	0.96 ± 0.69	1.04 ±0.72	1.15 ± 0.74	1.08 ± 0.58
Maximum radial growth (mm year^{-1})	7.24	6.64	5.15	3.65
Maximum sustained release*	5.27	4.54	8.54	1.67
Moderate release frequency (releases 100 year^{-1})†	2.4	1.66	2.16	0.9
Major release frequency (releases 100 year^{-1})†	0.76	0.34	1.13	0

SD, standard error of the mean.

*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.

†Release frequencies for the past 350 years were calculated by averaging the number of growth releases recorded for each tree and dividing by tree age.

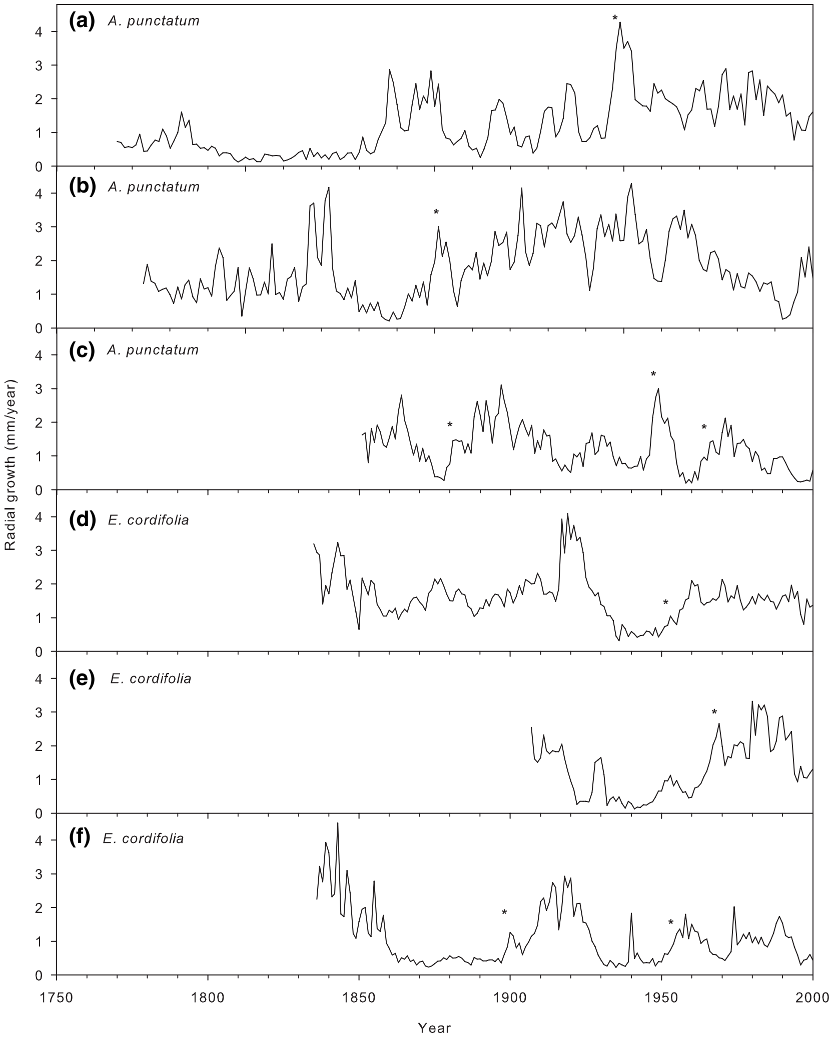

Figure 5 Radial growth rates (mm year^{-1}) for selected trees located along canopy gap edges. Data are for *Aextoxicon punctatum* (a–c) and *Eucryphia cordifolia* (d–f) in the coastal temperate rain forest of Guabún, northern Chiloé Island, Chile. Asterisks indicate years of moderate releases defined following Lorimer & Frelich (1989).

et al., 1981; Donoso *et al.*, 1985; Veblen, 1985) may facilitate regeneration from gap makers or trees growing along small gap edges. A similar regeneration pattern was found by Veblen *et al.* (1981) in the Cordillera Pelada, Chile (40°10′ S, elevation of 260 m) as suggested by the size structure and clustered spatial pattern of *E. cordifolia*.

Some differences emerge between this coastal forest and lowland (but not coastal) forests located in Chiloé Island (Donoso *et al.*, 1985; Veblen, 1985). We found a high relative dominance by *A. punctatum* in our study area versus its absence in the two cited studies that may be related to its ability to tolerate salt spray in coastal areas (Pérez, 1994). Also, the pioneer tree species *Weinmannia trichosperma* (Cunoniaceae) was absent or rare in our study area whereas it is present in lowland Chiloé forests (Donoso *et al.*, 1985; Veblen, 1985; Aravena *et al.*, 2002; Gutiérrez *et al.*, 2004). A possible explanation is that *E. cordifolia* can be a pioneer where soil conditions do not allow the establishment of *W. trichosperma* or *Nothofagus* spp. (Donoso *et al.*, 1984). The abundance of *Chusquea* bamboos may also have an important role as competitors in gaps in other forests, apparently inhibiting the regeneration of *E. cordifolia* and the shade-tolerant *A. punctatum* (González *et al.*, 1997; Donoso & Nyland, 2005). These differences reflect important site differences (e.g. coastal vs. non-coastal, soil differences) as well as differences in disturbance regime.

Disturbance regime and regeneration dynamics

The mean canopy gap area in this old-growth forest (< 300 m^2) was smaller than that reported for coastal, montane evergreen forests of Chiloé Island (Armesto & Fuentes, 1988). However, the fraction of the area in canopy gaps (8% in this old-growth forest), which included multiple tree-fall gaps, was consistent with previous estimates for lowland old-growth forest in Chiloé Island (Veblen, 1985). Large canopy openings (> 1000 m^2), produced by multiple tree falls, were infrequent and spatially confined to specific areas as reported in other Chiloé forests (Veblen, 1985; Armesto & Fuentes, 1988). Presumably, such openings are caused by infrequent, but severe, wind storms (Veblen, 1985). Trees growing along the edge of the extant tree-fall gaps did not show evidence of major growth releases (Fig. 5), indicating that single tree falls are more likely to produce moderate

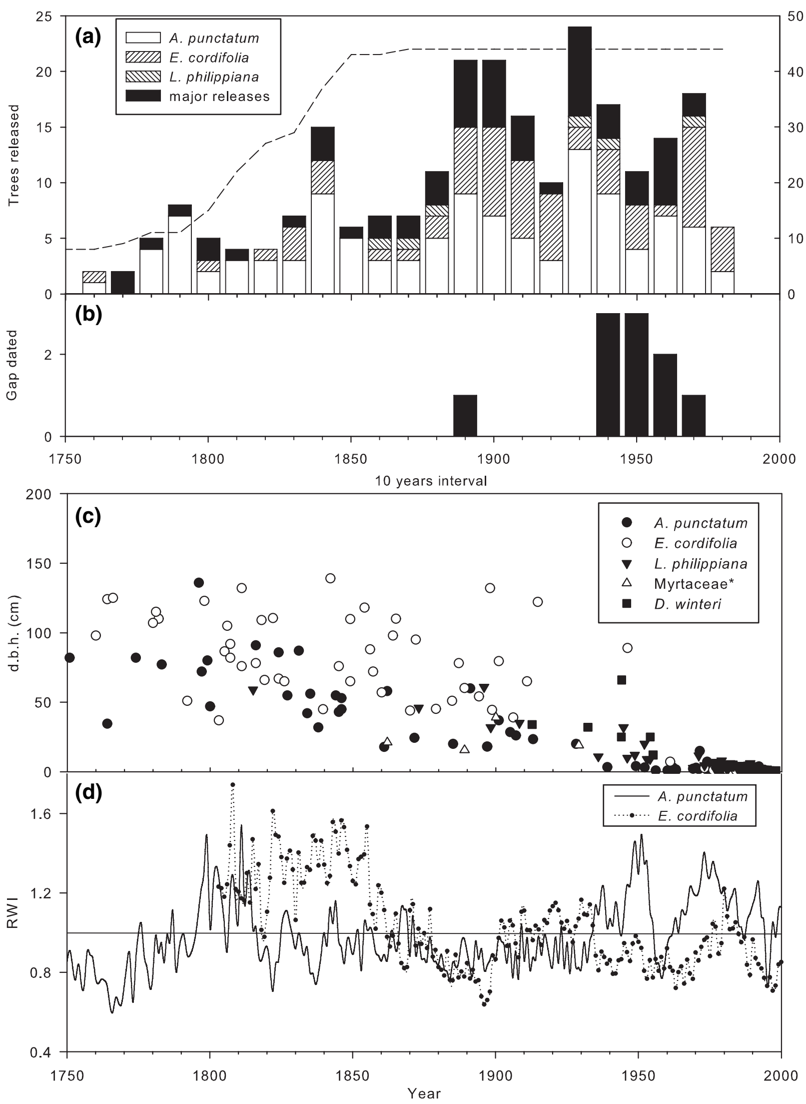

Figure 6 (a) Decadal distribution of major and moderate radial growth releases (after Lorimer & Frelich, 1989) in the oldest trees cored (n = 44, indicated by dotted line). (b) Frequency distribution of gap ages (n = 10). (c) Age–diameter (d.b.h.) relationships showing the minimum recruitment date and the present d.b.h. of sampled trees (n = 256). Myrtaceae* includes *M. planipes* and *A. meli*. (d) Radial growth index (RWI, estimated for periods with $n > 5$ trees) of *A. punctatum* and *E. cordifolia* [same trees as in (a)]. Note that the x-axis ticks don't line up for all of the graphs in this figure.

releases in the affected trees. Hence, the dominance of moderate releases in the release chronology and the observed tree recruitment patterns (Fig. 6) in this forest are consistent with a disturbance regime dominated by frequent, low-intensity disturbances (i.e. gap-phase dynamics), with sporadic large-scale disturbances (i.e. multiple tree falls).

The regeneration modes of canopy tree species and the disturbance regime in this old-growth coastal forest both resembled those documented for other southern temperate rain forests (Stewart & Rose, 1990; Lusk & Smith, 1998; Gutiérrez *et al.*, 2004; Pollmann & Veblen, 2004). The disturbance regime in these coastal forest differed from even-aged *Nothofagus* stands in the Andes, with catastrophic recruitment modes induced by large-scale disturbances (i.e. fires, mass movements induced by earthquakes) (Veblen & Ashton, 1978; Veblen *et al.*, 1992). Although extensive land-use changes on Chiloé Island started in the late 19th century (Willson & Armesto, 1996; Torrejón *et al.*, 2004), large disturbances were infrequent in this coastal forest as suggested by the presence of few major releases in the chronology. No shifts in tree-species composition are inferred from the recruitment patterns (Figs 4 & 6). Shade-tolerant tree species (Myrtaceae, *L. philippiana*, *A. punctatum*) (Table 4) are able to regenerate continuously under this disturbance regime, germinating and recruiting to sapling stage in both small canopy gaps and under a closed canopy. The largest and presumably oldest trees of shade-tolerant tree species (i.e. *A. punctatum*) may reach ages > 450 years (Fig. 4, Table 4). In contrast, most of the extant population of the comparatively shade-intolerant *E. cordifolia* was established sporadically (intermittently) in response to both small and larger gaps (Fig. 4). Based on these results, we propose that the canopy composition of the forest has remained relatively unchanged for at least 450 years.

Gap-phase dynamics and the coexistence of *A. punctatum* and *E. cordifolia*

Our results support the idea that long life spans, coupled with differences in sapling shade tolerance, and the creation of canopy gaps of different sizes by emergent and canopy trees are important factors for the non-equilibrium persistence of tree species mixtures (Lusk & Smith, 1998; Loehle, 2000). A long residence time in the canopy for *E. cordifolia* ensures that at least one gap of sufficient size will be produced to facilitate its recruitment (Loehle, 2000). Because of the large individual sizes that this species attains (Table 4) and its frequency as a gap-maker (Tables 3 & 6; see also Veblen, 1985), it is suggested that the death of large, emergent individuals of *E. cordifolia* creates conditions that favour its own regeneration mode (Shugart, 1984). Other traits of *E. cordifolia* that may enhance its long-term persistence in the canopy until the old-growth stage include its sprouting ability in small canopy openings, its rapid establishment immediately following a large disturbance event, its ability to tolerate long periods of growth suppression (Fig. 5f), and its rapid radial growth following release (Fig. 5d–f). These traits are comparable with those seen for *Weinmannia trichosperma*, which is a long-lived pioneer (Lusk, 1999) not present (or rare) in this coastal forest. In contrast, shade-tolerant *A. punctatum* persists and dominates the canopy because of its lower light requirement for germination (Figueroa & Lusk, 2001) and seedling growth compared with that of *E. cordifolia*, and its capacity to recruit (Fig. 2) and survive (Fig. 5a–c) both under canopy gaps and under the continuous forest canopy. Additionally, the long life span of *A. punctatum* increases its chances of survival in the understorey until the overtopping tree dies and a canopy gap forms in which an established subordinate tree can succeed.

Species-specific life-history traits (such as life spans, maximum height and shade tolerance) provide a basis for understanding the long-term coexistence of pioneer and shade-tolerant tree species in this coastal, old-growth rain forest, despite the rarity of major disturbances. To better understand the mechanism of tree-species coexistence, it would also be important to assess the importance of other reproductive traits, such as seed dispersal distances, under disturbance regimes varying in spatial and temporal scales (i.e. turnover rate, gap size distribution). Expanding these reconstructive studies of old-growth rain forests in coastal areas will also yield valuable insights for the protection and management of these threatened forests.

ACKNOWLEDGEMENTS

We gratefully acknowledge the Velazquez family for allowing us to work on their property. We appreciate the field assistance of M. Nuñez, M. P. Peña, C. Pérez and J. Cuevas. We thank M. P. Peña for laboratory assistance. We thank the Armada de Chile for access to climate data bases. T. T. Veblen, J. Calabrese and an anonymous referee provided useful comments. Financial support was provided by Contract ICA 4-CT-2001-10095 Biocores project funded by EC under the INCO IV programme, Millennium Nucleus Project P02-051-F ICM (CMEB), Fondecyt grant 1501-0001 to the Centre for Advanced Studies in Ecology and Biodiversity, and a DAAD fellowship to A.G.G. This is a contribution to the research programme of the Senda Darwin Biological Station, Chiloé. Other than the first and last author, the order of authorship is alphabetical.

REFERENCES

Aravena, J.C., Carmona, M.R., Pérez, C.A. & Armesto, J.J. (2002) Changes in tree species richness, stand structure and soil properties in a successional chronosequence in northern Chiloé Island, Chile. *Revista Chilena de Historia Natural*, **75,** 339–360.

Armesto, J.J. & Figueroa, J.A. (1987) Stand structure and dynamics in the temperate rain forest of Chiloé Archipelago, Chile. *Journal of Biogeography*, **14,** 367–376.

Armesto, J.J. & Fuentes, E.R. (1988) Tree species regeneration in a mid-elevation, temperate rain-forest in Chiloé Island, Chile. *Vegetatio*, **74,** 151–159.

Armesto, J.J. & Rozzi, R. (1989) Seed dispersal syndromes in the rain-forest of Chiloé – evidence for the importance of biotic dispersal in a temperate rain-forest. *Journal of Biogeography*, **16,** 219–226.

Armesto, J.J., Aravena, J.C., Villagrán, C., Pérez, C. & Parker, G. (1996) Bosques templados de la Cordillera de la Costa. *Ecología de los bosques nativos de Chile* (ed. by J. Armesto, C. Villagrán and M.K. Arroyo), pp. 199–213. Editorial Universitaria, Santiago.

Armesto, J.J., Díaz, I., Papic, C. & Willson, M.F. (2001) Seed rain of fleshy and dry propagules in different habitats in the temperate rainforests of Chiloé Island, Chile. *Austral Ecology*, **26,** 311–320.

Bailey, R.L. & Dell, T.R. (1973) Quantifying diameter distributions with the Weibull function. *Forest Science*, **19,** 97–104.

Bazzaz, F.A. (1979) Physiological ecology of plant succession. *Annual Review of Ecology and Systematics*, **10,** 351–371.

Brokaw, N.V.L. (1982) The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica*, **14,** 158–160.

Bustamante, R.O. & Armesto, J.J. (1995) Regeneration dynamics in canopy gaps of a montane forest of Chiloé Island, Chile. *Revista Chilena de Historia Natural*, **68,** 391–398.

Canham, C.D. (1989) Different responses to gaps among shade-tolerant tree species. *Ecology*, **70,** 548–550.

Chacón, P. & Armesto, J.J. (2005) Effect of canopy openness on growth, specific leaf area, and survival of tree seedlings in a temperate rainforest of Chiloé Island, Chile. *New Zealand Journal of Botany*, **43,** 71–81.

Christie, D.A. & Armesto, J.J. (2003) Regeneration microsites and tree species coexistence in temperate rain forests of Chiloe Island, Chile. *Journal of Ecology*, **91,** 776–784.

Cohen, A.C. (1965) Maximum likelihood estimation in Weibull distribution based on complete and on censored samples. *Technometrics*, **7,** 579–588.

Denton, G.H. (1999) Glacial and vegetational history of the southern Lake District of Chile – Preface. *Geografiska Annaler Series A–Physical Geography*, **81A,** 105–106.

Di Castri, F. & Hajek, E. (1976) *Bioclimatología de Chile*. Universidad Católica de Chile, Santiago.

Donoso, C. (1993) *Bosques templados de Chile y Argentina. Variación, estructura y dinámica*. Editorial Universitaria, Santiago, Chile.

Donoso, P.J. & Nyland, R.D. (2005) Seedling density according to structure, dominance and understory cover in old-growth forest stands of the evergreen forest type in the coastal range of Chile. *Revista Chilena De Historia Natural*, **78,** 51–63.

Donoso, C., Grez, R., Escobar, B. & Real, P. (1984) Estructura y dinámica de bosques del Tipo Forestal Siempreverde en un sector de Chiloe insular. *Bosque*, **5,** 82–104.

Donoso, C., Escobar, B. & Urrutia, J. (1985) Estructura y estrategias regenerativas de un bosque virgen de Ulmo (*Eucryphia cordifolia* Cav.)-Tepa (*Laurelia philippiana* Phil.) Looser en Chiloé, Chile. *Revista Chilena de Historia Natural*, **58,** 171–186.

Duncan, R. (1989) An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrycarpus dacrydioides*). *New Zealand Natural Sciences*, **16,** 31–37.

Figueroa, J.A. & Lusk, C.H. (2001) Germination requirements and seedling shade tolerance are not correlated in a Chilean temperate rain forest. *New Phytologist*, **152,** 483–489.

Fritts, H.C. (1976) *Tree rings and climate*. Academic Press, New York.

González, M., Donoso, C. & Fraver, S. (1997) Respuesta inicial de *Eucryphia cordifolia* Cav., *Laurelia sempervirens* R. et P Tul. y *Aextoxicon punctatum* R. et P. en plantaciones mixtas en sectores recientement florecidos con *Chusquea quila* Kunth en el centro-sur de Chile. *Bosque*, **18,** 53–59.

Gutiérrez, A.G., Armesto, J.J. & Aravena, J.C. (2004) Disturbance and regeneration dynamics of an old-growth North Patagonian rain forest in Chiloé Island, Chile. *Journal of Ecology*, **92,** 598–608.

Hall, M. & Witte, J. (1998) *Maderas del sur de Chile. Arboles, aplicaciones y procesos*. Editorial Universitaria, Santiago.

Holmes, R. (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree Ring Bulletin*, **43,** 69–75.

Lara, A. (1991) *The dynamics and disturbance regime of* Fitzroya cupressoides *in the south-central Andes of Chile*. PhD thesis, University of Colorado, Boulder.

Loehle, C. (2000) Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. *The American Naturalist*, **156,** 14–33.

Lorimer, C.G. & Frelich, L.E. (1989) A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research*, **19,** 651–663.

Lorimer, C.G. & Krug, A.G. (1983) Diameter distributions in even-aged stands of shade-tolerant and midtolerant tree species. *American Midland Naturalist*, **109,** 331–345.

Lusk, C.H. (1995) Seed size, establishment sites and species coexistence in a Chilean rain-forest. *Journal of Vegetation Science*, **6,** 249–256.

Lusk, C.H. (1996) Gradient analysis and disturbance history of temperate rain forests of the coast range summit plateau, Valdivia, Chile. *Revista Chilena de Historia Natural*, **69,** 401–411.

Lusk, C.H. (1999) Long-lived light-demanding emergents in southern temperate forests: the case of *Weinmannia trichosperma* (Cunoniaceae) in Chile. *Plant Ecology*, **140,** 111–115.

Lusk, C.H. & Del Pozo, A. (2002) Survival and growth of seedlings of 12 Chilean rainforest trees in two light environments: gas exchange and biomass distribution correlates. *Austral Ecology*, **27,** 173–182.

Lusk, C.H. & Smith, B. (1998) Life history differences and tree species coexistence in an old-growth New Zealand rain forest. *Ecology*, **79,** 795–806.

Mabberley, D.J. (1997) *The plant-book. A portable dictionary of the vascular plants*, 2nd edn. Cambridge University Press, Cambridge.

Marticorena, C. & Quezada, M. (1985) Catálogo de la flora vascular de Chile. *Gayana*, **42,** 1–157.

Nakashizuka, T. (2001) Species coexistence in temperate, mixed deciduous forests. *Trends in Ecology and Evolution*, **16,** 205–210.

Noble, I.R. & Slatyer, R.O. (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio*, **43,** 5–21.

Nowacki, G.J. & Abrams, M.D. (1997) Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs*, **67,** 225–249.

Parada, T., Jara, C. & Lusk, C.H. (2003) Distribución de alturas máximas de especies en rodales Antiguos de Selva Valdiviana, Parque Nacional Puyehue. *Bosque*, **24,** 63–67.

Pérez, C. (1994) Indices de esclerofilia en relación a la calidad química de la hojarasca y el grado de mineralización potencial del nitrógeno del suelo superficial del bosque de 'olivillo' (*Aextoxicon punctatum* R. et Pav.) en Chile. *Revista Chilena de Historia Natural*, **67,** 101–109.

Pollmann, W. & Veblen, T.T. (2004) *Nothofagus* regeneration dynamics in south-central Chile: a test of a general model. *Ecological Monographs*, **74,** 615–634.

Rüger, N., Gutiérrez, A.G., Kissling, W.D., Armesto, J.J. & Huth, A. (2007) Ecological impacts of harvesting scenarios for temperate evergreen rain forest in southern Chile – a simulation experiment. *Forest Ecology and Management*, **252,** 52–66.

Runkle, J.R. (1992) *Guidelines and sample protocol for sampling forest gaps*. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland.

Saldaña, A. & Lusk, C.H. (2003) Influence of overstorey species identity on resource availability and variation in composition of advanced regeneration in a temperate rainforest in southern Chile. *Revista Chilena de Historia Natural*, **76,** 639–650.

Schnitzer, S.A. & Carson, W.P. (2001) Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology*, **82,** 913–919.

Schulman, E. (1956) *Dendroclimatic change in semiarid America*. University of Arizona Press, Tucson.

Shugart, H.H. (1984) *A theory of forest dynamics. The ecological implications of forest succession models*. Springer, New York.

Smith-Ramírez, C. (2004) The Chilean coastal range: a vanishing center of biodiversity and endemism in South American temperate rainforests. *Biodiversity and Conservation*, **13,** 373–393.

Stewart, G.H. & Rose, A.B. (1990) The significance of life history strategies in the developmental history of mixed beech (*Nothofagus*) forests, New Zealand. *Vegetatio*, **87,** 101–114.

Stokes, M.A. & Smiley, T.L. (1968) *An introduction to tree-ring dating*. University of Chicago Press, Chicago.

Swaine, M.D. & Whitmore, T.C. (1988) On the definition of ecological species groups in tropical rain forests. *Vegetatio*, **75,** 81–86.

Torrejón, F., Cisternas, M. & Araneda, A. (2004) Environmental effects of the Spanish colonization from de Maullín river to the Chiloé archipelago southern Chile. *Revista Chilena de Historia Natural*, **77,** 661–677.

Veblen, T.T. (1985) Forest development in tree-fall gaps in the temperate rain forests of Chile. *National Geographic Research*, **1,** 161–184.

Veblen, T.T. (1986) Treefalls and the coexistence of conifers in subalpine forests of the Central Rockies. *Ecology*, **67,** 644–649.

Veblen, T.T. (1992) Regeneration dynamics. *Plant succession: theory and predictions* (ed. by C. Glenn-Lewin, R.K. Peet and T.T. Veblen), pp. 152–187. Chapman and Hall, London.

Veblen, T.T. & Ashton, D.H. (1978) Catastrophic influences on the vegetation of the Valdivian Andes, Chile. *Vegetatio*, **36,** 149–167.

Veblen, T.T., Ashton, D.H., Schlegel, F.M. & Veblen, A.T. (1977) Distribution and dominance of species in the understorey of a mixed evergreen–deciduous *Nothofagus* forest in south central Chile. *Journal of Ecology*, **65,** 815–830.

Veblen, T.T., Schlegel, F.M. & Escobar, B. (1980) Structure and dynamics of old-growth *Nothofagus* forests in the Valdivian Andes, Chile. *Journal of Ecology*, **68,** 1–31.

Veblen, T.T., Donoso, C., Schlegel, F.M. & Escobar, B. (1981) Forest dynamics in south-central Chile. *Journal of Biogeography*, **8,** 211–247.

Veblen, T.T., Hadley, K.S., Reid, M.S. & Rebertus, A.J. (1991) Methods of detecting past spruce beetle outbreaks in rocky mountain subalpine forest. *Canadian Journal of Forest Research*, **21,** 242–254.

Veblen, T.T., Kitzberger, T. & Lara, A. (1992) Disturbance and forest dynamics along a transect from Andean rain-forest to Patagonian shrubland. *Journal of Vegetation Science*, **3,** 507–520.

Willson, M.F. & Armesto, J.J. (1996) The natural history of Chiloé: on Darwin's trail. *Revista Chilena de Historia Natural*, **69,** 149–161.

BIOSKETCHES

Alvaro G. Gutiérrez studied forestry at the Universidad de Chile, Santiago. He is currently a doctoral student at the Helmholtz Centre for Environmental Research, Leipzig. His doctoral thesis focuses on the long-term forest dynamics of Chilean temperate rainforests with an emphasis on the impacts of climatic change. His main research interests are long-term forest dynamics, impacts of global change on forests, dendrochronology and ecological modelling.

Juan J. Armesto is a professor at the Universidad de Chile and P. Universidad Católica in Santiago, Chile. His main research interests are forest ecology and forest biodiversity conservation.

Editor: Pauline Ladiges