Stand dynamics of the shade-tolerant conifers *Podocarpus nubigena* and *Saxegothaea conspicua* in Chilean temperate rain forest

Lusk, Christopher H.

Departamento de Botánica, Universidad de Chile, Casilla 653, Santiago, Chile;
Present address: Depto. de Ciencias Biológicas, Universidad de Talca, Casilla 747, Talca, Chile;
Tel. + 56 071 200285; Fax + 56 071 200276; E-mail clusk@pehuenche.utalca.cl

Abstract. Population structures were used to infer regeneration patterns of the conifers *Podocarpus nubigena* and *Saxegothaea conspicua* and associated angiosperm tree species in six stands in the temperate rainforests of the coastal ranges of southern Chile. On poorly-drained, nutrient-poor and high altitude sites, where most of the associated species were fairly shade-intolerant and light-crowned, dense all-aged populations and the presence of numerous saplings beneath the canopy suggested continuous regeneration of both *P. nubigena* and *S. conspicua*. On more favourable sites, where several of the associated angiosperms were highly shade-tolerant and dense-crowned, both conifers, particularly *P. nubigena*, were less abundant, and their regeneration from seed appeared to be sporadic. *S. conspicua*'s great longevity ($\geq$ 750 yr) and frequent vegetative reproduction are probably crucial to its persistence in competition with shade-tolerant broadleaved species in undisturbed stands on favourable sites. Results of this study, and a review of related literature on southern temperate forests are not consistent with the hypothesis that heavily-shaded, infrequently-disturbed habitats are an evolutionary refuge for conifers. Sites likely to have high leaf area indices and infrequent disturbance are better exploited by shade-tolerant angiosperms.

Keywords: Conifer; *Nothofagus*; Podocarpaceae; Productivity gradient; Regeneration; Shade tolerance; Southern temperate forest; Treefall gap.

Nomenclature: Marticorena & Quezada (1985).

Introduction

Several hypotheses have been proposed to explain the historical rise of the angiosperms, and the present relegation of the conifers mainly to poor soils and cold sites. Bond (1989) proposed that this pattern can be explained in terms of competitive interactions in the regeneration phase, arguing that conifers are unable to compete with angiosperms on more productive sites as a result of phylogenetic contraints on the rate and plasticity of growth in gymnosperm seedlings.

Bond (1989) suggested that, in evolutionary terms, heavy shade would also be a refuge habitat for conifers, in that it would reduce the growth rate advantages of angiosperms in the same fashion as nutrient shortages or low temperatures. He therefore predicted that shade-tolerant conifers would perform well against angiosperm competitors in heavily-shaded, infrequently-disturbed understories, as well as on sites where climatic or edaphic conditions depress productivity.

Studies of the dynamics of southern temperate forests in South America, New Zealand and Tasmania provide little support for the extension of Bond's hypothesis to shaded environments, as most conifers discussed in the literature on these forests appear to be shade-intolerant (Enright & Ogden 1995). However, it must be borne in mind that a common motive for work on stand dynamics has been management concern about lack of regeneration of certain species in old stands (e.g. Veblen & Ashton 1982; Veblen & Stewart 1982), probably resulting in a research bias towards shade-intolerant species. Relatively shade-tolerant conifers are undoubtedly also present in southern temperate forests (e.g. Veblen et al. 1980; Lusk & Ogden 1992), and studies of the dynamics and distribution of these taxa may enhance the overall understanding of landscape partitioning between conifers and angiosperms.

All-sized populations of the podocarps *Podocarpus nubigena* and *Saxegothaea conspicua* have been described from Chilean rain forests (Veblen et al. 1980; Lara 1991; Innes 1992), and these two species are considered to be the most shade-tolerant conifers of temperate South America (Donoso 1989). However, most previous work on *S. conspicua* and *P. nubigena* has been incidental to studies of *Nothofagus* dynamics, and regeneration processes and response to environmental gradients have not been discussed in detail.

In this paper I describe population size and age structures of *P. nubigena* and *S. conspicua*, and associated angiosperm trees in six stands in the coastal ranges of southern Chile, and infer regeneration processes from these data (e.g. Veblen et al. 1980; Stewart & Rose 1989). Sites differing in soil parameters, elevation, floristic composition, canopy condition and disturbance history are compared, in order to characterize the site

and stand conditions most favourable for the establishment of these conifers.

Study area

Saxegothaea conspicua and *Podocarpus nubigena* are common on two broad site types in the coastal ranges of south-central Chile: at low altitudes on poorly-drained marine and fluvio-glacial deposits (Anon. 1981) and at mid to high altitudes (400 - 950 m) on shallow soils developed from micaschists (Veblen et al. 1981; Perez et al. 1991). Both species also occur in the Andes at similar latitudes.

The first site type is represented in this study by three plots at Yerba Loza on Isla Grande de Chiloé (Table 1), where extensive mixed stands of *S. conspicua* and *P. nubigena* occur on undulating terrain. Highly organic, acidic and generally poorly-drained soils have developed on fluvio-glacial sands and gravels overlying marine sediments (Anon. 1981). Soils were progressively less gleyed in the sequence of plots Y1 to Y3, indicating an ameliorating drainage gradient (Table 2). Precise climatic data were not available for the study sites, but interpolations from pluviometric maps in Almeyda & Saez (1958) indicate mean annual rainfall of ca. 3000 mm at Yerba Loza.

The second site type is represented by three plots from two sites in the Cordillera Pelada near Valdivia. Two plots were sampled at Hueicolla on the western slopes of the range and one at Piedra del Indio on the undulating plateau which forms the range summit. Interpolations from Almeyda & Saez (1958) suggest annual precipitation of ca. 3500 mm for Hueicolla and 4000 mm at Piedra del Indio.

Methods

Population structures

Plots (0.36 ha) were selected subjectively as representative of each site, except at Piedra del Indio where a smaller plot (0.15 ha) was used to characterize a stand of relatively simple structure. Within each plot, diameters at breast height (DBH) of all individuals ≥ 1.0 cm DBH were measured. Only the largest stem of multi-stemmed individuals was included in the diameter frequency distributions used to represent population structure. Stems of 1.0 - 4.9 cm DBH are referred to as saplings. Stems separated at ground level were classed as separate individuals, even when root suckering was suspected or proven. Seedlings ≥ 15 cm tall and < 1 cm DBH were counted in 1-m² subplots totalling 4 % of the total plot area, using a stratified random procedure.

As plots 2 and 3 at Yerba Loza were selectively-logged shortly after sampling, some of the age data at these site were obtained from cross-sections. At the other sites, stand age structure was examined by extracting increment cores from 4 - 5 individuals from each diameter class of *P. nubigena* and *S. conspicua*.

Many *Podocarpaceae*, including *P. nubigena* and *S. conspicua*, are prone to ring wedging and lobate growth, and so many rings may be missing from a given radius (Dunwiddie 1979). However, an examination of cross-sections of the New Zealand podocarp *Dacrycarpus dacrydioides* showed that age estimate errors due to missing rings could be minimized by counting on the longest radius (Duncan 1989). Accordingly, an attempt was made to obtain cores from the longest radius: for

Table 1. Plot locations and descriptions.

Locality	Plot	Alt. (m)	Slope range (˚)	% area in gap/building phases	Main associated spp.
Yerba Loza 42˚52'S 73˚51'S	Y1	220	0-5	9	*Drimys winteri* *Nothofagus nitida*
	Y2	170	0-10	20	*Amomyrtus luma* *D. winteri* *Laurelia philippiana*
	Y3	130	0-5*	8	*A. luma* *L. philippiana*
Hueicolla 40˚10'S 73˚34'E	H1	530	15-30	7	*Dasyphyllum diacanthoides* *Eucryphia cordifolia* *Gevuina avellana* *L. philippiana*
	H2	530	0-30	8	*D. winteri* *E. cordifolia* *Weinmannia trichosperma*
Piedra del Indio 40˚12´S 73˚26´E	P	880	10-15	0	*N. nitida*

* Up to 40° on banks of small stream bisecting plot

Table 2. Soil analyses of six plots from Chilean coastal ranges.

Plot	pH	% Organic matter	Total N (%)	C/N	P	K	Ca	Mg
Y1	4.3	45.5	1.08	24.4	6	107	65	119
Y2	4.3	44.3	1.12	23.0	3	117	113	130
Y3	4.2	39.8	1.21	19.1	4	198	340	523
H1	4.7	21.4	0.70	17.7	4	123	377	156
H2	4.3	15.4	0.37	24.1	5	107	78	82
P	3.5	18.3	0.27	34.0	5	46	131	210

large stems this usually required extraction of several cores per tree.

Small-diameter individuals ($<$ ca. 20 cm DBH) were cored at ground level. Larger stems were generally cored at 50 cm height, although sampling as high as 120 cm was occasionally preferred in order to minimise loss of radius due to butt rot. In view of the highly variable height growth rates of seedlings (Table 3), no correction was attempted for time to grow to sampling height (see Norton & Ogden 1990).

The total number of trees aged at each site varied according to the abundance of sound stems. As *S. conspicua* $>$ ca. 60 cm DBH usually contained heartrot, little reliable age data could be obtained from the larger diameter classes of this species. Procedures described in Norton et al. (1987) and Duncan (1989) were used to estimate the number of missing rings for incomplete cores, but cores that included less than 75 % of the geometric radius of the tree were rejected.

Sweda & Inoue (1987) cross-dated *P. nubigena* ring sequences at two sites in Patagonia, and annual ring formation has also been demonstrated for several other *Podocarpaceae* in southern temperate countries (e.g. Franklin 1969; Dunwiddie 1979). Growth rings were therefore assumed to be annual in *S. conspicua* and *P. nubigena.*

Linear regression showed diameter to be a significant predictor of age ($P < 0.01$) for both podocarp species at all sites. *R*-values ranged from 0.78 (*P. nubigena* at plots H2 & P2) to 0.99 (*P. nubigena* at plot Y2). No age data were obtained for other species, except for *Nothofagus nitida* at Piedra del Indio. However, significant age-diameter relationships have previously been demonstrated for populations of many of the main tree species in old-growth stands in the coastal ranges (Veblen et al. 1981). Stand dynamics of other common species were therefore inferred solely on the basis of population size structures.

Association of regeneration with canopy gaps

The degree of dependence of seedlings or saplings on canopy gaps can be assessed by comparing their abundance beneath gaps and beneath intact canopies (e.g. Armesto & Fuentes 1988). Canopy condition on each plot was mapped in 2.5 m × 2.5 m units as 'gap', 'building' or 'mature phase' (*sensu* Whitmore 1975; Clark & Clark 1992). The numbers of small stems (1-14.9 cm DBH) found in gap and building patches of ≥ 25 m^2 were compared with the totals to be expected if these stems were randomly distributed over the plot (*G*-test). Minor openings of < 25 m^2, resulting from branch-falls or standing death of small-crowned trees, were not recorded as gaps. Tests were performed separately for

Table 3. Time taken by saplings of *Podocarpus nubigena* and *Saxegothaea conspicua* to grow to a height of 50 cm and 100 cm at two sites (median and range, $n = 5$). Saplings harvested in treefall gaps.

Site	Species	Years taken to grow to	
		50 cm	100 cm
Y2	*P. nubigena*	18 (13-26)	29 (22-31)
	S. conspicua	9 (6-13)	13 (10-21)
P	*P. nubigena*	25 (10-66)	31 (14-75)
	S. conspicua	31 (9-44)	42 (22-59)

two diameter classes (1.0 - 4.9 cm and 5.0 - 14.9 cm DBH), in all cases where sample sizes were sufficient to avoid expected frequencies of < 5. At some sites the two classes were combined to provide totals sufficient for valid use of the test.

Results

Yerba Loza

At Y1, a ca. 20 m tall canopy was dominated by *Podocarpus nubigena*, *Drimys winteri* (*Winteraceae*) and *Saxegothaea conspicua,* with fewer *Tepualia stipularis* (*Myrtaceae*) and *Weinmannia trichosperma* (*Cunionaceae*), and overtopped by slightly taller *Nothofagus nitida* (*Fagaceae*). The sparse understorey consisted mainly of *Amomyrtus luma*, *Caldcluvia paniculata* (*Cunionaceae*), *T. stipularis* and the bamboo *Chusquea quila* (*Poaceae*). There were several small canopy gaps of less than 100 m^2, and several tip-up mounds and fallen logs in varying states of decay and different orientations indicating a history of sporadic treefalls.

Both *P. nubigena* and *S. conspicua* had all-aged populations indicative of continual establishment during the last 400 yr (Fig. 1a). *P. nubigena* of 1 - 15 cm DBH were significantly associated with gap and building phases (Table 5), but were also present beneath the canopy. Juveniles of *S. conspicua* and other species were not sufficiently abundant to permit analysis of their association with canopy gaps. Six of the nine saplings of *S. conspicua* had reproduced vegetatively, through re-iteration of toppled trees or juveniles, and suckering.

Although seedlings of *D. winteri* were abundant, stems in the 1-15 cm range were scarce relative to the numbers of larger stems (Fig. 1a). Development beyond seedling size therefore probably requires more open conditions than those afforded by the largely-intact canopy present at the time of sampling. The population structure of *N. nitida*, including very few small stems
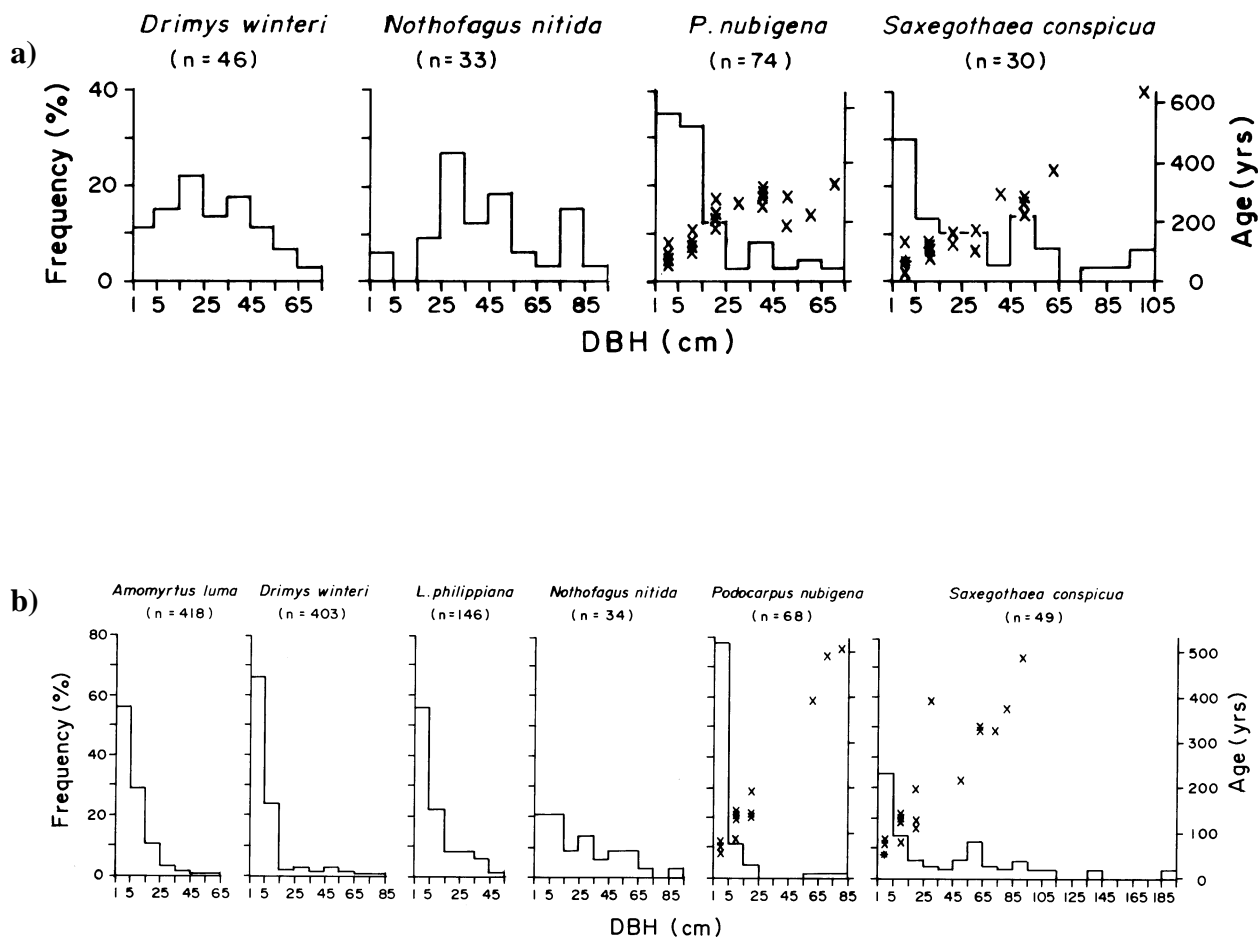
Fig. 1. Diameter frequency distributions of main tree species on five plots in Chilean coastal ranges. The first diameter class is 1.0-4.9 cm DBH, and subsequent classes are 10 cm wide (5.0-14.9 cm, 15.0-24.9 cm, etc.). The secondary y-axis shows ages (x) for up to five individuals in each diameter class of *Podocarpus nubigena* and *Saxegothaea conspicua*. **a.** plot Y1; **b.** Y2; overleaf: **c.** Y3; **d.** H1; **e.** H2.

(Fig. 1a) or seedlings (Table 4), suggests a similar, or greater, requirement for canopy openings.

At Y2 the main canopy species were *Saxegothaea conspicua*, *Drimys winteri* and *Laurelia philippiana* (Monimiaceae) up to 24 m tall, with slightly taller *Nothofagus nitida*. *Amomyrtus luma* was the dominant subcanopy and understorey species and *Chusquea quila* formed dense thickets, especially beneath the canopy gaps produced by numerous recent treefalls. Gap and building phases totalled nearly 20% of the plot area (Table 1).

The age distribution of *S. conspicua* indicated con-

tinual regeneration during at least the last 500 yr (Fig. 1b). As at Y1, there were several examples of reiteration from fallen juveniles and trees, and also suckering. *S. conspicua*'s remarkable powers of vegetative reproduction are illustrated by the production of new sapling-sized shoots from the fallen, completely severed trunk of a wind-snapped tree of ca. 85 cm DBH. Adult *P. nubigena* trees were very scarce on the plot (Fig. 1b), and the current abundance of saplings, highly significantly associated with canopy gaps (Table 4), seems likely to be a response to the numerous recent treefalls.

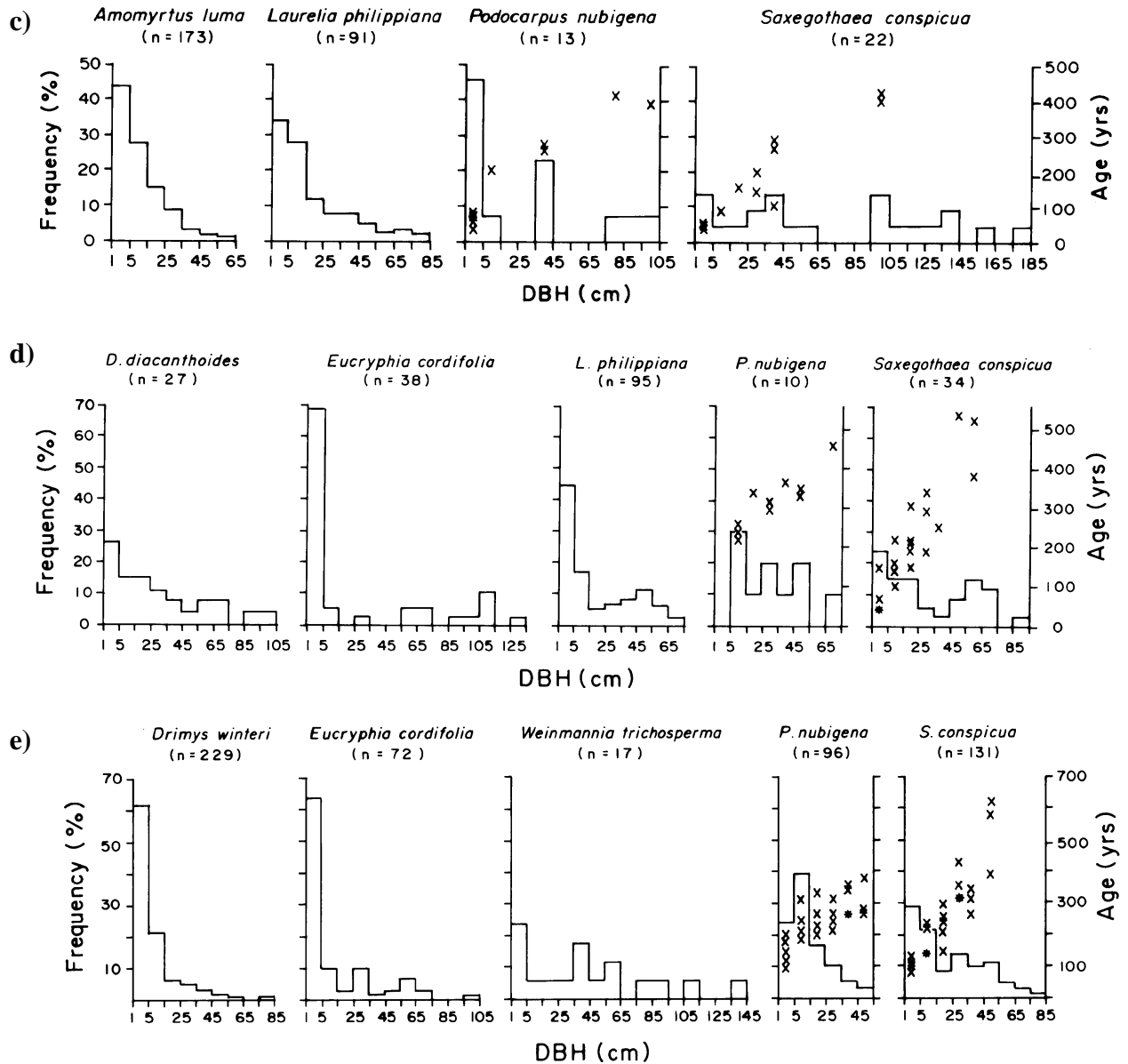Small stems of *A. luma*, *D. winteri* and *L. philippiana*

Fig. 1. (Continued)

were also significantly associated with canopy gaps (Table 4). The abundance of small stems of most species at Y2 (Fig. 1b) is therefore attributable to recent treefalls. This is especially true of *D. winteri*, which was represented by few small stems on the much-less-disturbed plot at Y1, despite similar densities of adult trees at the two sites. With the exception of *N. nitida*, all the main tree species were well-represented by seedlings (Table 5).

Plot Y3, bisected by a small sharply-entrenched stream, was the best drained of the three sites at Yerba Loza. *Saxegothaea conspicua* and *Laurelia philippiana* up to 30 m tall were the most common canopy trees,

with a few *Podocarpus nubigena*. *Amomyrtus luma*, *Myrceugenia ovata* (*Myrtaceae*) and *Chusquea quila* were the main subcanopy and understorey species.

Despite the intact canopy present on most of plot Y3 (Table 1), *A. luma* and *L. philippiana* presented 're-verse-J' type diameter distributions consistent with a continuous regeneration pattern (Meyer 1952). The diameter distributions and age data for both conifers suggested more sporadic recruitment to canopy (Fig. 1c). *S. conspicua* was represented in many diameter classes up to ca. 2 m DBH (Fig. 1c). Most of the smaller *S. conspicua* (58 % of stems < 65 cm DBH) had arisen

Table 4. Significant associations of small stems with canopy gaps (*G*-test).

Site	Species	DBH class (cm)	n	*P*
Y1	*Podocarpus nubigena*	1-15	50	< 0.05
Y2	*Amomyrtus luma*	1-5	229	< 0.001
Y2	*Drimys winteri*	1-5	267	< 0.001
Y2	*D. winteri*	5-15	99	< 0.001
Y2	*Laurelia philippiana*	5-15	34	< 0.02
Y2	*P. nubigena*	1-5	54	< 0.001
H2	*Saxegothaea conspicua*	1-5	66	< 0.01

from reiteration of fallen stems, indicating a predominance of vegetative reproduction during at least the last 300 yr of stand development. Several vertical stems containing 86 to 283 growth rings had arisen from different parts of one toppled *S. conspicua*, showing that fallen individuals may continue to produce new vertical stems for as much as 200 yr after the initial disturbance.

Hueicolla

Stand H1 was located on a moderate slope in a minor tributary valley of the Hueicolla stream. Scattered emergent *Eucryphia cordifolia* attained ca. 40 m. *Laurelia philippiana* (to 30 m tall) was the most common tree in a canopy which also included *Saxegothaea conspicua*, *Dasyphyllum diacanthoides*, *Podocarpus nubigena*, overtopping a variety of shorter tree species. *Chusquea macrostachya* and the fern *Lophosoria quadripinnata* formed a fairly dense understorey up to 3 m tall.

P. nubigena was represented at H1 by only 10 individuals of ≥ 1 cm DBH, all of which were at least 215 yr old (Fig. 1d). The lack of younger stems may indicate that development of *P. nubigena* on this site requires larger gaps than those present at the time of sampling, none of which exceeded 150 m².

The population structure of *S. conspicua* at H1, in-

cluding many stems less than 200 yr old, indicated more continuous regeneration than for *P. nubigena* (Fig. 1d). Most of the saplings present on the plot at the time of sampling appeared to have established directly from seed. However, suckering and production of epicormic shoots from old stems (see Veblen et al. 1980) were also noted on this site.

The diameter frequency distributions of *L. philippiana* and *D. diacanthoides* were consistent with all-aged population structures, and the former species in particular was represented by many saplings (Fig. 1d). Although many seedlings and saplings of *E. cordifolia* (mostly root suckers) were also present, the diameter distribution suggests sporadic rather than continuous regeneration. Evidence of repeated leader dieback noted in many of these small stems beneath the canopy, and the scarcity of intermediate-sized individuals (Fig. 1d), confirm that sizeable treefall gaps are probably required for development beyond sapling size (Veblen et al. 1981).

Plot H2 was located on a narrow ridge at the same elevation as H1. The shade-tolerant angiosperms which were common at H1 (*Laurelia philippiana* and *Dasyphyllum diacanthoides*) were scarce at H2 where the canopy was comprised mainly of *Saxegothaea conspicua*, *D. winteri* and *P. nubigena* up to 18 m tall, overtopped by scattered emergent *Eucryphia cordifolia* and *Weinmannia trichosperma* up to 27 m tall. The understorey included *Lophosoria quadripinnata*, *Chusquea macrostachya*, and numerous small stems of most overstorey species.

The age data for *P. nubigena* indicated continuous establishment during the last 400 yr. However, a similarity to H1 can be noted, in that < 200 yr old *P. nubigena* stems were scarce relative to those in the 200 - 400 yr range (Fig. 1e), suggesting linked recent disturbance histories at the two sites. Most stems in the modal size class (5 - 15 cm DBH) were suppressed individuals at least 200 yr old. *S. conspicua* at H2 showed a wider age

Table 5. Densities (ind./ha ± S.E.) of seedlings > 15 cm tall and < 1 cm DBH, estimated from sampling 1/25 of plot area (common tree species only).

| Species	Y1	Y2	Y3	H1	H2	P
Amomyrtus luma	3889 ± 1225	11458 ± 1000	5972 ± 900	3472 ± 539	347 ± 153	650 ± 251
Drimys winteri	9925 ± 2233	5694 ± 1225	556 ± 261	139 ± 97	2708 ± 472	10243 ± 1733
Eucryphia cordifolia	–	–	–	1319 ± 331	1042 ± 225	–
Laurelia philippiana	556 ± 289	2430 ± 583	2083 ± 650	903 ± 281	139 ± 97	–
Myrceugenia chrysocarpa	–	–	–	–	–	6341 ± 918
M. ovata	–	69 ± 69	556 ± 261	2361 ± 411	–	–
Nothofagus nitida	69 ± 69	–	–	–	–	1138 ± 350
Podocarpus nubigena	3541 ± 331	1736 ± 163	1319 ± 133	208 ± 43	1250 ± 121	650 ± 251
Pseudopanax laetevirens	–	–	–	347 ± 153	417 ± 239	325 ± 161
Saxegothaea conspicua	764 ± 250	903 ± 308	486 ± 200	625 ± 231	694 ± 289	1545 ± 490
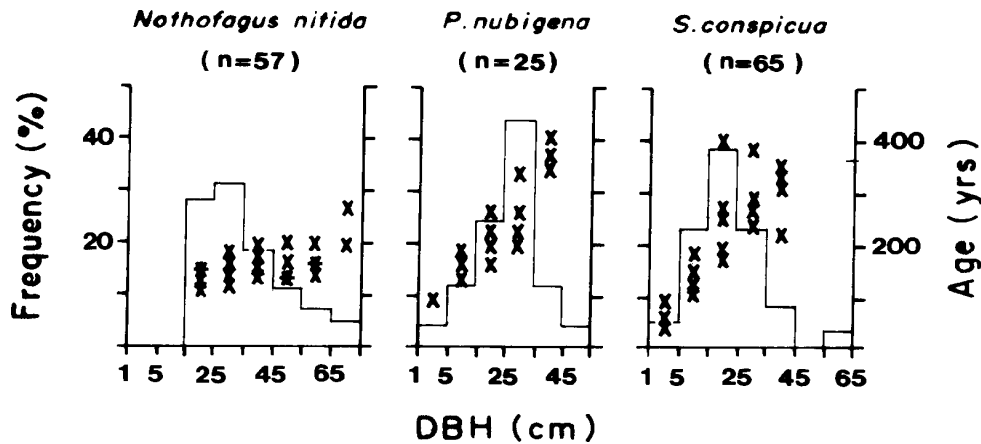
Fig. 2. Diameter frequency distributions of main tree species at plot P. Diameter classes and age data as for Fig. 1, except that age data are also shown for *Nothofagus nitida*.

range than *P. nubigena* (Fig. 1e), with saplings making up a larger percentage of its population.

Despite the relatively intact canopy (Table 1), and although the three main overstorey angiosperms are all fairly shade-intolerant (Donoso 1989), each of these presented all-sized populations at H2 (Fig. 1e). This can be attributed to light penetration permitted by the ridgetop location of the plot and by the prominence of light-crowned species in the overstorey (e.g. *Weinmannia trichosperma*).

H1 and H2 should not be regarded as different successional stages, as the age data suggest similar recent disturbance histories at the two sites, and invasion of the understorey by shade-tolerant dominants of H1 (*L. philippiana* and *D. diacanthoides*) was not evident at H2. They appear to be excluded from H2 by site conditions, possibly by the low nutrient status of the ridgetop soil (Table 2).

Piedra del Indio

Plot P was located near Piedra del Indio (ca. 880 m altitude), on a gentle slope near the eastern margin of the undulating plateau which forms the coastal range summit. *Nothofagus nitida* formed a largely-continuous overstorey up to 22 m tall, over a subcanopy of *Podocarpus nubigena* and *Saxegothaea conspicua,* and a sparse understorey of *Amomyrtus luma* and *Chusquea macrostachya*.

Nearly all of the *N. nitida* were between 113 and 215 yr old, with one older individual (Fig. 2). *P. nubigena* and *S. conspicua* showed bell-shaped diameter distributions, but were represented by a much wider range of ages, including stems that variously established before,

concurrently with, and after, the *N. nitida* cohort (Fig. 2). Seedlings of the three main tree species were present, but were greatly outnumbered by those of *Drimys winteri* and *Myrceugenia chrysocarpa* (Table 4), species which were not present in the overstorey.

Decaying logs and tip-up mounds were abundant on the floor of this stand, and most (83 %) of the *N. nitida* had established on these elevated microsites (cf. Lusk 1995). About half the *S. conspicua* (48%) and some of the *P. nubigena* (27 %) had also established on logs or tip-up mounds. In conjunction with the truncated age distribution of light-demanding *N. nitida* (Fig. 2), this evidence is consistent with a scenario of partial blowdown of the stand a little over 200 yr ago, producing a pulse of regeneration of all three overstorey species.

Discussion

Stand structure and dynamics

On poorly-drained or nutrient-poor soils, and at high elevations, *P. nubigena* and *S. conspicua* were most commonly associated with *Drimys winteri*, *Nothofagus nitida,* and *Weinmannia trichosperma*. Population structures at these sites indicate that *P. nubigena* and *S. conspicua* were the most shade-tolerant of the main canopy tree species: they typically presented all-aged populations (plots Y1, H2, P), with saplings frequently found beneath an intact canopy. Previous studies also show that small stems of *S. conspicua* and *N. nubigena* are often abundant in undisturbed stands where these species co-occur with *D. winteri*, *N. nitida,* and *W. trichosperma* (Lara 1991; Innes 1992).

Both conifers, especially *P. nubigena*, were less abundant on more favourable sites, where *Laurelia philippiana* and *Amomyrtus luma* were the most frequent associates. *L. philippiana* and *A. luma* approximated 'reverse-J' type diameter distributions consistent with continuous regeneration, indicating a high degree of shade-tolerance (Meyer 1952). Several previous studies have similarly ascribed a high degree of shade tolerance to these species on the basis of population structures (e.g. Veblen et al. 1980; Armesto & Fuentes 1988; Lara 1991). *P. nubigena* and *S. conspicua* were also represented by a wide range of size- and age-classes on some of the more favourable sites. However, the population structures of *P. nubigena* at H2 and Y2, and of both conifers at Y3, suggested that their regeneration had been more sporadic than that of *L. philippiana* and *A. luma*, possibly indicating a greater requirement for canopy openings. This apparent trend towards greater gap-dependance on the more favourable sites is more subtle than the striking variation in regeneration mode that has been described for a number of shade-intolerant tree species (e.g. Veblen & Stewart 1982; Rebertus & Veblen 1993).

Age structures indicated that *S. conspicua* regenerated more continuously than *P. nubigena* at many sites. This is at least partly attributable to its greater propensity for vegetative reproduction, enabling the initial subsidising of new individuals by the parent stem (Veblen et al. 1980). Suckering and production of epicormic shoots of *S. conspicua* were noted on most sites, whereas resprouting of toppled stems was found mainly on the wet soils at Yerba Loza. Suckering of *P. nubigena* was also noted at two sites. *S. conspicua* of all sizes seem to possess at least some potential for vegetative reproduction, enabling toppled or damaged individuals to capture, or recapture, canopy positions after treefalls. Toppled stems of *S. conspicua* may continue to produce new shoots over a period of at least 200 yr, which may in some way explain the lack of a direct relationship between recruitment and disturbance that is suggested by the often-continuous range of ages in *S. conspicua* populations.

The maximum ages attained by individual stems were greater in *S. conspicua* than in *P. nubigena*, and this is probably also decisive in the greater abundance of the former on favourable sites. Although the oldest *S. conspicua* reliably aged in this study was only ca. 650 yr old, a ca. 750-yr old tree was found at another site (Lusk in press), and extrapolation would suggest that the largest stems at Y2 and Y3 (ca. 2 m DBH) were ca. 1 000 yr of age. The limited available data on Chilean angiosperm overstorey rainforest trees species suggest maximum longevities ranging from 250 to 650 yr (Lara 1991; Lusk unpubl. data), figures which are comparable

with *P. nubigena*, but below the maximum ages probably attained by *S. conspicua*. On favourable sites where establishment from seed of both conifers appears to be sporadic, a longevity advantage over its associates, and vegetative reproduction, are probably important for the persistence of *S. conspicua* in old, undisturbed stands (see also Veblen et al. 1980). The life history of *S. conspicua* therefore shows similarities with that of the Tasmanian podocarp *Lagarostrobus franklinii*: individual genotypes of this species may hold a site for millennia through a combination of long-lived stems and highly effective vegetative reproduction (Gibson & Brown 1991).

On the distribution of shade-tolerant conifers

Bond (1989) predicted that shade-tolerant conifers would be favoured on infrequently-disturbed, heavily-shaded sites, as well as at cold sites and poor soils which conifers are generally associated with. This view was supported by Midgley et al. (1990), who considered that predominance of fine-scale processes favoured the prominence of shade-tolerant species of *Podocarpus* in the Southern Cape plateau forests.

Data presented in this and other papers on Chilean temperate rain forests confirm the association of conifers with edaphically and climatically-suboptimal sites, but not with especially heavy shade. Firstly, on the sites where *S. conspicua* and *P. nubigena* were most abundant, their principal associates were fairly light-crowned trees (*Nothofagus nitida*, *Weinmannia trichosperma*, *Drimys winteri*). In contrast, on sites where shade-tolerant, dense-crowned angiosperms were common, both conifers were more scarce, and did not have large sapling banks beneath the canopy. Secondly, this study produced no evidence that tree-by-tree replacement under conditions of minimal canopy disturbance favoured the conifers. *P. nubigena* regenerated abundantly in response to multiple treefalls at two sites (Y2, P); but in a largely-undisturbed stand at another site (H1) this species was not regenerating, in contrast to co-occurring angiosperms such as *Laurelia philippiana*. Furthermore, both conifers were common at a high elevation site (P), where the abundance of even-aged stands is consistent with frequent occurrence of stand-destroying disturbances (Lusk in press). Also relevant is the virtual absence of *S. conspicua* and *P. nubigena* from old-growth stands on well-drained sites at low to moderate elevations in the coastal ranges (not examined in this paper), which Armesto & Fuentes (1988) showed to be closer to a steady-state condition than most other forests in south-central Chile. These stands are composed almost exclusively of dense-crowned, shade-tolerant angiosperms (Veblen et al. 1981; Armesto & Fuentes

1988). The understories that are likely to be the least-disturbed and most heavily-shaded in the region are therefore better exploited by angiosperms than by conifers.

Comparisons with other southern temperate forests also fail to show evidence of conifers being favoured by heavy shade. All Tasmanian conifers appear to be light-demanding (Read & Hill 1988; Gibson & Brown 1991). Shade-tolerant podocarps (*Prumnopitys ferruginea, Podocarpus hallii*) occur in New Zealand (Lusk & Ogden 1992), but in similar fashion to less tolerant relatives, they attain greatest abundance on sites where edaphic or climatic conditions exclude or inhibit the most shade-tolerant angiosperms such as *Beilschmiedia tawa* and *Dysoxylum spectabile* (Beveridge 1983; Lusk & Ogden 1992; Leathwick 1995). On mesic, fertile sites with mild temperatures, where high leaf area indices (and hence deep shade) are most likely to occur (Waring et al. 1978), recruitment to canopy in undisturbed old-growth stands is dominated by angiosperms (Beveridge 1983; Smale & Kimberley 1983).

In conclusion, in contrast to other marginal habitats such as nutrient-poor or cold sites, heavily-shaded understories do not appear to serve as major refuges for conifers. Only a minority of conifers maintain large seedling and sapling banks beneath closed forest canopies, and most of these species do so only on climatically- or edaphically-suboptimal sites characterized by relatively low leaf areas.

References

Anon. 1981. *Mapa geológico de Chile, escala 1:1,000,000.* Servicio Nacional de Geología y Minería.

Almeyda, E. & Saez, F. 1958. *Recopilación de datos climáticos de Chile y mapas sinópticos respectivos.* Ministerio de Agricultura, Santiago.

Armesto, J.J. & Fuentes, E.R. 1988. Tree species regeneration in a mid-elevation, temperate rainforest in Isla de Chiloé. *Vegetatio* 74: 151-159.

Beveridge, A.E. 1983. Regeneration of podocarp forests and maintenance of productivity. In: Thompson, K., Hodder, A.P.H. & Edmonds, A.S. (eds.) *Lowland forests in New Zealand*, pp. 93- 112. University of Waikato, Hamilton.

Bond, W.J. 1989. The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. *Biol. J. Linn. Soc.* 36: 227-249.

Clark, D.A. & Clark, D.B. 1992. Life history diversity of canopy and emergent trees in a neotropical rainforest. *Ecol. Monogr.* 62: 315-343.

Donoso, C. 1989. Antecedentes para la silvicultura del tipo forestal siempreverde. *Bosque* 10: 37-53.

Duncan, R.P. 1989. An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrycarpus dacrydioides*). *N. Z. Nat. Sci.* 16: 31-37.

Dunwiddie, P.W. 1979. Dendrochronological studies of indigenous New Zealand trees. *N. Z. J. Bot.* 16: 251-266.

Enright, N. & Ogden J. 1995. The southern conifers - a synthesis. In: Enright, N. & Hill, R. (eds.) *Ecology of the southern conifers,* pp. 271-287. Melbourne University Press, Melbourne.

Franklin, D.A. 1969. Growth rings in rimu from South Westland terrace forest. *N. Z. J. Bot.* 7: 177-178.

Gibson, N. & Brown, M.J. 1991. The ecology of *Lagarostrobus franklinii* (Hook. f.) Quinn (*Podocarpaceae*) in Tasmania. 2. Population structure and spatial pattern. *Aust. J. Ecol.* 6: 223-229.

Innes, J.L. 1992. Structure of evergreen temperate rain forest on the Taitao Peninsula, southern Chile. *J. Biogeogr.* 19: 555-562.

Lara, A. 1991. *The dynamics and disturbance regimes of Fitzroya cupressoides forests in the south-central Andes of Chile.* Unpubl. Ph.D. thesis, University of Colorado, Boulder, CO.

Leathwick, J. 1995. Climatic relationships of some New Zealand tree species. *J. Veg. Sci.* 6: 237-248.

Lusk, C.H. 1995. Seed size, establishment sites and species coexistence in a Chilean rain forest. *J. Veg. Sci.* 6: 249-256.

Lusk, C.H. In press. Gradient analysis and disturbance history of rain forests of the coast range summit plateau, Valdivia, Chile. *Rev. Chil. Hist. Nat.*

Lusk, C.H. & Ogden, J. 1992. Age structure and dynamics of a podocarp-broadleaf forest in Tongariro National Park. *J. Ecol.* 80: 379-393.

Marticorena, C. & Quezada, M. 1985. Catálogo de la flora vascular de Chile. *Gayana* 42: 1-157.

Meyer, H.A. 1952. Structure, growth and drain in balanced, uneven-aged forests. *J. For.* 50: 85-92.

Midgley, J., Seydack, A., Reynell, D. & McKelly, D. 1990. Fine-grain pattern in Southern Cape plateau forests. *J. Veg. Sci.* 1: 539-546.

Norton, D.A. & Ogden, J. 1990. Problems with the use of tree rings in the study of forest population dynamics. In: Cook, E.R. & Kairiukstis, L.A. (eds) *Methods of dendrochronology*, pp. 284-288. Kluwer, Dordrecht.

Norton, D.A., Palmer, J.G. & Ogden, J. 1987. Dendroecological studies in New Zealand. 1. An evaluation of tree age estimates based on increment cores. *N. Z. J. Bot.* 25: 373-383.

Perez, C., Armesto, J. & Ruthsatz, B. 1991. Descomposición de hojas, biomasa de raíces y características de los suelos en bosques mixtos de coníferas y especies laurifolias en el Parque Nacional Chiloé, Chile. *Rev. Chil. Hist. Nat. 64*: 479-490.

Read, J. & Hill, R.S. 1988. The dynamics of some rainforest

associations in Tasmania. *J. Ecol.* 76: 558-584.

Rebertus, A.J. & Veblen, T.T. 1993. Structure and treefall gap dynamics of old-growth *Nothofagus* forests in Tierra del Fuego, Argentina. *J. Veg. Sci.* 4: 641-654.

Smale, M.C. & Kimberley, M.O. 1983. Regeneration patterns in *Beilschmiedia tawa*-dominant forest at Rotoehu. *N. Z. J. For. Sci.* 13: 58-71.

Stewart, G.H. & Rose, A.B. 1989. Conifer regeneration failure in New Zealand: dynamics of montane *Libocedrus bidwillii* stands. *Vegetatio* 79: 41-49.

Sweda, T. & Inoue, J. 1987. Dendrochronology of San Rafael and Soler areas, Patagonia. *Bull. Glacier Res.* 4: 125-132.

Veblen, T.T. & Ashton, D.H. 1982. The regeneration status of *Fitzroya cupressoides* in the Cordillera Pelada, Chile. *Biol. Conserv.* 23: 141-161.

Veblen, T.T., Donoso, C., Schlegel, F.M. & Escobar, B. 1981. Forest dynamics in south-central Chile. *J. Biogeogr.* 8: 211-247.

Veblen, T.T. & Stewart, G.H. 1982. On the conifer regeneration gap in New Zealand: dynamics of *Libocedrus bidwilli* stands on South Island. *J. Ecol.* 70: 413-436.

Veblen, T.T., Schlegel, F.M. & Escobar, B. 1980. Structure and dynamics of old-growth *Nothofagus* forests in the Valdivian Andes. *J. Ecol.* 68: 1-31.

Waring, R.H., Emmington, W.H., Gholz, H.L. & Grier, C.C. 1978. Variation in maximum leaf area of coniferous forests of Oregon and its ecological significance. *For. Sci.* 24: 131-140.

Whitmore, T.C. 1975. *Tropical rainforests of the Far East.* Clarendon Press, Oxford.