

Regeneration microsites and tree species coexistence in temperate rain forests of Chiloé Island, Chile

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Summary

1 We studied the importance of fallen logs as recruitment sites for tree species, their role in species coexistence, and also the influence of canopy openness and litter depth on tree species establishment in mid-successional and old-growth temperate rain forests of Chiloé Island, southern Chile.

2 Old-growth (OG) stands showed significantly more fallen logs than mid-successional (MS) stands. Concomitantly, the proportion of seedlings and saplings established on logs was significantly greater in OG than MS stands.

3 Of 13 tree species found at our study sites, eight showed a significant bias towards establishment on logs, especially those in advanced stages of decomposition.

4 In some stands, all seedlings of *Eucryphia cordifolia*, *Laureliopsis philippiana*, *Nothofagus nitida*, *Tepualia stipularis* and *Weinmannia trichosperma* occurred on decaying logs, whereas all *Podocarpus nubigena* seedlings were found on undisturbed soil sites.

5 Small-seeded species were more common on logs, whereas large-seeded trees occurred on soil.

6 On soil, litter depth negatively affected local abundance of log-dependent seedlings, suggesting that variation in litter accumulation influences species distributions across the forest floor mosaic.

7 The density of shade-intolerant seedlings was more enhanced by the presence of fallen logs under closed canopy than by the occurrence of canopy gaps over soil sites.

8 Seed size plays an important role in successful establishment of species across the mosaic of fallen logs and different litter depth on the forest floor. We suggest that this mosaic of microsites is an important factor for species coexistence.

Key-words: fallen logs, litter, regeneration niche, seed size, temperate rain forests

Journal of Ecology (2003) **91**, 776–784

Introduction

Far from being uniform, the forest floor is a mosaic of microsites, defined by either or both of the physical environment and biological effects (Whittaker & Levin 1977). Abundance, growth and survival of seedlings vary across microsites (Whittaker & Levin 1977; Christy & Mack 1984; Peterson & Pickett 1990; Peterson & Campbell 1993). The most common microsites are defined by the presence or absence of fallen logs (Harmon & Franklin 1989; Lusk 1995), differences in

thickness of the litter layer (Huenneke & Sharitz 1990; Molofsky & Augspurger 1992; Peterson & Facelli 1992; Peterson & Campbell 1993), and pits and mounds created by tree uprooting (Beatty 1986; Peterson & Campbell 1993).

This small-scale heterogeneity may affect the establishment of tree seedlings, which in turn influence the spatial distribution of tree species (Beatty 1984; Núñez-Farfán & Dirzo 1988; Harmon & Franklin 1989; Nakashizuka 1989). Thus, the presence of various kinds of microsites could allow differential fine-scale establishment of species with different safe site requirements (*sensu* Harper *et al.* 1965), and therefore the distinction of a regeneration niche among species having similar niches in their adult stages. This could contribute to local species coexistence (Grubb 1977),

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especially among temperate forest trees, which may be less dependent on chance events than are tropical ones (Nakashizuka 2001).

Fallen logs have been shown to be particularly important as recruitment microsites for some plant species in European coniferous forests (Hofgaard 1993, Hörnberg *et al.* 1995), northern hardwood forests (McGee 2001), and temperate rain forests of North America (Christy & Mack 1984; Harmon & Franklin 1989), Tasmania (McKenny & Kirkpatrick 1999), New Zealand (Lusk & Ogden 1992) and southern Chile (Lusk 1995). Harmon & Franklin (1989) postulated that, in *Picea-Tsuga* forests, the main cause of exclusion of woody seedlings from the forest floor was competition with herbs and mosses. In evergreen temperate forests of south-central Chile, however, such competition is unlikely because they lack a dense understorey of herbs and mosses.

Seed size is perhaps the most important factor influencing recruitment success in tree species (e.g. Gross 1984; Foster & Janson 1985; Turnbull *et al.* 1999; Dalling & Hubbell 2002). Species strongly associated with logs and mounds tend to have small seeds (Nakashizuka 1989; Lusk 1995), and a common feature of these elevated microsites is the absence of litter accumulation (Putz 1983; Beatty 1984; McKenny & Kirkpatrick 1999), which may be a critical factor excluding seedlings of some species from the forest floor.

Our main objectives were to use the structure and distribution of seedling and sapling communities to assess the importance of microsite heterogeneity provided by fallen logs and different litter depths, for tree species regeneration in mid-successional (MS) and old-growth (OG) temperate rain forests of Chiloé Island. We predict small-seeded species should be negatively affected by litter depth, and hence their recruitment should be greater on fallen logs, which are elevated above the litter layer. Differences in seed size, in association with heterogeneity of microsites may therefore promote species coexistence in temperate forests of different successional age. We also predict that the proportion of total regeneration occurring on logs will be greater in OG where logfalls are more abundant, than MS stands, where their limited availability may prevent recruitment of some tree species.

Materials and methods

STUDY SITES

We selected two old-growth (OG) and two mid-successional (MS) stands in which to compare tree recruitment patterns. Minimum stand ages were determined by Aravena *et al.* (2002) and Carmona *et al.* (2002) by coring 30 emergent and dominant trees per stand (Table 1). Forest stands studied were located in Chiloé National Park (OG2) and in northern Chiloé island (remain stands) (Fig. 1), where the rural landscape is characterized by a mosaic of grazing pastures,

Table 1 Stand locations, minimum stand ages and their dominant canopy species

Locality	Stand code	Stand age (years)	Main canopy species
El Quilar 41°50' S	MS1	51*	<i>Drimys winteri</i> <i>Amomyrtus luma</i> <i>Podocarpus nubigena</i>
Senda Darwin Biological Station 41°50' S	MS2	62*	<i>Drimys winteri</i> <i>Podocarpus nubigena</i> <i>Saxegothaea conspicua</i>
	OG1	199*	<i>Nothofagus nitida</i> <i>Podocarpus nubigena</i> <i>Drimys winteri</i>
Chiloé National Park 42°30' S	OG2	191**	<i>Nothofagus nitida</i> <i>Drimys winteri</i> <i>Podocarpus nubigena</i>

*Aravena *et al.* (2002); **Carmona *et al.* (2002).

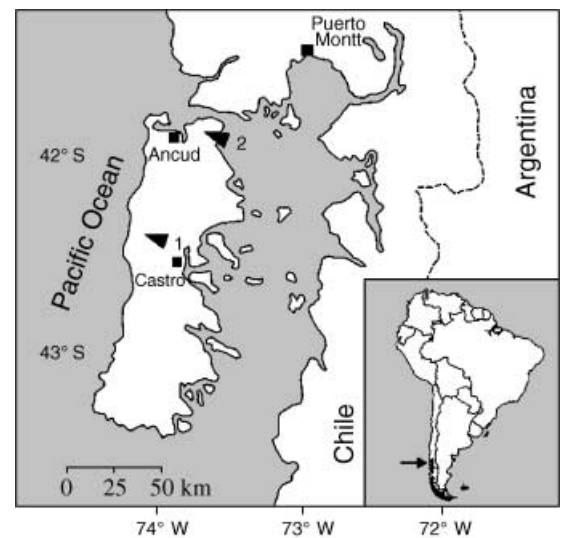


Fig. 1 Location of study sites in Chiloé Island, Chile. The arrows indicate Chiloé National Park (1) and 'Senda Darwin' Biological Station (2). The remaining site (El Quilar) is close to (2).

agricultural fields and remnant forest fragments. Disturbed stands and fragmentation are due to intense logging and widespread use of fire since the early 1800s to clear land for pastures and agricultural use (Willson & Armesto 1996).

In Chiloé National Park (42°30' S) we selected an old-growth stand (OG2) representative of the North Patagonian forest type (Veblen *et al.* 1995), located at 500 m a.s.l. The canopy was dominated by evergreen broad-leaved tree species, but also included a few narrow-leaved conifers (dominants in Table 1, details of these and other species in Table 2). Soils are highly organic and shallow (< 50 cm deep), derived from glacio-fluvial deposits. Annual precipitation has been estimated at 5000 mm, and monthly temperatures average 4 °C in winter and 15 °C in summer (Carmona *et al.* 2002). In northern Chiloé Island (41°50' S), we selected an old-growth stand (OG1) and two mid-successional

Table 2 Seed mass and shade tolerance of evergreen tree species in North Patagonian forests, Chiloé Island

Species	Family	Seed mass (mg)	Shade tolerance
<i>Amomyrtus luma</i>	Myrtaceae	35.0 ^a	Tolerant ^f
<i>Amomyrtus meli</i>	Myrtaceae	40.0 ^a	Tolerant ^f
<i>Drimys winteri</i>	Winteraceae	4.2 ^a	Intolerant ^f
<i>Eucryphia cordifolia</i>	Eucryphiaceae	1.7 ^d	Intolerant ^f
<i>Laureliopsis philippiana</i>	Monimiaceae	2.0 ^a	Tolerant ^f
<i>Myrceugenia parvifolia</i>	Myrtaceae	16.0 ^c	Tolerant ^f
<i>Myrceugenia chrysocarpa</i>	Myrtaceae	29.0 ^b	Tolerant ^g
<i>Nothofagus nitida</i>	Fagaceae	1.3 ^b	Intolerant ^h
<i>Podocarpus nubigena</i>	Podocarpaceae	450.0 ^b	Tolerant ^f
<i>Pseudopanax laetevirens</i>	Araliaceae	3.0–4.0 ^c	Intolerant ^f
<i>Saxegothaea conspicua</i>	Podocarpaceae	10.0 ^b	Tolerant ^h
<i>Tepualia stipularis</i>	Myrtaceae	0.3 ^d	Intolerant ^f
<i>Weinmannia trichosperma</i>	Cunoniaceae	0.1 ^a	Intolerant ^h

^aDonoso & Cabello (1978); ^bLusk (1995); ^cJ. A. Figueroa unpublished data; ^dCESAF (2002); ^eJ. J. Armesto, unpublished data; ^fFigueroa & Lusk (2001); ^gLusk (1995); ^hC. H. Lusk, unpublished data.

stands (MS1, MS2), also representative of the North Patagonian forest type (Veblen *et al.* 1995), located at 50–100 m a.s.l., and with similar vegetation to OG2 (Tables 1 and Table 2). Soils here are thin (< 1 m), derived from glacio-fluvial deposits, and are often poorly drained (Aravena *et al.* 2002). The climate was wet-temperate with a strong oceanic influence (di Castri & Hayek 1976). Meteorological records from Senda Darwin Biological Station (41°50' S, 73°40' W), indicate an annual precipitation of 2090 mm, 70% of which is concentrated between April and September. Periods of 1 week to 1 month without precipitation are not unusual during summer (January to March) (Willson & Armesto 1996). Average annual temperature is 11 °C, and the monthly maximum and minimum are 24 °C in January and 2.5 °C in June–July, respectively. In all study sites shrubs were rare or absent except along forest edges.

SAMPLING

Sampling was conducted in forest patches that represented different successional ages, defined by the age of canopy trees. This reflected the time since non-catastrophic anthropogenic fire for mid-successional sites, whereas OG stands seem to have remained free of major anthropogenic impact and apparently regenerated following windthrow (Veblen 1985; Armesto *et al.* 1996). In an area of about 0.5 ha in each of the four stands, 10 50-m long parallel transects were separated by intervals of 4 m. Along each transect, we randomly selected 25 points, where substrates were classified as log or soil. Tree seedlings (individuals < 30 cm tall) and saplings (individuals 30–150 cm tall), were counted and identified to species (nomenclature follows Marticorena & Quezada 1985), within a 50 × 50 cm (0.25 m²) quadrat placed at each point. We counted individuals originated from seeds and ignored those connected by root suckers to one another. Percentage canopy cover was visually estimated at each quadrat, and assigned to one of three categories; open (< 50% cover), intermediate (50–75% cover), and closed canopy (> 75% cover). A

total of 250 quadrats were registered in each stand, totalling 500 quadrats per successional stage. The percentage of the forest floor covered by logs in each stand was estimated from the percentage of quadrats classified as log substrate.

The state of decomposition of logs in quadrats was classified according to structural integrity, shape and texture (see Christy & Mack 1984; Spies *et al.* 1988), with tree classes: I = least decay, having intact twigs and bark, hard texture, and round shape; II = intermediate decay, absence of twigs, fragmented bark, partly soft texture, and round to oval shape; and III = most decayed, absence of twigs and bark, soft texture, and flat shape. The thickness of the leaf litter layer in soil quadrats was measured in millimetres with a vertical ruler at three points within each 0.25 m² quadrat, and averaged. The area sampled was considered sufficient to represent the tree species diversity and canopy heterogeneity of each stand (Armesto *et al.* 1996; Aravena *et al.* 2002).

DATA ANALYSIS

Distribution of saplings and seedlings among substrate types was analysed with a nominal logistic regression, with substrate type (log or soil) as predictor, and presence of seedlings and saplings on quadrats as response variable. Differences in the amount of logs between forest types (OG vs. MS) were tested by a nominal logistic regression, with forest type as the predictor variable and presence of logs as response variable. The distribution of saplings among different decay classes was analysed with an ordinal logistic regression, with decay class as the predictor variable and sapling presence on logs as the response variable. Although logistic regression is used predominantly when relating a binary response variable to a continuous predictor, it also works well when the predictor variable is ordinal or nominal (Hosmer & Lemeshow 1989).

Proportion tests (Zar 1996) were used to compare MS and OG stands in terms of the overall proportion of seedlings and saplings growing on logs regardless of

species identity. The effects of forest type (OG vs. MS), establishment substrate (log vs. soil), and canopy heterogeneity (open vs. closed) on density of shade-tolerant and shade-intolerant tree seedlings were assessed using three-way factorial ANOVAs, within multivariate ANOVA (MANOVA) in order to control for correlation among response variables. Non-parametric Spearman's rank correlations were calculated to assess the association between seed mass and species dependence on fallen logs as recruitment sites (expressed by the percentage of seedlings that were established on logs). To assess the effect of litter depth on tree regeneration, we calculated linear regressions between average litter depth in each soil quadrat and seedling density by species.

Results

FALLEN LOGS AND STAND AGE

The amount of logs varied significantly between OG and MS stands (nominal logistic regression, $\chi^2 = 13.12$, d.f. = 1, $P = 0.0003$, $n = 1000$). The probability of a

quadrat being classed as log, was 1.78 times higher on OG than MS stands (i.e. odds ratio = 1.78). The percentage of the forest floor covered by fallen logs was 16.4% in MS1 and 15.2% in MS2, vs. 24.8% and 25.2% in OG1 and OG2, respectively.

REGENERATION SUBSTRATE

The 13 tree evergreen species recorded in the study stands differed in their shade tolerance and seed mass (Table 2). More than 50% of the species regenerated preferentially on logs in all stands (Table 3). The estimated probability of presence of a seedling on a log quadrat, was significantly higher than on soil for seedlings of eight tree species, and for saplings of five (Table 3). The distribution of seedlings and saplings among substrates did not differ significantly for four species (*Amomyrtus luma*, *Amomyrtus meli*, *Myrceugenia parviflora* and *Myrceugenia chrysocarpa*, Table 3). Only for *Podocarpus nubigena* was the estimated probability of presence of seedlings and saplings significantly higher on soil than on logs for all stands.

Table 3 Nominal logistic regressions of the effect of substrate on presence of seedlings and saplings. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = not significant. P_l = estimated probability of presence on logs, P_s = on soil. (–) no saplings recorded, $n = 250$

Stand	Species	Seedlings				Saplings			
		χ^2	P	P_l	P_s	χ^2	P	P_l	P_s
MS1	<i>Amomyrtus luma</i>	0.02	NS	0.5	0.5	1.67	NS	0.1	0.1
	<i>Drimys winteri</i>	45.7	***	0.68	0.1	1.1	NS	0.1	0
	<i>Eucryphia cordifolia</i>	16.16	***	0.18	0	–	–	–	–
	<i>Laureliopsis philippiana</i>	8.22	**	0.13	0	4.58	*	0.1	0
	<i>Nothofagus nitida</i>	31.7	***	0.21	0	–	–	–	–
	<i>Podocarpus nubigena</i>	6.53	*	0	0.1	–	–	–	–
	<i>Pseudopanax laetevirens</i>	65.48	***	0.76	0.1	–	–	–	–
MS2	<i>Amomyrtus luma</i>	0.44	NS	0.1	0.1	0.43	NS	0	0.1
	<i>Amomyrtus meli</i>	1.05	NS	0.12	0.1	1.07	NS	0	0.1
	<i>Drimys winteri</i>	25.32	***	0.61	0.2	3.32	NS	0.1	0
	<i>Eucryphia cordifolia</i>	18.61	***	0.12	0	6.22	*	0.1	0
	<i>Laureliopsis philippiana</i>	22.47	***	0.15	0	7.53	**	0.1	0
	<i>Myrceugenia parvifolia</i>	1.29	NS	0.15	0.1	0.43	NS	0	0.1
	<i>Podocarpus nubigena</i>	2.55	*	0.15	0.3	4.18	*	0	0.2
	<i>Pseudopanax laetevirens</i>	59.91	***	0.51	0	11.03	***	0.1	0
	<i>Saxegothea conspicua</i>	9.18	**	0.22	0.1	0.68	NS	0.2	0.3
	<i>Tepualia stipularis</i>	26.38	***	0.17	0	–	–	–	–
<i>Weinmannia trichosperma</i>	26.38	***	0.17	0	–	–	–	–	
OG1	<i>Amomyrtus luma</i>	0.14	NS	0.26	0.2	2.46	NS	0	0.1
	<i>Amomyrtus meli</i>	0.04	NS	0.11	0.1	0.28	NS	0.1	0.1
	<i>Drimys winteri</i>	19.98	***	0.61	0.3	0.26	NS	0.1	0.1
	<i>Laureliopsis philippiana</i>	17.18	***	0.10	0	4.03	*	0.1	0
	<i>Nothofagus nitida</i>	26.14	***	0.15	0	41.67	***	0.2	0
	<i>Podocarpus nubigena</i>	6.54	*	0.15	0.3	4.71	*	0	0.1
	<i>Pseudopanax laetevirens</i>	54.24	***	0.53	0.1	56.26	*	0	0
	<i>Saxegothea conspicua</i>	7.79	**	0.11	0	1.71	NS	0.1	0
OG2	<i>Amomyrtus luma</i>	0.60	NS	0.3	0.3	0.60	NS	0	0
	<i>Drimys winteri</i>	16.29	***	0.97	0.8	3.41	NS	0.1	0.1
	<i>Laureliopsis philippiana</i>	10.51	**	0.3	0.1	4.68	*	0.1	0
	<i>Myrceugenia chrysocarpa</i>	1.49	NS	0.21	0.3	2.25	NS	0	0.1
	<i>Nothofagus nitida</i>	67.67	***	0.54	0.1	49.69	***	0.4	0
	<i>Podocarpus nubigena</i>	4.23	*	0.11	0.2	6.22	*	0	0.1
	<i>Pseudopanax laetevirens</i>	17.21	***	0.57	0.3	14.09	***	0.1	0
	<i>Saxegothea conspicua</i>	11.78	**	0.24	0.1	1.06	NS	0	0
<i>Tepualia stipularis</i>	8.14	**	0.13	0	5.13	*	0.1	0	

Table 4 Ordinal logistic regression of the effect of different decay classes of logs (I, II, III), on presence of saplings. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. P_I , P_{II} , and P_{III} = estimated probability of presence of saplings on each decay class

Species	χ^2	d.f.	n	P	P_I (%)	P_{II} (%)	P_{III} (%)
<i>Amomyrtus luma</i>	5.28	1	206	*	0	0.02	0.08
<i>Amomyrtus meli</i>	4.44	1	103	*	0.01	0.04	0.12
<i>Drimys winteri</i>	6.4	1	204	*	0.05	0.1	0.19
<i>Eucryphia cordifolia</i>	5.94	1	41	*	0.02	0.09	0.36
<i>Laureliopsis philippiana</i>	16.43	1	204	***	0	0.02	0.16
<i>Myrceugenia parvifolia</i>	4.03	1	41	*	0.01	0.05	0.23
<i>Myrceugenia chrysocarpa</i>	5.78	1	63	*	0	0	0.12
<i>Nothofagus nitida</i>	4.32	1	125	*	0.46	0.33	0.22
<i>Podocarpus nubigena</i>	8.32	1	166	**	0	0	0.07
<i>Pseudopanax laetevirens</i>	3.91	1	166	*	0.02	0.05	0.11
<i>Saxegothea conspicua</i>	8.52	1	166	**	0.02	0.06	0.18
<i>Tepualia stipularis</i>	3.96	1	63	*	0.01	0.06	0.20

For all species combined, 43.2% of seedlings in MS stands and 28.3% of saplings occurred on logs, compared with 49.7% of seedlings and 42% of saplings in OG stands. Seedlings growing on logs were much more common in OG stands ($n = 1787$) than in MS stands ($n = 366$) (Proportion test, $Z = 3.34$, $P < 0.05$). Saplings were also much more common on logs in OG stands ($n = 164$) than in MS stands ($n = 56$) (Proportion test, $Z = 3.15$, $P < 0.05$). Of the individual species, *Nothofagus nitida* showed the greatest contrast, with only 10 and 0 seedlings in the two MS stands vs. 39 and 144 in OG stands. Moreover, *Nothofagus* saplings were completely absent from MS stands, compared with 19 and 41 in OG. Seedlings of *Eucryphia cordifolia* and *Weinmannia trichosperma*, despite regenerating mainly on logs, occurred only in MS stands.

DECAY CLASSES

The estimated probability of presence of saplings varied significantly among log decay classes, with all species showing a logistic distribution (Table 4). *Nothofagus nitida* was most likely to occur on the least decayed logs (class I) (ordinal logistic regression, $\chi^2 = 4.32$, d.f. = 1, $P < 0.05$, $n = 125$), whereas all other species had the highest probability of presence on the most decayed class (III). Of these, *Myrceugenia chrysocarpa* and *Podocarpus nubigena* occurred only on decay class III.

EFFECTS OF FOREST TYPE, CANOPY COVER AND SUBSTRATE

The MANOVA showed highly significant effects of canopy opening (C), substrate (S), forest type (T), and their interactions, on seedling density (Table 5). Density of shade intolerant seedlings was greatly affected by forest type (three-way ANOVA; $F_{1,992} = 144.43$, $P < 0.001$), substrate ($F_{1,992} = 136.67$, $P < 0.001$), canopy opening ($F_{1,992} = 33.28$, $P < 0.001$), $T \times S$ ($F_{1,992} = 24.63$, $P < 0.001$), $T \times C$ ($F_{1,992} = 10.33$, $P < 0.01$), and $S \times C$ ($F_{1,992} = 7.05$, $P < 0.01$). In contrast, the density of

Table 5 MANOVA testing the effects of canopy opening (open vs. closed), substrate type (log vs. soil), and forest type (MS vs. OG) on density of shade-tolerant and shade-intolerant seedlings. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = not significant effect

Source	d.f.	Wilks' lambda	F	P
Forest type (T)	2	0.870	73.86	***
Substrate (S)	2	0.879	68.52	***
Canopy opening (C)	2	0.967	16.75	***
$T \times S$	2	0.976	12.37	***
$T \times C$	2	0.990	5.24	**
$S \times C$	2	0.989	5.46	**
$T \times S \times C$	2	0.998	1.04	NS
Error	991			

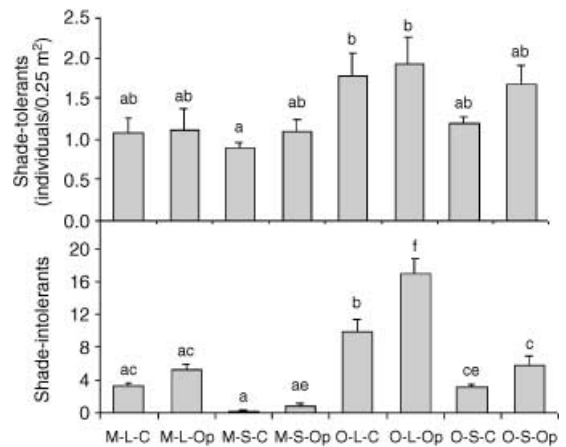


Fig. 2 Effect of forest type, substrate and canopy opening on density (individuals per 0.25 m² quadrat) of shade-tolerant and shade-intolerant seedlings. Values are means \pm 1 SE ($n = 1000$). M = mid-successional, O = old-growth, L = logs, S = soil, C = closed canopy, Op = open canopy. Different lower case letters indicate significant differences (three-way ANOVA, Tukey's a posteriori test, $P < 0.05$).

shade-tolerant seedlings was only affected by forest type (three-way ANOVA, $F_{1,992} = 19.71$, $P < 0.001$). The highest density of shade intolerant seedlings occurred on logs under open canopy and on OG stands (Fig. 2).

Table 6 Spearman's rank correlations between the percentage of seedlings established on logs and seed mass by species (n = number of species)

Stand	n	r_s	P -value
MS1	7	-0.96	< 0.01
MS2	11	-0.60	< 0.05
OG1	8	-0.96	< 0.01
OG2	9	-0.85	< 0.01

SEED SIZE

In both OG and MS stands, a significant inverse relationship was found between seed size and the proportion of seedlings regenerating on logs for each tree species (Table 6).

LITTER DEPTH

For tree species whose seedlings showed a significantly higher probability of presence on logs (*Drimys winteri*, *Eucryphia cordifolia*, *Laureliopsis philippiana*, *Nothofagus nitida*, *Pseudopanax laetevirens*, *Saxegothaea conspicua* and *Tepualia stipularis*), seedling density decreased significantly with increasing litter layer thickness (Table 7). In contrast, litter depth did not affect seedling density of *Podocarpus nubigena* (Table 7), the only tree species whose seedlings and saplings recruited preferentially on soil.

Discussion

DIFFERENTIAL USE OF MICROSITE MOSAIC

The distribution of tree species is influenced by microsite in the temperate rain forest of Chiloé Island.

Several species showed a strong preference for fallen logs as regeneration sites, in both MS and OG forests, with seedlings of some species occurring only on such substrate in some stands (e.g. *Eucryphia cordifolia*, *Laureliopsis philippiana*, *Nothofagus nitida*, *Tepualia stipularis* and *Weinmania trichosperma*). In the particular case of *Pseudopanax laetevirens*, which is frequently found growing as a hemi-epiphyte on large emergent trees of *Eucryphia cordifolia* or *Weinmania trichosperma*, all saplings were located on logs, demonstrating the importance of logs for establishment as well as recruitment in this tree species. Selective recruitment of these species on logs, as seedlings, remains unchanged through the sapling stage, which indicates long-term effects of this microhabitat on species establishment. The contrasting low or null probability of presence of seedlings and saplings of *Podocarpus nubigena* on logs may be a consequence of its larger seeds, which may not fit well in small crevices on the surface of logs, thus reducing their contact surface with the seed bed and impeding water uptake (Anderson & Winterton 1996) compared with smaller seeds (Harper *et al.* 1970).

Recruitment in plant populations may potentially be limited by the availability of suitable microsites as well as by seed rain (Eriksson & Ehrlén 1992). Thus, for the species that use logs as their main establishment site, regeneration may be substrate limited, because an increase or decrease in the fraction of the forest floor covered by logs would affect their regeneration success. Old-growth forests would have more logs and thus more safe sites for log-dependent species (see also Spies *et al.* 1988; Carmona *et al.* 2002), leading to the higher observed proportion of seedlings and saplings growing on logs in OG stands. This should apply to other forest

Table 7 Summary of linear regressions of the effect of litter depth on seedling density for tree species dependent on logs or soil for regeneration (Table 3) (n = number of quadrats on soil; L = logs, S = soil). * P < 0.05, ** P < 0.01, *** P < 0.001

Stand	Species	Slope	n	r^2	Substrate preference
MS1	<i>Drimys winteri</i>	-0.20	212	0.12***	L
	<i>Eucryphia cordifolia</i>	-0.02	212	0.02*	L
	<i>Laurelia philippiana</i>	-0.03	212	0.04***	L
	<i>Podocarpus nubigena</i>	0.01	212	0.00	S
	<i>Pseudopanax laetevirens</i>	-0.21	212	0.11***	L
MS2	<i>Drimys winteri</i>	-0.48	209	0.23***	L
	<i>Podocarpus nubigena</i>	-0.04	209	0.01	S
	<i>Pseudopanax laetevirens</i>	-0.05	209	0.07***	L
	<i>Saxegothaea conspicua</i>	-0.05	209	0.05***	L
OG1	<i>Drimys winteri</i>	-0.33	188	0.15***	L
	<i>Podocarpus nubigena</i>	-0.07	188	0.01	S
	<i>Pseudopanax laetevirens</i>	-0.10	188	0.07***	L
	<i>Saxegothaea conspicua</i>	-0.03	188	0.05*	L
OG2	<i>Drimys winteri</i>	-2.07	187	0.27***	L
	<i>Laurelia philippiana</i>	-0.10	187	0.06**	L
	<i>Nothofagus nitida</i>	-0.09	187	0.05**	L
	<i>Podocarpus nubigena</i>	-0.04	187	0.01	S
	<i>Pseudopanax laetevirens</i>	-0.77	187	0.07**	L
	<i>Saxegothaea conspicua</i>	-0.05	187	0.03*	L
	<i>Tepualia stipularis</i>	-0.06	187	0.03*	L

ecosystems, where more than 90% of the regeneration of some species occurs on fallen logs, as is the case for *Nothofagus dombeyi* in southern Chilean forests (Veblen *et al.* 1981), and *Picea sitchensis* and *Tsuga heterophylla* in North American temperate forests (Christy & Mack 1984; Harmon & Franklin 1989). The fact that we found *Eucryphia cordifolia* and *Weinmannia trichosperma* seedlings growing only in MS stands suggests that, despite the greater availability of logs in OG stands, recruitment limitation due to other microsite requirements or limited seed rain affected the regeneration process of these species (Hubbell *et al.* 1999).

Logs may be more important for the regeneration of shade-intolerant species than access to light on OG stands. This is demonstrated by the fact that the density of the shade-intolerant seedlings is enhanced to a greater extent by the presence of fallen logs under closed canopy than it is by open canopy over soil sites (Fig. 2). In this regard, Nakashizuka (1989) postulated that canopy gap formation *per se* in the absence of soil disturbance (pits, mounds or boles), did not substantially contribute to the maintenance of pioneer tree populations in Japanese old-growth temperate forests. In Chiloé forests, all shade-intolerant tree species demonstrated a preference for fallen logs as recruitment substrate. Thus, the greater the proportion of ground covered by logs, the greater are the chances that seeds of shade-intolerants can find an appropriate seedbed (Harmon 1989a). Logs were observed to be important recruitment sites for only two of the shade-tolerant species in this study (*Laureliopsis philippiana* and *Saxegothaea conspicua*) and regeneration of the majority of the shade-tolerant trees would not therefore be limited by the availability of decaying logs. Consequently, the removal of fallen logs from old-growth stands for timber use, or cleaning of woody detritus following logging, would limit regeneration particularly for shade-intolerant trees. Maintenance of pioneer tree populations might thus be affected, contributing to early dominance by shade-tolerant species (e.g. Armesto & Figueroa 1987).

LOG DECAY CLASSES AND TREE RECRUITMENT

In all study sites, tree species establishment was more likely at intermediate and more advanced stages of log decay, where the substrate has a lower density and greater moisture content than fresher logs, making root penetration easier (Lumley *et al.* 2001; Carmona *et al.* 2002), although seedlings would be faced with greater competition from bryophytes at such later states of decomposition (Harmon 1989b). The pioneer, shade-intolerant *Nothofagus nitida* was the only species that showed a higher probability of presence on fresher logs, where its seedlings could apparently enjoy a brief competition-free window.

Colonization of fresh logs by *N. nitida* may be possible because of its dependence on ectomycorrhizal (EM) association (Lusk 1995) rather than on arbuscular mycorrhizae (AM) (Garrido 1988). EM has epigeous fructifications and therefore their spores are easier to disperse to recently fallen logs. Moreover, EM associated with *Nothofagus* can develop on rotting wood (Palfner 2001); therefore, seedlings could find the fungus developing on fresh logs. All other tree species in the study sites have AM (Godoy *et al.* 1994), which in turn sporulate below ground (Sylvia *et al.* 1998), restricting their dispersal to well-decayed logs that are penetrated by roots infected with AM.

In the case of *Picea sitchensis*–*Tsuga heterophylla* forests, seedling abundance was greater on logs in early stages of decomposition (Harmon 1989b), while in forests of *Picea engelmanni*–*Abies lasiocarpa* recruitment was greater on intermediate and advanced stages of wood decay (McCullough 1948). Therefore, in addition to the availability of logs, decomposition state is also a significant variable for tree recruitment.

LITTER EFFECTS ON SEEDLING DENSITY

In Chiloé forests, litter depth may affect community structure through differential effects on the regeneration success of tree species with different seed mass. Thus, litter contributes to the creation of microsite heterogeneity. In our study, seed size was inversely related to seedling-dependence on fallen logs as recruitment sites, and for species that occurred preferentially on logs, litter depth had a significant negative effect on seedling density. Thus for tree species with small seed mass, recruitment was largely restricted to log substrate or exposed mineral soil. In Chilean forests, other tree species that use nurse logs, such as *Fitzroya cupressoides* (Rodríguez 1989; Donoso *et al.* 1993a) and *Nothofagus* spp. (Henríquez 1985; Veblen 1985), increase their recruitment when litter is removed, exposing the mineral soil, even under closed canopy (Burschel *et al.* 1976).

As the amount and composition of litter varies in both space (Peterson & Facelli 1992) and time (Pérez *et al.* 1991; Donoso *et al.* 1993b), litter would influence tree species establishment at small scales (Molofsky & Augspurger 1992; Peterson & Facelli 1992), affecting local species richness (Carson & Peterson 1990). Both influences of microtopography on litter distribution and the differential ability of seedlings to penetrate and emerge through the litter layer may be important in determining the distribution of regeneration on the forest floor (Sydes & Grime 1981). Logs prevent litter accumulation because of their elevated and convex surface (Beatty 1984; McKenny & Kirkpatrick 1999), and are therefore safe sites for smaller seeds. Species with a large seed mass, such as *Podocarpus nubigena*, having proportionally greater carbohydrate reserves (Tripathi & Khan 1990), N, P and K (Milberg *et al.* 1998), are better equipped to emerge from deeper soil and litter (Seiwa & Kikuzawa 1996).

Conclusions and prospects

Seed size is a major factor in the differential colonization of microsites (Nakashizuka 1989; Lusk 1995; Dalling & Hubbell 2002), and good predictor of seedling requirements for establishment. Regeneration niche partitioning and the coexistence of species that share much the same life-form and phenology, as well as occupying similar niches in their adult stages, would be facilitated by different seed sizes and forest floor heterogeneity in the temperate forest of Chiloé Island.

To understand the mechanisms of species coexistence in temperate forests we should elucidate the role of biotic interactions (e.g. seed dispersal, mycorrhizas), horizontal and vertical heterogeneity and disturbance on tree species diversity (Molino & Sabatier 2001). We should then be able to integrate the different stages of the life history and demography of co-occurring tree species in a community (Nakashizuka 2001). We must examine more carefully the importance of fine-scale heterogeneity (e.g. nurse logs, litter accumulation, microtopography and light availability) for the regeneration of different tree species and hence its implications for community patterns and recruitment limitation (Clark *et al.* 1999).

Acknowledgements

This research was funded by Núcleo Científico Milenio P99–103FICM, by Presidential Chair in Science to J.J.A. and by grant FONDAP-FONDECYT 1501–0001 to the CASEB. This is a contribution to the research programme of Estación Biológica 'Senda Darwin', Ancud, Chiloé. We thank J. C. Aravena, R. Bustamante, M. Carmona, G. Carvallo, P. Chacón, A. Christie, J. Dalling, I. Díaz, J. Figueroa, L. Haddon, A. Lara, C. Lusk, A. Muñoz, T. Nakashizuka, C. Peterson, C. Pérez, S. Reid, F. Sáiz, & M. C. Simpson for their help and for comments. M. Fuentes & H. Yáñez are thanked for field assistance during rainy days. The first author thanks Francisco Sáiz for his 'polyden-dritic' teaching way.

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Received 28 August 2002

revision accepted 2 June 2003