

Seed rain of fleshy and dry propagules in different habitats in the temperate rainforests of Chiloé Island, Chile

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Abstract In temperate rainforests on Chiloé Island in southern Chile (42°S), most canopy trees bear fleshy, avian-dispersed propagules, whereas emergent tree species have dry, wind-borne propagules. In the present study, the following hypothesis was tested: regardless of species, fleshy propagules are deposited in greater numbers in canopy gaps and in forest margins and hence have a more heterogeneous seed shadow than wind-dispersed propagules. To test this hypothesis, the seed rains of these two types of propagules were compared in the following forest habitats: (i) tree-fall gaps (edges and centre); (ii) forest margins with adjacent pastures; and (iii) under closed canopy (forest interior). Seed collectors (30-cm diameter) were placed in two (15 and 100 ha) remnant forest patches ($n = 60$ – 100 seed collectors per patch) distributed in the four habitats. Seeds were retrieved monthly from each collector during two reproductive seasons (1996, 1997). In both years, the seed rain was numerically dominated by two species with dry propagules (*Laureliopsis philippiana* and *Nothofagus nitida*) and three species with fleshy fruits (*Drimys winteri*, *Amomyrtus luma*, and *Amomyrtus meli*). The seed shadows of the two species with dry, wind-dispersed seeds differed markedly. Seeds of *L. philippiana* were deposited predominantly in canopy openings, whereas *N. nitida* seeds fell almost entirely in the forest interior. The fleshy-fruited species, *Drimys* and *Amomyrtus* spp., had similar seed deposition patterns in the various habitats studied, but the between-year differences in seed rain were greater in *Drimys winteri* than in *Amomyrtus* spp. Although no more than 10% of fleshy-fruited propagules reached the margins of the patch, approximately 7% of these were carried there by birds. Every year, canopy gaps (pooling data from edges and centres) concentrated approximately 60% of the total seed rain of both propagule types in both forest patches. Forest margins received less than 20% of the total seed rain, which was largely dominated by fleshy-fruited species. Seed shadows were a species-specific attribute rather than a trait associated with propagule type and dispersal mode.

Key words: Avian seed dispersal, Chiloé forests, fleshy fruits, forest edges, forest fragments, seed rain, seed shadow, tree-fall gaps, tree recruitment, wind-dispersed propagules.

INTRODUCTION

Seed dispersal by frugivores (endozoochory) is often considered to be a diffuse mutualistic interaction (Snow 1971; Herrera 1985; Armesto *et al.* 1987; Willson *et al.* 1996a), whereby in exchange for a meal, animals transport propagules to sites away from the parent plant, thus increasing the chances for seed germination and seedling establishment (Howe & Smallwood 1982; Wheelwright & Orians 1982; Malmborg & Willson 1988; Wenny & Levey 1998). The activity and behaviour patterns of frugivores influence the range of habitats over which propagules are disseminated and their chances of survival, hence

determining the outcome of the interaction. In the temperate forests of North America, fruit-eating birds are more active in canopy gaps and along forest edges (Thompson & Willson 1978; Malmborg & Willson 1988), where enhanced light conditions often favour seed germination and seedling growth. Likewise, in the tropical forests of Costa Rica, birds disperse seeds to favourable sites for seed establishment and survival (Wenny & Levey 1998).

In the temperate rain forests of Chiloé island, southern Chile, 51 of the 76 woody species, including epiphytes and vines, are fleshy-fruited (Armesto & Rozzi 1989) and 19 species of birds regularly or occasionally consume fruits, defecating the seeds undamaged (Armesto *et al.* 1987; Sabag 1993; Rozzi *et al.* 1996a; Willson *et al.* 1996a; Salvande & Armesto, unpubl. obs.). The major frugivores in Chiloé forests are generalist birds, which consume fruits of several fleshy-fruited species (Armesto *et al.* 1996a). As in Northern

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Accepted for publication March 2001.

Hemisphere temperate forests, avian frugivores in Chiloé are more frequently recorded in forest gaps and edges (Willson *et al.* 1994; Rozzi *et al.* 1996b). Thus, for avian-dispersed tree species, the spatial pattern of disseminating seeds or 'seed shadow' is expected to show some peaks associated with those habitats where bird activity is greater (Stiles 1989; Willson 1992). In contrast to this pattern, tree species bearing wind-dispersed (anemochorous) dry propagules often show strongly leptokurtic seed shadows, with a greater concentration of seed falling short distances from the parent plant (Janzen 1970; Augspurger 1984; Willson 1993). Consequently, in a forest environment, plant species with avian-disseminated propagules are expected to have a different spatial pattern of seed rain than species with dry, wind-blown propagules. Seeds dispersed by generalist avian frugivores are likely to exhibit a more patchy seed shadow, with greater numbers of seeds falling along edges and within tree-fall gaps, regardless of the species and spatial distribution of seeding trees. In contrast, the seed rain of wind-dispersed tree species should follow more closely a parent-centred negative exponential model (Willson 1993), resulting in a seed rain that is more restricted to the vicinity of seeding trees, with a lower concentration of propagules in habitats such as gaps and forest edges, where seeding tree density declines.

In the present paper we examine these hypotheses in two fragments of primary rain forest on Chiloé Island, southern Chile (42°30'S). We compare the relative abundance of seeds falling in three different forest habitats: (i) under the canopy in the forest interior; (ii) in forest margins adjacent to pastures; and (iii) under canopy gaps within the forest patch. We evaluated the prediction that the proportion of the seed rain falling in forest margins and under canopy gaps should be higher for fleshy-fruited plants than for tree species with wind-borne propagules. The latter should exhibit a less patchy seed shadow, with smaller proportions of seeds deposited in gaps and forest edges

relative to the forest interior, where the density of seeding trees is greater.

METHODS AND STUDY SITE

Study site

We characterized the seed rain in two lowland forest fragments on northern Chiloé Island in the locality of Huelden, 20 km north-east of Ancud (41°53'S), at an elevation of approximately 80 m a.s.l. Both forest fragments were dominated by evergreen broad-leaved tree species and are representative remnants of extensive primary forests that once covered most of the island (Darwin 1860; Willson & Armesto 1996). Forest patch A was nearly 100 ha in size with a closed canopy (> 80% cover) 25–30 m in height. Forest patch B was smaller, only 15 ha in size, with a more open (70% cover) and lower (20–25 m in height) canopy. Because of their similar canopy composition, we expected that the patterns of seed fall in each patch would be most closely associated with propagule types. The most frequent canopy species in both forest patches were the fleshy-fruited trees *Amomyrtus luma* (Mol.) Legr. et Kraus., *Amomyrtus meli* (Phil.) Legr. et Kraus, and *Drimys winteri* J. R. et Foster, with a few large emergent individuals (> 30 m in height) of wind-dispersed *Laureliopsis philippiana* Looser and *Nothofagus nitida* (Phil.) Krasser (Table 1). Human disturbance to these remnant patches has been limited to selective extraction of timber (especially the conifer *Podocarpus nubigena* Lindl.) and occasional grazing by cattle. Neither of the forest patches had been completely burned or commercially logged previous to the present study. Because of the type of land mosaic that exists on northern Chiloé Island, the habitat adjacent to forest margins was generally open pasture; however, often forest edges had an open cover of shade-intolerant low shrubs, with species such as *Berberis darwini* Hook and *Baccharis* sp.,

Table 1. Relative importance of tree species in each of four different habitats of two forest patches (A and B) where seed rain was characterized

Species	Family	Forest Interior		Gap Edges		Gap Centres		Forest Margins	
		A	B	A	B	A	B	A	B
Fleshy fruits									
<i>Amomyrtus</i> spp.	Myrtaceae	23	27	38	56	6	13	35	36
<i>Drimys winteri</i>	Winteraceae	19	13	26	15	1	0	41	27
Dry fruits									
<i>Laureliopsis philippiana</i>	Monimiaceae	39	30	36	30	11	13	0	0
<i>Nothofagus nitida</i>	Nothofagaceae	3	20	0	0	0	0	6	0
Other woody species ($n = 8$)		16	10	0	0	1	0	24	27
Total		100	100	100	101	19	26	106	90

Values are percentage cover in the canopy directly above the collectors (10 m transect lines, $n = 5$ per habitat).

and a narrow band of pioneer trees, mostly juvenile individuals of *D. winteri* that were 5–10 m in height. In both forests, the canopy was often interrupted by tree-fall gaps, which ranged in size from 80 to 200 m². These resulted from windthrow or selective logging. Canopy gaps were often covered by a dense undergrowth of native bamboo (*Chusquea quila* Khunt).

Tree regeneration in these forests is strongly dependent on disturbance regimes (Veblen & Alaback 1996; Veblen *et al.* 1996). For shade-intolerant pioneer tree species such as *D. winteri* (Winteraceae), *N. nitida* (Nothofagaceae) and *Eucryphia cordifolia* Cav. (Eucryphiaceae), regeneration from seed is largely restricted to large openings in the forest canopy that are caused by windstorms (Donoso *et al.* 1984; Veblen 1985; Armesto *et al.* 1996b; Veblen *et al.* 1996). Other tree species, such as *L. philippiana* (Monimiaceae), the conifer *Podocarpus nubigena* (Podocarpaceae) and all Myrtaceae (*Amomyrtus* spp.), are more shade tolerant and maintain dense seedling banks in the forest understorey, although they also regenerate in small tree-fall gaps (Donoso *et al.* 1984; Armesto & Figueroa 1987; Armesto & Fuentes 1988; Veblen & Alaback 1996).

Methods

Habitats

In each forest patch, we sampled the seed rain in the following habitat types: (i) canopy gaps (openings of the canopy created by a single or multiple tree falls, mean area = 150 m²); (ii) forest interior (areas under a closed canopy, at least 100 m away from the nearest edge); and (iii) forest margin adjacent to an open pasture (a band 20 m wide, starting from the outermost tree). In the case of tree-fall gaps, we made an additional distinction between gap edge (up to 10 m away from the base of large trees (> 10 cm d.b.h.) toward the forest interior) and gap centre (the area beginning 2 m away from the base of the trees surrounding the gap, toward the centre of the opening). We chose only gaps formed in the past 3–5 years, as inferred from the presence of small branches and twigs on fallen logs. The habitats where seed collectors were placed differed in tree species composition and percentage canopy cover (Table 1). The principal fleshy-fruited trees were *D. winteri* and *Amomyrtus* spp., both of which have heavy propagules (seed mass of *Drimys* = 0.0051 g and *Amomyrtus* spp. = 0.022 g) and were present in all four habitats, with a greater percentage cover in gap edges and forest margins (Table 1). Of the tree species with dry wind-dispersed propagules, the most common species in the study sites were *L. philippiana* and *N. nitida*. Both have light propagules (0.0013 and 0.0012 g dry mass for *L. philippiana* and *N. nitida*, respectively) bearing a pappus in the case

of *L. philippiana* and rudimentary wings in the case of *N. nitida*. *Laureliopsis philippiana* was present in all habitats except forest margins, while *N. nitida* was found in both forest interior and margins in patch A but exclusively in the forest interior of patch B (Table 1). Trees in forest margins were most commonly non-fruiting juveniles. Shrubs such as *B. darwini*, *Rhaphitammus spinosus* (A. L. Juss.) Mold. and *Baccharis* sp. occurred only in forest margins.

Sampling design

In both forest patches, areas representative of each habitat type were chosen to characterize the seed rain. Because of the size of patches and the definition of habitats, the relative extent of each habitat was greater for forest interior and lower for forest margins and tree-fall gaps (in that order). However, seed-collecting effort was equivalent in each type of habitat. Five seed collectors were placed 2 m apart along 10-m transects in each habitat. In edge habitats, transects extended from the base of the outermost trees toward the interior of the forest. To sample gap centres, the transect line started 2 m away from the base of the outermost trees to the centre of the opening, one transect per gap. To sample gap edges, the transect line extended from the base of the outermost trees to the forest interior, one transect per gap. In 1996, we placed seed collectors in four tree-fall gaps (with transects in both gap edges and centres) and along two transects in the forest interior and two in forest margins in each forest patch (60 collectors in total per patch). In 1997, seed collectors were set up along five transects (replicates) per habitat in each forest fragment (a total of 100 collectors per patch). The number of seed collectors actually analysed was slightly different from the number initially set up, because a few (< 5% overall) were damaged by animals or falling branches. Damage to collectors occurred mainly in forest margins and was associated with trampling by cattle.

Seed collectors

Seed collectors consisted of a metal ring, 30 cm in diameter (surface area of 0.07 m²), supported by four stakes at approximately 50 cm above the ground. Funnels made of plastic net (mesh size = 2 mm) were attached to each ring to collect the seeds. Falling seeds of most woody species in the forest, except for very small seeds (< 0.001 g), were retained inside the funnels. Collectors were emptied monthly and the contents were examined under a dissecting microscope. Seed collectors were exposed to seed rain in two consecutive fruiting seasons, January–March 1996 and December 1996–April 1997. All woody species in the forest patches studied bear ripe fruit between December and March (Smith-Ramírez & Armesto 1994). All seed

collectors in one transect were pooled to obtain replicate samples of sufficient size for each habitat. Mean seed rain for one habitat was then calculated as the average of all transects in that habitat for each forest patch. We standardized the data in terms of number of seeds m^{-2} per day in order to evaluate the differences in seed rain between habitats because the actual number of collectors analysed varied slightly between patches and years.

All propagules present in the collectors, with or without attached anatomical appendages, were identified to species if possible and considered in the analysis of the seed rain. Seeds of *A. luma* and *A. meli* were indistinguishable and were combined for analysis. In all counts, we separated fleshy and dry fruits. In 1997 we estimated the proportions of seeds dispersed by frugivorous birds. For fleshy fruits only, we made a distinction between whole fruits or seeds attached to arils, which presumably fell directly to the ground from the tree, and naked seeds, presumably the result of dispersal by avian frugivores.

Analyses

The following factors and levels were considered in evaluating differences in the distribution of seed rain among forest habitats: (i) year (1996 vs 1997 fruiting season); (ii) site (forest patches A and B); (iii) habitat (gap edges, gap centres, forest interior and forest margin); and (iv) species (only data for the four most abundant species in the seed rain). Analyses were conducted by using a multifactorial ANOVA, pooling the numbers of seeds collected during the entire fruiting

season. Square-root transformation ($x + 0.5$) was used to normalize the response variable, expressed as seeds m^{-2} per day (Zar 1996). Using separate factorial ANOVA, we evaluated differences in the pattern of seed rain by propagule type by pooling data in two categories: (i) fleshy (dispersed by animals/gravity); and (ii) dry (dispersed by wind/gravity) propagules. We also assessed the effects of habitat, site (forest patch) and species for the fraction of the seed rain (fleshy fruits only) attributed to dispersal by birds, using a separate factorial ANOVA. We tested the null hypothesis that the relative fraction of seed fall of each species or fruit type in the different habitats was the same. Significant interactions among factors affecting the pattern of seed rain were displayed graphically (Zar 1996). We also tested the dependency of the seed fall (both entire fruits and seed dispersed by birds) of every species on its abundance in the canopy of each habitat by means of Spearman's rank correlation.

RESULTS

Seed-fall patterns

Seeds of 13 woody species were collected in both forest patches during the 2 years of study (Tables 2,3). Species richness and composition of the seed rain differed somewhat among habitats in both patches, mainly because propagules of a greater number of species fell in forest margins (Table 2,3). Shrub seeds, that is, *Berberis* and *Baccharis* spp., and seeds of strongly shade-

Table 2. Estimated seed fall (number of seeds m^{-2} per day \pm 1 SE) in different habitats in forest patch A

Species	Gap centres		Gap edges		Forest interior		Forest margin		
	1996	1997	1996	1997	1996	1997	1996	1997	
Fleshy fruits									
<i>Amomyrtus</i> spp.	0.5 \pm 0.4	0.2 \pm 0.1	2.7 \pm 2.4	2.1 \pm 1.8	0.2*	0.9 \pm 0.6	0.09 \pm 0.01	0.2 \pm 0.1	
<i>Drimys winteri</i>	0.05 \pm 0.04	3.5 \pm 1.8	0.4 \pm 0.2	44.9 \pm 25.8	0.0	7.6 \pm 5.1	0.0	4.3 \pm 3.0	
<i>Berberis</i> sp.	0.0	0.0	0.01 \pm 0.01	0.0	0.0	0.0	0.0	0.04 \pm 0.02	
<i>Pseudopanax</i>									
<i>laetevirens</i>	0.01 \pm 0.01	0.01 \pm 0.01	0.0	0.04 \pm 0.04	0.0	0.0	0.0	0.01 \pm 0.01	
<i>Griselinia racemosa</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.04 \pm 0.02	
Dry wind-borne fruit									
<i>Laureliopsis</i>									
<i>philippiana</i>	7.4 \pm 1.4	42.0 \pm 11.5	9.0 \pm 5.6	24.3 \pm 6.8	0.4	7.4 \pm 3.8	0.6 \pm 0.5	0.4 \pm 0.2	
<i>Nothofagus nitida</i>	3.5 \pm 2.6	4.8 \pm 3.2	2.4 \pm 1.0	1.8 \pm 1.1	6.9	21.6 \pm 11.7	0.6 \pm 0.04	0.1 \pm 0.04	
<i>Eucryphia cordifolia</i>	0.01 \pm 0.01	0.02 \pm 0.01	0.04 \pm 0.02	0.05 \pm 0.01	0.2	0.0	0.0	0.01 \pm 0.01	
<i>Caldcluvia</i>									
<i>paniculata</i>	0.0	0.03 \pm 0.03	0.0	0.01 \pm 0.01	0.0	0.07 \pm 0.07	0.0	0.05 \pm 0.05	
Dry nut									
<i>Gevuina avellana</i>	0.0	0.0	0.0	0.0	0.0	0.01 \pm 0.01	0.0	0.02 \pm 0.01	
Undetermined	0.01 \pm 0.01	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
Total (all seeds)	11.5 \pm 1.8	50.5 \pm 10.8	14.6 \pm 5.2	73.1 \pm 24.4	7.7	37.5 \pm 11.4	1.2 \pm 0.5	5.1 \pm 3.1	
Number of species	6	7	6	7	4	6	3	10	

*No replicate for this habitat.

Table 3. Estimated seed fall (number of seeds m⁻² per day ± 1 SE) in different habitats in forest patch B

Species	Gap centres		Gap edges		Forest interior		Forest margin	
	1996	1997	1996	1997	1996	1997	1996	1997
Fleshy fruits								
<i>Amomyrtus</i> spp.	0.3 ± 0.05	1.6 ± 1.0	0.9 ± 0.5	3.0 ± 2.2	0.5 ± 0.4	1.1 ± 0.7	0.4 ± 0.2	0.6 ± 0.5
<i>Drinys winteri</i>	0.1 ± 0.05	64.1 ± 45.9	0.1 ± 0.1	35.3 ± 22.3	0.1 ± 0.01	58.4 ± 32.2	0.1 ± 0.1	26.1 ± 12.7
<i>Berberis</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.2 ± 0.3	0.1 ± 0.07
<i>Raphithamnus spinosus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.1 ± 0.1	0.06 ± 0.06
<i>Pseudopanax laetevirens</i>	0.0	2.1 ± 1.5	0.0	0.0	0.0	0.0	0.0	0.0
Dry wind-borne fruit								
<i>Laureliopsis philippiana</i>	7.5 ± 3.9	33.7 ± 9.7	3.9 ± 1.6	36.2 ± 13.1	3.2 ± 0.8	30.9 ± 7.4	0.6 ± 0.1	3.4 ± 1.8
<i>Nothofagus nitida</i>	0.2 ± 0.1	0.0	0.7 ± 0.7	0.04 ± 0.03	0.3 ± 0.2	0.2 ± 0.2	0.1 ± 0.1	0.0
<i>Encryphia cordifolia</i>	0.01 ± 0.02	0.06 ± 0.07	0.03 ± 0.02	0.1 ± 0.1	0.0	0.0	0.0	0.01 ± 0.01
<i>Embothrium coccineum</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.8 ± 1.0	0.0
<i>Caldeueta paniculata</i>	0.03 ± 0.04	0.0	0.1 ± 0.1	0.06 ± 0.07	0.0	0.0	0.0	0.0
<i>Baccharis</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	1.6 ± 1.6	0.0
Dry nut								
<i>Gevuma avellana</i>	0.0	0.0	0.03 ± 0.04	0.0	0.02 ± 0.02	0.02 ± 0.02	0.0	0.0
Undetermined	0.2 ± 0.1	0.0	0.2 ± 0.1	0.0	0.08 ± 0.02	0.0	0.1 ± 0.01	0.0
Total (all seeds)	8.3 ± 3.8	101.5 ± 44.7	5.7 ± 1.9	74.7 ± 21.1	4.3 ± 1.0	90.7 ± 27.1	4.8 ± 0.9	30.3 ± 11.8
Number of species	6	5	7	6	5	5	8	6

intolerant trees such as *Embothrium coccineum* J. R. et G. Foster (Proteaceae) and *Raphithamnus spinosus* (Verbenaceae) were found almost exclusively in collectors placed in forest margins, where these species usually grow. Seeds of the fleshy-fruited tree *Pseudopanax laetevirens* (Gay) Flanchet (Araliaceae), which is rare in the forest patches studied, were found mainly in canopy gaps (Tables 2,3).

In both forest patches, the seed rain was dominated numerically during the period of study by two large wind-dispersed canopy species *L. philippiana* and *N. nitida* and by three fleshy-fruited trees, *D. winteri*, *A. luma* and *A. meli* (Tables 2,3), regardless of their different representation in the canopy of each forest (Table 1). The main significant factors in the overall pattern of seed fall were year, habitat and species, and significant interactions were found between year × species, site × species and habitat × species (Table 4). The main effect of year was reflected in a significant increase in the total seed rain in 1997 in comparison with 1996 in both patches ($P < 0.001$; Table 4). Habitat effect was reflected in a lower number of seeds reaching the forest margins, given the total seed rain in both forest patches in both years of the study ($F_{3,1} = 5.4$, $P < 0.005$; Tukey's post hoc test, $P < 0.03$ for the comparison of the four habitats, or $P < 0.008$ when data from gap centres and edges are pooled). The fraction of seeds deposited along forest margins was less than half of that falling in other habitats (Fig. 1a). Total seed rain did not differ statistically among the other

Table 4. Multifactorial ANOVA for the effect of year, forest patch (site), habitat (forest interior, gap centre, gap edge and forest margin) and species (*D. winteri*, *Amomyrtus* spp., *L. philippiana* and *N. nitida*) on the seed rain in temperate rainforests of Chiloé Island, southern Chile

	d.f.	MS	F	P
Year	1	113.45	42.42	< 0.00001*
Site	1	2.25	0.84	0.36046
Habitat	3	14.36	5.37	0.00143*
Species	3	43.80	16.38	< 0.00001*
Year × site	1	9.32	3.48	0.06347
Year × habitat	3	3.68	1.37	0.25183
Site × habitat	3	1.79	0.67	0.57149
Year × species	3	35.94	13.44	< 0.00001*
Site × species	3	12.50	4.67	0.00355*
Habitat × species	9	6.19	2.32	0.01706*
Year × site × habitat	3	0.47	0.18	0.91177
Year × site × species	3	5.01	1.87	0.13548
Year × habitat × species	9	1.66	0.62	0.77784
Site × habitat × species	9	3.36	1.26	0.26251
Year × site × habitat × species	9	2.20	0.82	0.59538
Error		2.67		

*Significant effects ($P < 0.05$).

three habitats. However, if the data for gap centres and gap edges are pooled, canopy openings accumulated approximately 60% of the total seed rain in both forest patches (Fig. 1a). The species effect indicated that seed production was characteristic of each species, ranging between a low value of 15.2 seeds m⁻² per day for *Amomyrtus* spp. across all sites and years to a maximum of 253 seeds m⁻² day for *D. winteri* (Tables 2,3).

Year effect interacted significantly with individual species effects (Fig. 2a), indicating large increases in seed production for *Drimys* and *L. philippiana* in 1997, but smaller or no differences between years for *Amomyrtus* spp. and *N. nitida*. *Drimys winteri* showed the largest increase in seed rain between years, from 0.5 seeds m⁻² per day in 1996 to 60 seeds m⁻² per day in 1997 in site A, and from 0.4 seeds m⁻² per day to 180 seeds m⁻² per day in site B (Tables 2,3). Both *L. philippiana* and *N. nitida* had a greater seed rain in 1997 than in 1996, but the difference was less pronounced in *N. nitida*. The seed fall of *L. philippiana* increased from four- to sixfold in both patches (Tables 2,3). The seed rain of *N. nitida* doubled in 1997 in comparison with 1996, but only in forest patch A (Table 2). Likewise, another wind-dispersed species, *E. cordifolia*, decreased in 1997 in comparison with 1996 in patch A, but increased in patch B. Thus the sizes of annual

fruit crops of some species varied asynchronously between forest patches.

A significant site × species interaction indicated that for some species, seed-fall patterns differed significantly between forest patches (Fig. 2b). For instance, *D. winteri* and *N. nitida* had a greater seed production in site B, while the opposite was true for *L. philippiana* (Fig. 2b). No site effect was evident for *Amomyrtus*. Habitat effects also interacted significantly with species effects on seed-fall patterns (Table 4), indicating that for some species (e.g. *L. philippiana*) habitat effects on seed deposition were much larger than for other species.

Fleshy versus dry propagules

The total seed rain of species with fleshy fruits was similar in the four habitats, but dry propagules decreased markedly in abundance in forest margins (Fig. 1b). The same result was obtained by pooling data for gap centres and gap edges (Tukey's post hoc test, *P* < 0.0005).

For species with fleshy propagules, the overall pattern of seed deposition across the four habitats did not differ significantly in either *Amomyrtus* spp. or *D. winteri* (Fig. 3a), although *D. winteri* dominated the seed rain in absolute numbers. In the year of copious *D. winteri*

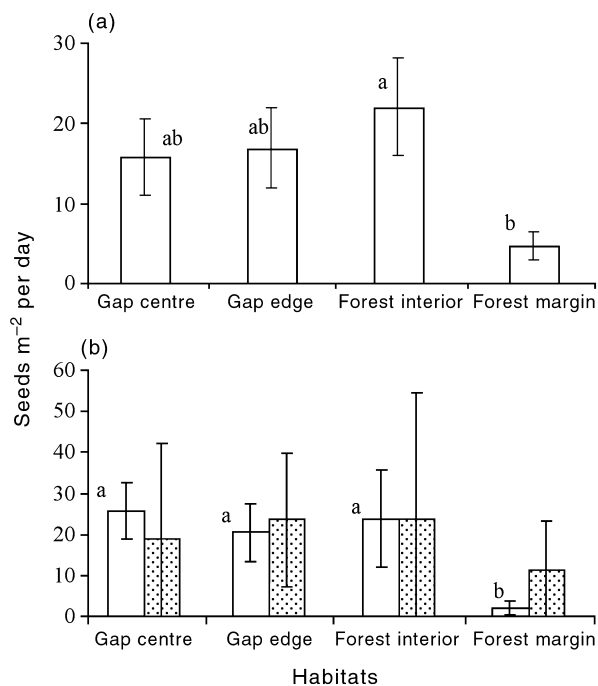


Fig. 1. Total seed fall in each forest habitat for (a) pooled 1996 and 1997 data and (b) by (▨) fleshy and (□) dry propagules (pooling data for all species in both years) in each forest habitat. Bars are means for each habitat ± 1 SE. Different letters above the columns indicate significant differences (*P* < 0.001; Tukey's post hoc test).

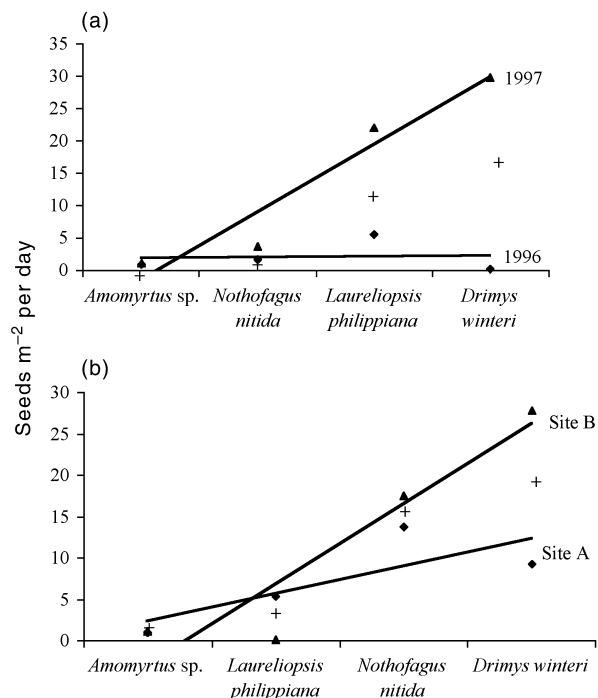


Fig. 2. Graphical illustration of significant interactions (a) year × species and (b) site × species. (a) Mean of seed rain for each tree species for (◆) 1996 and (▲) 1997; (b) mean of seed rain for each tree species in sites (◆) A and (▲) B; (+), mean for each species regardless of year or site (Zar 1996).

seeding (1997), approximately 60% of the total fruit fall was concentrated in canopy gaps (pooling gap edges and centres). Although *Amomyrtus* spp. had the greatest percentage cover among the fleshy-fruited species in most sites (Table 1), their fruit crop, inferred from seed deposition, was generally smaller than *D. winteri* and did not vary as much between years (Tables 2,3).

For both species with dry propagules (*N. nitida* and *L. philippiana*), there were significant differences among habitats, with the lowest proportion of seeds falling in forest margins (Fig. 3b; $P < 0.005$, Tukey's post hoc test). Seed deposition was higher under canopy gaps for *L. philippiana* and largely concentrated in the forest interior for *N. nitida* (Fig. 3b). For *L. philippiana*, 88% of the seed rain in both patches fell in canopy gaps (when data from gap edges and centres are pooled). The large difference in the seed deposition patterns between *N. nitida* and *L. philippiana* largely accounted for the significant habitat effect revealed in the ANOVA ($P < 0.001$, Table 4).

Seeds of fleshy fruits disseminated by birds

The proportion of the seed rain of fleshy propagules that represented actual dispersal by avian frugivores was

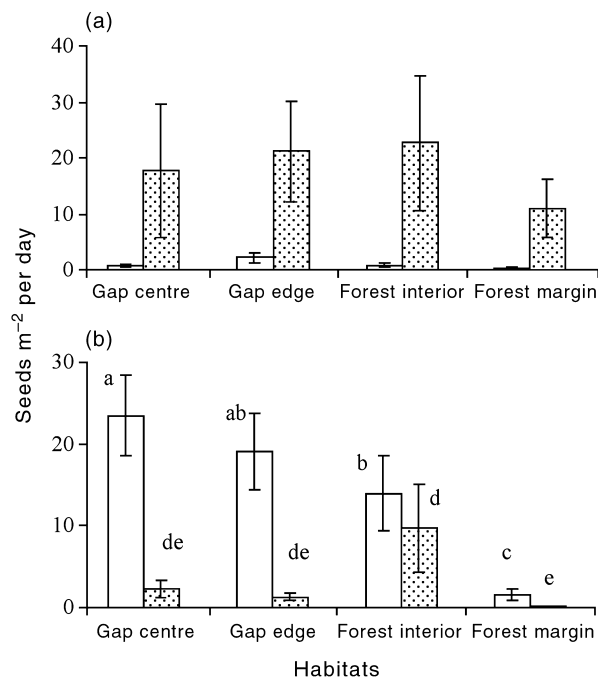


Fig. 3. Patterns of seed deposition for the four principal tree species represented in the seed rain in each forest. Different letters above the bars indicate statistically significant differences ($P < 0.05$; Tukey's post hoc test) between habitats for each species. Significant differences between habitats were only found for dry propagules. (a) (□), *Amomyrtus* spp.; (▨), *Drimys winteri*; (b) (□), *Laureliopsis philippiana*; (▨), *Nothofagus nitida*.

relatively small: 12% of the seed fall of *Amomyrtus* spp. and 5% of the total seed fall of *D. winteri*. For *D. winteri*, avian-disseminated seeds were collected primarily along the edges of canopy gaps, but did not differ significantly from the forest interior or forest margins (Fig. 4).

The forest margins and interior each received approximately 19% of all naked seeds dispersed by birds and 13–22% of all fleshy fruits that fell directly. The gap centre and gap edge received 30–47% of all naked seeds and 28–34% of the total seeds that fell directly, respectively. However, the percentage of naked seeds with respect to the total number of seeds deposited in each habitat was approximately 7% for both forest margins and gap edges, 2% for gap centres, and 4% for forest interiors.

Associations between tree cover by habitat and seed fall

To determine whether the patterns of seed deposition were associated with the differences in tree species cover among the four habitats, a Spearman's rank correlation test was performed between the percentage cover of each species in the canopy directly above the collectors (Table 1) and its seed rain in each habitat (Tables 2,3). Only for *Amomyrtus* spp. did we find a significant positive correlation between canopy cover by habitat and the total seed fall in that habitat ($R = 0.881$, $P = 0.004$). Seed fall of *D. winteri*, *L. philippiana* and *N. nitida* was unrelated to differences in tree cover among habitats and R -values were negative rather than positive ($R = -0.024$, $P = 0.955$, for *D. winteri*; $R = -0.335$, $P = 0.417$ for *L. philippiana*; $R = -0.136$, $P = 0.747$ for *N. nitida*).

DISCUSSION

There were two primary sources of variation in the patterns of seed fall in the two forest patches studied:

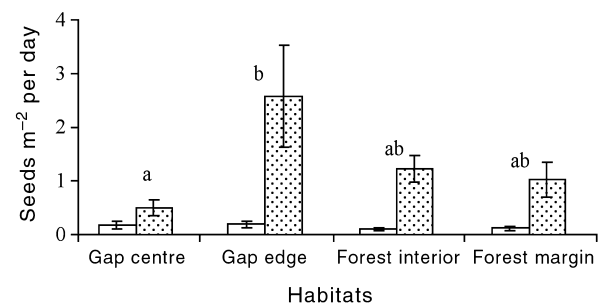


Fig. 4. Seed rain attributed to dispersal by frugivorous birds in each forest habitat. Different letters above the bars indicate statistically significant differences ($P < 0.05$; Tukey's post hoc test). (□), *Amomyrtus* spp.; (▨), *Drimys winteri*.

one temporal and one spatial. Inter-annual variation in seed fall was the result of large differences in fruit crops recorded for the same tree species between 1996 and 1997. In addition, patch-related differences in the magnitude of seed crops among species between years were documented, as shown by the significant interaction terms between the year and species factors. There were pronounced differences in the amount of seed fall between 1996 and 1997 in the tree species with the most copious seed rain in both patches, *N. nitida*, *D. winteri* and *L. philippiana*. These interannual differences appear to reflect the repeated temporal fluctuations in seed crops that characterize these tree species. Alternate years of high and low fruit crops have been reported for *D. winteri* and *N. nitida* in other southern Chilean forests (Murúa & González 1985; Donoso 1993). However, in the present study, the proportional distribution of the seed rain among habitats remained unaffected by large fluctuations of seed crops between years. Such spatial and temporal fluctuations may have important implications for the local abundance of avian frugivores and of seed predators (Murúa & González 1985; Wright *et al.* 1999), but other studies have shown that the abundance of avian frugivores remains unaffected by local variations in fruit production, although their patterns of activity may change (Sallabanks 1993; Restrepo *et al.* 1999).

The major differences in seed fall patterns in both forest patches were associated with a greater concentration of propagules under canopy openings generated by tree-falls and a lower seed fall in forest margins with adjacent non-forest habitat, which suggests a non-random pattern of seed rain (Loiselle *et al.* 1996). These tendencies are accentuated for some species but are not strictly related to propagule types (Figs 3,4). The general lack of a positive association between the amount of seed fall of each species in each of the four habitats and their presence in the canopy suggests that differences in seed fall are more likely to be a response to differences in fruit crop sizes and active seed dispersal by avian frugivores among habitats (Fig. 4). Juvenile trees of fleshy-fruited species, which are characterized by small fruit crops, predominate in forest margins. In contrast, a few large emergent individuals of *N. nitida* present in the forest interior seeded profusely. Although we did not explore this relationship further, our data suggest that the composition and magnitude of the seed rain in each habitat was strongly influenced by the presence, age and size of fruiting trees.

Overall, in both forest patches, the greatest number of seeds of woody species was concentrated in canopy gaps (including both gap edges and centres). Tree-fall gaps could thus act as strong 'sinks' for seed fall within the forest. However, the species richness of the seed rain was somewhat higher in forest margins, where propagules of shrub species (such as *Berberis* sp.,

Baccharis sp., *R. spinosus*) and shade-intolerant pioneer trees (such as *E. coccineum*) enriched the seed rain. In addition, some differences in species composition and abundance in the seed rain, on a finer spatial scale, were apparent within canopy gaps. Most seeds of fleshy-fruited species fell below the trees surrounding the tree-fall gap, whereas the centre of the opening received predominantly wind-dispersed seeds, particularly of *L. philippiana*. However, if data from gap edges and centres are pooled, we find that canopy openings were equally strong sinks for both fleshy-fruited and dry propagules.

In relation to our hypothesis, propagules of fleshy-fruited species did not differ from dry propagules in the location where their seed rain was concentrated. Fleshy fruits were not found in gap centres or forest margins to a greater extent than were those of wind-dispersed species. Rather, each of the major tree species in the forests had a particular seed shadow, with a different concentration of seeds in each habitat. For instance, the wind-dispersed propagules of *L. philippiana* fell primarily in the centres of canopy gaps, whereas the majority of dry seeds of *N. nitida* fell in forest interiors. In contrast, seeds of fleshy-fruited *D. winteri* were concentrated along the edges of tree-fall gaps. The pattern of deposition of fleshy propagules may be a consequence of both greater activity of fruit-eating birds in gap edges and greater seed crops in trees in gap edges, where big trees could be more exposed to sunlight after the creation of a canopy opening (Restrepo *et al.* 1999), in contrast to forest margins, which are frequently covered by a dense population of juvenile trees. Similar patterns of seed deposition for fleshy-fruited species have been reported in a Neotropical forest of Costa Rica, where seed rain was lower in the centres of tree-fall gaps than in gap edges, where branches served as perches for frugivorous birds (Loiselle *et al.* 1996).

The two major avian frugivores in Chiloé forests, *Elaenia albiceps* and *Turdus falcklandii* (Sabag 1993; Armesto *et al.* 1996a; Willson *et al.* 1996b), have been observed more frequently in trees that grow along forest margins. While foraging on ripe fruit on the trees in gap edges, birds may also drop a large number of fruits during manipulation or by accident, thus contributing to an increase the rain of fleshy propagules in this habitat. This behaviour has been reported for *T. falcklandii* feeding on the arillated seeds of *Podocarpus nubigena* (Podocarpaceae) in remnant patches of primary rainforest in Chiloé. This bird species also carries seeds of this tree away from the forest, across open areas and to forest margins (Willson *et al.* 1996b). Flocks of parrots (*Enicognathus leptorhynchus*) feeding on the fleshy fruits of *D. winteri* in forests of Chiloé have also been reported to cause massive fruit fall from trees where they feed (Hernández 1995).

From the spatial deposition pattern of naked seeds identified as 'bird-disseminated' (Fig. 4), we infer that avian frugivores often carry seed from large trees in the forest interior to juvenile trees in the forest margin. Although forest margins received a small amount of the total seed rain, most of these seeds belonged to fleshy-fruited species and at least 10% of these were carried there by frugivores. These data suggest that relative to dry, wind-dispersed seeds, trees with fleshy propagules have a better chance of reaching sites along the forest margin that are associated with the patterns of movement of avian frugivores. It is possible that in years of copious seed production such as 1997, birds could have little effect on the dispersal of fleshy fruits relative to the fruit that falls directly from the trees, because the amount of fruit produced can be much larger than the amount that birds can eat and disperse (Sallabanks 1993; Restrepo *et al.* 1999). However, in years of lower fruit production the effect of frugivorous birds on the seed rain of fleshy-fruited species in different habitats could be more intense.

Nothofagus nitida was the only tree species that exhibited a greater concentration of seeds in the interior of both forest patches (Figs 3,4). This pattern of seed fall may reflect a stronger fit to the parent-centred negative-exponential model of seed shadow that often characterizes wind-dispersed tree species (e.g. Willson 1993). The rudimentary wing appendages of *N. nitida* appear to confer upon them only a limited ability to disperse away from the source trees. In contrast to *N. nitida*, the dry seeds of *L. philippiana* have a conspicuous pappus (approximately 0.5–1 cm long) and our data suggest that these appendages facilitate their wind dispersal further away from the parental tree. Air currents above the forest canopy may 'funnel' the light propagules of *L. philippiana* toward tree-fall gaps.

Nothofagus nitida seeds fell predominantly under the canopy, despite the strong evidence that they are less likely to germinate and produce viable seedlings in this shaded habitat (Veblen & Alaback 1996). Thus, although less numerous, seeds falling in canopy gaps or forest margins may contribute more significantly to seedling recruitment of this species in undisturbed forests. We expected that the seeds of shade-intolerant *N. nitida*, because of their strongly limited spatial dispersal, might exhibit some type of seed dormancy in the forest understorey, but this has not been documented (Figueroa *et al.* 1996). However, *N. nitida* seedlings recruit more frequently on top of decomposing logs than on the forest floor (Lusk 1995). Seeds falling inside tree-fall gaps are more likely to reach large logs in advanced stages of decomposition, which should favour the regeneration of *N. nitida* and other tree species (Lusk 1995). A similar pattern has been described in early successional forest on Chiloé Island, where the establishment and survival of pioneer trees is associated with fallen logs in open areas (Pápic &

Armesto, unpubl. obs). In addition, the rate of seed predation in Chiloé forests was lower in canopy gaps formed by tree falls than in forest interior, for both *Amomyrtus* spp. and *D. winteri* (Díaz *et al.* 1999). This evidence suggests an important role of gaps in tree regeneration in Chiloé forests, despite the similarity in the seed-fall patterns among habitats. Levey (1988) reached a similar conclusion regarding the regeneration of tropical rainforest trees.

Finally, although propagules carried by birds seem to contribute only a small fraction (< 10%) of the total seed rain of fleshy-fruited species in these forest patches in a year of copious fruit crops, fruit-eating birds may play an important role in regeneration by transporting seed to forest margins and therefore accelerating the process of tree invasion of adjacent unmanaged pastures. In a similar manner, avian frugivores have been shown to influence the course of succession in open areas through their use of perch trees for roosting and feeding (McDonnell & Stiles 1983; Hernández 1995).

ACKNOWLEDGEMENTS

We thank Ana Montecino, Marcela Serrano, Sebastián Armesto, Sergio Castro and Wylie Harris for field assistance, and the landowners that allowed us to work in their properties. M. Cadenasso, J. Figueroa, Kris French, R. Ostfeld, S. Pickett, C. Smith and an anonymous referee provided useful statistical advice and comments on the manuscript. Field work was funded by Fondecyt grant 1950461 and by a National Science Foundation, International Program grant to M. F. Willson. Final manuscript preparation was supported by a J. S. Guggenheim Fellowship and an Endowed Presidential Chair in Science to J. J. Armesto, and by the Centre for Advanced Studies in Ecology and Research on Biodiversity (Grant No. P99–103F). This is a contribution to the research program of the 'Senda Darwin' Biological Station, Ancud, Chiloé.

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