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Effect of canopy openness on growth, specific leaf area, and survival of tree seedlings in a temperate rainforest of Chiloé Island, Chile

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Abstract Tree species of intermediate-shade tolerance may regenerate in canopy gaps as well as in the forest understory. However, seedling performance may vary widely between shaded and open habitats. In this study, we assessed the differences in relative growth rate (RGR), specific leaf area (SLA), and survival of seedlings of the tree species *Drimys winteri* (Winteraceae) and *Gevuina avellana* (Proteaceae) planted in three forest habitats differing in light availability: (1) forest interior, (2) forest edge, and (3) tree-fall gap (1%, 6%, and 12% of canopy openness, respectively). A total of 60 3-month-old seedlings of each species were monitored over 16 months (December 2001–April 2003) in the three habitats of a Valdivian rainforest fragment on Chiloé Island, southern Chile. RGR was greatest in the tree-fall gap in both species. Allocation to leaves was proportionally higher in the forest interior. SLA tended to be lower in the tree-fall gap, intermediate in the forest edge, and greater in the forest interior in both species. In addition, SLA of *D. winteri* seedlings was always greater than that of *G. avellana* in all three habitats. Survival of both species was greatest under the canopy gap and lowest in the forest interior.

Survival of seedlings of the larger-seeded species, *G. avellana*, was greatest during the first few months of the experiment in the forest interior, but then dropped significantly in the period during which seedlings of the smaller-seeded species, *D. winteri*, survived in greater numbers. Our comparative study of two intermediate-shade-tolerant tree species documented wide variation in growth and survival of seedlings among habitats differing in canopy openness.

Keywords canopy openness; forest edge; forest interior; seed size; shade tolerance; tree-fall gap; Valdivian temperate rainforests

INTRODUCTION

Among non-pioneer tree species, there is a gradation in responses to light (Canham 1989; Whitmore 1989). In the case of temperate forests of eastern North America, most tree species have been classified as shade-tolerant (*sensu* Whitmore 1982; Swaine & Whitmore 1988) because germination and seedling establishment can occur beneath a closed canopy. However, shade-tolerant species also respond to the formation of tree-fall gaps. As a consequence, the performance of shade-tolerant seedlings, in terms of growth and/or survival, may differ between open and closed habitats. For example, Walters & Reich (2000) showed that relative growth rate (RGR) and survival increased with increasing light for 10 North American tree species differing in shade tolerance. Given that tree crowns cover a greater proportion of the forest area in comparison to canopy gaps (Brokaw & Scheiner 1989), detailed knowledge of the performance of individuals under the canopy shade as well as in tree-fall gaps will be essential to gain a better understanding of forest dynamics. Further, most forest tree species spend long periods as suppressed seedlings or saplings in the understory (Connell 1989). This last point is important because, for many species, regeneration depends on the creation and maintenance of seedling banks (Nava & del Amo 1985).

A large seed size is known to provide an adaptive advantage for seedling survival under adverse conditions, such as shade (Harper 1977; Foster 1986; Crawley 1997; Walters & Reich 2000). One possible mechanism by which large seeds may provide an advantage in the shade is that their greater energy reserves enable seedlings to survive longer under net carbon deficit. This may be an advantage in habitats where gaps are created regularly (Leishman & Westoby 1994). Large-seeded species survived significantly longer than small-seeded species under 99% shade equivalent to light levels $< 5 \mu\text{mol m}^{-2} \text{s}^{-1}$ in a greenhouse experiment (Leishman & Westoby 1994). However, Walters & Reich (2000) showed that under extremely low light conditions, the relative benefits of greater seed mass to survival were temporary.

The Valdivian rainforests located in the Chilean Coastal Range between 38° and 44°S are subjected to disturbance regimes dominated by small and medium-sized tree-fall gaps ranging from 30 to 1000 m² (Armesto & Fuentes 1988). Most tree species in these forests possess some tolerance to shade, with more than 50% of the species occupying habitats with $< 10\%$ canopy openness (Figueroa & Lusk 2001). On the other hand, during past decades, coastal forests have been cleared to be replaced by crop fields and pastures, thus leaving remnants of forest habitat surrounded by extensive edges, i.e., margins or boundaries between forest and adjacent pastures (Willson et al. 1994; Willson & Armesto 1996). As in temperate forests of the Northern Hemisphere, avian frugivores in these forests are more frequently recorded in tree-fall gaps and edges (Willson et al. 1994; Rozzi et al. 1996). For a number of tree species dispersed by birds, seeds are not only deposited in forest interior and gaps, but also in forest edges (Armesto et al. 2001). Trees in Valdivian rainforests vary widely in seed size (Donoso 1989), ranging between 1.3 mg and 1040 mg (Díaz et al. 1999). Lusk (1995) and Lusk & Kelly (2003) suggested that seed size plays an important role in successful establishment of seedlings. In their work, seed size explained 45% of interspecific variation in site of establishment; most small-seeded species occurred on elevated microsites, whereas large-seeded species were more common on the forest floor (see also Christie & Armesto 2003).

Here, we address the following questions about tree regeneration in southern coastal forests: (1) how do relative growth rate (RGR), biomass allocation, specific leaf area (SLA), and survival of young seedlings of two intermediate-shade-tolerant

species (those that grow in shade as well as in open habitats, called “nomads” *sensu* Martínez-Ramos 1985) vary among habitats differing in light availability?, and (2) does seed size determine a greater survival of young seedlings particularly in low light habitats? We compared the survival of seedlings of two common tree species with contrasting seed sizes but with similar tolerance of shade, *Drimys winteri* (Winteraceae) and *Gevuina avellana* (Proteaceae). We expected that RGR and survival would increase, and that LMR (leaf mass ratio) and SLA would decrease with increasing light availability. We also expected that both species would have similarly low RGRs under low light, but that the larger-seeded species would have greater short-term survival.

MATERIAL AND METHODS

Study area

The study was conducted in a large (>100 ha) remnant patch of temperate rainforest in the north-eastern corner of Chiloé Island, about 20 km south-east of Ancud (41°53'S), at an elevation of approximately 80 m.a.s.l. The prevailing climate is described as wet-temperate with a strong oceanic influence (di Castri & Hajek 1976). Meteorological records at Senda Darwin Biological Station (41°51'S), less than 10 km from the study site, indicate average annual rainfall 2120 mm, mean minimum temperature 3.5°C, mean maximum 14.3°C, and mean annual temperature 8.9°C. The landscape is a mosaic of forest patches, shrublands, and anthropogenic pastures. Forest patches are representative of extensive primary forests that once covered most of the island (Willson et al. 1994; Willson & Armesto 1996). The canopy was dominated by evergreen broad-leaved tree species such as *Laureliopsis philippiana*, *Drimys winteri*, *Amomyrtus luma*, *A. meli*, and *Gevuina avellana*, with occasional emergent crowns of *Eucryphia cordifolia* and *Nothofagus nitida*. The forest edge consists of a narrow (5–10 m) belt of trees, dominated by 5–10 m high saplings of *D. winteri* combined with shrubby vegetation (<5 m tall). The forest canopy exhibits some medium-sized gaps (110–210 m²), most of which were created by natural tree falls.

Species

Relative growth rate (RGR), biomass allocation, specific leaf area (SLA), and survival of seedlings in habitats differing in light availability were assessed

in two common tree species, *Drimys winteri* and *Gevuina avellana*. Both species have been described by Donoso (1989) as having “intermediate” tolerance to shade (semi-shade-tolerant species), requiring medium-sized gaps to become established (Veblen & Alaback 1996). MSLR (mean seedling light requirements) is a relative measure that ranges between 0 and 100%, meaning that species with low values can grow and survive under low light levels. In Valdivian rainforest, MSLR values for tree species ranged between 2.4% (*Myrceugenia planipes*) and 25.6% (*Embothrium coccineum*), with *D. winteri* and *G. avellana* having values of 8.8% and 6.6%, respectively, indicating that *D. winteri* is slightly less tolerant than *G. avellana* (Figueroa & Lusk 2001). Mean seed mass of *D. winteri* was 5.1 mg, and of *G. avellana* was 1040 mg (Díaz et al. 1999).

Habitats

The types of habitats considered in this study were: (1) forest interior, area under a closed canopy, at least 100 m away from the nearest forest edge, (2) forest edge adjacent to an open pasture, a band 10 m wide, starting from the outermost tree, and (3) a tree-fall gap, opening of the canopy created by single or multiple tree falls formed in the last 3–5 years, mean area = 150 m².

The three habitats were characterised in terms of (1) percentage of canopy openness, (2) soil moisture, and (3) soil nitrogen availability. The latter two variables were measured to assess their role in explaining differences in seedling growth and survival. Light regimes in the three habitats were quantified using two LAI-2000 Canopy Analysers (Li-Cor, Lincoln, Nebraska, USA). Percent canopy openness directly above a randomly chosen point was determined by comparing two simultaneous readings of the LAI-2000, one inside the forest, and a second one stationed at an open pasture, outside the forest patch. Measurements of canopy openness with the LAI-2000 are a good surrogate of variation in total daily PPFD (Photosynthetic Photon Flux Density) in the forest understory (Machado & Reich 1999; Figueroa & Lusk 2001). Soil moisture was determined through the gravimetric method. We took 10 samples of soil from each habitat in October (spring), January (summer), April (autumn), and June (winter). Each sample was placed in a drying oven at 75°C for 72 h after the fresh weight had been obtained to the nearest 0.1 mg, and re-weighed following this period. Finally, the amount of total inorganic nitrogen (nitrate plus ammonium) was determined at the beginning of the experiment and

for winter samples (6 months later) by means of fractionated micro distillation, extracted with a 1% KAl(SO₄)₂ solution (Aravena et al. 2002). Winter samples were used for this analysis because this period was the mid point of the experiment and the data covered the six previous months. Although we began our experiment using homogenous soil in pots, we expected the amount of nitrogen to change during the experiment because of different rates of mineralisation in each habitat.

Field experimental design and measurements

Seedlings of each species were grown in a greenhouse from seeds collected from trees in the same forest where the experiment was conducted. After germination, seedlings were planted in individual 20 × 20 cm plastic pots using sieved topsoil and acclimated for one month outside the greenhouse at Senda Darwin Biological Station. At 10 randomly chosen points in each of the three habitats, we placed pots containing four 3 month old seedlings, two each of *D. winteri* and two of *G. avellana* ($n = 60$ seedlings per species). Pots were firmly positioned into the ground at experimental sites by placement into 5–10 cm deep holes. Initial shoot length of *D. winteri* was 3.0 ± 0.1 cm (mean \pm 1 SE) and of *G. avellana* was 4.9 ± 0.1 cm. Seedlings were periodically (once a month) disinfected with Dimetoato plus + piretrine (a wide spectrum systemic insecticide) with the purpose of reducing the differential effect of herbivores on growth and survival.

We monitored growth and survival of each seedling twice a month for 16 months (Dec 2001–Apr 2003). We measured total shoot length (i.e., primary and lateral shoots) using a vertical ruler and counted the number of leaves on each seedling. Only leaves that were fully expanded were recorded. Initial and final shoot length and the number of leaves were used to calculate total shoot length and leaf number increments, respectively. Values of shoot length were also used to calculate relative growth rate (RGR; Hunt 1982):

$$\text{RGR} = \frac{\ln(\text{final shoot length}) - \ln(\text{initial shoot length})}{\Delta t}$$

where t = time. Finally, a seedling was considered dead when we observed the senescence and fall of its leaves.

At the end of the experiment, we collected five live seedlings per habitat ($n = 15$ seedlings per species), placed them in a drying oven at 75°C for 72 h, and weighed them to the nearest 0.1 mg. Roots, shoots, and leaves were separated to determine the fraction of biomass allocated to roots (RMR = root

mass ratio), shoots (SMR = shoot mass ratio), and leaves (LMR = leaf mass ratio) in each habitat class in relation to total biomass.

Specific leaf area (SLA) (area/dry mass) was determined from leaves collected during winter (Jun 2002) and in summer (Feb 2003) from the same plants. Five leaves per habitat per species were collected each season. Leaves were scanned and leaf area was determined using the software Sigma Scan for Windows (version 5.0). Leaves were then placed in a drying oven at 75°C for 72 h and weighed to the nearest 0.1 mg.

Statistical analyses

We used a Repeated Measures Analysis of Variance (rANOVA) to assess differences in shoot length increments through time for seedlings growing in habitats differing in light availability. Further, an Analysis of Covariance (ANCOVA) with type of habitat as factor and initial shoot length or initial number of leaves as co-variables was used to test for differences in total shoot length and leaf number increments. Differences in RGR and biomass allocation were tested using a one-way Analysis of Variance (ANOVA), while SLA was analysed using

a two-way Analysis of Variance with type of habitat (canopy openness) and season as factors. Differences in seedling survival were tested for using a Binomial Linear Model with Logit (Statistica; StatSoft Inc. 1998), a type of logistic regression allowing the evaluation of the possible effects of two or more factors and their interaction on a discrete variable (live or dead seedlings). The factors considered in this analysis were species, habitat, and time. The final numbers of seedlings of each species that remained alive were compared using a multiple comparisons for proportions test (Zar 1996).

RESULTS

Habitat characterisation

Mean percentages of canopy openness differed significantly among habitats (ANOVA, $F = 58.560$; d.f. = 2, 27; $P < 0.001$), being lower in the forest interior, intermediate in the forest edge, and greater in the tree-fall gap (Table 1). In contrast, mean annual percentage of soil moisture (pooling all seasons) did not differ among habitats (ANOVA, $F = 2.086$; d.f.

Table 1 Characterisation of the three habitats compared in this study, in terms of percentage canopy openness, percentage soil moisture, and available nitrogen in the soil after 6 months of the beginning of the experiment. Means \pm 1 standard error are shown. Means with different letters differed significantly (*a posteriori* Tukey's tests, $P < 0.05$).

Parameter	Habitat		
	Forest interior	Forest Edge	Tree-fall gap
% canopy openness	1.0 \pm 0.2 ^a	5.7 \pm 1.1 ^b	11.5 \pm 1.1 ^c
% soil moisture	52.6 \pm 0.4 ^a	52.5 \pm 0.8 ^a	54.4 \pm 0.9 ^a
Soil inorganic nitrogen ($\mu\text{g g}^{-1}$ dry weight)	27.4 \pm 1.9 ^a	30.3 \pm 3.4 ^a	29.6 \pm 2.8 ^a

Table 2 Shoot length and leaf number increments in seedlings of *Drimys winteri* and *Gevuina avellana* grown in three habitats differing in canopy openness. The initial number of seedlings per species placed within each canopy openness class was 20. Means \pm 1 standard error are shown. Means with different letters differ significantly (*a posteriori* Tukey's tests, $P < 0.05$).

Habitat	Shoot length increment (cm)		Leaf number increment	
	<i>D. winteri</i>	<i>G. avellana</i>	<i>D. winteri</i>	<i>G. avellana</i>
Forest interior (1%)	2.5 \pm 0.4 ^a	1.6 \pm 0.7 ^a	1 \pm 0.30 ^a	1 \pm 0.32 ^a
Forest edge (6%)	7.2 \pm 1.2 ^b	7.4 \pm 1.0 ^a	5 \pm 0.57 ^b	3 \pm 0.70 ^b
Tree-fall gap (12%)	13.6 \pm 2.1 ^b	15.5 \pm 1.3 ^b	6 \pm 0.96 ^b	4 \pm 0.33 ^b

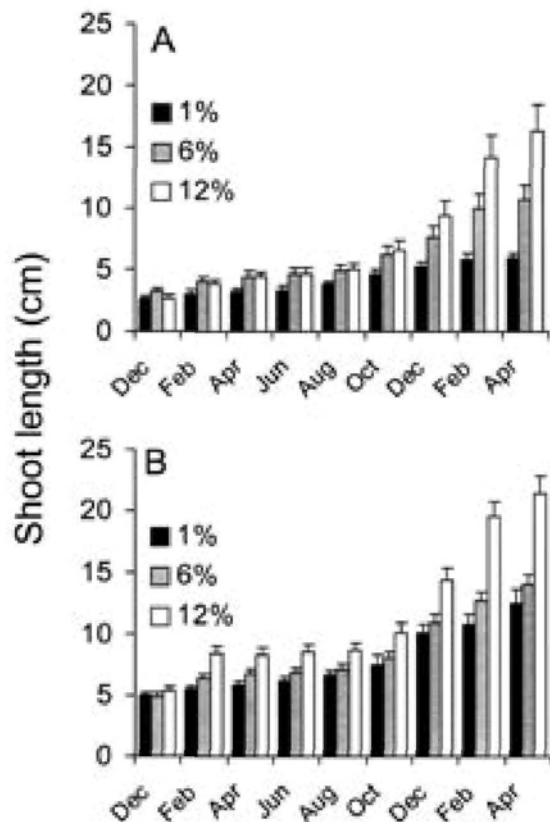


Fig. 1 Shoot length through time in seedlings of *Drimys winteri* (A) and *Gevuina avellana* (B) grown in three habitats differing in canopy openness. Bars show means + 1 SE. The initial number of seedlings per species planted in each habitat was 20.

= 2, 27; $P = 0.143$), ranging between 52% and 55% overall (Table 1). Total inorganic nitrogen (nitrate plus ammonium) available in the soil inside the pots, at the beginning of the experiment and 6 months afterwards, did not vary among habitats (ANOVA, $F = 0.693$; d.f. = 2, 27; $P = 0.503$) (Table 1). However, available-N decreased markedly over the course of experiment. At the beginning of the experiment, the amount of nitrogen was $83.3 \mu\text{g g}^{-1}$ dry weight and at the end ranged between 27.4 and $30.3 \mu\text{g g}^{-1}$ dry weight (Table 1).

Effects of light on growth

Seedling growth of both *D. winteri* and *G. avellana* was affected by canopy openness throughout the duration of the experiment (Repeated Measures ANOVA, $F = 3.151$; d.f. = 2, 47; $P = 0.05$ for *D. winteri* and $F = 3.893$; d.f. = 2, 34; $P = 0.03$ for *G.*

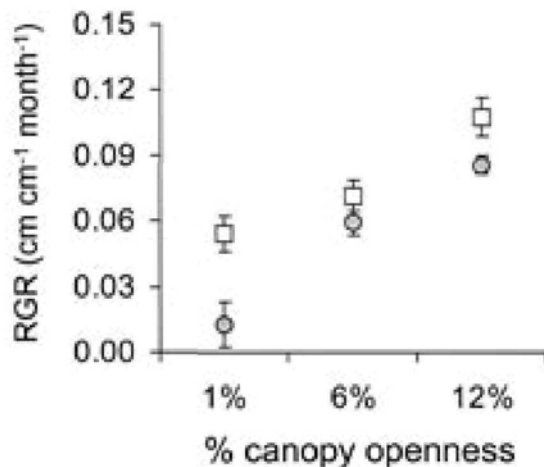


Fig. 2 Relative growth rate (RGR) of *Drimys winteri* seedlings (squares) and *Gevuina avellana* seedlings (circles) grown in three habitats differing in canopy openness. Symbols (squares or circles) show means \pm 1 SE. The initial number of seedlings per species planted in each habitat was 20.

avellana) (Fig. 1). Seedlings grown in the forest interior (1% of canopy openness) developed shorter shoots than those grown in the tree-fall gap (Fig. 1A,B) (*a posteriori* Student Newman-Keuls tests, $P < 0.05$). When we compared total shoot length and total leaf number increments, very similar trends were observed (Table 2). For both variables and both species, we found significant differences between seedlings grown in the forest interior and those grown in the tree-fall gap (Table 2) (*a posteriori* Tukey's tests, $P < 0.05$). In addition, mean shoot length and mean number of leaves were correlated in both species (Pearson correlation: $r = 0.73$, $n = 60$, $P < 0.05$ for *D. winteri* and $r = 0.61$, $n = 60$, $P < 0.05$ for *G. avellana*).

Canopy openness had a significant effect on RGR of seedlings in both species (ANOVA, $F = 11.628$; d.f. = 2, 53; $P < 0.001$ for *D. winteri* and $F = 28.032$; d.f. = 2, 54; $P < 0.001$ for *G. avellana*). In *D. winteri*, RGR differed significantly between seedlings growing in the forest interior and in the tree-fall gap (*a posteriori* Tukey's test, $P = 0.001$) and between those growing in the forest edge and in the tree-fall gap (Tukey's test, $P = 0.006$) (Fig. 2). In *G. avellana*, RGR was six times greater in the tree-fall gap than under closed canopy (Fig. 2). Further, mean RGRs of *G. avellana* seedlings growing in the three habitats differed significantly from each other (*a posteriori* Tukey's tests, $P < 0.05$) (Fig. 2).

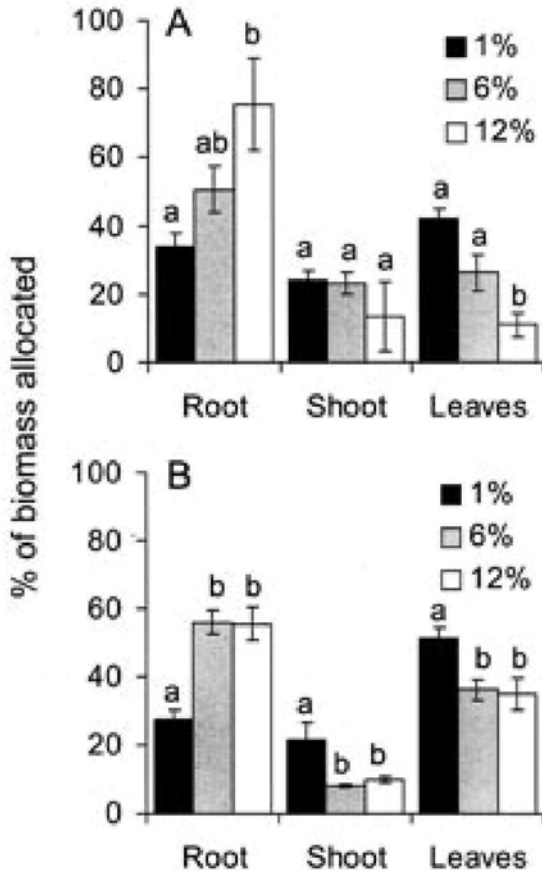


Fig. 3 Biomass allocated to roots, shoots, and leaves in seedlings of *Drimys winteri* (A) and *Gevuina avellana* (B) planted in three habitats differing in canopy openness. Bars show means \pm 1 SE. Means with different letters differed significantly ($P < 0.05$). $n = 5$ seedlings per habitat per species.

Biomass allocated to roots and leaves was significantly affected by canopy openness in seedlings of *D. winteri* (ANOVA, $F = 5.639$; d.f. = 2, 12; $P = 0.018$, and $F = 15.305$; d.f. = 2, 12; $P = 0.001$, respectively) (Fig. 3A). No differences were observed in shoot biomass among the three canopy openness classes ($F = 1.906$; d.f. = 2, 12; $P = 0.191$) (Fig. 3A). Canopy openness had a significant effect on the percentage of biomass allocated to roots, shoots, and leaves in seedlings of *G. avellana* (ANOVA: $F_{\text{Roots}} = 19.221$, d.f. = 2, 12, $P = 0.001$; $F_{\text{Shoots}} = 7.039$, d.f. = 2, 12, $P = 0.009$; and $F_{\text{Leaves}} = 5.779$, d.f. = 2, 12, $P = 0.017$) (Fig. 3B). Both species allocated more biomass to leaves in the forest interior than in the tree-fall gap and the opposite was true for biomass allocated to roots (Fig. 3).

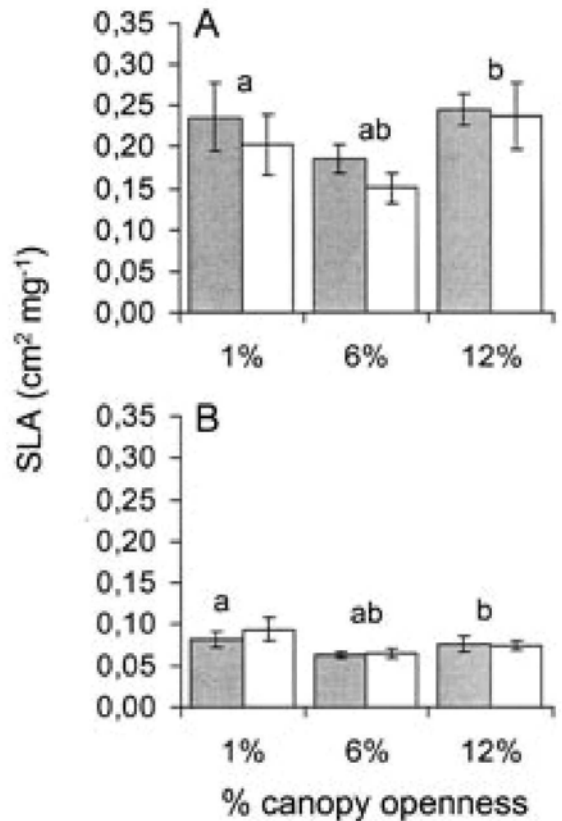


Fig. 4 Specific leaf area (SLA) of *Drimys winteri* (A) and *Gevuina avellana* (B) seedlings planted in three habitats differing in canopy openness measured in winter (shaded bars) and summer (open bars). Bars show means \pm 1 SE. Means with different letters differed significantly ($P < 0.05$). $n = 5$ leaves per habitat per species.

Light effects on specific leaf area

Specific leaf area was marginally affected by canopy openness in *D. winteri* (ANOVA, $F = 2.992$, d.f. = 2, 24, $P = 0.069$) and significantly affected in *G. avellana* (ANOVA, $F = 3.874$, d.f. = 2, 24, $P = 0.034$), while season had no effect on either species. SLA of *D. winteri* seedlings was greater in the forest interior, intermediate in the forest edge, and lowest in the tree-fall gap (Fig. 4A), differing marginally between habitats with 1% and 12% of canopy openness (*a posteriori* Tukey test, $P = 0.063$) (Fig. 4A). Seedlings of *G. avellana* showed a similar tendency (Fig. 4B), differing significantly between forest interior and tree-fall gap (*a posteriori* Tukey test's, $P = 0.027$) (Fig. 4B). However, SLA of *G. avellana*

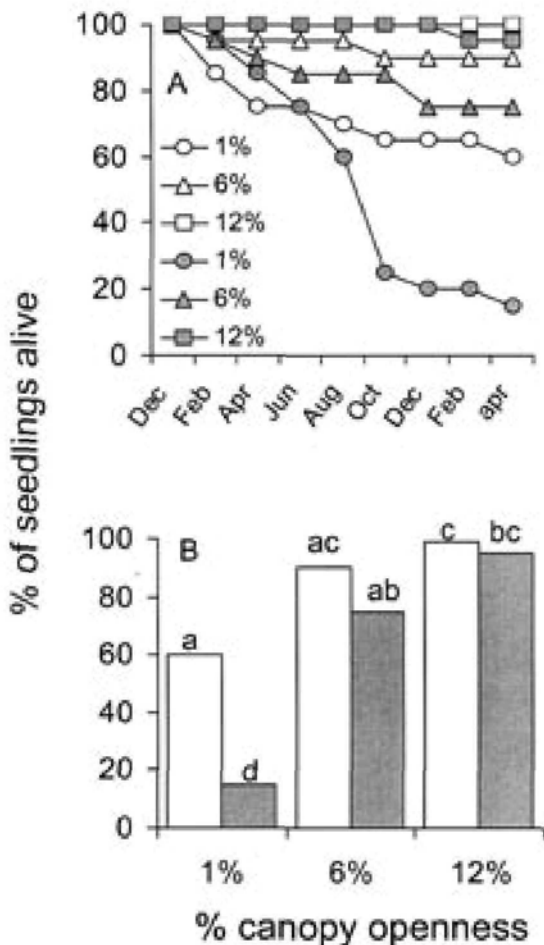


Fig. 5 Percentage of seedlings alive over time (A) and at the end of the experiment (16 months later) (B) in seedlings of *Drimys winteri* (open) and *Gevuina avellana* (shaded) in three habitats differing in canopy openness. The initial number of seedlings per species planted in each habitat was 20.

seedlings were always lower than those of *D. winteri* seedlings in all habitats (Fig. 4).

Seedling survival

Species, habitat, and time since the beginning of the experiment had significant effects on seedling survival (Binomial Model with Logit: $\chi^2_{\text{Species}} = 24.602$, d.f. = 1, $P < 0.001$; $\chi^2_{\text{Habitat}} = 164.569$, d.f. = 2, $P < 0.001$; $\chi^2_{\text{Time}} = 62.887$, d.f. = 8, $P < 0.001$). Further, no interaction between factors were detected although, the species \times habitat interaction was marginal ($\chi^2_{\text{Species-Habitat}} = 5.286$, d.f. = 2, $P = 0.071$).

For both species, a greater percentage of seedlings remained alive in the tree-fall gap (Fig. 5A). Survival was particularly reduced in *G. avellana* in the low light habitat (forest interior) (Fig. 5A). During the first few months of the experiment, more seedlings of *G. avellana*, the larger-seeded species, survived than *D. winteri*, the smaller-seeded species, in the forest interior (Fig. 5A). However, this difference disappeared rapidly as the survival rate of *G. avellana* declined.

At the end of the experiment after 16 months, the percentage of surviving seedlings of *G. avellana* in forest interior (1% canopy openness) differed significantly from the other habitats (*a posteriori* Tukey-type's tests for multiple comparisons, $P < 0.05$) (Fig. 5B). Final survival of *D. winteri* seedlings growing under the tree-fall gap was significantly higher than of *G. avellana* growing in the forest edge and from their conspecifics growing in forest interior (*a posteriori* Tukey-type's tests for multiple comparisons, $P < 0.05$) (Fig. 5B).

DISCUSSION

Our comparative study of two intermediate-shade-tolerant tree species of temperate rainforests of southern Chile documented wide variation in seedling growth and survival among habitats differing in canopy openness within a single forest patch. Growth and survival of *D. winteri* and *G. avellana* seedlings were greater in open habitats, the tree-fall gap and the forest edge (12% and 6% of canopy openness, respectively), and lower in the forest interior under closed canopy. The latter condition proved to be most unfavourable for the survival of *G. avellana*, especially after the first six months, i.e., during the winter months. A major cause of mortality of *G. avellana* seedlings was damping-off (pers. obs.). This phenomenon is attributed mainly to fungi in the genus *Fusarium*, and consists of a weakening of the upper portion of the shoot and subsequent loss of leaves. Walters & Reich (2000) also found that mortality rates of seedlings of the conifers *Larix laricina* and *Picea mariana* were highest under low light, suggesting that plants with severe carbon shortage may be more susceptible to pathogens (see also Augspurger 1984). In contrast, no obvious cause of mortality was identified for seedlings of *D. winteri*, although a few seedlings were uprooted during the first two months possibly due animal activity, presumably by birds or rodents. Our results differ from those reported by Figueroa &

Castro (2000), who found higher seedling mortality during summer (December to March), attributed to physiological disequilibrium (water or carbon deficit). These authors reported that seedling mortality attributable to pathogens was practically zero during winter-spring (July to October). One possible reason for this difference is the different size and age of the forest fragments. While the present study was conducted in a large old-growth forest fragment, Figueroa & Castro (2000) worked in a small young patch (<2 ha) where there would be a greater influence of the adjacent matrix. Williams-Linera (1990) suggested that biological responses of seedlings inside forest patches may be influenced by orientation, shape, size, and topographic features of the patches.

Although *D. winteri* has been described as a pioneer species by some authors (e.g., Veblen et al. 1980), our results show that its seedlings can survive in the forest interior and persist through time. This finding is important because in many forests, regeneration depends largely on the establishment of seedling banks (Nava & del Amo 1985; Armesto & Fuentes 1988). *D. winteri* usually forms seedling banks in advanced successional stages (Aravena et al. 2002). Results also suggest that *D. winteri* presents higher phenotypic plasticity than *G. avellana*. Pioneer species usually show higher plasticity than late or climax species (Bazzaz 1979).

We also showed that survival of the large-seeded species *G. avellana* was higher than that of the small-seeded species *D. winteri*, at least during the first few months of the experiment, particularly in the forest interior (Fig. 5A). Consequently, the relative benefits of a higher seed mass to survival under deep shade were only temporary, as shown in a greenhouse by Walters & Reich (2000) for 10 North American tree species varying in seed size. It is possible that in larger-seeded species, reserve translocation and cotyledon abscission take a longer time than in small-seeded species, thus favouring initial growth and survival. Uprooting was the only apparent cause of mortality of *D. winteri* seedlings in the beginning of the experiment. Seedlings of the smaller-seeded *D. winteri* may be at a disadvantage in this regard compared with the larger-seeded *G. avellana*, because their shorter radicle cannot penetrate the mineral soil well (Molofsky & Augspurger 1992). In contrast to the temporary benefits of the greater amount of energy stored in a large seed (Leishman & Westoby 1994), the benefits of enhanced RGR under low light would be expected to persist for longer. This suggests that

the positive effect of seed size on seedling survival under deep shade would change with seedling age (Walters & Reich 2000). Positive relationships between RGR and survival under low light conditions have often been reported for tree seedlings (Walters & Reich 1996) and saplings (Kobe & Coates 1997).

Relative growth rate (RGR) increased with light availability in both species, particularly in seedlings of *G. avellana*. For this species, mean RGR differed significantly among the three habitats. In contrast, RGR of *D. winteri* seedlings did not differ between the shaded forest interior and the forest edge. Light availability is known to limit seedling growth in the forest understory (Canham 1988; Kobe et al. 1995) while other factors such as nutrient availability are assumed to be less important in these carbon-limited environments (Denslow et al. 1990, 1998). In our study, available inorganic nitrogen and soil moisture did not differ among habitats, and hence they do not account for differences in RGRs. Although we did not statistically compare RGRs between species, it is interesting to note that each species behaved differently in the low light habitat (see Fig. 2). The higher RGR of *D. winteri* seedlings in the shaded forest understory could explain, in part, their greater survival. Recent reviews (e.g., Veneklaas & Poorter 1998; Walters & Reich 1999) concluded that seedlings of light-demanding tree species often grow faster than those of shade-tolerant counterparts, even under low light, reflecting the ability of the former to reduce their whole-plant light compensation point by greatly increasing SLA and LAR (leaf area ratio) under shade. However, it is also necessary to take into account that light-demanding tree species cannot maintain higher RGRs for a very long time. Given that this experiment ran for only 16 months, our results should be interpreted with caution.

As expected, seedlings of both species allocated relatively more energy to leaves in the forest interior than in the tree-fall gap. The net primary productivity of seedlings is positively correlated with photosynthetic to non-photosynthetic tissue ratios, especially when Photosynthetic Active Radiation (PAR) is above the leaf light compensation point (Foster 1986). The fact that seedlings allocated more biomass to leaves in light-poor habitats, such as forest interior, increases their chance of reaching the canopy when gaps are formed. Lusk & del Pozo (2002) showed, in a greenhouse experiment, that LMR (leaf mass ratio) was also higher in low light for most of the 12 Chilean temperate rainforest tree species they investigated.

Specific leaf area describes the light capture area deployed per unit leaf mass. As expected, SLA increased with light scarcity in both species. Wright & Westoby (2000) and others (e.g., Poorter & Remkes 1990; Reich et al. 1998; Wright & Westoby 1999), have shown that SLA was the strongest determinant of RGR. Moreover, Wright & Westoby (2001) also found that RGR scaled close to proportionally with SLA for 12 data sets comprising 250 species belonging to three growth forms. In our study, RGR was more strongly correlated with SLA in seedlings of *D. winteri* than in those of *G. avellana* (Pearson correlation: $r = -0.40$, $n = 30$, $P < 0.05$ for *D. winteri*; $r = -0.30$, $n = 30$, $P > 0.05$ for *G. avellana*). Wright & Westoby (2001) reported that a lack of correlation between RGR and SLA probably indicates the existence of a negative covariance between SLA and leaf nitrogen per area. This may reflect intrinsic differences in nitrogen use efficiency among species. Chapin (1980) suggested that the relationship between nitrogen and carbon gain could be partially uncoupled if species exhibit luxury consumption of nitrogen, such that increased nitrogen leads to a modest increase in growth. Such a conservative carbon allocation pattern, where growth potential is sacrificed in favour of traits that benefit persistence, such as chemical defences to protect tissues from herbivory, have been described by Augspurger (1984), Coley et al. (1985), and Kitajima (1994). Accordingly, we found that seedlings of *G. avellana* produced more carbon-based defences such as condensed tannins than *D. winteri*, resulting in lower foliar damage in the former (Chacón & Armesto unpubl. data).

Although only two species of Valdivian temperate rainforests were examined in this study, survival and growth of a cohort of seedlings in habitats differing in light availability were monitored in the field for at least an entire growing season. The forest edge proved to be a favourable site for survival and growth of seedlings of both species, a result that has management and restoration implications. Although forest edges receive less than 20% of the total seed rain, dominated largely by fleshy-fruited species (Armesto et al. 2001), the process of seedling establishment may be accelerated through restoration plans that consider planting additional seedlings of intermediate-shade tolerance as well as pioneer tree species.

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