

Seed germination responses in a temperate rain forest of Chiloé, Chile: effects of a gap and the tree canopy

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ABSTRACT. This study determined germination responses of 19 species, including trees, shrubs, vines, and herbs, under natural gap and non-gap conditions, in a secondary forest in Chiloé Island, southern Chile, in order to assess if there is any association between the habitat where the seedlings of these plant species occur and their germination requirements. Statistical differences in percentage seed germination were detected in six species in a gap habitat compared to the understory. Five forest edge species (*Embothrium coccineum*, *Escallonia rubra*, *Gunnera tinctoria*, *Nertera granadensis* and *Rhaphithamnus spinosus*) presented greater germination success in the canopy gap, while only one forest interior species (*Myrceugenia planipes*) germinated to a lesser extent in the gap. Percentages of seed germination were not statistically different between the two habitats neither in the remaining 10 edge species (*Gaultheria mucronata*, *Luma apiculata*, *Myrceugenia parvifolia*, *Tepualia stipularis*, among others) nor in the 3 forest interior species studied (*Luzuriaga radicans*, *Mitraria coccinea*, and *Myrceugenia ovata* var. *ovata*). Thus, there is no strong evidence of any association between the habitats where seedlings of these plant species grow and their germination requirement.

RESUMEN. Respuestas de germinación de semillas en un bosque templado de Chiloé, Chile: efectos de un claro y del dosel arbóreo: En condiciones naturales de un claro y bajo el dosel de un bosque secundario de Chiloé se realizaron ensayos de germinación en 19 especies, incluyendo árboles, arbustos, enredaderas e hierbas nativas, para determinar si el hábitat que ocupan las plántulas de cada especie está asociado a sus requerimientos de germinación. En seis especies, el porcentaje de germinación en el claro fue estadísticamente diferente al de bajo el dosel. En cinco especies de borde de bosque (*Embothrium coccineum*, *Escallonia rubra*, *Gunnera tinctoria*, *Nertera granadensis* y *Rhaphithamnus spinosus*), la germinación fue mayor en el claro, mientras que en una sola especie de interior de bosque (*Myrceugenia planipes*) el porcentaje de germinación resultó ser menor en el claro. Los porcentajes de germinación en el claro y bajo el dosel no fueron estadísticamente diferentes en las restantes 10 especies de borde (*Gaultheria mucronata*, *Luma apiculata*, *Myrceugenia parvifolia*, *Tepualia stipularis*, entre otras), ni en las 3 especies de interior de bosque estudiadas (*Luzuriaga radicans*, *Mitraria coccinea*, and *Myrceugenia ovata* var. *ovata*). Por ende, no parece haber suficiente evidencia como para postular que exista una asociación entre el hábitat que ocupan las plántulas de las especies y sus respectivos requerimientos de germinación.

INTRODUCTION

Plant regeneration promoted by natural disturbances in forests has been the subject of many studies in southern Chile (Veblen et al. 1981; Veblen 1989). Veblen (1982) and Armesto & Figueroa (1987) studied forests unaffected by massive natural disturbances (catastrophes) in the Coastal Cordillera of southern Chile, determining that they show a gap-phase

type regeneration, influenced by natural allogenic factors that may be critical to the regeneration of many forest species in Chile.

A gap is a discontinuity in the forest canopy that exposes the soil surface to environmental conditions different to those found under trees (Bazzaz & Pickett 1980). These conditions include higher density of photon flux and an increase in the red/far-red ratio of the light that strikes the soil (Wilson 1965; Goldberg & Werner 1983; Nakashizuka 1985; Lee 1987).

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Gaps stimulate germination of photoblastic seeds in many heliophytic species, due to an increase in the red/far-red ratio of light (Vázquez-Yanes & Orozco-Segovia 1990a, 1990b). Grubb & Whitmore (1966), Denslow (1980), and Collins & Pickett (1987) recorded greater temperature fluctuations in a gap's exposed soil than in the soil under the canopy, while Washitani & Takenaka (1987) recorded a thermosensitive germination response in some species typical of open sites in temperate regions. Higher temperatures and their greater daily variation in gaps have been shown to stimulate germination of pioneer forest species (Washitani & Takenaka 1987). In temperate forests of the Northern Hemisphere, air humidity is lower in a gap than under the canopy (Collins & Pickett 1987), while, in contrast, humidity in the upper levels of the soil is greater in gaps than under the canopy in tropical forests (Denslow 1987). These physical characteristics of gaps allow certain plant species with gap-favorable traits to invade these sites quickly. Some of these traits may be fast growth rates; low to medium height; short life cycles; small, wind-dispersed and photoblastic seeds; fast germination; and the ability to form seed banks below the canopy (Whitmore 1975; Vázquez-Yanes & Guevara-Sada 1985; Denslow 1987; Vázquez-Yanes et al. 1990). In the present study, we evaluated germination as a possible trait associated to the gap/non-gap dichotomy.

In the temperate rainforests of the island of Chiloé, southern Chile, most canopy species apparently regenerate better in gaps (Armesto & Figueroa 1987; Armesto & Fuentes 1988; Bustamante & Armesto 1995), where conditions are characterized by a high frequency of medium-to-small perturbations produced by tree falls, stem or branch decay, soil movement due to rain and wind storms, and the effect of the "epiphyte and vine loads" (Armesto & Fuentes 1988). However, knowledge of seed germination in this region is very scarce and limited to laboratory experiments (Figueroa et al. 1996; Figueroa 1997).

In this study, germination responses of different species under gap and non-gap conditions were evaluated in the field. We tested the hypothesis of differential germination responses of 19 species of plants commonly found in the forests of Chiloé, under gap and non-gap conditions, and tested for an associa-

tion between the habitat of seedlings of these plant species and their respective germination requirements. We expected seeds of species that regenerate in forest edges to germinate to a lesser extent in the understory than in gaps.

MATERIALS AND METHODS

Study site

Germination experiments assays were carried out under field conditions in the Estación Biológica Senda Darwin, 18 km northeast of Ancud, Chiloé, southern Chile (41°S; 75°W). The climate is humid-temperate with an oceanic influence, with a mean annual precipitation of 2200 mm and a mean annual temperature of 9.5 °C. A slight Mediterranean influence is reflected by a precipitation reduction during the summer months (di Castri & Hayek 1976).

Vegetation is dominated by typical Valdivian rainforest species of Myrtaceae, Fagaceae, Ericaceae and Berberidaceae (Armesto & Figueroa 1987; Armesto & Fuentes 1988; Gajardo 1994). While shrubs abound in gaps and in open spaces, they are absent or scarce within the forest where mosses, vines and epiphytes are abundant.

Seed collection

Mature fruits were collected of the 19 most common species of trees, shrubs, vines and perennial herbs present at the study site (Table 1). Most fruits were collected during winter and spring of 1998, with the exception of *Embothrium coccineum*, *Gunnera tinctoria*, and *Lomatia hirsuta*, whose fruits were collected during the summer of 1999. All the fruits were collected during the period of maximum fruit load at Chiloé (Smith-Ramírez & Armesto 1994; Figueroa et al. 1996; Smith-Ramírez et al. 1998). Seeds were extracted and cleaned manually as soon as they were collected. Seeds were then air-dried for three days in the laboratory. Any seed with evidence of fungal or insect attack was discarded.

Seed sowing

Seeds were sown immediately after drying was completed, and watered manually only once at the beginning of the experiment; afterwards the seeds received only natural

Table 1. Species of the temperate rainforest of Chiloé selected for the study. Their taxonomic assignment, life form, forest habitat, peak month of fruiting, dispersal syndrome, and seed viability are indicated. The last four characteristics were obtained from Armesto & Rozzi (1989), Smith & Armesto (1994), Figueroa (1997), and Smith et al. (1998). High seed viability corresponds to >75% of viability.

Tabla 1. Especies del bosque templado de Chiloé seleccionadas para el estudio. Se indican la asignación taxonómica, la forma de vida, el hábitat, el mes de máxima fructificación, el síndrome de dispersión y la viabilidad de las semillas. Las últimas cuatro características están tomadas de Armesto & Rozzi (1989), Smith & Armesto (1994), Figueroa (1997) y Smith et al. (1998). Una alta viabilidad de las semillas corresponde a >75%.

Species	Family	Life form	Forest habitat	Peak of fruiting	Dispersal syndrome	Seed viability
<i>Embothrium coccineum</i>	Proteaceae	Tree	Edge	Mar	Anemochory	High
<i>Escallonia rubra</i>	Escalloniaceae	Shrub	Edge	-	Multiple	High
<i>Gaultheria mucronata</i>	Ericaceae	Shrub	Edge	Jun	Endozoochory	High
<i>Gunnera tinctoria</i>	Gunneraceae	Herb	Edge	-	Endozoochory	High
<i>Lomatia ferruginea</i>	Proteaceae	Tree	Edge	Mar/May	Anemochory	-
<i>Lomatia hirsuta</i>	Proteaceae	Tree	Edge	Feb	Anemochory	-
<i>Luma apiculata</i>	Myrtaceae	Tree	Edge	May/Jul	Endozoochory	High
<i>Luzuriaga radicans</i>	Phylesiaceae	Vine	Interior	Apr/May	Endozoochory	High
<i>Mitrraria coccinea</i>	Gesneraceae	Vine	Interior	May/Mar	Endozoochory	High
<i>Myrceugenia exsucca</i>	Myrtaceae	Tree	Edge	Aug	Endozoochory	High
<i>Myrceugenia ovata</i> var. <i>nan.</i>	Myrtaceae	Shrub	Edge	Dec/Oct	Endozoochory	High
<i>Myrceugenia ovata</i> var. <i>ovata</i>	Myrtaceae	Tree	Interior	Sept	Endozoochory	-
<i>Myrceugenia parvifolia</i>	Myrtaceae	Shrub	Edge	Dec/Oct	Endozoochory	-
<i>Myrceugenia planipes</i>	Myrtaceae	Tree	Interior	Jan/Feb	Endozoochory	-
<i>Myrteola nummularia</i>	Myrtaceae	Shrub	Edge	Apr	Endozoochory	High
<i>Nertera granadensis</i>	Rubiaceae	Herb	Edge	Mar	Endozoochory	High
<i>Rhaphithamnus spinosus</i>	Verbenaceae	Shrub	Edge	Jun	Endozoochory	High
<i>Tepualia stipularis</i>	Myrtaceae	Shrub	Edge	Sep	Anemochory	High
<i>Ugni candollei</i>	Myrtaceae	Shrub	Edge	May/Jun	Endozoochory	-

rainwater. No scarification or stratification treatments were carried out before sowing. Large seeds (>0.1 mg) were sown in 15 x 6 x 10 cm plastic trays. Smaller seeds were sown in 3 x 3 x 3 cm plastic pots. The soil used for sowing was obtained directly from the forest under study after being sterilized in a high temperature oven (>150 °C). Seeds were sown directly on top of the soil and remained uncovered.

To avoid insect predation on seeds and seedlings the trays and pots were wrapped with a white polyester satilene mesh (code 520502) used for serigraphy (<0.5 mm of aperture). The photosynthetic photon flux density reduction resulting from the use of the mesh was estimated to be approximately 20%. To prevent seed predation by rodents and birds, trays and pots were placed inside 1 m³ cages lined with 15 x 15 mm chicken wire (a cage in the gap and other in the understory).

The gap and non-gap (understory) conditions were considered as separate treatments. Due to the limited number of seeds available, three replicates per treatment, each with 50 seeds, were used. To consider the possible effect of natural seeds falling from nearby plants, in each treatment a control was used consisting of a tray containing sterile soil but no seeds, also wrapped with polyester mesh. The selection of the gap and non-gap areas was carried out at random in a fragment of secondary forest. The trays and pots with seeds were assigned at random in the area of both treatments. The gap itself was approximately 80 m² and was surrounded by a fragment of secondary forest with small (6 m-tall) *Nothofagus nitida* and some medium-sized (12 m-tall) *Drimys winteri* trees on the eastern side. *D. winteri*, *N. nitida* and *Podocarpus nubigena* trees were dominant in the surrounding forest and the shade-tolerant seedlings of

Amomyrtus luma and *P. nubigena* dominated the understory. The forest edge was covered with small *Gaultheria mucronata* and *Myrteola nummularia* shrubs and ferns of the genus *Blechnum*. Introduced pastures were abundant in the center of the gap. Herbaceous species were cleared inside cages.

Thermal variations on the soil surface in the gap and under the canopy were recorded inside the cages every hour between 9:00 and 18:00 h for five consecutive days in winter (June) and spring (September). Photosynthetic photon flux density (PPFD), expressed in $\text{mmol of photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, was measured on the soil surface inside the cages every hour from 11:00 to 15:00 h during three consecutive days in winter and spring, both in the gap and under the canopy. PPFD was also measured outside the forest in an open site (under direct

sunlight). Temperature and PPFD were measured with a LI-1400 Data Logger (Licor, Lincoln, USA). The number of seeds that germinated in the trays was recorded once a month for six months (the proportion of viable seeds that might have germinated after six months was not determined). A seed was counted as germinated when its radicle became visible to the naked eye. An approximate indication of seed viability of each species is included in Table 1.

Statistical analysis

A fixed model repeated measures one-way ANOVA with three subsamples was used for the analysis of results obtained in the gap and under the canopy. Mean percentage germination in gap and under the canopy was obtained from three replicates per species. To satisfy ANOVA assumptions the arcsine square root transformation was applied to percent germination data. Germination within each replicate was calculated as (total number of emerged seedlings/total number of seeds sown) $\times 100$. A fixed model one-way ANOVA was used for analyses of results of temperature and PPFD in each hour from 9:00 until 18:00 h in the gap and under the canopy of the forest.

RESULTS

Gap vs. under the canopy microenvironment

In winter, although not significantly greater, a tendency for mean temperature in the gap to be highest between 11:00 and 17:00 h was detected ($P > 0.05$). Mean temperature in the gap decreased faster towards 18:00 h than under the canopy ($F_{1,8} = 120, P < 0.05$). Mean spring temperature in the gap was significantly greater than under the canopy ($P < 0.05$) between 12:00 and 16:00 h; there were no differences during morning and late afternoon hours (Figure 1). PPFD was about 40 times greater in the gap than under the canopy, and about 300 times greater in the open site than under the canopy during both winter and spring (Figure 2).

Gap and tree canopy effects on germination

Significant differences in percentage germination of seeds in the gap vs. the understory were detected in only six species. Of these,

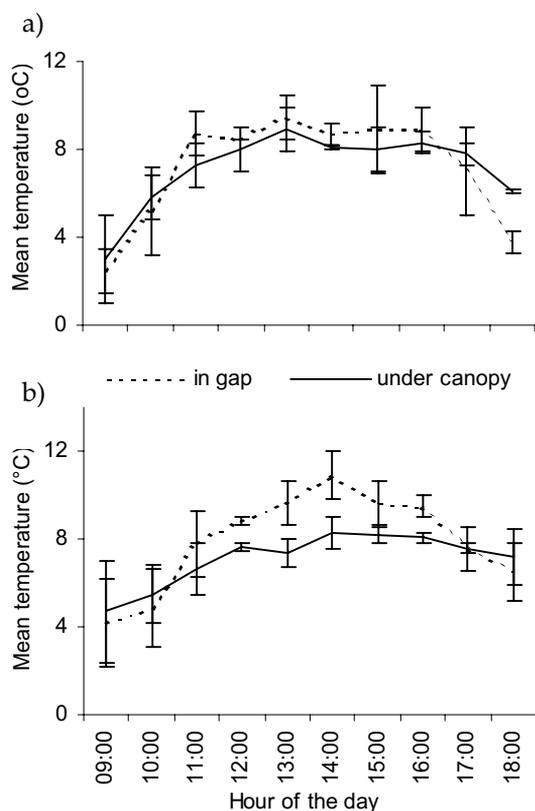


Figure 1. Mean (\pm SD) temperature measured hourly over a five-day period during (a) winter and (b) spring, in a canopy gap (dotted line) and under the canopy (full line) of a secondary forest in Chiloé.

Figura 1. Temperatura promedio (\pm DE) medida cada hora durante cinco días en (a) invierno y (b) primavera, en un claro (línea punteada) y bajo el dosel (línea entera) de un bosque secundario en Chiloé.

percent germination was highest in the gap in three species, *Escallonia rubra* (100% in the gap vs. $49 \pm 5\%$ under the canopy after six months; $F_{1,4} = 212$, $P < 0.01$), *Nertera granadensis* ($90 \pm 5\%$ in the gap vs. $23 \pm 5\%$ under the canopy after six months; $F_{1,4} = 33.4$, $P < 0.01$) and *Rhaphithamnus spinosus* ($73 \pm 3\%$ in the gap vs. $39 \pm 6\%$ after six months; $F_{1,4} = 71.4$, $P < 0.01$). Two of the six species did not germinate under the canopy even after six months, *Embothrium coccineum* and *Gunnera tinctoria* ($71 \pm 3\%$ and $86 \pm 4\%$, respectively, in the gap after six months). These five forest edge species represented 33% of all the edge species studied. The percentage germination in one out of four forest interior species stud-

ied, *Myrceugenia planipes*, was greater under the canopy ($82 \pm 5\%$ in the gap vs. 100% under the canopy after six months; $F_{1,4} = 17.4$, $P < 0.05$). Finally, for 13 of the species studied, namely ten edge species (e.g., *Gaultheria mucronata*, *Luma apiculata*, *Myrceugenia parvifolia*, *Tepualia stipularis*) and three interior species (*Luzuriaga radicans*, *Mitraria coccinea*, and *Myrceugenia ovata* var. *ovata*), there was no significant difference between germination in gap and under canopy after six months ($P > 0.05$).

In 12 of the species studied (e.g., *Escallonia rubra*, *Gaultheria mucronata*, *Myrteola nummularia*, *Rhaphithamnus spinosus*), seed germination was delayed for between one and three months (Figure 3). On the other hand, in seven species (*Lomatia ferruginea*, *Myrceugenia exsucca*, *M. ovata* var. *nannophylla*, *M. ovata* var. *ovata*, *M. parvifolia*, *M. planipes*, *Ugni candollei*), most of the seeds sown in the gap germinated during the second month. By the end of the first month, percentage germination, both in the gap and under the canopy, was high ($>50\%$) in all species within the genus *Myrceugenia* (Figure 3).

DISCUSSION

Gap vs. understory microenvironment

Results of temperature and light measures in gap vs. understory confirmed the thermal insulation effect of tree canopies, an effect that was accentuated during summer (Vázquez-Yanes et al. 1990). The measurements of PPFD ratified that the light environment of the understory and canopy gap sites selected for this study were significantly different. In effect, light measurements taken within this forest with two LAI 2000 Canopy Analyzers indicated that light penetration in this canopy gap and under the canopy was 34 and 1% of the total light received in an open site, respectively (Figuroa & Lusk, pers. obs.). The described differences in temperature (during spring) and PPFD (during winter and spring) between the canopy gap and the understory strongly suggest that the differences in germination could be associated with the microenvironmental conditions in each site (Vázquez-Yanes et al. 1990). Although we were not able to register temporal and spatial variations in microclimatic conditions in the gap and the understory with enough detail with the meth-

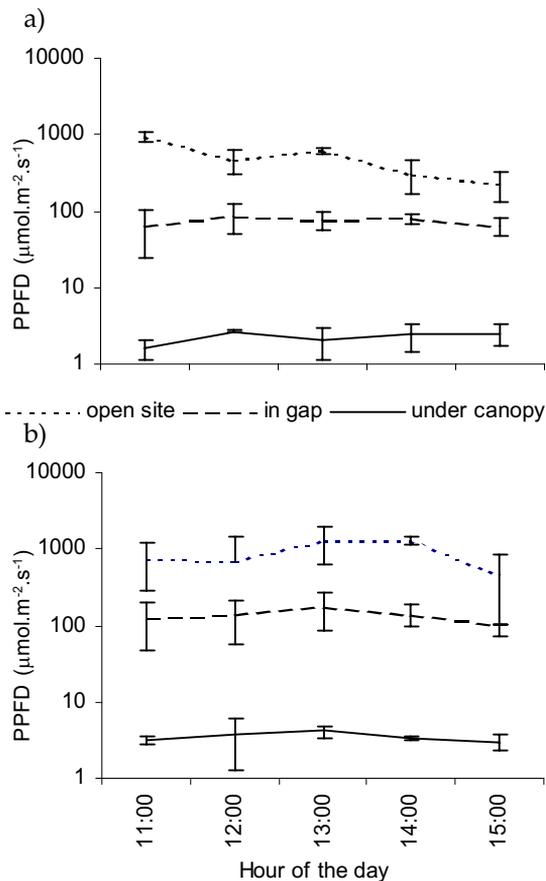


Figure 2. Mean (\pm SD) photosynthetic photon flux density (PPFD) recorded hourly over a three-day period during (a) winter and (b) spring, at an open habitat (outside the forest), in a canopy gap, and under the canopy of a secondary forest in Chiloé.

Figura 2. Densidad promedio (\pm DE) de flujo de fotones fotosintéticos (PPFD) registrada cada hora durante tres días en (a) invierno y (b) primavera, en un hábitat abierto (fuera del bosque), en un claro y bajo el dosel de un bosque secundario en Chiloé.

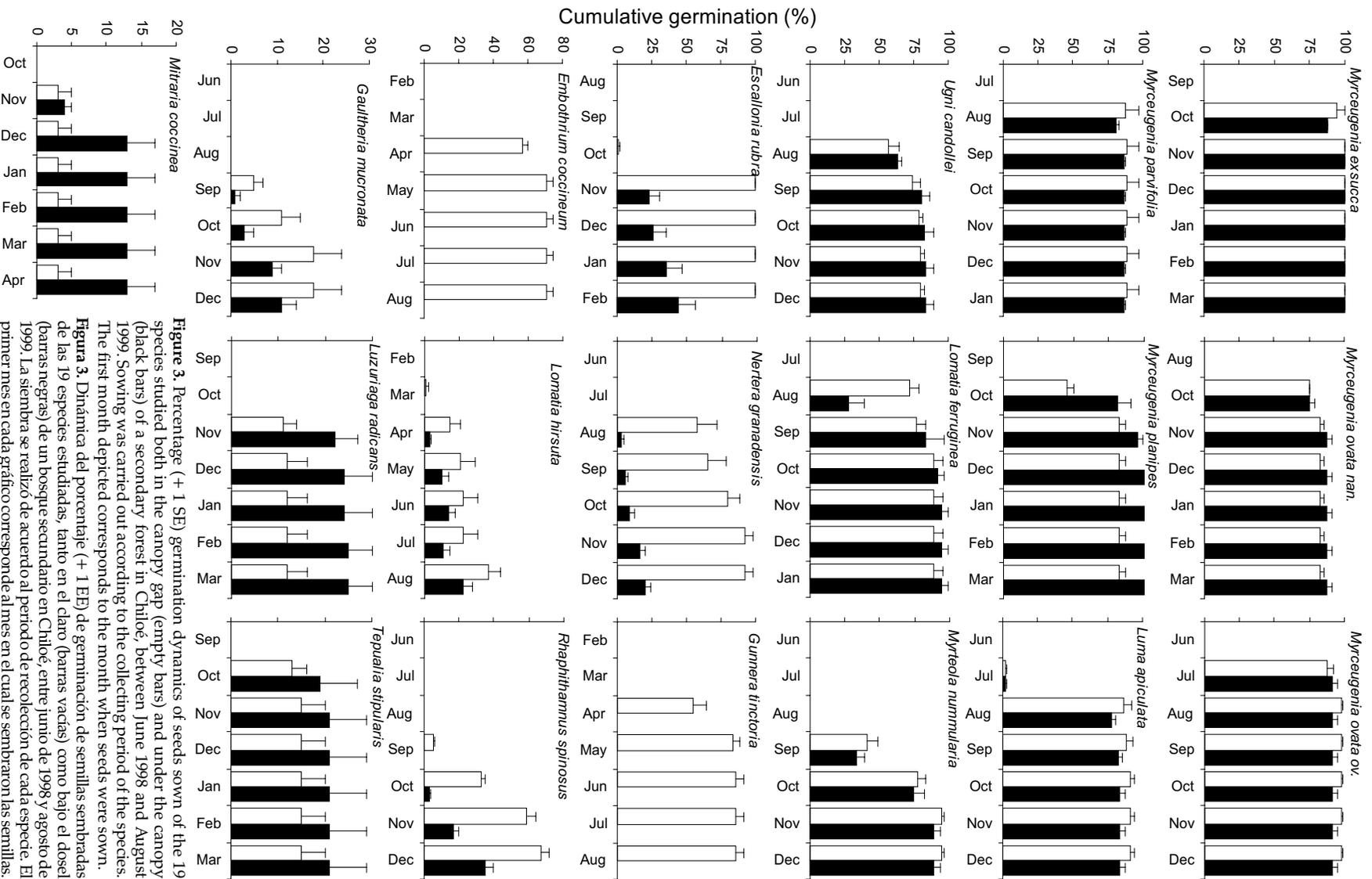


Figure 3. Percentage (+ 1 SE) germination dynamics of seeds sown of the 19 species studied both in the canopy gap (empty bars) and under the canopy (black bars) of a secondary forest in Chile, between June 1998 and August 1999. Sowing was carried out according to the collecting period of the species. The first month depicted corresponds to the month when seeds were sown.

Figura 3. Dinámica del porcentaje (+ 1 SE) de germinación de semillas sembradas de las 19 especies estudiadas, tanto en el claro (barras vacías) como bajo el dosel (barras negras) de un bosque secundario en Chile, entre junio de 1998 y agosto de 1999. La siembra se realizó de acuerdo al periodo de recolección de cada especie. El primer mes en cada gráfico corresponde al mes en el cual se sembraron las semillas.

ods we used in this study, we could nevertheless still demonstrate that there were noticeable differences between the two habitats in terms of PPFD. However, there might be differences in other factors (e.g., light quality, humidity) that, because of the lack of proper instruments, were not measured (see Vázquez-Yanes et al. 1990).

Gap vs. shading effects on germination

Our results strongly suggest that the association between the habitats where seedlings of these plant species are growing and their germination requirements is weak. We expected to find seed germination of species regenerating in forest edges to be somewhat inhibited under the darker forest understory conditions. However, germination of only five edge species, consisting of one tree, two shrubs, and two herbs, was significantly greater within the gap habitat. Only one tree species, *Embothrium coccineum* failed completely under the canopy, being analogous to pioneer trees that require open sites for explosive germination and fast growth of their seedlings (Vázquez-Yanes & Smith 1982; Washitani & Takenaka 1987; Raich & Khoon 1990). In contrast, germination in the other edge tree species (*Lomatia ferruginea*, *Lomatia hirsuta*, *Luma apiculata*, and *Myrceugenia exsucca*) was not inhibited under the canopy even though these species do not normally grow within this darker habitat.

Germination success of the shrub species *Escallonia rubra* and *Rhaphithamnus spinosus*, which are common in forest edges, was twice as high within the canopy gap than under the canopy. However, out of the eight shrub species assayed in this study, these were the only two in which germination was inhibited by the understory conditions. These observations contrast with the general scarcity of shrubs under the forest canopy in Chiloé forests; instead, shrubs grow mostly in abandoned fields and forest edges (Donoso et al. 1984; Donoso et al. 1985; Armesto & Figueroa 1987). Lack of seed dispersal does not seem responsible: 70% of the woody species of Chiloé are dispersed by birds (Armesto & Rozzi 1989), and birds are known to disperse tree seeds in gaps and forest interior with similar frequency (I. Díaz, pers. comm.). Therefore, it is likely that the scarcity of shrubs in understory habitats re-

sults from a low survival of shrub seedlings rather than from germination limitations within the understory.

Nertera granadensis and *Gunnera tinctoria* are two common non-woody herb species of edge sites in the forest. Both showed low or nil germination success (<23%) under the canopy and high percentages in the gap (>86%). Germination of both species has been shown to be inhibited by darkness (Willson et al. 1996; Figueroa, pers. obs.). Based on our previous results, we suggest that both species may present photoblastic dormancy (Borthwick et al. 1952). However, this should be corroborated by further studies.

Only one forest interior species showed significantly greater germination under the canopy and none of the four interior species studied showed significantly greater germination within the gap. Even in the two vine species, *Luzuriaga radicans* and *Mitraria coccinea*, germination was low both within the forest gap and the understory habitat. Seeds of *L. radicans* likely lose viability through dehydration when they remain in the soil for several months, given their high water content (Figueroa, pers. obs.). Furthermore, recruitment of vines in tropical forests has been proposed to be mainly vegetative (Peñaloza 1985). Hence, there is no evidence for specific germination requirements in these vines, let alone a role for such requirements in determining vine distribution. In contrast, germination of the two forest interior tree species studied here, *Myrceugenia planipes* and *M. ovata* var. *ovata*, was high, both in the gap and under the canopy (>82%). This result is consistent with the great abundance of seedlings of these two species commonly found in the understory (Armesto & Figueroa 1987; Armesto & Fuentes 1988). However, the high germination success of these species in the gap is not consistent with the scarce establishment of these trees in open sites. We suggest that seedling survival and establishment of these two tree species is restricted to the understory. Drought is probably an important cause of seedling mortality in the gap. During the summer of 1999, all *M. planipes* seedlings were found to die within the first year of life, likely due to severe dehydration, when the seedlings were exposed to gap conditions (Figueroa, pers. obs.). The summer season in Chiloé can be considered a

population bottleneck for the survival of tree seedlings within the understory (Figueroa & Castro 2000), and probably even more so in natural treefall gaps.

Our field germination data for trees and shrubs in Chiloé argue against the idea of a strong dichotomy in germination success under gap vs. non-gap conditions consistent with the common seedling habitat. Other investigations have also questioned the existence of this dichotomy (Raich & Khoon 1990; Kyereh et al. 1999), that had been previously proposed for tropical species (Whitmore 1975; Denslow 1987; Swaine & Whitmore 1988).

We suggest that many of the edge trees and shrubs are absent under the canopy because they cannot survive in the forest shade. This situation can be due in part to greater light requirements for photosynthesis in this species, and not solely because they do not germinate or have a lower germination success within the forest interior. Moreover, tradeoffs between light and nutrient requirements of plants (Lusk et al. 1997), and differential seed predation between light gaps, forest edges and understory environments (Díaz et al. 1999) may also be considered as other factors determining seedling and adult establishment patterns.

We conclude that in southern Chile temperate forest species, germination requirements do not underlie a dichotomy of habitat. This conclusion should be corroborated in studies that consider environmental variation through a gradient of gap sizes, the heterogeneity of conditions present in the understory, and the quality of the light reaching the soil (see Vázquez-Yanes & Orozco-Segovia 1990a).

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REFERENCES

- ARMESTO, JJ & J FIGUEROA. 1987. Stand structure and dynamics in the temperate rain forest of Chiloé Archipelago, Chile. *J. Biogeogr.* **14**:367–376.
- ARMESTO, JJ & ER FUENTES. 1988. Tree species regeneration in a mid-elevation, temperate rainforest in Isla de Chiloé, Chile. *Vegetatio* **74**:151–159.
- ARMESTO, JJ & R ROZZI. 1989. Seed dispersal syndromes in the rain forest of Chiloé: evidence for the importance of biotic dispersion in a temperate rainforest. *J. Biogeogr.* **16**:219–226.
- BAZZAZ, FA & STA PICKETT. 1980. Physiological ecology of tropical succession: a comparative review. *Ann. Rev. Ecol. Syst.* **11**:287–310.
- BORTHWICK, HA; SB HENDRICKS; EH TOOLE & VK TOOLE. 1952. A reversible photoreaction controlling seed germination. *P. Natl. Acad. Sci. USA* **38**:662–666.
- BUSTAMANTE, RO & JJ ARMESTO. 1995. Regeneration dynamics in canopy gaps of a montane forest of Chiloé Island, Chile. *Rev. Chil. Hist. Nat.* **68**:391–398.
- DI CASTRI, F & ER HAYEK. 1976. *Bioclimatología de Chile*. Editorial Pontificia Universidad Católica de Chile.
- COLLINS, BS & STA PICKETT. 1987. Influence of canopy opening on the environment and herb layer in a northern hardwood forest. *Vegetatio* **70**:3–10.
- DENSLow, JS. 1980. Gap partitioning among tropical rain forest trees. *Biotropica* **12**(supp.):47–55.
- DENSLow, JS. 1987. Tropical rainforest gaps and tree species diversity. *Ann. Rev. Ecol. Syst.* **18**:431–451.
- DÍAZ, I; C PAPIĆ & JJ ARMESTO. 1999. An assessment of post-dispersal seed predation in temperate rain forest fragments in Chiloé Island, Chile. *Oikos* **87**:228–238.
- DONOSO, C; B ESCOBAR & J URRUTIA. 1985. Estructuras y estrategias regenerativas de un bosque virgen de Ulmo (*Eucryphia cordifolia* Cav)-Tepa (*Laurelia philippiana* Phil. Looser) en Chiloé, Chile. *Rev. Chil. Hist. Nat.* **58**:171–186.
- DONOSO, C; R GREZ; B ESCOBAR & P REAL. 1984. Estructura y dinámica de bosques de tipo forestal siempre verde de un sector de Chiloé insular. *Bosque* **5**:82–104.
- FIGUEROA, JA. 1997. *Patrones de evaluación del tiempo de germinación: evaluación de condicionantes filogenéticas, biogeográficas, estructurales y ecológicas*. Doctoral thesis, Facultad de Ciencias, Universidad de Chile, Chile.
- FIGUEROA, J; JJ ARMESTO & JF HERNÁNDEZ. 1996. Estrategias de germinación y latencia de semillas en especies del bosque templado de Chiloé, Chile. *Rev. Chil. Hist. Nat.* **69**:243–251.
- FIGUEROA, JA & S CASTRO. 2000. Effect of herbivores and pathogens on the survival and growth of seedlings in a fragment of the Chiloé rainforest, Chile. *Rev. Chil. Hist. Nat.* **73**:163–173.

- GAJARDO, R. 1994. *La vegetación natural de Chile. Clasificación y distribución geográfica*. Editorial Universitaria. Santiago, Chile.
- GOLDBERG, DE & PA WERNER. 1983. The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrod (*Solidago* spp.). *Oecologia* **60**:149–155.
- GRUBB, PJ & TC WHITMORE. 1966. A comparison of montane and lowland rain forest in Ecuador. II. The climate and its effects on the distribution and physiognomy of the forest. *J. Ecol.* **54**:303–333.
- KYEREH, B; MD SWAINE & J THOMPSON. 1999. Effect of light on the germination of forest trees in Ghana. *J. Ecol.* **87**:772–783.
- LEE, DW. 1987. The spectral distribution of radiation in two Neotropical rainforests. *Biotropica* **19**:161–166.
- LUSK, CH; O CONTRERAS & J FIGUEROA. 1997. Growth, biomass allocation and plant nitrogen concentration in Chilean temperate rainforest tree seedlings: effects of nutrient availability. *Oecologia* **109**:49–58.
- NAKASHIZUKA, T. 1985. Diffused light conditions in canopy gaps in a beech (*Fagus crenata* Blume) forest. *Oecologia* **66**:472–474.
- PEÑALOZA, J. 1985. Dinámica de crecimiento de lianas. Pp. 147–169 in: A Gómez-Pompa & S del Amo (eds). *Investigaciones sobre la regeneración de selvas altas en Veracruz, México. II*. Editorial Alhambra. México DF, Mexico.
- RAICH, JW & GW KHOON. 1990. Effects of canopy openings on tree seed germination in a Malaysian dipterocarp forest. *J. Trop. Ecol.* **6**:203–217.
- SMITH-RAMÍREZ, C & JJ ARMESTO. 1994. Flowering and fruiting patterns in the temperate rainforest of Chiloé, Chile: ecological and climatic constraints. *J. Ecol.* **82**:353–365.
- SMITH-RAMÍREZ, C; JJ ARMESTO & J FIGUEROA. 1998. Flowering, fruiting and seed germination in Chilean rain forest myrtaceae: ecological and phylogenetic constraints. *Plant Ecol.* **136**:119–131.
- SWAINE, MD & TC WHITMORE. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* **75**:81–86.
- VÁZQUEZ-YANES, C & S GUEVARA-SADA. 1985. Caracterización de los grupos ecológicos de árboles de la selva húmeda. Pp. 67–78 in: A Gómez-Pompa & S del Amo (eds). *Investigaciones sobre la regeneración de selvas altas en Veracruz, México. II*. Editorial Alhambra. México DF, Mexico.
- VÁZQUEZ-YANES, C & A OROZCO-SEGOVIA. 1990a. Ecological significance of light controlled seed germination in two contrasting tropical habitats. *Oecologia* **83**:171–175.
- VÁZQUEZ-YANES, C & A OROZCO-SEGOVIA. 1990b. Seed dormancy in the tropical rain forest. Pp. 247–590 in: KS Bawa & M Hadley (eds). *Reproductive biology of tropical plants*. Vol. 7. Man and the Biosphere Series, Unesco (Paris, France) and Parthenon Publishing (Carnforth, Lancaster).
- VÁZQUEZ-YANES, C; A OROZCO-SEGOVIA; E RINCÓN; ME SANCHEZ-CORONADO; P HUANTE ET AL. 1990. Light beneath the litter in a tropical forest: effect on seed germination. *Ecology* **71**:1952–1958.
- VÁZQUEZ-YANES, C & H SMITH. 1982. Phytochrome control of seed germination in the tropical rain forest pioneer trees *Cecropia obtusifolia* and *Piper auritum* and its ecological significance. *New Phytol.* **92**:477–485.
- VEBLEN, TT. 1982. Regeneration patterns in *Araucaria araucana* forest in Chile. *J. Biogeogr.* **9**:11–28.
- VEBLEN, TT. 1989. Tree regeneration responses to gaps along a transandean gradient. *Ecology* **70**:541–543.
- VEBLEN, TT; C DONOSO; FM SCHLEGEL & BR ESCOBAR. 1981. Forest dynamics in south-central Chile. *J. Biogeogr.* **8**:211–247.
- WASHITANI, I & A TAKENAKA. 1987. Gap-detecting mechanism in the seed germination of *Mallotus japonicus* (Thunb.) Muell. Arg., a common pioneer tree of secondary succession in temperate Japan. *Ecol. Res.* **2**:191–201.
- WHITMORE, TC. 1975. *Tropical rain forests of the Far East*. Oxford Clarendon Press. London, UK.
- WILLSON, MF; C SABAG; J FIGUEROA; JJ ARMESTO & M CAVIEDES. 1996. Seed dispersal by lizard in Chilean rainforest. *Rev. Chil. Hist. Nat.* **69**:339–342.
- WILSON, JW. 1965. Stand structure and light penetration. *J. Appl. Ecol.* **2**:383–390.