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Facilitation of *Nothofagus antarctica* (Fagaceae) seedlings by the prostrate shrub *Empetrum rubrum* (Empetraceae) on glacial moraines in Patagonia

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Abstract: Although positive interactions among plants are believed to be common in primary succession, they have rarely been demonstrated on glacial moraines. In Patagonia, the prostrate shrub *Empetrum rubrum* is dominant in early succession in recently deglaciated valleys, eventually being replaced by the small tree *Nothofagus antarctica*. This study experimentally evaluates the effects of *E. rubrum* shrubs on density, biomass, growth and survival of *N. antarctica* seedlings. The initial density of the seedlings was significantly higher under the canopy of *Empetrum* than in open areas. A removal experiment was performed to evaluate the influence of *Empetrum* on survival and growth of seedlings that germinated naturally beneath the canopy of this species. The shrub cover was removed from half of a sample of randomly selected seedlings, and left intact above the remainder. One year later, seedlings with an intact cover of *E. rubrum* showed significantly higher survival, growth and leaf number than seedlings which had been exposed. The results suggest that the presence of *E. rubrum* facilitates the establishment of *N. antarctica* in post-glacial succession, mainly as a result of more favourable microclimatic conditions under the shrub canopy.

Key words: nurse plant, positive interactions, primary succession.

INTRODUCTION

Facilitation has been postulated as the main mechanism of primary succession in harsh terrestrial environments (Connell & Slatyer 1977; Tilman 1985; Callaway 1995), such as recently deglaciated areas. Pioneer species in these initially inhospitable environments may facilitate entry of other plants by buffering extreme temperatures, or increasing moisture and/or nutrient availability through their effects on soil development (Viereck 1966; Birks 1980; Walker & Chapin 1986; Walker 1991). However, few studies have experimentally demonstrated facilitation in post-glacial succession, and fewer still have identified the underlying mechanisms (Lawrence *et al.* 1967; Chapin *et al.* 1994; Jumpponen *et al.* 1998).

Although post-glacial successional seres in Patagonia have been described (Pisano 1978; Veblen *et al.* 1989; Dollenz 1991; Armesto *et al.* 1992), there has been no work on the underlying successional mechanisms. Intermoraines area in Patagonia are often colonized by the prostrate shrub *Empetrum rubrum* and the small tree *Nothofagus antarctica* (Heusser 1964; Pisano 1977; Henríquez 2002), two very cold-tolerant species of broad ecological amplitude (Weinberger 1973; Anchoreta 1985). The dynamics of interactions between these two species have not been clarified. Pisano (1977) has described the apparent invasion of *Empetrum* thickets by the later successional tree species *N. antarctica* and *Nothofagus pumilio*. On intermoraines at the Nueva Zelandia Glacier on Tierra del Fuego, seedling of *N. antarctica* are common under *E. rubrum* cover (J. M. Henríquez, pers. obs. 2001), possibly indicating that the presence of *E. rubrum* has a positive effect on establishment of *N. antarctica* in the early stages of succession.

We addressed two questions: (i) Does the presence of an *E. rubrum* cover facilitate establishment of *N. antarctica* seedlings? (ii) What are the mechanism by which *E. rubrum* influence seedling establishment? In order to do so, we compared natural abundance of *N. antarctica* seedlings within and outside patches of *E. rubrum*, and examined the effects of experimental removal of the shrub canopy on seedling growth and survival.

METHODS

Study area

Nueva Zelandia glacier (54°42′S–69°21′W) is located in Parry fjord, on Tierra del Fuego Island, Chile. The

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Fig. 1. General view of the study area: (a) Front view of the Nueva Zelandia glacier; (b) Inter-arc area of in-transit moraine dominated by *Empetrum rubrum*.

glacial area has a lake and three frontal moraine arcs. The study was carried out in a flat intermoraine area with free drainage, between the 2nd and 3rd frontal moraines, on sites where the plant cover is >95% (Fig. 1). The substrate is composed of silty sand, with frequent gravel and occasional boulders. *Empetrum rubrum* is the dominant vascular plant species on the study site, covering nearly 85% of the ground with thickets up to 20 cm tall. Other less common plants include the subshrub *Baccharis nivalis*, the perennial herb *Gunnera magellanica*, the small tree *Nothofagus antarctica*, and several species of perennial grasses and mosses.

Seedling density

A stratified random design was used to sample seedling density of *N. antarctica* in an area (100×15 m^2) with a patchy cover of *E. rubrum,* with a total of 40×1 m^2 quadrats. Twenty quadrats were randomly located on surfaces with shrub cover, and the other 20 on sites free of cover. The number of *N. antarctica* germinants was counted in each quadrat at the end of January 2000.

Survival and growth

A 10×10 m^2 plot was established in January 2000, within an area with a dense cover of *E. rubrum*. Cover of *E. rubrum* was estimated from 300 points placed randomly on line transects within the plot. The species was present at 268 of these points, indicating a cover of >89%. The plot was subdivided in 100×1 m^2 quadrats, and 60 of these were chosen at random, with the requirement that at least one germinant of *N. antarctica* was present. Quadrats without plants were replaced. Germinants were recognized by the presence of green cotyledons, which do not persist more than one growing season (J. M. Henríquez; pers. obs. 2001). One randomly chosen germinant per quadrat was marked, its height measured and its leaves counted. Any other seedlings present in the quadrat were removed, in order to eliminate potential effects of competition among seedlings. The same day, the cover of *E. rubrum* overtopping seedlings was removed from 30 randomly chosen quadrats, clearing a 10-cm radius around each germinant. Cover was left intact over the other 30 quadrats. Survival was registered after 1 year, and number of leaves and height measured. Survival of these 60 seedlings (with and without removal of *E. rubrum*) was compared with that of 30 seedlings of *N. antarctica* germinated in open areas outside the plot, randomly selected and marked in February 2000.

Microhabitat

The effect of *E. rubrum* on microclimate and microsite conditions was quantified by measuring temperature at ground level and selected soil variables. Temperature at ground level was measured with two automatic temperature recorders Minilog TR (Vemco Limited, Shad Bay, Canada) with a range of −30° to +40°C, which were programmed to take 16 temperature measurements each day. One temperature recorder was set up under the cover of *E. rubrum*, and the other was installed on a surface lacking plant cover. Both recorders were installed for 12 months, at 2 cm above the ground. We estimated the following temperature values for both summer (1 December–31 March) and winter (15 May–15 September) seasons: the overall average temperature (M), the average of daily maximum (MaA), the average daily minimum (MiA), and the average daily thermal oscillations (MaA-MiA).

Soil samples were taken from the uppermost 5 cm at three randomly chosen points in each of the three study situations: (i) open areas; (ii) sites with experimental removal of *E. rubrum* cover; and (iii) sites with intact cover of *E. rubrum*. Roots were extracted from soil samples. Soil was dried at room temperature and analysed for pH (ISO 1994), extractable N (Robarge *et al.* 1983), extractable P (Norma Chilena 1999), total P and N (Longeri *et al.* 1979), and organic matter (Schulte 1995), at the Laboratorio de Análisis de Suelos y Plantas, Universidad de Concepción.

Statistical analyses

Non-parametric Kruskall-Wallis ANOVAS were used to analyse growth and soil parameter data, due to their depent from normal distributions. Survival of seedlings in the three conditions (with and without removal of *Empetrum*, and open sites) was compared by randomization, using Resampling Stats software.

RESULTS

Density of *N. antarctica*

Average seedling density of *N. antarctica* under the cover of *Empetrum rubrum* was significantly higher ($4.7\ m^{-2} \pm$ SE1.0) than in open areas ($0.6 \pm 0.2\ m^{-2}$) ($F = 7.4$, $P < 0.001$ one-way ANOVA).

Survival, biomass and growth of *N. antarctica* seedlings

Seedlings of *Nothofagus antarctica* growing under the cover of *E. rubrum* showed significantly higher survival, leaf number and increase in height than those where the cover of *E. rubrum* were removed (Table 1). Ninety per cent of seedlings under the cover of *E. rubrum* survived, compared with 40% where *E. rubrum* was removed and 13% in the open area. All dead seedlings were located at the end of the study – none disappeared. Randomization tests showed that survival differed significantly among all three conditions ($P < 0.001$). Seedlings with an intact cover of *E. rubrum* increased in height more during the year, compared with the seedlings subject to removal of *E. rubrum* and the seedlings in open area (Table 1). Furthermore, seedlings whose cover was removed showed an average net decrease in leaf number during the 12-month study whereas those with cover the *E. rubrum* and seedling in open area increased their number of leaves.

Microhabitat

Soil temperature regimes were influenced by the shrub cover (Table 2). In winter these differences were low, although subzero daily mean temperatures were slightly less common under intact *E. rubrum* (117 days per year) than in the open (117 days). However, during summer time the plants in the open were exposed to higher maxima and wider daily temperature oscillations, as mean daily temperatures below 0° occurred on 117 days under the shrub canopy, compared to 128 days in the open.

All the nutrients measured in the soil samples had higher availability under the cover of *E. rubrum* than in open areas (Table 3). Soil pH was lower under *Empetrum* than in the open areas.

Table 1. Kruskal–Wallis ANOVA showing the effect of the *Empetrum rubrum* cover on height and mean number of leaves (±SD) of *Nothofagus antarctica* seedlings

Parameters	With cover	Without cover	Open area	*P*
Height growth	1.03 ± 0.47	0.62 ± 0.51	0.35 ± 0.19	0.0165
Number of leaves	1.26 ± 1.72	–0.67 ± 0.78	0.25 ± 0.96	0.0017

Table 2. Temperatures (°C) at 2 cm above ground under the canopy of *Empetrum rubrum*, and outside

	With shrub cover				Without shrub cover			
	M	MaA	MiA	Δ(T)	M	MaA	MiA	Δ(T)
Summer	9.2	18.2*	4.6*	13.6*	9.9	21.5*	3.2*	18.3*
Winter	–0.1*	0*	–0.1*	0.1	–0.3*	–0.2*	–0.3*	0.1

Asterisks indicate significant differences between the two microenvironments, $P < 0.05$ (one-way Anova).
M, temperature; MaA, absolute maximum temperature; MiA, absolute minimum temperature; Δ(T), (MaA–MiA).

Table 3. Soil parameters measured at sites with and without covering of *Empetrum rubrum* (means ± SD), with *P*-values for Kruskal–Wallis ANOVA

Soil parameters	Open area	With cover	Without cover	*P*
Available N (mg kg^{-1})	0.5 ± 0.01	6.8 ± 0.5	5.7 ± 0.6	0.028
P Olsen (mg kg^{-1})	2.5 ± 0.05	34.2 ± 0.6	28.6 ± 0.5	0.027
pH in water	5.3 ± 0.03	4.1 ± 0.2	4.6 ± 0.06	0.026
Organic matter (%)	1.01 ± 0.02	74.4 ± 5.8	55.6 ± 3.4	0.027
N Total (%)	0.1 ± 0.01	0.3 ± 0.02	0.27 ± 0.02	0.024
Retention of water (%)	10.8 ± 1.4	38.4 ± 5.2	36.7 ± 0.7	0.061

DISCUSSION

Our results support the hypothesis that the *E. rubrum* cover facilitates establishment of *N. antarctica* on the glacial moraine. The higher densities of *N. antarctica* seedlings under the cover of *Empetrum rubrum* can be attributed, at least in part, to higher survival there than in open areas (Table 1). However, we cannot rule out the possibility that differences in seedling density might also reflect higher germination under *E. rubrum*, and/or trapping of wind-dispersed *N. antarctica* seeds by the shrub cover (cf. Bullock & Moy 2004).

The greater growth of seedlings under the cover of *E. rubrum* (Table 1) suggests that the observed differences in survival are a function of differences in carbon balance. Intraspecific variation in growth is a good predictor of survival probability in juvenile trees subject to different levels of resource availability (Kobe *et al.* 1995; Walters & Reich 1996). The protection afforded by the cover of *E. rubrum* could therefore permit greater net carbon gain in seedlings, by ameliorating the effects of stresses such as moisture deficit (Vetaas 1992; Ryser 1993; Belsky 1994) and photoinhibition (Singla *et al.* 1997; Brittingham & Walker 2000; Walker *et al.* 2001; Holl 2002).

Survival differences between protected and open sites were not caused by herbivores. Some examples of facilitation in other ecosystems have been attributed to protection from vertebrate herbivores (Callaway 1995; Rousset & Lepart 1999). However, all dead seedlings remained at the site until the end of our study, showing that herbivores did not remove plants.

The temperature data (Table 2) suggest that the greater growth and survival of *N. antarctica* under the cover of *E. rubrum* could be linked to more favourable microclimate conditions. The lower maximum temperatures and narrower thermal range under the shrub canopy in summer, plus slightly lesser exposure to subzero temperatures in winter, suggest that *E. rubrum* confers some degree of protection from extremes of temperature, which are invariably more damaging to seedlings than to adult plants (Cook 1979; Shibata & Nakashizuka 1995).

Enhanced survival of seedlings of *N. antarctica* beneath *E. rubrum* may also reflect increased belowground resource availability (Table 3). Substrate conditions are an important factor restricting the establishment of plants in glacial environments (Matthews 1992). Survival of *N. antarctica* was significantly lower on open sites than in quadrats subjected to removal of *E. rubrum* cover (Table 1), where soil characteristics were very similar to those found under the intact canopy of *E. rubrum* (Table 3). The higher levels of nitrogen, phosphorus, organic matter and water on sites recently or currently occupied by *E. rubrum* suggest the facilitation of *N. antarctica* by the shrub cover is at least partly attributable to effects on soil resource availability. Several previous studies have shown that pioneer plants in primary successions increase soil organic matter and mineral nutrient availability to later-establishing plants (Walker & Chapin 1986; Blundon *et al.* 1993; Chapin *et al.* 1994).

In conclusion, our data suggest that the canopy of *Empetrum rubrum* has an important nurse effect in the early stages of succession on glacial moraines, by influencing microclimate and/or soil resource availability. Interestingly, another species of the same genus *Empetrum hermafroditum* appears to facilitate development of *Carex bigelowii* in the alpine/subarctic tundra of Swedish Lapland (Carlson & Callaghan 1991).

Mechanisms of successional changes have remained a topic of discussion throughout recent decades (Connell & Slatyer 1977; McIntosh 1981; Finegan 1984; Connell *et al.* 1987; Pickett *et al.* 1987; Walker & Chapin 1987). Facilitation has been proposed as the dominant mechanism of succession in harsh environments and in the early stages of primary succession, such as on glacial moraines and in high mountain environments (Walker & Chapin 1987; Matthews 1992; Bertness & Callaway 1994), where temperature extremes, low levels of soil resources and substrate instability pose many problems for seedlings. Our results are consistent with this proposal, in showing strong positive effects of a pioneer shrub on growth and survival of a longer-lived tree species that persists into later successional stages of post-glacial succession.

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