Nurse effect in seedling establishment: facilitation and tolerance to damage in the Andes of central Chile

Efecto nodriza en el establecimiento de plántulas: facilitación y tolerancia al daño en los Andes de Chile central

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ABSTRACT

Nurse effects, which occur when one plant species enhances the survival or growth of another plant species, are predicted to be most relevant in stressful environments. These effects are particulary important during seedling establishment due to their vulnerability to both biotic and abiotic factors, such as herbivory and drought. Tolerance to herbivory reflects the degree to which plants are able to regrow and reproduce after damage, and should vary with resource availability. In the high Andes of central Chile, the cushion plant *Laretia acaulis* (Apiaceae) acts as a buffer against environmental stress, enhancing survival of several associated plant species. We hypothesized that tolerance to herbivory of seedlings growing inside the canopy of *L. acaulis* should be greater than that of seedlings growing outside the cushion plant. We conducted a field experiment to test this hypothesis for two native perennial species in the high Andes of central Chile: *Hordeum comosum* (Poaceae) and *Haplopappus anthylloides* (Asteraceae). Seedlings of each species were planted inside and outside *L. acaulis* cushions and half of them received manual damage (50 % foliar tissue removed). Seedlings growing inside the nurse species showed high survival independent of the damage treatment. Whereas position (inside or outside the cushion plant) did not affect tolerance of *Haplopappus anthylloides*, it significantly affected tolerance of *Hordeum comosum*. Thus, we found similar survival of damaged and control seedlings of *H. comosum* inside the cushions, but survival of damaged seedlings in the bare ground was lower than that of control seedlings. We verified the occurrence of nurse effects of *Laretia acaulis* on the establishment of both species, and detected enhancement of tolerance to damage in *Hordeum comosum* in this stressful habitat.

Key words: facilitation, *Laretia acaulis*, herbivory, tolerance, nurse effect.

RESUMEN

Se ha sugerido que el efecto nodriza, el cual se evidencia cuando una especie vegetal incrementa la supervivencia o el crecimiento de otra, es más relevante en ambientes estresantes. Este efecto sería particularmente importante durante el periodo de establecimiento de las plántulas debido a su alta vulnerabilidad a factores bióticos y abióticos como herbivoría y desecación. La tolerancia a la herbivoría evidencia la capacidad de las plantas de recrecer y reproducirse después del daño, pero esta capacidad es recurso-dependiente. En los Andes de Chile central, la planta en cojín *Laretia acaulis* (Apiaceae) atenúa el efecto del estrés ambiental, aumentando la supervivencia de diversas especies de plantas asociadas. Proponemos que las plántulas que se encuentren creciendo dentro de los cojines de *L. acaulis* deberían evidenciar niveles mayores de tolerancia en relación a aquellas plántulas creciendo fuera de los cojines. Para probar esta hipótesis se llevó a cabo un experimento de campo con dos especies nativas perennes: *Hordeum comosum* (Poaceae) y *Haplopappus anthylloides* (Asteraceae). Plántulas de ambas especies fueron sembradas dentro y fuera de los cojines de *L. acaulis*, y la mitad de ellas recibieron daño manual (50 % tejido foliar removido). En general, las plántulas que se encontraron creciendo dentro del cojín evidenciaron una mayor supervivencia independientemente del tratamiento de daño. A pesar de que la ubicación de las plántulas no afectó la respuesta en tolerancia por parte de *H. anthylloides*, sí afectó significativamente la tolerancia de *H. comosum*. Por lo tanto, encontramos valores similares para la supervivencia de plántulas de *H. comosum* dentro de los cojines, pero la supervivencia de plántulas dañadas fuera de los cojines fue significativamente menor que la de plántulas control. Se pudo evidenciar la ocurrencia de efecto nodriza por parte de *L. acaulis* sobre el establecimiento de ambas especies y conjuntamente un aumento en la tolerancia al daño para *H. comosum* en este hábitat estresante.

Palabras clave: facilitación, herbivoría, tolerancia, *Laretia acaulis,* efecto nodriza.

INTRODUCTION

Positive interactions among plants occur when one plant species enhances the survival, growth or reproduction of another plant species (Callaway 1995, Callaway & Pugnaire 1999). These interactions have received special attention in recent years (Bruno et al. 2003, Lortie et al. 2004) and have been reported in several ecosystems (Callaway 1995, Callaway & Pugnaire 1999, Rand 2004), although they are particularly frequent in stressful habitats (Bertness & Callaway 1994, Callaway & Walker 1997, Brooker & Callaghan 1998). Positive interactions can occur through different mechanisms, involving both environmental conditions and biological interactions (Callaway 1995), and their magnitude varies through time and space (Choler et al. 2001, Pugnaire & Luque 2001, Callaway et al. 2002, Maestre et al. 2003). Nurse effect is a particular kind of positive interaction where one species (the nurse) provides microclimatic conditions that enhance the establishment of other (beneficiary) species (Franco & Nobel 1988, 1989). Because of the high vulnerability of seedlings to stressful conditions (Ibáñez & Shupp 2001), the nurse species may enhance seedling establishment via stress amelioration, which can be understood as an improvement of the environmental conditions experienced by the seedlings. This improvement can be achieved by the interaction of two mechanisms: the attenuation of some negative environmental factors such as herbivory, extreme temperatures or high solar irradiation, or by the increase of resource availability beneath the nurse species (Callaway 1995, Shumway 2000, Gómez-Aparicio et al. 2004).

Several studies have demonstrated the negative effect of herbivory on plant fitness (Strauss 1991, Hulme 1996, Harms & Dalling 1997, Thompson et al. 2003). Consequently, any interaction between plant species that minimizes the negative effects of herbivory, at least for one species, will fall into the definition of positive interactions (Callaway & Pugnaire 1999). This interaction could act through physical protection from herbivores, or via the enhancement of plant tolerance. Plant tolerance to herbivory has been defined as the ability to reduce the impact of damage on plant fitness (Strauss & Agrawal 1999, Tiffin & Inouye 2000). The maintenance of plant fitness after herbivory implies the enhancement of physiological functions in the remanent tissue (Nabeshima et al. 2001). Tolerance mechanisms include resource reallocation, increased photosynthetic rates, and increased meristem activity (Anderson & Briske 1995, Thompson et al. 2003). Therefore, tolerance to herbivory is a resource-dependent trait (Agrawal et al. 1999). Given that nurse species provide less stressful microhabitats inside or beneath their canopy in comparison with the surrounding environment, it is conceivable that this positive interaction may increase tolerance to herbivory.

The high Andes of central Chile are a potentially stressful environment. This ecosystem exhibits harsh winds and low temperatures during most of the year. At 2,800 m the soil is free of snow cover just a few months per year, presents low water availability and nutrient content (Cavieres et al. 1998), and a substantial microclimatic decoupling between bare ground and cushion surfaces (Cavieres et al. 2005). Stress levels in this ecosystem are buffered, at least in part, by the cushion plant *Laretia acaulis* (Cav.) Gill & Hook (Apiaceae). Cavieres et al. (1998, 2006) have proven this for the superficial air and soil temperatures, soil hydric content and soil nutrient concentrations. In this ecosystem, the cushion species *L. acaulis* facilitates the growth of at least nine plant species at the same altitude (Cavieres et al. 2006). These species were more frequently found (in some cases, exclusively) inside the cushion plant than on bare ground away from cushions (Cavieres et al. 2006). On the other hand, grazing by livestock is common during plant growth season in this habitat. The present study evaluates whether positive interactions at the high Andes of central Chile can be mediated by the enhancement of plant tolerance to damage. For this, we conducted a field experiment involving simulated herbivory. The study system was composed of the cushion plant *L. acaulis,* the "nurse species", and two native perennial species: *Hordeum comosum* J. Presl. (Poaceae) and *Haplopappus anthylloides* Meyen & Walp (Asteraceae).

MATERIAL AND METHODS

Study site

This study was carried out at La Parva (33º20'
S, 70º21' W), 70 km E from the city of
Santiago, in central Chile. The study site was
located at 2,800 m of altitude in a SW-facing
slope. Climate is alpine with influence of the
Mediterranean-type climate of lowlands. The
mean annual temperature is 5.4 ºC, with a
summer mean of 10 ºC (Cavieres & Arroyo
1999). Mean annual precipitation is 400-900
mm, mainly occurring during winter, and
showing high interannual fluctuations
(Santibáñez & Uribe 1990). A high proportion
of the precipitations falls as snow usually from
April-May to October-November, and snow
storms may occur even during the normally dry
summer (December-March) (Di Castri & Hajek
1976). According to Cavieres et al. (2000), the
study site belongs to the lower Andean belt,
which is located between 2,600 and 3,400 m of
altitude, showing in this range two dominance
peaks of cushion species. The first peak is
located at 2,700-2,900 m and corresponds to
Laretia cushions. Individual cushions are
randomly distributed and their size ranges from
10 to > 150 cm, being more frequent cushions
above 1 m diameter (Armesto et al. 1980). At
2,800 m *Laretia acaulis* cushions reach a
relative cover of 27.3 % from a total vegetation
cover of 40-50 % (Cavieres et al. 2000). Other
herbaceous species present are: *Senecio
pentaphyllus, Hordeum comosum, Haplopappus
anthylloides,* and *Hypochaeris tenuifolia*
(Cavieres et al. 2000).

Experimental design

To evaluate the effect of *Laretia acaulis*
cushions on the tolerance to damage of *H.
comosum* and *H. anthylloides,* we performed a
field experiment aimed to evaluate seedling
survival during the first growing season, which
has been suggested to be the main bottleneck in
seedling survival in alpine habitats (Forbis
2003). Damage (see below) was applied to
experimental seedlings planted within the
cushion species and on bare ground away from
cushions. Seedlings were obtained from seeds
collected from 120-150 individuals in the study
site during the previous growing season. They
were germinated in laboratory growth chambers
under controlled conditions (22 °C and 16/8 h
photoperiod), and were 2.5 month old at the
planting date. From the total seedling set, we
selected seedlings that had at least two fully
expanded leaves for *Hordeum* and four true
leaves for *Haplopappus* at the planting date. At
the field, we randomly chose eight *Laretia
acaulis* cushions and eight bare ground sites
(paired design) for each target species. All
chosen cushions had a diameter between 1 and
1.5 m. On January 11 2005, 12 seedlings of
each species were planted inside each selected
cushion. Another pool of 12 seedlings of the
same species was planted in each of eight sites
selected on the bare ground next to the cushion,
at a distance greater than 30 cm. Distance
between seedlings at planting was 5 cm, which
has been shown to be enough to minimize at
this stage intra-specific interactions (Cavieres
et al. 2006). For seedlings planted within
cushions, the distance to the cushion edge was
at least 30 cm. Seedling establishment was
supported by daily water addition during the
first four days after planting. All seedling
stands were covered with a 25 x 35 x 25 cm
herbivory exclosure to avoid subsequent
herbivory ("bird cage"; mesh size: 1 cm).
Seedlings that died during the first week were
immediately replaced.

Two weeks after planting (January 26), half
of the seedlings in each pool, both within and
outside cushions, received manual damage. We
cut 50 % of the foliar tissue: half of each leaf
was clipped with scissors along the mid vein.
Thus, we had a factorial design: species x
position x damage. Survival of each planted
seedling was recorded every two weeks during
46 days until the end of the growing season
(March 8). An unusual summer snowstorm
drastically reduced the number of replicates in
the experiment. Just two days before applying
foliar damage, an intense snowstorm killed
about 40 % of the experimental seedlings,
particularly those planted on the bare ground.
We replaced 62 seedlings of *Hordeum* (40
seedlings on bare ground and 22 inside the
cushions) and 48 seedlings of *Haplopappus* (38
seedlings on bare ground and 10 seedlings
inside the cushions). All replaced seedlings
were part of the same original cohort of
germinated individuals. Survivor seedlings and
the newly replaced ones were monitored daily

again during one week to ensure their survival. To continue with the experiment, we chose only those experimental groups (seedling pools) having at least ten seedlings: six cushions for *Hordeum* seedlings, five cushions for *Haplopappus* seedlings, and five stands on bare ground for each species.

We used differences in the mean survival (%) between pools of control and damaged seedlings (inside and outside the cushions) to assess the ocurrence of tolerance. If *Laretia acaulis* is, at least in part, facilitating the establishment of *Hordeum* and *Haplopappus* seedlings via tolerance enhancement, then the differences between the survival of control and damaged seedlings should be lower inside the cushion than outside.

Statistical analysis

Survival data were statistically analyzed for each species at the microsite level. Final mean survival (%) was used as a fitness measure. A Kruskal-Wallis ANOVA test was used to detect differences among experimental seedling pools (position and damage as factors). We used non-parametric statistics due to the non-normal distribution of field data. Within each position (cushion/bare ground), a Wilcoxon paired-test comparing final survival of control and damaged seedling pools was used to evaluate the effect of herbivory on plant fitness. Similar mean survival of damaged and control seedling pools would imply tolerance to damage. We recorded the cumulative survival proportions (Kaplan-Meier method) to describe the establishment process (Fox 1993).

RESULTS

Kruskal-Wallis ANOVA showed significant differences in survival for both species among all experimental groups (*Hordeum*: H_3 = 17.0475, P = 0.0007; *Haplopappus*: H_3 = 12.9674, P = 0.0047). These differences are mainly consequence of the position and show the same tendency for the studied species: high survival inside *Laretia* cushions in comparison with the bare ground regardless of damage. Interestingly, the effect of damage was not the same for both species. The Wilcoxon paired-test (Table 1) for *Haplopappus anthilloydes* found no differences in the survival of damaged and control seedlings neither inside cushions nor in the bare ground (P = 1.00 and P = 0.34, respectively). Hence, a similar tolerance to damage was detected in both substrates (Fig. 1A). For *Hordeum comosum* (Fig. 1B), damaged and control seedlings growing inside of *Laretia acaulis* cushions showed no difference in survival (i.e., tolerance occurred), but on the bare ground survival of control seedlings was higher (P = 0.0431, Wilcoxon matched-pairs test) than that of damaged seedlings. This could be evidence of nurse effect of *Laretia acaulis* on *Hordeum* seedlings via enhanced tolerance to damage.

DISCUSSION

Although *Hordeum comosum* and *Haplopappus anthylloides* had not been reported as "facilitated" species for this ecosystem in previous studies (Cavieres et al. 1998), our

TABLE 1

Wilcoxon matched paired test for *Hordeum comosum* and *Haplopappus anthylloides* mean survival values: C = control seedlings; D = damaged seedlings. Comparisons are made within each position

Prueba pareada de Wilcoxon para los valores promedio de supervivencia de *Hordeum comosum* y *Haplopappus anthylloides*: C = plántulas control; D = plántulas dañadas. Las comparaciones se realizaron entre grupos de plántulas pertenecientes a la misma posición

Species	*L. acaulis* C versus *L. acaulis* D			Bare ground C versus bare ground D		
	Z-value	P-value	n	Z-value	P-value	n
Hordeum comosum	0.53	0.5929	6	2.02	0.0431	5
Haplopappus anthylloides	0.00	1.0000	5	0.94	0.3452	5

results indicate that seedling establishment in these species increases when they are associated with *Laretia acaulis* cushions. Moreover, we detected in *H. comosum* enhancement of tolerance to foliar damage for seedlings growing inside *Laretia* cushions (Fig. 1B). A similar, albeit not significant, trend was found for *Haplopappus anthylloides* seedlings (Fig. 1A). It is likely that the reduced number of replicates caused the lack of significant differences for *Haplopappus* test. Due to the particularly stressful conditions of the mid summer at this altitude (Cavieres et al. 2005), any experimental seedling that survives this period of the season is assumed to be established. In this way, cumulative survival proportions show the establishment trend during the growth season for all treatments (Fig. 2A and 2B). These trends show that differences became to be relevant since mid February (second half of the season), when environmental conditions probably were more stressful due to shortage of soil moisture and extremely high soil temperature (Rada et al. 1999, Cavieres et al. 2005).

The damage level used in this study (50 % of foliar damage) has been shown to affect plant fitness in several studies of tolerance to herbivory (Welter & Steggall 1993, Strauss et al. 2003; but see Nowak & Caldwell 1984). This negative effect on fitness would suggest that herbivory may magnify the consequences of experiencing a given abiotic stress (Kaitaniemi et al. 1999, Thompson et al. 2003). Until now, positive interaccions involving herbivory had been related to a*ssociational resistance* (Tahvanainen & Root 1972). Associational resistance involves decreased preference of herbivores for the target plant when it is associated with another plant species instead of isolated (Hay 1986, Hamback et al. 2000, Stiling et al. 2003; but see Hjältén & Price 1997). It is surprising that, to our knowledge, just a single work has reported positive interactions via enhanced plant tolerance to herbivory (Rand 2004). Rand (2004) compared in a salt marsh the effect of herbivory on *Atriplex patula* var. *hastata* being spatially associated with *Juncus gerardi* or isolated. Attacked individuals of *A. patula* growing isolated showed 50 % less survival than attacked individuals associated with *J. gerardi*. Consequently, the present study seems to be the first evidence of "associational tolerance" in a terrestrial ecosystem.
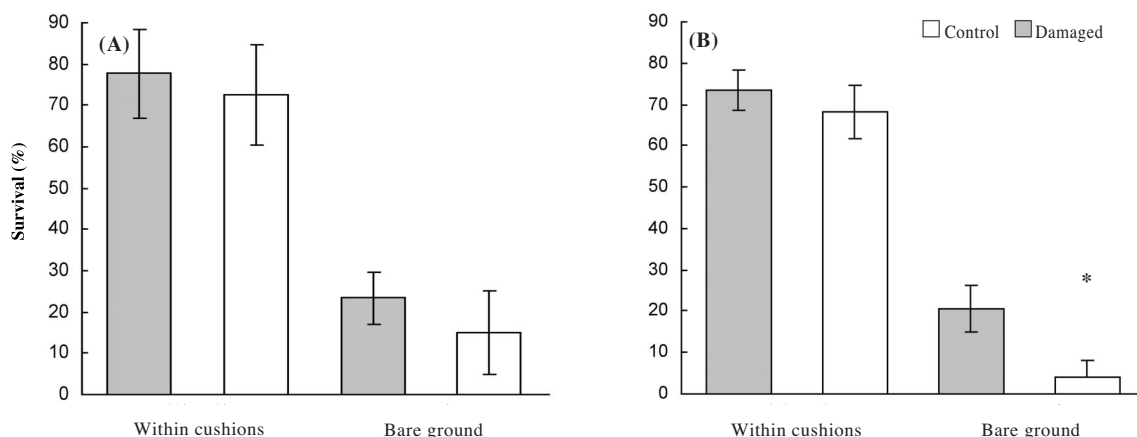

Fig. 1: Final survival average (%) for damaged and control seedlings of (A) *Haplopappus anthylloides*, and (B) *Hordeum comosum*. Significative differences between treatmens in each position means tolerance differences. Bars represent mean survival for each treatment ± 1 SE; ns = not significant, * P < 0.05, n = 6-5 cushions per bare ground stand.

Supervivencia promedio final (%) para las plántulas experimentales (daño/control) de (A) *Haplopappus anthylloides* y (B) *Hordeum comosum*. Diferencias significativas al interior de cada posición implican diferencias en los niveles de tolerancia. Las barras representan la supervivencia promedio para cada tratamiento ± 1 EE; ns = no significativo; * P < 0,05; n = 6-5 cojines por sitio en el suelo desnudo.
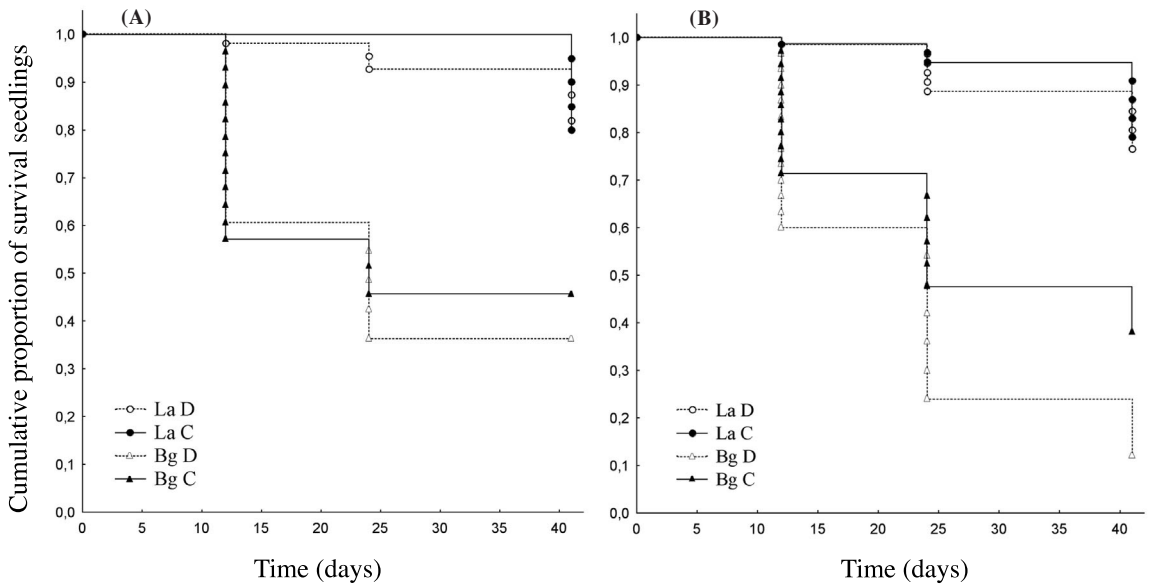
Fig. 2: Cumulative survival distributions at the individual level for experimental seedlings during the establishment process of (A) *Haplopappus anthylloides*, and (B) *Hordeum comosum*. La = *Laretia acaulis*, Bg = bare ground, D = damaged, C = control. Initial number of seedlings: LaC = 36, LaD = 36, BgC = 30, BgD = 30 for both species.

Distribución de la supervivencia durante el periodo de establecimiento para las plántulas experimentales de (A) *Haplopappus anthylloides* y (B) *Hordeum comosum*. La = *Laretia acaulis*, Bg = suelo desnudo, D = dañadas, C = control. Número inicial de plántulas: LaC = 36, LaD = 36, BgC = 30, BgD = 30 para ambas especies.

Tolerance implies resource costs for plants (Strauss & Agrawal 1999) and its expression could be limited by several environmental factors (Tiffin 2000). As Cavieres et al. (2006) showed, there are significant differences at 2,800 m for three important soil parameters (temperature, nutrients and moisture) between the soil below the cushions and the bare ground. Cavieres et al. (2005) further suggest that even though the survival and establishment of seedlings are mediated by the interaction of several factors, at this altitude it is the water economy of the individual the critical process. Thus, it might be suggested that *Laretia acaulis* improved a limiting resource in the substrate, probably soil moisture (see also Cavieres et al. 1998). It has been suggested that a reduction in tolerance must only occur when lost tissue implies a decrease in plant ability to capture the limiting resource in the environment (Wise & Abrahamson 2005). Therefore, we could suggest, at least for *Hordeum comosum*, that 50 % defoliation significantly affected its limitant resource acquisition rate when growing on the bare ground. Differences in survival between

damaged and control *Hordeum* seedlings in the bare ground (Fig. 1B) support this idea.

Hordeum comosum and *Haplopappus anthylloides* were reported as "not facilitated species" in a previous study: both species showed no differences in their frequencies of occurence inside and outside *Laretia* cushions (Cavieres et al. 1998). Present results seem to suggest a different trend, at least concerning the establishment process (Fig. 2A and 2B). It is possible that facilitation became evident during this period due to the higher vulnerability of seedlings to environmental stress. As has been shown in other studies (Karban & Thaler 1999, Rousset & Lepart 2000), the facilitation status could vary with ontogeny and can be influenced by the stress level of the environment. We certainly know that the generality of our results is restricted by the short-term nature of this study and the small sample size. However, at least for *Hordeum comosum*, our results seem to be consistent with our hypothesis and its corresponding theoretical framework. Further research in this habitat is needed to understand

the role of tolerance to herbivory in facilitation dynamics and also to determine which specific resource is involved in this process.

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