

Nurse effect of the native cushion plant *Azorella monantha* on the invasive non-native *Taraxacum officinale* in the high-Andes of central Chile

Lohengrin A. Cavieres^{a,*}, Constanza L. Quiroz^a, Marco A. Molina-Montenegro^a,
Alejandro A. Muñoz^a, Anibal Pauchard^b

^aECOBIOSIS, Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Casilla 160-C, Concepción, Chile

^bFacultad de Ciencias Forestales, Universidad de Concepción, Casilla 160-C, Concepción, Chile

Received 19 April 2005; accepted 12 September 2005

Abstract

Positive interactions among native plant species are common in alpine habitats, particularly those where one species (nurse plant) generates microclimatic conditions that are more benign than the surrounding environment, facilitating the establishment of other species. Nonetheless, these microclimatic conditions could facilitate the establishment of non-native species as well. A conspicuous component of the alien alpine flora of the central Chilean Andes is the perennial herb *Taraxacum officinale* agg. (dandelion). In contrast to other alien species that are restricted to human-disturbed sites, *T. officinale* is frequently observed growing within native plant communities dominated by cushion plants. In this study we evaluated if *T. officinale* is positively associated with the cushion plant *Azorella monantha*. Via seedling survival experiments and gas-exchange measurements we also assessed the patterns of facilitation between cushions and dandelions, and explore the potential mechanisms of invasion by dandelions. *T. officinale* grows spatially positively associated with cushions of *A. monantha*. Survival of seedlings, as well as their net-photosynthetic rates and stomatal conductance, were higher within cushions than in open areas away from them, suggesting that the microclimatic modifications generated by this native cushion facilitates the establishment and performance of a non-native invasive species. Our results, as well as other recent studies, highlight the role of native communities in facilitating rather than constraining non-native plant invasions, particularly in stressful habitats such as alpine environments.

© 2005 Rübél Foundation, ETH Zürich. Published by Elsevier GmbH. All rights reserved.

Keywords: Alpine; Andes; Cushion plants; Facilitation; Invasions; Positive interactions; *Taraxacum officinale*

Introduction

Invasion of native communities by non-native plant species is a growing conservation problem, threatening local and regional biodiversity (Drake et al., 1989;

Mooney and Hobbs, 2000). Although the presence and spread of non-native organisms into new areas where they have been deliberately or accidentally introduced by humans is occurring worldwide, few studies have addressed the magnitude of spread and the mechanisms involved in the invasion of alpine areas.

Alpine habitats are well known for their severe life conditions. Here, plants must confront low temperatures,

*Corresponding author.

E-mail address: lcaviere@udec.cl (L.A. Cavieres).

short growing seasons, excessive radiation and unstable substrates (Billings and Mooney, 1968; Bliss, 1985; Körner 2003). Although not clearly stated, it is believed that the climatic harshness of alpine habitats precludes the successful establishment of invasive species. For instance, Pauli et al. (2004) recently indicated that one of the threats for alpine areas due to global warming is that these areas may become more available for the colonization of invading species. Although this suggestion was made for colonization by lowland native species, it certainly can apply for lowland alien invasives as well. In fact, several studies have reported the presence of non-native species in a number of alpine habitats (e.g. Johnston and Pickering, 2001; Stohlgren et al., 2002; Dullinger et al., 2003).

In recent years, much research has been done with the purpose of unraveling the mechanisms responsible for successful invasions, with many of the suggested mechanisms relying on negative interactions among native and exotic species such as competition (Vilà and Weiner, 2004) and allelopathy (Callaway and Aschehoug, 2000). However, some reviews have highlighted the importance that positive interactions among species may have for the invasion process (Simberloff and von Holle, 1999; Richardson et al., 2000). For instance, introduced animals disperse seeds of invasive non-native plant species, increasing the magnitude of the invasion process and generating what has been termed as an ‘invasional meltdown’ (Simberloff and von Holle, 1999). The most commonly reported types of facilitative impacts on invasive processes are non-native animals pollinating and dispersing plants, and non-native animals and plants modifying the environment in ways that favor the spread of other non-native species (Simberloff and von Holle, 1999; Richardson et al., 2000; Crooks, 2002). Examples of direct positive interactions among plants, either between invasive species or between native and invasive species, are more scarce (Richardson et al., 2000), and usually involve the presence of microorganisms (but see Lenz and Facelli, 2003). For example, Maron and Connors (1996) showed that the nitrogen-fixing native species *Lupinus arboreus* facilitates the establishment of invasive weed species in coastal prairies of California.

Positive interactions among species are expected to be important in stressful habitats (Bertness and Callaway, 1994; Brooker and Callaghan, 1998), and several studies have reported that facilitative interactions are common in alpine habitats (Kikvidze, 1993, 1996; Kikvidze and Nakhutsrishvili, 1998; Choler et al., 2001; Callaway et al., 2002), particularly those that involve the presence of nurse plants (Núñez et al., 1999; Cavieres et al., 2002; Arroyo et al., 2003; Cavieres et al., in press). Recently, Bruno et al. (2003) has suggested that in stressful habitats, like alpine areas, facilitation between species could be an important mechanism for successful invasions.

In the Andes of central Chile, several non-native species have been observed (e.g. *Tanacetum parthenium*,

Lactuca serriola), mainly associated to perturbations generated by humans (e.g. roads) or introduced animals (horses and cattle). A conspicuous component of this alien alpine flora of the central Chilean Andes is the perennial herb *Taraxacum officinale* agg. or common dandelion. In contrast to other alien species *T. officinale* is frequently observed growing at varying densities within the native vegetation, particularly in communities dominated by cushion plants, which have been suggested to be nurse plants that facilitate the establishment and survival of several native species (Núñez et al., 1999; Cavieres et al., 2002, in press). Hence, cushion plants could also facilitate the establishment of non-native species.

In this study we evaluated the abundance of *T. officinale* in different vegetation patches in the high alpine zone of the Andes of central Chile. For vegetation patches dominated by cushion plants we specifically addressed the following questions: (i) Is *T. officinale* positively associated with cushions? (ii) Do cushions facilitate the survival of *T. officinale* seedlings? (iii) Do *T. officinale* individuals growing within cushions have a better photosynthetic performance than those individuals growing on bare ground? (iv) Is the presence of *T. officinale* related with changes in the frequency with which a particular native species is found both within and away from cushions?

Materials and methods

Study area

Our study area was located in the central Chilean Andes (33°S), in the surroundings of the Valle Nevado ski complex (33°20'S, 70°16'W) located ca. 50 km east to the city of Santiago. We restricted our vegetation sampling between 3100 and 3300 m a.s.l.

Central Chile possesses a Mediterranean-type climate (di Castri and Hajek, 1976), which is characterized by cool rainy winters and long dry summers spanning ca. 6–7 months. According to Santibáñez and Uribe (1990) mean total annual precipitation at 3200 m has been estimated to be 943 mm, falling predominantly as snow between May and September, with snow always occurring between June and August. Mean monthly air temperature during the growing season at 3150 m ranges from 3.0 °C in April to 7.6 °C in February (Cavieres and Arroyo, 1999).

At the elevations studied native vegetation is highly patchy (Cavieres et al., 2000). Some patches are dominated by cushion plant species such as *Azorella monantha*, with their cover reaching up to ca. 30% (Badano and Cavieres, in press). Other patches are dominated by tussock grasses, such as *Stipa chrysophylla*, with a cover of ca. 15%. Other species frequently found in both patches are rosette-forming perennial

herbs such as *Phacelia secunda*, *Nastanthus agglomeratus*, *Pozoa coriaceae*, *Barneoudia major*, *Nassauvia* spp. and *Viola philippii* (Cavieres et al., 2000).

Study species

Azorella monantha (Apiaceae), is a very flat and tightly knit cushion species, extending from 33°S to 55°S, and growing from above 3200 m elevation in the Andes of central Chile (33°S) and close to sea level at 55°S (Hoffmann et al., 1998). According to Armesto et al. (1980), the size of individual cushions of *A. monantha* at our study area ranges between 10 and >100 cm diameter, with mean size increasing with elevation.

Taraxacum officinale agg. (Asteraceae) probably originated in Europe, but is now found in most countries of the world (Holm et al., 1997). It is a stemless, deeply rooted perennial herb having a thick taproot and leaves in rosettes at soil level. Each plant has one or more 2–5 cm diameter capitula or flower heads terminally positioned on 5–45 cm long, hollow, cylindrical peduncles. Each capitulum has a composite of 50–250 small bright yellow ligulate or ray florets (Holm et al., 1997). *Taraxacum officinale* is generally apomictic although sexually reproducing biotypes have been described, and it is considered as a noxious weed in several countries (Holm et al., 1997).

Determining the abundance of *T. officinale* in different vegetation patches

Eighteen sites between 3100 and 3300 m a.s.l. were selected in order to evaluate the abundance of *T. officinale* in different vegetation patches. These sites were ca. 10,000 m² (1 ha) each, and were located at similar distances (ca. 50 m) from unpaved roads, which are mainly used by the maintenance staff of the Valle Nevado Ski Resort. We sampled five patches dominated by *A. monantha* cushions, three patches dominated by tussock grasses, five patches where vegetation is naturally disturbed by snowmelt runoff and dominated by *P. secunda*, and five vegetation patches disturbed by human activities. At each patch, a 50 cm diameter metallic hoop was randomly placed and the number of all individuals of *T. officinale* within the hoop was recorded. At each patch this procedure was repeated 100 times, and the frequency of *T. officinale* was subsequently calculated. No points were re-sampled in each of these patches.

Sampling within patches dominated by *A. monantha* cushions

To detect spatial associations of *T. officinale* with *A. monantha* cushions, fifty 50–60 cm diameter cushions were selected on a single slope at 3200 m a.s.l. We

selected this cushion size because it is the most abundant size class at this elevation (Armesto et al., 1980). Selection was done with a compass and random numbers between 0 and 1, which were converted to hexadecimal degrees, which indicated the direction (degrees from magnetic north) in which the first cushion that met our size criteria was selected. For each selected cushion, a 50 cm diameter metallic hoop was centered over the cushion surface, and all plant species found inside the hoop were identified and recorded. A hoop of identical size was located at random outside the cushion, where again all species included in the hoop were recorded. The random location of hoops outside cushions was determined with a similar procedure to that used in the selection of cushions, although the selected point outside had to be at least 50 cm away from the nearest cushion. Vegetation sampling was done during February 2004, in the middle of the growing season, and when the majority of the species were in bloom, thus facilitating the identification of specimens to species level.

To determine whether there were positive or negative associations between the *T. officinale* and native species, we sampled a different set of cushion and open areas to those described above and compared the incidence of each native species with and without *T. officinale* both within and outside cushions. For this, we selected 63 *A. monantha* cushions of >50 cm diameter size with at least one individual of *T. officinale* growing within, and further 57 *A. monantha* cushions of >50 cm diameter size without the presence of dandelions. In each cushion with *T. officinale*, a metallic-hoop of 50 cm diameter was centered on one *T. officinale* individual located preferably near the center of the cushion, and all plant species found inside the hoop were identified and recorded. We took care that the entire hoop was included within the sampled cushion. At each selected cushion without *T. officinale* a 50 cm diameter metallic-hoop was centered over the cushion surface and all plant species found inside the hoop were identified and recorded. Similarly, on the ground away from cushions, the metallic hoop used with cushions was placed in 64 points where *T. officinale* was present, and 86 random points where it was absent. At each point, all plant species found inside the hoop were identified and recorded.

Seedling survival

Seeds of *T. officinale* collected during March 2003 were germinated in growth chambers under controlled temperature conditions (20/10 °C day/night) during October 2003. Emerged seedlings from this trial were planted in small plastic bags (100 cm³) with commercial soil, and were maintained in a growth-chamber at 10/5

°C (day/night) during 1 month. The 1-month-old seedlings were taken to the field and planted in groups of ten individuals each into each of six previously random-selected cushions and in each of six randomly selected points on bare ground. Seedlings were planted on 28 November 2003, taking care that seedlings were distanced 5 cm from each other. Seedling survival was monitored every 2 weeks from December 2003 to March 2004.

Gas-exchange measurements

At each microhabitat, within and outside *A. monantha* cushions, we selected six *T. officinale* individuals of similar size and morphology. On each of these selected individuals, we measured foliar gas exchange with an IRGA (CIRAS-2, PP-Systems Haverhill, MA). Measurements were done on single days of December, January and February, which corresponded to early, mid and late growing season, respectively. At each day, gas-exchange measures were done at the same time: noon. For each measurement, on each of the selected individuals, a single leaf was randomly selected and was inserted inside the Parkinson leaf cuvette of the IRGA, where net-photosynthesis, stomatal conductance, photosynthetic active radiation (PAR) intensity and leaf temperature were registered.

Data analyses

Frequency of *T. officinale* at the different vegetation patches was expressed as the proportion of hoops where at least one individual was recorded, and was compared between habitats with a Kruskal–Wallis non-parametric test.

To detect either positive or negative spatial association between *T. officinale* and *A. monantha* cushions, we performed randomization tests (Slade and Hall, 1999; Kikvidze et al., 2001) with the software ‘Resampling Stats’ (Resampling Stats, Inc. 1990–1995). First, from the total frequency of incidence of *T. officinale*, we randomly redistributed the total number of presence recordings between the within and outside cushion habitats. We performed 1000 runs of random redistributions, and calculated the probability of the observed frequency within cushions being generated by chance (see also Cavieres et al., 2002, in press).

To assess if there was a relationship between the presence of *T. officinale* and native species richness both within and outside cushions, we performed ANCOVAs with the presence/absence of *T. officinale* as a factor. Native species richness was log transformed and used as the dependent variable and the abundance of *T. officinale* (log transformed) as a covariable. To determine if there were native species that showed

positive or negative spatial associations with *T. officinale* either within or outside cushions, randomization analyses for each native species were performed as described above.

Survival curves of seedlings at each position (within and outside cushions) were estimated by means of the Kaplan-Meier method and statistical differences were assessed with the Cox-Mantel test (Fox, 1993). All the gas-exchange variables measured on individuals growing within cushions and outside cushions were compared with repeated-measures ANOVA.

Results

Frequency of *T. officinale* in different vegetation patches

Among the sampled patches, *T. officinale* was more frequently found in patches dominated by cushion plants and in human-disturbed patches than in the other two types of patches (Fig. 1). The frequencies of *T. officinale* in naturally disturbed and tussock-grass-dominated patches were very low (<10% of the hoops contained at least one *T. officinale* individual) compared to that in the other patches.

While *T. officinale* was found within 28 out of the 50 sampled *A. monantha* cushions, it was only found in 16 out of 50 samples outside cushions, i.e. *T. officinale* was positively associated with cushions ($P < 0.05$). An average (± 2 SE) of 2.4 ± 0.7 *T. officinale* individuals per 50 cm diameter hoop was found within cushions,

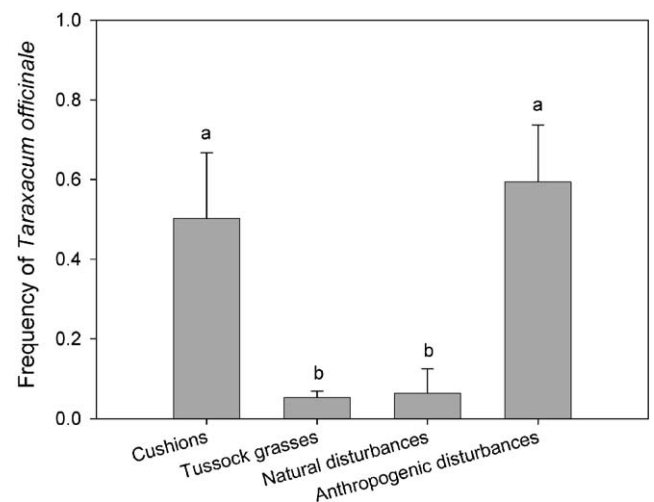


Fig. 1. Frequency of *Taraxacum officinale* expressed as the proportion of hundred 50 cm diameter hoops randomly placed at different vegetation patches occurring between 3100–3300 m a.s.l. in the Andes of central Chile. Error bars indicate 2 SE; different superscript letters indicate significant differences.

which was significantly higher than the abundance found outside the cushions (1.5 ± 0.3 ; Mann-Whitney test, $U = 888.7$, $P < 0.01$).

A mean (± 2 SE) of 5.0 ± 0.5 native species was found within the 50 cm diameter hoops positioned in cushions where *T. officinale* was present, this being significantly greater than native species richness found in cushions where *T. officinale* was absent (3.0 ± 0.5 ; ANCOVA, $F_{1,46} = 10.8$, $P < 0.01$). In contrast, outside the cushions there were no significant differences in native species richness within hoops with and without *T. officinale* (2.9 ± 0.4 vs. 3.9 ± 0.8 ; ANCOVA, $F_{1,47} = 0.7$, $P > 0.05$).

Only two native species (*Loasa sigmoidea* and *Thlaspi magellanicum*) showed significant differences in the frequency with which they were observed within cushions with and without *T. officinale*, being positively associated with the presence of the non-native species

(Table 1). In contrast, away from cushions, five species (*Chaetanthera lycopodioides*, *Montiopsis potentilloides*, *Oxalis compacta*, *P. secunda* and *V. philippi*) showed differences in their frequencies with and without the presence of *T. officinale*, with all the species showing lower frequencies in samples with the presence of *T. officinale*.

Seedling survival

Survival of planted seedlings of *T. officinale* was significantly higher within cushions than in the bare ground (Cox-Mantel test = 2.04, $P < 0.05$; Fig. 2), indicating that *A. monantha* facilitates the survival of *T. officinale*. Survival of seedlings was high (100%) during the first 20 days without differences between

Table 1. Incidence of native species growing within and outside *Azorella monantha* cushions, either with or without the presence of *Taraxacum officinale* individuals at 3200 m a.s.l. in the Andes of central Chile

Species	Within cushions			Outside cushions		
	With <i>T. officinale</i>	Without <i>T. officinale</i>	<i>P</i>	With <i>T. officinale</i>	Without <i>T. officinale</i>	<i>P</i>
<i>Acaena pinnatifida</i>	5	2	NS	1	0	NS
<i>Bromus setifolius</i>	—	—		3	2	NS
<i>Carex andina</i>	0	2	NS	13	10	NS
<i>Cerastium arvense</i>	44	37	NS	4	11	NS
<i>Chaetanthera euphrasioides</i>	—	—		10	11	NS
<i>Chaetanthera lycopodioides</i>	—	—		5	14	<0.05 (–)
<i>Chaetanthera planiseta</i>	—	—		9	8	NS
<i>Chaetanthera pusila</i>	—	—		3	2	NS
<i>Erigeron andicola</i>	7	6	NS	3	0	NS
<i>Festuca rubra</i>	2	4	NS	—	—	
<i>Hordeum comosum</i>	30	22	NS	14	10	NS
<i>Loasa sigmoidea</i>	9	2	<0.05 (+)	3	7	NS
<i>Microsteris gracilis</i>	12	6	NS	6	13	NS
<i>Montiopsis potentilloides</i>	16	13	NS	14	29	<0.05 (–)
<i>Nassauvia lagascae</i>	—	—		2	6	
<i>Nastanthus agglomeratus</i>	4	1	NS	2	3	NS
<i>Olsynium junceum</i>	3	2	NS	—	—	
<i>Olsynium scirpoideum</i>	—	—		3	3	NS
<i>Oxalis compacta</i>	—	—		1	8	<0.05 (–)
<i>Perezia carthamoides</i>	—	—		1	6	NS
<i>Perezia pilifera</i>	6	3	NS	0	4	NS
<i>Phacelia secunda</i>	4	2	NS	16	34	<0.01 (–)
<i>Poa pratensis</i>	6	2	NS	2	0	NS
<i>Poa</i> sp.	5	6	NS	18	15	NS
<i>Pozoa coriacea</i>	0	2	NS	5	10	NS
<i>Quinchamalium chilense</i>	—	—		0	4	NS
<i>Rytidosperma violaceum</i>	10	4	NS	1	0	NS
<i>Senecio francisci</i>	—	—		0	3	NS
<i>Thlaspi magellanicum</i>	22	9	<0.05 (+)	1	0	NS
<i>Trisetum preslei</i>	29	22	NS	8	5	NS
<i>Viola atropurpurea</i>	—	—		10	9	NS
<i>Viola philippi</i>	2	0	NS	13	28	<0.01 (–)

Signs indicate significantly positive (+) or negative (–) association with *T. officinale* according to randomization tests (NS, $P > 0.05$).

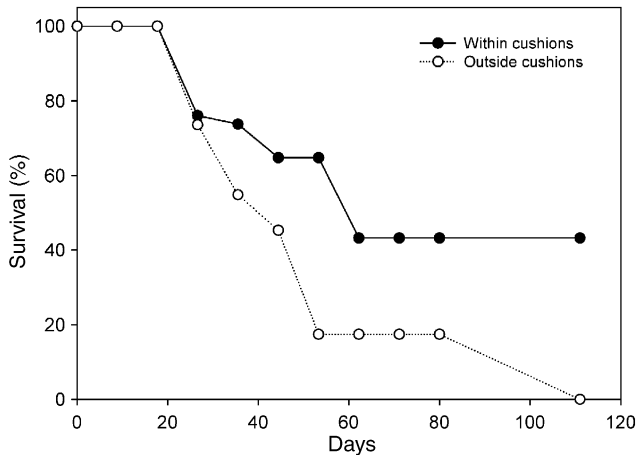


Fig. 2. Survival of experimentally planted seedlings of *Taraxacum officinale* within and outside *Azorella monantha* cushions at 3200 m a.s.l.

cushions and bare ground; however, after 1 month onward seedlings survival decreased, particularly in seedlings planted outside cushions where no seedlings survived after 110 days. Within cushions, however, ca. 45% of seedlings survived after 110 days.

Gas exchange of *T. officinale*

Overall, *T. officinale* individuals growing within *A. monantha* cushions showed significantly higher net-photosynthesis compared to individuals growing outside cushions (Table 2), particularly toward the end of the growing season when individuals growing within cushions had a photosynthetic rate of ca. $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ and those outside cushions had $5 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 3). Similarly, individuals growing within cushions had a higher stomatal conductance than those growing outside the cushions. This difference was also more pronounced toward the end of the growing season (Fig. 3). Neither leaf temperature nor PAR intensity differed between the individuals growing within cushions and outside them.

Discussion

As in other areas, non-native species in alpine areas typically occur in human-disturbed areas (Johnston and Pickering, 2001; Johnston and Johnston, 2004). *Taraxacum officinale* in alpine plant communities of the central Chilean Andes at 3200 m is also associated with disturbed areas, being more abundant in areas under anthropogenic disturbances. Given that all the sampled patches were located at similar distances from roads, it appears that the observed results are not strongly influenced by differences in propagule pressure. Thus, the observed differences among different vegetation

Table 2. Between-subject results of repeated measures ANOVA for variables recorded during gas-exchange measurements of *Taraxacum officinale* individuals growing at different position (within and outside *Azorella monantha* cushions) at three different periods during the growing season (early, mid and late) at 3200 m a.s.l. in the Andes of central Chile (cf. Fig. 3)

Variable	Factor	df	F	P
Net-photosynthesis (A)	Position (P)	1, 10	16.9	<0.01
	Time (T)	2, 20	12.7	<0.01
	P × T	2, 20	3.80	<0.05
Stomatal conductance (g)	Position	1, 10	5.44	<0.05
	Time	2, 20	14.4	<0.01
	P × T	2, 20	0.77	NS
Leaf temperature (Lt)	Position	1, 10	0.01	NS
	Time	2, 20	1.50	NS
	P × T	2, 20	1.04	NS
Photosynthetic active radiation (PAR)	Position	1, 10	0.11	NS
	Time	2, 20	2.72	NS
	P × T	2, 20	0.09	NS

patches are more likely to be related with microenvironmental differences.

It is well known that human disturbances increase the availability of resources, and that non-native species can, in many cases, take more advantage of these changes for a successful establishment than their native counterparts (e.g. Burke and Grime, 1996; Davis et al., 2000). For alpine habitats it has been reported that disturbances increase the availability of nutrients such as nitrogen and phosphorous (Chambers et al., 1990), which has enormous influences on recruitment success of seedlings (Forbis, 2003). Hence, the high abundance of *T. officinale* on anthropogenic-disturbed patches is likely to be related to local increases in nutrient availability. Indeed, other non-native species observed in this area (e.g. *L. serriola*) are also confined to these microhabitats.

Nonetheless, the importance of propagule pressure cannot be completely ruled out. In the study area we found patches dominated by *A. monantha* cushions where *T. officinale* was completely absent. These patches were characterized by their isolation from human-related activities (e.g. roads or tracking ways), corroborating the importance of propagule pressure as the first step in the invasion process (Richardson et al., 2000; Rouget and Richardson, 2003).

In contrast to other non-native species, *T. officinale* can be found in native undisturbed communities, particularly in those dominated by *A. monantha* cushions. Spatial association analyses indicated that *T. officinale* is positively associated with cushions and

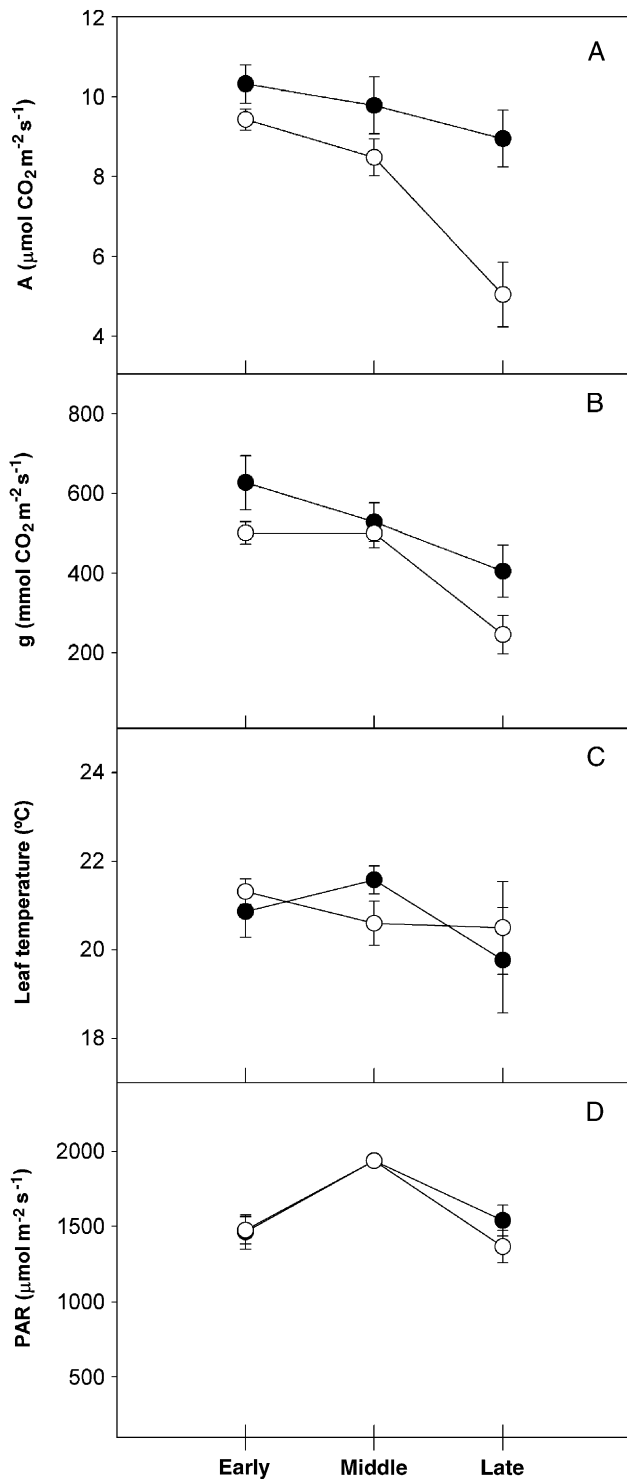


Fig. 3. Gas-exchange parameters of *Taraxacum officinale* individuals growing within (black circles) and outside (empty circles) *Azorella monantha* cushions at 3200 m a.s.l. in early, mid, and late periods of the growing season in the Andes of central Chile. A, net-photosynthesis (A , $\mu\text{mol m}^{-2} \text{ s}^{-1}$); B, stomatal conductance (g , $\text{mmol m}^{-2} \text{ s}^{-1}$); C, leaf temperature ($^{\circ}\text{C}$); D, photosynthetic active radiation (PAR, $\mu\text{mol m}^{-2} \text{ s}^{-1}$). Error bars indicate 2 SE.

the results of the seedling survival experiments suggest that this spatial association results, at least in part, from differential seedling survival. Although differences in seed rain and/or seed trap between cushions and areas away from them could be involved, initial observations indicate that this is unlikely. First, preliminary seed trap experiments performed in the study area have indicated that a greater number of seeds fall into traps located in open areas away from cushions than into traps located within cushions (L.A. Cavieres, unpubl. data). Secondly, and in contrast to other cushion species (e.g. *Silene acaulis*) that have ‘soft’ canopies that can trap seeds, *A. monantha* form tightly knit cushions, with very few spaces for seed trapping within the canopy. However, small fractures within the *A. monantha* canopy can occur that may function as seed traps and may be highly suitable for establishment.

The higher net-photosynthesis found in individuals growing within cushions provides further evidence that *A. monantha* facilitates growth and survival of *T. officinale*. High net photosynthetic rates are linked with higher availability of energy, which can be used to enhance survival, reproduction or both (Mooney, 1976). Positive relationships between instantaneous photosynthetic rates and plant productivity and/or fitness have been shown for several species (McAllister et al., 1998), including alien species (Nagel and Griffin, 2004). In fact, Molina-Montenegro (2003) showed that *T. officinale* individuals growing within cushions produced higher amount of seeds per capitulum than individuals growing outside them. Hence, all our evidence indicates that the native cushion species *A. monantha* facilitates the establishment and performance of the non-native species *T. officinale* in the high-alpine of the Andes of central Chile.

There are several reasons why cushion plants in alpine environments can facilitate non-native species. Cushion plants are one of the life forms best adapted to the extreme alpine climate (Körner, 2003), and because of their low stature and compact form, cushion plants favor the development of particular microenvironment within their canopies (Körner, 2003). For instance, cushion plants maintain higher soil moisture (Cavieres et al., 1998, in press) and higher temperatures (Arroyo et al., 2003; Körner, 2003) compared to their surrounding environment. In the Patagonian Andes of southern Chile, Arroyo et al. (2003) reported that *A. monantha* cushions maintained higher temperature within their canopies compared to that of the surrounding air. However, this does not seem to be the case for cushion plants in the Andes of central Chile, where temperature within cushions is lower than that outside (Cavieres et al., 1998, in press). At 3200 m in the Andes of central Chile, soil temperatures can reach ca. 40°C at midday during the summer, which could be lethal for some alpine plants (Cavieres et al., in press). In contrast,

cushions maintain significantly milder temperatures, which could be very important in terms of evaporative demands and their consequences for the hydraulic economy of the facilitated plant. The higher net-photosynthesis observed in *T. officinale* growing within cushions was linked with higher stomatal conductance which suggest that individuals within cushions have more water availability than those that grow on bare ground.

Higher availability of nutrients in soils beneath cushions has been previously reported (Núñez et al., 1999; Molina-Montenegro et al., 2000, 2005). This added to the fact that cushions maintained higher soil moisture could also have substantial influences on plant nutrition in general, but particularly on *T. officinale*, which is responsive to soil potassium content (Tilman et al., 1999). Molina-Montenegro et al. (2005) reported that potassium was the nutrient showing the highest increase in soils beneath *A. monantha* cushions in comparison with soils away from cushions, which suggests that the higher availability of potassium within cushion could be related with observed higher incidence and abundance of *T. officinale*. Thus, the facilitation of the invasive non-native *T. officinale* by the native *A. monantha* is likely to be the result of several factors acting in concert, although the provision of moisture and higher availability of nutrients, particularly potassium, seem to be very important.

The presence of *T. officinale* within *A. monantha* cushions was not correlated with reductions in the number of native species. Indeed, cushions where *T. officinale* was present had higher native species richness than those cushions where *T. officinale* was not found. Moreover, there were two species positively associated with the presence of *T. officinale* within cushions. In contrast, in open areas away from cushions, there were no differences in native species richness between points with and without *T. officinale*, and several species showed negative associations with the presence of *T. officinale*. Although the correlational nature of our evidence should be kept in mind, the former results suggest that while the net outcome of interactions between native species and *T. officinale* within cushions could be neutral and in some cases positive, outside cushions it is negative for several species. The latter suggests that future increases in the incidence and abundance of this invasive non-native species on open areas away from cushions could have detrimental effects on the diversity of this alpine site.

We have shown that besides man-made disturbances, which historically have been linked to the invasibility of a particular habitat, facilitation of non-native invasive species by native ones may be an important mechanism for the invasion of stressful habitats such as the high-alpine zone of central Chile. The importance of facilitation by native species for the success of non-

native invasive species is starting to be reported (Maron and Connors, 1996; Lenz and Facelli, 2003; von Holle, 2005) forcing us to question the current tenets on the role of species interactions on invasiveness (Bruno et al., 2003). Increasing propagule pressure and habitat disturbance may enhance the role of native communities in facilitating rather than constraining non-native plant invasions.

Acknowledgments

To Hansjörg Dietz for inviting us to write this contribution and to two anonymous reviewers for their comments on the manuscript. To Angela Sierra, Philippe Choler and Florence Baptist for their help in field sampling. To Chris Lusk for lending us the 'Resampling Stat' Software. Our research was funded by FONDECYT 1030821 (LC) and 1040528 (AP) and P02-051-F ICM supporting the Center for Advanced Studies in Ecology and Research in Biodiversity.

References

- Armesto, J.J., Arroyo, M.T.K., Villagrán, C., 1980. Altitudinal distribution, cover and size structure of umbelliferous cushion plants in the high Andes of central Chile. *Acta Oecol.* 1, 327–332.
- Arroyo, M.T.K., Cavieres, L.A., Peñaloza, A., Arroyo-Kalin, M.A., 2003. Positive associations between the cushion plant *Azorella monantha* (Apiaceae) and alpine plant species in the Chilean Patagonian Andes. *Plant Ecol.* 169, 121–129.
- Badano, E.I., Cavieres, L.A., in press. Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? *J. Biogeogr.*
- Bertness, M.D., Callaway, R.M., 1994. Positive interactions in communities. *TREE* 9, 191–193.
- Billings, W.D., Mooney, H.A., 1968. The ecology of arctic and alpine plants. *Biol. Rev.* 43, 481–529.
- Bliss, L.C., 1985. Alpine. In: Billings, W.D., Mooney, H.A. (Eds.), *Physiological Ecology of North American Plant Terrestrial Communities*. Chapman & Hall, New York, pp. 41–65.
- Brooker, R.W., Callaghan, T.V., 1998. The balance between positive and negative interactions and its relationship to environmental gradient: a model. *Oikos* 81, 196–207.
- Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. *TREE* 18, 119–125.
- Burke, M.J.W., Grime, J.P., 1996. An experimental study of plant community invasibility. *Ecology* 77, 776–790.
- Callaway, R.M., Aschehoug, E.T., 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290, 521–523.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D.,

- Cook, B.J., 2002. Positive interactions among alpine plants increase with stress. *Nature* 417, 844–848.
- Cavieres, L.A., Arroyo, M.T.K., 1999. Tasa de enfriamiento adiabático del aire en el valle del río Molina, Provincia de Santiago, Chile central (33°S). *Rev. Geogr. Chile Terra Australis* 44, 79–86.
- Cavieres, L.A., Peñaloza, A., Papic, C., Tambutti, M., 1998. Efecto nodriza del cojín *Laretia acaulis* (Umbelliferae) en la zona alto-andina de Chile central. *Rev. Chil. Hist. Nat.* 71, 337–347.
- Cavieres, L.A., Peñaloza, A., Arroyo, M.T.K., 2000. Altitudinal vegetation belts in the high-Andes of central Chile. *Rev. Chil. Hist. Nat.* 73, 331–344.
- Cavieres, L.A., Arroyo, M.T.K., Peñaloza, A., Molina-Montenegro, M.A., 2002. Nurse effect of *Bolax gummifera* (Apiaceae) cushion plants in the alpine vegetation of the Chilean Patagonian Andes. *J. Veg. Sci.* 13, 547–554.
- Cavieres, L.A., Badano, E.I., Sierra-Almeida, A., Gómez-González, S., Molina-Montenegro, M., in press. Positive interactions between alpine plant species and the nurse cushion plant *Laretia acaulis* do not increase with elevation in the Andes of central Chile. *New Phytol.* DOI:10.1111/j.1469-8137.2005.01573.x.
- Chambers, J.C., MacMahon, J.A., Brown, R.W., 1990. Alpine seedling establishment: the influence of disturbance type. *Ecology* 71, 1323–1341.
- Choler, P., Michalet, R., Callaway, R.M., 2001. Facilitation and competition on gradients in alpine plant communities. *Ecology* 82, 3295–3308.
- Crooks, J.A., 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97, 153–166.
- Di Castri, F., Hajek, E., 1976. *Bioclimatología de Chile*. Ediciones Universidad Católica de Chile, Santiago.
- Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* 88, 528–534.
- Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M., Williamson, M., 1989. *Biological Invasions: A Global Perspective*. Wiley, New York.
- Dullinger, S., Dirnböck, T., Grabherr, G., 2003. Patterns of shrub invasion into high mountain grasslands of the northern calcareous Alps, Austria. *Arct. Antarct. Alp. Res.* 35, 434–441.
- Forbis, T., 2003. Seedling demography in an alpine ecosystem. *Am. J. Bot.* 90, 1197–1206.
- Fox, G.A., 1993. Failure-time analysis: emergence, flowering survivorship, and other waiting time. In: Scheiner, S.M., Gurevitch, J. (Eds.), *Design and Analysis of Ecological Experiments*. Chapman and Hall, New York, pp. 253–289.
- Hoffmann, A., Arroyo, M.T.K., Liberona, F., Muñoz, M., Watson, J., 1998. *Plantas Altoandinas en la Flora Silvestre de Chile*. Fundación Claudio Gay, Santiago.
- Holm, L., Doll, J., Holm, E., Pancho, J., Herberger, J., 1997. *World Weeds. Natural Histories and Distribution*. John Wiley, Toronto.
- Johnston, F.M., Johnston, S.W., 2004. Impacts of road disturbance on soil properties and on exotic plant occurrence in subalpine areas of the Australian Alps. *Arct. Antarct. Alp. Res.* 36, 201–207.
- Johnston, F.M., Pickering, C.M., 2001. Alien plants in the Australian Alps. *Mount. Res. Devel.* 21, 284–291.
- Kikvidze, Z., 1993. Plant species associations in alpine-subnival vegetation patches in the Central Caucasus. *J. Veg. Sci.* 4, 297–302.
- Kikvidze, Z., 1996. Neighbour interaction and stability in subalpine meadow communities. *J. Veg. Sci.* 7, 41–44.
- Kikvidze, Z., Nakhutsrishvili, G., 1998. Facilitation in subnival vegetation patches. *J. Veg. Sci.* 9, 261–264.
- Kikvidze, Z., Khetsuriani, L., Kikodze, D., Callaway, R.M., 2001. Facilitation and interference in subalpine meadows of the central Caucasus. *J. Veg. Sci.* 12, 833–838.
- Körner, C., 2003. *Alpine Plant Life*. Springer, Berlin.
- Lenz, T.I., Facelli, J.M., 2003. Shade facilitates an invasive stem succulent in a chenopod shrubland in South Australia. *Aust. Ecol.* 28, 480–490.
- Maron, J.L., Connors, P.G., 1996. A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia* 105, 302–312.
- McAllister, C.A., Knapp, A., Maragni, L.A., 1998. Is leaf-level photosynthesis related to plant success in a highly productive grassland? *Oecologia* 117, 40–46.
- Molina-Montenegro, M.A., 2003. Intercambio gaseoso y eficiencia del PSII (Fv/Fm y θ PSII) en *Taraxacum officinale* en los Andes de Chile central: efectos de la asociación a plantas en cojín. Biology thesis, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción.
- Molina-Montenegro, M.A., Torres, C., Parra, M.J., Cavieres, L.A., 2000. Asociación de especies al cojín *Azorella trifurcata* (Gaertn.) Hook. (Apiaceae) en la zona andina de Chile central (37°S). *Gayana Bot.* 57, 161–168.
- Molina-Montenegro, M.A., Badano, E.I., Inostroza, P., Cavieres, L.A., 2005. Intercambio gaseoso en dos especies de plantas alto andinas de Chile central: efecto de la asociación a plantas en cojín. *Ecología Austral.* 15, 49–58.
- Mooney, H.A., 1976. The carbon balance of plants. *Ann. Rev. Ecol. System.* 3, 315–346.
- Mooney, H.A., Hobbs, R.J., 2000. *Invasive Species in a Changing World*. Island Press, Washington DC.
- Nagel, J.M., Griffin, K.L., 2004. Can gas-exchange characteristics help explain the invasive success of *Lythrum salicaria*? *Biol. Invas.* 6, 101–111.
- Núñez, C., Aizen, M., Ezcurra, C., 1999. Species associations and nurse plant effects in patches of high-Andean vegetation. *J. Veg. Sci.* 10, 357–364.
- Pauli, H., Gottfried, M., Dirnböck, T., Dullinger, S., Grabherr, G., 2004. Assessing the long-term dynamics of endemic plants at summit habitats. In: Nagy, L., Grabherr, G., Körner, C., Thompson, D.B.A. (Eds.), *Alpine Biodiversity in Europe*. Ecological Studies 167. Springer, Berlin, pp. 195–207.
- Richardson, D.M., Allsop, N., D'Antonio, C.M., Milton, S.J., Rejmánek, M., 2000. Plant invasions – the role of mutualisms. *Biol. Rev.* 75, 65–93.
- Rouget, M., Richardson, D.M., 2003. Inferring process from pattern in plant invasions: A semimechanistic model incorporating propagule pressure and environmental factors. *Am. Nat.* 162, 713–724.

- Santibáñez, F., Uribe, M., 1990. Atlas Agroclimático de la V Región y Región Metropolitana. Ministerio de Agricultura, Chile, Santiago.
- Simberloff, D., von Holle, B., 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biol. Invas.* 1, 21–32.
- Slade, N., Hall, D., 1999. Randomization test using standard statistical software. *Bull. Ecol. Soc. Am.* 80, 179–180.
- Stohlgren, T.J., Chong, G.W., Schell, L.D., Rimar, K.A., Otsuki, Y., Lee, M., Kalkhan, M.A., Villa, C.A., 2002. Assessing vulnerability to invasion by nonnative plant species at multiple spatial scales. *Environ. Manag.* 29, 566–577.
- Tilman, E.A., Tilman, D., Crawley, M.J., Johnston, A.E., 1999. Biological weed control via nutrient competition: potassium limitation of dandelions. *Ecol. Appl.* 9, 103–111.
- Vilà, M., Weiner, J., 2004. Are invasive plant species better competitors than native plant species? Evidence from pairwise experiments. *Oikos* 105, 229–238.
- Von Holle, B., 2005. Biotic resistance to invader establishment of a southern Appalachian plant community is determined by environmental conditions. *J. Ecol.* 93, 16–26.