Microclimatic Modifications of Cushion Plants and Their Consequences for Seedling Survival of Native and Non-native Herbaceous Species in the High Andes of Central Chile

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Abstract

Cushion plants are one of the most common growth forms in alpine habitats. Their low stature, dense canopy, and compact form allow them to decouple their microclimate from the surrounding environment, mitigating the effect of low temperatures and drought, enhancing the survival of other species. In this study, we evaluated the modifications on soil temperature and moisture over an entire growing season by two cushion species (*Laretia acaulis* and *Azorella monantha*) in alpine communities located at two different elevations in the central Chilean Andes. Additionally, we performed seedling survival experiments with two native herbaceous species (*Hordeum comosum* and *Erigeron andicola*) and the non-native forb *Cerastium arvense* to assess if seedling survival is higher within cushions than outside them. Our results indicated that cushions ameliorated extreme low and high substrate temperatures, improved soil moisture, and enhanced seedling survival of the three herbaceous plant species evaluated. Our results suggest that microclimatic modifications associated with cushion plants could be important for the establishment and survival of other plant species, both native and non-native, in the high alpine communities of central Chile.

Introduction

Alpine areas are characterized by low temperatures, high solar radiation, strong winds, unstable substrates, and short growing seasons (Billings and Mooney, 1968; Körner, 2003). Several different plant growth forms have adapted to grow and reproduce under such harsh environmental conditions (Bliss, 1971; Billings, 1974; Körner, 2003). Cushion-forming plants are one of the most conspicuous plants found in the most exposed alpine habitats and are especially abundant in temperate and subpolar regions, particularly in subantarctic mountains (Körner, 1995).

Due to their low stature and compact form, cushion plants can modify environmental conditions creating particular microclimates within their canopies (Körner, 2003; Cavieres et al., 2006). For instance, Körner (2003) has shown that in the Alps, cushions of *Silene acaulis* are efficient heat traps, maintaining higher temperatures than their surrounding environment. Similar enhancement of temperatures within cushions compared to that of the surrounding air has been reported for cushions of *Azorella monantha* in the Patagonian Andes of southern Chile (Arroyo et al., 2003). Hager and Faggi (1990) reported that cushions in Crete Island and in the southern Argentinean Patagonia reduced the wind velocity by 89–98%, decreasing the convective heat loss. Cushions of *Laretia acaulis* in the Andes of central Chile increase soil moisture (Cavieres et al., 1998) and soil nutrient availability (Cavieres et al., 2006). Most of these examples have been based on short-term records (e.g., single day measurements), and it is not known how persistent these microclimatic modifications are throughout the growing season.

In alpine communities from the Chilean and Argentinean Andes, ca. 30–50% of the plant species occurring in communities dominated by cushions grew more frequently within cushions than outside them (Nuñez et al., 1999; Molina-Montenegro et al., 2000; Badano et al., 2002; Arroyo et al., 2003; Cavieres et al., 1998, 2002, 2006), suggesting that cushions may influence the survival of other species. In alpine habitats, seed germination occurs immediately after snowmelt and successful seedling establishment has been proposed to vary according to substrate temperature and moisture (Chambers et al., 1990; Forbis, 2003). For instance, in sites exposed to constant low temperatures, seedling mortality is high because low temperatures decrease shoot and root growth (Scott and Billings, 1968; Roach and Marchand, 1984) or lower photosynthetic rates, decreasing the net carbon gain and the accumulation of reserves for survival (Billings and Mooney, 1968). In addition, sites exposed to drought during the growing season may experience increased seedling mortality (Bonde, 1968; Stöcklin and Bäumler, 1996; Forbis, 2003). Hence, the microclimatic modifications provided by cushion plants could enhance the survival for seedlings of other plant species. Although the presence of vegetation is important for seedling emergence (e.g., Chambers et al., 1990), results for seedling survival are less clear. While some studies show higher seedling survival in vegetated plots (e.g., Bell and Bliss, 1980), others have shown higher seedling survival in less vegetated patches (e.g., Erschbamer et al., 2001; Forbis, 2003). For the particular case of cushion plants, few studies have experimentally evaluated if there are differences in seedling survival within and outside cushions (see Cavieres et al., 2005, 2006).

In this study, we monitored the influence of two cushion species in the high Andes of central Chile: *Azorella monantha* Clos (Apiaceae) and *Laretia acaulis* (Cav.) Gill. et Hook. (Apiaceae) on soil temperature and moisture during the entire growing season. We also evaluated whether these environmental modifications enhanced survival of seedlings of three herbaceous species: the native grass *Hordeum comosum* J Presl (Poaceae), the native forb *Erigeron andicola* DC (Asteraceae), and the non-native forb *Cersatium arvense* L (Caryophyllaceae).

Materials and Methods

STUDY SITE

This study was carried out near Farellones, in the Andes of central Chile, 50 km east of Santiago. We selected two alpine sites of different elevation. The first site was located at 33°21′S, 70°19′W at 2800 m, on a northwest-facing slope, where vegetation is dominated by the cushion plant *Laretia acaulis*. The second site was located at 33°19′S, 70°15′W at 3600 m, on the summit of Cerro Franciscano, where vegetation is dominated by the cushion plant *Azorella monantha*. The lower and higher elevations correspond with the lower and upper altitudinal limit of cushion plants distribution in the area, respectively (Cavieres et al., 2000). Although cushion plants were the most abundant species in both sites, small annuals of the genus *Chaetanthera*, and rosette-forming perennial herbs such as *Phacelia secunda* and *Nassauvia* spp. also grow both within and outside cushions (Cavieres et al., 2000).

Precipitation in the high Andes of central Chile occurs mainly as snow during the winter. Summers are dry, with occasional rainstorms. Annual precipitation above the treeline (ca. 2200 m) fluctuates between 400 and 900 mm (Santibañez and Uribe, 1990). The growing season at 2800 m usually starts with snowmelt in October and finishes in April with the first snowfall. At 3600 m, the growing season starts in November and finishes in March (field observations). There are no weather stations in the study sites, but in a study conducted in the area during 1996 and 1997, Cavieres and Arroyo (1999) reported mean air temperatures during summer months of 11.4 °C at 2600 m and 6.7 °C at 3150 m. Estimated annual lapse rate for the area was 6.1 °C km^{-1}, with a seasonal variation from 4.7 °C km^{-1} in winter to 7.3 °C km^{-1} in summer (Cavieres and Arroyo, 1999). Thus, mean temperature during the growing season should be ca. 10 °C at 2800 m, and ca. 4 °C at 3600 m.

TARGET SPECIES

Azorella monantha and *Laretia acaulis* are low-growing and tightly knit cushion plants that occur throughout the Andes of Chile and Argentina. The distribution of *A. monantha* ranges from 3200 to 3600 m elevation in the Andes of central Chile at 33°S, to close to sea level at 55°S (Hoffmann et al., 1998). The latitudinal distribution of *L. acaulis* is more restricted and ranges from 30°S to 35°S, and between 2400 and 3200 m elevation (Hoffmann et al., 1998). *Hordeum comosum* J Presl (Poaceae) is a low-growing perennial grass of ca. 10–20 cm height, and is distributed along the southern Andes from central Patagonia in Argentina to central Chile, where it is abundant, particularly above 3000 m elevation (Nicora, 1978). *Erigeron andicola* DC (Asteraceae) is a caespitose perennial herb of ca. 10 cm diameter and 5–10 cm height that can be found from central Patagonia in Argentina to the Andes of central Chile, following the Andean steppe vegetation belt (Hoffman et al., 1998). *Cerastium arvense* L (Cariophyllaceae) is a small perennial herb that forms small mats <10 cm tall in the alpine habitats of central Chile. This species originated in the northern hemisphere and was introduced in Chile during the 19th century, and it now occupies different habitats throughout continental Chile (Matthei, 1995).

MICROCLIMATIC MEASUREMENTS

To characterize the climate in both study sites, air temperature and relative humidity were recorded between January and April 2004 using dataloggers (HOBO Pro RH/Temp, Onset Computer Corporation, Bourne, Massachusetts) placed 1 m above the soil surface. The dataloggers recorded air temperature and relative humidity once each hour.

To assess whether *Azorella monantha* and *Laretia acaulis* cushions maintained different temperatures than the surrounding bare ground, substrate temperatures within and outside cushions were recorded during the growing season, between December 2004 and March 2005. At each site, a temperature probe (TMCx-HD, Onset Computer Corporation) was placed at the center of each of four randomly selected cushions. For each selected cushion, a paired probe was placed in the surrounding bare ground 3 m away from the target cushion and in a random direction, but maintaining a minimum distance of 3 m away from any other cushion. Probes were placed at 2 cm depth and were connected to dataloggers (HOBO H8, Onset Computer Corporation) programmed to record temperature once each hour.

Differences in soil moisture between cushions and bare ground were assessed by measuring the soil matric potential using tensiometers (Jet Fill 2725 Series, Soilmoisture, Santa Barbara, California). These measurements were taken on a single day per site each month from December 2004 to March 2005. Soil moisture measurements were recorded from January to March 2005 at the high elevation site, as snow melts one month later. At each site on each measurement date, 4 cushions and 4 points on bare ground were randomly selected. Tensiometers were dug to 20 cm depth and allowed to stabilize for 1 h before recordings. For each site, soil matric potentials were compared between cushions and bare ground using one-way repeated measured ANOVAs where position (within cushions and outside them) was considered a fix factor.

SEEDLING SURVIVAL

Transplant experiments were performed with seedlings of *Hordeum comosum, Erigeron andicola*, and *Cerastium arvense*. We chose these species because they are present at both study sites, and previous field observations indicated that they have higher incidence and abundance within cushions than outside them (Cavieres et al., 1998, 2006). Seeds of each species, collected during summer 2004 (February–March), were germinated in growth chambers under controlled temperature conditions (20/10 °C day/night) during October 2004. Emerged seedlings from this trial were planted in small plastic bags (100 cm) with commercial soil, and were maintained in a growth chamber at 10/5 °C (day/night) for one month. The one-month-old seedlings were taken to the field, and at each study site, groups of 10 seedlings per species were planted within 6 previously randomly selected cushions and 6 randomly selected points in the bare ground. Seedlings were planted no less then 5 cm from each other. Seedling transplants were carried to the field sites on 15 December 2004 at 2800 m, and on 3 January 2005 at 3600 m. Seedling survival was monitored every two weeks for a total of 120 and 80 days at the lower and higher elevations, respectively. Survival curves of seedlings within and outside each cushion species were estimated by means of the Kaplan-Meier method, and statistical differences were assessed with the Cox-Mantel test (Fox, 1993).

Results

CLIMATIC CONDITIONS

Mean and mean maximum air temperature were higher at 2800 m than at 3600 m, whereas mean minimum temperature was lower at the higher elevation (Table 1). Although mean temperatures indicated that growing season at 2800 m was warmer than at

TABLE 1

Air temperatures and relative humidity at 2800 m and 3600 m elevation in the Andes of central Chile. Values are means ± 2 SE.

	Elevation	
	2800 m	3600 m
Mean temperature (°C)	10.9 ± 1.5	6.8 ± 1.3
Mean maximum temperature (°C)	20.4 ± 4.0	16.4 ± 2.9
Mean minimum temperature (°C)	4.4 ± 2.5	0.1 ± 0.6
Mean daily thermal amplitude (°C)	15.0 ± 2.1	16.9 ± 2.3
Mean relative humidity (%)	43.5 ± 5.2	43.5 ± 5.6

3600 m, this difference occurred only in January and February, and disappeared on March and April (Fig. 1).

At both elevations, maximum soil temperatures, both within and outside cushions, occurred between 13:00 and 16:00 (Figs. 2A and 2B). Cushions always maintained lower soil temperatures than bare ground at 2800 m, although this difference decreased toward the end of the growing season (March) (Fig. 2A). Cushions also maintained lower soil temperatures than bare ground at 3600 m, although the differences tended to be lower than that found at 2800 m, and disappeared at the end of growing season (Fig. 2B).

Soil temperature at 2800 m did not fall below freezing within cushions nor in bare ground during the measurement period. At 3600 m, however, soil temperatures in bare ground dropped to 0 °C or below on 32% of the days monitored, and for 122 h (6.0% of hours). In contrast, soil temperatures within *Azorella monantha* cushions fell below 0 °C only during two days.

At the higher elevation, soil moisture did not differ between *Azorella monantha* cushions and bare ground ($F_{1,6}$ = 0.85; N.S.), although soil moisture changed during the growing season ($F_{2,12}$ = 6.49; $P < 0.05$) (Fig. 3). At the lower elevation (2800 m), soil moisture decreased during the growing season ($F_{3,18}$ = 8.67; $P < 0.01$), and soil moisture beneath *Laretia acaulis* cushions was consistently higher than that on bare ground ($F_{1,6}$ = 73.19; $P < 0.01$) (Fig. 3).

SEEDLING SURVIVAL

At both elevations, seedling survival of the three species used in this study (*Hordeum comosum, Erigeron andicola*, and *Cerastium arvense*) was significantly higher within cushions than outside them (Table 2). In bare ground at 2800 m, a sharp decrease in survival was observed during the first month for *Erigeron andicola* and *Cerastium arvense* seedlings, with <20% of seedlings surviving after 30 days; no seedlings survived by the end of the experiment (Fig. 4). *Hordeum comosum* seedlings in bare ground at this elevation showed a sharp decrease in survival after 40 days, and no seedling survived after 120 days. In contrast, survival after 120 days within *Laretia acaulis* cushions was >28% in *E. andicola* and *C. arvense*, and >80% in *H. comosum* (Fig. 4). At 3600 m, similar patterns of seedling survival were observed for the three species (Fig. 4). Seedlings of *H. comosum* and *E. andicola* showed higher survival in bare ground at 3600 m than at 2800 m.

Discussion

Short-term data showing amelioration of the harsh alpine climate by cushion species have been previously reported for other Andean communities (e.g., Ruthsatz, 1978; Molina-Montenegro et al., 2000; Arroyo et al., 2003; Cavieres et al., 1998, 2006). However, as far as we are aware, this is the first continuous monitoring of the effects of cushion plants on soil temperature and moisture over an entire growing season period, enabling us to observe that while some effects are consistent during the entire growing season, others are not.

Our results indicate that both *Laretia acaulis* and *Azorella monantha* cushion species moderate substrate temperatures, creating more thermally stable sites. During the majority of the growing season cushions of both species maintained lower temperatures than bare ground during the day, but similar temperatures during the night. Soil temperature on bare ground during the day exceeded 30 °C, while temperature within cushions remained below 20 °C. These results suggest that cushion plants moderate substrate temperatures, providing milder habitats when the surrounding environment is relatively hot. The amelioration of high daytime soil temperatures by *L. acaulis* at 2800 was greater than for *A. monantha* at 3600 m, as indicated by the magnitude of the differences between soil temperature within cushions and outside them (Fig. 2), which is probably related to the higher air temperatures at 2800 m than at 3600 m (Fig. 1). At both sites, however, the decoupling in soil temperature was more evident during the middle of the growing season than at the end of the growing season, which corresponds to the period most critical for seedling survival and plant reproduction in this habitat (Arroyo et al., 1981, 1982, 1985). At both elevations there was a decrease in the magnitude of the amelioration effect of cushions with the progress of the growing season, which is clearly related to the decrease in the environmental temperature and proportion of sunny days that occur with the end of the snow-free period.

Arroyo et al. (2003) recorded temperatures during a single day in the Chilean Patagonian Andes (50°S) and reported that cushions of *Azorella monantha* maintained higher substrate temperatures than their surrounding environment. In contrast, we found that cushions of *A. monantha* in the Andes of central

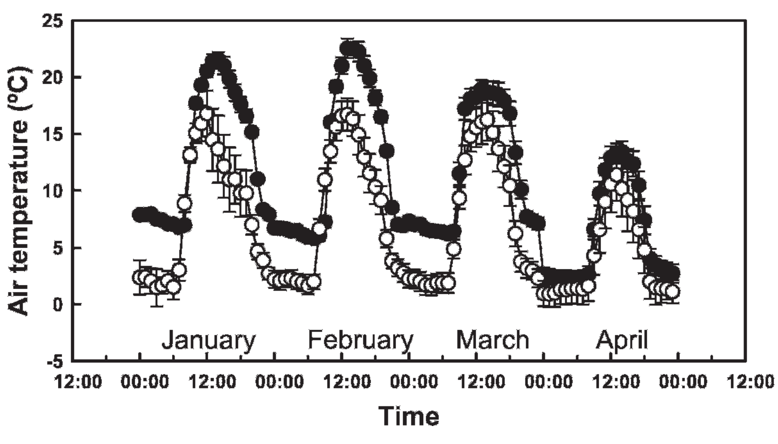

FIGURE 1. Daily cycles of average temperature of air at 2800 m (solid circles) and 3600 m elevation (empty circles). Values are hourly means ± 2 SE for each month during the study period.

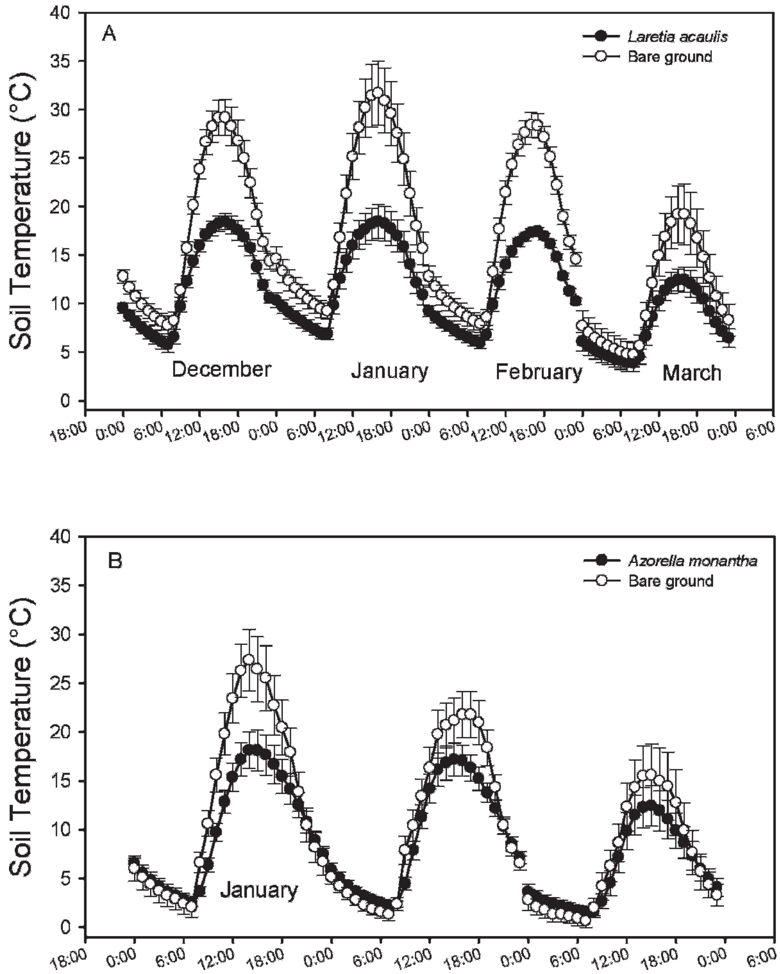

FIGURE 2. Daily cycles of average temperatures (± 2 SE) of substrate within cushion plants and bare ground at 2800 m (A) and 3600 m (B) elevation during one entire growing season.

Chile maintained lower substrate temperatures than its surrounding environments during the day over most of the growing season, but similar temperatures during the night. These results are similar to those reported in Ruthsatz (1978), who found that cushions of *Azorella compacta* in the Bolivian altiplano have lower substrate temperatures during the day, but similar temperatures than their surrounding environment during the night. Unlike the environmental conditions of the Andes of central Chile, the Patagonian Andes are colder and more windy, with ambient temperatures lower than 10 °C during the entire growing season and several days with overcast conditions (Arroyo et al., 2003), which could explain the sharp differences in the warming effect found for *A. monantha* between the two studies.

Our results also indicate that cushions generate microhabitats with less prevalence of extreme temperatures than bare ground, and that the importance of this phenomenon changes with elevation. In bare ground, the proportion of days with freezing temperatures (<0 °C) increased with elevation from 0% at 2800 m to 32% at 3600 m. Within cushions, however, the proportion of freezing days increased very little, from 0% at 2800 m to 1% at 3600 m, suggesting that the importance of cushions for protecting other species from subfreezing temperature effects during the growing season is higher at 3600 m than at 2800 m. Thus, the lower seedling mortality observed within cushions at the higher elevation could be related to a decrease in exposure to freezing temperatures, which protected roots of the herbaceous species from chilling, and from the instability that soil frost activity creates, which is an important cause of seedling mortality in several alpine habitats (Roach and Marchand, 1984). On the other hand, since the proportion of days with temperatures higher than 35 °C was similar at 2800 m (12%) and at 3600 m (14%), we suggest that protection from high temperatures by cushions could

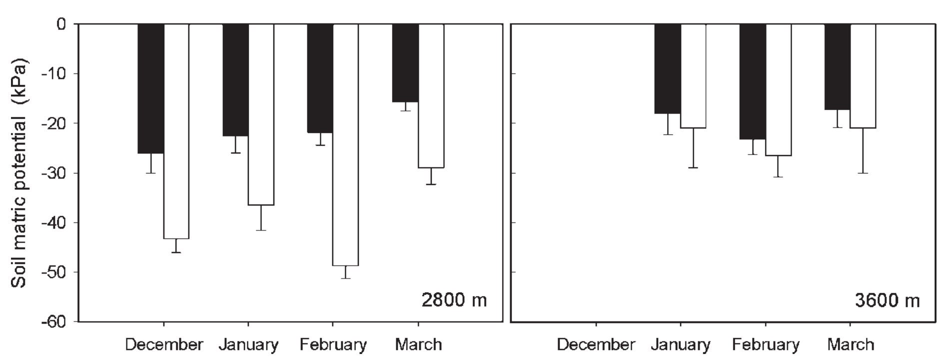

FIGURE 3. Soil matric potentials within cushion plants (black bars) and bare ground (white bars) at 2800 m and 3600 m elevation in the Andes of central Chile.

TABLE 2

Values of Cox-Mantel test for seedling survival in three herbaceous alpine species experimentally planted within and outside *Laretia acaulis* cushions at 2800 m and *Azorella monantha* cushions at 3600 m in the Andes of central Chile.

	Elevation	
Species	2800 m	3600 m
Hordeum comosum	13.4**	7.41**
Erigeron andicola	2.96*	8.34**
Cerastium arvense	7.1**	8.4**

* Indicates $p < 0.05$.
** indicates $p < 0.01$.

be equally important at both elevations. Mitigation of very high temperatures might also be important because it has been shown that temperatures higher than 40 °C could increase seedling mortality by negatively affecting net carbon gain (Körner, 2003).

High temperatures and scarce rainfall characterize the summer in the Andes of central Chile (Cavieres et al., 2006). Previous studies reported that cushion plants can enhance soil water availability in some alpine habitats (Griggs, 1956; Körner and De Moraes, 1979; Cavieres et al., 1998, 2006). In our study, soil moisture did not differ between bare ground and beneath cushions at 3600 m elevation, while at the lower elevation site soil moisture beneath cushion was higher than that on bare ground. The differences in soil matric potential between the bare ground and cushions at 2800 m and the lack of difference at 3600 m were consistent throughout the entire growing season. These results are consistent with others previously reported for the same study area. For example, Cavieres et al. (1998) found that gravimetric soil

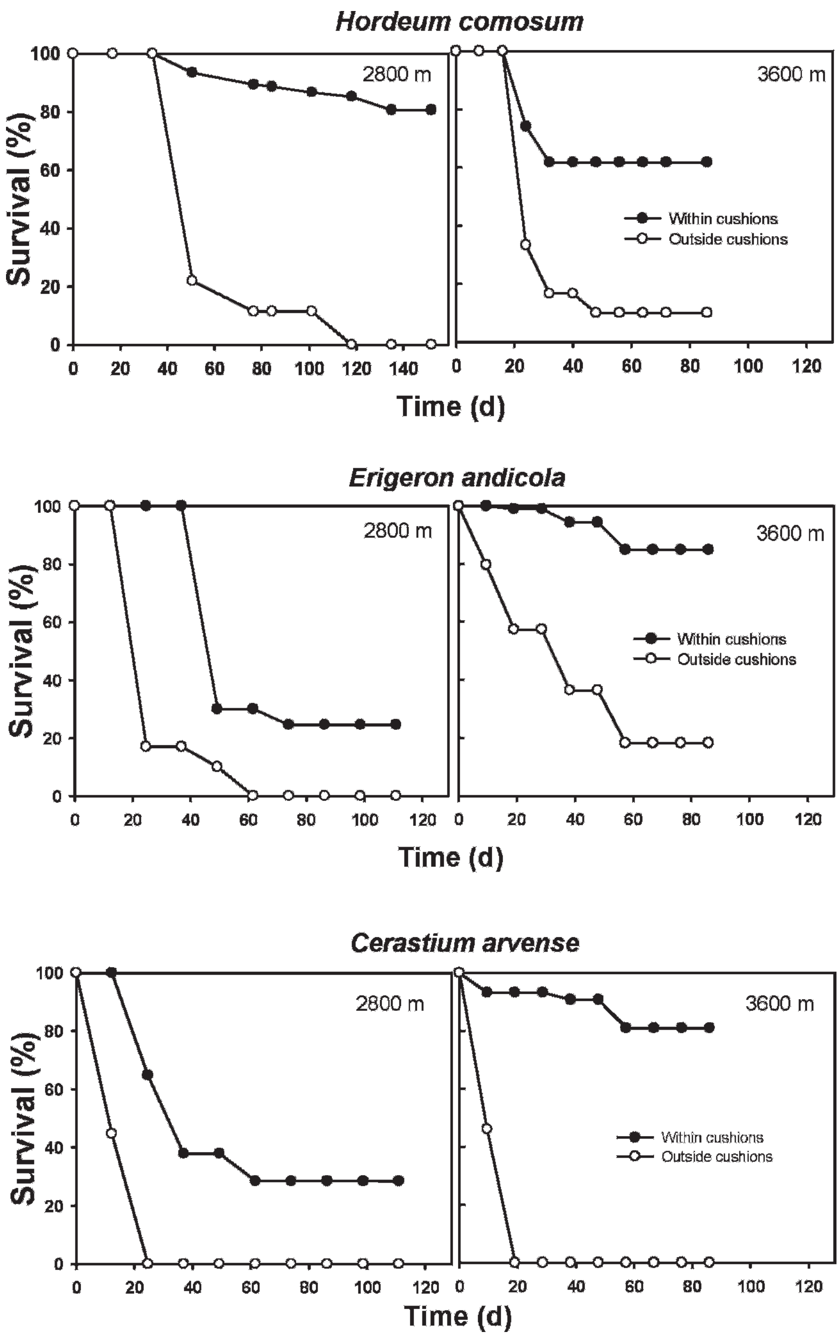

FIGURE 4. Kaplan-Meyer estimated survival of seedlings of *Hordeum comosum, Erigeron andicola*, and *Cerastium arvense* planted within cushions and bare ground at 2800 m and 3600 m elevation in the Andes of central Chile.

moisture on a single day in the mid-summer at 2800 m was higher beneath *Laretia acaulis* than bare ground. More recently, Cavieres et al. (2006) reported that the difference in moisture between *L. acaulis* cushion plants and bare ground at 2800 m increased over the course of the growing season during 2003 and 2004. Our results in the present study showed a similar pattern (Fig. 3), although the occurrence of small storms in March decreased the differences between the two microhabitats. The higher availability of water detected within *Laretia acaulis* cushions at the lower elevation may have been partially responsible for the increased survival of seedlings from desiccation. Seedling desiccation has been suggested as one of the most important causes of seedling mortality in alpine habitats (Bell and Bliss, 1980; Scherff et al., 1994; Stöcklin and Bäumler, 1996; Forbis, 2003). Moreover, the milder temperatures observed within cushions suggest that water loss due to evaporation could be lower within cushions, which is very important for the water economy of seedlings. For instance, in the alpine of southwestern U.S.A., Mooney et al. (1965) showed that transpiration rates of alpine species may exceed soil water absorption during drought events, producing strong water deficits and causing tissue injury and plant death. Thus, cushions may ameliorate the effects of drought events by providing moister and cooler microhabitats for recruitment of other species. Therefore, while amelioration of freezing temperatures can be more important at higher than at lower elevations, drought amelioration seems to be more important at lower than at higher elevations.

Several authors have suggested that the microclimatic modifications generated by cushions are related to higher occurrence and abundances of some plant species within cushions (Cavieres et al., 1998; Nuñez et al., 1999; Molina-Montenegro et al., 2000; Badano et al., 2002; Cavieres et al., 2002; Arroyo et al., 2003). Our transplant experiments demonstrated that cushions enhanced seedling survival of three herbaceous species in comparison with bare ground. Cavieres et al. (2006) reported that *Hordeum comosum* and *Cerastium arvense* are positively associated with *Laretia acaulis* cushions at 2800 m, whereas *Erigeron andicola* can be found growing only within cushions at this elevation. Badano et al. (2006) reported that at 3600 m *C. arvense* and *E. andicola* occurred only within *Azorella monantha* cushions, whereas *H. comosum* was significantly associated with cushions. Hence, it seems likely that the higher abundance within cushions of three study species is related to a higher survival of seedlings due to the microclimate generated by cushions. However, other processes (e.g., seed trapping, seed germination) also contribute to the greater abundance of these species in cushions. Regardless of the mechanism(s), cushions are establishing a positive interaction with other species of the community, facilitating the survival of some herbaceous species. Positive interactions among plants have been hypothesized to be particularly important in stressful habitats such as deserts, salt marshes, and dunes (Callaway, 1995). Recent studies have demonstrated that positive interactions are very important in alpine habitats as well (Kikvidze, 1996; Kikvidze and Nakhutsrishvili, 1998; Choler et al., 2001; Callaway et al., 2002), where the mitigation of extremely low temperatures and severe winds due to the presence of neighbors has been suggested as the main mechanism behind these positive interactions (Choler et al., 2001; Callaway et al., 2002). According to our result, drought mitigation might be another important mechanism for positive interactions in the alpine, particularly in arid mountains.

Finally, it is worth noting that one of the species evaluated in this study is non-native (*Cerastium arvense*). The climatic harshness of alpine habitats has been hypothesized to limit the successful establishment of non-native invasive species (Willard and Marr, 1971). However, several studies have reported the presence of non-native species in a number of alpine habitats (e.g., Johnston and Pickering, 2001; Dullinger et al., 2003; Arévalo et al., 2006; Beccker et al., 2006; McDougall et al., 2006). Although negative interactions among native and exotic species are proposed to be a key in explaining invasion success, recent studies have highlighted the importance of positive interactions among species in explaining invasion success (Simberloff and Von Holle, 1999; Richardson et al., 2000). Our results with *Cerastium arvense* indicate that cushions are facilitating the establishment of a non-native species at different elevations along the central Chilean Andes. This result concurs with a recent study of Cavieres et al. (2005) demonstrating that the non-native species *Taraxacum officinale* is facilitated by *A. monantha* cushions at 3200 m in the Andes of central Chile. Thus, our results, as well as other recent studies, highlight the role of native species in facilitating rather than constraining non-native plant invasions, particularly in stressful habitats such as alpine environments.

Conclusions

By monitoring soil microclimate during one entire growing season, we showed that two different species of cushion plants moderate soil temperatures and that one of these cushion species can change soil moisture. The microclimatic changes induced by cushions are correlated with a higher survival of seedlings of three herbaceous species within cushions, suggesting that cushions provided microhabitats more suitable for seedling establishment in the alpine ecosystems of central Chile. Moderation of extreme low substrate temperatures by cushion plants seems to be important for enhancing seedling establishment at higher elevations, while the enhancement of soil moisture occurred at lower elevations. One of the herbaceous species evaluated is non-native, suggesting that cushions can facilitate rather than constrain non-native plant invasions in the alpine habitats of the Andes. While the common climatic feature of alpine habitats is low air temperature, alpine communities vary enormously with respect to precipitation and wind conditions. Therefore, only long-term monitoring efforts of the microclimatic conditions generated by plants in combination with experiments and/or observations of their consequences for seedling survival will provide insights about the ultimate factors determining successful plant establishment in harsh alpine habitats.

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