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Authors: Kleier, Catherine, and Lambrinos, John G.

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The Importance of Nurse Associations for Three Tropical Alpine Life Forms

Catherine Kleier* and
John G. Lambrinos†

*Department of Biology, Metropolitan State College of Denver, Science Building 213, Campus Box 53, P.O. Box 173362, Denver, CO 80217, U.S.A.
ckleier@mscd.edu
†Department of Environmental Science and Policy, University of California, One Shields Avenue, Davis, CA 95616, U.S.A.
jglambrinos@ucdavis.edu

Abstract

We investigated biotic and abiotic associations for four growth forms in Chile's Parque Nacional Lauca, a tropical alpine puna ecosystem. We determined the biotic associations between *Parastrephia lucida* (Meyen) Cabr. [Asteraceae] and *Festuca orthophylla* Pilger. [Poaceae]. To determine if *F. orthophylla* was acting as a nurse plant for *P. lucida*, we used chi-square analysis to test for nurse plant effects. Our results indicated that *F. orthophylla* roots more often on bare ground and that *P. lucida* grows more often in association with *F. orthophylla* than would be expected. In testing for abiotic associations, we observed that both a tree, *Polylepis tarapacana* [Rosaceae], and a cactus, *Tephrocactus ignescens* [Cactaceae], showed positive abiotic associations with large boulders. These studies indicate that in an extreme environment, such as the South American puna, abiotic and biotic associations are important for plant survival.

Introduction

Examples of positive interactions shaping plant community dynamics and spatial structure are becoming increasingly well known (Bertness and Callaway, 1994; Callaway, 1998; Hacker and Gaines, 1997). How the strength and importance of positive interactions varies across ecosystems, however, is far from clear (Callaway and Walker, 1997). When abiotic stress is high, positive interactions become more important for plant survivorship; thus, facilitation is expected in stressful environments such as salt marshes (Hacker and Bertress, 1999), cobble beaches (Bruno and Kennedy, 2000), sand dunes (Kellman and Kading, 1992), desert (Cody, 1993), alpine (Callaway et al., 2002), and tundra ecosystems (Chapin et al., 1994).

In addition to facilitation, microhabitat plays an important role in shaping community patterns, particularly for recruitment and juvenile success (Sterling et al., 1984). Microhabitat requirements may differ between adults and juveniles (Ibañez, 2002). Abiotic structures may also play a role in creating adequate microhabitats for seed germination or seedling establishment. For example, a juvenile may need the shade and increased water availability from a large boulder (Nobel et al., 1992). Although facilitation and microhabitat have been studied individually, in this study we look at the combination of the two factors. We set out to determine the roles of facilitation and of abiotic microhabitat among three different plant growth forms: a tree, a cactus, and a shrub.

The high altitude, dry tropical region of the Andes is also known as a puna ecosystem. This landscape is semiarid (200–300 mm yr^{-1}), receives high irradiation, and has diurnal temperature fluctuations that may exceed 40°C. Because this area is tropical, but also high altitude, diurnal temperature variation is greater than seasonal temperature variation, thus being characterized as "summer every day and winter every night" (Rundel, 1994). Because of these stresses, nurse plant associations could have an important influence on community patterns.

In desert ecosystems, trees generally act as the nurse plants themselves, rather than needing a nurse for establishment, particularly leguminous trees such as *Olneya tesota*, ironwood (Suzan et al., 1996) and *Cercidium* spp., palo verde (Turner et al., 1966). For ironwood, it has been demonstrated that the nurse tree effects whole community diversity and is not limited to the facilitation of only one species (Tewksbury and Lloyd, 2001). In the Puna ecosystem, a high altitude tree, *Polylepis tarapacana*, may play a similar role. We investigated positive associations of *P. tarapacana* with other plants and with large boulders.

Shrubs often act as nurses for other herbaceous species (Shumway, 2000) and even as nurses for tree seedlings in revegetation programs (Castro et al., 2002). However, it has also been reported that seed predation by rodents increases under a shrub canopy (Rousset and Lepart, 2000). The puna also has a rich diversity of rodent herbivores, most notably the mountain viscacha, *Lagidium viscacia* [Rodentia]. This high rodent predation could drive reciprocal facilitation between bunch grasses and shrubs. Although grasses have also been shown to compete with establishing seedlings (Koukoura and Menke, 1995), here we test the hypothesis that establishment of a shrub is more common in the vicinity of bunchgrasses than in open soil.

The need for nurse plants has been well established for cacti. Saguaro will not germinate unless shaded by some other plant (Niering et al., 1963). The benefits of shade from a nurse plant to young cactus seedlings have also been demonstrated with leguminous trees (Arriaga et al., 1993), and leguminous trees may also protect cactus seedlings from frost (Nobel, 1980). Because the irradiation is so intense in this high altitude region and because temperatures may drop below freezing any night of the year, cacti may require facilitation to persist in the high puna. Here, we test the hypothesis that cacti will occur more frequently with large boulders than in open soil.

Materials and Methods

STUDY AREA

This study was conducted at Parque Nacional Lauca, Chile (18°12′S, 69°16′W) between 4000 and 4500 m above sea level (a.s.l.). The study site is located near a large lake, Laguna Chungara, and large series of smaller lakes, Lagunas Cotacotani. Laguna Chungara has a surface area of 21.5 km^2, and it is one of the highest lakes in the world at 4517 m a.s.l. (CONAF, 1986). Additionally, there are two high volcanoes on the eastern border of the park: Volcan Parinacota (6342 m a.s.l.) and Volcan Pomerane (6252 m a.s.l.).

The climate of P. N. Lauca is semiarid, with annual rainfall between 200 and 300 mm. Rainfall occurs seasonally, with the majority occurring between December and March, the so-called "Invierno Boliviano" (CONAF, 1986). Diurnal temperature variation for this region varies greatly, sometimes as much as 40°C in one day. Typical highs between December and March are 15°C, with lows around 0°C.

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TABLE 1

Percent cover of substrate, total plant cover, and *Polylepis tarapacana* between a high ridge site and a lower site within a boulder field is shown. Percentages do not sum to 100 because of overlap. An asterisk marks a significant difference of $p < 0.01$ as determined by Student's *t*-test.

	Rock (%)*	Sandy soil and cobble (%)*	Total plant cover (%)	*P. tarapacana* cover (%)
Higher site	14.95 ± 3	68.5 ± 3.4	19.1 ± 2.9	8.5 ± 2.8
Lower site	48.5 ± 12.6	28.3 ± 9.9	25.6 ± 16	9.5 ± 6.1

Parque Nacional Lauca is dominated by four main vegetation types. In low lying areas, bofedales (wet areas) are dominated by cushion-forming members of the Poaceae, Cyperaceae, and Juncaceae as described in Ruthsatz (1993). Just above the bofedales, and if sandy soils are predominant, mixed grasses and shrubs will predominate. On rocky slopes, diversity is higher than on sandy flats. If the slopes are north facing, a giant cushion plant, *Azorella compacta*, dominates (Kleier and Rundel, 2004). Slightly higher in elevation, rocky slopes are dominated by a low-growing tree, *Polylepis tarapacana*. The key plant communities are further described by Rundel and Palma (2000).

STUDY SPECIES

For this study, we investigated spatial dynamics for four species: *Polylepis tarapacana* Phil. [Rosaceae], *Festuca orthophylla* Pilg [Poaceae], *Parastephia lepidophylla* (Wedd.) Cabr. [Asteraceae], and *Tephrocactus ignescens* (Vaupel) Backeberg [Cactaceae]. *Polylepis tarapacana* forms possibly the world's highest forests, occurring up to 5100 m a.s.l. (Simpson, 1979). It is a low-growing, shrubby tree, reaching approximately 1–6 m in height with crown diameters ranging from 3 to 5 m (Kessler, 1995). It has been noted that the *Polylepis* forests are more dense in areas of increased rainfall, such as near large lakes and volcanoes (Braun, 1997). *Polylepis* is important both for ecosystem health and human use. The World Conservation Monitoring Centre has listed the genus *Polylepis* as "conservation dependent" (Hjarsen, 1997). *Festuca orthophylla* is a bunch grass that grows only a short time of the year, thus giving it an appearance like straw. One common name for this species is "paja brava" (wild straw). This bunchgrass is an important component of grazing for alpaca and llama, even though it has relatively low nutritive value (Genin et al., 2002). *Parastrephia lepidophylla* is a shrub that grows in sandy soils and commonly reaches 70–110 cm in height. It has been reported that *P. lepidophylla* is locally used as fuel for baking in Peru (Linares and Benavides, 1995). *Tephrocactus ignescens* is a cushion-forming cactus with spherical cladodes; it grows to about 50 cm in height and can reach a diameter of 100 cm. Although it is not grazed, the fruits are edible and eaten by local villagers near Arequipa, Peru (Vargas, 1988).

SAMPLING OF POLYLEPIS TARAPACANA

On 18–20 November 2000, two 25 × 15 m plots were constructed to determine *Polylepis* distribution. One plot was on a ridge top on the north side of highway 1 at 4650 m a.s.l. and had a slope of 13°. The other plot was located on a rocky slope of 18° about 2 km south of highway 1 (18°12′49.2″S, 69°13′22.5″W) at an altitude of 4635 m a.s.l. Four diagonal 25-m transects through both plots were laid, and all vegetation directly underneath the transects was recorded; bare ground was recorded as rock, cobble, or sandy soil. The following characteristics were recorded for each *P. tarapacana* individual within each plot: height, perimeter of the base of the trunk, and two widths of the canopy. If a large (>50 cm diameter) boulder occurred within a 1-m diameter of the tree, an association with a boulder was recorded for that individual. Maps of the plots were constructed to provide a visual image of the density and distribution of *P. tarapacana* and to determine qualitative association the trees with boulders. Temperature loggers (Onset HOBO® H8 Pro Temperature Loggers, Onset Computer Corporation, Pocasset, MA) were placed in both plots to determine differences potentially caused by a greater number of large boulders in the rocky plot.

SAMPLING OF FESTUCA ORTHOPHYLLA *PILG. AND* PARASTEPHIA LEPIDOPHYLLA *(WEDD.) CABR.*

Between 15 and 18 January 2000, four 25 × 25 m plots were constructed on open sandy flat areas within P. N. Lauca approximately 2 km northwest of the village of Parinacota. In these plots, all *P. lepidophylla* individuals were censused. If an *F. orthophylla* individual was present within 5 cm of the base of *P. lepidophylla*, an association was marked. Occasionally, a mat-forming species of *Azorella* sp. was also found within 5 cm of either *F. orthophylla* or *P. lepidophylla*, and such associations were noted for both species. Chi-square analysis was used to test for nurse plant effects. Expected numbers were calculated by multiplying the percentage of coverage of bare ground or vegetation times the total number of plants of a given species within the plot. Species richness was not measured in these plots since the overwhelming majority of species were either *F. orthophylla* or *P. lepidophylla*. On 14 January 2000, soil samples were taken in open soil and underneath *P. lepidophylla* shrubs to test for relative water content.

SAMPLING OF TEPHROCACTUS IGNESCENS

On 13 January 2000, six 25 × 25 m plots were established. Four plots were located in rocky flats, and two plots were located within 50 m of the rocky plots on sandy flats. Within each plot, all individuals of *Tephrocactus ignescens* were counted and all bunchgrass or boulders (>50 cm diameter) adjacent to the cacti were noted. A two-channel temperature logger (Onset HOBO® H8 Pro Temperature Logger) was placed at 5-cm and 10-cm depths into the root zone of *T. ignescens* growing in the rocky flats. This logger ran from 13 to 20 January 2002. From 20 to 27 January, the same two-channel logger measured temperatures on the surface and at 5-cm depth into the canopy of *T. ignescens*.

Results

POLYLEPIS TARAPACANA

The two sites of *Polylepis tarapacana* differed in substrate, but the sites did not differ in percentage of total plant cover or in percentage cover of *P. tarapacana* (Table 1). The lower site had more rocks, large boulders, but less cobble and sandy soil, while the higher ridge site was the opposite with more sandy soil and cobble than large boulders (Table 1). Species richness was about the same for both sites. Six species occurred at both the lower boulder site and the upper ridge site (Table 2). *Parastrephia lucida* (Meyen) Cabr. [Asteraceae] was not present on the ridge site, and *Festuca orthophylla* Pilger. [Poaceae] was not present in the lower site. As *P. tarapacana* occurred in robust populations at both sites, positive associations with either the shrub, *P. lucida*, or the bunchgrass, *F. orthophylla*, were not evident.

Although a difference in percent cover of *P. tarapacana* was not detected in the transect analysis, there was a difference in overall densities as measured by the plot censuses. The higher ridge plot contained only 48 individuals, while the lower boulder plot contained 75 individuals, and the plots were both 375 m^2. Trees were slightly taller at the lower site, mean = 0.79 m, than at the ridge site, mean = 0.573, although this difference was not significant as determined by a *t*-test ($p = 0.06$). The population structure between the two plots

TABLE 2

Species richness within two plots of *Polylepis tarapacana*. Numbers are means of four 25-m transects presented as percentages of total cover ± the standard deviation of the mean. The higher site refers to a plot located on a ridge, while the lower site represents a plot that was located among larger boulders.

Species [Family]	Higher site	Lower site
Polylepis tarapacana [Rosaceae]	8.5 ± 2.8	9.5 ± 6.1
Parastrephia lucida [Asteraceae]	0	3.5 ± 2.3
Parastrephia quadrangularis [Asteraceae]	1.5 ± 1.9	1.5 ± 1.2
Senecio rufescens [Asteraceae]	0.4 ± 0.4	0.3 ± 0.3
Picnophyllum bryoides [Caryophyllaceae]	0.5 ± 0.9	1.4 ± 0.9
Picnophyllum macropelatum [Caryophyllaceae]	2.2 ± 1.7	1.1 ± 1.7
Festuca orthophylla [Poaceae]	2.5 ± 3.0	0
Azorella compacta [Apiaceae]	1.1 ± 1.4	6.0 ± 7.1

appeared to differ with the boulder plot having a higher frequency of smaller seedlings than the ridge site (Fig. 1). Pooling both sites, positive associations with boulders were strong. Out of 120 individuals in both plots, only two occurred out of the vicinity (within 10 cm) of a large boulder (Fig. 2). The boulder site had slightly warmer temperatures than the ridge site, particularly at night (Fig. 3).

FESTUCA ORTHOPHYLLA *AND* PARASTREPHIA LEPIDOPHYLLA

For each plot surveyed, vegetation cover was estimated at 20% by a visual survey. Much bare ground was encountered, and the soils were sandy and visibly dry. Diurnal relative water content was measured both underneath *Parastrephia lepidophylla* and in the open soil (Table 3). Water content was always slightly greater in open soil, though these differences were not statistically significant.

Densities of *F. orthophylla* averaged 0.482 plants m^{-2}, and densities of *P. lepidophylla* averaged 0.156 plants m^{-2}. *Festuca orthophylla* did not form an association with *P. lepidophylla*, since *F. orthophylla* was found growing on bare ground more often than expected (mean $X^2 = 85.44 \pm 63.68$, $p \leq 0.001$). Of 390 *P. lepidophylla* individuals, none formed intraspecies associations with other *P. lepidophylla*. However, *P. lepidophylla* did form associations with *F. orthophylla* (mean $X^2 = 73.1 \pm 21.12$, $p \leq 0.001$) (Fig. 2).

TABLE 3

Relative water content taken from soil samples at 5-cm depth on 14 January 2000 at 8:00 a.m., 12:00 p.m., and 4:00 p.m. Samples were weighed and then oven dried for 36 h, and then reweighed.

	8:00 am	12:00 pm	4:00 pm
Under *P. lepidophylla*	21% ± 0.04%	21.5% ± 0.01%	20.3% ± 0.003%
In open soil	24% ± 0.01%	22.3% ± 0.02%	24.6% ± 0.002%

TEPHROCACTUS IGNESCENS

Density of *T. ignescens* averaged 0.0208 m^{-2} in four 25 × 25 m plots with more than 50% rock cover. In two 25 × 25 m plots with more than 50% sand cover, density averaged 0.004 plants m^{-2}. In the rocky plots, all *T. ignescens* were associated with boulders. In the sandy plots, all *T. ignescens* were associated with the bunchgrass, *Festuca orthophylla* (Fig. 2).

Discussion

This study supports the hypothesis that different life forms all use facilitation in a tropical alpine environment. In our study, facilitation occurred with either a large boulder for the tree (*P. tarapacana*), or with a bunch-grass for the shrub (*P. lepidophylla*). The cushion-forming cactus (*T. ignescens*) had positive associations with both boulders and bunchgrass. There were also varying dependencies on facilitation for the three growth forms. The tree did not have obligate facilitation, but the cactus did have an obligate facilitation requirement as no cacti were found that were not associated with either a boulder or a bunchgrass. The shrub was intermediate; it occurred more often by a nurse plant of the bunchgrass, but the bunchgrass was not obligate for shrub establishment.

There have been other studies of nurse associations with trees in tropical alpine regions. Smith (1984) has shown evidence of nurse tree

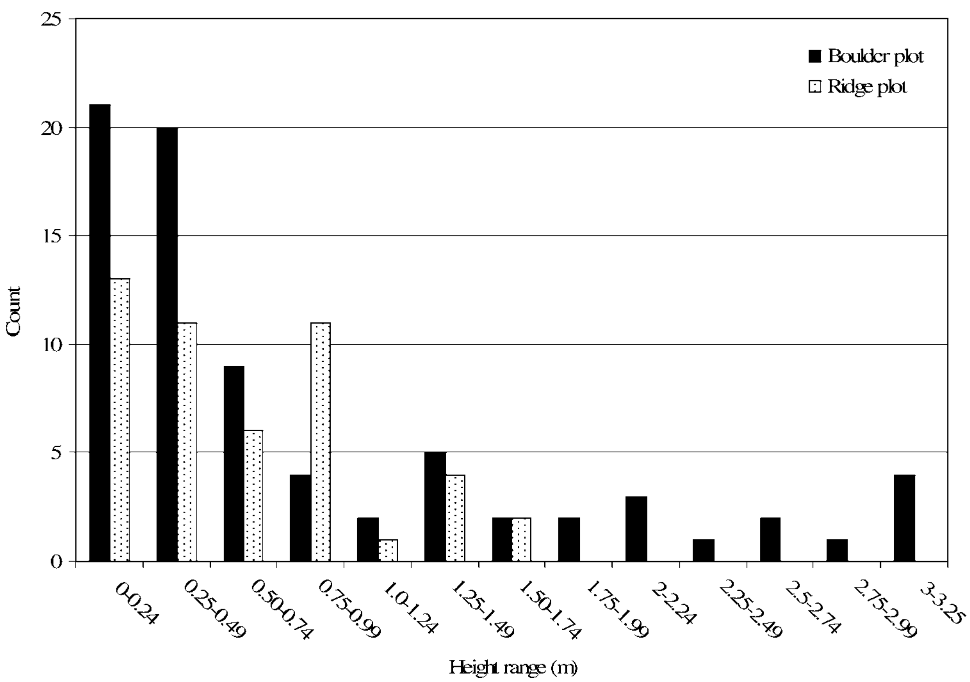

FIGURE 1. Population structure based on height for plots of *Polylepis tarapacana* from a boulder-dominated site and a ridge site. Plots were both 25 × 15 m and located at Parque Nacional Lauca, Chile.

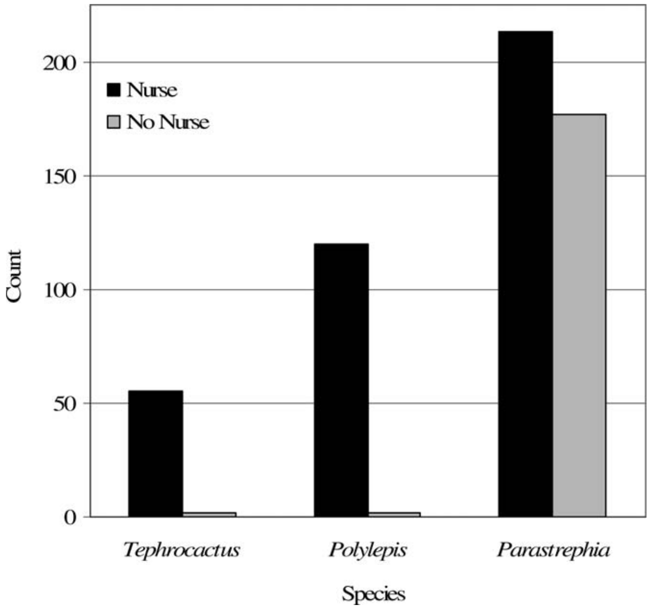

FIGURE 2. Histogram showing three species associations with other nurse plants or boulders (nurse). *Tephrocactus ignescens* is a cactus showing an obligate association with either a boulder or a bunchgrass. *Polylepis tarapacana* is a small tree showing an obligate association with a boulder, and *Parastrephia lepidophylla* is a shrub showing a greater association with bunchgrass (nurse) than shrubs in open soil (no nurse).

effects with *Senecio keniodendron* in Africa and also with *Espeletia schultzii* in South America. However, these associations are conspecific with other older trees acting as nurses for younger seedlings of the same species. Perez (1992) has demonstrated the effect of nurse rocks in a giant rosette plant, *Coespeletia tomentosis*. However in that study, boulder fields were providing more stability than bare ground. Because the slope angles were smaller in our study, the mechanism of support by the nurse is probably not soil stability. In another study by Perez (1991), boulders provided enhancement of soil moisture in the immediate environment. Soil moisture content was demonstrated to be higher in the vicinity of large boulders in P. N. Lauca during another study (Kleier and Rundel, 2004), so this is a probable explanation for positive associations between *P. tarapacana* and large boulders. Additionally, the temperature data from this study indicate that air temperatures just above the soil are warmer when boulders comprise more of the ground cover than sand. This difference may be especially important at night when freezing temperatures could limit seedling survival.

For the shrub *P. lepidophylla*, the bunchgrass *F. orthophylla* was acting as the nurse. Other cases of herbaceous plants acting as nurse plants for woody species are well documented (Buckley, 1984), though not all species are equally effective as nurses due to the possibility of competition (Connell and Slatyer, 1977). A valid question in the discussion of this nurse association has to do with recruitment versus establishment. It may be that *P. lepidophylla* grows preferentially near *F. orthophylla* simply because the bunchgrass is serving as a seed trap along the otherwise barren sandy soil. However, the bunchgrass may be acting as a facilitator for germination. Certainly, the first hypothesis is valid, though wind speeds in this area were never measured higher than 5 m s^{-1} (Kleier, 2001), so long-distance seed distribution from wind may not be a large factor. Additionally, there was no evidence of conspecific nurses, which would be expected if the bunchgrass, and potentially other *P. lepidophylla* shrubs, were acting only as seed traps.

Lastly, because the bunchgrass has fibrous roots (Linares and Benavides, 1995) and the shrub has longer taproots (Kleier, 2001), presumably to tap deeper water, the potential for competition would be lessened between the two species. Grass production can actually increase shrub production in some dryland areas (Williams et al., 2002). *Festuca orthophylla* has been used for restoration of a roadcut in central Peru, but it was not tested in terms of facilitating shrub survival (Woodward, 2001). Future studies of this grass in restoration could prove useful, particularly in central Chile, where the need for revegetation is great due to the degradation of the natural vegetation (Aronson et al., 1993).

Nurse plant associations for succulents are also well documented (Cody, 1993; Franco and Nobel, 1989; Niering et al., 1963). However, in these studies, it is another plant that is providing the nurse effect. In this study, the succulent *Tephrocactus ignescens* is sometimes using a boulder, and not always another plant, as a nurse. A boulder as a nurse prevents some challenges to the seedling that may become apparent during maturity. When a seedling matures, it may compete with the original nurse plant, and thus be limited in its productivity (Cody, 1993). A boulder could provide some of the same protection as a nurse plant and still avoid future competition. A large boulder will provide shade to a developing seedling, shading of the soil and thus reduced soil

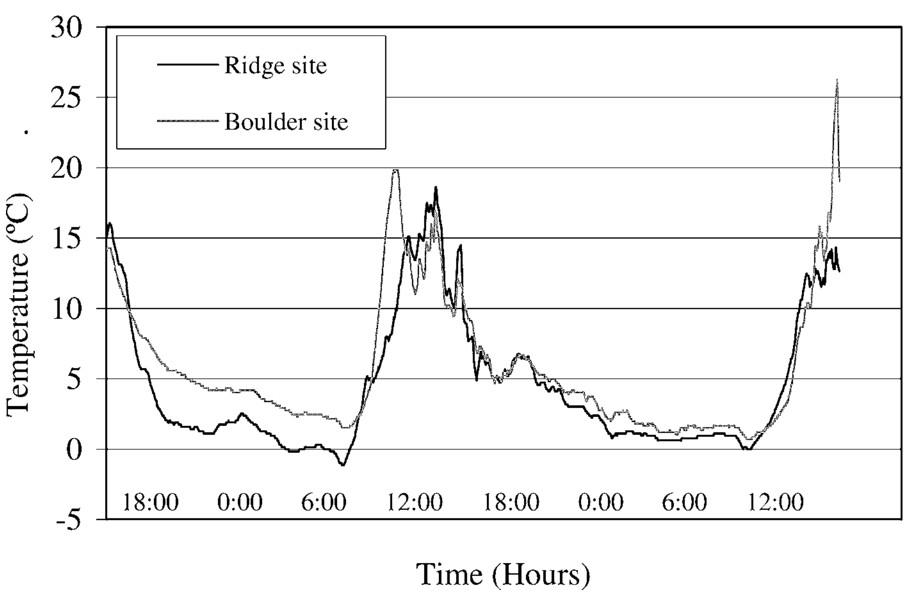

FIGURE 3. Temperature differences measured on 18–20 November 2000 for the two sites of *Polylepis tarapacana* at Parque Nacional Lauca. The ridge site contained far fewer large boulders than did the boulder site.

evaporation, and smaller temperature fluctuations. Due to the importance of boulder facilitation in desert areas (Pugnaire and Haase, 1996), the use of boulders could be an important consideration for restoration.

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