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Postdispersal Seed Predation on *Sisyrinchium arenarium* (Iridaceae) at Two Elevations in the Central Chilean Andes

Alejandro A. Muñoz and
Mary T. K. Arroyo

Laboratorio de Sistemática y Ecología
Vegetal, Facultad de Ciencias,
Universidad de Chile, Casilla 653,
Santiago, Chile.
amunoz@ciencias.uchile.cl

Abstract

Postdispersal seed predation in alpine communities has received surprisingly little attention. We evaluate the magnitude of seed predation by ants and avian granivores in the perennial herb *Sisyrinchium arenarium* through a field experiment at two different elevations (2700 and 2000 m) in the central Chilean Andes. A total of 96 pots, containing 50 seeds each, were placed at each elevation and randomly assigned to one of four treatments: control, bird exclusion, ant exclusion, and total exclusion (wind control). We also compare the activity of ants and avian granivores at the two elevations. Mean percentage seed removal by wind was 23 and 21% at 2700 and 2000 m elevation, respectively. Overall, after subtracting seed loss by wind, seed removal by granivores was low at both sites (2–14%), although it was significantly greater at the higher elevation (2700 m). This was concordant with the greater activity of ants and granivorous birds there. Seed removal by ants was greater than by birds at the higher site (14 vs. 4%, respectively), but did not differ at the lower elevation (3 vs. 2%, respectively). Results contrast with those reported for central Chilean mediterranean-type climate shrublands at lower elevations where avian and rodent granivory is important, while that by ants is low. Future studies considering plant species with different seed characteristics (e.g., size, shape, energetic value) and taxonomic affiliation will be necessary to assess the general importance of this ecological process in the central Chilean Andes and alpine areas in general.

Introduction

Postdispersal seed consumption by animals can have important effects on plant fitness, regeneration, species composition and the structure of plant communities (Janzen, 1971; Harper, 1977; Brown et al., 1986; Louda, 1989, 1995; Mackay, 1991; Wenny, 2000). Studies conducted in a wide range of environments have found postdispersal seed predation to be especially high in mediterranean-type climate shrublands (see reviews by Parker and Kelly, 1989; Louda, 1995), tropical forests (Schupp, 1988, 1990), temperate forests (Andersen, 1987; Whelan et al., 1991; Díaz et al., 1999) and, semiarid and desert lands (e.g., Davidson et al., 1985; Wellington and Noble, 1985; Brown et al., 1986; Brown and Heske, 1990). Activity of seed predators in these vegetation types has been shown to vary both spatially and temporarily, resulting in differences in the intensity of predation on seeds (e.g., Schupp, 1988, 1990; Whelan et al., 1991; Bustamante and Vásquez, 1995). Among the most important groups of postdispersal seed predators are ants, birds, and rodents (e.g., Abbott and van Heruck, 1985; Brown et al., 1986; Andersen, 1987; Pierce and Cowling, 1991; Díaz et al., 1999).

In contrast to the substantial amount of research on postdispersal seed predation carried out in low-elevation habitats, postdispersal predation has received surprisingly little attention in alpine environments (McGraw and Vavrek, 1989; Körner, 1999), although a limited number of studies have quantified seed losses to predispersal predators in the French Alps (Hemborg and Després, 1999), Swedish subalpine localities (Molau et al., 1989), New Zealand's Alps (Kelly and Sullivan, 1997), and Rocky Mountains, U.S.A. (Galen, 1990). This contrasts with the

large number of studies conducted on plant-pollinator interactions in these ecosystems (e.g., Arroyo et al., 1982, 1985; Erhardt, 1993; Totland, 1994; Bingham and Orthner, 1998; Sandvik et al., 1999).

The alpine habitat occurs above forests, deserts, and typical mediterranean-type ecosystems, and as such, levels of seed predation could be very different. A characteristic of alpine ecosystems is their low ambient temperature. In continental mountains temperatures decrease by approximately 6.5°C per 1000 m increase in elevation. Wind speeds of up to 200 km h⁻¹ have been measured at exposed sites in some mountain stations, although such high winds are invariably alternated with many calm days at high elevations (Körner, 1999). Insect pollination is abundant in alpine ecosystems, whereas bird pollination is uncommon (Körner, 1999). The spectrum of pollinators changes with elevation and is related to capacity to thermoregulate under low ambient temperatures (Arroyo et al., 1982; Corbet, 1990). Among seed predators, ambient temperature has been shown to affect the activity of both ants (e.g., Porter and Tschinkel, 1987; Heatwole and Muir, 1989; Cerdá et al., 1998a) and vertebrates (e.g., Platt, 1976; Schmidt-Nielsen, 1990; Bozinovic and Merritt, 1991). However, while the activity of ants decreases at low ambient temperatures (Porter and Tschinkel, 1987; Cerdá et al., 1998a), foraging rates and the activity of endothermic vertebrates should increase in order to maintain a constant body temperature (Schmidt-Nielsen, 1990). These ecophysiological properties could be expected to influence the composition of seed predators and predation levels at high elevations.

The aims of this study were to evaluate (1) postdispersal seed predation in the perennial herb *Sisyrinchium arenarium* (Ir-

idaceae) by ants and avian granivores, considering two elevational levels in the Andean Cordillera, central Chile, and (2) the activity of ants and avian granivores at these two elevational levels.

We hypothesized that seed predation on *S. arenarium* by ants should be more important at low elevations within the subalpine zone of the Andean Cordillera, while the magnitude of postdispersal seed predation by birds should be greater at higher elevations. Furthermore, activity of ants should be greater at the low site, while the activity of birds should be greater at the high-elevation site.

Materials and Methods

STUDY SITES

The study was undertaken in the Valle Nevado area (33°20'S, 70°18'W) in the Andean Cordillera, central Chile, approximately 45 km east of Santiago. We selected two sites at different elevations (2700 and 2000 m a.s.l.) within the subandean scrub zone (Arroyo et al., 1981, 1982). These elevations correspond with the upper and lower limit of the first vegetation belt above treeline in this area (Arroyo et al., 1982; Cavieres et al., 2000). Climate is mediterranean with some continental influence, characterized by a long, snow-free period of 5 to 8 mo. Mean annual precipitation at 2400 m elevation is 431 mm, falling predominantly as snow received during the winter months from June through August, although snow may fall as early as April and as late as October. Field work was conducted during April 2000 (mid-autumn), corresponding to the period of advanced seed dispersal for many plant species in the area (Arroyo et al., 1981).

The high-elevation (2700 m) site had a gentle (<5°) slope and was dominated by low, 20–40 cm, spiny shrubs of *Chusqueira oppositifolia* (Hook. & Arn.) Hook. & Arn., *Anarthrophyllum cumingii* (Hook. & Arn.) F. Phil., *Berberis empetrifolia* Lam., and *Haplopappus arbustoides* Remy in Gay. Herbaceous species, such as *Acaena pinnatifida* Ruiz & Pav., *Senecio* spp., and *Adesmia* spp. were also abundant. Rock cover was estimated to be 10 to 20%.

The low-elevation (2000 m) site was similar in slope to the former, but plant species composition was substantially different. The site was dominated by the herbaceous species *Madia sativa* Molina, *Malesherbia linearifolia* (Cav.) Pers., and *Acaena digitata* Phil., as well as the shrub *Solanum ligustrinum* Lodd. Rock cover at this site was 5 to 10%.

STUDY SPECIES

Sisyrinchium is a species-rich genus within the central Chilean Andes, from a bee-pollinated family (Arroyo et al., 1982; Hoffmann et al., 1998). *Sisyrinchium arenarium* Poepp. is an erect perennial herb, 20 to 50 cm tall. Flowers have six yellow tepals with gray-brown veins (Hoffmann et al., 1998). Flowers open during summer (Arroyo et al., 1981); fruits are capsules with locules containing 20 to 30 black, spherical seeds, 2 to 3 mm in diameter (mean fresh weight = 0.0062 g, range = 0.0051–0.0073 g). *Sisyrinchium arenarium* is patchily distributed throughout the subandean scrub zone, growing on dry sites between the dominant shrubs (personal observations).

COLLECTION OF SEEDS

We made bulk seed collections of *S. arenarium* in the general study area during the second half of March 2000. Capsules

of individual plants harvested were already open and dispersal was in process as evidenced by the presence of seeds on the ground near adult plants. We collected only completely mature (black-colored) seeds from open capsules. We refrained from collecting seeds from the ground in order to avoid any possibility of mixing seeds of other species.

SEED REMOVAL EXPERIMENT

In mid-April 2000, we established four parallel transects at 2000 m elevation and four at 2700 m. Transects were 15 m apart. Each transect had six replicate stations, separated by 10 m. At each station we placed four pots, (two on each side of the station), each diagonally distanced approximately 1 m from the station marker and from each other. The circular (8.5 cm diam. × 3.5 cm high) transparent, plastic pots were filled with native soil from the study sites (clay-type soil at 2700 m and loam-type soil at 2000 m elevation) to within 0.4 cm of the top of pots, and contained 50 seeds each, placed at the soil surface within pots. Pot bottoms were perforated to allow moisture drainage. The pots were dug into the ground so that the seeds were just below (<0.5 cm) the surrounding ground level. The four pots were randomly assigned into one of four treatments in order to evaluate seed removal by different biotic or abiotic agents: control—allowing access to all granivores as well as wind (Treatment 1); bird exclusion—through which seed removal by ants and wind combined was quantified (Treatment 2); ant exclusion—through which seed removal by avian granivores and wind combined was quantified (Treatment 3); and total exclusion—where access to all seed predators was denied, thus allowing assessment of seed removal by wind only (Treatment 4). This last treatment allowed us to estimate the proportion of seeds that had actually been removed by wind from the other treatment pots and not by granivores. The experiments considered 24 replicate pots per treatment and 96 pots, in total, at each elevation.

Bird exclusion was achieved by covering pots with 0.5 × 0.5 cm wire mesh raised ca. 0.5 cm above the pot surfaces and surrounding ground. Pots from which ants were excluded were surrounded by thin, 30-cm diameter transparent plastic sheets. The outer 5 cm of each sheet was covered by a thin layer of Tanglefoot (The Tanglefoot Company, Grand Rapids, MI) which prevented ants from entering the pots. Stones were placed on the plastic sheet between the pot rim and the Tanglefoot layer, in order to simulate the texture of the environment. The total exclusion treatment pots contained both the Tanglefoot paste and wire mesh in order to exclude all granivores from the pots, allowing assessment of seed loss by wind only. Finally, control pots allowing access to all types of seed predators as well as wind, were not covered at all.

The experiment ran for 10 d. Twenty-four hours after the initial setup of the experiment, we counted the number of seeds present in each pot by direct observation without removing the pots from the soil. Seed counts were subsequently repeated 3, 5, and 10 d after the start of the experiment.

ASSESSMENT OF ANT AND BIRD ACTIVITY

Seed predation by small mammals was not evaluated, given that the one species present in the area, *Spalacopus cyanus* (Rodentia: Octodontidae), is patchily distributed, forming colonies that are located 150 to 500 m away from the study sites. Measurements of ant and bird activity included presence and frequency. For these measurements, we set up one additional 50-m transect line at each elevation, parallel to the others. For ants,

TABLE 1

Results of a two-way, repeated measures ANOVA on the effects of study site (elevation) and type of exclusion through time on the percentage of *Sisyrinchium arenarium* seeds removed at two sites (elevations 2700 and 2000 m), under various granivore exclusion treatments in the central Chilean Andes^a

Source of variation	d.f.	MS	F	P
Site (elevation)	1	5769.56	22.01	0.000005
Type of exclusion	3	1529.10	5.83	0.000791
Time	3	8188.13	253.94	<0.000001
Site × Type of exclusion	3	583.18	2.22	0.0868
Site × Time	3	345.15	10.70	0.000001
Type of exclusion × Time	9	31.28	0.97	0.4637
Site × Type of Exclusion × Time	9	40.41	1.25	0.2510
Error	184	262.13		

^a Data were arcsine transformed. d.f. = degrees of freedom, MS = mean squares, F = F distribution value, P = probability value.

at the start of each seed monitoring session (i.e., day 0, 1, 3, 5, and 10), we placed approx. 30 g of a sweet bait consisting of apricot jam within 30 cm at six stations along each transect, separated by 10 m. At the end of each monitoring period (2–2.5 h), we determined the (1) number of species present, (2) number of stations at which ants were active, and (3) recorded the number of ant individuals at each station.

Avian seed predator species composition and number was determined through direct observation with binoculars by walking along the additional transect line once before and after each seed monitoring session (in conjunction with the assessment of ant predators). Observations were carried out at 40 to 50 m distance from the transect, and perpendicular to it.

DATA TREATMENT AND STATISTICAL ANALYSES

In order to eliminate the effect of seed removal by wind in the control, and ant and bird exclusion treatments, removal of seeds by wind as estimated in Treatment 4 (total exclusion treatment), was subtracted from the results for these treatments. Subtractions were made at the level of each replicate, where conditions were internally uniform. To assess the intensity of seed predation at the two sites in the various exclusion treatments, we expressed data as the percentage of seeds removed per pot and as the proportion of pots from which seeds had been removed since the start of the experiment. Percentage data were arcsine transformed for statistical analyses. Normal distribution of the transformed data under each treatment was determined through Shapiro-Wilks and Kolmogorov-Smirnov tests (Zar, 1996). Differences in seed removal from pots between sites and under different types of exclusion through time were assessed using a two-way, repeated measures, Analysis of Variance (site and type of exclusion as factors). In addition, the proportion of pots from which seeds had been removed under the different exclusion treatments and at the two sites were compared through a multiple proportions test (Zar, 1996).

Differences in ant activity between the two sites were assessed in two ways: (1) a one-way, repeated measures, ANOVA on ant abundance data through time, and (2) a proportions test in which the proportion of stations at which ants were active were compared (Zar, 1996). Differences in avian activity between elevations were also assessed through one-way repeated measures ANOVA.

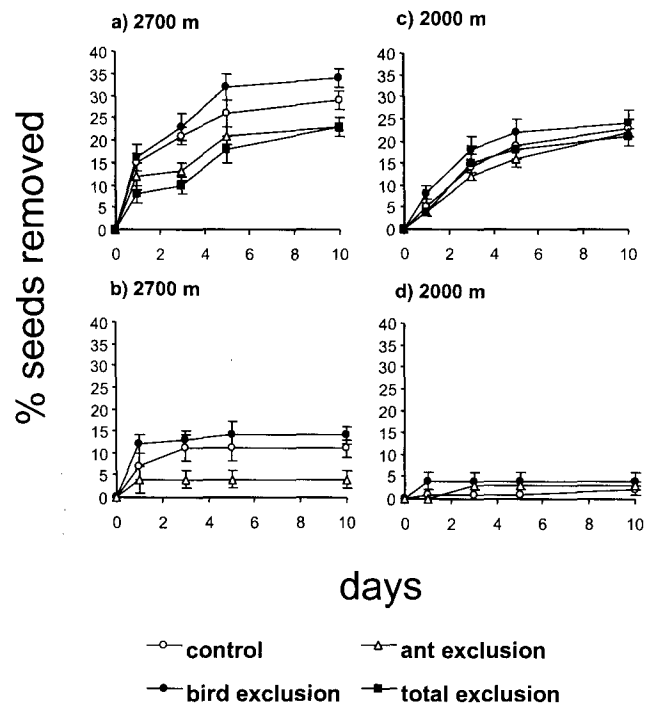


FIGURE 1. Percentage of *S. arenarium* seeds removed under various granivore exclusion treatments at 2700 and 2000 m elevation in the central Chilean Andes during the 10-d experiment. Seed loss when removal by wind is included in a) and c), and seed loss when removal by wind is excluded in b) and d). Bars represent ± 1 SE).

Results

EFFECT OF TYPE OF SEED PREDATOR AND ELEVATION ON SEED REMOVAL

Study site, type of exclusion, and time elapsed had significant effects on the percentage of *Sisyrinchium arenarium* seeds removed (two-way repeated measures ANOVA; Table 1). Seed removal through time, including by wind, was significantly greater at the high-elevation (2700 m) compared to the low-elevation (2000 m) site (*a posteriori* Tukey test; $P < 0.05$), and, overall, was also greater in the combination ants + wind than by avian seed predators + wind (*a posteriori* Tukey test; $P = 0.007$). The effect of study site was modified through time as suggested by a significant interaction between site and time (Table 1). Percentage seed removal by wind did not differ between the two elevations where the experiment was conducted (one-way repeated measures ANOVA; $F = 0.07$, $P = 0.79$; Fig. 1a, c).

At the high-elevation site, percentage seed removal (including losses due to wind) differed through time among treatments (one-way repeated measures ANOVA; $F = 12.58$, $P < 0.05$), ranging between 20 and 37% by the end of the experiment (Fig. 1a). After 10 d, a mean of 29 and 34% of seeds were removed from the control pots and bird exclusion treatments, respectively. However, when the effect of wind was considered, little seed removal could be attributed to granivores; on average 23% of seeds were removed from pots by wind, as evidenced from the average seed loss at the total exclusion treatment pots (Fig. 1a). Seed removal by predators, once wind removal had been accounted for, was on average only 4 (birds) to 14% (ants) by the end of the experiment (Fig. 1b).

Twenty-four hours after the start of the experiment in the high-elevation site, seed removal by ants alone did not differ

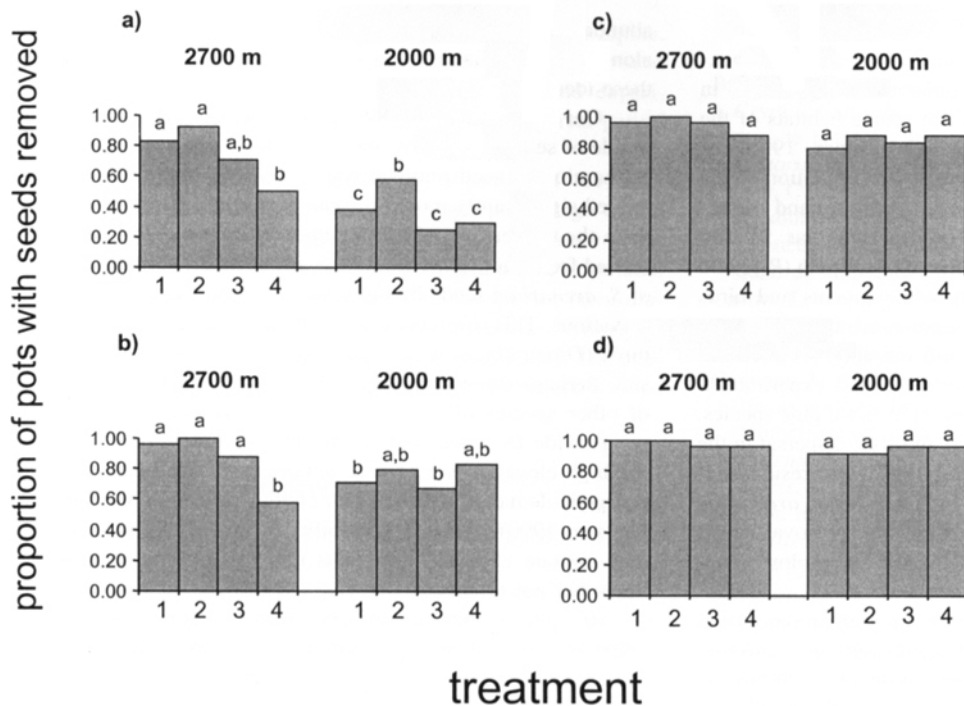


FIGURE 2. Frequency of removal of *S. arenarium* seeds (proportion of pots with seeds removed) under various granivore exclusion treatments at 2700 and 2000 m elevation in the central Chilean Andes, after a) 1 d, b) 3 d, c) 5 d, and d) 10 d. Exclusion treatments within the same monitoring event (day) sharing the same letter did not differ significantly ($P > 0.05$). Data for all treatments include removal by wind. Treatment codes: Treatment 1 = control, Treatment 2 = bird exclusion, Treatment 3 = ant exclusion, Treatment 4 = total exclusion.

from that by birds alone, but was significantly greater for ants from three days onward after the start (*a posteriori* Tukey test; $P < 0.05$; Fig. 1b). Removal of seeds by ants did not differ from that under the control (access to all granivores) treatment ($P = 0.10$; Fig. 1b), suggesting that seed removal by birds was very low at the high-elevation site. The fact that removal of seeds from the ant exclusion treatment pots did not differ from that at the total exclusion treatment pots (seed removal by wind) ($P = 0.27$; Fig. 1a), provides further evidence that removal by birds was very low at 2700 m.

At the low-elevation site, percentage of seeds removed through time (including by wind) was not affected by type of exclusion (one-way repeated measures ANOVA; $F = 0.75$, $P = 0.53$). Although seed removal increased through time ($F = 121.03$; $P < 0.05$), it was lower than at the high-elevation site (Fig. 1a, c; *a posteriori* Tukey test; $P < 0.05$). After 10 d a mean of 21% of seeds had been removed by wind (Fig. 1c). After subtracting the effect of wind on seed removal, only 2 (birds) to 3% (ants) of seed removal could be attributed to biotic agents (Fig. 1d), there being no significant difference between the two groups (*a posteriori* Tukey test; $P < 0.05$).

A comparison of seed removal by biotic agents between the two elevations revealed that, by the end of the experiment, seed removal by ants was significantly greater at 2700 m (Student's *t*-test; $t = 3.16$, $P < 0.01$), while in the case of birds there was no significant difference between elevations (Student's *t*-test; $t = 0.92$, $P = 0.36$; Fig. 1b, d).

Finally the proportion of pots from which seeds had been removed (including by wind) differed among elevations and exclusion treatments after 1 d (Multiple Proportions test: $\chi^2 = 41.48$; $P < 0.05$) and 3 d ($\chi^2 = 21.75$; $P < 0.05$) (Fig. 2a, b). However, from day 5 onward the proportion of pots from where seeds had been removed was very high and did not differ either among treatments nor between elevations (Multiple Proportions test: $\chi^2 = 9.34$, $P > 0.50$; and $\chi^2 = 4.35$, $P > 0.50$ at day 5 and 10, respectively, Fig. 2c, d).

SEED PREDATOR ACTIVITY

Number of ants observed at the baited stations was significantly greater at the higher elevation (mean 7 ± 2 individuals through time) than at the lower elevation, where no ants at all were recorded (one-way repeated measures ANOVA: $P < 0.001$). In addition, number of ants that were active did not change through time ($P = 0.20$) at the high-elevation site. All ants observed at baited stations at 2700 m were identified as *Solenopsis gayi* Spin. (Hymenoptera: Formicidae). The proportion of stations at the high-elevation site where ants were detected ranged from 50 to 100% among the different days during which this study was carried out, with no temporal trend of change. Although ants were never seen active at baited stations at the low-elevation site, *Camponotus chilensis* Spin. (Hymenoptera: Formicidae) individuals were seen on a number of occasions near experimental pots.

The only avian seed predator species that was observed during this study was the Fringillid *Diuca diuca* (Molina) (*diuca*), which was present at both elevations. However, its abundance was much greater at 2700 m (range 5–20 individuals) than at 2000 m (1–4 individuals) during single monitoring events (one-way repeated measures ANOVA: $P < 0.05$). Several non-granivorous birds were observed: the frugivorous Muscicapid *Turdus falcklandii* Quoy & Gaimond (*zorzal*) and insectivorous Tyrannids *Muscisaxicola* spp. (*papamoscas*) at 2700 m; and the insectivorous Emberizid *Curaeus curaeus* (Molina) (*tordo*) and the frugivorous and insectivorous Rhinocryptid *Pteroptochos megapodius* (Kittlitz) (*turca*) at 2000 m. However, these species were much less abundant in comparison to *D. diuca*.

Discussion

The alpine areas studied are located above the typical central Chilean mediterranean-type climate scrublands. In the latter, high levels of seed predation, as in many other mediterranean-type climate areas, have been documented (e.g., Abbott and van Heruck, 1985; Andersen, 1987, 1988; Louda, 1989, 1995; Bus-

tamante, 1995; Bustamante and Vásquez, 1995; Yates et al., 1995; Maron and Simms, 1997; Vila and Lloret, 2000). For example, seed losses to postdispersal predators averaged 51% in the tree *Cryptocarya alba* (Lauraceae) in sparse habitats of the central Chilean matorral (Bustamante and Vásquez, 1995; see also Bustamante, 1995). Similarly, average seed predation on the tussock grass *Ampelodesmos mauritanica* (Poaceae) and the perennial herb *Lobularia maritima* (Brassicaceae) was 91 and >80%, respectively, at two sites near Barcelona, Spain (Picó and Retana, 2000; Vila and Lloret, 2000), while rodents and birds consumed up to 96% of Scots pine seeds reaching the ground in a relict forest in southern Spain (Castro et al., 1999). To our knowledge, the present study constitutes the first experimental assessment of postdispersal seed predation in any alpine species. Indeed, in general, information on seed and fruit dispersal in the alpine seems to be wanting (cf., Körner, 1999). Our results suggest that postdispersal seed predation in *Sisyrinchium arenarium* at both elevations where we conducted the seed removal experiments in the central Chilean Andean Cordillera was low, ranging between 2 and 14%.

Although seed removal by ant and avian seed predators was generally low in *S. arenarium*, overall seed losses to granivores were significantly greater at the high-elevation site (2700 m). In fact, seed removal by granivores was almost negligible (2–3%) at 2000 m after subtracting the losses due to wind from the total percentage of seeds removed from the different treatment pots. Given the reported negative effects of low temperatures on the activity of ants (Porter and Tschinkel, 1987; Cerdá et al., 1998a), we predicted the amount of activity and magnitude of seed predation by ants to be greater at the low-elevation site, but this did not turn out to be the case.

A number of nonmutually exclusive factors may explain why activity of ants and seed removal by these granivores was lower at the low-elevation site. First, both low (Porter and Tschinkel, 1987; Cerdá et al., 1998a) and high (Heatwole and Muir, 1989; Medel and Vásquez, 1994; Cerdá et al., 1997, 1998a, 1998b; Cros et al., 1997) ambient temperatures have been shown to limit the activity in certain species of ants. For example, Heatwole and Muir (1989) found that some ant species in the pre-Saharan steppe of Tunisia that were active during the day at some times of the year shifted toward nocturnality in summer, avoiding the midday heat extremes. Similarly, Cerdá et al. (1997) found that foraging of some heat intolerant ant species was restricted mostly to late afternoon and night hours when temperatures were lower. Therefore, instead of low temperatures restricting the activity of ants at the high-elevation site, perhaps higher ambient temperatures at the low-elevation site restricted the number of hours in which ants were active, explaining the lower postdispersal seed predation registered at 2000 m. In this sense it is worthwhile recalling that air temperatures in the alpine in central Chile are not exceedingly low (Cavieres et al., 2000), and in fact can be still quite high at 2000 m in March and April, with mean monthly averages of 12 and 7°C, respectively (Rozzi, 1990). Soil temperatures can be much higher (Cavieres et al., 1998). For example, midday temperatures at ground level at 1800 m (where data are available) fluctuate between 17 and 29°C in March–April (Peñaloza, 1996). Secondly, although both sites were within the altitudinal range described as the subandean scrub by Arroyo et al. (1981, 1982), plant species composition was markedly different between the two sites. Differences in plant species composition could determine differences in the availability of alternative seed resources for granivores at the two sites, affecting the relative attractability of *S. arenarium* seeds as a food source. Additional information on ant and seed

abundance at both higher and lower elevations than those studied along the elevation gradient would be useful for testing some of these ideas.

Our experiment was designed to assess the relative magnitude of seed removal by ant versus avian granivores. Although as mentioned, seed removal was overall generally low, ants removed significantly more *S. arenarium* seeds than birds. In fact, once the percentage of seeds removed by wind had been subtracted from the results from the various treatment pots, removal of *S. arenarium* seeds by birds proved to be virtually nil at both elevations. This result contrasts with our finding that granivorous birds (*Diuca diuca*) were especially active at the high-elevation site. Perhaps these granivorous birds prefer to forage on seeds of other species of plants. *Sisyrinchium arenarium* seeds may not provide *D. diuca* with sufficiently high energetic returns at the high-elevation site, where temperatures are lower and thus energetic demands are higher for endothermic animals (Schmidt-Nielsen, 1990). Another possibility is that *S. arenarium* seeds may contain chemical deterrents that are toxic to avian granivores but not to ants.

In spite of this, we observed birds foraging around *S. arenarium* plants at both populations where we collected mature seeds. We carried out the experiments at sites away from patches of *S. arenarium* to avoid removal rates from possibly being affected by the large amount of seeds of this species around adult plants. If birds and/or ants were to use chemical or visual signals from patches of adult plants to cue in on the seeds (Fraenkel, 1969 in Price, 1996) it is possible that seed predation rates on this plant by both ants and birds may have been underestimated at these high elevations.

In addition, at least two other considerations should be taken into account when interpreting the generally low seed removal observed. First, as we do not know the final fate of seeds that were removed by ants or birds, we can not be sure that all seeds removed from pots represented actual mortality. For this reason, we have preferred to express the results as seed removal percentages rather than as seed predation. Overall postdispersal seed predation may be even lower than indicated by seed removal. Second, seed removal percentages reported might be considered conservative because, although we observed ants reaching seeds on a number of occasions, the pots' outer rim may have slightly decreased accessibility to ants.

A greater degree of seed removal by ants compared to birds contrasts with findings of other studies conducted at lower elevation mediterranean-type climate scrublands in central Chile, South Africa, California, U.S.A., and Spain where vertebrates are the most important postdispersal seed predators (Parker and Kelly, 1989; Herrera et al., 1994; Bustamante, 1995; Louda, 1995; Hulme, 1997). In fact previous work on seed predation by ants in mediterranean-type climate scrublands in central Chile have shown it to be particularly low in comparison to that encountered in other ecosystems (Medel and Vásquez, 1994). For instance ants are important seed predators within desert herbaceous plant communities in North America (e.g., Reichman, 1979; Brown et al., 1986; Mackay, 1991). The only lowland mediterranean-type climate area in which high levels of seed removal by ants has been reported is Australia (e.g., Abbott and van Heruck, 1985; Andersen, 1987). A comprehensive study of seed removal by ants in the high Andes of central Chile would be worthwhile. It should be kept in mind that in this paper we assessed seed predation on a single plant species. Further, the magnitude of seed predation may change over the dispersal period which stretches from December to May. We carried out this study during the latter part of the seed dispersal period on the

Andean site. In order to detect general patterns for the alpine, future studies considering plant species differing in their seed characteristics (e.g., size, shape, energetic value) and experiments conducted during different stages of the dispersal period are necessary.

Finally, although not originally an objective of the work reported here, we draw attention to the high percentage of the fairly large, round, and essentially smooth *Sisyrinchium* seeds that were removed by wind. A number of authors have pointed out that an exaggerated proportion of alpine species have diaspores without any apparent dispersal mechanisms (Willson et al., 1990; Cavieres et al., 1999; see also Castor, 2001). The possibility of wind dispersal in such seeds in alpine ecosystems should not be overlooked.

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