

A Multi-species Assessment of Post-dispersal Seed Predation in the Central Chilean Andes

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• **Background and Aims** Post-dispersal seed predation in alpine communities has received little attention despite evidence that seeds removed by granivores can decrease plant recruitment into ecosystems. Moreover, few studies have assessed the effects of removal of seeds of a range of species after dispersal on the seeds remaining in ecosystems. A comparison was made of the magnitude of seed removal by ants and birds of nine different shrubby-, herbaceous- and cushion-plant species in the central Chilean Andes in order to assess the interactions between birds, ants and wind, and the types of seeds.

• **Methods** A total of 324 soil-covered plates, each containing 50 seeds of one species, were placed in the field at an altitude of 2700 m and assigned to one of four treatments: control, exclusion of ants, birds, and both. The design also allowed the effects of wind to be assessed. Seed removal from plates was monitored over 20 d.

• **Key Results** Mean accumulative seed removal by granivores averaged over all nine species combined was 25%. However, large differences between species were evident, with limited seed removal (3–11%) in three herbaceous species (*Alstroemeria pallida*, *Sisyrinchium arenarium*, *Pozoa coriacea*), moderate (18–33%) in five species, including a shrub (*Chusqueira oppositifolia*), two herbs (*Taraxacum officinale*, *Rhodophiala rhodolirion*), and two cushion-plants (*Laretia acaulis*, *Azorella monantha*), and substantial (78%) in the shrub *Anarthrophyllum cumingii*. The magnitudes of losses caused by birds compared with ants did not differ for the majority of species, although removal by birds was greater than by ants in *A. cumingii*, and smaller for *C. oppositifolia*.

• **Conclusions** Post-dispersal seed removal is shown to be an important cause of decreased potential plant species recruitment into alpine ecosystems. The substantial differences in the magnitude of seed losses to ants and birds demonstrate the need for evaluation of seed removal on a wide range of species in any given ecosystem.

Key words: Post-dispersal seed predation, granivory, seed mortality, plant recruitment, plant–animal interactions, alpine ecosystems, central Chilean Andes.

INTRODUCTION

Seeds are a vulnerable stage in plant recruitment into ecosystems, which is affected by various abiotic and biotic factors causing the loss or death of seeds. Biotic factors include removal and consumption, generally called predation, of dispersed seeds by insects and vertebrates (rodents and birds) and are quantitatively important (e.g. Janzen, 1971; Brown *et al.*, 1986; Hulme, 1997). Plant recruitment, defined as the incorporation of new individuals into a population (Harper, 1977), may be substantially affected by post-dispersal seed predation, playing an important role in population dynamics (e.g. Harper, 1977; Louda, 1989, 1995; Crawley, 2000), community structure (e.g. Brown *et al.*, 1986; Howe and Brown, 1999), and maintenance of species diversity (e.g. Hubbell, 1980; Brown and Heske, 1990). Studies in a wide range of environments have found post-dispersal seed predation to be high in Mediterranean-type-climate scrublands (e.g. Hulme, 1997; Figueroa *et al.*, 2002), tropical forests (e.g. Schupp, 1990; Blate *et al.*, 1998), temperate forests (e.g. Whelan *et al.*, 1991; Díaz *et al.*, 1999) and, semi-arid and desert lands (e.g. Brown and Heske, 1990; Marone *et al.*, 2000; Kelt *et al.*, 2004).

Furthermore, there is much variation between species in the magnitude of losses caused by post-dispersal seed

predators (e.g. Hulme, 1997; Kollmann *et al.*, 1998; Díaz *et al.*, 1999; Figueroa *et al.*, 2002), which may be partially explained by variation in seed characteristics, such as size, nutritional, energy or water content, and in toxicity (Blate *et al.*, 1998; Kollmann *et al.*, 1998; Auld and Denham, 1999). Variation between species in seed predation may also be related to differences in preferences among the main groups of seed predators, including ants, rodents and birds (Hulme, 1997; Kollmann *et al.*, 1998; Figueroa *et al.*, 2002). Thus, results of studies on a single or few species cannot be generalized with respect to the importance of post-dispersal seed predation at the community level (cf. Vásquez *et al.*, 1995; Marone *et al.*, 2000; Kelt *et al.*, 2004).

In contrast to the substantial amount of research on post-dispersal seed predation in low-elevation habitats, this process has received little attention in alpine environments (McGraw and Vavrek, 1989; Körner, 1999). This is surprising because a number of granivores, including small mammals such as deer mice, birds including sparrows and finches, and ants, inhabit alpine ecosystems such as the Rocky Mountains of North America (Hoffmann, 1974; Raphael *et al.*, 2002), the central Alps of Europe (Meyer and Thaler, 2002) and the central Chilean Andes (Muñoz and Arroyo, 2002). Hence, there is a general lack of knowledge on the interactions between plant species and post-dispersal seed predators at high elevation habitats.

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Alpine ecosystems are characterized by low ambient temperatures and strong winds (Körner, 1999). Given that cold temperatures can sometimes limit the activity and abundance of ants (e.g. Porter and Tschinkel, 1987), as well as vertebrates (e.g. Schmidt-Nielsen, 1990), post-dispersal seed predation could be expected to be less important than in lowland ecosystems. To our knowledge, only one study (Muñoz and Arroyo, 2002) has assessed post-dispersal seed predation in any alpine ecosystem: very little seed removal (2–14%) by birds and ants occurred at two altitudes (2000 m and 2700 m) in the Andes of central Chile, a result agreeing with the above prediction. However, seed predation in that study was assessed on a single species only, the perennial herb *Sisyrinchium arenarium* (Iridaceae), which forms patches in between other dominant vegetation including dwarf shrubs, woody cushion-plants, and annual and perennial herbs (Cavieres *et al.*, 2000).

Here we report the results of a study in the central Chilean Andes to assess the importance of post-dispersal seed predation in this alpine ecosystem. In a manipulative seed predation experiment at 2700 m altitude, we assessed removal of seeds of nine species in five families, differing in life form (perennial herbs, dwarf shrubs and cushion plants) and seed traits (e.g. size).

Specifically, the following questions were addressed. (1) Is post-dispersal seed predation quantitatively important in the central Chilean Andes? (2) Does the magnitude of seed predation differ among plant species in this ecosystem? (3) If so, can this variation be partially explained by seed traits such as biomass? (4) What is the relative importance of ants and/or birds as seed predators in this ecosystem? (5) Are seeds of different species disproportionately preyed upon by ants or birds?

MATERIALS AND METHODS

Study site and system

The experiment was done on a gently (<5°) sloping site at 2700 m elevation near the Valle Nevado Ski Resort (33°21'S, 70°16'W), in the Andes of central Chile, distanced approx. 50 km east of the city of Santiago. The climate is alpine with Mediterranean influence, characterized by a long, snow-free summer period of 5–8 months (Santibáñez and Uribe, 1990). Long-term mean total annual precipitation at 2500 m is approx. 445 mm (Santibáñez and Uribe, 1990), falling predominantly as snow received during the winter months from June to August. The growing season at this altitude commonly extends from mid-October to mid-May. The experiment was done during March and April 2005 (mid-autumn), corresponding to the main period of advanced seed dispersal for many plant species in the area (Arroyo *et al.*, 1981).

Vegetation at 2700 m elevation is transitional between the first alpine belt above the tree line (the sub-andean scrub belt, 2100–2600 m elevation), and the lower alpine belt (the cushion-plant zone, 2700–3400 m elevation; Cavieres *et al.*, 2000). The former is dominated by low (<45 cm) spiny shrubs such as *Chuquiraga oppositifolia* (Asteraceae), *Anarthrophyllum cumingii* (Papilionaceae)

and *Berberis empetrifolia* (Berberidaceae). Herbaceous species, such as *Acaena pinnatifida* (Rosaceae), *Phacelia secunda* (Hydrophyllaceae), and various species of *Adesmia* (Fabaceae) and *Senecio* (Asteraceae), are also abundant (Cavieres *et al.*, 2000). In contrast, the lower alpine belt is dominated by cushion plants such as *Laretia acaulis* (Apiaceae) and *Azorella monantha* (Apiaceae) interspersed among herbaceous plants (Cavieres *et al.*, 2000).

The most conspicuous invertebrate seed predators at the study site are harvester ants, *Solenopsis gayi* (Hymenoptera: Formicidae), which actively forage at this altitude (Muñoz and Arroyo, 2002). Granivorous birds, *Diuca diuca* (Fringillidae) and *Zonotrichia capensis* (Emberazidae), are the most conspicuous vertebrate seed predators (Muñoz and Arroyo, 2002; A. A. Muñoz pers. obs.). Additionally, the Muscicapid *Turdus falcklandii*, which also includes seeds in its diet in central Chile (Araya and Millie, 1988), is also present here. Seed predation by small mammals was not evaluated as the only species present in the area, *Spalacopus cyanus* (Rodentia: Octodontidae), is patchily distributed, in colonies 150–500 m from the study site.

Study species

To assess the magnitude of post-dispersal seed predation by birds and ants in the ecosystem and, at the same time, to determine the differences in loss of seeds between plant species to these two important seed predators, nine plant species differing in life form and seed traits were chosen (Table 1). All species selected are characteristic of either the sub-andean scrub or the cushion-plant belt (Cavieres *et al.*, 2000). Seven of these nine species grow in the study area (*Alstroemeria pallida*, *Anarthrophyllum cumingii*, *Chuquiraga oppositifolia*, *Laretia acaulis*, *Rhodophiala rhodolirion*, *Sisyrinchium arenarium* and *Taraxacum officinale*). Two further species occurring only within the cushion-plant zone were included, the cushion-forming *Azorella monantha* and the herb *Pozoa coriacea*, both of which are more abundant above 2900 m, in order to increase the range of species studied from this alpine ecosystem.

Diaspores (dispersal units) of species were used in the seed removal experiment. In some cases this corresponds to the actual seed in the strict sense: *A. cumingii*, *R. rhodolirion*, *A. pallida*, *S. arenarium* (Table 1). For the other five species, the diaspore was the fruit. For instance, the two asteraceous species, *C. oppositifolia* and *T. officinale*, produce dry one-seeded achenes having a pappus: these cannot be separated. Hereafter the diaspores offered to predators are collectively called 'seeds'. Seed and fruit characteristics of the nine species vary widely (Table 1). Seed mass ranges from 0.33 mg in *T. officinale* to 25.6 mg in *A. pallida* (Table 1).

Collection of seeds

Bulk collections of seeds of all but two of the species were made from adult plants close (approx. 500–1000 m distance) to the study site (2500–2800 m elevation) between January and March 2005. Seeds of *A. monantha* and

TABLE 1. Characteristics of the nine species of plants used in the post-dispersal seed predation experiment at 2700 m in the Andes of central Chile

Species tested	Family	Life form	Fruit type	Diaspore ('seed')		Seed mass (mg)
				Size (mm)	Colour	
<i>Chusqueira oppositifolia</i>	Asteraceae	SHR	Dry, achene	5–6	Light brown	7.5 ± 0.2
<i>Anarthrophyllum cumingii</i>	Papilionaceae	SHR	Dry, pod	4–5	Greenish-brown	23.6 ± 0.5
<i>Taraxacum officinale</i>	Asteraceae	PH	Dry, achene	3–4	Light brown	0.33 ± 0.02
<i>Rhodophiala rhodolirion</i>	Amaryllidaceae	PH	Dry, capsule	12–15	Black	17.1 ± 0.4
<i>Alstroemeria pallida</i>	Amaryllidaceae	PH	Dry, capsule	3–4	Orange	25.6 ± 0.5
<i>Sisyrinchium arenarium</i>	Iridaceae	PH	Dry, capsule	2–3	Black	6.5 ± 0.1
<i>Laretia acaulis</i>	Apiaceae	CUS	Dry, 2 large round mericarps	8–14	Pale yellow	9.2 ± 0.3
<i>Azorella monantha</i>	Apiaceae	CUS	Dry, 2 large round mericarps	2–3	Light brown	0.75 ± 0.05
<i>Pozoa coriacea</i>	Apiaceae	PH	Dry, 2 mericarps	3–4	Brown	2.6 ± 0.1

Nomenclature follows Marticorena and Quezada (1985). Life forms according to Arroyo *et al.* (1981) and Cavieres *et al.* (2000) and fruit type according to Hoffmann *et al.* (1998). Seed mass indicates a mean value obtained from 100 seeds of each species \pm 1 s.e. Life form: PH = perennial herb, SHR = dwarf shrub, CUS = woody cushion.

P. coriacea were collected from adult plants at sites ranging between 2900–3100 m elevation, above the study site. Only completely mature seeds were taken directly from 15–75 different adult plants (depending on the size of individuals) where dispersal was in progress. Seeds were not taken from bare soil or from under adult plants, to avoid any possibility of mixing seeds of other species.

Seed removal experiment

The experimental design was similar to that used by Muñoz and Arroyo (2002). In late March 2005, nine parallel 80-m transects, 5 m apart, were established at the study site. Each transect had nine replicate 2 × 2 m plots, each having a central plot marker. Plot markers were separated by 10 m along each transect. Thus, there was a total of 81 replicate plots. At each plot we placed four 10-cm diameter circular cardboard plates, two on each side of the central plot marker, approximately 1 m from the marker and from each other. Each plate was placed on flat soil surface, firmly anchored to the ground with 6-cm nails, perforated to allow moisture drainage, and covered with a 2–3-mm thin layer of sieved clay-type soil from the area. Soils at the study site are very dry during autumn, with moisture content being <10% (A. A. Muñoz, pers. obs.). Wash-off of seeds and soil was not a problem as only light drizzle occurred during a single day towards the end of the experiment. Fifty seeds of a single species, which was randomly determined for each of the 81 replicate 2 × 2 m plots, were distributed evenly on the soil of each of the four plates within any given plot. The four plates within a plot were randomly assigned to one of four treatments to evaluate seed removal by different biotic or abiotic agents. (1) Control: allowing access to all granivores, as well as wind (Treatment 1); (2) ant exclusion: seed removal by birds and wind combined (Treatment 2); (3) bird exclusion: seed removal by ants and wind combined (Treatment 3); and (4) ant and bird exclusion: all ants and birds were excluded, thus allowing assessment of seed removal by wind only (Treatment 4). Thus, at each 2 × 2 m plot only one plant species was

represented but all exclusion treatments were applied. Therefore, this set-up corresponded to a random-block experimental design, which considered nine replicate plots of each species, nine replicate plates per exclusion treatment per species, and thus 324 replicate plates in total.

Ants (Treatment 2) were excluded by placing a 30 × 30 cm thin (6-mm high) wooden (4-cm wide) frame around a plate, set 4–5 mm into the soil in a small trench. The frame was totally covered throughout the experiment by a 1–2 mm thin layer of Tanglefoot (The Tanglefoot Company, Grand Rapids, MI, USA), an insoluble sticky paste, which acted as a highly effective barrier that prevented ants from entering the area within the frame. Tanglefoot paste has been shown to be effective in preventing access to seeds by walking/crawling insects (e.g. Hulme, 1997; Auld and Denham, 1999; Muñoz and Arroyo, 2002). Ants were never observed in the areas surrounded by the frames covered by Tanglefoot. We placed approx. five 3–5 cm diameter, roughly round stones between the rim of the plate and the inner edge of the wooden frame to simulate the natural texture of the ground surface and provide natural perches for birds, which could thus easily access these ant exclusion plates. Plates from where birds were excluded (Treatment 3) were surrounded by 30 × 30 × 30 cm galvanized wire mesh (1.8 × 1.8 cm aperture) mounted on four 40-cm long vertical steel bars, each dug approx. 5–8 cm into the ground. Ants could thus easily reach seeds within these bird exclusion cages. The ant and bird exclusion treatment plates (Treatment 4) were surrounded by the Tanglefoot paste and wire mesh to exclude all granivores, allowing assessment of seed loss by wind only. Finally, control plates (Treatment 1) allowing access to all types of seed predators as well as wind, were not covered at all. Given that the wire mesh cages had fairly large apertures (1.8 × 1.8 cm) throughout, and that the wooden frames with Tanglefoot paste were placed just above (<2 mm) ground level, we consider that wind speeds reaching seeds on the four plates under the different exclusion treatments within any given 2 × 2 m plot most probably did not differ (A. A. Muñoz, pers. obs.). Therefore, it is unlikely that the effects of wind could have been underestimated within ant and bird exclusion treatments.

The experiment ran for 20 d (until mid-April). Two days after the experiment had been set-up, the number of seeds remaining on each replicate plate were counted, by direct observation, without removing them from the soil. Identification and counting of seeds on the clay-type soil covering the plates was aided by the sharp contrast the colour of seeds of the different species provided against the clay-type soil. Seeds were counted 4, 6, 8, 10 and finally 20 d after the start of the experiment.

Data treatment and statistical analyses

To assess the intensity of seed predation on the nine different species under the exclusion treatments, the number of seeds removed, as a proportion of the original number of seeds applied per plate, was calculated and expressed as a percentage. Percentage data were arcsine transformed for statistical analyses. Normal distribution of the transformed data under each treatment and homogeneity of variances were determined through the Shapiro–Wilks and Bartlett tests, respectively (Zar, 1996). Differences in percentage seed removal from plates under different types of exclusion through time were assessed using one-way, repeated measures analysis of variance for all species combined and for each of the nine species separately. Differences between species in seed removal at the end of the experiment (day 20) attributable to (1) both granivores groups combined (ants and birds), (2) ants only, and (3) birds only were tested via one-way ANOVA with plant species as the factor. *A posteriori* multiple comparisons were conducted using the Tukey HSD Test. We followed the protocol used by Muñoz and Arroyo (2002) to estimate accumulative percentage seed losses attributable to both granivores only, or to either birds or ants only by the end of the experiment. For this, percentage seed losses due to wind as estimated in the ant and bird exclusion treatment (removal by wind only) were subtracted from percentage seed losses in the control (removal by all granivores + wind), ant exclusion (removal by birds + wind), and bird exclusion (removal by ants + wind). Subtractions were made for each replicate plot, where a replicate of each of the four exclusion treatment plates was present and where conditions were internally similar (Muñoz and Arroyo, 2002). Finally, the cumulative seed losses to ants compared with birds were determined at the end of the experiment for each plant species separately. These within-species comparisons were carried out by Student *t*-tests or non-parametric Mann–Whitney *U*-tests when the normality assumptions were not met by the transformed data.

RESULTS

Overall patterns of seed removal

Considering all plant species combined, mean seed removal from plates differed between the exclusion treatments and through time (Table 2), from 19 to 44 % by the end of the experiment at day 20 (Fig. 1). Seed removal attributable to wind (the ant and bird exclusion treatment) averaged 19 %. Therefore, final accumulated mean percentage seed removal

TABLE 2. Analysis by a one-way, repeated measures ANOVA showing the effects of exclusion of seed predation by ants and birds through time on the percentage of seeds removed for nine plant species studied under four granivore exclusion treatments over 20 d at 2700 m elevation in the central Chilean Andes

Source of variation	d.f.	M-S.	F	P
Between Subjects				
Type of exclusion	3	17084.6	10.982	< 0.001
Error	320			
Within Subjects				
Time	5	24665.9	232.144	< 0.001
Type of exclusion × Time	15	314.1	2.956	< 0.001
Error	1600	106.3		

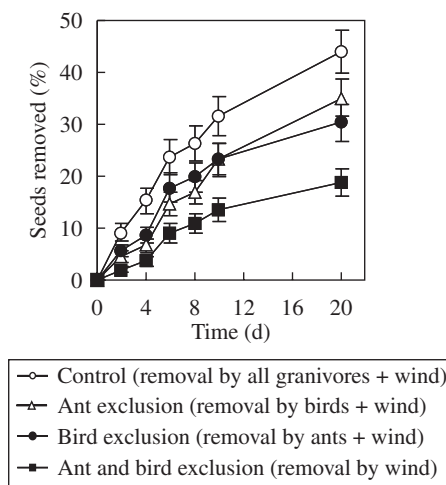


FIG. 1. Percentage of seeds of nine plant species combined, removed by birds, ants and wind in an experiment with four treatments: removal by ants, birds and wind (control); removal by birds and wind (ant exclusion); removal by ants and wind (bird exclusion); and removal by wind (ant and bird exclusion) at 2700 m elevation in the central Chilean Andes. Values are means ± 1 s.e., n = 81 replicate ‘plates’ for each exclusion treatment.

by ants was 10 % and birds 15 %: combined, they removed 25 % of seeds averaged over all species (*a posteriori* Tukey HSD test, *P* = 0.62; Fig. 1). The effect of the type of exclusion on percentage of seeds removed for all species combined changed throughout the experimental period, as shown by the significant type of exclusion × time interaction term (Table 2, Fig. 1).

Type of exclusion and time also had significant effects on the percentage of seeds removed for most species tested when analysed individually (Table 3, Fig. 2). Removal of seeds was not affected by type of exclusion only in *R. rhodolirion* and *A. pallida*. Further, the effect of type of exclusion only changed throughout the experimental period in *A. cumingii*, as suggested by a significant type of exclusion × time interaction for this species (Table 3, Fig. 2).

Species differences in seed removal by ants and birds combined

By the end of the experiment, final accumulated mean percentage seed removal (including losses due to wind)

TABLE 3. Analyses by one-way, repeated measures ANOVAs showing the effects of exclusion of granivorous ants and birds on the percentage of seeds removed, through time, of nine shrubby, herbaceous and cushion-forming species under four granivore exclusion treatments over 20 d in an experiment at 2700 m in the central Chilean Andes

Species	Type of exclusion (F-values)	Time (F-values)	Type of exclusion × time (F-values)
<i>Chuquiraga oppositifolia</i>	5.882 **	105.128 **	0.365 ns
<i>Anarthrophyllum cumingii</i>	8.872 **	26.513 **	7.958 **
<i>Taraxacum officinale</i>	4.998 **	99.756 **	0.390 ns
<i>Rhodophiala rhodolirion</i>	2.226 ns	33.570 **	1.011 ns
<i>Alstroemeria pallida</i>	1.552 ns	10.064 **	0.565 ns
<i>Pozoa coriacea</i>	3.038 *	81.916 **	1.380 ns
<i>Laretia acaulis</i>	4.320 *	58.321 **	1.248 ns
<i>Azorella monantha</i>	4.156 *	43.429 **	0.404 ns
<i>Sisyrinchium arenarium</i>	8.695 **	27.073 **	0.802 ns

Degrees of freedom: type of exclusion = 3, time = 5, type of exclusion × time = 15.

* = $P < 0.05$.

** = $P < 0.01$, ns = non-significant differences.

differed greatly between the nine species (Fig. 2). Losses were small in *A. pallida* and *S. arenarium* (4 and 12%, respectively), moderate in *P. coriacea*, *R. rhodolirion*, *A. monantha* and *L. acaulis* (24–36%), and large in *A. cumingii* (78%), *T. officinale* (86%) and *C. oppositifolia* (92%) (Fig. 2). Once losses attributable to wind alone were accounted for within each species, mean accumulated percentage seed removal by both ants and birds combined by day 20 differed significantly for species (one-way ANOVA, $F = 9.874$, d.f. = 8,72, $P < 0.001$, Fig. 3A). A significantly greater proportion of seeds of the shrub *A. cumingii* (78%) were taken compared to the eight other species (*a posteriori* Tukey HSD Test, $P < 0.05$). Between these eight species, losses were not significantly different with the exception of *A. pallida*, which had significantly lower losses than *C. oppositifolia* (*a posteriori* Tukey HSD Test, $P = 0.012$, Fig. 3A). For five species (*C. oppositifolia*, *T. officinale*, *R. rhodolirion*, *L. acaulis* and *A. monantha*, Fig. 3A) mean seed removal was intermediate (18–33%), and removal was small in *A. pallida* (3%), *S. arenarium* (10%) and *P. coriacea* (11%). Seed removal by granivores was not correlated with seed mass across the nine species tested (Spearman’s Rank Order Correlation, $R = -0.017$, $P = 0.97$).

Differences between plant species in seed removal by ants and by birds

Mean accumulated percentage of seeds removed by ants only (excluding the effect of wind) differed significantly among the nine species (one-way ANOVA, $F = 4.350$, d.f. = 8,72, $P < 0.001$, Fig 3B). Ants removed a significantly greater proportion of seeds of *C. oppositifolia* and *L. acaulis* (24%) than of *A. cumingii*, *A. pallida* and *S. arenarium* (2–5%) (*a posteriori* Tukey HSD Test, $P < 0.05$), while the losses to ants were intermediate and not significantly

different for the remaining species (*a posteriori* Tukey HSD Test, $P > 0.05$, Fig. 3B). On the other hand, removal attributable to birds by the end of the experiment was consistently small for all species tested (4–12%), with the sole exception of *A. cumingii*, with a large proportion (77%) removed by granivorous birds (Fig. 3C).

Differences between plant species in seed removal by ants vs. birds

A significantly greater proportion of seeds of *C. oppositifolia* were removed by ants than by birds (24 vs. 10%, respectively) by the end of the experiment (Students *t*-test, $t = 2.634$, d.f. = 16, $P < 0.05$; Figs 2 and 3B,C). The converse was observed for *A. cumingii*, with a large proportion taken by birds (77%) while very few seeds were removed by ants (1%; Mann-Whitney *U*-test, $U = 2.00$, $z = -3.399$, $P < 0.05$; Figs 2 and 3B,C). For all remaining species losses from birds were not significantly different compared with ants (Fig. 3B,C). Removal of seeds by either ants or birds was extremely small for *A. pallida* (3–7%) ($U = 32.00$, $z = -0.750$, $P = 0.453$), *S. arenarium* ($U = 34.5$, $z = -0.530$, $P = 0.596$) and *P. coriacea*, $t = 0.884$, $P = 0.389$; Figs 2 and 3B,C). Likewise, seed losses by ants and birds were both small (10–14%) for *T. officinale* ($U = 36.00$, $z = 0.397$, $P = 0.691$), *R. rhodolirion* ($t = 0.051$, $P = 0.959$) and *A. monantha* ($t = 0.574$, $P = 0.574$; Figs 2 and 3B,C). Finally, for *L. acaulis* losses to ants ($24 \pm 8\%$) and birds ($12 \pm 4\%$) were not statistically different ($t = 1.121$, $P = 0.279$, Figs 2 and 3B,C).

DISCUSSION

The seed removal experiment strongly suggests that seed-eating animals are an important source of post-dispersal seed mortality for shrubby, herbaceous and cushion-plant species in alpine habitats in the Andes of central Chile. Considering all the nine species studied combined, seed loss to granivores was considerable, being approx. 25% of the total number of seeds offered.

Post-dispersal seed predation as a process limiting recruitment in alpine plants has been neglected almost entirely in the literature, in contrast to environmental factors such as temperature, soil moisture and particle size, habitat disturbance regimes and species characteristics, such as seed dispersal mechanisms and life history (e.g. Reynolds, 1984; Chambers *et al.*, 1990; Scherff *et al.*, 1994; Chambers, 1995; Forbis, 2003; Shimono and Kudo, 2003). For instance, Körner (1999) discussed factors determining the number of dormant seeds (seed deposition, seed predation, germination) and their viability in the seed bank, but did not consider data regarding seed predation in alpine ecosystems. However, Chambers (1995) stressed that the potential for post-dispersal seed predation is relatively large in alpine ecosystems in the Rocky Mountains of North America, where a number of avian granivores are common (see also Hoffmann, 1974). Reynolds (1984) reported that most losses of individuals from populations of several alpine species occurred between seed dispersal and germination, but ascribed these to seeds being washed out of a suitable habitat.

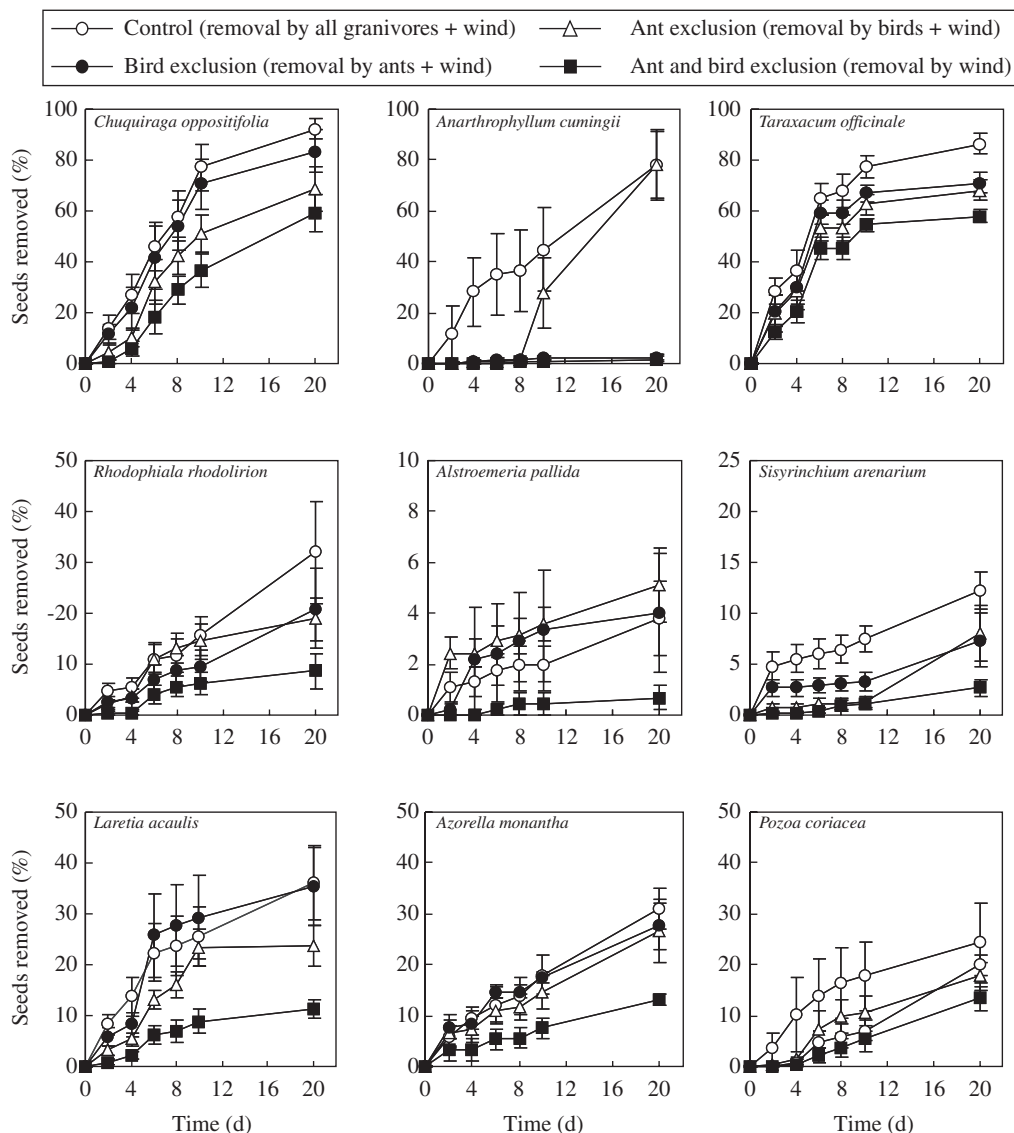


FIG. 2. Percentage of seeds removed for each of the nine plant species tested under the four treatments described in Fig. 1 during the 20-d post-dispersal seed predation experiment at 2700 m elevation in the central Chilean Andes. Values are means \pm 1 s.e., $n = 9$ replicate 'plates' per plant species for each exclusion treatment.

To our knowledge, this is the first experimental assessment of patterns of post-dispersal seed predation in an alpine plant community that considers several species differing in life form and seed characteristics. We found much variation between species in the proportion of seeds removed by granivores, varying from small to extremely large losses for the herb *A. pallida* and the shrub *A. cumingii*, respectively. An intermediate proportion of seeds of other species (*C. oppositifolia*, *T. officinale*, *R. rhodolirion*, *L. acaulis* and *A. monantha*) was removed. Considerable difference among species has been reported in other ecosystems, such as tropical forests (e.g. Blate *et al.*, 1998), temperate forests (e.g. Whelan *et al.*, 1991; Kollmann *et al.*, 1998; Hulme and Borelli, 1999), Mediterranean-type climate scrublands (Hulme, 1997; Figueroa *et al.*, 2002) and semi-arid communities (Brown *et al.*, 1986; Brown and Heske, 1990).

In our study, no relationship was detected between percentage seed losses and seed mass between the species, as observed in other systems (Kollmann *et al.*, 1998; Díaz *et al.*, 1999; Hulme and Borelli, 1999; Moles *et al.*, 2003). However, Blate *et al.* (1998) found a negative relationship between predation rates and seed mass in 40 species of trees in lowland tropical forest in south-east Asia, a result contrary to theoretical predictions, and which was explained by the scarcity of predators capable of penetrating the hard seed coats of large seeds. Apart from hardness, seed removal has also been reported to be related more to the viability of seeds, their water content and toxicity (Kollmann *et al.*, 1998). We suggest that differences between species in losses to predators may be partially related to their degree of hardness; removal of the hard seeds of *A. pallida*, *S. arenarium* and *P. coriacea* was

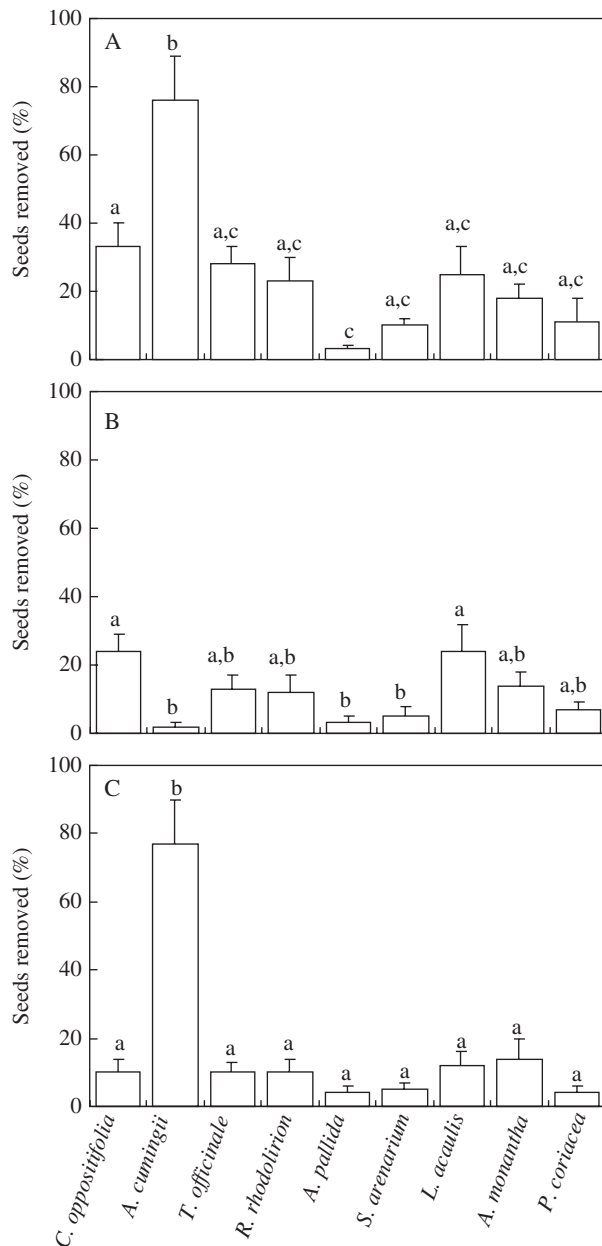


FIG. 3. Final accumulated percentage of seeds of each of the nine plant species removed by (A) ants and birds combined, (B) ants only, and (C) birds only, after 20-d exposure to seed predators at 2700 m in the central Chilean Andes. Values are means \pm 1 s.e. Each plant species had 9 replicate 'plates'. Means with the same letter do not differ significantly, $P > 0.05$.

low. Differences between species in seed losses may also be related to other traits such as nutritional content, given the requirement for energy associated with high metabolic costs that animals inhabiting alpine ecosystems probably experience (Hoffmann, 1974; Schmidt-Nielsen, 1990). However, we currently lack data on energy and nutritional contents of the seeds studied, and therefore the reasons for the differences between species can only be speculated upon. In any case, the large differences in the magnitude of seed predation for the different species in our study demonstrates that

generalizations on the importance of seed losses to granivores in any particular ecosystem should not be made based on studies of a single species (e.g. see Vásquez *et al.*, 1995, and review by Marone *et al.*, 2000).

The importance of distinguishing between removal of seeds by invertebrate and vertebrate granivores has been stressed in the literature (Hulme, 1997). Separation of the effects of these groups of animals is vital since they are likely to differ in time and space. Our study differentiated experimentally between seed removal by birds and ants, and showed different patterns of removal by these two types of granivores. Birds removed a large proportion (77%) of seeds from the shrub *A. cumingii*, while the remaining species experienced much smaller (4–12%) losses. The proportion of seeds removed by ants (24%) was moderate for the shrub *C. oppositifolia* and the cushion-plant *L. acaulis*. Nevertheless, for most species, seed removal by birds compared with ants was similar and small (e.g. *A. pallida*, *S. arenarium*, *P. coriacea*). Hulme (1997) showed that removal of seeds from three tree species in the highlands of Andalusia in south-eastern Spain was much greater by rodents than ants. Our results showed differences in seed predation by ants compared with birds for some of the species studied, again demonstrating that the importance of different predator groups in ecosystems can not be generalized when seeds of only one, or a few, species are offered (Vásquez *et al.*, 1995; Marone *et al.*, 2000; Kelt *et al.*, 2004).

Nonetheless, there is a caveat when interpreting the results. As we only quantified seed removal, the final fate of the seeds removed is unknown. Removal may not equate with death of the seed and may result in secondary seed dispersal (Chambers and MacMahon, 1994; Vander Wall *et al.*, 2005). However, although we can not rule out some secondary dispersal, two points argue for most seed removal actually representing consumption and death of seeds. Firstly, seed remnants were seen at many of the experimental plates. Secondly, none of the species tested produce fleshy fruits or special adaptations for animal dispersal, such as elaisomes. Nevertheless, the ant *Solenopsis gayi* in the ecosystem may cause some secondary dispersal of the seeds they remove. Thus seed predation by ants in this system may be over-estimated. We consider that seed removal by birds in the central Chilean Andes represents predation as all birds seen removing seeds are either described as granivores (*Diuca diuca*) or include seeds in their diet (e.g. *Turdus falcklandii*) (Araya and Millie, 1988). Future studies should focus on the fate of seeds in alpine ecosystems to gain a better understanding of the role of biotic agents.

Another caveat is that, given studies showing seed predation to differ spatially among microhabitats, such as open vs. closed canopy areas in woodlands (e.g. Whelan *et al.*, 1991; Díaz *et al.*, 1999), our study may have hidden potential differences in the magnitude of losses near dwarf shrubs of *C. oppositifolia* compared with open areas. Future studies of post-dispersal seed predation should take microhabitat differences into account.

It is necessary to point out the importance of allowing a sufficient experimental period (20 d), especially when considering a wide variety of species concurrently (cf. Moles

et al., 2003). A consistent effect of time on seed removal was evident for all species (Table 3) so that the magnitude of total loss to granivores would have been markedly smaller if the experiment had run for half the time, especially for species such as *A. cumingii*, *R. rhodolirion* and *A. monantha* (Fig. 2). However, for others the magnitude of seed predation levelled off between day 10 and 20 (e.g. *C. oppositifolia*, *T. officinale*, *A. pallida*), demonstrating that the time granivores took to detect seeds may have differed among plant species.

CONCLUSIONS

In alpine ecosystems, as elsewhere, an understanding of the processes limiting recruitment of plants of a species into an ecosystem clearly requires examination of not only abiotic factors causing mortality, such as desiccation, temperature and disturbance, but also biotic factors that may remove an important proportion of propagules from the soil even before abiotic factors become important. Considering seeds of a range of species of different life form, producing seeds of various sizes, up to 25 % of the total seeds dispersed in the alpine environment of the Chilean Andes may be lost over an period of 3 weeks to ant and bird predators, constituting an important source of mortality, and with potentially important effects on plant recruitment in alpine ecosystems.

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