

Granivore impact on soil-seed reserves in the central Monte desert, Argentina

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Summary

1. Mechanisms of grass- and forb-seed input and output in the central Monte desert of Argentina were studied in 1995 to test the hypothesis that seed consumption by autumn–winter granivores, especially birds, has qualitative as well as quantitative effects on soil-seed reserves.

2. The abundance of perennial grass seeds in late summer soils (≈ 2400 seeds m^{-2} or 0.36 g m^{-2}) remained unchanged the following early spring (≈ 2700 seeds m^{-2} or 0.39 g m^{-2}), despite the incorporation of about 3000 seeds m^{-2} or 0.71 g m^{-2} newly produced grass seeds during autumn–winter. Grass seeds appeared to be heavily consumed, especially the medium-sized ones.

3. The annual forb-seed bank was about the same size in late summer (≈ 5500 seeds m^{-2} or 1.34 g m^{-2}) as in early spring (≈ 6500 seeds m^{-2} or 1.53 g m^{-2}). Since forb-seed production had been relatively low (≈ 400 seeds m^{-2} or 0.12 g m^{-2}), these seeds apparently suffered negligible postdispersal losses.

4. This pattern of grass- and forb-seed loss coincides with the pattern of seed consumption by granivorous birds – on average, 93% of seed mass in bird stomachs was from grass seeds, while only 7% was from forb seeds.

5. Further evidence of a major impact of bird foraging on seed reserves is that the mass of particular grass seeds that was lost from soils was positively correlated with the mass of such seeds in bird diets, and that the main target of bird consumption, i.e. medium-sized grass seeds, suffered the highest postdispersal loss.

6. It is concluded that autumn–winter granivores in the central Monte desert, particularly birds, mainly consume newly produced grass seeds and that they might have major qualitative as well as quantitative impacts on soil-seed reserves.

Key-words: Granivory, granivorous birds, postdispersal seed loss, seed rain, soil-seed bank

Functional Ecology (1998) **12**, 640–645

Introduction

Seeds and granivores are conspicuous components of arid ecosystems. Though little is known about the fates of seeds once they land on the ground (Chambers & MacMahon 1994), there is convincing evidence of the impact that rodents, ants and fungi have on soil-seed reserves in several North American deserts (Reichman 1979; Brown *et al.* 1986; Crist & MacMahon 1992; Crist & Friese 1993; Price & Joyner 1997).

Mares & Rosenzweig (1978) experimentally assessed seed removal rates from ‘seed dishes’ in northern Monte and Sonoran deserts. Their results suggest that both vertebrate and overall granivory are ‘much depressed’ in the Monte, where mammal seed removal is ‘insignificant’, and birds are ‘relatively unimportant consumers’. A major failing of the ‘seed dish’ technique (Mares & Rosenzweig 1978;

Parmenter, MacMahon & Vander Wall 1984; Kerley 1991; Morton 1985) is the fact that birds might not remove seeds from trays left out for short periods (but see Vásquez, Bustamante & Simonetti 1995; Lopez de Casenave, Cueto & Marone 1998). In spite of this methodological warning, birds have been often considered unimportant granivores in desert ecosystems (e.g. Heatwole & Muir 1982; Abramsky 1983; Mull & MacMahon 1996; but see Parmenter *et al.* 1984; Thompson, Brown & Spencer 1991; Guo *et al.* 1995).

In 1994–95 we carried out a ‘seed dish’ experiment in the central Monte desert (Lopez de Casenave *et al.* 1998). We detected major consumption by vertebrates in autumn–winter, when birds were the primary seed eaters. Birds were responsible for almost 60% of total seed removal, while rodents removed about 35%. Ant removal, in contrast, was almost negligible during the

period (5%), because ant foraging is largely restricted to spring and summer. Our results did not coincide with those of Mares & Rosenzweig (1978) for the northern Monte. Here we use another approach (i.e. different from 'seed dish' experiments) to corroborate whether vertebrate granivory is important and has an impact on the central Monte's seed reserves.

We estimate soil seed reserves at the end of the summer of 1994–95 and compare them with those remaining in the soil-seed bank the following early spring, after granivore consumption in autumn–winter. Afterwards, we appraise whether seeds that suffered the largest postdispersal loss in the central Monte desert coincide with those regularly harvested by granivorous birds in order to test two hypotheses: (1) autumn–winter granivores, especially birds, cause major postdispersal seed losses and affect the floristic composition and size distribution of soil-seed banks; and (2) granivores focus their foraging on newly produced seeds, which prevents some seeds from entering a persistent soil-seed bank.

Materials and methods

STUDY SITE

The study was carried out in four 2-ha plots located in open woodlands of the Biosphere Reserve of Ñacuñán (34° 02' S, 67° 58' W), where *Prosopis flexuosa* and *Geoffroea decorticans* trees are scattered within a matrix of tall shrubs > 1 m (*Larrea divaricata*, *Capparis atamisquea*, *Condalia microphyla*), low shrubs < 1 m (mainly *Lycium* spp.) and perennial grasses (*Trichloris crinita*, *Pappophorum* spp., *Sporobolus cryptandrus*, *Aristida mendocina*, *Digitaria californica*, *Setaria leucopila*). Annual forb cover is usually lower than grass cover, and highly variable from year to year (Marone 1991). Ñacuñán's climate is dry and temperate with cold winters. Over 75% of the annual rainfall occurs in spring–summer (October–March average = 250 mm, $n = 25$ years), and seed production of almost all plants is restricted to summer months (Marone, Rossi & Horno 1998).

SEED BANK AND SEED RAIN SAMPLING

Owing to the great importance of predispersal seed predation (Louda 1989; Louda, Potvin & Collinge 1992), the term 'seed production' is avoided when referring to the cumulative newly produced seeds entering the soil-seed bank after summer production; instead the term potential seed bank (hereafter potential SB) is used. To assess the impact autumn–winter granivores had on soil-seed reserves, the soil-seed bank in late summer (12 February 1995; hereafter summer SB) was compared with the soil-seed bank present the following early spring (25 October 1995; hereafter spring SB). The total number of seeds that entered the soil from late summer to early spring (i.e.

the potential SB as defined above) was also estimated. Comparisons were focused separately on grass and forb seeds (i.e. those effectively consumed by granivorous birds) in an attempt to distinguish group-specific patterns of postdispersal seed loss.

Different microsites were sampled to obtain a representative sample of the soil-seed bank (summer SB and spring SB) and seed rain (potential SB) for the entire area. We located 84 core samples and the same number of seed traps accordingly to the percentage cover of three different microhabitats in the open woodland (Marone & Horno 1997): 'under the canopy of trees' (15% cover, $n = 14$ replicates), 'under the canopy of tall shrubs' (35% cover, $n = 28$ replicates), and 'in interspaces among shrubs or trees' (50% cover, $n = 42$ replicates). Roughly a quarter of the sampling effort was allocated to each 2-ha plot.

A cylindrical sampler, 3.2 cm in diameter and 2 cm deep, was used for taking soil samples. The cylinder was pushed into the soil, and then a metal scoop was pushed carefully just under the bottom edge of the cylinder to isolate the contained soil. In the laboratory, soil samples were searched for seeds under a dissecting microscope, after having been air-dried, sieved and sieved again under water pressure. Numbers and masses of 'apparently viable' (Roberts 1981) or 'sound' seeds (Mull & MacMahon 1996), i.e. those that did not crumble when probed with forceps, were recorded using a reference collection.

To measure the potential SB seed traps were used for catching seed rain. Each trap consisted of a 3.2-cm diameter and 5-cm deep plastic cup. Small holes in the bottom of the cup provided drainage. The cup was buried with its rim 0.5 cm above the soil surface to prevent trapping those seeds moving on the ground. Potential SB may be slightly overestimated, especially in exposed areas, because traps sometimes gathered wind-borne material (including seeds) from an area larger than the 8.04 cm² directly above the cup. Traps were initially installed on 13 February 1995, collected and replaced on 13 March, 19 April, 19 May and 3 August 1995. The final collection was on 27 August 1995. At that time the sampling was discontinued because seed trapping became negligible. Further, convective storms in the central Monte are rare in autumn–winter but gradually increase their frequency by spring, as does the likelihood of overestimating the potential SB by trapping seeds already standing on the soil. As with soil samples, the material that fell into seed traps was examined under a dissecting microscope. Numbers and masses of sound seeds were recorded.

DIET AND FORAGING BEHAVIOUR OF GRANIVOROUS BIRDS

Since the mid 1980s we have been surveying wintering and breeding bird populations over several belt transects in the Reserve of Ñacuñán (Marone 1992a; Marone, Lopez de Casenave & Cueto 1997). Four

species of the family Emberizidae are the most important seed-eater organisms that consume seeds from the soil surface in autumn–winter: *Zonotrichia capensis*, *Diuca diuca*, *Phrygilus carbonarius* and *Saltatricula multicolor*. Overall, birds from these species gleaned on the ground in 83% of 1457 observations recorded in the autumns and winters of 1993–97 (J. Lopez de Casenave, V. R. Cueto & L. Marone, unpublished data). *Poospiza torquata* is an important seed-eating species during autumn–winter in the central Monte. Nevertheless, it forages on seeds primarily from plant stalks and therefore it should be considered as a predispersal seed predator with insignificant impact on soil-seed reserves. All five bird species are year-round residents in the area, though they usually reach their maximum abundance in autumn–winter (Marone 1992b).

The contents of the digestive tract of mist-netted birds were obtained by using the flushing method (Moody 1970), which allows the effective collection of different food items with lower mortality than the emetic technique (Zach & Falls 1976; Zann & Straw 1984; Rosenberg & Cooper 1990). Droppings were also collected while handling the birds in order to increase the representation of each sample (Ralph, Nagata & Ralph 1985). Digestive tract contents from about 60 birds were preserved in alcohol, and the relative abundance of the different seed items was determined in the laboratory under a dissecting microscope (J. Lopez de Casenave, L. Marone and V. R. Cueto, unpublished data). Given our particular goals in this paper, we will exclusively consider the seed items present in bird diets (i.e. the granivorous diet of the birds will be depicted).

STATISTICAL ANALYSES

The sizes of the summer SB and spring SB were compared by using one-way ANOVA. Variables considered were the total number and total mass of grass and forb seeds. In all four cases ANOVA assumptions were met without data transformation. Conclusions were drawn about the magnitude of postdispersal grass- and forb-seed loss by testing whether the changes that occurred in the soil-seed bank were consistent with the amount of seeds incorporated after production (potential SB).

To test whether larger grass seeds suffered higher postdispersal loss than tiny ones, the size distribution of total grass-seed reserves before autumn–winter consumption (i.e. adding up seed numbers from summer SB and potential SB) was compared with that in spring SB, by using contingency tables. Grass seeds were classified into three size classes: 0–0.10 mg, 0.11–0.30 mg and 0.31–0.60 mg. The relationship between the mass of particular grass seeds that was lost from soils after granivore consumption and the mass of the same seeds in bird diets was assessed by using Spearman rank order correlation.

Results

SEED DYNAMICS

The means of 2428 and 2665 grass seeds m^{-2} in summer SB and spring SB, respectively (Table 1), were statistically indistinguishable (ANOVA, $F = 0.14$, $P > 0.70$, $df = 1166$). Such a lack of difference was recorded in spite of the incorporation of ≈ 3000 seeds m^{-2} during the autumn–winter of 1995. Likewise, 0.36 g m^{-2} of grass seeds in the summer SB and 0.39 g m^{-2} in the spring SB (ANOVA, $F = 0.11$, $P > 0.70$, $df = 1166$) was estimated, in spite of the 0.71 g m^{-2} that had entered in autumn–winter (Table 1). These results suggest that newly produced seeds from perennial grasses suffered major postdispersal loss and formed a mostly transient soil-seed bank in the study area.

The number and mass of annual forb seeds, like those of grass seeds, did not differ between summer SB and spring SB ($F = 0.25$ and $F = 0.16$, respectively; $P > 0.60$, $df = 1166$). In the case of forb seeds, however, their number and mass were more than an order of magnitude greater in the soil-seed bank than in the potential SB (Table 1). Thus, we conclude that forb seeds suffered almost no postdispersal loss, and were more likely to enter a persistent seed bank during this study.

Postdispersal losses of grass seeds were not homogeneous when different size classes were considered: tiny seeds were lost at lower rates than expected, whereas medium-sized seeds disappeared faster than expected, and larger seeds declined as expected ($\chi^2 = 29.9$; $P < 0.001$; $df = 2$; Fig. 1).

BIRD DIET

The percentage contribution in mass of every plant-seed genera to the granivorous diet of the birds that forage mainly on the soil in autumn–winter is shown in Table 2. On average, 93% of seed mass came from grasses. Forb seeds, on the other hand, contributed only 7%. Bird species such as *Diuca diuca* and *Saltatricula multicolor* appeared to forage exclusively on grass seeds, and these seeds represented almost 90% of the granivorous diet of *Phrygilus carbonarius*. Grass seeds also prevailed in *Zonotrichia capensis* diet (almost 70%), but this species also seemed systematically to consume some forb seeds (Table 2). Finally, 60% of seed mass found in stomach contents of birds belonging to the granivorous guild came from medium-sized grass seeds (*Trichloris crinita*, *Pappophorum* spp. and *Diplachne dubia*).

Discussion

Germination is a plausible alternative to consumption that may account for the seed losses reported here (Nelson & Chew 1977; Kemp 1989). Owing to its probable importance, the impact of germination loss will be addressed before discussing the effects of autumn–winter consumers on soil-seed reserves.

Table 1. Number of grass and forb seeds m^{-2} in soil-seed banks of the Monte desert of Argentina, in February 1995 (summer soil-seed bank) and October 1995 (spring soil-seed bank), and the cumulative number of seeds m^{-2} that entered the soils from 13 February 1995 to 27 August 1995 (potential soil-seed bank). Individual per seed masses are also given in the first column. Scientific names are after Roig (1981)

Species	Mass (mg)	Summer SB	Potential SB	Spring SB
Grasses				
<i>Sporobolus cryptandrus</i>	0.06	1599.1	370.2	1688.0
<i>Pappophorum</i> spp.	0.24	251.7	1347.4	577.5
<i>Trichloris crinita</i>	0.18	88.8	562.6	44.4
<i>Aristida</i> spp.	0.46	29.6	59.2	29.6
<i>Digitaria californica</i>	0.38	266.5	251.7	207.3
<i>Setaria leucopila</i>	0.60	103.6	177.7	59.2
<i>Diplachne dubia</i>	0.24	14.8	118.4	44.4
<i>Neobouteloua lophostachya</i>	0.08	14.8	88.8	14.8
<i>Chloris castilloniana</i>	0.20	29.6	14.8	–
<i>Bouteloua</i> spp.	0.14	14.8	–	–
<i>Stipa</i> spp.	0.10	14.8	–	–
Total number (SE)		2428 (397)	2991 (377)	2665 (490)
Total mass (g/m^2) (SE)		0.36 (0.06)	0.71 (0.08)	0.39 (0.06)
Forbs				
<i>Chenopodium papulosum</i>	0.24	4619.8	88.8	5626.6
<i>Parthenium hysterophorus</i>	0.45	14.8	–	–
<i>Heliotropium mendocinum</i>	0.63	29.6	–	–
<i>Conyza</i> spp.	0.04	44.4	–	29.6
Compositae unknown	0.20	–	59.2	–
<i>Phacelia artemisioides</i>	0.36	222.1	222.1	162.9
<i>Glandularia mendocina</i>	0.40	133.3	14.8	162.9
<i>Sphaeralcea miniata</i>	0.20	162.9	–	103.6
<i>Descurainia</i> sp.	0.08	222.1	–	340.6
<i>Lappula redowskii</i>	0.40	14.8	–	29.6
<i>Plantago patagonica</i>	0.38	–	14.8	–
Total number (SE)		5464 (1345)	400 (99)	6456 (1582)
Total mass (g/m^2) (SE)		1.34 (0.29)	0.12 (0.03)	1.53 (0.38)

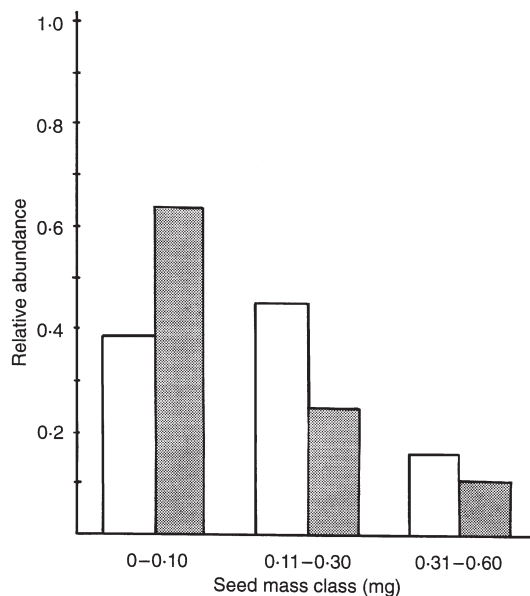


Fig. 1. Relative abundance of grass seeds in three different size classes before (summer SB + potential SB: open bars) and after (spring SB: shaded bars) postdispersal seed loss in the Monte desert of Argentina. Species-specific seed masses are shown in Table 1.

L. Marone and M. E. Horno (unpublished data) monitored the density of naturally emerging seedlings in open woodland from April to February in 1993–94 (140.3 mm) and 1994–95 (300.4 mm). Seedlings over 25 (1993–94) and 30 (1994–95) 1×1 m plots, randomly dispersed over an area of 3 ha, were recorded shortly after cotyledons appeared. Because seedling emergence was almost zero from June to September, a census of the plots was taken every 20–30 days only during the growing season. The number of emerged seedlings provides a coarse appraisal of germination loss, but is still a better estimator than the one most commonly used in community studies, i.e. the number of adult plants established (e.g. Nelson & Chew 1977). In 1993–94, 6.2 ± 1.7 (± 1 SE) seedlings m^{-2} were recorded, and in 1994–95 there were 11.2 ± 2.3 seedlings m^{-2} . These values represented $< 0.5\%$ of the minimum annual abundance of soil seeds in the central Monte desert (Marone & Horno 1997). Therefore, it is assumed that germination loss was almost negligible during this study, and that most postdispersal seed loss may be more parsimoniously attributed to other factors such as decomposition and consumption by autumn–winter granivores, especially birds.

This assumption was strengthened by our verification that seeds suffering higher postdispersal losses (i.e. grass seeds, see Table 1) were the same as those highly consumed by the main autumn–winter granivores (Table 2). Heavy consumption of grass seeds by taxonomically different seed-eating birds in several semiarid localities around the world has been already reported by Grant & Grant (1980), Schluter (1982), Schluter & Repasky (1991) and Read (1994). The preponderance of grass seeds in the diet of finches everywhere may be related to some morphological traits of these seeds that enhance their processing speed, and/or to the relatively low incidence of some toxic compounds, such as tannins and alkaloids, in seeds of the family Poaceae (Earle & Jones 1962; see Díaz 1996).

Two other lines of evidence also suggest that autumn–winter granivores may have an important impact on grass-seed reserves. First, the mass of grass-seed species in bird stomachs correlated positively with the amount of the species-specific production that was lost towards spring (Spearman rank order correlation, $R = 0.76$, $P < 0.01$, $n = 11$; Tables 1 and 2). Second, medium-sized grass seeds showed the greatest decline in the spring seed bank (Fig. 1), and were also the main food item in bird diets (Table 2).

We realize that our suggestion of a significant impact of autumn–winter granivores (particularly

birds) on seed reserves is based on circumstantial, non-experimental evidence, and that other avenues of autumn–winter seed loss (e.g. granivorous mammals, decomposition) should be investigated in the central Monte desert. Nevertheless, we think that our conclusions are robust and provide essential information to design the expensive field experiments that will be necessary to understand the organization of the seed–granivore system in semiarid South America thoroughly (e.g. Guo *et al.* 1995). Still, we contribute convincing evidence of:

1. a major impact of vertebrate granivores on the abundance, floristic composition and size distribution of seed reserves in the Monte desert, where vertebrate as well as overall granivory had been formerly considered to be very poor or even insignificant (Mares & Rosenzweig 1978; Abramsky 1983; Morton 1985);
2. the key role of newly produced seeds in maintaining the granivorous guild (Price & Joyner 1997), which would confirm the suspicion of a major effect of timing and amount of rainfall on the density and migratory movements of granivorous bird populations (Marone 1992a); and
3. the role vertebrate granivores may play, together with seed physiology, in determining what fraction of the seed bank is more likely to be transient or persistent in desert ecosystems (Grime 1989).

Table 2. Average seed mass (mg), corresponding to different plant genera, found in stomach contents of the most abundant granivorous bird species of the Biosphere Reserve of Ñacuñán during the autumns of 1993 and 1994, and the winters of 1994 and 1995. Note that plant-seed genera are arranged in order of increasing mass (see Table 1). Bird species acronyms: SAL (*Saltatricula multicolor*), PHR (*Phrygilus carbonarius*), ZON (*Zonotrichia capensis*), DIU (*Diuca diuca*), PTO (*Poospiza torquata*). Seed masses in *P. torquata* diet were not considered for estimating the general average (though they are shown in the last column) for this species forages mainly on seeds on plant stalks instead of on seeds on the soil (see the text) (J. Lopez de Casenave, L. Marone and V. R. Cueto, unpublished data)

Plant genera	Bird species				Average \pm SE	PTO
	SAL	PHR	ZON	DIU		
Grass seeds						
<i>Sporobolus</i>	0.07	0.01	0.81	0	0.22 \pm 0.20	0.29
<i>Neobouteloua</i>	0.04	0	0.07	0	0.03 \pm 0.02	0.08
<i>Trichloris</i>	0.09	0.14	0.13	0.12	0.12 \pm 0.01	0.16
<i>Pappophorum</i>	0.84	0.18	0.39	6.00	1.85 \pm 1.39	2.55
<i>Diplachne</i>	1.11	0.30	0.15	0	0.39 \pm 0.25	0
<i>Digitaria</i>	0	0.10	0.02	2.79	0.73 \pm 0.69	0.43
<i>Aristida</i>	0.11	0	0.02	0	0.03 \pm 0.03	0
<i>Setaria</i>	0.22	0	0.42	0.60	0.31 \pm 0.13	0.06
Total	2.48	0.73	2.01	9.51	3.68 \pm 1.98	3.57
Forb seeds						
<i>Sphaeralcea</i>	0	0	0.03	0	0.01 \pm 0.01	0
<i>Chenopodium</i>	0	0	0.72	0	0.18 \pm 0.18	0
<i>Glandularia</i>	0	0.10	0.19	0	0.07 \pm 0.05	0
Total	0	0.10	0.94	0	0.26 \pm 0.22	0
Richness	7	6	11	4		6
Total seed number	87	14	492	102		372
No. of stomachs	8	4	23	3		21

Acknowledgements

We thank V. R. Cueto, I. Peralta, N. Horak, R. González del Solar, S. Trione, G. Debandi, P. Villagra and M. Horno for valuable help. M. V. Price and J. Joyner kindly shared with us unpublished information on the seed/granivore system in the Mojave desert. M. V. Price, V. R. Cueto, F. Jaksic, M. Aguiar, R. González del Solar and two anonymous reviewers provided constructive comments on a first version of the manuscript. The study was supported by MAB-UNESCO, Association of Field Ornithologists, Manomet Bird Observatory and IADIZA-Gobierno de Mendoza. Contribution number 6 of the Desert Community Ecology Group (Ecodes), UF & EV, IADIZA.

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Received 11 April 1997; revised 10 December 1997;
accepted 19 December 1997