Post-dispersal fate of seeds in the Monte desert of Argentina: patterns of germination in successive wet and dry years

LUIS MARONE, MANUEL E. HORNO and RAFAEL GONZÁLEZ DEL SOLAR

Desert Community Ecology Research Team, IADIZA Institute, Casilla de Correo 507, 5500 Mendoza, Argentina

Summary

1 Patterns of seed germination of grass and forb species were studied in open *Prosopis* woodland of the central Monte desert (Argentina) during several years, to test the hypotheses that (i) seed germination is positively affected by both rainfall and protection afforded by vegetation cover (a facilitative effect), (ii) the number of surviving plants is positively influenced by rainfall but negatively affected by established vegetation (a competitive effect), and (iii) seed loss from soil banks owing to germination is lower than that caused by granivorous animals.

2 Forb species germinated during restricted periods, either in early autumn or in spring. Grasses, however, germinated throughout the growing season, but because seedlings could not be identified to species level, it was impossible to discern whether different species germinated in particular seasons, or if all grasses germinated in all seasons. Grass and forb germination were generally of similar magnitude, but grass germination increased by an order of magnitude during a summer of unusually abundant rainfall related to an El Niño Southern Oscillation (ENSO) event.

3 Overall, the spatial distribution of neither germinating seeds nor surviving plants could be explained by interactions with established vegetation (facilitation and competition effects, respectively). An alternative explanation may be provided by the distribution of forb and grass seeds in the soil.

4 Seed loss owing to germination was low in both dry and rainy years. For forbs, such loss totalled < 1% of soil-seed reserves, and no forb species suffered losses > 4%. Total grass-seed loss to germination was usually < 0.5%, and the 5% reached in 1997–98 corresponded to an interruption of a prolonged drought by unusually abundant rainfall associated with a reduced seed bank.

5 Grass-seed loss caused by germination was one to two orders of magnitude lower than that reported due to autumn-winter granivory in the central Monte desert.

Key-words: ENSO, granivory, grasses, seed loss, seedling

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Introduction

Seeds represent the only means of dispersal and therefore of access to new regions for most desert plants (Kemp 1989). Although seeds may be extremely abundant in desert soils, only a few of these 'potential plants' survive to produce seeds themselves. As well as removal due to germination, seeds may be lost as a result of consumption, deep burial and pathogen attack (Simpson *et al.* 1989; Chambers & MacMahon 1994). Research is however needed to establish which of the possible mechanisms effectively control seed flux in particular communities, and thus to evaluate the effects of seed-eating animals on plant dynamics (Kerley & Whitford 1994; Marone & Horno 1997).

Correspondence: Dr Luis Marone, Ecodes, UF & EV, IADIZA Institute, Casilla de Correo 507, 5500, Mendoza, Argentina (e-mail: Lmarone@lanet.com.ar).

L. Marone,
M. E. Horno &
R. G. del Solar

Post-dispersal seed loss in open *Prosopis flexuosa* woodland of the central Monte desert of Argentina is due to a number of causes, including seed-eating vertebrates, especially birds, which may consume about $7 \, kg \, ha^{-1}$ (i.e. almost all) the newly produced grass seeds during autumn-winter months (Marone *et al.* 1998a). Seeds are also lost by deep burial. About 80% of total seeds remains in the top $2 \, cm$ of soil (Marone *et al.* 1998b), a similar proportion to that seen in other warm deserts (Kemp 1989). Tiny seeds (e.g. those of the grass species *Sporobolus cryptandrus* or the forb species *Descurainia* sp.) were particularly prone to such loss as were some medium- and large-sized forb seeds (e.g. *Sphaeralcea miniata*, *Phacelia artemisioides* and *Glandularia mendocina*) that appear to be more likely to penetrate the soil than grass seeds of a similar size. The impact of pathogens and germination on the size of the seed bank remains to be established.

The feasibility of rehabilitating desert ecosystems, many of which are overgrazed (Milton 1995), will also depend on understanding the timing and spatial patterning of seed germination and plant establishment. Plant recruitment may be limited by insufficient rainfall (Milton 1995), scarcity of seeds (Aguiar & Sala 1997), lack of suitable sites (Moretto & Distel 1998), and/or competition from established plants (Potvin 1993; Defossé *et al.* 1997). The Monte desert is used for cattle rearing and information on the recruitment of forage plants (e.g. several perennial grasses) is therefore essential, although little is known about the effects of timing of rainfall and microhabitat on establishment of any of the species present.

Natural patterns of seed germination and the number of surviving plants were assessed during successive wet and dry years in order to test the following hypotheses: (i) grass and forb seeds germinate during restricted, species-specific periods (i.e. germination is widely seasonal), but seed germination ultimately depends on rainfall; (ii) seed germination is higher in protected microsites located under the canopy of established plants (facilitative effect), whereas survival is greater in exposed microsites where bare ground prevails (competitive effect); and (iii) post-dispersal seed loss owing to germination is highly variable from year to year, but is lower than that caused by seed-eating animals.

Materials and methods

STUDY AREA

Fieldwork was carried out in open woodland at the Biosphere Reserve of Ñacuñán ($34°02'$ S, $67°58'$ W), Mendoza province, Argentina. *Prosopis flexuosa* and *Geoffroea decorticans* are the major trees, although there are tall shrubs ($> 1 \, m$) of *Larrea divaricata*, *Capparis atamisquea* and *Condalia micro-*

phylla (Roig 1981). The main low shrubs ($< 1 \, m$) are *Lycium* spp., *Verbena* spp. and *Accantholippia seriphioides*.

The open woodland has 25–50% of grass cover, mostly of perennial C_4 Poaceae species (Cavagnaro 1988) with summer growth: *Pappophorum* spp., *Digitaria californica*, *Trichloris crinita*, *Aristida mendocina*, *Sporobolus cryptandrus*, *Setaria leucopila*, *Diplachne dubia* and *Neobouteloua lophostachya*. Perennial species represent $> 95\%$ of total grass cover in the open woodland (Marone 1990), although the annual grasses *Aristida adsencionis*, *Munroa mendocina* and *Cottea pappophoroides* do occur at low frequency. Most forb species in the reserve are annuals (e.g. *Chenopodium papulosum*, *Parthenium hysterophorus*, *Phacelia artemisioides*, *Lappula redowskii*, *Descurainia* sp. and *Plantago patagonica*), although biennials and perennials are also present (*Heliotropium mendocinum*, *Glandularia mendocina* and *Sphaeralcea miniata*). Forb cover is usually lower than grass cover, but is highly variable from year to year (Marone 1990). Climate in the central Monte desert is dry and temperate, with cold winters. On average $> 75\%$ ($258 \, mm$, $n = 26$ years) of the annual rainfall occurs in the spring and summer months (October–March).

SEED GERMINATION AND NUMBER OF SURVIVING PLANTS

We used seedling emergence as a surrogate for seed germination under field conditions. Although a proportion of all germinating seeds are expected to die without emerging, such pre-emergence mortality is extremely difficult to measure in the field (Wagner & Spira 1994). The number of emerging seedlings recorded at the cotyledon stage is, however, a better estimator of seed germination than the number of adult plants established, which has, nevertheless, been commonly used in community-level field studies (e.g. Nelson & Chew 1977).

We monitored the density of emerging seedlings and surviving plants from October 1993 to May 1995 and from May 1997 to March 1998, and the number of surviving plants only from October 1996 to May 1997, in $1-m^2$ quadrats ($n = 25$ until March 1994 and 30 thereafter). Seedlings were mapped as soon as cotyledons appeared and recensused every 15–30 days from October through May, the period over which emergence occurs in the central Monte desert (M. Horno & L. Marone, personal observations). At each census, we recorded any phenological change of previously mapped individuals as well as new emergences. Quadrats were located in three different 2-ha plots in open woodland and were randomly positioned along a transect, separated by at least $5 \, m$ ($n = 10$, 8 and 7; 12 in the later plot after May 1994).

Emerging seedlings of forbs were usually identified to species level but grass seedlings were indistinguishable and therefore combined. In all cases, surviving forbs had fruited and dispersed seeds by late spring, and all surviving plants were therefore considered to be established. In contrast, most of the surviving grasses did not fruit in the same season as they emerged but formed 'seedling banks' (Simpson *et al.* 1989), with the notable exception of *Cottea pappophoroides* whose fruit mature 8–10 weeks after the seedling stage (M. Horno & L. Marone, personal observations). For the sake of simplicity, we refer to 'number of surviving plants' for both forbs and grasses, even though the forbs had all matured and set seed, while most grasses were still juveniles at the end of the growing season.

The proportion of each quadrat that was covered by the canopy projection of trees, shrubs or grasses was estimated after division into four $0.25 \, m^2$ quadrants and measurement of the proportion of bare ground in each (protective cover = 1 − proportion of bare ground).

GERMINATION SEED LOSS

The magnitude of species-specific post-dispersal seed loss owing to germination was estimated as the proportion of germinating seeds (inferred from emerging seedlings) relative to previous seed reserves (determined from the size and composition of soil seed banks measured prior to germination).

Soil seed bank samples were taken from four 2-ha plots in the open woodland (including the three described previously). We sampled different microhabitats (under the canopy of trees, under the canopy of tall and low shrubs, among grasses and in exposed areas) to obtain a representative sample of the seed bank for the whole of this heterogeneous habitat ($n = 73$, spread approximately equally across the four plots). We used a cylindrical soil sampler to remove cores 3.2 cm in diameter and 2 cm deep, which were searched for seeds under a dissecting microscope after being sieved and washed under water pressure. Numbers of 'sound' seeds of each species (Mull & MacMahon 1996), i.e. those that did not crumble when probed with forceps, were recorded using a reference collection (see Marone & Horno 1997 for a detailed description of the method).

The number of seeds in the winter soil seed bank may underestimate the 'previous seed reserves' available for spring and summer germination, at least for those species that start to disperse seeds in spring. Studies on the timing of primary dispersal in the central Monte desert carried out in 1994 and 1995 showed that several grass species do indeed disperse their seeds in early summer (26 November−23 January; $6.9 \pm 1.4 \, mg \, m^{-2} \, d^{-1}$) as well as in late summer (24 January−19 April; $8.1 \pm 1.2 \, mg \, m^{-2}$

d^{-1}) (Marone *et al.* 1998b). If recently produced grass seeds are capable of germinating as soon as they land on the ground, they might constitute an unknown proportion of the spring-summer germination in addition to that due to seeds that have overwintered in the soil. Ripe seeds were therefore harvested from stalks of the most abundant grass species at the study site in early March 1998 and incubated at $30 \, °C$ in 9-cm diameter Petri dishes containing a cotton bed covered by a filter paper disc, saturated with a 0.1% w/v solution of a commercial fungicide. For each of the selected grass species (*Trichloris crinita*, *Pappophorum* spp., *Digitaria californica*, *Aristida mendocina*, *Setaria leucopila*, *Sporobolus cryptandrus*, *Diplachne dubia* and *Neobouteloua lophostachya*), germination capacity (cumulative germination percentage over 15 days; L. Marone & S.O. Trione unpublished data) was assessed in four sets of 50 seeds. The viability of any seeds remaining ungerminated was tested with 2, 3, 5 triphenyltetrazolium chloride.

Results

Seasonal rainfall was markedly variable among years during the study period (Fig. 1). Germination was also variable among years, and seemed to depend strongly on concurrent rainfall (Fig. 2). Total autumn germination differed among years ($H = 29.4$, d.f. = 2, $P < 0.001$; Kruskal–Wallis test; Zar 1996). The relatively wet autumns of 1994 and 1997 were statistically indistinguishable, but germination was lower in the dry autumn of 1995 (*a posteriori* Tukey-type tests, alpha = 0.05; Zar 1996). Total spring germination also differed among years ($H = 8.2$, d.f. = 2, $P < 0.05$), being significantly lower in the driest spring (1993) than in the wettest (1997), as did summer germination ($H = 64.2$, d.f. = 2, $P < 0.001$), which was low except in the unusually wet summer of 1998 (Fig. 2), when seedling density was over six times as high as at any other time.

The total number of surviving plants also differed among years with different rainfall ($H = 86.0$, d.f. = 3, $P < 0.001$; Fig. 3). The wettest period (1997–98) showed by far the highest survival, but 1996–97 values were also significantly higher than either 1993–94 or 1994–95 which were indistinguishable.

Seed germination of forb species was clearly seasonal (Fig. 2). Some species (autumn forbs: *Phacelia artemisioides*, *Glandularia mendocina*, *Sphaeralcea miniata*, *Descurainia* sp., *Lappula redowskii* and *Plantago patagonica*) germinated only in early autumn, usually in April–May, whereas others showed limited germination in autumn and summer, but typically had a peak in early October (spring forbs: *Chenopodium papulosum*, *Parthenium hysterophorus* and *Heliotropium mendocinum*). Overall, forb species germinated during short and restricted periods.
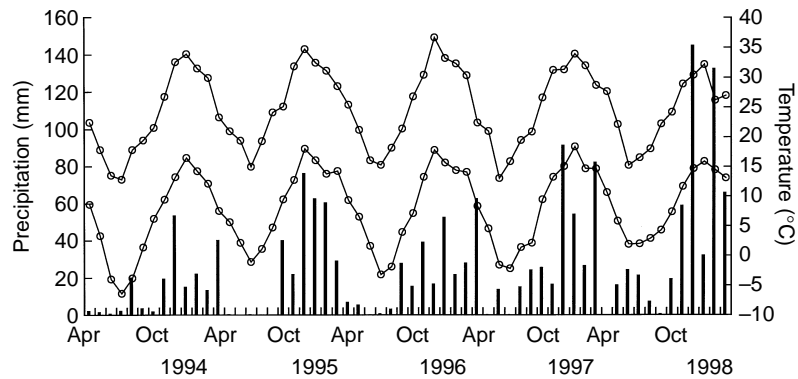
Fig. 1 Total monthly rainfall (vertical bars), and monthly averages of minimum and maximum daily temperatures (lines) in open *Prosopis* woodland of the central Monte desert, Argentina.

Grass species germinated in autumn, spring and summer (Fig. 2). Since grass seedlings could not be identified to species level, we were not able to distinguish whether this pattern was due to species-specific responses of particular grasses to particular weather conditions (as for forbs) or to continuing germination of all species throughout the growing season.

The number of germinating forb seeds always correlated positively and significantly with the presence

of protective cover (Spearman rank correlation; Zar 1996) as would be expected if facilitation were occurring; whereas the number of germinating grass seeds correlated positively with plant cover in only one of the three years analysed (Fig. 4). On the other hand, the number of surviving forbs and grasses never correlated negatively with protective cover (Fig. 5), as had been expected under the hypothesis of a competitive effect.

Seed loss by germination appeared to be very low throughout the study although it did vary between years. Such loss of autumn- or spring-forb species never reached 1% of soil reserves (Table 1), even under the extremely wet conditions of the spring and summer of 1997–98. Similarly, grass-seed loss was usually < 0.5%, but it did reach almost 5% of soil reserves in spring-summer 1997–98 (Table 1). Despite the limited loss to germination, the seed banks of both forbs and, especially, grasses showed marked interannual fluctuations in exposed as well as protected microhabitats (Table 2).

Germination trials showed that high proportions of the seeds of four of the eight species tested (*Trichloris crinita* (99%), *Aristida mendocina* (80%), *Pappophorum* spp. (62%) and *Digitaria californica* (44%)) were capable of germinating immediately after primary dispersal. The proportion of viable seeds of these species always surpassed 90%.

Discussion

SEED GERMINATION AND NUMBER OF SURVIVING PLANTS

The seasonal pattern of germination of forbs at Monte appeared to correspond with those of plants where germination is controlled by annual temperature cycles. Such seeds are generally subject to physical or physiological dormancy and thereby form persistent seed banks (Type III or IV, after Thompson & Grime 1979). Dormancy can be broken by either high temperatures (e.g. for species that
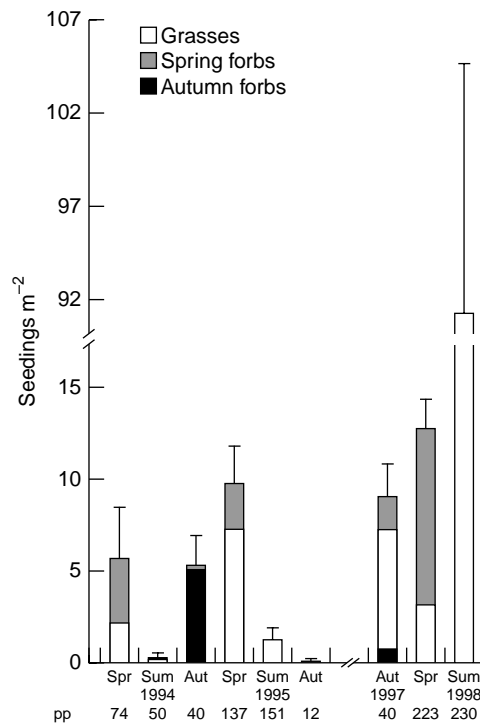

Fig. 2 Average (+ SE) number of total germinating seeds (inferred from emerging seedlings) in different seasons and years with different precipitation (mm). Although statistical comparisons among years are based on the total number of germinating seeds, the contribution of different plant groups is shown by different bar's textures.
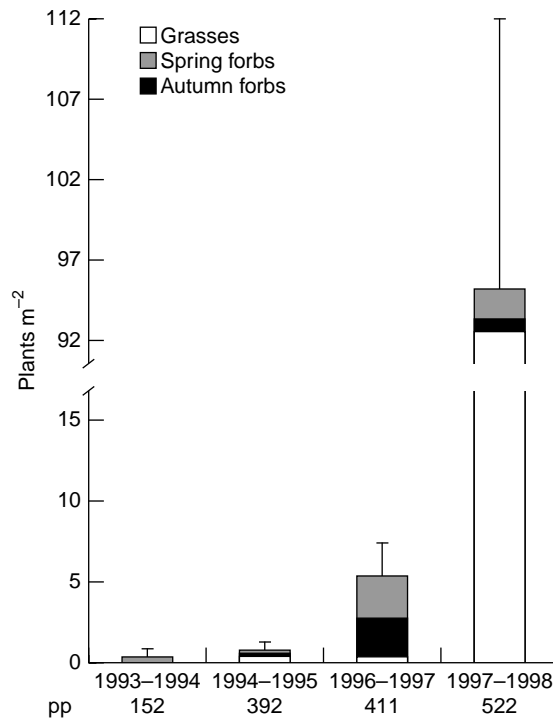
Fig. 3 Average number (+ SE) of surviving plants during 4 years (from May to the following March) subjected to different precipitation (mm).

germinate in early autumn) or low temperatures (e.g. species that germinate in early spring) (Baskin & Baskin 1989). By contrast, seeds from perennial grasses appeared to be able to germinate throughout the growing season, although they reached maximum germination in the warmer months (Fig. 2). This pattern corresponds to plant species with Type-I seed banks (grasses of dry or disturbed habitats, according to Thompson & Grime 1979), which always maintain a certain proportion of seeds capable of immediate germination.

Germination was sensitive to rainfall: for each season (spring, summer and autumn) total germination was least in the driest year and highest in the wettest year (Fig. 2). The number of surviving plants seemed to be also positively affected by precipitation (Fig. 3).

Under extremely rainy conditions, grass-seed germination in the summer of 1998 was two orders of magnitude higher than in previous, more mesic, summers (Fig. 2). Likewise, the number of surviving grasses in 1997–98 was 20 times higher than in previous years (Fig. 3). This pattern suggests that germination and recruitment of grasses in the Monte desert may be largely restricted to exceptional summers when rainfall surpasses a certain threshold, as implied by Neilson (1986), Westoby *et al.* (1989) and Potvin (1993) for other semiarid regions. *Bouteloua eriopoda* seedlings were observed in the

northern Chihuahuan desert (USA) in only seven of the years between 1915 and 1968 (Neilson 1986) and oceanic disturbances like the North Pacific sea-surface temperature (SST) anomalies may be needed to provide climatic conditions favourable for grass recruitment. Oceanic-atmospheric anomalies, such as the strong El Niño Southern Oscillation (ENSO) event which occurred in 1997–98, might also be important in the central Monte desert.

At the scale of a seed or seedling the environment may be strongly modified by established vegetation (Aguiar *et al.* 1992). In semi-arid regions, establishment/development of emerging seedlings may be facilitated by adult plants (e.g. via a decrease in potential evaporation rates or an increase in nutrient availability), although seedlings may subsequently suffer root competition from adult plants. Callaway (1997) indicated that facilitation among plants is likely to become stronger as abiotic stress increases (e.g. during dry periods). The positive correlation between vegetation cover and the number of forb seedlings could be due to facilitation, although no obvious association between precipitation and the strength of the effect was detected (Figs 1 and 4). In the case of grass seedlings, there was no consistent facilitative effect either (Fig. 4). Our results do not therefore provide conclusive data on the role of facilitation by established plants in seed germination.

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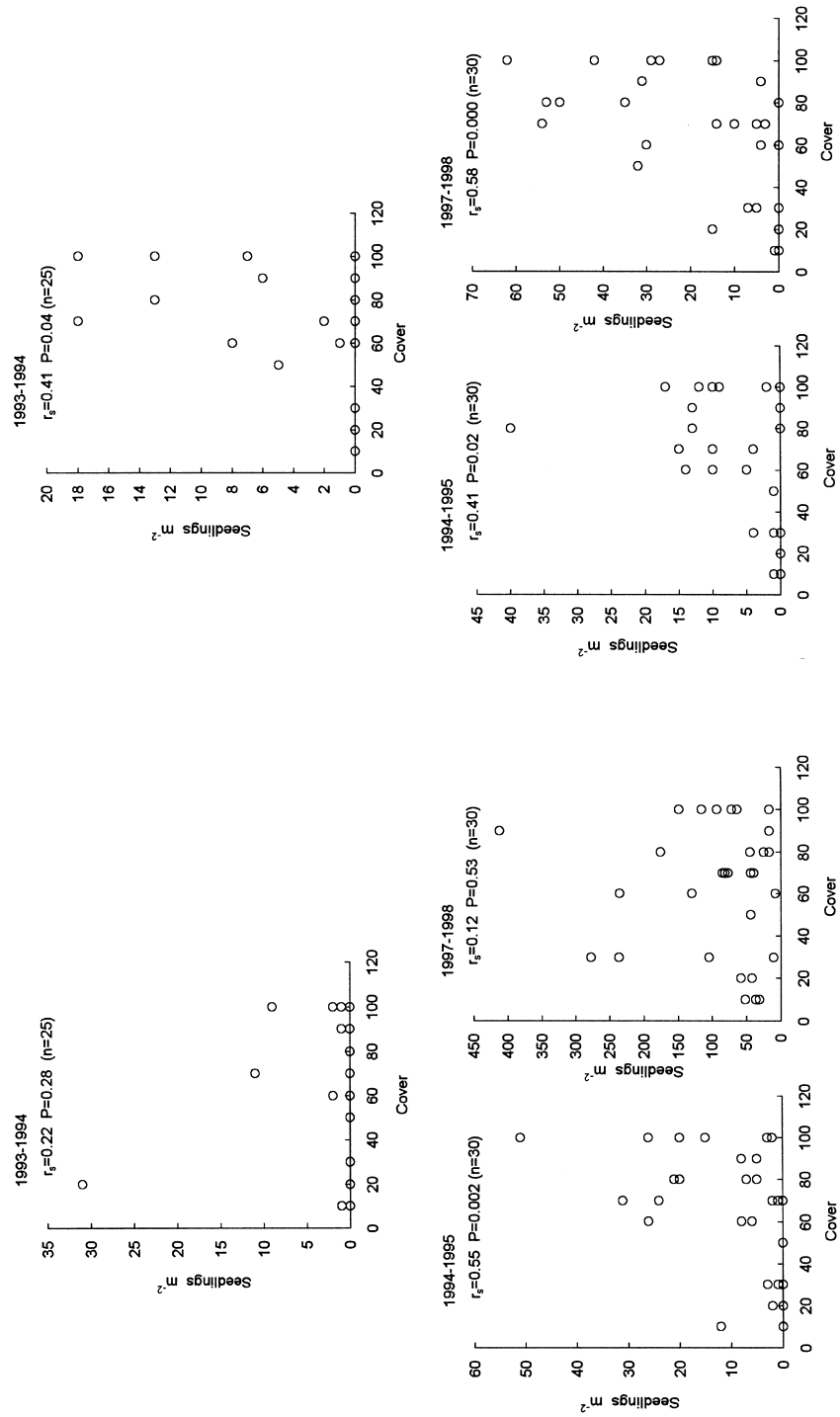R. G. del Solar

SEED GERMINATION

FORBS

GRASSES

Fig. 4 Relationship between the cover of perennial vegetation and total seed germination of forb and grass species. Statistics derived from Spearman rank order correlations.
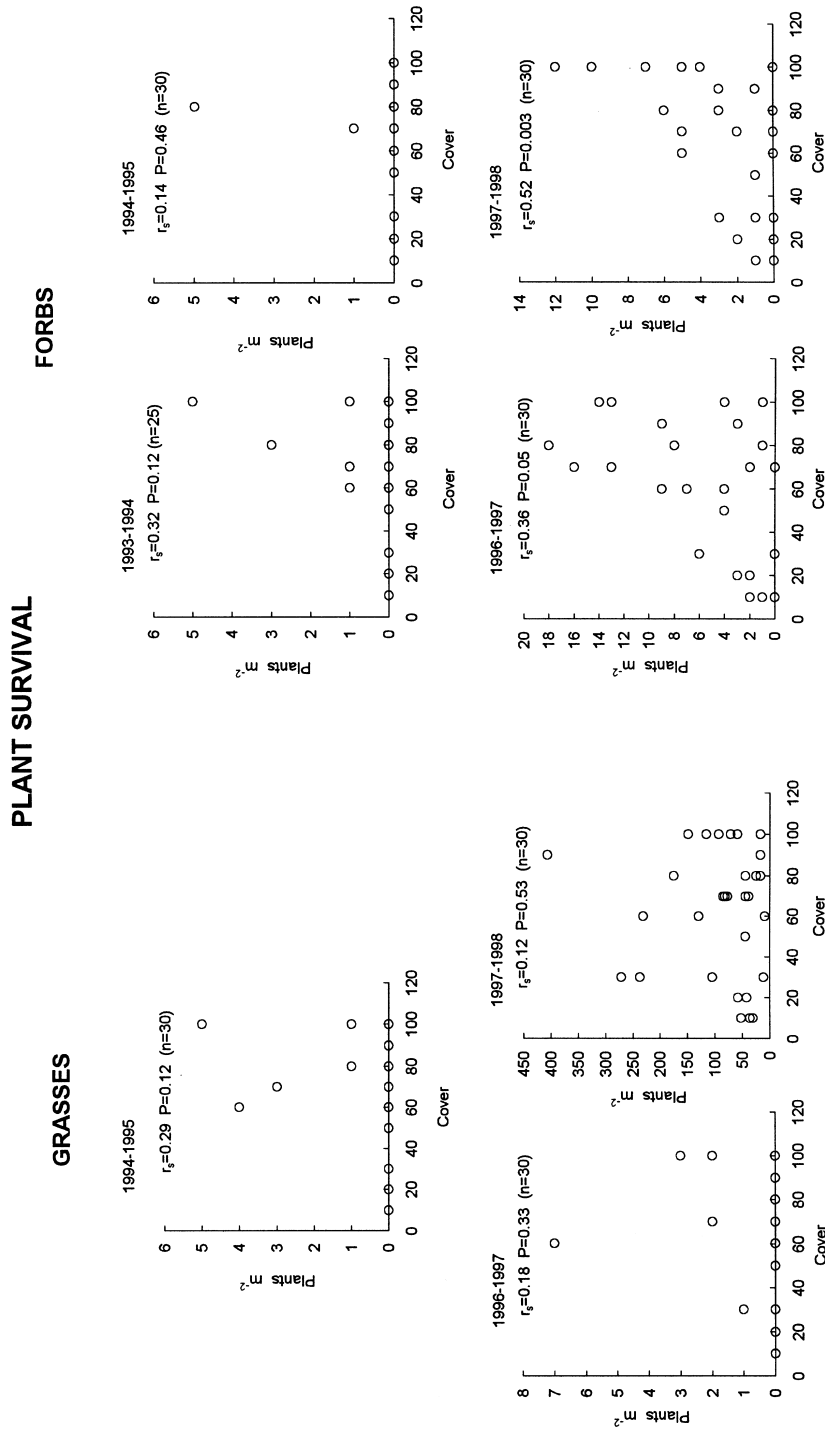
PLANT SURVIVAL

GRASSES

FORBS

Fig. 5 Relationships between the protective cover of perennial vegetation and the total number of surviving forbs and grasses. Statistics as in Fig. 4.

Table 1 Average (± SE) seed germination (SG; seeds m^{-2}) of specified plant species and the average (± SE) size of their previous soil seed bank (seeds m^{-2}). The number of autumn forbs germinated in April–May 1994, 1995 and 1997 were compared with corresponding soil seeds in February 1994 and 1995, and November 1996, respectively. The number of spring forbs germinated in September–October and of grasses germinated in October–March was compared with corresponding soil seeds in the previous winters (August 1993, 1994 and 1997)

Autumn forbs

	May 1994		May 1995		May 1997	
Plant species	SG	Soil bank	SG	Soil bank	SG	Soil bank
Phacelia artemisioides	0.23 ± 0.11	1414 ± 261	0	221 ± 70	0	323 ± 150
Glandularia mendocina	0.17 ± 0.11	119 ± 77	0	137 ± 63	0.37 ± 0.25	85 ± 37
Sphaeralcea miniata	0.83 ± 0.26	68 ± 33	0	170 ± 74	0.07 ± 0.05	204 ± 106
Descurainia sp.	1.33 ± 0.53	565 ± 159	0	460 ± 268	5.63 ± 1.71	188 ± 67
Lappula redowskii	0.90 ± 0.16	85 ± 56	0	17 ± 17	0	17 ± 17
Plantago patagonica	0.23 ± 0.16	0	0	0	0.63 ± 0.29	17 ± 17
Total	3.69 ± 0.89	2251 ± 386	0	1005 ± 334	6.7 ± 1.87	834 ± 240

Spring forbs

	October-November 1993		October-November 1994		October-November 1997	
Plant species	SG	Soil bank	SG	Soil bank	SG	Soil bank
Chenopodium papulosum	3.24 ± 1.13	13341 ± 3092	2.33 ± 1.05	4873 ± 1248	9.27 ± 2.46	5180 ± 1379
Parthenium hysterophorus	0.04 ± 0.04	17 ± 17	0.07 ± 0.05	17 ± 17	0.20 ± 0.11	68 ± 41
Heliotropium mendocinum	0	17 ± 17	0.07 ± 0.07	0	0	34 ± 24
Total	3.28 ± 1.13	13375 ± 3090	2.47 ± 1.06	4890 ± 1254	9.47 ± 2.45	5282 ± 1389

Grasses

	October 1993-March 1994		October 1994-March 1995		October 1997-March 1998	
Plant species	SG	Soil bank	SG	Soil bank	SG	Soil bank
Total grasses	2.36 ± 1.31	7127 ± 881	8.57 ± 2.10	4316 ± 636	92.6 ± 16.70	1925 ± 410

We predicted that competition from established plants would reduce seedling survival in the central Monte desert, but there was no association between cover and the number of surviving forbs or grasses except in two cases for forbs, where it was unexpectedly positive (Fig. 5). This evidence is, however, circumstantial and should be considered with caution as the measurement of both facilitation and competition on seedling dynamics requires careful experimentation (Aguiar *et al.* 1992; Potvin 1993; Defossé *et al.* 1997).

However, any experiment intended to measure facilitation or competition in the central Monte desert should take into account another plausible explanation for the spatial distribution of forb and grass seedlings and plants. Plant recruitment depends not only on appropriate conditions for germination and establishment, but also on seed availability (Aguiar & Sala 1997). Forb seedlings and plants were more abundant in under-canopy

patches, whereas grasses had a more homogeneous distribution across both protected and exposed patches (Figs 4 and 5), and such distributions could reflect patterns of seed availability. On average, 95% of forb seeds enter the habitat through under-canopy areas (Marone *et al.* 1998b), and a similar proportion remains there despite secondary dispersal in the winter (Table 2). Most grass seeds (70%), in contrast, enter the habitat through open patches (Marone *et al.* 1998b), and approximately 40% remains there (Table 2).

GERMINATION SEED LOSS

A negligible proportion of forb seeds was lost to germination (< 1% of previous soil-seed reserves, Table 1). Consistently, there was a persistent seed bank, at least in the soil of under-canopy patches, although many forb seeds were lost between 1993 and 1994 (Table 2). Such seeds are systematically
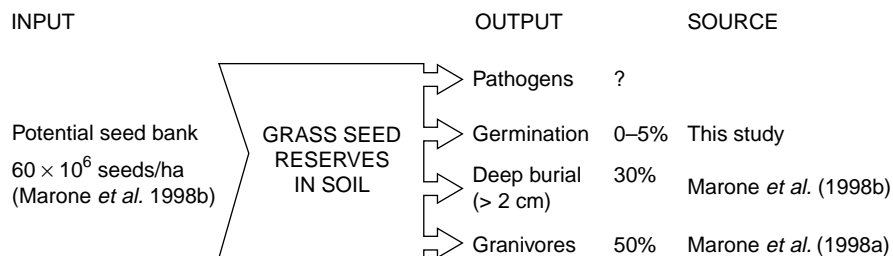
INPUT OUTPUT SOURCE

Pathogens ?

Potential seed bank — GRASS SEED RESERVES IN SOIL

60×10^6 seeds/ha
(Marone *et al.* 1998b)

Germination 0–5% This study

Deep burial (> 2 cm) 30% Marone *et al.* (1998b)

Granivores 50% Marone *et al.* (1998a)

Fig. 6 A quantitative model of the main mechanisms of seed input and output for grasses in the central Monte desert, Argentina. The potential seed bank (i.e. the cumulative production of new seeds that actually enter the soil) was measured in the spring-summer of 1994–95, a period of average rainfall. Grass-seed loss owing to deep burial was almost exclusively due to the small-seeded *Sporobolus cryptandrus*, and does not explain the loss of medium- and large-seeded species. Granivore seed loss was that caused specifically by birds and small mammals, which are the main autumn-winter seed consumers in the study area (see Lopez de Casenave *et al.* 1998).

consumed in autumn and winter by only one bird species (*Zonotrichia capensis*, Marone *et al.* 1998a), but little is known of the potential impact of ants and mammals on forb seeds in the Monte desert (Marone *et al.* 2000).

On the other hand, Marone *et al.* (1998a) found that granivorous vertebrates can consume a major fraction of the newly produced grass seeds during the subsequent autumn and winter, suggesting that granivory is responsible for the observed seed loss, although germination in autumn and early spring could be a contributing factor. Here, however, grass seed germination was mainly restricted to late spring and summer, and made a negligible contribution to the losses in autumn and early spring (Fig. 2; L. Marone, personal observations). Furthermore, total grass seed loss by germination was low (generally < 0.5% of previous soil-seed reserves) and even the 5% value in the spring-summer of 1997–98 (Table 1) might have been abnormally high due to a coincidence of low seed availability in winter 1997 due to drought (Table 2) and high precipitation in summer 1998 (Fig. 1), thus providing unusually suitable conditions for germination.

Germination trials showed that a major fraction of the newly produced seeds of several common species (from the genera *Trichloris*, *Pappophorum*, *Digitaria* and *Aristida*) appears to be capable of immediate germination. Thus, spring and summer germinants may come from seeds produced in the same growing season leading to an overestimate of the impact of germination on winter grass seed reserves. The contribution of germination to seed loss (relative to other factors) may be even less than suggested by Table 1.

Figure 6 summarizes the main mechanisms governing grass seed fluxes in open woodland. Our data, combined with other studies, support the hypothesis that autumn-winter granivory causes greater losses than do deep burial and germination, even if the number of seedlings that suffered pre-emergence mortality was several times higher than the number of the seedlings we actually recorded while emerging.

Year-to-year fluctuations in the number of grass seeds in the soil were marked (Table 2), even though germination loss was negligible (Table 1), suggesting that other losses were important. The main features

Table 2 Average ($\pm$ SE; $n = 73$) size of soil-seed banks (seeds m^{-2}) of grasses and forbs in different years, over two mesohabitats: beneath the canopy of trees and shrubs, and in exposed areas between trees and shrubs. Data correspond to winter soil banks (August), except for those of 1995, which were recorded in spring (October). Rainfall in the previous spring-summer (October–March) is also shown (L. Marone, unpublished data)

Season	Rainfall	Under canopy		Exposed	
		Grass seeds	Forb seeds	Grass seeds	Forb seeds
August 1993	269	6668 ± 1172	29402 ± 5756	7799 ± 1305	1513 ± 409
August 1994	124	5355 ± 1107	12023 ± 2356	3294 ± 612	840 ± 370
October 1995	289	3109 ± 858	10779 ± 2628	2454 ± 727	538 ± 262
August 1996	173	1900 ± 389	10538 ± 2817	840 ± 236	706 ± 349
August 1997	295	2073 ± 505	13094 ± 2615	1782 ± 651	403 ± 153
August 1998	453	5010 ± 1322	13509 ± 2351	3631 ± 703	1244 ± 480

of the foraging ecology of granivorous animals suggest that birds and, secondarily, mammals are important seed-eaters during the colder months, whereas ants prevail during the warmer months (Lopez de Casenave *et al.* 1998; Marone *et al.* 1998a; Marone *et al.* 2000). Although the impact of bacteria and fungi on grass seed reserves should be more carefully assessed, granivory seems to be increasingly likely to be the main mechanism governing grass-seed output in the central Monte desert of Argentina.

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