



Timing and spatial patterning of seed dispersal and redistribution in a South American warm desert

Luis Marone, Bertilde E. Rossi & Manuel E. Horno

Grupo de Ecología de Comunidades del Desierto (Ecodes), Ecofisiología Vegetal, IADIZA Casilla de Correo 507, 5500 Mendoza, Argentina

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Abstract

We measured newly-produced seeds entering the soil (Potential Seed Bank) to assess the timing and spatial patterning of Phase I dispersal in the central Monte desert, Argentina. Rates of forb- ($6.13 \text{ mg m}^{-2} \text{ d}^{-1}$) and shrub-seed input ($48.9 \text{ mg m}^{-2} \text{ d}^{-1}$) were maximum in early summer. The rate of grass-seed input, instead, was similar in early and late summer (7 to $8 \text{ mg m}^{-2} \text{ d}^{-1}$). About 90% of forb- and shrub-seed mass entered the habitat through protected (i.e., under canopy) areas, whereas 70% of grass-seed mass did so through exposed areas. Adult plant location and the uneven impact of wind on shrub, forb and grass seeds may explain such patterns.

We also compared the Potential Seed Bank with the soil seed bank in the following spring (Realized Seed Bank). Seeds that form transient banks in other ecosystems (e.g., shrub seeds of the genus *Larrea*, or perennial grass seeds like those of *Pappophorum* and *Trichloris*) prevailed in the Potential Seed Bank. Some annual forb seeds, instead, appeared to form a more persistent seed bank, and prevailed in the Realized Seed Bank (e.g., *Chenopodium*). Horizontal redistribution did not affect the spatial patterning of forb and shrub seeds, but produced a more homogeneous distribution of grass seeds in the habitat. The impact of wind could explain the redistribution pattern of grass seeds. Finally, we found almost 80% of total seeds in the top 2 cm of soil. The smallest grass and forb seeds (*Sporobolus* and *Descurainia*) as well as some medium-sized and large forb seeds (e.g., *Glandularia*, *Sphaeralcea*, *Phacelia*) were able to reach deeper soil layers in the central Monte desert.

Nomenclature: follows Roig, F. A. (1981) Flora de la Reserva Ecológica de Ñacuñán. Cuaderno Técnico de IADIZA (Argentina) 3-80: 5–176.

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Introduction

Phase I dispersal is movement of a seed from the parent plant to a surface, and Phase II dispersal or redistribution includes subsequent horizontal or vertical movements (Chambers & MacMahon 1994). There are few studies dealing with the timing and spatial patterning of primary dispersal for entire desert communities (but see Price & Joyner 1997), and the fate of seeds once they land on the ground is widely unknown in most ecosystems (Chambers & MacMahon 1994).

Phenology and adult-plant location are major determinants of the timing and spatial patterning of Phase I dispersal, respectively. Phenology largely

varies among desert plant species: some plants reach reproduction only after rainfall in an opportunistic fashion (e.g., annual forbs), whereas other species shed at least some seeds even under very dry conditions (e.g., perennial grasses and shrubs) (Kemp 1989). Once seeds leave the parent plant, the type of surface they land upon is a primary determinant of their subsequent movement. Abiotic seed dispersal is usually important in deserts, and vegetation structure as well as soil microtopography greatly influence redistribution, usually provoking highly heterogeneous soil seed arrangements (Reichman 1984).

Heterogeneous seed distribution in desert soils has been reported at several analytical scales (e.g., Re-

ichman 1984; Kemp 1989; Marone & Horno 1997; Price & Joyner 1997). The extent to which such heterogeneous pattern is caused by the heterogeneity of adult-plant distribution, by the action of physical and biological dispersal, or by the joint effect of these factors calls for a more thorough study that will enlighten important features of the spatial patterning of plants (Kemp 1989; Chambers & MacMahon 1994; Aguiar & Sala 1997), and of the reciprocal effect of seeds and granivorous animals (Price & Joyner 1997; Marone et al. 1998).

Owing to the importance of predispersal seed predation in natural communities (Louda 1989; Louda et al. 1992), we avoid the term 'seed production' to refer to the cumulative newly-produced seeds entering the soil bank in summer. Instead, we call those seeds the Potential Seed Bank (hereafter Potential SB). The soil seed bank in the following spring, in turn, is called the Realized Seed Bank (hereafter Realized SB). In this paper we compare seed input rates with phenological patterns of different plant species (e.g., shrubs, grasses and annual forbs) to discern the main attributes of Phase I dispersal in an open woodland of *Prosopis flexuosa*. We also compare seeds entering the soil bank after production with those that remain in the soil after several months of redistribution in order to detect changes in the composition and spatial patterning of Potential and Realized Seed Banks.

Methods

Study site

The study was carried out over four 2 ha plots randomly located in an open woodland of the Biosphere Reserve of Ñacuñán, Mendoza Province, Argentina (34° 02' S, 67° 58' W). This widespread habitat of the Monte desert has a tree stratum made up of scattered individuals of *Prosopis flexuosa* and *Geoffroea decorticans* within a dense matrix of tall shrubs > 1 m (*Larrea divaricata*, *Capparis atamisquea*, *Condalia microphyla*, *Atriplex lampa*), and low shrubs < 1 m (*Lycium* spp., *Verbena aspera*, *Acantholippia seriphioides*). The habitat has an important grass layer. Most Poaceae species are C4-perennial grasses, with summer growth (e.g., *Pappophorum* spp., *Digitaria californica*, *Sporobolus cryptandrus*, *Aristida mendocina*, *Trichloris crinita*, *Setaria leucopila*) (Cavagnaro 1988). Most forbs are annual; their cover is usually lower than grass cover, but highly variable from year to year (Marone 1991).

Ñacuñán's climate is dry and temperate, with cold winters. More than 75% of the annual rainfall occurs in the warmer months which coincide with the growing season (October to March). In this study we assessed seed dispersal in the 1994–1995 growing season. Cumulative rainfall in the period (288.8 mm) was slightly above the central-Monte's multiannual mean (248.2 mm, $n = 24$ yr).

Sampling design

We sampled different microhabitats to obtain a representative sample of seed bank (Realized SB) and seed rain (Potential SB) for the entire habitat. We distinguished two mesohabitats. The first one, 'under canopy' (hereafter UC), encompassed two microhabitats: 'beneath trees' and 'beneath tall shrubs' (> 1 m), covering 15.3% ($\pm 4.2\%$, 1SE) and 34.4% ($\pm 3.3\%$) of the general habitat, respectively. The second mesohabitat (the 'exposed' one or EX) comprised all microhabitats placed among the canopy projections of trees and shrubs: grassy areas (15.5 \pm 2.7%), shrubby areas (< 1 m tall, 13.4 \pm 2.2%), and bare soil (21.4 \pm 3.1%) (see Marone & Horno 1997). We proportionally arranged replications over the open woodland (for both traps and soil samples, $n = 84$) according to the cover of each microhabitat. Approximately one fourth of the sampling effort was allocated to each 2 ha plot.

The realized SB was sampled in late October 1995 by using a cylindrical soil sampler, 3.2 cm in diameter and 2 cm deep. 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 soil within. In the laboratory, soil samples were searched for seeds under a dissecting microscope, after being sieved and washed 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.

For assessing the distribution of seeds along a gradient of soil depth (i.e., vertical redistribution), we took 14 soil-samples from each of three layers: 0–2 cm deep, 2–4 cm deep, and 4–6 cm deep (total 42 samples), using the same method described above. Soil cores were collected under trees ($n = 12$) and tall shrubs ($n = 30$).

To measure the Potential SB we used seed traps 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 so as not to trap seeds while moving on the ground. The Potential SB could be slightly overestimated especially in exposed microhabitats because traps sometimes gather wind-borne material (including seeds) from an area larger than the 8.04 cm² directly above the cup.

We initially installed traps on 26 November 1994, and collected and replaced them on 13 and 23 December, 23 January 1995, 13 February, 13 March, 19 April, 19 May, and 3 August. The final collection was on 27 August 1995. We stopped the sampling because seed trapping was negligible by this date. Moreover, the probability of occurrence of convective storms, which is extremely low in autumn-winter, gradually increases by spring in the central Monte, and so does the likelihood of overestimating the Potential SB by trapping seeds already standing on the soil. During this study several sampling stations were discarded from analyses for some seed traps were unearthed by animals, so we used 84 of the 100 traps originally arranged. We examined the material that had fallen into seed traps under a dissecting microscope, recording all apparently viable seeds.

For the sake of simplicity we distinguished three periods of seed dispersal, which correspond with major phenological stages of Monte's plants (B. Rossi, unpubl.): early summer (26 November 1994–23 January 1995), late summer (24 January–19 April), and winter (20 April–27 August). The cumulative production was divided by the number of days in each sampling period (58, 85 and 130 d, respectively) to estimate the daily rate of seed input in each period.

We used seed masses to quantitatively assess seed dispersal. Masses were calculated by multiplying each species abundance by its per-seed mass, obtained from husked seeds (i.e., without any investing structures except those firmly attached to the seed). The dispersal behavior of grass, forb and tree/shrub seeds (hereafter shrub seeds) was analyzed separately given their group-specific differences in plant phenology, seed-bank strategy and vulnerability to granivores (B. Rossi, unpubl.; Grime 1989; Marone et al. 1998). The great number of zeroes and high variances in shrub-seed sampling make comparisons highly conservative, therefore we rejected the use of statistics for analyzing shrub-seed dynamics. Seed numbers and per-seed masses in the Potential and Realized Seed Banks are shown in Table 1.

Results and discussion

Timing of phase I dispersal

The rate of grass-seed input significantly differed between the periods of dispersal considered here (Kruskall–Wallis rank sum test $H = 37.7$, $P < 0.001$, d.f.=2; *a posteriori* contrasts, Zar (1984)). The grass-seed mass entering the soil in early summer was very similar to that entering in late summer, but both were significantly higher than the winter input (Figure 1). Forb-seed dispersal varied over the sampling period too (Kruskall–Wallis rank sum test $H = 26.9$, $P < 0.001$, d.f.=2; *a posteriori* contrasts), but in this case it prevailed in early summer (Figure 1). Lastly, shrubs also appeared to shed their seeds primarily in early summer (Figure 1).

Roughly 80% of the grass seeds that were incorporated to the soil in late-summer and winter did so between 13 March and 19 April of 1995, after full summer rainfall. Thereafter, primary dispersal of grass seeds was very low, though it might last for a longer time in years with abundant late summer rainfall (L. Marone & M. Horno pers. obs.). Like grass seed production has been considered to be principally restricted to late summer months in warm deserts (e.g., Pulliam & Brand 1975) the similar rate of grass-seed input observed in early and late summer deserves more attention.

Two factors contributed to the unexpectedly high grass-seed input in early summer. First, *Sporobolus* seeds that entered the soil bank in the early summer had been produced in the previous growing season. Such seeds constituted 53% (number), and 20% (mass) of the total early summer entrapment (Table 1). The reproductive growth of *Sporobolus* does not usually start until full summer (e.g., February in 1994 and 1995; B. Rossi pers. obs.), and a great fraction of the seeds are retained on dead stalks during the winter months. *Sporobolus* seed dispersal is usually completed during the following spring when seeds are ejected when hit by rain drops (Chamber & MacMahon 1994). Almost all *Sporobolus* seeds that dispersed in the early summer of 1994–1995 were trapped on 13 December, after a 37-mm rainfall the day before. Consequently, the seed-shedding behavior of *Sporobolus* overrated early summer grass-seed 'production'. The second factor was that at least some grass species reached seed production and dispersal in the spring of 1994. On our study sites, B. Rossi (unpubl.) found 20–30% of plant stems from *Pappopho-*

Table 1. Individual per-seed masses (mg); species-specific daily rate of seed input (seeds $m^{-2} d^{-1}$); and composition (seeds m^{-2}) of the Potential Seed Bank (i.e. seeds that entered the soil after being produced in the summer of 1994–1995), and of the Realized Seed Bank (i.e., seed standing crop in the spring of 1995). Daily rate of seed input was measured in three different periods: early summer (EaSu: 26 November 1994–23 January 1995), late summer (LaSu: 24 January–19 April), and winter (Win: 20 April–27 August).

Species	Mass	Rate of Seed Input			Seed Bank Composition	
		EaSu	LaSu	Win	Potential SB	Realized SB
<i>Trees & shrubs:</i>						
<i>Prosopis flexuosa</i>	24.00	1.53	–	–	88.8	14.8
<i>Condalia microphylla</i>	33.00	0.25	0.52	–	59.2	–
<i>Larrea</i> spp.	2.30	1.28	0.69	0.11	148.1	14.8
<i>Atriplex lampa</i>	0.62	0.25	–	–	14.1	–
<i>Lycium</i> spp.	0.42	1.02	0.17	–	74.0	207.3
<i>Verbena aspera</i>	0.60	0.25	0.17	–	29.6	–
<i>Acantholippia seriphioides</i>	0.25	–	–	–	–	29.6
<i>Total seed number</i>		4.58	1.55	0.11	413.8	266.5
<i>Grasses:</i>						
<i>Sporobolus cryptandrus</i>	0.06	23.49	1.57	2.39	1806.4	1688.0
<i>Pappophorum</i> spp.	0.24	15.83	16.72	1.48	2532.0	577.5
<i>Trichloris crinita</i>	0.18	1.02	5.57	0.91	651.5	44.4
<i>Aristida</i> spp.	0.46	0.77	0.69	0.11	118.4	29.6
<i>Digitaria californica</i>	0.38	0.51	2.79	0.57	340.6	207.3
<i>Setaria leucopila</i>	0.60	1.28	1.74	0.46	281.3	59.2
<i>Diplachne dubia</i>	0.24	0.51	1.39	–	148.1	44.4
<i>Neobouteloua lophostachia</i>	0.08	0.25	1.04	0.11	118.5	14.8
<i>Chloris castilloniana</i>	0.20	0.25	0.17	–	29.6	–
<i>Total seed number</i>		43.91	31.68	6.03	6026.4	2665.2
<i>Forbs:</i>						
<i>Chenopodium papulosum</i>	0.24	5.62	3.48	0.34	221.0	5626.6
<i>Conyza</i> spp.	0.04	–	–	–	–	29.6
Compositae unknown	0.20	–	0.69	0.11	74.0	–
<i>Phacelia artemisioides</i>	0.36	10.72	1.39	0.46	799.6	162.9
<i>Glandularia mendocina</i>	0.40	0.77	0.17	–	59.2	162.9
<i>Sphaeralcea miniata</i>	0.20	–	–	–	–	103.6
<i>Descurainia</i> sp.	0.08	–	–	–	–	340.6
<i>Lappula redowskii</i>	0.40	0.51	–	–	29.6	29.6
<i>Plantago patagonica</i>	0.38	1.02	0.17	0.11	88.8	–
<i>Total seed number</i>		18.64	5.90	1.02	1272.2	6455.8

rum, *Setaria*, *Aristida*, and *Neobouteloua* dispersing seeds by November–December of 1994. *Pappophorum* stood for 36% (number), or 55% (mass) of total early-summer entrapment (Table 1). We conclude that at least some grass species may contribute seeds to central Monte's soil banks in early summer, even after moderate rainfall.

Annual-forb seeds are produced sooner after the spring-summer rains than are most grass seeds. An-

nual forbs of the genera *Phacelia*, *Descurainia*, *Lappula*, *Glandularia*, *Sphaeralcea*, and *Plantago* largely germinate in early fall, and the seedlings that remain alive in the following spring usually mature seeds by November (L. Marone & M. Horno unpubl.). It is therefore not surprising that 85% of seeds from these plants entered the soil bank in early summer (Table 1). Further, *Chenopodium papulosum*, the most abundant summer forb species in the soil bank, mainly ger-

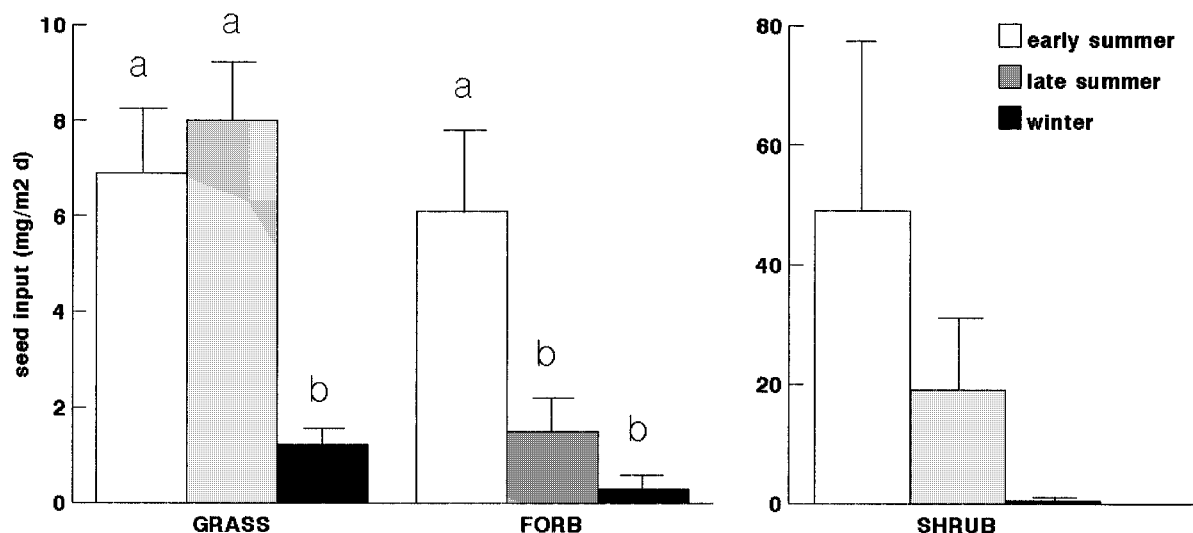


Figure 1. Rate of grass, forb and shrub seed input during early summer, late summer and winter. The values represent mean mass of seeds accumulated in seed traps per day per square meter. Error bars indicate 1 standard error of the mean. Different letters represent significant differences for grass and forb seeds. Note the different scale in the y axis for shrub seeds.

minates in early spring (99%, $n = 112$, and 96%, $n = 78$, of its seedlings emerged in October of 1994 and 1995, respectively), and fructificates 45–60 days later (L. Marone & M. Horno unpubl.). The higher rate of *Chenopodium* seed input in early summer (59%) than in late summer (37%) and winter (4%), was then widely expected from the phenological characteristics of this annual forb (Table 1).

Shrub seed production usually precedes grass seed production (but see Price & Joyner 1997), and it is not as sensitive to timing of rains as herb seed production (Pulliam & Brand 1975; Nelson & Chew 1977; Kemp 1989). Studies of tree and shrub phenology carried out during the 1993–1994 and 1994–1995 growing seasons in the study site (B. Rossi unpubl.) showed that *Atriplex* and *Lycium* began seed dispersal by December, whereas *Prosopis*, *Larrea*, *Condalia*, and *Capparis* were all dispersing seeds by January. Hence, the relatively early entrapment of shrub seeds (Figure 1) was widely expected from the phenological characteristics of woody plants.

Comparison of potential and realized seed banks

We found 21 seed species in the Potential SB, and 19 in the Realized SB. The seeds of *Condalia*, *Atriplex*, *Verbena*, *Chloris*, *Plantago* and unknown Compositae were observed in the Potential SB but not in soil samples, whereas those of *Acantholippia*, *Conyza*,

Sphaeralcea and *Descurainia* were present in the soil but absent from the Potential SB.

An average of 12.4 kg or 60.3×10^6 grass seeds entered the habitat per hectare, but only 3.9 kg or 26.6×10^6 seeds remained in the soil bank the following spring. These figures suggest that many grass seeds were lost soon after being dispersed, essentially the heaviest ones (e.g., *Trichloris*, *Pappophorum*, *Diplachne*, *Aristida*, *Setaria*; Table 1). Newly-produced grass seeds could persist for short periods in the soil either because of high germination rates or high mortality. L. Marone & M. Horno (unpubl.) assessed germination loss in the central Monte desert between 1993 and 1995, and concluded that it probably represented <0.5% of the minimum annual abundance of soil seeds (Marone et al. 1998). Desert granivores, instead, may have 'sieved' (sensu Harper 1977) newly produced seeds. On average, the diet of the main autumn-winter granivores (i.e., birds) consists of 93% grass-seed mass and 7% forb-seed mass in the central Monte. Further, the main target of birds appears to be medium-sized and large grass seeds (Marone et al. 1998). If birds are important granivores, grass seeds, especially the largest ones, will suffer higher postdispersal loss than forb seeds. Though such expectation was widely corroborated in the Monte desert (see below), both decomposition and rodent consumption may be additional plausible avenues of grass-seed loss that deserve investigation.

Forb seeds were more abundant in soil than in trap samples, whether abundances are expressed in terms of density (64.5×10^6 vs. 12.7×10^6 seeds ha^{-1} , respectively) or mass (15.3 vs. 4.2 kg ha^{-1} , respectively) (Table 1, *Chenopodium* seeds represented almost 90% of total forb seeds in the Realized SB). This is not surprising because seeds from annual forbs (i.e., ephemerals) are known to have high dormancy and form more persistent soil banks than seeds from perennial grasses (Grime 1989), and also because forb seeds would be subjected to low consumption by the main autumn-winter granivores in the central Monte desert (Marone et al. 1998).

Shrub seeds, especially those weighing >1.0 mg (e.g., *Prosopis*, *Condalia*, *Larrea*), prevailed in the Potential SB: while 45 kg or 4.1×10^6 shrub seeds entered the habitat per hectare, only 4.8 kg or 2.6×10^6 seeds remained in the soil the following spring (Table 1). Price & Joyner (1997) also reported a preponderance of seeds >1.0 mg in traps related to the soil in the Mojave desert (e.g., seeds from *Larrea* and *Acamptopappus* shrubs). Seeds of desert perennials, which tend to be large, do frequently lack the prolonged dormancy characteristic of ephemerals (Kemp 1989), and suffer great predation from seed-eating animals (e.g., ants and rodents). Mechanisms of post-dispersal seed loss of Monte's trees and shrubs remain to be determined.

Spatial patterning of phase I dispersal

Price & Joyner (1997) reported approximately the same amount of seed rain (measured as g m^{-2}) in EX and UC of the Mojave desert. In the central Monte desert we found group-specific seed dispersal for grasses, forbs and shrubs.

Most grass-seed primary dispersal occurred through EX (69% of total mass input; ANOVA $F = 14.3$, $P < 0.001$, d.f.=1,82; raw data were log-transformed; PSB in Figure 2). Forb seeds, on the other hand, entered the soil through UC (89% of mass, ANOVA $F = 21.8$, $P < 0.001$, d.f.=1,82; raw data were reciprocally transformed according to $y' = 1/(y+0.5)$; Figure 2). Likewise, 96% of shrub-seed mass was incorporated to the soil bank through UC (Figure 2).

Most seeds move only short distances from the parent plant during primary dispersal (Wilson 1992), especially the heaviest ones little affected by the wind, e.g., seeds from some shrubs in the Monte. In such cases, dispersal may only involve gravity and seeds

simply fall beneath the canopy of the parent tree or shrub, where they are usually trapped by the litter.

The significantly greater input of forb seeds through UC may be also a result of adult plant location. Desert herbs tend to be more abundant beneath shrubs than in the open (Turner 1973; Nelson & Chew 1977; Jaksic & Fuentes 1980). In the central Monte desert, 80% ($n = 205$) and 67% ($n = 106$) of forb-seedling emergence in spring and autumn, respectively, occurred under trees and shrubs between 1993 and 1995 (L. Marone & M. Horno unpubl.). Moreover, forb survival was very low in the period, but all forbs that matured seeds were located in UC.

Greater primary dispersal of grass seeds through EX, on the other hand, cannot be explained either by differential adult plant location (grass cover is similar in EX and UC), or by a larger cover of EX in the general habitat (49.7%, against 50.3% cover of UC). Instead, the greater proportion of grass seed dispersal through EX may be a consequence of a wind velocity gradient in favor of exposed areas. In arid ecosystems wind velocities in interspaces are higher than under the canopy of shrubs, and interspaces serve as avenues of seed transport (Soriano & Sala 1986; Chambers & MacMahon 1994). In the central Monte, grass seeds as a whole are the lightest ones and can be easily transported by the wind: the weighted mean masses of shrub, forb and grass seeds in the Potential SB were 10.8 mg, 0.35 mg, and 0.20 mg, respectively (see Table 1).

Spatial patterning of phase II dispersal

Forb-seed mass in the Realized SB was significantly higher in UC than in EX (ANOVA $F = 37.7$, $P < 0.001$, d.f.=1,82, raw data were reciprocally transformed according to $y' = 1/(y+0.05)$; RSB in Figure 2). A very similar pattern was previously reported for these seeds in the Potential SB (Figure 2). In both cases roughly 90% of forb-seed mass occupied protected areas. Similarly, shrub seeds also prevailed in UC ($>90\%$ of total mass; Figure 2) in both the Potential and Realized SB. This evidence suggests that forb and shrub seeds were subjected to low secondary horizontal dispersal, at least between the mesohabitats we compared. This could be the consequence of the higher proportion of forbs and obviously trees and shrubs in UC, combined with the sudden entrapment of such seeds by the litter strewn under woody plants.

Secondary dispersal notably modified the horizontal distribution of grass seeds: while EX received most

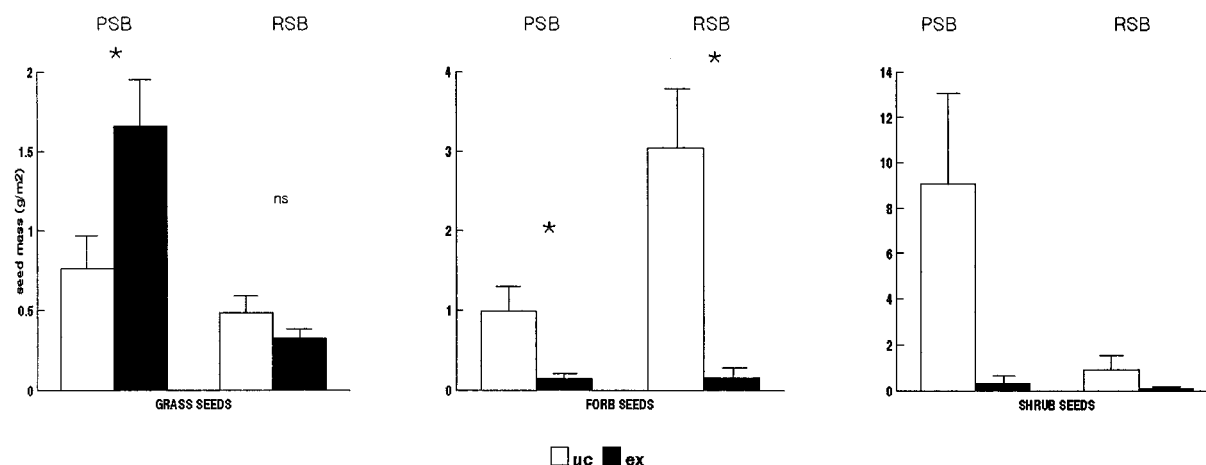


Figure 2. Grass-, forb- and shrub-seed mass that entered the soils after summer production (Potential Seed Bank: PSB), and found on the soils in the following spring (Realized Seed Bank: RSB) over two mesohabitats of the open woodland: under the canopy of trees and shrubs (UC, open bars), and in exposed areas among them (EX, black bars). Error bars indicate 1 standard error of the mean. Note the different scales in the y axis. Asterisks represent significant differences between mesohabitats (*: $P < 0.001$; ns: non-significant).

grass-seed mass, the size of the Realized grass-seed bank did not differ between EX and UC (ANOVA $F = 1.27$, $P > 0.25$, d.f.=1,82, raw data were reciprocally transformed according to $y' = 1/(y+0.5)$; Figure 2). Wind transport of seeds from interspaces to undershrub areas is usually much higher than seed movement in the opposite direction in deserts (Kerrick 1991; Mull & MacMahon 1996), and it may have caused the postdispersal spatial pattern shown in Figure 2. On the other hand, autumn-winter seed removal by granivores seems to be very similar in both EX and UC (Lopez de Casenave et al. 1998), therefore it could not account for the balanced mesohabitat distribution of grass seeds observed in spring.

The assessment of the vertical component of Phase II dispersal indicated that 78% of seeds were in the upper 2 cm of soil, whereas 14% were buried 2–4 cm deep, and 8% were buried 4–6 cm deep (Table 2). Most seeds in other deserts are also found near the surface, usually with >80% of them in the upper 2 cm of the soil (Childs & Goodall 1973; Reichman 1975; O'Connor & Pickett 1992).

We tested whether seed-size distribution at these three vertical layers was homogeneous or small seeds prevailed at greater depths, by using three size classes (0–0.10 mg; 0.11–0.30 mg, and 0.31–0.60 mg; see Table 2). Seed sizes were not homogeneously distributed ($\chi^2 = 27.7$, $P < 0.001$, d.f.=2) mostly because small and heavy seeds were more abundant than expected at a depth of 2–4 cm (Table 2). Hence, size alone was not a good predictor of which seeds are able to reach the

Table 2. Number of small, medium and large seeds found at three depth layers: in the top 2 cm of soil and litter (0–2 cm); and buried 2–4 cm and 4–6 cm into the soil. Individual per-seed masses are indicated in the first column.

Species	Mass	0–2 cm	2–4 cm	4–6 cm
<i>Sporobolus cryptandrus</i>	0.06	44	16	11
<i>Descurainia</i> spp.	0.08	7	5	1
<i>Total</i>		51	21	12
<i>Tricloris crinita</i>	0.18	3	0	0
<i>Sphaeralcea miniata</i>	0.20	0	2	4
<i>Chenopodium papulosum</i>	0.24	156	8	8
<i>Pappophorum</i> spp.	0.24	7	1	0
<i>Diplachne dubia</i>	0.24	1	0	0
<i>Total</i>		167	11	12
<i>Phacelia artemisioides</i>	0.36	16	5	1
<i>Digitaria californica</i>	0.38	1	0	0
<i>Glandularia mendocina</i>	0.40	3	6	2
<i>Lappula redowski</i>	0.40	1	0	0
<i>Lycium</i> spp.	0.42	2	0	0
<i>Parthenium hysterophorus</i>	0.45	0	1	0
<i>Setaria leucopila</i>	0.60	5	0	0
<i>Heliotropium mendocinum</i>	0.63	1	0	0
<i>Total</i>		29	12	3

deeper soil layers. When the tiny seeds of *Sporobolus* and *Descurainia* are discarded from analysis, only 1 grass seed (*Pappophorum*) but 43 forb seeds were buried >2 cm (*Sphaeralcea*, *Chenopodium*, *Phacelia*, *Glandularia* and *Parthenium*). This pattern suggests

that medium-sized and heavy forb seeds are best adapted to reach deeper soil layers than are grass seeds of similar size, which may in turn explain the faster recovery of forbs observed after habitat disturbances such as fires in the Monte desert (e.g., Marone 1990).

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