Spatial coherence between seasonal seed banks in a semi-arid gypsum community: density changes but structure does not

I. Caballero[1], J.M. Olano[2]*, A.L. Luzuriaga[3] and A. Escudero[3]

[1]Laboratorio de Botánica, Departamento de Biología Vegetal y Ecología, Facultad de Ciencias, Universidad del País Vasco, Apdo. 644, Bilbao E-48080, Spain; [2]Área de Biología Vegetal, Departamento de Ciencias Agroforestales, Escuela de Ingenierías Agrarias, Universidad de Valladolid, Los Pajaritos s/n, Soria E-42003, Spain; [3]Área de Biodiversidad y Conservación, ESCET, Universidad Rey Juan Carlos, C/ Tulipán s/n, Móstoles E-28933, Spain

Abstract

Seed banks play a crucial role in arid plant communities because they confer stability and long-term persistence. However, seed banks have high temporal and spatial variability, with dramatic changes in density and composition. The aim of this study was to test whether seasonal change affected seed bank community structure and spatial pattern. Moreover, we wanted to know if the effect driven by environmental factors on the seed bank was constant year round. We sampled the seed bank at 188 points along seven parallel transects through a gypsum system in central Spain. Soil samples were taken twice (September and April) in contiguous plots. In each plot we measured environmental parameters, including micro- and macroslope, vegetation band, shrub cover, lichen crust cover and landform. A nearly threefold decrease in seed bank density occurred between September (16,230 seeds m^{-2}) and April (5960 seeds m^{-2}). Seasonal changes in density varied widely among species; however, a seed bank was present for most species at both sampling dates. For several well-studied species (*Lepidium subulatum* and *Helianthemum squamatum*), seed losses were within the range of losses by emergence reported in the literature. In both seasons, seed bank composition was controlled mainly by community band and microslope. Sampling season had a significant, but minor effect on seed bank composition. Moreover, a high spatial correlation existed in terms of seed density and richness through the two studied seasons. These results show that the seed bank keeps a constant structure even under substantial variation in density.

Keywords: canonical correspondence analysis, *Helianthemum squamatum*, seasonal seed bank structure, seed density, semi-arid gypsum community

Introduction

There is general agreement that seed banks may reduce the demographic effects of environmental stochasticity (Thompson, 1992; Fenner, 1995), consequently promoting community stability. Seed banks favour plant population persistence by lowering extinction risk (Kalisz and McPeek, 1992) and act as genetic reservoirs (Morris *et al.*, 2002), slowing down the rate of evolutionary change (Nunney, 2002).

Despite their role in the promotion of above-ground stability, seed banks have remarkably high temporal variability (Hassan and West, 1986; Bertiller, 1992). Such dynamics are due to losses to predation, seed decay, deep burial, death and germination, to gains through primary and secondary dispersal (Harper, 1977) and to variation in seed production (Parmenter and MacMahon, 1983; Gutiérrez *et al.*, 2000). In fact, seasonal and annual changes in seed bank density may be as high as 20-fold (Reichman, 1984; Russi *et al.*, 1992). However, we still do not understand how these changes in abundance and composition affect community stability.

The high spatial heterogeneity in seed bank dynamics has long been recognized (Schupp, 1995; Guo, 1998). It is widely known that seed banks are spatially clumped (Ferrandis *et al.*, 1996; Pake and Venable, 1996) due to several factors, including

*Correspondence
Fax: +34 975129401
Email: jmolano@agro.uva.es

variation in adult distribution and seed rain (Clark *et al.*, 1999; Olano *et al.*, 2002), effects of shrubs as seed traps (Aguiar and Sala, 1997; Moro *et al.*, 1997; Bullock and Moy, 2004), effects of soil surface characteristics on secondary dispersal (Bigwood and Inouye, 1988; Schupp, 1988) and differential seed predation (Hyatt and Casper, 2000). Furthermore, seed bank spatial structure can have a strong effect on the subsequent life stages of plants (Laskurain *et al.*, 2004). Surprisingly, almost no information exists about how seed bank seasonal changes affect both demographic parameters at the population level and community structure and composition (Nakagoshi, 1984).

Gypsum systems have dense and highly spatially structured seed banks (Caballero *et al.*, 2003) that are strongly related to plant community composition and abundance. However, there is no information regarding seasonal patterns in gypsophile seed banks, either for the whole community or for any of the individual species. In order to fill this gap, we studied seed bank seasonal patterns in a gypsum system in central Spain. Two sampling periods were established, the first in September, after dispersal and prior to emergence, and the second in April, before seed dispersal and after the emergence pulse. We considered the first sampling period to correspond to the peak seed density and the second to the lowest density in the year. Roughly, the first comprised the transient and persistent seed bank and the second the persistent seed bank.

Our main objective was to assess the effect of seasonal change on the composition and spatial pattern of seed distribution. More specifically, we analysed the intensity and direction of the seasonal change, both in terms of seed density and species diversity. We also evaluated the effect on such changes of several variables belonging to three contrasting datasets. These sets can potentially exert a control on the process: soil surface variables, the above-ground perennial structure on small spatial scales and the landscape structure. We posed the following questions: (1) What are the factors controlling seed bank structure in both seasons? (2) Do composition and structure remain stable? (3) To what extent do species differ in their presence and abundance in both seasons?

Materials and methods

Study site

The study was carried out at Espartinas, close to Ciempozuelos, approximately 40 km south of Madrid, in central Spain (40°11′N, 3°36′W, 570 m above sea level). The climate is upper semi-arid mesomediterranean (Rivas-Martínez and Loidi, 1999), with an annual rainfall of 415 mm, but with almost no rainfall in summer. The mean daily temperature ranges from 0.6°C to 9.6°C in January and from 15.4°C to 32.7°C in July. The soils are classified as Calcic Gypsisols, developed over gypsum parental rocks (Monturiol and Alcalá del Olmo, 1990).

Three main vegetation bands dominate the surveyed gypsum system (Rivas-Martínez and Costa, 1970). First, the genuine gypsophyte community (*Gypsophylo struthii–Centaureetum hyssopifoliae*) is a sparse shrub community dominated by gypsophytes, occurring from the steeper slopes to the summit crest, where sometimes it has been considered another community (*Herniario fruticosae–Teucrietum pumili*). This community component has been named the *Lepidium* band. Secondly, in the upper piedmont, the *Lepidium* band contacts a dense shrub community (*Artemisio herba-alba–Frankenietum thymifoliae*), called the *Frankenia* band. Finally, the lower piedmont and bottom flats are colonized by a community dominated by the perennial tussock *Lygeum spartum* (*Lymonio dichotomi–Lygeetum sparti*) and called the *Lygeum* band.

Sampling design

Seed bank samples were collected twice: in September 2001, just after most seeds had been shed but prior to autumn emergence, and in April 2002, when most emergence had already taken place, prior to seed shedding.

We established seven parallel southern-exposed transects, running from the top of the ridge to the bottom and perpendicular to the maximum slope, because in a previous paper (Rubio and Escudero, 2000) we found soil components were spatially structured following this pattern. Transects were located parallel to each other and more than 15 m apart. The number of plots per transect ranged from 14 to 27, depending on slope extension. Quadrats (50 × 50 cm) were located every 2.5 m in each transect. In the centre of each quadrat, five soil cores (diameter 1.85 cm) were extracted and combined. Soil cores were 3 cm deep since, according to Childs and Goodall (1973), the first 2 cm accumulate most of the seed bank in arid environments. For each quadrat we measured: lichen soil crust and perennial plant cover, microslope (slope in the centre of each quadrat), macroslope measured on a 2-metre wooden frame located on the ground, and elevation (in metres) with respect to the first quadrat in each transect. Each quadrat was assigned to a landform type (crest, slope or piedmont) and to a vegetation band (*Lepidium*, *Frankenia* or *Lygeum* bands). The total number of quadrats was 188 and the total area cored was 0.253 m^2.

The viable seed bank was studied by monitoring seedling emergence (ter Heerdt *et al.*, 1996). Soil samples were kept at 4°C for 2 months. Thereafter, they were washed and sieved through a 0.5 cm-wide mesh to retain the coarse fraction. The resulting material was sieved over a 0.2 mm-wide mesh to reduce the fine material volume and to scarify the seeds to facilitate germination (Thompson *et al.*, 1997).

The resulting soil samples were placed in 10×10 cm plastic cells in a greenhouse. Soil samples were mixed with a sterile substratum of vermiculite and peat (2:1) until a depth of 1 cm was reached. Ten cells were filled only with the sterile mixture and located in the greenhouse to detect any contamination. Emergence trays were rotated regularly through the greenhouse. As soon as a seedling emerged, it was identified and removed. When identification at the species level was not feasible, seedlings were transplanted into individual pots and allowed to grow until identification was possible. After 5 months, the soil in the cells was regularly crumbled in order to enhance emergence during the following 3 months. Finally, the cells were watered with a gibberellic acid (GA_3) solution (1000 ppm) to germinate any seeds with endogenous dormancy, and emergence was monitored for another 2 months (Hartmann and Kester, 1999).

Data analysis

Our data did not fulfil normality assumptions, even after submitting them to different transformations. So we chose non-parametric techniques for data analyses. Differences between the two sampling seasons in species composition and seed density per plot were calculated using a Wilcoxon paired test. The same approach was used to check for differences among seed densities for individual species. Correlations between richness and seed density per plot were determined using a Kendall non-parametric correlation.

Seed aggregation patterns for the 24 most abundant species were tested using the Morisita index (Morisita, 1959). We used this index because it is not sensitive to density changes, so our values could be compared directly (Malhado and Petrere, 2004). Species composition and abundance were analysed using ordination techniques.

As a first step, in order to select the appropriate constrained ordination technique for hypothesis testing, the three matrices were submitted to a detrended correspondence analysis (DCA), detrending by segments and with non-linear rescaling of the axes. Since the lengths of the extracted gradients were always larger than 3 SD units, we used techniques assuming unimodal responses (ter Braak, 1986). These techniques allow for testing hypotheses concerning the relationships between a multivariate data matrix (i.e. seed bank composition) and an environmental data matrix (i.e. measured parameters) (ter Braak and Prentice, 1988). Our null hypothesis was that the seed bank composition is independent of the environmental variables.

Three matrices with species seed counts per quadrat (log-transformed) were built: the September dataset, the April dataset, and a third matrix comprising both datasets. All of the matrices were subjected to the same analytical procedure. Unidentified species (monocot and dicot classes comprising 13.5% of the emerged seeds) were excluded from the analyses. In order to reveal the effect of the environmental variables on seed species composition and abundance, we conducted a canonical correspondence analysis (ter Braak, 1986). The corresponding environmental matrix consisted of the following variables: crust and perennial cover, elevation, microslope, macroslope, landform (three dummy variables) and vegetation band (three dummy variables). When the whole dataset was considered, the sampling time was included in the model as a new dummy variable (season).

A Monte Carlo permutation test was performed to determine the significance of any model (999 randomizations) under a full model for September and April seed bank matrices, and a reduced model for the joint matrix. A forward selection of variables was undertaken to build a reduced model, including only the significant variables selected. Improvement of the reduced model with each new selected variable was determined by a Monte Carlo permutation test with 999 randomizations. The sum of all the canonical eigenvalues or trace was used to build the F-ratio statistic. Only when $P < 0.05$ was the relationship between the two datasets considered significant. The total variation explained (TVE) was calculated as the sum of all extracted canonical axes (Borcard *et al.*, 1992). Analyses were performed with Canoco for Windows, version 4 (ter Braak and Smilauer, 1997).

Results

A total of 5611 seedlings of at least 70 species emerged from the seed bank. Seed bank density was 16,230 seeds m^{-2} in September, and decreased to 5960 in April. This difference was highly significant according to the Wilcoxon test ($Z = -8.188$, $P < 0.0001$). When we compared data on a per plot basis, seed density in September was highly correlated with April values ($\tau = 0.45$, $P < 0.0001$). Richness was higher in September than in April ($Z = -9.536$, $P < 0.0001$), with 69 species in the September seed bank and only 42 in April. Richness at plot level was also correlated between September and April ($\tau = 0.48$, $P < 0.0001$).

A significant change in seed density was observed for 23 of the 31 most abundant species (Table 1). However, the intensity, and even the direction of change, varied widely among species. Of the 24 most abundant species, two species present in the fall seed bank were not detected in the spring seed bank. For 13 species, the size of the spring seed bank was less than 20% of the seed bank in September. For seven species, the April seed bank was still a significant proportion of September seed bank (within 20 and 50%). For five species, the April seed bank was at least 50% of September seed bank, including both *Campanula* species. Three species had a higher seed density in April. The difference was significant in only one case, *Centaurium gypsicola*, a typical autumn seeder.

The seed bank had a clumped distribution since values for the Morisita index were well above 1 (September $I_m = 2.38$, April $I_m = 2.45$). This aggregated pattern was maintained across seasons for almost all species (Table 1). Highly significant reduced models were constructed for the three matrices. Although they explained low percentages of total variance, ranging from 8.6% to 7.1% (Table 2), such low values are normal, given the characteristics of the data. The number and nature of the parameters that entered into the models differed slightly; however, similarities between the different models were obvious. The first variable included in all models was vegetation band (Table 3); two vegetation bands were included in the April and annual models, but only one in the September model. Microslope was the

Table 1. Seed bank density in September and April, percentage change (April/September density) and the Morisita index (I_m; only for the 24 most abundant species). Asterisks indicate significant seasonal differences in density. Seeds counts were transformed to densities by multiplying by 3.957

	Seeds m^{-2}		Change	I_m			Seeds m^{-2}		Change
	Sept.	April		Sept.	April		Sept.	April	
Total	16 230	5960	37%	2.38	2.45				
*Campanula erinus**	2216	1330	60%	7.9	7.7	*Hymenolobus procumbens*	24	12	50%
*Asterolinon linum-stellatum**	1923	178	9%	4.2	3.8	*Linaria glauca*	24	4	17%
*Vulpia unilateralis**	1852	245	13%	5.6	3.7	*Plantago coronopus*	24	0	0%
*Campanula fastigiata**	1053	641	61%	5.3	7.9	*Bromus madritensis*	16	0	0%
Galium spp. (3 spp.) *	788	32	4%	6.5	–	*Centaurea hyssopifolia*	16	0	0%
*Polypogon maritimus**	693	194	28%	37.6	59.5	*Anagallis arvensis*	12	0	0%
*Centaurium gypsicola**	649	906	140%	5.3	4.8	*Arenaria leptoclados*	12	12	100%
*Chaenorhinum reyesii**	586	91	16%	6.9	12.7	*Medicago minima*	12	0	0%
*Sedum gypsicola**	404	44	11%	35	10.4	*Caryophyllaceae*	8	0	0%
Frankenia thymifolia	376	772	205%	32.2	24	*Erodium cicutarium*	8	0	0%
*Filago pyramidata**	253	47	19%	9	20.1	*Helianthemum hirtum*	8	0	0%
Parentucellia latifolia	253	261	103%	13.8	6.7	*Liliaceae*	8	4	50%
*Sagina apetala**	253	8	3%	107.6	190	*Polygala monspeliaca*	8	0	0%
*Helianthemum squamatum**	245	63	26%	6.2	3.2	*Teucrium capitatum*	8	0	0%
Lepidium subulatum	241	154	64%	11	5.9	*Thymus lacaitae*	8	8	100%
*Reseda stricta**	232	107	48%	9.5	10.2	*Veronica arvensis*	8	0	0%
*Herniaria cinerea**	202	63	31%	18.4	23.7	*Arabis auriculata*	4	0	0%
*Cerastium pumilum**	166	0	0%	47.2	–	*Arabis parvula*	4	0	0%
Desmazeria rigida	142	12	8%	20.1	63.5	*Artemisia herba-alba*	4	0	0%
*Vulpia ciliata**	142	32	22%	5.6	3.7	*Asteraceae*	4	0	0%
*Stellaria media**	115	0	0%	3.1	–	*Cerastium glomeratum*	4	0	0%
*Plantago afra**	111	16	14%	5.5	0.3	*Euphorbia falcata*	4	0	0%
Sherardia arvensis	79	36	45%	37.9	78.9	*Heliotropium europaeum*	4	0	0%
Trisetum loeflingianum	75	24	32%	10	12.8	*Leontodon taraxacoides*	4	4	100%
*Euphorbia sulcata**	59	12	20%			*Lomelosia stellata*	4	0	0%
*Parapholis incurva**	59	8	13%			*Lophochloa cristata*	4	0	0%
*Neatostema apulum**	51	8	15%			*Scleranthus verticillatus*	4	0	0%
*Centaurea melitensis**	44	0	0%			*Gypsophila struthium*	0	4	
Helianthemum salicifolium	44	36	82%			*Hedypnois cretica*	0	4	
*Thesium divaricatum**	44	4	9%			*Limonium* sp.	0	4	
Valerianella coronata	44	4	9%			*Odontites viscosa*	0	8	
Blackstonia perfoliata	36	12	33%			*Sonchus* cf. *asper*	0	8	
Crepis capillaris	32	0	0%			*Thymelaea* cf. *passerina*	0	4	
Erophila verna	28	12	43%			Monocot	1278	396	
Erodium malacoides	24	0	0%			Dicot	1195	139	

Table 2. Canonical correspondence analysis (CCA) models using log-transformed seed count data as the main matrix and an environmental matrix (9 variables) as constraining matrix. The variables selected in the forward selection procedure were considered to build the reduced model. λ are the eigenvalues for the corresponding extracted axes. Σcons is the sum of all constrained axes and TVE is the variation explained by the constraining data set. Frat is the F-ratio statistic and P is the significance of the model (999 randomizations)

Constraining matrix	λ_1	λ_2	Σcons	TVE	Frat	P
September (5 variables)	0.265	0.142	0.652	8.6	3.430	0.001
April (4 variables)	0.373	0.275	0.925	8.0	3.965	0.001
Annual (6 variables)	0.252	0.198	0.826	7.1	4.687	0.001

next parameter included in the three models. The April model also included slope landform, whereas the September model included perennial and crust covers and macroslope. The annual model included season, indicating a seasonal effect in seed bank composition; however, its role was secondary, since it was included in fourth place and only accounted for 16% of the total variance explained, clearly less variability than the vegetation band and microslope variables (65%).

Discussion

Gypsum slopes at the study site maintained a dense and diverse soil seed bank all year round (Caballero *et al.*, 2003). Nevertheless, a sharp decline in both parameters was detected from September to April,

Table 3. Variables included in the reduced model. λ are the eigenvalues for the corresponding extracted axes, Frat is the F-ratio statistic and P is the significance of the model (999 randomizations)

			λ	Frat	P
Annual	step 1	*Lygeum* band	0.23	7.66	0.001
	step 2	*Lepidium* band	0.17	5.61	0.001
	step 3	Microslope	0.14	4.74	0.001
	step 4	Season	0.14	4.73	0.001
	step 5	Perennial cover	0.08	2.66	0.001
	step 6	Crust cover	0.07	2.14	0.001
September	step 1	*Lygeum* band	0.24	6.19	0.001
	step 2	Microslope	0.15	3.87	0.001
	step 3	Perennial cover	0.11	2.78	0.001
	step 4	Crust cover	0.08	1.95	0.001
	step 5	Macroslope	0.07	2.02	0.001
April	step 1	*Frankenia* band	0.36	6.01	0.001
	step 2	*Lepidium* band	0.24	4.04	0.001
	step 3	Microslope	0.19	3.21	0.001
	step 4	Slope landform	0.13	2.28	0.001

with nearly a threefold change in density. This combination of high density and steep seasonal turnover is in agreement with reports from other arid communities (Reichman, 1984; Price and Reichman, 1987; Kemp, 1989; Price and Joyner, 1997). This change is usually explained as a consequence of seed losses by death or emergence: transient and persistent seed banks, *sensu* Thompson and Grime (1979). Surprisingly, several species maintained, or even increased, their seed bank size during the study period. Such an increase in seed density can be attributed to a late seed-shedding strategy. Only 3 out of the 31 species with a dense seed bank in September were not present in April, suggesting that the possession of a persistent seed bank is a major trend in this system.

Species with persistent seed banks showed contrasting responses. Whereas, in some species, seed density decreased only moderately from September to April (less than 50% in *Campanula fastigiata*, *C. erinus* and *Lepidium subulatum*), the seed bank of other species suffered a steep reduction (more than the 80% in *Asterolinon linum-stellatum* or *Chaenorhinum reyesii*). Nevertheless, most of the species maintained dense seed banks all year round. These results suggest that a gradient from persistent seed bank to transient seed bank appears in this community. This gradient might be interpreted as a gradient from conservative to opportunistic seed bank strategies.

Obviously, emergence is one of the factors that decreases seed bank density. However, it has been considered to play a secondary role in arid environments. The highest emergence percentages detected by Marone *et al.* (2000) in arid environments in Argentina ranged from 1 to 5% of the seed bank. We have no direct emergence data in our study; however, field emergence data of two widely distributed Iberian perennial gypsophytes, *Helianthemum squamatum* and *Lepidium subulatum* in central Spain, showed emergence densities ranging from 8 to 130 seedlings m^{-2} and 50 to 165 seedlings m^{-2}, respectively (Escudero *et al.*, 1999, 2000; Caballero, unpublished data). These values are within the same order of magnitude as the seed bank losses estimated in our study (182 seeds m^{-2} for *H. squamatum* and 87 seeds m^{-2} for *L. subulatum*). These results may indicate that a major fraction of the seed bank losses can be attributed to emergence, at least for these species. Other seed losses, such as ant seed predation, have been suggested as important factors in semi-arid systems (Harrington and Driver, 1995; Longland *et al.*, 2001), although seed field sowings of *H. squamatum* in a nearby location showed very low predation rates (Romão and Escudero, 2005). In any case, extrapolation should be done with caution because most species in the seed bank are annuals.

Seed bank spatial pattern was clumped all year round (Table 1), a result that agrees with most seed bank studies (Bertiller, 1998; Marone *et al.*, 1998). Moreover, aggregation values were maintained across seasons. Several factors have been suggested to explain this aggregated pattern: seed predation due to seed-forager ants (Harrington and Driver, 1995), seed rain patterns and secondary dispersal movements of seeds, which favour seed accumulation in certain favourable microsites, a typical feature of semi-arid communities with sparse vegetation (Reichman, 1984). However, the aggregation index was much higher for individual species than for the whole seed bank, reflecting that factors determining each species' aggregation are not spatially coincident. We emphasize the role of seed rain, with the seed bank reflecting above-ground vegetation clumped structure. This hypothesis is supported by the fact that the highest aggregation values are found in species restricted to just one vegetation band, such as *Polypogon maritimus*, *Sagina apetala*, *Frankenia thymifolia*, confined to the *Frankenia*, or with strict habitat preferences as *Sedum gypsicola*, occurring only on steeper slopes.

In our study, environmental constraints on seed species composition and abundance showed similar patterns in both study periods (Table 3). Vegetation band and microslope significantly explained seed bank species composition in September and April, despite conspicuous variations in abundance. Above-ground vegetation type was the main factor controlling seed bank composition; thus the seed bank is filtered by community type. The effect of microslope on seed species composition has already been reported for this community (Caballero *et al.*, 2003), but in the present study we confirm that this effect is maintained all year round. The microslope interacts with seed morphological and chemical characters (Gutterman and Shem-Tov, 1996), differently affecting the lateral movement of each seed species in the soil, which ultimately determines the seed distribution pattern. Lateral movement is considered an important factor in seed dispersal in environments with sparse vegetation. Shrubs may act as seed traps (Bullock and Moy, 2004). Obviously, this effect is especially important in the case of the *Lepidium* band, because this vegetation type covers the steeper slopes, whereas the other two bands appear on almost flat surfaces. Furthermore, perennial and crust covers also play an important role in arid and semi-arid environments, affecting the distribution of safe sites for seeds, but also for detection by granivores (Fowler, 1988; Simonetti, 1989). Seasonal effects had a secondary role in structuring the seed bank. Thus, while seasonal changes exert a certain control on seed bank species, spatial processes were the main agents structuring soil seed banks.

The most striking result of this study deals with the strong spatial correlation of seed distribution through the two study seasons. Actually, although a large decline in seed bank density occurred from September to April, there was still a high point-to-point correlation between the two sampling dates for each plot. This suggests that in spite of a large change in numbers, a clear spatial structure is maintained all year round. The coherence of seed bank spatial distribution observed in the two sampling periods may have important implications in population and community development, at least for annual species, where seed bank and above-ground community performance are highly correlated (Olano *et al.*, 2005). Furthermore, a few studies have related seed location in the soil with the demographic consequences on the above-ground plant population in arid and semi-arid environments (Schupp, 1995; Schupp and Fuentes, 1995; Aguiar and Sala, 1997; Cabin and Marshall, 2000), since seedling recruitment is limited mainly by seed availability at a specific point, rather than by the presence of safe sites for plant recruitment (Aguiar and Sala, 1997; Cabin and Marshall, 2000). Consequently, our results suggest that the expected effect caused by the large decrease in seed density from September to April may be smoothed due to the spatial coherence of the seed distribution detected in the soil.

References

Aguiar, M.R. and Sala, O.E. (1997) Seed distribution constrains the dynamics of the Patagonian steppe. *Ecology* **78**, 93–100.

Bertiller, M.B. (1992) Seasonal variation in the seed bank of a Patagonian grassland in relation to grazing and topography. *Journal of Vegetation Science* **3**, 47–54.

Bertiller, M.B. (1998) Spatial patterns of the germinable soil seed bank in northern Patagonia. *Seed Science Research* **8**, 39–45.

Bigwood, D.W. and Inouye, D.W. (1988) Spatial pattern analysis of seed banks: an improved method and optimized sampling. *Ecology* **69**, 497–507.

Borcard, D., Legendre, P. and Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology* **73**, 1045–1055.

Bullock, J.A. and Moy, I.L. (2004) Plants as seed traps: interspecific interference with dispersal. *Acta Oecologica* **25**, 35–41.

Caballero, I., Olano, J.M., Loidi, J. and Escudero, A. (2003) Seed bank structure along a semi-arid gypsum gradient in Central Spain. *Journal of Arid Environments* **55**, 287–299.

Cabin, R.J. and Marshall, D.L. (2000) The demographic role of soil seed banks. I. Spatial and temporal comparisons of below- and above-ground populations of the desert mustard *Lesquerella fendleri*. *Journal of Ecology* **88**, 283–292.

Childs, S. and Goodall, D.W. (1973) *Seed reserves of desert soils*. US/IBP Desert Biome Research Memorandum, RM 73–75.

Clark, J.S., Beckage, B., Camill, P., Cleveland, B., HilleRisLambers, J., Lichter, J., McLachlan, J., Mohan, J. and Wyckoff, P. (1999) Interpreting recruitment limitation in forests. *American Journal of Botany* **86**, 1–16.

Escudero, A., Somolinos, R.C., Olano, J.M. and Rubio, A. (1999) Factors controlling the establishment of *Helianthemum squamatum* (L.) Dum., an endemic gypsophite of semi-arid Spain. *Journal of Ecology* **87**, 290–302.

Escudero, A., Iriondo, J.M., Olano, J.M., Rubio, A. and Somolinos, R. (2000) Factors affecting establishment of a gypsophyte: the case of *Lepidium subulatum* (Brassicaceae). *American Journal of Botany* **87**, 861–871.

Fenner, M. (1995) Ecology of seed banks. pp. 507–528 *in* Kigel, J.; Galili, G. (Eds) *Seed development and germination*. New York, Marcel Dekker.

Ferrandis, P., Herranz, J.M. and Martinez-Sanchez, J.J. (1996) The role of soil seed bank in the early stages of plant recovery after fire in a *Pinus pinaster* forest in SE Spain. *International Journal of Wildland Fire* **6**, 31–35.

Fowler, N.L. (1988) What is a safe-site?: neighbour, litter, germination date, and patch effects. *Ecology* **69**, 947–961.

Guo, Q.F. (1998) Microhabitat differentiation in Chihuahuan Desert plant communities. *Plant Ecology* **139**, 71–80.

Gutiérrez, J.R., Arancio, G. and Jaksic, F.M. (2000) Variation in vegetation and seed bank in a Chilean semi-arid community affected by ENSO 1997. *Journal of Vegetation Science* **11**, 641–648.

Gutterman, Y. and Shem-Tov, S. (1996) Structure and function of the mucilaginous seed coats of *Plantago coronopus* inhabiting the Negev Desert of Israel. *Israel Journal of Plant Sciences* **44**, 125–134.

Harper, J.L. (1977) *Population biology of plants*. London, Academic Press.

Harrington, G.N. and Driver, M.A. (1995) The effect of fire and ants on the seed-bank of a shrub in a semi-arid grassland. *Australian Journal of Ecology* **20**, 538–547.

Hartmann, H.T. and Kester, D.E. (1999) *Propagación de plantas, principios y prácticas*. México, CECSA.

Hassan, M.A. and West, N.E. (1986) Dynamics of soil seed pools in burned and unburned sagebrush semi-deserts. *Ecology* **67**, 269–272.

Hyatt, L.A. and Casper, B.B. (2000) Seed bank formation during early secondary succession in a temperate deciduous forest. *Journal of Ecology* **88**, 516–527.

Kalisz, S. and McPeek, M.A. (1992) Demography of an age-structured annual: resampled projection matrices,

elasticity analyses and seed bank effects. *Ecology* **73**, 1082–1093.

Kemp, P.R. (1989) Seed banks and vegetation processes in deserts. pp. 257–281 *in* Leck, M.A.; Parker, V.T.; Simpson, R.L. (Eds) *Ecology of soil seed banks*. San Diego, Academic Press.

Laskurain, N.A., Escudero, J.M., Olano, J.M. and Loidi, J. (2004) Seedling dynamics of shrubs in a fully closed temperate forest: greater than expected. *Ecography* **27**, 650–658.

Longland, W.S., Jenkins, S.H., Van der Wall, S.B., Veech, J.A. and Pyare, S. (2001) Seedling recruitment in *Oryzopsis hymenoides*: are desert granivores mutualists or predators? *Ecology* **82**, 3131–3148.

Malhado, A.C.M. and Petrere, M. (2004) Behaviour of dispersion indices in pattern detection of a population of angico, *Anadenanthera peregrina* (Leguminosae). *Brazilian Journal of Biology* **64**, 243–249.

Marone, L., Rossi, B.E. and Horno, M.E. (1998) Timing and spatial patterning of seed distribution in a South American warm desert. *Plant Ecology* **137**, 143–150.

Marone, L., Horno, M.E. and del Solar, R.G. (2000) Post dispersal fate of seeds in the Monte desert of Argentina: patterns of germination in successive wet and dry years. *Journal of Ecology* **88**, 940–949.

Monturiol, F. and Alcalá del Olmo, L. (1990) *Mapa de asociaciones de suelos de la Comunidad de Madrid*. Scale 1:200.000. Madrid, CSIC

Morisita, M. (1959) Measuring of the dispersion and analysis of distribution patterns. *Memoirs Faculty of Science, Kyushu University. Series E. Biology* **2**, 215–235.

Moro, M.J., Pugnaire, F.I., Haase, P. and Puigdefábregas, J. (1997) Mechanisms of interaction between a leguminous shrub and its understorey in a semi-arid environment. *Ecography* **20**, 175–184.

Morris, A.B., Baucom, R.S. and Cruzan, M.B. (2002) Stratified analysis of the soil seed bank in the cedar glade endemic *Astragalus bibullatus*: Evidence for historical changes in genetic structure. *American Journal of Botany* **89**, 29–36.

Nakagoshi, N. (1984) Buried viable seed populations in forest communities on the Hiba Mountains, southwestern Japan. *Journal of Science of the Hiroshima University, Series B, Division 2* **19**, 1–56.

Nunney, L. (2002) The effective size of annual plant populations: The interaction of a seed bank with fluctuating population size in maintaining genetic variation. *American Naturalist* **160**, 195–204.

Olano, J.M., Caballero, I., Laskurain, N.A., Loidi, J. and Escudero, A. (2002) Seed bank spatial pattern in a temperate secondary forest. *Journal of Vegetation Science* **13**, 775–784.

Olano, J.M., Caballero, I., Loidi, J. and Escudero, A. (2005) Prediction of plant cover from seed bank analysis in a semi-arid plant community on gypsum. *Journal of Vegetation Science* (in press).

Pake, C.E. and Venable, D.L. (1996) Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology* **77**, 1427–1435.

Parmenter, R.R. and MacMahon, J.A. (1983) Factors determining the abundance and distribution of rodents

in a shrub–steppe ecosystem: The role of shrubs. *Oecologia* **59**, 145–156.

Price, M.V. and Joyner, J.W. (1997) What resources are available for desert granivores: Seed rain or soil seed bank? *Ecology* **78**, 764–773.

Price, M.V. and Reichman, O.J. (1987) Distribution of seeds in Sonoran desert soils – implications for heteromyid rodent foraging. *Ecology* **68**, 1797–1811.

Reichman, O.J. (1984) Spatial and temporal variation of seed distributions in Sonoran desert soils. *Journal of Biogeography* **11**, 1–11.

Rivas-Martínez, S. and Costa, M. (1970) Comunidades gipsícolas del centro de España. *Anales del Instituto Botánico Cavanilles* **27**, 193–224.

Rivas-Martínez, S. and Loidi, J. (1999) Bioclimatology of the Iberian Peninsula. *Itinera Geobotanica* **13**, 41–47.

Romão, R. and Escudero, A. (2005) Gypsum soil surface crusts and the existence of gypsophytes in semi-arid central Spain. *Plant Ecology* (in press).

Rubio, A. and Escudero, A. (2000) Small-scale spatial soil–plant relationship in semi-arid gypsum environments. *Plant and Soil* **220**, 139–150.

Russi, L., **Cocks, P.S. and Roberts, E.H.** (1992) Seed bank dynamics in a Mediterranean grassland. *Journal of Applied Ecology* **29**, 763–771.

Schupp, E.W. (1988) Factors affecting post-dispersal seed survival in a tropical forest. *Oecologia* **76**, 525–530.

Schupp, E.W. (1995) Seed–seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany* **82**, 399–409.

Schupp, E.W. and Fuentes, M. (1995) Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* **2**, 267–275.

Simonetti, J.A. (1989) Microhabitat use by small mammals in central Chile. *Oikos* **56**, 309–318.

ter Braak, C.J.F. (1986) Canonical correspondence analysis, a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**, 1167–1179.

ter Braak, C.J.F. and Prentice, I.C. (1988) A theory of gradient analysis. *Advances in Ecological Research* **18**, 271–317.

ter Braak, C.J.F. and Smilauer, P. (1997) *Canoco for Windows Version 4.0*. Wageningen, The Netherlands, Centre for Biometry.

ter Heerdt, G.N.J., **Verweij, G.L.**, **Bekker, R.M. and Bakker, J.P.** (1996) An improved method for seed bank analysis: seedling emergence after removing the soil by sieving. *Functional Ecology* **10**, 144–151.

Thompson, K. (1992) The functional ecology of seed banks. pp. 231–258 *in* Fenner, M. (Ed.) *Seeds. The ecology of regeneration in plant communities*. Wallingford, CAB International.

Thompson, K. and Grime, J.P. (1979) Seasonal-variation in the seed banks of herbaceous species in 10 contrasting habitats. *Journal of Ecology* **67**, 893–921.

Thompson, K., **Bakker, J.P. and Bekker, R.M.** (1997) *The soil seed banks of North West Europe: Methodology, density and longevity*. Cambridge, Cambridge University Press.