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The fate of seeds in Mediterranean soil seed banks in relation to their traits

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Abstract

Question: Is there any change in seed density and species richness in Mediterranean surface soil banks during summer? Are there any relationships between these summer variations and seed traits (weight, length and shape), without and with controlling the phylogenetic effect?

Location: Central Spain.

Methods: Samples of the surface soil seed bank were collected in two Mediterranean systems, grassland and scrubland, at two points in the year: immediately after the summer production peak and immediately prior to the autumn germination peak. We used Canonical Correspondence Analysis ordination to check for changes in floristic composition and ANOVAs to check for changes in seed density and species richness between summer and autumn samples. We used multiple regression analysis to analyse the relationship between summer variations in soil seed density and form traits, with and without controlling phylogenetic relations.

Results: Soil seed density dropped significantly during the summer in the two systems (28% in grasslands, repeated measures ANOVA test; $F = 58.19, P < 0.01$; 72% in scrublands, repeated measures ANOVA test; $F = 75.67, P < 0.001$). Species richness, however, only dropped significantly in the scrubland (32%; repeated measures ANOVA test; $F = 9.17$, $P < 0.05$). Variation in the floristic composition of the shallow banks was only significant in the scrubland.

Changes in shallow bank density were related significantly to seed morphology features, with greater drops in species with heavier seeds in grasslands and species with longer seeds in scrubland.

Conclusions: Our results show a substantial loss of seeds in the uppermost soil layer during the summer period between the point of peak production and the autumn germination peak. This drop was clearer in the scrubland than in the grassland. Longer and/or heavier seeds underwent the greatest declines in density at the end of summer, indicating a more intense effect of post-dispersal predation on large-seeded species.

Keywords: Ant; Floristic composition; Phylogenetic effect; Post-dispersal seed density; Seed predation; Species richness; Surface soil bank; Seasonal variation.

Abbreviations: CSA = Cross-species analysis; PIA = Phylogenetically independent analysis; PIC = Phylogenetically independent contrast.

Introduction

The regeneration of vegetation cover in therophyte-dominated Mediterranean systems, characterized by autumn germination peaks (Bartolome 1979), depends primarily on the seeds that enter the soil seed bank in previous periods. Basic patterns of seasonal variation in seed density of soil banks in Mediterranean grasslands have been described, with autumn maxima prior to the point of peak germination, and spring minima immediately prior to the start of the seed production period (Bartolome 1979; Russi et al. 1992; Ortega et al. 1997). This variation is maximal in the first cm of the soil bank, while deeper fractions are more stable (Traba 2000), an indication of both slow burial and the presence of many transitory seeds in the seasonal inputs that quickly lose their viability (Roberts 1981; Traba 2000) or are predated (Hulme 1993).

However, summer changes in the soil bank have not been described to date in Mediterranean systems. Seed input to the soil depends on direct contribution via seed rain or through various medium- and long-distance dispersal vectors such as endozoochory, exozoochory, anemochory, etc. (Louda 1989). Seed output prior to the germination phase is due to factors such as secondary dispersal, including both horizontal and vertical movements (burial), post-dispersal seed predation and other hardly studied factors such as seed decay because of senescence or parasite attack (see review in Chambers & MacMahon 1994). All these processes determine the final composition of the bank prior to autumn germination.

Burial is a secondary dispersal movement that reduces the risk of desiccation and predation (Hulme 1993), although it can also restrict the capacity for successful germination, emergence and establishment (Traba et al. 2004), particularly in small-seeded species (Grundy et al. 2003). Burial capacity has been related to seed morphology features; it is greater when seed size decreases and sphericity increases (Thompson et al. 1993, 2001). Burial should result in a surface drainage of small seeds, which enter the deeper layers of the soil where they may remain viable for long periods

(Thompson et al. 1993, 2001; Funes et al. 1999; Peco et al. 2003, see however Leishman & Westoby 1998). In this context, species with small, rounded seeds should yield declining density in the shallow bank through summer, although this variation may not be appreciated in an analysis of the complete soil profile.

Post-dispersal seed predation has been mentioned as a key factor for explaining demographic changes in the plant community (Hulme 1998), and may affect seed survival more than pre-dispersal predation (Moles et al. 2003). While the importance of small mammals and birds in seed predation has been reported (Hulme 1998), the most important seed predators in open Mediterranean systems are ants, particularly *Messor* spp., during both pre- and post-dispersal stages (López et al. 2000; Azcárate & Peco 2003). Ants seem to predate mainly on the higher ranges of seed size (Detrain & Pasteels 2000; Azcárate et al. 2003) and seeds found on the surface (Azcárate 2003). This may lead to a decline in density of species with large and/or long seeds in the shallow bank in summer, the period of maximum ant predation. Similarly, in areas with the highest ant predation rates, large-seeded species experience greater summer drops in density than in zones with less ant activity.

We describe seasonal changes in seed density, species richness and floristic composition of shallow soil banks in two Mediterranean systems between the peak of seed input to the soil bank and the moment prior to autumn germination. We discuss two questions: 1. Do seed density and species richness change between summer and autumn? We expect to find a substantial decline in total density of viable seeds that triggers changes in the floristic composition between autumn and summer. 2. If changes occur, are they linked to morphological features of the seeds? If the changes are due to burial phenomena, small-seeded species should experience the largest drops in the density of the shallow bank during the summer. If, on the other hand, post-dispersal seed predation is the major change factor, long-seeded species should experience the most intense drop in density in the surface soil bank between summer and autumn.

Methods

Study area

The study area is 35 km north of Madrid (40°38' N; 3°70' W) at 850-900 m a.s.l. and has a gneiss bedrock. Mean temperature is ca. 13 °C and mean annual rainfall is ca. 500 mm, with large interannual fluctuations. The study year was wetter than average, with 660 mm during the 12 months prior to the sampling. The area contains two clearly different systems: a *Quercus ilex* ssp. *ballota* dehesa grassland extensively grazing by cattle and horses, and *Lavandula stoechas* ssp. *pedunculata* scrubland which developed after grazing abandonment 50 years ago. The herbaceous layer of the grassland is very rich in annual species, e.g. *Aphanes microcarpa*, *Leontodon taraxacoides* ssp. *longirostris*, *Hypochoeris glabra* and *Trifolium* spp., accompanied by a common perennial grass, *Poa bulbosa*. The scrubland harbours a less species-rich herbaceous matrix with annuals such as *Crepis capillaris*, *Xolantha guttata*, *Vulpia* spp., *Teesdalia coronopifolia* and *Mibora minima*. These two systems share 31% of the species (Traba 2000). The total study area covers ca. 600 ha.

Sampling design

At the start of July 1996, immediately after the production peak and seed rain, five 10 m × 10 m plots were chosen at random in each system (average distance between plots ca. 350 m) with ten shallow soil samples (10 cm × 10 cm × 1 cm; average distance between samples ca. 3 m), taken from each plot. No trees were found inside the plots, although some were growing in the vicinity. The ten July samples from each plot (henceforth summer control) were homogenized in the laboratory and carefully divided into three parts, two of which were discarded (total volume processed in each plot = 333 cm^3). The remaining third portion was placed in paper bags and stored cool and dry. In mid-September, before the germination had started, sampling was repeated at the same points, avoiding soil collection from areas affected by the previous samplings. These samples (henceforth autumn control) were processed like the summer control samples.

To estimate numbers of germinable seeds in the shallow bank samples, we used the greenhouse germination method (Traba et al. 1998; Peco et al. 2003), leaving samples in thin layers (no deeper than one cm) to facilitate seedling emergence (Traba et al. 2004). Samples were checked every day, and watered when necessary. There was no heating system in the greenhouse and temperatures ranged from 2 to 39 °C during the germination period. Samples were kept in the greenhouse for 20 months (two complete germination periods) beginning in October 1996. The soil samples were carefully stirred when no seedlings were detected for more than a month to facilitate the germination of the deepest seeds. Emerged seedlings were identified and counted as early as possible to avoid deleterious effects between individuals. At the end of the two germination cycles, 10% of the remaining samples were checked with a magnifying glass to detect ungerminated viable seeds, but no sound seeds were found. Germination attributed to *Poa bulbosa* was discarded due to the difficulty of distinguishing between seedlings and juveniles resprouting from bulbs or thickened roots.

Data for seed weight, length and shape (*sensu* seeds or fruits in their simplest form) were taken from Azcárate et al. (2002) and Sánchez et al. (2002) or measured following guidelines in Azcárate et al. (2002). Air-dried seeds were weighed, and seed length, width and depth were measured. Seed shape was calculated following Thompson et al. (1993) as the variance of the three main dimensions, first divided by length. Spherical seeds were given shape value = 0, which increased as they became flatter or elongated. For further information on methods, see the above-mentioned papers.

Statistical analysis

Summer variation in species richness and seed density were analysed using a separate one-way ANOVA for each system after data log-transformation and checking for homocedasticity. Changes in floristic composition of shallow seed banks between summer and autumn samples were analysed with a Canonical Correspondence Analysis (CCA) ordination (ter Braak & Šmilauer 1998). The matrix we used was number of seeds per plot, without data transformation or weighting. The contribution of the time factor to the explanation of variations in species data was analysed via conditional effects, and its relative importance was tested using a Monte Carlo permutation test.

The data for seasonal difference in seed density (*Ds*) for each species were calculated using the formula:

$$Ds = \ln(\text{autumn density} + 1) - \ln(\text{summer density} + 1) \qquad (1)$$

which permitted the standardization of seed density variation and the achievement of normality requirements in the residuals. To analyse the relationship between seasonal difference in soil seed density and form traits, we chose species that were present in more than three samples. To isolate the effect associated with phylogenetic relations, we used a phylogenetically independent analysis (PIA) (Martins & Hansen 1996), based on phylogenetically independent contrasts (PICs), which represent the difference in the corresponding trait values between two sister taxa (Felsenstein 1985). Differences were also calculated for internal nodes, and thus a data set of *n* species yields (*n*–1) PICs, assuming a dichotomous phylogeny. However, as a consequence of the lack of accurate phylogeny information, we used current non-dichotomous taxonomy to infer phylogeny, as suggested by Martins & Hansen (1996), which limited the number of PICs (App. 1).

To test whether the patterns detected in the PIA could also be found in the community we also performed a cross-species analysis (CSA). In both cases, a multiple regression analysis fitted the models to the PICs (PIA) or the species (CSA), depending on the case. The STATISTICA package (Anon. 1998) was used for all analyses.

Results

Seasonal variations in seed density, species richness and floristic composition of the soil bank

A total of 6586 germination cases for 117 species were detected in the set of samples over the 20 months in the greenhouse. Seed density (mean ± SD) fell significantly during the summer in both systems (Fig. 1a):

grassland: summer control: 462.00 ± 163.37;
autumn control: 331.00 ± 107.72;
repeated measures ANOVA test; $F = 58.19$; $df = 1$; $P < 0.01$;
scrubland: summer control: 411.80 ± 96.05;
autumn control: 112.40 ± 59.87;
repeated measures ANOVA test; $F = 75.67$; $df = 1$; $P < 0.001$.

Species richness (mean ± SD) fell significantly in the scrubland but not in the grassland (Fig. 1b):

scrubland: summer control: 33.80 ± 7.79;
autumn control: 22.80 ± 4.32;
repeated measures ANOVA test; $F = 9.17$; df = 1; $P < 0.05$;
grassland: summer control: 35.20 ± 7.66;
autumn control: 33.00 ± 6.16;
repeated measures ANOVA test; $F = 0.16$; df = 1; $P = 0.713$.

Variation in the floristic composition of the shallow banks was partially explained by the time factor, and was only significant in the scrubland (Table 1).

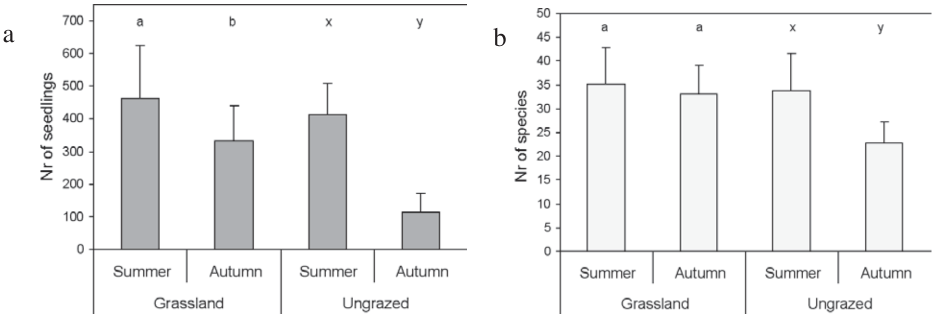

Fig. 1. a. Mean number of seedlings (± 1 SD); **b.** mean number of species (± 1 SD) per plot emerged from July and September surface soil bank samples taken at each system (*n* = 5). Different letters indicate significant differences ($P < 0.05$).

Table 1. Canonical Correspondence Analysis. The sum of all unconstrained eigenvalues (total inertia), inertia-conditional effects of the time factor and its *P*-value under the Monte Carlo permutation test using 499 permutations for grassland and shrubland. The inertia from the conditional effects is used to derive the multivariate correlation ratio (MCR), which represent the proportion of variation explained by time.

System	Total Inertia	Conditional effects	*P*-values	MCR (%) per factor
Grassland	0.93	0.11	0.25	11.8
Shrubland	1.04	0.15	0.02	14.4

Morphological traits

We obtained 29 PICs for the 42 species found in more than three samples in the grassland and 14 of 22 species in the scrubland (App. 1). Both the cross-species analysis (CSA) and the PIA for the grassland species showed significant negative correlations between seasonal variation in seed density and seed weight (Table 2). Greater seed weight was related to a greater drop in seed density during the summer. The CSA also showed this type of correlation with length. Shape did not yield significant correlations with variations in seed density in any case.

In the case of the scrubland, the CSA showed no significant correlations between variation in seed density and the three morphological variables. The analysis that monitored the phylogenetic effect yielded significant negative correlations between this variation in density and length (Table 2), showing that species with longer seeds experienced sharper drops in density over summer.

Table 2. Cross species analysis: [Ln (autumn density + 1) – Ln (summer density + 1)] vs. morphological variables, and phylogenetically independent analysis: PICs in [Ln (autumn density + 1) – Ln (summer density + 1)] *vs*. PICs in morphological variables, in grassland and shrubland. Significant correlations in bold. Grassland: cross species, *n* = 42; PICs, *n* = 29. Shrubland: cross species, *n* = 22; PICs = 14.

	Cross species		Phylogenetically independent	
	r	*P*	*r*	*P*
Grassland				
LnWeight	**–0.467**	**0.002**	**–0.368**	**0.048**
LnLength	**–0.387**	**0.011**	–0.316	0.094
Shape	–0.002	0.989	0.298	0.117
Shrubland				
LnWeight	–0.081	0.718	–0.245	0.398
LnLength	–0.256	0.249	**–0.573**	**0.032**
Shape	–0.133	0.556	–0.465	0.094

Discussion

These results show a substantial loss of seeds in the uppermost soil layer during the summer period between the point of peak production and the autumn germination peak. The reliability of the results lies on the relative synchrony of the germination phase and the low intensity of seed predation by ants during spring and early summer (F.M. Azcárate unpubl. data). In Mediterranean systems, spring or summer germination develops exceptionally, at least for C3 species (Ortega et al. 1997). In addition, some species could have seeded after July sampling, although undetected seed inputs during summer would reduce the significant decrease in seed density. Therefore, the substantial drop in seed density seems to be more important than those eventual inputs during summer.

The decrease in seed density was clearer in the scrubland, where we found a loss of 72% of seeds present at the start of summer, and in addition species richness fell by more than 30%, suggesting that the cause of the decline in density particularly affected certain species, which disappeared from the soil bank either totally (e.g. *Leontodon taraxacoides*, *Sanguisorba minor*, *Trifolium glomeratum)* or substantially (e.g. *Sedum caespitosum*, *Vulpia myuros* and *V. muralis* seed density decreased over 90%*)*. The results of the CCA reflect this change in the floristic composition of the scrubland, although effects deriving from rare species could be interfering. The drop in grassland seed density, while significant, did not trigger local disappearances of species from the shallow bank, which led to little seasonal variation in the floristic composition. The high heterogeneity of the soil seed bank, especially in Mediterranean systems (Ortega et al. 1997; Traba 2000), could hinder comparisons and explain a relevant fraction of these effects, although the number of rare species (only presented in one plot) was quite similar in both systems and dates: grasslands: 20 species in July, 23 in September; scrublands: 24 and 22 species, respectively.

Variations in seed density of the summer soil banks have rarely been analysed (but see Thompson & Grime 1979). The decrease in seed density found in the present study may be due to burial into deeper layers (Hulme 1993; Thompson et al. 1993). However, the decline could also be attributed to seed mortality caused by parasitism, desiccation or post-dispersal predation (Hulme 1998). Our correlations showed that species with longer and/or heavier seeds experienced the greatest declines in density at the end of summer. The greater burial capacity of small and rounded seeds (Thompson et al. 1993) should have promoted their rapid disappearance from the shallow bank while larger seeds remained on the surface. The burial of small seeds does not, however, seem to be a fast process as no losses of small seeds were detected in the first cm of soil in the summer. The variation noted in seed density may also be due to desiccation and death caused by pathogens. Although this aspect has hardly been studied at the community level, it seems that small seeds are more vulnerable to pathogens than larger ones (Crist & Friese 1993).

The correlations between seed morphology and changes in the shallow bank density seem to indicate a differential effect of post-dispersal seed predation with a more intense effect on large-seeded species, which are more attractive for predators (Detrain & Pasteels 2000; Willott et al. 2000; Azcárate et al. 2005; see however, Moles et al. 2003), less capable of escaping through burial (Thompson et al. 1993) and hence vulnerable to predators for a longer time (Bekker et al. 1998). Seed predation by *Messor* harvester ants plays a particularly important role in seed mortality in Mediterranean grasslands and scrubland (Detrain & Pasteels 2000; López et al. 2000; Azcárate & Peco 2003).

The pattern observed in the present study was relatively similar in the two analysed systems, although the effect of seed weight and length was intensified in grasslands and scrubland respectively, while the sign of the relationship was maintained, with increased size indicating decreased seed density in summer. These differences may be due to the different floristic composition of the herbaceous vegetation in the two systems, dominated by dicotyledons in the grassland and grasses in the scrubland (Peco et al. 2005). In accordance with these results, Azcárate et al. (2005) found that a combination of weight and length of the preys explained 57% of prey selection by ants in the grasslands of the study site, while in the scrublands prey length was enough to explain 64% of selection. In this sense, the differential predation may be responsible for the changes in the floristic composition of the shallow bank, particularly in very heterogeneous systems with low or medium seed densities (Traba et al. in prep.).

If large seeds are apt to more predation, we may expect this process to generate selective pressure towards a plant community dominated by small-seeded species (Louda 1989; Hulme 1998; Detrain & Pasteels 2000; Willott et al. 2000; Azcárate et al. 2005), as may be the case in our study site. Previous research has highlighted the predominance of high-productive, small-seeded species in Mediterranean grassland and scrubland, (Fernández Alés et al. 1993; Lord et al. 1997), capable of endozoochorous dispersal (Malo & Suárez 1995). These characteristics may prioritize colonization ability over competition ability, which is more characteristic of mesic habitats (Azcárate et al. 2002). Moreover, the greater burial ability of small seeds (Thompson et al. 1993) may increase their likelihood of escaping predation (Hulme 1993) although our results suggest that burial works more slowly than over the time period analysed in this study.

Mediterranean systems as grasslands and scrublands, dominated by annual species, depend primarily on soil seed banks for their regeneration. In these cases, drops in seed density during the summer season can generate significant effects on the vegetation dynamics. The fact that these decreases are related to selective disappearance of species with large and/or heavy seeds confirms the need for in-depth studies to establish the relative importance of these seeds for long-term changes in floristic composition.

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