Research

A model for small-scale seed bank and standing vegetation connection along time

Idoia Caballero, José M. Olano, Javier Loidi and Adrián Escudero

I. Caballero and J. Loidi, Laboratorio de Botánica, Depto de Biología Vegetal y Ecología, Facultad de Ciencia y Tecnología, Univ. del País Vasco, Apdo. 644, ES–48080 Bilbao, Spain. – J. M. Olano (jmolano@agro.uva.es) and IC, Área de Botánica, Depto de Ciencias Agroforestales, Escuela de Ingenierías Agrarias, Univ. de Valladolid, Los Pajaritos s/n, ES–42003 Soria, Spain. – A. Escudero, Área de Biodiversidad y Conservación, ESCET, Univ. Rey Juan Carlos, C/ Tulipán s/n, ES–28933 Móstoles, Spain.

Since inter-annual climatic variability influences composition and structure of seed bank and extant vegetation, it is expected that it also affects the relationship between both compartments at small scales along time. We hypothesize that seed bank and aboveground vegetation are closely and sequentially linked at small spatial and time scales. We conducted a field spatially explicit investigation to explore the spatial and temporal relationship between both compartments. Abundance, composition and spatial structure at different small-scales of seed bank and aboveground vegetation were analysed through 100 permanent plots during two consecutive (dry and wet) periods of growth. Following a conceptual transition path model, we analysed changes in correlation values in composition and spatial aggregation between both compartments along time including seasonal variations of seed bank. Shape of spatial structures were evaluated using partial Mantel correlograms. Annuals and perennials guilds were studied separately. During the wet year, annuals increased their aerial spatial aggregation and cover, whereas the opposite happened for perennials. Density and spatial aggregation of the seed bank increased for both guilds in the two seasons following the rain period, especially in annuals. The clumped structure of the transient seed bank is a consequence of the addition of spatial structure of extant vegetation and the persistent seed bank. Expression of the persistent seed bank is much lower during the dry period for the annual guild. In spite of the strong yearly variability, the community maintained a highly structured spatiotemporal pattern. The mechanisms promoting this stability differed for annual and perennial guilds. Temporal persistence in perennials relied mainly in established plants longevity, whereas annual guild persistence depended solely on seed bank. This tight structure was coherent with the existence of successional dynamics in the community, although persistent seed bank could moderate the pace. Longer term studies of seed bank–standing vegetation dynamics are required to fully understand this process.

Transition from seed to plant is probably the most important process in plant population and community dynamics (Eriksson and Ehrlén 1992, Tilman 1993, Burt-Smith et al. 2003). It connects two community compartments, seed bank and standing vegetation which occur spatially and temporally structured at several scales (Kemp 1989, Adler and Lauenroth 2001). As a consequence, knowledge on how both community components interact has become a priority for plant ecologists (Chambers and McMahon 1994) and for appropriate management and restoration of natural ecosystems (Chambers 2000, Matus et al. 2005).

Since dispersal is typically represented by a negative exponential function (Okubo and Levin 1989, Chambers and McMahon 1994), seeds tend to occur clumped in most habitats (Schmida and Ellner 1984). This mass effect which is modulated by local biotic and abiotic conditions over time (Miriti et al. 1998) such as the presence, composition and size of vegetated patches (Caballero et al. 2008) determines a strong spatial heterogeneity in the seed bank

structure at small scales (Jutila 1998, Olano et al. 2005). This effect is also partially responsible, at least in arid and semiarid regions, on the close relationship between aboveground vegetation and size and composition of soil seed banks (Kemp 1989, Chambers et al. 1991, Aguiar and Sala 1994, Moro et al. 1997, Pugnaire and Lázaro 2000, Marone et al. 2004, Caballero et al. 2008) which is mediated by the horizontal distribution of seedling emergences and survival (Aguiar and Sala 1997, Bisigato and Bertiller 2004, Olano et al. 2005).

Although a close spatial relationship between soil seed bank and vegetation has been revealed in Mediterranean communities (Levassor et al. 1990, Peco et al. 1998, Caballero et al. 2003), and in other stressful habitats where annuals are dominant (Henderson et al. 1988, Gul and Weber 2001, Olano et al. 2005, Capon and Brock 2006), some discrepancies have been also reported and associated to climate stochasticity (Gutiérrez et al. 2000, Gutiérrez and Meserve 2003). In this sense Clauss and Venable (2000), suggested that a higher emergence rate from a soil seed bank

should be expected in favourable years and therefore a higher correlation among seed bank and emergence and, definitively, on standing vegetation (Escudero et al. 2000).

Since inter-annual climatic variability highly influences composition and structure of both soil seed bank and extant vegetation, it is expected that it also affects the relationship between both compartments. Even more, spatial distributions (i.e. composition and small-scale abundance of plants and seeds) might also be affected by biotic but also abiotic climate-driven processes such as run-off or herbivory. However the number of papers focused on the relationship between these two community compartments during more than one reproductive period are scarce (Bonis et al. 1995, Dessaint et al. 1997, Cabin and Marshall 2000, Gutiérrez et al. 2000, Gul and Weber 2001, Gutiérrez and Meserve 2003, Matus et al. 2005) and to our knowledge none have considered how this interaction is modulated at very small scale along successive years or, specifically, how changes in one of the compartments is translated to the other.

We propose a model that hypothesizes that soil seed bank and above ground vegetation are closely and sequentially linked at small spatial and time scales. Consequently and point to point in space and time, composition and abundance of the seed bank will affect composition and abundance of the standing vegetation and in turn this will control soil seed bank structure in the following season. This connexion would constitute a spiral in the long time modulated by environmental conditions and favouring plant coexistence (Barot 2004). This dependence would vary in relation to climate but would remain intense along time: with higher correlation during favourable years (Clauss and Venable 2000). Moreover it would be weaker for the perennial guild which usually based its local persistence and dynamics on the longevity of mature individuals (García and Zamora 2003). In order to test our hypotheses and to unveil the degree of spatial and temporal dependence between aboveground vegetation and soil seed bank we conducted a field spatially explicit research in which standing vegetation was monitored annually during three years and seed bank was monitored every six months for two years. We propose a path model for the composition and abundance multivariate data controlling the spatial correlation among sample points (Legendre and Legendre 1998) and evaluating direct and indirect effects among compartments along time, partialling out the spatial structure effect. In addition, we want to answer the following questions: a) What is the relationship at small scale between the seed bank and the standing vegetation in a three year period? b) Does this relation vary between perennials and annuals? And c) Is the resemblance between seed bank-aboveground vegetation higher during favourable (wet) years?

Methods

Study site

The study was conducted at Belinchón (Cuenca province), 80 km southeast of Madrid, in central Spain (40°3′33.15″N, 3°3′3.67″W, 720 m a.s.l.). The climate is upper semi-arid mesomediterranean (Rivas-Martínez and Loidi 1997), with an annual rainfall of 441 mm, but with an extreme summer drought (only 5.6% of the rainfall during July and August). Average daily maximum and minimum temperatures in January are 10.6°C and –0.8°C, and in July 33.5°C and 14.5°C. Sampling years 2003 and 2005 were very hot and dry (354 and 178 mm respectively from September to August), whereas 2004 was a relatively wet year (542 mm). The soils are classified as Calcic Gypsisols, developed over gypsum parental rocks (Monturiol and Alcalá del Olmo 1990). Gypsum outcrops are characterized by a succession of small hills with steep slopes. Our working area is situated on a gentle slope, with a shrub community dominated by genuine gypsophytes and with some gypso-nitrophyllous perennials that are characteristic of piedmont communities. Shrubs are interspersed in well developed soil surface biological crust in which the presence of specialist annuals is important. Perennials ground cover projection rarely surpasses 20%. The area is exposed to light and occasional grazing.

Sampling design

A selected and representative 20 × 20 m area was divided in a 10 × 10 grid, obtaining 100 4-m² cells. In the centre of each cell we established a (0.5 × 0.5 m) sampling plot. In the middle of this plot we located three permanent nails forming an equilateral triangle of 30 cm with. On each sampling date one seed bank core was extracted from the close vicinity (5 cm distant) of each marked nail. The three soil cores were merged in a unique sample per grid cell and season. This sampling schema minimizes bias due to spatial heterogeneity and shrub cover at scales smaller than plot size.

Soil cores were 3 cm deep and 1.85 cm in diameter since, according to Childs and Goodall (1973), the first 2 cm accumulate most of the seed bank in arid environments. Local gypsum soil seed bank shows a strong seasonality (Caballero et al. 2003, 2005) with emergences occurring from autumn to spring and reaching a peak in early spring (Escudero et al. 1999, 2000). Contrarily, seed rain occurs almost exclusively in late spring and mainly in the summer (more than 95% of released seeds; Caballero 2006). Accordingly, we sampled at two dates: September, once seed rain has ceased and prior to the start of autumn rains and parallel emergence, and in late April, long before seed rain and after emergence period. As a consequence the September sampling corresponds to an almost perfect sum of transient and persistent seed bank components whereas the April sampling to only the persistent seed bank. The seed bank was measured at four dates covering two complete annual cycles: September 2003 and 2004, and April 2004 and 2005. Hereafter the April seed banks are termed persistent seed banks whereas the September seed banks are transient seed banks.

The aboveground percentage cover of all the species present in the standing vegetation was measured in a 50 × 50 cm quadrate around nails in April 2003, 2004 and 2005. Cover by species was visually estimated. In order to avoid an interference of seed bank sampling in standing vegetation measurements, these samplings did not take into

account the individuals growing in the holes performed during previous seed bank sampling.

We obtained data on the viable seed bank by monitoring seedling emergence in the glasshouse (ter Heerdt et al. 1996). Soil samples were kept at 4°C for two months. Thereafter, they were washed and sieved through a 0.5 cm mesh to retain the coarse fraction. The resulting material was sieved again through a 0.1 mm mesh, to reduce the fine material volume and produce the scarification of the seeds, which favours germination (Thompson et al. 1997). The resulting soil samples were placed in 0.1 mm meshes, laying on perlite-filled 8×8 cm plastic pots in a greenhouse. To improve the water carrying capacity of soil samples a sterile substratum of vermiculite and peat (2:1) was added and thoroughly mixed with the sampled soil until a 1 cm depth was reached. Ten pots were filled only with the sterile mixture and located in the greenhouse to detect contamination. Pot positions were regularly changed to prevent any localization effect. 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. After five months, the soil in the cells was crumbled to enhance germination and emergence was monitored for another three months. Finally, the cells were watered with a gibberellic acid (GA_3) solution (1000 ppm) to stimulate emergence for seeds with endogenous dormancy (Hartmann and Kester 1991) and emergence monitored for another two months. After such a long period the number of emerging seedlings was not significant.

Numerical analysis

We built a conceptual transition path model to explain seed bank and aboveground vegetation temporal relationships for annual and perennial guilds (Fig. 2). Point to point, transient seed bank composition affected the next persistent seed bank and vegetation compositions, whereas it was the result of previous persistent seed bank and standing vegetation. Aboveground vegetation was also related to previous year vegetation – this relationship being straightforward for perennial species.

As individual seed counts and vegetation cover were not normally distributed, original values were log transformed prior to the construction of distance matrices. The relationship between the different compartments of the community following our model (seed bank, aboveground vegetation) was evaluated using Mantel test. This is a procedure to compare two similarity matrices computed (Legendre and Legendre 1998). Results can be interpreted as a parametric Pearson correlation among similarity indices. Mantel statistical significance was tested using a randomisation approach with 999 permutations. The correlation between all the compartments was corrected from the dependence on spatial effect by a partial Mantel test with a geographic Euclidean distance matrix between cell positions as constant matrix. This technique is similar to a partial correlation, being able to detect the correlation between two matrices of interest when the effect of a third matrix, in our case the Euclidean distance matrix, is kept constant (Legendre and Legendre 1998).

In those cases in which the composition of a compartment might be influenced by the interaction of another two, partial Mantel tests were conducted to evaluate the independence of the effects and to estimate the relative contribution of each compartment. Specifically, we tested the relationship between former persistent seed bank and aboveground composition on autumn seed banks; and between the previous year standing vegetation and autumn seed bank on this year vegetation. The model was evaluated globally using a d-sep test (Shipley 2004).

The spatial structure of seed bank and vegetation at different scales was evaluated using a Mantel correlogram. This technique tests for spatial autocorrelation, computing a correlogram for multivariate data using the normalized Mantel statistic (R_M) and a permutation test for significance (Legendre and Legendre 1998, Escudero et al. 2003). The Mantel correlogram has the capability to test multidimensional data for the departure from spatial independence both in its totality and for each lag class. The distance interval used was 2 m (minimum distance between sampling points). In order to test the significance of each distance class, 999 permutations were carried out. The Bonferroni correction was used to account for multiple testing (Escudero et al. 2003). Finally, we used a partial Mantel correlogram to evaluate the dependence of the spatial pattern of autumn 2004 seed bank on those of spring vegetation and seed bank in the annual guild. More specifically we want to distinguish the differential contributions of standing vegetation and April (persistent) seed bank on September (transient) seed bank spatial pattern. Mantel tests were performed in R environment using the ecodist package (Goslee and Urban 2007).

Results

Temporal structure

A total of 9557 seedlings belonging to at least 61 species (45 annuals and 16 perennials) emerged from the 400 seed bank samples, ranging from 424 seedlings in April 2004 to 5910 in September 2004 after a relative wet and mild reproductive season. In the extant vegetation we recorded a total of 82 species (58 annuals and 24 perennials). Of these, 56 species were recorded also in the seed bank. Data on individual species characteristics and seed bank density are presented in Supplementary material Appendix 1.

Annuals seed densities were 10 times higher in magnitude than those of perennial species, whereas aboveground cover was quite similar (Table 1). Seed bank density and vegetation cover varied greatly over time for both plant groups (Fig. 1). Seed bank densities are higher in the transient seed bank than in the persistent for the same growing period. However, the 2005 persistent seed bank was still higher than the 2003 transient seed bank (Fig. 1). The increase of the seed bank in the the 2004 transient bank, immediately after a wet reproductive season, was notably higher for the annuals guild (Fig. 1, Table 1).

This is the only biologically feasible model, although d-sep tests (Shipley 2004) show that other paths could improve the adjustment of the model, but connecting compartments temporally separated. Consequently, we have

Table 1. Seed bank density (seeds m^{-2}) and vegetation cover in percentage (mean±SE) at different samples dates. Seed bank data based on seedling emergences counts.

	Annuals	Perennials
	Mean ±SE	Mean ±SE
Seed bank density		
Autumn 2003	15 252.8±1277.3	1612.1±230.8
Spring 2004	4203.8±513.2	905.2±177.9
Autumn 2004	70 411.0±6513.7	2566.9±300.3
Spring 2005	19 580.7±2101.2	1798.1±392.7
Vegetation cover		
Spring 2003	16.8±1.1	22.5±1.6
Spring 2004	24.3±1.3	16.6±1.6
Spring 2005	12.1±0.6	19.8±1.8

maintained our conceptual model which also presents high standardized path coefficients for both annual and perennial species (Fig. 2). This hypothesized model has R$_M$ values ranging from 0.219 to 0.815. Partialling out the spatial structure of the predictors did not significantly change the existing correlation values (unpubl.). Standing vegetation maintained very high correlation for perennials in both transitions (Fig. 2). In the case of the annuals correlation values changed depending on the year conditions, it was high for the spring 2003 – spring 2004 transition (wet year), but it was much lower for the spring 2004 – spring 2005 transition (dry year) (Fig. 2). In both life-forms, aboveground vegetation is better correlated with previous year vegetation than with the seed bank. Transient seed bank effect on next spring standing vegetation in annuals followed the same pattern with high values in annual for the 2004 transition (wet year) and lower values for the 2005 transition (dry year). Within the seed bank, transitions (persistent to transient and transient to persistent) maintained very similar values along time (Fig. 2).

Partial Mantel tests relationship of spring vegetation and persistent seed bank with transient seed bank (Fig. 3) show values similar to those of the general model, suggesting their additive and independent contribution to the transient seed bank formation.

The multivariable composition of the annual standing vegetation showed a significant spatial aggregation in the

first lags for the three analysed years, although the degree of aggregation varied among years, being more clumped in 2004 (Fig. 4). Seed bank composition was also spatially autocorrelated for the two first lags in September 2004 and April 2005 for annuals. Perennial vegetation composition showed a much more aggregated pattern in aboveground vegetation, extending from 0–8 m in 2003 and from 0–6 m in 2004 and 2005 (Fig. 4). The perennial seed bank showed spatial pattern only for the first lag (0–2 m) for September 2004 and smaller but still significant for the next seed bank in April 2005.

The 2004 transient seed bank revealed an even larger clumped spatial pattern in annuals when controlled for the effect of previous standing vegetation at scales ranging from 0 to 4 m (Fig. 5). A similar increase was observed when controlled for the previous persistent seed bank, although it was only close to significant (p < 0.1 for distances ranging from 0 to 4 m).

Discussion

A high inter-year variability in both vegetation and seed bank density and composition seems to be the norm in arid and Mediterranean environments (Kemp 1989), often as a response to changes in patterns and amount of rainfall (Gutiérrez et al. 2000, Lortie and Turkington 2002, Gutiérrez and Meserve 2003, Bisigato and Bertiller 2004, Capon and Brock 2006). Although extreme fluctuations in the cover of annuals in response to rainfall have been reported (Polis et al. 1997, Gutiérrez et al. 2000), the observed increase in the cover of annuals for our study area was fairly moderate (from 16 to 24%). In parallel, we also found significant differences in soil seed bank densities. These increases in seed bank showed a similar magnitude to those reported after ENSO events (Gutiérrez et al. 2000, Gutiérrez and Meserve 2003). Differences in seed bank can be attributed to the expected higher production of plants during the wet year and to a longer length of the vegetative season (unpubl.). Contrarily, the cover of perennials decreased during the wet year, mainly as a result of the high mortality and null recruitment during the previous year of *Helianthemum squamatum* (de la Cruz et al. 2008),
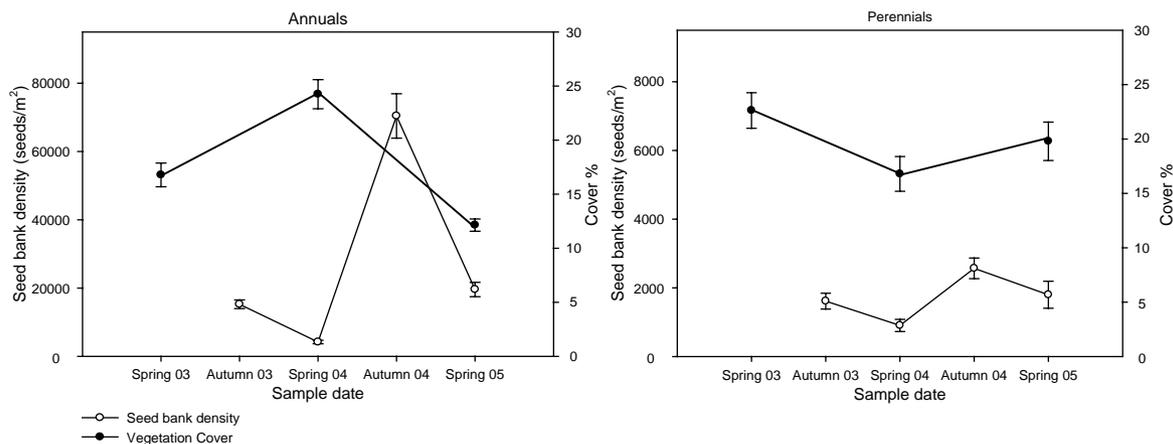

Figure 1. Abundance (mean±SE) in seed bank density and standing vegetation cover over the study period. Seed bank density scale in annuals is 10 × the scale of perennials. Data based on seedling emergences counts.
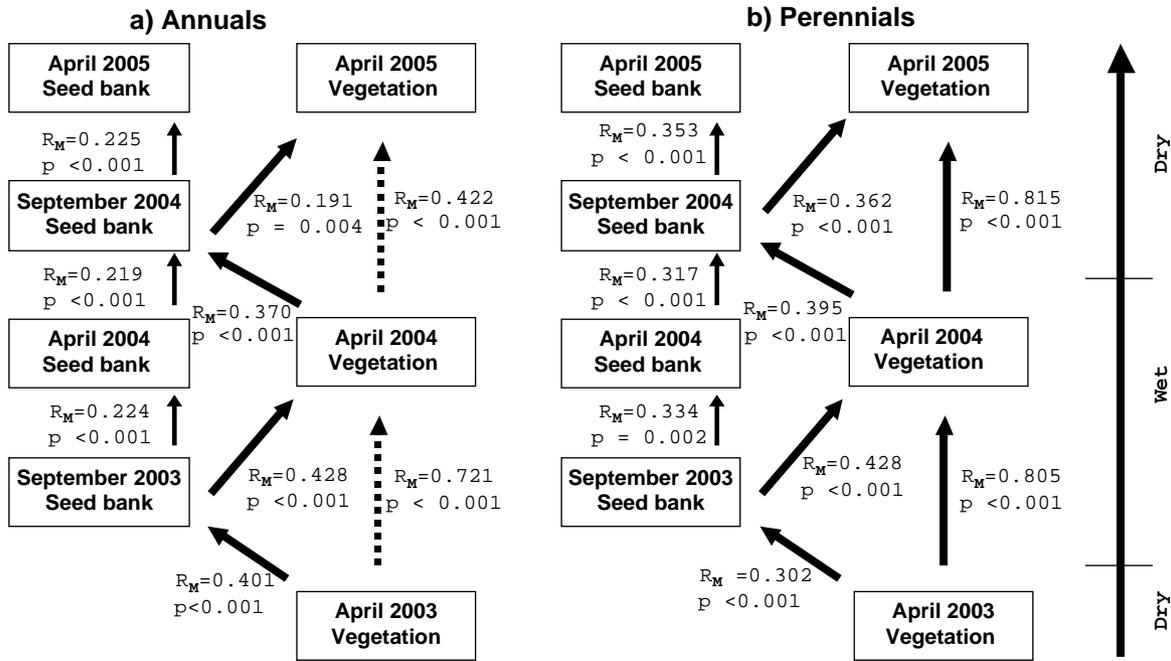
a) Annuals

b) Perennials

Figure 2. Path model based on Mantel correlations for annuals (a) and perennials (b) between seed bank and aboveground vegetation compartments along time. All the correlation results are corrected for spatial influence by a partial Mantel test with a geographic Euclidean distances matrix like constant matrix. The dashed arrows show not causal relationships. The arrow in the right side of the figure represents time in years. Years have been classified as dry or wet in relation to their annual rainfall.

the most abundant shrub in the community. Perennials show a milder reaction and less pronounced fluctuations to favourable conditions than annuals (Gutiérrez et al. 1997, 2000) and time-lagged responses may be common. In fact, the perennial cover increased during 2005, the driest year, but just after a favourable year. The seed bank also increased in the perennials guild, but in a minor proportion than in the case of the annuals guild, probably due to a more conservative strategy in perennials, devoting a higher proportion of their energy to persistence (García and Zamora 2003). Worth to note that which have been included as perennial might belong to at least two different plant strategies: genuine long-lived perennials and short term perennials. Among this last class we include *Helianthemum squamatum* with a sustained high reproductive output in a wide range of environmental conditions (Aragón et al. 2007) at the expense of exhaustion and early plant death, what together leads to a rapid turnover of plants

Accordingly with expectations from our model, field data showed the existence of a strong relationship between

standing vegetation and two sequential seed banks in our semiarid community at very small scale (Coffin and Lauenroth 1989, Peco 1989, Capon and Brock 2006), and extended this close relationship for several years despite climate conditions were markedly different. Moreover, the intensity of this dependence between both compartments was modulated by current environmental conditions. The strength of this relationship showed a two-fold increase during relatively wet 2004 (Fig. 2). A higher expression of the seed bank during favourable years has been widely reported (Espigares and Peco 1995, Clauss and Venable 2000). Nevertheless, the remaining relationships between all the transitions in the path model were quite stable, independently of the year climatic conditions. Not surprisingly, perennial standing vegetation was remarkably similar from year to year ($R_M > 0.8$), because a great part of the standing biomass remained alive from previous year and growth and recruitment is too slow in this stressful habitat to determine sharp changes in composition (Caballero 2006). Therefore, the meaning of the resemblance between persistent seed bank and perennial composition is different
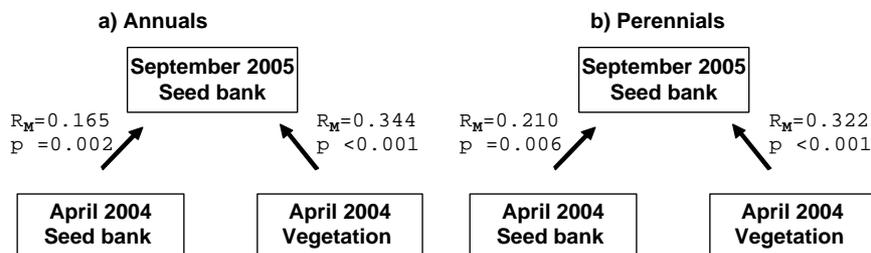
a) Annuals   b) Perennials

Figure 3. Path model based on partial Mantel tests for the relation between different compartments with 2004 transient seed bank; for annual (a) and perennial (b) species.
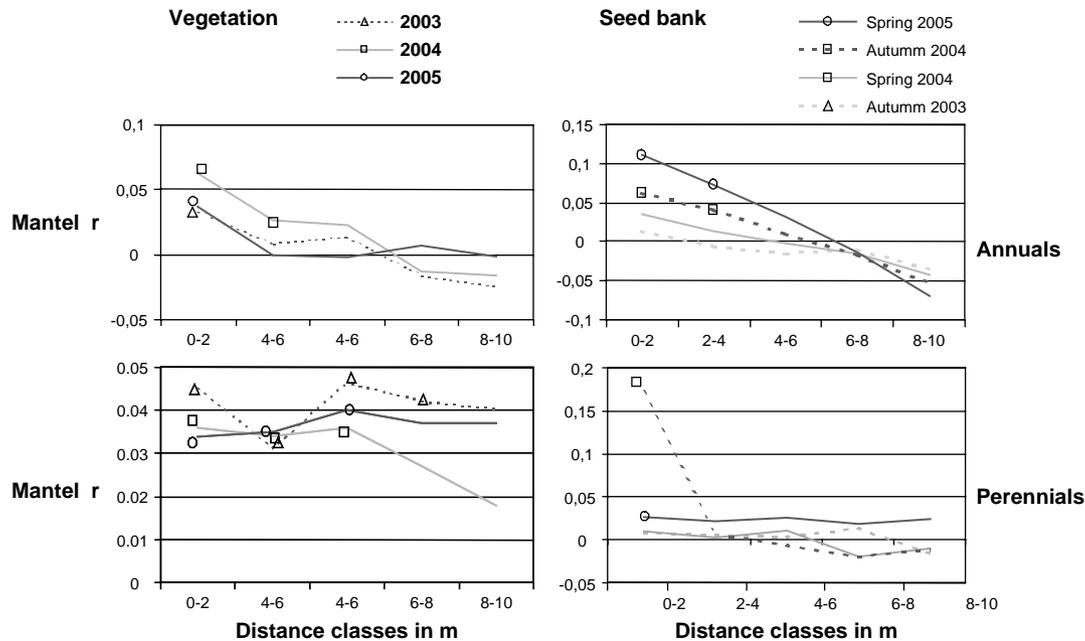
Figure 4. Mantel correlograms for annual and perennials seed bank and aboveground vegetation. Open symbols indicate p <0.05 after a sequential Bonferroni correction. The 2004 was a wet year whereas 2003 and 2005 were dry years.

from that of the annual guild, and should be simply interpreted as a direct effect of local seed rain.

The effect of a wet year was also reflected in the spatial structure of these compartments. For instance the annual standing vegetation pattern became more aggregated during this year. This clumped pattern was transferred to the seed bank compartment after dispersal (September 2004) and was still apparent in the next persistent seed bank (April 2005). However, the standing vegetation aggregation pattern in April 2005 reverted to similar levels to those of 2003. Changes in seed bank autocorrelation values have been reported in several studies, including those on annual species and communities (Chambers 1995, Houle et al. 2001, Lortie and Turkington 2002), and can be partially attributed to seed redistribution and the spatial patterns of germination during winter and early spring. Capon and Brock (2006) also found a spatial effect in the seed bank in response to variations in standing vegetation. Aboveground perennial vegetation cover showed a spatial structure more aggregated at larger scales than the annual guild. This is not a surprising result given the bigger size of perennial plants and their response to factors with a broader spatial grain than annuals (Escudero et al. 1999, 2000,
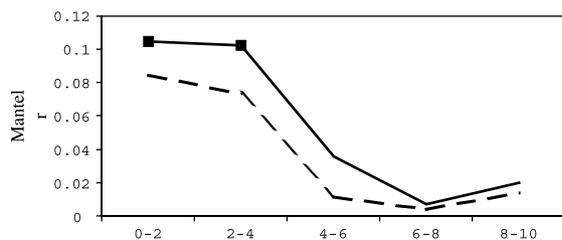

Figure 5. Partial Mantel correlogram for the 2004 September (transient) seed bank controlled by 2004 April (persistent) seed bank (dashed line) or by 2004 April standing vegetation (solid line). Filled squares indicate p <0.05. Distance classes in meters.

Caballero et al. 2008). Even so, the wet year promoted an increment of spatial structure in the perennials seed bank in September 2004, which extended with less intensity to April 2005.

High inter-annual variability in extant vegetation but also in seed bank in arid and Mediterranean environments has been related to patch dynamics (Pugnaire and Lázaro 2000, Lortie and Turkington 2002, Romão and Escudero 2005, Caballero et al. 2008). In this sense the accurate predictive ability of each single compartment on the next compartment could be interpreted as an indicator of absence of such a type of dynamics, because compartments would tend to remain stable with oscillations around an equilibrium point. But this would not be necessarily true. The community may be governed by patch dynamics or even directional changes and not remain constant. Such type of composition changes may be sustained by a spiral model: the close relationship between compartments will be maintained along time but small changes will lead for dynamic changes in the system and inter year variations in composition and structure both in soil seed banks but also in the standing vegetation would be feasible.

Highly unpredictable environmental conditions that characterize semiarid environments led to strong yearly variations in community cover and composition. In spite of this variability the community maintained a highly structured spatiotemporal pattern. Nevertheless, the mechanisms promoting this stability are substantially different for each of the two considered plant guilds: annual and perennial. Temporal persistence in perennials seems to rely mainly in established plants persistence, with a minor role of the seed bank, whereas annual guild persistence depends solely on seed bank. In both cases, the short range dispersal that characterise semiarid environments (Gutterman and Shem-Tov 1996) and the spatial heterogeneity of microsites (Quintana-Ascencio et al. 2008) may contribute to the

persistence of a finely grained spatial structure. However, this tight structure is coherent with the existence of successional dynamics, although persistent seed bank may moderate the pace. Longer term studies of seed bank-standing vegetation dynamics are required to fully understand these processes.

References

Adler, P. B. and Lauenroth, W. K. 2001. The effect of grazing on the spatial heterogeneity of vegetation. – Oecologia 128: 465–479.

Aguiar, M. R. and Sala, O. E. 1994. Competition, facilitation, seed distribution and the origin of patches in a Patagonian steppe. – Oikos 70: 26–34.

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

Aragón, C. F. et al. 2007. Environmental scales on the reproduction of a gypsophyte: a hierarchical approach. – Ann. Bot. 99: 519–527

Barot, S. 2004. Mechanisms promoting plant coexistence: can all the proposed processes be reconciled? – Oikos 106: 185–192.

Bisigato, A. J. and Bertiller, M. B. 2004. Temporal and micro-spatial patterning of seedling establishment. Consequences for patch dynamics in the southern Monte, Argentina. – Plant Ecol. 174: 235–246.

Bonis, A. et al. 1995. Seed bank dynamics and coexistence of annual macrophytes in a temporary and variable habitat. – Oikos 74: 81–92.

Burt-Smith, G. S. et al. 2003. Seedling resistance to herbivory as a predictor of relative abundance in a synthesised prairie community. – Oikos 101: 345–353.

Caballero, I. 2006. Estructura espacio-temporal de un banco de semillas: Las comunidades gipsícolas del centro de la Península Ibérica. PhD thesis. – Univ. del País Vasco, Spain.

Caballero, I. et al. 2003. Seed bank structure along a semi-arid gypsum gradient in central Spain. – J. Arid Environ. 55: 287–299.

Caballero, I. et al. 2005. Spatial coherence between seasonal seed banks in a semi-arid gypsum community, density changes but structure does not. – Seed Sci. Res. 15: 153–160.

Caballero, I. et al. 2008. Seed bank spatial structure in semi-arid environments: beyond the patch-bare area dichotomy. – Plant Ecol. 195: 215–223.

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*. – J. Ecol. 88: 283–292.

Capon, S. J. and Brock, M. A. 2006. Flooding, soil seed bank dynamics and vegetation resilience of a hydrologically variable desert floodplain. – Freshwater Biol. 51: 206–223.

Chambers, J. C. 1995. Relationships between seed fates and seedling establishment in an alpine ecosystem. – Ecology 76: 2124–2133.

Chambers, J. C. 2000. Seed movements and seedling fates in disturbed sagebrush steppe ecosystems. Implications for restoration. – Ecol. Appl. 10: 1400–1413.

Chambers, J. C. and McMahon, J. A. 1994. A day in the life of a seed – movements and fates of seeds and their implications for natural and managed systems. – Annu. Rev. Ecol. Syst. 25: 263–292.

Chambers, J. C. et al. 1991. Seed entrapment in alpine ecosystems, effect of soil particle size and diaspore morphology. – Ecology 72: 1668–1677.

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

Clauss, M. J. and Venable, D. L. 2000. Seed germination in desert annuals: an empirical test of adaptative bet hedging. – Am. Nat. 155: 168–186.

Coffin, D. P. and Lauenroth, W. K. 1989. Spatial and temporal variation in the seed bank of a semiarid grassland. – Am. J. Bot. 76: 53–58.

Dessaint, F. et al. 1997. Nine years' soil seed bank and weed vegetation relationships in an arable field without weed control. – J. Appl. Ecol. 34: 123–130.

De la Cruz, M. et al. 2008 Where do seedlings die? A spatio-temporal analysis of early mortality in a semi-arid gypsophyte. – Ecography 31. doi: 10.1111/j.2008.0906-7590.05299.x

Eriksson, O. and Ehrlén, J. 1992. Seed and microsite limitation of recruitment in plant populations. – Oecologia 91: 360–364.

Escudero, A. et al. 1999. Factors controlling the establishment of *Helianthemum squamatum* (L.) Dum., an endemic gypsophile of semi-arid Spain. – J. Ecol. 87: 290–302.

Escudero, A. et al. 2000. Factors affecting establishment of a gypsophyte: the case of *Lepidium subulatum* (Brassicaceae). – Am. J. Bot. 87: 861–871.

Escudero, A. et al. 2003. Spatial analysis of genetic diversity as a tool for plant conservation. – Biol. Conserv. 113: 351–365.

Espigares, T. and Peco, B. 1995. Mediterranean annual pasture dynamics-impact of autumn drought. – J. Ecol. 83: 135–142.

García, D. and Zamora, R. 2003. Persistence, multiple demographic strategies and conservation in long-lived Mediterranean plants. – J. Veg. Sci. 14: 921–926.

Goslee, S. and Urban, D. 2007. Ecodist: dissimilarity-based functions for ecological analysis, ver. 1.10. – Comprehensive R Archive Network. URL: <www.r-project.org>.

Gul, B. and Weber, D. J. 2001. Seed bank dynamics in a Great Basin salt playa. – J. Arid Environ. 49: 785–794.

Gutiérrez, J. R. and Meserve, P. L. 2003. El Niño effects on soil seed bank dynamics in north-central Chile. – Oecologia 134: 511–517.

Gutiérrez, J. R. et al. 1997. Effects of small mammals and vertebrate predators on vegetation in the Chilean semiarid zone. – Oecologia 109: 398–406.

Gutiérrez, J. R. et al. 2000. Variation in vegetation and seed bank in a Chilean semi-arid community affected by ENSO 1997. – J. Veg. Sci. 11: 641–648.

Gutterman, Y. and Shem-Tov, S. 1996. Structure and fuction of the mucilaginous seed coat of *Plantago coronopus* inhabiting the Negev Desert of Israel. – Isr. J. Plant Sci. 44: 125–133.

Hartmann, H. T. and Kester, D. E. 1991. Propagación de plantas: principios y prácticas. – CECSA. México, D.F.

Henderson, C. B. et al. 1988. Spatial and temporal patterns in the seed bank and vegetation of a desert grassland community. – J. Ecol. 76: 717–728.

Houle, G. et al. 2001. Spatiotemporal dynamics of *Floerkea proserpinacoides* (Limnanthaceae), an annual plant of the deciduous forest of eastern north America. – Am. J. Bot. 88: 594–607.

Jutila, H. M. 1998. Seed banks of grazed and ungrazed Baltic seashore meadows. – J. Veg. Sci. 9: 395–408.

Kemp, P. R. 1989. Seed banks and vegetation processes in deserts. – In: Leck, M. A. et al. (eds), Ecology of soil seed banks. – Academic Press, pp. 257–281.

Legendre, P. and Legendre, L. 1998. Numerical ecology. – Elsevier.

Levassor, C. et al. 1990. Seed bank dynamics of mediterranean pastures subjected to mechanical disturbance. – J. Veg. Sci. 1: 339–344.

Lortie, C. J. and Turkington, R. 2002. The small-scale spatio-temporal pattern of a seed bank in the Negev Desert, Israel. – Ecoscience 9: 407–413.

Marone, L. et al. 2004. Soil seed bank composition over desert microhabitats: patterns and plausible mechanisms. – Can. J. Bot. 82: 1809–1816.

Matus, G. et al. 2005. Impact of management on vegetation dynamics and seed bank formation of inland dune grassland in Hungary. – Flora 200: 296–306.

Miriti, M. N. et al. 1998. Spatial patterns of mortality in a Colorado desert plant community. – Plant Ecol. 136: 41–51.

Monturiol, F. and Alcalá del Olmo, L. 1990. Mapa de asociaciones de suelos de la Comunidad de Madrid. Escala 1:200.000. – Consejo Superior de Investigaciones Científicas, Madrid.

Moro, M. J. et al. 1997. Mechanisms of interaction between a leguminous shrub and its understorey in a semi-arid environment. – Ecography 20: 175–184.

Okubo, A. and Levin, S. A. 1989. A theoretical framework for data analysis of wind dispersal of seed and pollen. – Ecology 70: 329–338.

Olano, J. M. et al. 2005. Prediction of plant cover from seed bank analysis in a semi-arid plant community on gypsum. – J. Veg. Sci. 16: 215–222.

Peco, B. 1989. Modelling Mediterranean pasture dynamics. – Vegetatio 83: 269–276.

Peco, B. et al. 1998. Similarity between seed bank and vegetation in mediterranean grassland: a predictive model. – J. Veg. Sci. 9: 815–828.

Polis, G. A. et al. 1997. El Niño effects on the dynamics and control of an island ecosystem in the gulf of California. – Ecology 78: 1884–1897.

Pugnaire, F. I. and Lázaro, R. 2000. Seed bank and understorey species composition in a semi-arid environment, the effect of scrub age and rainfall. – Ann. Bot. 86: 807–813.

Quintana-Ascencio, P. F. et al. 2008. Qué sentido tiene una dispersión poco eficaz? Un modelo demográfico espacialmente explícito de Helianthemum squamatum. – In: Maestre, F. T. et al. (eds), Introducción al análisis espacial de datos en ecología y ciencias ambientales: métodos y aplicaciones. Univ. Rey Juan Carlos, Madrid, in press.

Rivas-Martínez, S. and Loidi, J. 1997. Bioclimatology of the Iberian Peninsula. – Itinera Geobotánica 13: 41–47.

Romão, R. L. and Escudero, A. 2005. Gypsum physical soil crusts and the existence of gypsophytes in semi-arid central Spain. – Plant Ecol. 181: 127–137.

Shipley, B. 2004. Analysing the allometry of multiple interacting traits – Persp. Plant Ecol. Evol. Syst. 6: 235–241.

Schmida, A. and Ellner, S. 1984. Coexistence of plants species with similar niches. – Vegetatio 58: 29–55.

ter Heerdt, G. N. J. et al. 1996. An improved method for seed bank analysis, seedling emergence after removing the soil by sieving. – Funct. Ecol. 10: 144–151.

Thompson, K. et al. 1997. The soil seed banks of northwest Europe, methodology, density and longevity. – Cambridge Univ. Press.

Tilman, D. 1993. Species richness of experimental productivity gradients – how important is colonization limitation. – Ecology 74: 2179–2191.

Supplementary material (available online at www.oikos. ekol.lu.se/appendix as Appendix O17138).