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Does aboveground vegetation composition resemble soil seed bank during succession in specialized vegetation on gypsum soil?

Abstract This paper evaluates the aboveground vegetation in relation to the soil seed bank throughout a 60-year succession process following agricultural abandonment in a semi-arid Mediterranean gypsum habitat. There is little information regarding the relationship between these two community components in the context of succession on semi-arid gypsum soils. Aboveground vegetation and the corresponding seed bank of gypsum plant communities were sampled through a chronosequence of 24 abandoned fields. Generalized linear models were used to model seed species richness and density, redundancy analyses to model the effect of time since abandonment and the effect of soil physicochemical parameters on seed bank species composition, and Mantel tests to analyze resemblance between above- and belowground species composition. In this last case, the effect of time since abandonment was controlled using a partial Mantel test. Mantel correlograms using time intervals instead of distances were used to describe the resemblance of above- to belowground species occurrence in different aged fields. No significant variability in seed species richness, seed density, or species composition due to time since abandonment was found. Differences in seed species composition were mainly due to small spatial scale predictors such as slope and soil calcium content. High correlations between species composition in the soil seed bank and the aboveground vegetation were detected during succession. The lack of a significant trend in aboveground species replacement over time was also reflected in seed bank composition. We concluded that the rapid establishment of strict gypsophyte species relied mainly on the long-term persistence of these species in the seed bank.

Keywords Gypsovags · Gypsophytes · Gypsum steppe · Soil seed bank · Soil physicochemical variables

Abbreviations GLM Generalized linear models · RDA Redundancy analyses · TVE Total variation explained

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Introduction

Soil seed bank is a key element in plant community dynamics. Seed banks enable plant populations to maintain their genetic variability and to withstand periods of adverse conditions and persist over time (Templeton and Levin 1979). It is well known from theoretical and observational studies that the existence of this community component confers an advantage in habitats where environmental conditions are unpredictable and can change dramatically (Venable and Brown 1988; Bonis et al. 1995). Seed bank composition and density therefore play a crucial role in vegetation dynamics aboveground after agricultural land is abandoned (Luzuriaga et al. 2005).

While it has been suggested that soil seed banks play a major role in community dynamics in determining the composition of aboveground vegetation (Fenner and Thompson 2005), the species composition of seed banks and aboveground communities does not always resemble each other closely (Leck 1989; Parker and Kelly 1989). This lack of correspondence may be partly due either to the dominance of vegetative reproduction over reproduction from seed in many plant species, or simply because some species do not form persistent seed banks and primarily base their establishment through efficient

seed dispersal. For instance, the similarity between aboveground and seed bank components is low in temperate grasslands dominated by perennial species (Milberg 1995; Bakker et al. 1996), but high in communities dominated by annuals, such as in most early successional stages and in Mediterranean grasslands (Peco et al. 1998; Ferrandis et al. 2001). An even closer relationship between these two components has been found at very small spatial and temporal scales in gypsum semiarid habitats (Caballero et al. 2008). Current theory suggests that the close relationship between these components will be maintained over time, but that small changes will lead to dynamic changes in the system (see spiral dynamics model in Caballero et al. 2008), but unfortunately, there is little information on how closely the above- and belowground components resemble each other during the long-term progression of a secondary succession.

Although significant research has been devoted to understand how plant communities are established and maintained over time, the role of seed banks remains little studied (Leck and Simpson 1987; Henderson et al. 1988; Caballero et al. 2008) and to our knowledge, no study of seed bank recovery over succession in gypsum soils has been carried out. Seed banks are especially important in gypsum steppes because of the limitations imposed by the particular physical and chemical characteristics of the soil, and the aridity of the climate (Bertiller 1998; Figueroa et al. 2004; Caballero et al. 2005). It has been suggested recently that community dynamics in this specialized system may be based on a close relationship between the aboveground and seed bank components at small scales that varies slowly over larger temporal and spatial scales (Caballero et al. 2008). Understanding the similarity of species composition in seed banks and aboveground vegetation, and how it varies over time, will not only provide insights into the mechanisms of succession but also inform the appropriate management of these habitats.

The chemical and physical characteristics of gypsum soils pose special problems for plants and some species have evolved gypsophilic abilities (Escudero et al. 1999, 2000; Guerrero-Campo et al. 1999a; Pueyo and Alados 2007) such that they are now restricted to areas where gypsum occurs in the soil (Pueyo and Alados 2007). Gypsum soils are characterized chemically by an imbalance in ion concentration, with an excess of sulphur and calcium ions (Boukhris and Lossaint 1975) and poor retention of ions such as phosphorous, potassium, and nitrogen due to their replacement with calcium in the soil complex (Guerrero-Campo et al. 1999a). In addition, seed establishment (Meyer et al. 1992; Escudero et al. 1999) and root penetration (Verheye and Boyadgiev 1997) are impeded by the hard physical and biological crust that forms on the surface of gypsum soils. It has even been suggested that gypsophily relies primarily on the ability of seedlings simply to be able to emerge through this extremely hard crust layer (Meyer 1986; Romao and Escudero 2005).

Because gypsum soils, together with serpentine soils, present one of the most hostile habitats for plant life (Harrison et al. 2004, 2006), they host one of the most conspicuously specialist endemic groups of plants (Guerra et al. 1995; Mota et al. 2003). The ecology of gypsum plant communities has been much studied recently (e.g., Meyer 1986; Guerrero-Campo et al. 1999a, b; Escudero et al. 1999, 2000; Palacio et al. 2007; Pueyo and Alados 2007), including their seed banks at small spatial and temporal scales (see Escudero et al. 1997; Caballero et al. 2003, 2005, 2008; Olano et al. 2005) and aboveground succession both primary (Mota et al. 2003; Dana and Mota 2006) and secondary (Martinez-Duro et al. 2010). However, many aspects of gypsophile community dynamics and the relationship between aboveground vegetation and seed bank composition during succession remain unknown. To fill this gap and to know to what extent the extreme soil physicochemical conditions modulate seed bank characteristics, we have conducted an observational study. Since we already know that aboveground vegetation and seed bank species composition are closely related in mature communities and at various spatial scales (Caballero et al. 2008), and that changes in aboveground vegetation composition after succession are negligible (Martinez-Duro et al. 2010), we hypothesized that both community components are also closely related during succession. We therefore did not expect to see marked changes in soil seed bank density and composition during secondary succession, contrary to reports from many other systems (Milberg 1995; Bakker et al. 1996). In addition, we wanted to test whether shallow and deep seed bank layers showed similar relationships to aboveground vegetation during succession. Specifically, we wanted to answer the following questions: (1) does aboveground vegetation mimic soil seed bank composition during succession in specialized gypsum vegetation?; and (2) to what extent do extremely challenging soil physicochemical conditions affect seed bank characteristics?

Materials and methods

Study site and plant communities

This study was carried out near Villarrubia de Santiago (39°59′N and 3°22′W; 750 m), in the province of Toledo (central Spain). The climate is semi-arid Mediterranean, with a typical pronounced summer drought (July–August) and an annual mean rainfall of ca. 400 mm. Mean temperature is 13.7°C with a mean minimum temperature in the coldest month of −0.2°C and a mean maximum temperature in the hottest month of 33°C. The soils are rich in massive calcic sulphate gypsum with gypsum content ranging between 50 and 70% (Rubio and Escudero 2000), which forms a hard physical crust at the surface (Ferrandis et al. 2005).

The landscape consists of low hills and flat-bottomed valleys, usually cultivated, leaving fragmented plant

communities on the hills. Gypsum soils are rich in calcium sulphate and calcium magnesium compounds that are inhospitable to plants. Plants living on gypsum soils are classified as gypsophytes when they occur exclusively on gypsum soils, and as gypsovags when they are able to grow on gypsisoils but grow optimally on non-gypsum soils (Meyer 1986). The natural vegetation on the hills is rich in endemic gypsophytes, such as *Centaurea hyssopifolia*, *Gypsophila struthium*, *Helianthemum squamatum*, *Koeleria vallesiana* subsp. *castellana*, *Ononis tridentata*, *Odontites longiflora* var. *gypsophila*, *Teucrium pumilum*, *Thymus lacaitae*, and *Reseda stricta*. Two plant communities can be distinguished on gypsum outcrops: (1) a scrubland dominated by *Gypsophila struthium*, *Centaurea hyssopifolia*, *Thymus lacaitae* and *Helianthemum squamatum* growing on slopes; and (2) a sparse dwarf scrubland dominated by *Teucrium pumilum* and *Herniaria fruticosa* subsp. *fruticosa*, which establishes on gypsum-crusted hill summits (Rivas-Martínez and Costa 1970).

Dry cereal crops and olive groves have traditionally been grown in the valleys. Rural exodus and European economic policies have led to changes in traditional land uses and lifestyle, resulting in field abandonment in recent decades. Dry grasslands rich in weeds (e.g., *Aegilops geniculata*, *Asterolinon linum-stellatum*, *Galium parisiense*, *Hippocrepis ciliata*) now grow in recently abandoned fields.

Sampling

Vegetation and the corresponding seed bank were sampled through a chronosequence of abandoned fields. We sampled 24 fields located on gypsophilous hills during spring and summer, 15 of which were abandoned between 1 and 60 years ago. The remaining nine fields were controls that had never been cultivated. The fields were dated according to records provided by the Castilla La Mancha Wildlife Service. Control fields were assigned an age of 100 years since abandonment for statistical purposes. Although arbitrary, this assignment enabled the effect of time since abandonment to be evaluated and provided consistent results in all of our analyses.

In each field, we chose a random sample plot 50 m^2 (5 × 10 m) with a 20-m buffer to avoid edge effect. The distance between the plot and the closest cropland was measured and included in our models. Vegetation was sampled using the "Point Quadrat" method (Groeneveld 1997). Four parallel 10-m-linear transects were established 1 m apart within each plot. Each transect consisted of 100 contact points located at regular 10-cm gaps (i.e., 400 contact points per plot; for more details see Martinez-Duro et al. 2010).

Soil samples were taken in May, before seed dispersal and after field germination, to estimate the persistent seed bank. On each plot, four soil cores (5 cm in diameter and 10 cm deep) were collected from each of five quadrats (1 × 1 m), positioned at random. Each core

was divided into two soil layers (0–5 and 5–10 cm deep). Soil samples from each quadrat were pooled for each layer, resulting in five soil samples per plot per layer (i.e., a total of 240 samples from 24 fields). The total area of the soil cores was 0.942 m^2 (0.008 m^2 per quadrat; 0.039 m^2 per plot). Soil samples were stored in dry conditions during summer for germination in the greenhouse in the autumn. The seed bank viability was assessed by monitoring seedling emergence (Thompson et al. 1997). Soil samples were washed and sieved through a 0.5-cm mesh to remove the coarse fraction. The resulting material was washed again through a 0.25-mm mesh to reduce the volume of fine material and to scarify the seeds to assist in germination (ter Heerdt et al. 1996). The concentrated samples were spread over a sterile substrate layer (vermiculite and peat; 2:1) in 20 × 30 cm plastic trays in a greenhouse. Five trays were filled with the sterile substrate only and placed at random in the greenhouse to detect contamination. A micro-sprinkler irrigation system watered the samples every 2–3 days. Seedlings were counted regularly, identified and then removed. Unidentified taxa were transplanted into individual pots and allowed to grow until identification was possible. Germination was monitored over 24 months.

Three soil samples (5 cm diameter and 10 cm deep) were taken per plot to determine soil chemical parameters and sent to the agrarian laboratory of the regional government to estimate: pH (in water 1:2.5), conductivity (mScm^{-1}), sodium (mEq 100 g^{-1}), potassium (mEq 100 g^{-1}), calcium (mEq 100 g^{-1}), total nitrogen (g 100 g^{-1}), available phosphorous (mg kg^{-1}), sulphate (mEq 100 g^{-1}), magnesium (mEq 100 g^{-1}), and organic matter (g 100 g^{-1}). Active limestone is the proportion of calcium carbonate (CaCO$_3$) that can be extracted with a CO$_2$ water solution and be taken up by plants. Soil texture was estimated for each plot (Bouyoucos Soil Hydrometer Method, Bouyoucos 1936). The crop type grown on each field prior to abandonment was recorded to evaluate the effect of prior land use on seed bank composition. Distance to the nearest cropland was measured to evaluate its influence on seed bank composition as a source of weed species (Supplementary material 1).

Statistical analyses

Total species richness, gypsophyte richness, and the total and gypsophyte seed densities at both soil depths were modeled using generalized linear models (GLM; McCullagh and Nelder 1989). GLMs can analyze larger distributions of the response variable than standard linear models. We applied a quasi-likelihood estimate of the regression coefficients for all the models, allowing estimation of the regression coefficients in data sets without fully knowing the error distribution of the response variable in cases when dispersion parameters were over- or under-dispersed. This method estimates

the dispersion parameter of the variance function that is otherwise set as a constant equal to 1 (MathSoft 1999). Significance of the regression coefficients were tested using a t test (H_0: coefficients are equal to 0).

The main variables determining species richness and seed density in the soil seed bank were examined with a forward stepwise procedure using the 19 variables measured in this study: time since abandonment, pH, conductivity, sodium, potassium, calcium, nitrogen, sulphate, phosphorus, magnesium, organic matter, fine sand, silt, clay, slope, altitude, longitude, distance to cropland, and agricultural practices (entered in the model as a multinomial variable with three categories: shallow, medium, and deep ploughing). One term was selected at each step on the basis of the magnitude of the Cp statistic estimated for each term, until additional terms no longer improved the power of the model (Escudero et al. 1999). The change of deviance of the model by the inclusion of a term was tested against an F distribution. The final model was characterized by fitted D^2, the equivalent to r^2 in least squares models (Guisan and Zimmermann 2000). These generalized linear models were built using R 2.4.1 statistical software (R Development Core Team 2006).

A standardized Mantel test was performed to test the similarities between the above- and belowground species composition (Legendre and Legendre 1998). We built two matrices of seed species densities, one for each soil layer (0–5, and 5–10 cm deep), another matrix for aboveground species composition, and a fourth matrix with differences in abandonment time (years) between each pair of samples. Abundance data were log-transformed and the distance matrix was built using the Bray–Curtis distance among samples. Bray–Curtis is the most commonly used coefficient for plant community analyses because, unlike most other coefficients, it obeys many of the natural biological axioms (Clarke and Gorley 2006). In order to check if the relationship between both matrices was the result of time-dependent changes, partial Mantel tests were conducted with distance in time since abandonment between sites as the co-variable matrix. This analysis is similar to a partial correlation; it enables us to detect the correlation between two matrices when the effect of a third matrix is kept constant. Mantel correlograms were built for each of the three community components (aboveground vegetation, seed bank at 0–5 cm deep, and seed bank at 5–10 cm deep). This technique allowed a comparison of the resemblance between pairs of stands at any given difference between sites in elapsed time since abandonment. The significances of the Mantel analyses were tested using a randomization approach with 5,000 permutations. Mantel tests were performed using R 2.4.1 statistical software (R Development Core Team 2006).

Ordination methods were used to evaluate compositional variation among the sites sampled. The major advantages of this technique over classical multivariate analysis of variance are that it is distribution-free and has no restrictive upper limit to the number of species included (Verdonschot and ter Braak 1994). The main matrix was built from the 24 plots (rows) and the densities of the 77 species recorded in the seed bank at 0-5 cm deep; the explanatory matrix consisted of the same 19 variables used for the GLMs. Because the axis length was below 3 standard deviation units, a redundancy analysis (RDA) was performed following the recommendations of Legendre and Anderson (1999). Square root transformation of the species data matrix was performed in order to reduce the impact of rare species. Total variation explained (TVE) by each constraining matrix was calculated as the sum of all canonical extracted axes (Borcard et al. 1992). Monte Carlo permutation tests were performed to determine the accuracy of every relationship (4,999 randomizations) between the two data sets. The sum of all canonical eigenvalues was used to build the F ratio statistic (Legendre and Anderson 1999). The relationship between the two data sets was considered significant when $p < 0.01$ (adjusted for multiple comparisons by the Holm's method; Legendre and Legendre 1998). A forward stepwise procedure was performed to detect the main physicochemical variables affecting soil bank seed species composition (see Martinez-Duro et al. 2010 for more details). Ordination analyses were performed using CANOCO v.4.

Results

A total of 10,998 seedlings (7,703 from 0–5 cm depth and 3,295 from 5–10 cm) grew from the 240 seed bank samples. Seventy-seven species were recorded: 13 gypsophytes (five annuals and eight perennials), 49 annual gypsovags, and 15 perennial gypsovags. Average seed density was 11,670 seeds/m^2 (of which 8,173 occurred in the 0–5 cm deep samples and 3,497 in the 5–10 cm deep samples). Most species (90%) had seeds at both depths, and 68% of species in the seed bank were recorded growing aboveground. We recorded 131 species aboveground. The most frequent species in the soil seed bank were annual gypsovags, such as *Bromus rubens*, *Asterolinon linum-stellatum*, *Trisetum loeflingianum*, and *Crucianella angustifolia*; and annual gypsophytes, such as *Campanula fastigiata*, *Chaenorhinum reyesii*, and *Reseda stricta*. Some perennial gypsophytes were mostly represented in the aboveground vegetation, such as *Centaurea hyssopifolia* and *Gypsophila struthium*, but were less abundant in the soil seed bank (see Supplementary materials 2 and 3).

Above- and belowground species richness were significantly correlated (Spearman's rho = 0.66; $p = 0.0005$). Time since abandonment had no significant effect on species richness in any of the three community components studied (Fig. 1) and did not explain any of the richness or density parameters in either soil seed bank layer (Table 1). The main variables explaining seed bank richness or density were soil texture, slope, and

conductivity. Slope had a negative effect on total richness and total density, explaining nearly 30% of the variation in seed species richness and total density. Increasing soil fine texture reduced total richness and gypsophyte density. Conductivity explained 23.5% of the variance in gypsophyte richness.

Mantel tests showed high correlations between seed bank species composition at 0–5 and 5–10 cm deep, 70% of species being shared; as well as between aboveground vegetation and both seed bank layers, 55–64% of species being shared. Neither of the seed bank layers showed a significant correlation with time since abandonment in terms of species composition, showing that time had no significant effect on seed species composition during succession (Table 2a). Partial Mantel tests showed that the correlation between aboveground vegetation and seed bank species composition remained almost constant after allowing for the effect of time (Table 2b). Mantel correlograms did not detect any significant autocorre-

lation in seed species composition between different aged plots, except for a single case of aboveground vegetation (Fig. 2), suggesting a very weak temporal autocorrelation of species composition.

The forward stepwise selection of the environmental variables considered in the ordination analyses (RDA) showed that neither time nor its quadratic term explained any significant fraction of the variation in seed bank species composition ($F = 1.16$; $p = 0.23$). In fact, many of the strict gypsophyte species were already detected at the early stages of succession both in the seed bank and in the aboveground vegetation (see Supplementary material 2). Nevertheless, slope and calcium content together explained a significant fraction of the species composition variation at the 0–5 cm deep seed bank level (Fig. 3), with most species associated with lesser slopes. Seeds of *Chaenorrhinum reyesii*, *Reseda stricta*, and *Koeleria vallesiana* subsp. *castellana* were more common in soils with higher calcium concentrations and seeds of other species such as *Odontites longiflora*, *Erophila* sp. and *Cerastium* sp. were more common in soils with lower calcium contents.
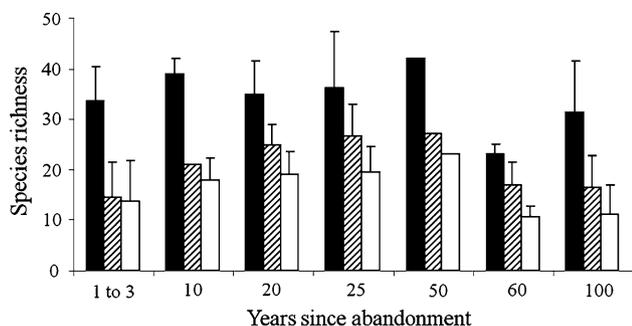

Fig. 1 Average species richness and standard deviation in different aged plots. *Black bars* aboveground vegetation. *Stripped bars* seed bank 0–5 cm deep. *White bars* seed bank 5–10 cm deep. For the class 50 years, there was only one stand

Discussion

Time since field abandonment did not influence seed bank species richness or seed species composition in these semi-arid gypsum habitats. Our results are not typical of Mediterranean seed banks (but see Figueroa et al. 2004 regarding Mediterranean scrublands), and differ from most results in other abandoned field systems (Falinska 1999) and in closely related Mediterranean grasslands (Levassor et al. 1990), where seed bank species richness decreased over time. Our findings also differ

Table 1 Parameters and fitting values of the reduced generalized linear models built after the forward selection analysis for four response variables

	Coef. (SE)	t	df	Res. dev.	D^2	F
Total richness						
Null			23	1,321.3		
Intercept	39.81 (5.52)	7.216***				
Slope	−0.36 (0.17)	−2.123*	22	931.7	0.295	10.98**
Silt	−0.70 (0.30)	−2.293*	21	745.2	0.436	5.26*
Gypsophyte richness						
Null			23	78.96		
Intercept	−7.799 (4.948)	−1.576				
Conductivity	0.006 (0.002)	2.601*	22	60.39	0.235	6.765*
Total density						
Null			23	2770919		
Intercept	705.35 (101.32)	6.962***				
Slope	−23.72 (7.78)	−3.047**	22	1948614	0.297	9.284**
Gypsophyte density						
Null			23	148059		
Intercept	265.59 (75.42)	3.522**				
Fine sand	−3.84 (1.50)	−2.551*	22	114255	0.228	6.509*

D^2 adjusted value is the equivalent of r^2
Coef. regression coefficient for each variable, *SE* standard error, *t* t statistic to test if the coefficient is different from zero, *df* residual degrees of freedom, *Res. dev.* residual deviance, *F* F statistic to test the fit of the model after introducing each variable
Significance is indicated at * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$

Table 2 Mantel tests and partial mantel tests for pairwise comparisons of aboveground vegetation, seed bank 0–5 cm deep, seed bank 5–10 cm deep, and time since abandonment of the 24 sampled plots

(a) Mantel tests

	Aboveground vegetation	Seed bank 5–10 cm deep	Time since abandonment
Seed bank 0–5 cm deep	0.6357 ***	0.7049***	0.16 n.s.
Seed bank 5–10 cm deep	0.5452***	–	0.15 n.s.

(b) Partial Mantel tests

	Aboveground vegetation	Seed bank 5–10 cm deep	Aboveground vegetation	Seed bank 5–10 cm deep
Covariable matrix	*Time since abandonment*	*Time since abandonment*	*Seed bank 5–10 cm deep*	*Aboveground vegetation*
Seed bank 0–5 cm deep	0.624***	0.6976***	0.423***	0.5537***
Seed bank 5–10 cm deep	0.5310***			

Vegetation and seed bank matrices were log + 1 transformed and each distance matrix was built using the Bray–Curtis index. Time since abandonment matrix was built using Euclidean distances. *p* value obtained after 5,000 permutations. *** $p < 0.00025$
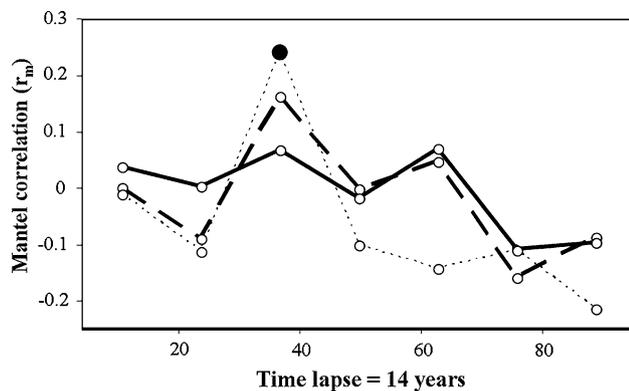*ns* not significant

Fig. 2 Mantel correlogram for the 24 plots sampled. Time lapse used was 14 years. *Thick line* seed bank 0–5 cm deep; *dashed thick line* seed bank 5–10 cm deep, *dashed thin line* aboveground vegetation. Significance was adjusted by means of the Holm's method. *Empty circles* not significant; *filled circle* significant correlation ($p = 0.01$). r_m Mantel correlation index

from those in semiarid Mediterranean forest seed banks (Ne'Eman and Izhaki 1999), where richness increased during succession. Nevertheless, our results were not unexpected because previous studies by Martinez-Duro et al. (2010) had shown that the aboveground vegetation composition in this semi-arid gypsum system was only slightly affected by time during succession. This did not match with other studies in which primary dynamics on gypsum quarries have been described as a typical replacement process (Mota et al. 2003; Dana and Mota 2006) with some peculiarities such as those related with the significant dominance of a genuine perennial gypsophyte, *Gypsophila struthium,* in the earlier stages.

Seed bank richness was relatively high, 77 species, especially considering that our results only reflected the persistent seed bank and not the transient one. However, our seed bank densities were in the middle range of those recorded in arid and semi-arid ecosystems (García-Fayos et al. 1995; Gutiérrez et al. 2000; Caballero et al. 2003). In other studies, seed bank diversity usually follows a humped distribution with increasing disturbance, with the richest seed banks often found in the most disturbed habitats (Grime 1979), and the lowest in more stable environments and during the pioneer stages of succession (Touzard et al. 2002). Our abandoned fields did not seem to follow this pattern, and time did not significantly affect species richness or seed bank density (see the attenuated hump-shaped trend of species richness during succession; Fig. 1). The moderate values of seed densities in our fields compared to other studies (see
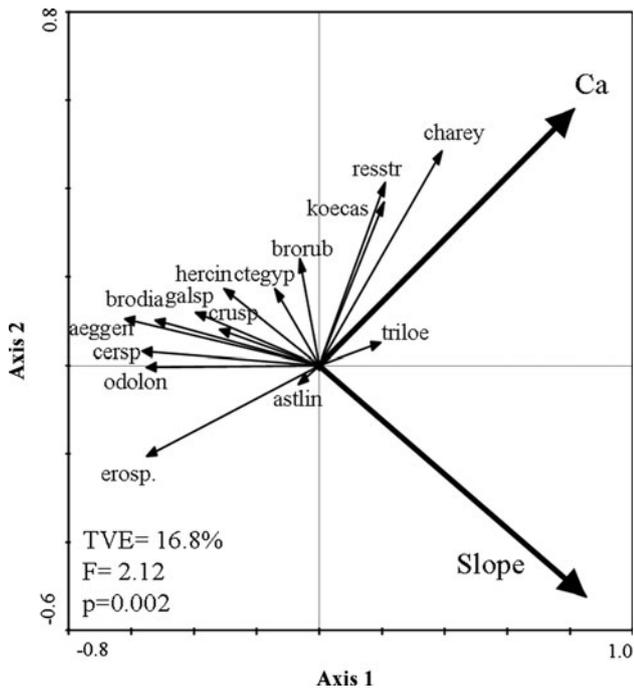
Fig. 3 RDA biplot with seed bank 0–5 cm deep as the main matrix and the two significant environmental variables obtained after a forward stepwise analysis (slope and calcium). Only the 16 most abundant species are represented in this figure. *TVE* total variance explained, *F* F ratio; aegova: *Aegilops geniculata*, astlin: *Asterolinon linum stellatum*, brodia: *Bromus diandrus*, brorub: *Bromus rubens*, campsp: *Campanula* sp., cersp.: *Cerastium* sp., charup: *Chaenorrhinum reyesii*, ctegyp: *Ctenopsis gypsophila*, crussp: *Crucianella* sp., erosp.: *Erophila* sp., galsp.: *Galium*, hercin: *Herniaria cinerea*, koecas: *Koeleria vallesiana subsp castellana*, odolon: *Odontites longiflora*, resstr: *Reseda stricta*, triloe: *Trisetum loeflingianum*

García-Fayos et al. 1995; Gutiérrez et al. 2000; Caballero et al. 2003) were probably due to the restricted plant productivity typical of gypsum soils. The soil seed bank at our study site was especially rich in annual gypsovags, most of which were nominally weeds, i.e., non-agricultural plants associated with cropland. This may partially explain why the original gypsum vegetation recovered so quickly after field abandonment, since most of these annual gypsovags that comprise so important a part of gypsum communities were already present as weeds in the croplands (Supplementary material 2). This result also mirrors other studies of semi-arid and arid systems, where perennial species made only a small contribution to richness and diversity (Gutiérrez et al. 2000; Caballero et al. 2003).

We found a high correlation between the species composition above- and belowground in the seed bank layers. Furthermore, this resemblance remained constant during succession. Our results suggest that the close relationship between above- and belowground species composition found in other studies at small spatial and temporal scales (the "spiral dynamics model"; see Caballero et al. 2008) was also maintained over the longer time scales evaluated in our study. These results highlight the comparative peculiarity of the semi-

arid gypsum system compared to most other systems, where the similarity between above- and belowground species composition decreases during secondary succession (see Kalamees and Zobel 1998; Wagner et al. 2003).

These results also conform to our previous findings regarding the development of aboveground vegetation during secondary succession in the same study area (Martinez-Duro et al. 2010). In these studies, we found that time since abandonment had almost no effect on the plant assembly on inhospitable soils. Specialized species appeared early in the first stages of secondary succession and the genuine gypsophyte community was rapidly established independently of the time since abandonment. In the prior study, we also recorded the maximum aboveground species richness soon after abandonment and observed no substantial changes in species composition as succession progressed. The sample plots were located far from other gypsophilous plant communities that might act as sources of propagules, and these species are not usually long-distance dispersers. We therefore conclude that time since abandonment has no effect on species richness, densities, and composition in the community studied because: (1) the existence of a plentiful and stable seed bank allows rapid recolonization by suitable species; and (2) it may be that many annual gypsovags are able to persist as "weeds" in nearby cropland and be available for colonization thanks to their ability to cope with a wide range of environmental conditions.

Although time since abandonment had little effect on these communities, topography and soil characteristics at small scale were major factors affecting richness and density of the soil seed bank in our study. Increasing slope had a negative effect on total diversity and density, highlighting the relevance of run-off processes as a key factor in distributing seeds in the soil. Run-off may therefore affect not only seed density but also total seed richness in arid landscapes. Our results highlight the consistent effect of run-off in the succession process beyond its effect on well-conserved areas studied elsewhere (see García-Fayos et al. 1995 and Caballero et al. 2003). Despite this, slope did not affect gypsophyte richness or density, probably because of their mucilaginous seeds and ability to anchor firmly onto the soil surface after primary dispersion (Escudero et al. 1997). As expected, salt concentration (conductivity) was highly and positively correlated to gypsophyte richness in the seed bank, and the presence of a sandy soil texture negatively affected gypsophyte seed species richness and abundance. These effects may simply reflect the preference of gypsophyte vegetation for the high salinity and fine textures typical of gypsum soils.

In conclusion, our results showed that the seed bank and aboveground vegetation were closely related over time. Although the composition and density of soil seed banks are crucial for community dynamics in inhospitable soils, seed bank features were not determined by the time elapsed since disturbance. In these ecosystems, there is an early persistent seed bank that drives the first

stages of secondary succession. Changes in the seed bank characteristics were driven mainly by changes in the abiotic chemical and physical soil environment, which in turn were most likely driven by changes in the composition of the aboveground vegetation. This pattern agrees with our previous studies on aboveground vegetation recovery (Martinez-Duro et al. 2010) and gives support to our "spiral dynamics model" connecting community components both above- and belowground (Caballero et al. 2008). Taken together, our results suggest that the recovery of gypsum habitats occurs naturally after crop abandonment, without the need for seeds from external sources, and most likely achieves the mature stages of succession after a relatively short time. This is particularly relevant since these habitats are extremely threatened, and also because habitat fragmentation is the most serious threat to some of their most outstanding plant species (Matesanz et al. 2009).

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