Seed bank structure along a semi-arid gypsum gradient in Central Spain

I. Caballero[a], J.M. Olano[b,*], J. Loidi[a], A. Escudero[c]

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

Abstract

The aim of this paper is to evaluate seed bank density and composition along a semi-arid gypsum gradient in Central Spain. Seed bank density was relatively high (16,214 seed/m^2) with a very clumped spatial distribution. Landform and microslope were the best predictors for seed density, indicating that density can be at least partly interpreted as a result of the physical processes regulating secondary dispersal. A high number of species appeared in the seed bank (68) being most of them annual gypsophytes. A relevant feature is that three widely distributed perennial gypsophytes occurred among the 10 more abundant species (*Helianthemum squamatum*, *Lepidium subulatum* and *Sedum gypsicola*). Presence of perennial among the most frequent species of the seed bank is not a shared characteristic with other arid and semi-arid systems. CCA model suggested that vegetation bands, microslope and vegetation perennial cover were factors shaping the composition of the seed bank.

1. Introduction

Seed bank enables plant populations to maintain their genetic variability, withstand adverse periods and persist through time (Harper, 1977; Baskin and

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*Corresponding author. Tel.: +349-751-29485.

E-mail address: jmolano@agro.uva.es (J.M. Olano).

Baskin, 1978; Grime, 1979; Templeton and Levin, 1979). It has been postulated that this biological trait is favourable in habitats where environmental conditions change dramatically and with unpredictable time patterns (Venable and Brown, 1988; Bonis et al., 1995). Plant communities of most arid and semi-arid regions, including those from large areas in the Mediterranean Basin, should be good candidates for the maintenance of important seed banks. This prediction has been widely confirmed, especially among their rich and heterogeneous annual plants community guilds (Inouye et al., 1980; Kemp, 1989, pp. 257–281; Levassor et al., 1990; Russi et al., 1992). In fact, the density and richness of seed banks occurring in these habitats range among the largest in the world (Leck et al., 1989), despite the sparse and usually patchy structure of plant above-ground biomass and cover of these ecosystems.

The relevance of seed bank as shaping factors of arid and semi-arid ecosystems has been long highlighted and intensively studied (Brown et al., 1979; Kemp, 1989). This research effort has involved a wide array of topics including density and composition measurements (Parmenter and MacMahon, 1983; Pugnaire and Lázaro, 2000), spatial patterns (Aguiar and Sala, 1997; Moro et al., 1997a; Marone et al., 1998), time patterns (Price and Joyner, 1997; Mayor et al., 1999), age structure (Moriuchi et al., 2000), dispersal and post-dispersal movements (Harrington and Driver, 1995; Marone et al., 1998), and seed predation control (Gutiérrez et al., 1997; Mandujano et al., 1997; Anderson and MacMahon, 2001). Even more, attempts have been conducted in these environments to establish appropriate links between seed bank and emergence and recruitment (Inouye, 1980; Cabin and Marshall, 2000) and to evaluate the evolutive role of seed banks in population dynamics and viability (Cabin, 1996; Cabin et al., 1998; Turelli et al., 2001).

Surprisingly, the knowledge of seed bank structure and composition in gypsum (hydrous calcium sulphate) environments remains extremely low, in spite of gypsophytes representing one of the most conspicuous and diversified set of arid endemic plants (Parsons, 1976; Powell and Turner, 1977; Meyer, 1986; Meyer and García-Moya, 1989; Escudero et al., 1999, 2000). Gypsum communities almost exclusively occur in gypsum outcrops under arid or semi-arid climates. Despite gypsisols, which are characterized by a gypsum content over 5%, extend over 1 million km^2 in the world (Verheye and Boyadgiev, 1997) and 35,000 km^2 (7%) in Spain (Riba and Macau, 1962), they have received remarkably little study (Meyer, 1986; Meyer et al., 1992; Escudero et al., 1999, 2000; Guerrero-Campo et al., 1999a, b). Furthermore, most of these plants conform a global biodiversity priority because most of them are narrowly distributed and seriously threatened (Meyer, 1986). In this sense, Mediterranean gypsum ecosystems are considered one of the most threatened habitats in the Mediterranean Basin (Gómez-Campo, 1987; European Community, 1992).

The aim of this research is to gain knowledge about seed bank structure and composition of gypsum environments in semi-arid central Spain. The possibility of extrapolating seed bank features of semi-arid regions to gypsum systems faces enormous difficulties due to the specialized behaviour of gypsophytes (Meyer, 1986; Escudero et al., 2000). With this in mind we address some basic questions: What is

the density and composition of the seed bank in gypsum systems? Which factors determine seed bank density? Which factors affect seed bank composition? Sharp changes in soil conditions in gypsum outcrops (Rubio and Escudero, 2000) conforms a very clear community gradient with conspicuous vegetation bands (Rivas-Martínez and Costa, 1970; Izco, 1974; Casas et al., 1989). The combination of different geomorphologic units in gypsum gradient landscapes and vegetation elements determines the existence of contrasting scenarios. So, which are the characteristics of seed bank within each of them?

2. Methods

2.1. Study site

The study was carried at Espartinas, a site close to Ciempozuelos, approximately 40 km south of Madrid, in Central Spain (40°11′N, 3°36′W, 570 m a.s.l.). The climate is upper semi-arid mesomediterranean (Rivas-Martinez and Loidi, 1997), with an annual rainfall of 415 mm, but with almost no rainfall in summer. Mean daily minimum and maximum temperatures in January are 9.6°C and 0.6°C, respectively, and 32.7°C and 15.4°C in July. The soils are classified as Calcic Gypsisols, developed over gypsum parental rocks (Monturiol and Alcalá del Olmo, 1990).

According to Rivas-Martínez and Costa (1970), three main community bands can be distinguished along the surveyed gypsum system: a perennial tussock community (*Limonio-Lygeetum spartii*) in the bottom flats and lower piedmont, a narrow and dense shrub community (*Artemisio herba-alba-Frankenietum thymifoliae*) in the middle piedmont, and a sparse shrub community dominated by genuine gypsophytes, occurring from the upper piedmont to the summit (*Gypsophylo struthii-Centaureetum hyssopifoliae* in the steeper slopes and *Herniario fruticosae - Teucrietum pumili* in the summit crests).

2.2. Sampling design

Sampling was performed in September 2001, just after all seeds had been shed and prior to autumn emergence. The timing of emergence does not allow to separate permanent from transient seed bank, but this seed bank is the most relevant to shape vegetation structure and composition. As our main goal was to evaluate seed bank features along a gypsum landscape, we established seven transects, running from the top of the ridge to the bottomland, perpendicular to the maximum slope and southern oriented. Quadrates (50×50 cm^2) were spaced every 2.5 m, so the number of quadrates per vegetation band reflects the size of the corresponding community within each transect. In the centre of each quadrate five soil cores ($\varnothing$ 1.85 cm) were extracted and merged. Soil cores were only 3 cm in depth, since, according to Chields and Goodall (1973), the first 2 cm accumulate most of the seed bank in arid environments. Perennial cover as a percentage, microslope (slope of the quadrate)

measured with a Suunto PM-5 clinometer on the ground and in the centre of each quadrate, macroslope measured on a 2-m wooden frame located on the ground, and height with respect to the first quadrate in each transect. Total number of quadrates was 188 and the total area cored was $0.253 \, \text{m}^2$.

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

The resulting soil samples were laid in $10 \times 10 \, \text{cm}^2$ plastic cells in a greenhouse. In order to improve the hydraulic conditions of the soil obtained after this procedure, a sterile substratum of vermiculite and peat (2:1) was provided and thoroughly mixed until a 1 cm depth was reached. Ten cells were filled only with the sterile mixture and located in the greenhouse to detect any contamination. As soon as a seedling emerged, it was identified and removed. When identification at the species level, was not feasible, seedlings were transplanted into individual pots and allowed to grow until identification was possible. After 5 months, the soil in the cells was regularly crumbled in order to enhance emergence during 3 months. Finally, the cells were watered with a gibberellic acid (GA_3) solution (1000 p.p.m.) to complete the data set and emergence monitored for another 2 months (16% of emerged seedlings).

2.3. Numerical analysis

A GLM model for total seed counts per quadrate was built assuming a Poisson distribution of errors and a logarithmic link function (McCullagh and Nelder, 1989). We chose GLMs instead of linear regressions because their capability to handle a larger class of distributions for the response variable. In our case the selected distribution was Poisson, although we have conducted a quasi-likelihood approach to overcome possible difficulties due to overdispersion. Several dummy variables (0, 1) were considered to deal with landform classes (piedmont, slope and summit) and for vegetation bands (*Artemisio-Frankenietum* band, *Limonio-Lygeetum* band and *Gypsophilo-Centaureetum* band which included the *Herniario-Teucrietum* fragments of the summit zones). These, together with four continuous variables (height, microslope, macroslope and perennial vegetation cover per quadrate), were considered in a forward stepwise procedure. Only variables explaining a significant amount of deviance were included in the statistical model. The change in the deviance was tested by the *F*-ratio test. Analyses were conducted with S-Plus 2000.

Lately, the evaluation of the relative importance of different parameters (vegetation band, landform and environmental parameters) on the seed bank composition was evaluated using constrained ordinations (ter Braak, 1986). These techniques allow for checking hypotheses concerning the relationships among a multivariate data matrix (i.e. seed bank composition) and an environmental data matrix (i.e. measured parameters) (ter Braak and Prentice, 1988; Legendre and Legendre, 1998). Our null hypothesis is that the seed composition is independent of

those control variables. In order to select the appropriate ordination technique the number of seeds matrix (species × quadrates) was submitted to a detrended correspondence analysis (DCA), with detrending by segments and non-linear rescaling of the axes. Since the length of the extracted gradients of the seed data was higher than 3 standard deviation units (4.85 S.D.), we followed the recommendations of ter Braak (1986) and we conducted a canonical correspondence analysis (hereafter CCA).

The constraining matrix was conformed by several dummy variables (three variables for landform and three for vegetation) and four environmental parameters (microslope, macroslope, height and vegetation cover). In order to avoid multi-collinearity problems, one dummy per set was released. The total variation explained (TVE) was calculated as the relation between the trace and the sum of all canonical extracted axes (Borcard et al., 1992).

A Monte Carlo permutation test was performed to determine the accuracy of the relationship (999 randomizations) between the two data sets. The sum of all canonical eigenvalues or trace was used to build the F-ratio statistic (ter Braak, 1986). Only when $p < 0.05$, adjusted for multiple comparisons by the Bonferroni correction (Legendre and Legendre, 1998), the relationship between the two data sets was considered significant. If the CCA model was significant, a forward stepwise procedure was carried out to select a reduced model including only significant variables for each matrix. Improvement of the reduced model with each new selected variable was determined by a Monte Carlo permutation test with 999 randomizations. These analyses were conducted using CANOCO for Windows v. 4.0 (ter Braak and Smilauer, 1997).

3. Results

3.1. Seed density

A total of 4102 seedlings, belonging to at least 68 species, were detected. Average density of seeds was 16,214 seed/m². Most of the emerged seedlings (78%) were identified at species level. From the rest 5% were assigned to a genus and 702 seedlings (17%) were recorded as either dicots or monocots. Among quadrates distribution of seed density was binomial, being relatively rare intermediate values (Fig. 1).

Seed density was affected by landform ($\chi^2 = 21.896$, $df. = 2$, $p < 0.0001$; summit $n = 35$, $x = 12,624$ seed/m²; slope $n = 74$, $x = 11,169$ seed/m²; piedmont $n = 79$, $x = 22,537$ seed/m²), being higher for piedmont than for summit ($U = 925$, $p < 0.005$) or slope ($U = 1670.5$, $p < 0.0001$). Similarly, seed density showed significant differences among vegetation bands ($\chi^2 = 12.553$, $df. = 2$, $p < 0.002$; *Gypsophilo-Centaureetum* band $n = 136$, $x = 14,175$ seed/m²; *Artemisio-Frankenietum* band $n = 19$, $x = 21,616$ seed/m²; *Limonio-Lygeetum* band $n = 33$, $x = 21,534$ seed/m²).
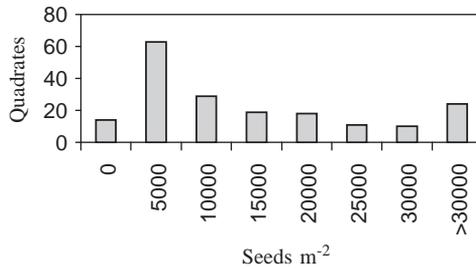
Fig. 1. Seed densities per quadrate. Number in abscises indicates seed number class upper value.

When all the parameters were considered together, the number of seeds was significantly related to microslope (coefficient -0.061 ± 0.01) and with two dummy landscape variables, piedmont (0.024 ± 0.19) and summit zone (-0.779 ± 0.26). A model including these three variables was highly significant and explained 25.7% of the deviance (Table 1).

3.2. Seed bank composition

The most frequent species are generalist annual plants or gypsovags sensu Meyer (1986), such as *Asterolinon linum-stellatum* (L.) Duby (55%), *Campanula erinus* L. (43%) and *Vulpia unilateralis* (L.) Stace (42%). Among genuine gypsophytes, the most frequent species are also annuals, such as *Campanula fastigiata* Dufour *ex* A. DC. (37%), *Chaenorhinum reyesii* (C. Vicioso and Pau) Benedí (33.5%) and *Centaurium gypsicola* (Boiss. and Reuter) Ronninger (29%). The most abundant perennial plants are also strict gypsophytes such as *Helianthemum squamatum* (L.) Pers. (20%), *Sedum gypsicola* Boiss. and Reuter (18%) and *Lepidium subulatum* L. (16.5%).

The distribution per vegetation band of the 24 most frequent species ($> 5\%$) showed that many of them preferentially accumulate their seeds in some vegetation band (33%, $p < 0.001$, see Table 2). The reduced CCA model (Table 3) selected five variables ($p < 0.01$): *Limonio-Lygeetum* band, microslope, vegetation cover, summit and macroslope. Drop in TVE in relation to the saturated model (eight variables) was only 2.4% (TVE $= 12\%$, F-ratio $= 5.93$; $p < 0.001$).

4. Discussion

Seed bank density in our studied gypsum system (16,214 seed/m^2 in average) is in the middle range of arid and semi-arid ecosystems (Reichman, 1984; Coffin and Lauenroth, 1989; García-Fayos et al., 1995; Lyaruu and Backéus, 1999; Cabin and Marshall, 2000; Gutiérrez et al., 2000). In any case this data must be taken with caution since it may correspond, at least partially, to a transient bank. The spatial distribution of seed density is also highly variable (Fig. 1), showing remarkable differences among, but also within, vegetation bands and landform units. This

Table 1
Seed counts per square meter at each vegetation band and in total

	Family	Bio type	Gypso.	Freq. (%)	Gyp.-Cent. band	Art.-Frank. band	Lim.-Lyg. band
*Asterolinon linum-stellatum**	Linaceae	A		55	2129	2579	675
*Campanula erinus**	Campanulaceae	A		43	2288	2345	1823
*Vulpia unilateralis**	Poaceae	A		43	1747	2853	1688
Campanula fastigiata	Campanulaceae	A	Yes	37	1141	781	833
Chaenorhinum reyesii	Scrophulariaceae	A	Yes	34	623	703	360
Galium sp.	Rubiaceae	A		29	557	1837	1125
Centaurium gypsicola	Primulaceae	A	Yes	29	639	665	675
*Helianthemum squamatum**	Cistaceae	P	Yes	20	322	118	0
Filago pyramidata L.	Asteraceae	A		19	306	274	22
*Sedum gypsicola**	Crassulaceae	P	Yes	18	551	39	0
Lepidium subulatum	Brassicaceae	P	Yes	16	311	156	0
*Reseda stricta**	Resedaceae	A	Yes	15	109	274	653
Teucrium sp.	Lamiaceae	A		12	284	313	90
Frankenia thymifolia Desf.	Lamiaceae	P	Yes	12	60	3244	22
Plantago afra L.	Plantaginaceae	A		11	125	118	45
Herniaria cinerea DC.	Caryophyllaceae	A		10	164	430	225
Stellaria media *	Caryophyllaceae	A		10	28	352	337
*Desmazeria rigida**	Poaceae	A		8	49	352	405
Euphorbia sulcata De Lens ex Loisel.	Euphorbiaceae	A		7	44	78	112
Trisetum loeflingianum (L.) C. Presl	Poaceae	A		7	66	118	90
Vulpia ciliata Dumort.	Poaceae	A		7	148	234	68
Lithospermum apulum (L.) Vahl	Boraginaceae	A		6	38	0	135
*Polypogon maritimus**	Poaceae	A		6	5	0	3915
Helianthemum salicifolium (L.) Miller	Cistaceae	A		6	38	78	45
Cerastium sp.	Caryophyllaceae	A		5	66	39	675
Centaurea melitensis L.	Asteraceae	A		4	16	196	68
Sagina apetala Ard.	Caryophyllaceae	A		4	33	78	1260
Crepis capillaris (L.) Wallr.	Asteraceae	A		4	11	39	112
Parapholis incurva	Poaceae	A		4	0	78	293
Thesium divaricatum Jan ex Mert. and Koch	Santalaceae	A		4	55	39	0
Erodium malacoides (L.) L'Hér.	Geraniaceae	A		3	11	118	22
Plantago coronopus L.	Plantaginaceae	A		3	22	39	22
Sherardia arvensis L.	Rubiaceae	A		3	16	0	383
Erophila verna (L.) Chevall.	Brassicaceae	A		3	22	78	22
Linaria glauca (L.) Chaz	Scrophulariaceae	A	Yes	3	28	0	22
Blackstonia perfoliata (L.) Hudson	Primulaceae	A		2	5	0	180
Bromus rubens L.	Poaceae	A		2	16	39	0
Hymenolobus procumbens (L.) Nutt. ex Torrey and A. Gray	Brassicaceae	A		2	16	0	68
Medicago minima (L.) Bartal.	Fabaceae	A		2	16	0	0
Arenaria leptoclados (Reichenb.) Guss.	Caryophyllaceae	A		1	0	0	68
Centaurea hyssopifolia *Vahl*	Asteraceae	P	Yes	1	11	39	0
Erodium cicutarium (L.) L'Hér.	Geraniaceae	A		1	11	0	0
Liliaceae				1	11	0	0
Teucrium capitatum L.	Lamiaceae	P		1	11	0	0
Valerianella coronata (L.) DC.	Valerianaceae	A		1	11	0	0
Anagallis arvensis L.	Primulaceae	A		1	0	0	68
Arabis auriculata Lam.	Brassicaceae	A		1	5	0	0
Arabis parvula Dufour	Brassicaceae	A		1	0	0	22
Artemisia herba-alba Asso	Asteraceae	P		1	5	0	0
Asteraceae				1	5	0	0
Caryophyllaceae				1	0	78	0
Euphorbia falcata L.	Euphorbiaceae	A		1	5	0	0

Table 1 (*continued*)

	Family	Bio type	Gypso.	Freq. (%)	Gyp.-Cent. band	Art.-Frank. band	Lim.-Lyg. band
Helianthemum hirtum (L.) Miller	Cistaceae	P		1	11	0	0
Heliotropium supinum L.	Boraginaceae	A		1	5	0	0
Leontodon taraxacoides (Vill.) Mérat	Asteraceae	A		1	5	0	0
Lithospermum arvense L.	Boraginaceae	A		1	0	0	22
Lophochloa cristata (L.) Hyl.	Poaceae	A		1	0	0	22
Polygala monspeliaca L.	Polygalaceae	A		1	11	0	0
Scabiosa stellata L.	Dipsacaceae	A		1	5	0	0
Scleranthus verticillatus Tausch	Caryophyllaceae	A		1	5	0	0
Veronica arvensis L.	Scrophulariaceae	A		1	0	0	45
Brassicaceae				1	0	39	0
Unidentified 1				1	0	78	0
Unidentified 2				1	44	0	0
Unidentified 3				2	45	0	22
DICOT				46	1245	1173	968
MONOCOT				38	623	1524	3825

Asterisk (*) indicates significant deviance ($p < 0.05$), with Bonferroni correction, from equal distribution among vegetation bands, based on a Kruskal–Wallis test (only for species with frequencies higher than 5%). *Biotype* indicates annual (A) or perennial (P) species; *gypsophyte* indicates if the species is restricted to gypsum outcrops; *Freq* indicates percentage of quadrates where the species occurs. *Gyp.-Cent.*, *Art-Frank* and *Lim-Lyg.* band indicates seed density per square meters in each of the vegetation bands. *Galium* sp. includes *G. murale* (L.) All. and *G. parisiense* L., *Cerastium* sp. includes *C. glomeratum* Thuill. and *C. pumilum* Curtis, *Liliaceae* includes two different taxa. Species are ranked according to their frequency.

Table 2
Analysis of deviance for total number of seeds

Model	Coefficient	Deviance	df.	Change in deviance	F	p
Null		4609.77	187			
+ Piedmont	0.024 ± 0.19	4199.01	186	410.76	19.64	< 0.0001
+ Microslope	-0.061 ± 0.01	3603.69	185	595.32	28.46	< 0.0001
+ Summit	-0.779 ± 0.26	3421.57	184	182.11	8.70	0.003

The level of significance refers to the change in deviance associated with the addition of the corresponding term.

spatial heterogeneity is also a typical feature of most arid systems (Kemp, 1989; Aguiar and Sala, 1997).

Accordingly, landform variables are selected among the best predictors in the GLM model. Consequently, seedling counts per quadrate might be interpreted as a result of physical processes regulating secondary dispersal and subsequent accumulation on the flattest bottom areas (piedmont has a significant positive coefficient, whereas summit negative). Relevance of run-off processes has been found in other gradient systems such as in Iberian semi-arid badlands (García-Fayos et al., 1995). The model for seedling counts per quadrate was completed with the significant inclusion of microslope. Its negative coefficient also suggested the relevance of

Table 3
Results of the stepwise CCA forward selection procedure using log-transformed seed counts

	Parameter	λ	Frat	P
Step 1	*Limonio-Lygeetum band*	0.26	7.95	0.001
Step 2	Microslope	0.16	4.86	0.001
Step 3	Vegetation cover	0.12	3.86	0.001
Step 4	Summit	0.09	2.80	0.002
Step 5	Macroslope	0.08	2.65	0.006

Only significant selected variables are represented. λ indicates the eigenvalues; *Frat* is the *F*-ratio statistic and *p* is the significance level of the reduced model (999 randomizations).

run-off as a key factor for seed density in gypsum landscapes. A clumped seed bank pattern is a typical characteristic in most arid systems (Kemp, 1989; García-Fayos et al., 1995; Lyaruu and Backéus, 1999). Seeds tend to accumulate in specific microsites, such as small depressions or even in ant nests (Harper, 1977; Reichman, 1984; Harrington and Driver, 1995). Nevertheless, these shaping mechanisms for seed density should be taken with care because most gypsophytes and gypsovags have mucilaginous seeds (Escudero et al., 1997), so they tend to anchorage firmly after primary dispersion. Even more, run-off processes on massive gypsum soils, percentage of gypsum in our massive outcrops is above 40% (Rubio and Escudero, 2000), is a marginal geomorphologic process (Guerrero-Campo et al., 1999a). Differential productivity could be also behind our results, since preliminary data on annuals performance on each landform measured as surface cover at May (biomass peak), indicates a rather similar pattern ($\chi^2 = 4.87$, $df. = 2$, $p < 0.0001$; summit $n = 35$, $x = 4.8\%$; slope $n = 74$, $x = 6.2\%$; piedmont $n = 79$, $x = 10.6\%$). Similar results occurred among vegetation bands ($\chi^2 = 20.092$, $df. = 2$, $p < 0.0001$; *Centaureetum* band $n = 136$, $x = 6.5\%$; *Frankenietum* band $n = 19$, $x = 9.9\%$; *Lygeetum* band $n = 33$, $x = 12.5\%$).

The seed bank was very rich in species (68), especially if we take into consideration that only a relatively reduced soil surface was cored (0.253 m^2). Annual species were dominant, both in number and density (Table 2). This result matches another seed banks in arid ecosystems, where perennials play a secondary role (Coffin and Lauenroth, 1989; Moro et al., 1997b; Marone et al., 1998; Lyaruu and Backéus, 1999; Gutiérrez et al., 2000). Nevertheless, in our gypsum system; three perennial shrubs (*H. squamatum*, *L. subulatum* and *S. gypsicola*) occurred among the 10 more frequent species. These three plants are genuine gypsophytes and have been included among the characteristic species of *Gypsophiletalia*, a phytosociological order for the gypsum shrubby communities of the western Mediterranean Basin (Loidi and Costa, 1997; Boira et al., 2002). This means that these three plants are widely distributed among gypsum outcrops in a very large territory. Probably, their relatively geographical success lies on an efficient sexual reproduction, with very dense seed banks and including the existence of complementary aerial seed banks in the case of *H. squamatum* (Romão *per. comm.*). Contrarily, other gypsophytes such as *Teucrium pumilum* L., or *Koeleria castellana* Boiss. and Reuter predominantly follow

vegetative reproduction. On the other hand, the most relevant element of the bottom piedmont vegetation communities, *Lygeum spartum* L. does not exert soil seed banks. It successfully follows clonal growth as usually occurs on communities developed on relatively halophyllous and wetter soils.

Reduced CCA model explained a significant fraction of the seed composition. The first variable included in the stepwise procedure was the *Limonio-Lygeetum* vegetation band (Table 3). This clearly reflects the marked fidelity of some annuals to this vegetation band. Some of these elements are *Desmazeria rigida* (L.) Tutin, *Parapholis incurva* (L.) C.E. Hubbard, *Polypogon maritimum* Willd., *Reseda stricta* Pers., *Stellaria media* (L.) Vill. (see also Table 2). Strikingly, microslope was the second selected parameter. Thus, microslope not only determine significant changes in the number of seeds (see GLM model, Table 1), but also exerts a relative control in the composition of the local seed bank. This may be due to the fact that run-off does not affects in the same way to every species (Reichman, 1984; García-Fayos and Cerdá, 1997). Some mechanisms, such as the presence of mucilaginous seed coats or other anchorage mechanisms may easily explain a differential spatial accumulation. The effect of perennial cover in seed composition may also reflect a similar differential movement of seeds. Although some authors have pointed out accumulation of seeds under canopies (Moro et al., 1997b; Guo et al., 1998) or in relation to specific microhabitat characteristics (Guo, 1998; Pugnaire and Lázaro, 2000), we have not detected a similar effect but exclusively on seed composition. Finally, the inclusion of the summit zone as a dummy variable and macroslope probably is due to the existence of an exclusive annual plant community interspersed among the creeping chamaephytes of the *Herniario-Teucrietum pumili* which is confined to the flat summit zones. This community, which is composed by annual rare gypsophytes such as *Chaenorhinum reyesii* and *Campanula fastigiata* has been named, *Chaenorhino rubrifolii-Campanuletum fastigiatae* (Izco, 1974) and exclusively occurs on the thicker and harder crusted gypsum surfaces.

Gypsophytes play a relevant role in the seed bank, as much as 10 Iberian endemic species (see Table 1), some of them clearly endangered (Gómez-Campo, 1987), comprised as much as a quarter of the total seed bank. Our results show that seed bank composition and density sharply vary between vegetation bands and independently between landform zones. A deeper knowledge of the gypsum seed bank dynamics may be also crucial to develop appropriate management tools for this endangered ecosystem.

Acknowledgements

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