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Soil seed bank and seedling dynamics in badlands of the Upper Llobregat basin (Pyrenees)

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Abstract

In the badlands of the Upper Llobregat basin, vegetation is sparse and heterogeneous. The harsh conditions generated with the formation of the badlands involve a regressive succession. On the upper part of the slope, a sharp change can be seen between dense communities and denuded badland slopes. Nevertheless, recolonization of the badlands rarely occurs. Scarce seed availability or low capacity of seeds to germinate in such unfavorable conditions may be the main causes. The soil seed bank was sampled in two micro-catchments; a total of 105 soil cores were extracted along three parallel transects. Soil samples were washed through a set of sieves, and seeds were separated and identified. Seedling emergence and mortality were also recorded monthly from April 1990 to December 1991, on two permanent plots in a nearby micro-catchment. An unexpected soil seed bank was found. A relatively high species number has been found with rather small and slightly heterometric seeds. Strong relation between seed bank composition and established vegetation has been detected. Seedling emergence occurred mainly from May to August. The species composition was also dominated by the most frequent species in the badlands and in the soil seed bank. Seedling mortality does not appear to be directly associated with the erosive processes, as it occurred throughout the year. It seems that seedling survival rates could be sufficient to ensure persistence of the current vegetation in badland areas. We conclude that there is no single reason that can explain the low vegetation cover in badlands but rather there is a

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combination of several restrictive factors. Lack of seed availability within the reduced favorable period for germination and low seedling establishment contribute in part to this low colonization.

Keywords: Seed bank; Seedlings; Population dynamics; Badlands; Erosion; Pyrenees

1. Introduction

Badland areas can develop in a variety of climatic conditions and they are characterized by high erosion rates and a rather sparse vegetation cover (Bryan and Yair, 1982). Under humid climates, active badland forms have been described associated with unconsolidated or non-cemented materials prone to rapid weathering. In the Upper Llobregat basin, badlands are widespread and, although they occupy only small areas, they are the main fluvial sediment source in the basin (Clotet et al., 1988).

In this area, badland vegetation is sparse and dynamically related to that of the non-eroded neighboring zones (Guàrdia and Ninot, 1992). The unstability and harsh environmental conditions of the badland surfaces generate a regressive succession from the initial community, usually a mesoxerophilous pasture, to almost denuded slopes. On the upper part of the slope, a sharp change between these pastures and badland vegetation can be observed within a few meters, with an abrupt headcut of the gradient slope. Although this adjacent vegetation may act as a seed source, recolonization of badland areas rarely occurs. Factors explaining the scarcity of vegetation on badland areas are rather unknown. In badland areas of southeastern of Spain, in semiarid climatic conditions, García-Fayos et al. (1995) found that seed removal by erosion is not enough to explain this lack of recolonization, but this may be quite different in wetter areas, with high quantity and more intense rainfalls.

In the life history of plants, seed and seedling stages are particularly vulnerable to environmental conditions (Symonides, 1974; Harper, 1977, etc.). The processes occurring during these stages influence the structure of both adult populations and communities. Colonization of denuded areas depends initially on seed availability from surrounding vegetation. In general, seeds that arrive on exposed soil surfaces remain trapped where they initially land, move over the surface, or move vertically through the soil column. The type and distance of movement depends on characteristics of the soil surface, on the abiotic or biotic forces that act upon the seeds and on the interactions between the seeds and their environment (Sheldon, 1974; Peart and Clifford, 1987). Finally, the characteristics of the microsite in which seeds settle determine the probabilities of seed germination, seedling emergence and survival (Chambers and MacMahon, 1994).

Seed availability in badland areas of the Upper Llobregat basin may be guaranteed from the neighboring communities. If seed rain is not scanty, then overland flow and sediment transport may be the main cause of lack of recolonization of badland areas, as they may carry away the seeds that arrive on the soil surface and turn seed rain into deficient. Moreover, the severe environmental conditions that characterize badland areas (water stress and low fertility) may be an insurmountable handicap for establishment from seed.

The aim of this study was to obtain a detailed demography of the seed and seedling phases in the badland areas of the Upper Llobregat basin. We sought to test the hypothesis that seed availability and seedling recruitment was not enough to guarantee colonization of these areas.

2. Area description and methods

2.1. Study area

The study area is located in Vallcebre, in the Upper Llobregat basin, which represents a sub-Mediterranean edge of the Pyrenees. Most of the geological material is carbonated and corresponds mainly to the Pedraforca mantle Unit and the Cadí Unit. The badlands sampled develop in materials of Cretaceous age, in a lacustrine formation dominated by smectite-rich clays. Erosion rates estimated in the study area were about 9 mm per year (between 90 and 150 tm/ha/year; Clotet et al., 1988).

The altitude of the plots is about 1120 m a.s.l. and the climate is sub-Mediterranean in character. The mean annual temperature is 9.2°C, and the range between monthly averages is about 17°C. As for rainfall, the annual average is 850 mm with very irregular distribution through the year; there are two main peaks in spring and autumn, and also high intensity storms occurred at the end of the summer.

The most frequent communities neighboring badlands are pastures and Scots pine (*Pinus sylvestris*) forests, ranging from xerophilous to mesophilous types in relation to slope aspect and altitude. On the north-facing aspects, where this study was centered, the dominant vegetation consists of mesophilous, calcicolous pastures (*Seslerio-Aphyllanthetum*), frequently bearing an open layer of Scots pine. Only in the less exploited areas remnants of the deciduous oak forest (*Buxo-Quercetum pubescentis*) occur on southern aspects, and more dense pine forests on the upper north-facing slopes (*Polygalo-Pinetum sylvestris*; Carreras et al., 1994).

2.2. Methods

The soil seed bank was sampled in two plots located in two badland micro-catchments near Vallcebre. The plots sloped 35–40° to the NNW, and had a homogeneous light vegetation coverage of less than 20%. In each plot, three transects perpendicular to

Table 1
Mean soil seed bank density (seeds.m^2 ± SE) recorded in each topographic position of each micro-catchment sampled and the overall average

	Catchment 1	Catchment 2
Upper slope	1783.44 ± 805.68	837.12 ± 482.05
Backslope	2388.54 ± 982.82	1426.75 ± 986.70
Footslope	1104.03 ± 942.29	886.18 ± 713.53
Mean	1729.48 ± 946.88	1063.26 ± 827.147

the maximum slope gradient were installed on the upper part, the backslope and the bottom part of each badland slope. Soil cores (5 cm diameter, 10 cm depth) were extracted at 50 cm intervals along these transects, which have a length variable according to the dimensions of the corresponding micro-catchment (between 14 and 23 m). A total of 48 and 57 soil cores were extracted at the first and second plots, respectively. Plant species intercepted by the transect were also recorded. Samples were collected in October 1991, after the seed fall of most of the species in the badlands and after the heavy storms that usually occur at the end of summer.

The soil samples were sieved through a set of 1, 0.5 and 0.2 mm meshes, and seeds were sorted and counted under a stereoscopic microscope (magnification, 10–40 ×). Seeds obtained from the samples appeared to be intact, but because no germination tests were performed, viability can not be presumed. Seeds were identified with the help of a

Table 2
Species composition of the soil seed bank

Plant taxa	Seeds.m^{-2}	Samples (%)
Thymus vulgaris	461.68	24.0
Ptychotis saxifraga	273.24	22.6
Rumex cf. *scutatus*	127.39	4.2
Laserpitium gallicum	113.39	9.6
Caryophyllaceae	107.54	8.0
Silene sp.	89.07	10.0
Tussilago farfara	77.85	2.8
Pastinaca sativa	76.43	4.4
Achnatherum calamagrostis	66.74	5.6
Poaceae	63.69	2.1
Campanula speciosa ssp. *affinis*	61.34	9.4
Hieracium sp.	47.47	2.0
Asteraceae	45.07	6.0
Sanguisorba minor ssp. *minor*	42.46	2.1
Thymelaea tinctoria ssp. *nivalis*	41.45	4.1
Plantago maritima ssp. *serpentina*	40.70	6.2
Sesleria coerulea	37.14	3.7
Taraxacum officinale	34.37	4.2
Teucrium polium ssp. *aureum*	31.56	4.9
Chenopodiaceae	28.31	2.1
Globularia cordifolia	22.16	0.9
Onobrychis supina	18.20	1.1
Fabaceae	18.20	1.1
Jasonia tuberosa	14.15	1.1
Avenula pratensis ssp. *iberica*	14.15	1.1
Potentilla neumanniana	12.74	0.9
Odontites sp.	11.08	0.9
Leontodon sp.	11.08	0.9
Sedum sediforme	11.08	0.9
Fabaceae	18.20	1.1
Unidentified	39.14	22.9

The first column expresses mean seed density (seeds.m^{-2}) for all samples and the second column indicates the percentage of samples with each taxa out of all the soil samples.

Table 3
Species in the soil seed bank and species present in the transects clustered according to its distribution (soil seed bank, established vegetation or both; percentages are the averages of the two micro-catchments)

Seed bank and established vegetation (32.2%)
Achnatherum calamagrostis
Avenula pratensis ssp. *iberica*
Campanula speciosa ssp. *affinis*
Genista scorpius
Hieracium sp.
Laserpitium gallicum
Pastinaca sativa
Plantago maritima ssp. *serpentina*
Potentilla neumanniana
Ptychotis saxifraga
Sanguisorba minor ssp. *minor*
Sesleria coerulea
Teucrium polium ssp. *aureum*
Thymelaea tinctoria ssp. *nivalis*
Tussilago farfara
Only in seed bank (30.2%)
Apiaceae
Asteraceae
Caryophyllaceae
Cerastium sp.
Chenopodiaceae
Jasonia tuberosa
Leontodon sp.
Odontites sp.
Onobrychis supina
Poaceae
Rumex scutatus
Sedum sediforme
Taraxacum officinale
Thymus vulgaris
Only in established vegetation (37.6%)
Aphyllanthes monspeliensis
Asperula cynanchica
Carex humilis
Carlina vulgaris
Cruciata glabra
Globularia cordifolia
Helianthemum oelandicum ssp. *italicum*
Koeleria vallesiana
Lavandula angustifolia ssp. *pyrenaica*
Linum tenuifolium ssp. *milletii*
Picris hieracioides
Pinus sylvestris

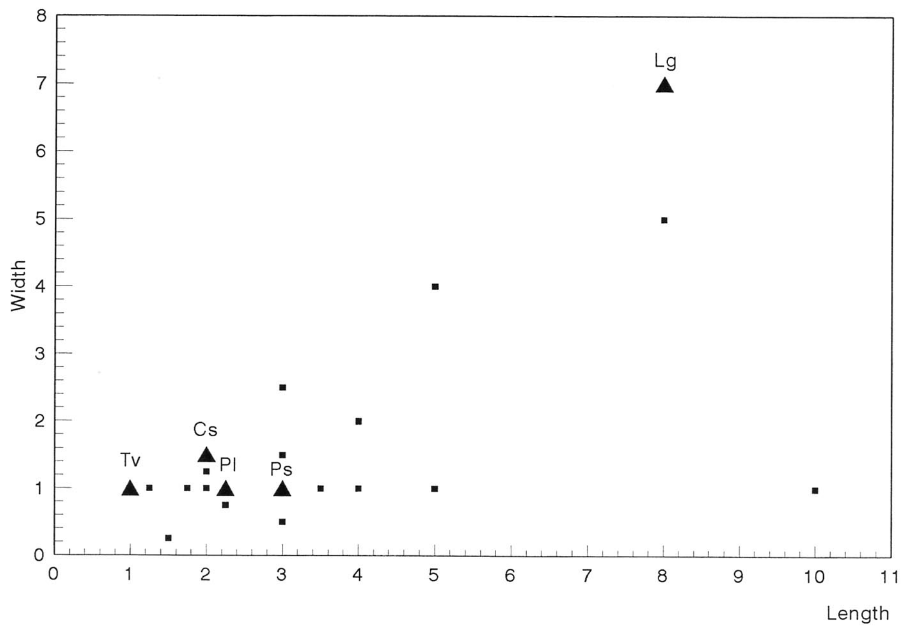

Fig. 1. Length and width (mm) of the seeds identified in the soil seed bank. The triangles represent main species: Ps, *Ptychotis saxifraga*; Tv, *Thymus vulgaris*; Cs, *Campanula speciosa* ssp. *affinis*; Pl, *Plantago maritima* ssp. *serpentina*; Lg, *Laserpitium gallicum*.

reference collection gathered from plants at the study site, and comparison with herbarium specimens.

Size and shape of seeds of species identified in the soil seed bank samples were also analyzed. For this purpose, 10 seeds of each taxa collected in the field were measured and mean length and width were calculated.

Seedling dynamics was recorded in a nearby micro-catchment, also north-facing and sloped about 40°. This sampling can not be carried out in the same plots where soil seed bank was analyzed because sampling involves a noticeable perturbation due to the low cohesion of the badland regolith. We installed two permanent plots, one (5 m × 0.5 m) in the upper part of the catchment and perpendicular to the maximum gradient slope, and the other (6.5 m × 0.5 m) parallel to the maximum gradient slope; both of them were subdivided into 0.25 m × 0.25 m quadrants to facilitate seedling monitoring. The sampling was done monthly, and extended from March 1990 to December 1991. At the first sampling, all the seedlings were marked by means of a numbered rigid plastic pin and in the following field visits, the new seedlings were marked and an inventory of the previous cohorts was made to detect the dead ones. The first sampling record, which represented a significant percentage of the total seedlings, was not used for calculations of the seedling dynamics, because we were not sure of the true ages of the seedlings.

Table 4
Mean seedling density (seedlings.m^{-2}) for the plots in the two topographic positions considered and total average (differences between both topographic positions are significatives at $p < 0.02$)

	Density
Upper slope	48.86 ± 8.60
Backslope	24.73 ± 3.80
Mean	36.80 ± 6.75

Differences among topographic positions in the values of seed and seedling densities were tested using one-way ANOVA analysis, performed using SPSS package. Nomenclature of plant species follows Flora Europaea (Tutin et al., 1964–1980).

3. Results

3.1. Soil seed bank

The soil seed bank had more than 1000 seeds.m^{-2} on average, with a high variability between samples (Table 1). Almost one-third of these (28%) had no seeds, while 37% of

Table 5
Total number and percentage of seedlings of each taxa recorded during the study period in the two sampled plots

Plant taxa	*N*	%
Ptychotis saxifraga	223	30.3
Sonchus sp.	90	12.2
Laserpitium gallicum	77	10.5
Campanula speciosa ssp. *affinis*	59	8.0
Helianthemum oelandicum ssp. *italicum*	47	6.4
Plantago maritima ssp. *serpentina*	41	5.6
Hieracium sp.	25	3.4
Avenula pratensis ssp. *iberica*	28	3.8
Genista scorpius	18	2.5
Onobrychis supina	14	1.9
Jasonia tuberosa	8	1.1
Poaceae	5	0.7
Pinus sylvestris	8	1.1
Rosa sp.	4	0.5
Sanguisorba minor ssp. *minor*	3	0.4
Centaurea scabiosa	3	0.4
Genista hispanica	5	0.7
Knautia dipsacifolia	3	0.4
Tussilago farfara	3	0.4
Koeleria vallesiana	2	0.3
Carex sp.	2	0.3
Galium sp.	1	0.1
Sesleria coerulea	1	0.1
Unidentified	66	9.0

them contained one or two seeds. Samples with more seeds were gradually less frequent; the richest sample contained 12 seeds. No significant differences could be established between the three topographic situations considered.

The soil seed samples showed a relatively high number of species (Table 2); 30 taxa were identified at least to the family level. Unidentified seeds comprised 15 different taxa, but their density was always very low. The spatial distribution of seeds was rather contagious, as each taxa appeared in general in few samples (second column of Table 2), mainly from the same transect or from the same micro-catchment.

About one-third of the taxa identified in the soil seed bank was intercepted by the transects done in the same catchment (established vegetation, Table 3); another third was not, but within this group most were species common in the badlands of the study area or in the neighboring communities.

Seed functional typology was rather diverse (Fig. 1). The general tendency was to be rather small and slightly heterometric (length greater than width). Seed length ranged from 1 to 10 mm but most were less than 5 mm long.

3.2. Seedling dynamics

The mean seedling density in July (Table 4), when it was maximum, was 36.8 ± 6.75 seedlings.m^{-2}. This value showed significant differences according to the topographic position in the micro-catchment, being considerably higher on the upper part of the slope (Guàrdia et al., 1996). Table 5 shows the number and percentages of taxa that emerged during the study period. The most frequent species, the biennial *Ptychotis saxifraga*, represented almost one-third of the total. The remaining species were mainly perennial herbs, most of them also present in the established vegetation.

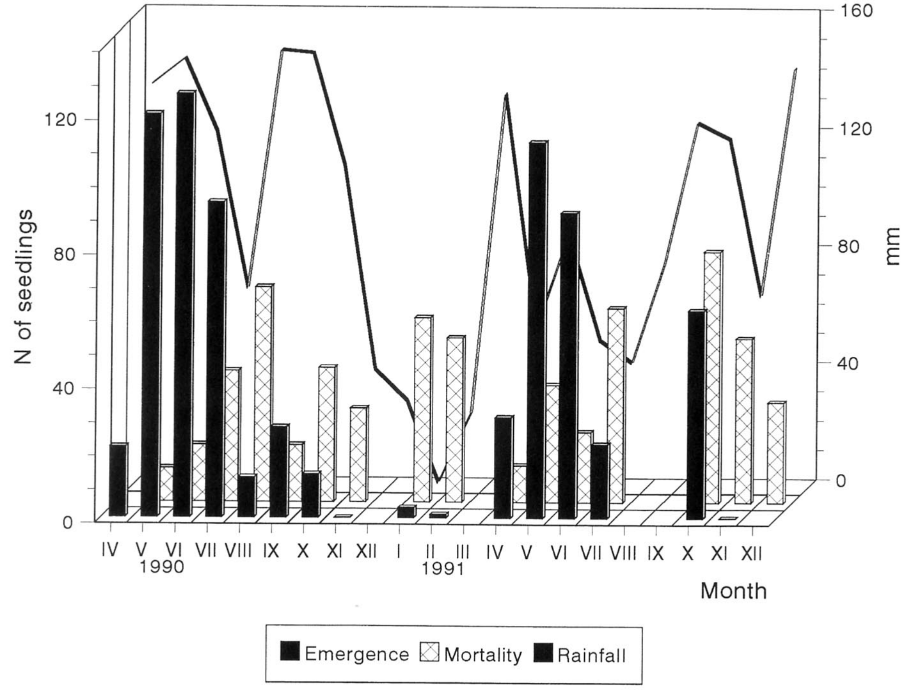

Fig. 2. Number of seedlings emerged and dead in each sample, and monthly rainfall during the study period. (The high value of October 1991 for seedling counts was due to a cumulative effect from the non sampled preceding August).

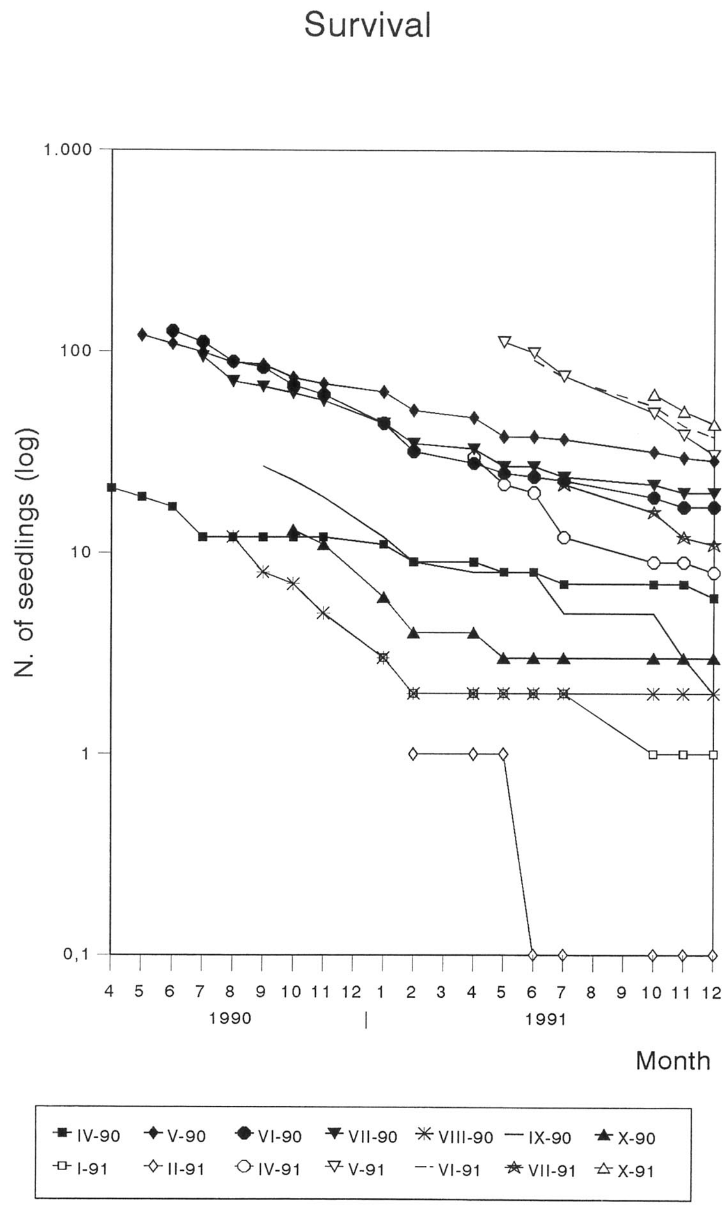

Fig. 3. Survival curves for total number of seedlings emerged at each sample data.

Table 6
Percentages of survival of all seedlings that emerged in 1990 at December 1990 (first column), at December 1991 (second column) and survival percentages of the seedlings that emerged in 1991 at December 1991 (third column) for all the seedlings computed and for the most abundant taxa

Plant taxa	1990–90	1990–91	1991–91
Total	56.7	19.1	41.4
Ptychotis saxifraga	80.3	26.2	52.9
Asteraceae	53.5	1.4	36.8
Laserpitium gallicum	9.1	0	6.8
Campanula speciosa ssp. *affinis*	49.0	18.4	80.0
Helianthemum oelandicum ssp. *italicum*	90.0	43.3	29.4
Plantago maritima ssp. *serpentina*	88.9	25.9	50.0
Hieracium sp.	73.7	31.6	50.0
Avenula pratensis ssp. *iberica*	61.9	33.3	100.0
Genista scorpius	60.0	30.0	37.5
Onobrychis supina	33.3	22.2	40.0

Seedling emergence took place mainly from May to July in both years (Fig. 2) and, moreover, was rather synchronized among the different species. In contrast, mortality occurred more or less gradually through the year, apparently with no relationship with precipitation distribution. This is also shown by the corresponding survivorship curves (Fig. 3), each one summarizing individuals of all the taxa of each sampling record. This graph shows that the risk of death is low and rather constant from the beginning. Unfortunately, we could not obtain these curves for the complete life cycle of the species.

Almost 50% of the seedlings that emerged in spring and summer had died by the start of winter (Table 6), and less than 20% remained one year later. Although total seedling survival was similar in the two years considered, analysis of the data concerning the most frequent taxa revealed that the mortality values were rather diverse among species and years. Some individuals of most of the species survived for a year, more so in 1990 than in 1991, but *Campanula speciosa* and *Avenula pratensis* ssp. *iberica* survived more in 1991. After the second year, all the survival values were lower than 50%, and mainly about 25%.

4. Discussion and conclusions

The number of diaspores found in the soil was higher than would be expected on the basis of the low vegetation cover in badlands, at about 1368 seed m^{-2} on average. This value is about six-fold the seed bank density detected in badland areas of the SE of Spain (García-Fayos and Recatala, 1992), but it is lower than the values obtained in habitats with comparable low vegetation cover, such as dune ecosystems (Symonides, 1978) and desert grassland communities (Henderson et al., 1988). No significant differences were detected between the three topographic positions considered.

The species composition of the soil seed bank was relatively diverse. Two species, *Ptychotis saxifraga* and *Thymus vulgaris*, accounted for almost 50% of the seeds in the soil, but there were many other species with lower percentages. One-third of the species present in the seed bank was also intercepted in the vegetation transects as established individuals, and many others corresponded to taxa of the communities neighboring the badlands. Similar levels of correspondence between established vegetation and the seed bank have been detected in other areas that are also affected by some sort of perturbation (Marlette and Anderson, 1986; Hutchings and Russell, 1989). These perturbed ecosystems return permanently to an initial stage of succession, and therefore, the enrichment of the soil seed bank that usually occurs in the progressive successional processes is not possible.

Some of the species present as established adults where seed bank was sampled had no seeds in the soil bank, such as *Pinus sylvestris, Aphyllanthes monspeliensis, Lavandula angustifolia* ssp. *pyrenaica* and *Linum tenuifolium* ssp. *milletii*. These plants were usually present in the adjacent non-disturbed communities and some of them were also present on other badland slopes. We may suppose that although these species could provide sufficient seed rain, this is not persistent in the soil. This lack of seeds may be due to predation or, more probably, to removal of seeds by erosion processes. In badland areas of southeastern Spain, Garcia-Fayos et al. (1995) found that seed removal by erosion is not the key factor explaining the lack of vegetation on badlands, but average annual rainfall in this area is about one-third of that in Vallcebre, and erosion presents a quite different dynamics.

Other explanation for this lack on soil seed bank, not exclusive with the precedent, could be that the seeds of these species do not disperse, or at least one fraction of their seeds, and they remain more or less protected within the fruits, as a seed store on the plants themselves (Fenner, 1985). These seeds are released and dispersed later by wind or rain water. This strategy has been described in many of the fire-adapted trees and shrubs of the arid regions of Australia and in many annuals inhabiting deserts (Gutterman, 1994). In badland areas, this mechanism seems to act in species with capsular fruits that contain many little seeds, as in *Helianthemum oelandicum* ssp. *italicum*, *Linum tenuifolium* ssp. *milletii*, or in plants whose fruits remain concealed in a persistent calix or bracts, as in *Lavandula angustifolia* ssp. *pyrenaica* and in some gramineous plants as *Koeleria vallesiana*.

Referring to the size and shape of the seeds in the soil bank, small slightly heterometric seeds were dominant. Seiwa and Kikuzawa (1996) pointed out that the importance of seed size in determining seedling establishment largely depends on the relationships between seasonal changes in environmental conditions and the phenological traits of the seedlings. Fenner (1987) concluded that many pioneer species produce numerous small seeds; this may facilitate dispersal into newly created open habitats. But in badland areas, small seeds have an additional benefit, as they may be more easily trapped in place than large seeds, in desiccation cracks or in the rough soil surface, and thus, present greater downward movement in the soil column. Harper and Benton (1966) suggested that in open habitats, small seeds are less liable to desiccation because they have a larger contact/surface area ratio and therefore, they make good contact with the available water in the soil. For larger seeds, such as those of *Achnatherum calamagrostis, Avenula pratensis* ssp. *iberica, Ptychotis saxifraga* and *Tussilago farfara*, the presence of appendices (hairs, awns, wings) or mucilage secretion may prevent seed removal by erosion processes and also, may act as an anchoring device (Peart, 1979).

Once seeds are incorporated into the soil, the physical and chemical properties of the soil determine temperature and nutrients regimes and have the greatest effects on seed germination and seedling growth and survival. The seedling recruitment observed on badland slopes was relatively low, especially if compared to the soil seed bank density. Possible causes of this disparity between the seed bank and seedling recruitment may be due to lack of suitable 'safe sites' for germination and establishment of the seeds (Harper et al., 1965). Soil fertility on badland slopes is very low (Guàrdia, 1997), as erosion has almost eliminated the superficial horizons and the substratum consists just of altered bedrock. Moreover, microenvironmental conditions are particularly extreme, as temperature and soil moisture vary over a wide range (Regüés et al., 1995). One fact that points out these environmental restrictions is the higher seedling density detected on the upper part of the slope even though this pattern could not be detected in the spatial soil seed bank distribution. On the upper part of the badland slopes, microclimatic conditions are more favorable and the vegetation is more dense (Guàrdia and Ninot, 1992). If the seed bank is regularly distributed along the slope, higher seedling density on the upper part suggests that less restrictive environmental conditions allowed more seed germination.

Seedling emergence took place fairly synchronously from May to July. Almost all the species had shed their seeds at the end of the summer and, therefore, they had to remain in situ during the winter. The high synchronization of seed germination among all the species is probably due to the relatively extreme environmental conditions that characterize badland areas. In a sowing experiment in the same study area with *A. calamagrostis* (Guàrdia and Ninot, 1998), we stated that seeds that were previously weathered and capable of germination in laboratory conditions delayed their germination in field conditions until June, after being sown in April. Since soil moisture content from April to June was not limiting in the study area, we assumed that low temperatures repress seed germination in the field. Unfortunately, we do not have any record of seed germination for the same species in less extreme habitats with which to contrast this hypothesis. In a wide review of seed germination characteristics at the Sheffield region, Thompson and Grime (1979) concluded that winter seed dormancy is strongly associated with species of the colder regions within the temperate zone. In these geographic areas, plant growth in late autumn and winter is severely restricted by low temperatures and the most favorable period for seedling establishment occurs only from spring onwards.

Seedling mortality occurred throughout the year, without any obvious relationship with the dynamics of the erosive processes. Heavy rainstorms did not cause any maximum in the mortality records, and burial or removal of seedlings due to water flow during rainfalls was not observed. On the other hand, on badland slopes space availability is not a limiting factor for seedling establishment, and survival of seedlings is more dependent on capability to endure severe environmental conditions than ability to withstand competition from neighboring plants. In contrast, as pointed out by Symonides (1977), in open habitats it would be advantageous for seedlings to grow in groups, as they protect each other from severe environmental hazards.

The continuous risk of mortality that was observed in the survival curves during the two first years reduced the number of seedlings to the half of those that emerged the first winter and to about 25% by the next year. This relatively high mortality rates is comparable to those observed in other perennial herbs from a wide range of habitats, where such rates do not impede population maintenance. For instance, Martínez and Moreno-Casasola (1992) found an annual mortality rate of 98% for *Chamaecrista chamaecristoides*, a perennial plant of the dunes of Mexico, which in spite of this high value was able to persist in this habitat.

Interannual variation in climatic conditions affected seedling emergence and survival values. In general the driest year, 1991, had lower emergence and survival values. This pattern of seedling dynamics has been detected in other Mediterranean communities, where it was correlated with rainfall distribution (Beatley, 1974; Guàrdia and Ninot, 1991; Peco et al., 1998). This variability affected the species composition of these communities in the long term. More extended studies are necessary to evaluate the true consequences of the interannual variability detected in seedling emergence in badlands.

In conclusion, the unexpected soil seed bank detected in the badlands of the Upper Llobregat indicates that, although erosion rates are high, seed inputs occur. Seedling emergence was observed on badland slopes, mainly from May to August. Seedling mortality occurred all around the year with any clear relation with erosive processes. Based on these results, predictions can be made on the future development of this vegetation. The low colonization of the badland areas is caused by a combination of factors such as low seed availability in the reduced favorable period for germination and subsequent poor seedling establishment. This prevents the advancement of a progressive succession to more advanced stages. Soil amelioration to improve microsite conditions for seed germination and seedling recruitment may be enough to start this succession that will lead to the recolonization of these areas.

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