

# Limitations to plant establishment on eroded slopes in southeastern Spain

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**Abstract.** The possible causes for the lack of vegetation in five badland sites from southeast Spain were experimentally tested. The main factors affecting seed germination and seedling survival considered were seed availability, regolith water dynamics in relation to rain events, regolith salinity, seedling predation by herbivores and seedling removal by erosion.

Four issues are addressed: 1. Both rainfall and the temporal and spatial dynamics of regolith water during the seedling emergence period were monitored in five different zones at one site (Petrer, Alicante). 2. Effects of salinity and water potential on the rate and speed of germination of local seeds were determined. 3. Seed reserve and seedling emergence and mortality were followed throughout one season. 4. Regolith characteristics of all five sites were compared and the consequences for plant colonization discussed.

The main factor limiting plant colonization in these sites was the very short duration of available water in the soil, due to the physical and chemical characteristics of the regolith. In addition, high regolith salinity and its effects on seed germination, the aspect of the site and the pattern of rain events, played a very important role reducing germination and survival. Herbivory and erosion were seldom responsible for seedling mortality. However, there were no highly erosive rain events during the study period, although several have been measured during the past few years.

**Keywords:** Badland; Germination; Plant colonization; Seedling dynamics; Soil salinity; Soil water dynamics.

## Introduction

A badland is a distinctive land form that develops in areas of accelerated slope erosion in soft-rock terrain. Badlands are particularly important landscapes in semi-arid regions, but they are also present under other climatic regimes (Bryan & Yair 1982; Campbell 1989; Calvo & Harvey 1996).

Seed availability, microsite limitations and predation by herbivores are the main factors potentially limiting recruitment in plant populations (Crawley 1990; Eriksson & Ehrlén 1992). Although badlands are characterized by very high rates of erosion, previous studies have shown that erosion does not affect the seed reserve as much as

expected. Seeds do accumulate in the badland surfaces in sufficient quantities to ensure plant recruitment (García-Fayos et al. 1995; Cerdà & García-Fayos 1997; García-Fayos & Cerdà 1997). Thus, if the lack of seeds is not the main cause for the lack of vegetation, then microsite factors and herbivore predation should be considered.

The regolith is the weathered surface layer of the badlands. It has very distinctive physical and chemical properties that may make it unsuitable for plant growth. First, the regolith usually has very high electrical conductivity, mostly because of the high concentration of sodium chloride and gypsum (Harvey 1982; Gerits et al. 1987; Imeson & Verstraten 1988). In addition, its physical structure is such that water may only be available for a short time after a rain event, regardless of the amount of rainfall (Cerdà 1997). Thus, we hypothesize that salinity and reduced water availability, through their effects on seed germination and seedling survival, could be the main factors accounting for the lack of vegetation on the badland slopes in southeast Spain.

The objective of this study is to test two possible causes for the lack of vegetation in badlands: the high salinity and reduced water availability of the regolith, and the predation of seedlings by herbivores. Specifically, we present evidence for: (1) the temporal and spatial dynamics of regolith water in relation to rainfall events during the seedling emergence period; (2) the effects of both salinity and water potential of the badland regolith on the rate and speed of germination of the main species of the local flora; (3) the main agents of seedling mortality; and (4) the trends of soil salinity and moisture dynamics in the regoliths of five representative badlands in southeastern Spain.

## Material and Methods

### Study sites

Five badland sites that encompass the main lithologic, climatic and geomorphological gradients across southeast Spain were selected. The sites are Petrer and

Monnegre, in the province of Alicante; Los Guillemos, in the province of Murcia; and Vera and Tabernas, in the province of Almería. The climate of all of them is Mediterranean with hot, dry summers and cool winters. Mean annual precipitation and temperature are around 350 mm and 16 °C in Petrer; 300 mm and 18 °C in Monnegre and Los Guillemos; 200 mm and 22 °C in Vera; and 250 mm and 23 °C in Tabernas. The substrate at Petrer and Monnegre is Senonian (Cretaceous) marls; Plio-Quaternary silts at Los Guillemos; Messinian (Tertiary) gypsiferous marls at Vera; and Tortonian (Cretaceous) mudstones at Tabernas. Plant cover at all sites is characterized by scanty individuals of *Salsola genistoides* (*Chenopodiaceae*), the medium size woody shrub *Cheirolophus inthybaceus* (*Asteraceae*), *Lygeum spartium* (*Poaceae*) and scattered populations of *Stipa capensis* (*Poaceae*) and *Moricandia arvensis* or *M. moricandioides* (*Brassicaceae*).

The experiments and observations designed to test the first three objectives were carried out only at the Petrer site, where the seed reserve and the rates of seed removal by erosion have been measured previously (García-Fayos et al. 1995; García-Fayos & Cerdà 1997). Measurements of the trends of regolith salinity and moisture dynamics were taken at all five sites.

At Petrer, we sampled five different zones that encompass the range in lithology, slope and aspect of the badland and adjacent terrain. The areas were defined following a detailed vegetation survey (unpubl. data). The first zone, called hereafter P-1, is located in the upper part of the north-facing slopes, outside the badland itself, and can be considered as a control zone. It is covered by a dense shrubs growing on Quaternary silts dominated by *Rosmarinus officinalis*, *Cistus albidus*, *Coronilla minima*, *Brachypodium retusum*, *Thymus moroderi* and *Rhamnus lycioides*. The second zone (P-2) is located immediately below P-1, on north-facing slopes, and represents a transition zone. Vegetation cover is open shrubland, growing on a mixture of Quaternary sediments and the underlying Senonian marls. The third zone (P-3) is characterized by unvegetated badland slopes, developed on Senonian white marls, with a northern exposure. The fourth zone (P-4) is similar to P3 but is south-facing. Finally, P-5 also occupies the south-facing slopes, but the clay has a different mineral composition than that of the white marls (A. Soriano pers. comm.). Slope ranges between 25° and 45° in all five areas.

#### Regolith moisture dynamics

During the germination period of 1992 from February to April, we sampled the upper 5 cm of regolith at the five zones in Petrer to determine moisture content. We

selected two sampling locations at P-1, two at P-2, two at P-3, three at P-4 and one at P-5. The regolith water content was measured after every rain event and daily until the soil dried below the wilting point. Afterwards, the regolith was sampled irregularly, with intervals ranging from weekly to monthly. The 5 cm sampling depth was chosen because previous studies showed that over 95% of all seeds were found at that depth (García-Fayos et al. 1995). Soil samples were taken using a 5.5 cm diameter core and moisture content was determined gravimetrically in the laboratory. Soil moisture characteristic curves were determined in the laboratory and were used to calculate water potentials from moisture content measurements (Table 1) (Mériaux 1979). In addition, five 0.5 kg samples were taken for chemical and physical analysis, the results of which are shown in table 1. Precipitation was measured using a rain gauge, and recorded into by data logger every 10 minutes.

#### Effects of water potential and salinity in the rate and speed of germination

We tested the effects of salinity and water potential on the speed and rate of seed germination at four levels of electrical conductivity (5, 10, 15 and 25 ms/cm) and four levels of water potential (−0.02, −0.10, −0.34 and −0.99 MPa). These values are within the wide range commonly observed in the regolith from the study area (Table 1). Salinity and water potential were simulated using sodium chloride (NaCl) and polyethylene glycol (PEG 6000) solutions, respectively. The appropriate concentration for each level of electrical conductivity or water potential was determined based on standard equations (Weas 1973; Michel et al. 1983) and distilled water controls were always included.

**Table 1.** Properties of regolith and moisture content at different water potentials of the different surface types 1, 2, 3/4 and 5 of the badland site Petrer, at 0–5 cm depth (values are means ± SE).

Surface type No. of samples	P-1 2	P-2 2	P-3/4 4	P-5 4
Sand (%)	46.30 ± 0.11	26.15 ± 5.69	13.95 ± 2.27	5.64 ± 0.19
Silt (%)	32.87 ± 0.76	42.64 ± 4.28	49.23 ± 1.81	60.58 ± 2.33
Clay (%)	20.83 ± 0.61	31.21 ± 1.41	36.82 ± 2.23	33.78 ± 2.46
Bulk density	1.38 ± 0.03	1.40 ± 0.10	1.44 ± 0.10	1.35 ± 0.00
EC (ms/cm)	1.86 ± 0.05	5.90 ± 1.56	26.36 ± 0.23	4.38 ± 0.41
CaCO <sub>3</sub> (%)	57.63 ± 1.68	74.47 ± 1.67	72.63 ± 1.05	53.60 ± 2.76
Na <sup>+</sup> (g/Kg)	0.03 ± 0.01	0.07 ± 0.02	3.79 ± 0.09	0.50 ± 0.04
Ca <sup>++</sup> (g/Kg)	0.04 ± 0.01	0.06 ± 0.03	0.26 ± 0.08	0.17 ± 0.02
Mg <sup>+</sup> (g/Kg)	0.08 ± 0.03	0.37 ± 0.19	0.37 ± 0.02	0.11 ± 0.03
K <sup>+</sup> (g/Kg)	0.02 ± 0.01	0.02 ± 0.01	0.08 ± 0.01	0.03 ± 0.01
RAS	0.12 ± 0.01	0.17 ± 0.01	8.34 ± 0.02	1.34 ± 0.01
Moisture at Ψ <sub>m</sub> (cm <sup>3</sup> water/cm <sup>3</sup> soil)				
−0.02 MPa	0.243 ± 0.003	0.237 ± 0.001	0.299 ± 0.039	0.234 ± 0.001
−0.10 MPa	0.189 ± 0.008	0.214 ± 0.003	0.243 ± 0.030	0.201 ± 0.011
−0.31 MPa	0.171 ± 0.006	0.188 ± 0.006	0.212 ± 0.022	0.161 ± 0.011
−1.00 MPa	0.081 ± 0.012	0.116 ± 0.009	0.167 ± 0.031	0.117 ± 0.003

The effect of salinity and water potential was tested for the following species:

- Asteraceae*: *Cheirolophus inthybaceus*, *Helichrysum stoechas*  
*Phagnalon saxatile*;  
*Poaceae*: *Dactylis glomerata* ssp. *hispanica*, *Lygeum spartium*;  
*Brassicaceae*: *Moricandia arvensis*;  
*Chenopodiaceae*: *Salsola genistoides*;  
*Crassulaceae*: *Sedum sedifforme*.

These species were selected because they were dominant in P-1 and P-2 and were also present in the other four badlands. Seeds were collected in the study area during 1993, air-dried and stored at room temperature until the autumn of 1993, when the germination experiments were run. Because seeds may have specialized dispersal structures, which may or may not be lost during dispersion, they were always used in the form they keep after the dispersion event.

Each level of electrical conductivity or water potential was replicated four times for each species. A replicate consisted of a Petri dish with filter paper moistened with 5 ml of the appropriate solution and 50 seeds. However, replicates for *L. spartium* and *S. genistoides* only had 25 seeds, because of their larger size. The Petri dishes were covered with PVC sheets to prevent evaporation and placed in a growth chamber with a 12:12 h photoperiod. Temperature was kept at 25 °C during daytime and 15 °C during night-time. These photoperiod length and temperatures correspond to conditions found in the field during the germination periods of 1991 and 1992. The dishes were checked daily until the first seed germinated. A seed was considered to have germinated when the radicle emerged from the seed coat. From then on the number of seeds that had germinated was counted 5 times per week, for a total of 28 days. At the end of this period the viability of the seeds that had not germinated was checked using the Tetrazolium test, and only viable seeds were considered for calculations. We calculated germination rate as the percentage of seeds that had germinated by day 28, and germination speed as the number of days until the first germination was detected.

The effects of water potential and salinity on the germination rate for each species were determined using analysis of variance. Tukey tests were applied to compare germination rates among treatment levels. The data were arcsin transformed to fit the assumptions of normality and homogeneity of variances. The effects of water potential and salinity on germination speed were analysed using the Kruskal-Wallis test, because data cannot be normalized. Also 'a posteriori' tests were performed to compare germination speed among treatment levels (Zar 1996).

### *Seedling emergence and survival*

A total of 78 0.5 m × 0.5 m plots were established in the five zones at Petrer prior to the 1993-1994 germination period. The location of the plots was determined following a stratified sampling procedure. Three plots were established in P-1, 15 in P-2, 18 in P-3, 31 in P-4, and 11 in P-5. Seedling emergence, survival and reproduction were monitored in each plot at least every 15 days from 30/09/93 to 01/07/94, and then monthly until 11/10/94. When a seedling was first detected, it was identified with a toothpick, so that each individual could be found in successive visits. Mortality was classified into four possible causes: drought, erosion, herbivory and undetermined. If a seedling was found desiccated, its death was attributed to drought. If the seedling could not be found and signs of regolith erosion were identified, its death was attributed to erosion. If a dead seedling had cotyledons or leaves partially or totally defoliated, its death was attributed to herbivory. If a seedling had disappeared, but we were not able to assign its death to any of the preceding causes, the cause of death was considered as undetermined. In addition, precipitation was registered daily during the same period using rain gauges connected to a data-logger.

In order to assess the effects of the soil seed bank on seedling emergence, we estimated the density of germinable seeds. In October 1991, before the period of seedling emergence, five 20 cm × 20 cm plots were randomly located in each of the P-1, P-2 and P-3 zones, and the top 6 cm of regolith collected. Each sample was desegregated and homogeneously distributed on trays. The soil sample was arranged in a 1 cm thick layer over a 5 cm bed of vermiculite. The trays were covered with a plastic mesh to prevent seed and seedling predation and placed outside. They were sprinkled with water three times per week. During the following four months, seedlings emergence was counted weekly, and the seedlings were removed after the species was identified.

### *Other badlands in southeast Spain*

We measured electrical conductivity and obtained soil moisture characteristic curves of the regolith in the five badlands during February 1994. Only the most representative substrate from each site was sampled. In Petrer, it was the substrate from P-3 and P-4. Five 5 cm deep subsamples were taken from five different south facing points at each badland site. After homogenizing the subsamples, they were air-dried, sieved through a 2 mm sieve and electrical conductivity and soil moisture characteristic curve determined.

To estimate the period of time during which soil water remained available after a rain event three 0.5 l

freely draining pots were filled with regolith from the upper 5 cm layer from each badland site. We added water to each pot until the soil reached saturation and then placed the pots into a growth chamber with the same temperature and photoperiod as those of the germination tests. The pots were weighed daily until their moisture content decreased to that of the wilting point. The measured daily loss of water and the soil-moisture characteristic curves for each regolith allowed us to determine the course of soil water potential for each badland site during the desiccation cycle. We compared the number of days that pots from each badland site remained between field capacity ( $-0.02$  MPa) and the wilting point ( $-1.00$  MPa).

## Results

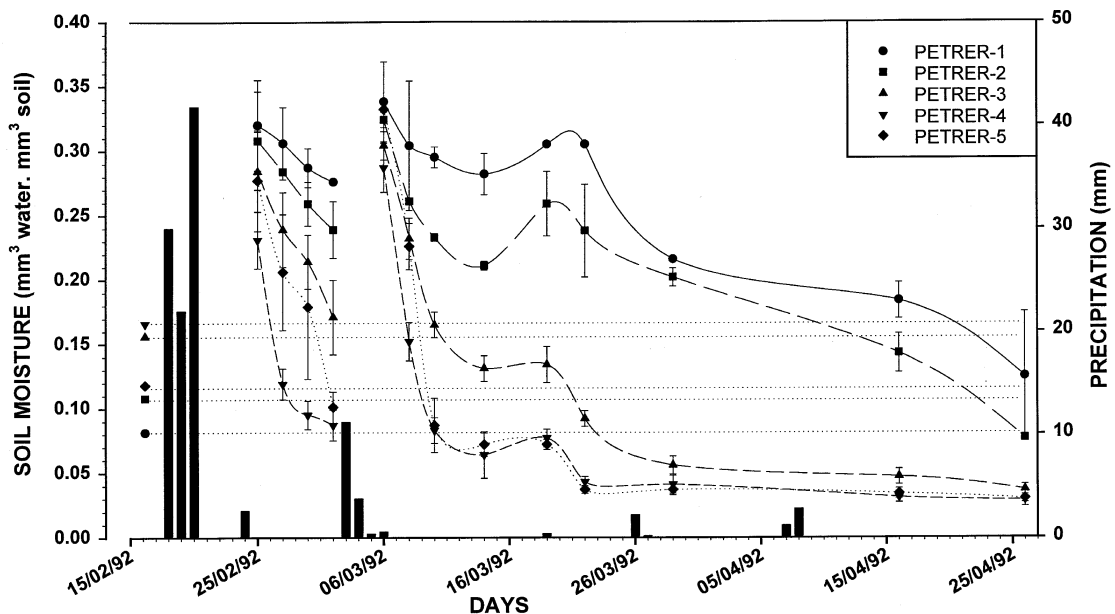
### Regolith moisture dynamics

Only three rain events noticeably moistened the regolith during the germination period of 1992. However, the number of days when water remained available in the soil after a rain event varied widely between zones. At P-4, the moisture content of the regolith stayed above the wilting point for only 1 to 4 days after the rain ceased; at P-3 and P-5, for 4 to 7 days; and at P-1 and P-2, for more than one month (Fig. 1).

### Effects of water potential and salinity on the rate and speed of germination

Not a single seed of any species germinated when water potential was at the wilting point ( $-0.99$  MPa) (Fig. 2). However, the effect of decreasing water potential between  $-0.02$  MPa and  $-0.34$  MPa on seed germination differed among species. The germination rate of *Lygeum spartium* remained close to 100 % at a water potential as low as  $-0.34$  MPa. Most species, such as *Cheirolophus intybaceus*, *Dactylis glomerata*, *Helichrysum stoechas*, *Salsola genistoides* and *S. sediforme* had a decreased germination rate when water potential decreased to  $-0.34$  MPa. Even then, the germination rate for most species remained close to 80%. Finally, the germination rate of *Moricandia arvensis* and *Phagnalon saxatile* decreased steadily as water potential decreased and reached levels as low as 20% at the lowest water potential. Interestingly, the effect of water potential on germination speed among the different species was different to its effect on germination rate. The seeds of *S. genistoides* germinated quickly, in less than three days, and the speed was not affected by a water potential as low as  $-0.34$  MPa. *D. glomerata*, *H. stoechas*, *L. spartium* and *S. sediforme* germinated relatively quickly, but germination speed decreased at  $-0.34$  MPa. Finally, the germination speed of *C. intybaceus*, *M. arvensis* and *P. saxatile* decreased steadily as water potential decreased.

Although most species were able to germinate at the highest level of electrical conductivity (25 ms/cm), the



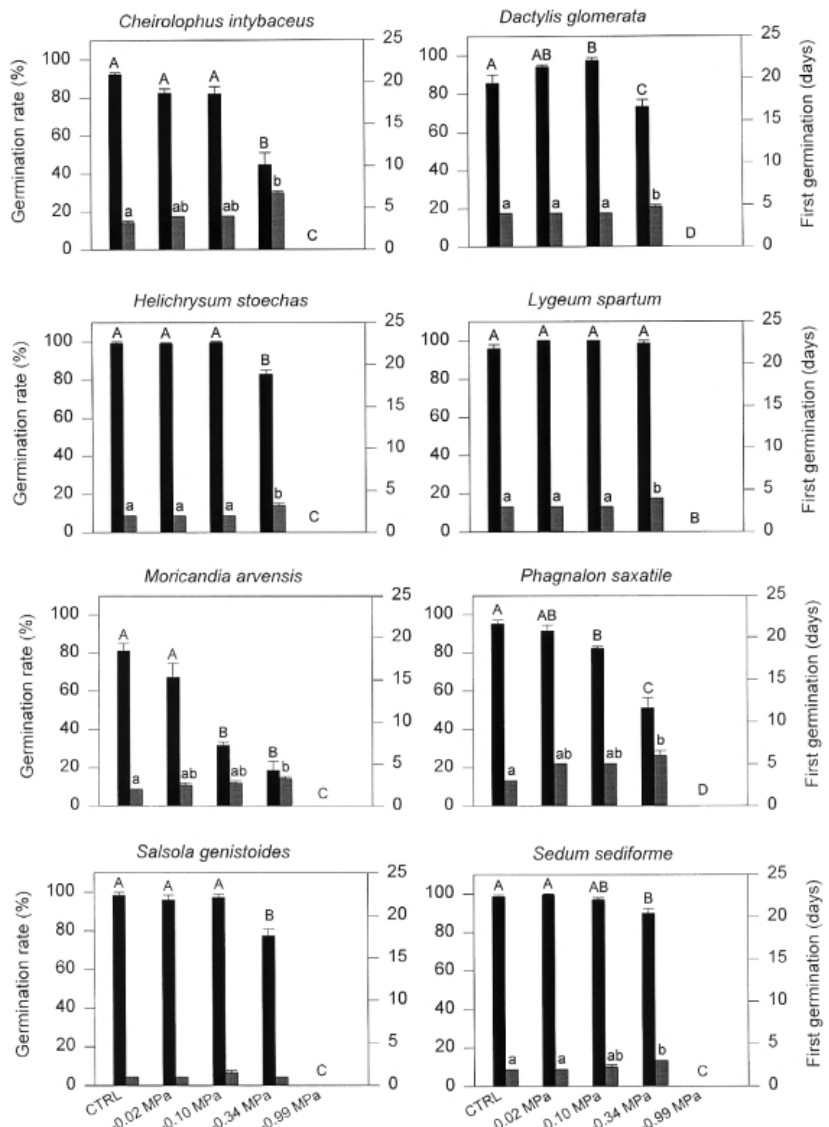
**Fig. 1.** Daily precipitation and regolith moisture content of the five zones in the Petrer site during the 1991-1992 seedling emergence period. Bars indicate daily precipitation; dotted, horizontal lines indicate soil moisture content at the wilting point. Error bars indicate SE ( $n = 4$ ).

effects of salinity on germination were more dramatic than the effects of reduced water potential (Fig. 3). With the exception of *L. spartium*, the germination rate or speed of all species was affected at an electrical conductivity greater than 5 ms/cm. At an electrical conductivity of 15 ms/cm or above only *L. spartium*, *S. genistoides* and *D. glomerata* maintained reasonably high germination rates and speeds.

*Seedling emergence and survival*

Germinable seed densities in P-2 and P-3 were similar, but they were much lower than the seed density in P-1, the control area outside the badland (Table 2). Four cohorts of seedlings were detected from September

1993 to June 1994, following four rainy periods. A total of 643 seedlings emerged. The cohort of November was the most numerous, with 67% of the seedlings. Although P-4 had the most intensive sampling (31 plots, covering a total of 7.75 m<sup>2</sup>), not a single seedling was detected during the 9 months of study (Table 2). In general, the number of seedlings and species decreased from the northern to the southern slopes, and from vegetated to unvegetated areas within the northern slopes. Thus, 273 seedlings/m<sup>2</sup> emerged in P-1; 55/m<sup>2</sup> in P-2; 0.8/m<sup>2</sup> in P-3; and none in P-4. Only seedlings from P-1 and P-2 had reproduced or survived by the end of the study (see App. 1). In P-5 10 seedlings/m<sup>2</sup> emerged, all *M. arvensis*, but none reproduced or survived. The number of species that emerged followed the same

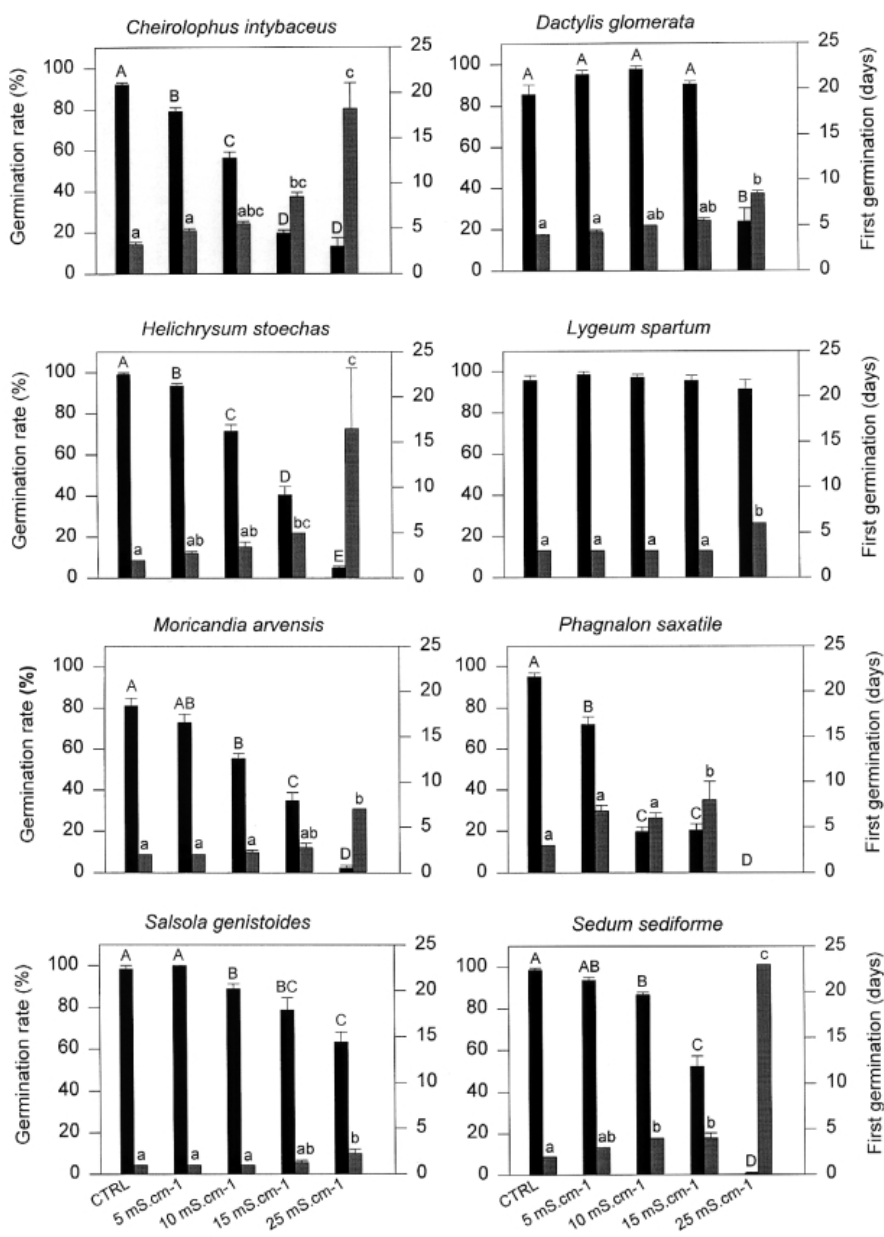


**Fig. 2.** Effect of water potential on germination rate (black bars), and germination speed (grey bars) for each species. Germination rate measures the percent of seeds that germinated after 28 days, while germination speed measures the number of days until the first seed germinated. Values are means ± SE. Different letters indicate significant statistical differences between treatment levels at the 0.05 level. No letters on bars indicate that the treatment had no significant effect.

**Table 2.** Germinable seed densities in the regolith in October 1991; seedling emergence, survival and causes of mortality for the recruitment period of 1993-1994 in the Petrer site. Values are means  $\pm$  SE.

	P-1	P-2	P-3	P-4	P-5
Seed bank (seeds/m <sup>2</sup> )	2335 $\pm$ 423.0	365 $\pm$ 133.3	315 $\pm$ 121.6	*	*
Emergence (seedlings/m <sup>2</sup> )	272.8 $\pm$ 38.2	54.8 $\pm$ 9.2	0.8 $\pm$ 0.4	0.0 $\pm$ 0.0	9.4 $\pm$ 3.2
Survival (seedlings/m <sup>2</sup> )	6.4 $\pm$ 4.2	1.2 $\pm$ 0.5	0.8 $\pm$ 0.4	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
Causes of mortality:					
Drought (%)	76.28	75.09	100.00	–	55.56
Erosion (%)	0.00	2.60	0.00	–	3.70
Predation (%)	2.10	3.72	0.00	–	0.00
Unknown (%)	21.62	18.59	0.00	–	40.74

\* These regolith surfaces were not sampled for seed bank, but seed density values might be similar to those in P-3 as inferred from García-Fayos et al. (1995).



**Fig. 3.** Effect of the salinity on germination rate (black bars), and germination speed (grey bars) for each species. Values are means  $\pm$  SE. Different letters indicate significant statistical differences between treatment levels at the 0.05 level. No letters on bars indicate that the treatment had no significant effect.

pattern. There were 13 species in total in the three plots of P-1; 11 species in the 15 plots of P-2; and two species in the 18 plots of P-3 (see App. 1). Only one species, *M. arvensis*, emerged in the 11 plots of P-5. *M. arvensis* was the most abundant species in all the zones where it was present, due to a better germination rate and high reproduction and survival rates. *C. inthybaceus* and *L. spartium* were the only species able to emerge at P-3, but none of them survived (see App. 1).

Drought was the main cause of death (Table 2), accounting for all seedling mortality in P-3, more than 75% in P-1 and P-2 and for more than 50% in P-5. Erosion and herbivory were responsible for less than 5% of the deaths in all zones. Erosion as a cause of mortality was only detected in P-3 and P-5, whereas herbivory was only detected in P-1 and in P-2.

#### Other badlands in southeast Spain

All of the badlands, except Los Guillemos, have moderate to highly saline regoliths. The Vera and Petrer badlands have the highest values, up to 51.8 and 36.5 ms/cm, respectively (Table 3). The salinity at Los Guillemos is similar to that of the Quaternary sediments at the Petrer site (P-1) (Table 1).

The regoliths from all but one of the sites retained water above the wilting point for ca. 5 days after the soil had been saturated. The only exception was the regolith from the Vera badlands, which retained available water for almost 15 days (Table 3).

## Discussion

The dynamics of soil water availability – determined by physical and chemical characteristics of the regolith such as its texture and sodium content – and the high soil electrical conductivity (Table 1), are the main factors responsible for the differences in seed emergence and seedling survival in the five zones in the Petrer badlands. Only the water retained in the regolith between field capacity (–0.02 MPa) and wilting point (–1.00 MPa) is usable by plants. In general, water availability increases as soil texture changes from sandy to loamy, and decreases again in clayey soils (Brady 1990). With regard to electrical conductivity, excessive salinity may cause ion toxicity to seeds and plants (Lima et al. 1990). In addition, high solute concentration has an osmotic effect, decreasing soil water potential and, therefore, seed water imbibition (Mayer & Poljakoff-Mayber 1989).

Neither water availability nor salinity seemed to limit germination in P-1 or P-2, the control and transition zones, where the highest seedling densities were detected. Regolith water potential remained close to

**Table 3.** Chemical and physical properties of the regolith of the badland study areas in SE Spain. Values are means  $\pm$  SE.

	Petrer	Monnegre	Guillemos	Vera	Tabernas
EC (ms/cm)	36.500	10.700	2.170	51.800	6.530
Na <sup>+</sup> (meq/100g)	0.590	0.645	0.015	0.687	0.652
Ca <sup>++</sup> (meq/100g)	0.332	0.235	0.165	0.595	0.410
Mg <sup>++</sup> (meq/100g)	0.130	0.135	0.074	0.215	0.179
K <sup>+</sup> (meq/100g)	0.283	0.178	0.018	1.159	0.129
RAS	1.228	1.500	0.042	1.079	1.201
DAWP*	5.60	4.67	5.72	14.67	6.67
	$\pm 0.42$	$\pm 0.22$	$\pm 0.27$	$\pm 0.29$	$\pm 0.17$

\*Number of days that pots remain above wilting point after artificial wetting.

field capacity (–0.02 MPa) for several weeks, a period of time much longer than the ca. 5 days needed for seed germination (Figs. 1 and 2). Likewise, electrical conductivity was too low to affect the speed or the rate of germination of the species of the local flora (Table 1 and Fig. 3). In fact, most of the species present in the area were able to germinate in these two zones (App. 1). The fivefold difference in seedling density between the sites may be caused by differences in seed availability, the density of germinable seeds at P-2 was almost an order of magnitude lower than that at P-1 (Table 2).

In the pure badland zones, P-3 and P-4, both regolith water availability and salinity had detrimental effects on seed germination. High clay and sodium content in the regolith resulted in large amounts of water held below the wilting point (ca. 0.167 cm<sup>3</sup> water per cm<sup>3</sup> soil) and significantly reduced the ability of the soil to retain available water. Thus, the soil dried quickly after a rain event and reached the wilting point more quickly than the soil at other zones. After the rain had ceased, the upper 5 cm of soil at P-3 and P-4 remained above the wilting point for only 1 to 7 days. However, the actual time available for seed germination was longer, because the regolith was also moist while it was raining or if two rain events occurred close enough to each other. Thus, during the germination season of 1992, the number of consecutive days when soil water potential remained above the wilting point was 8 at P-4 and 22 at P-3 (Fig. 1). Nevertheless, the laboratory experiments showed that germination rate and speed were also affected by water potentials above the wilting point. So, reduced water potential during those days may result in a reduction in the germination rate and/or an increase in the time needed to initiate germination (Fig. 2).

In addition to the effects of reduced water potential, high soil conductivity also affected seed germination rate and speed. Soil conductivity in the regolith from P-3 and P-4 was ca. 25 ms/cm (Table 1), a salinity level that completely inhibited germination of *Phagnalon saxatile* and strongly depressed germination of *Helichrysum*

*stoechas*, *Moricandia arvensis* and *Salsola sedifforme*. Even when electrical conductivity was 15 ms/cm, the germination of *Cheirolophus inthybaceus*, *Dactylis glomerata*, *H. stoechas* and *S. sedifforme* was delayed for eight or more days. This delay would prevent seed germination of all species except *Lygeum spartum* and *S. genistoides* at P-4, and could explain the failure to detect any seedling emergence in this zone. However, at P-3 water remained available for 22 days and, therefore, some seeds of *C. inthybaceus*, *D. glomerata*, *M. arvensis*, *L. spartum* and *S. genistoides* could germinate, even at a conductivity as high as 25 ms/cm.

The characteristics of P-5 were intermediate between the two types described above. Soil conductivity at this site was ca. 4 ms/cm, relatively low and similar in magnitude to that of P-2 (Table 1). However, the duration of available water in the soil was between that of P-3 and P-4. The abundance in this zone of *M. arvensis*, completely absent in P-3 and P-4, would support this explanation. *M. arvensis* is a species severely limited by soil salinity but only moderately affected by low water potentials.

The density of seedlings that emerged in the unvegetated badland zones (P-3, P-4 and P-5) was much lower than the  $36.8 \pm 4.1$  seedling/m<sup>2</sup> reported for a badland area in the Pyrenees mountain range (Guàrdia et al. 1996). However, this latter badland was located at a higher altitude, received a much higher precipitation (ca. 1000 mm) and had different parent material. Nevertheless, the seedling density at the Pyrenees site is much lower than that in the vegetated zones at our study site (P-1 and P-2), and certainly much lower than the seed bank of the regolith. Interestingly, the seed content from the P-3 zone was similar to that reported by García-Fayos et al. (1995) for March 1991 in the same area ( $280 \pm 74$  seeds/m<sup>2</sup>), despite methodological and chronological differences. The disparity between seed reserve and emergence suggests again that seedling emergence is not limited by seed availability, but by microsite conditions.

In addition to the reduced or inhibited seed germination, seedling survival was a very important factor limiting the recruitment of plants in the badlands. However, similar rates of mortality have been reported for other semi-arid environments outside badlands (Fuentes et al. 1984; Soriano & Sala 1986; Harrington 1991; Milton 1995). Not a single individual survived or reproduced in any of the badland areas (P-3, P-4 and P-5) and only 5.3% and 2.6% survived in P-1 and P-2, respectively. The main cause of mortality was drought, as expected from the water retention characteristics of the regolith discussed above. Seedling removal by erosion occurred infrequently and was not a major factor causing seedling mortality. Similar results have been found in other badland areas (Guàrdia et al. 1996), and are also in agreement with the negligible effects of erosion on seed dynamics (García-

Fayos et al. 1995).

The patterns of seed germination and seedling survival are consistent with the current distribution of adult plants in the badlands of Petrer (unpubl. data). The presence of adult plants of species of which not a single seedling was detected, could be explained by the occurrence of extraordinarily wet periods in the past. Climatic characteristics, such as the number of rainy days and the course of precipitation and temperatures throughout the year, influence the water dynamics of the regolith and, therefore, affect germination and survival. For instance, during the germination period of 1993-1994, there were five days of continuous rain, but only eight rainy periods longer than five days have been recorded between 1950 and 1990.

The same limitations to seed germination and seedling survival, caused by the interaction between the regolith physical and chemical characteristics and the climatic conditions, may also apply to other badland areas from southeastern Spain. The five sites sampled had similar regolith characteristics and are under a climatic regime similar or even drier than that at Petrer. The time it took the regolith to reach the wilting point after being saturated with water was equally short in all sites except Vera. However, the electrical conductivity of the regolith at Vera was almost twice that of P-3 and P-4 (Tables 1 and 3), which may explain the scarce and scattered vegetation there. Although it is possible that plant populations from different badlands have developed differences in their germination patterns (Acharya et al. 1989, 1992; Meyer & Monsen 1991), we do not think that these differences are so large and generalized as to invalidate the proposed explanations. For instance, a germination experiment with two levels of electrical conductivity (14.54 and 11.73 ms/cm) showed no differences on either germination rate or speed between seeds of *H. stoechas* from the Petrer and Monnegre populations (data not shown).

Although salinity and water availability seem to explain the lack of vegetation on badland areas, erosion could also occasionally play a mayor role in plant colonization. It is well-known that erosion processes in Mediterranean climates operate in a catastrophic mode (Wainwright 1994). Several highly erosive rain events, with important geomorphological consequences, have occurred in the studied areas during the last few years (Calvo et al. 1991). These events can affect the colonization processes by completely removing the regolith seed bank, killing already established plants and seedlings, and modifying the properties of the regolith. On the other hand, extreme events such as those reported here are not exclusive to badlands areas. In other environments such as road cuttings (Mineau & Puech 1987) and degraded slopes in Mediterranean and semi-arid regions (Francis et al. 1986; Agami 1987; Gutterman & Agami



1987; Tong 1987, 1989; Dargie 1987; González-Hidalgo et al. 1990), plant colonization is also controlled by erosive, lithologic and topographic factors.

In conclusion, short-lived water availability and high salinity of the regolith seem to be the key factors limiting colonization of vegetation on the badland slopes in southeast Spain. This limitation arises from the effects of the physical and chemical characteristics of the regolith on the water retention curve, and it is increased by other characteristics such as salt toxicity, aspect and climate. Although these factors may be present in other erosive and degraded environments, it is the degree and presence of all of them that make the badland environments so unique, and what results in the almost complete lack of vegetation so characteristic of these landscapes.

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**App. 1.** Number of seedlings that emerged, reproduced and survived of all species during the recruitment period of 1993-1994 on the different surface types in the badland area of Petrer. Dotted line in the column of plant reproduction indicates species that cannot reproduce the first year. (Values are means  $\pm$  SE.)

	PETRER-1			PETRER-2			PETRER-3			PETRER-4			PETRER-5		
	Emerged	Reprod.	Survived	Emerged	Reprod.	Survived	Emerged	Reprod.	Survived	Emerged	Reprod.	Survived	Emerged	Reprod.	Survived
<i>Brachypodium retusum</i>	0.8 $\pm$ 0.7	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0
<i>Cheirolophus inthybaceus</i>	6.4 $\pm$ 2.4	—	0.8 $\pm$ 0.7	3.0 $\pm$ 0.9	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0
<i>Coris monspeliensis</i>	4.8 $\pm$ 3.5	—	0.0 $\pm$ 0.0	0.2 $\pm$ 0.2	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0
<i>Dactylis glomerata</i>	32 $\pm$ 12.0	—	0.8 $\pm$ 0.7	9.8 $\pm$ 2.9	—	0.2 $\pm$ 1.9	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0
<i>Euphorbia exigua</i>	0.8 $\pm$ 0.7	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
<i>Fumana ericoides</i>	8.0 $\pm$ 3.8	—	0.0 $\pm$ 0.0	0.8 $\pm$ 0.4	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0
<i>Helianthemum syriacum</i>	0.8 $\pm$ 0.7	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0
<i>Helichrysum stoechas</i>	22.4 $\pm$ 10.4	—	0.0 $\pm$ 0.0	2.4 $\pm$ 0.9	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0
<i>Hippocrepis glauca</i>	0.8 $\pm$ 0.7	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
<i>Lygeum spartum</i>	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	1.0 $\pm$ 0.5	—	0.2 $\pm$ 0.2	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0
<i>Moricandia arvensis</i>	152.8 $\pm$ 36.8	8.0 $\pm$ 6.3	0.8 $\pm$ 0.7	25.8 $\pm$ 6.4	0.2 $\pm$ 0.2	0.6 $\pm$ 0.3	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
<i>Phagnalon saxatile</i>	7.2 $\pm$ 3.8	—	0.0 $\pm$ 0.0	3.8 $\pm$ 0.8	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
<i>Plantago albicans</i>	9.6 $\pm$ 7.7	—	0.0 $\pm$ 0.0	0.2 $\pm$ 0.2	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0
<i>Sedum sediforme</i>	22.4 $\pm$ 13.0	—	4.0 $\pm$ 3.6	6.8 $\pm$ 1.8	—	0.2 $\pm$ 0.2	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0
Not Determined	4.0 $\pm$ 1.6	—	0.0 $\pm$ 0.0	1.2 $\pm$ 0.5	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	—	0.0 $\pm$ 0.0
<b>TOTAL</b>	<b>272.8 <math>\pm</math> 85.4</b>	<b>8.8 <math>\pm</math> 13.7</b>	<b>6.4 <math>\pm</math> 4.2</b>	<b>54.8 <math>\pm</math> 9.2</b>	<b>0.2 <math>\pm</math> 0.2</b>	<b>1.2 <math>\pm</math> 0.5</b>	<b>0.8 <math>\pm</math> 0.4</b>	<b>0.0 <math>\pm</math> 0.0</b>	<b>0.0 <math>\pm</math> 0.0</b>	<b>0.0 <math>\pm</math> 0.0</b>	<b>0.0 <math>\pm</math> 0.0</b>	<b>0.0 <math>\pm</math> 0.0</b>	<b>9.8 <math>\pm</math> 3.2</b>	<b>0.0 <math>\pm</math> 0.0</b>	<b>0.0 <math>\pm</math> 0.0</b>