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Seed population dynamics on badland slopes in southeastern Spain

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Abstract. The dynamics of seed population on slope surfaces were studied to test the hypothesis that the lack of vegetation on badlands is caused by seed removal by erosion. The initial soil seed bank and two years of seed rain and seed removal by erosion were estimated in two small catchments, and a seed balance was constructed. In addition, six rainfall simulation experiments were performed to test the susceptibility of seeds to be removed by overland flow. A variety of soil surface conditions, rainfall characteristics and plot sizes were used in these experiments.

Soil seed bank densities are low, but enough for the development of plant cover. Seed losses due to erosion after natural rains were low (< 13 %), and in agreement with seed losses from simulated rainfall experiments. After two years, seed inputs in the seed rain were greater than seed outputs through seed removal, which resulted in a continuous increase in the numbers of seeds in the soil bank. These results point out that seed removal by erosion is not the key factor explaining the lack of vegetation on badlands. It is suggested that other factors, such as those related to seed germination and seedling survival, may play an important role.

Keywords: Colonization; Erosion; Seed rain; Soil seed bank.

Nomenclature: Tutin et al. (1964-1980).

Introduction

Badlands is a term of current use in earth sciences, especially in geomorphology. The term indicates a distinctive land form that develops in semi-arid regions, characterized by a highly dissected topography, very high drainage rates, rapid erosion rates and a sparse or even non-existant plant cover (Bryan & Yair 1982).

Important data are available on the geomorphological implications of the erosion processes involved in badland development (Bryan & Yair 1982; Calvo & Harvey 1989; López-Bermúdez & Romero-Díaz 1989; Harvey & Calvo 1991), but little is known about the implications for vegetation, especially plant colonization. The main topics in badland-vegetation studies have been the distribution of species and communities and its relations with physiography, soil properties and erosion rates (Brown 1971; Butler et al. 1986; Korzhenevskiy & Klyukin 1989; Alexander & Calvo 1990; Guardia & Ninot 1992). However, none of these studies looked at why there is almost no vegetation in badland slopes, although they implied that erosion processes are the main reason. In a general model on erosion and plant competition, the removal of sediments and litter has been proposed as the mechanism through which erosion influences vegetation development, because it affects plant establishment, growth and survival (Thornes 1985, 1990).

We hypothesized that the removal by erosion of seeds arriving at the soil surface is the main factor explaining the scarcity or the absence of vegetation on badland slopes. To test this hypothesis, we quantified the balance between seed inputs and outputs at the catchment scale in a badland area, and experimentally tested the susceptibility of the seeds to be removed by soil erosion at the plot scale.

Study site

This study was performed near Petrer, in the province of Alicante, Spain (38° 30' N, 0° 45' W.) The region has a semi-arid Mediterranean climate, characterized by dry summers lasting 4-5 months. Average annual rainfall is 370 mm, and average annual temperature is ca. 16 °C. The badlands occur on both sides of a small valley cut into Cretaceous (Senonian) marls (Anon. 1978). The general orientation of the valley is E-W, and badland development and extension differ on north- and south-facing slopes. On the south-facing slopes, badlands extend from the valley floor to the divide. However, on the north-facing slopes badland extension is limited, covering only the lower section of the slopes (Calvo & Harvey 1989). The slopes are very steep, ranging from 25° to 50°, and the regolith surface is characterized by a crack morphology. The dominant erosion processes are rill and interrill overland flow together with local piping and mass movements. Erosion rates recorded in these badlands are around 2000 g m^{-2} hr^{-1}, among the highest reported for southeast Spain (Calvo & Harvey 1989; Calvo et al. 1992).

Natural vegetation in this region has been highly influenced by human activity for centuries. The current vegetation is the result of the degradation of a dense and tall shrubland of the association *Rhamno-Quercetum cocciferae*. It consists of isolated individuals of *Moricandia arvensis* and *Lygeum spartum*, leaving most of the soil completely bare. Vegetation of the colluvial soils on the south slopes and terraces adjacent to the badlands is a sparse and low scrubland dominated by *Lygeum spartum, Salsola genistoides, Moricandia arvensis, Cheirolophus intybaceus, Helichrysum stoechas, Fumana ericoides, Sedum sediforme,* and *Phagnalon saxatile*. Vegetation of the adjacent north facing slopes is denser, especially on the upper parts where the colluvial soils are deeper. It is dominated by *Coronilla minima, Brachypodium retusum, Cistus albidus, Bupleurum fruticescens, Erica multiflora, Helictotrichon filifolium* and *Fumana ericoides*.

Methods

Seed population dynamics

A two-year complete seed balance was calculated in two adjacent small catchments. After estimating the initial soil seed bank, seed inputs and outputs were measured monthly and summarized for the study period. Measurements started in March 1991 and finished in April 1993. The areas of the catchments, to be called C-1 and C-2, were 245 and 335 m^2 respectively.

The initial soil seed bank in the catchments was sampled in March 1991, after seed dispersal and germination. At each catchment, 30 soil cores (5.5 cm diameter, 6 cm depth) were extracted, following an even design from the top to the bottom of the slopes. The samples were sieved through a 0.25-mm mesh and examined using a 7× - 40× microscope to determine the presence and amount of seeds of each species. Damaged and empty seeds were disregarded. The seed densities obtained were extrapolated to the catchment area, in order to estimate total seed numbers. The initial seed pools of the catchments were compared using a non-parametric Mann-Whitney test.

Seed inputs were measured monthly in three 0.34-m^2 seed rain traps installed on the upper, medium and lower parts of each catchment. Each trap consisted of four 33-cm diameter funnels kept 50 cm above the ground using a metal frame. Each funnel had a 0.25-mm mesh size bag attached to the end. The bag was replaced monthly, its content examined in the microscope, and the total number of seeds of each species determined. Damaged and empty seeds were rejected. The seeds of bird-dispersed species were discarded, because their presence was considered a consequence of the attractiveness of the trap for the birds. Seed predation by animals was not observed at any trap for the duration of the study. Total seed rain in each catchment was calculated by extrapolating the sampled densities, and compared yearly using a Mann-Whitney test.

Seed outputs were measured in sediment traps installed at the outlets of both catchments. The traps consisted of a metal frame holding a 0.25-mm mesh size bag that intercepted the sediments carried out by the run-off water. After each rainfall which led to run-off, the bags were replaced, their contents weighed and sieved, the sediments examined in the microscope, and the number of seeds of each species determined. Damaged and empty seeds were disregarded. The amount and intensity of the rainfall were measured in two rainfall gauges located at the higher and lower part of the study area.

Simulated rainfall experiments

A total of six rainfall simulation experiments on dyed seeds were performed, covering a variety of site and rainfall conditions, described in Table 3. Experiments SL-01 to SL-03 were carried out in February and March 1992, using a sprinkler rainfall simulator (Calvo et al. 1988). Plot size was 0.24 m^2, and rainfall intensity 55 mm/hr. The plot size used in these experiments was small, so new experiments using a larger sprinkler rainfall simulator were carried out in October and November 1992 (SL-04 to SL-06). In these experiments plot size was 3 m^2 and rainfall intensity 45 mm/hr. Rainfall intensities are similar to those of the heavier rainstorms registered in the area.

Seeds of *Cheirolophus inthybaceus, Cistus albidus, Helichrysum stoechas* and *Moricandia arvensis* were collected from populations living in the study area, air-dried in the laboratory and dyed with blue aniline. These species were chosen because of their dominance in the seed bank and adjacent vegetation. 24 seeds of each species were used in experiments SL-01 to SL-03 and 60 in the experiments SL-04 to SL-06. The seeds were placed on the soil surface, in the centre of each plot. During the rain simulation, samples of the overland flow were collected every minute. Run-off water, sediment content and seed losses were determined at each sample. The results from this experiment were not statistically analyzed because its objective was to experimentally verify the rates of seed losses obtained in the seed traps and thus there was no replication.

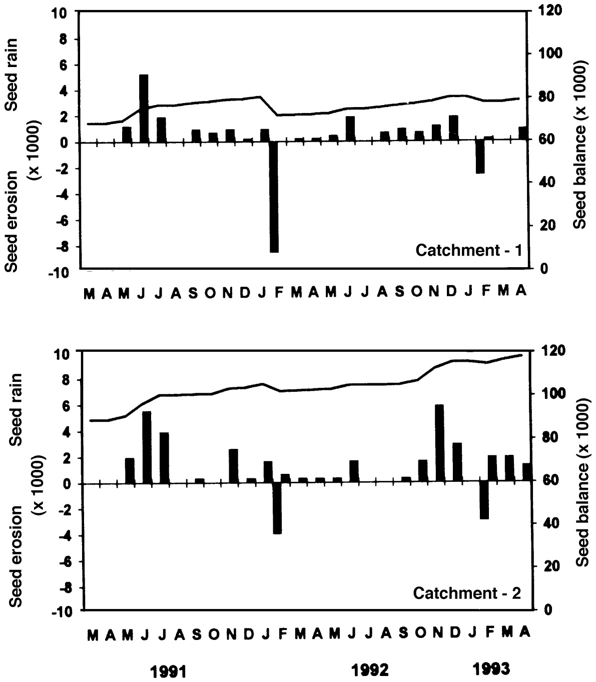

Fig. 1. Seed population dynamics in catchments C-1 and C-2. The initial value corresponds to the soil seed bank. (vertical bars=seed rain and seed removal by erosion; solid line=seed balance).

Table 1. Initial number of seeds in the soil bank and total number of seeds in two years of seed rain and seed removal by erosion, with indication of their dispersal agent (W=wind, X=others). The data are refered to the total study area (580 m^2).

Species	Dispersal agent	Seed bank	Seed rain	Seed removal
Sedum sediforme	W	48739	6957	4392
Erica multiflora	W	38835	4282	3043
Phagnalon saxatile	W	31582	5651	2578
Helichrysum stoechas	W	4692	6192	1891
Crepis vesicaria	W	4692	2348	505
Pallenis spinosa	X	4692	0	162
Lygeum spartum	W	4692	0	0
Sonchus oleraceus	W	3431	2411	683
Moricandia (2 spp.)	X	3431	326	1046
Salsola genistoides	W	3431	979	477
Dittrichia viscosa	W	0	9369	1102
Phragmites australis	W	0	5675	126
Dactylis glomerata	X	0	2762	916
Stipa parviflora	W	0	1218	0
Ulmus minor	W	0	955	0
Bupleurum fruticescens	X	0	803	0
Senecio linifolius	W	0	326	0
Piptatherum miliaceum	X	0	326	0
Stipa tenacissima	W	0	239	0
Cistus albidus	X	0	0	126
Thymus (2 spp.)	X	0	0	71
Globularia alypum	W	0	0	66
Brachypodium retusum	X	0	0	63
Foeniculum vulgare	X	0	0	63
Cheirolophus intybaceus	X	0	0	63
Teucrium pseudochamaepit.	X	0	0	3
Asteraceae (7 spp.)	W	8123	4044	385
Inderminated (6 spp.)	X	3431	2436	474

Results

Seed population dynamics

Initial soil seed bank density was 280 ± 74 and 266 ± 85 seeds/m^2 in catchments C-1 and C-2, respectively (see García-Fayos & Recatalá 1992 for additional information). These values are equivalent, as shown by the Mann-Whitney test ($U = 4.00$, $p = 1.000$, d.f = 1). Three species, *Sedum sediforme*, *Erica multiflora*, and *Phagnalon saxatile*, account for 75 % of the total seed bank (Table 1), a dominance that may be explained by the seed production of these species, the larger of all species in the study area. In addition, *Erica multiflora* disperses its seeds in February and March, when sampling was conducted. However, *Sedum sediforme* and *Phagnalon saxatile* disperse in October and May, respectively.

Seed inputs in catchments C-1 and C-2 were 52 ± 10 and 37 ± 7 seeds $m^{-2} yr^{-1}$ in the first year, and 53 ± 11 and 54 ± 13 seeds $m^{-2} yr^{-1}$ in the second year, respectively. These differences between catchments were not statistically significant in either year (Mann-Whitney test: $U = 7.00$, $p = 0.2752$, d.f. = 1 for the first year, and $U = 4.00$, $p = 0.8273$, d.f. = 1 for the second year). Seed inputs were continuous over the year, although some variability existed. In general, seed rain tended to be lower during summer and winter. The most abundant species in the seed rain, accounting for more than 60 % of the total, were *Dittrichia viscosa*, *Sedum sediforme*, *Helichrysum stoechas*, *Phragmites australis*, *Phagnalon saxatile* and *Erica multiflora* (Table 1).

Seed outputs for the two-year period accounted only for 12.5 % and 5.6 % of the total seed bank in catchments C-1 and C-2 respectively, including the two-year seed rain. For the duration of the study, there were only three rainfall events that produced seed losses, on 25 October 1991, 18 - 23 February 1992 and 3 - 8 February 1993. Again, *Sedum sediforme*, *Erica multiflora*, *Phagnalon saxatile*, *Helichrysum stoechas* and *Dittrichia viscosa* were the main species in the seed output, accounting for over 65 % of total losses (Table 2).

After two years, in both catchments, seed inputs in the seed rain were greater than seed outputs through seed removal, which resulted in a positive balance (Fig. 1).

Table 2. Rainfall events producing seed losses from March 1991 to April 1993 at catchments C-1 and C-2.

Date	Total precipitation	Maximum intensity	C-1 Seed losses n	C-1 Seed losses %	C-2 Seed losses n	C-2 Seed losses %
25th October 1991	5.6 l/m^2	59 mm/h	0	0	3	< 0.1
18-23th February 1992	97 l/m^2	12 mm/h	8577	10.7	4265	4
3-8th February 1993	66 l/m^2	14 mm/h	2712	3.4	2970	2.6

Simulated rainfall experiments

Seed losses were low in all experiments, less than 13 % of the total seeds present, despite the conditions of the experiment (Table 3). Seed losses increased as slope angle and rain duration increased, and decreased as total transport length increased. This behaviour is similar to that of sediment particles (Govers 1989; Parsons et al. 1993). However, increased run-off caused by high initial soil moisture did not result in an increase in seed losses, as expected with soil sediment particles (Govers 1991).

Each species showed a different susceptibility to removal (Table 4). While some species, such as *Cheirolophus inthybaceus*, presented high losses in all experiments, others, such as *Helichrysum stoechas* and *Moricandia arvensis* presented only least losses in one experiment.

Discussion

Soil seed densities were low, but there were seeds available for germination in the soil of the slopes in both catchments in 1991, 1992, and 1993, as data from the seed bank and seed balance showed. This result is in disagreement with the hypothesis that removal by erosion of the seeds arriving to the soil surface would be the main factor explaining the scarcity or absence of vegetation on badland slopes. Seed densities reported here, about 275 seeds/m^2, are comparable to those found in the Sonora and Mohave deserts and in the semi-arid sagebrush steppes of Utah. Soil in these areas contained 400, 269 and 92 seeds/m^2, respectively (Kemp 1989). The presence of vegetation in these ecosystems suggests that the lack of vegetation on the badlands cannot be explained only by the seed removal hypothesis.

The spatial distribution of the seed bank was highly heterogeneous. The frequency distribution of the number of seed in each sample has a skewed pattern; few samples have a large number of seeds but most have a few or none (Fig. 2). This pattern of highly clumped seeds is frequent in desert seed banks (Nelson & Chew 1977; Reichman 1984; Kemp 1989).

The seed rain values reported in this study are very low, compared with values from other environments where similar seed traps and methodology were used. Over a period of two years, average seed rain in Petrer ranged from 45 to 52 seeds m^{-2} yr^{-1}. Reported values in the literature range from 45 - 175 seeds m^{-2} yr^{-1} in the open ground of a fynbos community in S Africa (Manders 1990), to 7677 - 9622 seeds m^{-2} yr^{-1} in a recently burnt out plantation of *Cryptomeria japonica* in Japan (Kominami 1988), and to 35 000 seeds m^{-2} yr^{-1} in an old-field community in Central New York (USA) (Morris et al. 1986).

Seed losses through natural rainfall over the study period were lower than expected, although the results agree with those obtained in the rainfall simulation experiments. Maximum seed losses observed in the simulation experiments were 12.5 % of the total after 110 minutes of a 55 mm/hr rainfall. The probability of a rainfall of higher intensity and duration occurring is very low, and therefore the probability of complete

Table 3. Site and experimental conditions of the rainfall simulations, and rate of seed losses.

	SL-01	SL-02	SL-03	SL-04	SL-05	SL-06
Transport length (cm)	25	25	25	120	120	120
Slope (degrees)	25	40	40	40	45	45
Rain intensity (mm/h)	55	55	55	45	45	45
Rain duration (minutes)	40	40	110	40	40	40
Previous soil moisture	dry	dry	dry	dry	dry	wet
Run-off average (mm/h)	36.7	47.4	50.3	17.5	24.2	40.6
Erosion ($gr \cdot l^{-1} \cdot m^{-2}$)	1893.6	2505.5	3422.9	3212.0	3855.9	7099.4
Seed losses (%)	2.27	8.33	12.50	1.14	0.68	0.69

Table 4. Percentage of seed losses per species after rainfall simulations.

Experiment	*Cheirolophus intybaceus*	*Cistus albidus*	*Helichrysum stoechas*	*Moricandia arvensis*
SL-01	4.17	0.00	4.17	0.00
SL-02	25.00	8.33	0.00	0.00
SL-03	37.50	8.33	0.00	4.17
SL-04	3.33	3.33	0.00	0.00
SL-05	1.67	0.00	0.00	0.00
SL-06	4.35	0.00	0.00	0.00

depletion of the soil seed bank is remote. The results from the seed rain data suggest that, even if the soil seed bank is completely removed, the arrival of seeds would be enough to ensure a rapid re-establishment of the seed bank.

The same set of species dominates the soil seed bank and the seed input and output, indicating that the results are consistent. However, there was a relative lack of effectiveness of the soil seed bank and seed rain sampling design, because seeds of some species that appeared in the sediment traps were not found in the seed bank or rain (Table 1). This can most likely be attributed to the seed dispersal mechanisms of these species, which were either short distance, ballistic dispersion mechanisms (*Cistus albidus*), short pedicels (*Teucrium pseudochamaepitys*, *Thymus vulgaris* and *T. longiflorus*) or barochorous species (*Brachypodium retusum, Foeniculum vulgare* and *Cheirolophus inthybaceus*). As a consequence, total seed input was underestimated. Despite this fact, seed inputs were greater than outputs over the study period, and the seed balance showed a continuous increase in the number of seeds in both catchments. The positive results of the two-year seed balance may be caused by decreased seed losses due to scarce, low intensity precipitation during the study period. However, this low precipitation also affected seed production, thus reducing the amount of seeds available as inputs. Many individuals of *Erica multiflora* did not bloom in the winter of 1992 and the mortality of mature plants of *Fumana ericoides* from February 1991 till February 1992 was as high as 50 % in some stands.

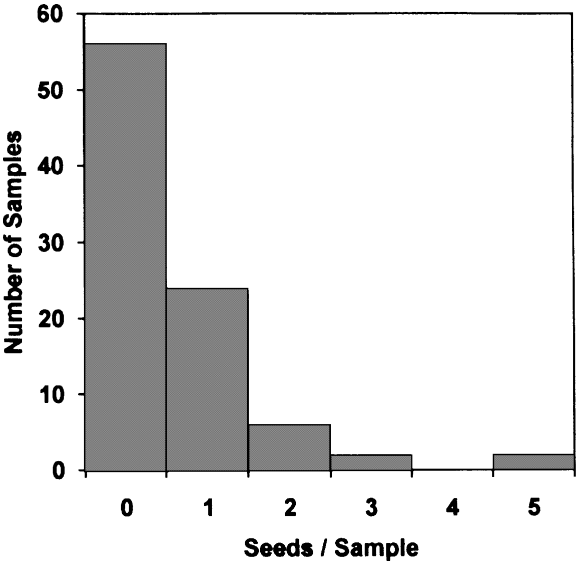

Fig. 2. Distribution of the soil seed bank samples that contained seeds (*n* = 90).

We can conclude that seed removal is not the cause of the lack of vegetation in the slopes of badlands. The presence of available seeds in the soil bank, the low losses caused by rainfall, and the number of seeds greater in the inputs than in the outputs support this conclusion. These results are reinforced by the agreement between observational and experimental data from the rain simulators. Low seed availability alone cannot explain the lack of vegetation in the badlands, and thus other factors such as seed germination and seedling survival should be considered.

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