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REGULAR ARTICLE

Soil water availability effects on seed germination account for species segregation in semiarid roadslopes

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Abstract Previous studies report that the low colonisation success on eroded roadslopes of semiarid environments is controlled by microsite limitations. We predicted that soil water availability, through its effect on seed germination, is a determinant factor in the colonisation process of roadslopes in semiarid environments. Moreover, we predicted that the success of species establishment on the harshest roadslope conditions (i.e., south-facing roadcuts) is either due to the ability of seeds to germinate fast at low water potentials (colonising species) or to the ability of plants to sprout (resistant species). Specifically we present evidence for: (1) soil drying occurs faster on roadcuts than on roadfills after a rainfall event; (2) germination is a filtering process that influences the success of species establishment on roadslopes; (3) species able to colonise successfully south-facing roadcuts have higher germination rates and a shorter time to germination under water-stress conditions than species able to colonise successfully but exclusively the most favourable roadslopes (i.e., roadfills); (4) species that live on south-facing roadcuts and have the ability to sprout do not necessarily germinate with germinating rates and speeds as high as species that colonise successfully these slopes but are unable to sprout. To test these hypotheses we compared water dynamics in the soil among roadslope types and aspects as well as the seed ability to germinate at low water potentials among species showing different regeneration strategies and establishment success on roadslopes. Soil water availability after rainfalls occurring during the germination period played a major role in the germination of seeds. The patterns of seed germination under water-stress conditions were consistent with the success of colonising species on roadslopes and with the distribution of adult plants in the roadslopes 8 years after these latter were built. We discuss the usefulness of these results for the improvement of revegetation projects in semiarid areas by means of an appropriate selection of species adapted to the local environmental conditions. We suggest that the ability of species to germinate under water stress could be an indication of a species' potential for success under semiarid conditions.

Keywords Colonisation · Ecological filters · Erosion · Regeneration strategy · Soil water potential · Resprouter

Introduction

The main factors that have been described as potentially limiting for plant recruitment are seed

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dispersal and microsite availability (Ericksson and Ehrlén 1992; Zobel et al. 1998; Butaye et al. 2002). The relative influence of these factors in plant recruitment depends on many characteristics of the local and regional environments (regional flora and fauna composition, proximity of the local flora, local environmental conditions, disturbance regime and severity) (i.e., Primack and Miao 1992; Turnbull et al. 2000; Verheyen and Hermy 2001; Tofts and Silvertown 2002; Foster and Tilman 2003).

In man-disturbed environments, several studies have revealed that plant colonisation is often limited by the too large distance between appropriate seed source areas and the target areas (Kirmer and Mahn 2001 for abandoned lignite-mining areas and Novák and Prach 2003 for basalt quarries). Roadslopes are man-disturbed environments that have received little attention to this respect, although they present favourable conditions to analyze the relative importance of seed availability versus microsite limitations in competition- and predation-free areas (Bochet et al. 2007). However, in semiarid conditions, recent studies have analysed the relative importance of seed availability and microsite limitations in roadslope colonisation (Alborch et al. 2003; Tormo et al. 2006; Bochet et al. 2007). These studies aimed at explaining the general low success of roadslope revegetation and the differences in revegetation success between roadslope types (roadcut and roadfill) and aspects (north and south) in semiarid conditions (Bochet and García-Fayos 2004). These authors found differences in species composition between roadslope types and aspects and recorded low vegetal covers especially on roadcuts (7.4% vs. 59.4% for roadfills) and south-facing slopes (26.7% vs. 47.0% for north-facing slopes). Similar results were obtained in natural semiarid ecosystems as regard the slope aspect (Kutiel and Lavee 1999; Sternberg and Shoshany 2001).

Alborch et al. (2003) and Tormo et al. (2006) demonstrated by means of observational and experimental approaches, respectively, that roadslope conditions were more limiting to plant colonisation than seed availability in the semiarid environments they studied. Slope angle, type and aspect were identified as the primary forces shaping the pool of species that established on semiarid roadslopes (Estarlich et al. 1992; Tolosa 2001; Bochet and García-Fayos 2004). Moreover, Bochet and García-Fayos (2004) reported that the slope characteristics influenced the general soil conditions of the roadslopes, especially the soil water availability for plants, which in turn may affect plant germination and establishment.

As it regulates the seed water intake (Evans and Etherington 1990), soil water potential is one of the main factors in addition to temperature that influences seed germination in arid and semiarid environments (Potter et al. 1986; Flores and Briones 2001; Lu et al. 2006). Several studies revealed that seeds of some arid plant species have an adaptation to germinate under water stress at water potentials as low as −1.0 MPa (Schütz et al. 2002) and even −1.5 MPa (Evans and Etherington 1990; Briedé and McKell 1992; Neil et al. 2003), and that desert plants have faster germination than plants living in wetter areas (Jurado and Westoby 1992). Accordingly, the ability to germinate fast and at low water potentials are advantages that may be vital for species colonising arid and semiarid environments (Evans and Etherington 1990).

Moreover, as roadcuts are built on soils where previously established vegetation exists, plant survival to both above- and belowground damage and the ability to sprout may also be a worthwhile strategy to ‘‘colonise’’ water-stressed slopes that suffer high rates of erosion. Resprouters have generally been related to disturbances such as fire, hurricane damage and herbivory (Bond and Midgley 2001; Vesk and Westoby 2004). However, some few studies have also reported their importance in relation to erosion and drought (Sakai et al. 1997; Ojeda 1998; Guerrero et al. 2006).

In this study, we hypothesise that reduced water availability, through its effects on seed germination, is a limiting factor to the colonisation of roadslopes in semiarid conditions. Moreover, we hypothesise that the success of species establishment on the harshest roadslope conditions (i.e., south-facing roadcuts) is either due to the ability of seeds to germinate fast at low water potentials (colonising species) or to the ability of plants to sprout (resistant species). More specifically, to test these hypotheses, we will check that: (1) soil drying occurs faster on roadcuts than on roadfills after a rainfall event; (2) germination is a filtering process that influences the success of species establishment on roadslopes; (3) species able to colonise successfully south-facing roadcuts (i.e., the harshest roadslopes in relation to water availability) have higher germination rates and a shorter time to germination under water-stress conditions than species able to colonise successfully but exclusively the most favourable roadslopes (i.e., roadfills); (4) species that live on south-facing roadcuts and have the ability to sprout do not necessarily germinate with germinating rates and speeds as high as species that colonise successfully these slopes but are unable to sprout.

Materials and methods

Study site

The study area is located in the region of ''La Plana de Utiel-Requena'' in the Valencian Community, East Spain (39°29′ N; 1°06′ W). The selected roadslopes are comprised in the road section between km 267 and km 307 of A-3 highway that links Madrid with Valencia. Soils are derived from calcareous marls and clays of Tertiary origin (García 1996). The climate is Mediterranean semiarid, with a mean annual precipitation and temperature of 418 mm and 14.2°C, respectively (Pérez 1994). Rainfall variability is high within and between years. Rainfall events are few and unreliable, in autumn they can be very intense with a high erosivity, and rain is almost absent in summer (<40 mm). The surrounding vegetation adjacent to the roadslopes is mainly covered by cultivated fields of vineyards, almond and olive groves, but some small patches of shrublands and open forests still remain between the cultivated fields. A broader description of the study site and roadslope characteristics can be found in Bochet and García-Fayos (2004) and Bochet et al. (2007).

Soil water dynamics in relation to rainfall events

Four humidity sensors (HOBO Soil Moisture smart sensor, ECH_2O^{TM}) were located in the soil at a depth of 5 cm, at mid-slope, one in each roadslope category, in order to record the temporal variability of soil water content during two successive germination periods (from 01/10/2002 to 30/04/2003 and from 01/10/2003 to 30/4/2004). Previous studies showed that over 95% of all seeds are found at that depth (García-Fayos et al. 1995). Measurements of soil water content were recorded into data loggers every hour. Precipitation was measured by a raingauge during the same time period.

Soil samples were taken at a depth of 5 cm in January 2004 in 16 roadslopes (four of each roadslope category: north- and south-facing roadcut and north- and south-facing roadfill). On each slope, three sub-samples were taken at mid-slope. They were air-dried, sieved through a 2 mm sieve and soil moisture characteristic curve determined using a Richard's standard pressure chamber (Klute 1986). Soil water content (cm^3 water/100 cm^3 soil), was determined in a wide range of values, ranging from saturation to the permanent wilting point (0; −0.01; −0.02, −0.05, −0.35 and −1.50 MPa).

To estimate the period of time during which soil water remained available for plants after a rain event in each roadslope category, we compared the number of days that the soil water content in the field remained above the value determined in the laboratory for each pressure class among the four roadslope categories. This number of days was calculated on the basis of an 8 days long rain event of 49 l/m^2 that occurred on the 12/10/2003.

Germination under different water potentials

Twenty-two species were selected among the local roadslope flora according to their establishment success on the roadslopes in order to test germination characteristics under a soil water potential gradient. Establishment success was assessed after performing vegetation surveys in spring and early summer on 46 roadslopes (10 north- and 11 south-facing roadcuts and 11 north- and 14 south-facing roadfills), including the 16 ones selected for soil sampling. Roadslopes were 6–8 years old at the time of vegetation survey. In all cases, roadslope length exceeded 5 m, slope width exceeded 20 m and slope angle was comprised between 25° and 45°. Rock outcrops did not reach in any case 5% of the roadslope surface. The success of species establishment was assessed by taking into consideration both the abundance and frequency of the species in the four categories of roadslopes. Species relative abundance was assessed in each slope after defining abundance classes from 0 to 3 (class 0: no single individual; class 1: less than 10 individuals scattered along the slope; class 2:

either individuals present regularly all along the slope or local monospecific patches of individuals; class 3: dominant species present abundantly all along the slope). A species was considered successful if it was present in more than 50% of the roadslopes surveyed from one category and if it had an abundance equal or greater than class ‘‘2’’ in at least one-third of the roadslopes of this category where the species was present. When a species did not fulfil both requirements, it was considered as ‘‘unsuccessful species’’.

The 22 species selected were grouped as follows: (1) ‘‘general successful species’’ (Gen) that were present successfully in all types of roadslopes; (2) ‘‘roadfill successful species’’ (R_f) that were exclusively successful on roadfills; (3) ‘‘south-facing roadcut successful species’’ (SR_c) that were present successfully, but not necessarily exclusively, on south-facing roadcuts (i.e., the most adverse slopes) and (4) ‘‘unsuccessful species’’ (Un) unable to establish successfully on any single roadslope category (Table 1). Furthermore, distinction between sprouting and non-sprouting species was made within the group of ‘‘south-facing roadcut successful species’’.

Seeds from the 22 selected species were harvested from adjacent areas to the roadslopes during the summer preceding germination experiments, except for *Santolina chamaecyparissus*, *Brachypodium retusum* and *Genista scorpius* which were obtained from a local seed supplier (Intersemillas, S.A.). The seeds were dried and stored in paper bags at room temperature for one to four months until the experiment started. Legume seeds were scarified (submerged in sulphuric acid 95–98% for 5 min, except *Genista scorpius* and *Medicago orbicularis* seeds that were submerged for 10 min). As *Anacyclus clavatus* and *Calendula arvensis* showed seed dimorphism, the most performant morphotype of each species was chosen to be included in the statistical analyses.

We tested the effects of water potential on the germination time and rate at five levels of water potential (0; -0.01; −0.05; −0.35 and −1.50 MPa). In order to mimic unaltered field capacity conditions of Mediterranean soils, the −0.01 MPa water potential was preferred to the −0.02 MPa (Bruand et al. 1996; Ingelmo et al. 1998). Water potential was simulated using polyethylene glycol (PEG 6000). The appropriate concentration for each level of water potential was determined based on standard equations (Michel et al. 1983). Distilled water served as a control. Germination experiments of each species were replicated four times. A replicate consisted of 50 seeds placed in a 9-cm diameter Petri dish on a filter paper moistened initially with 5 ml of either distilled water or treatment solution. Large-seeded species (*Avena barbata* and *Calendula arvensis*) had eight replicates with 25 seeds each. Petri dishes were sealed with PVC sheets to reduce loss of water and they were placed in a temperature-controlled plant growth chamber with 13 h light at 15°C during day-time and 11 h dark at 9°C during night-time simulating field conditions at the time of boom germination within the germination period (Tormo 2007; unpublished data). The dishes were checked daily until the first seed in each Petri dish germinated. Radical emergence from the seed coat was used as the criterion for germination. From then on, germinated seeds were counted and removed twice per week for a total period of 33 days. At the end of this period, the viability of the seeds that had not germinated was checked using the Tetrazolium test, and only germinated plus ungerminated but viable seeds were considered for calculations.

‘‘Germination rate’’ was calculated as the percentage of germinated seeds over 33 days and the ‘‘germination time’’ as the number of days until the first germination occurred. When no single seed germinated in a Petri dish, a ‘‘34’’ days fixed value, greater than the observation time period, was assigned to this replicate for statistical analysis. Moreover, as low seed viability was observed in the species *Plantago lanceolata* (<50%) causing high variability among replicates, Petri dishes were randomly grouped two by two, giving rise to two replicates of 100 seeds instead of four of 50 seeds.

Germination time was compared with the number of days water remained available above a specific water potential (equivalent to a soil-moisture content measurement determined in the laboratory) in the four categories of roadslope to explain the relative success of species establishment in the different roadslope categories.

Statistical analyses

The influence of slope type and aspect on the soil capacity to retain water at different water potentials determined in laboratory conditions was analysed

Table 1 Species selected for the study according to their establishment success on roadslopes (Gen = general successful species; R_f = roadfill successful species; SR_c = south-facing roadcut successful species (not exclusively); Un = unsuccessful species) and their regeneration strategy (sprouter versus non-sprouter)

Establishment success	Gen	Rf	SRc		Un
Regeneration strategy			Non-sprouter	Sprouter	
Species					
Alyssum simplex (*Brassicaceae*)	X		X		
Anacyclus clavatus (*Asteraceae*)	X		X		
Avena barbata (*Poaceae*)	X		X		
Bromus rubens (*Poaceae*)	X		X		
Diplotaxis erucoides (*Brassicaceae*)	X		X		
Santolina chamaecyparissus (*Asteraceae*)			X[a]		
Astragalus hamosus (*Fabaceae*)					X
Brachypodium retusum (*Poaceae*)					X
Helichrysum italicum (*Asteraceae*)					X
Medicago orbicularis (*Fabaceae*)					X
Plantago lanceolata (*Plantaginaceae*)					X
Plantago sempervirens (*Plantaginaceae*)					X
Calendula arvensis (*Asteraceae*)		X			
Carduus pycnocephalus (*Asteraceae*)		X			
Filago pyramidata (*Asteraceae*)		X			
Hirschfeldia incana (*Brassicaceae*)		X			
Medicago minima (*Fabaceae*)		X			
Convolvulus arvensis (*Convolvulaceae*)				X	
Eryngium campestre (*Apiaceae*)				X	
Euphorbia serrata (*Euphorbiaceae*)				X	
Genista scorpius (*Fabaceae*)				X	
Plantago albicans (*Plantaginaceae*)				X	

[a] *Santolina chamaecyparissus* was successful exclusively on south-facing roadcuts

with repeated measures ANOVA using the SPSS v.12.0 statistical package (SPSS Inc., Chicago, IL, USA).

The effect of water potential and species success (successful vs. unsuccessful) on the germination rate and time was analysed by a two-way GLM with quasibinomial and quasiPoisson functions, respectively, and with species nested to species success (R v.2.1 software, http://www.cran.r-project.org/). The effect of water potential and regeneration strategy of species (sprouter vs. non-sprouter) was also analysed by a two-way GLM. Three post-hoc comparisons were performed: Gen versus Un; Gen versus R_f; SR_c sprouter versus SR_c non-sprouter to test for the hypotheses 2, 3 and 4, respectively, stated in the introduction.

Results

Soil moisture characteristic curves

A general decrease of soil water content as water potential decreases was observed in laboratory conditions for the four roadslope categories studied ($F = 1.418$; $p = 0.240$ for the interaction between type and aspect, Table 2). However, there was a significant effect of roadslope type, with a higher water content for roadfill soils than for roadcut ones ($F = 49.529$; $p = 0.000$). Soil water content was 3–9% higher in roadfills than in roadcuts at the wilting point and saturation, respectively (Table 2). These differences are the expression of the textural and structural characteristics of the roadslope soils that influence

Table 2 Mean soil water content (% V/V) and standard error according to the different roadslope categories at 6 different levels of water potential

Roadslope category	Water potential (MPa)					
	0	−0.01	−0.02	−0.05	−0.35	−1.50
North roadfill	64.75 ± 1.03	31.50 ± 1.32	27.16 ± 0.68	22.02 ± 0.03	14.37 ± 1.33	12.32 ± 0.52
South roadfill	59.25 ± 1.70	33.00 ± 2.35	25.43 ± 1.26	20.03 ± 0.72	14.25 ± 0.65	11.05 ± 0.47
North roadcut	53.08 ± 0.42	28.75 ± 1.30	23.35 ± 2.62	16.75 ± 1.11	11.63 ± 1.00	8.42 ± 0.59
South roadcut	52.21 ± 1.94	29.24 ± 1.60	21.79 ± 2.23	17.63 ± 2.02	10.50 ± 0.65	8.92 ± 1.50

the water retention curve (Bochet and García-Fayos 2004). However, there was no effect of aspect on soil water content ($F = 1.812$; $p = 0.185$).

Soil water dynamics in relation to rainfall events

Rainfall amount was 253 and 244 mm, respectively, for the two successive germination periods considered. Only 10 rainfall events noticeably moistened the soil above the value of −0.35 MPa during each germination period. However, the maximum number of consecutive days the water remained in the soil after a rain event varied widely between roadslope types and aspect. The speed of soil drying increased in the order: north roadfill, south roadfill, north roadcut and south roadcut (Table 3). For example, after an 8 days long rain event of 49 l/m^2 that occurred on the 12/10/2003, the soil water content registered in the field remained above the value determined in the laboratory at −0.05 MPa during 1 day in south-facing roadcuts, 11 days in north-facing roadcuts, 13 days in south-facing roadfills and more than 1 month in north-facing roadfills. These estimates include the number of days rain was falling.

Influence of soil water potential, species success and regeneration strategy on germination rate and time

Not a single seed of *Diplotaxis erucoides* and *Euphorbia serrata* germinated at any of the water potentials selected, including the control with distilled water, and they were omitted from the analyses.

No germination occurred for any of the species selected at wilting point (Table 4). Therefore, germination data at −1.50 MPa were not used in the statistical analyses.

In general, germination performance was sensitive to water stress. Germination rate decreased and germination time increased as soil water potential decreased. However, the effect of increasing water stress on germination rate and time differed among species (Tables 4 and 5) and among groups of species with different success in plant establishment on roadslopes (Figs. 1–3). Whereas germination rates of the ‘‘general successful’’ and non-sprouting ‘‘south-facing roadcut successful’’ species remained higher than 90% at water potentials from 0 to −0.05 MPa, the other groups of species showed generally a steady decrease in germination rates as

Table 3 Maximum number of consecutive days (continuity $\leq$ 24 h) the soil water content remained in the four roadslope categories after an 8-days rain event of 49 l/m^2 (12/10/2003) above the respective values determined in the laboratory at five different water potentials

Roadslope category	Water potential (MPa)				
	−0.01	−0.02	−0.05	−0.35	−1.50
North-facing roadfill	4–33[a]	6–33[a]	>33	>33	>33
South-facing roadfill	4	6	13	>33	>33
North-facing roadcut	1	1	11	>33	>33
South-facing roadcut	0	1	1	8	8

[a] Gravimetric data to estimate the number of days for the north roadfill category were used because data recording on this roadslope category failed temporally

Table 4 Mean germination rates (%) and standard errors of the species studied at five levels of soil water potential

Establishment success	Species	Water potential (MPa)				
		0	−0.01	−0.05	−0.35	−1.50
Gen + SRc non-sprouter	*Alyssum simplex*	98.5 ± 0.7	97.7 ± 1.1	96.6 ± 1.5	83.0 ± 6.1	0 ± 0
Gen + SRc non-sprouter	*Anacyclus clavatus*	99.5 ± 0.5	95.7 ± 2.7	99.5 ± 0.5	70.1 ± 1.6	0 ± 0
Gen + SRc non-sprouter	*Avena barbata*	100.0 ± 0.0	100.0 ± 0.0	95.9 ± 1.5	41.5 ± 4.0	0 ± 0
Gen + SRc non-sprouter	*Bromus rubens*	100.0 ± 0.0	93.3 ± 2.6	92.5 ± 4.0	33.3 ± 2.8	0 ± 0
Gen + SRc non-sprouter	*Diplotaxis erucoides*	0 ± 0 [a]	0 ± 0[a]	0 ± 0[a]	0 ± 0[a]	0 ± 0[a]
SRc non-sprouter	*Santolina chamaecyparyssus*	100.0 ± 0	99.3 ± 0.4	95.5 ± 2.7	16.4 ± 4.6	0 ± 0
R_f	*Calendula arvensis*	76.5 ± 1.3	51.0 ± 2.6	39.3 ± 1.0	2.0 ± 1.4	0 ± 0
R_f	*Carduus pycnocephalus*	98.1 ± 1.2	95.7 ± 1.5	95.0 ± 3.7	89.0 ± 3.3	0 ± 0
R_f	*Filago pyramidata*	100.0 ± 0	68.7 ± 6.3	54.6 ± 11.6	7.2 ± 1.4	0 ± 0
R_f	*Hirschferdia incana*	90.5 ± 6.0	57.5 ± 5.3	63.7 ± 5.0	8.3 ± 3.1	0 ± 0
R_f	*Medicago minima*	92.6 ± 3.4	87.1 ± 7.6	85.6 ± 4.6	17.4 ± 5.8	0 ± 0
SR_c sprouter	*Convolvulus arvensis*	58.0 ± 8.4	54.3 ± 6.9	32.6 ± 3.6	0 ± 0	0 ± 0
SR_c sprouter	*Eryngium campestre*	80.8 ± 7.8	6.0 ± 2.6	0 ± 0	0 ± 0	0 ± 0
SR_c sprouter	*Genista scorpius*	100.0 ± 0	100.0 ± 0	7.9 ± 3.0	0 ± 0	0 ± 0
SR_c sprouter	*Plantago albicans*	93.6 ± 2.8	92.2 ± 5.6	89.5 ± 4.7	58.5 ± 4.1	0 ± 0
SR_c sprouter	*Euphorbia serrata*	0 ± 0[a]	0 ± 0[a]	0 ± 0[a]	0 ± 0[a]	0 ± 0[a]
Un	*Astragalus hamosus*	72.4 ± 4.5	24.6 ± 2.0	12.2 ± 4.8	3.3 ± 2.0	0 ± 0
Un	*Brachypodium retusum*	43.2 ± 6.7	25.3 ± 3.4	6.3 ± 2.1	3.2 ± 1.1	0 ± 0
Un	*Helichrysum italicum*	35.1 ± 10.1	21.7 ± 5.6	14.0 ± 5.3	3.4 ± 1.8	0 ± 0
Un	*Medicago orbicularis*	100.0 ± 0	95.1 ± 1.9	28.1 ± 6.1	3.6 ± 4.6	0 ± 0
Un	*Plantago lanceolata*	80.9 ± 0.0	50.0 ± 5.3	40.4 ± 10.6	3.2 ± 3.2	0 ± 0
Un	*Plantago sempervirens*	91.9 ± 1.0	90.4 ± 2.9	36.0 ± 6.9	0 ± 0	0 ± 0

[a] No single seed of *Diplotaxis erucoides* and *Euphorbia serrata* germinated. Gen = general successful species; R_f = roadfill successful species; SR_c = south-facing roadcut successful species (not exclusively); Un = unsuccessful species

water content decreased from field capacity to wilting point (Figs. 1–3). In some sprouting species such as *Eryngium campestre* and *Genista scorpius*, the decrease is much more pronounced reaching germination rates less than 10% at water potentials of −0.01 and −0.05, respectively (Table 4). Time to germination of ''unsuccessful species'' and especially sprouting ''south-facing roadcut successful species'' increased steadily with water stress, whereas for the species of the other groups it remained unchanged between 0 and −0.05 MPa and increased only at −0.35 MPa (Figs. 1–3).

Germination rates were significantly different between ''general successful'' and ''unsuccessful'' species ($t = 5.2851$; $p = 0.0007$), with lower rates for the latter than for the former species at all water potentials ($t = 1.6855$; $p = 0.0944$ for the interaction between success and water potential; Fig. 1A). On the contrary, a significant interaction existed between success and water potential for the germination time ($t = -1.5066$; $p = 0.0000$), indicating that differences in the first day of germination between ''general successful'' and ''unsuccessful'' species occurred at −0.35 MPa, but not at higher water potentials (Fig. 1B). Whereas at −0.35 MPa almost 50% of the seeds of ''general successful'' species germinated and the mean number of days until first germination occurred was 6.2, germination rates did not reach 5% for any of the ''unsuccessful'' species studied and mean time to germination raised to 23.6 days.

Similar trends were observed when comparing ''general successful'' and ''roadfill successful'' species (Fig. 2). The latter species were exclusively successful on roadfills and had significantly lower germination rates than that of the former species able to colonise successfully all kind of roadslopes

Table 5 Mean times to germination (days) and standard errors of the species studied at four levels of soil water potential

Establishment success	Species	Water potential (MPa)			
		0	−0.01	−0.05	−0.35
Gen + SRc non-sprouter	*Alyssum simplex*	5.0 ± 0.0	5.0 ± 0.0	5.0 ± 0.0	6.0 ± 0.0
Gen + SRc non-sprouter	*Anacyclus clavatus*	4.0 ± 0.0	4.0 ± 0.0	4.0 ± 0.0	4.3 ± 0.3
Gen + SRc non-sprouter	*Avena barbata*	6.0 ± 0.0	6.0 ± 0.0	7.0 ± 0.0	8.0 ± 0.5
Gen + SRc non-sprouter	*Bromus rubens*	4.0 ± 0.0	4.0 ± 0.7	4.3 ± 0.3	6.5 ± 0.3
Gen + SRc non-sprouter	*Diplotaxis erucoides*	–[a]	–[a]	–[a]	–[a]
SRc non-sprouter	*Santolina chamaecyparyssus*	7.0 ± 0.0	7.8 ± 0.3	8.3 ± 0.6	25.8 ± 1.7
R_f	*Calendula arvensis*	6.0 ± 0.0	6.0 ± 0.0	6.3 ± 0.3	29.3 ± 4.4
R_f	*Carduus pycnocephalus*	4.0 ± 0.0	4.0 ± 0.0	4.0 ± 0.0	6.0 ± 0.0
R_f	*Filago pyramidata*	3.5 ± 0.5	4.0 ± 0.0	4.0 ± 0.0	9.0 ± 2.2
R_f	*Hirschferdia incana*	4.0 ± 0.0	4.0 ± 0.0	4.0 ± 0.0	9.7 ± 0.7
R_f	*Medicago minima*	4.0 ± 0.0	4.0 ± 0.0	4.8 ± 0.3	11.8 ± 2.9
SR_c sprouter	*Convolvulus arvensis*	6.3 ± 1.4	8.8 ± 0.5	12.8 ± 2.1	34.0 ± 0.0
SR_c sprouter	*Eryngium campestre*	10.0 ± 0.0	25.0 ± 2.0	34.0 ± 0.0	34.0 ± 0.0
SR_c sprouter	*Genista scorpius*	7.3 ± 0.3	9.3 ± 0.9	25.0 ± 3.8	34.0 ± 0.0
SR_c sprouter	*Plantago albicans*	5.0 ± 0.0	5.0 ± 0.0	5.0 ± 0.0	5.0 ± 0.0
SR_c sprouter	*Euphorbia serrata*	–[a]	–[a]	–[a]	–[a]
Un	*Astragalus hamosus*	3.0 ± 0.0	3.0 ± 0.0	10.0 ± 6.5	18.8 ± 8.8
Un	*Brachypodium retusum*	9.3 ± 2.1	10.0 ± 2.5	16.5 ± 2.3	24.8 ± 3.6
Un	*Helichrysum italicum*	5.0 ± 1.0	7.7 ± 0.7	8.3 ± 0.7	19.3 ± 5.2
Un	*Medicago orbicularis*	3.0 ± 0.0	3.5 ± 0.3	6.3 ± 1.0	21.3 ± 6.3
Un	*Plantago lanceolata*	6.0 ± 0.0	6.0 ± 1.0	7.0 ± 0.0	29.5 ± 4.5
Un	*Plantago sempervirens*	8.0 ± 0.6	9.8 ± 0.3	10.3 ± 0.6	34.0 ± 0.0

Germination times at −1.50 MPa are not provided, as no single seed germinated at that water potential

[a] No single seed of *Diplotaxis erucoides* and *Euphorbia serrata* germinated. Gen = general successful species; R_f = roadfill successful species; SR_c = south-facing roadcut successful species (not exclusively); Un = unsuccessful species

including the harsh south-facing roadcuts. Although mean time to germination remained below 7 days and practically unchanged up to −0.35 MPa for ‘‘general successful species’’, it varied scarcely at water potentials above −0.05 MPa for ‘‘roadfill successful species’’ but reached 13.1 days at −0.35 MPa (Fig. 2B).

Sprouters had significantly lower mean germination rates and marginally significant higher mean times to germination than non-sprouters at all water potentials ($t = -3.1350$; $p = 0.0165$ and $t = -2.1234$; $p = 0.0714$, respectively). Mean germination rates of non-sprouting species remained above 95% and 50% at −0.05 and −0.35 MPa, respectively, whereas it dropped to 33% and 14% for sprouting species at the same water potentials. An opposite trend was obtained for the mean time to germination, with the highest differences between both groups occurring at −0.35 MPa (10 and 27 days, respectively, for non-sprouting and sprouting species). No interaction between water potential and regeneration strategy was detected ($t = 0.4039$; $p = 0.6870$ and $t = 0.3436$; $p = 0.7318$, respectively, for germination rate and time; Fig. 3). However, time to germination did not exceed 8 days in any case at −0.35 MPa for ‘‘non-sprouting species’’, except for *S. chamaecyparissus* which needed 26 days to germinate (Table 5). Unlike the other sprouting species, *Plantago albicans* showed a similar response to water potential to non-sprouting species, with germination rates remaining close to 90% at water potential as low as −0.05 MPa and times to germination remaining constant with increasing water stress (Tables 4 and 5).

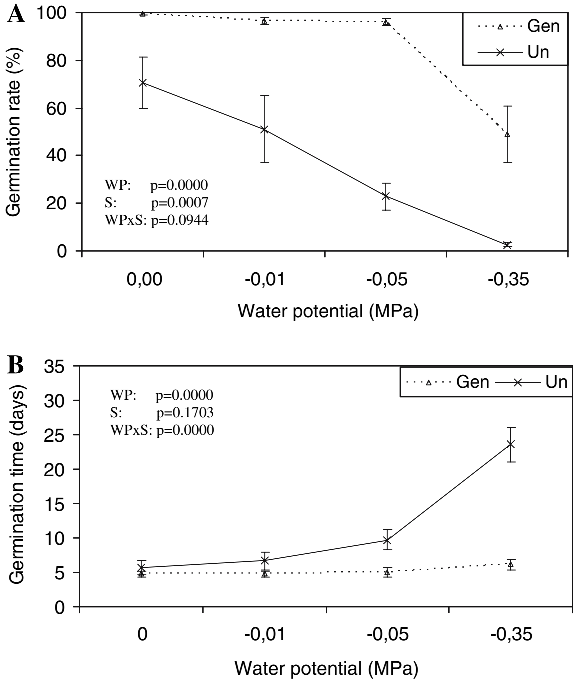

Fig. 1 Mean percent germination rate (**A**) and mean germination time (**B**) with their corresponding standard errors of successful (Gen) and unsuccessful colonisers (Un). Results of two-way GLM are indicated in the figure (WP = water potential; S = establishment success; WP × S = interaction between both factors; *p* = significance level)

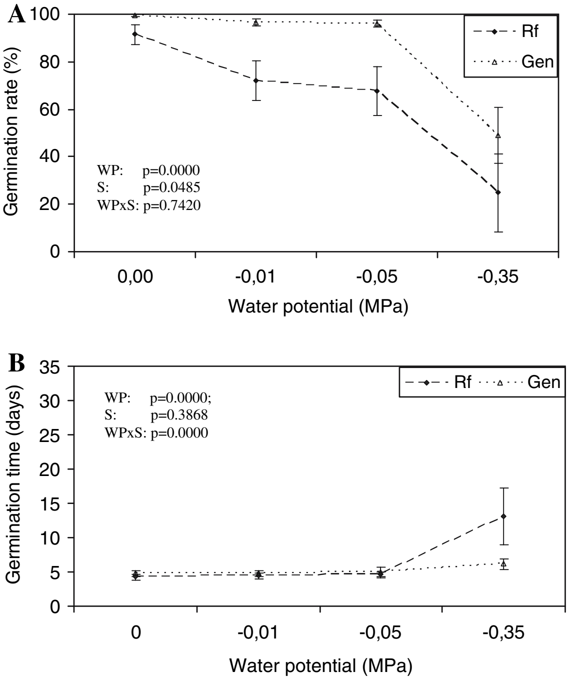

Fig. 2 Mean percent germination rate (A) and mean germination time (B) with their corresponding standard errors of successful (Gen) and roadfill successful colonisers (R_f). Results of two-way GLM are indicated in the figure (WP = water potential; S = establishment success; WP × S = interaction between both factors; *p* = significance level)

Discussion

This study provides evidences of differences in soil water availability for seeds during the germination period among the different roadslope categories and it reveals that germination performance of groups of species with different success in plant establishment on roadslopes was sensitive to these differences in soil water availability.

Our results show that soil drying velocity increased in the order: north-facing roadfills, south-facing roadfills, north-facing roadcuts and south-facing roadcuts. Water remained available on roadslopes at water potentials of −0.35 and −1.50 MPa for more than 1 month to only 8 days according to this gradient. Similar differences in soil drying features were described for eroded unvegetated versus vegetated slopes in semiarid badland areas in south-eastern Spain (García-Fayos et al. 2000). The germination rate of a species at a specific water potential in conjunction with the number of days the soil water content remaining above a specific water potential exceeded the time period a seed of that species needed to germinate, was correlated to the relative success of the species in the roadslope categories considered in this study. Our results also indicate that field soil conditions of all roadslope categories, except north-facing roadfills, are most of the time limiting to seed germination as the number of days water content is equal or higher than the value equivalent to −0.05 MPa is low. This, in turn, seems to indicate that seed germination in the field usually occurs under water conditions at water potentials lower than −0.05 and higher than −1.50 MPa for species that are able to germinate in a time lower than the number of days water remains in the soil above these water potentials.

Mean germination rates of ‘‘general successful species’’ were higher than those obtained for ‘‘unsuccessful’’ and ‘‘roadfill successful’’ species at all water potentials. Moreover, differences in germination time among these groups of species existed

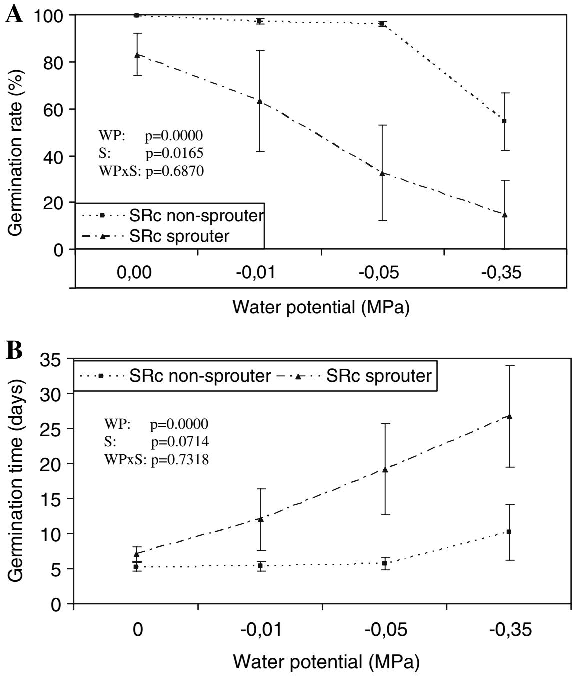

Fig. 3 Mean percent germination rate (**A**) and mean germination time (**B**) with their corresponding standard errors of south-facing roadcut successful sprouters (SR_c sprouter) and non-sprouters (SR_c non-sprouter). Results of two-way GLM are indicated in the figure (WP = water potential; S = establishment success; WP × S = interaction between both factors; *p* = significance level)

only at −0.35 MPa, with lower mean time to first germination for ‘‘general successful’’ than for ‘‘unsuccessful’’ or ‘‘roadfill successful’’ species. Therefore, germination time at water potentials between −0.05 and −0.35 MPa seems to represent a critical threshold that may explain differences in species success on roadslopes.

The presence of some individuals of ‘‘unsuccessful species’’ on roadslopes (not completely absent, but low colonising species) can be explained as time to germination of these species was in most cases slightly lower than the time to soil drying in all roadslope categories (except in south-facing roadcuts). Moreover, post-emergence competition between species in the roadslopes with high vegetation cover (78% and 44% on north- and south-facing roadfills, respectively; Bochet and García-Fayos 2004) may also explain the low success of this group of species.

Two of the species studied (*Carduus pycnocephalus* and *S. chamaecyparissus*), showed a different germination response to water stress from other species of their respective establishment success group. Unlike the other ‘‘roadfill successful species’’, *C. pycnocephalus*’ germination was similar to that of ‘‘general successful species’’. Factors other than germination performance under water stress, such as mechanical impedance to soil compaction (Atwell 1993) or susceptibility to uprooting might explain its low success on south-facing roadcuts.

Non-sprouting ‘‘south-facing roadcut successful’’ species were successful on south-facing roadcuts for the same reasons as ‘‘general successful species’’ (the former group of species include all of the ‘‘general successful species’’ plus *S. chamaecyparissus*). However, *S. chamaecyparissus* showed a lower germination performance than the other non-sprouting ‘‘south-facing roadcut successful species’’ which do not justify its successful presence on roadcuts (95% and 8 days to first germination at −0.05 MPa and 16% and 26 days at −0.35 MPa). As *S. chamaecyparissus* is a perennial species, it might have germinated on the roadcuts surveyed during longer wet events than that recorded along this study. Precipitation amount during the two germination periods recorded was 253 and 244 mm. Both values were close to 240.5 mm, the general mean of precipitation calculated for the same germination period (Oct–April) during 39 years at the Requena Meteorological station (Pérez 1994). Twenty-eight years of this long series had wetter germination periods than the ones we studied, thus providing higher possibilities for *S. chamaecyparissus*’ seeds to germinate on roadcuts.

The low germination performance of the sprouting ‘‘south-facing roadcut successful’’ species did not explain their success on south-facing roadcuts. This group of species had a low mean germination rate and a too high germination time (33% and 14% rate and 19 and 27 days) to be able to colonise successfully the roadslopes at −0.05 and −0.35 Mpa, respectively. Unlike *S. chamaecyparissus*, the successful presence of this group of species on south-facing roadcuts has to be attributed to their capacity to resprout and to resist on these slopes. Several studies have reported that plants that sprout vigorously as adults tend to be poor recruiters, and have generally less seed production, smaller seedbanks, slower growth rates and less seedling survival than non-sprouters (Iwasa and Kubo 1997; Bond and Midgley 2001, 2003). This is due to the characteristic allocation of resources to storage (carbohydrates) in sprouting species which has an important cost on growth or reproduction (Iwasa and Kubo 1997; Bond and Midgley 2001; Guerrero-Campo et al. 2006). The general trend of increasing resprouting rates in plant communities as the frequency and intensity of disturbance increases (Midgley 1996; Bond and Midgley 2001), may explain the successful presence of resprouting species in the driest and most eroded roadslopes (i.e., south-facing roadcuts). In highly eroded slopes under severe water stress, such as south-facing roadcuts, sprouting may be an advantageous strategy over seeding as it allows species to persist continuously after disturbance (Bellingham 2000; Bond and Midgley 2001, 2003). On the contrary, reseeders will be more vulnerable to recruitment failure after severe disturbance (Vesk and Westoby 2004). Species with both the ability to resprout and to germinate as response to perturbation have been described in relation to fire (Pausas and Verdú 2005). In our study, the resprouter *Plantago albicans* had the best of both regeneration strategies as it showed similar germination performance under water stress to non-sprouting ‘‘south-facing roadcut successful’’ species (Chaieb et al. 1992; Puech et al. 1998).

In conclusion, soil water availability after rainfalls occurring during the germination period played a major role in the germination of seeds. The patterns of seed germination under water stress were consistent with the success of colonising species on roadslopes and with the distribution of adult plants in the roadslopes 8 years after these latter were built. Similar conclusions were reported by García-Fayos et al. (2000) for semiarid badland areas in south-east Spain. However, processes others than germination, such as seed availability and plant survival, might also influence plant recruitment and success (Schupp 1995). To this respect, Bochet et al. (2007) and Alborch et al. (2003) demonstrated both, qualitatively (by means of species composition analysis) and quantitatively (data of seed density in the soil seed bank), respectively, that no significant differences existed in seed availability between both types of slopes and among slope aspects, and that seed availability was not limiting to roadslope colonisation in semiarid environments. Seed survival also represents a critical step in the life-cycle of most species living in semiarid ecosystems where rainfall is delivered in discrete pulses followed by intervening dry periods of variable length (Roundy et al. 1997; Snyder and Tarkowski 2006). However, the pattern of plant survival should reinforce the pattern of seed germination as both processes are more limiting in the most critical environments (García-Fayos et al. 2000; Montesinos et al. 2007).

Finally, our results may be very helpful in determining reasons for failure of many revegetation projects in semiarid areas (not only roadslopes but also abandoned degraded slopes) and in improving the success of such projects by the appropriate selection of species adapted to the local environmental conditions. To this respect, Briedé and McKell (1992) suggested that the ability of species to germinate under water stress could be an indication of a species’ potential for success under arid conditions and Matesanz et al. (2006) encourage future research aiming at identifying the limiting environmental conditions for the establishment of plants in semiarid environments.

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