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Topographic thresholds for plant colonization on semi-arid eroded slopes

E. Bochet,[1]* P. García-Fayos[1] and J. Poesen[2]
[1] Centro de Investigaciones sobre Desertificación (CSIC, Universidad de Valencia, Generalitat Valenciana), Valencia, Spain
[2] Physical and Regional Geography Research Group, K.U.Leuven, Geo-Institute, Heverlee, Belgium

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*Correspondence to: E. Bochet, Centro de Investigaciones sobre Desertificación (CSIC, Universidad de Valencia, Generalitat Valenciana), Camí de la Marjal s/n, Apdo Oficial, 46470 Albal, Valencia, Spain. E-mail: esther.bochet@uv.es

Earth Surface Processes and Landforms

ABSTRACT: Soil erosion plays an important role in plant colonization of semi-arid degraded areas. In this study, we aimed at deepening our knowledge of the mechanisms that control plant colonization on semi-arid eroded slopes in east Spain by (i) determining topographic thresholds for plant colonization, (ii) identifying the soil properties limiting plant establishment and (iii) assessing whether colonizing species have specific plant traits to cope with these limitations.

Slope angle and aspect were surrogates of erosion rate and water availability, respectively. Since soil erosion and water availability can limit plant establishment and both can interact in the landscape, we analysed variations in colonization success (vegetation cover and species number) with slope angle on 156 slopes, as a function of slope aspect. After determining slope angle thresholds for plant colonization, soil was sampled near the threshold values for soil analysis [nitrogen, phosphorous, calcium carbonate ($CaCO_3$), water holding capacity]. Plant traits expressing the plant colonizing capacity were analysed both in the pool of species colonizing the steep slopes just below the threshold and in the pool of species inhabiting gentler slopes and absent from the slopes just below the threshold.

Results show that the slope angle threshold for plant colonization decreased from north to south. For the vegetation cover, threshold values were 63°, 50°, 46°, 41° for the north, east, west and south slope aspect classes, respectively, and 65°, 53°, 49° and 45° for the species richness and the same aspect classes. No differences existed in soil properties at slope angle threshold values among slope aspects and between slope positions (just below and above the threshold) within slope aspect classes. This suggests that variations between slope aspect classes in the slope angle threshold result from differences in the colonizing capacity of plants which is controlled by water availability. Long-distance dispersal and mucilage production were preferably associated with the pool of colonizing species.

These results are discussed in the perspective of a more efficient ecological restoration of degraded semi-arid ecosystems where soil erosion acts as an ecological filter for plant establishment. Copyright © 2009 John Wiley & Sons, Ltd.

KEYWORDS: vegetation; erosion; eco-geomorphology; water availability; plant traits; soil properties; slope aspect; slope angle; restoration ecology; roots; dispersal; water stress

Introduction

Soil erosion is one of the most severe processes of land degradation in the Mediterranean region (Poesen and Hooke, 1997). It is a natural process which involves the movement of soil and rock as a result of gravitational force and flowing agents (Boardman and Poesen, 2006). On steep slopes, gravity tends to erode the soil giving rise to the reduction of the slope angle until equilibrium is reached between gravitational and cohesion forces. This equilibrium depends on various abiotic (climate, lithology, soil type, topographic features of the landscape) and biotic factors (presence of vegetation and animal life in the local environment) (Alexander *et al.*, 1994). Slope angle reduction slows down when soil materials show a high surface cohesion or when vegetation establishes, protecting the soil against the flowing agents (Thornes, 1985).

Thus, vegetation interacts actively with erosion processes as vegetation influences erosion and erosion influences vegetation development. The positive effects that vegetation has on water erosion control have been largely described in the literature (e.g. Morgan, 1986; Thornes, 1990) and summarized for a wide range of experimental conditions in a decreasing exponential relationship between the vegetation cover and the relative erosion rate (Gyssels *et al.*, 2005). Proportionately, few studies have examined the influence of erosion processes on vegetation establishment, although this trend is changing. In the last years, an increasing number of studies have described erosion as an ecological driver that influences vegetation composition, structure and spatial pattern (e.g. Thornes, 1990; Guerrero-Campo and Montserrat-Martí, 2000; Bochet *et al.*, 2000; Puigdefrábregas, 2005; Boer and Puigdefábregas, 2005; García-Fayos and Bochet, 2009). Soil erosion affects vegetation at all stages of plant life, directly by removing seeds, litter or the entire plant by runoff (e.g. García-Fayos and Cerdà, 1997; Cerdà and García-Fayos, 1997, 2002; Aerts *et al.*, 2006), or indirectly by modifying the soil properties that are relevant for seed germination and seedling establishment (Bochet *et al.,* 1999). In consequence, a decrease of vegetation cover and plant diversity with increasing erosion rate has been reported (Guàrdia and Ninot, 1992; Guerrero-Campo and Montserrat-Martí, 2000; García-Fayos and Bochet, 2009).

Given that plant colonization is a process that depends on the availability of seeds (seed dispersal, seed fixation) and on the local conditions for seedling establishment (seed germination, seedling survival and plant development) (Eriksson and Ehrlen, 1992; Zobel *et al.*, 1998; Turnbull *et al.,* 2000), erosion may play a fundamental role because of its influence on seed removal from the soil surface and on the soil properties to which plant establishment and development are sensitive (Guàrdia *et al.*, 2000). Several studies performed in badland areas and also roadslopes in semi-arid regions suggested the existence of a threshold in slope angle above which there is no plant cover anymore (Guàrdia and Ninot, 1992; Lázaro Suau, 1995; Bochet and García-Fayos, 2004; Cantón *et al.*, 2004a).

Although García-Fayos and Cerdà (1997) described an increasing exponential relationship between soil erosion rates and seed losses, the rates of seed losses they obtained, both in controlled laboratory (rainfall simulator) and field conditions, were too low (<13%) to explain the lack of colonization on highly eroded badland slopes. Furthermore, these authors evidenced that seeds of some species were more prone to be removed than others by water erosion. They found an inverse relationship between seed weight and seed removal but this relationship was altered by the presence of external appendages, such as pappus and wings, and also by the ability of seeds of some species to segregate mucilage in contact with water (García-Fayos and Cerdà, 1997; Cerdà and García-Fayos, 2002). As a consequence, seeds that segregate mucilage and seeds with external morphological structures had lower removal rates from steep slopes in relation to smooth and non-segregating mucilage seeds of similar weight.

Besides seed properties, soil erosion also selectively acts over a broader set of essential morphological and functional plant characteristics that affect plant performance and survival. For instance, a decrease in the frequency of annual species with increasing erosion rates has been repeatedly described in severely eroded areas (Guàrdia, 1995; Guerrero-Campo *et al.*, 2008; García-Fayos and Bochet, 2009). Guàrdia (1995) reported greater frequencies of tap-rooted compared to fibrous-rooted species in eroded badland slopes. Other plant traits such as root-sprouting capacity, clonality and woodiness proved to favour plants living in badland areas where severe erosion caused a simultaneous increase in stress (water and nutrient deficit) and edaphic disturbance (Guerrero-Campo *et al.*, 2008).

Further investigations on the factors that limit plant establishment and development on badland slopes demonstrated that neither seed removal nor seedling mortality caused by erosion were the main limiting factors to plant colonization on these steep slopes, but it was the duration of water availability during the germination period (García-Fayos *et al.*, 2000, Guàrdia *et al.*, 2000). Most of the potential colonizing species living in the surrounding areas to these badland slopes and producing seeds able to reach the soil surface in a large number (large enough for plants to establish) were unable to germinate in a number of days lower than the number of days water was available in the topsoil (above the wilting point) (García-Fayos *et al.*, 2000). The importance of suitable soil conditions for seed germination was also stressed by Bochet *et al.* (2007) for plant colonization of roadslopes in semi-arid conditions. These authors reported that the relative success of species on the harshest roadslope conditions (i.e. steep and eroded south-facing roadcuts) was explained by the ability of seeds to germinate fast in water-stressed conditions (soil water potential between −50 and −350 kPa).

Because topsoil water content decreases and soil drying rate increases from north- to south-facing slopes in the northern hemisphere, the interaction between seedling establishment and water availability may explain the lower vegetation cover on the south-facing compared to the north-facing slopes. This well-documented trend is caused by the greater solar radiation received by south-facing compared to north-facing slopes, resulting in a relatively warmer and drier south-facing slope microclimate (e.g. Desta *et al.*, 2004; Warren, 2008). However, solar radiation also depends on the angle of the slope, being higher on steep slopes than on flat ones. Hence, different combinations of slope aspect and angle must have the same consequences on water availability, and thus on plant establishment. Conversely, similar slope angles but with different slope aspects must have different consequences on water availability and on plant establishment. The reported variations of plant cover across south- and north-facing slopes in badland areas and roadslopes in semi-arid regions (Guàrdia and Ninot, 1992; Lázaro Suau, 1995; Cantón *et al.*, 2004a, Bochet and García-Fayos, 2004) support this influence of slope aspect and angle on plant establishment. Consequently, since slope angle influences the number of seeds remaining on hillslopes, and slope aspect and slope angle influence seed germination and establishment of these seeds through their influence on water availability, then a relationship must exist between these hillslope variables and the success of plant colonization. In this study, we hypothesize that:

(1) a threshold in slope angle exists above which plant colonization on slopes is not possible anymore (Figure 1);
(2) the slope angle threshold that controls plant colonization varies with the slope aspect and decreases from north to south in areas where the climate, lithology and opportunities for seed arrival are homogeneous (Figure 1);
(3) soil properties should neither differ between slope aspects at the threshold slope angle values nor around the threshold value within the same slope aspect ('around' refers to just below the threshold where colonization is incipient and just above it where no plant can establish anymore);
(4) potential colonizers from the local pool of species that are able to colonize the steep slopes near the slope angle threshold, should display a high colonizing capacity and resistance to seed removal (i.e. preferably annuals, high seed production, long distance-dispersal, seeds with mucilaginous seed coats or appendages, etc.) whereas species of more advanced stages of plant succession should be

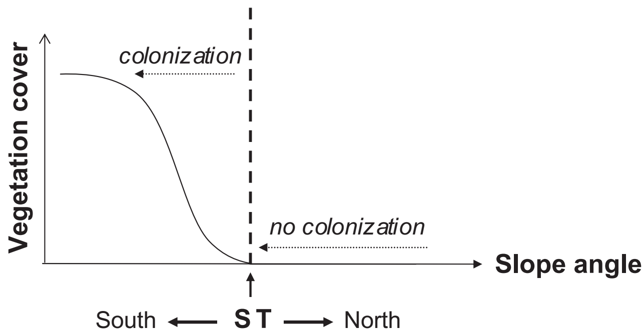

Figure 1. Structural model illustrating the relationship between slope angle, vegetation cover and plant colonization process in semi-arid areas. ST is the slope angle threshold for plant colonization which is influenced by the slope aspect.

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characterized by a high capacity to persist (preferably perennials, high sprouting ability).

In order to test these hypotheses, we analysed the relationships between vegetation cover, slope angle (as a surrogate of erosion rate) and slope aspect (as a surrogate of water availability) under the assumption that northern-exposed and flat slopes have better favourable water balance than southern-exposed and steep slopes respectively and that the former slopes will therefore enhance plant colonization compared to the latter ones (Figure 1). Finally, some implications of the findings in the field of ecological restoration and in the context of climate change are discussed.

Materials and Methods

Study area

The study area is located in the basin of the Alfambra River (Teruel, east Spain). This basin occupies 4000 km^2, with an altitude between 900 and 1300 m above sea level (a.s.l.). The dominant parent material consists of limestones of Tertiary origin, calcareous marls and sands which were highly eroded along the Quaternary by the Alfambra and Turia river systems. The resulting strongly eroded landscape with deep gullies and rills along the slopes shows frequent and abrupt changes in slope facets, with rapid alternations in slope orientation and exposure that affect vegetation pattern (Figure 2).

Within the studied area, climatic and geological conditions are homogeneous. Soils are poorly developed (<50 cm depth), have a loam to sandy-loamy texture (49·6% sand, 30·5% loam and 19·9% clay), are calcareous (15–45% $CaCO_3$) and are non-saline (<0·35 dS/m). The climate is semi-arid, with mean annual precipitation of 373 mm and a mean air temperature of 11·8°C (as recorded at Teruel over a period of 30 years, 1971–2000, AEMET, Ministerio de Medio Ambiente, URL: http://www.aemet.es/es/portada, last access on 16 December 2008). The region suffered from intense deforestation during the last 3500 years (Stevenson, 2000) and the present vegetation on deforested slopes is a sparse layer of shrubs and herbs with occasional trees. However, mature vegetation relicts remain on the flat highlands and consist of a juniper forest (*Juniperus thurifera*) with clearings covered with herbs and shrubs. The deforested slopes are moderately grazed at present with similar grazing pressures on slopes regardless of slope aspect and angle, at least up to the slope angle threshold values (field observations).

Figure 2. Overview of the study area. Strongly eroded landscape with deep gullies and rills along the slopes show frequent and abrupt changes in slope facets, with rapid alternations in slope orientation and exposure that affect vegetation pattern.

Vegetation surveys and slope threshold identification

156 (2 m × 2 m) plots, each on a different slope, were surveyed within the basin in order to identify topographic thresholds for plant colonization. Plot selection accounted for slope aspect and slope angle. We defined several aspect and slope classes in order to evenly sample them. So, four slope aspect classes were defined: north (315°–45°), east (45°–135°), south (135°–225°) and west (225°–315°) and, within each slope aspect class, slope angle classes were selected at every 5° slope angle interval (20°–25°, 25°–30°, 30°–35°, 35°–40°, 40°–45°, 45°–50°, 50°–55°, 55°–60°, 60°–65°, 65°–70°, 70°–75°). In every of each aspect and slope classes we searched for five different slopes and installed one sampling plot per slope. However, within a specific slope aspect class, when vegetation was absent in all plots of three successive slope angle classes, plots were no longer selected on steeper slopes. At each plot, aspect (azimuth degrees in a 0–360° compass scale) was measured with a compass and angle (horizontal angle in degrees) with a handheld clinometer. Slopes affected by the shadow of neighbouring slopes were avoided to ensure that aspect is a good indicator of the radiation received.

Plot selection did not account for other topographic features (contributing area, slope curvature and length of slope) that have a smaller influence on the vegetation cover compared to slope angle or aspect (Cantón *et al.*, 2004a). However, no plot was selected in the footslopes where colluvial material might accumulate and conditions may be more favourable for plant establishment (Calvo-Cases *et al.*, 2009).

Vegetation survey was carried out in the plots from May to June 2007. Colonization success on slopes was measured in terms of total vegetation cover (as a percentage) and species richness (in number of species). The line-intercept method was used to estimate vegetation cover, with three parallel lines – 2 m long and parallel to the contour – at the upper, middle, and lower part of each plot.

The opportunities for seed arrival were assumed to be the same for every slope at this spatial scale (10 ha area).

Soil sampling

After slope angle threshold inspection, 57 plots (20 north, 17 east, 8 west and 12 south) were identified 'around' the threshold values and they were sampled for soil analysis. Within each slope aspect class, a similar number of plots with slope angles just above and just below the corresponding threshold angle was considered. Soil samples were collected at 0–5 cm depth in October 2007, air-dried and sieved through a 2 mm mesh before laboratory analysis. Total nitrogen, total phosphorous, water holding capacity (expressed as the gravimetric difference between soil moisture content at field capacity and wilting point, in g/100 g), and calcium carbonate ($CaCO_3$) content were determined, in order to test whether there are differences in the degree of soil evolution between the different slope aspects at the threshold and between slope positions (below and above the threshold). The Walkley–Black method was used for total nitrogen and the Olsen method for total phosphorous analyses (Page *et al.*, 1986). Richard's standard

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pressure chamber (Klute, 1986) was used to determine soil moisture content at 33 kPa (field capacity) and 1500 kPa (wilting point) water potentials. The calcimeter of Bernard was used for $CaCO_3$ analysis (MAPA, 1986).

Plant trait measurements

Twelve traits describing three key features of plant dynamics (dispersal, regeneration and persistence) and mainly based on the minimal LEDA list of functional plant traits (Kleyer *et al.*, 2008) were selected and measured for each surveyed species, according to the following criteria: (1) they should express a capacity to colonize new areas (for the colonizers) or to persist at more advanced stages of plant succession (for non-colonizers), and (2) they should be easy to measure.

All plant material was collected from healthy, adult plants growing in unshaded areas in the study site. In case a trait could not be measured for a specific species (this is the case for some rare species), this latter was not included in the analysis of the corresponding missing trait. Measurements of leaf traits were conducted on 10 leaves/species and each leaf corresponded to a different individual. Fifteen seeds and 15 propagules (i.e. dispersing unit) were collected from at least 10 individuals of each species and seed and propagule measurements were conducted on 25 seeds and 25 propagules, respectively. Final trait values are the average of all replicates per species. Trait significance and more methodological details about trait measurements are given in Cornelissen *et al.* (2003).

(1) *Life-cycle* (categorical trait). Species were classified in two major life-cycles: annual and perennial. Annual species are known to be pioneer species in the early stages of succession, well-adapted to colonization in disturbed environments (Tzanopoulos *et al.*, 2007).
(2) *Woodiness* (categorical trait). Two broad categories were defined on the basis of the degree of lignification: herbaceous and woody species. Woodiness has been associated to plant persistence in disturbed environments (Guàrdia, 1995).
(3) *Specific leaf area (SLA)* (continuous trait, in mm^2/mg) is the one-sided area of a water saturated leaf (in mm^2) divided by its oven-dry mass (in milligrams). Species with high SLA values are known to display good competitive abilities (Domènech and Vilà, 2008).
(4) *Seed production* (categorical trait) or the estimated total number of seeds per individual plant. Two broad categories were defined: low <100 and high >100 seeds/plant with the assumption that a high production of seeds will increase species opportunities to colonize new areas.
(5) *Seed mass* (continuous trait, in grams) is the air-dried weight of the germinating unit. Seed mass was used as an indicator of seedling growth.
(6) *Dispersal mode* (categorical trait). Two broad categories were defined: long-distance (anemochorous or wind-dispersed; endo- and exo-zoochorous, or dispersed by animals but ants) and short-distance dispersal (barochores or gravity-dispersed; autochores or self-dispersed; ballistics or free-fall dispersal; and myrmecochores or ant-dispersed). Long-distance dispersed species have a higher probability of reaching a bare slope than do species in the other dispersal categories.
(7) *Propagule shape* (continuous trait, dimensionless) or the variance of its three dimensions (length, width and thickness), after each of these values has been divided by the largest of the three values (Thompson *et al.*, 1993). It is an indicator of the propagule capacity to resist removal by runoff (Cerdà and García-Fayos, 2002). Shape values range from zero to one, with low values of the index indicating a spherical shape and high values corresponding to flat shapes.
(8) *Propagule size* or propagule mass (continuous trait, in grams). Small propagules will tend to disperse to larger distances but to resist removal by runoff to a lesser extent than large propagules (Cerdà and García-Fayos, 2002).
(9) *Mucilage production* (categorical trait). Two broad categories were defined: capable and not capable to develop a mucilaginous seed coat when the propagule is wetted. This capacity is an advantageous trait to resist seed removal by runoff on steep slopes and to increase germination success in water-stressed environments (Harper and Benton, 1966; Gutterman and Shem-Tov, 1997).
(10) *Morphological dispersal syndromes* (categorical trait). The presence or absence of surrounding appendages (e.g. pappus, wings, commas, hairs) that influence the distance a propagule can cover and seed resistance to removal by runoff was also taken into account.
(11) *Root morphology* (categorical trait). Four major classes were defined: tap-, branched-, fibrous- and rhizomatous- (horizontal below-ground stems) roots, with the assumption that tap-rooted species will be less resistant to up-rooting than the other root systems considered (de Baets *et al.*, 2007; Stokes *et al.*, 2007).
(12) *Sprouting capacity* (categorical trait) or the ability of plants to form new shoots from the basal or below plant parts after removal of the above-ground biomass. Sprouting capacity has been usually associated with plant persistence in disturbed areas (Bond and Midgley, 2001). The assessment was based on visual observations after excavation in the field and descriptions reported in the literature (Guerrero-Campo, 1998).

In order to discern what plant traits were successful for plant colonization we compared the frequency of traits in the set of species colonizing the plots with values of slope angle immediately below that of the slope angle threshold (COL plots and colonizer species hereafter) with that in the set of species inhabiting plots with lower slope angles and absent from the COL plots (SOURCE plots and non-colonizer species hereafter). For COL plots we only used plots with values of vegetation cover lower than 20% and for SOURCE plots we only used plots with vegetation cover values between 20% and 45%. We assumed that below 20%, plant colonization is heavily affected by soil erosion and above that value plant cover lowers soil erosion rates (see Calvo *et al.*, 1991; Snelder and Bryan, 1995; Gyssels *et al.*, 2005). The 45% level was chosen because plant competition processes may occur above that value, as showed by the abrupt change, from 45% vegetation cover onwards, in the trend of the curve representing the relationship between species number and vegetation cover in the area (data not shown).

Traits that we assumed to be sensible to slope aspect were compared separately for the north+east and south+west slope classes and similarly, comparison of traits that do not depend on slope aspect (i.e. propagule appendages and dispersal mode), were made on the basis of the overall pool of species from north+east+south+west facing plots. We made this differentiation because after analysing species composition of the plots with Correspondence Analyses (CA), we found that the set of species of north-facing slopes was similar to the east-facing one and different from that of the south+west plots (data not shown).

Statistical analyses

Prior to analysis, data were checked for normality and homoscedacidity and transformed when necessary to fulfil these conditions. Slope angle thresholds of plant colonization were identified mathematically by means of linear regression analysis describing the relationship between slope angle and plant cover. Then, the inverse prediction procedure (Zar, 1996) was used to determine the slope angle threshold value that is to be expected for a vegetation cover equal to zero. Plots with 0% vegetation cover were excluded from the analysis and only plots where plant colonization occurred were taken into account. The 95% non-symmetrical confidence limits associated with the identified slope angle threshold values were also calculated (Zar, 1996: pp. 335–336). Analyses were performed separately for each slope aspect class.

Differences in soil properties among slope aspects were tested with a two-way General Linear Model (GLM), with slope aspect (four classes) and position with respect to slope angle threshold (two classes: above and below the slope angle threshold) as main factors, position being nested to slope aspect.

To assess whether categorical plant traits were associated with the species pools (colonizers versus non-colonizers), a contingency table was built up from the two classifications (plant trait categories and species pools) and a G-test was performed. This method contrasts the number of species with a specific trait to the number of species without the specific trait across the species pools, showing changes in the frequency of each trait among each species pool. The deviations from the expected frequencies with regard to the observed ones were examined to interpret the association under the assumption that traits that enhance colonization capacity should be over-represented in the species pool of colonizers, whereas traits indicating plant persistance should be over-represented in the species pool of non-colonizers. For continuous traits, *t*-Student tests were used to compare mean values between species pools.

All analyses were performed with the SPSS v.l5.0 statistical Package (SPSS Inc., Chicago, IL, USA).

Results

Determination of slope angle thresholds

Slope angle thresholds of plant colonization were identified for the four slope aspects (Table I and Figures 3 and 4). The values of slope angle threshold from which plants started to colonize the slopes decreased as aspect increased southerliness: 63°, 50°, 46° and 41° from north to east to west and to south, respectively, for the vegetation cover and 65°, 53°, 49° and 45°, respectively, for the species richness (Table I and Figures 3 and 4, respectively). So, differences as high as 20° and 22° were found for species richness and vegetation cover respectively between the slope angle threshold corresponding to the most contrasting hillslopes (Figure 5). The incipient colonization on steeper slopes for east-oriented compared to west-oriented slopes is responsible for the clear asymmetry of both curves in Figure 5.

However, although the slope angle threshold controlling plant colonization varied greatly with the slope aspect, 95% confidence intervals calculated for the four threshold values overlapped in both cases (Table I). From the slope angle thresholds on, the vegetation cover and species richness increased linearly with a decreasing slope angle for all slope aspects within the range of angles studied (Table I, Figures 3 and 4).

Soil parameters

No statistical differences in soil variables were detected in relation to the two factors considered in the analyses (i.e. slope aspect and position) (Table II). Total nitrogen, total phosphorous, carbonate content and water holding capacity did neither differ among slope aspect categories at the threshold values ($F_{3,39} = 0·626$, $p = 0·602$; $F_{3,39} = 0·4431$, $p = 0·732$; $F_{3,48} = 0·416$, $p = 0·742$ and $F_{3,49} = 1·577$, $p = 0·207$, respectively) nor among position with respect to the threshold within each slope aspect category ($F_{4,39} = 0·579$, $p = 0·679$; $F_{4,39} = 0·420$, $p = 0·793$; $F_{4,48} = 1·156$, $p = 0·342$ and $F_{4,49} = 1·201$, $p = 0·323$, respectively).

Plant traits

A total of 101 species were surveyed in the 86 plots, regardless of slope aspect (Table III). Among them, a total of 91 potential colonizers (colonizers + non-colonizers) were surveyed in the SOURCE plots and a total of 55 colonizer species in the COL plots near the threshold.

The number of potential colonizer species in the north+east and south+west SOURCE plots, was 77 and 60, respectively. Among these potential colonizer species, 42% and 53%,

Table I. Slope angle threshold (ST in degrees) for plant colonization, in terms of vegetation cover (COV as a percentage) and species richness (SPN), according to the slope aspect. The threshold values were determined by linear regression analyses and 95% confidence limits are given for the slope angle threshold values

	ST (deg)	Regression equation	*N*	*R*	*p*	Confidence limits (95%)
Vegetation cover						
North	63·46	COV = 108·765 − 1·714*S*	25	0·74	0·000	[45·64; 87·10]
East	49·56	COV = 83·511 − 1·685*S*	25	0·88	0·000	[40·23; 60·01]
West	45·69	COV = 78·580 − 1·720*S*	22	0·80	0·000	[35·76; 58·15]
South	41·46	COV = 70·232 − 1·694*S*	18	0·70	0·000	[31·03; 58·00]
Species number						
North	64·97	SPN = 48·598 − 0·748*S*	31	0·87	0·000	[52·32; 79·18]
East	53·45	SPN = 35·703 − 0·668*S*	29	0·83	0·000	[41·15; 67·45]
West	48·57	SPN = 37·887 − 0·780*S*	23	0·80	0·000	[38·52; 61·37]
South	45·03	SPN = 28·954 − 0·643*S*	21	0·81	0·000	[35·66; 57·03]

Note: *S*, slope angle in degrees; *N*, number of plots; *R*, regression coefficient; *p*-significance value of the simple linear regression test.

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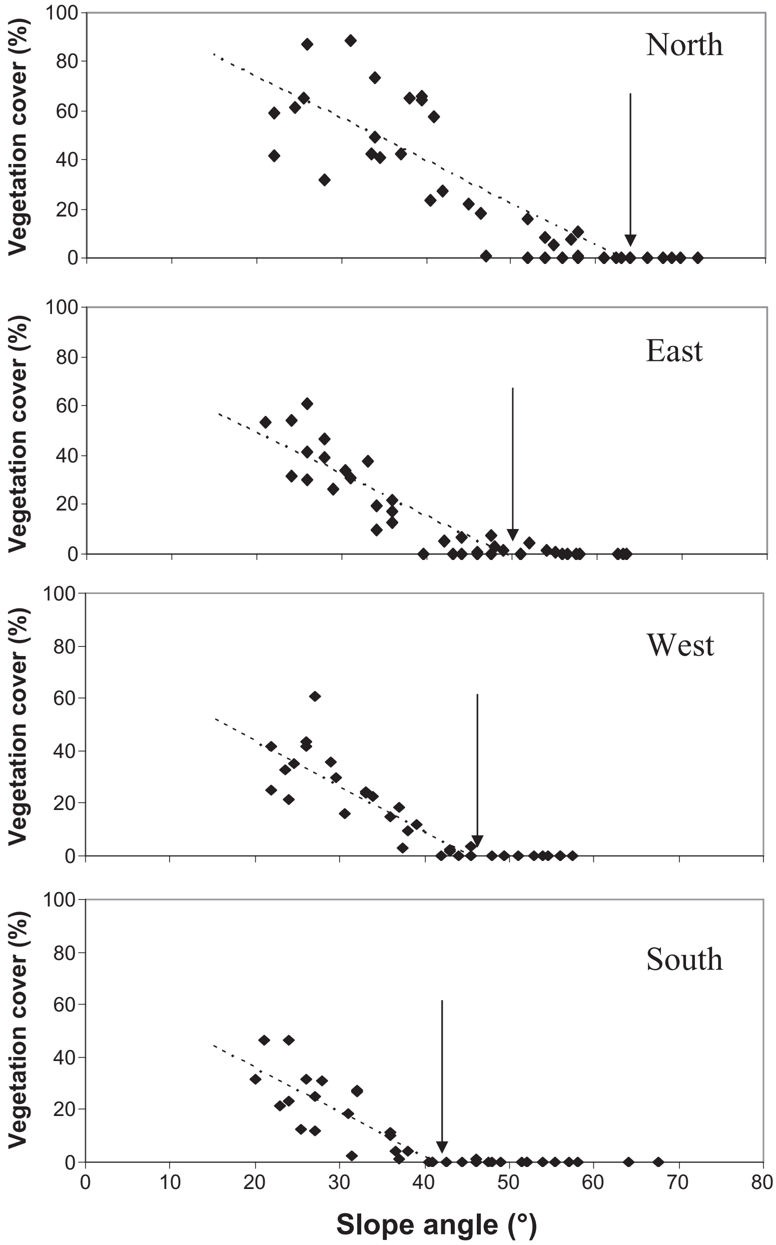

Figure 3. Identification of slope angle threshold of plant colonization (in terms of vegetation cover) according to the slope aspect. The arrow indicates the threshold determined by the simple linear regression (dotted line) corresponding to the vegetated plots (vegetation cover > 1%).

respectively, were colonizers (recorded in the COL plots). The remaining potential colonizer species (non-colonizers) were exclusively recorded in the SOURCE plots without occurring in the COL plots. Few species were exclusively surveyed in the COL plots (11 and four in north+east and south+west plots, respectively), either because they were not present in the areas surveyed (4 m^2 SOURCE plots) even if they were present in the slopes where plots were located or because they were dispersed from more distant areas (e.g. the highlands) by long-distance dispersal agents.

The most frequent colonizer species occurring in almost one half of the COL plots were *Plantago albicans*, *Alyssum simplex* and *Convolvulus arvensis* in the north+east facing slopes and *Plantago albicans*, *Artemisia campestris*, *Brassica nigra* and *Brachypodium retusum* in the south+west facing slopes (Table III). The most frequent species in the COL plots were also very frequent in their corresponding SOURCE plots (Table III). However, among the most frequent potential colonizers occurring in more than 50% of the SOURCE plots, almost one half occurred occasionally in the COL plots (in less than 25% of the plots). This is the case for example of *Filago pyramidata*, *Helianthemum violaceum*, *Thymus vulgaris*, *Scabiosa stellata*, *Atractylis humilis*, *Hippocrepis commutata*, *Anthyllis montana*, *Dactylis glomerata* and *Euphorbia exigua*. Moreover, non-colonizer species were in no case frequent species in the SOURCE plots.

According to plant trait analysis, the low frequencies obtained for some root morphology classes, forced us to analyse this trait considering only two broad categories: taproots versus all other root systems (branched, fasciculated, rhizomatous).

Four traits were significantly over-represented in one of the species pools (Tables IV and V, for continuous and categorical traits, respectively). Results related to the propagule mode confirmed the assumption that long-distance dispersal species are over-represented in the colonizing species pool with higher observed frequencies than expected by the co-occurrence hypothesis (Table V).

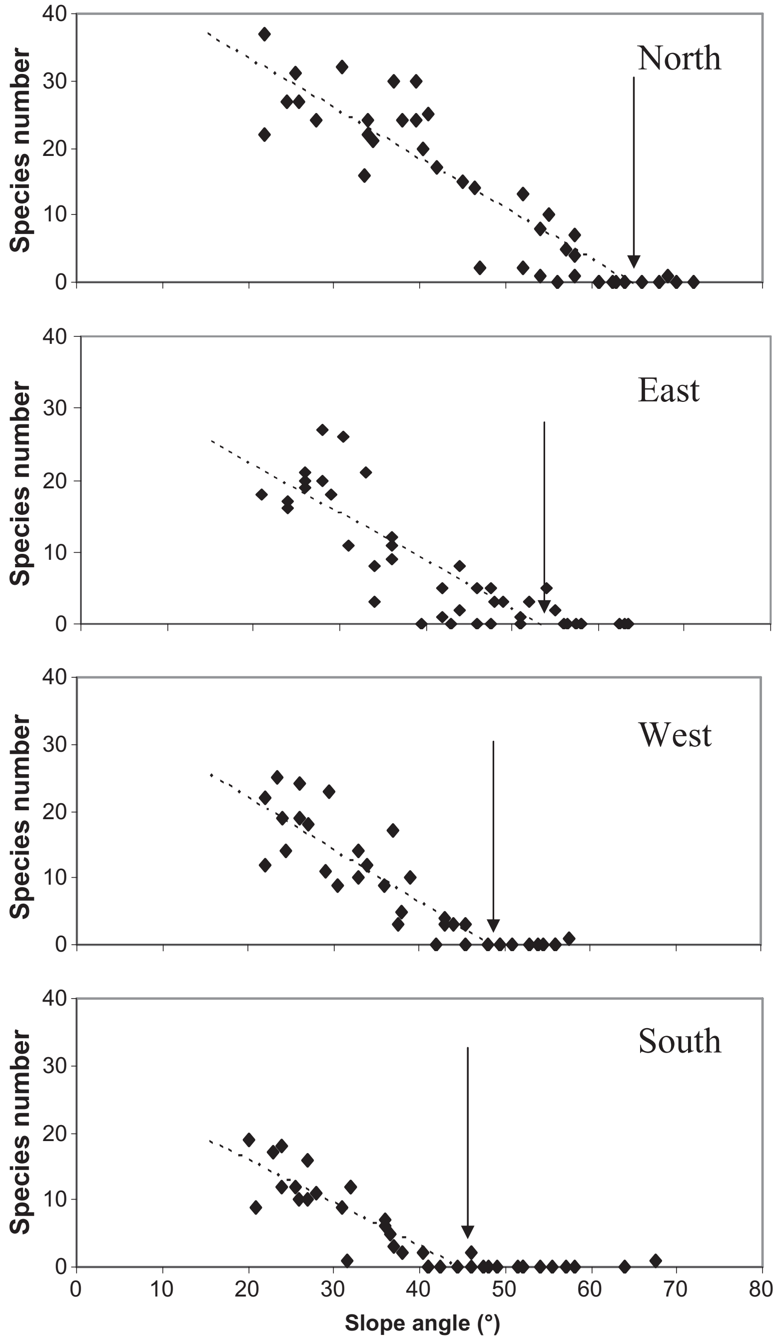

Figure 4. Identification of slope angle threshold of plant colonization (in terms of number of species) according to the slope aspect. The arrow indicates the threshold determined by the simple linear regression (dotted line) corresponding to the vegetated plots (number of species ≥1).

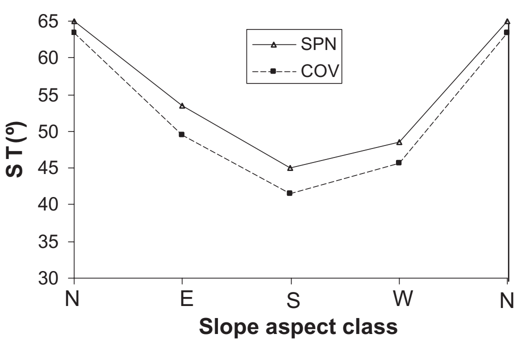

Figure 5. Differences in slope angle threshold (ST) for plant colonization between slope aspects. Plant colonisation is expressed in terms of total vegetation cover (COV) and total number of species (SPN). (N = north class from 315° to 45°; E = east class from 45° to 135°; S = south class from 135° to 225° and W = west class from 225° to 315°).

In relation to the traits sensible to slope aspect, specific leaf area (SLA) was the only trait in the north+east slopes that was significantly associated with the species pool, showing higher mean values in the non-colonizer than in the colonizer pool of species. In the south+west slopes, species capable to produce mucilage in contact with water were over-represented whereas sprouters were under-represented in the pool of colonizer species (marginal statistical significance).

Discussion

Our results indicate that topographic features (slope angle and aspect) play a major role in plant colonization in semi-arid conditions. Vegetation cover and species diversity showed both a decreasing trend with an increasing slope angle and

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Table II. Means ± standard errors (SE) of the set of soil variables analysed according to the slope aspect (four classes: north, east, west, south) and to the position with respect to the slope angle threshold (ST) within each slope aspect category (two positions: just below and just above ST)

Soil variable	Slope aspect	Position	Mean ± SE
N_{tot} (g/100g)	North	Below ST	287·90 ± 50·71
		Above ST	226·35 ± 32·65
		Total	257·13 ± 30·23
	East	Below ST	247·14 ± 11·00
		Above ST	262·38 ± 20·10
		Total	253·42 ± 10·29
	West	Below ST	233·82 ± 32·24
		Above ST	262·71 ± 42·4
		Total	253·08 ± 29·56
	South	Below ST	313·22 ± 37·64
		Above ST	279·75 ± 32·16
		Total	300·67 ± 25·58
P_{tot} (mg/kg)	North	Below ST	589·98 ± 126·86
		Above ST	658·97 ± 60·39
		Total	624·47 ± 67·22
	East	Below ST	726·78 ± 29·49
		Above ST	651·12 ± 46·95
		Total	695·63 ± 26·73
	West	Below ST	597·41 ± 95·48
		Above ST	650·52 ± 98·16
		Total	632·82 ± 70·52
	South	Below ST	712·60 ± 33·43
		Above ST	636·86 ± 43·21
		Total	684·20 ± 28·13
$CaCO_3$ (%)	North	Below ST	18·52 ± 3·34
		Above ST	12·72 ± 2·08
		Total	15·62 ± 2·03
	East	Below ST	15·49 ± 2·00
		Above ST	17·67 ± 2·01
		Total	16·39 ± 1·42
	West	Below ST	15·97 ± 0·74
		Above ST	20·41 ± 3·20
		Total	19·20 ± 2·38
	South	Below ST	16·38 ± 2·22
		Above ST	12·19 ± 4·77
		Total	14·81 ± 2·19
Water holding capacity (g/100g)	North	Below ST	10·99 ± 0·77
		Above ST	10·53 ± 0·63
		Total	10·76 ± 0·49
	East	Below ST	11·26 ± 0·69
		Above ST	13·06 ± 0·42
		Total	12·00 ± 0·48
	West	Below ST	11·18 ± 0·42
		Above ST	11·49 ± 0·73
		Total	11·38 ± 0·49
	South	Below ST	10·66 ± 0·71
		Above ST	12·00 ± 0·70
		Total	11·16 ± 0·54

Note: Total = average value of all soil samples at ST (just below and just above ST).

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Table III. List of the species with their respective frequency of occurrence (as a percentage) in the SOURCE (with vegetation cover from 20% to 45%) and COL plots (steep slopes near the slope angle threshold values with vegetation cover <20%) according to the slope aspect (N+E = north+east-facing plots; S+W = south+west-facing plots)

Species name	COL N+E	SOURCE N+E	Species name	COL S+W	SOURCE S+W
Alyssum simplex	46	75	*Plantago albicans*	86	90
Plantago albicans	46	63	*Artemisia campestris*	59	90
Convolvulus arvensis	43	31	*Brassica nigra*	41	50
Brassica nigra	32	63	*Brachypodium retusum*	41	95
Bromus rubens	32	44	*Medicago minima*	36	95
Brachypodium retusum	25	88	*Alyssum simplex*	32	45
Santolina chamaecyparissus	25	75	*Convolvulus arvensis*	27	20
Dactylis glomerata	14	63	*Atractylis humilis*	23	75
Artemisia campestris	14	56	*Thymus vulgaris*	18	80
Sedum sediforme	14	38	*Scabiosa stellata*	18	50
Papaver dubium	14	0	*Santolina chamaecyparissus*	18	40
Helianthemum violaceum	11	88	*Sedum sediforme*	14	25
Medicago minima	11	81	*Eryngium campestre*	14	30
Festuca sp.	11	31	*Dactylis glomerata*	14	50
Cirsium arvense	11	19	*Sideritis leucantha*	9	40
Senecio gallicus	11	6	*Genista scorpius*	9	40
Convolvulus lineatus	11	0	*Filago pyramidata*	9	65
Hippocrepis commutata	7	56	*Erodium cicutarium*	9	25
Eryngium campestre	7	44	*Echinaria capitata*	9	10
Koeleria vallesiana	7	44	*Xeranthemum inapertum*	5	10
Genista scorpius	7	31	*Stipa celakowski*	5	5
Xeranthemum inapertum	7	25	*Sisymbrium irio*	5	0
Silene sp.·3	7	13	*Scorzonera hispanica*	5	0
Biscutella alcarriae	7	0	*Medicago doliata*	5	25
Dorycnium pentaphyllum	7	0	*Koeleria vallesiana*	5	5
Scabiosa stellata	4	69	*Hippocrepis commutata*	5	25
Atractylis humilis	4	63	*Helianthemum violaceum*	5	85
Anthyllis montana	4	31	*Euphorbia polygalifolia*	5	5
Erodium cicutarium	4	31	*Euphorbia exigua*	5	40
Phlomis lychnitis	4	31	*Ephedra sp.·*	5	0
Cerastium sp.·	4	13	*Dorycnium pentaphyllum*	5	0
Echinaria capitata	4	13	*Cirsium arvense*	5	20
Scorzonera hispanica	4	13	*Centaurea aspera*	5	35
Lolium sp.	4	6	*Bromus rubens*	5	5
Species 3	4	6	*Brachypodium dystachion*	5	20
Vicia sp.	4	6	*Asperula sp.·1*	5	15
Aegilops geniculata	4	0	*Vicia sp.·*	0	0
Hordeum murinum	4	0	*Trifolium sp.·*	0	0
Lamium amplexicaule	4	0	*Thymus zygis*	0	0
Silene sp. 1	4	0	*Teucrium gnaphalodes*	0	20
Sonchus oleraceus	4	0	*Taraxacum sp.·*	0	0
Species 6	4	0	Species 9	0	5
Species 7	4	0	Species 8	0	5
Filago pyramidata	0	94	Species 7	0	0
Thymus vulgaris	0	75	Species 6	0	0
Euphorbia exigua	0	50	Species 5	0	0
Centaurea aspera	0	44	Species 4	0	0
Hymenolobus procumbens	0	44	Species 3	0	0
Sideritis leucantha	0	31	Species 2	0	0
Teucrium gnaphalodes	0	31	Species 18	0	5
Sisymbrium irio	0	25	Species 17	0	5
Asperula sp.·1	0	19	Species 16	0	0
Avenula bromoides	0	19	Species 15	0	0
Bupleurum fruticescens	0	19	Species 14	0	0
Desmazeria rigida	0	19	Species 13	0	0
Dipcadi serotinum	0	19	Species 12	0	0
Helianthemum marifolium	0	19	Species 11	0	5
Species 8	0	19	Species 10	0	0
Argyrolobium zanonii	0	13	Species 1	0	5
Astragalus incanus	0	13	*Sonchus oleraceus*	0	5
Galactites tomentosa	0	13	*Silene sp.·3*	0	0
Linaria glauca subsp· aragonensis	0	13	*Silene sp.·2*	0	5
Rochelia disperma	0	13	*Silene sp.·1*	0	0
Sanguisorba minor	0	13	*Senecio gallicus*	0	15
Silene sp.·2	0	13	*Scorzonera angustifolia*	0	0
Species 12	0	13	*Sanguisorba minor*	0	5
Thymus zygis	0	13	*Rochelia disperma*	0	5

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Table III. *Continued*

Species name	COL N+E	SOURCE N+E	Species name	COL S+W	SOURCE S+W
Asperula sp.·2	0	6	*Reseda undata*	0	0
Centranthus calcitrapae	0	6	*Reseda phyteuma*	0	20
Euphorbia polygalifolia	0	6	*Phlomis lychnitis*	0	30
Euphorbia serrata	0	6	*Papaver dubium*	0	0
Ferula sp.·	0	6	*Ononis tridentata*	0	5
Galium sp.·1	0	6	*Medicago orbicularis*	0	5
Galium sp.·2	0	6	*Lolium sp.·*	0	0
Medicago doliata	0	6	*Lithodora fruticosa*	0	5
Reseda undata	0	6	*Linaria glauca subsp· aragonensis*	0	0
Scorzonera angustifolia	0	6	*Lamium amplexicaule*	0	0
Species 2	0	6	*Hymenolobus procumbens*	0	0
Species 4	0	6	*Hordeum murinum*	0	0
Species 5	0	6	*Hieracium sp.·*	0	5
Species 10	0	6	*Helianthemum marifolium*	0	5
Species 13	0	6	*Galium sp.·2*	0	0
Species 14	0	6	*Galium sp.·1*	0	0
Species 15	0	6	*Galactites tomentosa*	0	0
Species 16	0	6	*Festuca sp.·*	0	0
Species 17	0	6	*Ferula sp.·*	0	0
Taraxacum sp.·	0	6	*Euphorbia serrata*	0	0
Trifolium sp.·	0	6	*Dipcadi serotinum*	0	10
Brachypodium dystachion	0	0	*Desmazeria rigida*	0	5
Coronilla minima	0	0	*Coronilla minima*	0	5
Ephedra sp.·	0	0	*Convolvulus lineatus*	0	0
Hieracium sp.·	0	0	*Cerastium sp.·*	0	0
Lithodora fruticosa	0	0	*Centranthus calcitrapae*	0	0
Medicago orbicularis	0	0	*Bupleurum fruticescens*	0	15
Ononis tridentata	0	0	*Biscutella alcarriae*	0	0
Reseda phyteuma	0	0	*Avenula bromoides*	0	5
Species 1	0	0	*Astragalus incanus*	0	10
Species 9	0	0	*Asperula sp.·2*	0	0
Species 11	0	0	*Argyrolobium zanonii*	0	15
Species 18	0	0	*Anthyllis montana*	0	55
Stipa celakowski	0	0	*Aegilops geniculata*	0	10

Note: The frequency of occurrence is defined as the proportion of plots, from the total number of plots surveyed (SOURCE and COL plots, respectively), where a given plant is present. For species that had no reproductive structures at the time of vegetation survey and could not be identified (i.e. 'species 1, species 2, . . .'), the non-reproductive parts of the plant were sampled to allow trait measurements (for root, leaf, and life-form determinations).

Table IV. Means ± standard errors (SE) of the continuous traits for the different pools of species (colonizers and non-colonizers)

	Colonizers (mean ± SE)	Non-colonizers (mean ± SE)	d.f.	*p*-value
North+east				
SLA (mm^2/mg)	11·42 ± 1·02	15·17 ± 1·33	46	0·028
Propagule shape	0·145 ± 0·019	0·106 ± 0·016	47	0·121
Seed mass (g)	0·00252 ± 0·00065	0·00211 ± 0·00058	47	0·634
Propagule mass (g)	0·00418 ± 0·00083	0·00570 ± 0·00294	49	0·617
South+west				
SLA (mm^2/mg)	13·08 ± 1·30	13·61 ± 1·54	45	0·796
Propagule shape	0·126 ± 0·017	0·126 ± 0·017	46	0·907
Seed mass (g)	0·00245 ± 0·00058	0·00354 ± 0·00073	46	0·249
Propagule mass (g)	0·00632 ± 0·00255	0·01133 ± 0·00542	46	0·358

Note: *p*-significance value of the *t*-test is given with the corresponding degrees of freedom (d.f.); SLA, specific leaf area.

with slope aspect varying from north to south (north > east > west > south) confirming the results of previous studies in a wide range of environments in the northern hemisphere (i.e. Hutchinson *et al.*, 1999; Bochet and García-Fayos, 2004; Cantón *et al.*, 2004a; Desta *et al.*, 2004; Warren, 2008). In these studies, differences in vegetation cover, species richness and plant composition were attributed to the influence of both topographical factors on soil–water distribution as southern-facing slopes receive greater rates of solar radiation than northern-facing ones and western-facing slopes receive greater rates of solar radiation than eastern-facing ones (Cantón *et al.*, 2004b; Nadal Romero *et al.*, 2007; Warren, 2008).

As expected, the process of plant colonization started at higher slope angles on north-facing slopes than on south facing ones and on east-facing slopes than on west-facing ones. At the slope angle thresholds, the soil showed similar

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Table V. Observed and expected frequencies of categorical traits in the two pools of species (colonizers and non-colonizers)

			North+east flora				South+west flora				Total flora			
Trait	Trait level	Species pool	Obs.	Exp.	*p*	*N*	Obs.	Exp.	*p*	*N*	Obs.	Exp.	*p*	*N*
Life-cycle	Annual	Col	12	14·1	0·321	32	13	13·3	0·861	32				
		Non-col	22	19·9		45	12	11·7		28				
Woodiness	Herbaceous	Col	23	24·9	0·281	32	22	21·9	0·941	32				
		Non-col	37	35·1		45	19	19·1		28				
Mucilage	Development	Col	6	5·7	0·848	26	7	4·7	*0·075*	29				
		Non-col	5	5·3		24	1	3·3		20				
Apendages	Presence	Col									22	19·5	0·189	39
		Non-col									9	11·5		23
Propagule mode	Long-distance	Col									20	16·2	*0·052*	43
		Non-col									6	9·8		26
Root	Tap (versus others)	Col	12	12·9	0·606	28	12	11·8	0·923	29				
		Non-col	12	11·1		24	8	8·2		20				
Sprouting capacity	Sprouter	Col	9	9·4	0·831	30	8	11·2	*0·077*	31				
		Non-col	12	11·6		37	13	9·8		27				
Seed number	High number	Col	26	24·3	0·257	30	25	25·5	0·681	31				
		Non-col	21	22·7		28	12	11·5		14				

Note: The pools of species accounted for the slope aspect (north+east, south+west, and total flora = north+east+south+west). Traits were analysed by means of a G-test, after contingency tables were built, under the assumption that traits are equally represented in both species pools. *G* = contingency coefficient resulting from the analysis of the contingency table (values in italic typeface indicate statistical significance at $p < 0{\cdot}10$ level). Col, colonizers; non-col = non-colonizers. As traits are bicategorical (two levels) and frequencies of the two levels are complementary (e.g. frequencies of annuals and perennials are complementary, the trend is opposite), observed (obs.) and expected (exp.) frequencies were given for a single level of the trait.

water holding capacities and similar nitrogen, phosphorous and carbonate contents among slope aspects suggesting a similar degree of soil evolution. Moreover, since slopes with angle values just above (unvegetated slopes) and just below (incipient colonization) the threshold did not show any difference in soil properties within each slope aspect class, we suggest that variations between slope aspect classes in slope angle thresholds result from differences in the colonizing capacity of plants which is controlled by water availability (i.e. time period water is available for plants) as described for other Mediterranean semi-arid areas (García-Fayos *et al.*, 2000; Bochet *et al.*, 2007). Contrary to these studies, in our study soil hydrological properties were homogenous across slope aspect classes and, consequently, the time that water is available for seed germination and plant development is expected to be controlled only by the solar radiation received.

Several traits were able to discriminate the colonizer as regard the non-colonizer pool of species. The higher frequency of species than expected displaying long-distance seed dispersal in the pool of colonizing species indicates that seed dispersal acts as a first selective filter regardless of slope aspect that might influence natural recruitment and condition subsequent vegetation structure. In these highly dynamic slopes where rejuvenation processes of the weathered material are frequent, seedbank density is low (García-Fayos *et al.*, 2000; Guàrdia *et al.*, 2000) and plant recruitment mainly depends on efficient seed dispersal from surrounding areas. Once seeds have reached the slope, seed fixation is a crucial issue in these steep slopes. In the south+west facing slopes, species that displayed mucilage production were over-represented in the colonizing pool of species. According to Gutterman and Shem-Tov (1997), mucilaginous seed coats enable seed adhesion to the soil crusts on steep slopes in semi-arid environments. However, this plant trait was not over-represented on the north+east facing slopes at early stages of colonization, even if slopes are approximately 20° steeper near the threshold on north+east compared to south+west facing slopes. Consequently, the high frequency of mucilaginous seeds among the colonizing species pool in the drier south+west facing slopes could be alternatively explained by the positive effect of mucilage on seed germination in water-limited environments. Harper and Benton (1966) described that mucilage enables a larger contact area between the seed and the soil surface that enhances water uptake by the seed.

Species with the ability to resprout were over-represented in the pool of non-colonizer species on south+west facing slopes. Several authors stated that plants that sprout vigorously as adults tend to be poor recruiters, and have generally less seed production, lower seedbank densities, slower growth rates and less seedling survival than non-sprouters (Iwasa and Kubo 1997; Bond and Midgley 2001, 2003). However, Guerrero-Campo *et al.* (2008) described high frequencies of root-sprouters among the pioneer species of highly eroded slopes in northeast Spain. These authors argued that vegetative reproduction (versus sexual) in water- and nutrient-limited eroded areas with high topsoil compaction is the most effective mechanism for species to colonize and resist on such degraded areas. Bochet *et al.* (2007) stated that the success of species establishment on the harshest roadslope types (south-facing roadcuts) was either due to the capacity of plants to resprout (resistant plants) or to the capacity of plants to germinate fast at low water potentials. *Plantago albicans*, one of the most frequent species in the early stages of colonization in our study area, was described by these authors as an adapted plant to eroded slopes of semi-arid environments as it has both regeneration strategies. *Alyssum simplex*, another frequent species in the colonizing pool of species of south+west-facing slopes was also described by these authors as a fast-germinating species in water-stressed conditions. All

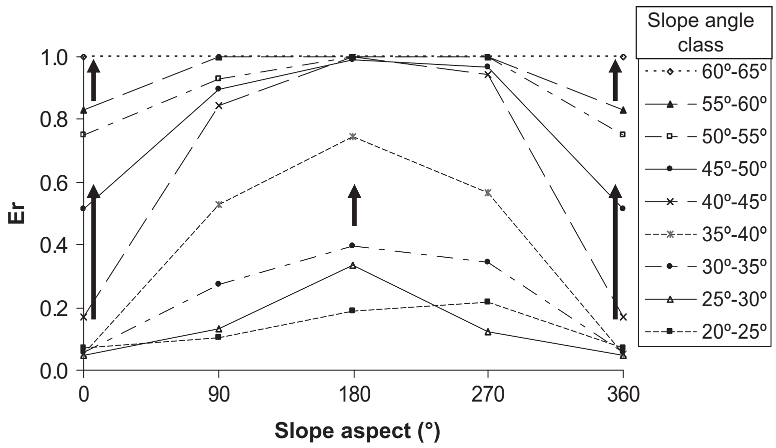

Figure 6. Trend of changes in the estimated actual relative water erosion rates (Er) at different slope aspect and angle classes in a scenario of climate change. Relative water erosion rate is defined as the ratio of soil loss rate by sheet and rill erosion from a vegetated surface compared to that of a bare soil surface. Actual erosion rates were calculated on the basis of the equation given by Gyssels *et al.* (2005): $Er = e^{-0.0492 \cdot COV}$, using as vegetation cover parameter (COV) the mean vegetation cover values obtained for each slope angle and aspect class. Arrow direction and length indicate the trend and magnitude of the change, respectively. (N = north class from 315° to 45°; E = east class from 45° to 135°; S = south class from 135° to 225° and W = west class from 225° to 315°).

these results support the idea that duration of water availability in the soil is one of the main limiting factors for plant establishment success in this semi-arid environment.

On the north+east-facing slopes, SLA was the only trait that showed differences among the two species pools. This trait has been usually used as easy trait to measure relative growth rate and competitive ability of plants (Cornelissen *et al.*, 2003; Doménech & Vilà, 2008). It is therefore not surprising that this trait was filtered in the more favourable north+east conditions where competition can be high at later stages of vegetation succession.

Species abundance (in terms of frequency of appearance on slopes) seems to be important in the outcome of the filtering process of colonizing species, as the most frequent species in the SOURCE plots were also the most frequent species in the COL plots. This apparent relationship may have influenced the results obtained in relation to the filtering of plant traits. Although the grazing pressure is moderate and homogeneous at present in the study area, it may have exerted a somewhat selective pressure on plant traits and influenced our results because of the impoverishment of the original flora. Thus, further research is needed to assess to what extent does present-day grazing affect vegetation cover and composition in the studied plots.

Our results have relevant practical consequences for the management of semi-arid degraded environments. The existence of topographic thresholds that condition water availability for plants which, in turn, limits the chances of plant establishment on steep slopes should be an important issue for ecological restoration of such environments. For example, revegetation of semi-arid roadslopes by hydroseeding will be doomed to failure as long as ecological knowledge on the topographic thresholds that limit vegetation establishment is not taken into account at the time of road building. Nowadays, roadcuts are in some cases steeper than the threshold slope angle identified in our study for south-facing slopes (roadcuts > 45°, see Bochet and García-Fayos, 2004).

Moreover, our results provide new insights in the field of species selection for the restoration of semi-arid degraded environments. This selection should focus not only on species able to overcome the eco-geomorphological filters that limit plant colonization from the very first stages of plant life (seed dispersal, seed fixation, seed germination, seedling establishment, and seedling survival), but also on the morphological and functional plant traits that enable the plant to overcome such filters and to colonize successfully new areas.

Moreover, the results obtained in our study at the slope scale reflect what may happen at the regional scale in a scenario of climate change with an increasing aridity and erosion rate (Lavee *et al.*, 1998; García Fayos and Bochet, 2009). In such a scenario, soil water content and water availability for plants are expected to decrease (Ruíz-Sinoga and Martínez-Murillo, 2009) and, hence, the slope angle threshold values for plant colonization should be expected to decrease leading to even more gentle slopes where colonization is impossible. Given the close relationship between vegetation density and erosion rate, such a shift in slope angle threshold should, in turn, affect erosion rates. Figure 6 illustrates the consequences that such a shift should have on erosion rates based on the model proposed by Gyssels *et al.* (2005) describing the relationship between vegetation cover and relative sheet and rill erosion rates. Thus, under a scenario of climate change, actual water erosion rates are expected to increase at all slope angle and aspect classes as a result of the predictable decrease of the vegetation cover (Lavee *et al.*, 1998; García-Fayos and Bochet, 2009). However, the magnitude of this change is expected to be larger on gentle north-facing slopes compared to both gentle south-facing or steep north-facing slopes (Figure 6). This is in line with García-Fayos and Bochet (2009) who give evidences that wet areas in Spain will suffer a higher magnitude of change in most soil and vegetation properties than dry areas under a scenario of increasing erosion rate and that gentle slopes will suffer a higher magnitude of change for the same properties than steep slopes under a scenario of increasing aridity.

Conclusions

Slope angle thresholds for plant colonization were identified on highly eroded slopes in a semi-arid area. Plant colonization started at higher slope angles on north-facing than on south-facing slopes. Variations in slope angle threshold values between slope aspects resulted from differences in the colonization capacity of plants which is controlled by the water availability. This latter is, in turn, controlled only by the solar

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radiation received (and not by the hydrological soil properties).

Species with long-distance dispersal and mucilage production were associated with the colonizer pool of species, whereas sprouting capacity and high SLA values were associated with the non-colonizer pool of species.

Obviously, the results presented in this study and the slope angle thresholds identified are site-dependent as they are dependent on the climate and lithology of our study area. However, this study provides relevant knowledge applicable to other semi-arid areas about the mechanism that control plant colonization on eroded slopes and confirm that water availability is a main ecological driver that shapes vegetation in such ecosystems.

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