Topographic thresholds for plant colonization on semi-arid eroded slopes

E. Bochet,¹* P. García-Fayos¹ and J. Poesen²

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

Received 15 January 2009; Revised 31 March 2009; Accepted 8 June 2009

*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 (CaCO₃), 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 vegeta-

tion 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:

- 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.

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 southernexposed 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 km², 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% CaCO₃) 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



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.

Copyright © 2009 John Wiley & Sons, Ltd.

(*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).

Vegetation surveys and slope threshold identification

156 (2 m \times 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 (CaCO₃) 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 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 CaCO₃ 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 mm²/mg) is the one-sided area of a water saturated leaf (in mm²) 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 eastfacing 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 overrepresented 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	Ν	R	р	Confidence limits (95%)
Vegeta	tion cover					
North	63.46	COV = 108.765 - 1.714S	25	0.74	0.000	[45.64; 87.10]
East	49.56	COV = 83.511 - 1.685S	25	0.88	0.000	[40.23; 60.01]
West	45.69	COV = 78.580 - 1.720S	22	0.80	0.000	[35.76; 58.15]
South	41.46	COV = 70.232 - 1.694S	18	0.70	0.000	[31.03; 58.00]
Species	s number					
, North	64.97	SPN = 48.598 - 0.748S	31	0.87	0.000	[52.32; 79.18]
East	53.45	SPN = 35.703 - 0.668S	29	0.83	0.000	[41.15; 67.45]
West	48.57	SPN = 37.887 - 0.780S	23	0.80	0.000	[38.52; 61.37]
South	45.03	SPN = 28.954 - 0.643S	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.



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 m² 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 \geq 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

Soil variable	Slope aspect	Position	Mean ± SE
N _{tot} (g/100g)	North	Below ST Above ST Total	$287.90 \pm 50.71 226.35 \pm 32.65 257.13 \pm 30.23$
	East	Below ST Above ST Total	247.14 ± 11.00 262.38 ± 20.10 253.42 ± 10.29
	West	Below ST Above ST Total	$233.82 \pm 32.24 262.71 \pm 42.4 253.08 \pm 29.56$
	South	Below ST Above ST Total	313.22 ± 37.64 279.75 ± 32.16 300.67 ± 25.58
P _{tot} (mg/kg)	North	Below ST Above ST Total	589·98 ± 126·86 658·97 ± 60·39 624·47 ± 67·22
	East	Below ST Above ST Total	726.78 ± 29.49 651.12 ± 46.95 695.63 ± 26.73
	West	Below ST Above ST Total	597.41 ± 95.48 650.52 ± 98.16 632.82 ± 70.52
	South	Below ST Above ST Total	712.60 ± 33.43 636.86 ± 43.21 684.20 ± 28.13
CaCO ₃ (%)	North	Below ST Above ST Total	$18.52 \pm 3.34 12.72 \pm 2.08 15.62 \pm 2.03$
	East	Below ST Above ST Total	15.49 ± 2.00 17.67 ± 2.01 16.39 ± 1.42
	West	Below ST Above ST Total	$\begin{array}{l} 15.97 \pm 0.74 \\ 20.41 \pm 3.20 \\ 19.20 \pm 2.38 \end{array}$
	South	Below ST Above ST Total	$16.38 \pm 2.22 \\ 12.19 \pm 4.77 \\ 14.81 \pm 2.19$
Water holding capacity (g/100g)	North	Below ST Above ST Total	10.99 ± 0.77 10.53 ± 0.63 10.76 ± 0.49
	East	Below ST Above ST Total	$11.26 \pm 0.69 \\ 13.06 \pm 0.42 \\ 12.00 \pm 0.48$
	West	Below ST Above ST Total	11.18 ± 0.42 11.49 ± 0.73 11.38 ± 0.49
	South	веlow ST Above ST Total	10.66 ± 0.71 12.00 ± 0.70 11.16 ± 0.54

Table II. Means \pm 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)

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

Table III.	List of the species	with their respective	frequency of occ	currence (as a pe	ercentage) in th	e SOURCE (with	vegetation cover	from 20%
to 45%) a	nd COL plots (steep	slopes near the slope	e angle threshold	d values with ve	egetation cover	<20%) according	to the slope aspe	ect (N+E =
north+east	-facing plots; S+W =	 south+west-facing p 	lots)					

Assam singlex 46 75 Mataga allicum 86 90 Plontaga allicum 40 63 Actentisic campestris 59 90 Convolvula anversis 13 13 Bassian night 14 30 Brown pope 13 64 Been pope 14 30 Brown pope 15 64 Been pope 12 45 Santolina chamaexpratisus 25 75 Convolvulus anonsis 27 20 Darchysocitam returns 14 63 Artecrylis Longinos 18 80 Santolina chamaexparisus 14 16 Trymur vulgaris 18 80 Papaer dublin 14 10 Santolina chamaexparisus 18 20 Cristian aronse 11 19 Subdettis baccuturus 14 25 Cristian aronse 11 10 Fulge provinitatis 9 40 Soncolina chamaexparisus 9 40 Convolvulus lineuts 9 10 C	Species name	COL N+E	SOURCE N+E	Species name	COL S+W	SOURCE S+W
Pinnang ublicans 46 0.1 Attemps a parties arangestrip 99 90 Draska nipa 12 0.1 Braska nipa 14 95 Draska nipa 12 0.1 Braska nipa 14 95 Brack popular tension 25 88 Alysum simplex 27 20 Dack fis gloment abor 14 63 Aracytis kumik 18 60 Standinar characyparisus 15 65 Convolvala arcensis 27 20 Standinar characyparisus 16 66 Trypnix vulgaris 18 60 Section saliforme 14 30 Scations saliforme 14 30 Section saliforme 11 18 Exclass saliforme 14 30 Cristian syn 11 19 Stelean section saliforme 14 30 Cristian syn 11 10 Iflags pryamiduta 9 10 Cristian syn 11 10 Iflags cangin 9 10	Alvssum simpley	46	75	Plantago albicans	86	90
Convolvulue anvensis 43 71 Rasks: ngpa 71 50 Branks: night 32 63 Barchypodium returm 11 95 Branks: night 32 64 Merkingga minima 66 95 Branks: nibers 32 64 Merkingga minima 14 95 Barchypodium reture 14 66 Trynux vulgaris 18 80 Station schlarmer 14 36 Trynux vulgaris 18 80 Speare reture 14 36 Station schlarmer 14 23 Hellanthemon vidacaum 11 61 Carbor schlarmer 14 23 Metting partia 11 66 Carbor schlarmer 14 25 Metting partia 7 56 Eradian schlarmer 9 40 Secreting article article artia 7 25 Symbritimin 3 3 Metochy article artia 7 25 Symbritimin 3 3 Secrantre artific art	Plantago albicans	46	63	Artemisia campestris	59	90
Daska nigo 12 63 Backpapelkon return 41 95 Brans rules 12 44 Medkago minina 16 95 Brackpapelkon 125 88 Ayesun simplex 12 45 Stanbias charascyparkus 25 75 Convolvilas swinsis 27 20 Dattylis plannetal 14 63 Atractylis humilis 23 75 Artentis campestris 14 65 Trymus vigaris 18 80 Sedum scellorine 14 0 Santolas charascyparsis 18 10 Helantherum vidaceum 11 81 Sedum scellorine 14 20 Calvan avenue 11 11 Darchylis glameata 14 30 Calvan avenue 11 10 Calvan avenue 9 25 Fyroglum campestre 7 31 Sigar calvania 5 30 Calvan avenue 7 31 Sigar calvania 5 30 Calvania visina	Convolvulus arvensis	43	31	Brassica nigra	41	50
incomes molecule 12 44 Medicago minima 56 95 Bochlypodum retusem 25 75 Convolvuts arcensis 27 20 Darchlys formerata 14 63 Attensifs humilis 23 75 Artensia compesties 14 66 Thymus volgaris 18 80 Space dubbur 14 0 Scaletos stellata 18 40 Papase dubbur 14 0 Scaletos stellata 18 40 Pelantheman volaceam 11 81 Conjugur campestre 14 30 Pentice ap, no 11 10 Darchy formerata 19 40 Sector gubleco 7 56 Erodium circutarium 9 40 Sector gubleco 7 13 Stipa cellatowski 5 5 Konelata staleta 7 25 Symbilian itrio 3 3 3 Dery form protopy foromata 7 25 Symbilian itrio 3 3 3 <td>Brassica nigra</td> <td>32</td> <td>63</td> <td>Brachypodium retusum</td> <td>41</td> <td>95</td>	Brassica nigra	32	63	Brachypodium retusum	41	95
naci grootani etterni production etterni Sentifica characes yunis serversis 27 Darcyki glomenta 28 Arceniska campestis 24 Arceniska campestis 25 Arceniska campestis 27 Arceniska campe	Bromus rubons	32	44	Modicago minima	36	95
indicing constraints 2 00 Constraints 2 25 05 Deryching bornestion 23 00 Constraints 27 5 Artershis campestis 14 56 Tyrus valgaris 18 80 Artershis campestis 14 56 Tyrus valgaris 18 40 Bapaver dubium 14 0 Santolina chamaceparistus 18 40 Belanterent violateum 11 88 Serdum selforme 14 30 Crision appeter dubium 11 88 Serdum selforme 14 30 Crision appeter 11 0 Flago prantidata 9 40 Convolutis lineatus 1 0 Flago prantidata 9 10 Convolutis lineatus 7 34 Evolution imagertum 5 5 Convolutis lineatus 7 3 Space blackowski 5 5 Seathers minatus 7 3 Space blackowski 5 5	Brachypadium ratusum	32	44	Alvesum simplex	20	95
Januaria 13 Canceration 2 23 23 Canceration 24 25 Section selfforme 14 26 Canceration 18 25 Section selfforme 14 26 Station accountscore 18 20 Section selfforme 14 28 Stationaccountscore 14 25 Deprecer dubtion 11 88 Section selfforme 14 20 Craiston aronse 11 10 Cancer and section 9 40 Sencero galificas 11 0 Chilago pornalidata 9 40 Convolvalis lineatus 11 0 Chilago capitata 9 40 Sencero galificas 11 0 Chilago capitata 9 10 Koeleria valostion 13 Signa cabitata 9 10 Koeleria valostion 13 Signa cabitata 5 5 Englising and section 7 14 Keantheemen inspectum 5 0	Santolina chamaagunariissus	25	75	Aryssum simplex	32	43
Deb(b)s generation 14 00 Articlys functions 13 33 Aremisia compactific 14 00 Santolina characcyparistus 18 40 Paparer doblam 14 00 Santolina characcyparistus 18 40 Paparer doblam 11 81 Expression 14 30 Medicago minima 11 81 Expression 14 30 Cristing arrense 11 19 Sideritis feucantia 9 40 Convolutius lineatus 11 0 Flago pyramidata 9 10 Convolutius lineatus 11 0 Flago pyramidata 9 10 Convolutius lineatus 7 31 Statu containa 3 0 Status acoptus 7 31 Statu containa 3 0 Status acoptus 7 31 Status containa 5 25 Status acoptus 7 31 Status containa 5 25 Status acoptus	Santolina Chamaecypanssus	23	/ 5	Atra atulia humilia	27	20
Atternisk Lampestra 14 36 Infrast Subject 0 0 Paparet dubim 14 0 Scalbas sublat 18 00 Paparet dubim 14 0 Scalbas sublat 18 00 Heintandemum violaceum 11 81 Scalbas sublat 9 40 Cirsian arcnes 11 10 Scalbas sublation 9 40 Considual Isratus 11 6 Censis acorptis 9 40 Consolvalis Isratus 7 56 Fradium cicutatium 9 10 Koeleit vallesiana 7 44 Recanhemum inapertum 5 10 Cicitia scorptus 7 13 Siga caloswaki 5 5 Scalbas sublat avalesiana 7 25 Signiphriam ino 5 0 Bocustal avalarias 7 0 Medicago dolsta 5 25 Scalbas sublata 4 31 Euphorbia polygitista 5 5 Scalbas sublata	Dactylis giomerata	14	63		23	/ 5
Sedun Section 14 38 Secultors stehular 16 30 Helantherum violaceum 11 88 Section sections 14 23 Medicago ninina 11 31 Darcylis glomenta 14 30 Crown arguer 11 31 Darcylis glomenta 9 40 Convolutis lineatus 11 0 Fights paramidata 9 40 Convolutis lineatus 11 0 Fights paramidata 9 45 Hyppaceptis commutata 7 34 Stentis catability 9 55 Kenelia vallexina 7 31 Stiga celukowski 5 5 Scholas stehula 4 63 Helantherum viagetum 5 5 Dorycnium pentphylum 7 0 Koeleria vallexina 5 5 Scholas stehula 4 63 Helantherum viagetum 5 5 Dorycnium pentphylum 7 0 Koeleria vallexina 5 5 0	Artemisia campestris	14	56	Inymus vulgaris	18	80
Paperer tablem 14 0 Santobia characeyparsas 18 40 Medicago misma 11 81 Exprigum campestre 14 30 Medicago misma 11	Sedum sediforme	14	38	Scabiosa stellata	18	50
Helasthermum violaceum 11 88 Sedum sedilorme 14 50 Cistua ay. 11 31 Datylis glomosta 9 40 Consion arense 11 19 Sidentis Everation 9 40 Convolvalis linestus 11 6 Censis acorpius 9 40 Convolvalis linestus 11 0 Filigo pyramioltat 9 40 Convolvalis linestus 11 0 Filigo pyramioltat 9 40 Convolvalis linestus 7 44 Echnical capitat 9 10 Consista scorpius 7 13 Siga calculatis capitat 5 0 Stema strain 7 0 Medicago chalata 5 25 Scabios stellata 4 69 Hippocrepis commutata 5 0 Derycnium pentiphyllum 7 0 Kederaj spi- 4 0 Condum citcutarium 4 31 Euphorbia polyaliolia 5 0 Conscinu inspinica 4 13 Constum anyo 0 0	Papaver dubium	14	0	Santolina chamaecyparissus	18	40
Medicago minima 11 81 Ergingum campestre 14 30 Cristura synces 11 19 Steterits keucantha 9 40 Caroling and sevenes 11 19 Steterits keucantha 9 40 Convolvulus lineatus 11 0 Filago pyramidata 9 65 Exponention campestre 7 44 Echinaria captata 5 0 Canoba scorpuis 7 31 Signa colakowski 5 0 Stene sp.3 7 13 Scorzanora lispancia 5 0 Stene sp.3 7 0 Kaclera vallesian 5 5 Exocuted acterate 7 0 Kaclera vallesian 5 5 Daryching polysition 7 0 Kaclera vallesian 5 0 Scaloos stella 4 61 Helpanthanum violaceum 5 0 Scaloos stella 4 13 Carvina values 5 0 Scaloos stela sp.1	Helianthemum violaceum	11	88	Sedum seditorme	14	25
Festica sp. 11 31 Dactylis glomerata 14 50 Cirsiom arense 11 10 Glenista scorpius 9 40 Sonecia gulleus 11 0 Filipocrepis commutata 9 65 Phippocrepis commutata 7 56 Erodium cicutarium 9 10 Koeleria vullesiana 7 44 Keranthermum inapertum 5 10 Koeleria vullesiana 7 13 Stopa celakowski 5 5 Keranthermum inapertum 7 0 Medicago dollata 5 0 Signes p.3 7 13 Scorromera bispanica 5 0 Scabiosa stellata 4 63 Helpocrepis commutata 5 5 Scabiosa stellata 4 31 Euphorbia polygallolita 5 0 Dorycnium pentphylum 4 13 Corstaine synthylum 5 0 Fondum circutatum 4 13 Corstaine synthylum 5 15 <	Medicago minima	11	81	Eryngium campestre	14	30
Cristom avenese 11 19 Sideritis leucantha 9 40 Convolvulus lineatus 11 0 Fridigo pyramidata 9 65 Engingum campestre 7 56 Frodium cicutarium 9 25 Engingum campestre 7 44 Metanthemum inapertum 5 10 Cenista scorpuis 7 31 Stipa celakovski 5 5 Secontrom inspertum 7 25 Signbrium irio 5 0 Silene sp.3 7 0 Medicago doltata 5 25 Dorycolium pentaphyllum 7 0 Medicago doltata 5 25 Scabios stellata 4 63 Helianthemum violaceum 5 35 Eodum cicutarium 4 31 Eupherbia sociauta 5 0 Creastium sp 4 13 Cortium entaphyllum 5 0 Creastium sp 4 6 Brachypanita 4 0 Trainomarphyllum 5	Festuca sp.	11	31	Dactylis glomerata	14	50
Senecic galikus 11 6 Censidus insatus 9 40 Convolutis lineatus 11 0 Flago pramidata 9 55 Propion camputste 7 44 Echinaria capitata 9 10 Kockri vallesiana 7 44 Keranthenum inapertum 5 10 Scenst scorptis 7 13 Stora calkowski 5 5 Scenseroptis 7 13 Scoracrea hispanica 5 0 Biscrella alcarriae 7 0 Medicago doltata 5 5 Scabios steldata 4 69 Hippocrepis commutata 5 5 Scabios steldata 4 11 Exphorbia polygalitofa 5 5 Fordum cicutarium 4 13 Exphorbia polygalitofa 5 5 Fordum scipata 4 13 Centarue aspera 5 5 Scoroneal hispanica 4 6 Branchypolitum optachifum 5 15 Scoroneal hispa	Cirsium arvense	11	19	Sideritis leucantha	9	40
Convolvidus lineatus110 <i>Filago pyramidata</i> 965Erongium campeste76 <i>Erodium cicutarium</i> 910Genista scorpius744Keanthermun inspertum510Genista scorpius731Sipa celakovski55Stranthermun inspertum725Sisynhirum inio500Sienes p.3713Scorzonera hispanica525Dorycnium pentaphyllum70Medicago doltata525Darycnium pentaphyllum70Medicago doltata525Artarchis humilis463Helanthermun voloceum585Endiski humilis431Euphorbia polygalifolia55Fondum cicutarium431Euphorbia polygalifolia500Censtim sp413Constum arenes520Scorzoren hispanica413Constum arenes55Species 346Brachypadum dystachion520Scorzoren hispanica413Constum aspera55Species 346Brachypadum dystachion520Statis sp.46Brachypaduschion520Scorzoren hispanica40Tridolian sp.00Species 346Brachypaduschion520Statis sp.46Brachypaduschion520 <t< td=""><td>Senecio gallicus</td><td>11</td><td>6</td><td>Genista scorpius</td><td>9</td><td>40</td></t<>	Senecio gallicus	11	6	Genista scorpius	9	40
Hippocepis commutata756Fodium icutanium925Koeleri vallesiana744Keinais capitata910Koeleri vallesiana744Keinais capitata510Genista scorpius713Stga caldkowski55Keanthemum inapertum725Skymbrium ino500Biscuella alcarriae70Medicago doltata525Dorychum pentphyllum70Koeleri vallesiana525Dorychum pentphyllum70Koeleri vallesiana525Dorychum pentphyllum431Explorible commutata536Frodhum crcutarium431Explorible exgua500Crasitium sp413Coristium avonse520Crasitium sp46Bronsitybrium535Socozonea hispanica413Certaurea aspera55Socies 346Brachypolium dystachion520Socies 346Brachypolium dystachion520Cristing pencivatia40Thinium synis00Leiniuria capitat40Thinium synis00Crasting pencivatia40Thinium synis00Crasting pencivatia40Thinium synis00Socias 340Thinium synis000Soci	Convolvulus lineatus	11	0	Filago pyramidata	9	65
Ir_nagine camposte 7 44 Ichinaria capitata 9 10 Genista scorpius 7 31 Stipa colakowski 5 5 Swarntherum inaperturn 7 25 Ssphrbum irio 5 0 Skene sp.3 7 13 Scorconers hispanica 5 0 Descuella alcariae 7 0 Medicago dollata 5 25 Stabiosa stelluta 4 69 Hippocrepis commutata 5 25 Scabiosa stelluta 4 63 Helantherum viokaceum 5 35 Aractylis humitis 4 31 Exphorbia polygaliolia 5 5 Cordum cicutarium 4 31 Corium arrense 5 20 Corastan spi- 4 13 Corium arrense 5 20 Corastan spi- 4 6 Brows rubers 5 5 Cordum cicutarium 4 0 Traino arrense 5 20 Vicia sp. 4	Hippocrepis commutata	7	56	Erodium cicutarium	9	25
Köckiravallesiana 7 44 Keranthemum inspertum 5 10 Cenista scorphis 7 13 Stipa celakowski 5 5 Neranthemum inapertum 7 25 Sisymbrium inio 5 0 Silene sp. 3 7 0 Medicago dollata 5 25 Darychium pentaphyllum 7 0 Koleina vallesiana 5 5 Scabios stellata 4 69 Hippocrepis commottata 5 5 Antryllis humilis 4 31 Exphorbia ovggaliolia 5 0 Cerastium sp. 4 31 Exphorbia vagualiolia 5 0 Cerastium sp. 4 13 Corstam arcense 5 20 Scorzonera hispanica 4 13 Corstam arcense 5 20 Scorzonera hispanica 4 13 Corstam scubens 5 5 Species 3 4 6 Brachypodium dystachion 5 20 Vicia sp.	Eryngium campestre	7	44	Echinaria capitata	9	10
Centst scorptis 7 31 Stipa celskowski 5 5 Skeanthenum inapertum 7 25 Sispmbrum inio 5 0 Silene sp. 3 7 13 Scorzonera hispanica 5 0 Bacutola alcarita 7 0 Medicago dollata 5 25 Scabiosa stellata 4 69 Hippocrepis commutata 5 25 Scabiosa stellata 4 63 Helanthemum violaceum 5 85 Anthylis montana 4 31 Euphorbia polygalifola 5 7 Codum ciccutarium 4 31 Euphorbia polygalifola 5 35 Codum ciccutarium 4 13 Cersium arronse 5 20 Cerastium sp. 4 6 Bromus rubers 5 35 Lolium sp. 4 6 Argeura sp1 5 15 Lolium sp. 4 0 Trainarronsee 20 Vici sp. Acaiga special 4	Koeleria vallesiana	7	44	Xeranthemum inapertum	5	10
Arrantheman 7 25 Signer by, 3 7 13 Securolia activity 5 0 Biscuella alcariae 7 0 Medicago dolata 5 0 Dorycnium pentaphyllum 7 0 Koeleria vallesiana 5 5 Scabios stellata 4 69 Hippocrepis comutata 5 5 Scabios stellata 4 31 Euphorbia polygalibila 5 5 Erodium cicutarium 4 31 Euphorbia polygalibila 5 0 Cerastium sp. 4 13 Consume aspera 5 35 Scorzonea hispanica 4 13 Consume aspera 5 35 Species 3 4 6 Branus rubens 5 5 Species 3 4 6 Asperula sp1 5 15 Acgilops geniculata 4 0 Trifolium sp. 0 0 Linum amplexicule 4 0 Trifolum sp. 0 0 0	Cenista scornius	7	31	Stipa celakowski	5	5
Attantional number 2 2 2 2 2 3 5 5 Biscutella alcarriae 7 13 Scaromera hispanica 5 25 Dorycnium pentaphyllum 7 0 Koleciai valicisiana 5 25 Scabiosa stellata 4 69 Hippocrepis commutata 5 25 Aractylis humilis 4 63 Helianthemun violaceum 5 5 Foodhum cicutarium 4 31 Euphorbia exigua 5 0 Cerastum sp. 4 13 Dorycnium pentaphyllum 5 0 Cerastum sp. 4 6 Brachysocian 5 35 Storzonera hispanica 4 13 Centaurea aspera 5 35 Storzonera hispanica 4 6 Brachysocian 5 5 Storzonera hispanica 4 6 Brachysocian 5 5 Storzonera hispanica 4 0 Tridolum sp 0 0	Yeranthemum inapertum	7	25	Sisymbrium irio	5	0
Jacent Sp. 5 7 13 Deriventian information in plantical 5 5 Dorycnium pentaphyllum 7 0 Koeleria vallesiana 5 5 Scabios stellala 4 69 Hippocrepis commutata 5 85 Artactylis humilis 4 63 Helianthernum violaceum 5 85 Anthyllis montan 4 31 Euphorbia polygalitolia 5 5 Erodium cicutarium 4 31 Euphorbia polygalitolia 5 0 Cerastiam sp. 4 13 Dorycnium pentaphyllum 5 0 Cerastiam sp. 4 6 Bromus rubens 5 5 Lolium sp. 4 6 Bromus rubens 5 5 Species 3 4 6 Bromus rubens 5 15 Aegilops geniculata 4 0 Triolium sp. 0 0 0 Hordeum murinum 4 0 Triolium sp. 0 0 0 0	Silono sp. 2	7	13	Scorzopera hispanica	5	0
Discussion P O Motion ago builing S 2.5 Dorycnium pertaphyllum 7 0 Kolecia valicisana S 2.5 Scabiosa stellata 4 6.9 Hippocrepis commutata S 2.5 Aractylis humilis 4 3.1 Euphorbia volgula 5 6.5 Cordum cicutarium 4 3.1 Euphorbia volgula 5 0 Corastum sp. 4 1.3 Orycnium pentaphyllum 5 0 Corastum sp. 4 6 Bromus rubers 5 3.5 Species 3 4 6 Brachygodium dystachion 5 20 Vicia sp. 4 6 Brachygodium dystachion 5 20 Vicia sp. 4 6 Brachygodium dystachion 5 20 Vicia sp. 4 0 Trinolum sp 0 0 0 Lamium amplexicaule 4 0 Trinolum sp 0 0 0 Species 6<	Silene sp.·s	7	15		5	25
Daylemin 7 0 Novema Valesiana 5 5 Atractylis humilis 4 69 Hippocepis commutata 5 55 Atractylis humilis 4 31 Euphorbia polygalifolia 5 55 Erodium cicutarium 4 31 Euphorbia polygalifolia 5 00 Cerastium sp. 4 13 Dorycnium pentaphyllum 5 00 Echinaria capitata 4 13 Cerastium avense 5 35 Lolium sp. 4 6 Brachypodium dystachion 5 20 Vicia sp. 4 6 Brachypodium dystachion 5 20 Vicia sp. 4 6 Brachypodium dystachion 5 20 Vicia sp. 4 0 Trifolium sp. 0 0 0 Lamium amplexicaule 4 0 Treucrium graphalodes 0 20 Sonchos oleraceus 4 0 Treucrium graphalodes 0 0 0	Bisculeira aicarriae	7	0	Medicago donata	5	25
Scabios steliata 4 09 Phipporcepts commutata 5 25 Aratcylis humilis 4 31 Euphorbia polygalifolia 5 55 Collum cicutarium 4 31 Euphorbia evigua 5 40 Phiomis lychnitis 4 13 Dorycnium pentaphyllum 5 00 Cerastium sp. 4 13 Cersian avense 5 20 Scorzonera hisparica 4 13 Certaurea aspera 5 5 Species 3 4 6 Bromus rubens 5 15 Acgilops geniculata 4 0 Vicia sp. 0 0 Lamium amplexicaule 4 0 Trainium sp. 0 0 0 Silene sp. 1 4 0 Trainium sp. 0 0 0 0 Species 6 4 0 Species 9 0 0 0 5 Silene sp. 1 4 0 Trainacum sp. 0 0 0<	Dorycnium pentapnyllum	/	0	Koeleria vallesiana	5	5
Attractivits humitis 4 63 Helanthermum volaceum 5 85 Attractivits montana 4 31 Euphorbia evigua 5 40 Pholms kychnitis 4 31 Euphorbia evigua 5 40 Pholms kychnitis 4 13 Cerastium properties 5 20 Cerastium sp. 4 13 Centaurea aspera 5 35 Lolium sp. 4 6 Brachypodium dystachion 5 20 Vicia sp. 4 6 Brachypodium dystachion 5 20 Vicia sp. 4 6 Asperula sp1 5 15 Aegilops geniculata 4 0 Trinolum sp 0 0 Lamium amplexicaule 4 0 Trinolum sp 0 0 20 Sonchus oleraceus 4 0 Traxacum sp 0 0 20 Species 6 4 0 Species 7 0 0 20 Species 7 4 0 Species 8 0 5 5	Scabiosa stellata	4	69	Hippocrepis commutata	5	25
Anthylis montana 4 31 Euphorbia polygalloolia 5 5 Erodium cicutarium 4 31 Euphorbia exigua 5 40 Phlomis lychnitis 4 31 Euphorbia exigua 5 0 Cerasium sp. 4 13 Darycrinium pentaphyllum 5 0 Echinaria capitata 4 13 Cersium arvense 5 20 Scorzonera hispanica 4 6 Bronus rubens 5 5 Species 3 4 6 Bronus rubens 5 15 Vicia sp. 4 6 Machypodium dystachhon 5 20 Vicia sp. 4 0 Trivinus zygis 0 0 0 Jamium amplexicaule 4 0 Travacum sp 0 0 0 Species 6 4 0 Species 7 0 0 0 Species 7 4 0 Species 7 0 0 0 Species 7	Atractylis humilis	4	63	Helianthemum violaceum	5	85
Erodium (ciutarium) 4 31 Euphorbia exigua 5 40 Pholmis kychnitis 4 31 Ephedra sp 5 0 Cerastium sp. 4 13 Dorycnium pentaphyllum 5 0 Echinaria capita 4 13 Cirsium arvense 5 35 Lolium sp. 4 6 Brachypodium dystachion 5 20 Scorzonea hispanica 4 6 Brachypodium dystachion 5 20 Vicia sp. 4 6 Asperula sp1 5 15 Aegilops geniculata 4 0 Tiriolium sp. 0 0 Idordeum munium 4 0 Travacum gaphalodes 0 20 Sonchus oleraceus 4 0 Travacum sp 0 0 20 Species 7 4 0 Species 8 0 5 5 Species 8 0 75 Species 6 0 0 0 Tymus vuligaris	Anthyllis montana	4	31	Euphorbia polygalitolia	5	5
Phomis lychnitis 4 31 Ephedra sp 5 0 Cerasitum sp 4 13 Dorycnium pentaphyllum 5 20 Echinaria capitata 4 13 Cirsium arvense 5 20 Scorzonera hispanica 4 13 Centaurea aspera 5 35 Species 3 4 6 Bromus rubens 5 50 Species 3 4 6 Bromus rubens 5 15 Aegilops geniculata 4 0 Vicia sp 0 0 Hordeum murinum 4 0 Trinoilum sp 0 0 0 Solenchus oleraceus 4 0 Traxacum sp 0 0 0 Species 6 4 0 Species 7 0 0 0 0 Species 6 4 0 Species 7 0 0 0 0 Species 6 4 0 Species 7 0 0 0 0	Erodium cicutarium	4	31	Euphorbia exigua	5	40
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 Bromus rubens 5 5 Aegilops geniculata 4 0 Vicia sp 0 0 Larnium amplexicaule 4 0 Triolium sp 0 0 0 Lamium amplexicaule 4 0 Travacum sp 0 0 0 Sonchus oleraceus 4 0 Species 9 0 0 0 Species 7 4 0 Species 6 0 0 0 0 Liphorbia exigua 0 54 Species 6 0 0 0 0 0 0 0 0 0 0 0 0 <	Phlomis lychnitis	4	31	Ephedra sp.·	5	0
Echinaria capitata413Cirsium arvense520Scorzonera hispanica413Centaurea aspera535Iolium sp.46Bromus rubens520Vicia sp.46Brachypodium dystachion520Vicia sp.46Asperula sp.:1515Aegilops geniculata40Vicia sp.00Hordeum murinum40Triholium sp.00Lamium anplexicaule40Trunus zygis00Sonchus oleraceus40Species 905Species 640Species 905Species 740Species 905Flago pyranidata094Species 700Ingo yranidata094Species 500Centaurea aspera044Species 300Centaurea aspera044Species 100Centaurea aspera031Species 1600Centaurea aspera019Species 1600Centaurea aspera019Species 1600Centaurea aspera019Species 1600Centaurea aspera019Species 1600Centaurea aspera019Species 1100Centaurea aspera019Species 1	Cerastium sp.·	4	13	Dorycnium pentaphyllum	5	0
Scorzonera hispanica 4 13 Centaurea aspera 5 35 Lolium sp. 4 6 Bromus rubens 5 20 Vicia sp. 4 6 Brachypodium dystachion 5 20 Vicia sp. 4 6 Asperula sp1 5 15 Aegilops geniculata 4 0 Vicia sp 0 00 Lamium mutinum 4 0 Trifolium sp. 0 00 Lamium amplexicaule 4 0 Trucirum gnaphalodes 0 200 Species 7 4 0 Trucirum gnaphalodes 0 200 Species 7 4 0 Species 7 0 00 Thymus vulgaris 0 75 Species 8 0 0 Lynchoxia exigua 0 50 Species 7 0 00 Lynchoxia exigua 0 50 Species 8 0 0 Lynchoxia exigua 0 50 Species 6 0 0 0 Lynchoxia exigua 0 31 Species 17 </td <td>Echinaria capitata</td> <td>4</td> <td>13</td> <td>Cirsium arvense</td> <td>5</td> <td>20</td>	Echinaria capitata	4	13	Cirsium arvense	5	20
Lolium sp. 4 6 Browns subers 5 5 Species 3 4 6 Brachypodium dystachion 5 20 Vicia sp. 4 6 Asperula sp1 5 15 Aegilops geniculata 4 0 Vicia sp. 0 0 Hordeum murinum 4 0 Trifolium sp. 0 0 Lanium amplexicaule 4 0 Trucrium gnaphalodes 0 20 Sonchus oleraceus 4 0 Species 9 0 5 Species 6 4 0 Species 7 0 00 Species 7 4 0 Species 7 0 0 Ikago pyranidata 0 50 Species 7 0 0 Ikago pyranidata 0 51 Species 7 0 0 Upmaniobus procumbens 0 44 Species 4 0 0 Upreuno hyranobus procumbens 0 131 Species 18 0	Scorzonera hispanica	4	13	Centaurea aspera	5	35
Species 3 4 6 Brachypodium dystachion 5 20 Vicia sp. 4 6 Asperula sp1 5 15 Aegilops geniculata 4 0 Vicia sp. 0 00 Hordeum murinum 4 0 Trifolium sp. 0 00 Lamium amplexicaule 4 0 Turcirum gnaphalodes 0 20 Sonchus oleraceus 4 0 Taraxacum sp. 0 00 Species 7 4 0 Species 8 0 0 Filago pyramidata 0 94 Species 6 0 0 Lymborida exigua 0 50 Species 5 0 0 Lymborida exigua 0 50 Species 3 0 0 Lymborida exigua 0 31 Species 13 0 0 Lymborida exigua 0 131 Species 18 0 0 Lymborida exigua 0 19 Species 15 0	Lolium sp.	4	6	Bromus rubens	5	5
Vicia sp.46Asperula sp. 1515Aegilops geniculata40Vicia sp.00Lamium amplexicaule40Trifolum sp.00Lamium amplexicaule40Thymus zygis00Silene sp. 140Teucrium gnaphalodes020Sonchus oleraceus40Species 905Species 640Species 905Species 740Species 700Ialgo pyramidata094Species 700Uphorbia exigua050Species 5000Euphorbia exigua050Species 5000Euphorbia exigua044Species 2000Sideritis leucantha031Species 1805Sisymbrium irio025Species 17000Desmazeria rigida019Species 15000Dipcadi seroinum019Species 13000Dipcadi seroinum019Species 1105Asperula sp1013Species 1105Asperula sp1013Species 1105Asperula sp3013Species 1105Asperula sp4013Species 1000Areural bron	Species 3	4	6	Brachypodium dystachion	5	20
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 0 Species 6 4 0 Species 8 0 55 Species 7 4 0 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 3 0 0 Sideritis leucantha 0 31 Species 18 0 5 Sisymbrium irio 0 25 Species 17 0 0 0 Avenula bromoides 0 19 Species 18	Vicia sp.	4	6	Asperula sp.·1	5	15
InclusionII	Aegilons geniculata	4	0	Vicia sp.	0	0
Initial and period 1 0 Information period 0 0 Silene sp. 1 4 0 Tecrim graphalodes 0 20 Sonchus oleraceus 4 0 Taraxacum sp 0 0 Species 6 4 0 Species 9 0 5 Species 7 4 0 Species 7 0 0 Inhymus zygis 0 94 Species 7 0 0 Species 7 4 0 Species 7 0 0 Thymus vulgaris 0 75 Species 6 0 0 0 Euphorbia exigua 0 50 Species 5 0 0 0 Hymenolobus procumbens 0 44 Species 3 0 0 0 Symbrium rio 0 25 Species 18 0 55 Symbrium rio 0 25 Species 17 0 0 0 Avenula bromoides 0 19 Species 16 0 0 0 Dipcadi serotinum 0	Hordeum murinum	4	0 0	Trifolium sp.	0	0
Landmin anipexitative40Intro-Stage00Silene sp. 140Teucrium gnaphalodes020Sonchus oleraceus40Species 905Species 640Species 905Filago pyramidata094Species 700Thymus vulgaris075Species 600Centaurea aspera044Species 300Centaurea aspera044Species 200Sideritis leucantha031Species 1805Sisymbrium irio025Species 1600Avenula bronoides019Species 1500Bupleurum fruticescens019Species 1500Dipcadi serotinum019Species 1200Dipcadi serotinum013Sonchus oleraceus05Galactites tomentosa013Silene sp100Argyrolobiur zanonii013Silene sp100Species 12013Silene sp300Galactites tomentosa013Sencies 1000Species 12013Sencies 1000Species 12013Sencies 1000Species 12013Sencies 1000Species 12013Silene		4	0	Thomas zvaic	0	0
Shehe Sp. 140Teranacum sp.020Sonchus oleraceus40Taraxacum sp.00Species 640Species 905Filago pyramidata094Species 700Thymus vulgaris075Species 600Centaurea aspera044Species 500Itymenolobus procumbens044Species 300Sideritis leucantha031Species 18055Sisymbrium irio025Species 1600Avenula bromoides019Species 1600Avenula bromoides019Species 1500Dipcadi serotinum019Species 1100Argyrolobium zanonii013Sonchus oleraceus05Astragalus incanus013Silene sp300Astragalus incanus013Silene sp100Silene sp1013Scorzonera angustifolia00Silene sp2013Scorzonera angustifolia00Species 12013Scorzonera angustifolia00Species 12013Scorzonera angustifolia00Species 12013Scorzonera angustifolia00Silene sp1013Scorzonera angustifolia00		4	0	Tourrium gnanhaladas	0	20
Solicitiz Geraceus 4 0 1 acadum sp. 0 0 0 Species 6 4 0 Species 9 0 5 Species 7 4 0 Species 8 0 5 Filago pyramidata 0 94 Species 6 0 0 Luphorbia exigua 0 50 Species 6 0 0 Euphorbia exigua 0 50 Species 5 0 0 Centaurea aspera 0 44 Species 2 0 0 Identition inio 0 31 Species 18 0 55 Sitymbrium inio 0 25 Species 17 0 50 Avenula bromoides 0 19 Species 15 0 0 Dipcadi serotinum 0 19 Species 12 0 0 Dipcadi serotinum 0 19 Species 13 0 0 0 Dipcadi serotinum 0 19 Species 12 0 0 0 Astragalus incanus 0 13 Species 14	Shere sp. 1	4	0	Teuchum gnaphaiodes	0	20
Species 6 4 0 Species 9 0 5 Filago pyramidata 0 94 Species 8 0 0 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 3 0 0 Centaurea aspera 0 44 Species 2 0 0 Sideritis leucantha 0 31 Species 18 0 5 Sisymbrium irio 0 25 Species 18 0 5 Asperula sp1 0 19 Species 16 0 0 Avenula bromoides 0 19 Species 13 0 0 0 Desmazeria rigida 0 19 Species 12 0 0 0 Desmazeria rigida 0 19 Species 12 0 0 0 Argyrolobium zanonii 0 13 Sonch	Sonchus Oleraceus	4	0	Taraxacum sp.	0	0
Species / 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 3 0 0 Hymenolobus procumbens 0 44 Species 2 0 0 Sideritis leucantha 0 31 Species 2 0 0 Fieldon procumbens 0 43 Species 18 0 5 Sigmbrium riro 0 25 Species 17 0 0 0 Avenula sp1 0 19 Species 16 0 0 0 Avenula spc.ingida 0 19 Species 13 0 0 0 Dipcadi serotinum 0 19 Species 10 0 0 5 Species 8 0 19	Species 6	4	0	Species 9	0	5
Hago pyramidata 0 94 Species / 0 0 Thymus vulgaris 0 75 Species 6 0 0 Euphorbia exigua 0 50 Species 5 0 0 Centaurea aspera 0 44 Species 3 0 0 Hymenolobus procumbens 0 31 Species 2 0 0 Sideritis leucantha 0 31 Species 18 0 5 Sizymbrium irio 0 25 Species 16 0 0 Avenula bromoides 0 19 Species 15 0 0 Bupleurum fruticescens 0 19 Species 13 0 0 Dipcadi serotinum 0 19 Species 13 0 0 Asyrolobium zanonii 0 19 Species 11 0 5 Species 8 0 19 Species 11 0 5 Astragalus incanus 0 13 Sonchus oleraceus 0 5 Galactites tomentosa 0 13 Silene sp3 0 <td>Species /</td> <td>4</td> <td>0</td> <td>Species 8</td> <td>0</td> <td>5</td>	Species /	4	0	Species 8	0	5
Ihymus vulgaris 0 75 Species 6 0 0 Euphorbia exigua 0 50 Species 5 0 0 Centaurea aspera 0 44 Species 3 0 0 Hymenolobus procumbens 0 44 Species 3 0 0 Sideritis leucantha 0 31 Species 2 0 0 Sideritis leucantha 0 31 Species 18 0 5 Sisymbrium irio 0 25 Species 17 0 5 Asperula sp1 0 19 Species 15 0 0 Avenula bromoides 0 19 Species 15 0 0 Bupleurum fruticescens 0 19 Species 13 0 0 Dipcadi serotinum 0 19 Species 11 0 5 Species 8 0 19 Species 12 0 0 Astragalus incanus 0 13 Solenes p3 0 0 Calactites tomentosa 0 13 Silene sp3 0	Filago pyramidata	0	94	Species /	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 18 0 55 Sisymbrium irio 0 25 Species 16 0 0 Asperula sp.·1 0 19 Species 16 0 0 Avenula bromoides 0 19 Species 15 0 0 Bupleurum fruticescens 0 19 Species 13 0 0 Dipcadi serotinum 0 19 Species 13 0 0 Dipcadi serotinum 0 19 Species 11 0 5 Species 8 0 19 Species 10 0 0 Argyrolobium zanonii 0 13 Sonchus oleraceus 0 5 Galactites tomentosa 0 13 Silene sp.·3 0 </td <td>Thymus vulgaris</td> <td>0</td> <td>75</td> <td>Species 6</td> <td>0</td> <td>0</td>	Thymus vulgaris	0	75	Species 6	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 16 0 0 Asperula sp.·1 0 19 Species 16 0 0 Avenula bromoides 0 19 Species 15 0 0 Bupleurum fruticescens 0 19 Species 13 0 0 Desmazeria rigida 0 19 Species 13 0 0 Dipcadi serotinum 0 19 Species 11 0 5 Species 8 0 19 Species 10 0 0 Argyrolobium zanonii 0 13 Sonchus oleraceus 0 5 Galactites tomentosa 0 13 Silene sp.·3	Euphorbia exigua	0	50	Species 5	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 13 0 0 Dipcadi serotinum 0 19 Species 13 0 0 0 Perical serotinum marifolium 0 19 Species 13 0 0 0 Argyrolobium zanonii 0 19 Species 13 0 0 0 Argyrolobium zanonii 0 19 Species 13 0 0 0 Argyrolobium zanonii 0 13 Species 10 0 5 Galactites tomentosa 0 13 Silene sp.·3 0 0 0 <	Centaurea aspera	0	44	Species 4	0	0
Sideritis leucantha 0 31 Species 2 0 0 Teucrium gnaphalodes 0 31 Species 18 0 5 Sisymbrium irio 0 25 Species 18 0 5 Asperula sp.1 0 19 Species 16 0 0 Avenula bromoides 0 19 Species 15 0 0 Bupleurum fruticescens 0 19 Species 13 0 0 Desmazeria rigida 0 19 Species 13 0 0 0 Dipcadi serotinum 0 19 Species 12 0 0 0 Pecies 8 0 19 Species 11 0 5 5 Species 8 0 19 Species 11 0 5 Argyrolobium zanonii 0 13 Species 10 0 0 Astragalus incanus 0 13 Species 1 0 5 Galactites tomentosa 0 13 Silene sp3 0 0 0 Inaria glauca subsp- aragonensis	Hymenolobus procumbens	0	44	Species 3	0	0
Teucrium gnaphalodes031Species 1805Sisymbrium irio025Species 1705Asperula sp. 1019Species 1600Avenula bromoides019Species 1500Bupleurum fruticescens019Species 1300Desmazeria rigida019Species 1300Dipcadi serotinum019Species 1105Species 8019Species 1000Argyrolobium zanonii013Species 105Galactites tomentosa013Silene sp. 300Linaria glauca subsp- aragonensis013Silene sp. 100Sanguisorba minor013Scorzonera angustifolia015Silene sp. 2013Scorzonera angustifolia00Species 12013Scorzonera angustifolia05Species 12013Scorzonera angustifolia05Thymus zygis013Rochelia disperma05	Sideritis leucantha	0	31	Species 2	0	0
Sisymbrium irio025Species 1705Asperula $sp. \cdot 1$ 019Species 1600Avenula bromoides019Species 1500Bupleurum fruticescens019Species 1400Desmazeria rigida019Species 1300Dipcadi serotinum019Species 1200Helianthemum marifolium019Species 1000Species 8019Species 1005Astragalus incanus013Species 105Calactites tomentosa013Silene $sp. \cdot 3$ 00Linaria glauca subsp- aragonensis013Silene $sp. \cdot 1$ 00Sanguisorba minor013Senecio gallicus015Silene $sp. \cdot 2$ 013Scorzonera angustifolia00Species 12013Scorzonera angustifolia00Species 12013Sanguisorba minor05Thymus zygis013Rochelia disperma05	Teucrium gnaphalodes	0	31	Species 18	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 Galactites tomentosa 0 13 Sonchus oleraceus 0 0 Linaria glauca subsp- aragonensis 0 13 Silene sp.·3 0 0 Sanguisorba minor 0 13 Silene sp.·1 0 0 15 Silene sp.·2 0 13 Scorzonera angustifolia 0 0 15 Silene sp.·2 0 13 Scorzonera angustifolia 0 0 5 Sil	Sisymbrium irio	0	25	Species 17	0	5
Avenula bromoides019Species 1500Bupleurum fruticescens019Species 1400Desmazeria rigida019Species 1300Dipcadi serotinum019Species 1200Helianthemum marifolium019Species 1105Species 8019Species 1000Argyrolobium zanonii013Species 105Galactites tomentosa013Silene sp.·300Linaria glauca subsp- aragonensis013Silene sp.·205Sonchelia disperma013Senecio gallicus015Silene sp.·2013Scorzonera angustifolia00Species 12013Sanguisorba minor05Thymus zygis013Rochelia disperma05	Asperula sp.·1	0	19	Species 16	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 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 Galactites tomentosa 0 13 Sonchus oleraceus 0 0 Linaria glauca subsp- aragonensis 0 13 Silene sp.·3 0 0 Sanguisorba minor 0 13 Silene sp.·1 0 0 15 Silene sp.·2 0 13 Senecio gallicus 0 15 Silene sp.·2 0 13 Scorzonera angustifolia 0 0 Species 12 0 13<	Avenula bromoides	0	19	Species 15	0	0
Desmazeria rigida 0 19 Species 13 0 0 Dipcadi serotinum 0 19 Species 13 0 0 Helianthemum marifolium 0 19 Species 12 0 0 Species 8 0 19 Species 10 0 0 Argyrolobium zanonii 0 13 Species 10 0 5 Astragalus incanus 0 13 Sonchus oleraceus 0 5 Galactites tomentosa 0 13 Silene sp.·3 0 0 0 Linaria glauca subsp. aragonensis 0 13 Silene sp.·2 0 5 Rochelia disperma 0 13 Senecio gallicus 0 15 Silene sp.·2 0 13 Senecio gallicus 0 15 Silene sp.·2 0 13 Senecio gallicus 0 0 Species 12 0 13 Sanguisorba minor 0 5 Species 12 0 13 Sanguisorba minor 0 5 Thymus zygis 0	Bupleurum fruticescens	0	19	Species 14	0	0
Dipcadi serotinum 0 19 Species 12 0 0 Helianthemum marifolium 0 19 Species 12 0 0 Species 8 0 19 Species 10 0 0 Argyrolobium zanonii 0 13 Species 10 0 0 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 Senecio gallicus 0 15 Silene sp.·2 0 13 Senecio gallicus 0 15 Silene sp.·2 0 13 Senecio gallicus 0 15 Silene sp.·2 0 13 Senecio gallicus 0 0 Species 12 0 13 Sanguisorba minor 0 5 Thymus zygis 0 13 Ro	Desmazeria rigida	0	19	Species 13	0	0
Dependent Services (12)O13O14Helianthemum marifolium019Species (12)05Species 8019Species 1000Argyrolobium zanonii013Species 105Astragalus incanus013Sonchus oleraceus05Galactites tomentosa013Silene sp.·300Linaria glauca subsp. aragonensis013Silene sp.·205Rochelia disperma013Senecio gallicus015Silene sp.·2013Scorzonera angustifolia00Species 12013Sanguisorba minor05Thymus zygis013Rochelia disperma05	Dipcadi serotinum	0	19	Species 12	0	0
Species 1Species 11Species 11Species 8019Species 1000Argyrolobium zanonii013Species 105Astragalus incanus013Sonchus oleraceus05Galactites tomentosa013Silene sp.·300Linaria glauca subsp- aragonensis013Silene sp.·205Rochelia disperma013Silene sp.·100Sanguisorba minor013Scorzonera angustifolia00Species 12013Sanguisorba minor05Thymus zygis013Rochelia disperma05	Helianthemum marifolium	0	19	Species 12	0	5
Argyrolobium zanonii013Species 1005Argyrolobium zanonii013Species 105Astragalus incanus013Sonchus oleraceus05Galactites tomentosa013Silene sp300Linaria glauca subsp- aragonensis013Silene sp205Rochelia disperma013Silene sp100Sanguisorba minor013Scorzonera angustifolia00Species 12013Sanguisorba minor05Thymus zygis013Rochelia disperma05	Species 8	0	19	Species 10	0	0
Argyrobbulin Zahohin013Species 105Astragalus incanus013Sonchus oleraceus05Galactites tomentosa013Silene sp.·300Linaria glauca subsp· aragonensis013Silene sp.·205Rochelia disperma013Silene sp.·100Sanguisorba minor013Senecio gallicus015Silene sp.·2013Scorzonera angustifolia00Species 12013Sanguisorba minor05Thymus zygis013Rochelia disperma05	Argurolobium zanonii	0	12	Species 1	0	E E
Astragalas incantas013Sonchus oferaceus05Galactites tomentosa013Silene sp.·300Linaria glauca subsp- aragonensis013Silene sp.·205Rochelia disperma013Silene sp.·1000Sanguisorba minor013Senecio gallicus015Silene sp.·2013Scorzonera angustifolia00Species 12013Sanguisorba minor05Thymus zygis013Rochelia disperma05	Astrogalus inconus	0	15	Sonchus claracous	0	5
Galactules tomentosa013Silene sp300Linaria glauca subsp- aragonensis013Silene sp205Rochelia disperma013Silene sp100Sanguisorba minor013Senecio gallicus015Silene sp2013Scorzonera angustifolia00Species 12013Sanguisorba minor05Thymus zygis013Rochelia disperma05	Asuagaius incanus	0	13	SUNCHUS OIEFACEUS	U	5
Linaria glauca subsp- aragonensis013Silene sp.·205Rochelia disperma013Silene sp.·100Sanguisorba minor013Senecio gallicus015Silene sp.·2013Scorzonera angustifolia00Species 12013Sanguisorba minor05Thymus zygis013Rochelia disperma05	Galactites tomentosa	0	13	Silene $sp.3$	0	0
Rochelia disperma013Silene sp.·100Sanguisorba minor013Senecio gallicus015Silene sp.·2013Scorzonera angustifolia00Species 12013Sanguisorba minor05Thymus zygis013Rochelia disperma05	Linaria glauca subsp∙ aragonensis	0	13	Silene sp.·2	0	5
Sanguisorba minor013Senecio gallicus015Silene sp.·2013Scorzonera angustifolia00Species 12013Sanguisorba minor05Thymus zygis013Rochelia disperma05	Rochelia disperma	0	13	Silene sp.·1	0	0
Silene sp2 0 13 Scorzonera angustifolia 0 0 Species 12 0 13 Sanguisorba minor 0 5 Thymus zygis 0 13 Rochelia disperma 0 5	Sanguisorba minor	0	13	Senecio gallicus	0	15
Species 12013Sanguisorba minor05Thymus zygis013Rochelia disperma05	Silene sp.·2	0	13	Scorzonera angustifolia	0	0
Thymus zygis 0 13 Rochelia disperma 0 5	Species 12	0	13	Sanguisorba minor	0	5
	Thymus zygis	0	13	Rochelia disperma	0	5

Copyright © 2009 John Wiley & Sons, Ltd.

Table III. Continued

Species name	cies name COL SOURCE N+E N+E Species name		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 \pm SE)	Non-colonizers (mean ± SE)	d.f.	<i>p</i> -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

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.	р	Ν	Obs.	Exp.	р	Ν	Obs.	Exp.	р	Ν
Life-cycle	Annual	Col Non-col	12 22	14·1 19·9	0.321	32 45	13 12	13·3 11·7	0.861	32 28				
Woodiness	Herbaceous	Col Non-col	23 37	24∙9 35∙1	0.281	32 45	22 19	21·9 19·1	0.941	32 28				
Mucilage	Development	Col Non-col	6 5	5∙7 5∙3	0.848	26 24	7 1	4.7 3.3	0.075	29 20				
Apendages	Presence	Col Non-col									22 9	19∙5 11∙5	0.189	39 23
Propagule mode	Long-distance	Col Non-col									20 6	16∙2 9∙8	0.052	43 26
Root	Tap (versus others)	Col Non-col	12 12	12·9 11·1	0.606	28 24	12 8	11·8 8·2	0.923	29 20				
Sprouting capacity	Sprouter	Col Non-col	9 12	9∙4 11∙6	0.831	30 37	8 13	11·2 9·8	0.077	31 27				
Seed number	High number	Col Non-col	26 21	24·3 22·7	0.257	30 28	25 12	25∙5 11∙5	0.681	31 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 < 0.10 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

Copyright © 2009 John Wiley & Sons, Ltd.

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 (southfacing 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): $\text{Er} = e^{-0.0492.COV}$, 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 southfacing 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 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.

Acknowledgements—This research was financially supported by the Spanish Government, Ministerio de Ciencia y Tecnología (CGL2005–03912/BOS; Programa Ramón y Cajal) and EU-FEDER funds. We thank the staff of the laboratories of the CIDE for soil analyses and Jaume Tormo for field assistance (vegetation surveys). We also thank two anonymous referees and the Assistant Editor for their critical comments which helped in improving this article.

References

- Aerts R, Maes W, November E, Behailu M, Poesen J, Deckers J, Hermy M, Muys B. 2006. Surface runoff and seed trapping efficiency of shrubs in a regenerating semiarid woodland in northern Ethiopia. *Catena* **65**: 61–70.
- Alexander RW, Harvey AM, Calvo A, James PA, Cerdà A. 1994. Natural stabilisation mechanisms on badland slopes: Tabernas, Almeria, Spain. In *Environmental Change in Drylands*, Millington AC, Pye K (eds). John Wiley & Sons: Chichester; 85–111.
- Boardman J, Poesen J. 2006. *Soil Erosion in Europe*. John Wiley & Sons: Chichester.
- Bochet E, Rubio JL, Poesen J. 1999. Modified top soil islands within a patchy Mediterranean vegetation in SE Spain. *Catena* **38**: 23–44.
- Bochet E, Poesen J, Rubio JL. 2000. Mound development as an interaction of individual plants with soil, water erosion and sedimentation processes on slopes. *Earth Surface Processes and Landforms* 25: 847–867.
- Bochet E, García-Fayos P. 2004. Factors controlling vegetation establishment and water erosion on motorway slopes in Valencia, Spain. *Restoration Ecology* **12**: 166–174.
- Bochet E, García-Fayos P, Alborch B, Tormo J. 2007. Soil water availability effects on seed germination account for species segregation in semiarid roadslopes. *Plant and Soil* **295**: 179–191.
- Boer M, Puigdefábregas J. 2005. Effects of spatially structured vegetation patterns on hillslope erosion in a semiarid Mediterranean environment: a simulation study. *Earth Surface Processes and Landforms* **30**: 149–167.
- Bond WJ, Midgley JJ. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution* **16**: 45–51.
- Bond WJ, Midgley JJ. 2003. The evolutionary ecology of sprouting in woody plants. *International Journal of Plant Science* **164**: 103–114.
- Calvo A, Harvey AM, Paya J, Alexander RW. 1991. Response of badland surfaces in south east Spain to simulated rainfall. *Cuaternario y Geomorfología* **5**: 3–14.
- Calvo-Cases A, Alexander RW, Arnau-Rosalén E, Bevan J, Cantón Y, Lázaro R, Puigdefábregas J, Solé A. 2009. Interacción de procesos geomórficos y distribución de componentes de la superficie del suelo en relación a la evolución de los abarrancamientos de Tabernas, Almería.
- Cantón Y, del Barrio G, Solé-Benet A, Lázaro R. 2004a. Topographic thresholds on the spatial distribution of ground cover in the Tabernas badlands of SE Spain. *Catena* **55**: 341–365.
- Cantón Y, Solé-Benet A, Domingo F. 2004b. Temporal and spatial patterns of soil moisture in semiarid badlands of SE Spain. *Journal of Hydrology* **285**: 199–214.

- Cerdà A, García-Fayos P. 1997. The influence of slope angle on sediment, water and seed losses on badland landscapes. *Geomorphol*ogy 18: 77–90.
- Cerdà A, García-Fayos P. 2002. The influence of seed size and shape on their removal by water erosion. *Catena* **48**: 293–301.
- Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, van der Heijden MGA, Pausas J, Poorter H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**: 335–380.
- de Baets S, Poesen J, Knapen A, Galindo P. 2007. Impact of root architecture on the erosion-reducing potential of roots during concentrated flow. *Earth Surface Processes and Landforms* **32**: 1323–1345.
- Desta F, Colbert JJ, Rentch JS, Gottschalk KW. 2004. Aspect induced differences in vegetation, soil, and microclimatic characteristics of an Appalachian watershed. *Castanea* **69**: 92–108.
- Doménech R, Vilà M. 2008. Response of the invader *Cortaderia* selloana and two coexisting natives to competition and water stress. *Biological Invasions* **10**: 903–912.
- Eriksson O, Ehrlen J. 1992. Seed and microsite limitation of recruitment in plant populations. *Oecologia* **91**: 360–364.
- García-Fayos P, Cerdà A. 1997. Seed losses by surface wash in degraded Mediterranean environments. *Catena* **29**: 73–83.
- García-Fayos P, García-Ventoso B, Cerdà A. 2000. Limitations to plant establishment on eroded slopes in southeastern Spain. *Journal of Vegetation Science* **11**: 77–86.
- García-Fayos P, Bochet E. 2009. Evidence of antagonistic interaction between climate change and erosion on plant species richness and soil properties in semiarid Mediterranean ecosystems. *Global Change Biology* **15**: 306–318.
- Guàrdia R. 1995. La colonització vegetal de les áreas erosionades de la conca de la Baells (Alt Llobregat), PhD Thesis, Universitat de Barcelona.
- Guàrdia R, Ninot JM. 1992. Distribution of plant communities in the badlands of the upper Llobregat Basin (Southeastern Pyrenees). *Studia Geobotanica* **12**: 83–103.
- Guàrdia R, Gallart F, Ninot JM. 2000. Soil seed bank and seedling dynamics in badlands of the Upper Ilobregat Basin (Pyrenees). *Catena* **40**: 189–202.
- Guerrero-Campo J. 1998. *Respuesta de la vegetación y de la morfología de las plantas a la erosión del suelo. Valle del Ebro y Prepirineo aragonés.* Consejo de Protección de la Naturaleza de Aragón, Serie Investigación: Zaragoza.
- Guerrero-Campo J, Montserrat-Martí G. 2000. Effects of soil erosion on the floristic composition of plant communities on marl in northeast Spain. *Journal of Vegetation Science* **11**: 329–336.
- Guerrero-Campo J, Palacio S, Montserrat-Martí G. 2008. Plant traits enabling survival in Mediterranean badlands in northeastern Spain suffering from soil erosion. *Journal of Vegetation Science* **19**: 457–464.
- Gutterman Y, Shem-Tov S. 1997. Mucilaginous seed coat structure of Carrichtera annua and Anastatica hierochuntica from the Negev Desert highlands of Israel, and its adhesion to the soil crust. *Journal* of Arid Environments **35**: 695–705.
- Gyssels G, Poesen J, Bochet E, Li Y. 2005. Impact of plant roots on the resistance of soils to erosion by water: a review. *Progress in Physical Geography* **29**: 1–28.
- Harper JL, Benton RA. 1966. The behaviour of seeds in soil. II. The germination of seeds on the surface of a water supplying substrate. *Journal of Ecology* **54**: 151–166.
- Hutchinson TF, Boerner REJ, Iverson LR, Sutherland S, Sutherland EK. 1999. Landscape patterns of understorey composition and richness across a moisture and nitrogen mineralization gradient in Ohio (USA) Quercus forests. *Plant Ecology* **144**: 177–189.
- Iwasa Y, Kubo T. 1997. Optimal size of storage for recovery after unpredictable disturbances. *Evolution Ecology* 11: 41–65.
- Kleyer M, Bekker RM, Knevel IC, Bakker JP, Thompson K, Sonnenschein M, Poschlod P, van Groenendael JM, Klimes L, Klimesova J, Klotz S, Rusch GM, Hermy M, Adriaens D, Boedeltje G, Bossuyt B, Dannemann A, Endels P, Götzenbergber L, Hodgson JG, Jackel A-K, Kühn I, Kunzmann D, Ozinga WA, Römermann C, Stadler M, Schlegelmilch J, Steendam HJ, Tackenberg O, Wilmann B, Cornelissen JHC, Erikson O, Garnier E, Peco B. 2008. The LEDA Traitbase:

a database of life-history traits of the northwest European flora. *Journal of Ecology* **96**: 1266–1274.

- Klute A. 1986. Methods of Soil Analysis. Part 1. Physical and Mineralogical Properties, Agronomy Monograph 9, 2nd edition. American Society of Agronomy – Soil Science Society of America: Madison, WI.
- Lavee H, Imeson AC, Sarah P. 1998. The impact of climate change on geomorphology and desertification along a Mediterranean-arid transect. *Land Degradation & Development* **9**: 407–422.
- Lázaro Suau R. 1995. *Relaciones entre vegetación y geomorfología en el área acarcavada del Desierto de Tabernas,* PhD Thesis, Universidad de Valencia.
- MAPA. 1986. *Métodos oficiales de análisis,* Tomo III. Ministerio de Agricultura, Pesca y Alimentación: Madrid; 101–103.

Morgan RPC. 1986. Soil Erosion and Conservation. Longman: Harlow.

Nadal Romero E, Regüés D, Martí-Bono C, Serrano-Muela P. 2007. Badland dynamics in the central Pyrenees: temporal and spatial patterns of weathering processes. *Earth Surface Processes and Landforms* **32**: 888–904.

Page AL, Miller RH, Keeney DR. 1986. *Methods of Soil Analysis. Part*2. *Chemical and Microbiological* Properties, Agronomy Monograph
9, 2nd edition. American Society of Agronomy – Soil Science Society of America: Madison, WI.

- Poesen JWA, Hooke JM. 1997. Erosion, flooding and channel management in Mediterranean environments of southern Europe. *Progress in Physical Geography* **21**: 157–199.
- Puigdefrabregas J. 2005. The role of vegetation patterns in structuring runoff and sediment fluxes in drylands. *Earth Surface Processes and Landforms* **30**: 133–147.
- Ruiz-Sinoga JD, Martínez-Murillo JF. 2009. Eco-geomorphological system response variability to the 2004–06 drought along a climatic gradient of the Littoral Betic Range (southern Spain). *Geomorphology* **103**: 351–362.

- Snelder DJ, Bryan RB. 1995. The use of rainfall simulation tests to assess the influence of vegetation density on soil loss on degraded rangelands in the Baringo District, Kenya. *Catena* **25**: 105–116.
- Stevenson AC. 2000. The Holocene forest history of the Montes Universales, Teruel, Spain. *The Holocene* **10**: 603–610.
- Stokes A, Lucas A, Jouneau L. 2007. Plant biomechanical strategies in response to frequent disturbance: uprooting of *Phyllostachys nidularia* (*Poaceae*) growing on landslide-prone slopes in Sichuan, China. *American Journal of Botany* **94**: 1129–1136.
- Thompson K, Band SR, Hodgson JG. 1993. Seed size and shape predict seed persistence in the soil. *Functional Ecology* 7: 236–241.

Thornes JB. 1985. The ecology of erosion. *Geography* **70**: 222–236.

- Thornes J. 1990. Vegetation and Erosion: Processes and Environments – Symposium Proceedings, British Geomorphological Research Group Symposia Series. John Wiley & Sons: Chichester.
- Turnbull LA, Crawley MJ, Rees M. 2000. Are plant populations seedlimited? A review of seed sowing experiments. *Oikos* 88: 225–238.
- Tzanopoulos J, Mitchley J, Pantis JD. 2007. Vegetation dynamics in abandoned crop fields on a Mediterranean island: development of succession model and estimation of disturbance thresholds. *Agriculture, Ecosystems and Environment* **120**: 370–376.
- Warren II RJ. 2008. Mechanisms driving understorey evergreen herb distributions across slope aspects: as derived from landscape position. *Plant Ecology* **198**: 297–308.
- Zar JH. 1996. *Biostatistical Analysis*. Prentice-Hall International: Upper Saddle River, NJ.
- Zobel M, van der Maarel E, Dupré C. 1998. Species pool: the concept, its determination and significance for community restoration. *Applied Vegetation Science* **1**: 55–66.