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REGULAR ARTICLE

Seed removal susceptibility through soil erosion shapes vegetation composition

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Abstract Soil erosion and vegetation cover are negatively related in semiarid slopes due to the influence of erosion on important soil surface properties for plant establishment and development, but also because the removal of seeds and plants. Previous published work concluded that seed mass is the main factor explaining the seed susceptibility to removal by soil erosion but that this susceptibility can be modified by the presence of seed appendages (hairs, wings, awns) and the ability of seeds to segregate mucilage in contact with water. In the present work we first analyzed how the presence of seed appendages and the ability of seeds to segregate mucilage modify the susceptibility of seeds to removal by soil erosion, and then if soil erosion, through its effects on seed removal can explain plant community composition of semiarid slopes. Results indicate that segregation of mucilage reduces seed susceptibility to be removed and that this seed susceptibility to removal is lower for plants living on steep slopes than that of species living in communities of flat sites. We then argue that soil erosion by water has the potential to affect plant communities of semi-arid Mediterranean slopes.

Keywords Semiarid · Soil erosion · Vegetation–erosion relationships · Plant community assembly · Seed mass · Seed shape

Introduction

The relationship between vegetation and soil erosion may be viewed not only as the effect of vegetation cover on the geomorphic processes but also as the effect of geomorphic processes on plant cover, structure and composition (Thornes 1985). Despite the long recognized influence of geomorphic processes on vegetation patterns at landscape scale, lesser attention has been put on the influence of geomorphic processes at smaller scales such as slopes or portions of slopes (Buxbauma and Vanderbilt 2007; Murray et al. 2008; Renschler et al. 2007; Saco et al. 2007; Valentín et al. 1999). Soil erosion acts on vegetation through the removal of nutrients stored in the soil, but also through the removal of seeds, fragments of plants or even entire plants. Therefore, soil erosion has the

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potential to affect species establishment and persistence, and as a consequence it also influences the species composition and its spatial distribution (Schlesinger et al. 1990).

Soil erosion by water is an important natural geomorphic process in semiarid areas but, at the same time, is one of the main processes of land degradation of these areas because intensive live stocking, farming, and fuel wood (Poesen 1995). Research has been done about the influence of plant cover and species composition on soil erosion at catchment's and plot's scales (Boix-Fayos et al. 2005; Boardman and Poesen 2006 for recent reviews), but the effect of soil erosion by water on vegetation establishment, structure and composition through space and time was and still is poorly documented. Casado et al. (1985) and Puerto et al. (1990) found that primary production in grasslands of Central Spain increases from the upper to the bottom parts of slopes in a source-sink system that enhances differences in development and reproduction of individuals of the species living in the two parts of the system. Kadmon (1993) obtained similar results for other grasses, like *Stipa capensis*, in wadis of Palestine. At the community level, a decrease in the vegetal cover and species richness of plant communities has been reported as a consequence of increasing soil erosion (Guerrero-Campo and Montserrat-Martí 2000). García-Fayos and Bochet (2009) reported a decrease up to 10% in vegetal cover and up to 40% in species richness when they compared plant communities developing in the flat upper part of the hillslopes—i.e. low erosion levels—with those developing on 20–25° steep hillslopes—i.e. high erosion levels.

After dispersal, seeds remain at the soil surface until they germinate or enter into the soil seed bank (Chambers and McMahon 1994). The fate of these seeds depends on their attractiveness to seed predators and on their resistance to be removed down slope by overland flow. In dryland slopes, variations in slope angle and the presence of obstacles such as rocks and established plants control overland flow distribution along slopes and can aid to explain the spatial heterogeneity of plant recruitment. In those slopes, a decrease in water velocity along the slope can cause water reinfiltration and sediment deposition in specific sites, enhancing plant establishment and development locally and therefore, increasing the control over water overland flow at that point (Cerdà 1997). In consequence, vegetation often forms patches where litter, water and seeds accumulate (Boeken and Orenstein 2001; Chambers 1995; Montaña 1992; Puigdefábregas et al. 1999) in a self-organizing process (Puigdefábregas 2005).

The resistance of the seeds to be removed downslope by water erosion depends on the characteristics of the seeds (size and shape) as well as on the characteristics of the soil surface (Chambers et al. 1991; Traba et al. 2006). Although there has been research about the ecological and evolutionary implications of seed size and shape (Harper et al. 1970; Hodkinson et al. 1998; Moles et al. 2005, 2007) however, there is a lack of information about the relationships between seed characteristics and seed susceptibility to be removed by water erosion as a potential mechanism controlling plant establishment and then the assembly of plant communities. Our previous published work on susceptibility of seeds to be removed by erosion on slopes of degraded areas of southeast Spain concluded that seed mass is the main characteristic explaining seed susceptibility to removal by water erosion (García-Fayos and Cerdà 1997; Cerdà and García-Fayos 2002) and that seed shape becomes important only after seeds reach a threshold mass. So, seed susceptibility to removal by water erosion decreases with seed mass, but when seeds reach a mass greater than 50 mg this trend reverses, and seed removal susceptibility increases with seed mass. Likewise, this response was modulated by seed shape. That is, this rule only applies for spherical or near to spherical seeds. In the case of flatter seeds heavier than 50 mg, seeds weren't removed in any way (Cerdà and García-Fayos 2002). It was also suggested that the susceptibility of a seed to be removed by erosion can be modified by the presence of seed appendages (hairs, wings, awns) or by the seed ability to segregate mucilage in contact with water (García-Fayos and Cerdà 1997).

Awns can aid seeds getting deep into the soil through hygroscopic movements (Stamp 1984; Peart and Clifford 1987) and mucilage segregation can attach seeds to the soil surface (Gutterman and Shem-Tov 1997). Both mechanisms have been related to antitelechory, the active mechanism of plants to avoid seed dispersal in space hindering seeds from predation by ants and removal by erosion (Ellner and Shmida 1981). Species with mechanisms against seed removal by erosion may be favoured in communities if their survival and development increase in relation to that of species whose seeds lack these mechanisms. Seeds lacking mechanisms against removal by erosion may be removed along the slopes and predictably clustered in (micro)-sites where survival, germination and development may be performed in conditions of higher plant competition than isolated seeds fixed at the slope surface. Thus, the existence of such mechanisms against seed removal may be expected in the case of poor competitive plants (sensu Grime 2001). In semiarid and poor soil areas, low competitive ability is frequent in plant species that colonize open spaces (Grime 2001) and therefore, mechanisms that obstruct seed removal by erosion in steep slopes may be important for species permanence. We hypothesize that in dryland areas, other environmental conditions being similar, mechanisms hindering seed removal by soil erosion (i.e. seed appendages and mucilage segregation) should be more frequent in plant communities on steep slopes with active soil erosion processes than in plant communities developed on flat sites with no signs of erosion activity.

To test this hypothesis, we first analysed, using a rainfall simulator under experimental conditions, how the relationships between seed size and susceptibility of seeds to soil erosion is modified by the presence of seed coat appendages (hairs, wings, awns) or by the ability of seeds to segregate mucilage when put in contact with water (species level approach). Later, we analysed whether seed susceptibility to removal by soil erosion through water differs between plant communities living on flat areas (highlands) vs. steep slopes (hill slopes) with active soil erosion processes in semiarid climatic areas (community level approach). To the present, still lacks empirical analysis of the effect of appendages and mucilage segregation on seed susceptibility to be removed by water erosion and on the importance of seed susceptibility to removal by soil erosion in determining species composition of eroded slopes.

Material and methods

Seed susceptibility to removal by soil erosion at the species level

One hundred and forty one plant species were selected from wild plants living in dry and semi-arid habitats in East Spain and representative of the Mediterranean flora. Some of them were trees and shrubs but we also tested grasses and annual plants. For the purposes of the present work, we refer here to "seeds" as the dispersal units of plants. In many cases they are true seeds but in some others, however, they are fruits or seeds with some gynoecium's structures attached. Studied species were sorted in three classes according to seed characteristics: "Smooth", species whose seeds have neither appendage nor segregate mucilage from the seed coat when wetted (77 species); "Appendage", species whose seeds bear wings, awns or long hairs that remain attached to the seed coat once seeds have reached the soil surface (35 species); and "Mucilage", species whose seeds segregate mucilage from the seed coat after wetting (29 species). The assignation of the species to a category was made after inspecting the seeds (presence of appendages) and performing microscope observations on the seed coat of ten to 25 seeds/species, soaked for 10 min in water (mucilage segregation). Longer time to mucilage segregation would be not fast enough to avoid seed removal by water erosion since time to runoff is typically shorter than 10 min in these environments (Cerdà and García-Fayos 1997; Arnau-Rosalen et al. 2008) and then, species needing more than 10 min to segregate mucilage may be not considered in this category. Several species whose seeds have appendages and also segregate mucilage (*Alyssum simplex* and *Helichrysum stoechas*) were included into the class with the lowest seed susceptibility ratio predicted from their respective seed mass (see below).

For each species, we collected mature seeds from at least ten different individuals within a population. Then, seeds were stored in paper bags under laboratory conditions (dry and dark place 20–25°C in average) for less than 1 year, until the experiments were carried out. Fresh mature and healthy seeds were weighed individually in a laboratory balance to the nearest 0.01 mg (n=25). To characterise the seed shape we first determined the length (L, longest axis), width (W, intermediate axis) and height (H, shortest axis) of each seed species (n=20) with the aid of an optical microscope to the nearest 0.1 mm. A Flatness Index, $FI = (L + W)/2H$ (Poesen 1987) was calculated for every species. Flatness Index ranged from 1 for spherical seeds to greater values for flat and spindle seed shapes. The Flatness Index was not calculated for seeds with appendages because appendages heavily modify the shape of the seeds in an unpredictable manner, depending on the position of the seed after reaching the soil and the pattern of the wetting process (soil moisture conditions, drop impact and runoff).

Five rainfall simulation experiments were performed for each species with a rainfall simulator (Eijkelkamp, the Netherlands) (see Cerdà and García-Fayos 2002 for more details). This apparatus consists of a sprinkler with a built-in pressure regulator and a support frame for the sprinkler. The original stainless steel frame at the basis was substituted by a square 26×26 cm PVC plate covered by sandpaper with a roughness of 320 µm in order to simulate a minimum surface roughness and to avoid rolling of the spherical seeds along the 11° slope angle. In this study water discharged from the sprinkling head with mean rainfall intensity of 54.73±5.13 mm h^{-1}. At each experiment, 25–50 seeds, according to their size, were located at the top of the 26×26 cm plot. Rainfall simulations lasted 25 min and the total number of seeds coming out of the plot was counted at the end of the experiment. A Seed Susceptibility to Removal index (SSR) was then calculated for each species ($SSR = \Sigma(x_i/X_i)$; where x_i is the number of seeds lost in the experiment i, and X_i the number of seeds used in that experiment). SSR varies from 0 (0% of the seeds removed) to 1 (100% of the seeds removed). The relation between the logarithm of seed mass (expressed in milligrams) and the SSR index within each seed category ("Smooth", "Appendage" and "Mucilage") was explored with regression analysis (linear and curvilinear models) and the model with the higher determination coefficient was selected for each category.

Seed susceptibility to removal by soil erosion at the plant community level

Plant community composition of two geomorphic positions consisting of highlands and hillslopes was compared to test for the effects of the specific SSR index on plant community composition. Highlands were selected as surrogates of areas with low erosion rates and hillslopes were selected as surrogates of areas with high erosion rates.

Two study systems were selected at the basin of the Alfambra River (Teruel, Spain), one at the north (Villarejo area) and the other at the south part of the Basin once the Alfambra and Guadalaviar rivers have joined (Carrascalejo area). This basin occupies 4,000 km^2, with an altitude between 900 m a.s.l and 1,300 m a.s.l. Every study system was composed of highlands ("Muelas") and steep hillslopes excavated by the rivers during the Quaternary on Tertiary limestones, calcareous marls and sands. The region suffered from intense deforestation from Neolithic times, mainly for fuel, domestic livestock and dryland agriculture (see García-Fayos and Bochet 2009 for more details on Study Area and sampling conditions). Flora of highlands and hillslopes shared 40% of the species in the Villarejo area and 38% in the Carrascalejo area.

For every geomorphic position we selected 15 independent sites in each study system. Site selection criteria for highlands were forest clearings greater than 0.05 km^2 located at least 100 m apart from each other, with a slope angle less than 5° and south-oriented. Site selection criteria for hillslopes were midslope trams of hillslopes longer than 100 m, south-oriented, 25–30° slope angle, separated by ravines from each other and with similar rill development (25.5±6.2% of rill cover in average). To avoid the differential influence of land use on the study variables, we sampled only sites with no signs of cultivation or outcrops. Vegetal cover in the plots varied between 15% and 45%. In the spring 2006, we marked one 1×20 m plot perpendicular to the slope in every sampling site, measured the slope angle and aspect and recorded all the plant species present in all the 1×1 m sub-plots. Two plant variables were obtained per plot, the presence of a species in the whole 1×20 m plot (the variable takes values of 1 = presence or 0 = absence) and its abundance, measured as the frequency of the species in the twenty 1×1 m sub-plots (values ranging from 0 to 20).

Along the summers of 2006 and 2007 we collected seeds from near all the species in the study areas and determined seed mass, the presence of appendages and the ability to segregate mucilage when wetted in the same way that for the species used to obtain the models of seed susceptibility to removal by soil erosion. For every species the value of SSR was obtained from its seed mass with regression models according to its seed coat category. For each plot we calculated the average value of the SSR index according to the value of SSR of every plant species present in the plot and also according to its abundance (SSR x abundance). Then, we compared the value of

SSR of plots at different geomorphic positions within each study system. All the statistical analyses were performed with SPSS v. 15.0.

Results

Seed susceptibility to removal by soil erosion at the species level

Seed mass ranged from 0.040 mg (*Sedum sediforme*) to 514 mg (*Chamaerops humilis*) and the SSR index ranged from 0.000 (several species such as *Ceratonia siliqua* in the "Smooth" category, *Avena barbata* in the "Appendage" category or *Fumana thymifolia* in the "Mucilage" category) to more than 0.900 (*Erica multiflora* in the "Smooth" category, and *Erigeron canadensis* in the "Appendage" category) (Table 1) (see "Supplementary Material").

Figure 1 shows the model best fitting the relationships between SSR and seed mass for every seed category and Table 2 the model parameters. The model for the "Mucilage" category shows the best fit and the model for the "Smooth" category the poorest one as expressed by the determination coefficient. In all cases, seed losses decrease with the increase of seed mass until a value around 5 mg, reaching almost no losses at that point. The best fit for all seed categories was the quadratic model when the logarithm of seed mass was used. For the lightest seeds (≤0.7 mg), the model for "Mucilage" seeds showed significant lower SSR values than for the seeds of the other seed categories (one-way ANOVA $F=6.889$, $P=0.013$; Dunnet post-hoc test).

Seed susceptibility to removal by soil erosion at the plant community level

The average SSR of the species per plot was lower for plots located at steep slopes than those located at flat sites and it was consistent at both study sites and for presence and abundance data of species (Figs. 2 and 3), and the differences were statistically significant. So, for presence/absence data in the Villarejo study site, plots of the flat sites had 45% higher values of SSR than that of the plots in the hillslopes (*t-test*=6.143; df=28; $P<0.0001$), and those differences were 29% at the Carrascalejo study site (*t-test*=4.042; df=28; $P<0.0001$). The same pattern was found when we used the abundance of the plant species in the plots (*t-test*=4.654; df=28; $P<0.0001$ and *t-test*=3.472; df=28; $P=0.002$ for the Villarejo and Carrascalejo study sites respectively).

Discussion

From the inspection of the relationships between seed mass and the index of seed susceptibility to removal we realize that (i) seed size is the major factor in determining seed removal by water erosion, (ii) an inverse relation exists between seed susceptibility to be removed and seed mass until a threshold around 5 mg mass and it is general to all the seed categories and (iii) species with light seeds (≤0.7 mg) and segregating mucilage experience 10% lower losses than the seeds with similar mass of the other categories.

The model for the "Smooth" seed category showed that seed susceptibility to removal decreases with seed weight until it reaches a value near 50 mg, henceforth SSR increases with seed weight (Fig. 1). However, and accordingly with Cerdà and García-Fayos (2002), seeds heavier than 50 mg behaved in two different ways. Spherical or near to spherical seeds, like those of *Osyris quadripartita* and *Olea europaea* (Flatness Index lower than 1.3), fitted the model and SSR increased with seed weight but flat or near to flat seeds, like those of *Ceratonia siliqua* and *Retama sphaerocarpa* (Flatness Index higher than 1.3), had lower values of the SSR than expected by the model (open circles in Fig. 1) thus indicating a higher resistance to be removed.

Table 1 Seed characteristics (minimum-maximum value)

	Smooth	Appendage	Mucilage
Seed weight (mg)	0.04–514.50	0.067–79.86	0.04–9.04
Flatness index	1.00–14.76	–	1.10–4.40
Seed susceptibility to removal	0.000–0.928	0.000–0.932	0.000–0.236

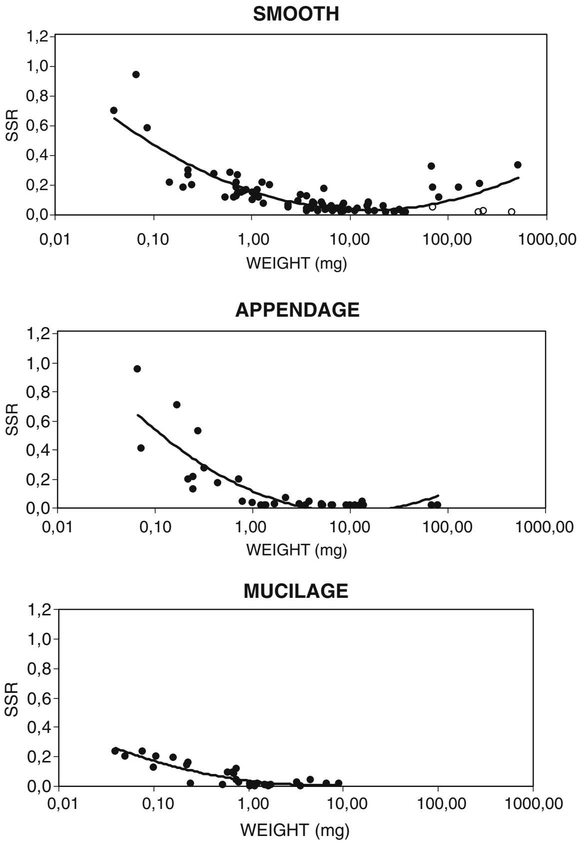

Fig. 1 Regression models of seed susceptibility to removal (SSR) for three different seed class category (i.e. smooth, appendage, and mucilage). *Empty circles* in the "Smooth" category indicate seeds heavier than 50 mg with a flat form (Flatness Index >1.3)

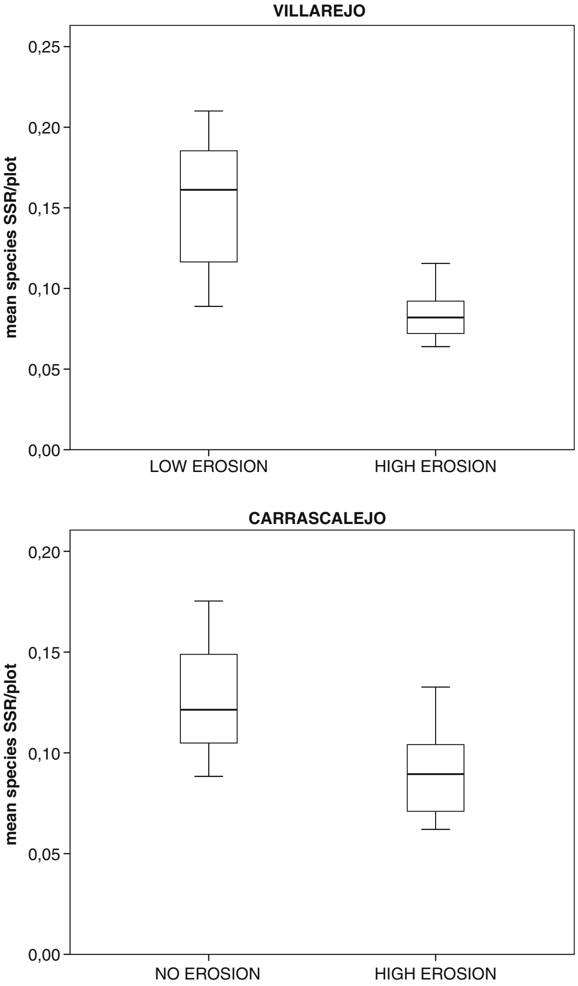

Fig. 2 Differences in mean species value of seed susceptibility to removal (SSR) per plot (species presence data)

The model for seeds in the "Appendage" category also fit a quadratic model, thus paralleling the pattern of the relations between seed mass and SSR as of the "Smooth" category. However, seeds heavier than 50 mg didn't increase SSR values with the increase of seed weight behaving like "smooth" seeds with low Flat Index. It may be the consequence that seed appendages (i.e. awns, pappus or hairs) have on the shape of the entire dispersal unit when wetted, because they increase dimensions (*L* and *W*) of the dispersal unit and then its Flatness Index, reaching a flatter shape.

Table 2 Model parameters

	Smooth	Appendage	Mucilage
R^2	0.696	0.725	0.785
F	84.687	42.130	47.380
df	2, 74	2, 32	2, 26
p	<0.0001	<0.0001	<0.0001
a	0.142±0.012	0.096±0.025	0.036±0.009
b_1	−0.221±0.017	−0.282±0.031	−0.081±0.015
$\boldsymbol{b_2}$	0.094±0.009	0.140±0.026	0.055±0.017

The model for seeds in the "Mucilage" category showed the same pattern that the other models. However, it differed in an important way. Seeds lighter than 1 mg were less susceptible to be removed by water erosion and had SSR values lower than seeds with the same mass in "Smooth" and "Appendage" categories.

The SSR index of the entire plant communities was affected by the increase of slope angle and the intensity of erosion processes as predicted, and it was consistent using both, species presence and species abundance in

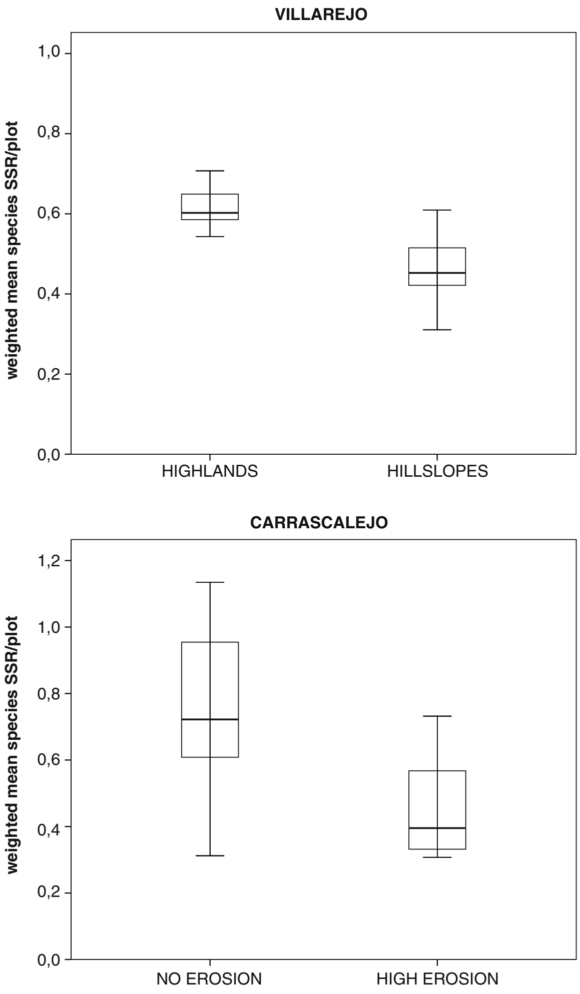

Fig. 3 Differences in weighted mean species value of seed susceptibility to removal (SSR) per plot (species abundance data)

the plots. So, plant communities with high slope angle and more soil erosion intensity had lower values of SSR than plant communities living in flat sites with low or no erosion and we can then conclude that soil erosion by water is able to modify species composition and abundance of plant communities.

To the present, this is the first evidence that soil erosion processes plays a role in species selection in plant communities and that seed susceptibility to erosion may play a crucial role on it. The way how soil erosion by water proceeds on species selection is still under investigation (Engelbrecht et al. in preparation), but we predict that species with mechanisms to reduce seed susceptibility to removal by water erosion may be more frequent in plant communities living on severely eroded areas than in plant communities living on poorly eroded areas.

Nevertheless, we are aware of the risks of over interpreting the role of seed removal by erosion in structuring plant communities. On the one hand, seed removal by erosion is not so high in field conditions. Our present experiment in laboratory conditions with very short plots (26 cm) without relief or obstacles such as stones, litter or roughness never showed total seed losses in any species. Empirical data and observations of seed removal after intense rains on very steep badland slopes never surpassed 13% (García-Fayos et al. 1995). On the other hand, seed size is the main factor explaining the variation in the susceptibility of seeds to be removed, but seed size is also related to many other important plant characteristics. Changes in seed mass during seed plant evolution have been more consistently associated with divergences in growth form than with divergences in any other plant and environmental variable (Moles et al. 2005), but divergences in seed mass have also been associated with divergences in temperature, precipitation, and leaf characteristics (Harper et al. 1970; Moles et al. 2007). In consequence, several other pressures on plant performance are then shaping plant composition on these communities and then direct or indirectly affecting plant community composition. For example, García-Fayos and Bochet (2009) found that the number of annual and shrub species increases with soil erosion in the same plant communities we studied in this paper, and then changes in seed size associated to this different plant growth form composition can indirectly be affecting seed size.

In conclusion, although seed size is the main determinant of the susceptibility of a seed to be removed by soil erosion this relation is modulated by the shape of the seeds and the presence of seed coat appendage in seeds heavier that 50 mg. Also, the secretion of mucilage by seeds when wetted increases seed resistance to be removed thus lowering the relation between seed size and removal. In Mediterranean semiarid environments soil erosion by water acts over species composition of plant communities at plot and hillslope scales by favouring species with lower susceptibility to be removed by water erosion.

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