Plant Ecol (2013) 214:941–952
DOI 10.1007/s11258-013-0220-z

Post-dispersal seed anchorage to soil in semiarid plant communities, a test of the hypothesis of Ellner and Shmida

Patricio García-Fayos · Meike Engelbrecht · Esther Bochet

Received: 1 November 2012 / Accepted: 28 May 2013 / Published online: 6 June 2013

Abstract In this paper we test the Ellner and Shmida's hypothesis that in semiarid environments aridity may select for the lack of seed dispersal mechanisms (atelechory) of many plants, whereas post-dispersal selective forces such as soil erosion, seed predation or limitations to water uptake by seeds may select for structures facilitating seed anchorage to the ground (antitelechory). We analyzed the proportions of species with seed anchorage mechanisms and that of atelechoric species in shrublands colonizing flat areas and hillslopes in two sites differing in climate dryness. Their relation with several soil properties involved in runoff generation, seed–soil contact and water uptake by seeds and with nest density of granivorous ants was also explored. Our results support the hypothesis that in semiarid shrublands the proportion of species with seed anchorage mechanisms increases because of soil erosion but not because of climate dryness. This is the first time that a direct relation between the proportion of species with seed anchorage mechanisms and soil erosion is shown in plant communities; supporting the view that soil erosion shapes species composition in communities.

Keywords Vegetation · Soil erosion · Climate dryness · Seed dispersal · Myxospermy

Introduction

It has been repeatedly observed that long-distance seed dispersal syndromes are less frequent in arid and semiarid than in mesic habitats and even that mechanisms constraining spatial seed dispersal are a common trait of arid and semiarid floras (Van der Pijl 1982; Ellner and Shmida 1981; Rheede et al. 1999).

Early predictions claimed that plants inhabiting spatially heterogeneous environments benefits from long-distance seed dispersal because it allows plants to reach distant favourable patches and spread extinction risk in space (Levin et al. 1984; Cohen and Levin 1987). Contrary to this view, Stebbins (1971) and Friedman and Stein (1980) argued that the continuous occupation of the few favourable sites that exist for plant development in those environments may be a superior adaptative strategy for plants (mother-site theory). Accordingly, these authors suggested that, in plant communities inhabiting open environments, long-distance seed dispersal syndromes (telechory) should be selected against whereas short-distance seed dispersal syndromes, including both the lack of syndromes for seed dispersal (atelechory) and the presence of syndromes to avoid seeds to disperse

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P. García-Fayos (✉) · M. Engelbrecht · E. Bochet
Centro de Investigaciones sobre Desertificación—CIDE (CSIC-UV-GV), Carretera Moncada-Náquera, Km. 4.5, 46113 Moncada, Spain
e-mail: patricio.garcia-fayos@uv.es

(antitelechory), should be favoured. On the grounds of these arguments, spatial restrictions to seed dispersal have been widely proposed to explain the origin and maintenance of patches in semiarid vegetation (Kefi et al. 2008; Pueyo et al. 2008).

There are two groups of antitelechoric mechanisms used by plants to avoid seed dispersal. One of them is based on the control of the time that seeds disperse and the other is based on mechanisms that anchor the seeds to the ground. Ellner and Shmida (1981) suggested that seed anchoring mechanisms should not be considered adaptations to claim the mother site in the same way that atelechory does, as the mother site theory proposed, because in plants with seed anchorage mechanisms seeds need to be dispersed before seed anchoring mechanisms can operate. They argue that "the openness of desert vegetation and the patterns of climatic variation favour atelechory while antitelechory is generally a side-effect of mechanisms whose adaptative value is not directly related to seed dispersal". They maintain that anchoring mechanisms are adaptative, given that providing fruits or seeds with mechanisms that actively restrict post-dispersal movement has an additional cost to plants in terms of carbon allocation during their development, but they also argue that these mechanisms may be related to post-dispersal events, such as the loss of opportunities for seeds to germinate derived from seed removal by erosion, seed predation or insufficient seed–soil contact in coarse textured soils.

There are only two reputed mechanisms related to seed anchorage on the ground surface in plants living in semiarid areas, trypanocarpy and myxospermy (Rheede et al. 1999). Trypanocarpic diaspores have the ability to sink into the cracks or holes of the soil surface by means of hygroscopic movements of appendages attached to the upper part of the diaspore. This mechanism keeps diaspores safe from seed harvesters and removal by wind or water erosion, and also increases the chance for seed germination by increasing the contact surface of seeds with soil particles in coarse textured soils (Stamp 1989; Schöning et al. 2004). Typical examples of trypanocarpic species can be found in the Geraniaceae and Graminae families. Myxospermy is the ability of seeds or fruits to secrete mucilage from their testa or pericarp respectively, once they become moistened. It is a common feature in many families of Angiosperms (Grubert 1974; Western 2012). Rain, fog, dew or even soil moisture when soil is at field capacity are effective enough to stimulate the secretion of mucilage (García-Fayos and Cerdà 1997; Huang et al. 2004). The increase of the diaspore surface due to mucilage secretion reduces the probability of the diaspore being removed (García-Fayos et al. 2010) because when the mucilage turns dry, it strongly anchors the diaspore to the surface it is in contact with. Further research proved that mucilage secretion highly reduces seed predation by granivorous ants (Fuller and Hay 1983; Gutterman and Shem-Tov 1997; Engelbrecht and García-Fayos 2012), significantly reduces seed losses by runoff (García-Fayos and Cerdà 1997; García-Fayos et al. 2010) and, similar to trypanocarpy, increases the amount of surface contact between the seed coat and soil, aiding seed hydration and thus facilitating germination (Harper and Benton 1966; Gutterman and Shem-Tov 1996; Chambers et al. 1991).

Semiarid vegetation is characterized by a two-phase structure of vegetated patches and bare soil (Aguiar and Sala 1999). Rainfall in arid and semiarid regions of the world is mostly concentrated into few high intensity events (Rodriguez-Iturbe and Porporato 2004) with the potential to trigger strong soil erosion processes (Poesen and Hooke 1997). Several authors have shown that the interaction of plant growth with soil erosion can explain the origin and maintenance of patchy vegetation in hillslopes (Aguiar and Sala 1999; Puigdefàbregas 2005). In these hillslopes, seeds reaching the ground are at risk of being removed downslope by runoff water and deposited in the lower parts of slopes where they can get deeply buried (García-Fayos et al. 1995; Han et al. 2011) or where the seedlings they produce may be affected by stronger competition than those seedlings emerging on the upper and medium parts of the hillslopes (Cantón et al. 2004; Alados et al. 2006). Although there has been less research on the subject, wind erosion also has the potential of putting seeds at risk in the same way as surface runoff (Whitford 2002). Erosion also affects important soil properties related to plant establishment and development. Raindrop splashes break soil aggregates and sheet flow removes the finest particles and organic debris from the upper layer of soil, thus reducing soil fertility, the rate of water infiltration into the soil and the amount of available water for plants (Calvo-Cases et al. 2003; Monger and Bestelmeyer 2006). In addition, granivorous animals, mainly harvester ants, have a strong impact on seed survival in arid and semiarid ecosystems (Louda 1995; Hulme and Benkman 2002).

Consequently, the loss of seed germination opportunities in semiarid slopes because seed removal by erosion, predation or soil degradation can be a major difficulty for plants to overcome and, therefore, post-dispersal mechanisms allowing diaspore anchorage to the ground, burying the seed into the soil or increasing the amount of contact of the surface of seeds with soil particles could be favourable adaptations. At the same time, seed anchorage mechanisms should be the instrument because a new patch of vegetation originate and maintain in hillslopes. Once a plant develops from the anchored seed it can restrain locally the downslope movement of water and sediments, increasing soil moisture and fertility at the microsite where plant established (Cerdà 1997; Puigdefàbregas 2005) and favouring the growth of the plant and the patch, which in turn increases the ability of the patch to restrict the downslope movement of water and sediments.

If, as Ellner and Shmida (1981) proposed, seed anchorage mechanisms, such as myxospermy and trypanocarpy, are the outcome of agents of selection that operate after seed dispersal, but not the outcome of selective forces shaping seed dispersal, then it should be predicted that an increase in the intensity of all, or some, of the agents of selection that operate on seeds once they have dispersed (i.e. soil erosion, seed predation) must lead to an increase in the proportion of plants with seed anchorage mechanisms, but should not affect the proportion of plant species with atelechory seed dispersal syndromes. On the contrary, increasing the intensity of selective forces that shape seed dispersal only (i.e. climate aridity), must lead to an increase in the proportion of species with atelechory syndromes, but should not affect the proportion of plant species with seed anchorage mechanisms.

To test this hypothesis we compared the proportion of plant species with atelechory seed dispersal syndromes and the proportion of species with seed anchorage mechanisms (myxospermy plus trypanocarpy) in plant communities colonizing flat areas and steep hillslopes at both extremes of an aridity gradient that has been proved to negatively affect soil properties (García-Fayos and Bochet 2009). The area comprising the aridity gradient is mainly composed of calcareous clays and marls and characterized by superficial soil erosion processes more influential in shaping the hillslope landscape than those occurring in other materials such as limestone or sandstone (Cerdà 2002). We also explored the relationships between these proportions of species and physical soil properties related to runoff generation (bulk density, as a surrogate of the rate of water infiltration in soils) and to water uptake by seeds (fine sand content, indicative of the amount of contact between the seed surface and the ground, and soil water availability as a surrogate of the amount of available water for seeds to germinate and establish). At the same time, since seed harvesting pressure by ants may also influence our results, we analyzed the current nest density of granivorous ants in the study area as a surrogate of seed harvesting pressure. All other factors being similar, the density of granivorous ants in semiarid areas highly depends on vegetation structure, food availability and microsite conditions for winter survival (Diaz 1991; Arnan et al. 2007) and we have no reason to expect that density of granivorous ants is affected by climate and erosion in the same way that these factors affect plant species composition. We predict that (i) an increase in climate dryness, but not an increase in soil erosion, should increase the proportion of species with atelechory syndromes; (ii) an increase in soil erosion, but not an increase in climate aridity, should increase the proportion of plant species with seed anchorage mechanisms in plant communities; and (iii) the effect of soil erosion on physical soil properties related to runoff generation and water uptake by seeds may explain the effect that soil erosion has on the proportion of plant species with seed anchorage mechanisms.

Materials and methods

Study area

The study area is located in the Alfambra river basin (province of Teruel, Spain). The basin is 4,000 m^2 in area and lies at an altitude of 900–1,100 m a.s.l. It is composed mainly of calcareous marls. While the seasonal pattern is homogeneous in the whole basin, the amount of precipitation and average temperature differ between the southern and northern extremes of the basin with marked consequences on the plant communities. The extreme northern area, hereafter "cool&wet" area, has annual average temperature and total precipitation of 10.3 °C and 484 mm, respectively, and the southern area, hereafter"warm&dry" area, 11.9 °C and 368 mm, respectively (data from the 1990–2009 period, provided by AEMET: www.aemet.es).

In spring 2006, we selected and marked one sampling plot (1 × 20 m) perpendicular to the main slope direction in each of 30 hillslopes in the "cool&wet" and in the "warm&dry" areas, all of them south-oriented. In each area, 15 plots were placed in flat sites (hereafter "no erosion" sites) and 15 in 25°–30° steep hillslopes (hereafter "severe erosion" sites). Marked differences in erosion severity exist between flat and steep sites, varying from 0 to 25 % rill development respectively (García-Fayos and Bochet 2009); the latter rill density indicates a notorious sign of erosion processes on steep sites (Cerdan et al. 2010). Wind erosion has not been taken into account in our experimental design, because it has been reported as unimportant in the eastern part of the Iberian Peninsula (Solé-Benet 2006). Vegetation cover in all the plots was low (<50 %) and it was mainly composed of dwarf shrubs and some herbs.

Plant species present in each plot were identified and, when necessary, the plots were surveyed several times during the growing season to ensure that all plant species were recorded. From 2006 to 2009 we collected seeds from all species and 10 mature and fully developed seeds per species were checked and assigned to the following categories: trypanocarpy, myxospermy and atelechory. Trypanocarpy corresponds to diaspores with hygroscopic awns or hairs that are able to enter into the soil; myxospermy corresponds to diaspores that secrete mucilage from their testa or pericarp when wet; and atelechory corresponds to diaspores with mechanisms for short-distance seed dispersal (ballistic, barochory, etc.) or diaspores lacking such mechanisms but also lacking mechanisms for long-distance seed dispersal. Since trypanospermy and myxospermy act after seed dispersal, a species can be classified at the same time into the atelechory category and one of the two seed anchoring categories.

At the end of the summer of 2006, we took five soil subsamples 5 cm deep and 300 cm^3 volume at regular distances in each plot, that were mixed up in a single sample per plot. Samples were air-dried and sieved through a 2 mm mesh and fine sand content (mineral fraction size between 0.10 and 0.25 mm) and the soil moisture content available for plants were determined following the methodology proposed by Klute (1986). Additionally, we took three 57.7 cm^3 soil cores per plot for bulk density determination at the same depth as previous soil sampling and the average value per plot was used for comparisons. These soil properties were significantly and negatively affected by both climate dryness and soil erosion in our study area (García-Fayos and Bochet 2009). Bulk density is a key property influencing water infiltration into the soil and it was chosen as a surrogate of runoff generation. The higher the soil bulk density, the lower the soil water infiltration and consequently, in steep hillslopes lying on calcareous marls, the faster and higher the runoff generation (Cerdà 2002). Fine sand content and water availability were chosen respectively as surrogates of the extent of seed–soil contact and the amount of water stored in soils. The relation of these soil properties with the energy that seeds need to obtain water from soils was considered to be direct for fine sand content and inverse for water availability (Williams and Shaykewich 1971). So, the higher the fine sand content and the lower the water availability in soils, the higher the pressure that seeds need to exert in order to obtain enough water for germination and establishment (García-Fayos et al. 2000; Bochet et al. 2007).

To analyze the current nest density of granivorous ants we sampled six hillslopes per treatment and counted all the ant nests of granivorous species in an area of 250 m^2. Ant nests were attributed to granivorous ants after identification of the worker ants or inspecting the vast pile when direct ant identification was not possible.

Analyses of the influence of climate dryness and soil erosion treatments on the proportion of species with seed anchorage mechanisms and the proportion of atelechoric species per plot were performed with Linear Models, considering climate dryness and erosion as main factors and the proportions of atelechoric species and of species with seed anchorage, as response variables. Analyses were firstly performed on the total set of species with seed anchorage mechanisms, either myxospermic or trypanocarpic, and secondly, separately on each of both categories. We checked residuals for departure from normal distribution.

Because the size of the plots we used to sample ant nest density was greater than that used to sample plant species composition, it was not possible to directly analyze the effect of nest density on the proportion of plant species with seed anchorage mechanisms. Instead, we analyzed the effect of climate dryness and seed erosion on ant nest density per hillslope, and compared this result with that obtained from the analysis of the effect of the same factors on the proportion of species with seed anchorage mechanisms per plot. Statistical analyses were performed with the *lm* function of the R package v. 2.14.1 (R Development Core Team at http://cran.r-project.org/ last accessed 25/05/2012).

Results

We found a total of 167 plant species in the study area. Of them, 139 were unambiguously assigned to the different dispersal and seed anchoring diaspore categories (see Appendix in Table 3). Among these, 108 (77 %) were considered to be atelechoric and 31 (22 %) having any seed anchorage mechanism (26 myxospermic species -several Brassicaceae, Cistaceae, Lamiaceae, Asteraceae, Linaceae, Rosaceae, Plantaginaceae and Aristolochiaceae species- and only 5 trypanocarpic species-four Graminae, *Stipa parviflora*, *S. celakowsky*, *S. lagascae*, *Avenula pratensis* and one Geraniaceae, *Erodium cicutarium*). At the plot level, 67–94 % of the species have atelechoric diaspores (79 % in average, see Table 1) and 17–45 % of the species have diaspores with anchorage mechanism (30 % in average) and the proportion of myxospermic species is higher (15–44, 26 % in average) than that of trypanocarpic species (0–8, 2.4 % in average).

Table 1 shows the variation among plots in the proportion of atelechory and seeds with anchorage mechanisms. The linear model significantly explained the variation in the proportion of atelechoric species (Adjusted $R^2 = 0.1366$; $F_{3,56} = 4.112$; $p = 0.0105$) indicating that it is affected, although marginally ($p = 0.0753$), by climate dryness (81.2 ± 4.5 % (Mean ± SD) in the "warm&dry" plots versus 77.5 ± 3.9 % in the "cool&wet" plots), but that neither soil erosion ($p = 0.3572$) nor the interaction of both factors ($p = 0.4178$) affected the proportion of atelechoric species.

Relative to the proportion of species with seed anchorage mechanisms, the linear model significantly explained a moderate proportion of the variance (Adjusted $R^2 = 0.3481$; $F_{3,56} = 11.5$; $p < 0.0001$) showing that the proportion of species whose diaspores have anchorage mechanisms is positively affected by soil erosion ($p = 0.0002$) but neither by climate dryness ($p = 0.6616$) nor by their interaction ($p = 0.7426$). On average, the proportion of species with seed anchorage mechanisms is 26.7 ± 4.3 % in the "no erosion" plots and 33.5 ± 4.6 % in the "severe erosion" ones.

When the proportion of species with myxospermic and trypanocarpic mechanisms was analyzed separately, we found in the case of myxospermy that the model significatively explained almost 41 % of the variance ($F_{3,56} = 14.62$; $p < 0.0001$) indicating that soil erosion ($p = 0.0081$), but not climate dryness ($p = 0.8075$), significantly increased the proportion of myxospermic species in plots. However, the significant interaction term ($p = 0.0376$) indicates that the increase in the proportion of myxospermic species due to the effect of soil erosion is higher when climate dryness is greater. In the case of trypanocarpy, the model (Adjusted $R^2 = 0.3033$; $F_{3,56} = 9.561$; $p < 0.0001$) shows that climate dryness does not have a significant effect ($p = 0.6645$) but that soil erosion increases the proportion of trypanocarpic species ($p = 0.0086$). However, again, the significant interaction term between climate dryness and soil erosion ($p = 0.0010$) indicates that the proportion of trypanocarpic species in the "cool&wet" end of the climate gradient, is a little higher in the "no erosion" plots than in the "severe erosion", but that the contrary occurs in the "warm&dry" end of the climate gradient (see Table 1).

As hypothesized, both seed anchorage mechanisms (myxospermy and trypanocarpy together) and myxospermy were significantly and directly related to fine sand content and bulk density and also significantly but inversely related to water content (Table 2) indicating that there is an increase in the proportion of species with anchoring mechanisms (mainly myxospermy) when physical soil properties related to runoff generation and water uptake worsen. Atelechory was positive and significatively related to fine sand content and inversely to water availability but not to bulk density (Table 2).

Nests of ants collecting diaspores in the studied hillslopes were attributed mainly to the genus *Messor* (granivorous) and to a lesser extent to *Aphenogaster* (omnivorous). The total density of nests of these ants

Table 1 Average and standard deviation of the number (sp) and percentage (%) of species with different dispersal and soil anchorage mechanisms in 20 m^2 plots and ant nest density per hectare (nests) in hillslopes for the different treatments ($N = 15$)

		Total	"Cool&wet"		"Warm&dry"		Terms in the model
			"No erosion"	"Severe erosion"	"No erosion"	"Severe erosion"	
Atelechory	sp.	26.3 ± 8.5	39.3 ± 3.0	24.5 ± 4.5	21.6 ± 3.9	20.0 ± 3.8	C
	%	79.3 ± 4.5	79.2 ± 3.3	76.8 ± 4.3	81.0 ± 5.8	81.3 ± 2.8	
Seed anchorage mechanisms	sp.	9.8 ± 3.0	13.5 ± 1.4	10.6 ± 1.7	7.0 ± 2.0	8.2 ± 1.9	E
	%	30.1 ± 5.6	27.0 ± 3.1	33.5 ± 4.1	26.3 ± 5.3	33.5 ± 5.2	
Myxospermy	sp.	8.4 ± 2.5	11.5 ± 1.5	8.6 ± 1.3	6.0 ± 1.6	8.6 ± 1.3	E, CxE
	%	26.0 ± 5.5	22.9 ± 3.0	29.3 ± 3.0	22.5 ± 4.7	31.4 ± 5.7	
Trypanocarpy	sp.	0.8 ± 0.7	1.1 ± 0.5	1.3 ± 0.5	0.6 ± 0.7	0.3 ± 0.5	E, CxE
	%	2.4 ± 2.2	2.1 ± 1.0	4.2 ± 1.6	2.1 ± 2.6	1.1 ± 1.9	
Ant nest density	nests	100.2 ± 87.1	186.7 ± 96.1	36.6 ± 40.6	97.6 ± 89.1	81.8 ± 38.6	C, E, CxE

"Terms in the model" gives information about factors that have significant effect on the response variable in the linear model (see text for details)

Table 2 Pearson correlation indices between the percentage of species with different dispersal and soil anchorage mechanisms and soil properties

	Fine sand content (%)	Water availability	Bulk density
Atelechory	0.2713*	−0.3233*	0.0169
Seed anchorage mechanisms	0.2753*	−0.2948*	0.3479**
Myxospermy	0.3277**	−0.4260***	0.3745**
Trypanocarpy	−0.1048	0.2708*	−0.0489

p value: n.s. < 0.05; * 0.05–0.01; ** <0.01; $N = 60$

in hillslopes was highly variable (from 0 to 317.5 nests.ha^{-1}, Table 1) and the linear model fitting our data (Adjusted $R^2 = 0.2668$; $F_{3,24} = 4.276$; $p = 0.0149$) showed that ant nest density significantly decrease because of climate dryness ($p = 0.0295$) and soil erosion ($p = 0.0019$), but the decrease of ant nest density because of soil erosion is higher in the "cool&wet" than in the "warm&dry" treatment (interaction term, $p = 0.0287$, Table 1).

Discussion

The proportion of species with diaspore anchorage mechanisms in our study area is similar, or even higher, to that found in desert and semi-desert areas of Africa (Rheede et al. 1999). At least 22.3 % of the plant species in our study area and 17.0 % of the species living in Namaqualand (Namibia) have anchorage mechanisms in their diaspores and 18.7 % of the species in our study area, 15.7 % in southeast Spain, 11.3 % of the species in Namaqualand and 11.1 % in northwest Africa are myxospermic (Rheede et al. 1999; Navarro et al. 2009). In relation to trypanocarpy, only 3.6 % of the species in our study area are trypanocarpic, a similar value as in Namaqualand (5.7 %) and in semi-desert areas of southeast Spain (<4 %, Navarro et al. 2009). The proportion of species with short-distance dispersal syndromes (atelechory) was very high, ~80 %, and is similar to that of desert areas of Israel (75.0 %) but higher than that of Mediterranean and semi-desert areas of Israel (50.0 %) and semiarid areas of Namaqualand (21.6 %) (Ellner and Shmida 1981; Rheede et al. 1999). Interestingly, 100 % of the myxospermic species also have short-distance dispersal mechanisms and 22 % of atelechoric species are myxospermic (see Appendix in Table 3). Ant nest density was also in the range of values reported for other semiarid shrublands (Diaz 1991; Azcárate and Peco 2003).

According to the prediction of the Ellner and Shmida's hypothesis, soil erosion but not climate dryness, increased the proportion of species with anchoring mechanisms living on hillslopes in our study area. Similarly, and in agreement with our prediction, atelechory increased, although slightly, with climate dryness, but soil erosion did not affect it. These results and the correlations between the proportions of species having atelechoric or seed anchorage mechanisms with the studied soil properties strongly suggest that the need to resist seed removal by water runoff and to enhance the rate and the amount of water uptake by seeds are selective forces affecting the proportion of species with seed anchoring mechanisms, mainly myxospermy, in our study area. However, the significant correlation of atelechory with fine sand content (positive) and water availability (negative) and the fact that all myxospermic species have also atelechoric syndromes, supports the idea that soil degradation because of vegetation openness positively selects plant species with short-distance seed dispersal mechanisms (Ellner and Shmida 1981; Kefi et al. 2008; Pueyo et al. 2008) but that myxospermy should be a specific adaptation to soil erosion.

It is interesting to note that although the proportion of seed anchorage and myxospermic species are positively correlated with bulk density and bulk density increased with both, climate dryness and soil erosion, only soil erosion, but not climate dryness, positively affected the proportion of species with seed anchorage mechanisms and myxospermy. This can be explained by the fact that although bulk density decreased from the flat "warm&dry" plots to the flat "cool&wet" plots (García-Fayos and Bochet 2009), the low slope angle recorded in these areas ($<5^{\circ}$) prevents water sheet flow from increasing in the same way. Therefore, plants of the flat "warm&dry" plots do not suffer from more intense erosion than their equivalents in the "cool&wet" area and consequently they do not need to increase mechanisms against seed removal by erosion.

Our results also shed some light on the different roles that myxospermy and trypanocarpy play as seed anchorage mechanisms, although the very low frequency of trypanocarpic species ($<1.5 \pm 0.9$ species.plot^{-1} in average) precludes obtaining robust conclusions. Whereas almost all the conclusions about seed anchorage mechanisms are applicable to myxospermy, this is not the case for trypanocarpy. In fact, the percentage of trypanocarpic species per plot is only significantly correlated with water availability and this relationship is positive, unlike myxospermy. This reinforces the results from the linear model indicating that trypanocarpic species seem to be selected by soil erosion only in the wetter extreme of the climatic gradient, but that myxospermic species are selected positively in both extremes of our climate gradient, although more intensely in the "warm&dry" extreme.

It is unlikely that the interpretation of our results on seed anchorage and myxospermy was masked by the pressure exerted by harvester ants on plant species composition. Ant nest density was negatively related to soil erosion, especially in the "cool&wet" extreme of the gradient, probably because of the negative effect of soil erosion on the standing biomass and productivity. That is, the pattern of variation of the proportion of species with seed anchorage mechanisms and that of myxospermic species we found in our study was the opposite that it can be expected because of the pressure of harvester ants on plants. This does not mean that ant harvesting pressure cannot be a relevant force selecting anti-predatory mechanisms for seeds, such as myxospermy and trypanocarpy (see Schöning et al. 2004 and Engelbrecht and García-Fayos 2012 for recent reports on this issue), but it simply means that this pressure cannot explain the proportion of species with seed anchorage mechanisms in our study design.

Our results have implications for the controversies on the role of seed dispersal in buffering unpredictable small or medium-scale differences in patch quality in semiarid environments. It has been repeatedly suggested that atelechory and seed anchorage mechanisms contribute to the origin and maintenance of arid and semiarid patchy landscapes (Schurr et al. 2004; Kefi et al. 2008; Pueyo et al. 2008) but to date this assumption remains untested and needs to be directly verified. Siewert and Tielborger (2010) found that in Mediterranean semiarid communities most species do not rely on seed dispersal mechanisms to buffer unpredictable small-scale differences in patch quality, but rather that the major contribution of plant species to population recruitment was through the investment in seed numbers and dormancy. In this context, investing in seed anchorage mechanisms, such as those analyzed here, can be another way for plant species to survive in semiarid landscapes where soil erosion plays an important selection pressure.

In conclusion, our report is, to our knowledge, the first attempt to examine systematically the importance of various factors associated with the selection of plant species whose diaspores have anchoring mechanisms to ground. Although the role of myxospermy and trypanocarpy as mechanisms enhancing seed–soil contact had already been widely studied, it is the first time that a direct relation of soil erosion with the proportion of myxospermy and trypanocarpy in plant communities has been shown, supporting the hypothesis that anchorage mechanisms in diaspores play a role shaping species composition in communities affected by intense soil erosion (see also Bochet et al. 2009 and García-Fayos et al. 2010). The correlative approach of our study and the complex nature of the explanatory characteristics used make it difficult to interpret unambiguously the ultimate causes behind the observed associations. Nevertheless, the patterns that we detected support the idea that in water-limited environments anchorage mechanisms can be a way for seeds to overcome the direct effects of soil erosion—seed removal—and the negative effects of soil erosion on soil properties related to water uptake by seeds, an important limiting factor for plant establishment in such environments (García-Fayos et al. 2000; Bochet et al. 2009; Moreno-de las Heras et al. 2011).

Acknowledgments This research was supported by the Spanish "Plan Nacional de I+D+i" [projects CGL2005-03912 and CGL2009-07262]. We thank M^{a} Clara Castellanos, Miguel Morales, Jose Pavía and Helene Heyd for their help in the field and to J. Gabriel Segarra for his aid with plant determination. Thanks are also given for support of the whole 'Llavoratori' team. Meike Engelbrecht was funded by grants from the Spanish National Research Council [JAEPre-0800758] and the CSIC-Fundación BANCAJA [2007] of Spain. We are also grateful to Christopher Allen for his English revision and to Glenda Wardle and two anonymous reviewers for their suggestions. The National Meteorological Agency of Spain kindly provided the climatic data for the period 1990–2009.

Appendix

See Table 3

Table 3 List of the species in the study area with information about seed dispersal, seed anchorage and life-form syndromes

Species[a]	Atelechory	Myxospermy	Trypanospermy	Life-form[b]
Allium senescens subsp. montanum	1	0	0	G
Alyssum simplex	1	1	0	T
Androsace maxima	1	0	0	T
Anthyllis montana	1	0	0	H
Anthyllis vulneraria	1	0	0	H
Aphyllantes monspeliensis	1	0	0	H
Arabis auriculata	1	1	0	T
Arctostaphyllos uva-ursi	0	0	0	F
Argyrolobium zanonii	1	0	0	C
Aristolochia pistolochia	1	1	0	G
Artemisia campestris	1	1	0	C
Asperula aristata subsp. scabra	1	0	0	H
Asphodelus ramosus	1	0	0	G
ASTERACEAE (undetermined)	0	0	0	T
Astragalus incanus	1	0	0	H
Astragalus stella	1	0	0	T
Atractylis humilis	0	0	0	C
Avenula pratensis subsp. gonzaloi	0	0	1	H
Biscutella alcarriae	0	0	0	C
Brachypodium retusum	1	0	0	C
Brassica nigra	1	1	0	T
BRASSICACEAE (undetermined)	1	1	0	T
Bromus erectus	1	0	0	H
Bupleurum fruticescens	1	0	0	C
Bupleurum rigidum	1	0	0	H

Table 3 continued

Species[a]	Atelechory	Myxospermy	Trypanospermy	Life-form[b]
Carduncellus monspelliensium	0	0	0	H
Carex humilis	1	0	0	H
Centaurea aspera	1	0	0	H
Cephalaria leucantha	1	0	0	H
Cerastium sp. 1	1	0	0	T
Cerastium sp. 2	1	0	0	T
Cerastium sp. 3	1	0	0	T
Convolvulus lineatus	1	0	0	H
Coris monspeliensis	1	0	0	C
Coronilla minima subsp. lotoides	1	0	0	C
Coronilla minima subsp. minima	1	0	0	C
Crucianella patula	1	0	0	T
Dactylis glomerata subsp. hispanica	1	0	0	H
Dianthus algetanus subsp. turolensis	1	0	0	C
Dianthus pungens subsp. hispanicus	1	0	0	C
Digitalis obscura	1	0	0	C
Dipcadi serotinum	1	0	0	G
Dorycnium pentaphyllum	1	0	0	C
Echinops ritro	0	0	0	H
Erinacea anthyllis	1	0	0	C
Erodium ciconium	1	0	1	T
Eryngium campestre	0	0	0	H
Euphorbia exigua	1	0	0	T
Euphorbia isatidifolia	1	0	0	G
Euphorbia polygalifolia	1	0	0	C
Euphorbia serrata	1	0	0	G
Filago pyramidata	0	0	0	T
Fritillaria lusitanica	1	0	0	G
Fumana ericifolia	1	1	0	C
Fumana procumbens	1	1	0	C
Galactites tomentosa	0	1	0	H
Genista mugronensis	1	0	0	C
Genista scorpius	1	0	0	F
Globularia vulgaris	1	0	0	H
Helianthemum apenninum subsp. stoechadifolium	1	1	0	C
Helianthemum marifolium	1	1	0	C
Helianthemum origanifolium subsp. glabratum	1	1	0	C
Helianthemum salicifolium	1	0	0	C
Helianthemum violaceum	1	1	0	C
Helichrysum stoechas	0	1	0	C
Hieracium sp	0	0	0	H
Hippocrepis commutata	1	0	0	C
Hormatophylla lapeyroussiana	1	1	0	C
Hymenolobus procumbens	1	0	0	T
Iris germanica	1	0	0	G

Table 3 continued

Species[a]	Atelechory	Myxospermy	Trypanospermy	Life-form[b]
Juniperus communis	0	0	0	F
Juniperus thurifera	0	0	0	F
Koeleria splendens	1	0	0	H
Koeleria vallesiana	1	0	0	H
Lavandula latifolia	1	0	0	C
Leuzea conifera	0	0	0	H
Linaria glauca subsp. aragonensis	1	0	0	T
Linum narbonense	1	1	0	H
Linum suffruticosum	1	1	0	C
Lithodora fruticosa	1	0	0	C
Matthiola fruticulosa	1	1	0	C
Medicago minima	0	0	0	T
Muscari neglectum	1	0	0	G
Myosotis sp	1	0	0	T
Onobrychis viciifolia	0	0	0	H
Ononis fruticosa	1	0	0	F
Paronychia sp	1	0	0	C
Phagnalon saxatile	0	0	0	C
Phlomis lychnitis	1	0	0	C
Pilosella pseudopilosella	0	0	0	H
Plantago albicans	1	1	0	C
POACEAE (undetermined sp. 1)	1	0	0	T
POACEAE (undetermined sp. 2)	1	0	0	T
Potentilla cinerea	1	1	0	H
Potentilla neumanniana	1	1	0	H
Quercus faginea	1	0	0	F
Quercus ilex	1	0	0	F
Ranunculus gramineus	1	0	0	G
Rapistrum rugosum	1	0	0	T
Reseda lutea	1	0	0	T
Reseda phyteuma	1	0	0	T
Reseda undata	1	0	0	H
Rhamnus alaternus	0	0	0	F
Rhamnus saxatilis	0	0	0	F
Ruta chalepensis	1	0	0	C
Salvia lavandulifolia	1	1	0	C
Sanguisorba minor	1	0	0	H
Santolina chamaecyparissus	1	1	0	C
Satureja intricata	1	0	0	C
Scabiosa stellata	1	0	0	T
Scleranthus annuus	1	0	0	T
Scorzonera angustifolia	0	0	0	H
Scorzonera hirsuta	0	0	0	H
Sedum sediforme	1	0	0	C
Senecio gallicus	0	0	0	T

Table 3 continued

Species[a]	Atelechory	Myxospermy	Trypanospermy	Life-form[b]
Serratula nudicaulis	0	0	0	H
Seseli montanum	0	0	0	H
Sideritis ilicifolia	1	0	0	C
Silene nutans	1	0	0	H
Sisymbrium irio	1	1	0	T
Sonchus tenerrimus	0	0	0	H
Spergularia diandra	1	0	0	T
Stipa celakowskyi	0	0	1	H
Stipa lagascae	0	0	1	H
Stipa parviflora	0	0	1	H
Stipa pennata	0	0	0	H
Teucrium capitatum	1	0	0	C
Teucrium chamaedrys	1	0	0	C
Teucrium gnaphalodes	1	0	0	C
Teucrium webbianum	1	0	0	C
Thalictrum tuberosum	1	0	0	G
Thesium humifussum	1	0	0	H
Thymelea pubescens	1	0	0	C
Thymus leptophyllus	1	1	0	C
Thymus vulgaris	1	1	0	C
Tribulus terrestris	0	0	0	T
Trinia glauca	1	0	0	H
Vicia sp	1	0	0	T
Viola willkommii	1	0	0	H

[a] Nomenclature follows Castroviejo S. (coord.) (1986–2012) Flora Iberica. CSIC, Madrid but still unpublished families that follows Mateo G. (1992) Claves para la flora de la Provincia de Teruel. Instituto de Estudios Turolenses-Diputación de Teruel, Teruel

[b] Raunkiær life-forms: *T* terophyte, *G* geophyte, *H* hemicriptophyte *C* camephyte *F* fanerophyte

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