Abundance and habitat segregation in Mediterranean grassland species: the importance of seed weight

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Abstract. We analysed the relationship between seed traits (weight, shape and dispersal structures) and the abundance and habitat segregation of Mediterranean grassland species. To take into account possible correlations with other plant traits, the study also includes 5 vegetative traits (growth form, plant longevity, clonality, onset of flowering and plant size) of commonly accepted functional importance. Data were recorded for 85 species from *dehesa* grasslands in central Spain. Species abundance was measured in upper (dry and less productive, high stress) and lower (moist and more productive, low stress) slope zones in the same area. Habitat segregation was estimated using an index based on the relative frequencies of species in upper and lower slope zones. Multiple regression models were fitted using species, as well as phylogenetically independent contrasts, as data points. Annual small-seeded species without specialised dispersal structures are over-represented in *dehesa* grasslands. Abundance was negatively related to seed weight in upper slope zones. None of the recorded plant traits were related to abundance in the lower slope zones. Habitat segregation was mainly related to seed weight, but also to some vegetative traits. Annual, early flowering and small-seeded species were relatively more abundant in the upper than the lower slope zones. This pattern is independent of phylogeny. Our results suggest that in dry Mediterranean grasslands, abundance of many species is determined by dispersal (production of numerous small seeds) rather than by competitive ability.

Keywords: Plant community; Seed shape; Seed size; Vegetative trait.

Abbreviations: CSA = Cross species analysis; PIA = Phylogenetically independent analysis; PIC = Phylogenetically independent contrast.

Nomenclature: Castroviejo (1986-1999), except taxa yet to be covered which follow Tutin et al. (1964-1980).

Introduction

Seed traits have generally been studied in order to understand plant strategies (Harper et al. 1970; Primack 1987; Mazer 1989). More recently, they have also been used in the interpretation of plant abundance and distribution patterns at local (Rees 1995), regional (Eriksson & Jakobsson 1998; Thompson et al. 1999) and macroscales (Edwards & Westoby 1996; Lord et al. 1997; Thompson et al. 1999).

According to the literature, large seed size improves recruitment success and competitive ability (Leishman & Westoby 1994; Haig 1996; Turnbull et al. 1999). On the other hand, development of large seeds reduces the number of seeds produced. Species with large seeds will have a lower dispersal and colonisation ability solely on the basis of low seed numbers (Harper et al. 1970; Haig 1996; Jakobsson & Eriksson 2000). A model linking seed size with colonization ability has been proposed based on the trade-off between seed size and seed production (Eriksson & Jakobsson 1998). The model predicts that species with intermediate seed sizes will be more abundant. The model has been supported with a so-called phylogenetically independent analysis in Swedish semi-natural grasslands (Eriksson & Jakobsson 1998). Other studies have shown that local species abundance can be related to seed (or diaspore) weight, either positively (Rabinowitz 1978) or negatively (Rees 1995; Thompson et al. 1999). Furthermore, the importance of seed weight in predicting abundance seems to depend on scale and does not appear to be a good indicator at macro-scales (Eriksson et al. 1995; Edwards & Westoby 1996; Thompson et al. 1999).

There is also evidence that different habitats may favour different seed sizes. In general, large seeds are better represented in productive or shady habitats, while less productive environments and disturbed areas are rich in species with smaller seeds and higher seed outputs (Mazer 1989; Fernández Alés et al. 1993; Lord et al. 1997). Biotic interactions may also favour certain seed weights. Predation risk and the type of seed predators

modulate seed size in several ways (Davidson et al. 1984), while the presence of herbivores capable of endozoochory seed dispersal favours small-seeded species (Malo & Suárez 1995). In addition, models based on the 'game theory' have linked optimum seed size and output to the type of seeds produced by potential competitors (Geritz 1995; Rees & Westoby 1997; Haig 1996).

In contrast to size, the relationship between other seed traits and abundance and their suitability to different environmental conditions have been less thoroughly investigated. The presence and type of certain dispersal structures (fleshy fruits, elaiosomes, hooks, spines, awns, wings, hairs, pappus, etc.) are obviously related to dispersal strategies (Westoby et al. 1990; Hughes et al. 1994), but can have other ecological implications. Spherical seeds without appendages are more likely to penetrate the soil and tend to be located deeper than seeds with hygroscopic or twisted structures (Peart 1984; Bekker et al. 1998). The vertical distribution of seeds in the soil is also closely related to seed longevity, with small, appendage-free seeds forming more persistent banks (Thompson et al. 1993; Bekker et al. 1998; Funes et al. 1999). Nevertheless, exceptions have been found in Australian and New Zealand floras (Leishman & Westoby 1998; Moles et al. 2000). Some studies link the possession of dispersal structures to certain environmental conditions. Arid systems, for example, have a high proportion of unassisted diaspores (Ellner & Shmida 1981) possibly because, under extreme conditions, the area around the mother plant is a relatively favourable microhabitat (Pugnaire et al. 1996).

In Mediterranean grasslands, few studies have focused on linking plant traits with ecological features. Most have dealt with vegetative traits and relationships with grazing (Noy-Meir et al. 1989; Fernandez Alés et al. 1993; Sternberg et al. 2000), mechanical disturbance (Lavorel et al. 1999) and summer drought (Espigares & Peco 1995). Seed traits have rarely been considered (Fernández Alés et al. 1993; Lavorel et al. 1999), although these environments are primarily composed of annual species and are heavily dependent on seed traits for regeneration (Peco 1989). Because Mediterranean grasslands have a relatively low production and open structure, we expect a positive selection of small-seeded species here. Moreover, large inter-annual rainfall fluctuations in mediterranean climates may favour species with a persistent seed bank, which is possibly related to the production of small seeds (Thompson et al. 1993; Bekker et al. 1998). Other factors, such as intense grazing, may also promote the selection of small seeds (Thompson et al. 1996; Westoby 1998), perhaps adapted to dispersal by herbivorous mammals.

In these grasslands, topography-related spatial heterogeneity defines a stress gradient between nutrient-poor dry zones and areas on more fertile and moist soils, where there is a greater proportion of perennials and a higher similarity to mesic grasslands (Casado et al. 1985; Puerto et al. 1990). This gradient may be expected to produce a differential distribution of diaspore types so that small-seeded species will be more abundant towards the drier and less productive upper slope zones.

Our study searched for support for these hypotheses. In particular, we addressed 2 questions: 1. Are seed traits good predictors of species abundance in Mediterranean grasslands? 2. Can these traits help predict species habitat segregation between upper and lower slope zones?

Methods

Study area and field survey

The field work was conducted on the southern pediment of the Guadarrama Mountains in a 20 km × 20 km area 15 km north of Madrid (40° 38' N, 3° 70' E). The altitude ranges between 700 and 900 m a.s.l. and the climate is typically mediterranean, with a drought period in summer, mean annual temperature of ca. 13 °C and 450 - 500 mm mean annual rainfall. The area has a predominance of shallow soils on siliceous substrata. The vegetation consists of open woodlands (*Quercus ilex* ssp. *ballota* and *Juniperus oxycedrus*) and dry grasslands dominated by annual species such as *Xolantha guttata*, *Vulpia muralis*, *V. myuros* and *Trifolium glomeratum* and the perennial *Poa bulbosa*. Other perennials such as *Agrostis castellana* and *Festuca rothmaleri* are abundant in depressions, where water and nutrient availability is higher. The vegetation is a result of centuries of mixed farm husbandry which is maintained to the present day.

Species abundance was estimated on 3 slopes (< 5%) where we distinguished an upper and a lower slope zone which differed in water and nutrient availability and soil texture (Table 1). In each zone we established a 10 m × 10 m plot and noted the frequency of each species in 10 quadrats (20 cm × 20 cm) randomly distributed in each plot. For each species and slope an index of habitat segregation was calculated, using the difference between the number of presences in the upper and lower slope zones divided by 10, the index ranged between + 1 and −1. Finally, mean species abundance in the upper and lower slope zones and mean habitat segregation index for the 3 slopes were calculated.

Table 1. Mean values (±s.d.) of soil parameters from upper and lower slope zones in the study area (A. M. Sánchez et al. in prep.).

Slope zone	Organic matter (%)	N total (%)	Clay (%)	Available water (%)	pH
Upper	2.55 ± 0.31	0.17 ± 0.02	8.77 ± 1.78	13.35 ± 1.49	5.05 ± 0.22
Lower	3.94 ± 0.65	0.26 ± 0.04	20.12 ± 3.22	22.13 ± 3.04	5.12 ± 0.18

Seed and vegetative plant traits

Fresh seeds were collected between 1996 and 1999 for the 85 species recorded in the quadrats. The definition of 'seed' used throughout this paper is taken from Bekker et al. (1998), i.e. seeds or fruits in their simplest form. The 'seed' coincides with the diaspore (*sensu* Jurado et al. 1991) for a large number of species, given their lack of dispersal structures.

Seeds were air-dried and weighed individually whenever possible, or otherwise in small groups (*n* max = 10). For the majority of species 30 weights were obtained. The 3 main seed dimensions were measured semi-automatic analysis equipment (Leica Q500 Iw). Between 20 and 30 propagules were measured from each species. Seed shape was defined as the variance of the 3 main dimensions (first divided by length), following Thompson et al. (1993). Totally spherical seeds would have a shape value = 0, with this value increasing with elongation. For each species, we considered the mean of all individual values as an estimate of the seed shape. Species were also classified according to the presence of dispersal structures in the diaspore. The seeds were also classified as being (1) unassisted, (2) wind-dispersed or (3) with adhesive structures (App. 1; see *JVS* Electronic Archive; www.opuluspress.se).

Seed traits may be associated with vegetative traits (Primack 1987; Thompson & Rabinowitz 1989; Leishman et al. 1995), and the variability of the latter may be also related to the environmental conditions. To account for this potentially confounding effect, our study also included 5 vegetative traits (plant size, growth form, clonality, longevity and onset of flowering) whose importance in Mediterranean grasslands has been proven in other studies (Montalvo et al. 1991; Fernández Alés et al. 1993; Sternberg et al. 2000). Information on vegetative traits was taken from the literature (Valdés et al. 1987; Castroviejo 1986-1999; González Bernáldez 1997) and is shown in Table 2. We also collected data on maximum stem length, considering this to be indicative of plant size under non-limiting conditions, plant weight might have been a more exact indicator but this information was not available for most plants.

Phylogenetically independent contrasts

Individual species in a species-by-attributes data set cannot be considered as independent data points (Felsenstein 1985; Harvey et al. 1995; Harvey 1996; Martins & Hansen 1996). We therefore used a phylogenetically independent analysis (PIA) as the most appropriate means of evaluating statistical hypotheses, as in other similar comparative studies (Edwards & Westoby 1996; Eriksson & Jakobsson 1998; Thompson et al. 1999). At the same time, we performed a cross-species analysis (CSA) the value of which is merely descriptive and ascertains whether the PIA patterns detected could be observed in the plant communities.

The PIA was based on phylogenetically independent contrasts (PICs), which were obtained following Felsenstein (1985). Because phylogeny data were not available, we used current taxonomy (Bremer 1987; Bremer et al. 1992; Jansen et al. 1990; Hufford 1992; Kim et al. 1992; Davis & Soreng 1993; Kubtzki et al. 1993; Muñoz 1995; Takhtajan 1996) to infer phylogeny as suggested by Martins & Hansen (1996). The maximum number of available PICs was limited to 58 as a consequence of dealing with non-dichotomous phylogeny (for details of species or nodes used for contrasts, see App. 2; see *JVS* Electronic Archive; www.opuluspress.se). Finally, given that the character state for inter-

Table 2. Frequencies found for each category of the 5 nominal variables, *n* = 85 species.

Variable	Categories	Frequency (%)
Dispersal structures	Unassisted	73
	Adhesive	14.1
	Wind-dispersed	12.9
Longevity	Annual	71.8
	Biennial	3.5
	Perennial	24.7
Clonality	Clonal	20
	Non-clonal	80
Growth form	Bulbs	3.5
	Graminoids	22.3
	Rosette	15.9
	Straight stem	38.8
	Prostrate stem	20
Onset of flowering	Early spring	29.4
	Spring	40
	Late spring	28.2
	Autumn	2.3

nal nodes cannot be estimated using categorical variables, only the 25 contrasts at the species level were used when these types of variables were involved.

Statistical analysis

Cross-species analysis

The effect of vegetative and seed attributes on species abundance and habitat segregation was analysed by fitting multiple regression models. To achieve normality of residuals, seed weight and maximum stem length variables were log-transformed and species abundance arcsin transformed. All the categorical variables were coded into dummy variables for the CSA. To select the relevant independent variables, we followed a backward elimination procedure (P to remove $= 0.05$), which is more appropriate than the forward selection procedure when dealing with dummy variables (Zar 1996).

Phylogenetically independent analysis

Multiple regression models were also fitted for the PICs. Initially, we included both quantitative and categorical variables in the models, and thus excluded pairs involving internal nodes leading to a sample size of $n = 25$. The original dummy variables were transformed into 3-level factors ($-1, 0, +1$), indicating the existence and direction of divergences. The need for a minimum number of observations for each level reduced the sample size to 19 pairs. However, in cases where all categorical variables were rejected by the backward elimination procedure, the models were re-estimated for the quantitative variables using all available pairs ($n = 58$). All analyses were performed with STATISTICA (Anon. 1998).

Results

Seed weight varied by 3 orders of magnitude (Table 3): the species with the lightest seeds was *Sagina apetala* (8.88×10^{-3} mg) and the heaviest seeds were produced by *Trifolium subterraneum* (6.22 mg). *Merendera pyrenaica* had the most spherical seeds (0.0104) and *Vulpia myuros* had the most elongated seeds (0.277). The community was essentially composed of annual species with spring flowering and variable growth forms (with a slight predominance of the erect type) and diaspores generally lacking dispersal structures (Table 2). The most represented families were *Fabaceae*, *Asteraceae*, *Poaceae* and *Caryophyllaceae* (each ca. 15%).

The most abundant species in the lower slope zones was the perennial *Agrostis castellana*, which appeared in more than 93% of the sampled quadrats (Table 3). Other species with high abundance were *Trifolium dubium*, *Juncus bufonius*, *Carex divisa* and *Trifolium cernuum* (App. 1). In the upper slope zones, the annual *Xolantha guttata* was the most abundant species (83%), followed by *Moenchia erecta* and *Logfia minima*. With respect to habitat segregation, the tussock-forming grass *Festuca rothmaleri* was the most clearly linked to more mesic zones while *Xolantha guttata* was connected to dry zones. The majority of the species (58) had positive habitat segregation values, while only 25 had negative values and hence a greater relative abundance in the lower slope zones. This is reflected in the fact that both the mean and the median of this variable were positive. However, while all 85 species were present in the lower slope zone, 13 species were com-

Table 3. Distribution type, mean, median and range of the quantitative variables considered in the study, $n = 85$ species. D (K-S): Kolmogorov-Smirnov D_{max} statistic for the specified distribution type. None of the commonly used distribution types fitted to species abundance in upper and lower slope zones.

Variable	Distribution	D (K-S)	P	Mean	Median	Range Lower limit	Upper limit
Abundance in lower zones (%)	-	-	-	15.2	6.6	3.3 various spp.	93.3 *Agrostis castellana*
Abundance in upper zones (%)	-	-	-	22.6	13.3	0 various spp.	83.3 *Xolantha guttata*
Habitat segregation	Normal	0.1041	Ns	0.107	0.033	−0.567 *Festuca rothmaleri*	0.767 *Xolantha guttata*
Seed weight (mg)	Log-normal	0.0609	Ns	0.471	0.191	8.88×10^{-3} *Sagina apetala*	6.223 *Trifolium subterraneum*
Seed shape	Normal	0.0761	Ns	0.122	0.119	0.0104 *Merendera pyrenaica*	0.277 *Vulpia myuros*
Maximum stem length (cm)	Log-normal	0.1909	Ns	44.81	40	3 *Scleranthus delortii*	200 *Convolvulus arvensis*

pletely absent from the upper slope zone.

No significant predictors were found for abundance in the lower slope zones. In the case of the upper slope zones, only one predictor (seed weight) was included in both the CSA and PIA models. Abundance was negatively related to seed weight, a pattern that may be regarded as independent of phylogeny (Table 4). The hypothesised non-linear relationship between abundance and seed weight (Eriksson & Jakobsson 1998) was tested by including species seed size deviation from median seed size in the community (after the log transformation) in the models (CSA and PIA). This new variable did not predict abundance in any of the slope zones.

According to the model constructed using independent pairs (Table 5b), habitat segregation depends on 3 traits: seed weight, onset of flowering and plant longevity. Species with small seeds, early flowering and annual life cycle were associated with upper slope zones. The model accounted for nearly 80% of the variance. Using the individual species as data points (Table 5a), 3 variables were included: seed weight, clonality and onset of flowering. The model reveals that species with small seeds, early flowering and absence of clonality are better represented in upper slope zones. Overall, the model accounts for almost 40% of the variance.

Discussion

Our results show that small-seeded species lacking specialised dispersal mechanisms predominate in Mediterranean grassland vegetation. The median seed weight (0.19 mg) was close to the findings of Fernández Alés et al. (1993) for Mediterranean grasslands in southern Iberia (0.25 mg, $n = 42$) and was much lower than the results of Eriksson & Jakobsson (1998) in Swedish mesic grasslands (0.44 mg; $n = 81$). The proportion of unassisted diaspores (73%) was similar to findings in other communities that have aroused interest due to the lack of dispersal structures, as in Israeli deserts (75% of the species; Ellner & Schmida 1981).

Seed weight was the only trait retained when species abundance in the upper slope zones was modelled. No vegetative traits were linked to species abundance. The coincidence between the species-based model and that estimated from PICs indicates that the relationship is independent of phylogeny, underscoring the functional importance of this trait.

Although the wide range of seed weights shows that different strategies are viable in the same community, the models indicate that in the upper slope zones, small seeds are advantageous. Similar results were found by Rees (1995) in British sand dune communities and by

Table 4. Models of abundance in upper slope zones estimated from the cross-species analysis (a) and the phylogenetically independent analysis (b). The table shows the proportion of variance accounted for by the models (r^2), the F-value associated with the ANOVA and its P-level. Partial correlation coefficients, estimated slope values (B), standard errors of B and corresponding P-levels are shown for the retained variables.

a. Cross species analysis

Arcsin (abundance in upper slope zones)
$r^2 = 0.074$, F(1,83) = 6.63, $P = 0.012$

	Partial corr.	B	s.e. of B	P
Intercept		−0.1842	0.166	0.271
Ln seed weight (mg)	−0.272	−0.049	0.019	0.012

b. Phylogenetically independent analysis

Abundance in upper slope zones
$r^2 = 0.147$, F(1,56) = 6.63, $P = 0.0029$

	Partial corr.	B	s.e. of B	P
Intercept		−0.004	0.0146	0.770
Seed weight (mg)	−0.38	−0.339	0.109	0.0029

Table 5. Models of habitat segregation estimated from the cross-species analysis (a) and the phylogenetically independent analysis (b). The table shows the proportion of variance accounted for by the models (r^2), the F-value associated with the ANOVA and its P level. Partial correlation coefficients, the estimated slope values (B), standard errors of B and corresponding P levels are shown for the retained variables.

a. Cross species analysis

Habitat segregation $r^2 = 0.396$, F(4,80) = 12.78, $P < 0.0001$

	Partial corr.	B	s.e. of B	P
Intercept		−0.182	0.134	0.179
Ln seed weight (mg)	−0.371	−0.017	0.005	<0.001
Clonality	−0.328	−0.157	0.051	0.0029
Onset of flowering (spring)	−0.249	−0.109	0.048	0.0254
Onset of flowering (late)	−0.503	−0.268	0.052	<0.001

b. Phylogenetically independent analysis

Habitat segregation $r^2 = 0.781$, F(3,15) = 17.817, $P < 0.001$

	Partial corr.	B	s.e. of B	P
Intercept		0.036	0.015	0.04
Seed weight (mg)	−0.610	−0.399	0.081	<0.001
Longevity (perennial)	−0.389	−0.090	0.028	0.006
Onset of flowering (late)	−0.543	−0.129	0.029	<0.001

Thompson et al. (1999) in the herbaceous flora of Central England. Comparisons are impeded, however, by the lack of a phylogenetically independent analysis in the former and the diversity of habitats covered in the latter. Rabinowitz (1978) found a positive relationship between seed size and abundance in North American prairie grasses, but this study only included 7 species in the community, without consideration of phylogeny. One of the most comparable studies, carried out by Eriksson & Jakobsson (1998) in perennial-dominant mesic grasslands, found that greater abundance was associated with intermediate seed sizes, a relationship that could not be confirmed in our study. Bruun (2001) found no relationship either between abundance and seed mass for perennial-dominant grasslands. Small seeds may thus only be an advantage in certain xeric Mediterranean grasslands.

Small seeds imply reduced competitive ability, but also certain benefits related to a greater number of recruitment opportunities. While this analysis did not yield data on seed production, several observations (Primack 1987; Fernández Alés et al. 1993; Jakobsson & Eriksson 2000) and theoretical models (Smith & Fretwell 1974; Geritz 1995; Haig 1996) suggest that species with the smallest seeds should be those that also produce the largest numbers of seeds. The upper slope zones are dominated by annuals, which regenerate every year after the autumn rains when the ground is almost bare as a result of the death of most individuals before the summer. Competition in the early establishment stages is therefore very weak in this type of system (Peco & Espigares 1994).

In addition, small seeds are more capable of penetrating the soil (Grime 1979; Bekker et al. 1998) and tend to survive longer in the seed bank (Thompson et al. 1993), which can be particularly advantageous in the unpredictable rainfall patterns of the Mediterranean systems (Espigares & Peco 1993, 1995). Also, the unfavourable dry season coincides with the period of greatest activity by granivore ants (*Messor* spp.), implying a risk of seed loss by predation (Azcárate et al. unpubl.). Small seed size reduces this hazard, not only because they are not the ideal prey size (Hulme 1994) but also due to their greater burial capacity. Finally, small seeds are better adapted to endozoochory than large ones, which are more likely to be chewed and destroyed by herbivores (Janzen 1984).

Neither of the other 2 diaspore traits analysed (presence of dispersal structures and seed shape) had any relationship with species abundance. Endozoochory is considered to be an important dispersal mechanism in Mediterranean grasslands (Malo & Suárez 1995). This may explain the lack of appendages for wind dispersal and exozoochory, which involve added energy cost and provide no advantage to this type of dispersal. There is also evidence that small seeds can be dispersed epizoochorously without the need for specialised appendages (Fischer et al. 1996).

The production of small seeds cannot be claimed to be advantageous in all types of Mediterranean grassland. In the lower slope zones, which characteristically have less water and nutrient stress, there is no relationship between species abundance and the analysed plant traits, including seed weight. In this type of grassland, with possibly intermediate characteristics between typical Mediterranean pastures and mesic grasslands, species abundance depends on unknown factors other than seed weight.

Most species had a positive habitat segregation index, indicating a higher relative abundance in the upper slope zones. However, while all 85 species appeared at least once in the more moist zones, 13 were not recorded in the dry zones. If we assume low levels of competition in the dry zones and that the short distance between the moist areas is not a serious impediment to dispersal, the absence of these species in the dry zone can only be explained in terms of abiotic limitations. On the other hand, the existence of records for the whole set of species in the moist zones suggests that there are no abiotic impediments to their establishment, although many species have a very low level of representation. The rarity of these species may be a consequence of the higher levels of competition in this type of habitat.

In this context, the habitat segregation models can help to explain which designs make Mediterranean grassland species better prepared to survive under either stressed or competitive environments. Two vegetative traits (onset of flowering and longevity) are retained by the PIA model in a way that is consistent with results reported in other papers (Casado et al. 1985; Noy-Meir et al. 1989; Montalvo et al. 1991; Fernández Alés et al. 1993). Late flowering makes better use of the longer duration of the favourable period in the productive lower zones but not in the upper zones, where the summer drought dries the soil 1 or 2 months earlier. A perennial strategy may be more competitive in moist areas, but a disadvantage through the summer months in drier habitats, which is indicated by the fact that 10 of the 13 species absent from the upper slope zones are perennials. The longevity variable is replaced by clonality in the CSA model, which is not surprising considering the redundancy between the 2 features (almost all species with clonality are perennials).

In summary, seed traits, especially weight, should be regarded as key features in understanding Mediterranean grassland communities. In these systems, seed weight is a better predictor of species abundance and habitat segregation than some vegetative traits of recognized functional importance. Small seeded species are better

represented in heavily stressed habitats, where they predominate over large-seeded species. In such systems, dispersal ability (production of small, numerous seeds) is selected for rather than competitive ability. This may be related to certain distinctive environmental features of these communities such as the need for complete regeneration every autumn under conditions in which there is no competition with established individuals and competition amongst seedlings is very weak. The fact that Mediterranean grasslands are semi-natural systems under long-term human management suggests that the predominance of small-seeded species should not only be interpreted as a consequence of species adaptation, ecological selection is also a potential cause.

References

Anon. 1998. *STATISTICA for Windows*. Tulsa, OK.

Bekker, R.M., Bakker, J.P., Grandin, U., Kalamees, R., Milberg, P., Poschlod, P., Thompson, K., & Willems, J.H. 1998. Seed size, shape and vertical distribution in the soil: indicators of seed longevity. *Funct. Ecol.* 12: 834-842.

Bremer, K. 1987. Tribal interrelationships of the *Asteraceae*. *Cladistics* 3: 210-253.

Bremer, K., Janzen, R.K. & Karis, P.O. 1992. A review of the phylogeny and classification of the *Asteraceae. Nord. J. Bot.* 12: 141-148.

Bruun, H.H. 2001. On the seed mass-regional abundance relationship: the Eriksson & Jakobsson (1998) model does not apply to Danish grasslands. *J. Ecol.* 89: 300-303

Casado, M. A., De Miguel, J.M., Sterling, A., Peco, B., Galiano, E.F. & Pineda, F.D. 1985. Production and spatial structure of Mediterranean pastures in different stages of ecological succession. *Vegetatio* 64: 75-86.

Castroviejo, S. (coord.). 1986–1999. *Flora iberica*. Vols. 1–8. Real Jardín Botánico. CSIC, Madrid, ES.

Davidson, D.W., Inouye, R.S. & Brown, J.H. 1984. Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. *Ecology* 65: 1780-1786.

Davis, J.I. & Soreng, R.J. 1993. Phylogenetic structure in the grass family (*Poaceae*) as inferred from chloroplast DNA restriction site variation. *Am. J. Bot.* 80: 1444-1454.

Edwards, W. & Westoby, M. 1996. Reserve mass and dispersal investment in relation to geographic range of plant species: phylogenetically independent contrasts. *J. Biogeogr.* 23: 329-338.

Ellner, S. & Shmida, A. 1981. Why are adaptations for long-range dispersal rare in desert plants? *Oecologia* 51: 133-144.

Eriksson, O. & Jakobsson, A. 1998. Abundance, distribution and life histories of grassland plants: a comparative study of 81 species. *J. Ecol.* 86: 922-933.

Eriksson, O., Eriksson, Å. & Berglund, H. 1995. Species abundance patterns of plants in Swedish semi-natural pastures. *Ecography* 18: 310-317.

Espigares, T. & Peco, B. 1993. Mediterranean pasture dynamics: the role of germination. *J. Veg. Sci.* 4: 189-194.

Espigares, T. & Peco, B. 1995. Mediterranean annual pasture dynamics: the impact of drought. *J.Ecol.* 83: 135-142.

Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125: 1-15.

Fernández Alés, R., Laffarga, J. M. & Ortega, F. 1993. Strategies in Mediterranean grassland annuals in relation to stress and disturbance. *J. Veg. Sci.* 4: 313-322.

Fischer, S.F., Poschlod, P. & Beinlich, B. 1996. Experimental studies of the dispersal of plants and animals on sheep in calcareous grasslands. *J. Appl. Ecol.* 33: 1206-1222.

Funes, G., Basconcelo, S., Díaz, S. & Cabido, M. 1999. Seed size and shape are good predictors of seed persistence in soil in temperate mountain grasslands of Argentina. *Seed Sci. Res.* 9: 341-345.

Geritz, S.A.H. 1995. Evolutionarily stable seed polymorphism and small-scale spatial variation in seedling density. *Am. Nat.* 146: 685-707.

González Bernáldez, F. 1997. *Gramíneas pratenses de Madrid.* 2nd. ed. Comunidad de Madrid, Madrid, ES.

Grime, J.P. 1979. *Plant strategies and vegetation processes.* Wiley, Chichester, UK.

Haig, D. 1996. The pea and the coconut: seed size in safe sites. *Trends Ecol. Evol.* 11: 1-2.

Harper, J.L., Lovell, P.H. & Moore, K.G. 1970. The shapes and sizes of seeds. *Annu. Rev. Ecol. Syst.* 1: 327-357.

Harvey, P.H. 1996. Phylogenies for ecologists. *J. Anim. Ecol.* 65: 255-263.

Harvey, P.H., Read, A.F. & Nee, S. 1995. Why ecologists need to be phylogenetically challenged. *J. Ecol.* 83: 535-536.

Hufford, L. 1992. *Rosidae* and their relationships to other non magnolii dicotiledons: a phylogenetic analysis using morphological and chemical data. *Ann. Mo. Bot. Gard.* 79: 218-248.

Hughes, L., Dunlop, M., French, K., Leishman, M.R., Rice, B., Rodgerson, L. & Westoby, M. 1994. Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. *J. Ecol.* 82: 933-950.

Hulme, P.E. 1994. Post-dispersal seed predation in grassland: its magnitude and sources of variation. *J. Ecol.* 82: 645-652.

Jakobsson, A. & Eriksson, O. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos* 88: 494-502.

Jansen, R.K., Holsinger, K.E., Michaels, H.J. & Palmer, J.D. 1990. Phylogenetic analysis of chloroplast DNA restriction site data at higher taxonomic levels: An example from the Asteraceae. *Evolution* 44: 2089-2105.

Janzen, D.H. 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. *Am. Nat.* 123: 338-353.

Jurado, E., Westoby, M. & Nelson, D. 1991. Diaspore weight,

dispersal, growth form and perenniality of central Australian plants. *J. Ecol.* 79: 811-830.

Kim, K.J., Janzen, R.K., Wallace, R.S., Michaels, H.J. & Palmer, J.D. 1992. Phylogenetic implications of rbcL sequence variation in the *Asteraceae*. *Ann. Mo. Bot. Gard.* 79: 428-445.

Kubitzki, K., Rohwer, J.G. & Bittrich, V. (eds.) 1993. *The families and genera of vascular plants.* Springer-Verlag, Berlin, DE.

Lavorel, S., Rochette, C. & Lebreton, J.D. 1999. Functional groups for response to disturbance in Mediterranean old fields. *Oikos* 84: 480-498.

Leishman, M.R. & Westoby, M. 1994. Hypotheses on seed size: tests using the semiarid flora of western New South Wales, Australia. *Am. Nat.* 143: 890-906.

Leishman, M.R. & Westoby, M. 1998. Seed size and shape are not related to persistence in soil in Australia in the same way as in Britain. *Funct. Ecol.* 12: 480-485.

Leishman, M.R., Westoby, M. & Jurado, E. 1995. Correlates of seed size variation: a comparison among five temperate floras. *J. Ecol.* 83: 517-530.

Lord, J., Egan, J., Clifford, T., Jurado, E., Leishman, M., Williams, D. & Westoby, M. 1997. Larger seeds in tropical floras: Consistent patterns independent of growth form and dispersal mode. *J. Biogeogr.* 24: 205-211.

Malo, J. & Suárez, F. 1995 Herbivorous mammals as seed dispersers in a Mediterranean dehesa. *Oecologia* 104: 246-255.

Martins, E.P. & Hansen, T.F. 1996. The statistical analysis of interspecific data: a review and evaluation of phylogenetic comparative methods. In: Martins, E.P. (ed.) *Phylogenies and the comparative method in animal behavior*, pp. 23-75. Oxford University Press, Oxford, UK.

Mazer, S.J. 1989. Ecological, taxonomic and life history correlates of seed mass among Indiana dune angiosperms. *Ecol. Monogr.* 59: 153-175.

Moles, A.T., Hodson, D.W & Webb, C.J. 2000. Seed size and shape and persistence in the soil in the New Zealand flora. *Oikos* 89: 541-545.

Montalvo, J., Casado, M.A., Levassor, C. & Pineda, F.D. 1991. Adaptation of ecological systems: compositional patterns of species and morphological and functional traits. *J. Veg. Sci.* 2: 655-666.

Muñoz, A.F. 1995. Morfología de las seeds de las species del género *Trifolium* de la Península Ibérica. *Lazaroa* 15: 131-144.

Noy-Meir, I., Gutman, M. & Kaplan, Y. 1989. Responses of Mediterranean grassland plants to grazing and protection. *J. Ecol.* 77: 290-310.

Ortega, M., Levassor, C. & Peco, B. 1997. Seasonal dynamics of Mediterranean seed banks along environmental gradients. *J. Biogeogr.* 24: 177-195.

Peart, M.H. 1984. The effects of morphology, orientation and position of grass diaspores on seedling survival. *J. Ecol.* 72: 437-453.

Peco, B. 1989. Modelling Mediterranean pasture dynamics. *Vegetatio* 83: 269-276.

Peco, B. & Espigares, T. 1994. Floristic fluctuations in annual pastures: The role of competition at the regeneration stage.

J. Veg. Sci 5: 457-462.

Primack, R.B. 1987. Relationships among flowers, fruits and seeds. *Annu. Rev. Ecol. Syst.* 18: 1409-1430.

Puerto, A., Rico, M., Matias, M.D. & García, J.A. 1990. Variation in structure and diversity in Mediterranean grasslands related to trophic status and grazing intensity. *J. Veg. Sci.* 1: 445-452.

Pugnaire, F.I., Haare, P. & Puigdefábregas, J. 1996. Facilitation between higher plant species in a semiarid environment. *Ecology* 77: 1420-1426.

Rabinowitz, D. 1978. Abundance and diaspore weight in rare and common prairie grasses. *Oecologia* 37: 213-219.

Rees, M. 1995. Community structure in sand dune annuals: Is seed weight a key quantity? *J. Ecol.* 83: 857-863.

Rees, M. & Westoby, M. 1997. Game-theoretical evolution of seed mass in multi-species ecological models. *Oikos* 78: 116-126.

Smith, C.C. & Fretwell, S.D. 1974. The optimal balance between size and number of offspring. *Am. Nat.* 108: 499-506.

Sternberg, M., Gutman, A., Perevolotsky, E.G., Ungar, E.G. & Kigel, J. 2000. Vegetation response to grazing management in a Mediterranean herbaceous community: a functional group approach. *J. Appl. Ecol.* 37: 224-237.

Takhtajan, A. 1996. *Diversity and classification of flowering plants.* Columbia University Press, New York, NY.

Thompson, K. & Rabinowitz, D. 1989. Do big plants have big seeds? *Am. Nat.* 133: 722-728.

Thompson, K., Band, S.R. & Hodgson, J.G. 1993. Seed size and shape predict persistence in soil. *Funct. Ecol.* 7: 236-241.

Thompson, K. Hillier, S.H., Grime, J.P., Bossard, C.C. & Band, S.R. 1996. A functional analysis of a limestone grassland community. *J. Veg. Sci.* 7: 371-380.

Thompson, K., Gaston, K.J. & Band, S.R. 1999. Range size, dispersal and niche breadth in the herbaceous flora of central England. *J. Ecol.* 87: 150-155.

Turnbull, L.A., Rees, M. & Crawley, M.J. 1999. Seed mass and the competition / colonization trade-off: a sowing experiment. *J. Ecol.* 87: 899-912.

Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.) 1964-1980. *Flora Europaea.* Cambridge University Press, Cambridge, UK.

Valdés, B., Talavera, S. & Fernández-Galiano, E. (eds.) 1987. *Flora vascular de Andalucía Occidental.* Ketres, Barcelona, ES.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199: 213-227.

Westoby, M., Rice, B. & Howell, J. 1990. Seed size and plant growth form as factors in dispersal spectra. *Ecology* 71: 1307-1315.

Zar, J.H. 1996. *Biostatistical analysis.* 3rd ed. Prentice-Hall, Englewood Cliffs, NJ.

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