



# The effect of grazing abandonment on species composition and functional traits: the case of dehesa grasslands

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## Summary

This study attempts to identify the consequences of grazing abandonment for changes in floristic and functional vegetation composition in dehesa systems. Species cover was quantified in plots on grazed and abandoned dehesas in Central Spain. Using literature and field measurements, we analysed plant attributes linked to dispersal, establishment, and persistence for the 85 most abundant species. A Detrended Correspondence Analysis of the species  $\times$  plots matrix and the traits  $\times$  plots matrix was used to describe differences in species composition and functional traits in relation to grazing. The latter matrix was obtained by multiplying the traits  $\times$  species matrix by the species  $\times$  plots matrix.

Grazed sites had a higher proportion of prostrate species, medium specific leaf area, early flowering, cryptophytes, unassisted seeds and clonal reproduction. Ungrazed sites had a higher proportion of taller plants, heavy leaf dry weight, late flowering species and chamaephytes as well as species with heavy seeds and fruits with adhesive structures.

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## Zusammenfassung

Diese Untersuchung versucht die Konsequenzen zu identifizieren, die eine Aufgabe der Beweidung für die Veränderungen der floristischen und funktionellen Vegetation in Dehesasystemen hat. In Zentralspanien wurde die Artendeckung in Versuchsflächen sowohl in beweideten als auch aufgegebenen Dehesas quantifiziert. Unter Verwendung von Literaturdaten und Messungen im Feld analysierten wir für die 85 häufigsten Arten die Pflanzenmerkmale, die mit der Verbreitung, Etablierung und der Persistenz verknüpft sind. Es wurde eine enttendete Korrespondenzanalyse der Arten  $\times$  Versuchsflächen-Matrix und der Merkmale  $\times$  Versuchsflächen-Matrix benutzt, um

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die Unterschiede in der Artenzusammensetzung und den funktionellen Merkmalen in Beziehung zur Beweidung zu beschreiben. Dabei wurde die letztere Matrix gewonnen, indem die Merkmale  $\times$  Arten-Matrix mit der Arten  $\times$  Versuchsflächen-Matrix multipliziert wurde.

Beweidete Flächen hatten einen höheren Anteil an kriechenden Arten, an mittlerer spezifischer Blattfläche, an früherem Blühen, an Kryptophyten, an barochoren Samen und klonaler Reproduktion. Nicht beweidete Flächen hatten einen höheren Anteil an größeren Pflanzen, an Trockengewicht schwerer Blätter, an spätblühenden Pflanzen und Chamaephyten sowie an Arten mit schweren Samen und Früchten mit anhaftenden Strukturen.

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## Introduction

Extensive grazing has been linked to high species richness in Mediterranean grasslands (Whittaker, 1977; Naveh & Wittaker, 1979; Noy-Meir, Gutman, & Kaplan, 1989). This intermediate level of disturbance, with low livestock density and no external inputs (fodder, fertilizers, pesticides) has changed dramatically in the recent years in Europe due to the intensification of livestock management, causing overgrazing in some areas and abandonment in others (Baldock, Beaufoy, Brouwer, & Godeschalk, 1997; Ostermann, 1998).

The modelling of the effect of land use changes in vegetation structure and ecosystem function is a key issue for the management of economic and environmental benefits of grasslands. Many studies have described changes in floristic composition in relation to grazing but their results are difficult to use in cross-regional comparisons or do not necessarily provide a better understanding of the mechanisms underlying the observed changes. There is widespread international consensus that in order to model vegetation response to environmental change on a regional or global scale, it is necessary to understand and predict plant responses to different land management factors in terms of plant traits that are ecologically meaningful but at the same time easily measured (Díaz & Cabido, 1997; Lavorel, McIntyre, Landsberg, & Forbes, 1997; Westoby, 1998; Hodgson, Wilson, Hunt, Grime, & Thompson, 1999; McIntyre, Díaz, Lavorel, & Cramer, 1999a; Weiher, van der Werf, Thompson, Roderick, Garnier et al., 1999).

Several authors have tried to identify plant traits linked to grazing (Friedel, Bastin, & Griffin, 1988; Noy-Meir et al., 1989; Díaz, Acosta, & Cabido, 1992; Fernández Alés, Laffarga, & Ortega, 1993; Díaz, Acosta, & Cabido, 1994; Díaz, Cabido, Zak, Martínez Carretero, & Aranibar, 1999; Landsberg, Lavorel, & Stol, 1999; Lavorel, McIntyre, & Grigulis, 1999; Hadar, Noy-Meir, & Perevolotsky, 1999;

review in McIntyre, Lavorel, Landsberg, & Forbes, 1999b). However, few general patterns have emerged beyond the fact that heavy grazing tends to favour small prostrate plants over tall erect types, and annuals over perennials. Furthermore, trends linking plant responses to disturbance (grazing and fire), previously accepted as universal, seem to depend on the regional context in a global-scale synthesis (Díaz, McIntyre, Lavorel, & Pausas, 2002). Another reason for the few generalities about plant traits and disturbance at the global scale is that a consistent set of traits has rarely been systematically screened in several different situations. Recently, there has been some progress on deciding how and which traits should be measured. Weiher et al. (1999) propose a list of easily measured core traits for comparative studies of functional ecology related to dispersal, establishment and persistence as well as standardized protocols for their measurement, while acknowledging that not all traits are relevant in all situations, and that trait selection should depend on the specific purpose, scale and system involved (see also McIntyre et al., 1999b). It is therefore necessary to document grazing-related changes in the vegetation covering as many particular floras under as many different circumstances as possible and using a core set of traits.

This paper analyses the consequences of grazing abandonment in dehesa systems in Central Spain and tests the indicator value of different plant traits for describing such changes. Firstly, we analysed changes in floristic composition of the vegetation using an ordination method and we identified species associated with grazed and ungrazed situations. Secondly, we described changes in the trait composition of the vegetation using an ordination method. We also tested 10 functional plant traits in relation to grazing abandonment. These traits were selected from the core list proposed by Weiher et al. (1999) and included morphological as well as regenerative traits.

## Methods

### Study area

The study area is 35 km north of Madrid (Central Spain, 40°38'N, 3°70'E), on the gneiss pediment of the Sierra de Guadarrama at a mean altitude of 900 m. The landscape has an undulating topography with <5% slopes, shallow acid soils and numerous rocky outcrops. The continental Mediterranean climate has a mean annual temperature of 13 °C, with an intense summer drought. The mean annual rainfall varies around 450 mm, with large inter-annual fluctuations.

The potential vegetation is a woodland dominated by Holm oak (*Quercus ilex* subsp. *rotundifolia*) and juniper (*Juniperus oxycedrus*). The woodlands have been cleared and maintained as dehesa grasslands for several centuries to permit extensive grazing by local breeds of cattle, sheep and goats. These grasslands are primarily composed of annual species, although perennials may also be found in the areas with greater water availability. Species richness is very high ( $58.8 \pm 5.17$  spp/100 m<sup>2</sup>, Traba, 2000). Over the last 40 years, dehesas have undergone a dual process of intensification and abandonment. In the more productive zones, intensification of land use has led to the conversion of pastures into herbaceous crops, mainly for the production of silage and fodder, a heavier stocking rate and the replacement of the local livestock species with commercial cross-breeds. In marginal zones, husbandry has gradually been abandoned, leading to scrub invasion. In the study area, species colonizing after abandonment of grazing are mainly lavender (*Lavandula stoechas* subsp. *pedunculata*) and broom (*Cytisus scoparius*). The communities also support a species-rich herbaceous matrix ( $49.3 \pm 3.53$  spp/100 m<sup>2</sup>, Traba, 2000).

### Vegetation and plant traits data

In spring 1996, we chose five sites with similar habitat features (flat dry zones over acidic shallow soils, outside the tree canopy) in both the grazed zones and the areas abandoned more than 20 years ago (scrubland). The minimum distance between sites was 200 m and the maximum 2 km. At each site we established a 10 × 10 m plot and we measured species cover in 20 quadrats (20 × 20 cm) set at random in each plot. Cover was estimated using five classes: (0) absent, (1) cover <12.5%, (2) 12.5–25%, (3) 25–50% and (4) >50%. For each site and species, we calculated

the average cover in the 20 quadrats after having designated each species in each quadrat with the median of its cover class. Nomenclature follows Tutin, Heywood, Burges, Valentine, Walters et al. (1964–1980).

We also collected data on functional traits of the most abundant species (those present in more than 10% of the quadrats in grassland or scrubland). The traits were chosen from those proposed by Weiher et al. (1999) as indicators linked to the main plant population processes: dispersal, establishment and persistence. The attribute data for each species were taken from the literature and field data (Table 1).

Seed mass and the presence of dispersal structures were taken from previous field measurements in the study area (Azcárate, Sánchez, Arqueros, & Peco, 2002), where air-dried seeds collected from 1996 to 1999 were weighed individually or in small groups ( $n_{\max} = 10$ ). For the majority of species, seed weight was obtained by averaging 30 measurements. The species were also classified according to the presence of dispersal structures of the diaspore. Information on life form, growth form, longevity, onset of flowering and clonality was taken from literature (Valdés, Talavera, & Fernández-Galiano, 1987; Castroviejo, 1986–1999; González-Bernáldez, 1997). Specific leaf area (SLA), leaf dry weight (LDW) and canopy height were measured in at least 10 mature well-developed individuals of each species collected at random in the field in spring 2001. These measurements followed the protocols recommended by Weiher et al. (1999). SLA is the area of a single leaf divided by its dry mass. Leaf area was measured using image analysis software (Leica Q500 Iw) in fully developed and hydrated mature leaves, leaving the petiole attached. These leaves were dried at 60–80 °C until a constant mass was reached, and then weighed to obtain measurements of LDW. Canopy height was measured as the difference between the height of the tallest photosynthetic tissue in the canopy and the base of the plant.

### Data analysis

Detrended Correspondence Analysis (DCA; Hill, 1979) of cover data for the 85 most abundant species in the 10 plot matrix was used to analyse the main variation trends based on species composition. In order to identify the predominant variations in plant traits, we used a conventional analytical scheme, multiplying the species × traits matrix by the plots × species matrix to produce a traits × plots matrix (Feoli & Scimone, 1984; Díaz,

**Table 1.** Traits recorded for the 85 most abundant species of the study area

Trait	Description	Classes in the matrix
Seed mass*	Average seed weight	Light: <0.05 mg; Medium: 0.05–1 mg; Heavy: > 1 mg
Dispersal structures*	Type of structures in the diaspore to dispersion in space	1: Unassisted; 2: Wind dispersal; 3: Adhesive
Life form*		1: Hemicryptophyte; 2: Pterophyte; 3: Chamaephyte; 4: Cryptophyte
Grow form*		1: Graminoid; 2: Rosette; 3: Prostrate; 4: Straightstem; 5: Bulb
Longevity*	Life span	1: Perennial; 2: Annual
Clonality*	Capacity to spread laterally	1: Clonality; 2: No clonality
Onset flowering†	Mean flowering start date	1: Autumn; 2: Early spring; 3: Spring; 4: Late spring
Canopy height†	Average plant height	Very short: 1–49 mm; Short: 50–99 mm; Medium: 100–299 mm; High: 300–599 mm; Very high: 600–1000 mm.
Leaf Dry Weight (LDW)†	Average leaf dry weight	Light: <0.5 mg; Medium: 0.5–10 mg; Heavy: >10 mg
Specific Leaf Area (SLA)†	Average leaf area (mm <sup>2</sup> )/Average LDW (mg)	Small: <20; Medium: 20–40; High: >40

\*Azcarate et al. (2002).

†Field measurements.

et al., 1992; Díaz & Cabido, 1997; Díaz Barradas, Zunzunegui, Tirado, Ain-Lhout, & García Novo, 1999). In order to homogenize the type of variables in the species x traits matrix, quantitative variables were assigned to three classes using the 25 and 75 percentiles as cut-off points (Table 1). Prior to matrix calculations, multistate traits were recoded into “dummy variables” as binary traits. The traits x plots matrix was analysed with a DCA performed following the CAP package procedure (Henderson & Seaby, 1999).

Species and plant traits associated with grazing were identified using Mann-Whitney U-tests, comparing species cover and relative cover values per trait in grazed vs. ungrazed plots. SPSS package (SPSS Inc., 2001) was used in this case.

## Results

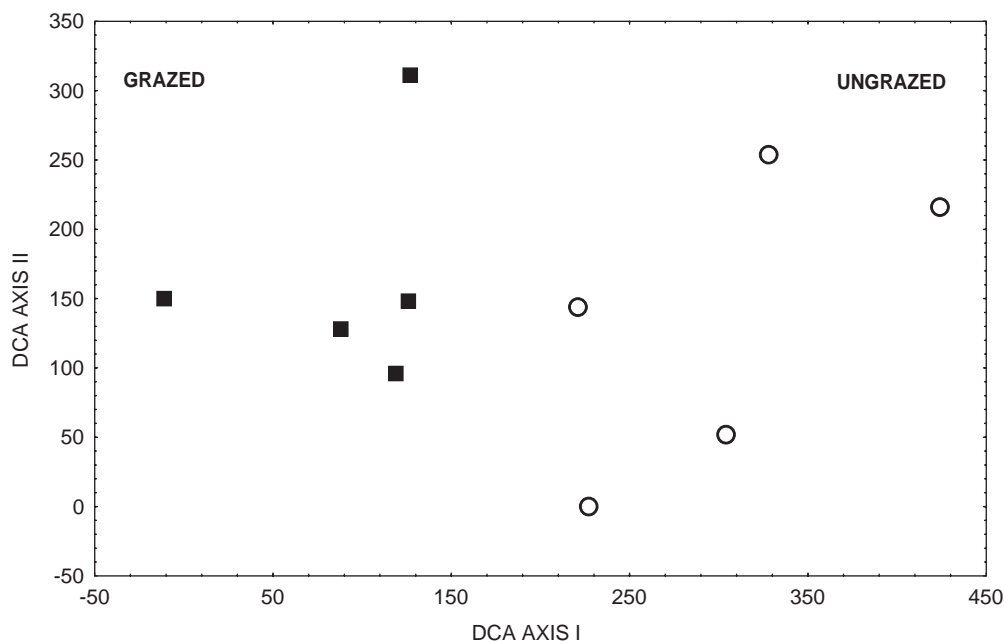
### Floristic composition and grazing

A total of 85 species were present in more than 10% of the samples (65 annuals and 20 perennials), of which 46 were common to both systems, 18 exclusive to grasslands and 21 exclusive to scrubland.

The major variation trend of the DCA obtained from species cover data was related to grazing. DCA-Axis 1 of this analysis clearly distinguishes between the grazed and ungrazed plots (Fig. 1). Species including *Anthemis arvensis*, *Aphanes microcarpa*, *Herniaria hirsuta*, *Parentucellia latifolia*, *Poa bulbosa*, *Trifolium glomeratum*, *Trifolium suffocatum* and others were significantly linked to grazing, while *Anthyllis lotooides*, *Campanula lusitanica*, *Coronilla repanda*, *Jasione montana*, *L. stoechas* and others were linked to grazing abandonment (Table 2).

### Plant traits, community structure and processes

The major variation trend in the analysis of the traits x plots matrix was also related to grazing (Fig. 2). U-tests showed that grazing resulted in a higher proportion of prostrate species, cryptophytes, intermediate SLA and early flowering. Unassisted seeds and clonal reproduction were also associated with grazing. Grazing abandonment involved a higher proportion of taller plants, heavy LDW, late flowering, heavy seeds and fruits with adhesive structures, and a high proportion of chamaephytes (Table 3).



**Fig. 1.** DCA-ordination of the 85 most abundant species  $\times$  plots matrix. Squares indicate grazed plots, circles indicate ungrazed plots. Total variance explained by these two axis was 72%.

## Discussion

Grazing abandonment produced large changes in floristic composition in dry dehesa grassland, with a floristic similarity between the grazed and ungrazed communities of only 54%. Floristic differences were even larger when all species were considered, in which case similarity is 30% (Traba, 2000). Relatively large changes in the species composition of the vegetation in relation to abandonment have also been found elsewhere in the Mediterranean region (Noy-Meir et al., 1989; Fernández Alés et al., 1993; Hadar et al., 1999), but not in similar agrosystems such as the Portuguese *montados* (Lavorel et al., 1999). These results should be compared with some caution as most of the studies refer to short-term experiments (2 or 3 years after change of use), while the changes documented in the present paper and in Noy-Meir et al. (1989) refer to a longer period (at least 20 years of abandonment) and the magnitudes and even the direction of change may vary considerably with the history of abandonment (Olff & Ritchie, 1998).

Several differences in the occurrence of traits were detected in addition to floristic changes. Height and habit were found to be important attributes in relation to grazing. Our results confirm the early findings that grazing favours small-stature species and species with rosette or prostrate morphology (Noy-Meir et al., 1989; Fernández Alés,

Laffarga, & Ortega, 1993; Lavorel, Touzard, Lebreton, & Clement, 1998; Hadar et al., 1999). Height was also the best single predictor of grazing response for herbaceous communities in Argentina and Israel (Díaz, Noy-Meir, & Cabido, 2001). The mechanism underlying these patterns is probably the differential defoliation on a vertical gradient caused by large herbivore grazing. Tall, erect plants or plants with raised regeneration buds are eliminated, while small or prostrate species survive (Noy-Meir et al., 1989). However, habit should be considered in combination with canopy height (Lavorel et al., 1999).

Grazing did not favour therophytes, contrary to what has been documented in other studies (McIntyre, Lavorel, & Tremont, 1995). The similar relative cover of annuals vs. perennials in grazed and ungrazed zones (1.6 and 1.8, respectively) may be related to the 3- or 4-month summer drought with barely any rainfall, which could restrict the cover of perennials in ungrazed environments. Amongst perennials, grazing appeared to promote cryptophytes while abandonment promoted chamaephytes. Hemicryptophytes seemed to be indifferent to grazing, probably because in this case, the feature should be considered in combination with habit. The capacity for clonal reproduction also seemed to be favoured by grazing. In fact, one unexpected result of the present study was the positive association between perennial grasses and grazing. This result was due exclusively to the

**Table 2.** Species with significant differences in their abundance between grazed and ungrazed sites (Mann-Whitney U-test;  $n = 5$ )

Species	Grazed	Ungrazed	P
<b><i>Anthemis arvensis</i></b>	3.44	0.00	0.008
<i>Anthyllis lotoides</i>	–	0.94	0.005
<b><i>Aphanes microcarpa</i></b>	6.88	1.25	0.009
<i>Arrhenatherum album</i>	–	0.94	0.018
<i>Asterolinon linum-stellatum</i>	–	1.56	0.005
<i>Campanula lusitanica</i>	–	4.06	0.005
<b><i>Cerastium semidecandrum</i></b>	3.12	0.32	0.021
<i>Coronilla repanda</i>	0.00	3.12	0.007
<i>Corynephorus canescens</i>	–	3.44	0.019
<b><i>Erodium cicutarium</i></b>	1.25	0.32	0.020
<b><i>Erophila verna</i></b>	2.81	0.31	0.009
<b><i>Herniaria hirsuta</i></b>	4.38	0.00	0.008
<i>Holcus setiglumis</i>	–	0.62	0.018
<i>Jasione Montana</i>	0.00	5.94	0.007
<i>Lavandula stoechas</i>	–	15.00	0.005
<b><i>Logfia gallica</i></b>	0.94	–	0.005
<i>Micropirum tenellum</i>	0.00	1.25	0.007
<b><i>Parentucelia latifolia</i></b>	1.88	0.00	0.008
<b><i>Plantago lagopus</i></b>	0.32	–	0.018
<b><i>Poa bulbosa</i></b>	46.88	3.44	0.009
<b><i>Rumex acetosella</i></b>	8.44	0.00	0.008
<i>Scilla autumnalis</i>	–	0.63	0.018
<b><i>Sedum caespitosum</i></b>	4.38	0.00	0.008
<i>Silene scabrifolia</i>	–	1.88	0.018
<b><i>Spergula arvensis</i></b>	5.94	–	0.005
<b><i>Spergularia purpurea</i></b>	5.00	0.31	0.016
<b><i>Trifolium dubium</i></b>	0.31	–	0.018
<b><i>Trifolium glomeratum</i></b>	3.75	0.00	0.008
<b><i>Trifolium subterraneum</i></b>	1.88	–	0.019
<b><i>Trifolium suffocatum</i></b>	4.38	–	0.005
<i>Valerianella carinata</i>	–	1.25	0.019
<i>Vicia lathyroides</i>	–	1.88	0.005

For each site and species we calculated the average cover in the 20 quadrats after having designated each species in each quadrat with the median of its cover class. The values in the table represent the median of these cover values for the 5 replicates. Species with significantly higher abundance in grazed sites are shown in bold type.

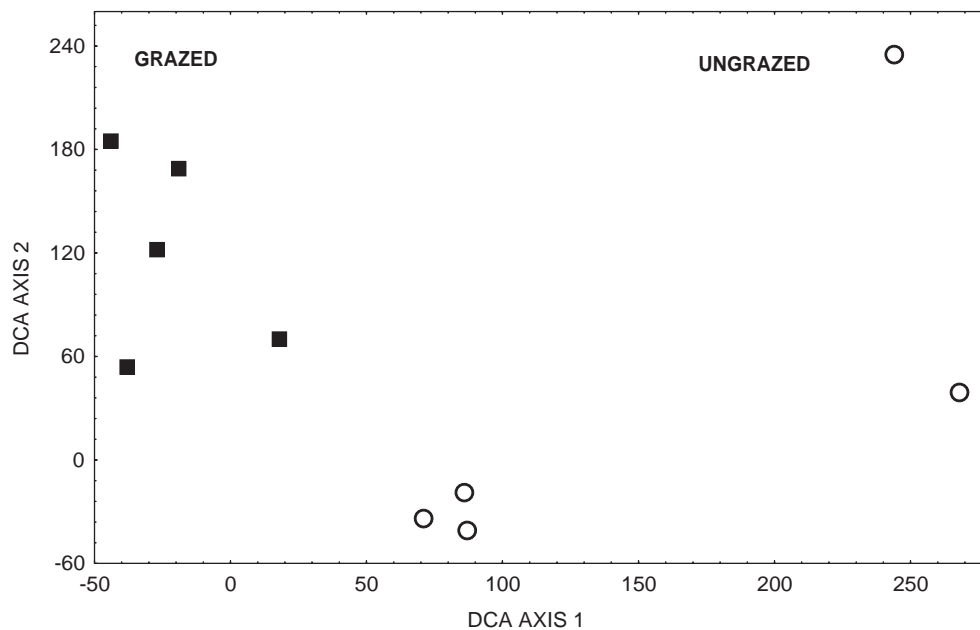
extremely high *P. bulbosa* cover in grasslands in comparison with scrublands (49% as opposed to 5%), as the relationship ceased to be significant when this species was eliminated. *P. bulbosa*, a very small perennial grass with fundamentally clonal reproduction and early phenology, is remarkable for its resistance to sheep grazing under the dry conditions of the Mediterranean basin and its soil-retention capacity (Montserrat, 1980a, b; Ofir & Kerem, 1982).

The phenological niche is also an important factor in determining community composition under grazing pressure. Early flowering in particular appears to be promoted by grazing. The same

result was found in southern Spain and Israel (Fernández Alés et al., 1993; Hadar et al., 1999), in systems with continuous seasonal grazing and a predominance of annual species. Early flowering and fruiting has been interpreted as an avoidance strategy in relation to grazing (Briske, 1996), which may be particularly useful for annual species whose fitness is linked to seed production but not to the survival of implanted individuals. However, 12 years of livestock grazing did not modify the periodicity of flowering or fruiting in an Argentinian montane grassland dominated by perennial species (Díaz et al., 1994).

LDW and SLA were also associated with grazing in our study area. In general, species with medium SLA (values between 20 and 40) were more abundant in grazed than ungrazed areas while heavy leaves were more common in ungrazed areas. This result partially concurs with Díaz et al. (2001) and Westoby's (1998) prediction for heavily grazed areas, suggesting that a higher growth rate (high SLA) is a grazing tolerance mechanism while small leaves (low LDW) are an avoidance mechanism (*sensu* Briske, 1996). The indifference to grazing by species with SLA values below 20 or over 40, however, could indicate that the relationship between SLA and grazing in Mediterranean grasslands is not linear.

With respect to seed traits, our research confirms that seed mass and dispersal structures are traits associated with grazing. Unassisted seeds tend to be associated with grazing, while heavy-seeded species are more frequent in ungrazed habitats. Large heavy seeds seem to have a lower chance of surviving the herbivore gut passage and the mechanical chewing process (Staniforth & Cavers, 1977), which could be a selective force against species with heavy seeds in grazed environments. In addition, the presence of dispersal structures appears to be less important in grazed than abandoned dehesas. Similar results have been found by other authors. In southern Portuguese Mediterranean grasslands, Lavorel et al. (1999) found that grazing favours forbs with small unassisted seeds while abandonment favours grasses with heavy seeds. More recently, McIntyre and Lavorel (2001) found that in Australian subtropical pastures, intensive grazing on both perennial grasses and forbs generally favours species that produce smaller seeds and grasses without dispersal appendages, while wind dispersal is associated with low grazing intensity. In contrast, no consistent seed size pattern in response to grazing was found in Australian semi-arid woodlands by Landsberg et al. (1999), or in southern Spanish Mediterranean grasslands by Fernández Alés et al. (1993).



**Fig. 2.** DCA-ordination of the traits x plots matrix. Squares indicate grazed plots, circles indicate ungrazed plots. Total variance explained by these two axis was 10%.

**Table 3.** Traits with significant differences in their relative cover between grazed and ungrazed sites (Mann-Whitney U-test;  $n = 5$ )

Traits	Grazed	Ungrazed	<i>P</i>
<b>Seed mass</b>			
Heavy (> 1 mg)	0.56	1.27	0.047
<b>Dispersal structures</b>			
<b>Unassisted seeds</b>	16.18	14.76	0.047
Adhesive seeds	0.98	2.84	0.009
<b>Life form</b>			
Chamaephyte	—	2.37	0.005
<b>Cryptophyte</b>	5.46	0.89	0.009
<b>Grow form</b>			
<b>Prostrate</b>	2.44	1.58	0.028
<b>Clonality</b>			
<b>Clonality</b>	7.15	1.33	0.016
<b>Onset of flowering</b>			
<b>Early spring</b>	4.62	2.56	0.028
Late spring	2.00	6.07	0.028
Autumn	—	0.10	0.018
<b>Canopy height</b>			
Medium (100–229 mm)	3.83	9.20	0.016
High (300–599 mm)	—	0.46	0.005
<b>Leaf Dry Weight</b>			
Heavy (> 10 mg)	0.97	4.64	0.028
<b>Specific Leaf Area</b>			
<b>Medium (20–40)</b>	13.43	9.59	0.016

Values in the table represent the median of the relative cover of each trait in the 5 replicates. Traits with significantly higher abundance in grazed sites are shown in bold type.

## General considerations

Our methodological approach permitted the identification of a series of individual attributes that are positively or negatively associated with grazing. There is no doubt that the results from this study are linked to a series of methodological decisions. The choice of traits was necessarily pragmatic in an attempt to minimise the number of chosen traits and the effort required for their measurement, while at the same time maximising their functional relationship to grazing (McIntyre et al., 1999a; Weiher et al., 1999). We did not evaluate the importance of interpopulation variations of species traits present in grazed and ungrazed zones, although this aspect possibly carries more weight in communities that do not evidence large changes in floristic composition in relation to grazing pressure (Díaz et al., 1994). The product of the species x traits matrix by the species x plots matrix facilitates the typification of the functional composition of the communities, but fails in the detection of groups of species with syndrome attributes, since it does not consider the natural association between attributes in each of the species. Individual attributes are not the targets of natural selection, rather it is the fitness of the whole plant, which is important (Coughenour, 1985). However, even considering the whole

plant, the combination of attributes may be suboptimal for surviving grazing since many of the attributes may have developed due to different types of selection pressure. We believe that, for global modelling purposes, individual attributes whose functional relationship with grazing has been proven experimentally may be more useful than attribute syndromes, as the latter may vary between floras with different evolutionary histories.

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