

Species and life-forms composition of Mediterranean mountain pastures in two years of contrasting precipitation

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Summary

Twenty sites, representing different pasture types in NW Spain, were sampled with respect to their floristic composition and structural characteristics for two years of contrasting precipitation. The first year was characterised by a severe regional drought and the second year had normal precipitation. Four plant community types were identified by consensus classification techniques of plant species composition. These community types were associated with grazing regime, percentage cover of herbaceous vegetation, rocks and bare ground, and soil characteristics. One community type included mesic sites on acidic parent materials with low grazing, whereas the other three were all intensely grazed, and included either xeric or mesic sites on calcareous parent materials, or mesic sites on acidic parent materials. Species composition varied between years according to well defined directional trends within the intensely grazed communities. Compositional differences between calcareous and acidic pastures increased in the normal year. On average 49 to 73% of the species appeared only in one year. This high species turnover was also high when analysed separately for different life-forms, namely annuals, perennial grasses, perennial forbs and undershrubs. In spite of this, both the life-form spectrum, and the relative abundance of each life-form remained unaltered for each community type in both years. This suggests that such characteristics of the communities' structure are in equilibrium with habitat characteristics, as well as the existence of a deterministic structure in the grasslands studied.

Key words: Grasslands, plant species richness, biological spectrum, drought, fluctuations, grazing regime

1. Introduction

Most of the works studying temporal changes of natural communities emphasise problems related with ecological succession (e.g. TRAMER 1975; INOUE et al. 1987; PINEDA et al. 1987; MESLÉARD et al. 1991). Fluctuations, i.e. functional or structural changes of communities with no defined direction are typically less analysed (e.g. AUSTIN 1981; COLLINS et al. 1987; PECO et al. 1988; TILMAN & EL HADDI 1992). However, the effects of yearly climatic fluctuations on grasslands' structure are receiving increased attention; in part because they offer good opportunities to analyse natural situations which could resemble those occurring during an eventual global warming. Such studies have been carried out by comparing one dry with one wet year (e.g. FRANK & McNAUGHTON 1991, 1992, RODRÍGUEZ & GÓMEZ-SAL 1994), or in a larger time scale (COLLINS et al. 1987,

HOULE & PHILLIPS 1989, MILCHUNAS et al. 1989, FIGUEROA & DAVY 1991, TILMAN & EL HADDI 1992, TILMAN & DOWNING 1994, SILVERTOWN et al. 1994, TILMAN 1996). Weather fluctuations may affect plant communities by altering seed set and dispersal, germination, plant growth, and the relative competitive ability of the participating species. For many ecosystems, droughts are unusual events that upset normality, causing the death of some individuals, and local species extinctions, and can be viewed as disturbances (sensu GRIME 1977). This is not the case of the Mediterranean ecosystems, since these have typically evolved under the influence of a fluctuating climate, in which dry, average, and wet years alternate in an unpredictable fashion. The aim of this study is to document the effects of climate fluctuation on species composition and life-form structure in different mesic and more xeric Mediterranean pasture communities. The study spanned two

years, the first one coincided with a severe regional drought, whereas the second one had average precipitation.

2. Materials and methods

The study area has been described in RODRÍGUEZ *et al.* (1995). Briefly, it covers 3000 ha in the Revero Valley (Cantabrian Mountains, NW Spain). The altitude varies from 1000 to 1900 m, although the study sites were all between 1150 and 1400 m. The climate is transitional between Mediterranean-Continental and Atlantic, with a mean annual precipitation of 1220 mm. The mean minimum and maximum temperatures range from -3 to 29 °C with extremes of -11 and 32 °C, respectively. Only three months are guaranteed frost-free (typically from June to August), while for five months frosts are normal (from November to March), the remaining months have occasional frosts. Plant growth stops during the coldest winter months, and from August to early September due summer drought (RIVAS-MARTÍNEZ *et al.* 1984).

The study spanned 1986 and 1987. October-December precipitation for 1985 and 1986; i.e., for the Autumn seasons preceding each sampling, was 64% and 45% of normal, respectively. The total precipitation between 1 January and 31 May for 1986 and 1987 was 72% and 76% of normal. January-March precipitation was 288 mm for 1986, and 302 mm for 1987; whereas April-May precipitation was 115 mm for 1986, and 125 mm for 1987. The greatest differences between years occurred in June-July; i.e., coinciding with the main germination and growing period in this area. In this period, the precipitation was only 20 mm in 1986, but was 129 mm in 1987, equalling 19% vs 123% of the average precipitation respectively.

A stratified sampling programme was adopted, based on parent material and broad vegetation type (e.g. meadow, pasture, scrub and forest). These were identified by means of published lithological maps and aerial photographs. Starting at the sites that first become dry, sampling took place in late-July in both years, coinciding with the end of the growing season. There were 20 sites, each 10 m \times 10 m. For the classification of plant communities, the aerial percentage cover of all angiosperm species (nomenclature follows TUTIN *et al.* 1964–1980) was estimated in each site in four 50 cm \times 50 cm permanent quadrats. These quadrats were placed at random at each site in 1986 and resampled in 1987. Cover was estimated by eye using a modified Daubenmire cover scale: 1 = <1% cover (e.g. present), 2 = 2–10%, 3 = 11–25%, 4 = 26–50%, 5 = 51–75%, 6 = >76%. Average cover was determined for each species by converting the Daubenmire scale value to the midpoint of the cover range and averaging across the four quadrats at a site.

Major physical and structural characteristics of the sites were also recorded: elevation, slope, topographic position, parent material type, apparent soil moisture (four subjective categories), and percentage of soil surface covered by herbaceous plants, gaps, small stones and rocks. The pastures studied were all grazed by cattle, and each site was assigned to a category of grazing regime using a nominal scale: concentrated intense grazing in early spring, extended intense grazing

throughout spring, and non-intense grazing. These categories were established from direct observations and information provided by farmers. In 1986, four soil subsamples were taken at each site to a depth of 10 cm and after plant material had been manually removed. For soil analyses, the subsamples corresponding to each site were combined into one sample that was air-dried and sieved to remove coarse fragments (particles >2 mm diameter), then analysed for pH, organic matter, total nitrogen, carbon, carbon/nitrogen ratio, available phosphorous, and exchangeable potassium and calcium. (See RODRÍGUEZ *et al.* 1995, for details on the estimation of the environmental variables).

Species richness (S) was calculated as the number of species per site. Interannual variation of species composition was assessed as $IVS = 100 \cdot (b + c) / (a + b + c)$, where b was the number of species appeared only in 1986, c was the number of species appeared only in 1987, and a was the number of species which were present in both years. (Note that this index is the inverse of the Jaccard's Community Index). Identification of community types was made taking into account relevant compositional traits of the sites in both years. The data matrix of sites-by-percentage cover of plant species of each year was separately subjected to a Correspondence Analysis, and Generalised Procrustes Analysis (GOWER 1975) was then used to produce an overall ordination of the sites. The sites were classified according to their respective scores in this ordination, using Euclidean Distances and the centroid method as clustering criterion (DIGBY & KEMPTON 1987). Correspondence Analysis was also used to explore the main overall trends of variation of the vegetation by analysing jointly the data matrices of sites-by-percentage cover of species of each year. Association of community types with qualitative environmental variables was examined by constructing all the possible two-way contingency tables. These tables were tested for significance with Chi-square, applying Yates' correction (ZAR 1984). Differences between communities, years or life-forms in relation with different structural parameters were studied by analysis of variance (ANOVA). When comparisons involved more than two means, the differences among them were tested by means of Tukey-Kramer HSD test. For comparisons among communities we used the HSD test for unequal sample sizes (Spjøtvoll and Stoline test; see SOKAL & ROHLF 1981), since community types differed in the number of sites representative of each of them (see below). Proportional data were angularly transformed, absolute data, except pH, were subjected to logarithmic transformation, whereas data of species counts were subjected to square root transformation prior to analysis. In the tables presented here, the mean values resulted from the analyses have been transformed back to untransformed parameters following ZAR (1984).

3. Results

3.1. Plant community types

The sites were clustered into four groups (Fig. 1). One site (# 17) was compositionally very different from the others, and remained unclustered down to a similarity value of 10%, for which it was omitted from further ana-

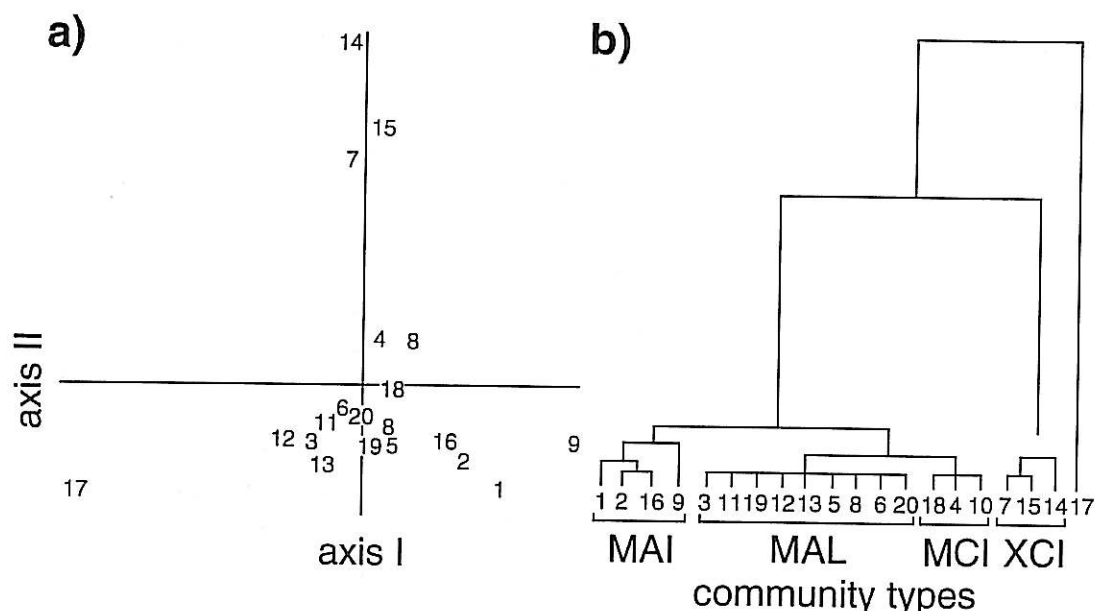


Fig. 1. Consensus ordination (a) and classification (b) of the study sites. The consensus ordination is based on the results of two correspondence analysis, each performed on the data matrix of sites-by-percentage cover of plant species corresponding to a particular year. The classification analysis was done according to the scores of the sites in the consensus plane.

lyses. To denote the site groupings we used three letters; the first one refers to the character mesic (M) or xeric (X) of the sites, the second one indicates whether their parent material was acidic (A) or calcareous (C); and the third letter indicates whether they received intense (I) or low (L) grazing pressure. A synthesis of those characteristics, including others referred to structural features of the sites is given in Table 1. Following JANCEY (1979), the differential species of these groupings of sites were identified by means of ANOVA using percentage cover data (see Table 3). (Note that the use of ANOVAs here is for the only purpose of helping characterizing community types in terms of composition, and that we do not base our conclusions on these analyses).

Cluster XCI (Fig. 1) grouped three sites which occurred in steep slopes, with soils of nearly neutral pH

and intermediate values of organic matter, nitrogen and calcium (Table 2). The high percentage of ground covered by gaps and stones ($\approx 40\%$) suggest that these sites had high levels of soil erosion. To this may have contributed their steep slopes, and the intense grazing pressure they typically receive in early spring, when the ground is still moist (soon after snowmelt) and potentially highly sensitive to trampling. High levels of erosion may also account for the abundance of perennial caespitose species (e.g. *Koeleria vallesiana*, *Festuca hystrix*) particularly capable of growing in such situations. Similarly, the large number of annual species (e.g. *Bupleurum baldense*, *Xeranthemum inapertum*, *Crucianella angustifolia*) present in these pastures (see Table 4) may be associated with the abundance of bare ground. The relative cover of perennial forbs (e.g. *Asperula*

Table 1. Environmental and structural characteristics of the community types that were analysed as qualitative variables. Only those variables co-varying nonrandomly with community type (as indicated by Chi-square tests, $P \leq 0.050$) are presented.

Variable	Community type				P <
	XCI	MCI	MAI	MAL	
Soil moisture	Dry	Medium	Medium-wet	Wet	0.050
Parent material	Calcareous	Calcareous	Acidic	Acidic	0.001
Grazing regime	Intense, early spring	Intense, spring-early summer	Intense, spring-early summer	Low pressure	0.001
Percent cover of herbaceous plants	Low	Medium	High	Medium	0.010
gaps	High	Low-medium	Low	Low	0.050
small stones	High	Low-medium	Low	Low	0.010
rocks	High	Low-medium	Low	Low	0.001

cynanchica, *Galium mollugo*, and the bulbs *Allium sphaerocephalon* and *Muscari neglectum*) was lower in these pastures than in the other intensely grazed communities (Table 4). Conversely, the percentage of undershrub species (17.5%) as well as their relative

cover (19.9%) was highest in XCI (Table 4). Among these species, *Lithodora diffusa*, *Helianthemum canum*, *Thymus mastigophorus* and *Teucrium chamaedrys* were the most characteristic (Table 3). These species develop relatively small hairy leaves and persistent large roots,

Table 2. Mean values of the quantitative soil variables, and results of the one-way ANOVAs comparing community types. For each variable, community types not sharing a common letter were significantly different ($P < 0.050$) as indicated by HSD test.

Variable	Community type				$F_{3,15}$	$P \leq$
	XCI	MCI	MAI	MAL		
Organic matter (%)	8.3 _{ab}	13.1 _a	5.1 _b	8.2 _{ab}	4.4	0.019
Nitrogen (%)	39.9 _{ab}	59.1 _a	25.1 _b	38.2 _{ab}	5.3	0.010
Carbon/Nitrogen	12.2	12.9	11.8	12.3	0.4	n.s.
pH	6.6 _a	6.4 _{ab}	5.6 _{ab}	5.3 _b	5.7	0.008
CaO (mg/100 g)	313 _{ab}	514.3 _a	194.5 _b	181.8 _b	5.1	0.010
P ₂ O ₅ (mg/100 g)	2.3	1.9	2.1	2.7	0.6	n.s.
K ₂ O (mg/100 g)	42.2	58.5	20.2	27.3	2.3	n.s.

Table 3. Species exhibiting significantly different ($P < 0.050$) percentage cover in at least two community types in one year. Comparisons were made by analyses of variance performed separately for each year. Each analysis involved one species and a pair of community types. (+) indicates significant differences in 1986; (x) indicates significant differences in 1987; and (*) indicates significant differences in both years. For each pairwise comparison, symbols are placed below the initials identifying the community type in which the species was more abundant.

	Pairwise comparisons between communities					
	XCI-MCI	XCI-MAI	XCI-MAL	MCI-MAI	MCI-MAL	MAI-MAL
Annual grasses						
<i>Bromus squarrosus</i>	.	x	x	.	.	.
<i>Cynosurus echinatus</i>	.	.	x	.	.	.
<i>Bromus hordeaceus</i>	x	+
<i>Vulpia bromoides</i>	+
<i>Aira caryophyllaea</i>	+
Annual and biennial forbs						
<i>Crucianella angustifolia</i>	+	*	*	.	.	.
<i>Xeranthemum inapertum</i>	x	x	*	.	.	.
<i>Hornungia petraea</i>	.	x	x	.	.	.
<i>Filago pyramidata</i>	.	+	*	.	.	.
<i>Petrorhagia prolifera</i>	.	x	*	.	.	.
<i>Arnoseris minima</i>	.	.	x	.	.	.
<i>Linum trigynum</i>	.	.	x	.	.	.
<i>Logfia minima</i>	.	.	x	.	.	.
<i>Medicago lupulina</i>	.	.	x	.	.	.
<i>Arenaria serpyllifolia</i>	.	.	x	.	x	.
<i>Bupleurum baldense</i>	x	*	*	x	x	.
<i>Linum catharticum</i>	.	.	.	x	x	.
<i>Bellardia trixago</i>	.	.	.	x	x	.
<i>Trifolium scabrum</i>	.	.	.	x	x	.
<i>Linum bienne</i>	x	.
<i>Trifolium campestre</i>	.	.	*	.	.	.
<i>Seseli libanotis</i>	x
<i>Dipsacus spec.</i>	x
<i>Tragopogon pratensis</i>	x
<i>Crepis capillaris</i>	.	+	.	+	.	+

Table 3. (Fortsetzung)

	Pairwise comparisons between communities					
	XCI-MCI	XCI-MAI	XCI-MAL	MCI-MAI	MCI-MAL	MAI-MAL
Perennial grasses (+ sedges)						
<i>Festuca hystrix</i>	.	.	*	.	.	.
<i>Bromus erectus</i>	.	*	.	*	.	.
<i>Koeleria vallesiana</i>	.	*	*	.	*	.
<i>Avenula bromoides</i>	.	×	×	.	×	.
<i>Carex flacca</i>	×	.
<i>Agrostis capillaris</i>	.	+
<i>Phleum pratense</i>	.	+	.	+	.	+
<i>Cynosurus cristatus</i>	.	+	.	+	.	+
<i>Poa compressa</i>	.	+	.	.	.	×
<i>Phleum phleoides</i>	+
<i>Carex caryophylla</i>	.	.	×	.	.	.
<i>Luzula caespitosa</i>	.	.	×	.	.	×
<i>Festuca gr. rubra</i>	+	+
Perennial forbs (non graminaceous species)						
<i>Galium mollugo</i>	+	+	*	.	.	.
<i>Asperula cynanchica</i>	+	*	*	.	.	.
<i>Muscari neglectum</i>	.	+	+	.	.	.
<i>Allium sphaerocephalon</i>	.	+	+	.	.	.
<i>Leontodon taraxacoides</i>	.	×	*	.	.	.
<i>Geum sylvaticum</i>	.	.	+	.	.	.
<i>Coronilla minima</i>	.	.	+	.	.	.
<i>Silene legionensis</i>	.	.	×	.	.	.
<i>Sedum album</i>	.	.	×	.	.	.
<i>Anthyllis vulneraria</i>	.	×	*	×	×	.
<i>Potentilla tabernaemontani</i>	.	*	*	.	*	.
<i>Sanguisorba minor</i>	.	.	.	+	.	.
<i>Ononis spinosa</i>	.	.	.	+	.	.
<i>Hippocrepis comosa</i>	.	.	.	+	*	.
<i>Leontodon pyrenaicus</i>	+	.
<i>Galium verum</i>	.	.	.	+	.	.
<i>Carduncellus mitissimus</i>	.	.	.	*	×	.
<i>Linum narbonense</i>	×	.
<i>Leucanthemum vulgare</i>	×	+
<i>Lotus corniculatus</i>	.	+	.	.	+	+
<i>Hieracium pilosella</i>	×
<i>Plantago lanceolata</i>	.	*
<i>Bellis perennis</i>	.	×
<i>Trifolium pratense</i>	.	*	.	×	.	.
<i>Eryngium campestre</i>	+
<i>Ranunculus bulbosus</i>	+
<i>Ranunculus acris</i>	×
<i>Hypochaeris radicata</i>	+
Undershrubs (woody species)						
<i>Lithodora diffusa</i>	×	×	×	.	.	.
<i>Teucrium chamaedrys</i>	×	×	*	.	.	.
<i>Helianthemum canum</i>	.	×	*	.	.	.
<i>Thymus zygis</i>	.	.	×	.	.	.
<i>Thymus mastigophorus</i>	*	*	*	×	.	.
<i>Linum suffruticosum</i>	+	.
<i>Thymus pulegioides</i>	.	.	×	+	.	×

Table 4. Percentage of species and percentage cover corresponding to each life-form in each community type. For both parameters, a MANOVA analysis with community type and year as main factors showed significant effects of community type but not of year. Similarly, two-way ANOVAs with year and life-form as main factors performed separately for each community type only showed significant effects of life-form. Since there were not significant effects of year in any case, this factor is not included in the table. Within each life-form, differences among communities are indicated by left hand superscripts (Tukey-Kramer HSD test). In each row, the significant differences among life-forms are indicated by right hand subscripts (Spjøtvoll and Stoline HSD test). Significant effects for which the HSD test was not sensitive to differences among means are indicated by asterisks. Conventions as in Table 2.

Variable	Community	Life-form			
		Annuals	Perennial grasses	Perennial forbs	Undershrubs
Percentage of species	XCI	^a 29.3 _a	^b 16.4 _b	^b 38.9 _a	^a 17.5 _b
	MCI	^{bc} 10.8 _b	^a 24.0 _b	^a 48.8 _a	^{ab} 11.9 _b
	MAI	^{ab} 24.3 _b	^a 26.5 _b	^{ab} 42.7 _a	^b 4.1 _c
	MAL	^c 10.2 _c	^a 29.5 _b	^{ab} 47.2 _a	^{ab} 11.4 _c
Percentage cover	XCI	^a 19.5	[*] 27.8	^b 31.4	^a 19.9
	MCI	^{ab} 7.4 _c	[*] 28.2 _{ab}	^a 50.5 _a	^{ab} 9.3 _{bc}
	MAI	^a 16.9 _b	[*] 31.6 _{ab}	^a 46.7 _a	^b 2.0 _c
	MAL	^b 3.8 _b	[*] 45.1 _a	^{ab} 38.4 _a	^{ab} 9.7 _b

which suggests that they are capable of making an effective use of scant water resources (see GRIME 1994). This may indeed account for the relatively high abundance of these plants in XCI.

The three remaining site groupings were all clustered into a major group of mesic pastures (Fig. 1), which differed in parent material characteristics and/or in grazing regime. Cluster MCI grouped three sites with similar parent material to XCI pastures (i.e. limestone and calcareous conglomerates). This may explain why some of the characteristic species of XCI were also common in MCI (see Table 3). MCI sites were intensely grazed through spring. The soils of these sites exhibited the greatest amounts of organic matter and nitrogen (Table 2), and had an apparent good water supply (Table 1). These MCI sites were dominated by herbaceous plants (83% and 88% of the above ground biomass in 1986 and 1987, respectively; RODRÍGUEZ 1992), and had a low proportion of ground covered by gaps and stones (Table 1). Characteristic species of this cluster were (Table 3) *Potentilla tabernaemontani*, *Hippocrepis comosa*, *Sanguisorba minor*, *Thymus pulegioides*, *Leontodon pyrenaicus* (perennial forbs), *Bromus erectus* (perennial grass), *Bromus hordeaceus* and *Linum catharticum* (annuals). In phytosociological terms, the MCI pastures could be classified into the alliance Mesobromiom erecti (Festuco-Brometea class, see RIVAS-MARTÍNEZ et al. 1984).

Cluster MAI grouped four mesic sites which were also intensely grazed through spring. The soils of these sites were on acidic parent materials consisting of quaternary deposits which were relatively poor in terms of

organic matter and nitrogen (Table 2). Whereas undershrubs showed the lowest contribution in terms of percentage of species (4.1%) and relative cover (2% Table 4), the percentage cover of the herbaceous vegetation reached nearly 100%. Characteristic species of these sites were *Crepis capillaris* (annual forb), *Trifolium pratense* (perennial forb), *Cynosurus cristatus*, *Phleum pratense* and *Poa compressa* (perennial grasses) (Table 3). Accordingly, these pastures could be included into the alliance Cynosurion cristati (Molinio-Arrhenatheretea class).

Cluster MAL had nine sites, mainly located on the lower, more moist part of slopes. The soils of these sites were also on acidic parent materials, and had low pH and intermediate values of organic matter and nitrogen (Table 2). In spite of their usually high yield (RODRÍGUEZ et al. 1995), the grazing pressure in these pastures was low in both years, probably because both the farmers believe that these pastures have low nutritional value for cattle, and because their grazing period (late spring and summer) often coincide with the time in which the hay meadows of the valley floors (not considered in this study) are used for grazing. Characteristic species of the cluster MAL were *Festuca* gr. *rubra*, *Luzula caespitosa*, *Carex caryophylla* (perennial monocots), and *Thymus pulegioides* (undershrub) (Table 3).

In sum, there were three mesic community types (MCI, MAI and MAL) which had many species common to one another, and where mainly dominated by herbaceous perennial plants. Conversely, in the xeric pastures XCI, there were no significant differences

among life-forms in terms of their relative cover, although annuals and perennial forbs significantly contributed more species than perennial grasses and undershrubs (Table 4).

3.2. Changes in species composition

The arrangement of the sites along the axes 1 and 2 of the Correspondence Analysis (Fig. 2) reflected the delineation of communities, although it was less clear in the dry year (i.e. 1986), where all the mesic sites appeared closely packed toward the negative end of the axis 1, than in the normal year (i.e. 1987). The compositional differences among community types clearly increased in the normal year (Fig. 2). The sites on calcareous parent materials (XCI and MCI community types) showed a well defined displacement toward the positive end of the axis 1, whereas those representative of mesic pastures on acidic parent materials with intense grazing (MAI) did the same toward the negative end of the axis 2. Only the mesic sites on acidic parent materials with low grazing pressure (MAL) did not show definite trends of interannual variation in the multifactorial space (we note here that this absence of definite trends of variation in MAL persisted in the axes 4 and 5 of the Correspondence Analysis).

Average species richness per community type per year ranged from 42 to 56. Species richness did not vary between years in any of the community types, and was higher in the calcareous communities (MCI and XCI) (Table 5). Although the community types were fairly stable in terms of the percentage of species and percentage cover contributed by each life-form (Table 4), the interannual variation of species composition (*IVS*) was remarkably high in all of them (Table 6). On average across the 19 sites, annual species showed significantly

higher values of *IVS* than perennial grasses, perennial forbs and undershrubs, which did not differ to each other in this respect (Table 6). Comparing between communities, the greatest *IVS* value was shown by the mesic pastures on acidic parent materials MAI, in which 72.7% of the species were present in only one year. In contrast, the xeric pastures on calcareous parent materials XCI were significantly more stable (*IVS* = 48.6%), whereas MCI and MAL showed intermediate species turnover. The differences in *IVS* between MAI and XCI were particularly apparent in the case of undershrubs, which were significantly less variable in XCI (*IVS* = 13%) than in MAI (*IVS* = 91.2%). The high variability of undershrubs in MAI may have been due to their low abundance (relative cover = 2%) and the low percentage of species they contributed to this community (4.1%).

4. Discussion

The species turnover we observed could be due to sampling noise (NILSSON & NILSSON 1985), even though we have used the same methods and did the same sampling effort in the two years studied (TILMAN & EL HADDI 1992). GAUCH (1982) estimated that the maximum dissimilarity among replicate samples that can be attributed to sampling noise is 50%. The interannual variability showed by the communities we studied equals this theoretical value for one community (XCI), and is greater than that for the three remaining communities (Table 6). Therefore, the compositional variability we observed likely reflects properties of the study system, and not simply sampling noise. The well defined interannual patterns of change of species composition shown by the three intensely grazed communities (i.e. XCI, MCI and MAI) reinforces such interpretation,

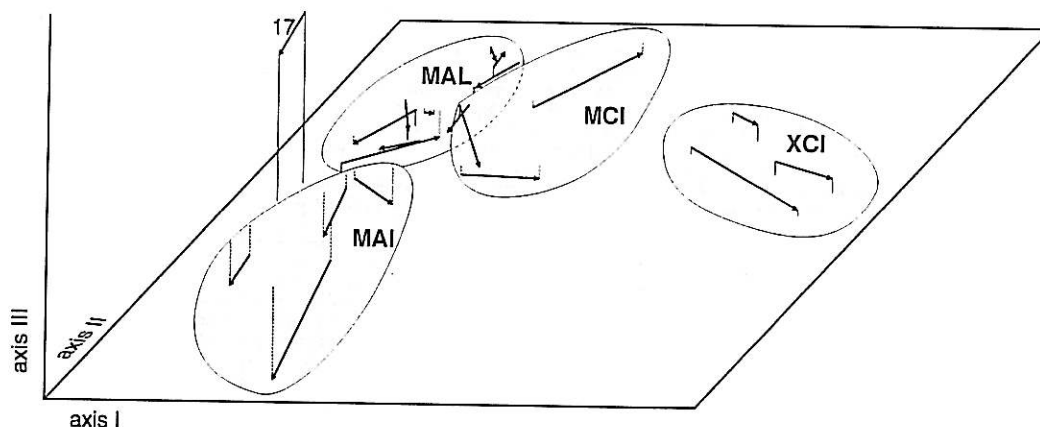


Fig. 2. Ordination of the sites according to the percentage cover of the species. Each arrow starts in the position of a site in the dry year, and ends in the position of this site in the normal year. Shaded regions group sites belonging to the same community type.

Table 5. Average values of species richness per community type per year. Subscripts indicate significant differences among communities. There were not significant differences between years. Conventions as in Table 2.

Variable	Year	Community types				Average
		XCI	MCI	MAI	MAL	
Richness	1986	52	53	43	42	47
	1987	49	56	46	46	49
	Average	51 _{ab}	55 _a	44 _{bc}	44 _c	

Table 6. Interannual variation of species composition (IVS) in four different pasture community types and four life-forms. Right hand superscripts and subscripts indicate significant differences due to the main factors community type and life-form, respectively. Left hand subscripts indicate significant effects of the interaction between community type and life-form. Conventions as in Table 2.

Variable	Community types	Life-form				Average
		Annuals	Perennial grasses	Perennial forbs	Undershubs	
IVS	XCI	_{ab} 63.3	_{ab} 53.3	_{ab} 68.9	_b 13.0	48.6 ^b
	MCI	_a 78.8	_{ab} 42.9	_{ab} 49.8	_{ab} 65.6	61.3 ^{ab}
	MAI	_a 82.0	_{ab} 50.7	_{ab} 60.2	_a 91.2	72.7 ^a
	MAL	_a 80.4	_{ab} 49.3	_{ab} 57.5	_{ab} 58.9	61.9 ^{ab}
	Average	77.8 _a	49.0 _b	59.2 _b	57.8 _b	

and suggests that weather variation (e.g. by modifying plant species germination and survival) was relevant in conditioning species turnover.

The absence of definite interannual trends of species composition variation within the community type MAL may have been associated with its management. Grazing is known to be a major force in shaping community composition and structure (e.g. CRAWLEY 1983). Potential small habitat differences among sites otherwise located in analogous habitats, may have been lesser relevant in conditioning the response of the communities to the change of precipitation under intense grazing (e.g. as in XCI, MCI and MAI) than under low grazing (MAL). In other words, in the less grazed MAL, where there was no uniformizing grazing effect, small environmental differences between sites could have been enough for them to show diversified patterns of interannual compositional change.

Habitat differences seemed to be less important in determining compositional differences among community types in the dry than in the normal year (see Fig. 2). Water stress tolerant species may have contributed to this result, as it is likely that these species were favoured in the dry year in all the communities, thus increasing their similarity. The parent material also conditioned the direction of the variation of species composition, leading to different interannual changes in calcareous and acidic pastures. In agreement with this,

AUSTIN et al. (1981) found that soil differences can modify the type of response of the community to environmental changes.

Since RAUNKIAER (1934) first proposed that the location of a plants' renewal buds (as differentiated in various life-forms) expresses plants' adaptations to the unfavourable season for plant life, the biological spectrum of the vegetation and local climate have repeatedly been linked in the vegetational literature. The extent of this linkage is so strong that many authors assume that biological spectra are predictive attributes from which local climates can be deducted (see for example HALLOY 1983). Our observations suggest that the life-form categories we considered may also be used as predictive attributes of communities' ecological properties. In particular, as each community type exhibited similar life-form profile in the two years (Table 4), and this occurred despite the strong interannual compositional changes experienced by all the communities. Taking into account the marked interannual variation of the precipitation, and that community types differed in habitat characteristics, this suggests that the life-form categories we considered vary with environmental factors operating at the habitat scale. Moreover, this suggests that the percentage of species and percentage cover contributed by each life-form to a community can be used as predictive attributes of local environmental characteristics.

A detailed inspection of the data revealed that, virtually, all the colonisations and extinctions occurred at each site in the transition from the dry to normal year affected rare species (those having an abundance <10%). This is not surprising, since it is more likely to find a greater species turnover within rare than within common species (MAY 1973; HUBBEL 1979). On the other hand, this indicates that the invariability of the life-form spectra arose from both a low species turnover within the common species, and from a trade-off in which the loss of some rare species from particular life-forms in the normal year, was compensated by the recruitment of other species belonging to the same life-forms (cf. COLLINS et al. 1987).

The dynamics of the rare species could be associated to direct habitat effects, but also to the invariability exhibited by the common species, particularly if these species were stable enough as to keep similar abundance in both years. If this was the case, the basic structure of the communities would remain stable over time, thus maintaining analogous functional and/or structural limitations for species colonisation in both years. On average, only 6.5% (± 0.4 S.E.) of the species present in the communities exhibited a relative abundance value of >10%, but notably these species contributed 59% (± 2.7 S.E.) of the biomass. Such characteristics were general properties of the communities analysed here, since there were no significant differences among communities, nor between years in these respects. According to previous analyses (RODRÍGUEZ & GÓMEZ-SAL 1994), in 8 out of the 19 sites there were no abundant species changing significantly ($P < 0.050$) their relative abundance from one year to another, and only 4 sites exhibited 1 abundant species showing a variation of its relative abundance of 20–44%. Indeed, this reduced variability of common species suggests that they create an invariant structure in the communities (GRUBB 1986), which seems to be in equilibrium with local conditions, and with general climatic characteristics of the study area. Moreover, the maintenance of similar basic structural features within each community in both years supports the suggestion that common species contributed for the stability of the life-form spectra.

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