

The vertical distribution of below-ground biomass in grassland communities in relation to grazing regime and habitat characteristics

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Abstract. 40 sites, representing different pasture types in Northwest Spain, were sampled in respect of their floristic composition, distribution of above and below-ground biomass and environmental and physical variables. Five plant community types were identified by classification techniques of plant species composition. These communities were then characterized in terms of the percentage of ground covered by herbaceous and shrub vegetation, stones, rocks and gaps as well as their topographic location and characteristics of the shallow soil (pH, organic matter, nitrogen and calcium content). Biomass was assessed in terms of above-ground structures, surface crowns and three below-ground layers to a depth of 10 cm. Three types of grazing regime were distinguished: Concentrated Intense Grazing in early spring (CIG), Extended Intense Grazing throughout the spring (EIG), and Non-Intense Grazing (NIG). Grazing regime showed the highest association with plant community type and three broad categories were identified: xeric stressed pastures, which nevertheless received CIG, mesic pastures with EIG, and three kinds of NIG mesic pastures.

The xeric communities had the highest proportion of above-ground biomass, as a consequence of their greater proportion of woody perennials. These xeric communities displayed a more gradual reduction in below-ground biomass with depth than mesic pastures, a likely consequence of the low water content in the upper soil layers. The mesic communities had a high concentration of below-ground biomass in the upper layers when they were intensely grazed. However, when grazing was low (i.e. NIG situations), these communities had greater variability in biomass profiles than any of the other pasture types. Possible causes of the patterns in biomass distribution of the intensely grazed pastures are discussed.

Keywords: Community structure; Correspondence Analysis; Grazing intensity; Plant root; TWINSpan.

Abbreviations: CIG = Concentrated Intense Grazing in early spring; EIG = Extended Intense Grazing throughout the spring; NIG = Non-Intense Grazing.

Nomenclature: Tutin et al. (1964-1980).

Introduction

The structure of grazed plant communities depends on the interaction of many factors, including climate, soil type, water and nutrient availability and grazing intensity (e.g. Chapin et al. 1987). Despite this multiplicity of sources of variation, the plant root/shoot ratio may be highly predictable under a great variety of external conditions (e.g. Crawley 1983). Brouwer (1983) claims that plants concentrate their growth in parts of their anatomy whose function is most constrained by the environment. Thus, "when growth is limited by an essential substance to be absorbed by the roots, root growth is relatively favoured; when the limiting factor has to be absorbed by the shoot, growth of above-ground parts is relatively favoured". Similarly, "disturbance of the root/shoot ratio that exists in any condition, either by root cutting or by defoliation, leads to such changes in the growth pattern that the original ratio is restored rapidly". Although some exceptions have been reported (e.g. Coughenour et al. 1985), these appear to be general rules governing plant growth partitioning in many species (Chapin et al. 1987). One can therefore predict that stress (or disturbance) will affect species similarly and will lead to consistent plant developmental responses at the community level. From a structural stand point, this implies that the greater the stress or disturbance (as long as certain limits are not exceeded), the greater will be the uniformity of the distribution of the biomass in the community. In accordance with this, Milchunas & Lauenroth (1989) found that long-term heavy cattle grazing of short-grass steppe pastures of North America had a large influence on the horizontal distribution of all vertical components of the plant community. These communities showed a more uniform horizontal distribution of above- and below-ground biomass than did non-grazed communities in adjacent similar habitats.

This study aims to assess the effects of grazing and

habitat characteristics upon the spatial distribution of below-ground biomass at the community level. With the exception of the work of Milchunas & Lauenroth (1989), this has not been addressed. We therefore analyse the vertical distribution of the below-ground biomass in two types of communities, namely mesic and xeric pastures, subjected to different grazing regimes. We hypothesize that, within each of these communities, those pastures growing in similar habitats, i.e. with analogous environmental constraints, will show a more consistent below-ground structure if they are intensely grazed than lightly grazed. This would be the result of the altered below-ground morphology of the intensely grazed plants, which may have greater implications for plant-plant interactions than above-ground structure, because the majority of plant biomass in many pastures is below-ground (Milchunas & Lauenroth 1989). On the other hand, we predict different patterns between the two community types, since in xeric pastures plant growth will be limited by water stress as well as by grazing.

Material and Methods

Study area

The study area covers 3000 ha in the Reyero Valley in the Cantabrian Mountains in North West Spain. The altitude varies from 1000 m to 1900 m, and the climate is transitional between Mediterranean-continental and Atlantic. Mean annual precipitation is 1220 mm. The mean minimum and maximum temperatures range from -2.9 to 27.8°C with extremes of -10.8 and 32.4°C , respectively. The area is geologically diverse, varying from massive limestone and other calcareous conglomerates to sandstone or quartzite. The valley floors and lower slopes are of alluvial and colluvial material. The vegetation has characteristics associated with both types of climate, and varies according to altitude and exposure. Although the climate would categorize the pastures as subhumid (Milchunas et al. 1988), the great variability in aspect, altitude and soils generates such a wide variety of microclimatic conditions that some pastures (e.g. south facing slopes on limestone) resemble semi-arid communities. This area was selected for the study because of its unusual diversity of vegetation types and because the history of land use was well documented (e.g. Martín-Galindo 1987; Gómez-Sal et al. 1993).

Most of the pastures had been cultivated and ploughed until ca. 40 yr ago. This, together with the steeper slopes characteristic of mountain environments, have contributed to the development of shallow soils seldom in excess of 15 cm. The pastures are now used for live-

stock, mainly dairy cows, but some zones are also grazed by sheep or goats (ca. 5% of the area). The populations of wild herbivores, such as Chamois (*Rupicapra rupicapra*) and Roe deer (*Capreolus capreolus*), are not important in these pastures because they normally occur at higher elevations. The timing and intensity of cattle grazing is determined by plant phenology, which differs markedly according to aspect and soil type. Grazing begins on the calcareous south-facing slopes in early spring. These pastures have low yields because they rapidly become dry; but, nevertheless, are intensely grazed in early spring. Subsequently, grazing is moved to pastures on other aspects and only reaches the coolest northerly slopes in mid summer, which consequently receive far lower grazing pressure, particularly in wet seasons when cattle are allowed to spend more time on better pastures. Grazing intensity also depends on the ownership of the pastures. Privately owned lands are carefully and intensely grazed under the direct control of the farmers. Communal grazing lands, owned jointly by all the village farmers, are more variable and when access is difficult may be neglected for long periods.

Sampling

Our aim was to sample a variety of pasture types subjected to different grazing conditions. The influence of altitude was reduced by restricting the sampling between 1150 and 1400 m, as the vertical distribution of below-ground biomass is known to vary with altitude (see Körner & Renhardt 1987 and references therein). A stratified sampling programme was adopted, based on parent material, aspect and broad vegetation type (e.g. meadow, pasture, scrub and forest). These were identified by means of published lithological and topographical maps and aerial photographs.

Sampling was performed in 1987, a relatively wet year with a precipitation of 397 mm between March and July, whereas the 30 yr average rainfall for this period is 280 mm. Sampling took place between mid June and late July, coinciding with the end of the growing season and after grazing was finished. There were 40 pastures, each with a station of $10\text{ m} \times 10\text{ m}$. For the classification of plant communities, data were collected using four $50\text{ cm} \times 50\text{ cm}$ quadrats placed at random at each station. The aerial percentage cover of all angiosperm species was visually estimated. Species present, but not sampled by the quadrats, were arbitrarily assigned a cover value of 1%. For biomass estimates, at each station, four randomly-positioned soil blocks with a surface area of $20\text{ cm} \times 20\text{ cm}$ were removed together with the above-ground vegetation to a depth of 10 cm, depending on the depth of the soil. The blocks were cut with metal blades,

separated from the surrounding soil and placed in a layered frame for transportation to the laboratory. The soil blocks were sliced into five layers, namely above-ground biomass (a), crowns (c) and below-ground material at depths of >1-4, >4-7 and >7-10 cm (d1, d2 and d3, respectively). The soil layers were washed and the plant material was collected in a 0.5 mm mesh sieve. All components of the above- and below-ground plant material were dried to constant weight in a drying oven at 60°C, and then weighed. Consistent with many other studies, ash corrections were not undertaken, since preliminary biomass assessments in 1986 revealed that the nature of the soil made soil washing very effective at removing mineral fragments. A maximum depth of 10 cm was selected for the investigation of below-ground structures, since a very high proportion of biomass is concentrated in this zone which also represented the maximum soil depth in many pastures. Detached roots below this depth were negligible.

In addition to vegetational aspects, major physical and structural characteristics of the stations were noted: altitude, aspect, slope, topographic position, parent material type, apparent soil moisture (four subjective categories) and percentage of soil surface covered by herbaceous plants, shrubs, gaps, small stones and rocks. Each site was also assigned to a category of grazing regime. We differentiated three types of grazing using a nominal scale: Concentrated Intense Grazing in early spring (CIG), Extended Intense Grazing throughout the spring (EIG), and Non-Intense Grazing (NIG). These categories were established from direct observations and information provided by farmers. Finally, at each of the 40 sites, four soil subsamples were taken to a depth of 10 cm and after plant material had been 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 phosphorus, and exchangeable potassium and calcium. Exchangeable potassium and calcium were extracted with NH_4OAc , 1.0 mol/l (pH = 7) and their concentration determined by atomic absorption spectrophotometry. Available phosphorus was extracted with NH_4F , 0.03 mol/l plus HCl, 0.025 mol/l and its concentration determined colorimetrically (Olsen & Sommers 1982). Organic carbon concentration was determined by the Walkley-Black procedure (Nelson & Sommers 1982), and converted to organic matter concentration by multiplying by the conventional factor of 1.724. Total nitrogen was measured using a macro-Kjeldahl procedure (Bremner & Mulvaney 1982). Soil pH was measured with a pH-meter in soil saturated with water.

Data analysis

The identification of community types was carried out using TWINSpan (Hill 1979), based on estimates of aerial percentage cover of the angiosperm species present in at least 10% of the samples. These data were sorted according to categories (>0-1, >1-5, >5-10, >10-20, >20% cover) for each species. Differences between community types in quantitative soil variables were analysed by one-way ANOVA. To increase the homoscedasticity of variances, all proportional data were angularly transformed, and absolute data, except pH, were logarithmically transformed prior to analysis. Association of community types with qualitative environmental factors was examined by constructing all possible two-way contingency tables. These tables were tested for significance with Chi-square, applying the Yates' correction (Zar 1984). The degree of association between community types and environmental factors was also assessed by the Information Index $I(X,Y)$ (e.g. Abramson 1966). To make all the indices comparable, each was divided by its maximum value (I_{max}). This limits the range of $I(X,Y)$ from 0 to 1, where 0 indicates complete independence.

Analyses of the associations between community types and environmental factors are insufficient to describe overall, multivariate patterns of variation. To examine this, Correspondence Analysis was performed over the contingency matrix of species by classes of environmental variables. In the resulting ordination, the area corresponding to each community type was delimited by the position of its characteristic plant species. This method is appropriate to look for broad correlations between groups of environmental variables and groups of species (Montaña & Greig-Smith 1990).

Differences between the average vertical biomass profiles of the community types were assessed by multivariate analysis of variance (MANOVA) and Chi-square goodness of fit. One-way ANOVA was also used to determine differences between community types in above-ground biomass, total non-aerial biomass and the allocation of non-aerial biomass to the crown and below-ground layers. Proportional data were again angularly transformed. In all the ANOVA analyses, differences between means were compared by the HSD test for unequal sample sizes (Spjøtvoll & Stoline test; see Sokal & Rohlf 1981).

Biomass profiles of the 40 stations were also subjected to TWINSpan analysis, based on the proportion of non-aerial biomass corresponding to crown and root biomass (i.e. c, d1, d2 and d3). These data were sorted according to categories >0-5, 5-10, 10-15, 15-20, 20-30, 30-40, 40-50, 50-60, >60% biomass. The association of the profile types identified by this analysis

and the community types was established by means of Chi-square. Above-ground biomass was excluded from this analysis, to avoid confounding the effects of removal of the current-year's above-ground structures and the long-term effects of grazing on non-aerial biomass.

Results

Community types and their relation to grazing and environment

Through TWINSpan we identified five community types (Table 1). Grazing regime showed the greatest significant association with community type (Table 2). In addition, community type was also highly associated with percentage cover of herbaceous vegetation and of small stones on soil surface. Among the remaining variables, slope, topographic position, soil moisture and percentage cover of shrubs, gaps, and rocks were also significant, but not as strongly.

The community types differed significantly in chemical and organic soil characteristics, particularly in terms of pH, and content of calcium, nitrogen and organic matter ($F_{4,35} = 12.7$, $P < 0.0001$; $F_{4,35} = 5.1$, $P < 0.008$; $F_{4,35} = 3.5$, $P < 0.02$; $F_{4,35} = 3.3$, $P < 0.03$, respectively), but not in available phosphorus, potassium and carbon/nitrogen ratio (Table 3). Community types A, B and C had nearly neutral soils, whereas those of D and E were significantly more acidic. The soil calcium content was significantly greater in community type A than in D and E, whereas B and C showed intermediate values. In addition, the poorest and richest soils in terms of nitrogen and organic matter were shown by community types C and E, respectively, which were significantly different in each case.

Fig. 1 shows the results of the ordination of species and environmental variables. Axis 1 contrasts community types A and C, both of which are separated from community E by axis 2. Community types B and D occupy intermediate positions. Community type A is characterized by intense grazing levels concentrated in early spring (CIG), i.e. in the short period when the xeric pastures reach their peak production. This type of community occurred on shallow, lithic soils, generally on limestone or calcareous matrix conglomerates, with neutral pH, low edaphic moisture, and plant cover generally below 60%. Characteristic species of this community type are *Helianthemum canum*, *Lithodora diffusa*, *Teucrium chamaedrys* (woody chamaephytes), *Koeleria vallesiana*, *Festuca hystrix* (perennial caespitose grasses), *Anthyllis vulneraria*, *Asperula cynanchica* (perennial forbs), *Xeranthemum inapertum* and *Bupleurum baldense* (annuals). Community type B was found on slopes and

Table 1. Summary of the TWINSpan analysis of the floristic data, with abbreviations of the species names. All species present in at least four stations (a total of 122) were included, although only those giving a good discrimination between communities are cited. For each species, the number of stations in which it appeared in each community type (value to left of hyphen) and its average relative cover in these stations (value to right of hyphen) are shown. The latter is indicated by 1 to 5, corresponding to the categories of percent cover: > 0-1, > 1-5, > 5-10, > 10-20, > 20%.

Community type		A	B	C	D	E
Number of stations		8	5	13	5	9
<i>Seseli libanotis</i>	SESE LIB	1-2		8-2		
<i>Cytisus scoparius</i>	CYTI SCO		1-1		4-2	
<i>Dactylis glomerata</i>	DACT GLO		2-2	10-2	2-1	1-1
<i>Eryngium campestre</i>	ERYN CAM		1-2	7-2		
<i>Malva moschata</i>	MALV MOS			5-1	2-2	
<i>Poa compressa</i>	POA COM			5-2		
<i>Trifolium striatum</i>	TRIF STR	1-1	4-2	8-3	4-2	
<i>Cynosurus cristatus</i>	CYNO CRI		3-2	12-3	1-1	3-2
<i>Phleum pratense</i>	PHLE PRA		2-2	12-2	2-2	4-3
<i>Trifolium repens</i>	TRIF REP		1-2	9-4	1-2	3-3
<i>T. pratense</i>	TRIF PRA		1-2	12-4	1-2	8-3
<i>Agrostis capillaris</i>	AGRO CAP	1-2	4-3	11-4	5-5	8-4
<i>Calluna vulgaris</i>	CALL VUL		2-1			5-2
<i>Galium pinetorum</i>	GALI PIN					4-2
<i>Lathyrus pratensis</i>	LATH PRA		1-1			3-3
<i>Digitalis parviflora</i>	DIGI PAR				1-2	3-2
<i>Leontodon hispidus</i>	LEON HIS					4-2
<i>Nardus stricta</i>	NARD STR			1-2	1-2	6-5
<i>Cerastium fontanum</i>	CERA FON	1-1		1-1	1-1	4-2
<i>Deschampsia caespitosa</i>	DESC CAE		1-1			3-4
<i>Chamaespartium sagittale</i>	CHAM SAG	1-2	1-1	1-1	1-3	5-4
<i>Thymus pulegioides</i>	THYM PUL	1-2	2-2	2-3	2-2	7-2
<i>Avenula marginata</i>	AVEN MAR	2-2	1-1	3-2	3-2	8-3
<i>Briza media</i>	BRIZ MED	1-4	1-2	4-2		8-3
<i>Rosa canina</i>	ROSA CAN	1-2	2-1	4-2	1-1	2-3
<i>Festuca gr. ovina</i>	FEST OVI	4-2	5-4	4-2	4-4	
<i>Cytisus purgans</i>	CYTI PUR	1-3				4-2
<i>Leontodon taraxacoides</i>	LEON TAR	3-2	2-3	1-1		
<i>Potentilla tabernaemontani</i>	POTE TAB	7-2	4-3	2-2	3-2	
<i>Helianthemum nummularium</i>	HELI NUM		2-2			3-2
<i>Primula veris</i>	PRIM VER	2-2	1-1			3-2
<i>Bromus erectus</i>	BROM ERE	8-3	4-3	2-2		
<i>Lithodora diffusa</i>	LITH DIF	6-2	1-2		1-3	2-2
<i>Filago pyramidata</i>	FILA PYR	3-2	1-2	2-2		
<i>Crucianella angustifolia</i>	CRUC AGU	2-3	2-2			
<i>Helianthemum croceum</i>	HELI CRO	4-2	3-3			
<i>Avenula bromoides</i>	AVEN BRO	6-2	4-2			
<i>Anthyllis vulneraria</i>	ANTH VUL	8-2	3-2	1-2		
<i>Asperula cynanchica</i>	ASPE CYN	5-2				
<i>Bupleurum baldense</i>	BUPL BAL	5-2	2-1			
<i>Festuca hystrix</i>	FEST HYS	5-3				
<i>Galium mollugo</i>	GALI MOL	5-2	2-1	1-1	1-1	1-2
<i>Helianthemum canum</i>	HELI CAN	8-4				
<i>Koeleria vallesiana</i>	KOEL VAL	8-4	2-4			
<i>Pimpinella tragium</i>	PIMP TRA	5-2	1-1			
<i>Silene legionensis</i>	SILE LEG	3-2	2-2			
<i>Teucrium chamaedrys</i>	TEUC CHA	6-2	1-2			
<i>T. pyrenaicum</i>	TEUC PYR	3-2	1-1			
<i>Thymus mastigophorus</i>	THYM MAS	4-4	2-1			
<i>Sedum forsteranum</i>	SEDU FOR	3-1				1-1
<i>Xeranthemum inapertum</i>	XERA INA	5-2				

more distant communal pastures, with less intense grazing (NIG). Stations characteristic of this type had parent material and aspect similar to type A, although the environment was less harsh with higher humidity, deeper soil and more scrub. Thus, the characteristic species of community type B were a mixture of species commonly present in xeric (*Festuca gr. ovina*, *Avenula bromoides*,

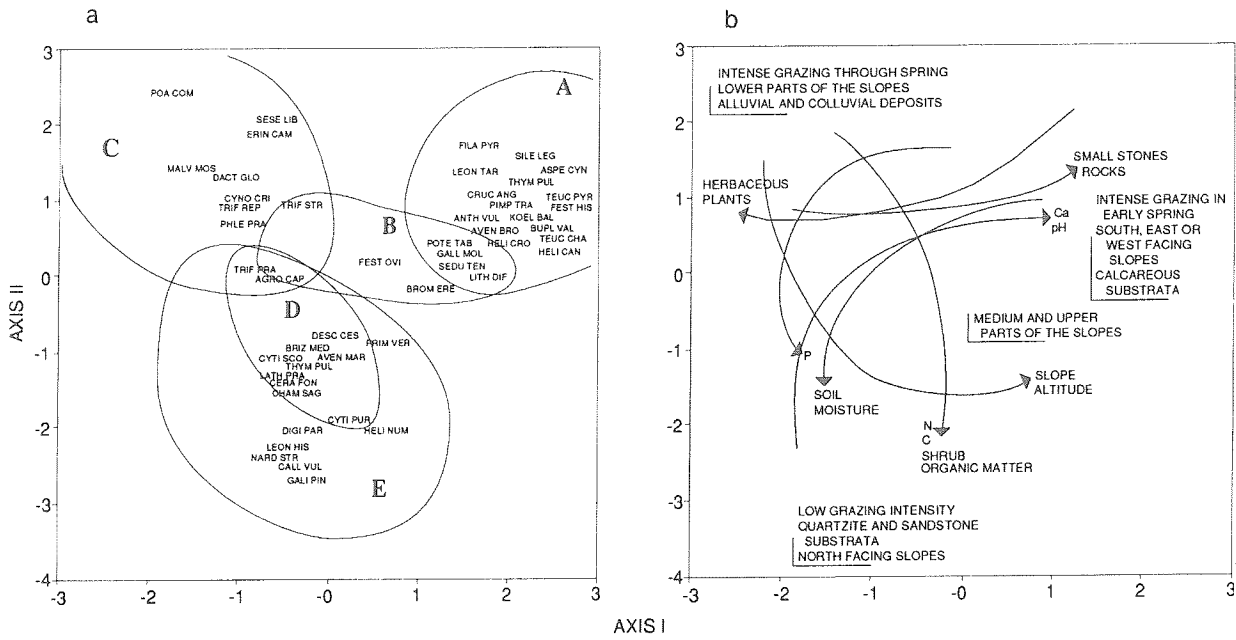


Fig. 1. Ordination of species and classes of the variables. Figs. **a** and **b** are given separately to facilitate interpretation, but may be directly superimposed. Axes I and II account for the 36% and 14% of the variance, respectively. **a.** The areas corresponding to each community type were identified according to the positions of their characteristic species. Of the 122 species included in the analysis, only those differentiating the communities are included. Abbreviations correspond to the names of the species given in Table 1. **b.** Position of the qualitative variables indicated by \square . Ordinal variables indicated by arrowed lines, showing directional gradients (increase in values). The arrows were drawn by connecting the positions of the states of the ordinal variables in the plane.

Bromus erectus, *Potentilla tabernaemontani*) and mesic pastures (*Trifolium striatum*, *Agrostis capillaris*; see Table 1). Type C communities were mesic pastures which supported the highest grazing pressure, evenly

extended throughout the spring (EIG), and represented most of the privately owned pastures sampled. This community showed the highest herbaceous cover and occurred on alluvial or colluvial material of the lower

Table 2. Association of community type with environmental factors. Pairs of variables marked with asterisks co-vary nonrandomly (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$). The Information Index (I) close to 1 indicates high association. Community types A and C represented CIG and EIG respectively, whereas B, D and E were NIG.

Variables	Community type		
	χ^2 (df)	Significance	I
Habitat characteristics			
Grazing regime	80.0 (8)	***	1.0
Slope	24.6 (12)	*	0.3
Soil moisture	22.5 (12)	*	0.3
Topographic position	21.7 (12)	*	0.3
Parent material type	20.6 (12)	n.s.	0.2
Altitude	18.5 (12)	n.s.	0.2
Structural characteristics (% cover)			
Herbaceous plants	41.0 (12)	***	0.4
Small stones	37.3 (12)	***	0.4
Rocks	30.9 (12)	**	0.4
Gaps	30.8 (16)	*	0.3
Shrubs	25.4 (12)	*	0.2

Table 3. Mean values (± 1 SE) of the quantitative soil variables in the community types. For each variable, community types with different letters are significantly different ($P < 0.05$) as indicated by HSD test for unequal sample sizes.

Variables	Community type				
	A	B	C	D	E
Organic matter (%)	9.0 ^{ab} (1.53)	6.7 ^{ab} (1.2)	5.1 ^b (0.45)	7.0 ^{ab} (0.76)	10.0 ^a (1.45)
Nitrogen (%)	0.45 ^{ab} (0.08)	0.35 ^{ab} (0.06)	0.26 ^b (0.03)	0.33 ^{ab} (0.04)	0.47 ^a (0.06)
Carbon/Nitrogen	12.0 (0.9)	11.6 (0.51)	11.7 (0.39)	12.5 (0.29)	12.0 (0.71)
pH	6.7 ^a (0.08)	6.4 ^a (0.24)	6.1 ^a (0.19)	5.1 ^b (0.16)	5.1 ^b (0.18)
CaO (mg/100g)	330.4 ^a (36.7)	268.6 ^{ab} (37.7)	186.0 ^{abc} (19.0)	104.6 ^c (18.4)	166.1 ^{bc} (31.3)
P ₂ O ₅ (mg/100g)	1.98 (0.37)	1.65 (0.09)	2.25 (0.35)	2.12 (0.23)	3.06 (0.38)
K ₂ O (mg/100g)	31.7 (7.3)	24.3 (6.0)	23.3 (1.1)	23.2 (2.7)	26.8 (3.1)

part of the slopes. The most characteristic species were *Cynosurus cristatus*, *Dactylis glomerata*, *Phleum pratense* and *Trifolium repens*. The stations comprising type D community had uneven use, as in the case of type B. Although the plant species were similar to those of type C, the stations were characterised by a higher abundance of *Agrostis capillaris* and *Cytisus* spp. and *Genista florida* scrub, indicative of a lower grazing pressure. Type E communities included pastures in which grazing was insufficient to make a good use of their usually high yield. These pastures typically are grazed in late spring or early summer, when the others have become too dry. Nevertheless, grazing is often low because cattle are moved to wet hay meadows, previously harvested in late June and then irrigated. The stations of the E community type were found on moist, acidic organic soils. Woody perennials (mainly *Calluna vulgaris* and *Chamaespartium sagittale*) were abundant and, among the herbaceous species, plants with good root development and biomass (*Briza media*, *Avenula marginata*, *Nardus stricta* and *Thymus pulegioides*) were common, as were many species occurring in community types C and D. In general, community types B, C, D and E are mesic pastures, with adequate water supply and soil nutrients. B, D and E are less intensely grazed than type C. They are typically less intensely grazed.

Distribution of biomass in different layers

The community types were quite variable in the proportion of above-ground biomass contributed by the major plant life-forms, namely, perennial grasses (including sedges), perennial forbs (non-graminaceous species) and woody perennials ($F_{4,35} = 2.94$, $P = 0.034$; $F_{4,35} = 4.55$, $P < 0.005$; $F_{4,35} = 8.35$, $P < 0.0001$, respectively). Grasses were dominant in community types D and, particularly, E, while forbs were most abundant in type C (Table 4). Community A was the only type where woody plants made an important contribution to the plant community, accounting for its greater relative accumulation of above-ground biomass. The above-ground/below-ground biomass ratio – i.e. $a / (c+d)$ – of the five community types differed significantly ($F_{4,35} = 2.67$, $P < 0.05$), with community A having the highest relative accumulation of above-ground biomass.

The total non-aerial biomass (i.e. $c + d1 + d2 + d3$), as well as that at each layer of the five community types differed significantly (total: $F_{4,35} = 15.08$, $P < 0.0001$; c: $F_{4,35} = 14.3$, $P < 0.0001$; d1: $F_{4,35} = 6.3$, $P < 0.001$; d2: $F_{4,35} = 8.5$, $P < 0.0001$; d3: $F_{4,35} = 4.2$, $P < 0.01$). The HSD test indicated that community E, on moister, acidic more organic soils, had significantly higher values of non-aerial biomass, whereas values for A, B, C and D were not significantly different (Table 5). A similar

Table 4. Percentage contribution to vegetation cover (Mean \pm 1 SE) contributed by perennial grasses, perennial forbs and woody perennials in five community types. Conventions as in Table 3.

Life form	Community type				
	A	B	C	D	E
Perennial grasses	33.79 ^b (5.3)	39.14 ^{ab} (3.53)	43.2 ^{ab} (5.52)	56.19 ^{ab} (7.22)	60.19 ^a (6.0)
Perennial forbs	24.17 ^b (4.43)	35.22 ^{ab} (5.46)	45.91 ^a (5.13)	25.92 ^{ab} (4.53)	23.01 ^b (2.82)
Woody perennials	35.91 ^a (5.71)	15.52 ^{ab} (6.22)	3.06 ^b (1.32)	12.08 ^b (5.6)	16.53 ^b (4.36)

pattern emerged for crown biomass, whereas for the three root layers, community E and the intensely grazed type C mesic pastures were the only two which differed significantly, having the highest and lowest biomass values, respectively.

The relative contribution of non-aerial biomass to the various layers is given in Table 6. The proportion of this biomass allocated at crown level ranged from 49-68%, while below-ground structures accounted for 25-31, 6-17 and 1-6%, at d1, d2 and d3 layers, respectively. The differences among community types in terms of vertical non-aerial biomass distribution were highly significant, as indicated by MANOVA analysis (Wilk's Lambda $_{16,98} = 0.3$, $P < 0.0005$). Such differences were mainly due to community type C, since it was the only one that showed an average non-aerial biomass profile significantly different ($P < 0.05$) from those of the other communities when compared by Chi-square. When con-

Table 5. Mean biomass (dry weight g/m², \pm 1 SE) of different vertical layers for the five types of communities. Conventions as in Table 3.

Biomass layer	Community type				
	A	B	C	D	E
Above-ground (a)	310.76 ^{ab} (24.99)	264.3 ^b (71.47)	263.5 ^b (20.27)	311.85 ^{ab} (49.16)	532.72 ^a (78.83)
Crowns (c)	254.27 ^b (27.99)	243.88 ^b (36.0)	365.94 ^b (22.76)	371.04 ^b (29.97)	614.6 ^a (55.15)
Below-ground >1 - 4 cm (d1)	130.7 ^{ab} (29.35)	165.66 ^{ab} (34.09)	131.6 ^b (8.72)	205.55 ^{ab} (34.19)	294.66 ^a (37.39)
Below-ground >4 - 7 cm (d2)	75.78 ^{ab} (14.25)	93.61 ^{ab} (36.25)	34.25 ^b (4.06)	80.69 ^{ab} (15.88)	202.94 ^a (36.21)
Below-ground >7 - 10 cm (d3)	26.05 ^{ab} (3.03)	24.6 ^{ab} (10.87)	5.14 ^b (1.14)	37.58 ^{ab} (12.76)	40.22 ^a (9.61)
Non-aerial biomass (c + d1 + d2 + d3)	486.79 ^b (70.48)	527.75 ^b (91.0)	536.93 ^b (29.96)	688.85 ^b (77.3)	1152.42 ^a (95.19)

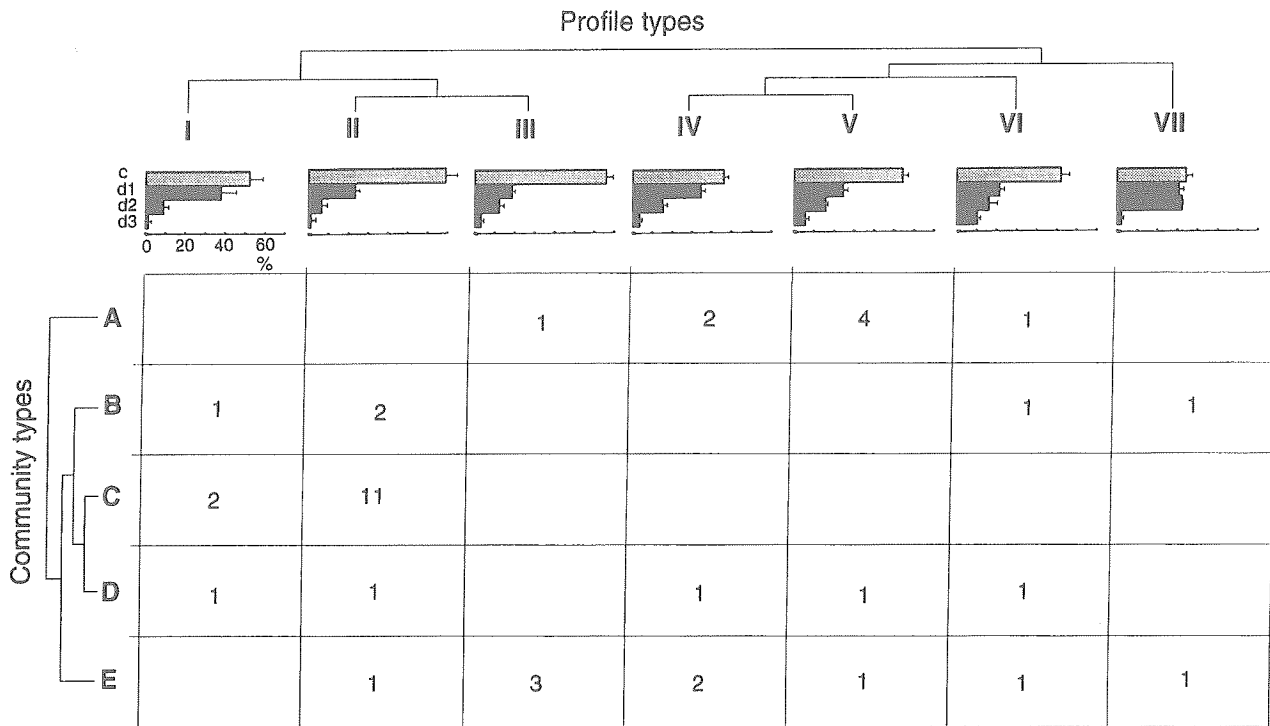


Fig. 2. Summary of the types of vertical biomass profiles (I - VII) in community types A - E. The types of vertical profiles were established by TWINSPLAN analysis, using the percentage of non-aerial biomass allocated to crowns and the three below-ground layers, i.e. c, d1, d2 and d3.

sidering each layer individually, one-way ANOVA showed that the contribution of root biomass at layer d1 did not differ significantly between communities, whereas that corresponding to crowns and roots at d2 and d3 did (c: $F_{4,35} = 6.40, P < 0.0006$; d2: $F_{4,35} = 8.38, P < 0.00001$; d3: $F_{4,35} = 6.22, P < 0.0007$, respectively). According to the HSD test, the greatest differences between communities occurred at the crown level, where community C showed significantly higher values than A, B and E. There were no differences in d1, while in d2,

the proportion of biomass in community C was significantly lower than in communities A and E, and in d3 it was smaller than A.

Biomass profiles in the different communities

TWINSPLAN analysis of the biomass profile data (Table 7) revealed seven profile types (I - VII). From this, it was possible to relate these to the five community types (Fig. 2), since both classifications were significantly associated ($\chi^2_{24} = 43.3, P < 0.01$). Generally, the grazed communities (C, A) were less variable in their below-ground profiles than those with lower levels of grazing (B, D, E). Stations representing intensely grazed mesic communities (C) were characterized by highly consistent profiles, mainly Type II ($\chi^2_1 = 23.8, P < 0.0001$), in which crowns accounted for $\geq 60\%$ of the non-aerial biomass, while biomass below 7 cm was negligible. Intensely grazed xeric pastures (A) were mainly concentrated in the profiles IV-VI (see Fig. 2), showing significant association with Type V ($\chi^2_1 = 9.6, P < 0.002$). In these profiles, the decrease of below-ground biomass with depth was more gradual than in profile Type II, characteristic of intensely grazed mesic pastures. In contrast, the less intensely grazed commu-

Table 6. Proportion of biomass (Mean \pm 1 SE) allocated to the below-ground layers. Conventions as in Table 3.

Biomass layer	Community type				
	A	B	C	D	E
Crowns (c)	54.1 ^b (2.46)	49.37 ^b (4.82)	68.25 ^a (1.94)	55.43 ^{ab} (3.26)	54.33 ^b (3.41)
Below-ground > 1 - 4 cm (d1)	25.09 (2.13)	30.72 (4.39)	24.62 (1.27)	28.99 (1.99)	25.15 (2.24)
Below-ground > 4 - 7 cm (d2)	15.03 ^a (0.71)	15.16 ^{ab} (4.22)	6.19 ^b (0.7)	11.07 ^{ab} (1.75)	17.07 ^a (2.12)
Below-ground (d3) > 7 - 10 cm	5.79 ^a (0.83)	4.75 ^{ab} (1.58)	0.94 ^b (0.21)	4.51 ^{ab} (2.0)	3.45 ^{ab} (0.8)

Table 7. Percentages of non-aerial biomass allocated to surface crowns and three below-ground layers (i.e. c, d1, d2 and d3) at the 40 sites. TWINSpan analysis was applied over these data yielding seven types of vertical biomass profiles. The sites are arranged according to profile types, and the community types to which they belong are also indicated.

Site	Profile type	Community type	Non-aerial biomass layers (%)			
			c	d1	d2	d3
6	I	B	44.5	48.7	6.5	0.3
26	I	C	49.1	35.9	11.9	3.1
21	I	C	59.8	32.6	6.4	1.2
31	I	D	54.7	34.5	10.3	0.5
17	II	B	59.0	27.7	10.7	2.5
35	II	B	62.2	21.2	8.1	8.5
20	II	C	66.0	25.6	7.4	1.0
30	II	C	66.2	25.2	7.1	1.5
5	II	C	67.8	25.8	6.3	0.2
19	II	C	69.8	24.8	4.7	0.8
12	II	C	70.2	22.5	7.0	0.3
40	II	C	70.5	22.6	6.1	0.8
15	II	C	70.7	20.9	7.9	0.6
32	II	C	71.2	22.9	4.5	1.4
34	II	C	72.7	19.9	6.4	0.9
16	II	C	75.3	19.5	4.8	0.3
22	II	C	77.8	22.0	0.1	0.1
11	II	D	69.7	25.5	4.4	0.5
25	II	E	60.0	25.7	13.5	0.8
14	III	A	66.2	18.3	11.7	3.8
9	III	E	63.1	19.9	15.3	1.7
27	III	E	63.3	20.0	12.4	4.3
8	III	E	70.4	16.4	9.9	3.2
2	IV	A	43.5	35.6	16.7	4.3
28	IV	A	45.9	33.0	17.9	3.2
10	IV	D	49.9	34.2	11.8	4.2
1	IV	E	43.7	38.2	16.1	2.0
7	IV	E	47.3	32.9	14.9	4.9
24	V	A	51.3	25.3	16.0	7.5
37	V	A	53.6	21.7	16.6	8.0
3	V	A	53.8	27.0	14.7	4.5
39	V	A	59.9	21.4	14.0	4.8
18	V	D	51.9	26.9	16.6	4.7
33	V	E	54.9	24.2	17.0	3.9
4	VI	A	58.6	18.4	12.7	10.3
38	VI	B	49.0	23.3	18.3	9.4
36	VI	D	51.1	24.0	12.2	12.8
29	VI	E	49.4	19.9	21.6	9.0
23	VII	B	32.1	32.6	32.2	3.1
13	VII	E	36.8	29.1	32.9	1.2

ities B, D and E displayed a far larger spectrum of profile types.

Discussion

The study of the biomass distribution enables us to look for differences between community types and for consistent patterns within communities. Community C was found to be significantly different from other community types in that most of the non-aerial biomass was concentrated in the surface crowns. Furthermore, pastures

representing this community and community type A had consistent patterns of biomass distribution, whereas those belonging to B, D and E were far more variable. There are several factors which can explain these trends, of which grazing is undoubtedly of key importance, since consistent patterns of biomass distribution have only been found in community types receiving some form of intense grazing (i.e. CIG in A and EIG in C). Nevertheless, the occurrence of consistent biomass profiles within two very contrasting community types suggests the existence of other mechanisms which could determine the vertical distribution of the biomass. In the following, we discuss these taking into account previous work and current theories on the effects of disturbance and stress on plant community structure.

Grazing and below-ground biomass distribution in mesic communities

Grazing may determine the vertical distribution of the plant community biomass through several mechanisms. Firstly, the below-ground biomass patterns observed in the intensely grazed mesic communities could be the consequence of low rates of root growth and the high proportion of roots that die and are not replaced. Whenever intense defoliation occurs, plants lose photosynthetic area, at least in the short term. This usually leads to an increase in their investment of nonstructural carbohydrates to green leaf production. In some cases, it has been reported that defoliation also increases nutrient uptake (e.g. Ruess et al. 1983; McNaughton & Chapin 1985). This is associated with an extra investment in production of photosynthetic area. According to Ruess et al. (1983 and references therein), photosynthesis rather than stored root reserves supplies the substrate necessary for root respiration, which is the principal source of energy for nutrient absorption (but see Oesterheld & McNaughton 1988). From this, it follows that root growth tends to decrease after defoliation (but see Coughenour et al. 1985, for an exception). Both the decrease in root growth and an overall decrease in root number due to a reduction in their turnover would explain the concentration of subterranean biomass towards the soil surface shown by the intensely grazed mesic communities (type C).

Secondly, Dickinson & Polwart (1982) observed that intense mowing increased investment in grassland below-ground reserves, while the reduction of mowing frequency increased above-ground production by depleting below-ground reserves. They concluded that reserve organs would provide resilience to mowing or grazing. These observations are consistent with the highest proportion of crown biomass (i.e. the plant's perennating organs) being shown by the intensely grazed

mesic communities. Hence, concentration of the non-aerial biomass at the soil surface could be associated with a high investment in reserve organs to enhance their chance of persistence.

Thirdly, the below-ground biomass pattern of the intensely grazed mesic pastures could be associated with the concentration of nutrients on the soil surface, as a result of cattle dung and urine. Since the soils of these pastures are poor in nitrogen and organic matter (Table 3), plants are likely to be particularly dependent on these additional nutrients and would therefore allocate more roots towards the soil surface.

Finally, the rare occurrence of profiles characteristic of intensely grazed areas in other less intensely grazed communities may be also related to grazing. For example, in these situations it would be possible for small areas to be heavily grazed, within an otherwise non intensely grazed area. It is probably this 'mosaic' effect of grazing intensity which gives rise to the greater heterogeneity in biomass profiles seen in the non-intensely grazed communities.

Xeric pastures

The different profiles found in intensely grazed mesic and xeric pastures suggest that the influence of grazing on the subterranean structure of the community may be different depending on the constraints of the environment. The high abundance of woody perennials in xeric communities (36% of the vegetation) may explain both the accumulation of above-ground biomass observed in these communities, and the more gradual diminution of their below-ground biomass with depth. Woody plants are characterized by secondary growth and by the continuous conversion of structural tissue into non-living biomass, which remains an integral part of the individual (Schulze 1983; Klepper 1991). Above-ground, this woody biomass can confer some protection to the plant from grazing (see Coley et al. 1985). Below-ground, this biomass allows the development of robust tap roots, capable of reaching the deeper and wetter horizons of the soil (see Crick & Grime 1987; Grime 1991). The contribution of these roots to the deep below-ground biomass of the community accounts for the greater proportion of biomass at deeper levels in the xeric pastures than in the intensely grazed mesic pastures.

Implications for plant-plant interactions

Grazing results in both injury to individual plants and changes in community physiognomy. The effects of grazing upon community structure are better known above-ground than below-ground. In general, plant developmental responses to grazing lead to a concentra-

tion of above-ground biomass in a small volume near the soil surface (Stobbs 1973), which serves as a spatial refuge inaccessible to grazers (McNaughton 1984). When grazing pressure is moderate or low, pasture communities are often a mosaic of short, heavily grazed patches and taller, lightly grazed areas (Bakker et al. 1983). The greater the grazing intensity, the greater the area of the short grazed patches, and, in consequence, the greater will be the uniformity of the horizontal distribution of the above-ground biomass (barring damage by other herbivore activities). The tendency to maximize occupation of the horizontal aerial space leads to important changes in above-ground plant-plant interactions (see Milchunas et al. 1988). However, herbivore-induced changes on below-ground physiognomy of the community may have even more important effects on plant-plant relationships, especially as the majority of plant biomass is commonly below-ground (Sims & Singh 1978; Leatham & Milchunas 1985). Our data indicate that intense grazing can have significant effects on the distribution of subterranean biomass. Here, we specifically focus on the vertical distribution of biomass. However, the uniformity in the vertical distribution of this biomass in intensely grazed pastures suggests that grazing can impose greater horizontal uniformity as well, as has been found by Milchunas & Lauenroth (1989) in semi-arid grassland communities of the United States. According to these authors, the more uniform the distribution of crown and root biomass in the soil, the greater the extent of soil exploitation which results in reduced opportunities for seedling establishment. Our results suggest that this situation may also occur in the intensely grazed pastures we studied, implying low colonization of plant species. In addition, such phenomena can be exaggerated in the intensely grazed mesic pastures (type C), where the biomass showed a clear tendency to accumulate in the surface crowns and therefore favourable locations for establishment would be less likely to occur. This may indeed be an explanation for why species richness was lower in type C grasslands than in other types.

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