

Vertical distribution of below-ground biomass in intensively grazed mesic grasslands

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Abstract. Previous work has shown that below-ground biomass is more concentrated in surface soil layers in intensively grazed mesic grasslands than in moderately grazed grasslands. However, since the mesic grasslands previously studied shared similar compositional traits, the question remained whether grasslands with differing species composition, and intensive defoliation, showed similar biomass distribution patterns. Eight grasslands at four sites distributed along an elevational gradient were investigated. The upper and lower zones of a slope were sampled at each site. Four of these grasslands were grazed by livestock and the other four were grazed and mown. Biomass was divided into above-ground, root crown and three root layers.

Species composition varied according to management and topography. Annuals and perennial forbs had relatively more above-ground biomass at the upper part of the slopes, while perennial grasses dominated the lower parts. The above-ground biomass and root biomass at 4 - 7 cm depth attained maximum values in the lower, potentially more fertile, parts of the slopes. Crown biomass increased with altitude at the upper part of the slopes. Despite their differences in composition and structure, seven out of the eight stands showed a remarkable concentration of the below-ground biomass near the soil surface, which decreased drastically with soil depth. This pattern is similar to that observed in the intensively grazed mesic communities studied earlier. This similarity was more evident in the more mesic-like grasslands, since it increased from the upper, potentially drier parts of the slopes, to the lower parts, and, when each topographic position was considered separately, from low to high elevation.

Keywords: Community structure; Herbivory; Pasture; Plant root.

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

Introduction

Grazing can cause injury to individual plants and alter community structure. Functional implications of grazing for plant-plant relationships are better known above-ground, where they are related to the effects of

canopy structure on the light regime (e.g. Crawley 1983). However, the altered below-ground morphology of grazed plants may have greater implications for plant-plant interactions (Milchunas & Lauenroth 1989) because the greater proportion of the grassland's biomass is often below-ground (Sims & Singh 1978a; Dickinson & Polwart 1982; Leetham & Milchunas 1985; Titlyanova et al. 1988; van der Maarel & Titlyanova 1989). Milchunas & Lauenroth (1989) hypothesized that grazing may increase below-ground plant-plant interactions through its effects upon the spatial distribution of root biomass.

Rodríguez et al. (1995) found that livestock grazing can be important in determining the spatial distribution of the subterranean biomass of pasture communities. They found that intensively grazed mesic communities had a majority of root biomass concentrated in the uppermost soil layers, while only a small proportion was present below 7 cm soil depth. In contrast, mesic communities not exposed to intensive grazing exhibited a variety of vertical distributions of below-ground biomass, and, in general, had a lesser proportion of roots in the uppermost soil layers. In spite of these differences, Rodríguez et al. (1995) found that both intensively and less intensively grazed communities had similar amounts of total non-aerial biomass. These authors suggested that below-ground plant-plant interactions could be stronger in the intensively grazed mesic situations, since the roots in such communities were confined to a small soil volume near the surface. However, it was not known whether the patterns in vertical distributions of below-ground biomass were due to above-ground herbivore mediated alterations of plant allocation or were related to changes in species composition. In the present study we addressed this question.

Our main aim was to quantify the vertical distribution of below-ground biomass in largely defoliated (grazed or mown) pastures at sites along an elevational gradient of temperature and precipitation. The experimental design ensured that the pasture communities

examined differed in species composition and environmental variables that could have important effects on the vertical distribution of the below-ground biomass. In semi-arid grasslands of North America, Milchunas & Lauenroth (1989) found that grazing had less effect on the amount of crown and root biomass than the difference between topographical positions. On the other hand, plant growth theory predicts that plants growing at high altitudes and in cold habitats allocate greater proportions of photosynthates to below-ground organs than plants in warmer sites (Sims & Singh 1978b; Grime 1979; Schulze 1983; Bloom et al. 1985; but see Körner & Renhardt 1987). This prompted us to examine potential altitude effects on biomass distribution in these grasslands.

Material and Methods

Four grassland sites in the Cantabrian Mountains in NW Spain were studied. Altitudinal differences between sites spanned more than 500 m: site A at 990 m, site B at 1200 m, site C at 1250 m and site D at 1500 m. The macroclimate is transitional between Mediterranean and Atlantic; the mesoclimate varies strongly with altitude, from warm, more semi-arid to cool and moist. Mean annual precipitation, mean temperatures, mean (and extreme) minimum and mean (and extreme) maximum temperatures are:

Site A:	535 mm	11.0 °C	-1.1 (-7.4) °C	27.8 (34.4) °C
B and C:	1009 mm	9.9 °C	-3.1 (-10.1) °C	27.1 (33.8) °C
D:	1294 mm	8.6 °C	-4.0 (-12.9) °C	26.2 (32.4) °C

At each site, stands at the lower and upper zones of a selected south-facing slope were studied; they will be indicated with the letters L and U, respectively, following the capital letter identifying the stand: AL, AU, BL, etc. The stands, particularly those in the upper slope positions, had very shallow soils, with an underlying layer of stones typically located at 10-15 cm depth. The fact that the sites had been cultivated and ploughed until ca. 40 yr ago may account for the development of such shallow soils. All stands were grazed by livestock (mainly dairy cows), and BL, BU, CL and CU were also mown. The grazing management system was similar in all sites. Grazing typically takes place all-year-round, although it may stop for some time when the grasslands are covered by snow in winter, and also in mid-summer, due to summer drought. Sampling was performed between late June and mid July in 1988, coinciding with the end of the spring season at each site. Estimates of the defoliation intensity showed that the vegetation was nearly completely utilized in all stands, and that the remaining above-ground biomass consisted of small green portions

which were virtually inaccessible to grazers. None of the stands showed structural characteristics commonly associated with heavily grazed pastures (e.g. bare areas due to trampling or scratching). In all of them the percentage of ground covered by herbaceous vegetation was nearly 100% and the vegetation was composed of native species.

For analysis of the composition of the plant communities, data were collected using four 50 cm × 50 cm quadrats placed at random in each stand within an area 10 m × 10 m. The percentage cover of all angiosperm species was estimated visually. Species present within the reference area, but not sampled by the quadrats were arbitrarily assigned a cover value of 1% (e.g. Collins 1987). For biomass analysis, a 20 cm × 20 cm soil block was removed from the centre of each quadrat together with the above-ground vegetation. The blocks were cut with metal blades to a depth of 10 cm, separated from the surrounding soil and placed in a layered frame for transportation to the laboratory. The blocks were sliced into five layers: above-ground biomass, crown plus other superficial structures biomass (hereafter called crown biomass), and below-ground material at depths of 1-4, 4-7 and 7-10 cm. Above-ground plant litter was almost absent in all samples, so we did not attempt to separate it. Below-ground biomass beyond 10 cm could not be accurately sampled, because it was embedded in a dense layer of stones. Nevertheless, crude estimations of this biomass indicated that it was negligible in all samples. The soil layers were thoroughly washed and the plant material was collected in a 0.5-mm-mesh sieve. All components of the above-ground and below-ground plant material were oven-dried at 60 °C and weighed. Consistent with many other studies, ash corrections were not undertaken, since preliminary biomass assessments revealed that the nature of the soil made soil washing very effective in removing mineral fragments.

Variation in community composition was analysed through Correspondence Analysis ordination of the sites (Benzécri 1973), based on estimates of the cover/abundance of the angiosperm species. Two-way analysis of variance (ANOVA) was used to determine if topography, location in the altitudinal sequence, or the interaction between both factors significantly affected the proportion of above-ground biomass corresponding to different life forms: annuals, perennial grasses and perennial forbs. Woody plants were not considered in this analysis as they only appeared in three stands and contributed less than 5% of the total biomass. ANOVA was also used to compare both biomass values at different layers and the proportional allocation of non-aerial biomass into crowns and the three root layers. Significant ($P \leq 0.05$) differences between means were determined by the Tukey-Kramer unplanned comparison

test. All percentage data were angular transformed prior to the analyses.

Rodríguez et al. (1995) classified 40 grasslands according to proportions of non-aerial biomass in the same layers as considered in this study. This classification revealed seven clusters, six containing four or more sites and one containing only two sites. The differences among the six bigger groups in terms of vertical non-aerial biomass distribution were highly significant, as indicated by MANOVA analysis (Wilk's $\lambda = 0.04$; $P < 0.001$; $N = 38$). In the present study, the average profiles of these six groups were compared with those of the study sites by using χ^2 goodness of fit. In this case, if the hypothesis that intensively defoliated mesic pastures tend to develop a particular kind of profile is correct, then the communities analysed here should fit with the profile of the intensively grazed mesic communities studied by Rodríguez et al. (1995).

Results

Axis I of the ordination of the sites separated pastures where grazing was complemented with mowing (B and C) from those that were only grazed (A and D) (Fig. 1). Axis II distinguished between upper (U) and lower (L) zones of the slopes. At the site level, the differences in species composition were larger between the stands of the two lower sites (i.e. AL-AU and BL-BU) than between those of the two more elevated sites (CL-CU and DL-DU), which meant that topographic position had a greater effect on the differentiation of vegetation at sites with intensive Mediterranean influence (i.e. A and B).

Above-ground biomass related to the plant material remaining after defoliation. There were significant effects of site and topography on the percentage of this biomass relating to annual and perennial grasses, while perennial forbs were affected only by topography (Table 1). Differences among sites did not follow the sequential variation of altitude. Instead, differences in the pasture management (i.e. grazing vs. grazing + mowing) seemed to be more important, since annuals had relatively less and perennial grasses relatively more above-ground biomass in sites that were only grazed (i.e. sites A and D) than in those that were grazed and mown (sites B and C, Table 1). In general, annuals and perennial forbs exhibited relatively more above-ground biomass in the upper parts of the slopes, whereas the percentage of biomass contributed by the perennial grasses was greater in the lower parts. Nevertheless, at the site level, only site B showed a significant effect of topography, as on this site biomass contributed by annuals was greater in the upper part of the slope.

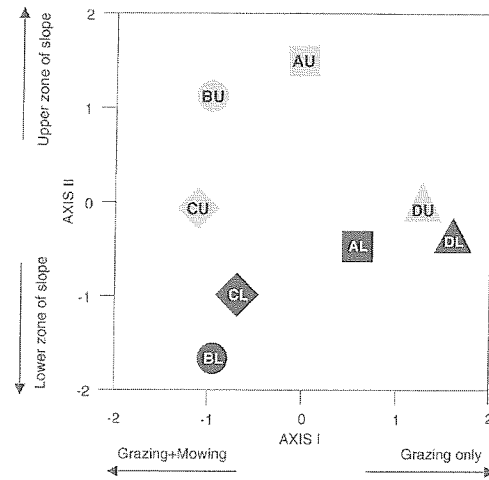


Fig. 1. Ordination of the sampling stands in terms of their species composition. Axes I and II account for 27% and 19% of the variance, respectively. A = stands of the lowest elevation; B and C = intermediate elevations; D = highest elevations; L = lower part of the slope; U = upper part.

There were significant effects of topography upon above-ground biomass and root biomass at 4 - 7 cm depth (Table 2). Both showed greater values in the lower part of the slopes than in the upper parts. There were also significant main effects of site characteristics on all biomass layers except from 7 - 10 cm. In this way,

Table 1. Mean values of the percentage of above-ground biomass for annuals, perennial grasses and perennial forbs. Superscripts and subscripts to the right of a value indicate significant differences due to the main effects of topographic position and location on the altitudinal sequence, respectively. Superscripts to the left of a value indicate significant effects of the interaction between these variables. In each case, means not sharing the same letter are significantly different at $P < 0.05$. Values have been back-transformed following Zar (1987), and represent the biomass contribution of the life forms to the above-ground biomass portion remaining after grazing (i.e. that inaccessible to grazers).

Growth form	Percentage of plant biomass				
	A	B	C	D	Average
Site					
Annuals					
Upland	^{abc} 22.0	^a 42.5 ^{ab}	33.1	^c 2.7	22.5 ^a
Lowland	^c 3.7	^{bc} 11.4 ^{ab}	32.6	^c 6.7	11.9 ^b
Average	11.1 ^{bc}	25.3 ^{ab}	32.9 ^a	4.5 ^c	
Perennial grasses					
Upland	29.3	2.2	28.4	33.6	21.3 ^b
Lowland	80.2	40.5	46.7	58.5	57.0 ^a
Average	55.6 ^a	16.5 ^b	38.2 ^{ab}	46.0 ^a	
Perennial forbs					
Upland	47.6	50.5	35.6	63.3	49.3 ^a
Lowland	15.7	42.4	12.7	29.8	24.3 ^b

altitude appeared to be of some importance in the case of crown and the top root layers (1-4 cm) and total root mass (1-10 cm), since the greatest biomass values for these layers occurred in the highest site (D, Table 2). In addition, the crown biomass on the upper parts of the slopes gradually increased from the lowest to the highest site (Table 2). One-way ANOVA detected highly significant differences ($F[3,12] = 16.9$; $P < 0.001$) in this case, and the Tukey-Kramer test showed that the arrangement of the crown biomass values was $AU < BU = CU < DU$ ($P < 0.05$). This result suggests a positive relationship between the amount of crown biomass and the increase of environmental constraints with altitude. However, no such relationship was observed between altitude and plant biomass of pastures located at the lower parts of the slopes (Table 2).

All stands, except AU, showed similar biomass profiles, in which surface crowns accounted for $\geq 60\%$ of the non-aerial biomass, while the percentage biomass below 7 cm was negligible (Fig. 2a). Thus, there was a significant interaction of site and topography only in the case of the percentage of non-aerial biomass contributed by crowns and a significant effect of site for the percentage of this biomass contributed by roots between 4 and 7 cm ($F[3,18] = 3.3$, $P < 0.05$ and $F[3,18] = 5.8$, $P < 0.01$, respectively). The Tukey-Kramer test revealed that the significant interaction for crowns was due to the lower

value observed at stand AU, and that the site effect for roots between 4-7 cm was due to a larger concentration of roots in this layer at the lowest site of the elevational sequence (A).

Rodríguez et al. (1995) found that intensively grazed mesic communities had a characteristic vertical distribution of non-aerial biomass (profile Type II, Fig. 2b). This vertical distribution was similar to those found in the majority of stands analysed in the present study (i.e. a large proportion of biomass at the uppermost soil layers and relatively small below 7 cm depth). This similarity was statistically confirmed by the fitting of the profiles of the stands to the average profiles of the clusters given by the classification (Table 3). The six stands at higher elevations (BL, BU, CL, CU, DL and DU) fit best in profile Type II. The stand AL appeared to fit best in profile Type III. The similarity between profile Types II and III (Fig. 2b) may account for this result. Only stand AU was associated with different profiles, particularly with profile Type V, which was characterized by a gradual decrease with depth in the below-ground biomass. This type of vertical distribution was associated with intensively grazed xeric pastures (Rodríguez et al. 1995). Stand AU was potentially the most xeric of all stands sampled, because it was located in the upper part of the slope at the end of the climatic gradient where the Mediterranean influence was more intensive. This may explain why the vertical profile of this stand showed the characteristic pattern observed in xeric communities. This hypothesis was supported by the relationship showed by the values of χ^2 with both topography and altitude. For all sites, the lower slopes showed a better fit with profile Type II than the upper slopes (Table 3), which were potentially more affected by water stress. When the stands of the same topographic position were ranked according to their degree of fit with profile Type II, the pattern that emerged with respect to altitude was $A < B = C < D$, for both the upper and lower slopes (Table 3). Both the potential major stresses, i.e. water and nutrient stresses influencing the pastures located at the upper part of the slopes, and the decrease in these stresses with the increase of the altitude may account for these patterns.

Table 2. Mean values of plant biomass in above-ground parts, crowns and root layers. Conventions as in Table 1.

Plant part	Plant biomass (g/m ² dry weight)				Average
	A	B	C	D	
Site					
Above-ground					
Upland	183.5	211.6	332.9	155.3	220.8 ^b
Lowland	309.1	279.3	412.9	298.9	325.1 ^a
Average	246.3 ^{ab}	245.4 ^{ab}	372.9 ^a	227.1 ^b	
Crowns					
Upland	116.1	157.6	212.9	411.7	
Lowland	355.9	150.4	379.4	384.3	
Average	236.0 ^{ab}	154.0 ^b	296.2 ^{ab}	398.0 ^a	
Roots (1-4 cm)					
Upland	56.4	42.4	103.8	97.9	
Lowland	94.8	67.2	73.2	127.3	
Average	75.6 ^{ab}	54.8 ^b	88.5 ^{ab}	112.6 ^a	
Roots (4-7 cm)					
Upland	43.2	7.3	10.5	27.3	22.1 ^b
Lowland	50.9	17.9	30.4	46.3	36.4 ^a
Average	47.1 ^a	12.6 ^c	20.4 ^{bc}	36.8 ^{ab}	
Roots (7-10 cm)					
Upland	5.8	0.3	7.4	10.0	
Lowland	5.8	3.9	11.3	7.7	
Average	5.8	2.0	9.4	8.9	
Roots (1-10 cm)					
Upland	105.4	49.9	121.6	135.1	
Lowland	151.4	89.1	114.9	181.3	
Average	128.4 ^{ab}	69.5 ^b	118.3 ^{ab}	158.2 ^a	

Discussion

All sources of environmental variation considered in the study had effects upon grassland structure. Thus, whereas above-ground biomass and the percentage of this biomass contributed by perennial grasses, showed maximum values in the lower part of the slopes, annuals and perennial forbs had relatively more above-ground biomass at the upper parts. The potentially lower water

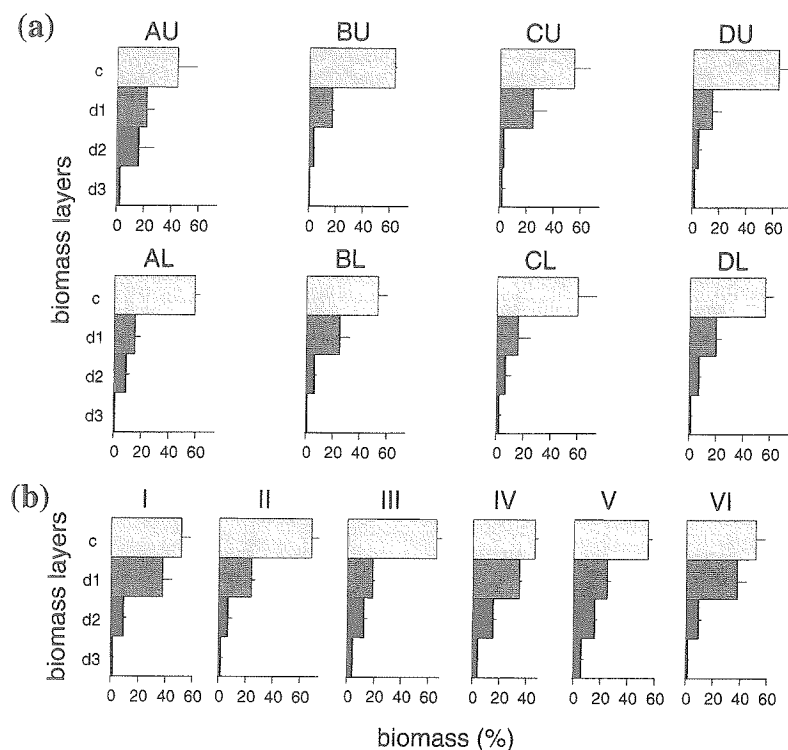


Fig. 2. Biomass profiles of the stands (a), and biomass profile types as defined by Rodríguez et al. (1995) (b). Bars are means (± 1 S.E.) of the percentage of non-aerial biomass corresponding to the four biomass layers; namely c, crowns; d1, 1-4 cm soil depth; d2, 4-7 cm depth; and d3, 7-10 cm depth. Conventions as in Fig. 1. Biomass profile types (b) are average profiles of groups of grasslands obtained by cluster analysis (see Rodríguez et al. 1995). Profile Types I, III and particularly II are characterised by a high concentration of biomass close to the soil surface. Profile Types IV, V and VI show a more gradual reduction of the biomass with depth. According to the results of Rodríguez et al. (1995) intensely grazed mesic and xeric pastures showed a highly significant association with profile types II and V respectively. Conversely, mesic pastures with low grazing pressure did not show a significant association with any of the profile types.

and nutrient availability of the upper parts of the slopes (e.g. Barnes & Harrison 1982; Schimel et al. 1985) may account for these results (cf. Schimel et al. 1985; Abrams et al. 1986; Montalvo et al. 1993). The elevational decrease in temperatures may be related to the increase in crown biomass (i.e. the layer where most plant reserve organs occur). We base this interpretation upon plant growth theory predicting an increase in reserve biomass with a decrease in temperature (see Körner & Renhardt 1987 and references therein). Finally, differences in management and topography were relevant in determining the species composition of the pastures, as

indicated by the ordination result (Fig. 1).

The structural differences between stands clearly contrast with the remarkably similar vertical profiles shown by seven of them. This, however, does not support the hypothesis that the development of a characteristic biomass profile (specifically profile Type II) in these grasslands was associated with species composition. Conversely, the similarity between this profile and the biomass profiles of the intensely grazed mesic grasslands studied earlier (Rodríguez et al. 1995) support the hypothesis that vertical distributions of biomass are associated with intensive defoliation (see Rodríguez et al. 1995 for a discussion on the ways by which intensive grazing or mowing may lead to the development of Type II profiles). On the other hand, although all study grasslands were intensely grazed and virtually all biomass accessible to grazers had been removed, the livestock spent more time at the more productive lower part of the slopes than at the upper parts (pers. obs.). Thus, the fact that the majority of both the upper and lower slope stands exhibited a similar biomass profile suggests that the vertical biomass distribution was not due to the removal of a particular amount of biomass.

In dry pastures, plant growth would be limited not only by defoliation but also by water stress. Crick & Grime (1987) observed that a persistent subterranean structure with deep, robust roots can provide a selective advantage to plants in dry habitats. Accordingly, we may

Table 3. Degree of fitting between six biomass profile types (i.e. those presented in Fig. 2b) and the profiles of the stands (Fig. 2a). Only χ^2 values and probabilities (in parentheses) of the fits that were not significantly different at 95 %, are given. Values in bold indicate the best fit for each stand.

Stands	Profile types					
	I χ^2 (P)	II χ^2 (P)	III χ^2 (P)	IV χ^2 (P)	V χ^2 (P)	VI χ^2 (P)
DU		3.3 (0.4)	6.8 (0.08)			
DL		0.4 (0.9)	3.7 (0.3)			
CU		3.6 (0.3)				
CL		1.8 (0.6)	3 (0.4)			
BU		3.4 (0.3)				
BL	4.8 (0.2)	1.7 (0.6)				
AU				4.5 (0.2)	2.2 (0.5)	7.1 (0.07)
AL		3.2 (0.3)	2.3 (0.6)			

(d.f. = 3 for all cases)

expect a more gradual decrease of below-ground biomass with depth in dry habitats than in less stressed situations; our observations are consistent with this prediction. They further suggest a continuum in the variation of the form of the biomass profiles in defoliated grasslands which would vary from the characteristic distributions of mesic situations (i.e. with high proportions of biomass concentrated at the uppermost soil layers) to those typical of xeric pastures (i.e. showing a more gradual decrease of the below-ground biomass with depth) (Rodríguez et al. 1995). Thus, the lower parts of the slopes (potentially with higher water and nutrient supply) appeared to fit profile Type II better than the corresponding upper parts.

In conclusion, intensively grazed and mown mesic grasslands developed characteristic patterns of subterranean biomass distribution and this occurred irrespective of species composition characteristics. Patterns were, however, modified to some extent by environmental factors (e.g. temperature, topographical position). Although our studies involved a variety of grassland communities, the patterns observed may not be general. If these patterns are found in other communities comprehensive theories describing grassland structure and function (e.g. McNaughton 1979) could be improved by including the below-ground component. In this way, Milchunas & Lauenroth (1989) extended the scope of the 'grazing-lawn concept' to include below-ground structural characteristics of the communities.

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