COMMUN. SOIL SCI. PLANT ANAL., 26(9&10), 1323–1341 (1995)

PATTERNS OF ABOVEGROUND HERBAGE PRODUCTION AND NUTRITIONAL QUALITY STRUCTURE ON SEMIARID GRASS-LANDS

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ABSTRACT: Botanical composition, aboveground biomass, protein, fibre content, and dry matter digestibility (DMD) were used as tools for studying the production and nutritional quality in semiarid grasslands. The study was carried out in herbaceous communities from Central-West of Spain over a period of five consecutive years (1986-1990). The grassland typologies were mainly related to their positions in topographical gradients (slopes) which characterize the regional landscape. The mean values for the production of aboveground biomass in the communities range between 126 and 304 g/m^2 which seem fitted with the possibilities of those areas. The botanical composition is different in the two zones of the slope (upper and lower) and it responds to a defined pattern. Vegetation in the lower zones is dominated by grasses and in the upper zones by forbs. The correlation between production and botanical fractions considered (grasses, legumes and forbs) is significant for the grass group. The results show also that allocation of biomass among organic compounds is different in the three botanical groups.

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In relation to topographical gradient, production and nutritional parameters (protein, fibre content and DMD) for each botanical group show differences between the two zones of the slope. Parameters like organic composition and DMD characterize clearly the botanical fractions. The grasses are always related with high hemicellulose proportions while legumes with cellular contents. Considering the community, grasslands from the lower zones are better characterized by higher protein contents and DMD. The communities from the upper zones are characterized by high contents in cell components. The nutritional quality of communities is clearly related with the percentages of botanical fractions forming the grassland and with organic contents and dry matter digestibility as well.

INTRODUCTION

Structural and functional changes in semiarid grassland vegetation have been studied by some authors in relation with environmental factors, like geomorphology, precipitation, or grazing (Naveh, 1982; Milchunas et al., 1989; Noy-Meir et al., 1989; Perez-Corona et al., 1991) and with certain temporal aspects connected with the ecological succession (Casado et al., 1985). Those changes usually have been only recorded as variations in the floristic composition or production of the communities. However, environmental variations and perturbations are also reflected in the chemical organic composition of the plants, either in the proportion and allocation of these organic compounds. The particular distribution of organic compounds to different plant parts in each specie or group of species must lead to particular and specific strategies in the competition for the resources in semiarid grassland systems.

The nutritional parameters studied in this paper (organic composition and DMD) could also be related with changes that grazing hervibores induced in the vegetation development (Van Soest, 1982), since they can select their food and subsequently this would affect to the growth grassland processes. The organic composition of the plants is also related with phenological phases. In this way the oldest plants have more cell wall proportions and less protein content and digestibility than the youngest ones (Seoane, 1981; Minson, 1982; Kirby et al., 1989; Gill et al., 1989; Perez Corona, 1992).

In the present work, the vegetation has also been studied according to a geomorphological gradient which is regarded as elemental landscape unit (Troeh, 1965; Montserrat, 1975; Gomez et al., 1978). This gradient determines two extreme zones: upper and lower. They are connected by a vectorial transport of water and nutrients from the upper towards the lower parts (Diaz Pineda and Peco, 1988). Consequently, the residence time of nutrients and water in the upper parts is lesser than in the lower parts (Gonzalez Bernaldez, 1981). This means that the upper parts lose nutrients and water in favour of the lower ones, and leads to a faster development and maturation (in the season) in the communities from the upper parts (Perez Corona, 1992). On those gradients, also called slopes locally, successional processes take place as well but always conditioned by the particular dynamic of the geomorphological system. The slope is continually renovated in its upper part so that the succession, that usually would replace annual species by perennials (Bornkamm, 1981; Pickett, 1982), cannot be possible in the upper zones due to their constant rejuvenating. Only when the adverse conditions in the upper parts are softer (due to the action of other factors as a climatical regional gradient), the slope gradient is less drastic and we can find more perennials in the upper zones (Montalvo, 1991; Perez Corona, 1992). In these cases, the successional stages of the two gradient zones will be more proximate.

The aims of this work were (i) to evaluate the aboveground herbage production and nutritional quality of semiarid grasslands, (ii) to know if any patterns can be recognized in the aboveground production of the grassland community and in their distribution in the botanical groups which compound the grasslands according to the regional landscape scale characterized by the slopes, (iii) to know if any pattern can be identified in the nutritional quality, both for the communities and botanical groups, and (iv) if the botanical composition of grassland can be related to the nutritional quality of the community.

MATERIALS AND METHODS

Study Area

Representative semiarid grassland communities from central-western Spain were selected. The study area is characterized by "dehesa" systems. Those consist of low density *Quercus ilex* subsp. *rotundifolia* woodlands with wide-open spaces occupied by grasslands. The climate in the zone is characterized by cold winters and dry, warm summers. The average annual rainfall is around 500 mm, although the regime varies considerably throughout the year. The presence of these grasslands also belongs to geomorphologic units which respond to a slope-bed system with upper and lower zones connected by a vectorial relation of nutrients, water, and information (Diaz Pineda, 1989). These slopes characterize the regional landscape. The substrate is siliceous with many slaty or granitic zones. The soils are Brown Mediterranean, although the ridge zones are occupied by skeletal soils. The number of considered slopes was 34.

Sampling and Experimental Analyses

In both zones, it was made an aboveground biomass production control, botanical composition, organic parameters (crude protein, cellular content, cellulose, hemicellulose and lignin), and dry matter digestibility (DMD) of grassland vegetation. This control was annually made during five consecutive years (1986-1990) at the moment considered of maximum production on the semiarid grassland cycle (Perez Corona et al., 1991). The phenological phase of each community was also recorded. Sampling was made at random in an area of the grassland that it was considered homogeneous. A square of 0.50 m size was thrown four times over the grassland. The vegetation included within the four squares was cut using electric scissors and put into polystyrene bags which were transported to the laboratory.

Afterwards, each grassland community sample was separated into three botanical fractions that traditionally have been considered in these grasslands (grasses, legumes, and forbs). Botanical fraction subsamples were dried in a forced air oven at 60°C till constant weight. Then the dried weight of each fraction and community was determined. The proportion of botanical group in the grassland was quantified as a percentage of its dry weight biomass in the total community biomass production. The samples were ground in a Rescth mill to a sieve size of 0.5 mm and homogenized. The original initial community samples were reconstructed maintaining the same proportion of families as found in the separation.

All the samples (communities and botanical fractions) were analyzed for the following parameters: crude protein content by Kjeldahl digestion/distillation method; cellular content (CC), cell wall (NDF), cellulose (CELL), hemicellulose (HEM), lignin (LIG), and dry matter digestibility (DMD) by using the Goering and Van Soest method (1970) with modifications introduced by Garcia Criado (1975).

The data were statistically analyzed using ANOVA and LSD tests for comparisons among pairs of means (Statgraphics, 1991). A Principal Component Analysis (PCA, BMDP) for factorial analysis of data was used for establishing which organic parameters or DMD would characterize to each botanical group.

RESULTS

Production and Botanical Composition of Grassland Communities

The communities from upper zones have a mean biomass production of 126 g/m^2 (Table 1) being less than those from the lower ones (304 g/m^2). The production shows significant differences between the two zones ($p<0.01$; Table 1). The percentage of grasses does not show significant differences between years for the upper zone of the slope but it does in the lower one ($p<0.01$; Table 1). The differences between zones are also significant ($p<0.01$) being the percentage of the lower zones larger than the upper ones (Table 1).

The percentage of legumes in the community (Table 1) does not show any zonal differences but both zones have significative differences between years ($p<0.01$; Table 1).

Forbs are represented better in the communities of the upper parts than in the lower ones, and the differences between two values are significant (Table 1). Therefore, they may be the dominant group of the grassland in the upper zones. In general, the grasses are the dominant fraction in the lower zone of the slope.

With respect to the phenological stage of the communities at the sampling time, it is clear that the lower zone communities usually have a phenological delay with respect to the upper ones (data not shown).

We have also tried to determine the possible relation between community biomass production and percentage of botanical groups in the community. Our results are in Table 2. The biomass production of the community is not related with the proportions of the families in the grassland. However, when the two zones are considered together, the production is positively correlated with the

TABLE 1. Dried Aboveground Biomass Production (g/m²) of two slope zones (upper and lower) and percentages of botanical fractions (grasses, legumes and forbs) in the community in different zones and years. ANOVA LSD ($p<0.01$) significative differences among community productions and botanical fraction percentages.

		N	Community	Grasses	Legumes	Forbs
UPPER	a	102	126	30.5	18.5	51
	b		7.0	1.6	1.8	1.8
	LSD (year)		*	n.s.	*	*
LOWER	a	150	304	62.1	21.3	16.6
	b		9.6	1.5	1.1	0.9
	LSD (year)		*	*	*	n.s.
	LSD (zones)		*	*	n.s.	*

a = Mean b = Standard error N = Number of samples. * = LSD significant; n.s. = LSD not significant.

TABLE 2. Correlations between proportion of botanical fractions and aboveground biomass production of communities.

	GRA			LEG			FORBS		
	upper	lower	all	upper	lower	all	upper	lower	all
PRO	0.16	-0.01	0.44*	-0.05	0.08	0.08	-0.10	-0.09	0.52*

* = significant ($p<0.01$).
GRA = Grasses percentage; LEG = Legumes Percentage; FORBS = Forbs Percentage
PRO = Biomass Production of Community

percentage of grasses and negatively with the forbs one. There is no relation between production and legumes proportion.

Organic Composition of Grassland Communities and Botanical Fractions in Relation with Topographical Gradient

Protein contents for the considered botanical groups and the community are larger in the samples from the lower zones than in the upper ones (Table 3). The

TABLE 3. Protein, NDF, Cellulose, Hemicellulose, and Lignin contents and DMD in both communities and botanical fractions according to topographical position.

	Communities		Grasses		Legumes		Forbs	
	upper	lower	upper	lower	upper	lower	upper	lower
PROT	9.1	10.3*	7.2	8.9*	14.3	15.5*	9.0	10.3*
NDF	51.2	53.7*	65.5	63.0*	44.9	37.1*	44.5	43.1
CELL	29.3	29.8	33.0	32.5	26.7	23.8*	27.0	26.7
HEM	15.9	19.7*	28.1	26.7*	11.4	7.4*	10.1	10.1
LIG	6.0	4.3*	4.3	3.9*	6.9	6.2	7.5	6.4*
DMD	61.0	65.5*	62.4	65.2*	61.2	65.1*	60.2	63.4*

PROT = Protein; NDF = Neutral Detergent Fibre; CELL = Cellulose; HEM = Hemicellulose; LIG =Lignin; DMD = Dry Matter Digestibility. * significant differences ($p<0.01$).

differences between zones are significant ($p<0.01$). Protein contents are also larger in the lower zones for the three groups of plants. Protein values are quite variable among families (Table 3), but in both zones of the gradient, the largest content always corresponds to legumes group and the differences with the rest of the groups are significant ($p<0.01$).

The cell wall components (Table 3) have different patterns in each botanical fraction as well. For the three fractions, the cell wall content (NDF) is larger in the upper part of the slope than in the lower part, although the differences are not significant in forbs. However, the community shows larger contents of cell wall in the lower zone of the gradient. This is due to the high influence of the grass percentage in the lower zones of the slopes (Table 1), so that it is the botanical fraction with largest contents of NDF (Table 3). The cellulose percentage has only significant zonal differences ($p<0.01$) for the legumes. The group of grasses has the highest values in both zones. The hemicellulose content is also larger in grasses than in the rest of the botanical fractions ($p<0.01$; Table 4). The zonal differences are significant in grasses and legumes, with larger contents in the upper part of the gradient. However, the community has always higher contents of

TABLE 4. ANOVA-LSD differences among organic parameters in botanical groups.

	PROT	NDF	CELL	HEM	LIG	DMD
UPPER	G,L,F	G,L=F	G,L=F	G,L=F	G,L,F	G=L,L=F
LOWER	G,L,F	G,L,F	G,L,F	G,L,F	G,L=F	G=L,F

G,L,O: significant differences.
L = O; G = L: no significant differences.
G = Grasses; L = Legumes; F = Forbs.

HEM in the lower zone of the slope than in the upper ones due to, again, the effect of the higher percentages of grasses in this zone of the gradient. Lignin content is always larger in the upper part of the gradient, although the differences are not significant in legumes (Table 3).

The DMD is always larger in the lower zone of the gradient (in the community and botanical fractions) (Table 3). Forbs is the botanical fraction with smallest DMD.

Considering the community level, it is observed that the organic composition and DMD, in the upper and lower zones of the slopes, are significantly different ($p<0.01$) in five out of six parameters studied. These results are clearly belonged to the organic composition of each botanical fraction, their proportion in the community and the phenological phase of the plants on every part of the gradient. In general, the upper zones appear characterized by a higher lignin content and lower NDF. The upper zone has a more advanced phenological phase which should lead to an increase of cell wall components. But this was observed only for some of them, like lignin. However, the content of protein, NDF, hemicellulose, and DMD value are larger in the lower parts.

The results of the PCA made in the matrix composed by the data of organic parameters considered (PROT, CC, CELL, HEM, LIG, and DMD) in all three botanical groups in the two zones of the slope and years of sampling are shown in the Figures 1 and 2. It is observed a clear differentiation of the groups according to some organic components. In the upper zone (Figure 1), it is produced a

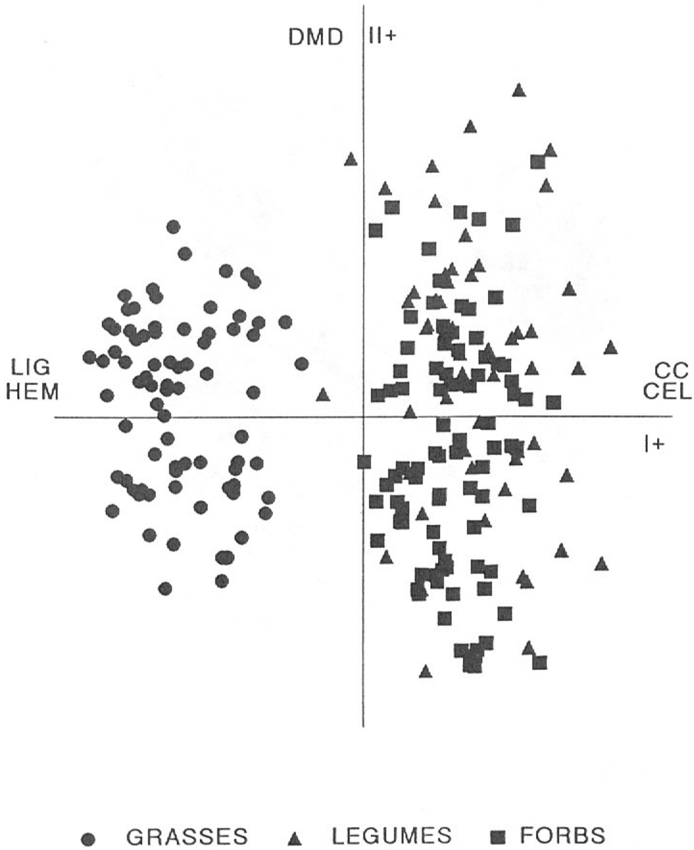

FIGURE 1. Grasses, legumes and forbs samples situation in the factorial plane defined by two first axes of principal components analysis in the upper zones of slope. CELL = Cellulose; CC = Cellular Content; HEM = Hemicellulose; LIG = Lignin; DMD = Dry Matter Digestibility.

separation between grasses and another group that joins the other two botanical fractions (legumes and forbs). The grasses, in the negative part of the first axis, are characterized by high hemicellulose and lignin contents. The other group, in the positive part of the axis, is related with cellulose and cellular content. In the lower part of the slope (Figure 2), the grasses are in a similar position to the upper

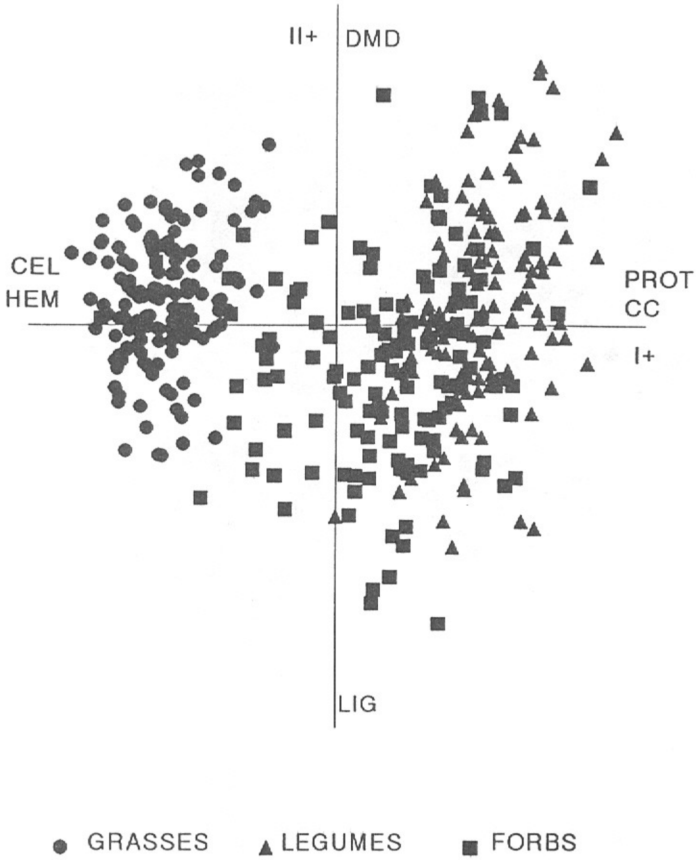

FIGURE 2. Grasses, legumes and forbs samples situation in the factorial plane defined by two first axes of principal components analysis in the lower zones of slope. PROT = Protein; CELL = Cellulose; CC = Cellular Content; HEM = Hemicellulose; LIG = Lignin; DMD = Dry Matter Digestibility.

zone, but here the variables related with it are cellulose and hemicellulose. The other group is now broken into two groups: legumes, close to the extreme of this axe, and forbs in the centre of the projection figure. The legumes are mainly related with high contents in protein and cellular content. The results suggest the possibility of characterize the botanical groups according to the organic composition. It is noted that the variables determining this separation are different in the two slope positions. The grasses from the upper zone also increase their lignin content according to their advanced phenological stage, but in both zones, the hemicellulose is the parameter related to them. Legumes are related to the cellular content and to protein in the lower zone. The differentiation in the lower part is clear between compounds of the wall (grasses) and compounds of the cytoplasm (legumes).

The organic content and DMD of the botanical fractions are the main factors that rule the nutritive quality of the community. Consequently, the botanical fraction percentages in the community are also very important. We wanted to find which organic variables dominate the zonal and annual differentiation in these communities. A PCA was made in the matrix determined by communities and their organic contents and DMD (Figure 3) as well. The results show that the first factorial axis seems related to the time of the growing season. Cellulose, in the negative part, and CC in the positive one are the main load factors. The second factorial component would be responsible for the spatial variations. In this way, the samples from the upper parts of the slopes are close to the positive part of the second factorial axis. Those samples are characterized by high lignin contents. The samples from the lower zones are situated in the negative part of the axis with larger values in hemicellulose and DMD.

DISCUSSION

Botanical Composition and Production of Semiarid Grassland Communities

Both the spatial segregation of the communities from the slope zones, due to the geomorphological structure of those units, and the annual variations bear different growth and development responses, which in this case, have been recorded like production measurements and changes in the botanical composition.

The differences between production in the two zones of the slope are justified by the larger availability of water and nutrients in the lower part owing to the vectorial transport in the slope (upper zones towards lower zones). The differences in production between the two zones are related to factors limiting for the production, like the hydric availability and pools of accessible nitrogen (Caballero

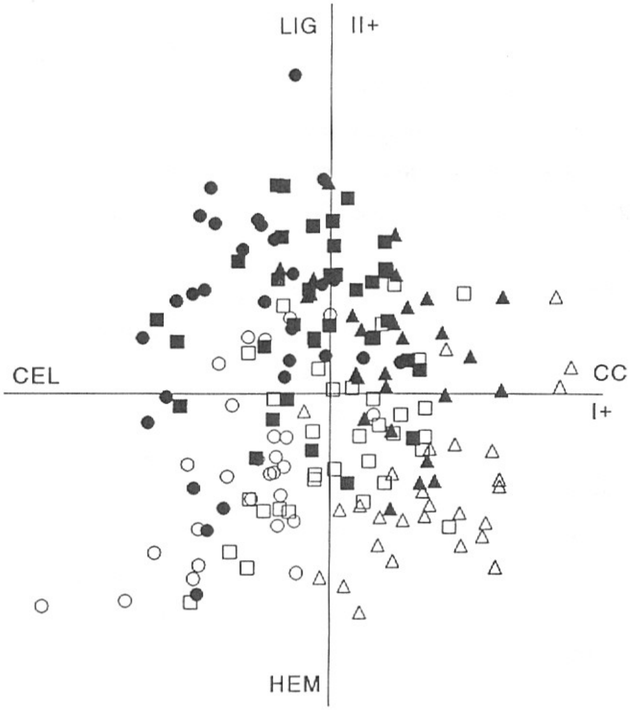

FIGURE 3. Community samples situation in the factorial plane defined by the two first axes of principal component analysis in upper and lower zones of slope. CC = Cellular Content; CELL = Cellulose; HEM = Hemicellulose; LIG = Lignin. Δ Lower zone 1987; ▲ Upper zone 1987; O Lower zone 1988; ● Upper zone 1988; □ Lower zone 1989; ■ Upper zone 1989.

et al., 1977) which are larger in the lower zone. Furthermore, it is joined with the influence of livestock which tends to graze in the lower zones. This behaviour is accentuated with the progress of secondary succession and leads also to larger nitrogen availability in the naturally fertilized zones (Miguel de, 1989). It is reflected in the structure of grassland, in terms of maintaining of diversity with grazing (Montalvo et al., 1993) and in productivity as well. For example, the presence of livestock in the lower parts makes also a more continuous growth of the plants from those zones (Casado et al., 1985). So, the phytomase production should be increased due to the establishment of plants with basal meristemes which could stand herbivores pressure. Contrary to that, the grassland loss of quality in absence of animal exploitation which is related to the decrease of productivity (Diaz Pineda and Peco, 1988). This process takes place in the upper parts of the slopes. Our results showed a lower productivity in the upper zones.

From the results refereed to the botanical composition of the grasslands, it can be deduced that grasses are the dominant component in dehesa grassland systems. The dominance is accentuated in the lower parts of the slopes, reaching sometimes 100% values of the grassland (Perez Corona et al., 1991). Some authors have suggested the relationship between high productions and percentages of grasses in the grassland (Milchunas et al., 1989), being also clear in the present work. These results indicate that the extreme spatial heterogeneity in the slope is reflected in the botanical composition of the communities as well. The poorest edaphic conditions are related to higher proportions of forbs and the grasses which are the next important fraction. In the lower zone, where the edaphic conditions are better than in the upper zone (Casado et al., 1985), the dominant group is clearly grasses followed by the legumes.

It is also observed that grasses have clear zonal and annual differences in the lower zones of the slope while forbs do so in the upper zone. This means that changes in the annual meteorological fluctuations affect mainly the botanical groups dominating the zone. Legumes could follow a different strategy and their percentages in the communities are more sensible to the annual variations than to the zonal ones. Consequently, the legumes seem to be responsible of the annual variation of the grasslands within each zone.

Patterns in Organic Composition of Grassland Communities

The protein percentages of the three botanical groups are larger in the lower zone of the gradient. It is due to two main reasons, (i) the lower zone has better environmental conditions than the upper one (McDonald et al., 1986) and (ii) that the protein content decreases with the plant maturity which appears earlier in the upper zones (Perez Corona et al., 1994). Some authors have suggested the possibility of a protein content increase in grasses growing together with legumes (Mallarino and Wedin, 1990) but it is not so clear in these grasslands (Perez

Corona, unpl.). Grass and legume values of protein are fitted to those that other authors have shown in grasslands (Garcia Criado et al., 1980; Garcia Ciudad et al., 1984). Legumes are considered as a good quality indicator in the grasslands (Chocarro et al., 1987) due to their higher content with respect other groups (Lyttleton, 1973; Norton, 1982; Shennan et al., 1985) and their lower variability in relation with environmental conditions (Perez Corona, 1992). With special reference to the semiarid grassland, some authors have indicated that the largest percentage of protein in the legumes is due to the symbiosis with some indigenous stocks of *Rhizobium* (Almazan and Bermudez de Castro, 1991).

Among the studied cell wall constituents, two have special interest in the differential proportion in the plants. First, for some authors (Van Soest, 1982) hemicellulose is the most complex and specific polisacharid in plant species. In this sense, we can indicate the larger values in grasses and the significant differences between zones in grasses and legumes but not in forbs. Second, lignin is the cell wall component which varies not only in quantity with species or with the maturity stage, but also with the structure or localization in plant and cells (Van Soest, 1982). For example, legumes have a large lignin content in their stems, but leaves rarely are subjected to the lignification processes. However in grasses, the leaves are a bit more lignificated, so that they are more suitable for carrying out supporting jobs. It is possible that our lignin content results for the legumes were biased by the sampling method. The lignification process does not affect leaves considerably, and the leaves are mainly the sampling parts in legumes. On the other hand, lignin has certain properties which can modify the nutritive characteristics of the herbaceous community. Lignin is not a homogeneous material in all plants which have different chemical and biological properties in each group. In the case of legumes, lignin is more reactive to the digestion than grasses (Gordon, 1975). Lignin content affects the nutritional quality of the communities since it limits the digestion of cellulose and other components of the cell wall (Van Soest, 1968).

Cellulose is also very important in relation to the nutritional quality of these communities. Van Soest (1982) consider this parameter directly related to the intake of herbivores. Cellulose is also related to the nutritional quality of the plant because of the digestibility of the plants belongs to the grade of lignification in cellulose. The digestibility is also influenced by other factors like silica levels, cutin, and others intrinsic proprieties of cellulose. The communities from the lower zones have similar quantity of cellulose than those from the upper ones, but the DMD is higher due to likely differences in the lignification of this organic compound.

Grasslands communities from the lower zone of the slopes have larger quality related to their organic content and DMD than the upper zones, like some authors have indicated in other semiarid grasslands (Montalvo et al., 1989). This is related to the tendency of the upper zones of the slopes to accumulate biomass in form of lignin like supporting element. This behaviour is also related to the advanced phenological stage of upper zones with respect the lower ones since this means an anticipate lignification. It can be related to different strategies in the community. Diaz Pineda (1989) suggests that the upper zone communities may follow the plant strategy of capitalization of energy in form of lignin, forced by the drastic and hard environmental conditions in which they are developed and matured. The communities, either in the upper and lower zones, have the same age but their maturation speeds have been different. The upper zones have strategies of growing which lead towards fast developments to lignin accumulation in the cell walls. However in the lower zone, good DMD values are maintained longer. The speculations about whether the lignin contents affect the behaviour consumption of the herbivores are divided. For Montalvo et al. (1989), clearly the high contents of lignin in the communities influence intake, meanwhile for Van Soest (1965,1982), lignin does not have any relation with intake.

In summary, the communities from the lower zones of the slope have different patterns in organic composition and production than the upper zones. Lower zones have higher renovation rates (Casado et al., 1985) that can be associated to the larger protein contents and DMD, and also due to the continuous pressure that livestock have on them. We can not postulate anything about the influence of the herbivores on the organic contents of the communities, although we seem right that plants in the two extremes zones of the gradient have been chosen by different adaptative strategies in the course of their evolution and succession both to the climatic conditions and livestock pressure. The ecological succession has different results in each zone, selecting a certain way that more adapted to maximum exploitation of the qualities and resources of each zone in each moment. This is also reflected in their pattern of distribution of biomass and energy in different organic compounds that must be related with the botanical groups and geomorphological landscape structure.

CONCLUSIONS

The botanical composition and production of semiarid grassland communities are related with their position in the topographical gradients. Production of the community is also related with the proportion of grasses in the grassland.

Grasses, legumes, and forbs show a characteristic allocation pattern of biomass into certain organic compounds and several differences between slope zones. The position in the slope also determines differences in the nutritional quality of the grassland community which is related with the botanical group proportion within the community.

This multivariate study detected an association of the position in the slope and certain organic parameters. The grassland communities from the lower zones were characterized by higher protein content and DMD (higher nutritional quality) than the upper zones.

ACKNOWLEDGEMENTS

This work was supported by European Union Research Project (Contract No 800 -CT90-0021) and a Grant of Programa Nacional de Formacion de Personal Investigador en el Extranjero of Spanish Government in the Department of Plant Ecology and Evolutionary Biology of Utrecht University. We are indebted to P. M. Pelaez-Campomanes de Labra and R. Villar Montero for the critical discussion of the manuscript. Thanks are also due to L. Garcia, J. C. Estevez, and M. Hernandez for their technical assistance.

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