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Variations in nutritional quality and biomass production of semiarid grasslands

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Abstract

The effect of the growing season and topographic zone on biomass production, protein content, cell content (CC), lignin, cellulose, hemicellulose, digestibility (DMD), and mineral element concentrations (P, K, Ca, Mg, Na, Mn, Fe, Cu, Zn) were studied in herbage samples collected from semiarid grasslands in Central-Western Spain. Protein and mineral contents decreased as the growing season progressed whereas fibre properties tended to increase. Topographic gradient significantly affected peak biomass production, fibre properties, protein and mineral contents. Stepwise multiple regression showed that the prediction of biomass production on these areas was related to cellulose, Na, Fe, and Mg contents in the grassland community whereas fibre properties were mainly predicted by Ca, Na, and Cu. Principal component analysis indicated that the temporal evolution (component II) of the organic variables determined pasture quality whereas most of the variation in mineral content was related to the topographical gradient (component I). Some organic and inorganic parameters may cause deficiencies in cattle grazing on the upper and middle zones, mostly at the end of the growing season. The data suggest that information about the temporal and spatial variations of the production and nutritional quality of semiarid grassland is necessary for making correct management.

Key Words: macronutrients, Mediterranean ecosystems, relationships, seasonal variation, topographical gradient

Resumen

Se estudiaron los efectos de la posición topográfica y de la estación de crecimiento en la producción de biomasa, contenido en proteína, contenido celular (CC), lignina, celulosa, hemicelulosa, digestibilidad (DMD) y concentraciones de elementos minerales (P, K, Ca, Mg, Na, Mn, Fe, Cu, Zn) en comunidades de pastizales semiáridos del centro-oeste español. Los contenidos en proteína y elementos minerales de los pastizales tendieron a disminuir al avanzar la estación de crecimiento, mientras que las variables relacionadas con el contenido en fibra (lignina, celulosa y hemicelulosa) tendieron a incrementar. El gradiente topográfico de ladera tuvo un efecto significativo en la producción de biomasa y en los contenidos de celulosa, lignina, hemicelulosa, proteína y elementos minerales. Un análisis de regresión múltiple paso a paso mostró que la predicción de la producción de biomasa en estas áreas estaba relacionada con el contenido en celulosa, Na, Fe, y Mg del pastizal, mientras que los parámetros relacionados con el contenido en fibra fueron principalmente predichos por los contenidos de Ca, Na, y Cu. Un análisis en componentes principales indicó que la calidad del pastizal estaba determinada principalmente por la evolución temporal (componente II) de las variables orgánicas y que la mayor parte de la variación en el contenido mineral estaba relacionada con el gradiente topográfico (componente I). Algunos parámetros nutricionales del pasto pueden resultar deficientes para el ganado al final de la estación de crecimiento. El análisis de los datos sugiere que el conocimiento de las variaciones temporales y espaciales de la producción de biomasa y la calidad nutricional de la hierba es necesaria para un adecuado manejo de estos pastizales semiáridos.

Grassland nutritional quality is affected by abiotic and biotic environmental factors including soil type, climatic regime, botanical composition and management (Lyttelton 1973, Norton 1982, Angell et al. 1990). Herbivores also influence botanical composition through selective grazing and change the organic and mineral properties of the grassland communities through fertilization with dung and urine (Norton 1982, Van Soest 1982, Georgiadis and McNaughton 1990, Jaramillo and Detling 1992). In the semiarid areas of Western Spain, the quality and production of the grassland varies with temporal and spatial gradients (Casado et al. 1985, Pérez Corona et al. 1994), producing a complex environment which is difficult to manage for optimal livestock production. The climatic characteristics are severe and unpredictable, causing a strong seasonality in grassland production (Pérez Corona 1993). From energetic and economic view points, grassland quality determines the rational use of these ecosystems. Often supplementary feed is required to compensate animals for pasture deficiencies. Inappropriate management contribute to these deficiencies (McDowell 1985).

Protein and digestibility of grasslands have been emphasized as the main determinants of forage quality (Ballard et al. 1990, Pérez Corona et al. 1994). However, much less attention has been paid to minerals even though they also influence forage quality and can depress feed intake when levels are low (Provenza 1995).

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The aim of this study was to describe the effects of seasonality and slope position on the relationships between biomass production, mineral content and organic content (forage quality) in semiarid grassland pastures. A second point was to determine to what extent spatial and/or temporal gradients affect the adequacy of the nutritive value of these Mediterranean grasslands for grazing cattle.

Materials and Methods

Study Area

The study was conducted in the "Dehesa" ecosystem located in Salamanca province (Western Spain). The Dehesa systems are characterized by low density *Quercus ilex* subsp. *rotundifolia* woodlands with wide open grassland where large ruminants graze between the sparsely scattered shrubs. The climate of the Dehesa area is semiarid Mediterranean, characterized by cold winters and dry, warm summers. In 1990, annual precipitation was 411 mm and average temperature was 12° C. The average monthly minimum temperature was in January -1.0° C and the average monthly maximum temperature in July was 31.5° C. The soil substrate is mainly siliceous but with many slate or granitic zones also present. The soils are described as Brown Mediterranean, although skeletal soils occupy the ridge zones. The grasslands belong to geomorphologic units which correspond to the slope-bed systems. Topographic gradients are characterized by an increase in soil fertility, soil depth and water availability along upland to lowland gradients (Díaz Pineda 1989).

In the study area, 2 slopes on similar substrate (at 40° 55' N and 6° 00' W and 820 m in elevation; 40° 57' N and 6° 08' W and 840 m in elevation) were selected, and on each slope upper, middle, and lower zones topographic zones were differentiated. Altitude differences between zones were 15 m and slope length 100 m. Vegetation was dominated by short-lived annual species although perennial species were also present. *Agrostis castellana* Boiss et Reut, *Vulpia bromoides* (L.) S.F. Gray, and *Anthoxanthum aristatum* (Boiss) were the dominant grasses. Forb species were represented by *Plantago lanceolata* (L.), *Tuberaria guttata* (L.) Fourr. The dominant legumes were *Trifolium hybridum* (L.) and *T. striatum* (L.).

Sampling and Experimental Analyses

On each slope zone, one 24 m^2 plot was protected from grazing by a 1 m high fence, in March 1989. Plots within each slope zone were located in areas of uniform botanical composition and away from the inter-zone boundaries. In early autumn, 1989, all the vegetation inside the enclosures was cut at ground level to simulate the impact of herbivores grazing outside the enclosure. Sampling of the herbage was performed inside the enclosure, on the 2 slopes, at each of the 3 topographic positions, during spring–summer period (10 April, 25 April, 10 May, 25 May, 10 June, and 25 June) in 1990. Different areas were sampled on each date so that each sampling represented the accumulated pasture biomass. Sampling was made inside the enclosure by cutting the herbaceous vegetation in 4 randomly selected units (0.50 × 0.50 m) at 2 cm above ground level. After 25 May, sampling was not possible in the upper and middle zones because the plants died almost completely. Each sample was separated manually into grasses, legumes, and forbs. Each botanical subsample was dried to constant weight, ground in a Retsch mill with a sieve size of 0.5 mm and homogenized. The proportion of each botanical group in the grassland was calculated as the percentage of its dry weight in the total community biomass. Samples were reconstructed by weighting and mixing the proportion to dry weights of each botanical group to represent the pasture community.

The pasture community samples were analyzed for: a) crude protein content by the Kjeldahl distillation method; b) cellular content (CC), cellulose, hemicellulose, lignin, and dry matter digestibility (DMD) using the Goering and Van Soest method (1970); c) combustion of sub-samples preceded analysis for phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sodium (Na), manganese (Mn), iron (Fe), copper (Cu) and zinc (Zn) (Duque Macias 1971). P concentrations were measured colorimetrically as molybdovanadato-phosphoric acid. K, Ca, Mg, Na, Mn, Fe, Cu and Zn were determined by atomic absorption spectrophotometry.

The data were analyzed statistically using one-way ANOVA testing for the effects of sampling date and topographic position separately (Statgraphics 5.0). Analysis of correlation, multiple stepwise linear regression and principal component analysis (PCA) (SPSS 6.0) were performed with the mineral and organic variables.

Results and Discussion

Phenology of Biomass Production and Botanical Composition

There was a significant effect of the slope position on biomass production ($P < 0.01$; Table 1). Biomass production on the lower parts was higher than on the upper and middle slope positions. These differences became more apparent and were greater as the growing season progressed (Fig. 1). Slope positions differed ($P < 0.01$) temporally in peak biomass production (accumulative total of annual pasture growth) with the middle zones reaching a maximum earlier whereas the upper parts did not show a maximum (Fig. 1). Pasture growth was maintained for a longer period on the lower slope positions than on the upper and middle positions.

Table 1. Results of one-way ANOVA showing the significance of the effects of harvests and slope position on different parameters studied.

	Sampling date	Slope position
Production (g)	**	**
Grasses (%)	NS	**
Legumes (%)	NS	**
Forbs (%)	NS	**
P (g kg^{-1})	NS	**
K (g kg^{-1})	NS	NS
Ca (g kg^{-1})	**	**
Mg (g kg^{-1})	NS	**
Na (g kg^{-1})	**	**
Mn (kg kg^{-1})	NS	NS
Fe (kg kg^{-1})	**	**
Cu (kg kg^{-1})	**	NS
Zn (kg kg^{-1})	**	NS
Protein (%)	**	**
CC (%)	**	**
Hemicellulose (%)	NS	**
Lignin (%)	**	**
Cellulose (%)	**	**
DMD (%)	**	**

Level of significance **$P < 0.05$; NS not significant.

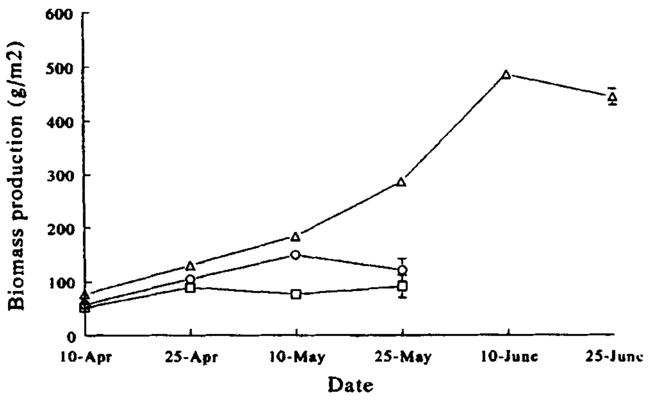

Fig. 1. Biomass production of grassland (g/m2 over dry weight) during the growing season in the upper (□), middle (O), and lower (Δ) zones of slope. Symbols are means of 2 sampling sites. Bars (I) are standard errors of the differences for comparison between slope positions.

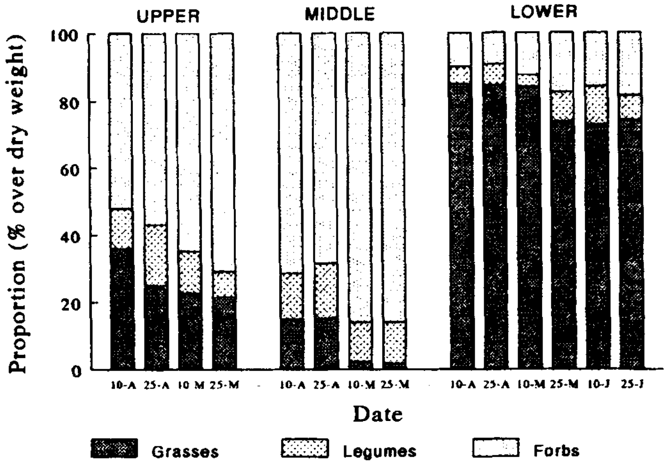

Fig. 2. Proportion (% dry weight) of grasses, legumes, and forbs in the community, during the growing season in the upper, middle, and lower zone of slope.

According to Pearson and Ison (1987), the typical shape of grassland growth is a sigmoid curve, increasing to a maximum and then decreasing. Biomass production on the lower zones of this Mediterranean grassland resembled this pattern. However, clear trends were not recognized in the upper and middle zones. Higher soil moisture levels and soil fertility accounts for the higher production in the lower zones (Pérez Corona 1993). High production in the lower zones was also favored by successional processes (Casado et al. 1985) and by the higher grazing pressure (Díaz Pineda and Peco 1988).

The proportion of plant groups in the grassland did not vary significantly with the sampling date, but they did change significantly ($P < 0.05$) with the slope position (Table 1). The upper and middle zones were characterized by higher proportions of forbs whereas the lower zones were dominated by grasses (Fig. 2). The proportions of legumes were higher on the upper and middle zones than on the lower zones.

Changes in Fibre Properties, Protein Content, Digestibility, and Mineral Content with Date and Slope Position

Except for hemicellulose (Table 1), the percentages of cell wall constituents increased significantly over time (Fig. 3). Protein content and DMD declined with time ($P<0.01$) resulting in a decrease in grassland quality as the growing season progressed. This pattern has been documented for other areas (Kirby et al. 1989).

The topographical position significantly affected all fibre variables ($P < 0.01$). Compared with the lower parts of the slope, the upper and middle positions had higher lignin content and lower

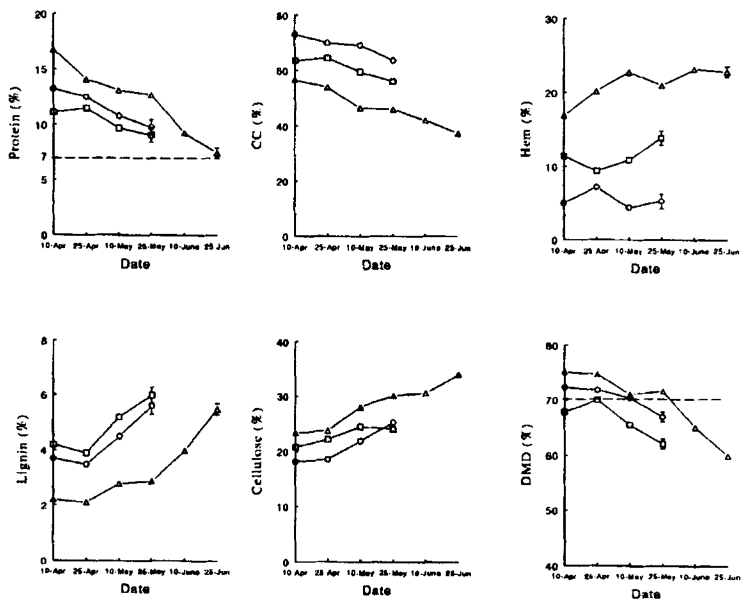

Fig. 3. Protein, cellular content (CC), hemicellulose (Hem), lignin, cellulose, and dry matter digestibility (DMD) in the community during the growing season in the upper (□), middle (O), and lower (Δ) zones of slope. Symbols are means of 2 sampling sites. Bars (I) are standard errors of the differences for comparison between slope positions. Where no error bars are visible, standard errors are smaller than the diameters of the symbol. The dotted line indicates critical values recommended for cattle nutrition.

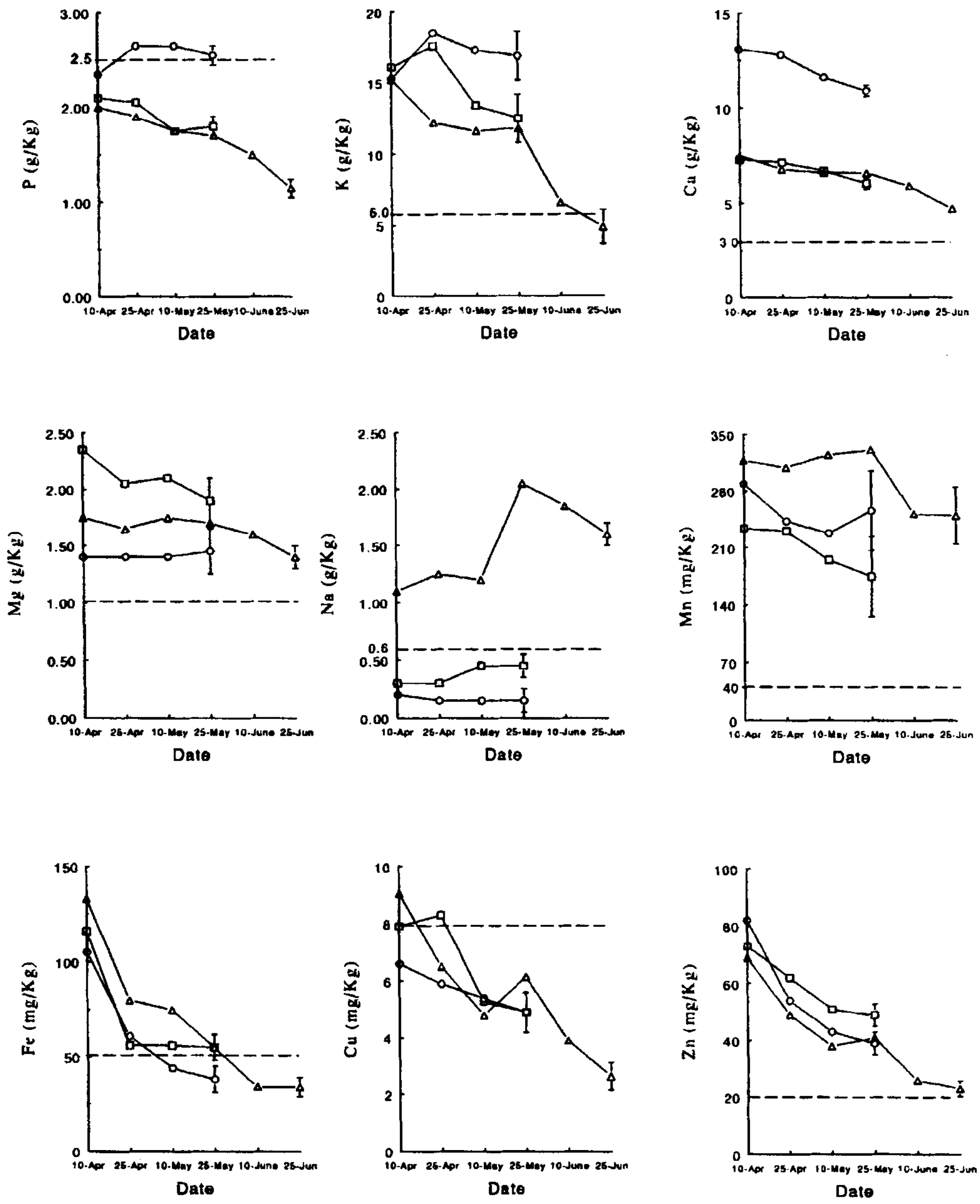

Fig. 4. Mineral concentrations in the community during the growing season in the upper (□), middle (O), and lower (Δ) zones of slope. Symbols are means of 2 sampling sites. Bars (I) are standard errors of the differences for comparison between slope positions. The dotted line indicates critical values recommended for cattle nutrition.

protein, cellulose and DMD levels at the same respective sampling. The middle zones stood out by virtue of their lower hemicellulose and higher cellular contents. Differences in nutritional quality between slope positions, as indicated by protein and DMD, were related to differences in phenology and botanical composition (Lyttleton 1973, Norton 1982, Pérez Corona et al. 1995). Due to their lower DMD and protein content, annuals, and other early maturing species tend to decrease grassland quality (Biddiscombe 1987). In our study, pasture matured earlier on the upper zones than on the lower zones and annual species were more frequent on the upper and middle parts of slopes (Pérez Corona 1993).

Plant Ca, Fe, Cu, and Zn contents in the community varied significantly ($P < 0.05$) with the sampling date (Table 1) and decreased with time (Fig. 4). The concentrations of P, K, Mg, and Mn in the community did not change significantly as the growing season progressed. This suggests that P, K, Mg, and Mn are not retranslocated to below ground structures as the season progressed. Ca contents changed seasonally, contrary to the results of Georgiadis and McNaughton (1990) in savannah grasslands. The absence of a fixed pattern in Na concentrations may be related to its non-essential nature for plants.

The effect of the topographic gradient was different for each mineral element. Thus, Mg contents were higher on the upper

Table 2. Coefficients associated with mineral elements and fibre properties for significant variance in a stepwise multiple regression analysis of the production (as dependent variable).

Regression equation	R^2
Production = 267 + 1447 Na-622 Mg-1.6 Fe	0.79
Production = -449 + 25 Cellulose	0.68

Level of significance $P < 0.05$.

zones; P and Ca on the middle; Na and Fe on the lower zones of slope; and K, Mn, and Zn were not affected by slope position (Table 1; Fig. 4). These differences in mineral contents of the vegetation between slope zones reflect differences in the botanical composition between slope zones (Vázquez de Aldana et al. 1993) since legumes and forbs usually have higher mineral content than grasses. The higher Na concentrations on the lower zone pastures than on the upper and middle zones may be related to subterranean lateral movement of the highly soluble Na which accumulated in the soil of lower zones (this study; Vázquez de Aldana 1993).

Relationships between Fibre, Mineral Elements, Protein and Biomass Production

Stepwise multiple regression analyses were performed to quantify the interrelationships between grassland biomass production, the mineral elements and the fibre properties as independent variables (Table 2). The concentrations of 3 mineral elements in pasture tops were associated with biomass production: Mg (negatively), Na (positively), and Fe (negatively). Cellulose was the only fibre property significantly related to production. This indicates that biomass production varied over the growing season at different topographic positions as cellulose content does it.

Correlation coefficients between DMD, organic, and mineral contents are shown in Table 3. Protein and DMD were positively correlated with K, Fe, Cu, and Zn contents. DMD was also positively correlated with P and Ca. CC was negatively correlated only with Na and positively with P, K, Ca, Cu, and Zn. The lignin content had significant negative correlation coefficients only. None of the organic variables had significant correlation coefficients with Mg or Mn contents.

In general, the mineral element contents were positively correlated to variables that increase with grassland quality (protein, CC, DMD) and negatively correlated to variables that decrease with forage quality (cellulose, hemicellulose, lignin). The results could support some physiological evidence. For example, Cu is an important enzyme co-factor located in the cytoplasm of plants (Spears 1994) and its concentration was expected to vary with crude protein. The negative correlation coefficients between mineral elements and cell wall components and the positive correlation coefficients between mineral elements and cell content variables suggest that mineral elements are located in the cytoplasm or vacuole and not in the cell walls. However, larger amounts of Ca, Mn, Zn, and Cu are present in the cell walls of different grassland species (Whitehead et al. 1985). Calcium is an important structural element of the cell wall and is present in the form of calcium pectate. This suggests that the results of the correlation analysis may be related to similar patterns of temporal change since protein, CC, DMD, and most of mineral element concentrations tended to decrease as the growing season progressed while lignin, cellulose, and hemicellulose tended to increase. The positive relationship between Na and cellulose and hemicellulose could be related to the similar variation in their concentrations between slope positions: compared to the upper and middle, the lower zones have higher proportions of grasses, which have higher cellulose and hemicellulose contents than legumes and forbs (Pérez Corona et al. 1994), and higher Na contents in the botanical groups (Vázquez de Aldana et al. 1993).

Nutrient Status of Grassland in Relation to Animal Nutrition

Figures 3 and 4 show (dotted line) the concentrations below which the samples were deficient for beef cattle. The critical digestibility is based on Rico Rodríguez and García Criado (1985), and cattle mineral requirements are based on ARC (1980). Digestibility, intake and the energetic efficiency of ruminants have been used as an estimate of the nutritional value of grasslands (Gill et al. 1989). Milford and Minson (1966a) showed that 7% is the minimum protein concentration for maintaining intake and adequate digestion (Milford and Minson 1966b). Mineral deficiencies may depress feed intake (Provenza 1995). Pasture production also limits intake (Christian 1987). With less than 500–600 kg/ha of DM on offer (regardless of how high the nutritive value), cattle may not be able to obtain intake at a maintenance level. Therefore, protein contents, digestibility, biomass production and mineral contents should all be included in guidelines for efficient pasture management.

In general, protein, K, Ca, Mg, Mn, and Zn in the 3 zones and over the season provided adequate nutrition for cattle (Figs. 3 and 4). However, the upper and middle zones were deficient in Na and DMD, and P was deficient in the upper and lower zones. P deficiency is widespread due to low available P levels in soils (Underwood 1981, Montalvo et al. 1982). Fe and DMD became deficient at the end of the season while Cu was below the critical value in samples from the 3 zones. Cu deficiency in grazing ruminants is also widespread in many areas, and is mainly induced by Cu antagonists such as Mo, S, and Fe (Spears 1994).

Table 3. Correlation coefficients between organic parameters and mineral element contents.

	Protein	CC	Hemicellulose	Cellulose	Lignin	DMD
P		0.78**	–0.74**	–0.72**		0.39*
K	0.42*	0.71**	–0.62**	–0.69**		0.48**
Ca		0.81**	–0.78**	–0.71**		0.39*
Mg						
Na		–0.86**	0.89**	0.77**	–0.38*	
Mn						
Fe	0.55**			–0.48**	–0.44*	0.46*
Cu	0.73**	0.43**		–0.54**	–0.48**	0.63**
Zn	0.56**	0.65**	–0.45**	–0.77**		0.44*

Level of significance: **$P < 0.01$;*$P < 0.05$; missing values were not significant.

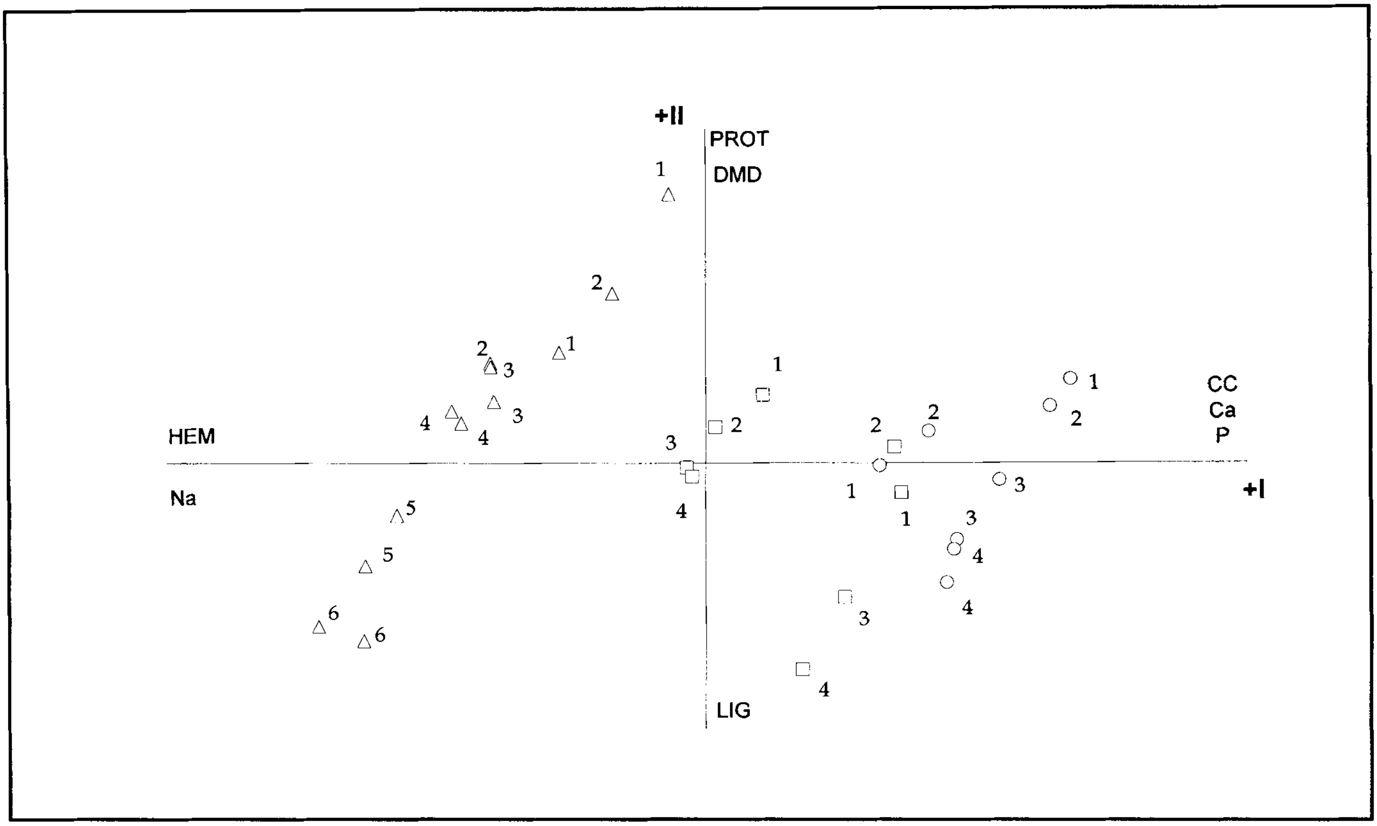

Fig. 5. Ordination of the samples in the factorial plane defined by axis I and II of principal component analysis (PCA). Variables accounting for high weight in each axis are indicated (CC = cellular content; Ca = calcium; P = phosphorus; HEM = hemicellulose; Na = sodium; PROT = protein; DMD = dry matter digestibilty; LIG = lignin). Zones of slope: upper (❑), middle (O), and lower (Δ). Numbers indicate harvest (1 = 10 April; 2 = 25 April...).

Dry matter production or accumulative total of annual pasture growth reached its maximum at the end of the season (Fig. 1) when the pasture quality was at its lowest.

Ordination of Grassland Samples by Organic Content and Mineral Composition

The ordination of the grassland samples on the factorial plane delimited by the first and second PCA axes is shown in Figure 5. Component I accounted for 45.5% of the total variance of the data. This first principal component is interpreted as representing the topographic gradient: samples from the upper and middle zones were positioned on the positive side and were correlated with cellular content, P, and Ca concentrations whereas samples from the lower zones were positioned on the negative side of the axis and were correlated with hemicellulose and Na contents. The second principal component accounted for 22.5% of the total variance. The variables with a high weight on this axis were protein and DMD on the positive part, and lignin on the negative part. This second axis was related to phenological development. Earlier samples were located on the positive side of the axis (high protein content) whereas samples harvested at the end of the season were generally on the negative side (high lignin content).

The results indicate that grassland quality is mainly determined by the phenology of the pasture components and its effect on temporal evolution (component II) of the organic variables since earlier samples have greater protein content and DMD which are positively correlated with grassland quality. Samples of different zones positioned by the topographic gradient (component I) were not related to the main variables which determine forage quality. However, the first component would be a useful tool in determining sample differentiation along the topographic gradient. The results showed that most of the variation in mineral content was related to the topographical gradient which means in turn that mineral deficiencies for cattle (when they occur) are related to slope zones and not to the phenological development (e.g. P in the upper and lower zones, and Na in the upper and middle zones Fig. 4).

Conclusions

Nutritional value of feed-on-offer indicated by organic, mineral, and DMD values, declined as the growing season progressed. There was a strong influence of slope position on these parameters. The upper and middle zones, which mature earlier than the lower zones, were lower in quality (low protein, DMD), higher in the proportion of cell wall compounds, and higher in P and Ca concentrations.

The Dehesa system seems to fulfill the requirement of cattle for organic and most essential minerals, especially at the beginning of the growing season. Although there is spatial variation of biomass production, organic contents, and mineral contents, it seems that grassland quality is mainly determined by the temporal evolution of the organic variables (protein content, DMD and lignin). Temporal variation is also the factor most likely to cause critical deficiency in DMD and Fe whereas the topographical gradient is more likely to explain deficiency for P and Na. Thus, both spatial and temporal dynamics of production and grassland nutritional quality should be taken into account in developing better management strategies. Based on our findings, we recommend fence construction to separate the upper and middle zones from the lower zone as a management procedure which could optimize livestock performance in these semiarid grasslands. Upper and middle zones, which mature earlier and have shorter cycles than the lower zones, should be grazed earlier in the season than the lower zones. This management procedure would ensure that cattle consume pasture on each zone when quality is at its peak.

Literature Cited

Agricultural Research Council (ARC). 1980. The nutrient requirements of ruminant livestock. CAB, Farnham Royal.

Angell, R.F., R.F. Miller, and M.R. Haferkamp. 1990. Variability of crude protein in crested wheat grass at defined stages of phenology. J. Range Manage. 43: 186–189.

Ballard, R.A., R.J. Simpson, and G.R. Pearce. 1990. Losses of digestible components of annual ryegrass (*Lolium rigidum* Gaudin) during senescence. Aust. J. Agr. Res. 41:719–731.

Biddiscombe, E.F. 1987. The productivity of mediterranean and semiarid grasslands. p. 19–25. *In*: R.W. Snaydon (ed.). Ecosystems of the World 17B. Managed grasslands. Analytical studies. Elsevier Sci. Publ., Amsterdam.

Casado, M.A., J.M. De Miguel, A. Sterling, B. Peco, E.F. Galiano, and F.D. Pineda. 1985. Production and spatial structure of mediterranean pastures in different stages of ecological succession. Vegetation 60:75–86.

Christian, K.R. 1987. Matching pasture production and animal requirements. p. 463–476. *In*: J.L. Wheeler, C.J. Pearson and G.E. Robards (eds.). Temperate pastures; their production, use and management. CSIRO, Australia.

Díaz Pineda, F. 1989. Ecologia: Ambiente Fisico y Organismos Vivos. Sintesis, Madrid.

Díaz Pineda, F. and B. Peco. 1988. Pastizales adehesados del area de El Pardo. Mundo Cientifico 79:386–395.

Duque Macías, F. 1971. Determinacion conjunta de P, K, Ca, Mg, Fe, Mn, Cu, y Zn en plantas. An. Edafol. Agrobiol. 30:207–229.

Georgiadis, N.J. and S.J. McNaughton. 1990. Elemental and fibre contents of savanna grasses: variation with grazing, soil type, season and species. J. Appl. Ecol. 27:623–634.

Gill, M., D.E. Beever, and D.F. Osbourn. 1989. The feeding value of grass products. p. 89–130. *In:* W. Holmes (ed.) Grass: its production and utilization. Blackwell Scientific Publ., Oxford.

Goering, H.K. and P.J. Van Soest. 1970. Forage fiber analysis. Agr. Handb. Nß 379. USDA-ARS. Washington, D.C.

Jaramillo, V.J. and J.K. Detling. 1992. Small-scale heterogeneity in a semiarid North American grassland. 1. Tillering, N uptake and retranslocation in simulated urine patches. J. Appl. Ecol. 29:1–8.

Kirby, D.G., D.M. Green, and T.S. Mings. 1989. Nutrient composition of selected emergent macrophytes in Northern prairie wetlands. J. Range Manage. 42:323–326.

Lyttelton, J.M. 1973. Proteins and nucleic acids. p. 63–103. *In*: G.W. Butler and R. Bailey (eds.). Chemistry and Biochemistry of Herbage. Vol. 1. Academic Press, London.

McDowell, L.R. 1985. Nutrition of grazing ruminants in warm climates. Academic Press, Orlando.

Milford, R. and D.J. Minson. 1966a. The feeding value of tropical pastures. p. 106–114. *In:* W. Davies and C.L. Skidmore (eds.). Tropical pastures. Faber and Faber, London.

Milford, R. and D.J. Minson. 1966b. Intake of tropical pasture species. p. 815–822. *In*: Proc. 9th Int. Grassl. Cong., Sao Paulo.

Montalvo, M.I., B. García, and J.M. Gómez. 1982. Producción y composición mineral en pastizales de zona semiárida. II. Majadales. Stud. Oecologica 3:181–200.

Norton, B.W. 1982. Differences between species in forage quality. p. 89–110. *In:* J.B. Hacker (ed.). Nutritional limits to animal production from pastures. CAB, Farnham Royal.

Pearson, C.J. and R.L. Ison. 1987. Vegetative Growth. p. 28–47. *In:* C.J. Pearson and R.L. Ison (eds.). Agronomy of grassland systems. Cambridge Univ. Press, Cambridge.

Pérez Corona, M.E. 1993. Producción de biomasa aérea neta y calidad nutricional de pastizales semiáridos. Desarrollo y aplicación de la tecnología NIRS en estudios ecológicos. Ph.D. Thesis. Univ. Complutense Madrid, Madrid.

Pérez Corona, M.E., B. García-Criado, B.R. Vázquez de Aldana, and A. García-Ciudad. 1994. Effect of topographic and temporal (maturity) gradients on the nutritive quality of semiarid herbaceous communities. Commun. Soil Sci. Plant Anal. 25:2047–2061.

Pérez-Corona, M.E., A. García-Ciudad, B. García-Criado, and B.R. Vázquez de Aldana. 1995. Patterns of aboveground herbage production and nutritional quality structure on semiarid grasslands. Commun. Soil Sci. Plant Anal. 26:1323–1341.

Provenza, F.D. 1995. Postingestive feedback as an elementary determinant of food preference and intake in ruminants. J. Range Manage. 48:2–17.

Rico Rodríguez, M. and B. García Criado. 1985. Ordenacion de especies dominates en pastizales salmantinos segun su calidad nutricional. Anu. Cent. Edafol. Biol. Apl. Salamanca 11:311–325.

Spears, J.W. 1994. Minerals in forages. p. 281–317. In: C.G. Fahey, Jr. (ed.). Forage quality, evaluation and utilization. Amer. Soc. Agron., Inc., Madison, Wisc.

Underwood, E.J. 1981. The mineral nutrition of livestock. CAB, Slough, England.

Van Soest, P.J. 1982. Nutritional ecology of the ruminant. O & B Books Inc., Oregon.

Vázquez de Aldana, B.R. 1993. Elementos minerales en comunidades de pastizal. Desarrollo y aplicación de la tecnología NIRS para el analisis rápido. Ph.D. Thesis. Univ. Salamanca, Salamanca.

Vázquez de Aldana, B.R., A. García Ciudad, E.P. Corona, and B. García Criado. 1993. Elemental content in grassland of semiarid zones: effect of topographic position and botanical composition. Commun. Soil Sci. Plant Anal. 24:1975–1989.

Whitehead, D.C., K.M. Goulden, and R.D. Hartley. 1985. The distribution of nutrient elements in cell wall and other fractions of the herbage of some grasses and legumes. J. Sci. Food Agr. 36:311–318.