Full text DOI
10.1046/j.1365-2494.2000.00217.x

Vázquez de Aldana B.R., García Ciudad A., Pérez Corona M.E., García Criado B. 2000. Nutritional quality of semi-arid grassland in western Spain over a 10-year period: changes in chemical composition of grasses, legumes and forbs. *Grass and Forage Science*, 55: 209-220.

Nutritional quality of semi-arid grassland in western Spain over a 10-year period: changes in chemical composition of grasses, legumes and forbs

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Received 8 October 1998; revised 19 July 1999

Abstract

From 1987 to 1996, nutritional quality of the main botanical components (grasses, legumes and forbs) in semi-arid grasslands in the dehesa ecosystem in western Spain was analysed. Herbage samples were collected at the end of spring season, in 30 locations, at two different topographic positions (upper and lower slope zones). Herbage mass over 2 cm and proportion of botanical components were estimated and samples were analysed for crude protein, neutral-detergent fibre (NDF), hemicellulose, cellulose, lignin and *in vitro* dry matter digestibility (DMD). Analysis of variance revealed a significant effect of sampling year on the herbage mass, proportion of botanical components and their nutritional quality. The three botanical groups followed similar year-to-year trends in their crude protein, cellulose and lignin contents and *in vitro* DMD. Herbage mass was not significantly related to any meteorological variables, suggesting that inter-annual variation in biomass production of botanically complex pastures cannot be explained by a single factor. However, annual precipitation was significantly related to the proportion of the botanical group which was dominant at each slope zone: grasses in the lower zone and forbs in the upper zone. In the upper zone spring precipitation explained part of the inter-annual variation in the NDF, cellulose, lignin contents and *in vitro* DMD of the botanical components.

Introduction

Semi-arid grasslands located in the central, western and south-western Iberian Peninsula form part of the "Dehesa" ecosystems which occupy more than 5,500,000 hectares. These grasslands are semi-natural pastures maintained by grazing, burning, ploughing and other traditional management practices (e.g. pruning of oak-trees) that have not allowed woodland to regenerate in the ecosystem. Nowadays, Spanish semi-arid grasslands maintain more than 500,000 head of cattle under extensive management (Miguel and Gómez-Sal., 1992). These grasslands not only provide forage for domestic herbivores but they also perform other functions, such as, to be specific habitats for wild flora and fauna, to provide a protective land cover and to add diversity to the aesthetic value of the landscape.

Quantity and quality of forage produced are primary determinants of the level of livestock production derived from grazing lands (Heitschmidt *et al*., 1995). It is known that forage production varies with several ecological factors. Regional variability of above-ground biomass production in grasslands has been related to climatic variables (Naveh, 1982; Sala *et al*., 1988), disturbances such as fire, and management (Milchunas *et al*., 1989; Smith *et al.,* 1996). At more reduced spatial scales, additional factors such as topographic relief and soil texture need to be considered (Briggs and Knapp, 1995; Pérez Corona *et al*., 1995). Forage quality is commonly evaluated by laboratory analysis for crude protein, fibre and digestibility. Generally, the quality of grasslands for livestock production is a result of the species present, amount of forage available, and chemical and physical characteristics of each species. Several studies have shown that forage nutritional quality varies with topographic relief, botanical composition, soil characteristics, climate, season and management (Lyttelton, 1973; Morrison, 1980;

Norton, 1982; Papanastasis and Koukoulakis, 1988; Angell *et al*., 1990; Georgiadis and McNaughton, 1990; Pérez Corona *et al*., 1994). The topographic gradient is an important factor influencing structural and functional characteristics of plant communities in the dehesa system, such as primary production, nutritional quality and plant mineral content (Pérez Corona *et al*., 1995; Vázquez de Aldana *et al*., 1996). So far, few studies have considered long-term variations of nutritional quality apart from our previous study on the interannual variations of herbage samples (Vázquez de Aldana *et al*., 1998). There is a clear need for long term studies: for most vegetation types, the analysis of the effects of changing climate and/or disturbance regimes is difficult because changes and responses take place over time scales of decades, centuries or even millennia (Hobbs and Mooney, 1995).

Grasslands from the dehesa system are characterised by a great diversity of species (Marañón, 1985). In these botanically-complex grasslands, there are interspecific ecological relationships that control the growth and maturity of each species so that the effective nutritive value of grasses and legumes in mixed permanent meadows may be different from that in monocultures. The general objective of this study was to estimate over a 10-year period the nutritional quality of semi-arid grasslands in relation to the main botanical groups (grasses, legumes and forbs). Specific objectives were: (1) to evaluate the effect of year-to-year variation on the herbage mass production and the chemical composition of grasses, legumes and forbs; (2) to determine whether inter-annual variations in chemical composition are affected by the topographic position; and (3) to evaluate the relationships between climatic variables, herbage mass, proportion of botanical groups and nutritional quality of botanical groups.

Material and methods

Study area

Research was conducted in the dehesa area of Salamanca province (western Spain) which is located between 40º30´ and 41º15´ N and 5º25´ and 6º30´ W. The dehesa system occurs on gently undulating hills and features low-density *Quercus ilex* ssp. *rotundifolia* with a semi-natural grassland. Land is mainly used for extensive grazing with beef, bull-fighting cattle but Iberian pigs and game animals (deer, rabbits, hares, etc.) are also consumers of the dehesa primary production resources. The grassland substrate is mainly siliceous with many slate or granitic zones. Overall, soils are district cambisols (García, 1987). The climate is dry supra-Mediterranean with cold winters and dry, warm summers. The average annual rainfall is around 500 mm, with considerable variation throughout the year (Figure 1). The study area is defined by landscape and functional units, called slopes. These slopes are characterized by fertility gradients which are a function of soil nutrient and water availability. Topographic gradients result in differences in species composition of the grassland.

Sample collection

Thirty-seven gentle slopes were identified within the dehesa area (Figure 2) and 30 of the 37 were selected at random each year for sampling. On each slope two zones were differentiated: upper and lower zones. The slope lengths were approximately 100 m and the altitude differences between zones were approximately 15 m. On each zone sampling was made at the end of the spring season (June) for eight years: 1987-1996 (1990 and 1992 excluded). Samples were collected at the flowering-fruiting stage; those obtained from the upper zones were at a later stage of ripening than those from the lower zone. In all cases sampling was made by cutting the herbaceous vegetation in four randomly selected quadrats (0.50 m × 0.50 m) to 2 cm above ground level. Those plant species present in the quadrats with a cover value above 15% were considered as dominant plant species (Table 1). Each sample was manually sorted into three botanical groups; grasses, legumes and forbs. Dry weights were determined by drying samples at 60ºC for 48 h in a forced-air oven. The proportion by oven-dry weight of each botanical group was calculated. Samples were ground in a Retsch ZM1 mill (Haan, Germany) with a 0.5 mm mesh sieve and stored in polyethylene bags before analysis.

Chemical analysis

Each sample was analysed for: crude protein (by the Kjeldahl distillation method) neutral-detergent fibre (NDF), hemicellulose, cellulose, lignin and *in vitro* dry-matter digestibility (DMD) (using the methods described by Goering and Van Soest, 1970).

Statistical analysis

The data were analysed statistically by two-way analysis of variance (ANOVA) using STATISTICA 4.3 (StatSoft, Inc, 1993), for the effects of slope zone, sampling year and their interaction. Barlett´s test for homogeneity of variance and Kolmogorov-Smirnoff test for normality were used but no transformation of the data were needed. Least square differences (LSD) were used to determine significant differences among means when significant ANOVA results occurred. Correlation analysis was used to analyse relationships between chemical composition variables.

Meteorological variables were obtained from five local weather stations (province of Salamanca). The longest distance between a weather stations and a sampling location was 10 km. Data from the five weather stations were combined and mean values were used for statistical analysis. The following climatic variables were used: total annual precipitation, seasonal precipitation (winter, spring, summer, autumn), mean annual daily temperature, and mean seasonal daily temperatures. Total annual precipitation and mean annual daily temperature were calculated from 1 October of the year previous to sampling to 30 September of the sampling data year; autumn precipitation and temperature were calculated for the year previous to the sampling data. The relationships between these variables and herbage mass, proportion of botanical components, and nutritional quality variables were tested using linear regression over mean values of each of the botanical group and each of the slope zones.

Results and discussion

Herbage mass and proportion of botanical components

Dry-matter production was significantly ($P<0.001$) higher in the lower slope zones than in the upper ones (Figure 3). The influence of topographic position on biomass production has been shown previously (Milchunas *et al.*, 1989; Pérez Corona *et al.*, 1995) and is related to differences in soil fertility between slope zones (Schimel *et al.*, 1985; Burke *et al.*, 1995). In the lower slope zone, the highest mean herbage mass was recorded in 1996 and in the upper zone the highest value was recorded in 1988; the interaction effect (zone × year) was significant ($P<0.001$). However, there was a significant correlation ($r=0.45$, $P<0.05$) between herbage mass in upper and lower zones across years. The variation in herbage mass between years was greater in the upper than in the lower zones.

Figure 4 shows mean values of the proportion (oven dry weight) of the three botanical groups of the grassland: grasses, legumes and forbs. Over all sampling years, in the lower zone the major contribution to the herbage mass over 2 cm was by grasses and in the upper zone was by forbs. The relative contribution of the legumes was greater in the lower than in the upper zone ($P<0.05$).

There was a significant effect of year ($P<0.05$, Table 2) on the proportion of botanical components. The effect of the interaction zone × year on the proportion of grasses and forbs was not significant. The differences in proportion of legumes between zones varied among years (zone × year, $P<0.001$). Thus, in 1987 the proportion of legumes was higher ($P<0.05$) in the upper zone but in 1989-91-93-95 it was higher in the lower zone. Silvertown *et al.* (1994) suggested that variations in botanical composition over years were related to changes in environmental variables, such as precipitation and temperature, through preferential effects on some species.

Chemical composition and digestibility

Grasses, legumes and forbs had significantly higher ($P<0.001$, Figure 5) crude protein contents on the lower than on the upper slope zone. These differences in the crude protein content have been related to differences in soil characteristics (Vázquez de Aldana *et al.*, 1996) and to differences in phenological stages. The lower zones have better growth conditions and plants on these zones are maintained for a longer growing period (Puerto *et al.*, 1985). Given that the crude protein content declines with stage of maturation (Kirby *et al*., 1989; Pérez Corona *et al*., 1994), it is possible that the greater crude protein content in the lower zone partly reflects a later maturation stage of plant species.

There were significant effects of year ($P<0.001$, Figure 5) and of the interaction of zone × year (Table 3) on the crude protein content of grasses, legumes and forbs. In the lower zone, all three botanical groups had the greatest crude protein content in 1991 and 1993. Analysis of variance showed that the differences in the crude protein content between slope zones were not affected by years and the sign of the difference was maintained over all years. By contrast, the differences between years were affected by the zone of slope ($P<0.05$). These results and the significant correlation coefficients between zones (Table 4) suggest that the inter-annual variation in crude protein content of grasses, legumes and forbs follow similar patterns in both slope zones. Also according to correlation coefficients between the protein content of botanical components across sampling years (Table 5), it appears that in both slope zones inter-annual variations followed the same trend in grasses, legumes, and forbs.

The mean NDF contents of grasses and legumes were significantly higher ($P<0.001$, Figure 6) in the upper than in the lower zone but the differences in NDF content of forbs between slope zones was not significant ($P>0.05$). The NDF contents of botanical groups differed significantly ($P<0.001$, Table 3) among years. In the lower zone, grasses, legumes, and forbs had the highest mean values of NDF content in 1996. The stage of maturity of plants or age of tissue has been related to the NDF content which increases in older tissue (Pérez Corona *et al.*, 1994; Heitschmidt *et al.*, 1995). The differences among years may be attributed partially to differences in maturity of plants at the time of harvest which could be affected by climatological factors. There were significant correlation coefficients ($P<0.001$, Table 4) between the upper and lower zones of the NDF content of the three botanical groups. In both slope zones there were significant correlation coefficients between the NDF content of grasses, legumes and forbs except between legumes and forbs in the lower zone (Table 5). These results suggest that the NDF content in the three botanical components varies in a similar pattern across years.

Grasses and legumes had a significantly (*P*<0.01, Figure 7) greater hemicellulose content in the upper than in the lower slope zone. The hemicellulose content of the three botanical groups differed among years (*P*<0.001). There was a significant effect of the interaction zone × year on the hemicellulose content of forbs (*P*<0.001) and the differences between zones varied with year but the effect of zone was not significant (Table 3). There was a significant positive correlation between hemicellulose contents of legumes and forbs in the upper zones but a significant negative correlation in the lower zone (Table 5).

Legumes had a greater (P<0.001) cellulose content in the upper zone but there was no significant effect of zone on the cellulose contents of grasses and forbs (Figure 8). The effect of year on the cellulose content of the three botanical components was significant (*P*<0.001, Table 3). In the lower zone, grasses and legumes had the highest mean cellulose content in 1988 and 1996. In both zones, forbs had the highest mean value in 1996. The significant correlation coefficients between the cellulose contents of grasses, legumes and forbs in upper and lower zones (Table 4) suggest that in both zones the cellulose contents followed similar trends through years. In both the upper and lower zones there were significant correlation coefficients between cellulose content of grasses, legumes and forbs (Table 5).

The lignin content of grasses, legumes and forbs differed significantly between topographical zones (*P*<0.01, Figure 9) with the upper having a greater mean value than the lower zone. This is partly consistent with the results of previous studies on semi-arid grasslands in the same area (Pérez Corona *et al*., 1995) that showed a significant effect of the slope zone on the lignin content of botanical components except legumes. The lignin content of grasses, legumes and forbs differed significantly (*P*<0.001) among years. In all three botanical groups the lowest mean value was recorded in 1991 (Figure

9), when the lowest spring precipitation was recorded (Figure 1). Lignin content of grasses, legumes and forbs was significantly correlated between upper and lower zones (Table 4) suggesting similar year-to-year variations on both slope zones. In the upper and lower zones of the slope, the lignin content of each of the botanical groups was significantly correlated to that of the other groups (Table 5), suggesting a similar yearly variation of the lignin content in the three botanical groups.

The *in vitro* DMD of grasses, legumes and forbs was significantly (P<0.01) greater in the lower than in the upper zone (Figure 10). There were inter-annual differences in the *in vitro* DMD of the three botanical fractions (P<0.001). In all cases, the highest *in vitro* DMD value was reached in 1991 when the NDF and lignin contents were lowest. These results are consistent with those of Van Soest (1982) who indicated that interannual variations in DMD are mainly related to those of crude protein, fibre and lignin. The correlation coefficients (Table 4) suggest that the *in vitro* DMD values of grasses, legumes and forbs showed similar trends in the upper and lower zones through years. There were significant correlation coefficients among *in vitro* DMD values of grasses, legumes and forbs in both slope zones (Table 5) indicating that, across years, the *in vitro* DMD followed a similar trend in the three groups.

Effect of meteorological variables on herbage mass, botanical composition and nutritional quality of botanical groups

Autumn precipitation, summer precipitation, mean daily winter temperature and mean daily summer temperature were not significantly related to herbage mass, proportion of botanical components, or any aspect of chemical composition. Futhermore, linear regression analysis did not disclose any other significant relationship between herbage mass over 2 cm and climatic variables. Similarly, Gutman *et al.* (1990) concluded that the herbage production of Mediterranean grasslands in Israel was not sensitive to total precipitation and they suggested that level of production may be determined mainly by the seasonal patterns of soil moisture availability in a restricted rooting zone. On the other hand, inter-annual variations in above-ground biomass production have been related to annual precipitation in an annual rangeland in California (Duncan and Woodmansee, 1975), and to seasonal water evaporation in a Kansas tallgrass prairie (Abrams *et al.*, 1986). Our results for semi-arid Mediterranean grassland, which are characterized by a high species richness, showed an absence of significant relationship between herbage mass over 2 cm and single factors such as precipitation or temperature. This is consistent with the idea that patterns of production in permanent grasslands with a complex botanical composition are a product of spatial and temporal variability in light, water and nutrients driven by a combination of topography and climate (Briggs and Knapp, 1995).

Annual precipitation was positively related ($P<0.01$) to the proportion of grasses from the lower zone and negatively related ($P<0.05$) to the proportion of forbs from the upper zone (Table 6). This means that grasses and forbs had a different response to precipitation in different slope zones. It seems that an increase in water availability favoured the proportion of grasses and reduced that of forbs on the lower and upper zones, respectively, where each botanical component comprises the largest proportion of the pasture. Forbs have been found to be favoured when soil moisture conditions are low (Briggs and Knapp, 1995), suggesting that forbs are more limited by biotic interactions that by abiotic factors. Hufstader (1976) reported that precipitation was related to the proportion of dominant species in the Californian grasslands, whilst the proportion of subdominant species was related to competition for light and variable germination time. This is consistent with our results.

In the upper zone, mean annual temperature was positively related to the proportion of grasses and negatively related to the proportion of legumes (Table 6). In the lower zone, mean spring temperature was negatively related to the proportion of legumes which could be attributable to a direct effect of temperature on the legume growth or to an indirect effect through favourable conditions for grasses, especially since grasses were the highly dominant group.

The nutritional quality variables of botanical groups were mainly related to spring precipitation (Table 6). Annual precipitation was related (negatively) to only crude protein content of grasses and forbs. In the upper zone, spring precipitation was significantly positively related to NDF and lignin contents of the three botanical fractions, to cellulose of grasses and forbs, and negatively related to *in vitro* DMD of grasses, legumes and forbs. This occurred only in the upper zones of the slopes, where the soil water content is low and consequently plants are more likely to be limited by water availability than in the lower zones (Puerto *et al*., 1985). These results suggest that the inter-annual variability in chemical composition of grasses, legumes and forbs explained by spring precipitation was affected by the slope position with the lower zones responded in a lesser extent. The results of correlation analysis between upper and lower zones of nutritional quality variables (Table 4) suggested that in both zones chemical composition followed similar trends through years. However, part of the inter-annual variation of chemical composition was explained by spring precipitation in the upper but not in the lower zone. This suggests that part of the inter-annual variation, which is explained by spring precipitation, could explain differences between slope zones.

In the upper zone, fibre contents of grasses, legumes and forbs decreased and *in vitro* DMD increased with increasing spring rainfall. Most of the papers reviewed by

Wilson (1982) indicated that low soil moisture has either no effect or increases the digestibility of the pasture and leaf and stem material. Water stress with minimal associated heat stress often improves forage nutritive quality because moisture stress slows growth and delays stem development resulting in leafier swards of higher digestibility (Nelson and Moser, 1994). This could explain the negative relationship between measures of nutritional quality and spring precipitation in the present study, since in spring there is minimal heat stress in the dehesa ecosystem.

Conclusions

The inter-annual differences in the herbage mass over 2 cm of the Mediterranean dehesa grasslands, at the en of June, in Spain cannot be explained by any single climatological factor. This could be attributed to the complexity of the botanical composition of the grassland and the multiplicity of factors controlling the growth and maturity of species. However, annual precipitation was significantly positively related to the proportion of the dominant botanical group in both upper and lower slope zones.

As indicated by correlation analysis, part of the inter-annual variation in chemical composition of grasses legumes and forbs was similar in the upper and lower zones. However, the part of the inter-annual variability in chemical composition of grasses, legumes and forbs explained by spring precipitation was affected by the position in the slope. In the upper zone, spring precipitation could explain most of the year-to-year variation in NDF, cellulose, lignin contents and *in vitro* DMD of grasses, legumes and forbs while in the lower zones the response was much less. The different response in the two zones could be related to the lower soil moisture contents in the upper parts of the slopes.

Acknowledgments

We are grateful to L. García, J.C. Estévez and M. Hernández for practical assistance. This work was financially supported by the Directorate General for Agriculture of the European Union (Contract 8001-CT90-0021) and the Spanish "Comisión Interministerial de Ciencia y Tecnología" (C.I.C.Y.T.; AGF96-0423).

References

ABRAMS M.D., KNAPP A.K. and HULBERT L.C. (1986) A ten-year record of aboveground biomass in a Kansas tallgrass prairie: effects of fire and topographic position. *American Journal of Botany*, **73**, 1509-1515.

ANGELL R.F., MILLER R.F. and HAFERKAMS M.R. (1990) Variability of crude protein in crested wheat grass at defined stages of phenology. *Journal of Range Management*, **43,** 186-189.

BRIGGS J.M. and KNAPP A.K. (1995) Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position and fire as determinants of aboveground biomass. *American Journal of Botany*, **82**, 1024-1030.

BURKE I.C., ELLIOT E.T. and COLE C.V. (1995) Influence of macroclimate, landscape position, and management on soil organic matter in agroecosystems. *Ecological Applications*, **5**, 124-131.

DUNCAN D.A. and WOODMANSEE R.G. (1975) Forecasting forage yield from precipitation in California´s annual rangeland. *Journal of Range Management*, **28**, 327-329.

GARCÍA A. (1987) *Mapa de suelos de Castilla-Leon*. Valladolid: Junta de Castilla León.

GEORGIADIS N.J. and MCNAUGHTON S.J. (1990) Elemental and fibre content of savannah grasses. Variation with soil type, season and species. *Journal of Applied Ecology*, **27**, 623-634.

GOERING H.K. and VAN SOEST P.J. (1970) *Forage Fiber Analysis. Agricultural Handbook nº 379*. Washington DC: United States Department of Agriculture.

GUTMAN M., SELIGMAN N.G. and NOY-MEIR I. (1990) Herbage production of

Mediterranean grassland under seasonal yearlong grazing systems. *Journal of Range Management*, **43**, 64-68.

HEITSCHMIDT R.K., GRINGS E.E., HAFERKAMP M.R. and KARL M.G. (1995) Herbage dynamics on 2 northern great plains range sites. *Journal of Range Management*, **48**, 211-217.

HOBBS R.J. and MOONEY H.A. (1995) Spatial and temporal variability in California annual grassland: results from a long-term study. *Journal of Vegetation Science*, **6**, 43-56.

HUFSTADER R.W. (1976) Precipitation, temperature, and the standing crop of some southern California grassland species. *Journal of Range Management*, **29**, 433-435.

KIRBY D.G., GREEN D.M. and MINGS S. (1989) Nutrient composition of selected macrophytes in Northern prairie wetlands. *Journal of Range Management*, **42**, 323-326.

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

MARAÑÓN T. (1985) Diversidad florística y heterogeneidad ambiental en una dehesa de Sierra Morena. [Floristic diversity and environmental heterogeneity in a dehesa of Sierra Morena]. *Anales de Edafología y Agrobiología,* **44**, 1183-1197.

MIGUEL J.M. DE and GOMEZ-SAL A. (1992) Los paisajes de la dehesa y su papel en el comportamiento del ganado extensivo. [The dehesa landscape and its influence on the behaviour of free-ranging cattle]. *Quercus*, Noviembre 1992, 16-22.

MILCHUNAS D.G., LAUENROTH W.K., CHAPMAN P.L. and KAZEMPOUR M.K. (1989) Effects of grazing, topography and precipitation on the structure of a semiarid grassland. *Vegetatio*, **80**, 11-23.

MORRISON I.M. (1980) Changes in the lignin and hemicellulose concentrations of ten varieties of temperate grasses with increasing maturity. *Grass and Forage Science*, **35**, 287-293.

NAVEH Z. (1982) The dependence of the productivity of a semiarid Mediterranean hill pasture ecosystem on climatic fluctuations. *Agriculture and Environment*, **7**, 47-61.

NELSON C.J. and MOSER L.E. (1994) Plant factors affecting forage quality. In: Fahey Jr., G.C. (ed.) *Forage Quality, Evaluation and Utilization*. pp. 115-154. Madison, Wisconsin: American Society of Agronomy, Crop Science Society of America, Soil Science Society of America.

NORTON B.W. (1982) Differences between species in forage quality. In: Hacker J.B. (ed.) *Nutritional Limits to Animal Production from Pastures*. pp. 89-110. Farnham Royal: Commonwealth Agricultural Bureaux.

PAPANASTASIS V.P. and KOUKOULAKIS P.H. (1988) Effects of fertilizer application to grasslands in Greece. *Grass and Forage Science*, **43**, 151-158.

PÉREZ CORONA M.E., GARCÍA CRIADO B.,VÁZQUEZ DE ALDANA B.R. and GARCÍA CIUDAD A. (1994) Effect of topographic and temporal (maturity) gradients on the nutritive quality of semiarid herbaceous communities. *Communications in Soil Science and Plant Analysis,* **25**, 2047-2061.

PÉREZ CORONA M.E., GARCÍA CIUDAD A., GARCÍA CRIADO B. and VÁZQUEZ DE ALDANA B.R. (1995) Patterns of aboveground herbage production and nutritional quality structure on semiarid grasslands. *Communications in Soil Science and Plant Analysis*, **26**, 1323-1341.

PUERTO A., RICO M. and GOMEZ GUTIERREZ J.M. (1985) Comparacion de la produccion primaria aerea neta de dos unidades de explotacion ("dehesas") en relacion con la topografia, litologia y regimen climatico.[Comparison of the net primary aerial production of two exploitation units (dehesas) with respect to topography, lithology and climatic conditions]. *Anales de Edafologia y Agrobiologia,* **44,** 529-547.

SALA O.E., PARTON W.J., JOYCE L.A. and LAURENROTH W.K. (1988) Primary production of central grassland region of the United States. *Ecology*, **69**, 40-45.

SCHIMEL D., STILLWELL M.A. and WOODMANSEE R.G. (1985) Biogeochemistry of C, N, and P in asoil catena of the shortgrass steppe. *Ecology,* **66**, 276-282.

SILVERTOWN J., DOOD M.E., McCONWAY K., POTTS J. and CRAWLEY M. (1994) Rainfall, biomass variation, and community composition in the Park Grass Experiment. *Ecology,* **75**, 2430-2437.

SMITH R.S., CORKHILL P., SHIEL R.S. and MILLWARD D.A. (1996) The conservation management of mesotrophic (meadow) grassland in northern England. 2. Effects of grazing, cutting date, fertilizer and seed. *Grass and Forage Science,* **51**, 292-305.

STATSOFT, Inc. (1993) *Statistica for Windows, Release 4.3*. Tulsa, OK, USA: StatSoft, Inc.

VAN SOEST P.J. (1982) Composition, fiber quality and nutritive value of forages. In: Heath M.E., Barnes R.F., Hetcalfe D.S. (eds) *Forages: The Science of Grassland Agriculture*. pp. 412-421. Ames: Iowa State University Press.

VÁZQUEZ DE ALDANA B.R., PÉREZ CORONA M.E., GARCÍA CIUDAD A. and GARCÍA CRIADO B. (1996) Mineral content in semiarid grassland systems as affected by community structure and soil characteristics. *Acta OEcologica*, **17**, 245-259.

VÁZQUEZ DE ALDANA B.R., GARCÍA CIUDAD A., PÉREZ CORONA M.E. and GARCÍA CRIADO B. (1998) Interannual variations of nutritional quality in semiarid grasslands under extensively grazing management. In: Nagy G., Petö K. (eds) *Ecological Aspects of Grassland Management. Proceedings of the 17th General Meeting of the European Grassland Federation, Debrecen, Hungary, 1998*. pp. 325-328.

WILSON J.R. (1982) Environmental and nutritional factors affecting herbage quality. In: Hacker J.B. (ed.) *Nutritional Limits to Animal Production from Pastures*. pp. 111-131. Farnham Royal: Commonwealth Agricultural Bureaux.

Table 1 Plant species with cover values above 15% present in June at each slope position.

Slope position	Botanical group	Species	Life form
Upper	Grasses	*Agrostis castellana*	Perennial
		Bromus hordaceus	Annual
		Dactylis glomerata	Perennial
		Poa bulbosa	Perennial
		Vulpia bromoides	Annual
	Legumes	*Anthyllis lotoides*	Annual
		Ornithopus compressus	Annual
		Trifolium striatum	Annual
		Trifolium arvense	Annual
	Forbs	*Cerastium glomeratum*	Annual
		Plantago lanceolata	Perennial
		Thapsia villosa	Perennial
		Tuberaria guttata	Annual
Lower	Grasses	*Agrostis castellana*	Perennial
		Anthoxantum aristatum	Annual
		Cynodon dactylon	Perennial
		Cynosurus cristatus	Perennial
		Festuca rubra	Perennial
		Holcus lanatus	Perennial
		Poa pratensis	Perennial
	Legumes	*Lotus corniculatus*	Perennial
		Trifolium pratense	Perennial
		Trifolium hybridum	Perennial
		Trifolium dubium	Annual
	Forbs	no dominant species cover < 3%	

Table 2 Results of 2-way ANOVAs showing degrees of freedom, *F* statistic and the significance of the effects of slope zone, year and factor interaction on above ground dry-matter production and proportion of botanical groups.

Source of variation	d.f.	*F*	*P*
Dry matter			
zone	1	327	0.0000
year	7	15.4	0.0000
zone × year	7	3.33	0.0018
Proportion of grasses			
zone	1	219	0.0000
year	7	7.68	0.0000
zone × year	7	1.95	0.0610
Proportion of legumes			
zone	1	18.0	0.0000
year	7	15.4	0.0000
zone × year	7	9.17	0.0000
Proportion of forbs			
zone	1	401	0.0000
year	7	2.07	0.0449
zone × year	7	1.78	0.0890

Table 3 Results of 2-way ANOVAs showing degrees of freedom, *F* statistic and the significance of the effects of slope zone, year and factor interaction on crude protein, neutral detergent fibre (NDF), hemicellulose, cellulose, lignin and *in vitro* dry matter digestibility (DMD) of grasses, legumes and forbs.

Source of variation	Grasses			Legumes			Forbs		
	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
Crude protein									
zone	1	119	0.0000	1	35.1	0.0000	1	60.7	0.0000
year	7	19.8	0.0000	6	13.9	0.0000	7	23.5	0.0000
zone × year	7	5.36	0.0000	6	3.58	0.0019	7	2.39	0.0209
NDF									
zone	1	17.6	0.0000	1	94.6	0.0000	1	3.27	0.0714
year	7	26.4	0.0000	6	48.9	0.0000	7	17.1	0.0000
zone × year	7	4.23	0.0002	6	3.22	0.0044	7	5.24	0.0000
Hemicellulose									
zone	1	8.51	0.0037	1	62.5	0.0000	1	0.222	0.6376
year	7	4.13	0.0002	6	19.4	0.0000	7	7.02	0.0000
zone × year	7	1.64	0.1216	6	1.98	0.0682	7	4.26	0.0001
Cellulose									
zone	1	3.60	0.0583	1	41.0	0.0000	1	0.027	0.8680
year	7	25.9	0.0000	6	35.8	0.0000	7	39.51	0.0000
zone × year	7	4.59	0.0001	6	3.37	0.0031	7	5.63	0.0000
Lignin									
zone	1	9.79	0.0018	1	23.5	0.0000	1	43.52	0.0000
year	7	45.8	0.0000	6	55.3	0.0000	7	42.05	0.0000
zone × year	7	3.62	0.0008	6	2.48	0.0233	7	2.50	0.0160
In vitro DMD									
zone	1	10.6	0.0012	1	62.9	0.0000	1	44.0	0.0000
year	7	42.3	0.0000	6	71.6	0.0000	7	37.5	0.0000
zone × year	7	3.40	0.0015	6	1.77	0.1048	7	1.29	0.2530

Table 4 Correlation coefficients of nutritional quality parameters between upper and lower zone values, for each of the three botanical fractions.

	Grasses (n=221)	Legumes (n=117)	Forbs (n=199)
Crude protein	0.43***	0.24**	0.50***
NDF	0.41***	0.51***	0.36***
Hemicellulose	-0.02	0.33***	0.15*
Cellulose	0.40***	0.48***	0.52***
Lignin	0.59***	0.69***	0.40***
In vitro DMD	0.59***	0.73***	0.50***

Significance levels: * *P*<0.05; ** *P*<0.01; *** *P*<0.001
n=number of samples

Table 5 Correlation coefficients between chemical composition and digestibility of the botanical fractions at each slope zone.

	Upper zone		Lower zone	
	Legumes	Forbs	Legumes	Forbs
Crude protein				
Grasses	0.276** n=125	0.69*** n=188	0.70*** n=182	0.71*** n=207
Legumes		0.21* n=131		0.62*** n=175
NDF				
Grasses	0.60*** n=125	0.58*** n=188	0.47*** n=182	0.30*** n=207
Legumes		0.73*** n=131		0.15 n=175
Hemicellulose				
Grasses	-0.002 n=125	0.12 n=188	0.05 n=182	0.13 n=207
Legumes		0.28*** n=131		-0.21** n=175
Cellulose				
Grasses	0.66*** n=125	0.60*** n=188	0.59*** n=182	0.48*** n=207
Legumes		0.68*** n=131		0.55*** n=175
Lignin				
Grasses	0.70*** n=125	0.58*** n=188	0.59*** n=182	0.45*** n=207
Legumes		0.74*** n=131		0.55*** n=175
In vitro DMD				
Grasses	0.59*** n=125	0.62*** n=188	0.53*** n=182	0.44*** n=207
Legumes		0.74*** n=131		0.66*** n=175

Abbreviations as in Table 4

Table 6 The amount of variance (r^2) explained by linear regression analysis of botanical fractions (proportion in the dry matter [DM]), and nutritional quality parameters of the botanical fractions on meteorological measurements from 1987 to 1996 at the upper and lower slope zones.

		Grasses						Legumes			Forbs		
	Slope zone	Pan	Pwi	Psp	Tan	Tau	Tsp	Psp	Tan	Tsp	Pan	Psp	Tau
Proportion	Upper				0.57*				0.87***(-)		0.52*(-)		
	Lower	0.53**								0.43*(-)			
Crude protein	Upper	0.72**(-)									0.69*(-)		
	Lower		0.54*(-)								0.49*(-)		
NDF	Upper			0.56*				0.63*				0.65*	
	Lower					0.43*							
Hemicellulose	Upper								0.57**(-)				
	Lower						0.52*						
Cellulose	Upper			0.62*				0.74*					
	Lower												0.53*
Lignin	Upper			0.89***				0.93***				0.83**	
	Lower												
In vitro DMD	Upper			0.84**(-)				0.82**(-)				0.74**(-)	
	Lower												

Significance levels: * $P<0.05$; ** $P<0.01$; *** $P<0.001$

Pan, annual precipitation from autumn to summer; Pwi, winter precipitation; Psp, spring precipitation; Tan, mean annual temperature from autumn to summer; Tau, mean autumn temperature; Tsp, mean spring temperature. (-) indicates a negative relationship.

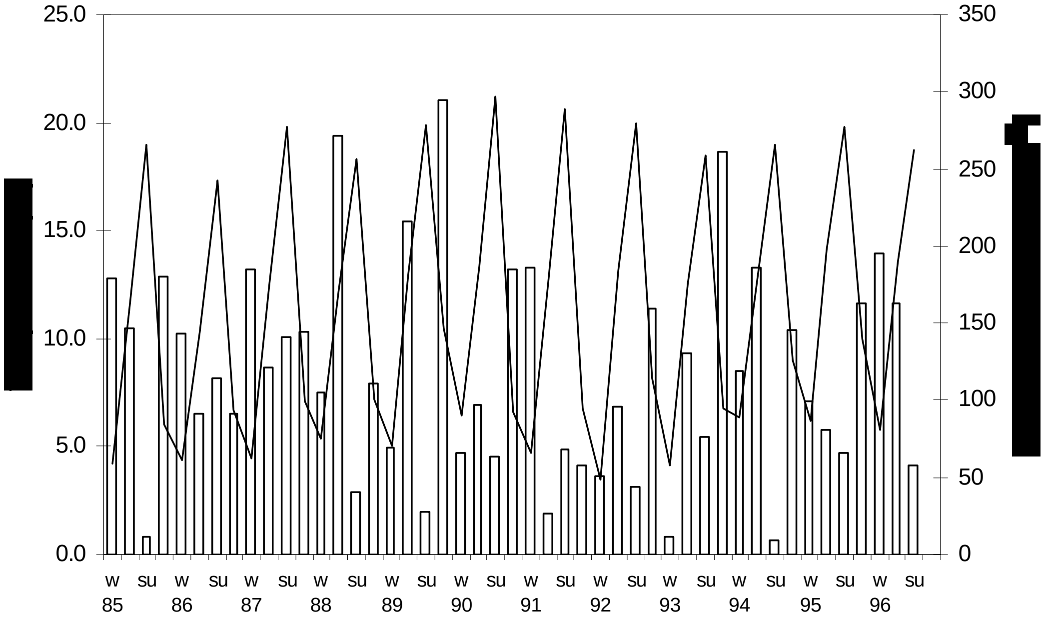

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Figure 1 Seasonal precipitation (quarterly total, mm) (□) and average daily temperature (quarterly mean, ºC) (—) during 1986-1996; w, winter; su, summer. Spring and autumn seasons unlabelled.

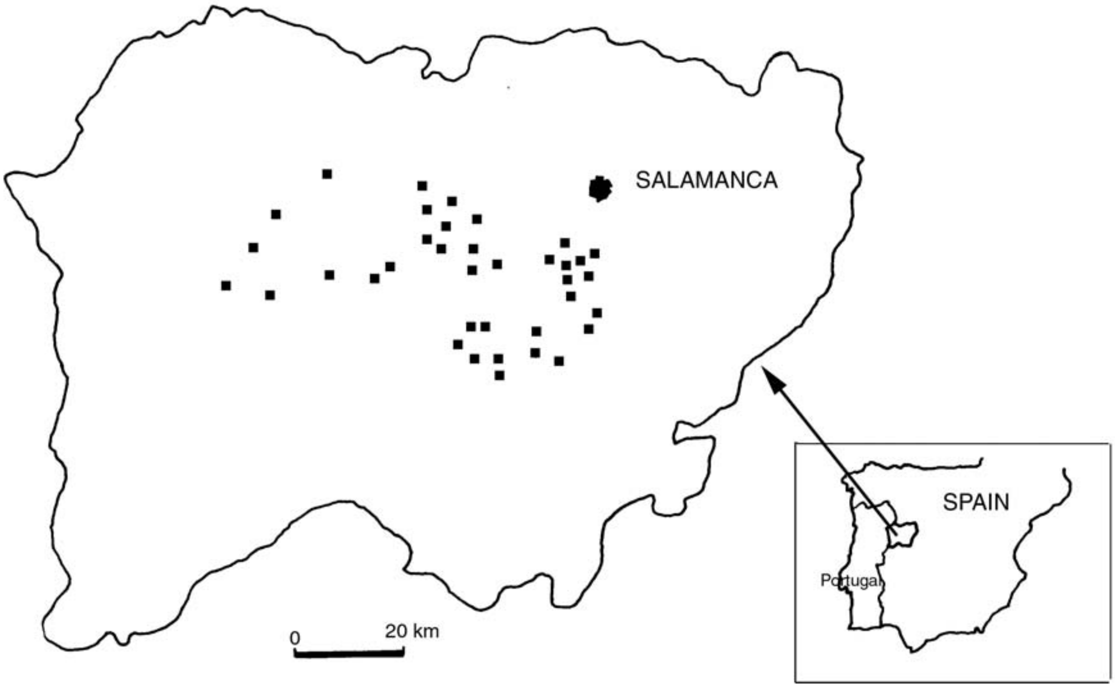

Figure 2 Location of sampling sites within the dehesa are in the province of Salamanca (Spain).

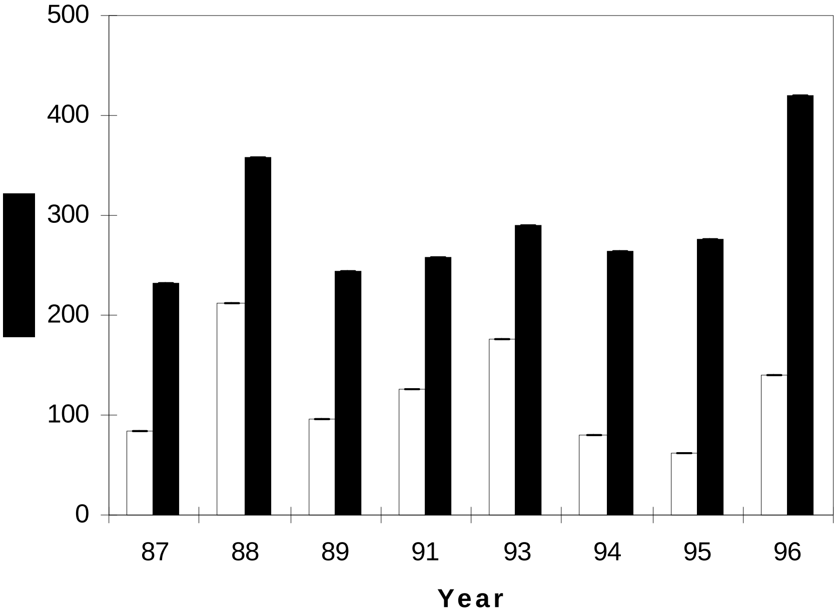

Figure 3 Mean herbage mass above 2 cm at the end of June (g m^{-2}) in the upper (□) and lower (■) slope zones over ten years. Vertical bars ± s.e.

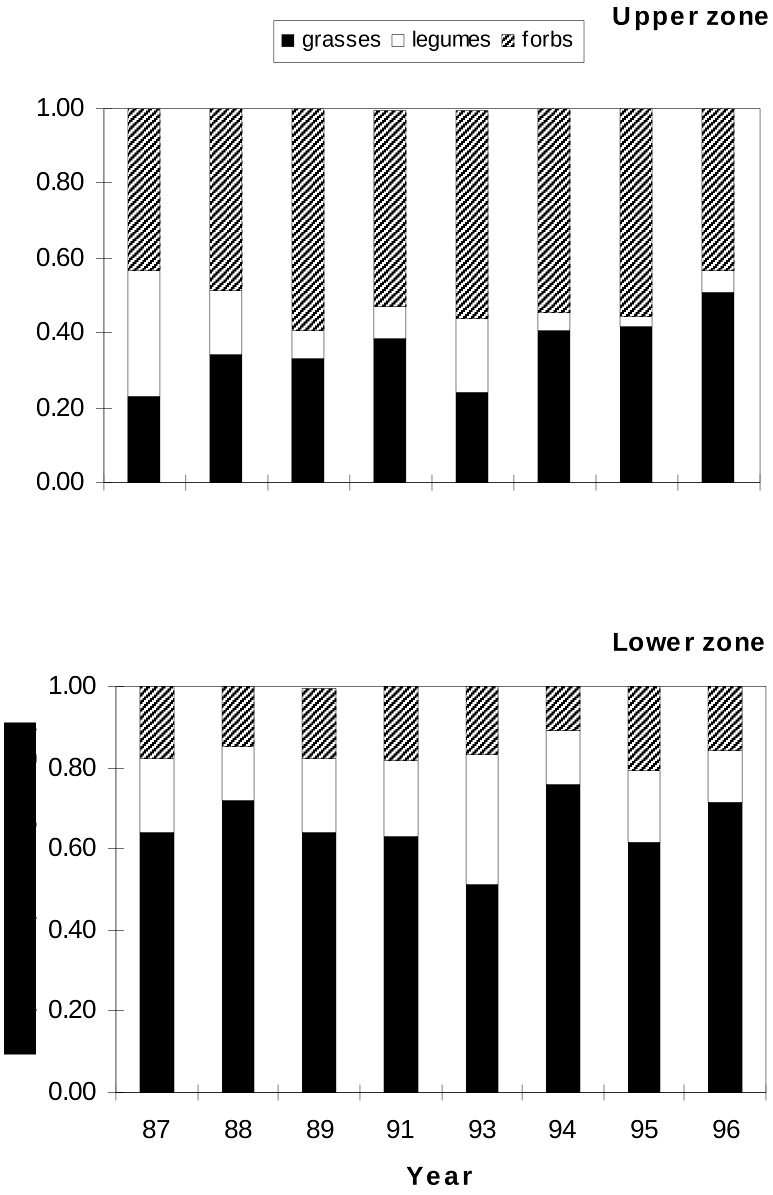

Figure 4 Proportion (oven dry weight) of grasses, legumes and forbs in the herbage mass above 2 cm at the end of June, in the upper and lower slope zones, from 1987-96.

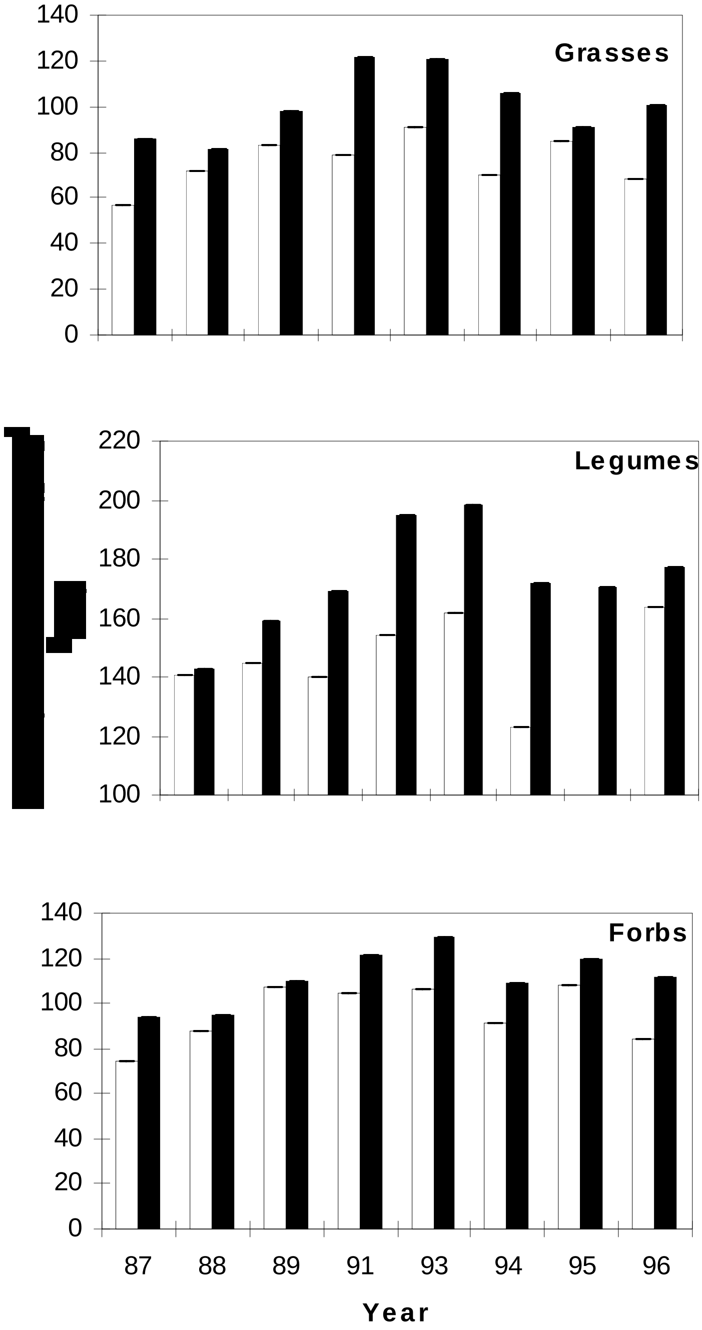

Figure 5 Mean crude protein content (g kg^{-1} DM) in grasses, legumes and forbs from semi-arid grasslands, in the upper (□) and lower (■) zones, from 1987-96. Vertical bars ± s.e.

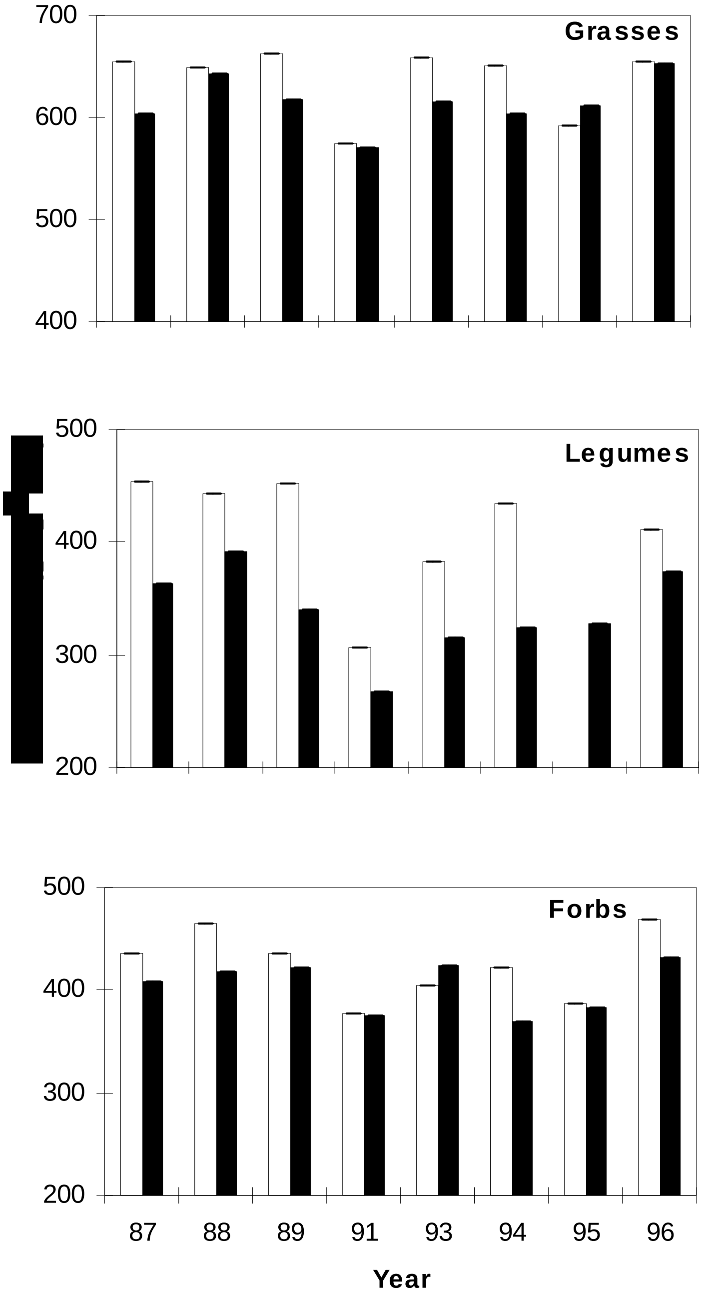

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Figure 6 Mean neutral-detergent fibre (NDF) content (g kg^{-1} DM) in grasses, legumes and forbs from semi-arid grasslands, in the upper (□) and lower (■) zones, from 1987-96. Vertical bars ± s.e.

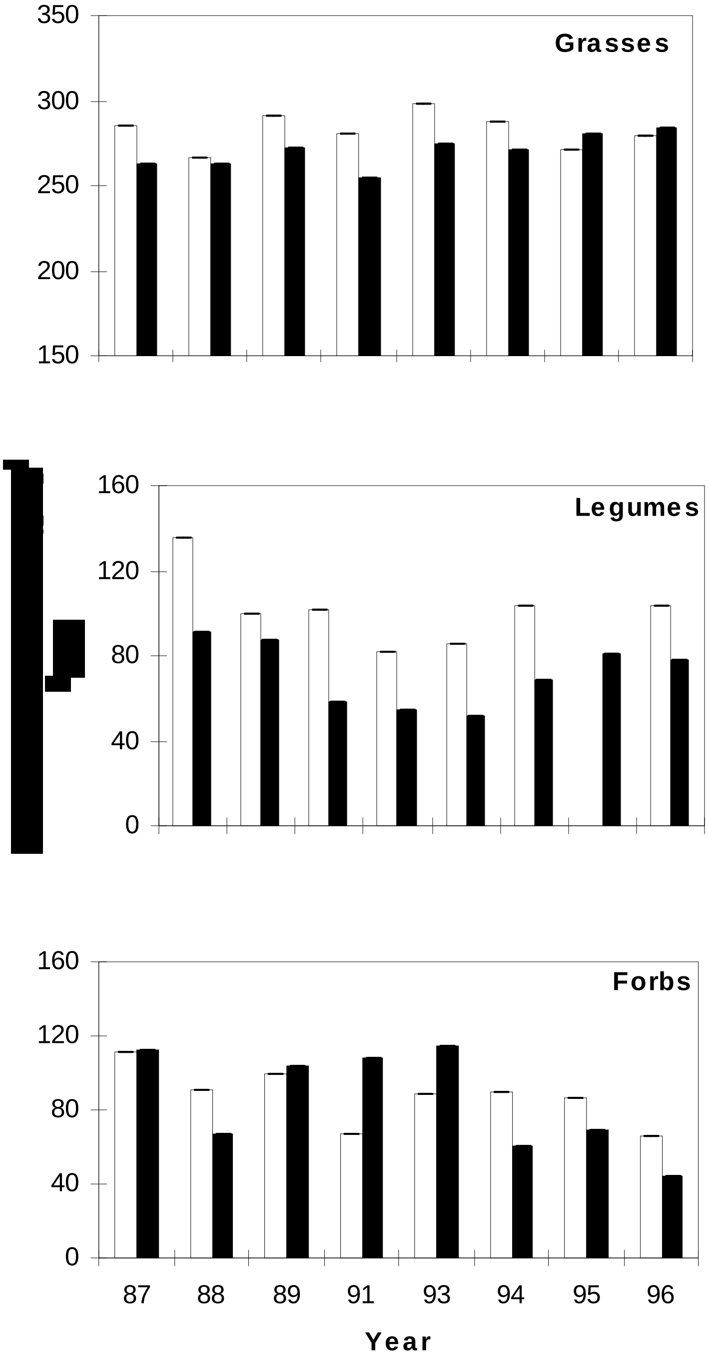

Figure 7 Mean hemicellulose content (g kg^{-1} DM) in grasses, legumes and forbs from semi-arid grasslands, in the upper (□) and lower (■) zones, from 1987-96. Vertical bars ± s.e.

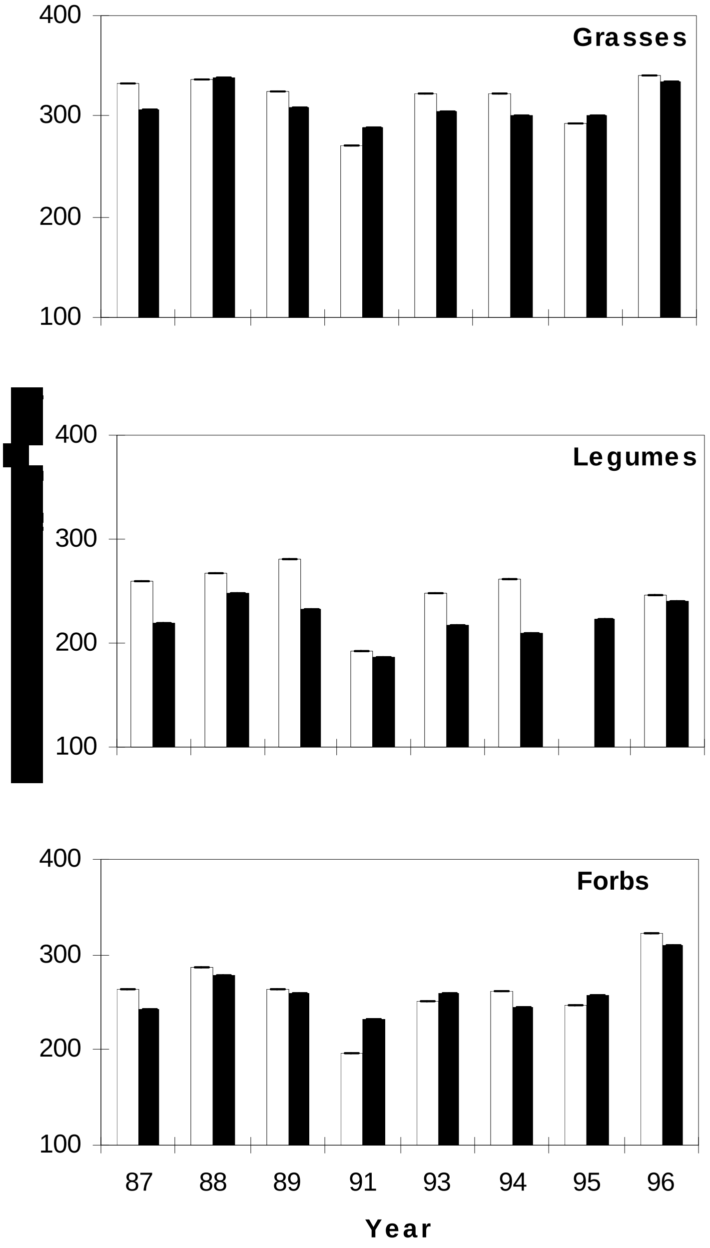

Figure 8 Mean cellulose content (g kg^{-1} DM) in grasses, legumes and forbs from semi-arid grasslands, in the upper (□) and lower (■) zones, from 1987-96. Vertical bars ± s.e.

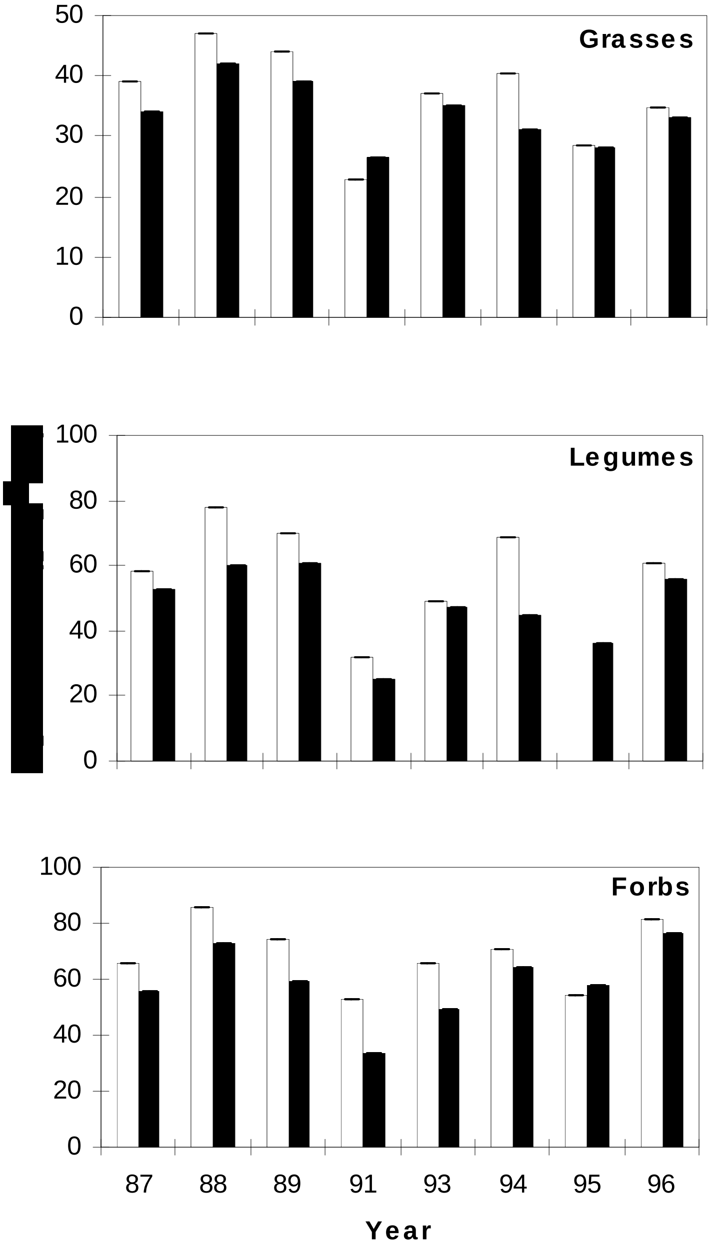

Figure 9 Mean lignin content (g kg^{-1} DM) in grasses, legumes and forbs from semi-arid grasslands, in the upper (□) and lower (■) zones, from 1987-96. Vertical bars ± s.e.

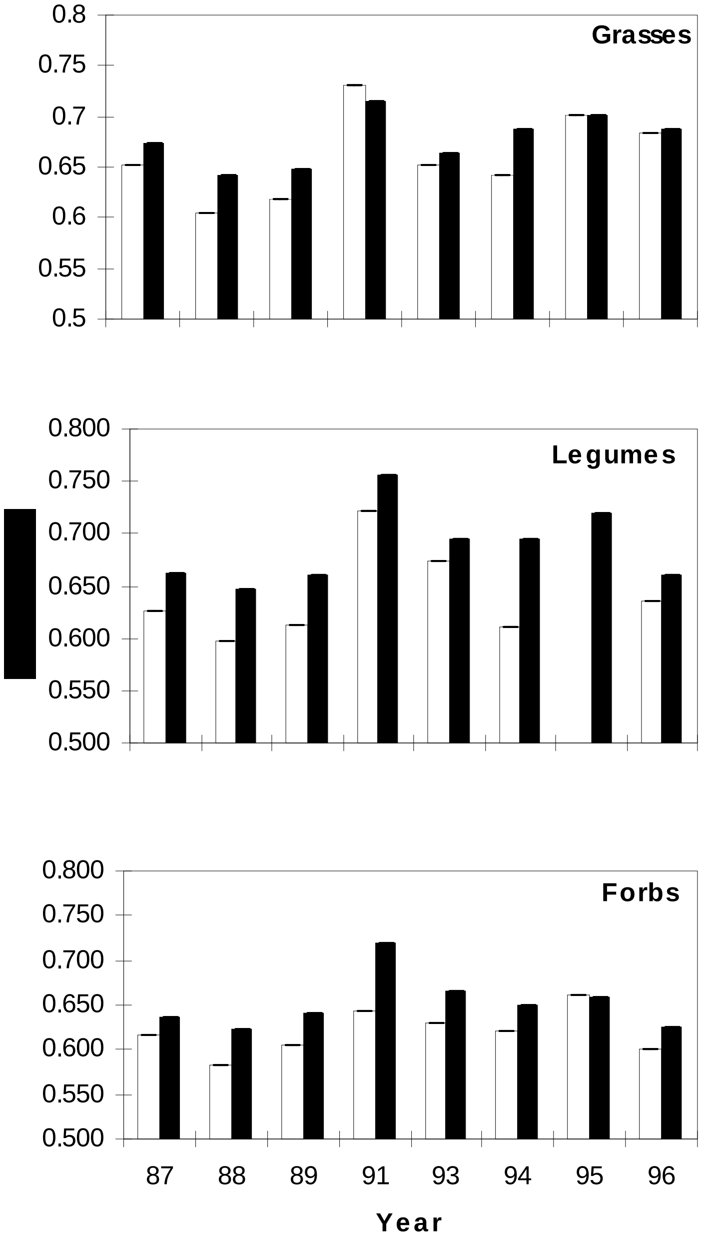

Figure 10 Mean *in vitro* DMD in grasses, legumes and forbs from semi-arid grasslands, in the upper (□) and lower (■) zones, from 1987-96. Vertical bars ± s.e.