J. Range Manage.
46:232-236, May 1993

Plant structure and the acceptability of different grasses to sheep

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Abstract

Plant structure should be an important determinant of species acceptability to grazing ungulates functioning under various time-energy constraints. The acceptability of 9 grasses to sheep grazing a secondary grassland community in spring, summer, and autumn in South Africa was related to the following species attributes: plant height, leaf table height, tussock diameter, stemminess, percent leaf, leaf density, percent dry matter (DM), leaf tensile strength, and leaf crude protein (CP). Species acceptability over the grazing season was positively related to tussock diameter ($P \leq 0.05$) but negatively related ($P \leq 0.01$) to leaf tensile strength and DM. Discriminant function analysis successfully discriminated between species in different acceptability classes in summer ($P \leq 0.05$) and autumn ($P \leq 0.01$) using a combination of plant structure and leaf quality attributes. Correspondence analysis indicated that preferred species were generally short and nonstemmy and had leaves of low DM, low tensile strength, and high crude protein content. Conversely, avoided species tended to be tall and stemmy with a high leaf table height, and had leaves of high DM and tensile strength but low CP levels. It is concluded that, for sheep, acceptability is determined by a combination of plant structure and leaf quality attributes.

Key Words: leaf quality, tensile strength, stems, African rangelands, leaf accessibility

Plant species selection by grazing ungulates has been extensively documented, yet understanding of the underlying factors determining species acceptability remains tenuous. While acceptability is generally correlated with plant nutrient content (Heady 1964), attempts to predict species selection on this basis alone have largely been unsuccessful (e.g., Westoby 1974, Owen-Smith and Novellie 1982).

Optimal foraging theory predicts that the utility of a food to an animal is determined by the ratio of nutrient content to handling costs (Stephens and Krebs 1986). For grazing ungulates, where search time may be assumed to be low, handling costs arise directly from the time and energy expended in harvesting leaf from a particular plant. As these costs are largely determined by plant structure (Ruyle et al. 1987) in terms of the amount and 3-dimensional distribution of leaf present, this variable should be an important determinant of acceptability to these animals. In a study with cattle (O'Reagain and Mentis 1989), species acceptability was found to be positively correlated with leaf table height and tussock diameter but negatively correlated with stemminess.

Different ungulate species function under time-energy constraints (Hanley 1982) which are unique for a particular body size (Demment 1983). Consequently, the relative importance of plant structure in determining acceptability could vary widely between different ungulate species. The present study was initiated to repeat the experiment of O'Reagain and Mentis (1989) using sheep, which were assumed to function under constraints significantly different from those of cattle. The objectives were, first, to determine the relationship between plant structure and species acceptability to sheep, and secondly, to identify specific components of structure important in determining acceptability to these animals. The study adopted the hypothesis generating approach (Loehle 1987) in an attempt to facilitate maturation of current theories on dietary selection.

Procedure

Study Area

The study was conducted on the Dundee Research Station situated 10 km east of the town of Dundee, South Africa, (28° 10'S, 30° 14'E) in the Natal Sour Sandveld (Acocks 1975). Mean annual rainfall is 730 mm (20 year mean) concentrated over the summer months, with a peak in January. Summers are warm with a mean maximum air temperature of 27° C, while winters are cool with grass minimum temperatures below 0° C.

The 0.5-ha experimental site was situated on a deep, well-drained soil of the Hutton form (Macvicar et al. 1977). The area had previously (>10 years) been cultivated and was dominated by a secondary grassland community comprised largely of *Hyparrhenia hirta* (L.) Stapf and various *Eragrostis* species.

Methods

The site was burnt in October 1987 in order to remove residual material and, thereafter, grazed by 22 Merino wethers (average mass 45 kg) for periods of 10 days in a simulated rotational grazing system on 3 December (spring), 9 February (summer), and 14 April (autumn). Between grazing periods, animals grazed veld of a composition similar to the study area. Animals received supplementation in accordance with the recommended procedure for the area, i.e., mineral-phosphate lick in spring and summer and a nitrogen-based lick thereafter.

Nine perennial grass species, common to the area, were selected for the study. Species were chosen so as to obtain a wide range of acceptabilities and plant structures. These were *Cynodon dactylon* (L.) Pers., *Eragrostis capensis* (Thunb.) Trin., *Eragrostis curvula* (Schrad.) Nees, *Eragrostis gummiflua* Nees, *Eragrostis plana* Nees, *Hyparrhenia hirta* (L.) Stapf, *Michrocloa caffra* Nees, *Paspalum notatum* Fluegge, and *Sporobolus africanus* (Poir.) Robyns and Tournay. (Nomenclature follows Gibbs Russell et al. 1990). With the exception of *C. dactylon* and *P. notatum,* which are creeping stoloniferous grasses, all are tussock species.

Immediately before each grazing period, 100 tussocks of each species were randomly selected from the total species population, to allow measurement of the attributes listed below. (For stolonif-

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The author thanks Raymond Ntshangase, for field assistance, Neil Miles for Kjeldahl analyses, Marlene McMaster for typing, and Johan Du Toit, Tim O'Connor, Norman Owen-Smith, and 2 anonymous referees for constructive criticism of an earlier draft.
Manuscript accepted 2 Oct. 1992.

Table 1. Means of species attributes for 9 perennial grasses in spring (1), summer (2), and autumn (3) in South Africa.

Species	Season	Plant height	Leaf table height	Stemminess	Tussock diameter	Leaf	Leaf	Leaf tensile strength	Dry matter	Leaf CP
		(cm)	(cm)	(0–5)	(cm)	(%)	(mg/cm)	Dynes	(%)	(%)
C. dactylon	1	16.14	4.74	1.03	30.00	46	1.48	2252	44	10.07
E. capensis	1	61.75	6.83	3.89	11.35	35	4.53	2334	51	656
E. curvula	1	84.48	15.57	2.63	12.27	47	0.95	7612	52	6.74
E. gummiflua	1	45.51	19.02	1.41	20.25	60	1.66	3375	44	564
E. plana	1	50.66	13.33	0.67	17.02	57	1.42	9247	44	6.36
H. hirta	1	45.99	18.98	0.75	19.38	53	2.42	2819	39	8.02
M. caffra	1	26.86	2.61	3.18	3.98	41	1.20	7887	59	6.63
P. notatum	1	13.86	6.71	0.06	30.00	66	1.24	2630	—	9.36
S. africanus	1	33.92	11.93	0.08	13.06	60	2.41	8366	45	8.34
C. dactylon	2	16.75	5.68	1.86	30.00	48	2.02	2252	54	9.48
E. capensis	2	62.29	12.35	3.06	15.39	42	2.56	2334	64	5.77
E. curvula	2	80.42	16.66	2.60	16.98	51	1.65	7612	66	5.79
E. gummiflua	2	61.53	19.65	2.60	16.85	53	2.07	3375	51	4.17
E. plana	2	67.13	17.23	1.80	16.21	—	3.39	9247	51	5.67
H. hirta	2	81.91	19.97	3.27	14.72	32	1.84	2819	46	7.02
M. caffra	2	23.54	3.45	2.07	5.54	55	0.50	7887	68	5.58
P. notatum	2	28.65	6.89	1.29	30.00	54	1.33	2630	44	7.72
S. africanus	2	67.45	21.23	1.38	13.55	49	2.28	8366	46	6.09
C. dactylon	3	13.10	4.99	0.73	30.00	45	1.78	2252	56	8.48
E. capensis	3	31.26	6.95	1.40	13.48	55	1.81	2334	52	5.02
E. curvula	3	75.22	17.66	2.59	20.98	56	1.59	7612	65	5.34
E. gummiflua	3	60.41	15.71	2.30	16.86	63	5.23	3375	53	3.99
E. plana	3	63.60	14.88	1.28	18.33	59	2.24	9247	60	5.02
H. hirta	3	87.09	20.77	3.57	16.71	25	1.92	2819	51	5.01
M. caffra	3	15.88	3.11	0.75	4.01	55	1.04	7887	58	5.68
P. notatum	3	17.20	4.38	0.37	30.00	60	1.16	2630	51	6.01
S. africanus	3	88.51	11.64	2.48	9.63	48	2.47	8366	55	3.76

erous species, a 'tussock' was arbitrarily defined as a 30 × 30-cm quadrat.) Of the tussocks selected, 10 were clipped to ground level and removed for laboratory analysis. To reduce subjectivity, all measurements, with the exception of the Kjeldahl analyses, were performed by the author. Expectation bias in the subjective measurements was unlikely given the extreme range in structures between species.

The following attributes were measured for each species (see Table 1) with the sample size (n) given in parentheses: plant height—the height above ground level of the tallest, extended part of the plant (n=100); leaf table height—the height below which 80% of the plant's leaves were subjectively judged to occur (n=100); tussock diameter—the diameter at the widest part of the tussock (n=100); stemminess—the proportion of stems present, subjectively estimated on a scale of 0 to 5 where 0=no stems and 5=many stems (n=100); leaf percentage—the percentage (%) contribution of leaf mass to total tussock mass expressed on a dry mass basis (n=10); leaf density—the mass of leaf (dry mass) per unit volume of leaf space (n=10) where:

$$\text{Leaf space} = \pi \, \frac{(\text{tussock diameter})^2}{2} \times \text{leaf table height x.} \qquad (1)$$

dry matter percentage—the percent dry matter (DM) of freshly cut herbage (n=10) x; leaf tensile strength—the force required to break a single leaf per unit width of the leaf at the broken edge, measured using a leaf tensilmeter (Martens and Booysen 1968). Measurements of leaf tensil strength (n=20) were made only once (autumn) as this variable does not change significantly over the growing season (Theron and Booysen 1968); leaf crude protein (CP)—samples were dried at 65° C for 48 hours, milled (1-mm sieve) and analyzed using the macro-Kjeldahl procedure (AOAC 1970) (n=10).

Species acceptability, expressed as a percentage, was determined at the end of each grazing period by systematically selecting 100 tussocks of each species using a wheel-point apparatus (Tidmarsh and Havenga 1955) and visually classifying tussocks as either 'grazed' or 'ungrazed'. A grazed tussock was defined as one where plant material had been removed, the exception being where only seed heads had been consumed. Confusion with earlier grazing was unlikely as regrowth was good. As the area was fenced and indigenous ungulates absent, sheep can be assumed to have been responsible for all defoliations.

Statistical Analysis

The G-test (Sokal and Rohlf 1981), using the ratio of grazed to ungrazed tussocks per season, was used to determine whether species acceptability was independent of season. The relationship between species attributes and acceptability was investigated using standard least squares regression (Statistical Graphs Corporation 1987). For multivariate analysis species were classified into groups on the basis of acceptability, i.e., preferred (>60% acceptability), intermediate (30–60% acceptability), or avoided (<30% acceptability). For each season, discriminant function analysis (DFA) was used (Statistical Graphics Corporation 1987) to identify attributes which could best discriminate between groups of different acceptability. Correspondence analysis (Greenacre and Vrba 1984) using SIMCA (Greenacre 1985) was used to detect patterns of association between acceptability classes over all seasons and the various species attributes. Attributes of a particular species were classified as being either low (1), medium (2), or high (3) by dividing the total range of a variable for all species over all seasons into 3 equal groups.

Plants were not used as replications, but were the sampling units, as plant species were the experimental units. Replication was not considered essential to achieve stated objectives given the hypothesis generating approach adopted. Animals operate under fixed constraints, so under optimal foraging theory (Stephens and Krebs 1986) the relative importance of different factors in determining dietary selection should be consistent in space and time (Dearing and Schall 1992).

Results

Species Acceptability

The most acceptable species were *P. notatum* and *H. hirta* in spring, *E. capensis* and *P. notatum* in summer, and *P. notatum* in autumn (Table 2). In general, the least acceptable species were *E. curvula, E. plana, E. gummiflua,* and *M. caffra.* With the exception of *E. plana* and *E. curvula* there was a significant interaction between acceptability and season (Table 2) with some species (e.g., *M. caffra*) increasing while others (e.g., *H. hirta*) declined in acceptability over the grazing season.

Table 2. The acceptability (percentage of tufts grazed) of 9 grass species to sheep in spring, summer, and autumn. G-values indicate significance of seasonal effects on acceptability.

Species	Spring	Summer	Autumn	G-value
	---------- % Grazed ---------			
C. dactylon	51	56	68	6.07*
E. capensis	44	84	65	36.06**
E. curvula	10	04	05	3.29
E. gummiflua	21	07	42	36.66**
E. plana	09	11	13	0.814
H. hirta	91	64	65	27.08**
M. caffra	02	03	33	54.26**
P. notatum	92	81	95	10.92*
S. africanus	76	78	58	11.32*

* ($P \leq 0.05$; $x^2 = 5.99$)
**($P \leq 0.01$; $x^2 = 13.81$)

Correlation Analysis

In spring, no significant relationship could be detected between acceptability and any species attribute, although there appeared to be a negative relationship with tussock height, leaf tensile strength, and dry matter, and a positive relationship with tussock diameter (Table 3). Similarly, in summer no significant relationship was evident, although acceptability was negatively related to leaf tensile strength and percent leaf. In autumn, a strong ($P \leq 0.01$) negative relationship was evident between species acceptability and both dry matter and leaf tensil strength. Over the grazing season as a whole, species acceptability was positively related to tussock diameter ($P \leq 0.05$) but negatively related to leaf tensile strength ($P \leq 0.01$) and dry matter ($P \leq 0.01$).

Table 3. Correlation coefficients (r) for the relationship between the acceptability of 9 different grasses to sheep and species parameters measured in spring, summer, autumn, and over all seasons.

Attribute	Spring (n = 9)	Summer (n = 9)	Autumn (n = 9)	G-value (n = 27)
Leaf %	0.427	–0.546	–0.488	–0.151
Leaf CP	0.224	0.327	0.329	0.287
Leaf tensile strength	–0.522	–0.529	–0.742*	–0.582**
Leaf table height	0.049	–0.015	–0.433	–0.094
Stemminess	–0.063	–0.035	–0.162	0.053
Dry matter %	–0.592	–0.485	–0.885**	–0.475**
Leaf density	–0.363	–0.489	–0.273	–0.304
Tussock height	–0.434	–0.076	–0.371	–0.358
Tussock diameter	0.540	0.354	–0.371	–0.447*

* ($P \leq 0.05$)
**($P \leq 0.01$)

Correspondence Analysis

Axis 1 accounted for 60.8% of the inertia, and separated avoided species and species of intermediate to preferred acceptability (Fig. 1). Axis 2 accounted for 39.2% of the inertia and appeared to separate preferred from species to intermediate acceptability. In terms of species parameters, the main opposition in axis 1 appears to be between short, mat-forming grasses with leaves of high quality on the right, and tall-growing grasses with leaves of low quality on the left. Axis 2 appears to reflect separation between species with low dry matter and stemminess at the top from species of intermediate dry matter intermediate to high leaf density at the bottom. In general, avoided species had associated attributes of a high leaf table height, a high DM%, high leaf tensile strength and an intermediate to low leaf crude protein content. Conversely, species of intermediate and preferred acceptability had a low leaf table height, were nonstemmy, and possessed leaves of low leaf tensile strength but high crude protein content.

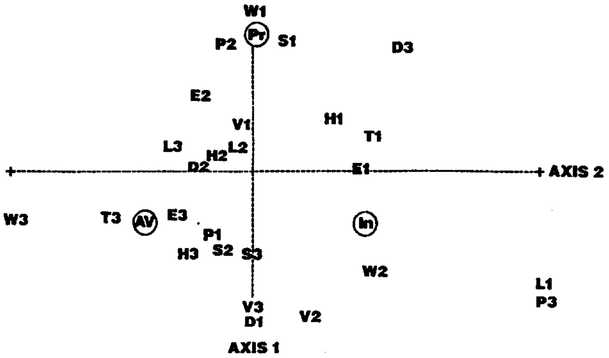

Fig. 1. Graphical display of the first 2 axes of inertia for sheep, derived from correspondence analysis of different acceptability classes and their associated species characteristics (AV=avoided, PR=preferred, and IN=intermediate acceptability class; 1=low, 2=medium, 3=high; W=dry matter percentage, V=leaf density, S=stemminess, D=tuft diameter, P=leaf crude protein, E=leaf table height, T=leaf tensile strength, L=leaf percentage, H=tuft height).

Discriminant Function Analysis

For all seasons, a combination of plant structure and leaf quality attributes provided the strongest discriminatory power between different acceptability classes (Table 4). In spring, leaf table height, percent leaf, percent dry matter and leaf tensile strength best discriminated between classes, although the function derived was nonsignificant. Tussock diameter, stemminess, leaf crude protein,

Table 4. Discriminant analysis of the attributes of species of preferred intermediate and avoided acceptability to sheep in spring, summer, and autumn. (DM = dry matter percent; CP = crude protein; LTS = leaf tensile strength; LTH = leaf table height).

Species attributes	Canonical r^2	Probability >F	Misclassified species (n)
Spring			
LTH, DM, Percent leaf, LTS	.940	.149	1
Summer			
LTS, stemminess, leaf CP	.920	.049*	1
Tussock diameter, stemminess, leaf CP, DM	.985	.027*	0
Autumn			
LTS, stemminess, DM			
LTH, leaf CP	.992	.008*	0
DM, stemminess, LTS	.965	.006*	1
DM, stemminess, leaf CP	.987	.0003**	0

* ($P \leq 0.05$)
**($P \leq 0.001$)

and dry matter formed a significant ($P \leq 0.05$) discriminant function in summer with all species correctly classified. Similarly, in autumn, a highly significant ($P \leq 0.01$) discriminant function correctly classified all species using the attributes of stemminess, leaf protein, and dry matter. Of the attributes used only dry matter was common to the functions derived from all seasons while stemminess and leaf crude protein were common to both summer and autumn.

Discussion

Sheep appeared to avoid tall, stemmy species but tended to select for short, nonstemmy species with a low leaf table height. This suggests that plant structure is an important determinant of species acceptability to these animals as has been found with cattle (O'Reagain and Mentis 1989), buffalo (Field 1976), and kudu (Cooper and Owen-Smith 1986). As leaf forms in excess of 80% of sheep diets (Arnold 1960), the effects of plant structure must be interpreted in terms of its effects on leaf accessibility and hence the rate of nutrient ingestion by the grazing animal. Thus, sheep may select for shorter grass species as the amount of leaf harvested per unit time is maximized at these heights; evidence from temperate pastures indicates that for sheep, intake rates are maximized at a sward height of 6 cm but decline above or below this height (Penning et al. 1991). If preference is correlated with intake rate (Kenney and Black 1984), this may explain why very short (e.g., *M. caffra)* and very tall grasses (e.g., *E. curvula*), tended to be avoided.

These results conflict with those for cattle (O'Reagain and Mentis 1989), which selected strongly for species with tall leaves. This difference may best be explained in terms of the allometric scaling of mouth dimensions with body mass. As larger animals have a proportionately greater bite depth than small animals, bite size is likely to be maximized at a relatively greater sward height for the former animals (Illius and Gordon 1987). Large animals should therefore select for comparatively tall swards or species. Sheep may also experience difficulty in harvesting tall leaves with their nibbling method of grazing (personal observation) while cattle readily sweep such leaves into their mouths using their prehensile tongues.

Sheep also appeared to select for nonstemmy plants (Fig. 1), in agreement with the findings of Murray (1984). Stemminess may reduce bite size by physically restricting access to leaf (Arnold 1962) and may also increase bite time (Ruyle et al. 1987) thereby increasing nutrient handling costs. Stemminess may therefore modify species acceptability through its effects upon the cost:benefit ratio, and hence profitability of harvesting leaf from a particular species. Interestingly, the effects of stemminess on acceptability appear to be less extreme for sheep than for cattle (O'Reagain and Mentis 1989). For example, the marked increase in stemminess in *H. hirta* from spring to autumn resulted in a 26% decline in its acceptability to sheep (Table 1) compared with a decline of nearly 50% for cattle over a similar range (O'Reagain and Mentis 1989). This discrepancy may be attributed to the different morphological and physiological constraints under which the 2 animals operate. First, as a consequence of their 'nibbling' method of grazing, relatively narrow muzzles, and the greater degree of curvature of the incisor arcade (Gordon and Illius 1988), sheep have an inherently superior ability to select small, highly dispersed leaf items. Secondly, as foraging time increases with body size (Owen-Smith 1988), small ungulates have a relatively greater potential to increase grazing time to compensate for physical restrictions on intake than their larger counterparts.

Leaf quality in terms of tensile strength, dry matter, and protein content was also an important determinant of species acceptability (Table 4) with leaf tensile strength possibly being the most important in the present study (Table 3). Theron and Booysen (1966) similarly noted that the acceptability of different African grasses to sheep was most strongly correlated with tensile strength. Sheep may avoid species with high strength leaves for a number of reasons. First, handling costs in terms of time and energy are likely to be significantly greater for high stength leaves. Consequently, rates of dry matter consumption are greater for low strength leaves, even within a particular species (Mackinnon et al. 1988). Secondly, leaf strength is negatively correlated with leaf quality (Evans 1964, Wilson 1965, John et al. 1989), and may thus act as an index of leaf nutrient content. Thirdly, leaf strength adversely affects rumen processing costs. In general, rumination times are longer, dry matter disappearance rates slower, and voluntary intakes lower for high compared to low strength leaves (Inoue et al. 1989). Significantly, leaf tensile strength appeared to be a relatively more important determinant of acceptability to sheep than to cattle (O'Reagain and Mentis 1989), possibly reflecting the comparatively shorter retention times and lower digestive ability (Demment and Van Soest 1985) of small ruminants.

Sheep also appeared to avoid grass species with high DM (Fig. 1) in accordance with Theron and Booysen's (1966) findings that sheep select for succulent species with a high water content. Dry matter percent may give an indication of the concentration of cell wall constituents and hence potential digestibility of a particular species. Sheep may also avoid species with high dry matter as this factor is negatively correlated with intake of fresh herbage (Kenny et al. 1984). Although intake may be restricted by water content at very low dry matter levels (Arnold 1962), these levels are unlikely to be encountered under range conditions.

In general, sheep tended to select for species with a high crude protein content and avoid species with low to intermediate levels of the nutrient. However, considering the relatively high energy requirements of small ungulates such as sheep (Kleiber 1961) it is surprising that the relationship between acceptability and leaf crude protein was not stronger (Table 3). Removal of the outlier points belonging to *C. dactylon* did not have the effect of improving the relationship between the crude protein and acceptability ($r=0.522$; $P \leq 0.01$) although this is still considerably weaker than that recorded for cattle (O'Reagain and Mentis 1989). As with cattle (O'Reagain and Mentis 1989), leaf crude protein appeared to be a relatively more important determinant of acceptability in summer and autumn (Table 4) when herbage quality in the study area declines and may approach sub-maintenance levels (O'Reagain and Mentis 1988).

Significantly, acceptability could not be explained solely in terms of any single factor, with the strongest relationship, tensile strength, only explaining 30% of the variation in the data (Table 3). This indicates that acceptability is not determined by any single factor but rather by a range of factors. For example, although *H. hirta* is a tall-growing stemmy grass, it was strongly selected (Table 1), possibly due to its soft, high-quality leaves. Acceptability to sheep therefore appears to be determined by the interplay between plant structure and leaf quality attributes. Animals appear to balance the unfavourable and favourable characteristics of a particular species and then select accordingly (Arnold 1964).

Other factors, not considered in the present study, may also be involved in determining species selection by sheep. Secondary plant compounds affect dietary selection by browsers (Cooper and Owen-Smith 1985) and may also be of importance for grazers. Some indigenous grasses have been observed to possess tannin-like substances (Ellis 1990) while others such as *C. dactylon* produce cyanogenic compounds (Timson 1943). The costs associated with the digestion and passage of food are also likely to be of importance in dietary selection (Owen-Smith and Novellie 1982). Slowly digestible foods may depress intake as their long retention times depress rumen turnover rate while foraging time may be restricted due to the greater rumination requirements of such foods (Spalinger et al. 1986). Future studies of dietary selection in grazing ungulates should therefore take into account handling costs associated with both the ingestion and digestion of food, as well as the possible presence of secondary chemicals.

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