The influence of large mammalian herbivores on growth form and utilization of mopane trees, *Colophospermum mopane*, in Botswana's Northern Tuli Game Reserve

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Abstract

Mopane veld is of great value to the general ungulate spectrum in times of drought, and it is capable of retaining its dominance in a community even in the presence of extremely heavy browsing pressure imposed by large browsing mammals. Scrub mopane (hedges) has been regarded as resulting from excessive browsing pressure by large mammals, especially elephants. Both the nutrient and chemical composition of mopane twig bark were investigated, the seasonal results being related back to the seasonal utilization of branches by large mammals. Mopane twigs were most palatable in winter. Eland feed on mopane throughout the year irrespective of palatability. Elephants were rarely present in the scrub mopane area before the onset of spring rains, when the major mopane leaf flush occurs independently of rainfall. The impact of both species was not excessive and recruitment of mopane seedlings does occur. Herbivore browsing is responsible for a mopane morph which buds early and continues to produce accessible, nutritious leaves even when heavily browsed. Many browsing ungulates are reliant on this resource during the stressful transition from spring to summer in south-eastern Botswana.

Key words: branches, *Colophospermum mopane*, eland, elephants, palatability

Résumé

Le ''veld'' à Mopane est très important pour l'ensemble du spectre des ongulés en temps de sécheresse, et est à même de conserver sa dominance dans une communauté même en cas de pression extrêmement lourde exercée par les grands mammifères brouteurs de feuilles. On a considéré que les buissons de mopane (formant des haies) étaient le résultat d'une pression excessive du broutage par les grands mammifères, particulièrement les éléphants. On a analysé les nutriments et la composition chimique de l'écorce des rameaux de mopane, et on a mis les résultats saisonniers en relation avec l'utilisation saisonnière des branches par les grands mammifères. Les rameaux de mopane sont plus goûteux en hiver. Les élands se nourrissent de mopane toute l'année quel qu'en soit le goût. Les éléphants sont rarement présents dans les buissons de mopane avant l'arrivée des pluies du printemps alors que la plus grande poussée des feuilles de mopane a lieu indépendemment des pluies. L'impact des deux espèces n'est pas excessif, et on observe une repousse de jeunes mopane. Le broutage par les herbivores est responsable d'une morphologie qui bourgeonne tôt et qui continue à produire des feuilles accessibles et nutritives même lorsque le broutage est intense. Beaucoup d'ongulés qui broutent dépendent de cette ressource lors de la transition difficile entre le printemps et l'été au sud-est du Botswana.

Introduction

The food choices and food-related habitat preferences of African elephants *Loxodonta africana* have been exhaustively documented in the literature (Buss, 1961; Guy, 1976; Lewis, 1986; Ruggiero, 1992). However, due to uncertainties as to how many elephants an area can indeed support, still more needs to be known about their

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impact on tree communities and, in turn, the responses of woody plants to utilization by elephants (Walker *et al.*, 1987). Elephant browsing has long been considered a prime factor in the suppression of woody vegetation, preventing tree regeneration and eventually reducing species richness. Consequently, the management of elephants within Southern African conservancies has caused great concern (Anderson & Walker, 1974; Lewis, 1991; Nott & Stander, 1991). Although elephants tend to eat the majority of woodland tree species, more or less in proportion to their occurrence, some species such as *Colophospermum mopane* (mopane) are definitely favoured (van Wyk & Fairall, 1969; Guy, 1976; Skinner & Smithers, 1990). Hence, such species tend to exhibit signs of damage more quickly than do less utilized species (Styles, 1993).

In Botswana's Northern Tuli Game Reserve (NTGR), this mopane veld is the dominant veld type (McKenzie, 1990) and mopane trees exhibit two very definite morphs. One morph, loosely referred to by managers within the area as a 'bonsai', is a very short robust tree which does not usually exceed 4 m in height. These mopane trees are encountered in the open areas away from the drainage lines, where, due to obvious extensive utilization by browsers, they have been cropped into hedges. The other mopane tree morph is much taller, usually exceeds 10 m in height, is relatively undamaged as it is far less utilized by browsers and is encountered along the riparian zones of the conservancy's water courses. When extensive areas of mopane began to show obvious signs of damage, this being hedging, managers within the NTGR, considered the need to either cull or translocate elephants in order to reduce this browsing pressure. These concerns motivated this study, which was designed to investigate which agents were responsible for the hedging of mopane away from the rivers; to determine the seasonal chemistry of mopane twig bark, a resource much sought after within the NTGR; to relate these chemical data to seasonal utilization; and to determine the ecological implications of these mopane hedges for the dominant plant community of the NTGR, the mopane veld.

Study site

The vegetation of the NTGR falls within the broad classification of Mopane Veld (Acocks, 1975). The NTGR lies in the eastern corner of Botswana, between 21°55′ S and 22°15′ S and between 28°55′ E and 29°15′ E, where Botswana, South Africa and Zimbabwe converge. The NTGR constitutes the north-eastern extremity of a 350-km long strip of land known as the Tuli Block (McKenzie, 1990). The climate of the region is semiarid tropical, with a low and unpredictable rainfall (Harrison, 1984). The long-term average rainfall is 370 mm (1965–89), with peak rainfall years receiving up to 660 mm (1976) and low rainfall years receiving as little as 180 mm (1989).

Materials and methods

Fresh elephant faecal samples were collected seasonally so that the amount of twig material in the diet could be assessed. Samples were placed in large paper bags and stored in a cool place. The sample was kept moist, by sealing the paper bag, to prevent the twig material from disintegrating when sifting. All pieces of undigested mopane twig material were removed from the samples using forceps. Finally, the twig material, and what remained of the sample, were oven-dried at 50°C for 72 h and their respective masses determined. The percentage dry twig mass of mopane in the faecal sample was determined by dividing the dry mass of the leaf or twig sample by the mass of the dry faecal sample plus the dry mass of the twig material. Variation in the overall seasonal content of material was tested using a Kruskall–Wallis (K–W) Analysis by Ranks Test. Differences between the seasonal content of undigested twig material in samples were tested using the Mann–Whitney Test (Siegel, 1956).

The investigation of the seasonal removal of mopane branches was done in the NTGR in Elephant Valley, an area where the hedged bonsai mopane morph predominates; hedging is an indicator of the occurrence of regular branch browsing. Five hundred branches (ten on each of 50 tagged trees) were marked unobtrusively with a mocca-coloured non-volatile paint where they emerged from the main stem. Branches were recorded as either new or old growth. The site was visited on a seasonal basis and the tagged trees checked for the presence/absence of marked branches. Seasonal variation in the intensity of removal of both the young and old branches was tested using the Mann–Whitney Test.

The mopane trees along the riverine fringe are tall and relatively undamaged, whereas those on the open plains are the bonsai morph. The phenologies of the two morphs were compared during the last week of October 1992.

Three sites were selected in each area, 100 trees were sampled at each site. Records were made of the following:
ia. No pods
ib. Pods thinly scattered over the canopy, not easily visible from 50 m (Few)
ic. Numerous pods in the canopy, easily visible from 50 m (Abundant)
iia. No old leaves
iib. Old leaves thinly scattered over the canopy, not easily visible from 50 m (Few)
iic. Numerous old leaves in the canopy, easily visible from 50 m (Abundant)

The seasonal chemical composition of mopane twig bark was investigated in an attempt to correlate these factors with branch browsing. Twig bark was removed with a scalpel. Analysis was carried out as follows. Samples were oven-dried at 50°C for 96 h, and then ground in a Wiley mill (40-mesh). Per cent crude protein content (CP) was calculated from the percentage nitrogen content, determined using a macrokjeldahl method. The amount of available energy (EN) in the samples, was determined using a CP 400 bomb calorimeter (Coalab supplies (Pty) Ltd, Johannesburg). The results are expressed in kJ/g plant material. The condensed tannin content (CT) of the samples was determined using a slight modification of the vanillin assay (Terrill *et al.*, 1990). The protein precipitation capacity (PP) was determined following Hagerman (1987). Total phenolic content (TP) was determined using a modification of the Prussian blue redox assay described in Price & Butler (1977). The methods used to determine the percentage Neutral Detergent Fibre (NDF), and percentage Acid Detergent Fibre (ADF) content of the samples, followed Robertson & van Soest (1981) and Goering & van Soest (1970). The moisture content (MO) of the samples was determined as follows: samples were sealed in pre-weighed plastic packets, weighed, dried in an oven for 72 h and their dry masses determined. The percentage moisture in the sample collected was calculated by dividing the mass lost during drying by its wet mass. All results for each parameter for each season were ranked (in reverse order for tannins, total phenols, protein and detergent fibre) and the differences between overall seasonal contents for each parameter assessed using the Kruskall–Wallis Analysis by Ranks Test. If this was significant, each season was tested against every other season using the Mann–Whitney Test. A palatability index was calculated for each season by averaging the ranks of all parameters. Where seasons were not being compared, the results obtained for the respective parameters of the respective plant parts were compared using the Mann–Whitney Test.

Results

In Table 1, the seasonal content of mopane twigs and leaf material in elephant faeces are shown. There was at least 14% more twig material in summer than in any of the other seasons (mean for winter, spring and autumn $8.9 \pm 1.7\%$).

In Table 2, the number of old and new marked branches removed over a 10-month period is shown. Eland removed the 33 branches in spring, the sharp increase between spring and summer coincided with the return of elephants to the area. The decrease in the percentage of new branches removed between spring and summer ($P < 0.001$) can also be attributed to the elephants because they are less selective feeders than eland (Styles, unpubl.).

The chemical composition of mopane twig bark is shown in Table 3 and the palatability ranking in Table 4. Although the seasonal differences were highly significant the value for the lowest season was within 10% of the highest season for all characteristics except for moisture, protein, neutral detergent fibre and acid detergent fibre. Moisture in winter was only 86% of that in autumn the second lowest season which did not differ from spring and summer. Protein precipitation was very variable but was 27% higher in spring than in winter or autumn.

There were too few samples of detergent fibre to assess the seasonal differences, but both NDF 53 and ADF 44 were higher in spring and autumn than they were in winter and summer (NDF 48 and ADF 39). Four samples of highly palatable lucerne had 50.9 NDF and 40.5 ADF. Winter is the season when bark is most palatable largely because of the low tannin, total fibre, total phenols, protein precipitate and fibre. Bark is more nutritious in summer but has high tannins and total phenols.

The number of bonsai and riverine trees with pods and old leaves is shown in Table 5. The heavy browsing pressure that large mammals impose upon the bonsai morph does not prevent it from setting seed, but the number with abundant pods was lower than for riverine trees (18.7 and 28.7, respectively). The bonsai trees are not completely stripped of old leaves, although there was a marked difference between the two morphs in the

Table 1 Values showing the seasonal content (%) of undigested mopane twigs in fresh elephant faecal samples

				Significance		
Season	n	Mean ± SD	K–W Test	Spring	Summer	Autumn
Winter	15	9.7 ± 2.0	**	NS	**	NS
Spring	06	9.2 ± 1.3		–	*	NS
Summer	15	12.0 ± 2.0		–	–	*
Autumn	15	10.1 ± 1.9		–	–	–

Significance values: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; NS, non-significant.

Table 2 Table of values showing the seasonal removal of new and old mopane branches from marked trees in a hedged area

								Significance		
SN	REV.	TTL.	REM.	No. new	%	No. old	%	Spring	Summer	Autumn
Wi	0	500	0	0	0	0	0	–	–	–
Sp	33	467	33	31	94	2	6	–	***	***
Su	106	361	139	75	71	31	29	–	–	***
Au	49	312	188	36	73	13	27	–	–	–

REV: No. removed that season; TTL: Total no. branches remaining; REM: Total no. branches removed to date.

number with abundant old leaves (17 and 55, respectively).

Discussion

Observations revealed that mopane hedges were structures induced largely by the browsing activities of elephants and eland. According to the 1991 aerial survey, the number of eland in the NTGR was within the range of previous five surveys (0.34/km^2, mean 0.49 ± 0.18), but the number of elephants was rather high (0.63/km^2, mean 0.49 ± 0.15). On the other hand, the rainfall over the period during the course of the study was 47.5 mm, in contrast to the mean for the previous 12 years of 329.5 mm. The combination of average or high animal numbers and very low rainfall placed an extra demand on the mopane over the study period because most other tree species were devoid of browsable material. In spite of this, the mopane survived, possibly because of the timing of the major browsing by elephants, which was in summer, as shown by branch removal and the contents of faecal samples.

In spring, before the onset of rain and in the absence of surface water, the major leaf flush occurs independently of rainfall (Styles, 1993), and elephants, which need to be near free water, were rarely present in the area (Table 1, $n = 6$ for spring). On the other hand, herds of more than 200 eland were not an uncommon sight in the mopane hedges over the dry period before the spring rains.

It appears that availability, rather than twig bark palatability, as determined in our bark palatability index, seems to be the factor most closely related to consumption of twigs. Eland feed readily on mopane throughout the year, irrespective of palatability (especially polyphenolics) of the phenophases. Recently it has been shown that mammalian herbivores may possess defensive mechanisms against polyphenolics such as tannins, through the secretion of proline-rich salivary compounds, which render substances like tannins inactive to a degree, so reducing their effects (Mole, Bulter & Iason, 1990). This may well explain why, throughout the year, eland are encountered in mopane hedges, probably the most unforgiving areas within the NTGR. In addition, the extensive utilization of twig bark by eland over the early spring period, before the spring leaf flush, may well be to obtain sufficient moisture at a time when moisture is usually very scarce.

The vast areas of scrub or 'bonsai' mopane trees within the NTGR have been regarded as areas of ecological

Table 3 The seasonal chemical composition of mopane twig bark

SN	PAR	*n*	Mean ± SD	K–W	Significance		
					Spring	Summer	Autumn
WI	CP	20	5.3 ± 0.2	***	**	***	***
SP		20	5.4 ± 0.1		–	***	***
SU		20	5.7 ± 0.1		–	–	***
AU		20	5.8 ± 0.2		–	–	–
WI	EN	20	18.5 ± 1.0	***	NS	*	***
SP		20	17.7 ± 0.1		–	**	***
SU		20	17.6 ± 0.2		–	–	**
AU		20	17.3 ± 0.3		–	–	–
WI	MO	15	33.7 ± 2.8	***	***	***	***
SP		15	41.0 ± 5.0		–	NS	NS
SU		15	38.3 ± 2.8		–	–	NS
AU		15	38.4 ± 3.1		–	–	–
WI	CT	10	65.0 ± 0.9	***	**	***	***
SP		10	66.6 ± 0.9		–	*	NS
SU		10	68.5 ± 1.7		–	–	NS
AU		10	67.6 ± 1.7		–	–	–
WI	TP	10	425.1 ± 3.5	***	***	***	***
SP		10	447.8 ± 6.1		–	***	***
SU		10	482.2 ± 3.6		–	–	***
AU		10	436.6 ± 2.9		–	–	–
WI	PP	10	44.2 ± 10.2	***	NS	NS	NS
SP		10	61.2 ± 9.9		–	*	NS
SU		10	30.4 ± 4.5		–	–	NS
AU		10	44.2 ± 10.2		–	–	–
WI	NDF	4	48.5				
SP		4	53.2				
SU		4	47.1				
AU		4	53.3				
WI	ADF	4	38.3				
SP		4	45.2				
SU		4	39.1				
AU		4	42.3				

WI – winter; SP – spring; SU – summer; AU – autumn; CP – crude protein; EN – energy; MO – moisture; CT – condensed tannin; TP – total phenolic; PP – protein precipitation; NDF – neutral detergent fibre; ADF – acid detergent fibre.
Significance values: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; NS, non-significant.

disorder, resulting from excessively heavy browsing pressures on mopane trees by elephants, a situation demanding an eventual decision on the culling of elephants. However, the results from the present study question the supposed impact that elephants are having on mopane trees within the NTGR, hedging being a phenomenon largely resulting from browsing by eland. Riney (1982) states that mopane about 1.5–3.0 m high could have been modified by both eland and elephants to a hedge shape and that it is impossible to distinguish between hedged forms created by the two species. According to Lewis (1986), the dependence of elephants on mopane appears to have been overemphasized. Our results are consistent with their conclusions. Clearly, what emerges from this study is the bias that managers within the NTGR exhibit towards elephants, viewing them as the sole agents responsible for the hedging of mopane within the conservancy.

The present study found that when mopane twigs were at their most palatable in winter, mopane branches were

Table 4 Seasonal palatability of mopane twig bark

Season	Rank values								Mean value	Final rank	Palatability
	CP	EN	MO	CT	TP	PP	NDF	ADF			
Winter	4	1	4	1	1	2	2	1	2.0	1	
Spring	3	2	1	2	3	3	3	4	2.6	=3	
Summer	2	3	3	4	4	1	1	2	2.5	2	
Autumn	1	4	2	3	2	2	4	3	2.6	=3	

CP – crude protein; EN – energy; MO – moisture; CT – condensed tannin; TP – total phenolic; PP – protein precipitation; NDF – neutral detergent fibre; ADF – acid detergent fibre.

Table 5 Comparative ecological differences revealed by the two dominant mopane morphs

		Pods			Old leaves		
Site	*n*	No. with pods	No. abundant	No. few	No. with old leaves	No. abundant	No. few
Bonsai							
A	100	36	11	25	98	19	79
B	100	46	30	16	85	5	80
C	100	39	15	24	88	27	61
Mean		40.3	18.7	21.7	90.3	17	73.3
Riverine							
A	100	36	19	17	99	32	67
B	100	57	38	19	100	85	15
C	100	51	29	22	97	48	49
Mean		48	28.7	19.3	98.7	55	43.7

browsed on up to three times. Thus, to be satisfied that the impact eland and elephants were having on the mopane tree community was not excessive, the phenological ecology of the hedges had to be monitored, as according to Caughley (1976) abundant regeneration is a necessary condition for the continued health of the mopane association. Within this suppressed tier or scrub mopane, it has been suggested (Caughley, 1976) that very few seedlings ever grow to form tall mature trees. Lewis (1991) found that in Zambia's Luangwa Valley, only mopane trees exceeding 5 m in height produced seeds. By contrast, our results indicate that the hedged areas of mopane within the NTGR are producing seeds and that there is indeed recruitment in such areas, hence current levels of utilization do not appear to be detrimental to the mopane tree community.

The impact that eland and elephants are having on the mopane trees of the NTGR may not be aesthetically pleasing, but their activities are responsible for a mopane morph which comes into leaf early and which continues to produce accessible, nutritious leaves even in the presence of heavy utilization, a resource upon which many browsing ungulates are reliant during the stressful transition from spring to summer within the NTGR. Culling or translocating elephants in an attempt to curb the hedging effect will be a misguided attempt to manage a system which appears to be currently functioning to the benefit of all species concerned.

Acknowledgements

We wish to thank the Government of Botswana, the Office of the President, and the Department of Wildlife and National Parks, for permission to undertake the project; Dr A. A. McKenzie who facilitated field work for the project; Dr M. J. Coe of Oxford University, for guidance in the field; the land-owners of the Northern Tuli Game Reserve of Botswana, for their consent to conduct the study in the area, and the wardens for their assistance in the field; Mr and Mrs E. Steyn for their kindness and hospitality; Dr H. M. Dott for advice; the Foundation for Research Development who funded the project and provided a Studentship to C.V.S., who was also the recipient of the Bob Blundell Memorial Scholarship and a study bursary from the University of Pretoria.

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(Manuscript accepted 9 April 1999)