

REGROWTH AND PALATABILITY OF *ACACIA* SHOOTS FOLLOWING PRUNING BY AFRICAN SAVANNA BROWSERS¹

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Abstract. Stands of two species of African *Acacia* were monitored for 1 yr in a natural savanna ecosystem, to compare shoot regrowth and leaf chemistry in lightly browsed and heavily browsed trees. Where ungulates concentrated at a seasonal waterhole, *A. nigrescens* was more severely browsed than the thornier and finer leaved *A. tortilis*. Shoot regrowth in heavily browsed *A. nigrescens* more than compensated for herbivory, as net annual shoot extension was not significantly different from that in lightly browsed trees. Foliage of heavily browsed *A. nigrescens* was higher in nutrients and lower in condensed tannins than foliage of lightly browsed trees. We propose that severe pruning by browsing ungulates reduces intershoot competition for nutrients, promoting rapid shoot regrowth. Carbohydrate demands of rapid regrowth reduce carbon-based secondary metabolite synthesis. This results in patches of highly palatable browse that attract further browsing, generating a browsing–regrowth feedback loop. Such patches may be considered analogous to grazing lawns.

Key words: *Acacia* shoots; browsing ungulates; regrowth; pruning; African savanna; grazing lawns; palatability; secondary metabolites.

INTRODUCTION

For African savanna grazers, McNaughton (1984) proposed that individual grazers benefit by feeding in a herd because of the greater forage yield per bite from “grazing lawns” compared with lightly grazed vegetation. A grazing lawn is a patch of dense, closely grazed grass that is more productive and nutritious than tall, sparser grass growing on the lightly grazed periphery. McNaughton (1984) suggested that the dense, highly branched canopy surfaces of heavily browsed woody plants are analogous to grazing lawns. While the generality of the grazing lawn principle has been contested (Belsky 1986), it has been demonstrated that browsing by giraffe (*Giraffa camelopardalis*) does stimulate *Acacia* shoot production in the Serengeti ecosystem of East Africa (Pellew 1983). Moreover in Sweden, browsing by moose (*Alces alces*) on birch (*Betula* spp.) can induce regrowth that is more palatable than foliage on unbrowsed plants (Danell et al. 1985, Danell and Huss-Danell 1985). Similar findings have been reported for shrubs browsed by black-tailed prairie dogs (*Cynomys ludovicianus*) in North America (Coppock et al. 1983). In this paper we consider the applicability of the grazing lawn principle to browsing ruminants and *Acacia nigrescens*, one of the principal food plants of browsers

in the central Kruger National Park (KNP), South Africa.

In *Sclerocarya birrea*/*Acacia nigrescens* savanna on basalt plains in the central KNP, *A. nigrescens* trees dominate the woody vegetation but become locally less abundant near surface water (Codd 1951). The canopies of those that occur around surface water are typically pruned by impala (*Aepyceros melampus*) from below and giraffe from above (du Toit 1988). This pruning results in a clear browse line beneath a dense, highly branched canopy, which may be sculptured into a cone, sphere, or hourglass shape, as is characteristic of severe browsing by giraffe (Sinclair and Norton-Griffiths 1979, Pellew 1984, Coe and Coe 1987). Impala are mixed feeders with a high rate of water turnover (Fairall and Klein 1984) and, in the KNP, are seldom found more than a few kilometres from surface water (Young 1972, du Toit 1988). The reason for giraffe exerting such a high browsing pressure around waterholes is, however, less apparent.

Unlike grass, woody foliage retains a high water content throughout the seasonal cycle, which enables savanna browsers to be largely independent of surface water (Taylor 1969, Western 1975, Louw 1984). Consequently giraffe would be expected to avoid waterholes where, in the central KNP, lions (*Panthera leo*) concentrate their hunting activities (Smuts 1982). Because giraffe risk this predation threat by browsing around waterholes that they do not need to drink from, especially in the wet season, the most likely explanation

¹ Manuscript received 12 December 1988; revised 5 May 1988; accepted 12 May 1988.

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is that they are attracted by the quality of their staple diet, *Acacia* foliage. Hence this investigation was designed to test the hypothesis that severe browsing by giraffe and impala results in regrowth of enhanced palatability in *Acacia* patches that are frequented by both species. We tested this hypothesis by comparing shoot growth, leaf chemistry, and local soil nutrients available to specific trees of two *Acacia* species across a gradient of browsing intensity.

METHODS

Study sites and research design

Three sites were chosen at the top of the catenary drainage sequence, on basaltic clay soil, in the *Sclerocarya birrea*/*Acacia nigrescens* savanna landscape of the Tshokwane area (24°47' S, 31°52' E) in the central KNP (described by Gertenbach 1983). Rainfall in this area averages 590 mm per annum, with 80% of this falling during the wet season between October and March.

One site was at a seasonal waterhole. The heavily grazed and trampled area immediately about this waterhole was vegetated with *Acacia tortilis* and severely pruned *A. nigrescens* trees. Five mature trees were chosen at random from both species at this site. On each tree 10 growing shoots were marked with numbered plastic tags, tied with string \approx 50 cm in from the canopy surface. The tags were distributed all round the canopy from the lower browse line to the upper surface. The length of shoot (including all side branches) distal to each tag was measured. Tagging was done in mid-September, just before the spring flush.

A second site, the *A. nigrescens* control site, was in a monospecific stand of mature, lightly browsed *A. nigrescens* trees, 7 km from the waterhole and > 3 km from alternative water. Here, five trees were chosen at random and tagged in the same way (and during the same week) as at the waterhole site.

A third site, the *A. tortilis* control site, was in a monospecific stand of *A. tortilis* at the Tshokwane ranger station, 4 km from the waterhole. Large herbivores visited this site relatively infrequently due to the disturbance of human activity. It was nevertheless representative of the surrounding *A. tortilis* savanna vegetation, which was heavily grazed and trampled by large herbivores drawn to permanent water in pools of the Nwaswitsontso River (< 1 km from the *A. tortilis* control site). Five mature trees were chosen at random and individually marked, and 10 shoots on each were tagged in the same way (and during the same week) as previously described.

All three sites were revisited during the same week at 3-mo intervals: in late December (after the early growing season), early April (after the late growing season), early July (after the early dry season), and early October (after the late dry season period of dormancy). On each visit all tagged shoots were inspected for signs

of recent browsing, recorded on a presence/absence basis for the whole shoot, irrespective of which part of the shoot had been browsed. The length of shoot distal to each tag, including all side shoots, was measured on each visit.

Estimation of browsing pressure and net shoot extension

The proportion of tagged shoots showing signs of recent browsing was calculated for each tagged tree of each species at each site, during each quarter of the seasonal cycle (October–December, January–March, April–June, July–September). For each tagged tree, the four seasonal proportions were averaged to give an index of mean browsing pressure per tagged tree per species per site for the complete seasonal cycle. For each tree species at each sampling site, the five (one per tree) mean proportions of browsed shoots were arcsine transformed and browsing pressure was compared across species and sites using ANOVA and the a posteriori Student-Newman-Keuls (SNK) test (SAS 1985).

Net annual shoot extension (total growth minus browsed growth) was calculated for each tagged shoot as the difference between the length of shoot measured at the time of tagging, and the length of shoot measured after 1 yr. Net annual shoot extension was compared across *Acacia* species and sites using the same statistical procedure (ANOVA and SNK) as described for browsing pressure comparisons.

Chemical analyses

In December (middle of the wet season), leaf and soil samples were collected on the same day at each marked tree at each site. Leaf samples were collected by plucking leaves all round the canopy over the same height range as the tagged shoots. For each marked tree, the plucked leaves were well mixed and a handful was placed in a paper packet, giving five replicate samples (one from each tree) per species per site. These packets were hung in the shade to dry, and then milled and stored at low temperature until analyzed. Leaf samples were analyzed for condensed tannin, total nitrogen, and total phosphorus. Details of methods are as described by Bryant et al. (1985). Condensed tannins were quantified by the proanthocyanidin assay using a hot butanol-HCl extraction. The result of this assay is an absorbance value (at 550 nm, using a Perkin-Elmer Lambda 1 spectrophotometer), which is presented in the results as an index of condensed tannin concentration in place of an absolute value derived from a standard curve. This avoids the inaccuracies of estimating condensed tannin concentration from a standard curve that is based on a tannin other than that extracted from the plant being assayed (Wisdom et al. 1987). Nitrogen and phosphorus were analyzed on a Technicon auto-analyzer, using a sulphuric/selenious acid digest and colorimetric assay with a ferricyanide blue reaction for

TABLE 1. Plant and soil data (mean \pm SE per variable per site) from waterhole and control sites. Comparators indicate differences determined by the Student-Newman-Keuls multiple range test ($\alpha = .05$).

Variable	<i>Acacia tortilis</i>				<i>Acacia nigrescens</i>			
	Control	Diff	Waterhole	Diff	Waterhole	Diff	Control	
Browsed shoots* (mean %)	0.50 \pm 0.50	<	12.08 \pm 4.73	<	30.75 \pm 5.00	>	3.21 \pm 2.42	
Net shoot extension (cm/yr)	31.20 \pm 5.68	NS	35.91 \pm 9.19	>	10.67 \pm 3.05	NS	15.28 \pm 3.10	
Leaf tannin† (A_{550})	0.35 \pm 0.02	NS	0.32 \pm 0.02	>	0.21 \pm 0.02	<	0.42 \pm 0.01	
Leaf total N (% dry mass)	3.06 \pm 0.05	NS	2.97 \pm 0.11	<	3.67 \pm 0.20	>	3.01 \pm 0.05	
Leaf total P (% dry mass)	0.14 \pm 0.001	NS	0.14 \pm 0.006	<	0.18 \pm 0.007	>	0.16 \pm 0.005	
Soil total N (mg/kg)	1174 \pm 123	<	1946 \pm 303	NS	1934 \pm 247	<	2784 \pm 156	
Soil nitrate N (mg/kg)	0.81 \pm 0.13	<	3.97 \pm 0.60	NS	5.74 \pm 1.17	>	2.00 \pm 0.25	
Soil ammonium N (mg/kg)	4.67 \pm 0.18	<	12.61 \pm 1.66	NS	14.18 \pm 1.86	>	8.52 \pm 0.68	
Soil total P (mg/kg)	355 \pm 16	<	1303 \pm 51	NS	1163 \pm 62	NS	1109 \pm 43	
Soil soluble P (mg/kg)	Trace	<	10.29 \pm 2.63	NS	16.32 \pm 2.36	>	2.52 \pm 0.81	

* Percentage of marked shoots within each sample of trees that showed signs of recent browsing, averaged over four quarterly inspections.

† Absorbance value obtained in the proanthocyanidin assay, at 550 nm.

nitrogen and a molybdate blue reaction for phosphorus.

Soil samples were collected beneath each tagged tree at each site by removing surface litter and collecting \approx 1 kg of soil from the top 10 cm at four places beneath the canopy, 1 m out from the stem. These samples were then pooled and a subsample was collected, resulting in five replicate samples of soil from beneath each tree species at each site. These were air-dried and stored at low temperature until analyzed. Soil samples were analyzed for total nitrogen, nitrate nitrogen, ammonium nitrogen, total phosphorus, and water-soluble phosphorus. Total nitrogen and phosphorus were analyzed by the methods described by Bryant et al. (1985). Soil nitrate (NO_3), ammonium (NH_4), and water soluble phosphorus (P) were assayed by standard agronomic methods (Black 1982); NO_3 and NH_4 were extracted for 1 h from 15 g soil with 75 mL of 2 mol/L KCl; water soluble P was extracted overnight from 2 to 3 g soil with double-distilled deionized water (7 mL/g soil). These extracts were analyzed colorimetrically on a Technicon autoanalyzer.

Assumptions

Samples from each site are not assumed to be representative of the regions in which these sites occur, as the research design would then be flawed by pseudoreplication (Hurlbert 1984). We attempted to minimize intrinsic site differences (i.e., excluding herbivory-induced differences) by choosing sites in the same landscape and soil type, and in the same position at the top of the catenary drainage sequence. The furthest distance between sites was 10 km (the two control sites) and so rainfall differences were assumed to be negligible.

RESULTS

To facilitate comparisons between tree species and sites, all results are summarized together in Table 1. *Acacia nigrescens* was browsed significantly more heavily at the waterhole site than at the *A. nigrescens*

control site. Furthermore, *A. nigrescens* was browsed more heavily than *A. tortilis* at the waterhole site, where browsing pressure on *A. tortilis* was also higher than that at the *A. tortilis* control site. Browsing pressure did not differ significantly between *A. nigrescens* and *A. tortilis* at the two control sites.

Net annual shoot extension was greater in *A. tortilis* than *A. nigrescens* at both waterhole and control sites. Within each species, net annual shoot extension did not differ significantly between waterhole and control sites. This finding is important, as it shows that despite being browsed significantly more severely, shoots on trees at the waterhole site achieved net annual growth increments equivalent to those at control sites. Hence shoot regrowth in the heavily browsed trees, especially *A. nigrescens*, was exceptionally rapid to compensate for continual removal as well as achieve a net annual growth increment equivalent to that of lightly browsed trees.

Leaves on heavily browsed *A. nigrescens* trees at the waterhole were significantly lower in condensed tannins, and higher in total nitrogen and total phosphorus, than leaves on any of the other trees sampled.

Soil total nitrogen was highest at the *A. nigrescens* control site and lowest at the *A. tortilis* control site, with the waterhole site intermediate. Soil total phosphorus was highest at the waterhole site and lowest at the *A. tortilis* control site, with a *A. nigrescens* control site intermediate. The same applied for nitrate nitrogen and ammonium nitrogen. Water-soluble phosphorus was higher in soil at the waterhole than at the two control sites. In all comparisons, the *A. tortilis* control site had the lowest levels of soil nutrients assayed. At the waterhole site, soil nutrient levels beneath *A. nigrescens* canopies were not significantly different from those beneath *A. tortilis* canopies in all comparisons.

In both *Acacia* species leaf N and P levels were not correlated with soil N and P levels. However, browsing pressure on *A. nigrescens* was strongly positively correlated with leaf total nitrogen content (Fig. 1), and negatively correlated with leaf condensed tannin con-

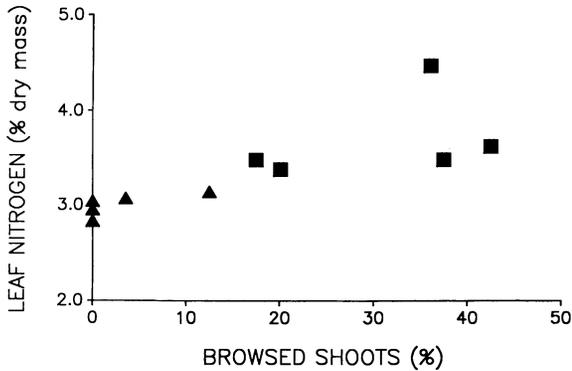


FIG. 1. *Acacia nigrescens* leaf nitrogen content (% dry mass) plotted against the percentage of marked shoots that were browsed on each of five trees at control (▲) and waterhole (■) sites. Spearman's rank correlation, $R_s = 0.95$ ($P < .01$).

tent (Fig. 2). Alternatively, the distribution of data points in Fig. 2 suggests that *A. nigrescens* leaf tannin concentration could be a complex function of browsing pressure. That is, there may be no change at low levels of browsing but a large change to a lower concentration (with high variability among trees) when browsing intensity exceeds a critical threshold ($\approx 15\%$ browsed shoots). Browsing pressure on *A. tortilis* was not correlated with any of the leaf chemistry variables assayed.

DISCUSSION

In a mixed stand of *Acacia tortilis* and *A. nigrescens* at a seasonal waterhole, browsing pressure was significantly 2.5 times as high on *A. nigrescens* as on *A. tortilis*. Browsing pressure on both species was higher at the waterhole than at control sites. To replace tissue lost to browsers, shoot regrowth occurred on trees of both species at the waterhole, so that net annual shoot extension was not significantly different from that among lightly browsed control trees. Furthermore, the nutritional quality of foliage on severely browsed *A. nigrescens* trees at the waterhole was significantly higher (higher in nutrients and lower in condensed tannin) than that of foliage on lightly browsed *A. nigrescens* trees at the control site. For the less heavily utilized *A. tortilis*, no difference in forage quality was detected between waterhole and control sites.

The difference between *A. tortilis* and *A. nigrescens* in terms of browsing pressure at the waterhole can be explained by differences in feeding preference. Large browsers feed on *A. nigrescens* in preference to *A. tortilis* (du Toit 1988), probably because of the greater spinescence and smaller leaf size of the latter (Cooper and Owen-Smith 1986). An explanation for the higher browsing pressure and forage quality on *A. nigrescens* trees at the waterhole, relative to the control site, requires consideration of two possibilities.

Firstly, it could be argued that severe browsing at the waterhole resulted from the high leaf nutrient levels

expected among trees growing in soils enriched with dung. However, in both *Acacia* species, leaf total nitrogen and phosphorus levels were not related to total levels of these nutrients in the soil. "Available" soil nutrients in the form of ammonium, nitrate, and water-soluble phosphorus were all highest at the waterhole site, and so both *A. tortilis* and *A. nigrescens* leaf nutrients should also have been higher at the waterhole than at the control sites. This was not the case, however. In fact, *A. tortilis* leaf nitrogen at the waterhole site did not differ significantly from that at the *A. tortilis* control site, which had the lowest soil nutrient levels. Finally, soil nutrient differences cannot account for the significant difference between waterhole and control sites with respect to *A. nigrescens* leaf condensed tannin levels, as no such difference was detected for *A. tortilis*.

An alternative hypothesis, which is suggested by our results, is that severe browsing induces a physiological response in some woody plants that increases palatability, leading to a feedback loop of further browsing. The mechanics of this feedback loop (refer to Fig. 3) are outlined below.

Browsing ruminants, such as giraffe and impala, often bite off or damage shoot ends during feeding (Dunham 1980, Pellew 1984, Cooper 1985, du Toit 1988). This is equivalent to pruning (step 1) which induces a plant physiological response quite different from that due to severe defoliation, such as caused by insects (Danell and Huss-Danell 1985, Bryant et al., *in press*). Pruning the shoot system of mature woody plants reverses ageing (step 2), reducing between-shoot competition for nutrients (Moorby and Wareing 1963). The result is increased concentrations of nutrients in remaining shoots (step 3), which together with a release of apical dominance, stimulates growth (step 4). From this study it appears that the pruning effect, widely employed in orchard management, also works to the advantage of

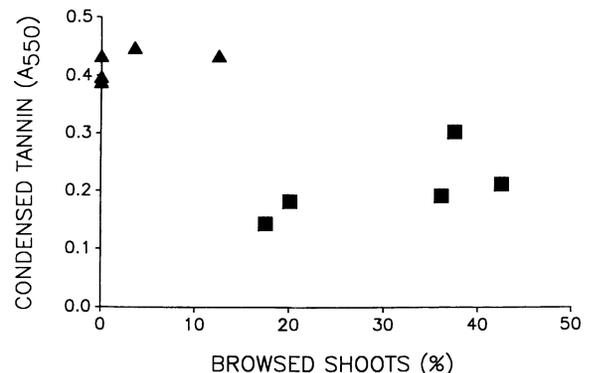


FIG. 2. *Acacia nigrescens* leaf condensed tannin content (A_{550}) plotted against the average percentage of marked shoots that were browsed on each of five trees at control (▲) and waterhole (■) sites. For the overall relationship ($P < .05$). The absorbance value was measured at 550 nm in the proanthocyanidin assay (see Methods).

browsing ruminants. Evidence is stimulation of shoot regrowth and significantly higher levels of leaf nitrogen and phosphorus in severely pruned *A. nigrescens* relative to less pruned *A. nigrescens* and *A. tortilis* (Table 1). Furthermore, carbohydrate demands incurred by rapid regrowth (step 5) cause substrate limitation (step 6) of carbon-based secondary metabolite synthesis (Bryant et al. 1983, Danell and Huss-Danell 1985, Bryant et al. 1987, Bryant et al., *in press*). Hence leaf-condensed tannin levels in heavily browsed *A. nigrescens* at the waterhole were significantly reduced (halved) relative to lightly browsed plants at the control site (Table 1). Reduced chemical defense and increased shoot nutrients (steps 6 and 3) increase the palatability (step 7) of most woody plants (Bryant et al. 1983, Cooper and Owen-Smith 1985, Danell and Huss-Danell 1985, Cooper et al. 1988, du Toit 1988, Bryant et al., *in press*), thereby attracting increased browsing pressure (feedback loop to step 1).

For the above cause-and-effect system to be initiated and maintained, it requires that browsing pressure become focused on a localized patch of *A. nigrescens*. We suggest that this focus is provided by waterholes, to which impala are attracted for their water requirements, and where they severely browse *A. nigrescens* to the upper limit of their feeding height range. Even moderate browsing by giraffe would then raise the browsing pressure on these patches above the "background" level. If this was sufficient to produce the pruning effect leading to increased palatability, then more giraffe would be attracted to these patches and the browsing feedback loop would come into effect.

Stimulation of *Acacia* shoot production by browsing has been demonstrated in controlled experiments with giraffe (Pellew 1983) and domestic goats (Teague 1987). Pellew (1983) suggests that this could be induced by salivary plant-growth-promoting agents (Reardon et al. 1972, Dyer 1980, McNaughton 1985). Evidence from this study indicates that browsing not only stimulates *Acacia* shoot production, but may also enhance browse quality. Hence the effects of concentrated browsing could be considered analogous to the effects of gregariousness in grazers, which may modify the sward to the benefit of individual grazers in a herd (McNaughton 1984). However, the analogy is not complete. Firstly, the greater forage yield per bite from grazing lawns results largely from improved grass leaf: stem ratios, and increased green leaf nutrient concentrations (Ruess et al. 1983, Ruess 1984, McNaughton 1984) while leaves of severely pruned *Acacia* trees also have improved nutrient:condensed tannin ratios. Secondly, while grazing lawns apparently maintain high productivity despite repeated grazing by migratory ungulates (McNaughton 1979; but see Belsky 1986), the benefits of concentrated browsing appear to be relatively short lived. Preliminary evidence indicates that severe selective browsing ultimately leads to the replacement of *A. nigrescens* by less palatable and productive species

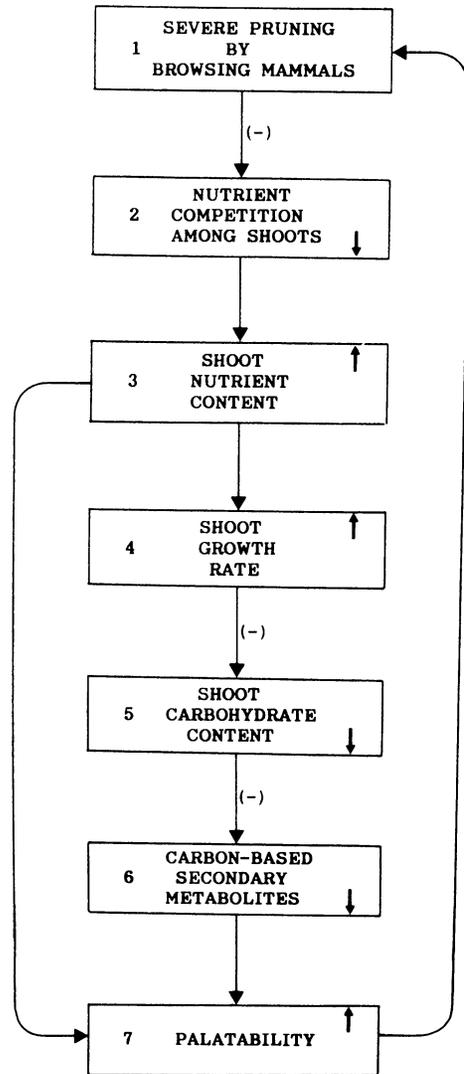


FIG. 3. Cause-and-effect model of woody plant chemistry changes induced by severe browsing, showing positive effects on palatability that induce further browsing. Arrows between boxes indicate positive effects unless marked (-). Small arrows within boxes indicate directions of change. Adapted from Bryant et al. (*in press*).

(J. T. du Toit and J. P. Bryant, *unpublished manuscript*).

ACKNOWLEDGMENTS

Previous drafts were improved through the constructive comments of M. Caldwell, N. Owen-Smith, R. Scholes, B. Walker, and two anonymous referees. The study was made possible by generous support from the National Parks Board of South Africa. Research funds were provided by the C.S.I.R. and the University of the Witwatersrand.

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