

# Morphological responses of woody species to simulated twig-browsing in Botswana

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**Abstract:** Increased shoot growth has recurrently been recorded following real or simulated shoot browsing, although responses may vary between different woody species. We investigated morphological responses to simulated dry-season browsing on *Colophospermum mopane*, *Acacia tortilis*, *Grewia flava*, *Peltophorum africanum* and *Ziziphus mucronata*, which differ in growth rate, occurrence of spines and use by mammalian herbivores. Treatment groups included a control, four clipping intensities and cutting at ground level. Responses were monitored during the following growth season on three annual shoots, located in the bottom, middle and top height interval, on each sapling. All five species showed compensatory growth responses, although no obvious relation was found between the strength of responses and growth rate or natural browsing pressure. The general pattern was an increased shoot length, shoot diameter, number of lateral shoots and shoot biomass with increased clipping intensity. These responses are probably an effect of the reduction of competing growing points and disrupted apical dominance. Growth responses were stronger in shoots with higher location on the sapling, which may reflect the pressure on saplings to attain a certain height to avoid browsing, reproduce and increase resistance to fire. We found no evidence of the number of spines being an induced defence in either of the two spinescent species studied.

**Key Words:** *Acacia tortilis*, *Colophospermum mopane*, *Grewia flava*, growth, herbivory, *Peltophorum africanum*, plant–herbivore interactions, spines, *Ziziphus mucronata*

## INTRODUCTION

A plant's ability to compensate for tissue loss due to browsing is influenced by several factors, including timing and degree of damage (Canham *et al.* 1994, Danell *et al.* 1994), competition and nutrient availability (Hjältén *et al.* 1993, Maschinski & Whitham 1989) and plant intrinsic factors (Bryant *et al.* 1983). It has been suggested that plants, due to limited resources, either invest in defensive traits or greater regrowth capacity (Herms & Mattson 1992, van der Meijden *et al.* 1988), with some plants even overcompensating in terms of growth (McNaughton 1979, 1983; Owen & Wiegert 1976, Paige & Whitham 1987). Slow-growing, low-resource-adapted plants are expected to invest in chemical defences against herbivory, while high-resource-adapted plants instead may rely on rapid growth to replace lost tissues and escape from the

browsing zone (Bryant *et al.* 1983, 1989; Coley *et al.* 1985, Herms & Mattson 1992).

Several different responses to simulated winter browsing in trees have been demonstrated in temperate zones, with effects on growth varying between species (Bilbrough & Richards 1993, Campa *et al.* 1992, Canham *et al.* 1994, Danell *et al.* 1994, 1997; Katsma & Rusch 1980, Krefting *et al.* 1966). Studies in boreal forests on the effects of simulated winter browsing on birches (*Betula* spp.) have shown that browsed birches may increase shoot size, branching and leaf size on individual shoots during the following summer (Danell *et al.* 1994, 1997), although overall shoot biomass production may decrease (Danell *et al.* 1994). Similar responses are expected following dry-season browsing in African savannas, although fewer such studies have been undertaken there. Bergström *et al.* (2000) found that late-dry-season clipping of *Combretum apiculatum* produced larger but fewer annual shoots and increased individual shoot biomass and leaf area during the following growth season.

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In addition, du Toit *et al.* (1990) reported that *Acacia nigrescens* and *A. tortilis* compensated for herbivory as net annual shoot extension did not differ between lightly and heavily browsed trees. Simulated twig-biting during the rainy season also induced compensatory regrowth in *Acacia erubescens* (Dangerfield & Modukanele 1996). Increased growth following shoot browsing therefore seems to be a recurring pattern in African savanna trees. As saplings are vulnerable to fires and most species must attain a certain height before starting to reproduce, growth in height may be especially important in this system with frequent fires (Bond 1997, Bond & van Wilgen 1996, Dangerfield & Modukanele 1996). As a consequence, growth responses may be more pronounced in shoots higher in the crown, which would promote growth in height over lateral growth.

Although browsing is common on spinescent woody species, spines and thorns are believed to limit total intake (Milewski *et al.* 1991), primarily by restricting bite size (Belovsky *et al.* 1991, Cooper & Owen-Smith 1986, Gowda 1996). As such, spines seem to function as a defence against twig-biting, but less so against leaf picking (Gowda 1996). Previous studies have reported increased spine length, or biomass of spines, on *Acacia* trees subjected to browsing or hand pruning, compared with unbrowsed or unpruned trees (Gowda 1997, Rohner & Ward 1997, Young & Okello 1998, Young *et al.* 2003), and longer spines on shoots within reach of browsers, compared with shoots above browsing height (Milewski *et al.* 1991, Young 1987). Increased spine densities on browsed shoots have also been found (Dangerfield *et al.* 1996).

On woody species, large herbivores mostly forage for shoots and leaves by twig-biting, leaf-picking or leaf-stripping (Bergström 1992). As most savanna trees are deciduous (Scholes 1997), leaf herbivory mostly occurs during the growth season, while twig-biting is especially common during the dry season and droughts. The mode of feeding, and the season in which it occurs, is of course essential to the outcome in terms of plant responses (Canham *et al.* 1994, Danell *et al.* 1994). To study responses to simulated dry-season browsing (twig-biting), we performed clipping treatments, at different intensities, on five different woody species in Botswana. The species studied included both fast- and slow-growing species and spinescent and non-spinescent species. Under natural conditions, the studied species are browsed by large herbivores to varying extents. During the following wet (growth) season we monitored the emerging annual shoots and recorded shoot length, shoot base diameter, lateral shoot production, leaf size and shoot biomass. The study included annual shoots growing at different height levels (bottom, middle and top third of the sapling). To study responses in terms of defence we also monitored spine production.

We presumed that simulated dry-season browsing would affect growth and morphology of annual shoots during the following wet season and expected growth responses to be most evident in the fast-growing species. As clipping disrupts apical dominance (Aarssen 1995), and may lessen the competition for nutrients between shoots by reducing the number of growth points (Danell & Bergström 1989, du Toit *et al.* 1990, Fontanier & Jonkers 1976, McNaughton 1983), we predicted that clipping would result in an increased growth of annual shoots and larger leaf size, during the following growth season. We also expected that many responses would be more pronounced in the upper part of the crown and that clipping would induce an increased production of spines in spinescent species.

## METHODS

The trial was performed during 1996–97 in south-eastern Botswana. Two experimental fields were used, one at Veld Products Research (VPR), Gabane, 20 km west of Gaborone (24°39'S, 25°47'E, altitude 1230 m asl) and one at Botala Farm (BF), Notwane, 20 km south of Gaborone (24°47'S, 25°50'E, altitude 1020 m asl). We used five woody species in the trial, all common in Botswana and differing in terms of growth rate, presence of spines and palatability to large herbivores (Table 1). Saplings (1–2.5 y old depending on species) were planted at the experimental sites in mid-January 1995. *Colophospermum mopane* Kirk ex Benth. (Cm) and *Acacia tortilis* (Forsk.) Hayne (At) were planted at VPR, with every third sapling being a *C. mopane* (i.e. At, At, Cm, At, At, Cm, . . .) at a spacing of 2 m. *Grewia flava* DC. (Gf), *Peltophorum africanum* Sonder (Pa) and *Ziziphus mucronata* Willd. (Zm) were planted at BF, alternating the species (i.e. Pa, Gf, Zm, Pa, Gf, Zm, . . .) at a spacing of 1.9 m. Between the time of planting and the start of the trial, both sites were weeded and watered when necessary.

## Treatments

Individuals of each species were randomly allocated to six different treatment groups; control, four clipping intensities, and cutting at ground level (hereafter called stump treatment). In mid-August 1996, during the dry season and before leafing, the clipping treatments, simulating large herbivore browsing, were performed at four intensities by removing 25, 50, 75 and 100% respectively of the number of living twigs (longer than 1 cm) on individual saplings. The exception was *C. mopane* that, due to a shorter supply of saplings, was clipped only at 50 and 100% intensities. Twigs were clipped at a diameter of  $\leq 4$  mm (except twigs of *P. africanum* which

**Table 1.** Description of species used in this study. Classification of species according to Coates Palgrave (2000).

Species (Family, subfamily)	Growth rate <sup>1,2,3</sup>	Spines	Use by mammalian herbivores
<i>Acacia tortilis</i> (Leguminosae, Mimosoideae)	Slow	Yes <sup>a</sup>	Palatable in all savanna vegetation types <sup>4</sup> . Leaves and pods nutritious <sup>1,2</sup> , well-known fodder tree <sup>2</sup> . Leaves and shoots eaten by antelope, branches by rhino <sup>5</sup>
<i>Colophospermum mopane</i> (Leguminosae, Caesalpinioideae)	Slow	None	Eaten but not selected in arid and <i>Acacia</i> savannas, palatable in <i>C. mopane</i> savannas <sup>4</sup> . Foliage eaten by elephant <sup>5,2</sup> , giraffe and rhino <sup>5</sup> . Especially young leaves eaten by game <sup>6</sup> and cattle <sup>2</sup>
<i>Grewia flava</i> (Tiliaceae)	No info.	None	Very palatable in arid savannas, palatable in mixed savannas and eaten but not selected in <i>Acacia</i> savannas <sup>4</sup> . Leaves heavily browsed by game and stock, especially when grass is scarce <sup>1</sup>
<i>Peltophorum africanum</i> (Leguminosae, Caesalpinioideae)	Fast	None	Browse by game limited <sup>2</sup> . Foliage may contain saponins which function as chemical defence <sup>7</sup>
<i>Ziziphus mucronata</i> (Rhamnaceae)	Fast	Yes <sup>b</sup>	Palatable in <i>Acacia</i> and mixed savannas, unpalatable to palatable in arid savannas <sup>4</sup> . Leaves and fruits eaten by game and stock <sup>1,2</sup> , valuable fodder in times of drought <sup>1</sup>

<sup>a</sup> Pairs of long straight or short curved stipular spines.

<sup>b</sup> Pairs of one short straight and one short curved stipular spine.

References on growth rate and use by mammalian herbivores: <sup>1</sup>Coates Palgrave (2000), <sup>2</sup>van Wyk (1990), <sup>3</sup>Palmer & Pitman (1973), <sup>4</sup>Walker (1980), <sup>5</sup>Berry (undated), <sup>6</sup>Styles & Skinner (1997), <sup>7</sup>Cooper & Owen-Smith (1985).

were cut at  $\leq 6$  mm), starting the counting at ground level to obtain a random clipping of the leading shoot. The diameter used for clipping roughly represented the upper limit of bite diameter for large herbivores in the adjacent Mokolodi Nature Reserve (Bergström & Skarpe, pers. obs.). For the stump treatment each sapling was cut at ground level, while saplings in the control group were left intact. In January 1997, i.e. during the following rain season, we randomly selected and marked three new annual shoots (growing from lateral buds on older shoots) per sapling, one shoot within each of three height intervals (bottom, middle and top section).

### Data collection

At the end of the wet season (April 1997) leaf lengths (mm) were measured on all saplings except *A. tortilis*. These measurements were performed on a sample of approximately 20 leaves, selected evenly along the marked annual shoots in the upper section of each sapling, excluding leaves not fully developed or badly damaged by insect herbivores. Simple leaves (*G. flava* and *Z. mucronata*) were measured from leaf base to apex, compound leaves with two leaflets (*C. mopane*) from leaf base to the apex of the right leaflet, and twice-compound leaves (*P. africanum*) along the rachis, from the first to the last rachilla node. In August 1997, during the dry season 1 y after treatment, we cut each marked shoot at the base, measured shoot length (cm) and base diameter (mm), counted the number of lateral shoots (longer than 1 cm) and weighed all shoots (g fresh weight). All shoots were brought back to the laboratory where they were dried at 40 °C to constant weight and weighed again (g dry weight). Due to logistic problems, only fresh weights were recorded for *A. tortilis*. On each marked shoot on the

two spinescent species, we also counted the number of pairs of spines (separating between long straight vs. short curved spines on *A. tortilis*). The height of the saplings (mean  $\pm$  SD), excluding stump-treated individuals, was at this stage; 134  $\pm$  42 cm for *A. tortilis*, 53  $\pm$  23 cm for *C. mopane*, 125  $\pm$  40 cm for *G. flava*, 124  $\pm$  49 cm for *P. africanum*, and 197  $\pm$  50 cm for *Z. mucronata*. During the growth season following treatments, 96% of *G. flava* (n = 24), 9% of *P. africanum* (n = 17) and 70% of *Z. mucronata* (n = 24) individuals in the control group bore reproductive organs. *Acacia tortilis* and *C. mopane* had not yet reached reproductive maturity.

### Statistical analyses

At time of data collection, 17 to 24 saplings of each species remained in each control and clipped group, providing 13–24 shoots for each combination of species (five species), clipping treatment (five levels: 0, 25, 50, 75 and 100% intensity) and shoot location (three levels: top, middle and bottom location) for statistical analyses.

To test for general differences between clipping treatments and shoot locations across species, response variables which met the assumptions of an ANOVA, after square-root (for data on shoot length) and logarithmic transformations (for data on shoot base diameter and biomass), were analysed in multi-way ANOVAs with replication (Sokal & Rohlf 1995). Three fixed and crossed factors were entered (species, clipping treatment and shoot location), except for one species, *C. mopane*, that was only subjected to 50% and 100% clipping treatments, and was analysed separately with only two factors (clipping treatment and shoot location). Shoot biomass of *A. tortilis* (measured as fresh weight) was also analysed separately

from shoot biomass of the other species (measured as dry weight).

Remaining response variables, which violated the assumptions of an ANOVA (normal distribution and homogeneity of variances) in spite of transformation (data on leaf length, number of lateral shoots and number of spines on shoots), were analysed with Scheirer–Ray–Hare tests, an extension of the Kruskal–Wallis test and a non-parametric equivalent to multi-way ANOVAs with replication (Dytham 1999, Scheirer *et al.* 1976, Sokal & Rohlf 1995). Leaf lengths, which were only measured on shoots in top locations, were analysed with two factors (species and clipping treatment), while number of lateral shoots per annual shoot were analysed with three factors (species, clipping treatment and shoot location). As before, *C. mopane* was analysed separately without the species factor. The two spinescent species, *A. tortilis* and *Z. mucronata*, were analysed separately for number of spines per unit shoot length (separating the two types of spines on *A. tortilis*), with two factors (clipping treatment and shoot location).

As we were only interested in general patterns, not detailed differences in interactions between clipping treatments and locations, further trends were sought in graphic presentations and no post-hoc analyses were performed. For comparison, data from shoots on ‘stump’ saplings (from 17–18 individuals per species) have been added to the graphs, although they were not included in the statistical analysis as they all grew from the base of the sapling and were therefore not comparable with shoots at different locations on the control or clipped saplings.

All tests were considered significant at the  $P < 0.05$  level. All statistical analyses were performed with MINITAB™ release 13.32 (MINITAB 2000a, b).

## RESULTS

Analyses across four species (*A. tortilis*, *G. flava*, *P. africanum* and *Z. mucronata*) showed effects of all three factors (species, clipping intensity and shoot location on sapling) on shoot length, shoot base diameter and number of lateral shoots per annual shoot, while leaf lengths only differed between species (Tables 2 and 3). Interaction effects of species and clipping were found for shoot base diameter and number of lateral shoots, and of clipping and shoot location for shoot diameter. Analyses of *C. mopane* (which was subjected to fewer clipping treatments and therefore analysed separately) showed an effect of clipping intensity alone on shoot length and leaf length, and effects of both clipping and shoot location on shoot diameter and number of lateral shoots (Tables 2 and 3). Analyses across three species (*G. flava*, *P. africanum* and *Z. mucronata*) showed effects of all three factors (species, clipping intensity and shoot location) on shoot biomass

**Table 2.** ANOVA for effects of species, dry-season clipping treatment (0, 25, 50, 75 and 100% of shoot removed) and shoot location (bottom, middle and top third of sapling) on length and diameter of annual shoots of *A. tortilis* (At), *C. mopane* (Cm), *G. flava* (Gf), *P. africanum* (Pa) and *Z. mucronata* (Zm). Cm was only clipped at 0, 50 and 100%, and therefore analysed in a separate ANOVA.

Source	At, Gf, Pa, Zm			Cm		
	df	F	P	df	F	P
Shoot length	Species	3	66.8	< 0.001	–	–
	Clipping	4	26.2	< 0.001	2	23.0
	Shoot location	2	21.4	< 0.001	2	1.07
	Species × Clip.	12	1.54	0.103	–	–
Shoot base diameter	Clip. × Loc.	8	1.84	0.067	4	0.33
	Species	3	203	< 0.001	–	–
	Clipping	4	32.3	< 0.001	2	19.6
	Shoot location	2	52.5	< 0.001	2	5.28
Species × Clip.	Species × Clip.	12	2.86	0.001	–	–
	Clip. × Loc.	8	2.20	0.025	4	0.60

(dry weight) (Table 4). Shoot biomass (dry weight) of *C. mopane* was only significantly affected by clipping, while shoot biomass (fresh weight) of *A. tortilis* was only significantly affected by shoot location (Table 4).

The graphical presentation of effects of clipping treatments shows a general pattern, most noticeable in the slow-growing *C. mopane*, and the fast-growing *P. africanum* and *Z. mucronata*, of increased shoot length, shoot base diameter and number of lateral shoots with increased clipping intensity (Figures 1a–c). In addition, leaf length increased with clipping intensity in *C. mopane* (Figure 1d). In all species, except the slow-growing *A. tortilis*, there is a trend towards higher shoot biomass with increasing clipping intensity (Figure 1e). In comparison to shoots on control or clipped saplings, shoots on ‘stump’ saplings of *A. tortilis*, *G. flava* and *Z. mucronata* have an increased length, diameter, number of lateral shoots and shoot biomass, but differ less from heavily clipped shoots in *C. mopane* and *P. africanum* (Figures 1a–c, e). The graphical

**Table 3.** Scheirer–Ray–Hare Test for effects of species, dry-season clipping treatment (0, 25, 50, 75 and 100% of shoot removed) and shoot location (bottom, middle and top third of sapling) on number of lateral shoots (> 1 cm) and leaf length (only measured on top shoots) on annual shoots of *A. tortilis* (At), *C. mopane* (Cm), *G. flava* (Gf), *P. africanum* (Pa) and *Z. mucronata* (Zm). Cm was only clipped at 0, 50 and 100%, and therefore analysed in a separate test.

Variable	Source	At, Gf, Pa, Zm	Cm
		P-value	P-value
Number of lateral shoots	Species	< 0.001	–
	Clipping	< 0.001	0.004
	Shoot location	< 0.001	0.003
	Species × Clip.	0.007	–
Leaf length	Clip. × Loc.	0.162	0.545
	Species	< 0.001	–
	Clipping	0.626	0.005
	Species × Clip.	0.904	–

**Table 4.** ANOVA for effects of species, dry-season clipping treatment (0, 25, 50, 75 and 100% of shoot removed) and shoot location (bottom, middle and top third of sapling) on shoot biomass (fresh or dry weight) of *A. tortilis* (At), *C. mopane* (Cm), *G. flava* (Gf), *P. africanum* (Pa) and *Z. mucronata* (Zm). Cm was only clipped at 0, 50 and 100%, and therefore analysed in a separate ANOVA.

Source	At (fresh weight)			Gf, Pa, Zm (dry weight)			Cm (dry weight)		
	df	F	P	df	F	P	df	F	P
Species	–	–	–	2	114	< 0.001	–	–	–
Clipping	4	2.08	0.084	4	29.3	< 0.001	2	22.3	< 0.001
Shoot location	2	4.83	0.009	2	37.4	< 0.001	2	2.89	0.059
Species × Clip.	–	–	–	8	1.56	0.133	–	–	–
Clip. × Loc.	8	0.53	0.834	8	1.27	0.253	8	0.50	0.738

presentation of shoots at different locations shows that all species increased shoot length, shoot diameter, number of lateral shoots and shoot biomass with shoot height on the sapling, with the exception of *C. mopane* which differed little in shoot length and biomass between shoot locations (Figure 2a–d).

Analyses of the number of pairs of spines per unit shoot length did not reveal any significant effect of clipping intensity (Table 5, Figure 3a), and only showed an effect of shoot location in *Z. mucronata* (Table 5) which had fewer spines on higher shoots (Figure 3b).

## DISCUSSION

All studied species showed a compensatory response to the simulated browsing. However, we found no obvious relation between strength of response to clipping and growth rate or natural browsing pressure of species. Of the three species which showed the most distinct responses to clipping intensity, *C. mopane* is slow-growing, while *P. africanum* and *Z. mucronata* are fast-growing. In addition, the severe stump treatment gave the strongest growth response in *A. tortilis* and *Z. mucronata*, which are slow- and fast-growing species, respectively. Although *P. africanum* is rarely browsed, its responses to clipping were similar to the other species. According to general hypotheses concerning plant defences, fast-growing species, adapted to high-resource environments, should be able to respond to herbivory by rapid regrowth, while slow-growing species should invest in defence

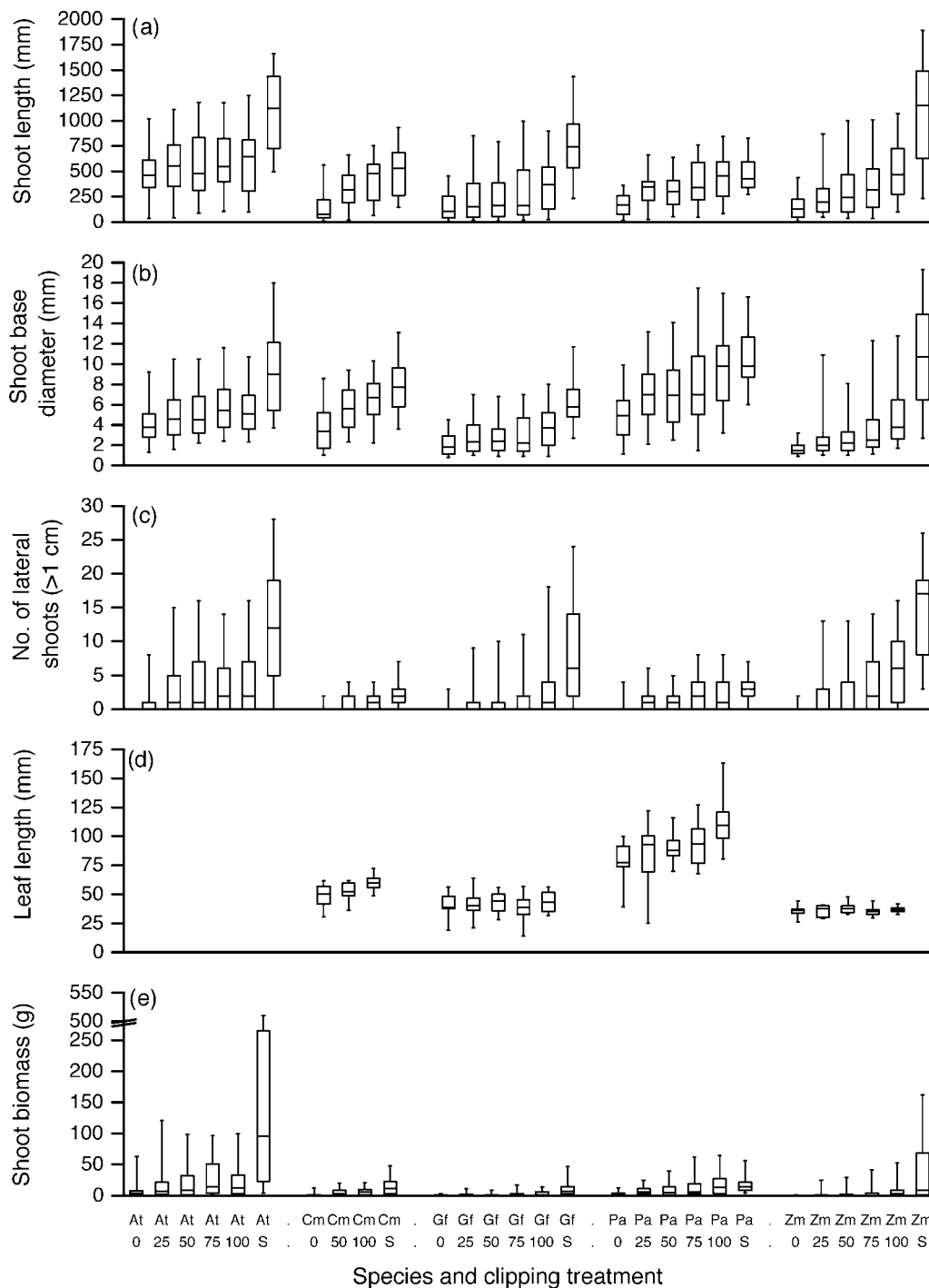
**Table 5.** Scheirer–Ray–Hare Test for effects of dry-season clipping treatment (0, 25, 50, 75 and 100% of shoot removed) and shoot location (bottom, middle and top third of sapling) on number of pairs of spines on annual shoots of *A. tortilis* (At) and *Z. mucronata* (Zm).

Source	At (straight spines)	At (curved spines)	Zm
	P-value	P-value	P-value
Clipping	0.849	0.275	0.393
Shoot location	0.411	0.098	0.002
Clip. × Loc.	0.064	0.418	0.168

(Bryant *et al.* 1983, 1989; Coley *et al.* 1985, Herms & Mattson 1992). Nevertheless, even if we use the shoot lengths on control saplings in our study as a measure of growth rate, the prediction that fast-growing species would respond stronger to clipping does not hold.

As predicted, simulated dry-season browsing resulted in a general pattern of increased shoot length, shoot diameter, number of lateral shoots and, consequently, increased shoot biomass during the following wet (growth) season. Increased leaf length with clipping intensity was, however, only found in *C. mopane*. These compensatory growth responses, which increased with increased clipping intensity, may be an effect of modified root–shoot ratio (Danell & Bergström 1989, du Toit *et al.* 1990, McNaughton 1983) and removal of apical dominance suppressing lateral meristems (Aarssen 1995), and consequently, an effect of competition for light, rather than an adaptation to herbivory (Aarssen 1995, Hjältén *et al.* 1993, Järemo *et al.* 1996). Similar responses have also been reported for *Combretum apiculatum*, which produced larger, but fewer, annual shoots and increased shoot biomass and leaf area in the growth season following late-dry-season clipping (Bergström *et al.* 2000). Furthermore, these findings, including increased responses with increased clipping, correspond to those of winter browsing on birch (*Betula* spp.) in the relatively well-studied system of moose (*Alces alces*) and woody plants in the boreal forest (reviewed in Danell *et al.* 1994).

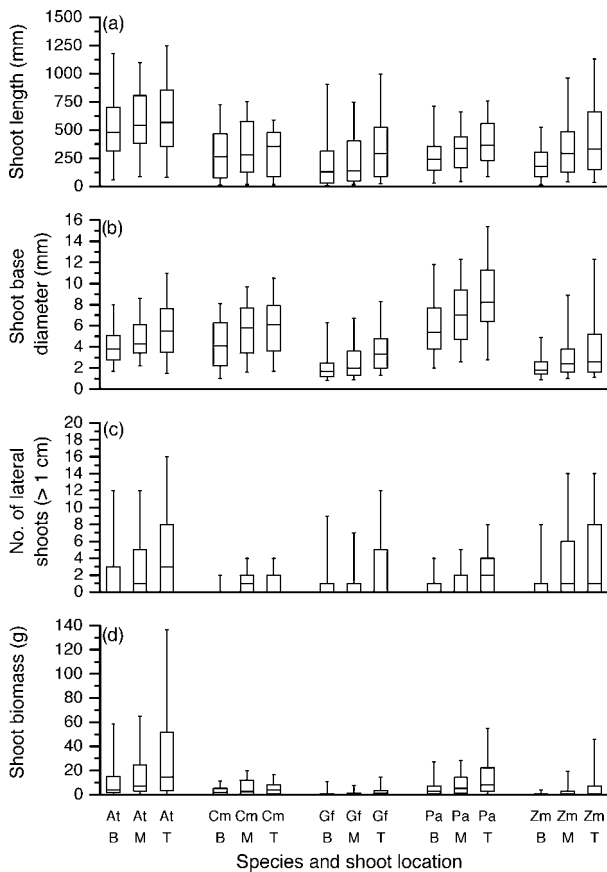
Of the five species studied, all except *A. tortilis* showed a pattern of increased shoot biomass with increased clipping intensity. Nevertheless, *A. tortilis* showed the strongest response in basal shoots in the stump treatment. Accordingly, the most intense clipping treatments may have induced growth of basal shoots instead of axillary shoots in this species. In systems with frequent fires, the ability to sprout from the base of the stem is important for juvenile survival in many species, although this ability may decline when trees grow taller (Bond 1997, Bond & Midgley 2001). Regrowth after severe damage also requires stored reserves, which is traded off against normal growth or reproduction (when trees have



**Figure 1.** Effects of dry-season clipping treatments (0, 25, 50, 75 and 100% of shoots removed) and stump treatment (S) on five woody species (*Acacia tortilis* (At), *Colophospermum mopane* (Cm), *Grewia flava* (Gf), *Peltophorum africanum* (Pa) and *Ziziphus mucronata* (Zm)) in Botswana. Boxes show 25th, 50th (median) and 75th percentiles, and the vertical line marks the 5th and 95th percentile for (a) length of annual shoots, (b) shoot base diameter, (c) number of lateral shoots per annual shoot, (d) leaf length and (e) shoot biomass (measured as g fresh weight for At, and g dry weight for remaining species) at the end of the following growth season. (Note that Cm was only treated with 0, 50 and 100% clipping treatment.)

reached reproductive maturity) (Bellingham & Sparrow 2000, Bond & Midgley 2001). In other words, sprouting behaviour should be more common in juvenile trees, and in species with slow growth or maturation rates.

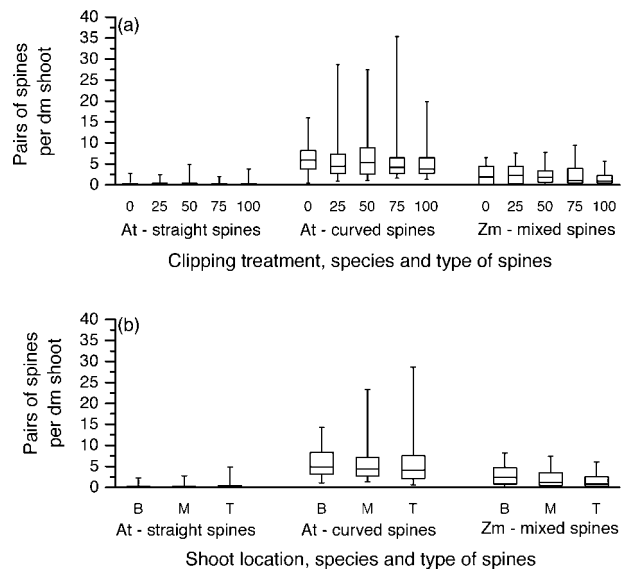
Interestingly, all our species sprouted, irrespectively of growth rate or stage of maturation (in three species, flowers and fruits were produced by individuals in the control group). This also indicates that these species,



**Figure 2.** Effects of shoot location (bottom (B), middle (M) and top (T)) on five woody species (*Acacia tortilis* (At), *Colophospermum mopane* (Cm), *Grewia flava* (Gf), *Peltophorum africanum* (Pa) and *Ziziphus mucronata* (Zm)) in Botswana. Boxes show 25th, 50th (median) and 75th percentiles, and the vertical line marks the 5th and 95th percentile for (a) length of annual shoots, (b) shoot base diameter, (c) number of lateral shoots per annual shoot, and (d) shoot biomass (measured as g fresh weight for At, and g dry weight for remaining species) at the end of the following growth season.

at least as juveniles, have stored reserves which can be allocated to regrowth following fire or herbivory.

The general pattern of differences between shoot locations was an increase in shoot length, diameter, number of lateral shoots and biomass higher up on saplings. This indicates that growth in higher shoots may be important to reach above browsing height and attain reproductive size, and to increase probability of surviving frequent fires (Bond 1997, Bond & van Wilgen 1996, Dangerfield & Modukanele 1996). Few significant interaction effects between treatment and shoot location were found in our study, although some trends were indicated (Tables 2–5). We had expected stronger effects of shoot location, but the observed pattern may be explained by the relatively small size of the saplings, and canopies, and also a lack of competition between the saplings.



**Figure 3.** Effects of (a) dry-season clipping treatments (0, 25, 50, 75 and 100% of shoots removed) and (b) shoot location (bottom (B), middle (M) and top (T)) on spine production of two woody species, *Acacia tortilis* (At) and *Ziziphus mucronata* (Zm), in Botswana. Boxes show 25th, 50th (median) and 75th percentiles, and the vertical line marks the 5th and 95th percentile for number of pairs of spines per dm annual shoot at the end of the following growth season. Note that At produces pairs of both long straight spines and short curved spines, while Zm produces pairs of one short straight and one short curved spine (mixed spines).

Contrary to our predictions, we did not find any significant increase in spine density with increasing clipping intensity in either *A. tortilis* or *Z. mucronata*. The trend (Figure 3a) rather is towards a reduced spine density with clipping intensity. Previous studies indicating that spinescence may be an inducible defence have in most cases found increases in spine length (Gowda 1997, Rohner & Ward 1997, Young & Okello 1998, Young *et al.* 2003). Density of stipular spines, on the other hand, is dependent on internode length, and the increased growth in clipped shoots in this study would naturally reduce spine density. Supporting this idea, under reversed conditions, other studies have reported increased spine densities in browsed shoots following reduced growth rates and internode lengths (Dangerfield *et al.* 1996, Milewski *et al.* 1991). This may also explain why we found a trend in *Z. mucronata* towards a higher density of spines on lower shoots, compared to those higher up which grew longer.

Although pronounced responses were observed, no evidence was found for a clear connection between growth responses and growth rate or earlier reported natural browsing pressure of the species. The present study showed that the five species seem to have a high tolerance to twig biting during the dry season and are able to react strongly through re-growth during the following growth season. One striking result is the increased shoot

size with increasing clipping intensity, which may affect the probability of future browsing (cf. Bergström *et al.* 2000). On most occasions the results only indicated a slight effect of shoot location, a pattern that might be different on trees growing naturally with higher intra- and interspecific competition. The significant growth responses could be interpreted as an investment in competitive ability, in opposition to allocation to defensive traits, and purely physiological in nature. However, even if the growth responses were a direct result of altered apical dominance and root–shoot ratio, they may still be adaptive responses to different types of physical damage, including herbivory.

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