

## Shoot characteristics of *Acacia tortilis* (Forsk.) in wildlife and rangeland habitats of Botswana

J. M. DANGERFIELD\*<sup>1</sup>, J. S. PERKINS<sup>2</sup> and S. K. KAUNDA<sup>1</sup>

<sup>1</sup>*Department of Biological Sciences and* <sup>2</sup>*Department of Environmental Science, University of Botswana, Private Bag 0022, Gaborone, Botswana*

### Summary

Length, branch production, orientation, spinescence and biomass were measured for current shoots of *Acacia tortilis* shrubs in a range of habitats in Botswana. All shoot characteristics varied between individuals and between habitats with longer, less spinescent shoots produced in the habitat recently protected from wildlife. Biomass allocated to woody material increased with shoot length at the expense of leaf mass, whilst investment in straight prickles was as much as 6% of shoot dry mass. Shoot length had significant effects on total current shoot mass per shrub which was greatest in the recently protected area but the mean number of shoots per shrub also varied between habitats. Age and history of disturbance, including herbivory, appear to be important determinants of morphology and growth pattern of individual shrubs. Fitness of *A. tortilis* individuals and the consequence of flexibility in growth responses for vegetation structure and community organization are discussed.

*Key words:* biomass allocation, browsers, herbivory, production, spinescence

### Résumé

On a mesuré la longueur, la production de branches, l'orientation, l'épinescence et la biomasse des pousses récentes des arbustes d'*Acacia tortilis* dans différents habitats du Botswana. Toutes les caractéristiques des pousses variaient selon les individus et les habitats, avec des pousses plus longues et moins épineuses dans l'habitat protégé depuis peu contre la faune. La biomasse de la matière ligneuse augmentait avec la longueur des pousses au détriment de la biomasse des feuilles, tandis que l'investissement dans les raides épines pouvait atteindre 6% du poids sec des pousses. La longueur des pousses avait un impact significatif sur la masse totale des pousses par arbuste, qui était la plus élevée dans la zone récemment protégée, mais le nombre moyen de pousses par arbuste variait aussi selon l'habitat. L'âge et le taux de dérangement, comme par exemple par les herbivores, semblent être des facteurs déterminants dans la morphologie et la croissance de chaque arbuste. La santé de chaque *Acacia tortilis* et la conséquence de la flexibilité des réponses de croissance sur la structure de la végétation et l'organisation des communautés sont discutées.

\*Corresponding author.

## Introduction

An individual plant can respond to herbivory by (a) absorbing the consequences of shoot or leaf loss, (b) increasing the production of new leaves and/or shoots to compensate for the loss (Belsky, 1986), or (c) protecting against future attack (Cooper & Owen-Smith, 1986). Adoption of a general strategy is generally a species level trait, e.g. palatable shrubs in southern Africa tend to produce spines (Owen-Smith & Cooper, 1987), but individual variation in responses can be large and is related to past herbivory, plant age and current environmental conditions.

In southern Africa there are few studies of browse production (Pellew, 1983a; Du Toit, Bryant & Frisby, 1990) and the impact of browsing on trees and shrubs (Bergstrom, 1992). This is surprising as large areas of fine-leaved savannas, typical of the drier regions on Kalahari sand, have only seasonal and highly variable grass production. For example, in Botswana browse is considered important for cattle in the sandveld areas and northern mopane tree savanna (Skarpe, 1990), but is not often considered in carrying capacity estimates (Arntzen & Veenendaal, 1986). Locally abundant wildlife species include specialist browsers and mixed feeders but their impact on the vegetation has been underestimated (Skarpe, 1986, 1990).

Herbivory and its consequences for plant production, morphology and physiology are very difficult to measure (Canham, McAninch & Wood, 1994; Sand-Jensen & Jacobsen, 1994). Where information on basic responses of plants to herbivory are not known, comparative observations of plant characteristics and growth pattern in different environmental conditions within a growing season are valuable. Such comparisons also provide insights into the evolutionary responses of individual species to edaphic conditions and disturbance from herbivores.

In this study we measured shoot characteristics in an invasive and widespread savanna species *Acacia tortilis* from a range of habitats that differed in browsing pressure and edaphic conditions. *A. tortilis* occurs most frequently on enriched or loamy soils, particularly those modified by livestock, and because of this association with human impact is considered an important bush encroachment species in Botswana (Timberlake, 1980).

## Study sites

Three contiguous areas were selected on the southern floodplain of the Thamalakane River, Maun (19°59'S, 23°30'E), within and adjacent to the Maun Education Park (MEP). The sites were located on the upper terrace approximately 5 m above and 800 m distant from the current channel on eutric arenosols. Mean annual rainfall of 500 mm is seasonal and variable both between years and spatially within a season.

Trees and shrubs on the terrace are dominated by *A. tortilis* and *A. nilotica* (L.) Willd. ex Del. with occasional *Dichrostachys cinerea* L. and *Combretum imberbe* Wawra. At the time of sampling (February 1994) grass cover was significant and the annual herb *Amaranthus* sp. was abundant. Wildlife within the park includes kudu, impala and a small number of giraffe together with zebra and wildebeest on the grassed terraces.

One of the sites was a fenced boma of approximately 1 ha, erected in March 1993 as a holding pen for giraffe. Two yearling giraffe were kept in the boma for 6 weeks in July and August 1993 after which no grazing or browsing ungulates were allowed access, hence *A. tortilis* were not browsed for 7 months prior to and during the 1993–94 growing season.

The rangeland habitat was contiguous with the boma but separated by a 3 m tall game fence. Although data on stocking rates were not available, utilization by cattle, goats and donkeys was, at best 16 ha per large stock unit (LSU) (Arntzen & Veenendaal, 1986), but probably closer to 6 ha per LSU (de Ridder & Wagenaar, 1984) (1 LSU  $\equiv$  450 kg body mass).

Three further sites were selected in and around Gaborone (24°40'S, 25°52'E) in southeastern Botswana where rainfall averages 510 mm but with only 50% reliability. Firstly, a fenced area of 2.5 ha dominated by *Acacia erubescens* Welw. ex Oliv. and *D. cinerea* on the University of Botswana campus was chosen. This site was set aside as a Nature Reserve (UBNR) with minimal human disturbance, no recent fires and no large mammalian herbivores (Dangerfield, Milner & Matthews, 1993).

A second site was selected within the Gaborone Game Reserve (GGR) which, although small (500 ha), contains kudu, impala, eland, steenbok and bushbuck that are either obligate or seasonal browsers and occasional browsers such as red hartebeest and gemsbok (McColaugh, 1993). A third site, heavily utilized by cattle and goats, was selected in communal rangeland in the village of Tlokweng less than 5 km from the GGR.

## Methods

On each of the five sites 30 *A. tortilis* shrubs between 0.5 and 4.0 m high were selected at random with respect to location and individual, but stratified to ensure that all size classes were evenly represented. On each shrub eight current annual shoots were selected in a semi-stratified random manner to cover all zones and aspects of the crown up to 250 cm. On the taller plants (>3.0 m) the centre of the crown was inaccessible.

The base of each current shoot was distinguished by a change in colour and softer texture of the stem and the length, height of the shoot base above the ground and the horizontal distance from shoot base to the main trunk were recorded. Any branches on the shoot were measured. The orientation, or direction of growth, of each shoot with respect to the vertical was recorded as 1 if the orientation was between 90° and 60°; 2 if it was between 60° and 30°; 3 if it was between 30° and horizontal and 4 if it was orientated below the horizontal.

On 10 isolated shrubs between 0.5 and 1.2 m high, selected at random, all new shoots were located and their length measured to estimate current season's production still present on the shrub. Not all current shoots were accessible in shrubs >1.2 m. The total length of current shoots was converted to biomass which was assessed by cutting between 50 and 60 shoots from each of three shrubs, one in each of the sites in the MEP. Replicate shrubs were not taken in order to minimize disturbance prior to more detailed shoot marking and clipping experiments. Cut shoots were dried at 40°C for 14 days after which the leaves were separated from the woody stem and weighed. The number of hooked and

straight prickles were counted, and for straight prickles, their length and position with respect to the shoot base were recorded.

## Results

### *Growth pattern of shoots*

Most current shoots were single stems although some were branched with up to 23 separate branches off the main shoot. Frequency of branching varied between sites from 2.4% of all shoots in the wildlife areas to 8.9% in the boma (Table 1). In the GGR  $2.31 \pm 1.7\%$  of shoots were branched compared to  $1.03 \pm 0.7\%$  in the UBNR where eight of the 10 shrubs sampled had no branched shoots. The length of these branches did not vary significantly with position on the main shoot until near the apex of the shoot where branches tended to be shorter. This suggests an even pattern of branch development that was likely to produce a dense crown.

In the Maun sites, most shoots were growing at approximately  $45^\circ$ , with no significant difference in mean orientation ( $F_{2,85} = 1.51$ ,  $P > 0.1$ ) which ranged from 2.22 in the wildlife site to 2.41 in the boma. Shoot orientation in the Gaborone sites differed significantly ( $F_{2,77} = 15.1$ ,  $P < 0.0001$ ), being more vertical in the UBNR ( $1.91 \pm 0.10$ ) than the Tlokweng range ( $2.53 \pm 0.07$ ) and Game Reserve ( $2.36 \pm 0.07$ ).

In the boma, shoots tended to be longer when they were proportionately further from the bole ( $r = 0.173$ ,  $P < 0.05$ ,  $n = 230$ ) and higher on the shrub ( $r = 0.267$ ,  $P < 0.001$ ,  $n = 240$ ), suggesting that, in the absence of browsing, shrubs were growing both vertically and laterally. There were no significant relationships between shoot length and relative position of shoot in the wildlife site, whilst in the rangeland, shoots higher on the shrub tended to be longer ( $r = 0.284$ ,  $P < 0.001$ ,  $n = 240$ ). In the University Reserve shoots further from the bole tended to be shorter ( $r = 0.259$ ,  $P < 0.001$ ,  $n = 158$ ) and in the rangeland the longest shoots were closest to the bole ( $r = 0.191$ ,  $P < 0.01$ ,  $n = 240$ ) and near the top of the shrub ( $r = 0.326$ ,  $P < 0.001$ ,  $n = 240$ ).

### *Spinescence*

*A. tortilis* shoots have two types of paired prickles on or close to the leaf axils as antiherbivore defence (Cooper & Owen-Smith, 1986): (a) short curved prickles that occur in pairs and (b) straight prickles that usually occur in pairs but occasionally are singular.

On all three Maun sites significant linear relationships were observed between shoot length and the number of hooked and straight prickles (Table 2). Slope coefficients differed such that regression equations predict a greater number of hooked and straight prickles in the sites with greatest browsing pressure. However, pairwise comparisons of slope coefficients were not significant ( $t$  values 0.13–1.42). Negative intercepts for the number of straight prickles suggest that shoots of less than 10 cm fresh length are less likely to develop this type of herbivore protection.

### *Biomass of shoots*

Regressions of dry mass of leaves, woody stem plus hooked prickles and straight prickles on fresh shoot length were significant after square root transformation

**Table 1.** Measurements of all current shoots on randomly selected *A. tortilis* shrubs within the height range 80–120 cm from sites with and without browsers. Number of shrubs sampled is 10 in all sites except GGR where  $n=8$  values are means  $\pm 1$  s.e.

	Boma			Wildlife			Rangeland			Maun		Gaborone	
										<i>F</i> values	UBNR	GGR	<i>t</i> values
Mean shrub height (cm)	94 $\pm$ 5	97 $\pm$ 3	96 $\pm$ 4	96 $\pm$ 4	0.14 <sup>ns</sup>	102 $\pm$ 7	99 $\pm$ 6	–0.33 <sup>ns</sup>					
Mean number of shoots per shrub	70 $\pm$ 15	98 $\pm$ 11	88 $\pm$ 10	88 $\pm$ 10	1.3 <sup>ns</sup>	44 $\pm$ 7	86 $\pm$ 14	2.73 <sup>**</sup>					
Mean percentage of branched shoots	8.9 $\pm$ 3.0	2.4 $\pm$ 1.6	4.6 $\pm$ 1.6	4.6 $\pm$ 1.6	2.35 <sup>ns</sup>	1.03 $\pm$ 0.7	2.31 $\pm$ 1.7	0.80 <sup>ns</sup>					
Range in percentage of branched shoots	0–27.1	0–12.4	0–16.3	0–16.3	—	0–6.0	0–13.7	—					
Mean shoot length (cm)	23.1 $\pm$ 3.1	11.5 $\pm$ 1.8	8.8 $\pm$ 0.8	8.8 $\pm$ 0.8	13.2 <sup>***</sup>	11.5 $\pm$ 0.9	15.4 $\pm$ 1.8	1.89 <sup>ns</sup>					
Mean total of current shoots per individual	1657 $\pm$ 454	1027 $\pm$ 130	815 $\pm$ 150	815 $\pm$ 150	2.34	508 $\pm$ 83	1378 $\pm$ 208	3.88 <sup>**</sup>					

<sup>ns</sup>, not significant, \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

**Table 2.** Regression coefficients for the relationship between spinescence and shoot fresh length in current shoots from *A. tortilis* shrubs in three habitats

	Boma	Wildlife	Rangeland
Coefficients for number of hooked prickles			
Slope	0.428	0.564	0.570
Intercept	4.42	5.14	7.46
Number of prickles predicted for			
10 cm shoot	9	11	13
20 cm shoot	13	16	19
Coefficients for number of straight prickles			
Slope	0.289	0.335	0.164
Intercept	-2.84	-0.98	-0.77
Number of prickles predicted for			
10 cm shoot	0	2	1
20 cm shoot	3	6	3

All regressions were linear and significant at  $P < 0.001$ .

**Table 3.** Regression coefficients for the relationship between cube root of biomass (dry mass in mg) and shoot fresh length in current shoots from *A. tortilis* shrubs in three habitats

	Boma	Wildlife	Rangeland			
Coefficients for:						
(a) mass of leaves						
slope	0.839	0.436	0.983			
intercept	10.0	-0.53	5.74			
(b) mass of straight prickles						
slope	1.14	0.398	1.160			
intercept	4.15	-2.02	1.05			
(c) mass of woody shoot and hooked prickles						
slope	0.946	0.438	0.962			
intercept	8.21	0.33	5.38			
Biomass of 10 cm and 20 cm shoots						
Leaves	338	717	242	726	312	736
Straight prickles	15	67	4	35	22	83
Woody stem	242	645	160	588	225	606
Total	595	1429	406	1349	559	1425

All regressions were significant at  $P < 0.001$ .

of mass estimates (Table 3). Leaves accounted for at least half the total biomass of shoot with the proportion decreasing slightly as shoot length increased. Investment in straight prickles was as much as 5.8% of total biomass on longer shoots and overall was greatest in the rangeland habitat.

On 10 randomly selected shrubs mean shoot length varied significantly (Table 1) mainly due to longer shoots in the boma. *A. tortilis* in the GGR produced almost twice the number of shoots and nearly four times the mean total current shoot biomass as those in the protected UBNR (Table 1). On conversion an

**Table 4.** Estimates of the amount of new biomass per shrub (mg) based on mean number and length of current shoots per shrub between 50 cm and 120 cm height. UBNR and GGR estimates are based on pooled biomass regressions from Maun sites

	Boma	Wildlife	Range	UBNR	GGR
Mean number of shoots	70	98	88	44	86
Mean shoot length	23.1	11.5	8.8	11.5	15.4
Leaf mass per shoot	863	298	273	332	480
Mass straight prickles	91	6	18	16	33
Woody mass per shoot	809	207	192	240	384
Total biomass per shoot	1763	511	483	588	897
Total biomass per shrub (g)	123.4	50.1	42.5	25.9	77.1

'average' 50–120 cm high shrub in the boma had greater biomass than a similar individual in the wildlife or rangeland habitats (Table 4).

## Discussion

*A. tortilis* shoots are produced seasonally, primarily after rainfall events (Pellew, 1983a). Growth is opportunistic and potentially variable in response to current conditions. In evolutionary terms investment in shoot growth, rather than storage or reproductive structures, is a relevant 'decision' for the individual. Flexibility in these investment allocations would be expected if an individual was to maximize reproductive potential in an unpredictable or risky environment (Schultz, 1991; Yoshimura & Clark, 1991).

In *A. tortilis* shoot length, branching of current shoots, orientation of shoots and spinescence all varied considerably between individuals and with habitat. The absence of browsers for only a brief period allowed shrubs in the Boma to produce longer shoots with a greater frequency of branching and ultimately a greater overall biomass of current shoots than equivalent shrubs exposed to wild and domestic browsers. In older individuals exposed to browsing for long periods, a smaller number of short shoots were produced compared with apparently younger saplings of similar size. Clearly plant history has implications for current growth pattern (Coughenour *et al.*, 1990; Bergstrom, 1992) which may, in turn, be passed on to influence behaviours and responses of browsers (Pellew, 1984).

If browsing is sufficient to retard vertical development of shrubs, they remain susceptible to fires, more browsing or competition from neighbours (Pellew, 1983b; Owen-Smith, 1988). In semi-arid systems there is an additional trade-off for the plant between overall morphology and the impact of fire on individual fitness. When moisture is limited, canopy cover provides a more suitable micro-climate for herbaceous cover to flourish (Walker, 1979; Weltzin & Coughenour, 1990). Without herbivore impact this herbaceous layer provides greater fuel loads for fire and the potential for fire damage to the tree increases. When the tree is small, the pattern of shoot production and branching of *A. tortilis* provides a dense canopy cover and prevents development of herbaceous plants below the canopy with consequently lower risk of fire damage.

This also implies that there is considerable competition between plants for available nutrients and moisture in savannas (see review by Skarpe, 1992) and an important consequence of herbivory, including root herbivory (McPherson, 1993), on an individual plant is the effect it has on the plant's competitive ability. In the UBNR *A. tortilis* shrubs were in the more disturbed areas towards the periphery of the reserve or were crowded by mature *A. erubescens* and, to a lesser extent, *D. cinerea*. Vigorous growth in these adjacent trees may have contributed to the low number of current shoots in *A. tortilis*. As an invasive species *A. tortilis* may only be competitive in open systems similar to those in the MEP, whilst heavy browsing may disadvantage the plant, even if it overcompensates through a greater production of tissue (Halten, Danell & Ericson, 1993).

Hooked and straight prickles deter browsers with hooks being more effective against smaller selective browsers (e.g. impala, steenbok) (Cooper & Owen-Smith, 1986), and straight prickles being more effective against larger species such as giraffe (Pellew, 1984). More hooked prickles were produced per unit length in the rangeland and wildlife habitats compared to shrubs in the boma. One mechanistic explanation is that internode length was shorter in the rangeland and wildlife areas; however, the net effect is a higher density of hooked prickles and an improved deterrent. Percentage biomass investment in straight prickles increased with shoot length and there were more straight prickles produced on shoots in the rangeland sites. This is consistent with observations by Young (1987) on the effects of goat browsing on spinescence in *Acacia drepanolobium* Harms ex Sjöstedt. A specific test of the deterrent hypothesis of straight spines against shoot biters, in areas with and without browsing pressure from giraffe, would be instructive given the observation of Timberlake (1980) and the present authors that large *A. tortilis* lose their straight prickles.

Plant responses to herbivory include positive effects on growth and biomass production and an increased physical or chemical protection (Whitham *et al.*, 1991). Individual *A. tortilis* shrubs produce these types of responses in terms of shoot characteristics very rapidly, and perhaps uniquely. The history of browsing, moisture availability combined with ambient soil conditions may determine the morphology and current shoot production more than the genotype. Such phenotypic plasticity (Bradshaw, 1965; Caswell, 1983) may be the only way to maximize fitness for plants where the intensity and frequency of herbivore attack cannot be determined by an individual. Such flexible responses have implications for the browsers themselves given that shoot size affects food preference (e.g. Bergstrom & Danell, 1987) and the proportion of woody material changes with shoot size (Danell & Bergstrom, 1987), as shown here for *A. tortilis*.

The structure and functioning of southern African savannas is believed to be determined by a combination of moisture, nutrients, fire and herbivory (Walker, 1987). In these models herbivory is treated generally, e.g. heavy browsing may prevent shrubs reaching maturity and seed set, ultimately affecting recruitment. The interplay between mammalian herbivore and plant not only affects the plant (Harper, 1977) and shapes individual phenotypes, as here, but may also influence the development of plant communities (Crawley, 1989). Rapid compensation or allocation to protection by a plant in response to browsing might affect its competitive ability, and subsequent reproductive potential. How much this influences plant communities remains to be tested.

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