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Shoot Production by *Acacia tortilis* under Different Browsing Regimes in South-East Botswana

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ABSTRACT

We investigated shoot production by *Acacia tortilis* under three distinct land-use types and browsing regimes in south-eastern Botswana: a large mammal exclosure (UB Nature Reserve, UBNR), a conservation area (Gaborone Game Reserve, GGR), and a livestock area (Tlokweng Rangelands, TR). We applied one-way ANOVA to determine variation in shoot production within and amongst land-use types, and also across vertical browsing levels ("Low", "Medium" and "Upper"). Mean shoot length varied significantly amongst the three habitats, being highest in GGR, TR, and lowest in UBNR. Spinescence (spine number and mass) differed significantly under the three land-use types, being highest in GGR, TR, and UBNR, respectively. Within land-use types, shoot length differed significantly between the three browsing levels. Shoot length declined from the "Upper" to the "Low" browsing levels or zones. Leaf dry-mass differed significantly between the three browsing levels, decreasing from the highest to the lowest levels. The highest number of thorns produced was significantly higher on the "Upper" browsing zones. Thorn mass did not vary significantly across the browsing zones. We postulate that differential browsing pressure elicited the variable response in shoot production across the three land-use categories, and further discuss the implications for wildlife and rangeland management.

Keywords: habitat, herbivory, rangeland, savanna woodland, spinescence, wildlife

INTRODUCTION

We sought through the present study, to compare patterns of shoot production by *Acacia tortilis* under three distinct land-use types and browsing regimes within a 10 km^2 radius of an *Acacia* savanna woodland in south-eastern Botswana. The three sites comprised: a 35-year large mammal exclosure, a 22-year old conservation area, and a century old communal grazing area (Timberlake 1980).

Phenotypic plasticity can be inclusively defined as the ability of an organism to produce multiple phenotypes from a single genotype, moderated by variable environmental pressures (Strauss and Agrawal 1999; Strauss *et al*. 2002; Rohner and Ward 2005; Heil 2010). It is now widely accepted that a wide diversity of plant species express phenotypic plasticity in response to biotic and abiotic aspects of their environments (Begon *et al*. 1996; Rooke 2003; Rohner and Ward 2005; Young and Augustine 2007; Heil 2010). Such plasticity becomes particularly apparent when plants alter their transcriptome after predation by herbivores (Strauss and Aggrawal 1999; Strauss *et al*. 2002; Heil 2010). These plastic responses include changes in biochemistry, physiology, morphology, growth, behaviour, life history, demography, and can be expressed either within the lifespan of a single individual or across generations (Strauss and Aggrawal 1999; Strauss *et al*. 2002; Rooke 2003; Scogings and Macanda 2005; Fornara and du Toit 2007; Fornara and du Toit 2008a, 2008b; Rohner and Ward 2009; Heil 2010). All these expressions of plasticity confer upon plants, relatively high fitness differentials in the face of variable environmental adversity.

Across several African savannas, the physiognomic structure and species diversity of plant communities has been reported to be significantly altered by the feeding activities of different types of herbivores (Skarpe 1990a, 1990b; Oba 1998; Rooke 2003; Fornara and du Toit 2007; Fornara and du Toit 2008a, 2008b). Plants respond to herbivore browsing pressure by altering relative resource allocation to growth, reproduction, or defence (Barbour *et al*. 1987; Strauss and Aggrawal 1999; Mathieu *et al*. 2009; Heil 2010). The effects of herbivory on plants depend on the timing of defoliation relative to plant development, and also on the specific plant components that are targeted (Begon *et al*. 1996; Fornara and du Toit 2008a, 2008b; Scogings and Macanda 2005; Heil 2010). Herbivore impact can result in mortality or induced redistribution of shoot production and flowering away from vulnerable points (Coe and Coe 1987; Skarpe 1992; Scogings and Macanda 2005; Young and Augustine 2007). As such the tolerance of plants to herbivory reflects the degree to which a plant can re-grow and reproduce after damage from herbivores (du Toit *et al*. 1990; Strauss and Agrawal 1999; Mathieu *et al*. 2009; Heil 2010).

Because plant-herbivore interactions assume several forms, plant defence mechanisms in terms of variable shoot production and architecture under different browsing regimes, has attracted considerable theoretical and applied interest (Pellew 1983; Cooper and Owen-Smith 1986; Skarpe 1992; Gowda 1996; Moleele and Perkins 1998; Oba 1998; Strauss *et al*. 2002; Scogings and Macanda 2005; Young and Augustine 2007; Fornara and du Toit 2008a; Mathieu *et al*. 2009; Rohner and Ward 2009; Heil 2010). Shoot production in terms of spinescence is a common physical deterrent by plants against herbivory among African savannas (Fornara and du Toit 2008a; Mathieu *et al*. 2009). Most physically defended plants, notably acacia species, naturally show much individual variation in spinescence (Milewski *et al*. 1991; Rooke 2003; Young and Aug-

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ustine 2007; Fornara and du Toit 2008b). This variation is usually attributed to individual plant histories of environmental stresses (Grubb 1992; Dangerfield *et al.* 1996; Gowda 1996; Heil 2010), and particularly to browsing by large mammals (Young 1987; Milewski *et al.* 1991; Young and Augustine 2007; Fornara and du Toit 2007, 2008a).

Given predictions of woody plant production in southern Africa under global climatic change (Midgley and Bond 2001) and the reported impacts of human activities on savannas (Scholes and Archer 1997; du Toit and Cumming 1999), predictive understanding of woody plant ecology in subtropical regions is critical for the conservation and management of savannas (Mathieu *et al.* 2009). As such, comparative field studies investigating patterns of plant production under different environmental histories are necessary to enhance our understanding and application of savanna ecosystem dynamics in the sub-region.

STUDY SPECIES

In the semi-arid areas of Botswana such as the Kalahari, there has been an invasion of encroacher species such as *Acacia tortilis*, *A. erubescens*, *A. fleckii*, and *A. mellifera* over the years (Skarpe 1991; Abel 1997; Moleele 1998). Our motivation for nominating *A. tortilis* hinged upon previous reports (e.g. Dangerfield *et al.* 1995; Abel 1997; Moleele 1998) and field observations of extensive utilisation of this species by wildlife and livestock in south-eastern Botswana.

A. tortilis is commonly known as the "umbrella thorn" tree on account of the umbrella-like conformation of mature trees subjected to sustained browsing by large herbivores in semi-arid savannas. Its specific name (*tortilis*) denotes the contorted form of the pods (Palgrave 1983). The leaves, flowers, and mature pods are a rich source of plant protein and are generously consumed by livestock and wildlife species. As a tree, *A. tortilis* can reach up to 20 m in height, but only around five metres as a shrub (Timberlake 1980; Palgrave 1983), with branching commencing at 1-2 m above the ground. *A. tortilis* thorns are of two forms; the straight, sharp, white spines of up to 5 cm in length, and the short hooked prickles. Both the straight spines and hooked prickles can be found on the same twig, and are assumed to confer differential anti-herbivory functions. The leaves and numerous small leaflets (0.5-3 mm long) of *A. tortilis* can produce a dense canopy cover (Ross 1979), while inflorescences in southeast Botswana typically appear from November to January as white to yellowish feathery balls.

STUDY SITES

Three study sites, representing three distinct land-use types and browsing regimes in an Acacia savanna woodland of south-eastern Botswana (24° 38′ S, 25° 57′ E) were identified for the present study. The three sites, occurring within a 10 km^2 radius presented the requisites for conducting a comparative ecological field study: a large mammal exclosure (UB Nature Reserve); an enclosed wildlife reserve (Gaborone Game Reserve); and an open communal livestock area (Tlokweng Rangelands). For studies on comparative shoot characteristics under different management or herbivore regimes, these habitats were adjudged appropriate (see below). In much of Botswana, the rainy season (October-April) occurs in summer, while the dry period (May to September) occurs in winter. The mean annual rainfall for south-eastern Botswana is 500 ± 50 mm (Botswana Department of Meteorological Services). Total rainfall for the greater study area during the present study was 1200 mm, indicating an exceptionally wet rainy season for the region (Kaunda *et al.* 2004). The mean maximum temperature is 32°C for summer and 23°C for winter, while mean minimum temperature is 19°C in summer and 6°C for the winter period.

UB Nature Reserve

The University of Botswana Nature Reserve (UBNR; 24^o 39'S, 25^o 55'E) was a fenced *Acacia* savanna woodland measuring approximately 2 ha, and situated at the Gaborone Main Campus. Since its inception and fencing in the mid 1970's, the UBNR has been characterised by a conspicuous absence of large mammalian herbivores, no fire history, and minimal human disturbance from students and wood collectors (Kaunda 1994; Dangerfield *et al.* 1996). Due to the absence of large mammalian herbivores, the herbaceous layer was well established (Weltzin and Coughenor 1990; Kaunda 1994) containing *Hibiscus* sp., *Philyrophyllum schinzii*, *Kalanchoe rotunifolia*, and *Protoasparagus flavicaulis* beneath patches of *Acacia erubescens*, *Dichrostachys cinerea*, and *Euclea undulata*. *Aloe grandidentata* was also abundant over most of the study site. Open areas were characterised by grass species, notably, *Eragrostis rigidior* and *Tragus berteronianus* (Kaunda 1994). Small mammals (Lagomorpha and Rodentia) were the only few mammalian herbivores resident in the Reserve. Regrettably, the UB Nature Reserve was deliberately cleared off in 2009, after 35 years of fire and large herbivore exclusion to give way to infrastructural development. Hence in some respect, the present report partly embodies a tribute to the ecological utility of the UB Nature Reserve towards understanding Acacia savanna ecosystem dynamics in Botswana and the Southern African sub-region.

Gaborone Game Reserve

The Gaborone Game Reserve (GGR; 24^o 38'S, 25^o 57'E) is a fenced 5 km^2 educational game reserve situated in the periphery of the Gaborone City in south-eastern Botswana. GGR was gazetted in 1978 and falls under the jurisdiction of the Department of Wildlife and National Parks, Botswana Government. For the present study we nominated the Acacia savanna woodland component of GGR, which was comparable to the other two sites in vegetation composition and geomorphologic expression (Kaunda *et al.* 2004). Other vegetation types in the Reserve were Acacia shrubland, Riverine woodland, Artificial wetland, Floodplains, and Kopje woodland (Kaunda *et al.* 2004)

Resident large mammalian herbivores included obligate or seasonal browsers such as kudu *Tragelaphus strepsiceros*, impala *Aepyceros melampus*, eland *Taurotragus oryx*, and steenbok *Raphicerus campestris*. Occasional browsers included gemsbok *Oryx gazella*, red hartebeest *Alcelaphus buselaphus*, while the preferential grazers were represented by wildebeest *Connochaetes taurinus* and plains zebra *Equus burchelli*. Warthogs *Phacochoerus africanus* were also abundant in GGR. Large predators were conspicuously and deliberately absent, save for the occasional itinerant black-backed jackal *Canis mesomelas*. The reserve lies in the valley of the Ngotwane River, with about half of it situated on the floodplain and the remainder, to the west, being on a plateau that is about 10 m higher (McColaugh 1993; Kaunda *et al.* 2004). The plateau, predominantly Acacia savanna woodland vegetation, is overlain by Kalahari sands of varying depths, while the south of the park is characterised by shallow sands, and several granite outcrops that form small kopjes.

Tlokweng Rangelands

The Tlokweng Rangelands (TR; 24^o 39'S, 25^o 57'E), less than 5 km away from both UB Nature Reserve and GGR, is on communal rangeland and has been heavily utilised by cattle, goats, sheep, donkeys, and related anthropogenic activities for over a century (Timberlake 1980). Similar to the other sites, the dominant woody species were *Acacia tortilis*, *Acacia erubescens*, and *Dichrostachys cinerea*. Past and extant anthropogenic activities such as farming and livestock production typified this study site (Timberlake 1980; Dangerfield *et al.* 1996)

Table 1 Mean (± SE) shoot production by *A. tortilis* shrubs in UB Nature Reserve, Gaborone Game Reserve, and Tlokweng Rangelands. *= Significant at P<0.05

Parameter	**Study site/Habitat**			
	UB Nature Reserve	**Gaborone Game Reserve**	**Tlokweng Rangelands**	**Significance**
Shoot length (cm)	12.29 ± 0.66	13.43 ± 0.44	12.16 ± 0.52	0.018*
Leaf mass (g)	0.28 ± 0.17	0.29 ± 0.02	0.24 ± 0.03	0.966
Shoot mass (g)	0.21 ± 0.03	0.26 ± 0.04	0.22 ± 0.02	0.013*
Number of thorns	0.92 ± 0.15	2.11 ± 0.24	2.04 ± 0.14	0.001*
Thorn mass (g)	0.03 ± 0.003	0.07 ± 0.005	0.08 ± 0.006	0.003*

MATERIALS AND METHODS

Shoot production was determined in 20 randomly chosen *Acacia tortilis* shrubs in Tlokweng Rangelands and Gaborone Game Reserve. Only 14 shrubs could be sampled in the UB Nature Reserve since the rest were clearly older senescent trees beyond the present study jurisdiction. All data were collected from the study sites within 10 days of February 2000 in order to reduce variations in environmental conditions such as available soil moisture and temperature among the three study sites or habitats. On each individual plant, 30 current shoots, distinguished by their lighter colouration, were chosen; 10 each from the upper (>1.5 m), middle (0.75-1.5 m), and lower (<0.75 m) browsing levels or zones. The upper levels were accessed using a ladder. For each shoot, length was measured in the field. Immediately thereafter, the shoot was clipped with a pair of secateurs and its wet biomass recorded. The clipped shoots were then dried to constant mass in the laboratory at 37°C for two weeks. The number of hooked and straight white thorns was then determined per shoot. The straight white thorns were cut off, and leaflets brushed off the shoots to determine the dry leafy, and woody (shoot with thorns) biomass. All data were then subjected to one-way analysis of variance (ANOVA) using the statistical package MINITAB.

RESULTS

We assessed for inter- and intra-habitat variation in shoot characteristics for five measurement parameters: mean shoot length, shoot mass, leaf mass, thorn number, and thorn mass.

Inter-habitat variation in shoot characteristics

Differences across habitats were determined using one-way ANOVA at the 95% confidence interval. Mean shoot length varied significantly between the three land use areas or habitats (P = 0.018; **Table 1**), being highest in the Gaborone Game Reserve. Variation in the mean leaf dry mass was not statistically different among the three habitats (P = 0.966). Mean shoot dry mass varied significantly among the three habitats (P = 0.013; **Table 1**), being highest in the GGR and least in the UB Nature Reserve. The mean number of thorns was significantly different between the three habitats (P < 0.001; **Table 1**). The highest thorn production was in the Gaborone Game Reserve and least in the UB Nature Reserve, with thorn mass varying significantly between the habitats (P = 0.003; **Table 1**). The proportion of resource allocation to thorn production was highest in the Tlokweng Rangelands and Gaborone Game Reserve, which had resident ungulate browsers, than in the UB Nature Reserve exclosure (**Table 2**).

Intra-habitat variation in shoot characteristics

1. Shoot production by A. tortilis shrubs within the UBNR

Mean shoot length differed significantly among the three browsing zones (P < 0.0001), decreasing from the upper zones to the bottom of the shrubs (**Table 3**). Mean leaf dry mass differed significantly between the three levels (P < 0.0001), decreasing from the upper to the low levels. From the upper level of the shrubs to the lower zone, mean shoot dry mass differed significantly (P < 0.0001; **Table 3**). The mean number of thorns produced was significantly higher on the upper levels (P = 0.0046; **Table 3**). Thorn mass did not vary significantly between the levels (P = 0.0893; **Table 3**).

Table 2 Proportionate (%) resource allocation to shoots, leaves, and thorns by *A. tortilis* shrubs in the three study sites.

Habitat	**Relative allocation (%)**		
	Shoots	**Leaves**	**Thorns**
UB Nature Reserve	40	54	6
Gaborone Game Reserve	42	47	11
Tlokweng Rangelands	41	44	14

2. Shoot production by A. tortilis within the Gaborone Game Reserve

There were significant differences in shoot length between the three levels (P = 0.0005, **Table 4**), with the longest shoots on the upper levels. No significant differences were found between the three levels for leaf dry mass (P = 0.1600; **Table 4**). Shoot dry mass was significantly different between the three levels (P = 0.0221; **Table 4**), decreasing from the upper to the low height levels of the shrubs. A significantly higher number of thorns were produced on the low browsing levels of the shrubs (P = 0.0070; **Table 4**). The dry mass of thorns was not significantly different between the three levels (P = 0.2210; **Table 4**)

3. Shoot production by A. tortilis shrubs within the Tlokweng Rangelands

Mean shoot length differed significantly between the three levels (P = 0.0285; **Table 5**), decreasing from the highest to the lowest shrubs. There were no significant differences in mean leaf dry mass (P = 0.1839; **Table 5**) and shoot dry mass (P = 0.1248; **Table 5**) among the three browsing levels. There were no significant differences in the number of thorns (P = 0.0579) produced at each browsing level and in their dry weight (P = 0.6403).

DISCUSSION

While we acknowledge the limited thrust of descriptive and correlational studies to elucidating underlying ecological patterns, we are mindful that manipulative experiments remain the ultimate protocol for adequately gauging cause-effect relationships in biotic nature, notably plant-herbivore interactions. However, baseline studies such as the present comparative one, serve to provide a useful premise and yardstick from which to progressively decipher the fundamental question in ecology; "Why is what where when?" question using the Scientific Method (Berry 1984; Kaunda 2000).

A general finding gleaned from the present study is that shoot biomass production was much pronounced for Gaborone Game Reserve than for Tlokweng Rangelands and UB Nature Reserve, presumably as a relative response to enhanced browsing pressure that would have had a "positive" effect on shoot re-growth in the two sites inhabited by ungulates. Studies elsewhere have reported that acacia shoot production can be stimulated by browsing (Young 1987; du

Table 3 Mean shoot production for *A. tortilis* shrubs across three browsing zones in the UB Nature Reserve. Values are means of 10 replicates ± SE. *= Significant at P<0.05

Parameter	Lower	Middle	Upper	Significance
Shoot length (cm)	9.20 ± 0.79	11.07 ± 0.59	16.59 ± 0.61	0.001*
Leaf dry mass (g)	0.22 ± 0.02	0.25 ± 0.19	0.39 ± 0.03	0.001*
Shoot dry mass (g)	0.17 ± 0.02	0.18 ± 0.01	0.29 ± 0.02	0.001*
Number of thorns	0.64 ± 0.13	0.74 ± 0.14	1.39 ± 0.23	0.0046*
Thorn mass (g)	0.02 ± 0.01	0.02 ± 0.004	0.04 ± 0.007	0.0893

Table 4 Mean shoot production for *A. tortilis* shrubs across three browsing zones in the Gaborone Game Reserve. Values are means of 10 replicates ± SE. *= Significant at P<0.05

Parameter	Lower	Middle	Upper	Significance
Shoot length (cm)	12.92 ± 0.29	12.80 ± 0.35	14.56 ± 0.40	0.0005*
Leaf dry mass (g)	0.29 ± 0.01	0.28 ± 0.01	0.31 ± 0.02	0.1600
Shoot dry mass (g)	0.24 ± 0.01	0.25 ± 0.01	0.28 ± 0.01	0.0221
Number of thorns	2.48 ± 0.20	2.20 ± 0.18	1.66 ± 0.18	0.0070*
Thorn mass (g)	0.08 ± 0.01	0.08 ± 0.01	0.06 ± 0.01	0.2210

Table 5 Mean shoot production for *A. tortilis* shrubs across three browsing zones in the Tlokweng Rangeland. Values are means of 10 replicates ± SE. *= Significant at P<0.05

Parameter	Lower	Middle	Upper	Significance
Shoot length (cm)	11.53 ± 0.32	11.95 ± 0.43	13.00 ± 0.44	0.0285*
Leaf dry mass (g)	0.22 ± 0.01	0.24 ± 0.01	0.25 ± 0.01	0.1839
Shoot dry mass (g)	0.20 ± 0.01	0.22 ± 0.01	0.23 ± 0.01	0.1248
Number of thorns	2.40 ± 0.19	1.86 ± 0.17	1.87 ± 0.18	0.0579
Thorn mass (g)	0.09 ± 0.01	0.08 ± 0.01	0.08 ± 0.01	0.6403

Toit *et al.* 1990; Rooke 2003; Scogings and Macanda 2005; Rohner and Ward 2009), possibly due to plant growth-promoting agents in the saliva of herbivores (Pellew 1983; Strauss *et al.* 2002; Rooke 2003). It is possible that indigenous wildlife species have such stimulants due to likely co-evolutionary relationships with woody species in African savannas (Strauss and Aggrawal 1999; Strauss *et al.* 2002; Young and Augustine 2007; Heil 2010), unlike the domestic browsers in the Tlokweng Rangelands. But it is also plausible that *A. tortilis* shrubs on rangeland responded differently to frequent and sustained herbivory by livestock, particularly goats (Gowda 1997; Oba 1998; Scogings and Macanda 2005; also see below).

For intra-habitat variation, current shoots in the UBNR grew longest in the upper browsing zone of the *A. tortilis* shrubs. A possible explanation for this is that shoots in the upper levels had more access to light than those well below the canopy (Weltzin and Coughenor 1990). In specific parts of the UBNR, it was notable that *A. tortilis*, together with *A. erubescens* and *D. cinerea* stands, engaged in an interlocking canopy formation that nearly impeded light access to understory vegetation. As such, in an environment not mediated by disturbances such as large mammalian herbivory and fire, an increase of shoot production in the upper height zone might have been elicited by inter- and intra-specific competition for resources such as sunlight, moisture, and nutrients since this is the shrub zone that usually harbour *A. tortilis* reproductive organs (Dangerfield *et al.* 1996; Palgrave 1983; pers. obs.). To further lend credence to the competition hypothesis, *A. tortilis* shrubs sampled at the fenced extremes of UB Nature Reserve were crowded by large mature trees and had branches overhanging beyond the perimeter fence (Dangerfield *et al.* 1996; pers. obs.), suggesting some competition avoidance. Vigorous growth in, and suppression by, these adjacent trees may have contributed to the relatively low current shoot production in *A. tortilis* in the UB Nature Reserve. As an invasive species, *A. tortilis* may only compete better in more open systems (Skarpe 1991) similar to those in Gaborone Game Reserve and Tlokweng Rangelands.

That spines protect plants by limiting the rate of herbivory by large browsers, is no longer in dispute but well established (Cooper and Owen-Smith 1986; Belovsky *et al.* 1991; Gowda 1996; Scogings and Macanda 2005; Rohner and Ward 2009; Heil 2010). However, some small mammals such as rodents resident in UB Nature Reserve likely possess abilities to climb through the upper level to the canopy of acacia shrubs to harvest fruits, seeds, and foliage (Cooper and Ginnet 1998). Although they may not have much individual impact on savanna community dynamics, small mammals may collectively during population explosions, have deleterious effects on the competitive and reproductive potential of individual plants via herbivory and seed predation (Ostfeld *et al.* 1996; Weltzin *et al.* 1997; Young and Augustine 2007). Spinescence in the upper level may indeed protect plants from damage to reproductive organs by small mammals (Young and Augustine 2007). Small mammals may be able to manoeuvre around spines on moderately spiny plants as opposed to densely spiny branches (Grubb 1992). Protection from small mammal browsing is mediated by the physical impedance created by the dense mesh of spines coupled with the discomfort of foraging among the spines. Although plant spines are generally thought to be an evolved defence against browsing by ungulate herbivores (Strauss *et al.* 2002; Young and Augustine 2007; Mathieu *et al.* 2009; Rohner and Ward 2009; Heil 2010), small mammal browsing may also be a factor affecting plant allocation to structural defences (Grubb 1992).

The *A. tortilis* shrubs in the GGR, which had a wider variety of obligate browsers such as kudu and eland, as well as facultative browsers such as impala, gemsbok, and red hartebeest, produced more spinescent shoots on the lower levels, possibly as impedance to sustained browsing (Dangerfield *et al.* 1996; Woolnough and du Toit 2001; Fornara and du Toit 2007; Young and Augustine 2007; Fornara and du Toit 2008a). In spite of this, *A. tortilis* shoots on the lower levels in the GGR were still observed to be browsed by the smaller selective browsers like impala and steenbok, because prickles do not effectively deter mammalian herbivores that are adapted to cope with them (Cooper and Owen-Smith 1986; Dangerfield *et al.* 1996; Strauss *et al.* 2002; Heil 2010). From field observations, *A. tortilis* shrubs in the GGR had numerous thorns, even embedded deep within individual plants, but despite this seemingly aggressive array of spines, some browsers could still access the foliage as also observed by Coe and Coe (1987). Proportionate allocation of resources to thorn production was higher on the game reserve and on rangeland, than for the UB Nature Reserve, further suggesting that current thorn production was an induced response to historical differences in herbivore pressure.

In the Tlokweng rangelands, it was not immediately apparent from a study of this nature, why spinescence in particular, and other shoot characteristics in general, would not predominate in the lower and middle zones that were potentially within reach of domestic mammalian browsers. Fitness costs are a common explanation for the evolution of inducible resistance expression (Strauss and Aggrawal 1999; Heil 2010). However, variability in the resistance phenotype can per se be beneficial, because it makes counter-adaptations by predators more difficult. In the case of indirect defences, which are mediated by plant-herbivore mutualisms, signal reliability and reciprocal responses among phenotypically plastic partners appear necessary prerequisites for their evolutionary stabilisation (Strauss and Aggrawal 1999; Strauss *et al.* 2002; Mathieu 2009; Heil 2010).

It has further been reported elsewhere (Oba 1998; Rooke 2003) that more than 25% defoliation of *Acacia* during the leaf flush phase at the beginning of the growth season does not stimulate shoot production. Frequent, heavy browsing of woody plants in African savannas does not invariably stimulate shoot production, but infrequent, heavy browsing does (Skarpe 1990b; Oba 1998; Rooke 2003; Rohner and Ward 2009). Prolonged browsing, however, reduces plant growth and increases mortality rate (Fornara and du Toit 2008a). The stimulatory effect of browsing subsides sooner than the recovery of plant growth rate after cessation of browsing. From field observations, cattle and goats often grazed on rangeland during summer, rather than investing foraging time on apparently cumbersome browsing of *A. tortilis* shrubs. Besides, given a choice between woody and grass species, livestock would most likely preferentially graze on the herbaceous layer. Du Toit *et al.* (1990) likened the feeding mechanism on *A. tortilis* and *A. nigrescens* species to a pruning effect. With browsing, competition between shoots for nutrients is reduced and so the growth rate of the remaining shoots possibly increases. Though we did not analyse nutrient levels in the present study, other studies have reported variable levels of nutrients and tannins under different levels of simulated and material herbivory (du Toit *et al.* 1990; Skarpe 1991, 1992; Gowda 1997; Rooke 2003; Scogings and Macanda 2005; Fornara and du Toit 2008a; Rohner and Ward 2009).

Suffice to note that the current *A. tortilis* shoots that were measured during the present study were produced soon after the first summer rains in the study area (pers. obs.). Summer browsing stimulates browse production during the growth season because the rate of recovery is quickest then. Winter browsing, however, would generally have little effect on shoot production. Increased spinescence accompanies browsing-induced changes in shoot morphology and demography. Prevailing biotic and abiotic conditions dictate the “opportunistic” and “potentially variable” growth of *A. tortilis* shoots (Skarpe 1990a; Dangerfield *et al.* 1996; Heil 2010). As such, in unstable environments, there might be plasticity in the resource allocations to the fundamental faculties of growth, maintenance, and reproduction. According to the resource availability hypothesis, plants in poor habitats invest heavily in anti-herbivore defence because losses to browsers are costly when growth rates are low (Rohner and Ward 2005). Further, few plants invest simultaneously in different categories of defence, suggesting an existence of trade-offs, albeit little is known about how individuals allocate resources to defence in natural populations.

The encroachment and success of *A. tortilis* on degraded rangeland and wildlife habitats has attracted considerable controversy from both theoretical and management perspectives. Bush encroachment has been reported to constitute land undergoing reduced biological productivity as a result of human induced or climatic factors (Skarpe 1991; Scholes and Archer 1997; Moleele and Perkins 1998; Midgley and Bond 2001). Acacia bush encroachment in particular, has been viewed in this negative light primarily on the basis of received wisdom on classical rangeland management practices. First, cattle are traditionally known to be preferential grazers and so bush encroachment was envisaged to potentially lower cattle production (Moleele and Perkins 1998; du Toit and Cumming 1999). Secondly, since bush encroachment has usually been attributed to overgrazing of grasslands by livestock grazers (Skarpe 1991; Scholes and Archer 1997), it has been imagined that browse would therefore nutritionally contribute much less to cattle production in savannas. Contrastingly, in south-eastern Botswana, we have observed cattle resorting to browsing on woody plants, notably *A. tortilis* in areas where the grass sward was almost absent (Moleele, 1999; pers. obs.). With the upsurge in cattle numbers, a marked change from grass savannas with few scattered trees to thick bush has been further reported (Skarpe 1990a, 1992; Scholes and Archer 1997; Moleele 1999; du Toit and Cumming 1999). Such transformation might have far-reaching implications for rangeland management since *A. tortilis* might be a significant browse species that can support wildlife and livestock in degraded rangeland in the semi-arid savannas of southern Africa. For Botswana, this resolve is well-placed in light of the country’s commitment to revive the productivity and relative economic potential of its wildlife and agricultural land resources in the face of temporally and spatially variable environmental influences.

CONCLUDING REMARKS

The findings from the present study suggest that a history of differential large mammalian herbivory was a significant contributor to shoot biomass production and architecture. Comparative investigations such as the present study provide a useful window for crafting incisive experimental protocols to understand Acacia savanna ecosystem dynamics. For applications, browser species, including both domestic and wild herbivores, may thus become the alternative option for secondary production in overgrazed and acacia-encroached areas. Even generically preferential grazers like cattle are likely to at least marginally subsist on *Acacia tortilis* browse in semi-arid savanna woodlands of Africa, in the face of unpredictable environmental insults.

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