CHAPTER 5

Plant tolerance, resistance and phenology: responses from *Acacia nigrescens* to ungulate browsing in an African savanna

Abstract

I examined defensive traits of two stands of *Acacia nigrescens,* Miller, in a eutrophic southern African savanna under a natural regime of ungulate browsing. Mass compensation after artificial clipping, tree branching, prickle spacing and size, annual shoot growth, leaf nitrogen, specific leaf area (SLA), and seed production were measured over a two-year survey period among stands of *Acacia* trees that have undergone very different histories of attack from herbivores. The results show that *Acacia* trees in a heavily browsed stand developed (1) tolerance traits such as high mass compensatory growth abilities, extensive tree branching and rapid shoot growth rates during the main growing season, as well as (2) resistance traits such as short prickle spacing and large prickle size. However, efforts of phenological escape from browsers were similar in both stands, and presumably resulted from the interplay of different key environmental factors. Overall, tree pruning strongly affected plant morpho-functional traits and decreased pod production in heavily browsed trees. Hence, I present experimental evidence that tolerance and resistance traits may have evolved first, as a strategy to reduce mass loss and increase plant survival under chronic herbivore disturbance rather than as a strategy to increase reproductive success over undamaged trees. Finally, I suggest that tolerance and resistant traits may coexist only if, (1) costs related to produce structural defences (resistance traits) are relatively low and amortized over several years in a semi-arid eutrophic savanna, and (2) browsers trigger a positive feedback loop with their plant resources indirectly supporting plant compensatory growth abilities. I discuss the role of nutrient remobilization mechanisms, and herbivore-mediated linkages between above- and below-ground processes, to support plant growth under high browsing intensity.

KEY WORDS: compensatory growth, defensive traits, eutrophic savanna, nitrogen, plant fitness, prickles, spines, thorns

5.1 INTRODUCTION

Plant responses to herbivore attack involve chemical and mechanical defences, as well as alternative defensive traits (i.e. mass compensation, changes in plant phenology), which often increase plant fitness under herbivore damage (Paige 1992; Houle and Simard 1996; Lennartsson et al. 1997; Agrawal 1998, 2000; Oba et al. 2000). Herbivore-induced defences may be categorized (see Agrawal 2000) into (1) plant resistance traits that reduce herbivore performance or damage, (2) tolerance traits (i.e. mass compensatory growth abilities) that reduce negative effects when herbivore damage has already occurred, and (3) phenological "escape" that reduces plant availability when herbivores are most active.

Recently, attention has been paid to the interplay of such defensive traits and their consequences on plant ecological and/or evolutionary traits (Rosenthal and Kotanen 1994; Strauss and Agrawal 1999; Karban et al. 1999; Stinchcombe and Rausher 2002). For example, consistent compensatory growth abilities of both grass and herb species have been observed after chronic damage by grazers (McNaughton 1983; Paige and Whithmann 1987; Nilsson et al. 1996). Empirical studies have shown positive relationships between compensatory ability and plant fitness in terms of increased reproductive success (Lennartsson et al. 1997, 1998; Agrawal 1998; Freeman et al. 2003). Mass compensation after herbivore damage has also been observed in woody plant species under ungulate browsing in different ecosystems, from tropical savannas to boreal forests (Bergström and Danell 1987; du Toit et al. 1990; Edenius et al. 1993; Dangerfield and Modukanele 1996; Gadd et al. 2001). Although, plant eco-physiological mechanisms responsible for enhancing compensatory growth have been proposed for grasses (McNaughton 1983; Holland et al. 1992), less information is available on potential mechanisms supporting mass compensation in woody species.

Recently, Ayres et al. (2004) established that tree physiological responses to foliar herbivory are capable of modifying soil processes. Herbivores through indirect effects on the plant root system (i.e. increasing root exudation and/or fine root turnover) may increase C inputs in the soil, thereby enhancing plant productivity and sustaining mass compensatory growth. However, overall plant responses to herbivory are most likely dependent on the levels of habitat resource availability (Coley et al. 1985; Bryant et al. 1983; Herms and Mattson 1992; Bardgett and Wardle 2003), as well as on interspecific competition and/or frequency and intensity of disturbance events. A trade-off between different defensive strategies may, or may not occur, depending on the interactive effects of different key environmental factors on plant fitness (Rosenthal and Kotanen 1994).

The question still remains whether alternative plant defensive traits (tolerance, resistance and phenological traits) are influenced by herbivores and may coexist, in terms of cost-benefits, in natural woody plant stands with consistently different histories of attack from herbivores. Moreover, it is still debated whether tolerance or resistant traits are necessarily related to plant fitness in terms of increased reproductive success, which might confer advantage to damaged either tolerant or resistant plants over less damaged plants (Belsky et al. 1993; Strauss and Agrawal 1999). Here I measure resistant, tolerant and phenological traits of two stands of a palatable woody species, *Acacia nigrescens* Miller, that have experienced markedly different levels of browsing intensity, presumably for centuries, in a central area of the Kruger National Park, South Africa (Naiman et al. 2003; du Toit 2003).

I tested whether mass compensatory growth abilities, tree branching, rates of shoot growth (tolerance traits) of heavily and lightly browsed *Acacia* trees, differed between each others when an artificial clipping was imposed in the mid growing season. Mass compensation can be considered as the degree of tolerance exhibited by plants and/or an estimate of the amount by which fitness is reduced for a given amount of damage (Fineblum and Rausher 1995; Strauss and Agrawal 1999).

Furthernore, I tested whether prickle size and prickle spacing on external branches of *Acacia* trees (resistance traits) were different between heavily and lightly browsed sites. As with many other *Acacia* species, *A. nigrescens*, has increased resistance to mammalian herbivores through physical defences, which reduce rates of damage as has been shown in previous studies (Cooper and Owen-Smith 1986; Milewski et al. 1991; Spalinger and Hobbs 1992; Gowda 1996). Spinescence is a distinctive feature of many woody species in arid southern African savannas (Huntley 1982), and especially of fine-leaved savannas on relatively nutrient rich geological substrates (Scholes 1990). In addition I tested whether changes in phenological traits, such as the occurrence and length of the main period of plant annual growth, were affected along a strong browsing gradient.

Finally, I quantified seed production for *Acacia* trees along the browsing gradient over two consecutive years. My study aimed to: (1) establish the degree of mass compensation between heavily versus lightly browsed trees, (2) address how prickle spacing and size, as well as main annual growth were affected along the strong browsing gradient, (3) examine how other morpho-functional traits (i.e. leaf N, SLA, shoot growth rates within tree branches) changed between heavily and lightly browsed trees, and finally (4) address how differences in body size among browser species might affect net shoot growth and tree branching.

5.2 METHODS

5.2.1 Mass compensation and morpho-functional traits

Two stands of *A. nigrescens* trees were identified according to canopy physiognomy and degree of browsing damage. A preliminary vegetation survey (February 2003) assessed levels of ungulate browsing on 70 trees according to distance from water sources. A total of 40 exposed shoots all around the tree canopy were randomly counted at different height levels. Specifically, 20 twigs were exposed to browsers between 0-2 m and 20 twigs between 2-4 m in height. The number of shoots that have been browsed during the current growing season was then checked and expressed as percentage of total number of shoots counted. In heavily browsed trees 50 to 70% of the exposed shoots had been damaged, trees had narrow canopies and mainly occurred < 2 km from permanent or seasonal watering points. Lightly browsed trees showed damage to between 10 and 20 % of the exposed shoots. At a distance of more than 7 km from watering points, trees were taller with wider canopies. Subsequently, three sites where randomly chosen under high browsing intensity (H) and three sites under low browsing intensity (L). Five trees per site within each browsing level (15 heavily browsed and 15 lightly browsed *Acacia* trees) were selected and tagged with numbered aluminium tags. On each tree, 12 shoots (six shoots between 0 - 2 m and six shoots between 2 - 4 m) were randomly chosen and an artificial clipping was performed at the end of February 2003 using, as sampling unit, the giraffe browsing unit (G.B.U.) in order to simulate mass loss due to browser damage. The G.B.U. is equivalent to the length of a twig pruned or leaf-stripped by a giraffe in a single "bite" and on average corresponds to 144 mm (see Woolnough and du Toit 2001).

The number of leaves per shoot was counted and shoot diameter was measured with a calliper at the cut section. Then an aluminium tag was secured on the remaining part of the shoot at a distance of 5 cm from the same cut section. For each of the 360 clipped samples the effective shoot length was measured using a string, which allowed us to follow all shoot curvatures and eventually, included all side shoots comprised in the G.B.U. Each clipped sample was then divided into its woody and leafy components (shoots and leaves), oven dried for 3 days at 80 °C and separately weighed to the second decimal unit. Tagged shoots of the same trees were checked in June, September, and November for evidence of potential regrowth. However, new shoots sprouted only during a 3-4 week window between October and November (see results). New shoots sprouted from lateral buds close to the previously cut section and were easily recognizable from their light green colour and the soft thorns. Only new shoots grown between the tag and the old cut section were re-clipped, oven dried and weighed as above.

I measured other morpho-functional parameters between November 2002 and June 2003 on the same 30 *Acacia* trees. Specifically, in February 2003, 10 external branches per tree were randomly chosen and the length of the first three branch internodes from the canopy surface inwards, were measured with a string and values determined with a plastic ruler. On the same branches the distance between the first five pairs of prickles were measured to estimate prickle spacing. Additionally, prickle size was measured on the same branches, such as the projection of the prickle hooked tip down to the perpendicular intersect of the prickle base. At the end of February 2003, leaf samples (50 leaflets per tree) were collected from the same 30 trees to examine potential differences in specific leaf area (SLA) along the strong browsing gradient. I followed the protocol proposed by Garnier et al. (2001), in terms of sample preparation. Leaf collection was done early in the morning (06h00 - 07h00) to minimize leaf dehydration. Samples were stored in moist paper in a cool box, leaf area measured within 24 h with a LI-COR Model Area Meter and finally, leaf samples oven dried at 70 °C for 2 days.

5.2.2 Annual net shoot growth, leaf N and tree phenology

I performed a second set of experiments to quantify annual rates of shoot growth within different branches of *A. nigrescens* trees according to browsing level, tree height and seasonality. Effects of ungulate browsing were considered at two main height levels within tree canopies (0 – 2 m and 2 – 4 m) since giraffes were the only animals able to feed above 2 m (see du Toit 1990). This allowed me to address potential differences in shoot growth responses due to giraffe only versus all browser species.

I initially identified two sites within the landscape surveyed; the first site was less than 1 km from a seasonal waterhole where *Acacia nigrescens* trees were heavily browsed. The second site (control site) was in a monospecific stand of lightly browsed *A. nigrescens* trees > 8 km from the waterhole and > 3 km from alternative water sources. I then randomly identified 10 trees as heavily browsed (H) and 10 lightly browsed trees

(L). For each tree, 10 branches were marked with aluminium tags, which were tied approximately 30 cm in from the canopy surface (five branches between 0 – 2 m and five branches between 2-4 m). The length of all internodes and apical shoots distal to each tag was measured using a string, which allowed me to follow all branch curvatures. A sketch was made of the branch architecture, showing the position and distribution of all measured shoots and internodes. All tree branches were checked for signs of browsing and each shoot/internode re-measured after 2, 9, 12 and 14 months respectively. Hence, any changes in shoot length and branch architecture due to browsing damage were reported in successive drawings. Leaf samples were collected from each *Acacia* tree in November 2002 (early growing season), February 2003 (late growing season), and at the end of June 2003 (early dry season). Leaves were air dried and stored in paper bags before N analysis using the Kjeldahl standard method (Benton 1991).

In order to test differences in tree branching between lightly and heavily browsed trees a branching ratio was calculated *sensu* Archibold and Bond (2003), which gives indications of whether branch growth is in the form of shoot elongation or lateral branching. For each branch unit, the ratio between the total length of all shoots and the length of the longest shoot was calculated and expressed as a mean of values collected after two growing seasons (Nov '02 ad Nov. '03). The higher the ratio, the more numerous will be the side branches and therefore the tree branching. Finally, the number of flowers and pods were checked in 2002 and 2003 on 100 trees randomly selected under each browsing level (50 trees in heavily browsed sites and 50 trees in lightly browsed sites).

5.3 DATA ANALYSIS

A two-way ANOVA was performed to test for significant effects of browsing and site, on variation in mass compensated after artificial clipping and changes in plant morpho-functional traits. Values were previously log transformed to meet the assumptions of ANOVA. A Spearman rank R correlation was computed using mean values of both shoot and leaf mass compensated versus browsing intensity expressed as percentage of browsed shoots counted on a total of 40 shoots ranging between 0 and 4 m in height. Repeated measures ANOVA were also performed on mean values of annual net shoot growth for tree branches according to browsing intensity, seasonality and canopy height levels (0 – 2 m and 2 – 4 m in height). Mean values of net shoot growth between consecutive measurements were log transformed to meet the requirements of a normal distribution. A post-hoc Tukey HSD test was then performed to evaluate interactive effects of different variables. A Friedman ANOVA and Kendall coefficient of Concordance was performed to test for significant variation in tree branching ratio between heavily and lightly browsed trees, and also according to tree height. Finally, a two-way ANOVA was performed on mean values of leaf N concentration according to browsing levels and seasonality after data were log transformed.

5.4 RESULTS

5.4.1 Mass compensation and morpho-functional traits

Percentage of mass compensated in leaves and shoots after 9 months from artificial clipping was significantly higher in heavily browsed plants than lightly browsed plants (Fig. 5.1; Table 5.1). Heavily browsed plants were exposed to ungulate browsing in-between clipping periods. Heavily browsed trees compensated with 12.9 % ± 1.2 % shoot mass and 62.8 % ± 8.7 % leaf mass, whereas lightly browsed trees compensated with 5.46 % ± 0.65 % shoot mass and 27 % ± 3.42 % leaf mass (Fig. 5.1). Mean values of all other measured morpho-functional traits, except prickle size, were all significantly affected by ungulate browsing (Table 5.1). However, prickle size was affected by browsing-site interactions and a Tukey HSD Test showed that such results depend on variation in prickle size across the lightly browsed sites. Indeed, few trees among the lightly browsed sites still have large prickle size. There was a positive correlation between biomass compensated in both shoots and leaves and the percentage of browsed shoots. Biomass allocated to shoots and leaves increased at higher levels of browsing (Fig. 5.2). Mean values of SLA measured in the mid- to late growing season were similar in heavily (94.1 ± 2.5 cm^2/g) and lightly (92.4 ± 2.5 cm^2/g) browsed trees. There was no significant variation between different browsing levels ($F = 2.87$, $df = 1$, $p = 0.92$).

5.4.2 Annual net shoot growth, leaf N and phenology

Overall, my results show that *Acacia nigrescens* trees, regardless of browsing levels, concentrated their main annual growth between September and November (Fig. 5.3). In 4 weeks, net shoot length (calculated from data collected in two consecutive years), increased by 36.5 % ± 2.78 % in heavily browsed trees and by 18 % ± 0.97 % in lightly browsed trees (Fig. 5.3). Seasonal effects of mean shoot length were significant (Table 5.2), and a Tukey HSD Test showed that such differences were mainly due to shoot sprouting between Sept.-Nov. ‘02 and Sept.-Nov.’03. Moreover, annual shoot growth was significantly affected by both browsing intensity and tree height (Table 5.2). Mean net shoot growth was higher within branches of heavily browsed trees (398 ± 63 mm in Nov.’02 and 434 ± 52 mm in Nov. ’03) than in lightly browsed trees (165 ± 43 mm in Nov. ’02 and 105 ± 19 in mm Nov.’03). However, there was no interaction between browsing, seasonality and height (Table 5.2). The mean number of new shoots produced after 14 months (two growing seasons) within branches of *Acacia* trees was 9.3 ± 0.68 in heavily browsed trees and 3.44 ± 0.37 in lightly browsed trees (Wilcoxon Matched Pairs Test, $N = 48$, $p < 0.001$). Branching ratio was positively correlated with browsing intensity ($F = 23.8$, $df = 3$, $p = 0.0003$; Fig. 5.4) and heavily browsed trees showed greater branching than lightly browsed trees. Variation in leaf N concentration was related to seasonality (Fig. 5.5). Indeed, regardless of browsing levels, leaf N content was higher in *Acacia* trees during the main growing season (November), and decreased in the late growing season (February) and shown the lowest values in the early dry season ($F = 180.2$, $df = 2$, $p < 0.0001$; Fig. 5.5). Browsing intensity was responsible for significant variation in leaf N content ($F = 12.8$, $df = 1$, $p < 0.0001$), as well as browsing-seasonality interactions ($F = 111.1$, $df = 2$, $p < 0.0001$, Fig. 5.5) since heavily browsed *A. nigrescens* trees likely withdrawn N from their leaves more efficiently than lightly browsed trees. The number of flowering trees averaged (after the two years counting) ~ 36 % in lightly browsed sites and ~ 25 % in heavily browsed stands, while the number of flowers was extremely variable. Browsing pressure was not significant if related to the number of flowers per tree (Wilcoxon Matched Pairs Test, $N = 13$, $p = 0.81$). The number of trees that carried pods differed between lightly browsed sites (~ 25 %) and heavily browsed sites (16 %). However, the number of pods differed significantly between lightly (25 ± 5.6) and heavily (10 ± 2.4) browsed trees (Wilcoxon Matched Pairs Test, $N = 8$, $p = 0.03$).

Table 5.1. Mean values ± SE and ANOVA results for variation of morpho-functional traits measured in heavily and lightly browsed *A. nigrescens* trees after 9 months since artificial clipping was performed. Mean of 15 trees per browsing level and 12 shoots measured per tree.
NS = not significant

	High browsing	Low browsing	Browsing			Site			Interaction		
			df	F	p	df	F	p	df	F	p
Shoot mass (g)	0.12 ± 0.02	0.03 ± 0.07	1	14.5	< 0.001	2	0.36	NS	2	0.23	NS
Leaf mass (g)	0.39 ± 0.05	0.17 ± 0.04	1	17.5	< 0.001	2	0.30	NS	2	0.29	NS
Shoot length (mm)	202 ± 26.8	60.1 ± 8.9	1	27.5	< 0.001	2	0.77	NS	2	0.45	NS
Number of leaves	14.5 ± 1.94	4.85 ± 0.45	1	21.65	< 0.001	2	2.74	NS	2	0.11	NS
Shoot diameter (mm)	3.37 ± 0.15	2.75 ± 0.11	1	12.4	< 0.01	2	2.21	NS	2	0.51	NS
Internode length (mm)	58.5 ± 3.37	107 ± 14.1	1	39.1	< 0.001	2	1.80	NS	2	0.72	NS
Prickle size (mm)	4.33 ± 0.19	3.97 ± 0.16	1	1.09	NS	2	2.3	NS	2	5.27	< 0.01
Prickle spacing (mm)	19.3 ± 0.80	26.5 ± 1.45	1	13.1	< 0.01	2	5.09	< 0.05	2	7.45	< 0.01

Table 5.2. Results from repeated measures of variance (ANOVA) for values of net shoot growth within *Acacia* tree branches depending on seasonality, canopy height level (0 – 2 m and 2 – 4 m) and browsing level (high and low).

	SS	df	MS	F	p
Seasonality	1.09	3	0.36	4.52	0.004
Height	0.66	1	0.66	8.19	0.004
Browsing	1.65	1	1.65	20.4	0.00001
Seasonality x height	0.03	3	0.01	0.12	NS
Seasonality x browsing	0.61	3	0.20	2.52	NS
Height x browsing	0.001	1	0.001	0.02	NS
Seasonality x height x browsing	0.07	3	0.02	0.32	NS

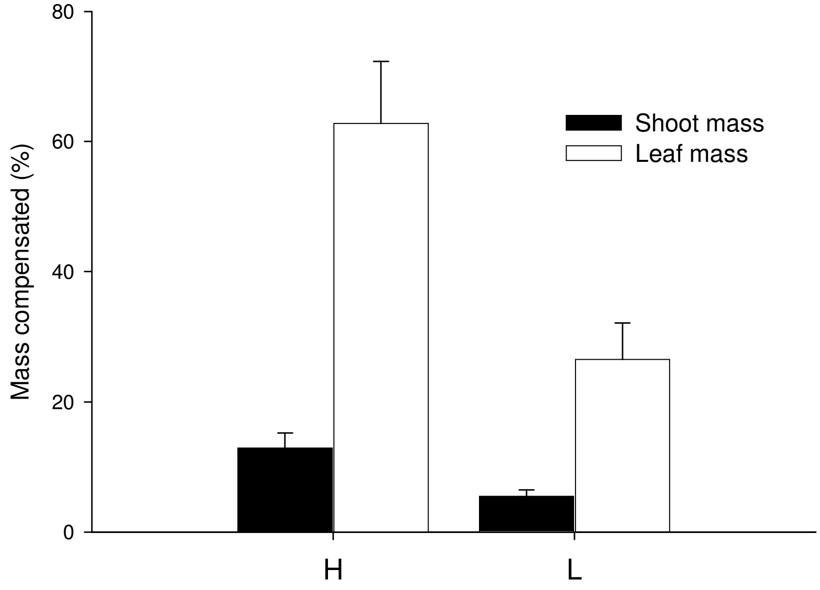

Fig. 5.1. Mass compensated (%) in shoots and leaves of heavily browsed (H) and lightly browsed trees (L) of *Acacia nigrescens* 9 months after artificial clipping.

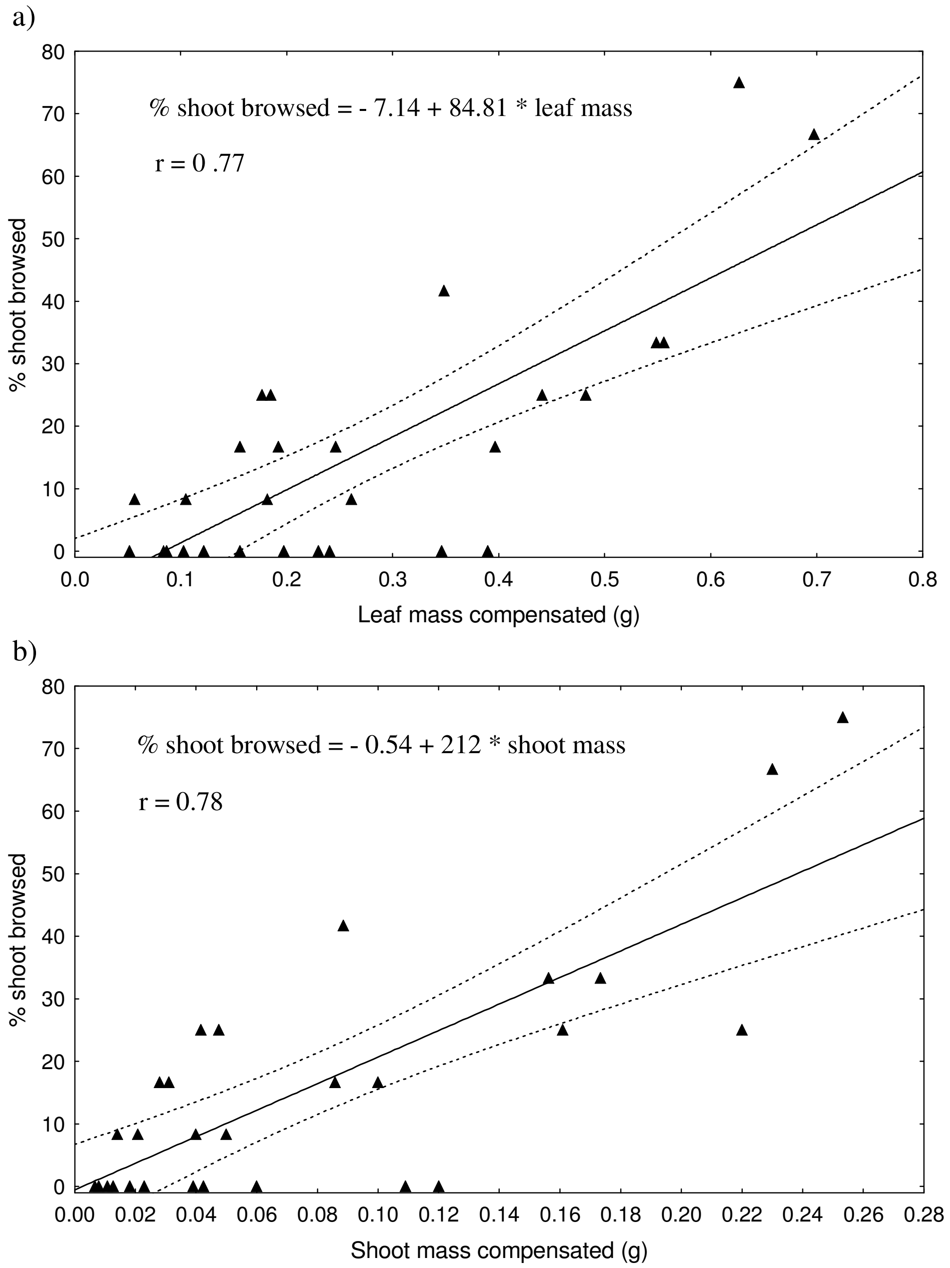

Fig. 5.2. Results from Spearman rank R correlation of both leaf (a) and shoot mass (b) compensated in heavily and lightly browsed trees after artificial clipping vs percentage of browsed shoots around the canopy tree.

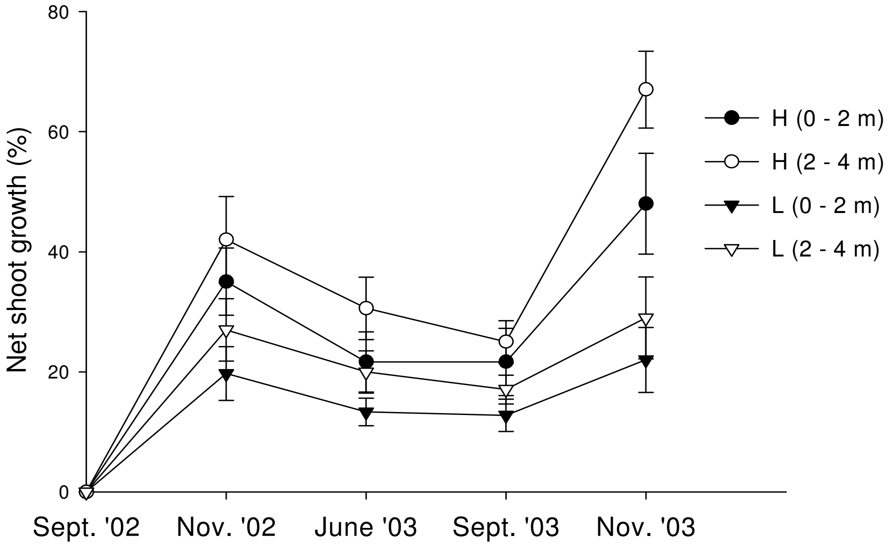

Fig. 5.3. Mean net shoot growth (%) within branches of heavily (H) and lightly (L) browsed *A. nigrescens* trees at two different canopy height levels (0-2 m and 2-4 m) measured at five time intervals.

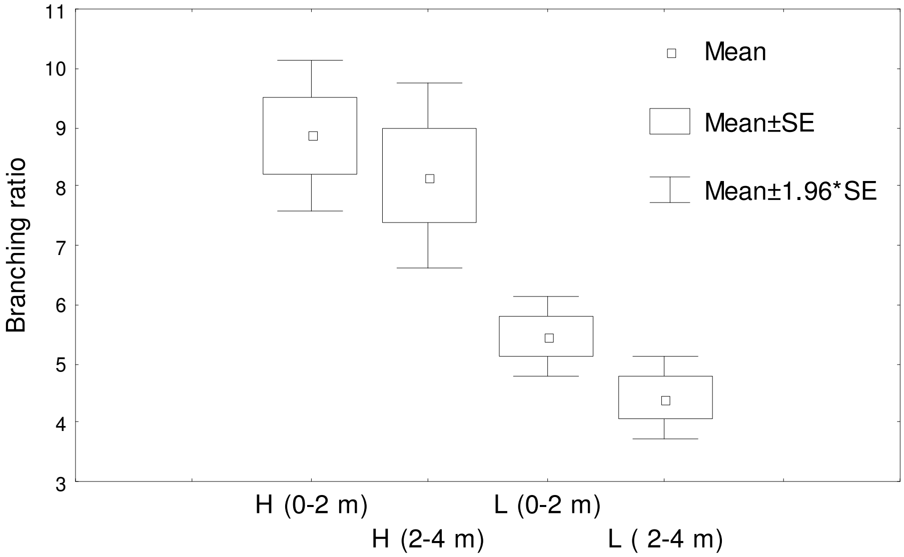

Fig. 5.4. Results from Friedman ANOVA and Kendall Coeff. of Concordance on branching ratio differences between browsing levels (H = high browsing; L = low browsing) and between canopy height levels (0-2 m and 2-4 m).

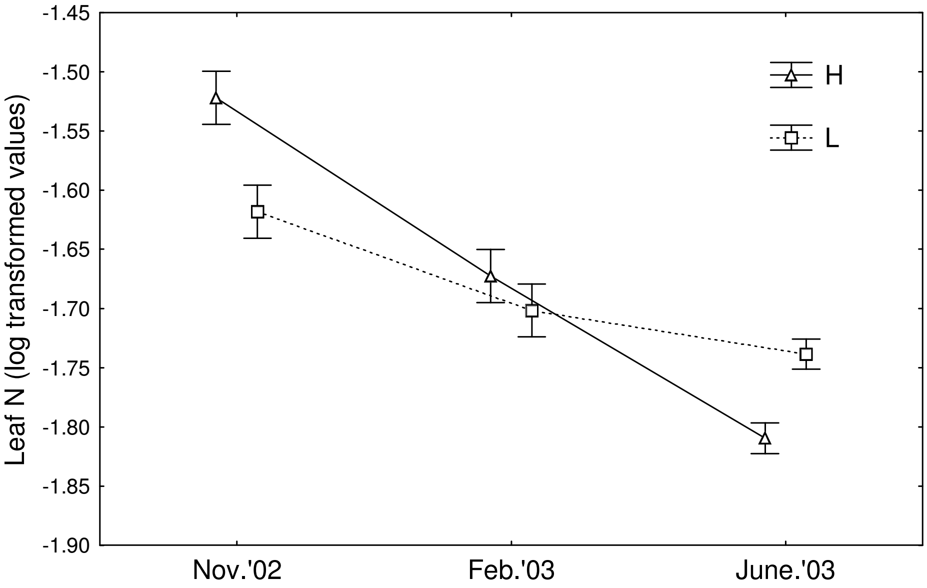

Fig. 5.5. Plotted results from ANOVA of leaf N content in heavily (H) and lightly (L) browsed *Acacia* trees depending on seasonality.

5.5 DISCUSSION

My results show that long-term selective browsing enhanced the compensatory growth abilities of trees within heavily browsed stands of *A. nigrescens*. This partly corroborates earlier findings, which established high mass compensation in *Acacia* species of African savannas (Pellew 1984; du Toit 1990; Dangerfield and Modukanele 1996; Gadd et al. 2001), as well as in palatable woody species of temperate and boreal forests (Danell et al. 1985; Bergström and Danell 1987; Edenius et al. 1993; Peinetti et al. 2001).

However, this study highlights some important aspects related to the plant-browser system, including: (1) the presence of an important positive feedback loop between browsers and their food resource in terms of enhanced plant ability to support mechanisms of mass compensation, (2) the evidence that tree pruning influenced tolerance and resistant traits while comparing two stands of *Acacia* trees with different histories of attack from browsers, and (3) increased tolerance and resistance traits in heavily browsed trees appear to be an efficient response in reducing the impact of browsers rather than in increasing plant reproductive success over undamaged *Acacia* trees.

However, I showed that tree pruning may strongly affect morpho-functional traits and reduce pod production (i. e. plant fitness) in woody plants that have experienced long-term chronic browsing disturbance (Peinetti et al. 2001).

In fact, increased tolerance and resistance in heavily browsed trees is associated with important changes in tree branching, prickle spacing, shoot growth rates, shoot diameter and shoot number. It is likely that tree branching increased after suppression of apical dominance by mammalian browsers, which leads to an increased number of side shoots (du Toit et al. 1990; Bergström et al. 2000; Gadd et al. 2001). Although prickle size (resistant trait) was greater in heavily rather than in lightly browsed trees, such an increase in size was not as apparent as that induced by browsers in *A. drepanolobium* in an East-African savanna (Young 1987; Young et al. 2003). This may primarily depend on prickle form/function effectiveness in reducing mass loss under herbivore damage. For example, prickles of *A. tortilis* are effective in retarding biting rates by kudu and impala (Cooper and Owen-Smith 1986).

In the present study short prickle spacing might have similar retarding effects on browser ability to remove leaves, such as leaf stripping by giraffes. However, long straight thorns are more efficient against giraffe browsing (Pellew 1984). The fact that they are absent in *A. nigrescens* suggests that trees may also rely on other defensive traits, such as tolerance traits. Prickles represent a relatively ‘cheap’ form of plant protection if amortized over many years on relatively N rich soils (Craine et al. 2003), such as soils of eutrophic southern African savannas (Scholes 1990; Venter et al. 2003). However, thorns, prickles and spines still allow plants to be eaten and mechanisms of compensatory growth might have evolved in response to severe damage by ungulate browsers.

Specific leaf area (SLA) values were similar between heavily and lightly browsed trees in the late growing season (February) when leaf N content was similar among browsing levels (Fig. 5.5). Such results, according to the strong relationship between leaf nitrogen, SLA and photosynthetic capacity (see Reich et al. 1995; Reich et al. 1999), indicate that heavily and lightly browsed *Acacia* trees may have similar growth rates in the late growing season. However, I found higher leaf N in heavily than lightly browsed trees in the early growing season (Fig. 5.5). This may explain the high compensatory growth abilities of heavily browsed trees when supported by high photosynthetic rates.

The main period of plant growth occurred during only a few weeks for both heavily and lightly browsed plants. This suggests the presence of mechanisms of N remobilization as a response to key environmental factors when plants are in critical phenological stages (see Tolsma et al. 1987). There was evidence to suggest that browsing may influence mechanisms of N relocation from leaves to perennial organs since heavily browsed trees withdrawn N more efficiently than lightly browsed trees before the beginning of the dry season (Fig. 5.5). This, combined with a reduced canopy volume may explain why heavily browsed plants compensated much more biomass than lightly browsed trees during the main plant growth period.

Severe pruning, reducing canopy size and increasing overlapping of photosynthetic tissues has an indirect negative impact on C storage in below-ground compartments (Peinetti et al. 2001). Therefore, long-term browsing pressure may affect nutrient uptake and stimulate internal nutrient remobilization in plants (Chapin et al. 1990; Millard 1993). However, it is unlikely that the high compensatory growth abilities observed in heavily browsed *Acacia* trees rely only on mechanisms of nutrient remobilization, and other eco-physiological mechanisms may support plant growth.

Indeed, since litterfall was scarce under *Acacia* tree canopies due to high tree pruning (see Chapter 4) and mineralization rates, being highly variable in semi-arid African savannas (Scholes et al. 2003), compensatory growth abilities may be supported by important herbivore-mediated linkages between above- and below-ground processes (see Bardgett and Wardle 2003). In fact, above-ground herbivory via indirect effects on the root system, whether through an increased number of fine roots and/or root exudation, may enhance N mineralization and inorganic N availability in the soil which in turn increases plant productivity and therefore support mass compensatory growth (see Ayres et al. 2004). The apparent contradiction between low litterfall and high compensatory growth abilities of heavily browsed trees, as Prof. Pastor suggested, may be due to the fact that leaf biomass in heavily browsed sites may simply be converted into dung which in turn may represent an important source of nutrients for woody plants.

Hence, woody plant responses to selective browsing would partly resemble those observed in grasses under ungulate grazing. Grazers are able to induce changes in nutrient cycle within individual plants and increase grass compensatory growth abilities promoting and sustaining the "grazing lawns" (McNaughton 1979, 1983). I demonstrated here that *Acacia nigrescens* trees are able to persist *in situ* under long-term browsing pressure, which suggests the presence of analogous "browsing lawns" where heavily browsed *Acacia* trees rely on different eco-physiological mechanisms and/or nutrient source-sinks to sustain plant compensatory growth (see also du Toit et al. 1990). However, *Acacia* morpho-functional traits are profoundly modified by browsers, and the overall effects on nutrient cycling either within the plant-browser system or at the ecosystem level are possibly different from those described for the grazing guild (see Chapter 4).

I did not find evidence to support the presence of potential differences in phenology between heavily and lightly browsed trees of *A. nigrescens*. Seasonality and environmental constraints (i. e. water availability) may have contributed to concentrate annual plant growth for both heavily and lightly browsed trees during the few weeks before the main rainy season. However, this may also represent an efficient response to herbivory. Indeed, *Acacia nigrescens* trees concentrate main annual growth during a short period, protect themselves with new prickles, and "dilute" at a landscape scale the biomass available to browsers, therefore decreasing chances of mass loss per individual tree.

I found fewer trees carrying pods in heavily browsed sites and pod number was also lower in heavily than in lightly browsed trees. This suggests a general negative effect of browsing on plant reproductive success. It is likely that only the few individuals that escape browsing during favourable years will produce pods within heavily browsed stands of *A. nigrescens,* and only those above giraffe's reach would have more chance to be successfully released. Pruning effects of giraffes significantly increased both mean annual shoot growth (Fig. 5.3; Table 5.2) and tree branching (Fig. 5.4). This implies that giraffe pruning at higher canopy levels has a stronger impact on *Acacia* trees than other browser species, and partly supports the findings of Woolnough and du Toit (2001) that large browsers gain a bite-size advantage by browsing above the reach of the smaller species.

5.6 CONCLUSION

Comparing two stands of *A. nigrescens* with extremely different histories of attack from herbivores I found that heavily browsed trees showed (1) increased tolerance in terms of mass compensatory growth ability, extensive tree branching and high leaf N during the main growing season, (2) increased resistance as shown by the short prickle spacing and the evidence of large prickle size. I also showed that increased tolerance and resistance traits were not positively related to pod production, but presumably enhance plant survival over a life-time period. Evidence of differences in phenological escape from browsers between heavily and lightly browsed trees, such as shortening the period of main annual growth, was not obvious, and is likely dependent on the interplay of different environmental constraints.

In order for *A. nigrescens* to show tolerance and resistant traits I propose that costs related to produce physical defences (i.e prickles) must be relatively low in a semi-arid eutrophic African savanna, as we might expect from the resource economics of chemical/structural defences across a N supply gradient (Craine et al. 2003). Moreover, I suggest that important nutrient source-sinks may support plant compensatory growth abilities, such as mechanisms of nutrient remobilization, high levels of N_2 fixation in fine-leaved savannas (Scholes et al. 2003), and increased abilities of root mining triggered by above-ground herbivory (Bardgett and Wardle 2003). However, the browser-plant system might be specific to semi-arid eutrophic savannas, thus more research on differences between eutrophic and oligotrophic systems would be necessary.

5.7 REFERENCES

Agrawal, A. A. 1998. Induced responses to herbivory and increased plant performance. *Science* 279:1201-1202.

Agrawal, A. A. 2000. Overcompensation of plants in response to herbivory and by-product benefits of mutualism. *Trends in Plant Science* 5:309-313.

Archibald, S. and Bond, W. 2003. Growing tall vs growing wide: tree architecture and allometry of *Acacia karoo* in forest, savanna, and arid environments. *Oikos* 102:3-14.

Ayres, E., Heath, J., Possell, M. et al. 2004. Tree physiological responses to above-ground herbivory directly modify below-ground processes of soil carbon and nitrogen cycling. *Ecology Letters* 7:469-479.

Bardgett, R. D. and Wardle, D. A. 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84:2258-2268.

Belsky, A. J., Carson, W. P., Jensen, C. L. and Fox, G. A. 1993. Overcompensation by plants: herbivore optimization or red herring? *Evolutionary Ecology* 7:109-121.

Benton, J. J. 1991. Kjeldahl method for nitrogen determination. Athens GA:Micro-Macro Publishing.

Bergström, R. and Danell, K. 1987. Effects of simulated winter browsing by moose on morphology and biomass of two birch species. *Journal of Ecology* 75:533-544.

Bergström, R., Skarpe, C. and Danell, K. 2000. Plant responses and herbivory following simulated browsing and stem cutting of *Combretum apiculatum. Journal of Vegetation Science* 11:409-414.

Bryant, J. P., Chapin, F. S. and Klein, D. R. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40:357-368.

Chapin, F. S. I., Schulze, E. D. and Mooney, H. A. 1990. The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics* 21:423-447.

Coates Palgrave, K., Coates Palgrave, M., Drummond, R. B. et al. 2002. *Trees of Southern Africa*. 3rd Edition Struik Publishers.

Coley, P., Bryant, J. P. and Chapin, F. S. 1985. Resource availability and plant antiherbivore defense. *Science* 230:895-899.

Cooper, S. M. and Owen-Smith, N. 1986. Effects of plant spinescence on large mammalian herbivores. *Oecologia* 68:446-455.

Craine, J., Bond, W., Lee, W. G., Reich, P. B. et al. 2003. The resource economics of chemical and structural defenses across nitrogen supply gradients. *Oecologi*a 137:547-556.

Danell, K., Huss-Danell, K., and Bergström, R. 1985. Interactions between browsing moose and two species of birch in Sweden. *Ecology* 66:1867-1878.

Dangerfield, J. M., and Modukanele, B. 1996. Overcompensation by *Acacia erubescens* in response to simulated browsing. *Journal of Tropical Ecology* 12:905-908.

du Toit, J. T. 1988. *Patterns of resource use within the browsing ruminant guild in the central Kruger National Park*. PhD thesis, University of the Witwatersrand, Johannesburg, South Africa.

du Toit, J. T. and Owen-Smith, N. 1989. Body size, population metabolism, and habitat specialization among large African herbivores. *American Natutalist* 133:736-740.

du Toit, J. T. 1990. Feeding-height stratification among African browsing ruminants. *African Journal of Ecology* 28:55-61.

du Toit, J., Bryant, J. P. and Frisby, K. 1990. Regrowth and palatability of *Acacia* shoots following pruning by African Savanna browsers. *Ecology* 71:140-154.

du Toit, J. T. 2003. Large herbivores and savanna heterogeneity. – In: du Toit, J., Rogers, K. and Biggs, H. (eds), *The Kruger experience. Ecology and Management of savanna heterogeneity.* Island Press, Washington, DC, US, pp 292-309.

Edenius, L., Danell, K., and Bergström, R. 1993. Impact of herbivory and competition on compensatory growth in woody plants: winter browsing by moose on Scots pine. *Oikos* 66:286-292.

Fineblum, W. L. and Rausher, M. D. 1995. Tradeoff between resistance and tolerance to herbivore damage in a morning glory. *Nature* 377:517-520.

Freeman, R. S., Brody, A. K., and Neefus, C. D. 2003. Flowering phenology and compensation for herbivory in *Ipomopsis aggregata. Oecologia* 136:394-401.

Gadd, M. E., Young, T. P., and Palmer, T. M. 2001. Effects of simulated shoot and leaf herbivory on vegetative growth and plant defense in *Acacia drepanolobium*. *Oikos* 92:515-521.

Garnier, E., Shipley, B., Roumet, C., and Laurent, G. 2001. A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology* 15:688-695.

Gowda, J. H. 1996. Spines of *Acacia tortilis*: what do they defend and how? *Oikos* 77:279-284.

Herms, D. A., and Mattson, W. J. 1992. The dilemma of plants: to grow or defend? *The Quarterly Review of Biology* 67:283-335.

Holland, E. A., Parton, W. J., Detling, J. K. et al. 1992. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. *American Naturalist* 140:685-706.

Houle, G. and Simard, G. 1996. Additive effects of genotype, nutrient availability and type of tissue damage on the compensatory response of *Salix planifolia* ssp. *Planifolia* to stimulated herbivory. *Oecologia* 107:373-378.

Huntley, B. J. 1982. Southern African Savannas. In: Huntley B. J. and Walker, B. H. (eds), *Ecology of Tropical Savannas*. Springer-Verlag Berlin Heidelberg, New York, pp.101-119.

Karban, R., Agrawal, A. A., Thaler, J. S. et al. 1999. Induced plant responses and information content about risk of herbivory. *Trends in Ecology and Evolution* 14:443-447.

Lennartsson, T., Tuomi, J. and Nilsson, P. 1997. Evidence for an evolutionary history of overcompensation in the grassland biennial *Gentianella campestris* (Gentianaceae). *American Naturalist* 149:1147-1155.

Lennartsson, T., Nilsson, P., and Tuomi, J. 1998. Induction of overcompensation in the field gentian *Gentianella campestris*. *Ecology* 79:1061-1072.

McNaughton, S. J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *American Naturalist* 113:691-703.

McNaughton, S. J. 1983. Compensatory growth as a response to herbivory. *Oikos* 40:329-336.

Milewski, A. V., Young, T. P., Madden, D. 1991. Thorns as induced defenses: experimental evidence. *Oecologia* 86:70-75.

Millard, P. 1993. A review of internal cycling of nitrogen within trees in relation to soil fertility. In: Fragoso, M. A. C. and van Beusichem, M. L. (eds), *Optimization of Plant Nutrition*. Kluwer Academic Publishers, Dordrecht, pp 623-628.

Naiman, R. J., Braack, L. Grant, R. et al. 2003. Interactions between species and ecosystem characteristics. In: du Toit, J., Rogers, K. and Biggs, H. (eds). *The Kruger experience. Ecology and Management of savanna heterogeneity.* Island Press, Washington, DC, US, pp. 221-241.

Nilsson, P., Tuomi, J. and Astrom, A. 1996. Even repeated grazing selects for overcompensation. *Ecology* 77:1942-1946.

Oba, G., Mengistu, Z. and Stenseth, N. C. 2000. Compensatory growth of the African dwarf shrub *Indigofera spinosa* following simulated herbivory. *Ecological Applications* 10:1133-1146.

Owen-Smith, N. 1979. Assessing the foraging efficiency of a large herbivore, the kudu. *South African Journal of Wildlife Research* 9:102-110.

Owen-Smith, N. 1990. Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall. *Journal of Animal Ecology* 59:893-913.

Paige, K. N., and Whithman, T. G. 1987. Overcompensation in response to mammalian herbivory: the advantage to be eaten. *American Naturalist* 129:407-416.

Paige, K. N. 1992. Overcompensation in response to mammalian herbivory: from mutualistic to antagonistic interactions. *Ecology* 73:2076-2085.

Peinetti, H. R., Menezes, R. S. C. and Coughenour, M. B. 2001. Changes induced by elk browsing in the aboveground biomass production and distribution of willow (*Salix monticola* Bebb): their relationships with plant water, carbon, and nitrogen dynamics. *Oecologia* 127:334-342.

Pellew, R. A. 1984. The feeding ecology of a selective browser, the giraffe (*Giraffa camelopardis tippelskirchi*). *Journal of Zoology* 202:57-81.

Reich, P. B, Kloeppel, B. D, Ellsworth, D. S. et al. 1995. Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. *Oecologia* 104:24-30.

Reich, P. B., Ellsworth, D. S., Walters, M. B. et al. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80:1955-1969.

Rosenthal, J. P. and Kotanen, P. M. 1994. Terrestrial plant tolerance to herbivory. *Trends in Ecology and Evolution* 9:145-148.

Scholes, R. J. 1990. The influence of soil fertility on the ecology of southern African dry savannas. *Journal of Biogeography* 17:415-419.

Scholes, M., Scholes, R. J., Otter, L. B. et al. 2003. Biogeochemistry: the Cycling of Elements. In: du Toit, J., Rogers, K. and Biggs, H. (eds), *The Kruger experience. Ecology and Management of savanna heterogeneity*. Island Press, Washington, DC, US, pp 131-148.

Spalinger, D. E. and Hobbs, N. T. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. *American Naturalist* 140:325-348.

Stinchcombe, J. R. and Rausher, M. D. 2002. The evolution of tolerance to deer herbivory: modifications caused by the abundance of insect herbivores. *Proceedings of the Royal Society of London* 269:1241-1246.

Strauss, Y. S. and Agrawal, A. A. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution* 14:179-185.

Tolsma, D. J., Ernst, W. H. O., Verweij, R. A. et al. 1987. Seasonal variation of nutrient concentrations in a semi-arid savanna ecosystem in Botswana. *Journal of Ecology* 75:755-770.

Venter, F. J., Scholes, R. J., and Eckhardt, H. C. 2003. The abiotic template and its associated vegetation pattern. In: du Toit, J., Rogers, K. and Biggs, H. (eds). *The Kruger experience. Ecology and Management of savanna heterogeneity.* Island Press, Washington, DC, US, pp. 83-129.

Woolnough, A. P. and du Toit, J. P. 2001. Vertical zonation of browse quality in tree canopies exposed to a size-structured guild of African browsing ungulates. *Oecologia* 129:585-590.

Young, T. P. 1987. Increased thorn length in *Acacia drepanolobium*: an induced response to browsing. *Oecologia* 71:436-438.

Young, T. P., Stanton, M. L. and Christian, C. E. 2003. Effects of natural and simulated herbivory on spine lengths of *Acacia drepanolobium* in Kenya. *Oikos* 101:171-179.