CHAPTER 6

Ungulate browsing and its effects on suppressed juvenile forms of woody species in a eutrophic African savanna

Abstract

Suppressed growth forms of woody species ("gullivers") are common in highly variable, fire prone ecosystems such as African savannas. Despite their critical role in maintaining population viability and influencing vegetation dynamics, previous studies have neither quantified gullivers resprouting abilities, nor the set of plant traits which might confer resilience to ungulate browsing in the absence of fire. Here I tested compensatory growth abilities of 120 gullivers of two common species, *Acacia nigrescens* Miller, and *Acacia tortilis* (Forsk.), Hayne, after a severe artificial clipping along strong herbivory gradients. I also selected five gullivers' morpho-functional traits and compared them between the two *Acacia* species. Finally, I measured net annual height growth, leaf N and plant density variation throughout a study area where fire had been absent for 13 years. Overall, *Acacia* gullivers showed high mass compensatory growth abilities under high browsing pressure. Increased root size supports high mass compensation after artificial clipping and stresses the role of below-ground organs as important nutrient storage to enhance resprouting abilities. Ungulate browsing strongly affected plant morpho-functional traits and reduced net annual height growth. Gullivers in heavily browsed sites were (1) shorter, with (2) more stems originating above the main root crown, (3) smaller stem diameter at ground level, and (4) greater root diameter at 5 cm depth than gullivers in lightly browsed sites. Finally, gullivers were more abundant and showed a clumped dispersion within heavily browsed sites opposite to the lightly browsed sites. I propose, at the landscape scale, gullivers density and distribution to be positively related to the presence of mammalian browsers, which increase chances of gullivers establishment but limits their recruitment to mature size classes. Since gullivers show high persistence under long-term browsing regimes and with plant recruitment opportunities highly variable in semi-arid African savannas, I suggest gullivers presence and persistence may be ascribed to the "storage effect". Gulliver morpho-functional traits associated with high resprouting

abilities increase the likelihood of plant population survival in a semi-arid eutrophic African savanna exposed to withstanding levels of browsing and fire.

KEY WORDS: *Acacia*, compensatory growth abilities, fire, functional traits, gulliver, herbivory, storage effect

6.1 INTRODUCTION

Mechanisms responsible of species turnover in space and time represent a central topic in plant ecology. Plant species distribution mainly results from the interaction between environmental factors and plant eco-physiological traits (Whittaker 1967; Grime 1977; Hubbell and Foster 1986; Grime et al. 1988; Tilman 1988; Matthews 1992; Bazzaz 1996; Westoby 1998). Although interspecific competition is considered a key driver of plant community composition, more attention has been recently paid to the role of disturbance (e.g. herbivory, fire) in influencing both spatial and temporal variation in plant species assemblages (Bond and van Wilgen 1996; Hobbs 1996; Pastor and Cohen 1997; Ritchie et al. 1998; Westoby 1999).

Disturbance events might determine shifts in vegetation structure and composition, as shown, for example in African savannas where state changes are likely triggered and maintained by fire and herbivory (Skarpe 1992; Jeltsch et al. 1996; Van de Koppel and Prins 1998; Roques et al. 2001; van Langevelde et al. 2003). Despite strong research interest on mechanisms responsible for the coexistence of trees and grasses in African savannas (see Scholes and Archer 1997; Higgins et al. 2000a), comparatively little attention has been directed at understanding the determinants of tree species distribution and abundance along herbivory gradients. Bond et al. (2001) showed that a disturbance gradient defined by fire and mammalian herbivory was responsible for shifts in population structure of two *Acacia* species in an African savanna. The study also demonstrated the vulnerability of trees in their early life-history stages resulted in adaptations that optimize persistence and/or recruitment strategies. For example, species with enhanced resprouting abilities can occupy a 'persistence niche' as a temporary alternative to the "grow or die" gamble (Bond and Midgley 2001).

In their seedling-sapling stage, savanna woody plants are most susceptible to fire and herbivory (Bond and van Wilgen 1996). Nevertheless, there is consistent evidence that many woody species in fire prone ecosystems are resprouters (Le Maitre and Midgley 1992; Midgley and Cowling 1993; Kruger et al. 1997; Canadel and Lopez-Soria

1998; Higgins et al. 2000a; Espelta et al. 2003), and evolutionary studies have shown that resprouters are favored where disturbance regimes are frequent and severe in relation to plant regrowth rates (Bond and Midgley 2003).

Consequently, it is not surprising that suppressed juveniles forms of tree species, resilient to disturbance, have been described in southern African savannas (Bond and van Wilgen 1996; Midgley and Cowling 1993; see also Wilson and Witkowski 2001). This phenomenon has been ascribed to the 'Gulliver effect' (Bond and van Wilgen 1996), which methodologically explains young trees struggle to emerge from the herbaceous layer because of fire fuelled by grasses ("Lilliputians").

Moreover, gullivers are able to persist *in situ* for decades relying on high resprouting abilities, when recruitment events are rare and episodic. Hence, the set of morpho-functional traits that enhance gullivers survival, may represent a direct consequence of the 'storage effect' (see Warner and Chesson 1985; Higgins et al. 2000b; Bond and Midgley 2003), since they 'store' the reproductive potential as persistent juvenile forms until favorable conditions occur (e.g. episodes of decreased browsing, increased rainfall). The storage effect is based on the evidence that population growth is dependent upon (1) plant recruitment, and (2) survival strategies, such as the storage of reproductive potential over generations which may increase population viability in highly variable ecosystems (Higgins et al. 2000b).

The present study was motivated by field observations during a two-year vegetation survey in a semi-arid eutrophic southern Africa savanna. I observed the scarcity of true seedlings and high resprouting abilities of gullivers of common *Acacia* species, especially under high browsing intensity (Fornara, *unpublished data*). Despite their critical role in increasing the likelihood of population survival and influencing the structure of *Acacia* woodlands, previous studies, neither have quantified compensatory growth abilities of gullivers after browsing damage, nor measured variation in morpho-functional traits within gulliver species along strong herbivory gradients in the absence of fire. Nevertheless, we lack information on patterns of abundance and dispersion of gulliver species along strong browsing-grazing gradients. Therefore, my study set out to investigate:

- How gulliver resprouting abilities vary along a strong browsing gradient in two common *Acacia* species;
- Whether gulliver morpho-functional traits, and net annual height growth are influenced by browsers in the absence of fire;

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- If there is a consistent effect of herbivory on gullivers distribution and density across a strong gradient of grazing and browsing.

6.2 METHODS

Three sites of approximately 10 km² were identified in February 2002. A set of 30 plots (25 m x 25 m), were then randomly established in each site along a strong browsing gradient on the basaltic clay plains at the top of the catenary drainage sequence. Plots were positioned along 10 transects of 600 m each in length (3 plots per transect). The transects were placed to be accessible from the road network and were at least 50 m from main roads. I definied the browsing gradient by considering both plant physiognomy (e.g. tree canopy shape and size) and percentage of shoots that had been browsed in the current growing season all around the canopy of adult *Acacia* trees.

Along with the browsing gradient, a grazing gradient was also identified since environmental conditions created by the grass layer and grazer disturbance likely affect tree seedling establishment and recruitment (Brown and Archer 1989; Davis et al. 1998). Grazing intensity was determined using a number of quadrats (1 m²) that were laid out at the end of the growing season in February 2002. Four quadrats were randomly located per plot and data were collected on distinctive grass traits affected by grazing: (1) density of grass tufts, (2) mean tuft height, (3) ground area covered by tufts, (4) percentage of stems recently grazed (see Chapter 3). Browsing and grazing intensity is strongly related to distance from permanent or seasonal water sources (see Redfern et al. 2003). Hereafter, according to the browsing and grazing levels observed, I refer to the three site types as follows: high browsing/high grazing site (HH) situated < 2 km from water sources, high browsing/low grazing site (HL) < 4 km from permanent water, and low browsing/low grazing site (LL) > 8 km from permanent water and also > 3 km from any seasonal water sources. There are consistent indications that the HH and HL sites have been undergoing heavy browsing pressure for decades, and presumably for centuries (du Toit et al. 1990; du Toit 2003).

I attempted to minimize intrinsic site differences by choosing sites with the same soil type and rainfall regime. First, since the furthest distance between sites was ~ 10 km, rainfall differences were assumed to be negligible. Second, all sites were located on the basaltic clay plains at the top of the catenary drainage sequence. Third, my study area within the Tshokwane section of the Kruger Park, where all our investigations were carried out, had not been burnt for 13 years.

Gulliver morpho-functional traits and distribution

Gullivers of two common *Acacia* species, *A. nigrescens,* Miller, and *A. tortilis* (Forsk.) Hayne, were selected and tagged among the study sites. The knobthorn *Acacia nigrescens* Miller, which is a staple food resource for mammalian browsers, has double pinnately compound leaves with 4-6 large leaflets per leaf. Trees bear hooked thorns and are usually leafless for three-four months during the dry season (see Coates Palgrave et al. 2002). The umbrella thorn *A. tortilis* (Forsk.), Hayne was also common across the study sites. It bears both hooked and straight thorns and compound leaves with numerous small leaflets. Gullivers of both *A. nigrescens* and *A. tortilis* were observed to resprout from the base of the stem just above the main root crown. Therefore, following sprouting typologies reviewed by Del Tredici (2001), both *Acacia* species presented a collar sprouting type rather than specialized underground organs (i.e. lignotubers or rhizomes) or root suckering.

6.2.1 Compensatory growth and leaf N

Initially, 100 gullivers for each of the two *Acacia* species were identified and tagged in February 2002. In order to select a sample size as homogeneous as possible, I estimated the age of individual gullivers by the size of the taproot system measured at a depth of five cm. I assumed this was a good indicator of gullivers age under the same disturbance regime and soil type. I therefore selected gullivers of the two *Acacia* species for which the mean values of the of root diameter were contained within the confidence intervals of 99% (p = 0.01) at each browsing-grazing level. I finally selected 60 gullivers for each *Acacia* species (30 gullivers per species per site) at the opposite ends of the browsing-grazing gradient (HH and LL sites).

Five morpho-functional traits were measured as follows: (1) maximum height measured from ground level to the highest photosynthetic part, (2) maximum width, (3) number of stems generated from the same root crown, (4) stem diameter at ground level measured on vegetative parts avoiding dead stems still in place after fire or elephant damage (in case of multiple stems the largest diameter was measured), (5) measuring the root diameter at five cm depth using a caliper. To quantify the compensatory growth abilities of the two *Acacia* species a severe artificial clipping was performed at the end of February 2002 on the selected gullivers distributed along the browsing gradient.

Since gulliver architecture differed between the two *Acacia* species I established a standard method of clipping only the shoots exposed to ungulate pruning all around the gulliver canopy. For each individual the main stem, internodes and apical shoots were

given a hierarchical order. I considered as 1st order the stem/s directly originating from the root crown, 2nd order internodes were those starting from nodes on the main stem and 3rd order internodes (or terminal shoots) originated from ramifications of the 2nd order internodes. Then, according to increased chances of pruning by different browser species, 3rd order internodes were clipped in *Acacia nigrescens*. Woody architecture was simpler for gullivers of *Acacia tortilis*, which often had multiple stems originating from the root crown then flattening on the ground and bearing 2nd order (sometimes 3rd order) shoots. In this case clipping was performed on 2nd order shoots since they were the most likely pruned by browsers. Before clipping, all shoots exposed to ungulate browsing (3rd order shoots for *A. nigrescens* and 2nd order shoots for *A. tortilis*) were checked for signs of damage and browsing intensity was expressed as percentage of browsed *vs* total number of shoots.

Clipped material was separated in wood and leaf components, oven dried at 70 ˚C for three days and weighed. Gullivers were monitored monthly for signs of resprouting, which occurred, however, only during a few weeks between October and November. Clipped gullivers were not protected by exclosures during the experiments since most of the leaves where removed by artificial clipping and they were no longer targeted as food resources by browsers. Nine months later a second clipping was performed in November 2002 (just after the main annual growth) on the new shoots that resprouted from the gullivers since the first clipping in February 2002. New shoots and leaves were then oven-dried and weighed as above. Leaf samples from newly produced shoots of 10 individuals of *A. nigrescens* and *A. tortilis* in the HH site were analyzed for N concentration using the Kjeldahl standard methodology (Benton 1991).

6.2.2 Net annual height growth, density and gulliver distribution
A total of 251 gullivers of *A. nigrescens* and *A. tortilis* were randomly tagged with aluminum tags in the HH and HL sites in May 2002. Gulliver maximum height was measured from ground level to the highest photosynthetic part. The same gullivers were re-measured one year later to assess main browsing effects on net annual height growth. Moreover, in May 2002, all gullivers < 50 cm height found inside each of the 90 plots across the browsing-grazing gradients, were identified at the species level when possible. Finally, in each plot three quadrats of 25 m² each were located using coordinates given by a random number generator. In each of the three 5x5 m quadrats the number of *A.*

nigrescens gullivers' were counted to test whether the observed frequency distribution differed from its expected pattern if they had a random distribution.

6.3 DATA ANALYSIS

A Mann-Whitney U Test was repeatedly used to check for significant differences in the amount of biomass compensated in shoots and leaves of the two *Acacia* species along the strong browsing gradient (HH *vs* LL sites). Proportions of browsed shoots were arcsine transformed and values from morpho-functional traits were ln-transformed to meet assumptions for ANOVA.

We expected the five morpho-functional traits of the two *Acacia* species to covary as response variables to ungulate browsing. Therefore, the data were first analyzed by multivariate analysis of covariance (MANCOVA) using the proportion of browsed shoots (browsing intensity) as the covariate. Repeated measures ANOVA were then performed for each plant trait using browsing and species identity as predictor factors. The interaction between species and browsing was not considered in the ANOVA since MANCOVA would not show significant differences (see results). A Tukey HSD test was adopted for post-hoc comparison of independent effects of species identity and browsing on the measured traits.

A t-test was then performed to investigate differences in leaf N content between the two gulliver species. A Pearson correlation matrix was used to test significant relationships between morpho-functional traits and mass compensated by the *Acacia* gullivers after artificial clipping. Finally, frequencies of occurrence of gullivers of *A. nigrescens*, recorded in the randomly located quadrats along the browsing gradient, were fitted to a Poisson distribution to test if the observed frequency distribution differed from that expected. However, since expected frequencies of *A. nigrescens* gullivers in the LL site and A. *tortilis* gullivers across all sites, would result being less than 1.0 per plot, I did not use them to fit a Poisson distribution (see Zar 1999).

6.4 RESULTS

6.4.1 Compensatory growth ability

Mass compensated by gullivers of the two *Acacia* species was significantly greater at HH than LL sites (Fig. 6.1), even though 20 % of plants in the HH site experienced browsing damage in-between the two clipping treatments. Mortality rates after clipping were low, only 2 % of the total number of gullivers. In total, 70 % of gullivers of *A. nigrescens*

produced new shoots in the HH site and only 50 % in the LL site, whereas all gullivers of *A. tortilis* resprouted in the HH site and only 47 % of them in the LL site. In the HH site gullivers of *A. nigrescens* compensated 18.4 % ± 10.7 % (mean ± SE) of mass loss in shoots from artificial clipping. In the LL site biomass compensation was only 3.5 % ± 2.6 % (Fig. 6.1; Mann-Whitney U-Test, $Z = 2.18$, $p = 0.029$).

Leaf dry mass of *A. nigrescens* compensated 91.2 % ± 40 % in the HH site, but only 10 % ± 4.3 % in the LL site (Fig. 6.1; Mann-Whitney U-Test, $Z = 2.56$, $p = 0.01$). Similarly, shoots of *A. tortilis* showed in percentage higher compensation rates in the HH site, 26 % ± 7.5 % than in the LL site where mass compensated 11 % ± 6.4 % (Fig. 6.1; Mann-Whitney U-Test, $Z = 4.28$, $p = 0.001$). Finally, leaf dry mass of *A. tortilis* compensated for 46 % ± 10.2 % in the HH site *vs* only 17 % ± 6.5 % in the LL site (Fig. 6.1; Mann-Whitney U-Test, $Z = 4.31$, $p = 0.001$).

6.4.2 Morpho-functional traits

Results from MANCOVA show that significant variation in the morpho-functional traits measured, were due to species identity and browsing level (Table 6.1). Contrary, plant traits were not affected by the interaction between species identity and browsing levels ($p = 0.93$). The proportion of browsed shoots was higher in the HH than in the LL site and between species higher for *A. nigrescens* than *A. tortilis* (Table 6.2). Ungulate browsing similarly affected morpho-functional traits of the two *Acacia* species (Table 6.2). Specifically, root diameter at five cm soil depth, and stem number were positively correlated to browsing intensity. Gulliver maximum height and diameter at ground level (for both species) were negatively correlated to browsing intensity.

Gulliver maximum width was significantly different between species (higher in *A. tortilis* than in *A. nigrescens* gullivers; Table 6.2) but did not vary according to browsing intensity. A Pearson correlation matrix between root diameter and percentage of mass compensated after artificial clipping, showed a positive significant regression line for the two *Acacia* species (Fig. 6.2). Finally, *A. tortilis* gullivers showed higher leaf N concentration than gullivers of *A. nigrescens* (Fig. 6.3; t-test, N=10, $p = 0.0001$).

6.4.3 Gullivers demography and distribution

The vegetation survey along the browsing-grazing gradients yielded 16 woody species (*Acacia exuvialis, A. nigrescens, A. tortilis, Albizia harveyi, Balanites maughamii, Combretum hereroense, C. imberbe, Dalbergia melanoxylon, Dichrostachys cinerea,*

Eheritia rigida, Gymnosporia senegalensis, Lonchocarpus capassa, Maerua parvifolia, Ormocarpum trichocarpum, Securinega virosa and *Ximenia caffra*). Mean number of woody species per hectare was higher in the HL site than in the other two sites (Fig. 6.4). Mean (± SE) density of gullivers of *A. nigrescens* was higher in the HL (116 ± 22/ha) and HH sites (96 ± 18/ha) than in the LL site (44 ± 4.5/ha). In contrast, gullivers of *A. tortilis* were absent from all 30 plots in the HL site. Frequencies at which gullivers of *A. nigrescens* were recorded across heavily sites (HH and HL) made me reject the null hypothesis for a random gulliver distribution. Instead, there was evidence for a clumped or clustered distribution of gullivers of *A. nigrescens* across the HH and HL sites ($\sigma^2 > \mu$, see Zar 1999; Fig. 6.5).

When I do not consider the percentage of gullivers that died during the same year (5% in total), I found that gullivers of *A. nigrescens* in the HH site had a marked negative annual growth (Fig. 6.6) as their height was negatively affected by browsers (Wilcoxon matched pair test, $N = 98$, $p = 0.001$). Significant positive growth was measured for *A. nigrescens* in the HL site ($N = 87$, $p = 0.0002$), whereas not significant growth, was apparent for *A. tortilis* in the HH site ($N = 66$, $p = 0.46$).

a)

Acacia nigrescens

b)
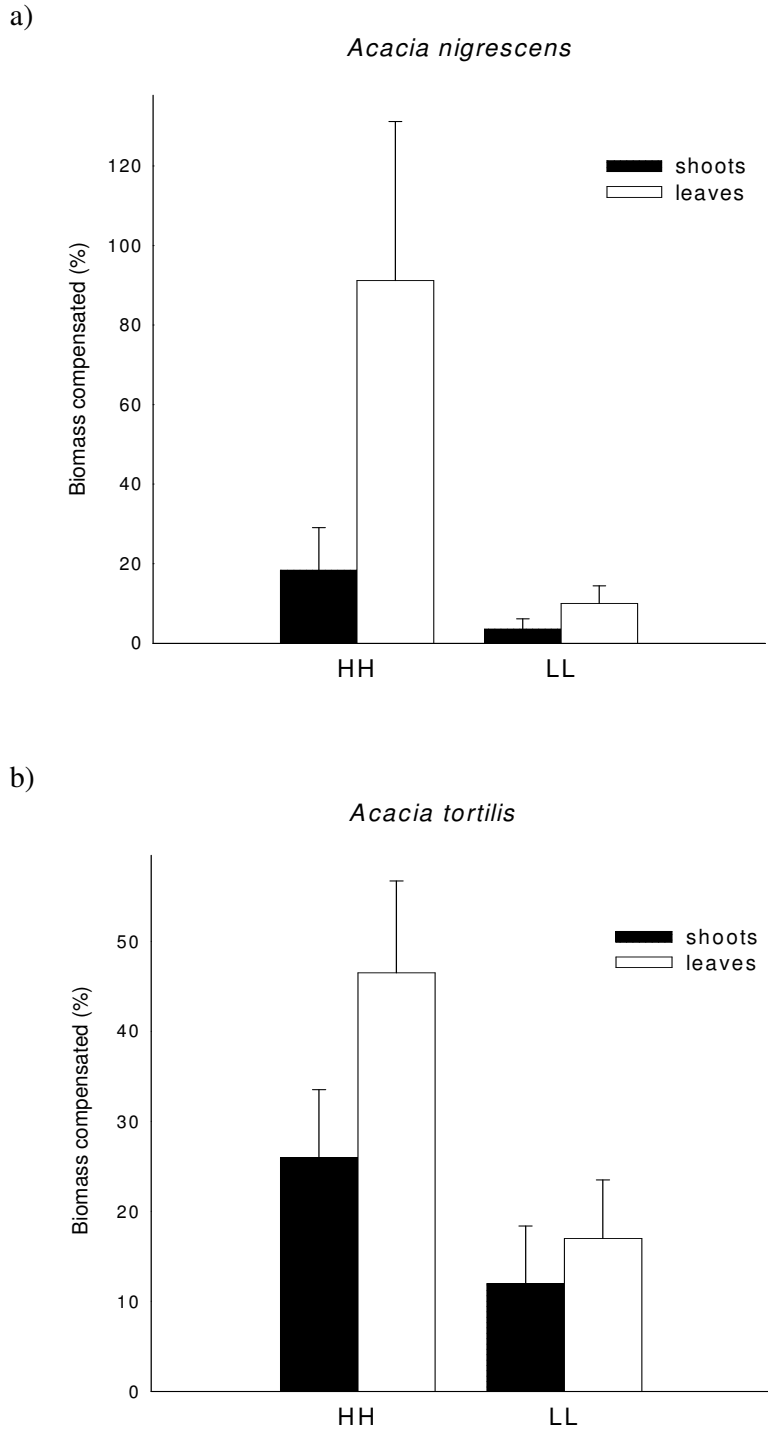
Acacia tortilis

Fig. 6.1. Biomass compensated in leaves and shoots by gullivers of *Acacia nigrescens* (a) and *Acacia tortilis* (b) after 9 months from severe artificial clipping.

Table 6.1. MANCOVA results for the effects of browsing, species identity and browsing-species interactions on five morpho-functional traits. Proportion of browsed shoots was used as covariate. Response variables were max height, max width, stem number, diameter ground level and root diameter 5 cm depth.

|	Wilks value	F	*df*	P
Proportion browsed shoots	0.924	2.299	4.112	0.033
Species	0.811	6.542	4.112	0.01
Browsing	0.786	7.611	4.112	0.0001
Species x browsing	0.992	0.22	4.112	0.927

Table 6.2. Repeated measures analysis of variance (ANOVA) for the effects of browsing and species identity on changes in five plant morpho-functional traits of the two *Acacia* species.

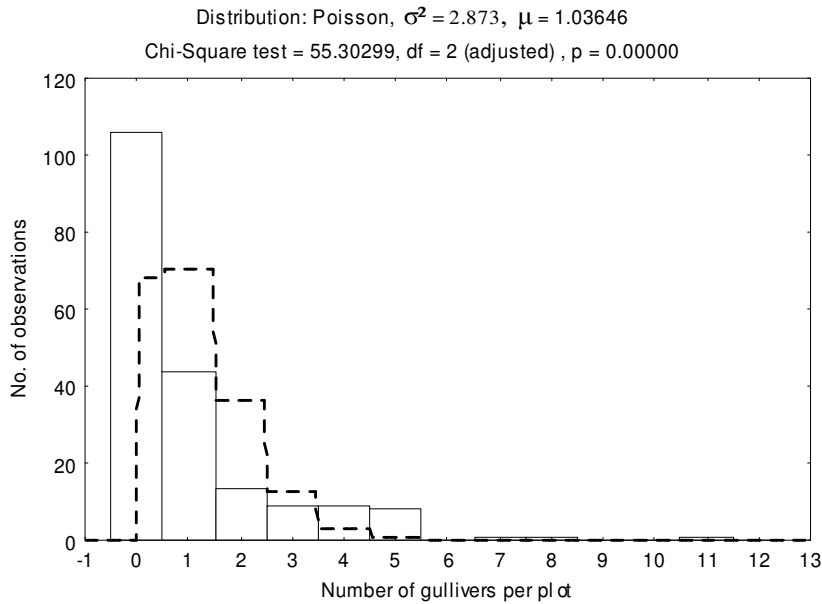|	*A. nigrescens*		*A. tortilis*		Species	Browsing
	HH	LL	HH	LL	P	P
Browsed shoots (%)	41.5 ± 3.7	3.63 ± 0.4	6.66 ± 0.7	2.7 ± 0.3	< 0.001	< 0.001
Max height (mm)	345 ± 3.4	452 ± 5.7	299 ± 4.6	433 ± 5.3	NS	< 0.001
Max width (mm)	479 ± 5.9	462 ± 6.8	734 ± 34.7	813 ± 30.5	< 0.001	NS
Stem Ø ground level (mm)	9.13 ± 0.1	9.3 ± 0.1	6.36 ± 0.7	11.8 ± 0.7	NS	< 0.001
Root Ø at 5 cm depth (mm)	22.1 ± 2.1	11.3 ± 0.4	21.2 ± 2.3	11.1 ± 3.5	NS	< 0.001
Stem number	3.7 ± 0.1	2.1 ± 0.08	4.73 ± 0.5	1.83 ± 0.1	NS	< 0.001

NS = not significant.
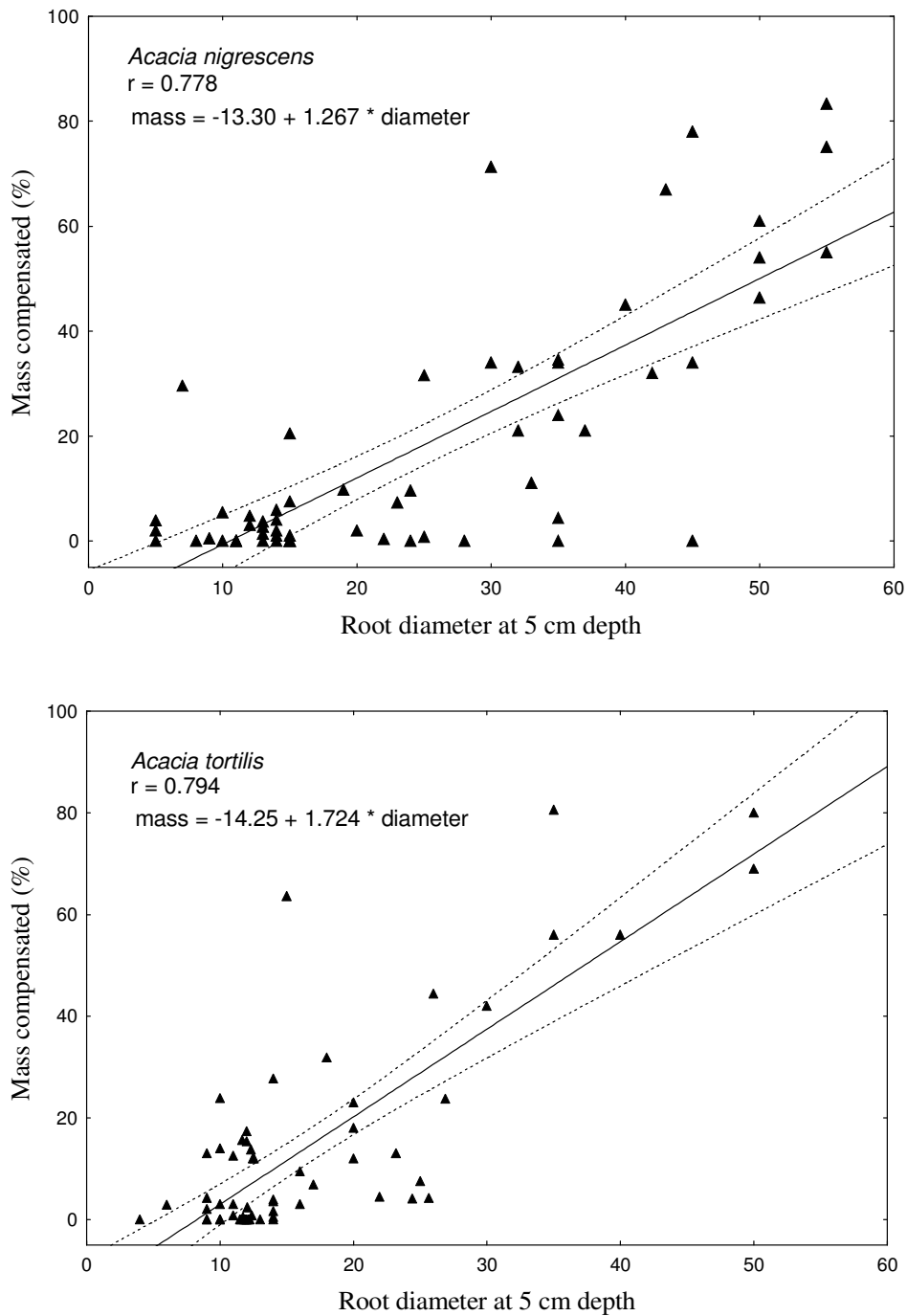
Fig. 6.2. Results from Pearson correlation matrix between root diameter at five cm soil depth and percentage of mass compensated in *A. nigrescens* and *A. tortilis* after 9 months from artificial clipping.
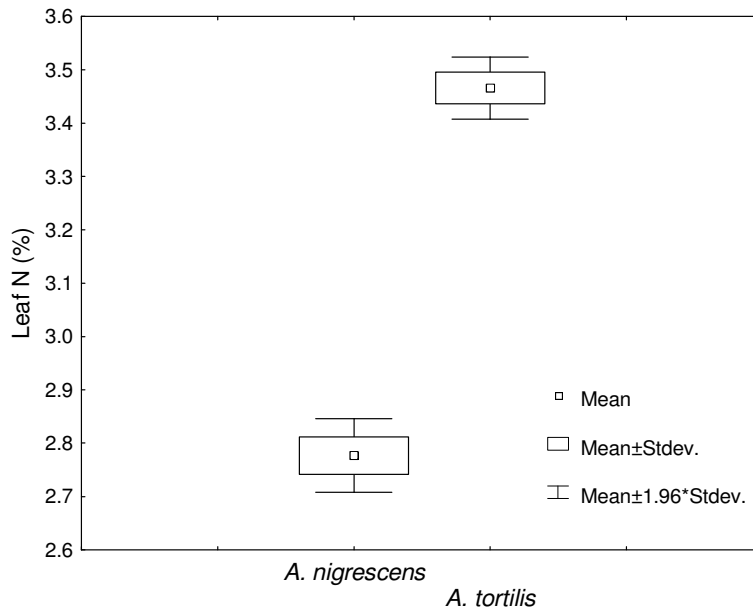
Fig. 6.3. Mean percentage of leaf N concentration from samples of 10 individuals of *A. nigrescens* and *A. tortilis* collected during the main growing season (November).
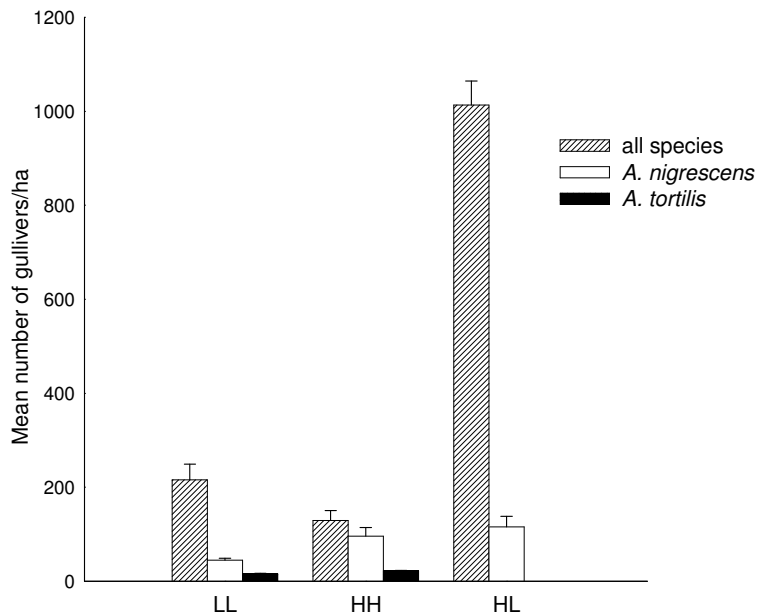
Fig. 6.4. Density of plant individuals < 50 cm in height of woody species recorded among 90 plots established between 3 sites along a browsing-grazing gradient (HH = heavily browsed-heavily grazed; HL = heavily browsed-lightly grazed; LL = lightly browsed-ligthly grazed).

Distribution: Poisson, $\sigma^2 = 2.873$, $\mu = 1.03646$

Chi-Square test = 55.30299, df = 2 (adjusted) , p = 0.00000

Fig. 6.5. The observed frequency of individuals of *A. nigrescens* recorded in each plot across heavily browsed sites (HH and HL sites) and the distribution expected from the Poisson distribution (dashed line).
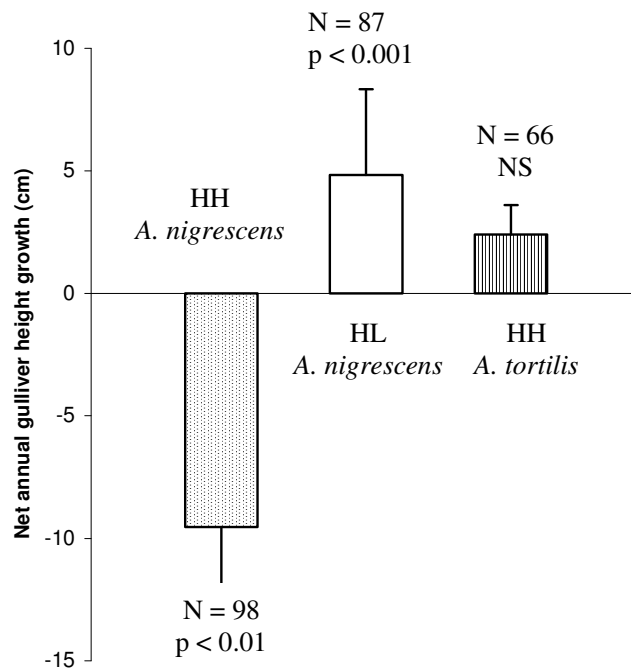
Fig. 6.6. Net changes in annual gulliver height growth (cm) of randomly selected individuals distributed along the browsing-grazing gradient.

6.5 DISCUSSION

6.5.1 Gulliver resprouting abilities

Overall, my results showed high resprouting abilities of juveniles of both *Acacia* species under high browsing pressure (Fig. 6.1 a, b). The ability to compensate mass loss after herbivory damage has been already established for adult *Acacia* trees in African savannas (du Toit et al. 1990; Dangerfield and Modukanele 1996). However, gullivers of *A. nigrescens* recovered 91 % and *A. tortilis* 46 % of the mass loss from leaves after artificial clipping in the heavily browsed site, which suggest high reliance on resprouting mechanisms.

The significant correlation between root diameter at five cm soil depth and percentage of mass compensated (Fig. 6.2) implies the role of roots as important storage organs to support plant resprouting (Bond and Midgley 2003). More importantly, this may suggest that in the absence of fire, browsing influences the mechanisms of biomass allocation to below-ground organs and indirectly increases gulliver chances of survival first, as it would be expected after fire damage (Gignoux et al. 1997; Hoffmann 1998) or drought periods in semi-arid conditions (Otieno et al. 2001; Heilmeier et al. 1997). Interestingly, the few incomplete taproot samples of gullivers of *A. nigrescens,* that were dug out in the HH, HL and LL sites showed that total root mass in heavily browsed gullivers was at least three times higher than in lightly browsed gullivers (Fornara, *unpublished data*).

It is not clear yet, however, how carbohydrates and nutrients are used by gullivers to enhance resprouting abilities and how their storage is yearly replenished to support plant growth under constant browsing damage. For example, recent findings on lignotubers of two Mediterranean shrubs and temperate tree seedlings show that carbohydrate reserves in roots are depleted after multiple artificial defoliations (Canadell and Lopez-Soria 1998; Canham et al. 1999). It might be that gullivers responses to pruning under natural conditions are mediated by linkages between above- and below-ground processes. Leaf litter input in heavily browsed sites is generally low and mineralization rates extremely variable in semi-arid African savannas. Therefore, nutrients availability to support resprouting may be enhanced by pruning, which triggers and maintains a positive feedback loop between browsers and their food resource. It is plausible that tree pruning affects below-ground processes through indirect effects on the root system, such as stimulating root exudation which in turn enhances C inputs in the

soil with overall positive effects on mineralization and nutrient uptake rates (Bardgett et al. 1998; Ayres et al. 2004; Bardgett and Wardle 2003).

However, mass compensation only occurred in few weeks between October and November just before the onset of the rainy season. This might be due to remobilization of stored reserves in below-ground organs (see Cherbuy et al. 2001), allowing plants to be partly independent of soil nutrients at critical phenological stages (Chapin et al. 1990). Nutrient remobilization is common in woody plants of semi-arid African savannas (see Tolsma et al. 1987) since effective soil nutrient mineralization rates mainly occur after rainfall events, and are otherwise very low throughout the rest of the year (Scholes et al. 2003).

Gullivers of *A. tortilis* showed higher concentrations of leaf nitrogen than gullivers of *A. nigrescens* (Fig. 6.3). This suggests a more efficient use of N and/or likely higher photosynthetic and growth rates in early life-history stages (see Field and Mooney 1986; Reich et al. 1995), which may represent an advantage under herbivory damage. In fact, all gullivers of *A. tortilis* were able to resprout in the HH site versus 70 % of those of *A. nigrescens*, with important consequences for plant community composition in the long-term period. Interestingly, the number of resprouting gullivers of both species was higher in the HH site than in the LL site despite the higher levels of browsing.

6.5.2 Morpho-functional traits

Changes in plant traits were related to browsing intensity rather than gulliver species (Table 6.2). Overall, *Acacia* gullivers under high browsing pressure, (1) were shorter, (2) had higher number of stems, (3) smaller diameter at ground level, and (4) greater diameter at five cm depth than those situated at the LL site. However, although net annual height growth of gullivers of *A. nigrescens* was negatively affected in the HH site, in contrast variation in height growth was positive in the HL site (Fig. 6.6). These results draw attention on the interactive effects of browsing-grazing-fire regimes on the structure and dynamics of woodlands in semi-arid eutrophic savannas. Firstly, it seems that long-term selective browsing in heavily grazed sites in the absence of fire (i.e. sites relative close to permanent water sources) enhances survival of gulliver species with high resprouting abilities. Secondly, browsing limits gulliver recruitment to mature size classes and could in turn negatively affects woodland regeneration (Belsky 1984; Augustine and McNaughton 2004). Therefore, browsers may play the same role as fire strongly limiting

gulliver recruitment in heavily grazed sites where fire occurrence is low (i.e. low fuel load).

Interspecific differences in the set of morpho-functional traits adopted by gulliver species may influence their response to browsing damage and affect plant community structure and composition. Indeed, browsing effects were higher on *A. nigrescens* than on *A. tortilis* (Table 6.2) partly due to the efficient physical armament of the latter and might explain the increased abundance of *A. tortilis* gullivers throughout the HH site. I stress the negative impact of common browsers such as impala (*Aepyceros melampus*) on changes in gulliver net annual growth in the HH site, probably due to the high dependence of impala on water sources (Redfern et al. 2003). I found evidence that in sites where fire had not occurred for 13 years and grazing intensity was low, the overall negative effects of browsing on gulliver annual height growth were attenuated (Fig. 6.6). This suggests that under low grazing pressure and in the absence of fire, the grass layer protects gullivers from being over-utilized by large herbivores (see below), and may offer the opportunity to some individuals to grow above the topkill height set by fire (Bond and van Wilgen 1996).

However, architectural differences may also play a role in gulliver competitive abilities with grasses. Although gulliver maximum width was not related to browsing intensity, changes in canopy width were significant between the two species, as gullivers of *A. tortilis* had a wider canopy than *A. nigrescens.* Interestingly, gullivers of *A. tortilis* were completely absent from the HL site, which may suggest grasses to inhibit their establishment (see Bond et al. 2001).

6.5.3 Gulliver distribution and abundance

The highest plant density was in the HL site (Fig. 6.4) where medium grass height was ~ 40 cm suggesting facilitation mechanisms of grasses playing a role in enhancing gulliver establishment (Brown and Archer 1989; Davis et al. 1998). This might depend on numerous low-competition microsites for woody seedlings within the lightly grazed grassland matrix (Jurena and Archer 2003), and the increased protection by grasses against browsers in the absence of fire. In general, gullivers of both *Acacia* species were more abundant in heavily browsed than lightly browsed sites. Moreover, the distribution frequencies of *A. nigrescens* gullivers were not those predicted by a random Poisson distribution in the HH and HL sites (Fig. 6.5). Such results support the hypothesis of a clumped or clustered distribution of gullivers in heavily browsed sites associated to a high

browser density. Indeed, in heavily browsed sites I often observed clumps of gullivers surrounded by areas where no gullivers were found. The higher abundance of gullivers in heavily browsed sites, associated to a general clumped distribution might be due to a positive effect on mechanisms of seed germination after seeds being ingested by large mammalian herbivores (Miller and Coe 1993; Miller 1996; Rohner and Ward 1999). Nevertheless, the high density of large mammalian herbivores in the HH sites may enhance seedling establishment (from seed to the seedling stage), indirectly decreasing the impact of other small predators (i.e. rodents, insects) as has been shown by exclosure experiments in an east African savanna (Shaw et al. 2002; Goheen et al. 2004). However, I suggest other environmental factors critical to seedling survival (e.g. available moisture due to frequency and intensity of rainfall events) may interact with herbivores to determine clumpiness in *Acacia* gulliver distribution.

6.6 CONCLUSION

I mentioned in the Introduction paragraph that the set of morpho-functional traits that enhance gullivers survival may represent a direct consequence of the 'storage effect'. Indeed, according to Higgins et al. (2000b), the "storage effect" may successfully be used as model to explain the coexistence of strongly competing organisms when two conditions are met: (1) organisms are able to persist *in situ* under intense disturbance events, and (2) recruitment events are rare and episodic.

Here I presented evidence that gullivers of the two *Acacia* species showed high mass compensatory growth abilities and a set of morpho-functional traits adapted to browsing damage (i.e. mechanisms of biomass allocation to below-ground organs). These responses likely enhance gulliver's resilience and persistence when recruitment events are highly variable such as in semi-arid African savannas (Bond and van Wilgen 1996; Wilson and Witkowski 1998; Higgins et al. 2000a; Scholes et al. 2003).

It appears, therefore, that the gulliver bank, together with long-lived adult trees, play a critical role in maintaining population viability under frequent and intense disturbance regimes set by fire and browsing. To what extent gulliver species may persist and functioning as storage of potential reproductive is not clear yet, it is likely, however, that gulliver life-history traits strongly influence vegetation structure and composition in semi-arid eutrophic African savannas.

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