UNGULATE BROWSING AS AN ECOSYSTEM PROCESS: BROWSER-PLANT-SOIL INTERACTIONS IN A SOUTHERN AFRICAN SAVANNA

by

Dario Arturo Fornara

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SUMMARY

Ungulate browsing and its ecological effects at plant, population, community, and ecosystem levels were addressed in a eutrophic southern African savanna. This was to test predictions of prevailing hypotheses, which are based on research in boreal and temperate forests. Changes in plant morpho-functional traits and population structure of a staple palatable species, *Acacia nigrescens* Miller were addressed over a two-year survey among vegetation stands with very different histories of attack from herbivores. Moreover browser-induced effects on functional composition of a woody plant community were addressed along a strong browsing gradient. Nutrient cycling was investigated through measurements of leaf litter decomposition rates, as well as soil and leaf chemistry analyses. Finally, a modelling approach was used to make predictions on plant productivity and changes in soil nutrient availability under ungulate browsing according to opposite plant defensive traits (i.e. tolerance *vs* resistance).

I found evidence that long-term selective browsing may negatively affect soil nutrient pool, at least in the vicinity of palatable woody plants. I proposed this might be due to the drastic reduction of leaf-twig litter mass returned to the soil, which likely decreased decomposer activity and negatively affected N mineralization rates. Hence, the processes responsible for a loss of nutrients in the soil were different from those proposed for northern hemisphere scenarios, which were instead due to decreased litter quality. However, I found evidence of high plant resilience in heavily browsed sites where *Acacia* stands shown (1) higher leaf N during the main growing season, (2) higher N release from leaf litter, (3) high concentrations of nitrate (NO_3) and ammonium (NH_4), and (4) similar, or even faster, litter decomposition rates than in lightly browsed sites. Firstly, this suggests that tree pruning triggers and maintains a fast nutrient cycling within the plant-browser system. The accelerating effect is supported by high mass compensatory growth abilities from highly palatable, fast-growing *Acacia* trees that produce highly decomposable litter. Secondly, browsing may have a long-term decelerating effect on N cycling through quantitative changes in litter production rather than through qualitative changes in litter chemistry. Further studies should better address processes related to soil nutrient cycling to confirm such hypothesis. I discuss how the interactive effects of browsing-grazing-soil fertility may influence nutrient cycling trough different ecological processes.

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CONTENTS

CHAPTER 1

Introduction

1.1 BACKGROUND AND JUSTIFICATION

The African savanna biome includes more large mammalian herbivores (> 5 Kg) than any other continent (McNaughton and Georgiadis 1986; Owen-Smith and Cumming 1993), as would be expected from the suitable combination of precipitation and soil fertility (see du Toit 1995; Olff et al. 2002). The exceptional species richness in African savannas likely depends on the high degree of specialization of ungulate species to particular habitats and the highly variable savanna ecosystem over temporal and spatial scales (du Toit and Cumming 1999; du Toit 2003).

It has been proved that large mammalian herbivores influence terrestrial ecosystem processes both directly by consuming plant material and indirectly by altering litter quality and nutrient cycling (McNaughton et al. 1988; Hobbs 1996). In African savannas the literature on mammalian herbivory in relation to the composition and structure of vegetation communities has been dominated by studies on the grazing guild (Sinclair and Norton-Griffiths 1979; Sinclair and Arcese 1995). Former studies have shown that grazing induces changes in reallocation of nutrients within individual plants and indirectly stimulates soil mineralization processes (McNaughton 1979, 1983). Moreover grazing increases root exudation in grassland plants, which in turn stimulates microbial biomass and activity in the rhizosphere (Hamilton and Frank 2001). Hence, grazing may enhance net primary productivity at the community level and create a positive feedback loop within the grazer-plant-soil system that improves grazing efficiency at moderate herbivore densities (McNaughton et al. 1988).

The only studies of browsing as an ecosystem process have been conducted in boreal forests, where the evidence is that the long-term consequences of intensive browsing are opposite to those for grazers (Naiman et al. 1986; Pastor et al. 1988; Kielland and Bryant 1998). The difference appears to be that selective browsing on palatable deciduous woody plants provides a competitive advantage to chemically defended slow-growing evergreens, which produce leaf litter that decomposes slowly (Pastor et al. 1988). Consequently, with slow nutrient uptake by slow-growing plants, combined with leaching and reduced microbial activity, there could be a net loss of nutrients down the soil profile (Bryant and Chapin 1986).

So far, I'm not aware of previous studies that have addressed ungulate browsing as an ecosystem process in eutrophic southern African savannas, where the set of environmental key drivers are different from those of boreal and temperate forest ecosystems (see Scholes et al. 2003). Moreover, it is important to uncouple the effects of browsing from those of grazing on aspects related to the ecosystem nutrient cycling. Finally, plant-animal interactions and their effects on ecosystem properties assume particular importance in protected areas where management decisions have to be taken according to vegetation status and animal distribution and density. Naiman et al. (2003), highlight the exceptional habitat diversity in the Kruger National Park, South Africa, due to the interactions between soil characteristics, rainfall regime and animal activities. They also suggest that, although soils determine the composition of plant communities, individual plants may influence soil characteristics at the local scale. I therefore addressed the responses of savanna woody plants to ungulate browsing at different hierarchical levels from (1) plant to, (2) population, (3) community, and (4) ecosystem level.

1.2 UNGULATE BROWSING AND *ACACIA* TREE RESPONSES

Plants may reduce herbivore damage through resistance, tolerance and/or changes in phenological traits (see Agrawal 2000). Specifically, (1) plant resistance traits (i.e. thorns) reduce herbivore performance or damage, (2) tolerance traits (i.e. mass compensatory growth ability) reduce negative effects when herbivore damage has already occurred, and (3) phenological "escape" reduces plant availability when herbivores are most active. Plant responses to herbivory likely depend on 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.

Indications of compensatory growth abilities (tolerant trait) after herbivore damage have been found in woody plant species under ungulate browsing in different ecosystems (Bergström and Danell 1987; du Toit et al. 1990; Dangerfield and Modukanele 1996; Bergström et al. 2000; Gadd et al. 2001). Resistance traits such as spine and thorns are quite common in woody species of arid eutrophic savannas (Huntley 1982) and represent an efficient physical protection against tree pruning (Cooper and Owen-Smith 1986; Young 1987). In general, defensive traits vary across plant communities depending on the interactions between different environmental factors. A useful approach is to compare populations or stands of vegetation with very different histories of attack from herbivores (Agrawal 1998, 2000).

In Chapter 5, I examine defensive traits of two stands of *A. nigrescens* Miller in a eutrophic southern African savanna under a natural regime of ungulate browsing. *Acacia nigrescens* Miller, is a staple food resource for ungulate browsers and is very common throughout all my study area (see Chapter 2). The leaves are characteristics of this species and quite different from other common *Acacia* species, being double pinnately compound and having 4-6 leaflets per leaf which are comparatively large with oblique (lopsided) bases (Fig. 1.1a). Trees bear prickles and are usually leafless for two-three months during the dry season (June to September). Mass compensation after artificial clipping, tree branching, prickle spacing and size, annual shoot growth, leaf N, specific leaf area (SLA), and seed production, were measured over a two-year survey (see Chapter 5) among stands of *Acacia* trees that have undergone very different levels of browsing presumably for centuries (see du Toit 2003; Naiman et al. 2003; see Fig. 1.1 and Fig. 1.2).

Similarly, I tested compensatory growth abilities of 120 suppressed juveniles forms of two common woody species, *Acacia nigrescens* Miller and *Acacia tortilis* (Forsk.), Hayne, after severe artificial clipping (see Chapter 6). I also measured five gulliver morpho-functional traits including net annual height growth and plant density variation throughout a study area where fire had been absent for 13 years.

1.3 BROWSING EFFECTS ON PLANT COMMUNITY COMPOSITION

Impacts of ungulate browsing on vegetation structure and dynamics have been recognized as significant in boreal forests (Kielland and Bryant 1998; Horsley et al. 2003) where historically, much emphasis had been given to abiotic factors as main responsible for vegetation structure and dynamics (see Bryant and Chapin 1986). Indeed selective browsing negatively affects species with nutrient rich tissues (Ritchie et al. 1998; Peinetti et al. 2001), and contributes to a shift in dominance towards unpalatable evergreen species within the vegetation community (Pastor et al. 1988; Kielland and Bryant 1998; Wardle et al. 2001; Horsley et al. 2003). In African savannas browsing induced effects have been described as limiting woodland regeneration (Belsky 1984), affecting vegetation structure (Pellew 1983) or influencing species composition and distribution (Bond and Loffell 2003).

However, there is a lack of information on how functional type composition might change along a strong browsing gradient in an extensive wildlife area where mammalian browsers are free to move according to resource availability. Vegetation responses under permanent browsing pressure are sometimes contradictory and do not always lead to a clear dominance of unpalatable species especially when trees and shrubs rely on compensatory growth abilities (Augustine and McNaughton 1998). Therefore we may expect different responses from woody plants in a eutrophic savanna where soil N concentration is relatively high due to the basaltic igneous substrate (Scholes 1990). Browsing impact on vegetation communities assumes particular importance in protected areas where management decisions have to be taken according to vegetation status, and animal distribution and density.

For example, in the Kruger National Park, one of the largest conservation areas in Africa, trends in woody vegetation structure and composition have been historically explained by the reciprocal effects of fire and elephants (see Eckhardt et al. 2000; Whyte et al. 2003), but the few published studies on the effects of browsing on woody plant ecology have been restricted to the central region of the Park (du Toit et al. 1990; du Toit 2003; Naiman et al. 2003). Hence, in Chapter 3 I test the following prediction derived from browser-woody plant interactions that have been elucidated in boreal and temperate forests:

- Ungulate browsing influences vegetation traits and species composition within woody plant communities through selective damage to palatable woody plants, resulting in increases in number of spinescent, evergreen and unpalatable species at increasing levels of browsing.

1.4 PLANT-BROWSER-SOIL INTERACTIONS: NUTRIENT CYCLING AT THE ECOSYSTEM LEVEL

To test predictions based on hypotheses proposed for boreal and temperate forest ecosystems I examine (Chapter 4) aspects of aboveground nutrient cycling between two stands of *Acacia nigrescens* with very different histories of attack from. herbivores. I specifically measured (1) leaf litter decomposition rates of five common savanna woody species, (2) leaf chemistry (mainly N) of *A. nigrescens* in wet and dry seasons, (3) soil chemistry (total N, NH_4, NO_3, P, Ca, K, Mg, Na, cation exchange capacity, pH) and (4) litter biomass and composition distributed across browsing and grazing gradients. If long-term selective browsing has a negative effect on ecosystem properties and nutrient cycling as shown in boreal forests we might expect that: (1) leaf litter among heavily browsed sites has lower decomposition rates than litter placed in lightly browsed sites, (2) soil nutrient pool in heavily browsed sites is more depleted than in lightly browsed sites.

Nonetheless, the 'top-down' effects, exerted by large mammalian herbivores on ecosystem properties (Pastor and Naiman 1992; Kielland et al. 1997; Scholes et al. 2003; Bardgett and Wardle 2003) are likely mediated by "bottom up" effects exerted by soils and climate since large herbivores use their landscapes according to the spatio-temporal distribution of food resources. For example, in N limited boreal forest ecosystems, browsers are responsible to decrease number of palatable species with N rich tissues (see above) contributing to increase the number of unpalatable species over a long-term scale (McInnes et al. 1992).

However, the overall effects of browsing on ecosystem properties are likely more complex and driven by the interactions of different environmental factors. For example, although soils determine the composition of plant communities, individual plants may influence soil characteristics and nutrient concentrations at the local scale (Naiman et al. 2003). Indeed, Persson et al. (2005) found that in a N-limited Swedish boreal forest, selective browsing on medium preferred woody species, negatively affected ecosystem productivity through a reduction of litter quantity returned to the soil, rather than changes in plant community composition and litter chemical quality.

Alternatively, relatively fast-growing, highly-palatable woody plants of semi-arid eutrophic savannas, according to the resource economics of chemical and structural defences along a nitrogen gradient (Craine et al. 2003) may have evolved different defence strategies (e.g. increased physical defence) to cope with browsing damage. This in turn influences plant responses to tree pruning as, for example, enhancing compensatory growth abilities in savanna tree and shrub species (Augustine and McNaughton 1998), which therefore may have important consequences on nutrient cycling and ecosystem functioning.

Finally, I propose a simulation model that makes predictions on the effects of ungulate browsing on changes in plant productivity and soil nutrient availability according to varying plant defensive traits (see Chapter 7). The modelling results are confronted with empirical data and predictions are made in terms of nutrient cycling and functional type composition within a semi-arid eutrophic savanna.

a)

b)

Fig. 1.1. Unbrowsed shoot of *Acacia nigrescens* showing pairs of prickles and the double pinnately compound leaves with 4-6 leaflets each (a). Heavily browsed branches of *A. nigrescens,* 60% to 80% of the shoots have been browsed in the current growing season.

Fig. 1.2. Examples of heavily browsed *A. nigrescens* trees that show different canopy shapes due to the impact of different browsers species. Note the clear height limit for the giraffe's reach in the second tree (b).

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CHAPTER 2

Study area

2.1 KRUGER NATIONAL PARK AT A GLANCE

The present research has been carried out in a central region of the Kruger National Park, South Africa (Fig. 2.1). The Park is situated in the *lowveld* of north-eastern South Africa covering an area of about 2 million ha. It stretches 350 km from north to south and has an average width of 60 km. The park is bordered on the west mainly by high-density communal areas and by private and provincial game reserves. Geologically, Kruger is split down its long axis with the western parts characterized by granite substrate and the more eastern parts underlain by basalt (Fig. 2.2; see Mabunda et al. 2003). The park straddles two climatic transitional zones: the tropical and subtropical north and the temperate south. Summer temperatures regularly exceed 35°C and winter temperatures are moderate. Rain falls mostly from October to March with a dry season that occurs mainly between April and September. The long-term average annual rainfall for the whole park is 530 mm. Rainfall cycles of 15-20 years are recognizable. Kruger is drained by five perennial rivers that flow from west to east through the park and into Mozambique and a large number of seasonal rivers of varying sizes. The vegetation in all but the wettest part of Kruger is classified as subarid to arid wooded savanna (see Mabunda et al. 2003). Vegetation structure varies from open plains with low shrubs and a sparse tree canopy to close gallery forest along certain rivers. The savannas of Kruger are split between the two main ecological types, broad-leaved savannas occupy approximately 75% of Kruger, 50% of which are mopane (*Colophospermum mopane*) and 25% are made up by fine-leaved savanna (Venter et al. 2003). The response of the vegetation and animal population to the template presented by the geology (which is reflected by the soils), and changes caused by the ecosystem drivers such as rainfall and fire, have led to a complex patch mosaic. The abiotic template heterogeneity at different spatial and temporal scales supports an impressive array of species. So far, the following species have been identified: 147 mammals, 505 birds, 119 reptiles, 49 fishes, 34 amphibians, 1,980 plants and many thousands of invertebrates.

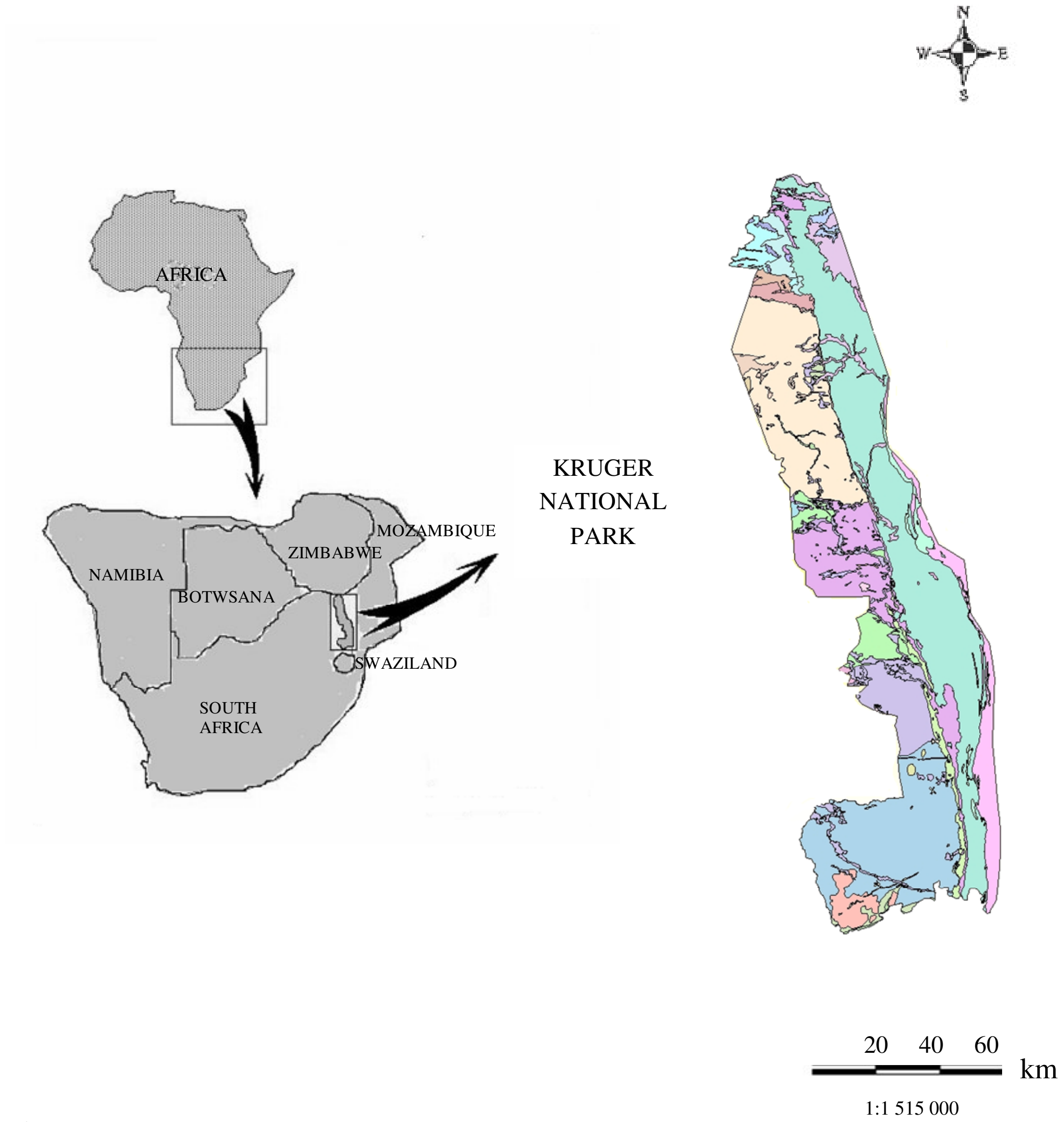
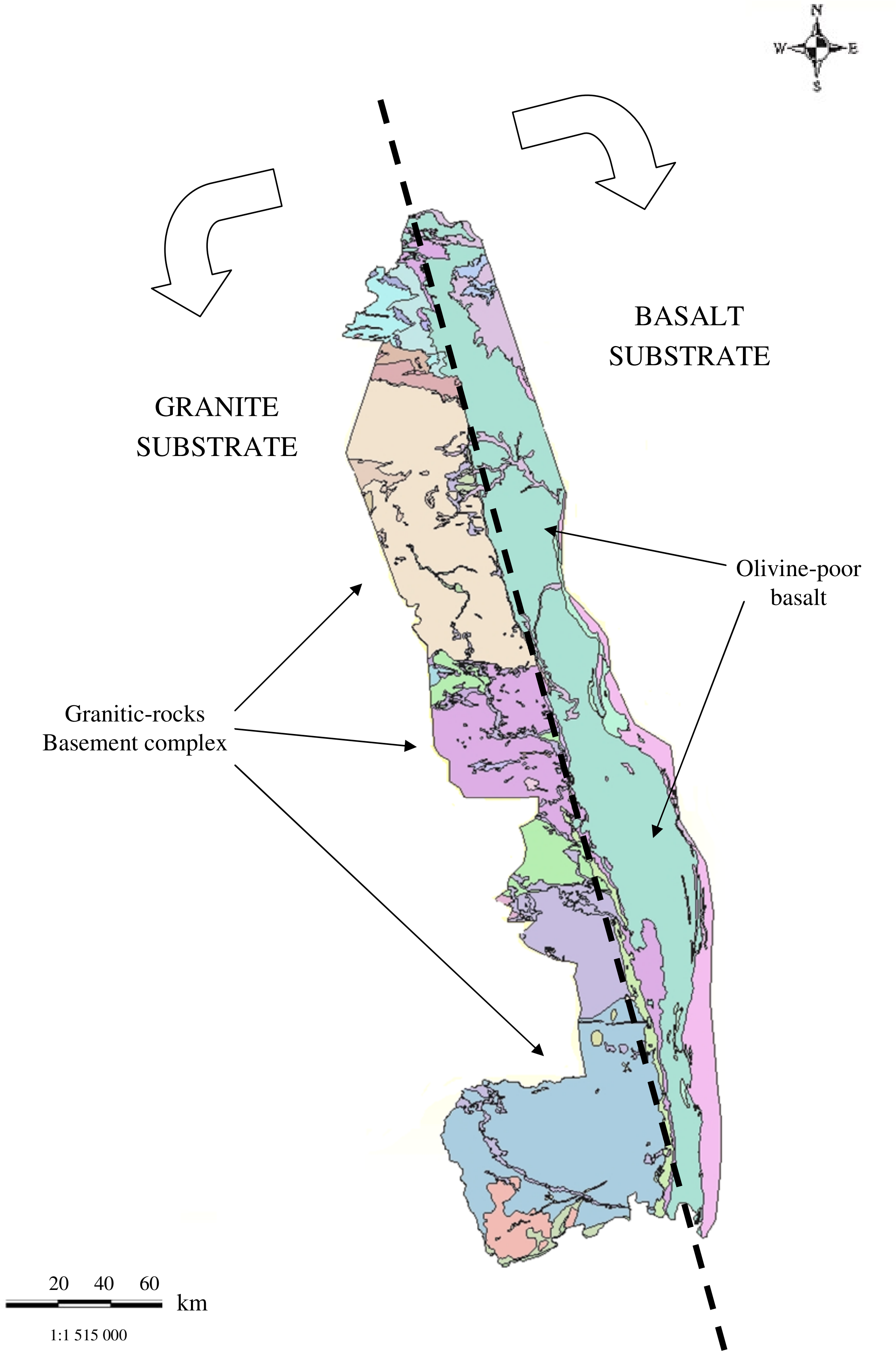


Fig. 2.1. Kruger National Park in relation to Africa.



2.2. Main geological features of the Kruger National Park.

2.2. STUDY AREA: THE TSHOKWANE SECTION OF THE KRUGER PARK

The study was conducted in a central-eastern region of the Kruger National Park (Fig. 2.3), based at the Tshokwane ranger station (24° 47´ S, 31° 52´ E). The experiments were carried out in the Satara land system on basaltic soil, which consists mainly of fine-leaved tree savanna or bushveld, dominated by *Acacia nigrescens*, *Sclerocarya birrea* and *Dichrostachys cinerea* (Fig. 2.3; Venter et al. 2003). The soil is general high in clay and nutrients and dominated by *Acacia* trees that enhance nitrogen availability and therefore attract herbivores. Along the basalt catena there is an increase in pH and most of the exchangeable cations, in a downslope direction (see Venter et al. 2003). Rainfall regime averages 560 mm per annum, with 80% of the precipitation concentrated in the wet season from October to March. Distance from surface water is a powerful determinant of the distribution of herbivore biomass and density, which determines strong browsing-grazing gradients departing from permanent and/or seasonally waterholes (see Redfern et al. 2003).

2.3 SITE DESCRIPTION AND RESEARCH ASSUMPTIONS

Large concentrations of game occur in the Satara land system (Owen-Smith and Ogutu 2003). The ungulate browsing guild is mainly composed by giraffe (*Giraffa camelopardis*), kudu (*Tragelaphus strepsiceros*), steenbok (*Raphicerus campestris*), and the mixed feeders impala (*Aepyceros melampus*), and elephant (*Loxodonta africana*). Former studies on the Kruger browsing guild started in the 1970s (Owen-Smith 1979; du Toit and Owen-Smith 1989; du Toit et al. 1990; Owen-Smith 1990) and monitoring data from Kruger indicate that large mammalian density has been consistently high in the Tshokwane section of the Park. Hence we can assume the woody vegetation has been experiencing consistently high browsing pressure for decades and presumably for centuries (see du Toit 2003). The giraffe density is estimated at 2.52 animals per km² (du Toit 1988), and the kudu density at 2.46 animals per Km² (Owen-Smith 1990), impala are very common and in general elephants and large herbivore densities high in this central part of the Kruger on basalt substrate. Soil nutrient pool was tested in previous studies (du Toit et al. 1990; du Toit 2003), which indicated relatively high concentration of N, P and cations. Field experiments on individual trees were performed on *Acacia nigrescens* trees, which represent the staple food source for large mammalian browsers. The leaves are double pinnately compound and differ from those of many *Acacia* species since are not fine-leaved but have 4 – 6 leaflets relatively large with oblique (lopsided) bases.

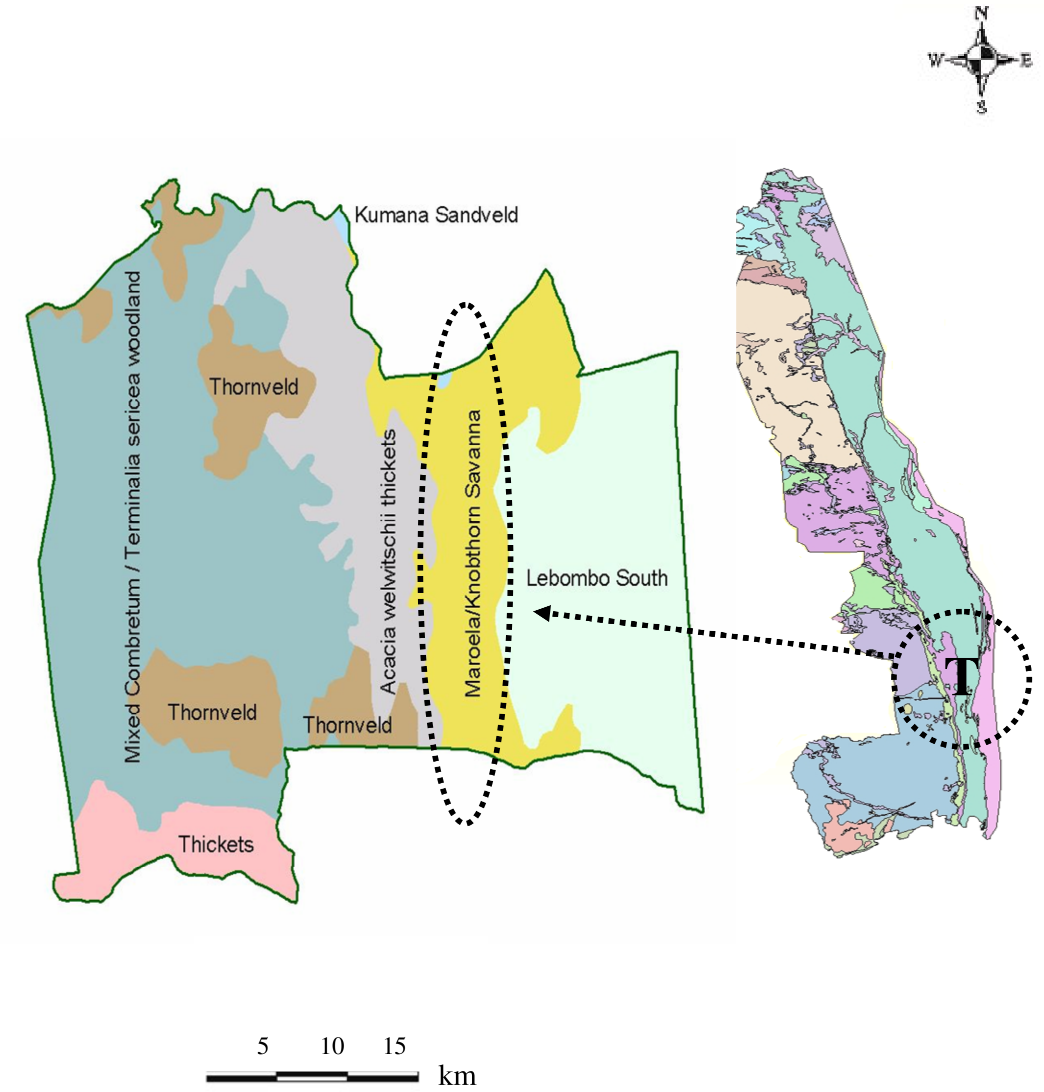


Fig. 2.3. Vegetation types of the Tshokwane section (T) of the Kruger National Park Experiments were carried out in the Maroela (*Sclerocarya birrea*)-Knobthorn (*Acacia nigrescens*) savanna.

Branches bring paired of prickles whose tips are oriented from the canopy surface in, offering resistance to pruning and leaf stripping by ungulate browsers. The study sites were chosen to minimize environmental variation across them. First, all study sites were on basalt soil at the top of the catenary drainage sequence. Second, the entire study area covered ~ 230 km² and so rainfall differences were assumed to be negligible. Third, fire events hadn't been recorded for 13 years in all the study sites. Finally, I assumed the impact of ungulate herbivores on vegetation has been stable for decades or presumably for centuries (du Toit 2003). I therefore addressed browsing effects on structure and composition of a woody plant community exposed to an intact indigenous browsing guild in an ecosystem in which large herbivores move freely in response to seasonal variation in resource availability.

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CHAPTER 3

Responses of a woody plant community to long-term browsing by indigenous ungulates in a southern African savanna

Abstract

Ungulate browsing and vegetation responses were investigated in a eutrophic southern African savanna to test predictions of existing hypotheses, which were based on studies in boreal and temperate forests. I focused on (1) browsing impact on population structure of a palatable woody species, *Acacia nigrescens* Miller, and (2) browser-induced effects on functional composition of a savanna woody plant community (i.e. ratio palatable:unpalatable species). As predicted, the *A. nigrescens* population was strongly affected by browsing with striking physiognomic differences between heavily and lightly browsed individuals, as well as variation in tree density and representation of different height classes along the browsing gradient. However, contrary to predictions, high ungulate browsing was not associated with any changes in the mix of unpalatable, evergreen, or spinescent plants within the vegetation community surveyed. Moreover, the density of palatable species was comparatively high in vegetation sites that have experienced high browsing pressure for several decades. I propose that woody plants in eutrophic African savannas are adapted for impacts of mammalian herbivores (and fire) through: (1) physical rather than chemical defences against browsing, (2) plant compensatory growth after browsing damage, and (3) resprouting abilities of saplings in their critical height class. I discuss these properties of woody plant resilience under ungulate browsing in comparison with studies in boreal and temperate forests.

KEY WORDS: African savanna, compensatory growth, evergreen, grazing, palatable, plant-herbivore interactions, spines

3.1 INTRODUCTION

Large mammalian browsers indirectly determine changes in structure and dynamics of vegetation communities across terrestrial ecosystems (Jachmann and Croes 1991; McInnes et al. 1992; Belsky 1984; Ammer 1996; Harmer 2001; Augustine and McNaughton 1998). Impacts of ungulate browsing on patterns of vegetation succession have been recognized as significant in boreal forests (Kielland and Bryant 1998; Horsley et al. 2003) where historically, much emphasis was given to abiotic factors as main responsible for vegetation structure and dynamics (see Bryant and Chapin 1986). Nevertheless, an increasing body of literature has been focusing on forest-ungulate interactions to improve management and conservation solutions (see Weisberg and Bugmann 2003). At high latitudes selective browsing on palatable trees and shrubs (Brookshire et al. 2002; Rao et al. 2003; Motta 2003; Heikkilä and Härkönen 1996), negatively affected species with nutrient rich tissues (Ritchie et al. 1998; Peinetti et al. 2001), and contributed to a shift in dominance towards unpalatable species within the vegetation community (Wardle et al. 2001; Horsley et al. 2003). Moreover, long-term browsing in boreal forests may negatively affect nutrient cycling and hence speed up the vegetation succession to later stages dominated by evergreens (Pastor et al. 1988; Pastor and Naiman 1992; Kielland and Bryant 1998).

The extent to which large herbivores might affect vegetation physiognomy and species composition is expected to increase in eastern and southern African savannas where large herbivore diversity represents a distinctive ecosystem feature (Huntley 1982; du Toit and Cumming 1999). Biomass densities of mammalian herbivores in African savannas are at the highest levels yet quantified in terrestrial ecosystems (McNaughton and Georgiadis 1986), as would be expected from the suitable combination of precipitation and soil fertility (see du Toit 1995; Olff et al. 2002). Moreover, the feeding constraints among herbivores resulting from body size/dietary tolerance (du Toit and Owen-Smith 1989) and the assemblages of herbivores in different "functional groups" or guilds (Prins and Douglas-Hamilton 1990; Fritz et al. 2002) interact with environmental factors affecting structure and dynamics of African savannas. In fact, woody species responses to ungulate browsing are strictly related to soil resource availability (Bryant et al. 1989), and consequently plants might evolve morpho-functional traits (i.e. physical and/or chemical defences) that may have important consequences on plant community composition and function.

In African savannas browsing induced effects have been described as limiting woodland regeneration (Belsky 1984), affecting vegetation structure (Pellew 1983) or influencing species composition and distribution (Bond and Loffell 2003). However, vegetation responses under permanent browsing pressure are sometimes contradictory and do not always lead to a clear dominance of unpalatable species (Jachmann and Bell 1985; Tilghman 1989), due probably to the compensatory growth abilities of browsed trees (du Toit et al. 1990; Augustine and McNaughton 1998; Oba and Post 1999). Indeed, when Styles and Skinner (2000) investigated the impact of elephants (*Loxodonta africana*) and elands (*Taurotragus oryx*) on mono-specific mopane (*Colophospermum mopane*) communities on poor soils in south-eastern Botswana, they found browsing to be neither detrimental to net shoot growth nor a constraint on seedling recruitment.

Browsing impact on vegetation communities assumes particular importance in protected areas where management decisions have to be taken according to vegetation status and animal distribution and density. For example, in the Kruger National Park, one of the largest conservation areas in Africa, trends in woody vegetation structure and composition have been historically explained by the reciprocal effects of fire and elephants (see Eckhardt et al. 2000; Whyte et al. 2003), but the few published studies on the effects of browsing on woody plant ecology, have been restricted to the central region of the Park (du Toit et al. 1990; du Toit 2003; Naiman et al. 2003). In this study, I identified a strong browsing gradient at a landscape scale on the eutrophic basaltic plains of central Kruger and then examined its potential consequences at, plant population and community levels. More specifically, I tested the following prediction derived from browser-woody plant interactions that have been elucidated in boreal and temperate forests:

(1) Ungulate browsing influences vegetation traits and species composition within woody plant communities through selective damage to palatable woody plants, resulting in increases in number of spinescent, evergreen and unpalatable species at increasing levels of browsing.

3.2 METHODS

Three areas of approximately 40 km² each were previously identified for our vegetation survey on the basaltic clay plains at the top of the catenary drainage sequence. Although, previous studies shown relatively high soil fertility throughout all the study area (du Toit et al. 1990), I collected more data on soil chemistry and soil depth (see Chapter 4, Table

4.3, 4.4 and Fig. 4.4). Such data which reveals differences in soil characteristics along the browsing gradient will be considered in the Discussion paragraph to complete my main conclusions on vegetation changes and plant species composition.

The three areas were chosen according to field observations based on changes of browsing-grazing intensity starting from permanent water sources. The vegetation survey based on woody plant physiognomic traits and grass species composition allowed us to establish *a priori* three browsing/grazing levels according to distance from water sources as follows: HH = high browsing/high grazing area, situated < 2 km from water sources; HL = high browsing/low grazing area < 4 km from permanent water, and LL = low browsing/low grazing > 8 km from a waterhole and > 3 Km from other seasonal water sources. In each area, three sites were identified in July 2002 and a set of four plots (25 m x 25 m each), were established within each site (12 plots per each browsing/grazing level), being the plots randomly arranged and at least located 300 m apart each other. Finally, among the 36 plots (our sample units) the following series of data were collected:

1) Browsing intensity on 72 focal trees of *Acacia nigrescens* was assessed in the mid dry season and expressed as percentage of number of plant shoots (produced in the current growing season) which have been damaged by ungulate browsers on a total of 20 randomly chosen, ranging in height between 1.5 m and 4 m all around the tree canopy. Specifically, 5 shoots per each height class (1.5, 2, 3 and 4 m height) were randomly checked all around the tree canopy for browsing damage. Each of four shoots per height class was exposed to browsers towards each of the four cardinal directions being the fifth shoot in-between and its position changing in turn per height class and tree investigated. Browsing pressure was also established on different tree/shrub species which individuals were recorded within 10 m apart from the focal trees of *Acacia nigrescens* previously chosen. Browsing pressure on shrubs was established between 0-2 m in height with the same modalities.

2) Number of pods for each tree/shrub, were counted all around the whole canopy and furthermore, the number of flowering trees of *Acacia nigrescens* was recorded in September 2002 among low and high browsed vegetation sites.

3) Grazing intensity was addressed using a number of quadrats (1 m^2) established at the end of the growing season in February 2003. Eight quadrats per plot were randomly located and inside each we recorded: (a) the number of grass tufts, (b) the average height of the grass layer from ground to up the base of the inflorescence, (c) the total ground area covered by the tufts (estimated as the grass canopy projection on the ground), (d) the

mean number of green stems higher than 5 cm, (e) the percentage of recently grazed stems.

4) All woody plants in each plot were identified at the species level, then, the number of individuals per species was recorded as well as classified by height (0-1 m, 1-2 m, 2-4 m, and above 4 m).

5) According to field observations and literature available woody plant species were sorted in groups defined by three functional traits as spinescence, evergreenness and palatability. A species could be classified and counted in two different functional groups if it would simultaneously show two or more of the recorded traits (i.e. a species that was evergreen and spinescent). I considered spinescent species those bearing all kind of spines, thorns and prickles that defended themselves against ungulate browsers. Foliage acceptability of common species was in part estimated (as above), according to the number of shoots damaged in the current year. Palatability indices were also assigned to the woody species occurring in our plots and according to data from previous research in the same area (du Toit 1988; du Toit 2003).

Assumptions

The study sites were chosen to minimize environmental variation between them. First, the 9 study sites were on basalt soil at the top of the catenary drainage sequence. Mean altitude is 283 m a.s.l. Second, the entire study area covered ~ 230 km² and so rainfall differences were assumed to be negligible. Third, fire events hadn't been recorded for the last 13 years in all the study sites. Finally, I assumed the impact of ungulate herbivores on vegetation has been stable for decades or centuries (see du Toit 2003) allowing us to address browsing intensity on structure and composition of a woody plant community exposed to an intact indigenous browsing guild in an ecosystem in which large herbivores move freely in response to seasonal variation in resource availability.

3.3 DATA ANALYSIS

Analyses on differences in the number of browsed shoots of *Acacia nigrescens* and other common woody species across browsing/grazing levels, as well as, across sites within the same browsing/grazing level, were performed using a Kruskal-Wallis non-parametric test for variance based on ranks. Analysis of variance (ANOVA) was performed to test for significant variation in grazing intensity across browsing/grazing levels and sites. Values were firstly log transformed for normality and then a Tukey post-hoc test was performed on ANOVA results. Significant changes in observed frequencies of plant species bearing a specific trait as spinescence, palatability and evergreenness among the nine sites were tested performing a Cochran Q Test. This tests whether several matched frequencies might differ significantly among themselves. Hence, data on woody plant species traits recorded in the 25m x 25m plots were artificially dichotomized, as assigning values of 0 = absence of trait (i.e. absence of spines) and 1 = presence. Therefore, differences in frequencies of plant species showing that specific trait were tested among the 36 plots among the nine study sites. A Kruskal-Wallis test was then performed on data of species richness according to a particular trait in each of the 36 plots (spinescence, palatability and evergreeness) along the browsing/grazing gradient. Finally, to test for floristic variation within the vegetation community across the nine sites a Cluster Analysis (CA) was performed on data collected from the 36 plots established in our fieldwork.

3.4 RESULTS

3.4.1 Browsing intensity

Browsing pressure varied significantly across the three browsing-grazing levels (Table 3.1), with *Acacia nigrescens* trees in the HH and HL sites that experienced a higher browsing impact than those in the LL sites. In the heavily browsed vegetation patches (HH and HL), *Acacia nigrescens* experienced levels of browsing > 3 times higher than in the LL sites more distant from water sources (Kruskal-Wallis, $H = 25.1$, $df = 2$, $N = 36$, $p < 0.0001$). A similar trend was observed in *Dichrostachys cinerea* (Kruskal-Wallis, $H = 14.1$, $df = 2$, $N = 21$, $p < 0.001$), *Acacia tortilis* between HH and LL sites (Kruskal-Wallis, $H = 14.9$, $df = 1$, $N = 24$, $p < 0.001$), as well as *Securinega virosa* (Kruskal-Wallis, $H = 7.60$, $df = 1$, $N = 11$, $p < 0.006$) and *Maerua parvifolia* (Kruskal-Wallis, $H = 17.9$, $df = 1$, $N = 25$, $p < 0.001$). Instead, for all woody species no significant variation was found in the number of browsed shoots across sites within the same browsing/grazing level.

Plants in HH sites, shown low or nil fruit production (Table 3.1), whereas plants in the LL sites had a slight increase in fruit number. Interestingly, *Combretum hereroense* carried a consistent number of pods even in highly browsed vegetation stands (HL sites; Table 3.1). Finally, total number of flowering trees estimated per ha was very low (5 trees among the HH sites, 8 trees in both HL and LL sites) and therefore didn’t substantially differ between lightly and heavily browsed sites.

3.4.2 Grazing intensity

Grazing intensity didn't vary across sites within each browsing/grazing level but variation was consistent between the three browsing-grazing levels identified (Fig. 3.1). All the parameters measured showed significant variation, as tufts number ($F_{1, 95} = 10.01$; $p < 0.001$), tufts mean height ($F_{1, 95} = 180.4$; $p < 0.001$; Fig. 3.1), tufts ground cover ($F_{1, 95} = 263$; $p < 0.0001$; Fig. 3.1), number of green stems higher than 5 cm ($F_{1, 95} = 104$; $p < 0.0001$), and percentage of grazed stems ($F_{1, 95} = 122$; $p < 0.0001$; Fig. 3.1).

3.4.3 Population structure of Acacia nigrescens

Among the 36 plots, *Acacia nigrescens* was the most abundant tree species counting on average 332 individuals per ha in the HL sites (26% as relative abundance within the vegetation community), 197 per ha in the HH area (20% relative abundance) and 134 per ha in the LL area (10% relative abundance; see Table 3.2). Individuals of few shrub species were more numerous than *A. nigrescens* among the LL sites, namely *Dicrostachys cinerea, Eheritia rigida* and *Maerua parvifolia* whereas *Solanum sp.* was more common among heavily browsed sites (HH and HL; Table 3.2). Small individuals of *Acacia nigrescens* in the 0-1 m height class were more abundant among the HL and HH sites respectively than in the LL sites (Kruskal-Wallis, $H = 12.4$, $df = 2$, $N= 36$, $p = 0.002$; Fig. 3.2).

Hereafter, we will call these small individuals as "gullivers" *sensu* Bond and van Wilgen (1996) since they are not proper seedlings being sometimes several years old with well-developed root systems and being kept short in the grass layer by fire and ungulate browsing. Tall adult trees of *A. nigrescens* were at the highest density among the LL sites (Kruskal-Wallis $H = 21.6$, $df = 2$, $N= 36$, $p < 0.0001$). Saplings 1-2 m tall, also displayed significant variation among the study sites, being more numerous in the heavily browsed (HH and HL) vegetation sites (Kruskal-Wallis, $H = 11.9$, $df = 2$, $N = 36$, $p < 0.002$; Fig. 3.2). No significant variation was found in the number of trees in the 2-4 m height class (Kruskal-Wallis, $H = 5.50$, $df = 2$, $N= 36$, $p < 0.06$), even if they were slightly more abundant in the heavily browsed sites.

Table 3.1. Percentage of browsed shoots ± SE, pod number of *Acacia nigrescens* (mean of 24 trees per browsing/grazing level) and neighbour trees which presence, in each plot, was recorded within 10 m from focal trees of *A. nigrescens* in the dry season. Browsing/grazing levels: LL = Low/Low, HL = High/Low, HH = High/High.

HH			HL			LL		
Species	% browsed shoots (SE)	N° pods (SE)	Species	% browsed shoots (SE)	N° pods (SE)	Species	% browsed shoots (SE)	N° pods (SE)
Acacia nigrescens	70.6 ± 3.9	0	*Acacia nigrescens*	80 ± 3.4	0	*Acacia nigrescens*	24 ± 0.38	2.91 ± 1.5
Dichrostachys cinerea	42.7 ± 1.2	4.77 ± 2.6	*Dichrostachys cinerea*	32.2 ± 0.8	10.5 ± 5.5	*Dichrostachys cinerea*	9.44 ± 0.6	30.6 ± 7.2
Acacia tortilis	35 ± 4.5	0	*Combretum hereroense*	57 ± 4	140 ± 17.2	*Acacia tortilis*	13.4 ± 2.3	7 ± 1
Maerua parvifolia	43.8 ± 3.1	0	*Combretum imberbe*	58 ± 1.3	6 ± 2.3	*Maerua parvifolia*	15 ± 1	0
Securinega virosa	74.5 ± 6.4	0	*Maytenus senegalensis*	20 ± 0.8	1.64 ± 0.6	*Securinega virosa*	26.3 ± 2.9	0.91 ± 0.08
			Euclea divinorum	6 ± 0.6	1.73 ± 0.6			

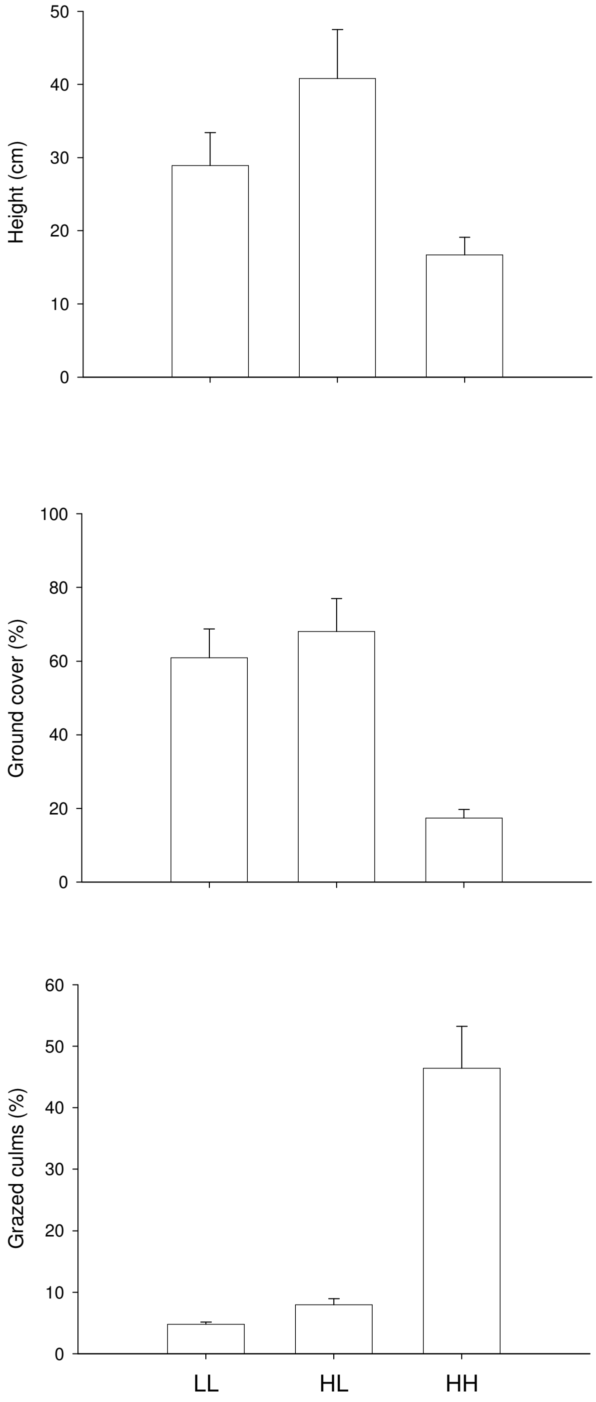

Fig. 3.1. Parameters related to grazing intensity measured in 288 quadrats (1 m² each) established within plots distributed along the browsing/grazing gradient in February 2003 (end of wet season). Browsing/grazing levels: LL = Low/Low, HL = High/Low, HH = High/High.

Table 3.2. Plant density (individuals/ha) ± SE, relative abundance (%), species presence/absence (X = absence) and plant traits as spinescence (S), palatability (P), evergreenness (E) and, deciduousness (D) of the woody species recorded in 36 plots established along the browsing/grazing gradient. Abbreviations as for Fig. 3.1.

		LL		HL		HH	
		plant/ha ± SE	(%)	plant/ha ± SE	(%)	plant/ha ± SE	(%)
Acacia exuvialis	S,P,D,	X	X	98.7 ± 0.78	7.86	64 ± 2.68	6.58
Acacia gerrardii	S,P,D	6.6 ± 0.04	0.49	40 ± 0.23	0.18	X	0.00
Acacia nigrescens	S,P,D	134 ± 0.4	9.98	332 ± 1.2	26.4	197 ± 3.77	20.3
Acacia tortilis	S,P,D	42.7 ± 0.21	3.16	2.7 ± 0.03	0.21	101 ± 1.26	10.4
Albizia harveyii	D	5.3 ± 0.4	0.4	44 ± 0.20	3.50	2.7 ± 0.17	0.27
Albizia petersiana	P,D	X	0.00	2.7 ± 0.03	0.21	X	0.00
Balanites maughamii	S	2.7 ± 0.29	0.2	X	0	X	0.00
Cassia abbreviata	P,D	X	0.00	17.3 ± 0.12	1.38	X	0.00
Combretum hereroense	P,D	X	0.00	105 ± 0.37	8.39	5.6 ± 0.19	0.55
Combretum imberbe	P,D	X	0.00	14.7 ± 0.07	1.77	6.7 ± 0.34	0.69
Commiphora africana	S,P,D	17 ± 1.05	1.28	7 ± 0.11	0.64	18.7 ± 0.59	1.92
Dalbergia melanoxylon	S,P,D	X	0.00	33 ± 0.86	2.27	2.6 ± 0.17	0.27
Dichrostachys cinerea	S,P,D	154.7 ± 3.8	11.5	108 ± 0.51	8.60	67 ± 1.17	9.19
Eheritia rigida	D	158.6 ± 4.7	11.8	17.3 ± 0.10	1.38	1.3 ± 0.08	0.14
Elaeodendron transvaalense	P,D	X	0.00	X	0	1.3 ± 0.08	0.14
Euclea divinorum	E	1.3 ± 0.14	0.1	8 ± 0.09	0.64	2.7 ± 0.17	0.27
Gardenia volkensii	P,D	17.3 ± 0.92	1.28	6.7 ± 0.07	0.53	X	0.00
Grewia flavescens	P,D	1.3 ± 0.14	0.1	8 ± 0.06	0.64	25 ± 0.54	2.61
Grewia hexamita	D	X	0.00	1.3 ± 0.02	0.11	9.3 ± 0.29	0.96
Grewia monticala	D	7 ± 0.31	0.49	2.7 ± 0.03	0.21	57 ± 1.25	5.90
Lonchocarpus capassa	P,E	X	0.00	32 ± 0.21	2.55	X	0.00
Maerua parvifolia	P,E	633 ± 25	46.1	8 ± 0.08	0.64	66.7 ± 3.55	6.86
Maytenus senegalensis	S,P,E	24 ± 1.14	1.78	78 ± 0.52	6.26	8 ± 0.29	0.82
Ozoroa engleri	E	14.7 ± 1.15	1.09	X	0	1.3 ± 0.08	0
Ormocarpum trichocarpum	P,D	84 ± 2.75	6.23	36 ± 0.22	2.87	8 ± 0.42	0.82
Sclerocarya birrea	P,D	X	0.00	25 ± 0.19	2.02	X	0.00
Securinega virosa	P,D	28 ± 0.77	2.08	42 ± 0.22	3.40	13.3 ± 0.39	1.37
Solanum sp.	D	9.4 ± 0.87	0.69	180 ± 2.04	14.33	274 ± 7.04	28.3
Ximenia americana	S,P,D	6.6 ± 0.52	0.49	X	0	X	0.00
Ziziphus mucronata	S,P,D	X	0	X	0	14.7 ± 0.29	1.51
TOT.		**1349**	**100**	**1256**	**100**	**972**	**100**

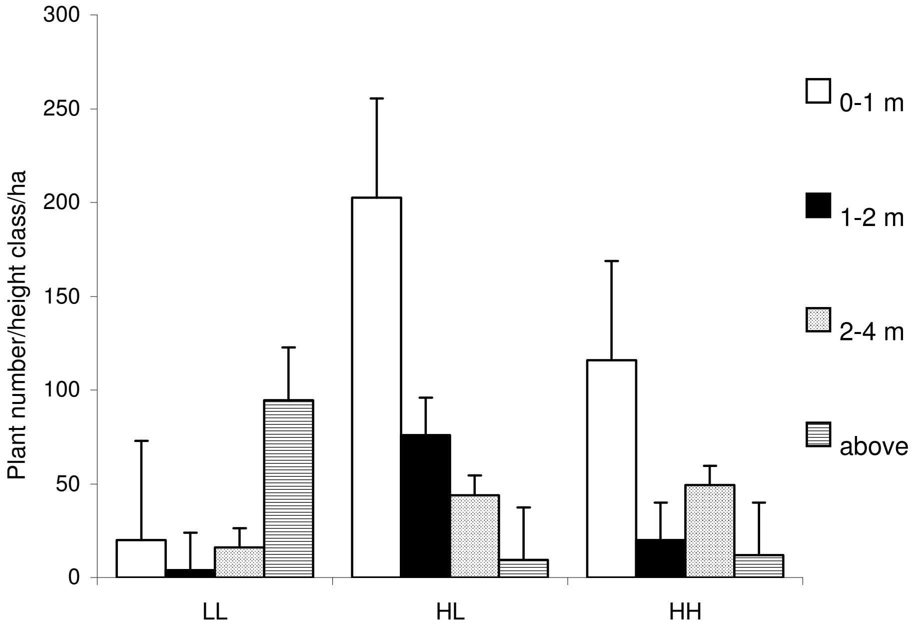

Fig. 3.2. Population structure of *Acacia nigrescens* along the browsing/grazing gradient. Abbreviations as for Fig. 3.1.

Table 3.3. Total number of plant species according to a specific trait and results of Cochran Q test on frequencies of species presence/absence occurring in sites among the three browsing/grazing levels. Abbreviations as for Fig. 3.1.

Species	LL	HL	HH	Cochran Q Test	df	p
Spinescent	8	8	8	29.48	35	NS
Non-spinescent	11	17	14	65.30	35	0.0013**
Evergreens	4	5	4	40.32	35	NS
Deciduous	15	20	18	52.20	35	0.030*
Palatable	12	18	15	58.54	35	0.007**
Unpalatable	7	7	7	43.23	35	NS

* $p < 0.05$; ** $p < 0.01$; NS = not significant

3.4.4 Effects of browsing on spinescence, palatability and evergreenness

Frequencies of spinescent, unpalatable and evergreen species across the 36 plots didn't show significant variation along the browsing/grazing gradient (see Q test results; Table 3.3). To the contrary, I found significant variation in the frequencies of non-spinescent, palatable and deciduous species across browsing-grazing levels, which is likely due to a higher richness of the same species in the HH and HL sites (Table 3.3). Palatable species were particularly abundant in heavily browsed sites. Further, variation in abundance of spinescent and unpalatable species weren't significant across all sites. However, abundance of evergreen species showed significant variation across browsing/grazing levels and this seemed due to the high number individuals of *Maerua parvifolia* which is a evergreen dwarf shrub found at high densities (633 plants/ha) in most of the plots established within the LL sites (Table 3.2). Nevertheless *Maerua parvifolia*, being classified within the palatable species, contributed to the significant number of palatable woody plants among the LL sites.

3.4.5 Vegetation community composition and species distribution

Cluster analysis (CA) based on species presence/absence recognized some differences in the floristic composition among the 36 plots grouping the 12 plots in the HL sites, apart from those established in the LL and HH sites (Fig. 3.3). Indeed, species richness was higher in the HL than the HH and LL sites (Table 3.2). Specifically, four species (*Albizia petersiana, Cassia abbreviata, Lonchocarpus capassa* and *Sclerocarya birrea*), for which presence was only recorded in the HL sites, may partially explain the cluster grouping. Other two more similar groups are recognizable in the dendrogram: the first is mainly built by plots established in the HH sites, while the second group is discriminated by plots established in the LL sites. Although *Balanites maughamii* and *Ximenia africana* were only found in the LL sites and, *Ziziphus mucronata* and *Elaeodendron transvaalense* only in the HH sites, it is interesting to note that species composition in these two opposite browsing/grazing levels (LL and HH) are floristically very similar.

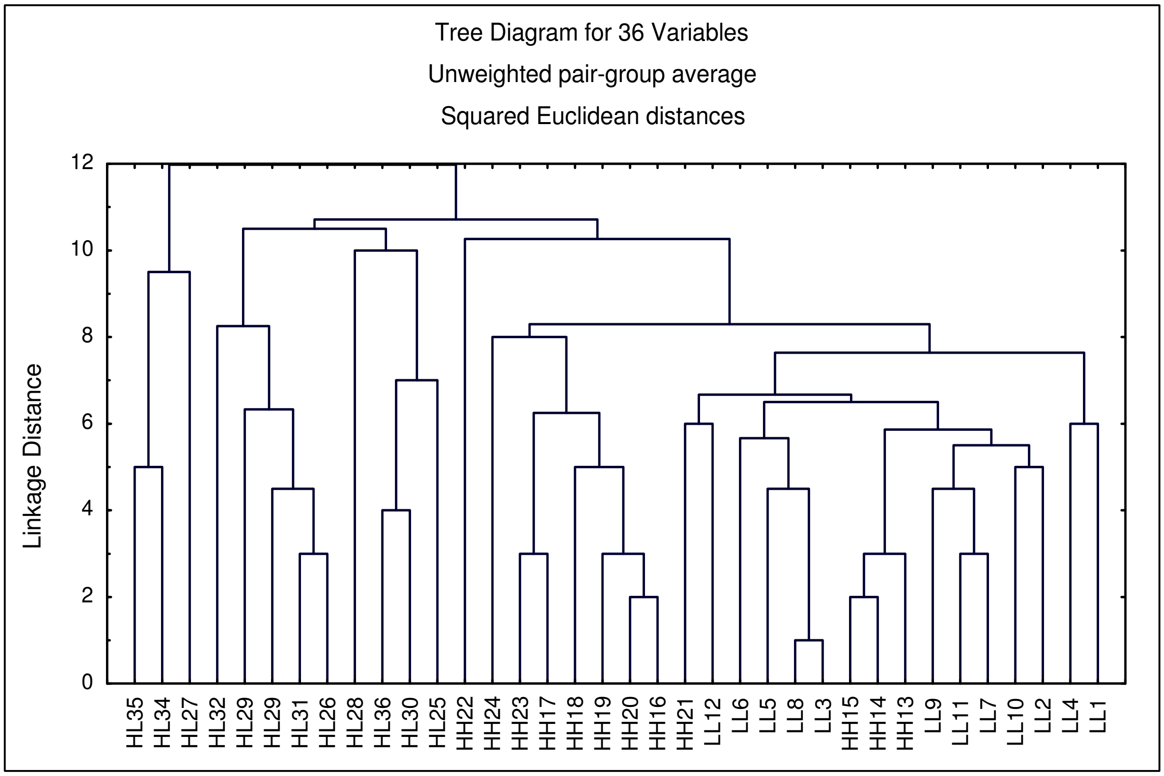

Fig. 3.3. Results from a cluster analysis (CA) based on data of species presence/absence among 36 plots along the browsing/grazing gradient. Abbreviations as for Fig. 3.1.

3.5 DISCUSSION

3.5.1 Browsing-grazing gradient

I established the existence of strong browsing/grazing gradients at the landscape scale on the same geological substrate and under the same rainfall regime. Distribution of natural and artificial water sources, the former being dependent on catenary drainage gradients and the latter on human management, might partially explain such herbivory gradient according to the distribution and dietary requirements of the large herbivore community (du Toit and Owen-Smith 1989; du Toit et al. 1990). Both woody plants and grasses experienced high herbivore pressure < 2.5 Km from water sources but browsing levels were still very high at 4 km from a permanent waterhole (HL sites; see Table 3.1). This might be due to large ungulate browsers being relatively water-independent (Redfern et al. 2003) and therefore able to exploit their food resource farther than grazers from the same watering points. Herbivore impact in our study was most apparent in terms of induced changes in vegetation structure, though Brits et al. (2002) also found differences in shrub density (lower at water points) in the same landscape type. This is probably due to an elevated density of sedentary, water-dependent large mammalian herbivores in areas with introduced watering points. The asymmetry of browsing *vs* grazing in the HL sites might be partially related to the absence of fire for 13 years from the portion of the *Acacia nigrescens/Sclerocarya birrea* landscape surveyed. This likely contributed to the local accumulation of biomass and growth of coarse high grasses, which consequently decreased grazing pressure but not browsing intensity.

3.5.2 Browsing effect on population structure of Acacia nigrescens

Population structure of *A. nigrescens* was strongly affected by browsing pressure as tall trees with wide canopies and branches with long internodes occurred at low browsing levels whereas small trees with narrower canopies and branches with shorter internodes and numerous side shoots, where likely to be found at high levels of browsing. Among the HH and HL sites, 70 to 80% of the current yearly shoots of *A. nigrescens* were damaged by ungulate browsers *vs* only 24% in the LL sites (Table 3.1) with obvious consequences on tree height and canopy volume. This agrees with previous findings from temperate forests where ungulate browsing was recognized as a major factor in significantly damaging and reducing tree height of palatable woody species (Ammer 1996; Heroldova et al. 2003; Motta 2003; Relva and Veblen 1998; Brookshire et al. 2002). Instead, we didn’t find clear indications that *Acacia* reproductive success might be negatively correlated to browsing intensity since pod production was low or null at different browsing levels (see Table 3.1). Also, the number of *Acacia nigrescens* flowering trees didn't differ among heavily and lightly browsed sites. Such results might depend on the very low rainfall during the year of vegetation survey (<200 mm between 2002 and 2003).

Interestingly, density of *A. nigrescens* gullivers was higher across heavily browsed sites (HH and HL) than LL sites, which seems to suggest (1) higher rates of seed dispersal related perhaps to positive mechanisms of seed survival after being ingested by large mammalian herbivores (Miller 1996; Milton and Dean 2001), (2) higher success rate of seedling establishment and (3) lower recruitment success (from sapling to adult trees) being the gulliver bank maintained by browsing. Moreover, among heavily browsed sites the number of *Acacia nigrescens* gullivers was higher in the high browsed-low grazed sites (HL). Likely, establishment of these seedlings has occurred in favourable years (i.e. suitable rainfall and low fire frequencies), and might have been facilitated by the presence of grasses (Brown and Archer 1989; Davis et al. 1998; Jurena and Archer 2003). Nevertheless, the gulliver bank is currently protected from herbivore damage by the high grass layer in the absence of fire.

3.5.3 Browsing effect on vegetation community composition

My main prediction was rejected and in disagreement with temperate and boreal forest scenarios, I firstly, did not find any significant changes in the number of unpalatable, spinescent and evergreen species among sites under different browsing levels. Secondly, number of palatable species that have been experiencing high browsing pressure for decades was still higher among heavily browsed sites (HH and HL; see Table 3.3) than LL sites. Such results might be primarily explained by the different set of environmental key drivers in African savannas *vs* their northern hemisphere forest counterparts (see Scholes et al. 2003) that selected for different plant-herbivore interactions over variable spatio-temporal scales. In boreal and temperate forests, for example, palatable woody species tend to occur in early stages of vegetation succession when new sites rich in nutrients and increased availability of light and moisture are created by stochastic events (i.e. flooding, fire, landslides etc.). It has been shown, then, ungulate browsers (Pastor et al. 1988; Wardle et al. 2001; Seagle and Liang 2001) can accelerate the rate of the natural succession contributing to earlier dominance of evergreen unpalatable slow-growing late successional species over pioneers.

In our savanna system the fact that the number of evergreen and other unpalatable species did not differ between browsing levels, suggests that their distribution is more related to local water and soil nutrient availability than browsing induced effects. My survey, indeed, was conducted in non-riparian areas where evergreen species usually constitute less than 5 % of the woody plant community (Scholes et al. 2003), are relatively drought tolerant and often have chemically protected and distasteful leaves (i.e. *Euclea divinorum*).

Different are the causes for the increased number of palatable woody species in the HH and HL sites where browsing has a high impact on vegetation structure. We would have rather expected palatable woody species decrease in number among heavily browsed sites since they experienced high browser pressure. Such finding suggests palatable species have evolved efficient adaptations (i.e. mechanical defence) to persist under ungulate browsing and/or fire disturbances. Indeed, many woody species from arid, semi-arid and more fire prone ecosystems as African savannas, Mediterranean shrub-lands, chaparral etc. (Bond and Van Wilgen 1996; Higgins et al. 2000; Espelta et al. 2003 for review), appear to be very resilient to chronic disturbance and able to persist *in situ* over long-time periods. Moreover, fire-herbivory interactions and soil nutrient levels in savanna ecosystems may switch vegetation state from woodland to grassland or vice versa (Van Langevelde et al. 2003) rather than cause changes in woody species composition.

Specifically, I propose palatable woody species might persist under high browsing pressure because of (1) inherent mechanisms of biomass allocation to mechanical defences (spines, thorns, prickles) instead of chemical defences (Owen-Smith and Cooper 1987; Bryant et al. 1989; Craine et al. 2003), (2) increased compensatory growth abilities after damage by ungulate browsers (du Toit et al. 1990; Augustine and McNaughton 1998), and (3) resprouting abilities of gullivers after disturbances (see Higgins et al. 2001). Firstly, spines, thorns and prickles are effective in protecting plants against browser activity (Cooper and Owen-Smith 1986; Gowda 1996), and have a high incidence in African arid eutrophic savannas, which recurrence also shows a strong correlation between high herbivore diversity and abundance in the past in South America (Huntley 1982).

Secondly, inherently fast-growing plants in eutrophic savannas as shown by Bryant et al. (1989) are expected to increase mechanical armament and show higher compensatory growth abilities against herbivores than expected from slow-growing species in moist dystrophic savannas. Indeed, du Toit et al. (1990) suggested that severe pruning on *Acacia nigrescens* trees in a eutrophic savanna reduced intershoot competition for nutrients and promoted rapid shoot regrowth after disturbance. However, within spinescent woody species, different armament levels might involve different costs/benefits for plant relative growth rate (RGR) and/or life history traits, which in turn might have consequences on their distribution within the vegetation community. If we compare, for example, *Acacia nigrescens* with the thornier and finer leafed *Acacia tortilis*, the latter experienced less damage in the HH area than *A nigrescens* (Table 3.1), was very common within the heaviest browsed patches of vegetation (HH sites) but, was almost absent among the HL sites (Table 3.1), perhaps being the seedlings of *A. tortilis* enable to establish and growth in the grass layer.

Thirdly, in my study area I recorded high compensatory growth abilities among *A. nigrescens* gullivers after herbivore damage (see Chapter 6). This suggests savanna woody plants might be less dependent on seeds and more on modalities of vegetative reproduction (Hoffmann 1998), as resulting from evolutionary responses to frequent disturbances (Bond and Midgley 2001, 2003). In my survey, gullivers of different woody species were more abundant in the HL sites where presumably grasses protected them from being heavily browsed in the absence of fire. Hence, it might be that the asymmetry of browsing *vs* grazing in the HL sites, contributed to shifts in the plant community more than those observed in high browsed-high grazed sites were all the palatable species might have a greater likelihood of being hammered by herbivores. The HL sites have shown indeed the richest plant community counting small individuals of *Sclerocarya birrea, Cassia abbreviata, Lonchocarpus capassa*, and *Albizia petersiana*, otherwise absent in the HH and LL sites. Finally, floristic differences across sites might also be due to soil chemistry differences. Indeed, the lightly browsed sites show higher concentrations of various metallic cations, total soil N and P respect to the heavily browsed sites (see Table 4.3, 4.4, Chapter 4).

3.6 CONCLUSION

In a eutrophic southern African savanna the browsing guild was responsible for dramatic changes in population structure of a palatable *Acacia* woody species. This agrees with previous studies from temperate and boreal forests which shown ungulate browsers consistently damaged palatable woody species and maintained plant population structure at a reachable browser height.

However, no functional changes in species composition were found within the vegetation community along a strong browsing gradient whereas a high number of palatable plants were recorded among heavily browsed sites. The reason of this discordance with boreal and temperate scenarios should be searched in the main ecological factors responsible for ecosystem functioning in semiarid southern African savannas. Abiotic drivers such as soil nutrient concentration and water availability contributed to a patchy distribution of evergreen and other unpalatable slow-growing species throughout the landscape regardless browsing intensity.

Instead palatable woody species show high resilience under high browsing intensity due to increased mechanical defences, increased compensatory growth abilities for adult trees and high resprounting abilities for gullivers. In an arid-eutrophic savanna it appears that fast-growing palatable woody species are the better competitors against more chemically defended, slow-growing tree species, which is contrary to the pattern in boreal-temperate forests.

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CHAPTER 4

Ungulate browsing as an ecosystem process: browser-plant-soil interactions in a semi-arid eutrophic African savanna

Abstract

This study examined the consequences of long-term ungulate browsing at the ecosystem level in a semi-arid eutrophic African savanna. I tested whether large mammalian browsers were responsible for positive or negative feedbacks with their food resource, and whether such effects would decelerate or accelerate the nitrogen (N) cycling. A set of experiments was performed to investigate (1) leaf litter decomposition rates in five common woody species (*Acacia nigrescens*, *Securinega virosa*, *Combretum hereroense*, *Euclea divinorum*, and *Maytenus senegalensis*) by mean of 690 litterbags placed under natural conditions, (2) leaf N in wet and dry seasons, (3) soil chemistry and (4) litter biomass and composition distributed across browsing and grazing gradients. My results show a general depletion of total soil N in heavily browsed sites. This agrees with long-term decelerating effects of browsing on nutrient cycling, previously established for temperate and boreal forest ecosystems. However, I found evidence of high plant resilience in heavily browsed sites where *Acacia* stands shown (a) higher leaf N during the main growing season, (b) higher N release from leaf litter, (c) high concentration of labile soil nutrient forms, such as nitrate (NO_3) and ammonium (NH_4), and (d) similar, or even faster, litter decomposition rates than in lightly browsed sites. Firstly, this suggests that tree pruning triggers and maintains a fast nutrient cycling within the plant-browser system. The accelerating effect is supported by high mass compensatory growth abilities from highly palatable, fast-growing *Acacia* trees that produce highly decomposable litter. Secondly, browsing has a long-term decelerating effect on N cycling drastically reducing the quantity of leaf-twig litter biomass that is returned to the soil rather than through qualitative changes in litter chemistry. I discuss how the interactive effects of browsing-grazing-soil fertility may influence nutrient cycling through different ecological processes.

KEY WORDS: *Acacia*, compensatory growth, litter decomposition, leaf nitrogen, nutrient cycling, nutrient remobilisation, termites

4.1 INTRODUCTION

Large mammalian herbivores influence terrestrial ecosystem processes both directly by consuming plant material and indirectly by altering litter quality and nutrient cycling, therefore mediating linkages between above- and below-ground communities (McNaughton et al. 1988; Hobbs 1996; Kielland and Bryant 1998; Wardle et al. 2002; Bardgett and Wardle 2003). The literature on mammalian herbivory in relation to the composition, dynamics and structure of plant communities in African savannas has been dominated by studies on the grazing guild (Norton-Griffiths 1979; Sinclair and Arcese 1995). Former studies on ‘grazing lawns’ have shown that herbivory directly induces changes in reallocation of nutrients within individual plants and indirectly stimulates soil mineralization processes (McNaughton 1979, 1983, 1984). Herbivory, manuring and enhanced nutrient uptake by grass plants maintains a fast nutrient cycling close to the soil surface in a sustainable positive feedback cycle (McNaughton 1983).

The only studies investigating browsing as an ecosystem process have been conducted in boreal and temperate forests, where the long-term consequences of intensive browsing are often opposite to those for grazers (Naiman et al. 1986; Pastor et al. 1988; Pastor et al. 1997; Harrison and Bardgett 2004). The difference appears to be that selective browsing on palatable deciduous woody plants provides a competitive advantage to chemically defended slow-growing evergreens, which produce leaf litter that decomposes slowly (Bryant et al. 1991; Pastor and Naiman 1992; Pastor et al. 1993). Consequently, with slow nutrient uptake by slow-growing plants combined with reduced soil microbial activity and leaching (Bryant and Chapin 1986; Pastor et al. 1988), there is a net loss of available forms of soil nutrients (i.e. reduced mineralization rates). Nevertheless, the ‘top-down’ effects, exerted by large mammalian herbivores on ecosystem properties (Kielland et al. 1997; Bardgett and Wardle 2003) are mediated by “bottom up” effects exerted by soils and climate which influence plant community structure and functional species composition.

For example, Wardle et al. (2001) show that ungulate browsing may have accelerating, decelerating and neutral effects on processes in New Zealand natural forests, despite consistent changes in vegetation composition. Moreover, Persson et al. (2005) have recently proposed that a reduction in litter mass rather than changes in litter chemistry was responsible for a decrease in productivity in a N-limited Swedish boreal forest. The fact is that varying browsing intensity on medium preferred woody species, which represent the "bulk food" for moose (*Alces alces*), is not responsible for changes in the plant species mix, and therefore does not affect litter quality.

In southern African savannas comparatively, little attention has been paid to the potential effects of the browsing guild on the growth of highly preferred woody species and nutrient cycling, and whether this varies with geological substrate. African ungulate browsers may contribute to negative feedbacks on nutrient dynamics decreasing the abundance of woody species with N-rich tissues (Ritchie et al. 1998). This might cancel out the positive effects of grazing on nutrient cycling and contribute to increase the number of unpalatable woody species within the plant community. Furthermore, this would decrease leaf litter decomposition rates in heavily browsed sites, affecting mineralization rates and contributing to a general degradation of ecosystem properties (i.e. decelerating effect).

Alternatively, in semi-arid eutrophic savannas, inherently fast-growing palatable woody plant species (Bryant et al. 1989) may have adaptations including eco-physiological responses to pruning, such as mass compensatory growth abilities (Augustine and McNaughton 1998). This might buffer the effects of browsers, and limit changes in the functional composition of the plant community. These resilient plants may compensate for browsing damage, have high nutrient tissue concentrations and provide high litter quality with consequent positive effects on soil microbial processes and rates of nutrient turnover (i.e. accelerating effect; see Ritchie et al. 1998; Bardgett and Wardle 2003).

The question still remains whether, and how, the positive or negative feedbacks within the plant-browser system may affect the nutrient cycling at larger scales along a strong browsing gradient where large mammalian herbivores are free to move throughout an extensive wildlife area. In my study I addressed the effects of the ungulate browsing guild on stands of vegetation dominated by the highly palatable *Acacia nigrescens,* Miller, in a central region of the Kruger National Park, South Africa. I used leaf N content as index of browse and litter quality (see Cooper et al. 1988; Gallardo and Merino 1993; du Toit 2003), and conducted litter decomposition experiments, as well as soil analyses in *Acacia nigrescens* stands that have experienced markedly different levels of browsing for centuries. If the long-term browsing pressure had negative effects on ecosystem properties and nutrient cycling we would then expect that: (1) soil nutrient pool in heavily browsed sites is more depleted than in lightly browsed sites, (2) leaf litter among heavily browsed sites has lower decomposition rates than litter placed in lightly browsed sites. I specifically tested the following hypotheses in a semi-arid eutrophic savanna:

a) Browsing induces negative ecosystem-level responses (i.e. retarding nutrient cycling), reducing the quantity of organic matter that is returned to soil rather than negatively affecting litter quality;
b) Rates of litter decomposition are positively correlated with leaf palatability for woody species occurring within the vegetation community dominated by *Acacia nigrescens*.

4.2 METHODS

4.2.1 Browsing/grazing intensity

Nine sites were chosen in June 2002 at the top of the catenary drainage sequence, on the same basaltic clay soil to minimize intrinsic site differences. The furthest distance between sites was ~ 15 km, so rainfall differences were assumed to be negligible. The scale of my study allowed me to address browsing effects on woody vegetation where large herbivores moved freely in response to seasonal variation in food availability. Moreover, fire had not been recorded for 13 years in all the nine study sites, thus offering homogeneous conditions to evaluate the independent effects of large herbivores on ecosystem processes.

The nine sites chosen at the landscape level were previously identified according to preliminary field observations based on changes of browsing-grazing intensity, which generally decreased with distance from permanent water sources. Browsing intensity was assessed by randomly checking 40 twigs all around the canopy of each of 45 *Acacia nigrescens* trees, being 20 twigs exposed to browsers between 0-2 m in height and 20 twigs between 2-4 m in height. The number of twigs that have been browsed in the current growing season was recorded and the mean percentage used to define three browsing levels (high, medium, low). Grazing intensity was addressed among the study sites by randomly establishing 80 quadrats (1 m^2) per each study site. In each quadrat grass species were identified and tuft number, grass maximum height and percentage of culms damaged by grazers were measured. As a consequence of this preliminary survey three different browsing and grazing gradients were established: three sites were low browsed/low grazed (LL) situated > 7 km from watering points, three more sites were high browsed-high grazed (HH) < 2 km from water, three sites were medium browsed-low grazed (ML), 3-7 km from water sources.

4.2.2 Litter decomposition: August placement

Leaf samples from 45 *Acacia nigrescens* trees (5 trees per site) were collected in two days in June 2002 during the peak period of leaf-fall, which for *Acacia nigrescens* occurs from June to August in the dry season (Coates Palgrave et al. 2002). Leaves from each tree were kept separated and air-dried (3 days at ~ 25 °C), weighed till constant mass and used to fill 135 (15 x 15 cm) steel mesh bags (2 mm mesh size). At the same time other 135 mesh bags were filled with common straw (dried under the same conditions), collected at one site at Tshokwane ranger station. Both leaves and straw were weighed after the bags were stuffed, yielding 5 ± 1 g (mean ± SE). The experimental design consisted of units of six mesh bags each (3 mesh bags of common straw and 3 of *Acacia* litter), evenly fixed along a steel wire that was fastened around the tree trunk and carefully placed on the soil horizontally under each of the *A. nigrescens* tree canopies. Each pair of litterbags was then retrieved after 3, 6 and 12 months. Therefore, 2 litterbags (*Acacia* and straw) x 3 collections (November, February and August) x 45 trees gave a total of 270 litterbags.

I used common litter (straw) to take into account across-site variations in decomposition rates of *A. nigrescens* tree leaves that might be due to either variation in leaf chemistry or local microbial activity. After retrieval the litterbags were carefully emptied, the content oven dried at 70 °C for two days and weighed to measure weight loss (dry matter), whereas to measure the effective biomass loss (without soil inorganic particles) a correction factor was applied by igniting all samples for 4 hours at 550 °C and using the ash free weight in the final calculations. Initial sub-samples of *Acacia* leaves and all the samples retrieved during the year were analyzed for N and C. Nitrogen was determined by Kjeldahl standard method (see Benton 1991) and carbon by dry combustion. Finally, fresh leaf sub-samples from heavily and lightly browsed trees were collected in December (early growing season) and June (early dry season) to test for potential seasonal variation in leaf N concentration.

4.2.3 Litter decomposition across species and sites

Leaves of *Acacia nigrescens* and four other common woody species, *Securinega virosa*, *Combretum hereroense*, *Euclea divinorum* and *Maytenus senegalensis* were collected during two days in June 2002. *Acacia nigrescens* and *Securinega virosa* (deciduous shrub) are palatable browse species whereas *Euclea divinorum* (evergreen shrub), *Combretum hereroense* (deciduous shrub-small tree) and *Maytenus senegalensis* (evergreen shrub) are unpalatable (du Toit 2003; for tree nomenclature see Coates Palgrave et al. 2002). Leaf samples from 10 individuals per species were mixed, air-dried and stuffed in steel mesh bags to make up experimental units of six mesh bags consisting in three mesh bags of straw and three in turn of each of the other woody species. Common straw was used as previously as a control to test for across-site variation in decomposition rates.

The experiment was started at the end of June and mesh bags were retrieved after 5, 8 and 12 months. Two litterbags (straw + one of the woody species) x 3 yearly collections x 4 species x 10 replicates per species gave a total of 240 mesh bags. Finally, mesh bags with leaf samples of *Acacia nigrescens* were distributed in two sites per each browsing-grazing level (HL, ML, HH), so 2 litterbags (straw and *Acacia*), x 3 yearly collections x 30 trees gave a total of 180 mesh bags. After retrieval the content of the mesh bags was oven dried, weighed and the ash free weight determined as above.

4.2.4 Litter biomass, soil depth and soil nutrient pool

In addition to litter decomposition experiments for our 45 *Acacia nigrescens* trees (August placement), litter samples were collected from the soil surface inside quadrats of 25x25 cm each, located in two places 1.5 m away from the tree trunk of each of the tagged *Acacia nigrescens* trees, just before soil sample collection. Litter was separated into its different components (wood, grasses, leaves and dung), oven dried at 70°C for two days and weighed to give an estimate of litter dry mass composition around each of the 45 trees in the study sites. Soil samples were collected in the same places as litter sampling. A 10 cm deep soil core of 5 cm diameter was collected, put in paper bags, air dried, and then sent for chemical analyses. Samples were analyzed for total N, NO3, NH4, total P, extractable cations (Ca, Mg, K, Na), pH, and cation exchange capacity (CEC). Soil depth was checked using a manual auger digging 30 cm away from the two places where soil and litter were collected.

4.2.5 Termite activity

Since termites are very common in arid semi-arid savanna ecosystems and their role in litter decomposition very important (see Bignell and Eggleton 2000), our litterbags were chosen as having 2 mm mesh size to allow termite access to the litter samples placed along the browsing-grazing gradient. The experimental design for litter decomposition (June and August placements) allowed us to test potential effects of termites on litter removal during the driest winter months. Signs of termite activity were considered as presence of workers and soldiers during monthly inspections, as well as earth debris left inside our mesh bags at the time of mesh bag retrieval. Specimens were collected if found at the time of mesh bag retrieval, conserved in alcohol and sent off for identification.

4.3 DATA ANALYSIS

Repeated measures ANOVA were performed to test effects of different browsing/grazing intensity on decomposition rates of two litter types (*Acacia* and straw) at the end of the period of incubation. Data were expressed as proportions of organic mass remaining and were then arcsine transformed to meet the uniformity assumptions of ANOVA. A Wilcoxon matched pairs test was performed on proportional weight loss after one year of incubation from litter samples of the four common woody species and straw placed in June 2002.

To compare annual decay constants among our woody species in term of mass loss and N release along the browsing-grazing gradient and placement period, a standard exponential model (Olson 1963) was applied using the equation: ln (X0/Xt) = kt, where X0 is the initial mass of litter and Xt is the mass of litter remained after time t. The constants (k) were calculated as means of litter decomposition rates throughout the year and linear regressions of ln (X0/Xt) against time (months) were performed to quantify the variance explained by the exponential model, using the STATISTICA software package.

Pearson correlation coefficients were calculated to test significant differences between mass loss and N release, as well as C/N ratio along the browsing/grazing gradient. Significant variation in soil nutrient concentration (N, NO3, NH4, P) was tested using a two-way ANOVA, being data log transformed. Further significant statistics in soil cation concentration (Ca, Mg, Na and K), was performed by a Friedman ANOVA and Kendall Coefficient of Concordance. Finally, a chi-square test was performed to test for variation in frequencies of termite occurrence at the litterbag sites after one year of litter incubation.

4.4 RESULTS

4.4.1 Litter decomposition rates - August placement

As expected, litter samples from single trees of *Acacia nigrescens* placed in August 2002, showed increasingly mass loss with increasing time of litterbag incubation (F = 38.57, df = 2, p < 0.001; Fig. 4.1 a, b). Browsing effects on litter decay rates after one year of incubation did not vary significantly along the browsing-grazing gradient (F = 1.921, df = 2, p = 0.15), also no differences were found between decomposition rates of *Acacia* and straw litter types (F = 0.56, df = 1, p = 0.45), and finally, there was no significant browsing-litter type interaction on decomposition rates (F = 0.44, df = 2, p = 0.64). I further didn't find variation in litter decomposition rates across sites established within sites with similar browsing/grazing intensity (F = 0.78, df = 2, p = 0.46), but browsing-site interactions played a role in influencing litter decay rates (F = 10.19, df = 4, p < 0.001). A Tukey post-hoc test showed such variation was due to different litter decomposition rates among the three LL sites.

Straw litter showed a more linear decay rate than *Acacia* during the period of incubation (Fig. 4.1 b), and decomposition constants (k values) of both litter types *Acacia* and common straw, fitted into an exponential decay model (Table 4.1). However, straw and *Acacia* litter had higher k values in the HH sites than in the LL and ML sites (Table 4.1), which suggests faster decomposition rates associated with high browsing/grazing intensity whereas, decomposition constants of *Acacia* along the browsing/grazing gradient didn't fit an exponential decay model for the June placement period. This was mainly caused by a high termite foraging activity among all study sites during the June placement period (see below percentage of litterbag visited by termites), which determined no linear decomposition rates for *Acacia* litter (Fig. 4.2 a).

Total leaf N content was significantly higher in heavily than lightly browsed trees in the early wet season in December (N = 10, p < 0.0123) just after the main leaf flush. This roughly occurs for *Acacia nigrescens* between October and November before main rainfall events (see also Scholes et al. 2003b). However, leaf N content was lower in heavily than lightly browsed trees when leaf samples were collected in June (N = 15, p < 0.0006). Indeed, the average initial leaf nitrogen content (N %) in June was higher in trees located in the LL sites (1.82 ± 0.02) *vs* trees in the HH sites (1.55 ± 0.03). The amount of N released from the litterbags during the year of incubation was higher in the HH sites as shown by the decomposition constants (k = - 0.045) than in the LL (k = - 0.015) and ML (k = - 0.009) sites and, also fitted an exponential decay model in the HH sites ($R^2 = 0.137$, $p < 0.038$), as well as in the ML sites ($R^2 = 0.11$, $p < 0.036$), but this was not the case for N release in the LL sites ($R^2 = 0.009$, $p = 0.263$). Pearson correlation coefficients were significant for both N released from leaf litter ($r = - 0.492$; $p < 0.05$) and C/N ratio ($r = 0.499$; $p < 0.05$) only in the HH sites confirming a quite constant and faster decay rate at increasing levels of organic mass loss during the year, than in the LL and ML sites. This was also due to increases in N and decreases in C concentrations in the leaf litter.

4.4.2 June placement

As for the August placement, although increased time until mesh bag retrieval affected rates of decomposition (F = 10.8, df = 2, $p < 0.001$; Fig. 4.2 a, b), browsing effects on percentage of mass loss from litter samples of *Acacia* and common straw were not found significant after one year of incubation (F = 2.49, df = 2, p = 0.088). Decomposition rates between *Acacia* and straw were significant (F = 81.58, df = 1, $p < 0.0001$) because of the faster rate of decomposition of *Acacia* leaf than straw litter (see also k values, Table 4.1). Indeed, litter samples of *Acacia* decomposed much faster and had a peak in mass loss during the first five months of incubation than those of straw and especially in the ML and HH sites (Fig. 4.2 a, b). Browsing-litter type interaction was significant (F = 8.38, df = 2, $p < 0.0004$) and a post-hoc Tukey's test shown such results were mainly due to a different decomposition rate of *Acacia* and straw within the ML area that was probably due to termite activity (see Table 4.1; see also par. 4.4.4). Common straw showed a linear decay rate throughout the year (Fig. 4.2 b) and the k values (higher among the HH sites) fitted an exponential decay model (Table 4.1). As opposite *Acacia* litter didn't have a constant decay rate during the year but as straw samples, shown higher k values in the HH and ML sites *vs* the LL sites (Table 4.1; Fig. 4.2 a). Decomposition rates of *Euclea divinorum, Securinega virosa* and *Combretum hereroense*, shown significant differences if compared to straw decay rates (Table 4.2), whereas *Maytenus senegalensis* had similar trends of decomposition as common straw. *Combretum* and *Euclea* decomposed slower than straw and had the lowest k values (Table 4.1, 4.2), whereas *Maytenus* seemed to have intermediate k constants and, finally *Securinega* had faster decomposition rates than both straw and all the other woody species (Table 4.1). Only the decay rates of *Maytenus* fitted an exponential decay model (Table 4.1).

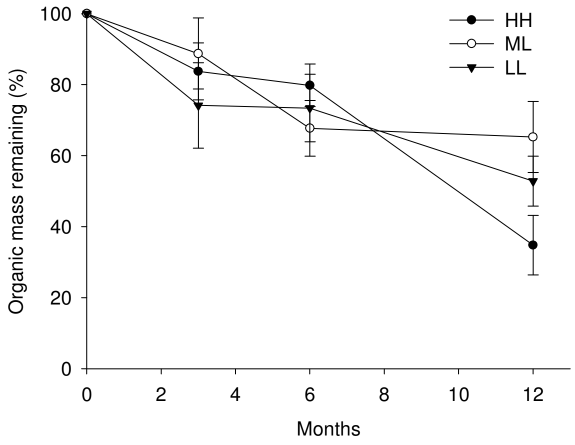
4.4.3 Soil analysis and litter composition

Levels of soil nutrients were relatively high all among my study sites (Table 4.3), which is likely explained by the basic igneous basaltic substrate (see Scholes 1990; Venter et al. 2003). Total soil N (%) was significantly higher in both LL and ML sites than in the HH sites (Table 4.3). However, NH4 and P didn't vary among the study sites whereas NO3 was significantly higher in the HH sites (Table 4.3). All the cations showed significant high concentrations in both the ML and LL sites (Table 4.4), which is likely due to the higher clay soil content (pers. obs.). Indeed, clay has the property to attract and retains positive charged particles as, can be also inferred by the substantial differences in the cation exchange capacity (CEC) between LL and HH sites (Table 4.4). Also, cation concentrations were found highly variable due to site effects within similar browsing-grazing levels (Table 4.4). No significant variation was found between pH values all among our study sites ($F = 1.34$, $p = 0.123$). Topsoil depth was higher in the LL sites than in high browsed/grazed sites (Fig. 4.4). Finally, litter composition analyses shown dung component was relatively higher into the litter collected among the HH sites than in the LL and ML sites (Fig. 4.3; $\chi^2 = 13.45$, $N = 15$, $df = 2$, $p < 0.0012$).

4.4.4 Visitation of termites to litter bags

Termite activity varied according to litter type and period of litter placement. Litter samples from June placement period were visited at higher frequencies by foraging termites than those of the August placement. Frequencies of straw and *Acacia* litterbags visited by termites among browsing/grazing levels after one year of incubation starting in June 2002 were statistically significant for straw ($\chi^2 = 21.19$, $df = 2$, $p < 0.00002$), being straw preferred in the HH sites, but not for *Acacia* ($\chi^2 = 2.73$, $df = 2$, $p < 0.24$) which was visited at high frequencies at all sites. After one year from August placement, frequencies of litterbags visited by termites among browsing/grazing levels were neither significant for straw ($\chi^2 = 3.67$, $df = 2$, $p < 0.16$), nor for *Acacia* ($\chi^2 = 4.55$, $df = 2$, $p < 0.11$). Specimens of both workers and soldiers, collected at the litterbag bait sites were identified and classified in to the family Termitidae represented by the Termitinae with one species (*Amitermes sp.*) and Macrotermitinae more numerous represented by 5 species (*Macrotermes sp.*, *Macrotermes ukuzii*, *Ancistrotermes latinotus, Microtermes sp.* and *Odontotermes sp.*).

a)



b)

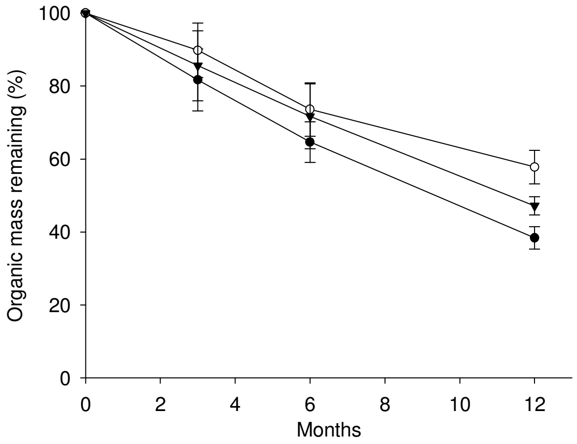


Fig. 4.1. Ash free litter mass remaining of samples collected from individual trees of *Acacia nigrescens* (a) and common straw (b), after 3, 6 and 12 months from August litterbag placement along different browsing/grazing levels. Browsing/grazing levels: HH = high/high; ML = medium-high, LL = low-low.

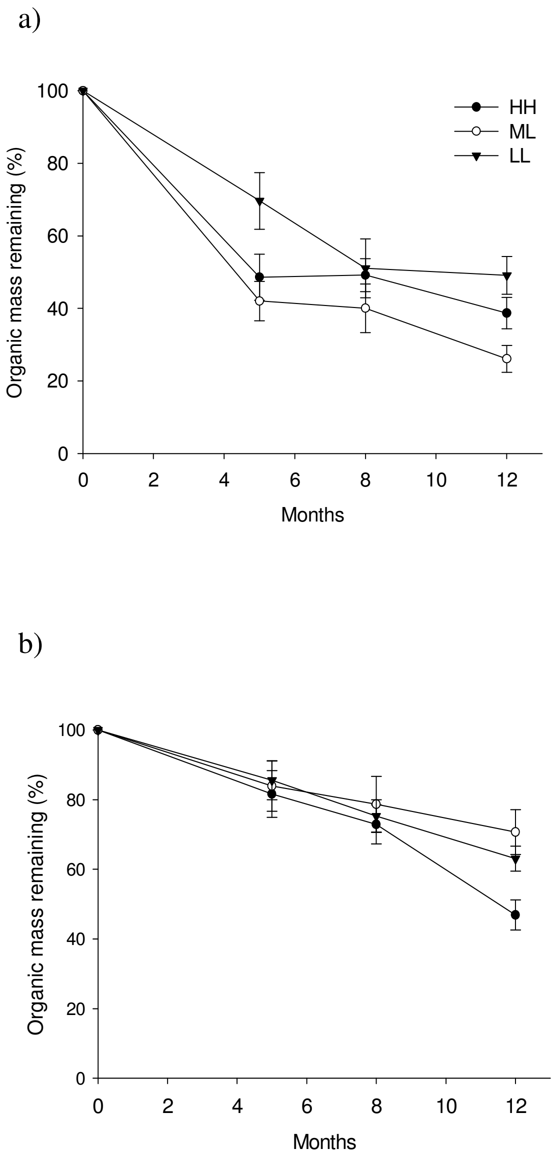


Fig. 4.2. Ash free litter mass remaining from mixed leaf samples of 10 *Acacia nigrescens* trees (a) and common straw collected (b), after 5, 8 and 12 months from June litterbag placement along the browsing/grazing levels. Browsing/grazing levels: HH = high/high; ML = medium-high, LL = low-low.

Table 4.1. Decomposition constants (k), as mean values of mass loss calculated for each period of mesh bag retrieval (month^{-1}) of litter samples of *Acacia nigrescens* placed in August 2002 and all species placed in June 2002. Mean of 3 sites per browsing/grazing level: HH = high/high; ML = medium-high, LL = low-low.

June placement				August placement			
Litter type	k values ± SE	R^2	P	Litter type	k values ± SE	R^2	P
Acacia nigrescens				*Acacia nigrescens*			
HH	0.123 ± 0.02	0.04	NS	HH	0.085 ± 0.02	0.46	< 0.001
LL	0.084 ± 0.03	0.01	NS	LL	0.081 ± 0.02	0.41	< 0.001
ML	0.148 ± 0.01	0.03	NS	ML	0.069 ± 0.01	0.46	< 0.001
Straw				Straw			
HH	0.072 ± 0.01	0.18	< 0.02	HH	0.102 ± 0.01	0.18	< 0.05
LL	0.037 ± 0.003	0.18	< 0.02	LL	0.075 ± 0.01	0.24	< 0.001
ML	0.033 ± 0.001	0.17	< 0.02	ML	0.051 ± 0.01	0.14	< 0.05
Combretum hereroense	0.015 ± 0.01	0.001	NS				
Maytenus senegalensis	0.025 ± 0.01	0.59	< 0.001				
Euclea divinorum	0.007 ± 0.001	0.003	NS				
Securinega virosa	0.09 ± 0.001	0.04	NS				

NS = Not significant.

Table 4.2. Results of Wilcoxon Matched Pairs Test on values of weight loss after one year of incubation from litter samples of four woody species and straw litter (% mass remaining ± SE) placed in June.

Species	Leaf litter	Diff	Straw litter	P
Maytenus senegalensis	76.8 ± 3.54	NS	69.2 ± 1.35	0.313
Securinega virosa	36.9 ± 4.76	>	62.5 ± 3.43	0.009
Euclea divinorum	93.2 ± 2.34	<	81.4 ± 1.45	0.004
Combretum hereroense	91.6 ± 5.65	<	79.2 ± 2.56	0.043

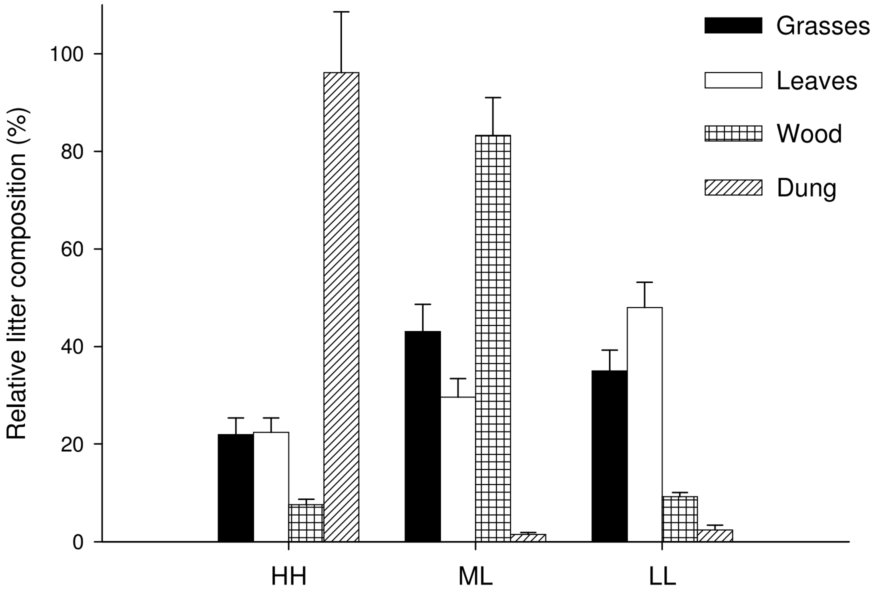


Fig. 4.3. Relative litter mass composition (%) established, along the browsing/grazing gradient (mean of 3 sites per browsing-grazing level). Abbreviations as for Table 4.1.

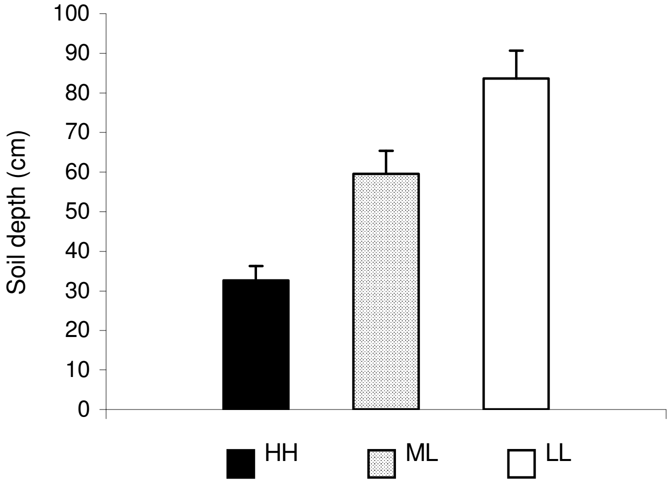


Fig. 4.4. Top-soil depth measured using a manual auger digging 30 cm away from the two places where soil and litter were collected. Abbreviations as for Table 4.1.

Table 4.3. Soil nutrient concentration (± SE) and results from ANOVA on significant differences along the browsing-grazing gradient (mean of 3 sites per browsing-grazing level). Abbreviations as for Fig. 4.1.

	Browsing/grazing levels			Browsing effect		Site effect		Interaction	
	HH	ML	LL	F	P	F	P	F	P
Total N (%)	0.14 ± 0.01	0.18 ± 0.01	0.18 ± 0.01	12.2	0.003	1.97	NS	0.89	NS
NH4 (mg/kg)	75.6 ± 11.1	69.5 ± 0.72	73.2 ± 1.11	0.86	NS	0.69	NS	0.12	NS
NO3 (mg/kg)	60.1 ± 1.45	66.1 ± 4.39	52.7 ± 2.59	7.18	0.016	1.77	NS	5.57	< 0.005
P (mg/kg)	61.2 ± 7.98	67.7 ± 3.60	74.2 ± 4.04	1.58	NS	2.57	NS	7.82	< 0.001

NS, Not significant.

Table 4.4. Soil cation concentration (± SE) and Friedman ANOVA, Kendall Coeff. of Concordance on soil parameters and cation exchange capacity (CEC), along the browsing/grazing gradient (mean of 3 sites per browsing-grazing level). Abbreviations as for Table 4.1.

	Browsing/grazing levels			Browsing effect		Site effect	
	HH	ML	LL	χ^2	P	χ^2	P
Ca (mg/kg)	1615 ± 34.8	2200 ± 99.9	2785 ± 93.8	22.8	< 0.001	36.4	< 0.001
K (mg/kg)	477 ± 15.5	762 ± 39.3	1048 ± 10.4	23.3	< 0.001	32.1	< 0.001
Mg (mg/kg)	538 ± 26.1	780 ± 16.2	1021 ± 63.5	28.13	< 0.001	35.14	< 0.001
Na (mg/kg)	73.4 ± 4.5	92 ± 5.03	110 ± 8.58	12.13	< 0.002	29.79	< 0.001
CEC	15.8 ± 0.61	24.7 ± 0.90	26.1 ± 1.12	31.5	< 0.001	10.2	< 0.005

4.5 DISCUSSION

Overall my results suggest that long-term selective browsing on stands of palatable *Acacia* trees may have a negative effect on nutrient cycling. This is likely to happen in the immediate vicinity of palatable woody species, as inferred from a general depletion of total soil N at heavily browsed vegetation sites (Table 3). However, (Naiman, *personal comments*) this must be better addressed through a more detailed analysis of processes involved in the nutrient cycling within the plant-browser-soil system (e.g. N denitrification, mineralization, N2-fixation, N dung content etc.). Moreover, the fact that I found less total soil N at heavily browsed sites doesn't necessarily mean that it is associated with a decreased nitrogen cycling (Pastor, *personal comments*). Indeed, N and P availabilities to plants are determined not by pool sizes but by the supply rate into those pools through mineralization of organic matter (Pastor, *personal comments*). Therefore my first hypothesis that ungulate browsing may have a decelerating effect on nutrient cycling (Pastor et al. 1988; Pastor et al. 1993; Kielland et al. 1997; Harrison and Bardgett 2004) must be tested further. However, I propose the intermediate processes affecting nutrient cycling and leading to a depletion of soil nutrients are likely different in a semi-arid eutrophic African savanna from those proposed in northern emisphere scenarios (see Fig. 8.1). I suggest that soil nutrient cycling might be primarily due to a drastic reduction of litter input into the soil from heavily browsed palatable trees (Fig. 4.3; Fig. 8.1). Though, I didn't directly measured litter input from heavily browsed trees, the percentage of leaf litter on the ground was very low under heavily browsed trees. This would lead to a C deficit for microbial activity, which in turn has negative effects on soil N mineralization rates (Bardgett and Wardle 2003). In fact, the part of N mineralized from soil organic matter before to become available to plants is likely immobilized in microbial biomass, which could better incorporate it back again into soil organic matter if plant litter provides enough C to increase microbial activity (Knops et al. 2002). Nonetheless, this stresses the importance of both microbial nitrogen loop and plant impact on nitrogen inputs and losses since a drastic reduction in plant carbon input (e.g. litter) lead to a negative feedback through microbial nitrogen immobilization (see Knops et al. 2002; Harrison and Bardgett 2004).

However, I observed important positive feedbacks within the plant-browser system which can be inferred from the higher leaf N content and higher rates of N release from leaf litter of heavily browsed trees than lightly browsed trees. Moreover, litter decay constants observed for both *Acacia nigrescens* and common straw in heavily browsed sites were similar or even higher than those in lightly browsed sites (Table 1). Finally, concentrations of nitrate (NO_3) and ammonium (NH_4) were still high among the HH sites. At first sight, such results wouldn't match with the overall depletion of soil nutrients (low N in the soil of heavily browsed sites), for which browsers were considered responsible in our system. On the contrary, these general findings would be expected from predictions of the accelerating nutrient cycling hypothesis (see Ritchie et al. 1998). Indeed, the presence of spinescent woody plants in eutrophic savannas (see Craine et al. 2003) with relatively high N tissue contents and high compensatory growth abilities (Augustine and McNaughton 1998) would still be the dominant species within the vegetation community over unpalatable slow growing woody tree/shrubs. Hence, the modalities through which ungulate browsing can depress nutrient cycling in semi-arid eutrophic savannas might lie in the interactions between browsers and resilient palatable woody plants rather than in a decreased quality of litter due to changes in vegetation composition as shown, for example, in boreal forests (Pastor et al. 1988; Bryant et al. 1991; Pastor and Naiman 1992, Pastor and Cohen 1997).

Accordingly, there are important indications for a positive feedback loop between browsers and their food resource, which resemble at least in part those proposed for the grazing guild. In fact, ungulate browsing seems to be able to stimulate and maintain a fast nutrient cycling within the plant-browser system but not with the same positive consequences at the whole ecosystem level as shown for the "grazing lawns". Grazer-induced stimulation of aboveground productivity benefits from the fast nutrient uptake rates by grass species, which are supported by mechanisms of increased microbial activity and root exudation in the rhizosphere (Bardgett and Wardle 2003). The result is a positive feedback loop between grazers and grasses, which is sustained by a closed nutrient cycle (Fig. 8.2).

On the other hand, the fast nutrient cycle between browsers and woody plants is triggered by tree pruning, which is likely to decrease competition between plant shoots (du Toit et al. 1990) and increase N availability, as I found in leaves of heavily browsed trees during the main growing season. The result is a positive feedback loop between browsers and trees, which is sustained by an open nutrient cycle (Fig. 8.2).

It is not clear yet, however, (1) how different plant nutrient source-sinks and/or eco-physiological processes may sustain plant compensatory growth after browsing damage, and (2) why litter of heavily browsed trees releases more N than litter of lightly browsed trees. Likely, herbivores enhance plant compensatory abilities indirectly acting on below-ground processes as stimulating production of new fine roots or increasing root exudation which in turn increases C inputs in the soil and plant productivity (Ayres et al. 2004; Bardgett and Wardle 2003). Additionally, nutrients might be supplied by consistent rates of biological nitrogen fixation in plants of semi-arid eutrophic savannas (see Högberg 1992; Scholes et al. 2003; Ayres et al. 2004). Excretion of N in dung and urine of grazers in the HH sites might also accelerate N mineralization and turnover, hence increasing its availability to plants and microbes growth (Ruess and McNaughton 1987; Hobbs 1996). This would temporarily enhance microbial activity and N mineralization explaining the higher release of N from litter of heavily *vs* lightly browsed plants. However, the higher levels of NO_3 in the HH rather than in the LL sites whether resulting from high nitrification rates from soluble urea or from low NO_3 utilization by grasses during the winter months, likely would support grass rather than woody plant compensatory growth. High concentration of NO_3 across the HH sites may be related to termite foraging-harvesting activities. Zaady et al. (2003) found consistent evidence of conversion of organic N and C to inorganic compounds (especially NO_3) due to harvester termites in the Negev desert. Whether such nutrient release would be available to sustain compensatory growth abilities of woody plants is still to be demonstrated. I found no variation in the proportion of litterbags visited by termites along the browsing/grazing gradients and we agree on the importance of fine scale patchiness in litter availability, as for example, the increased termite activity around woody plants as suggested by Tracy et al. (1998) from a desert grassland study. Finally, my data on leaf N content in the early wet and dry seasons, suggest that heavily browsed *Acacia nigrescens* trees may adopt an efficient mechanism of N remobilization from leaves to perennial organs which likely starts long before the beginning of the dry season (see Tolsma et al. 1987).

My second hypothesis was also accepted since the most palatable woody species (*Securinega virosa*) had higher decomposition rates than straw, and comparatively had lost more litter mass than the other less palatable species (Table 2; *Euclea, Maytenus, Combretum*). Interestingly, the less palatable species tended to create monospecific stands of different size, patchily distributed regardless browsing-grazing levels. This suggests that nutrient cycling may be negatively affected at a local scale within monospecific stands of woody species with slow decomposing litter.

To conclude, my main hypothesis is that ungulate browsing in a euthropic savanna affects nutrient cycling through two different processes: (1) promoting a positive feedback loop with highly palatable woody plants, which accelerates nutrient cycling and is triggered by tree pruning (i.e. effect similar to those observed for the "grazing lawns"; see du Toit et al. 1990); (2) decelerating nutrient cycling through long-term changes in quantity of organic matter returned to the soil rather than qualitative changes in plant community composition. I finally suggest that the movements and feeding activities of large mammalian herbivores in the HH sites might have enhanced soil erosion and compaction, as well as decreased water infiltration (see Cumming and Cumming 2003; Snyman and du Preez 2005), contributing over a long-term period to a reduction of soil depth (Fig. 4), and the availability of soil nutrients. Although I showed important interactions across tree palatability, litter decomposability, soil fertility, and disturbance by mammalian herbivores, future research should closely address the linkages between below- and above-ground processes, as well as track N, C fluxes within the plant-browser system.

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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

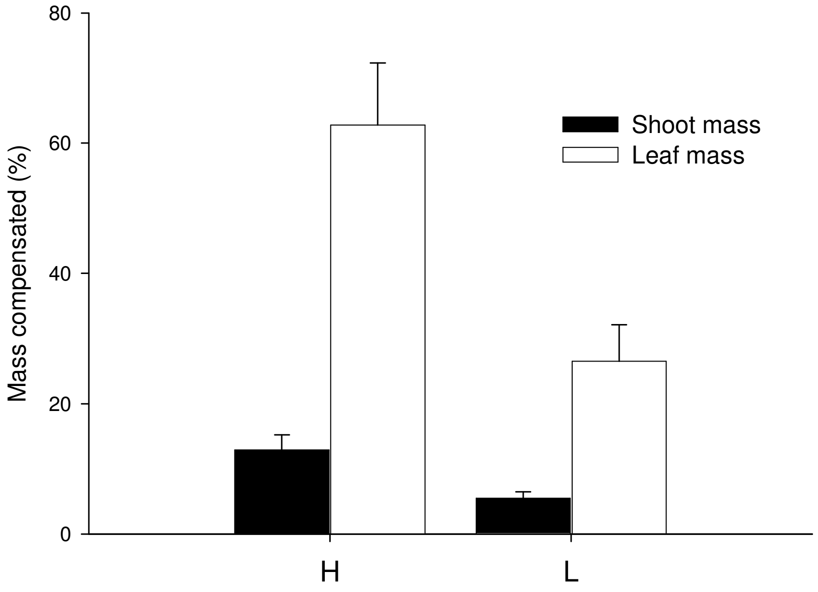

Fig. 5.1. Mass compensated (%) in shoots and leaves of heavily browsed (H) and lightly browsed trees (L) of *Acacia nigrescens* 9 months after artificial clipping.

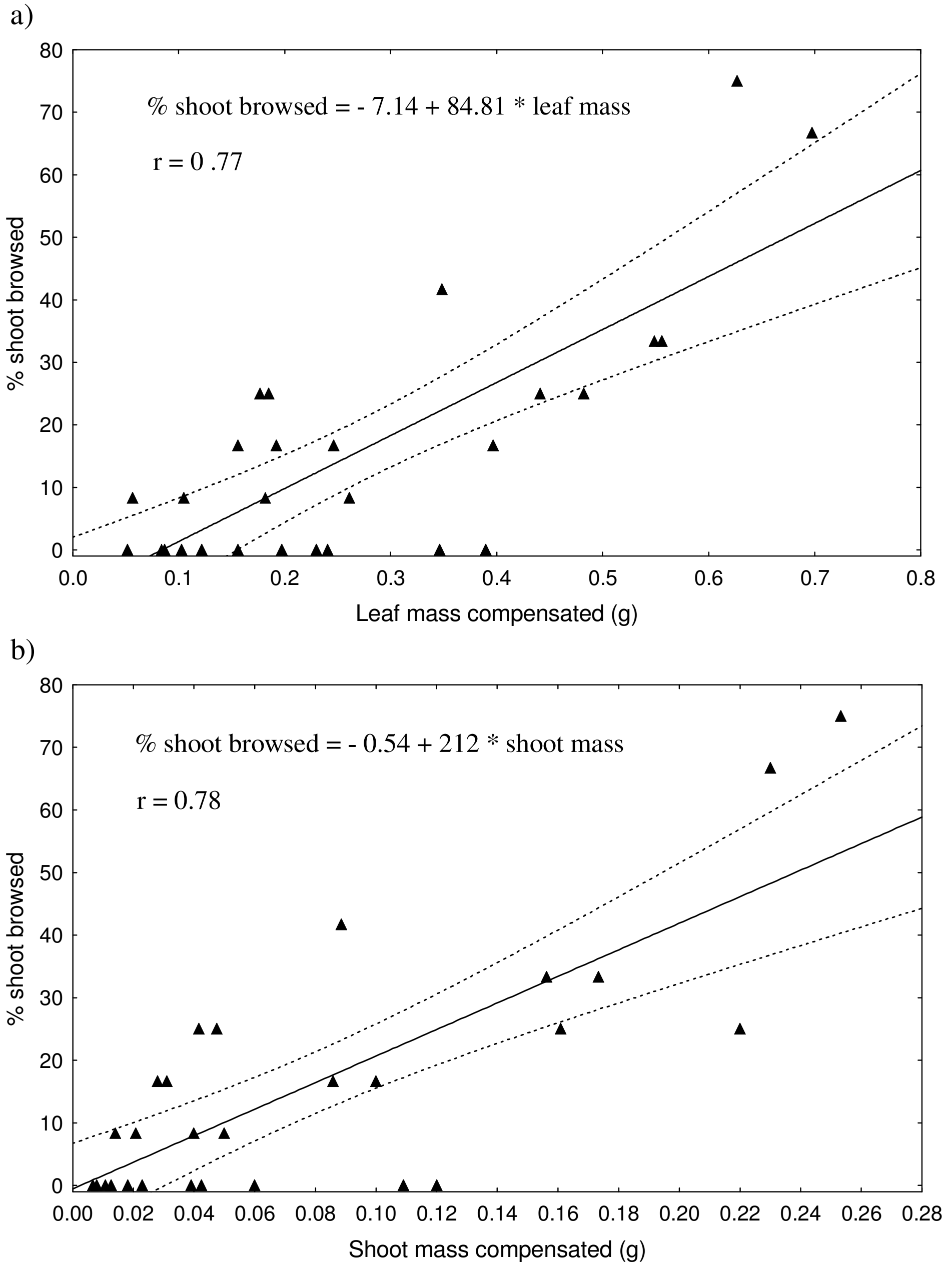

Fig. 5.2. Results from Spearman rank R correlation of both leaf (a) and shoot mass (b) compensated in heavily and lightly browsed trees after artificial clipping vs percentage of browsed shoots around the canopy tree.

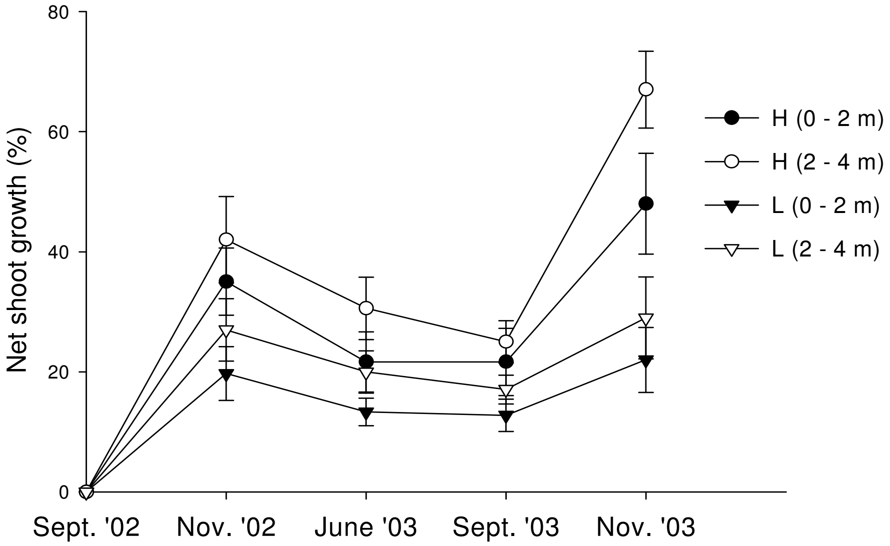

Fig. 5.3. Mean net shoot growth (%) within branches of heavily (H) and lightly (L) browsed *A. nigrescens* trees at two different canopy height levels (0-2 m and 2-4 m) measured at five time intervals.

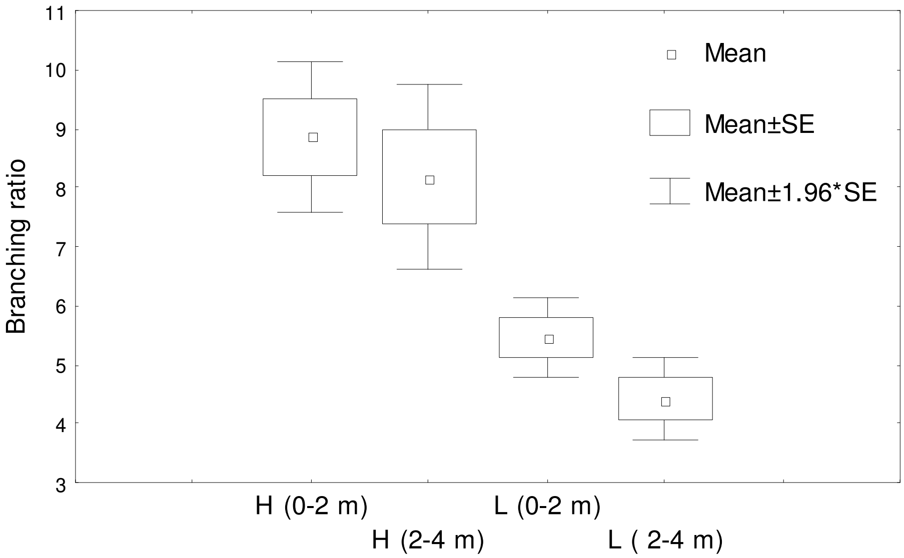

Fig. 5.4. Results from Friedman ANOVA and Kendall Coeff. of Concordance on branching ratio differences between browsing levels (H = high browsing; L = low browsing) and between canopy height levels (0-2 m and 2-4 m).

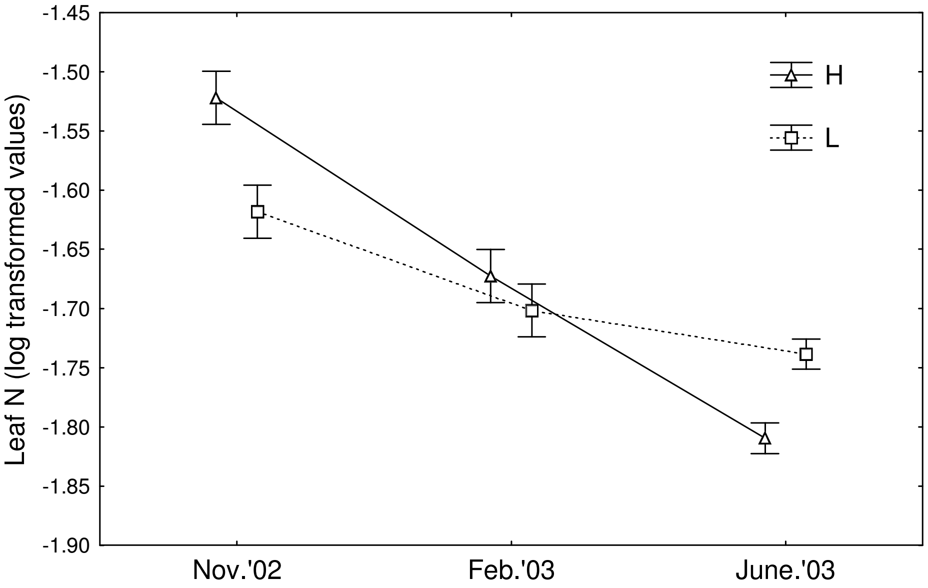

Fig. 5.5. Plotted results from ANOVA of leaf N content in heavily (H) and lightly (L) browsed *Acacia* trees depending on seasonality.

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.

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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;

- 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.

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).

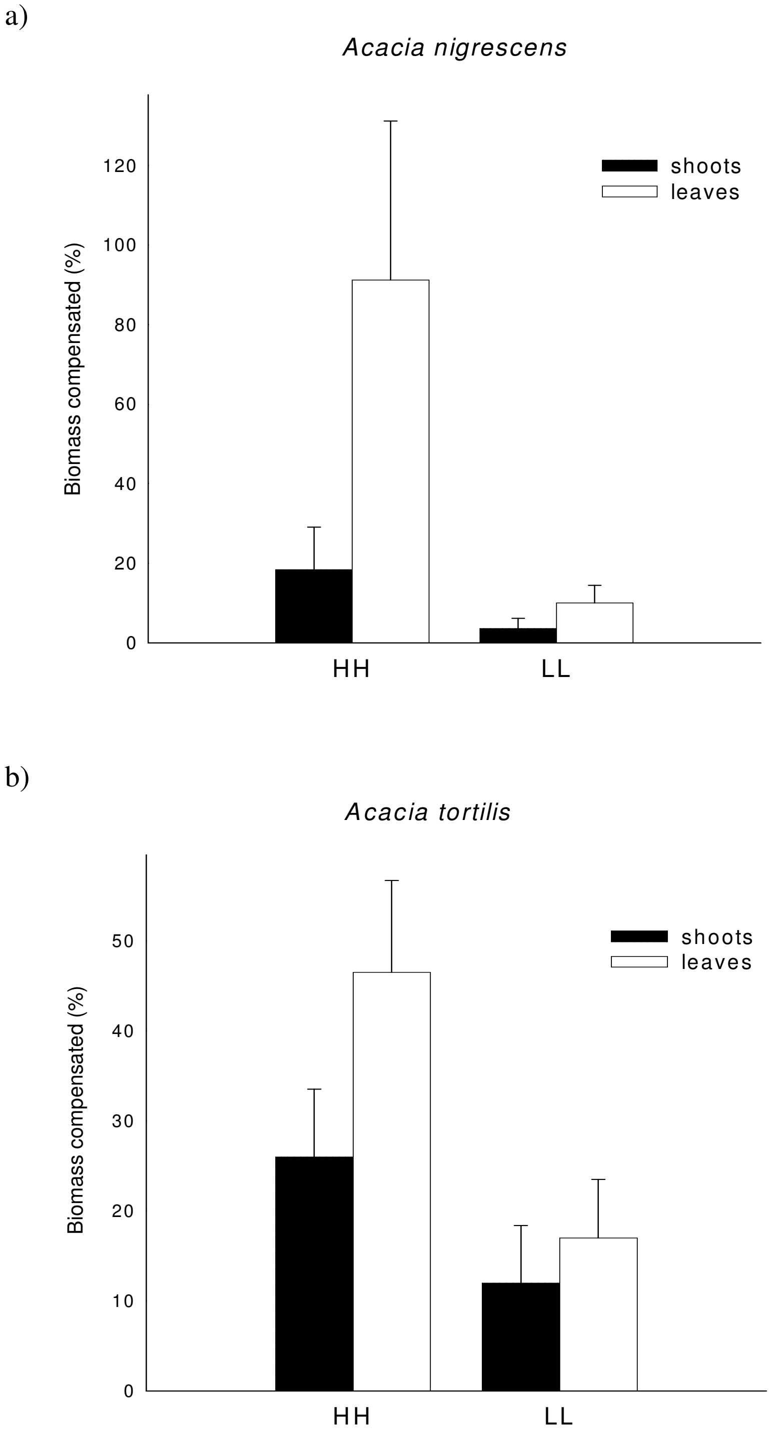


Fig. 6.1. Biomass compensated in leaves and shoots by gullivers of *Acacia nigrescens* (a) and *Acacia tortilis* (b) after 9 months from severe artificial clipping.

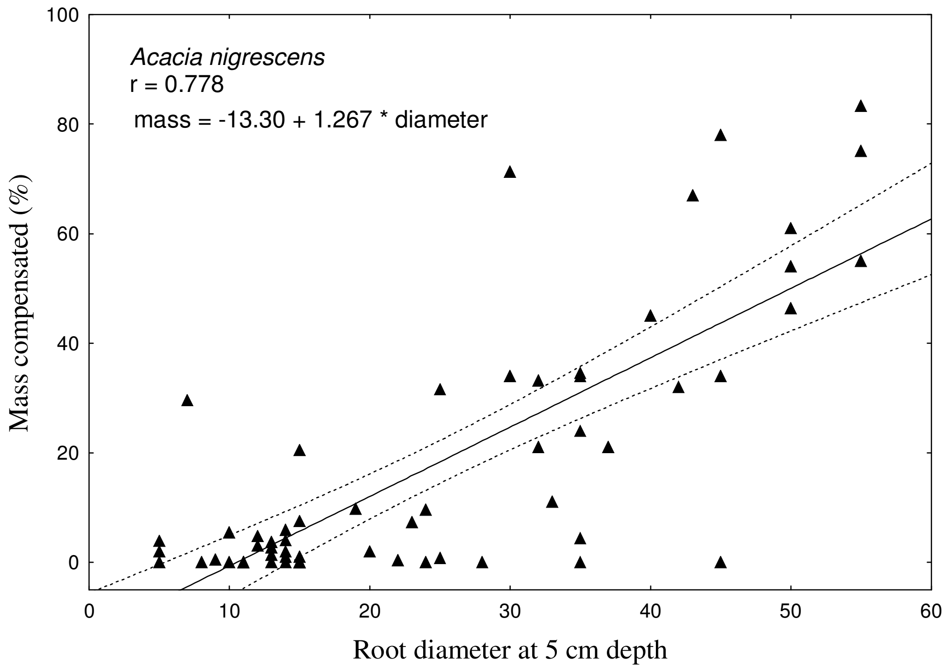
Table 6.1. MANCOVA results for the effects of browsing, species identity and browsing-species interactions on five morpho-functional traits. Proportion of browsed shoots was used as covariate. Response variables were max height, max width, stem number, diameter ground level and root diameter 5 cm depth.

	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.



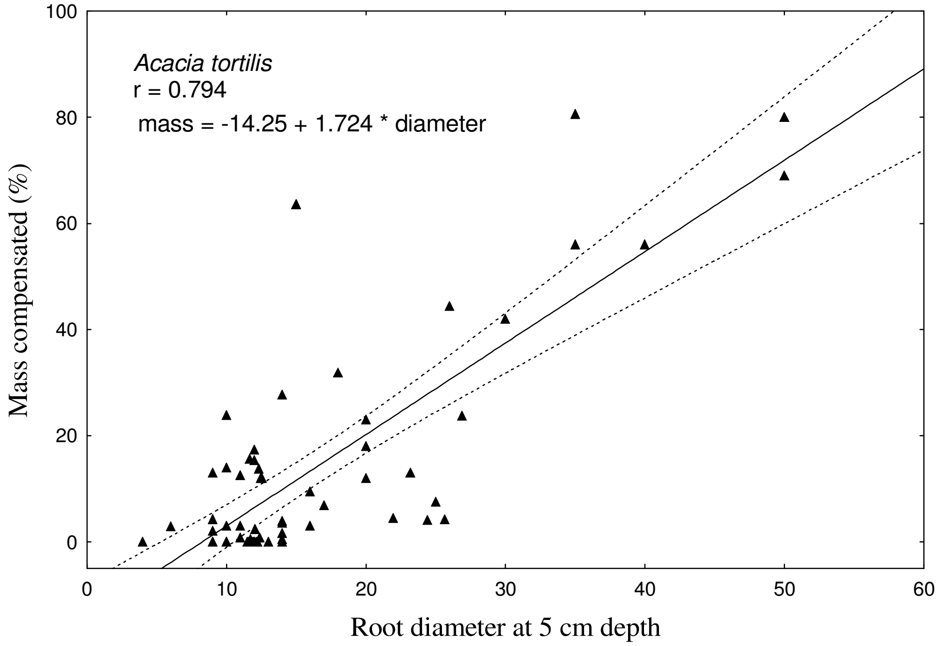


Fig. 6.2. Results from Pearson correlation matrix between root diameter at five cm soil depth and percentage of mass compensated in *A. nigrescens* and *A. tortilis* after 9 months from artificial clipping.

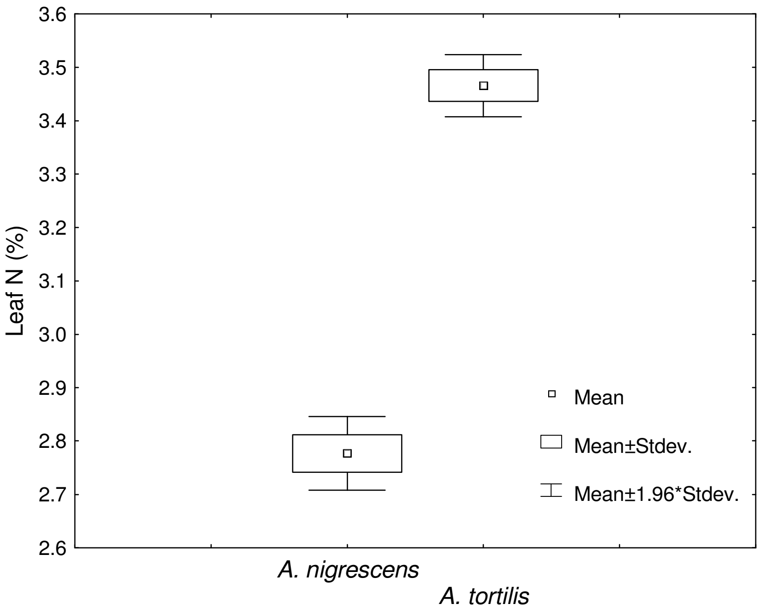


Fig. 6.3. Mean percentage of leaf N concentration from samples of 10 individuals of *A. nigrescens* and *A. tortilis* collected during the main growing season (November).

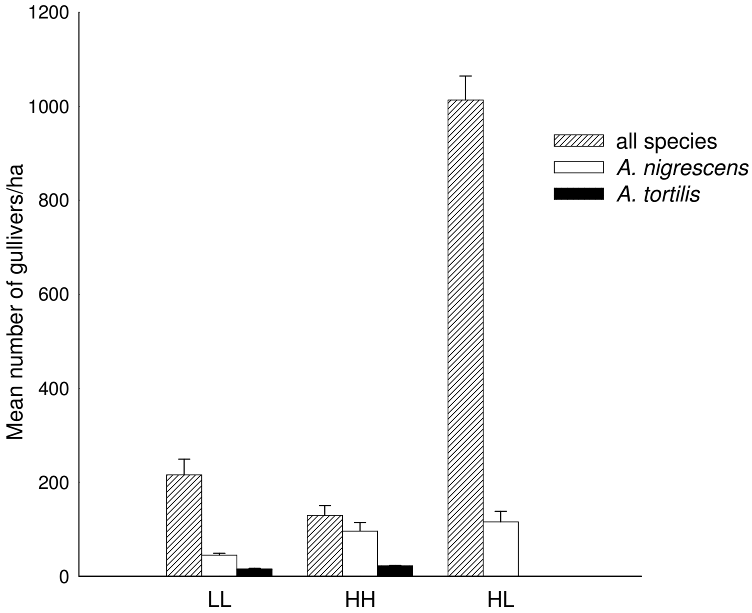


Fig. 6.4. Density of plant individuals < 50 cm in height of woody species recorded among 90 plots established between 3 sites along a browsing-grazing gradient (HH = heavily browsed-heavily grazed; HL = heavily browsed-lightly grazed; LL = lightly browsed-ligthly grazed).

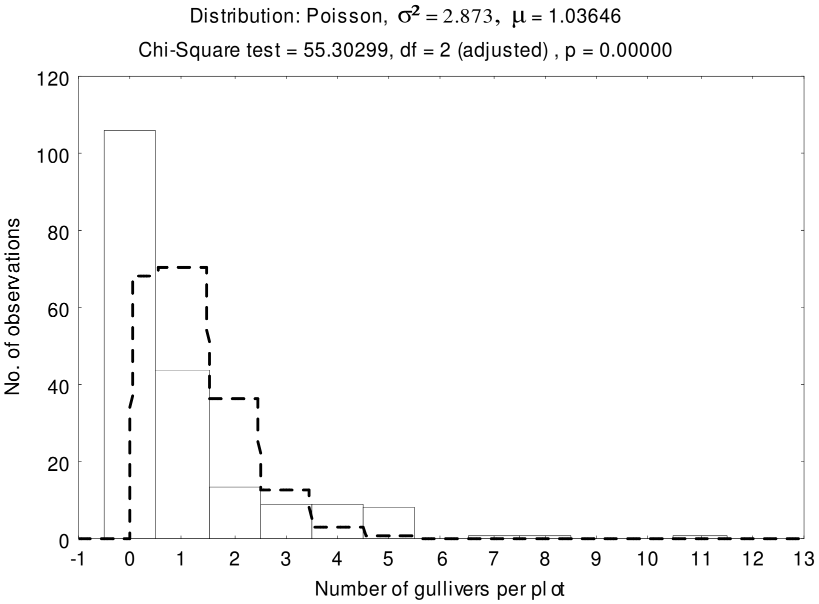


Fig. 6.5. The observed frequency of individuals of *A. nigrescens* recorded in each plot across heavily browsed sites (HH and HL sites) and the distribution expected from the Poisson distribution (dashed line).

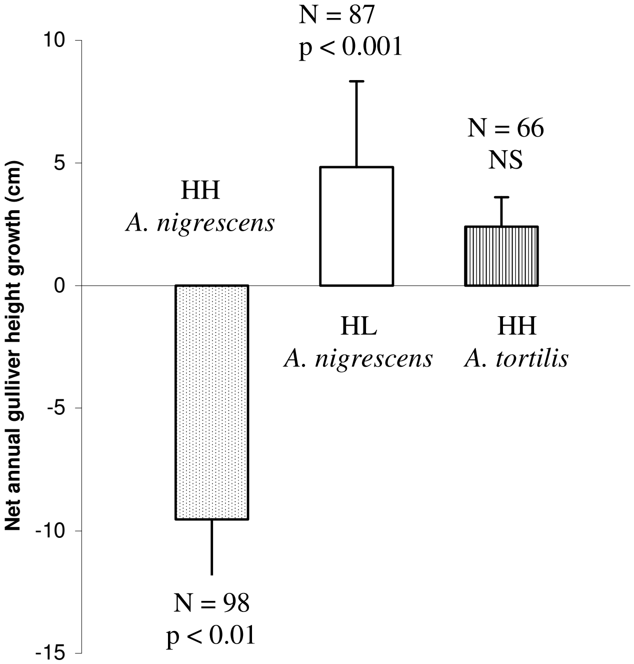


Fig. 6.6. Net changes in annual gulliver height growth (cm) of randomly selected individuals distributed along the browsing-grazing gradient.

6.5 DISCUSSION

6.5.1 Gulliver resprouting abilities

Overall, my results showed high resprounting 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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CHAPTER 7

Ungulate browsing and plant defensive traits: modelling changes in plant productivity and soil nutrient availability in savanna

Abstract

I propose a simple simulation model that makes predictions on the effects of ungulate browsing on changes in plant productivity and soil nutrient availability in a semi-arid eutrophic savanna. I assumed that percentage of yearly plant biomass lost as leaves and stems due to browsers is dependent upon plant defensive stategy (i.e. resistance and tolerance). Hence browser-tolerant plants experience high damage but show high compensatory growth abilities rather than relying on physical or chemical defence. If we Holding constant default parameters for the model runs, the results show that resistant plants have low nutrient requirements, reduce soil nutrient uptake, produce less compensatory biomass, and keep soil resources at higher levels than tolerant plants. On the other hand, tolerant plants have high nutrient requirements, increase soil nutrient uptake and potentially grow faster than resistant plants. However, populations of browse-tolerant plants can be maintained only at suitable nutrient supply rates (e.g. mineralization rates), which are highly variable in semi-arid African savannas. Moreover, when costs related to the increased resprouting abilities were considered for early plant life-history stages, then tolerant plants decreased productivity more than resistant plants. Modelling results partially confirm those from empirical data collected during a two-year vegetation survey in a southern African savanna where spinescent *Acacia* trees predominate within the vegetation community. However, field observations and literature show that many savanna woody species may often rely on both resistance and tolerance traits. I suggest that the existence of these functional types in semi-arid eutrophic savannas may be explained by the fact that (1) costs related to resistance traits (i.e. spines) are relatively low and amortized overall several years, and (2) tolerant traits, such as enhanced plant compensatory growth abilities, may rely on different nutrient source-sinks (i.e. N_2 fixation, plant internal N remobilization, indirect positive effects of browsers on

mineralization rates via the root system etc.) other than those provided by leaf litter or manuring by mammalian herbivores.

KEY WORDS: *Acacia*, ALLOCATE model, compensatory growth, resistance, tolerance

7.1 INTRODUCTION

Plant responses to damage induced by large mammalian herbivores have been addressed at levels ranging from tree species (Danell et al. 1985; Young 1987; du Toit et al. 1990; Edenius et al. 1993; Young and Okello 1998; Bergström et al. 2000; Oba et al. 2000), through plant communities (Jachmann and Croes 1991; McInnes et al. 1992; Liang and Seagle 2002; Augustine and McNaughton 2004) to ecosystems (Pastor et al. 1988; Pastor and Naiman 1992; Ritchie et al. 1998; Wardle et al. 2001; Bardgett and Wardle 2003). Empirical and theoretical studies have demonstrated that such responses have important consequences for primary productivity and mediate interactions between producers, consumers, and decomposers (McNaughton et al. 1988; Pastor et al. 1988, 1997; Bryant et al. 1991; Ritchie et al. 1998; de Mazancourt and Loreau 2000; Bardgett and Wardle 2003). Qualitative and quantitative plant responses to herbivory are likely dependent on levels of habitat resources (Coley et al. 1985), which influence from the “bottom-up” the type of defensive trait adopted.

Plants may enhance either chemical or physical *resistance* traits (*sensu* Strauss and Agrawal 1999) to reduce the amount of biomass removed by herbivores (Cooper and Owen-Smith 1985, 1986; Young 1987; Gowda 1996) or may show *tolerance* (Strauss and Agrawal 1999; Chase et al. 2000) by enhancing compensatory growth abilities to recover from mass loss due to herbivore damage (Dangerfield and Modukanele 1996; Oba 2000; Abu-Zanat et al. 2004; see Strauss and Agrawal 1999 for review). Differences in plant resistance and tolerance traits within vegetation communities may have important ecological and evolutionary implications (Chase et al. 2000), and it is likely that a trade-off between these two opposite defensive traits occurs depending on the interplay of key environmental constraints (Rosenthal and Kotanen 1994). Moreover, the type of defence adopted may be related to important plant eco-physiological traits, such as leaf palatability, relative growth rate or nutrient use efficiency (see Ritchie et al. 1998).

Former hypotheses, which aimed to explain patterns of plant responses to herbivory (see Stamp 2003 for review), have focused on cost/benefits of different defensive traits according to tradeoffs across plant growth-defence-reproduction processes (Lerdau and Gershenzon 1997). We might then expect highly protected resistant plants to have high costs associated with increased mechanical or chemical defences (see Chase et al. 2000), and would grow slower than less protected tolerant plants, which rely on high compensatory growth abilities when subjected to high mass loss rates. Nonetheless, this may have consequences on plant nutrient requirements (i.e. nutrient uptake rates), which in turn affects availability of soil nutrients (Ritchie and Tilman 1995; Ritchie et al. 1998). For example, in temperate and boreal forests ungulate browsers preferentially feed on tolerant, fast-growing plants (i.e. pioneer woody species in the early stages of vegetation succession) than on more resistant unpalatable woody species (i.e. evergreens) with important implications for both plant community composition and ecosystem functioning (Pastor 1988, McInnes et al. 1992; Kielland and Bryant 1998; Ruess et al. 1998). Therefore, simulation models have been proposed in the last few decades to better predict the effects of ungulate browsing on forest structure-dynamics, as well as to support decision-making processes for forest management (Jorritsma et al. 1999; Kramer et al. 2003; Weisberg and Coughenour 2003; Tremblay et al. 2004 for review).

Whether these complex gap models were spatially explicit or individual based, great attention has been paid to key parameters, such as plant leaf area and light-use efficiency of simulated tree species to evaluate browsing effects on plant community structure and patterns of vegetation succession. However, there is a need to address how ungulate browsing can affect plant productivity and the soil nutrient pool according to opposing plant defensive traits (i.e. resistance *vs* tolerance) in ecosystems where light is not a major constraint in structuring the vegetation community. A good example is the *Acacia* savannas of eastern and southern Africa, which have co-evolved with a high density and variety of large mammalian herbivores (du Toit and Cumming 1999; Olff et al. 2002).

Since the investment in different plant defensive traits indirectly influence plant productivity and soil nutrient uptake (see Lerdau and Gershenzon 1997), a modelling approach that addresses such interactions may improve our understanding of the mechanisms affecting nutrient cycling within the plant-browser system.

Here, I propose a simple simulation model applicable to a semiarid eutrophic southern African savanna for which empirical data had been collected during a two-year survey (see Chapter 3, 4, 5 and 6). The model simulates the effects of ungulate browsing on woody plants, which alternatively show three different defensive traits: high tolerance, high resistance and an intermediate defensive trait. The model is neither thought to simulate vegetation dynamics nor interspecific competition. The aim of the model is to quantify the effects of different plant defensive traits on changes in plant biomass and in the concentration of available soil nutrients along a strong browsing gradient.

7.1.1 Conceptual definition

Tree pruning by ungulate browsers causes mass loss in woody plant species and affects plant morpho-functional traits. This influences resource allocation patterns to different plant compartments such as roots, stems and leaves (Fig. 7.1). The amount of biomass removed also depends on the type of defensive trait adopted, which is related to important plant eco-physiological traits. For example, tolerant plants must grow quickly and allocate biomass to new leaves and stems after severe herbivore damage. This in turn modifies the use of soil resources by woody plants (e.g. plant nutrient requirements), and in a long-term period affects soil nutrient levels (Fig. 7.1). It must be noticed that the model doesn't incorporate complex plant-animal interactions, neither feedbacks within the plant-browser-soil system. Moreover aspects related to turnover rates of roots and the activities of fossorial animals were not incorporate into the model to limit as much as possible complexity. Hence the simulation model focuses on the effects of tree pruning on both changes in plant biomass and soil nutrient availability along a strong browsing gradient and its predictions must be interpreted under the above-mentioned limitations. I started considering the important theoretical framework of the model ALLOCATE, proposed by Tilman (1988), which already incorporates critical aspects and mechanisms of plant growth according to key environmental factors. ALLOCATE can make predictions on the outcomes of plant interspecific competition according to varying light and plant resource requirements, but interspecific competition was not considered in my model. Instead, I specifically focus on individual plant species, which are assumed to grow in monospecific stands.

7.1.2 Assumptions

First, light is not considered a key factor among those structuring woody vegetation communities in open eutrophic savannas (see Sinclair and Norton-Griffiths 1979; Huntley 1982). Second, the model assumes that plant growth is affected by soil nutrient availability, which in turn depends on nutrient requirements by plants (Tilman 1988).

Plant nutrient requirements are affected by nutrient supply rates, as well as by the amount of biomass removed by browsers according to varying defensive traits. Third, I assume that plant individuals grow under density independent loss rates. Finally, the model is neither spatially explicit nor individual based, and has only a vertical structure, therefore all the individuals of the same cohort experience the same nutrient availability and grow under the same environmental constraints.

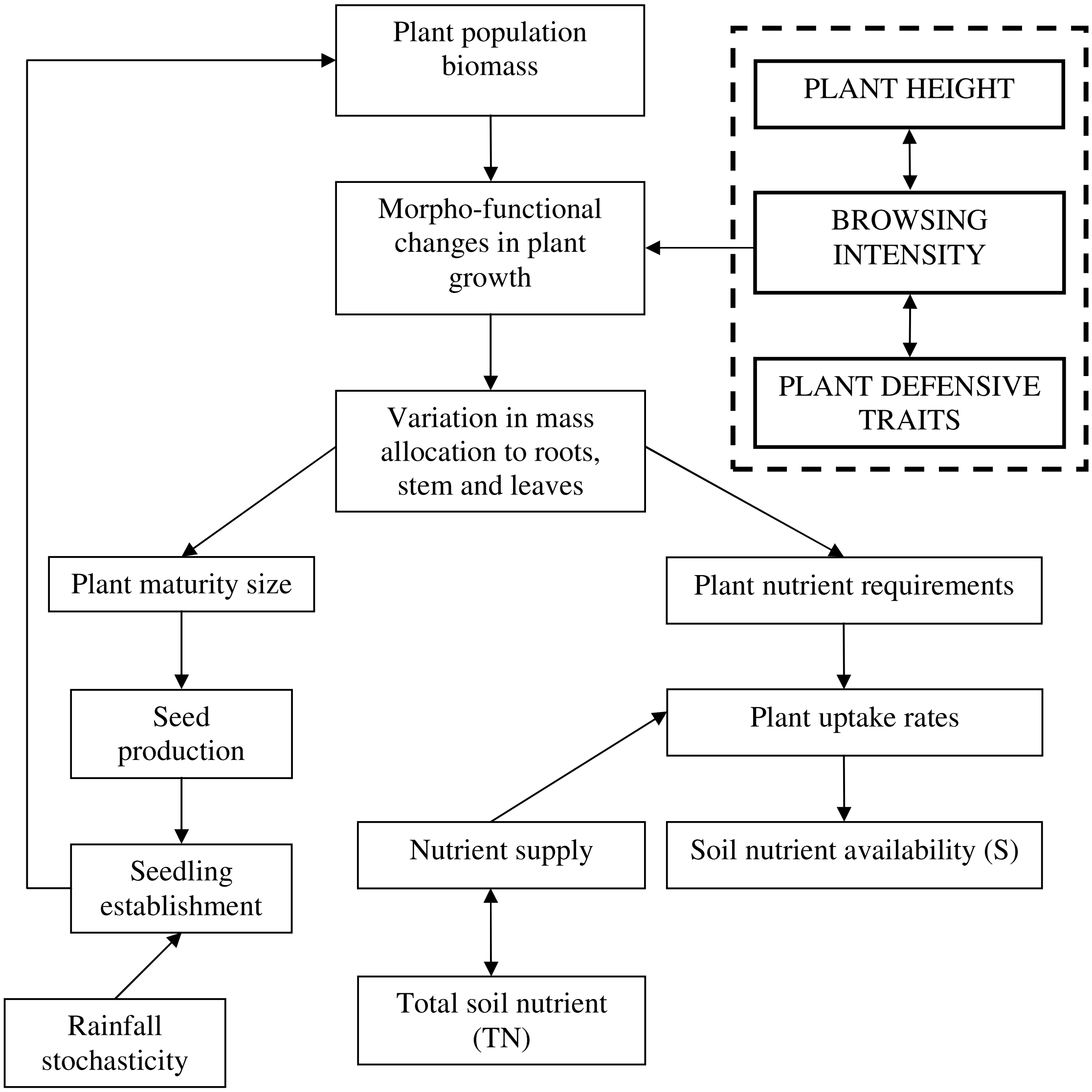


Fig. 7.1. Conceptual model of the potential effects of browsing intensity, defensive traits and plant height on changes in plant biomass and soil nutrient availability (S). Note – the above elements of the system are those that were incorporated in the model only. The influence of browsing on litter quantity, quality and decomposition (for example) were not included. Moreover important feedbacks from leaf litter which may better incorporate nutrient cycling were excluded for simplicity.

7.2 OPERATIONAL DEFINITION

Specific formulae used to simulate plant growth can be found in Tilman (1988) and are summarized below as part of the ALLOCATE model. Meanwhile, I introduced definitional and ecological rules (*sensu* Jeltsch et al. 1997) to optimize my modelling approach on ungulate browsing-woody plant interactions in a eutrophic African savanna.

7.2.1 Specific formulae of the ALLOCATE model

A) A size-structured population with individuals germinating from seeds and undergoing continuous vegetative growth until reaching adult size was considered. Starting as seed the individual allocates biomass according to varying proportional allocation to roots, stems and leaves. Biomass to roots (BR), leaves (BL) and, stem (BS) increases daily due to allocation of new photosynthate (DBt, see Table 7.1) to different plant compartments as follows:

BR = rAR*DBt + BR;

BL = rAL*DBt + BL;

BS = rASt*DBt + BS;

Here rAR, rASt and rAL are the proportional allocation, respectively to roots, stems and leaves (see Table 7.1). According to phenological traits of common *Acacia* trees growing in a eutrophic savanna (e.g. *Acacia nigrescens, A. tortilis, A. exuvialis*; see Coates Palgrave et al. 2002), I consider one simulated year including 180 days during which woody plants could actively photosynthesize before to shed their leaves.

B) Photosynthetic efficiency is nutrient dependent and production of new photosynthate is positively correlated to leaf biomass according to the function (modified from Tilman 1988):

DBt = ((BL*r*C)/C+K)) – RESP;

Here, DBt is the amount of photosynthate produced daily, RESP includes plant respiration rates (see below), r is the maximal photosynthetic rate, K is an half saturation constant for soil nutrients, C is the effective availability of soil nutrients (see Table 7.1) and is calculated, as follows: C = S * (BR/BL). Here S is the measurable concentration of available forms of the limiting nutrient in the soil. The sum of respiration rates of leaves, roots and stem was expressed as:

RESP = (BR*RR+BS*RS+BL*RL), where RR, RS and RL are the per unit biomass respiration rates for roots, stem and leaves (see Table 7.1).

Table 7.1. State variables, names and unit measure used for the simulation runs.

Symbol	Variable name	Unit measure
BR	Root biomass per individual of each cohort	g
BL	Leaf biomass per individual of each cohort	g
BS	Stem biomass per individual of each cohort	g
rAR	Proportional allocation to roots	Scaled 0 - 1
rAL	Proportional allocation to leaves	Scaled 0 - 1
rASt	Proportional allocation to stem	Scaled 0 - 1
HT	Plant height	m
DBt	Amount of photosynthate produced daily	g g^{-1} d^{-1}
C	Effective availability of soil resource	mg/kg
TN	Total nutrient pool in the soil	mg/kg
S	Availability of the limiting soil nutrient	mg/kg
a	Proportional rate constant defining resources supply rates	Scaled 0-1
BN	Total amount of nutrient contained in plant biomass	mg/kg
Supply	Rate of nutrient supply	mg/kg

Table 7.2. Parameter symbols, names and default values used for the simulation runs.

Symbol	Parameter name	Default value
Bseed	Seed biomass	0.02 g
RR	Respiration rates per unit of root biomass	0.024 g g^{-1} d^{-1}
RL	Respiration rate per unit of leaf biomass	0.03 g g^{-1} d^{-1}
RS	Respiration rate per unit of stem biomass	0.02 g g^{-1} d^{-1}
NR	Nutrient content per unit biomass of root	0.003 mg g^{-1}
NL	Nutrient content per unit biomass of leaf	0.002 mg g^{-1}
NS	Nutrient content per unit biomass of stem	0.004 mg g^{-1}
NSeed	Nutrient content per unit biomass of seeds	0.004 mg g^{-1}
r	Maximal rate of photosynthesis per unit leaf biomass	0.08 g g^{-1} d^{-1}
K	Half saturation constant for nutrient	0.5

C) Nutrient availability in the soil is determined by mineralization rates and rates of nutrient uptake by plants. Soil nutrients are taken up by plants in the amount required to meet the nutrient demand related to the production of stem, roots, leaves and seeds (Tilman 1988). Nutrient uptake is determined by adding nutrients required per unit biomass of roots, stem, leaves and seeds according to tree reproductive age (seeds were produced only when a plant reached adult size). Nutrient supply rates (i.e. mineralization rates) of the limiting soil resources result from the "equable" mode through which they are supplied to the soil (Tilman 1982). This represents a useful approximation of the amount of available forms of the limiting resource in the soil such as N or P. The nutrient supply is calculated according to Tilman (1988) as follows:

Supply rate = a*(TN-BN-S);

Here a, is the proportionality rate constant defining resource supply rates (Tilman 1982), TN is the total amount of nutrient in the soil, and BN is the total amount of nutrient in plant biomass and depends on plant uptake rates.

7.2.2 Aspects related to the plant-browser system in a semi-arid eutrophic savanna

Photosynthetic and respiration rates

To simulate plant growth in a southern African savanna, photosynthetic, as well as respiration rates for savanna woody plants were deduced from empirical data and parameterized according to average values resulting from eco-physiological studies in semi-arid environments as southern African savannas and/or sub-tropical biomes (see Medina 1982; Cresswell et al. 1982; Eamus et al. 1999; Reich et al. 1998; Hoffman and Franco 2003; Midgley et al. 2004). Nutrient content per unit plant biomass was also estimated according to studies of savanna woody species (Tolsma et al. 1987; Atkin et al. 1998; Reich et al. 1998; Schmidt and Stewart 2003; Midgley et al. 2004; see also Scholes et al. 2003, Table 7.2).

Tree height and maturity size

Based on information of feeding height stratification among savanna ungulate browsers (see du Toit 1990; Woolnough and du Toit 2001) and according to field observations on pod production, I introduced an ecological rule assuming that individual plants are able to produce seeds once they have reached 4 m in height, having then escaped from browsing damage by the tallest browsers, namely giraffes (*Giraffa camelopardis*). Plant height is considered dependent on biomass allocated to stem, is thus proportional to the square root of stem biomass (Tilman 1988).

Seed production

I tried to estimate the number of seeds produced per year by common *Acacia* species using data from the literature. However, due to limited published information and the highly variable environmental influences on seed-set (see Wagner 1997; Brown et al. 2003; Walters and Milton 2003), I assumed (according to Tilman 1988) that current photosynthate is entirely devoted to seed production once individual plants have reached the maturity size. This represents a simplification of the model by excluding constant eco-physiological processes, such as the allocation of new photosynthate to respiration, branch and root elongation, and the replacement of biomass due to high turnover of leaves and fine roots once the individual has reached maturity size. It follows that the number of seeds is equal to the ratio DBt/seed mass. Seed biomass was estimated using literature for *Acacia* species in sub-tropical biomes and/or semi-arid environments (see Brown et al. 2003; Moles and Westoby 2003).

Rainfall and seedling establishment

Although the magnitude and seasonality of annual rainfall events may play an important role in shaping vegetation communities of African savannas (Walker and Noy-Meir 1982; Walker 1987), I assumed that savanna woody plants have evolved efficient eco-physiological mechanisms to deal with rainfall stochasticity, regardless browsing pressure or fire regime such as, for example, increased nitrogen use efficiency at increasing moisture availability (Midgley et al. 2004). Hence, plant-available moisture (PAM, see Walker 1993) was not considered a factor influencing browsing effects on woody plants with different defensive traits across the same landscape type. Instead I considered PAM to influence the chances of seedling establishment. Indeed, the number of seedlings that germinate and survive their first year is very low in semi-arid savannas, and probably only in exceptionally wet years may they escape herbivory and fire to become established as a cohort of young trees (Bond and van Wilgen 1996). Therefore, based on an evaluation of rainfall data from weather stations distributed across the Kruger National Park (see Venter et al. 2003), I assumed that wet episodes when a woody seedling may successfully establish occur in ~ wet 20% of the overall simulated years. Then the number of seedlings established during a wet year is proportional to the total amount of precipitation occurred, which is given by a random number generator sampled from a normal distribution.

Defensive traits

As a definitional rule, three plant defensive traits (Di) were introduced as follows: resistant plants (D_1), intermediate (D_2) and tolerant plants (D_3). Hence, in our savanna system resistant plants are protected through either physical (e.g. spines) or chemical defences (e.g. tannins). They experience low browsing pressure as we might expect from a negative correlation between amount of biomass removed and the presence of efficient either mechanical or chemical defences (Cooper and Owen-Smith 1986; Bryant et al. 1991; Milewski et al. 1991; Gowda 1996). On the other side, tolerant plants, though partially protected by thorns and/or prickles, experience high browsing pressure (i.e. high mass loss) and show higher resprouting abilities (see du Toit et al. 1990; Chapter 5) than resistant plants.

Browsing intensity

According to empirical data (Chapter 3, 4, 5 and 6; Fornara *unpublished data*), three different browsing intensity levels (i.e. browsing gradient) were identified representing different amounts of leaf and stem biomass yearly removed by browsers, as follows: R_1 = high removal, R_2 = medium removal, R_3 = low removal. Therefore, under each browsing intensity level, plants with different defensive traits experienced different yearly removal rates (see below). Moreover, the amount of mass removed was associated with tree height since the shorter individuals are vulnerable to a higher number of browser species (du Toit 1990). Three height classes were then defined as follows: HT_1 = 0-1.5 m, HT_2 = 1.5-4 m, HT_3 > 4 m. Hence, the percentage of biomass yearly removed was imposed depending upon: (1) type of defensive trait adopted, (2) browsing intensity level, and (3) tree height class (see Table 7.3 for plants in the HT_1 height class).

Mortality

The number of individuals that survive the end of each year was calculated according to different mortality rates, which are applied depending on tree height. The highest mortality rates are applied to individuals shorter than 1.5 m, since they are damaged by the highest number of browser species and generally, mortality decreases with increasing tree height.

Table 7.3. Percentage of mass yearly removed from leaves (BL) and stem (BS) of individuals ranging between 0-1.5 m height (HT_1) along the browsing gradient (R_1 = high removal; R_2 = medium removal; R_3 = low removal) and according to different defensive traits (D_1 = resistant; D_2 = intermediate; D_3 = tolerant).

	D_1		D_2		D_3	
	BL (%)	BS(%)	BL (%)	BS (%)	BL (%)	BS(%)
R_1	20	20	35	30	50	40
R_2	10	5	30	20	35	30
R_3	5	2	20	10	25	15

7.3 RESULTS

Model sensitivity was tested varying in turn by ± 20%, parameter values and percentages of mass yearly removed from stem and leaves according to different defensive traits. The model was run for 100 years a single run was used for each parameter setting. This procedure has shown that the levels of variable values changed but the dynamics of the model and the effects on plant productivity and nutrient availability were not affected across defensive traits.

Only a limited number of allocation patterns to roots, leaves and stems allowed a plant population to growth and persist till the end of a simulation period of 100 years. Overall, within the range of feasible allocation patterns plant growth was possible when at least 40% of the current photosynthate was allocated to leaves (AL = 0.4). Regardless of defensive traits, increased browsing pressure ($R_3<R_2<R_1$) was positively associated with the availability of soil nutrients (Fig. 7.2 a, c, e) and negatively correlated with plant biomass (Fig. 7.2 b, d, f). This means that both tolerant and resistant plants increased productivity and depleted soil nutrients more efficiently at low than at high browsing intensities.

Among different allocation patterns (Fig. 7.3 a, b, c) tolerant plants reduced soil nutrients (S) at lower levels than resistant plants along the simulated browsing gradient (R_1, R_2, R_3). Consequently, for certain allocation patterns and at low browsing intensity (R_3; Fig. 7.3 a, b) populations of tolerant plants went extinct before the end of the simulated period for total exploitation of soil nutrients. This was also due to the fact that tolerant plants were able to produce a high number of offspring under low browsing pressure (see below).

The high exploitation of soil nutrients by tolerant plants in the model was primarily due to the high root:leaf ratio (BR/BL), which increased the effective availability of soil nutrient (C; Table 7.1) and in turn supported high nutrient uptake to enhance production of new leaves after browsing damage. Plants with intermediate defensive traits (D_2) appeared to be less efficient (Fig. 7.3) in reducing soil nutrients than tolerant and resistant plants for different allocation patterns considered (Fig. 7.3 a, b, c).

In this case the non-linear relationship between defensive traits was due to the different response of resistant plants (D_1), which were supposed to maintain available soil nutrients (S) at higher levels than intermediate species (D_2) since their higher efficiency in protecting leaves and the potential lower nutrient requirements. Instead, D_1 plants reduced soil nutrients more than D_2 plants (Fig. 7.3).

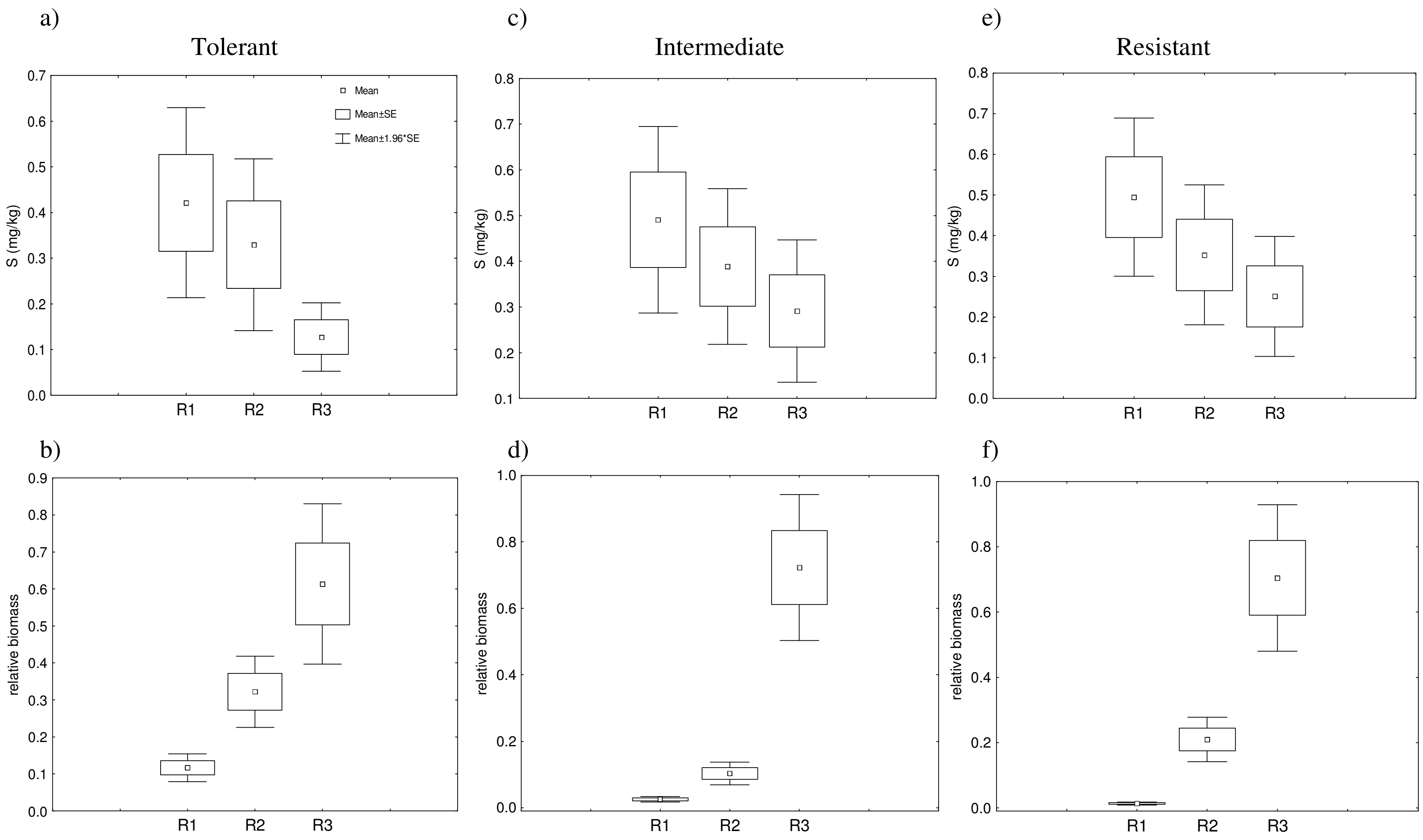
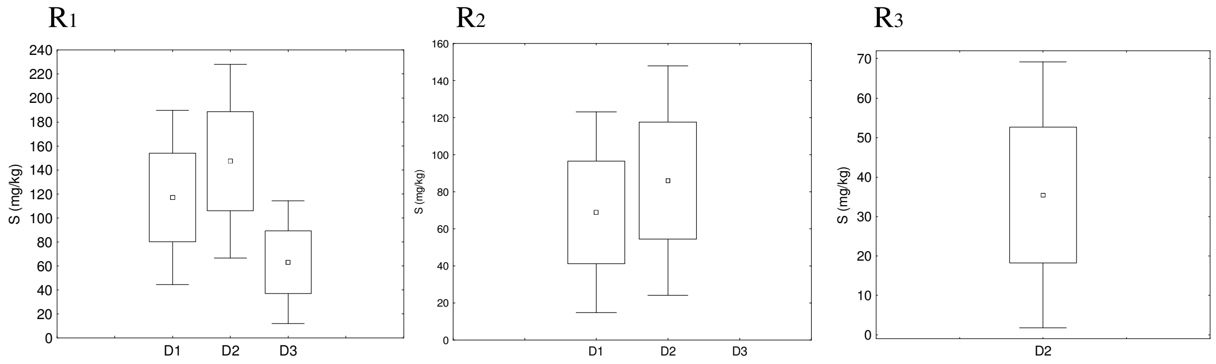
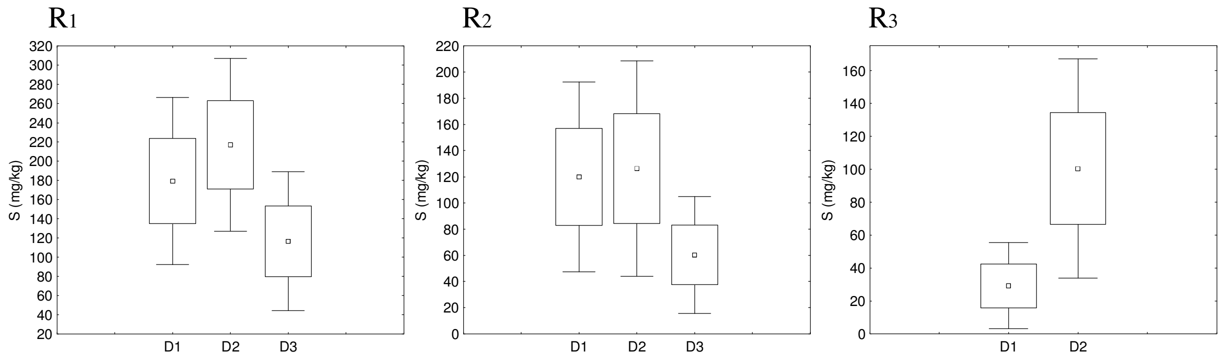


Fig. 7.2. Relative concentration of nutrient available in the soil (S) and relative biomass produced by a plant population under different browsing intensity (R_1 = high; R_2 = intermediate; R_3 = low) after a simulation period of 100 years. Individuals show respectively, high tolerance (a, b), intermediate defensive trait (c, d) and high resistance (e, f). Allocation patterns: AR=0.1, AS=0.5, AL=0.4.

a) AR = 0.3, AS = 0.3, AL = 0.4



b) AR = 0.2, AS = 0.4, AL = 0.4



c) AR = 0.1, AS = 0.5, AL = 0.4

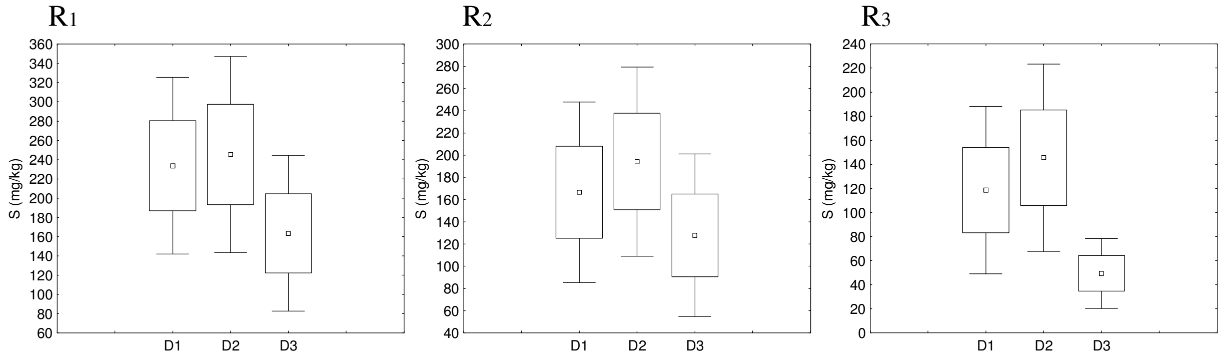


Fig. 7.3. Changes in soil nutrient availability (S) after a simulation period of 100 years according to different allocation patterns (a, b, c). S values (mg/kg) for each browsing level (R_1 = high; R_2 = medium; R_3 = low) and defensive traits (D_1 = resistant, D_2 = intermediate; D_3 = tolerant) were calculated as mean of varying nutrient concentration in the soil (TN). Rate of photosynthesis = 0.08 g g^{-1} d^{-1}.

The mechanism responsible for such result is likely explained by the trade-off between nutrient uptake rates high for D_2 plants since they experience high mass removal and productivity represented by the amount of photosynthate produced (high for resistant plants since they experience low mass removal). Simply, high leaf protection, conserved photosynthetic tissue which in turn increased productivity (DBt) and enhanced soil nutrient uptake more efficiently than for medium defended plants whose productivity was lower (due to high leaf removal).

In my simulations both tolerant and resistant plants increase plant biomass and reduce soil nutrients more efficiently than plants with an intermediate defensive trait (Fig. 7.3). This trend is also confirmed under different photosynthetic rates and along the browsing gradient (Fig. 7.4). When default parameters were held constant, tolerant plants always increased biomass and reduced soil nutrient availability more efficiently than plants with the other two defensive traits. This because mechanisms of plant growth in the model conferred costs to resistant plants in terms of reduced soil nutrients uptake, whereas they didn't lead to growth related costs for tolerant plants. Therefore D_3 plants could potentially deplete soil nutrients and quickly grow reaching maturity size faster than individuals showing the other two defensive traits even under high browsing pressure (Fig. 7.5). However, holding plant traits constant, a first disadvantage for tolerant plants appears to be their high nutrient demand to support fast growth. Indeed, populations of tolerant plants could be only sustained at high nutrient supply rates (Fig. 7.6).

To further investigate potential costs for tolerant plants I considered (without changing default parameters) the importance of the root system assuming that below-ground compartments represent important storage organs to support regrowth after damage (Fig. 7.7). For all plant defensive traits (D_1, D_2, D_3) the increased allocation to roots (from AR = 0.1 to AR = 0.3), enhanced plant productivity (Fig. 7.7). Moreover, in some cases high resistant (D_1) and medium defended plants (D_2) with a high proportional allocation to roots (AR = 0.3) were able to produce more biomass than those tolerant plants, which allocated less biomass to roots (Fig. 7.7). Although somewhat speculative I assumed that the high browsing pressure and consequent high mass removal from tolerant plants might have a negative impact on plant growth rates in early life-history stages (i.e. seedling-sapling) when individuals likely rely on root reserves for resprouting after herbivory (see Bond and Midgley 2003). For further simulations I then assumed that at the end of each year following browsing damage, the proportional allocation to roots for saplings (0-1.5

m in height), was reduced in direct proportion with the mass loss in above-ground organs (stem and leaves). My assumption finds justification in recent studies on functional responses of seedlings and lignotubers to artificial clipping, which show that carbohydrates reserves in roots are seriously depleted after severe and multiple defoliations (Canadell and Lopez-Soria 1998; Canham et al. 1999). Hence relative to whole plant biomass, tolerant saplings were yearly experiencing higher decreases in the proportional allocation to roots than resistant saplings in order to support higher compensatory abilities (i.e. higher allocation to leaves).

When mean plant productivity (photosynthate) was simulated for saplings under high browsing pressure, and allocation costs to roots are considered (Fig. 7.8), tolerant plants were less productive than resistant plants while intermediate plants still showed the lowest production of photosynthate. Accordingly, when I simulated relative time for an individual plant to reach adult size I found that resistant plants grew faster (in net effect) and produced more biomass when compared with the other two defensive traits (Fig. 7.9).

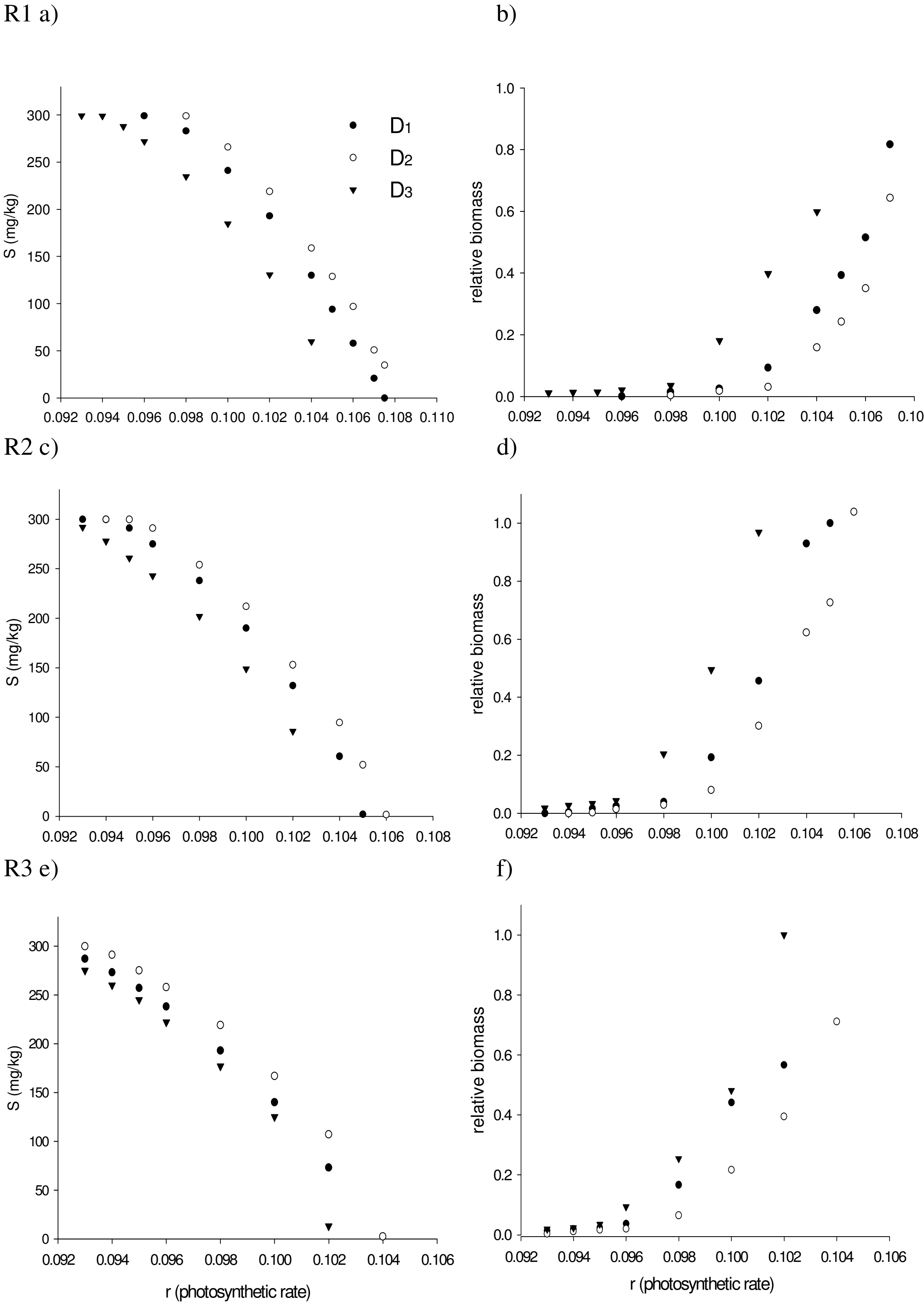


Fig. 7.4. Changes in soil nutrient availability (S) and relative biomass at increased photosynthetic rates for different defensive traits and browsing intesity levels. Allocation patterns as follows: AR=0.3, AS=0.3, AL=0.4, and total soil nutrient TN = 300.

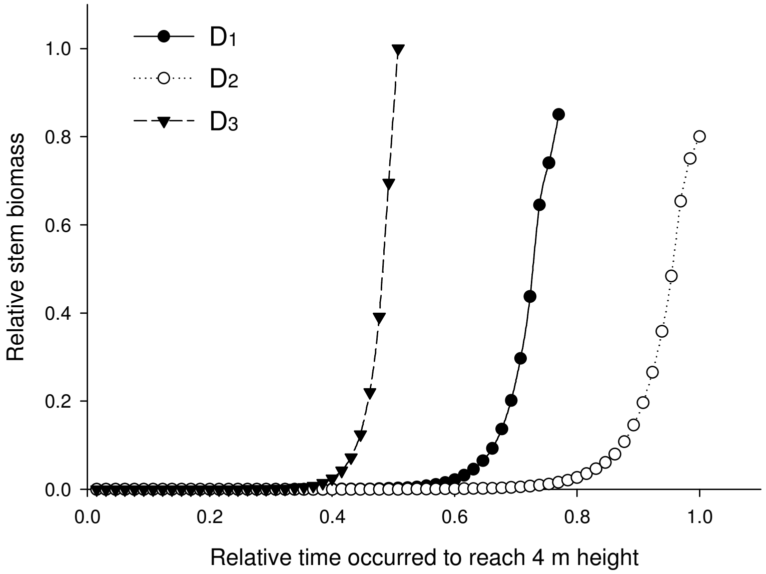


Fig. 7.5. Relative time occurred for an individual to reach adult size under high browsing (R_1) according to different defensive traits (Abbreviations as for Fig. 7.3) and not costs involved. Amount of nutrients in the soil, TN = 300, and allocation patterns: AR=0.2, AS=0.4, AL=0.4.

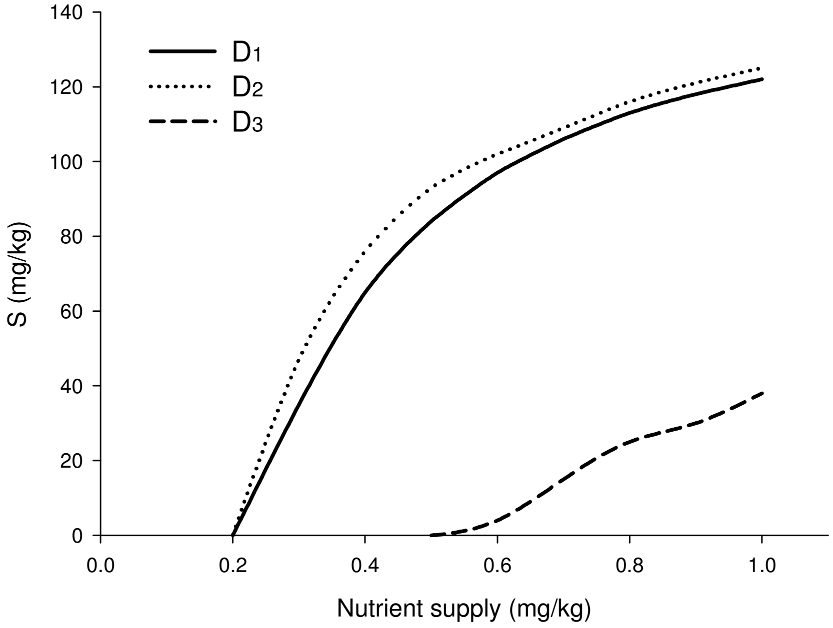


Fig. 7.6. Availability of soil resources to support plant growth after a simulation period of 100 years according to increased nutrient supply rates (i.e. mineralization rates) for different defensive traits (Abbreviations as for Fig. 7.3). R_1, TN=200, AR=0.2, AS=0.2, AL=0.4.

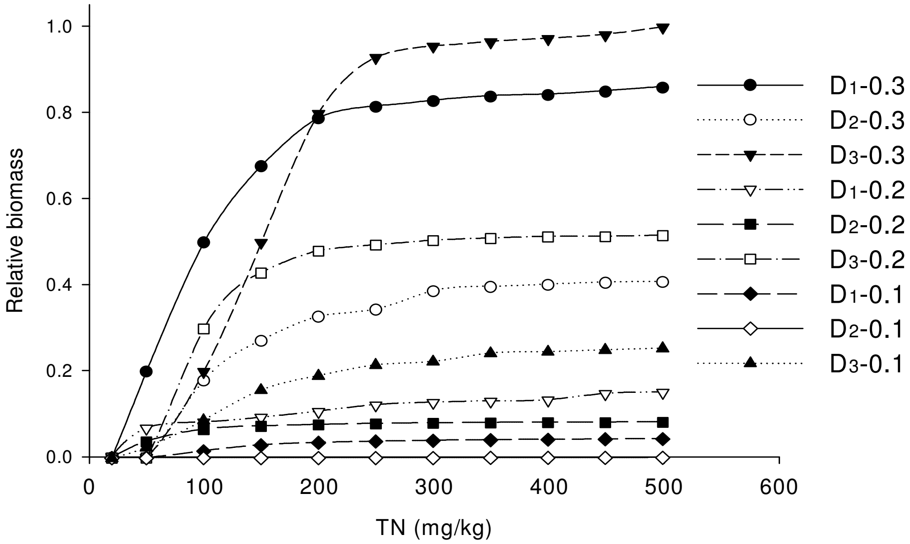


Fig. 7.7. Relative biomass produced by an individual, which alternatively shows the three defensive traits (D_1, D_2, D_3) and grows until to reach adult size (4 m height). Allocation patterns to roots (AR) are respectively: 0.3, 0.2 and 0.1.

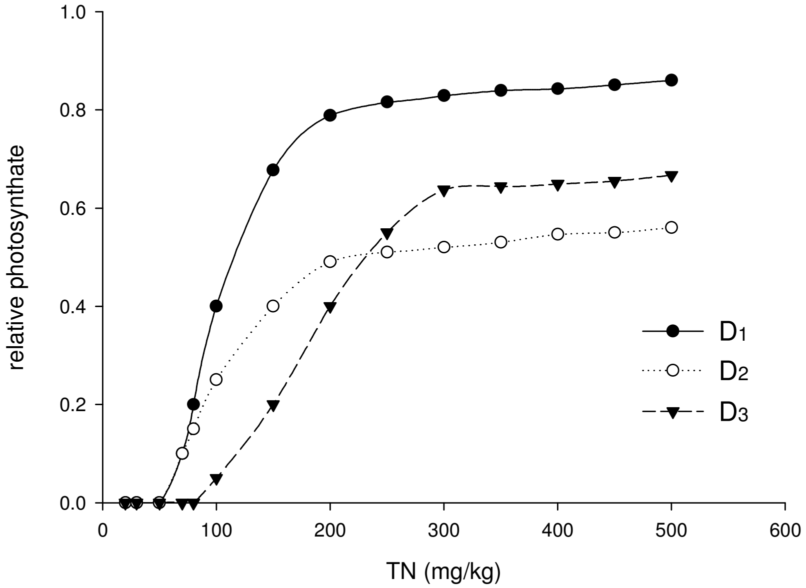


Fig. 7.8. Mean relative productivity (photosynthate) of an individual, which starts as seed and grows till 1.5 m in height. Roots are assumed to be the main storage organ to support regrowth after damage. Allocation patterns: AR=0.3, AS=0.3, AL=0.4.

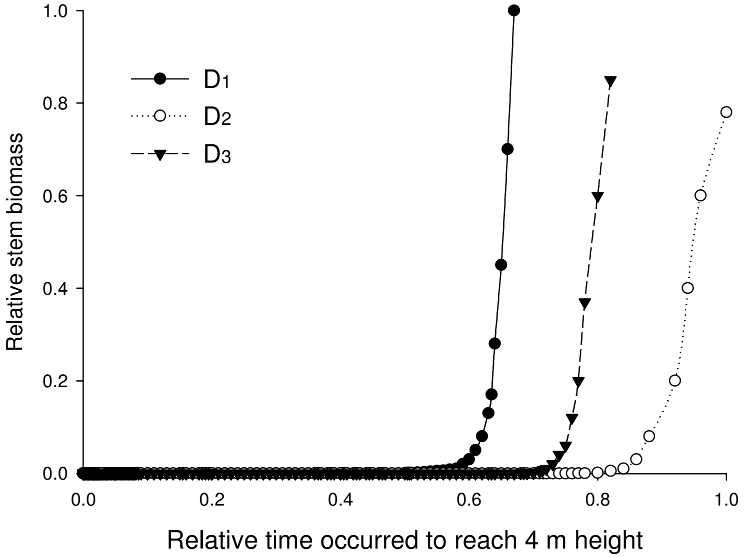


Fig. 7.9. Relative time occurred for an individual to reach adult size assuming that the proportion of biomass yearly allocated to roots is negatively correlated to the amount of biomass removed in above-ground organs (stem and leaves). TN = 300, browsing level = R1, and allocation patterns: AR=0.2, AS=0.4, AL=0.4.

7.4 DISCUSSION

7.4.1 Tolerance vs resistance: plant biomass and soil nutrient availability

Overall, my results show that at low browsing intensity regardless of defensive traits and allocation patterns, plants produce more biomass and deplete soil nutrients more efficiently than at high browsing intensity. Nevertheless, under high browsing intensity more nutrients are left in the soil after the simulation period of 100 years as we might expect from a positive correlation between the availability of soil resources and rates of mass loss (Tilman 1988). Comparing different defensive traits without changing default parameters in the model, I obtained two main results.

First, tolerant plants show high productivity and are able to low soil nutrients more efficiently than intermediate and resistant plants. Second, intermediate plants neither optimizing resistance nor tolerance against herbivory, under similar allocation patterns, have low productivity, need long time to reach maturity size, and finally maintain soil nutrients at high levels. Hence, plants which show a poor compromise between tolerance and resistance traits likely would be disadvantaged within a mixed plant community with individuals showing the three different defensive traits.

The mechanisms responsible involve tradeoffs across nutrient uptake rates, plant nutrient requirements, and photosynthetic efficiencies. Indeed, the increased uptake rates of tolerant plants depends on the effective availability of soil resources (in the model called ‘C’, see Table 7.1), which increases with their high root:leaf ratio that results when photosynthetic tissue is removed by browsers. In turn, the high plant nutrient requirements of tolerant plants contribute to increase amount of photosynthate and allow them to grow quicker than resistant plants. However, populations of tolerant plants could only be maintained in the model simulations at high nutrient supply rates (i.e. high mineralization rates), but these are highly variable and especially concentrated after rainfall events in semi-arid eutrophic savannas (Scholes et al. 2003). Moreover, although mechanisms of plant growth and nutrient use efficiency conferred costs to resistant plants in terms of reduced nutrient uptake rates, the same mechanisms did not impose costs on tolerant plants. The same findings have been suggested by Chase et al. (2000), who used an analytical approach under a similar conceptual framework to address soil resource-plant-herbivore interactions. They suggested that tolerant plants might incur costs only if an increase in tolerance also involves a strong increase in density-independent mortality.

This might occur, for example, through the use of protected storage organs and stored meristems (Marquis 1996; Stowe et al. 2000; see also Chase et al. 2000).

I attempted to evaluate costs for tolerant plants assuming in the seedling-sapling stage, the root system is the main storage organ that supports resprouting abilities (see Canadell and Lopez-Soria 1998; Canham et al. 1999; Bond and Midgley 2003). I therefore speculated that at the end of each year (after browsing damage) the proportion of mass allocated to roots was decreased in direct proportion with the biomass removed from leaves and stem. Consequently, I found that seedlings of tolerant plants produced less photosynthate (Fig. 7.8) and reached maturity size later than resistant plants (Fig. 7.9).

Such results indirectly stress the role of roots as important storage organs for surviving herbivory (and fire), especially during critical plant life-history stages as the seedling-sapling stage. Indeed, I showed that large root systems were associated with increased resprouting abilities in gullivers of two *Acacia* woody species in a semi-arid eutrophic savanna (see Chapter 6). Interestingly, gullivers of the less resistant knobthorn (*A. nigrescens*) experienced higher mortality than the more resistant umbrella tree (*A. tortilis*) after severe artificial clipping while being exposed to high browsing pressure. This confirms modelling results and suggests that mass allocation to below-ground reserves is likely more cost effective for tolerant than resistant plants since the former experience high removal rates of above-ground tissues.

7.4.2 Plant community composition and nutrient cycling

Modelling results suggest that resistant traits may strongly enhance woody species persistence under long-term browsing pressure when compared to either intermediate or tolerant traits. Indeed, resistant plants experience low mass loss rates, have more photosynthetic tissue available, and increase their productivity more than plants with intermediate defensive traits.

Nevertheless, though resistant plants grow slower than tolerant plants, they are less nutrient-dependent and may persist under high browsing pressure at relatively low nutrient supply rates. Indeed I found that highly resistant (i.e. highly spinescent) individuals of different *Acacia* woody species are very common in heavily browsed sites (see Chapter 3, 4). This also agrees with recent outcomes of the resource economics of chemical and structural defences across nitrogen supply gradients as we may expect an increased number of spinescent species in semi-arid eutrophic savannas (see Craine et al. 2003).

Therefore there are indications that resistant plants would predominate the plant community in heavily browsed sites over long-term periods with local and/or temporary dominance of fast growing tolerant plants whenever the combination of nutrient supply and browsing rates would be favourable to sustain their populations.

However, field observations and data from literature clearly show that many savanna woody plants have developed both efficient resistance and tolerance traits in response to mammal herbivory and frequent fire regimes (Bond and van Wilgen 1996; Hoffmann 1998; Higgins et al. 2000; Midgley and Bond 2001). Indeed, many woody species are both spinescent in order to reduce intake rates of ungulate browsers (Cooper and Owen-Smith 1986; Young 1987; Mileswski et al. 1991; Gowda 1996), and are also able to recover after herbivore damage through increased compensatory growth abilities (du Toit et al. 1990; Dangerfield and Modukanele 1996; Oba et al. 2000; see Chapter 5).

For a plant showing both tolerance and resistance traits we would expect that costs related to resistance traits (i.e. spines and thorns) should be relatively low in a semi-arid eutrophic savanna. Moreover, I propose that important source-sinks of nutrients, other than nutrients recycled from leaf litter and manuring by mammalian herbivores, play a critical role in supporting plant compensatory growth abilities after browsing damage.

Physical defences may not cost a lot of resources especially when amortized overall several years but clearly, they still allow leaves to be eaten (Craine et al. 2003). Moreover, there are indications from recent studies in the Kruger National Park (see Scholes et al. 2003) that many woody species of the Mimosoideae family, which are often protected by physical defences, are able to fix nitrogen. In fact, N_2 fixation is far higher in eutrophic fine-leafed than in broad-leafed savannas on relatively poor soil (Scholes et al. 2003). Moreover, the Kruger National Park receives some of the highest atmospheric inputs of nitrogen in the world (~ 20kg/ha/yr; M. Scholes, personal communication) and some influence on some plant characteristics. This may represent an important source of nutrients to support regrowth in plants that experience high removal rates from ungulate browsers. Nevertheless, mechanisms of N remobilization (see Chapter 4, 5 and 6) and indirect positive effects of tree pruning on mineralization rates via the root system may also enhance plant compensatory growth abilities after herbivore damage (Bardgett et al. 1998; Bardgett and Wardle 2003; Ayres et al. 2004). The model, however, doesn't address efficiently how the nutrient cycling is closed and how nutrients are reimported to the system through either external N inputs or feedbacks from the leaf litter. Therefore, the model predictions should be seen in terms of responses of woody plant species under ungulate browsing but with limited significance to what concerns potential changes in soil nutrient cycling.

It is likely that fire and browsing have different roles in maintaining species with enhanced tolerance and resistance traits at the landscape level. Undoubtedly, both disturbances select for tolerant plants with high resprounting abilities in their early life-history stages, which rely on important below-ground nutrient storage organs (Bond and van Wilgen 1996; Canadell and López-Soria 1998; Canham et al. 1999; Hoffman and Franco 2003). However, ungulate browsing may represent a stronger selective force than fire for the expression of resistance traits, such as physical defences (see Young 1987; Young and Okello 1998). It is likely then, that in heavily browsed and heavily grazed sites (i.e. sites within few km from waterholes) where fire occurs less frequently due to the low grass fuel, woody species that rely more on resistant than on tolerant traits would be favoured in a long-term period. Our results suggest that the degree of tolerance and/or resistance shown by different woody species plays a key role in influencing vegetation structure in highly disturbed arid-eutrophic African savannas.

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CHAPTER 8

8.1 CONCLUSION

Overall, my results showed that ungulate browsing may negatively influence nutrient cycling in the immediate vicinity of palatable tree species (i.e. decelerating effect) through a drastic reduction of organic matter returned to the soil rather than through changes in litter quality as has been proposed for boreal forest ecosystems (Fig. 8.1). However, (Naiman, *personal comments*) this must be better addressed through a more detailed analysis of processes involved in the nutrient cycling within the plant-browser-soil system (e.g. N denitrification, mineralization, N2-fixation, N dung content etc.). Indeed, the fact that I found less total soil N at heavily browsed sites doesn't necessarily mean that it is associated with a decreased nitrogen cycling (Pastor, *personal comments*). Nitrogen and phosphorus availabilities to plants are determined not by pool sizes but by the supply rate into those pools through mineralization of organic matter (Pastor, *personal comments*). Therefore my first hypothesis that ungulate browsing may have a decelerating effect on nutrient cycling must be tested further.

However, ungulate browsers are able to establish a positive feedback loop with highly palatable, inherent fast growing woody plant species, which produce highly decomposable litter and show high mass compensatory growth abilities (i.e. accelerating effect). These plant responses resemble those observed in grasses under ungulate grazing (Fig. 8.2). Grazers are able to induce changes in the 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 highly resilient to browsing pressure in the long-term. This suggests the presence of analogous "browsing lawns" where heavily browsed *Acacia* trees rely on different eco-physiological mechanisms and/or nutrient sources to sustain plant compensatory growth (Fig. 8.2). However, although ungulate browsing seems to be able to stimulate and maintain a fast nutrient cycling within the plant-browser system, it is unlikely that this will have the same consequences at the whole ecosystem level as shown for the "grazing lawns" (Fig. 8.2). Nevertheless, it might be possible that within the woody plant community, individual plants might affect nutrient cycling at local scales in different ways (Naiman et al. 2003). For example, there are indications that total soil N beneath heavily browsed *A. nigrescens* trees is lower than in lightly browsed sites (Chapter 4; du

Toit et al. 1990). The opposite trend was observed for *A. tortilis* (du Toit el al. 1990), soil N being still high under trees that experienced browsing damage at a waterhole site. Although waterhole sites might represent hotspots of elevated soil nutrients (Naiman et al. 2003), it is plausible that the interactions between individual woody plants and browsing intensity may influence soil nutrient concentrations beneath the tree crowns.

The study was motivated by the need to improve our understanding of the effects of ungulate browsing on ecosystem properties since most of the previous studies in African savannas have been focused on the grazing guild. Nevertheless, the study has tested predictions of prevailing hypotheses, which are based on research in boreal and temperate forests (Naiman et al. 1986; Pastor et al. 1988; Pastor et al. 1993; Persson et al. 2005). Those studies showed that large mammalian browsers through their selective feeding on preferred woody plant species are able to modify fundamental ecosystem processes such as nutrient cycling and habitat productivity.

In N-limited boreal forest ecosystems, browsers preferentially feed on fast growing palatable species in the early stages of vegetation succession. This leads to an increased number of unpalatable evergreens, which produce less decomposable litter with consequent negative effects on ecosystem nutrient cycling (Fig 8.1). It has been shown however, that litter quantity rather than leaf litter quality may also be responsible for reducing productivity in N-limited Swedish boreal forests (Persson et al. 2005). This because browsers when feeding on medium preferred “bulk food” species, and not only on highly preferred deciduous species, may not cause changes in the functional species composition of the plant community. Consequently, the reduction of organic matter returned to the soil might be the main factor responsible for the decreased microbial activity and decreased nutrient cycling rather than the chemical composition of leaf litter. These findings demonstrate that the effects of ungulate browsing on ecosystem processes are complex and depend on the interactive effects of many critical environmental factors.

Here I’ve focused my research on browser-plant-soil interactions in a semi-arid eutrophic African savanna where the set of abiotic and biotic factors is markedly different from their boreal forest counterparts. I showed that the browsing guild is responsible for dramatic changes in the population structure of a palatable *Acacia* woody species and proposed new hypotheses on how ungulate browsing may affect nutrient cycling within few meters from highly palatable woody species. Indeed, no changes in plant functional type composition were found within the vegetation community along a strong browsing gradient whereas a high number of palatable plants were recorded among heavily browsed sites. The reason for this discordance with boreal and temperate scenarios should be searched for in the main ecological factors responsible for ecosystem functioning in semi-arid southern African savannas. Abiotic drivers such as soil nutrient concentration and water availability contribute to a patchy distribution of evergreens and other unpalatable slow-growing species throughout the landscape, regardless of browsing intensity. Moreover, palatable woody species showed high resilience under high browsing intensity due to increased physical defences, increased compensatory growth abilities in adult trees, as well as high resprounting abilities in gullivers. Therefore, in an arid-eutrophic savanna it appears that fast-growing palatable woody species are the better competitors against more chemically defended, slow-growing tree species, which is contrary to the general pattern in boreal-temperate forests.

Measurements of gullivers morpho-functional traits and modelling results suggest that ungulate browsing strongly limits plant recruitment from seedling to adult size. This might be more critical for individuals of tolerant plants in their early life-history stages. They are highly damaged by browsers, likely use nutrients stored in the roots to re-sprout and need efficient mechanisms to replenish root reserves since mineralization rates are low and highly variable in semi-arid African savannas. Hence, ungulate browsing may represent a stronger selective force than fire for the expression of resistance traits in sites associated with high grazing pressure. It might be then, that in heavily browsed and heavily grazed sites (i.e. sites within few km from water sources) where fire occurs less frequently due to the low grass fuel, woody species that rely more on resistant than on tolerant traits would be favoured within the vegetation community in the long-term period.

In general, my results suggest that long-term selective browsing on stands of palatable *Acacia* trees may have a negative effect on nutrient cycling, as inferred from a general depletion of total soil N at heavily browsed vegetation sites. I suggest that soil nutrients depletion is primarily due to a drastic reduction of litter input into the soil from heavily browsed palatable trees (Fig. 8.2). This would lead in a long-term to a C deficit for microbial activity, which in turn has negative effects on soil N mineralization rates. However, more data are needed to conferm such results since I didn’t measure important nutrient cycling processes such as nitrogen mineralization, denitrification, nitrogen inputs and nitrogen released from dung. I suggest there are important indications of a positive feedback loop between browsers and their food resource, which resemble at least in part those proposed for the grazing guild (Fig. 8.2). In fact, ungulate browsing seems to be able to stimulate and maintain a fast nutrient cycling within the plant-browser system but not with the same positive consequences at the whole ecosystem level as shown for the "grazing lawns". The fast nutrient cycle is triggered by tree pruning which is likely to decrease competition between plant shoots (du Toit et al. 1990) and simultaneously increase N availability for plant sprounting which was indeed supported by the higher leaf N content found in heavily browsed trees during the growing season.

To conclude, my data show that ungulate browsing affects nutrient cycling through two different processes, (1) promoting a short-term positive feed-back loop with palatable woody plants which is triggered by tree pruning (i.e. effect similar to those observed for the "grazing lawns"), and (2) a potential negative long-tem impact due to constant browsing pressure on plant species driven by changes in quantity of organic matter returned to the soil rather than qualitative changes in plant community composition.

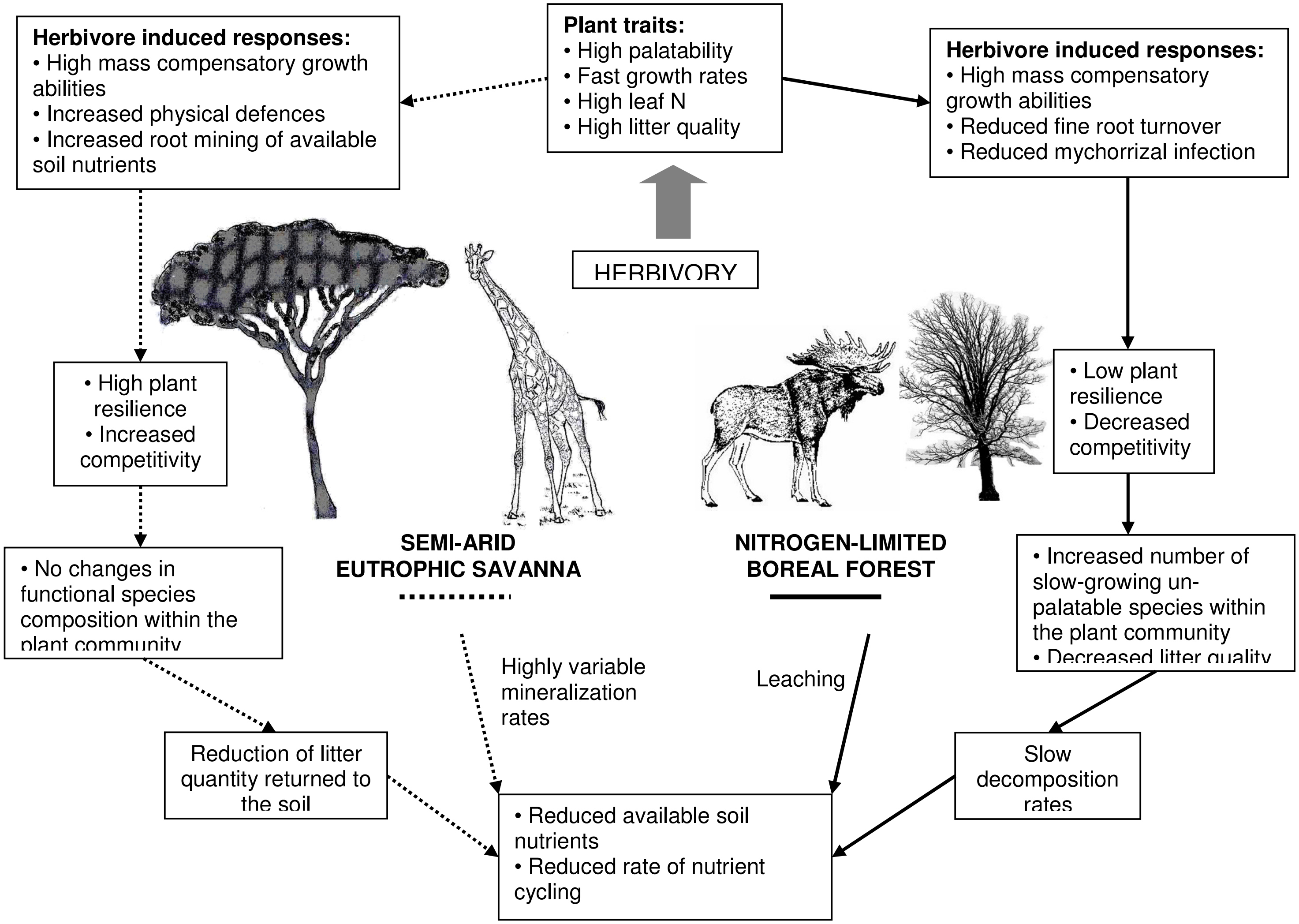

FIG. 5. Schematic of the effects of ungulate browsing on nutrient cycling in semi-arid African savannas and boreal forest ecosystems.

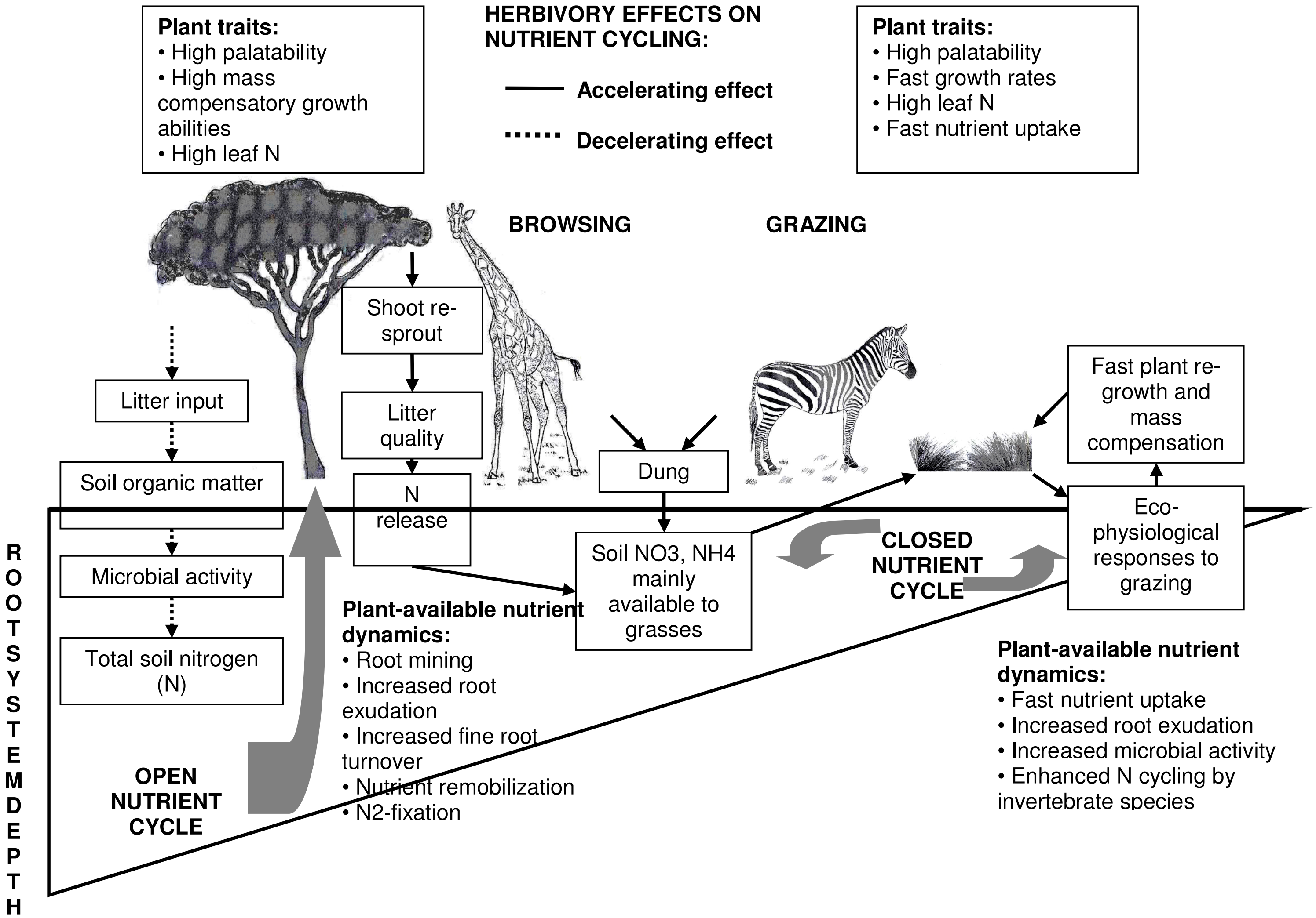

FIG. 6. Mechanistic basis on how browsers and grazers may differently affect nutrient cycling in semi-arid eutrophic savannas.

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