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.

Ungulate browsing and plant community composition

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 m²) 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

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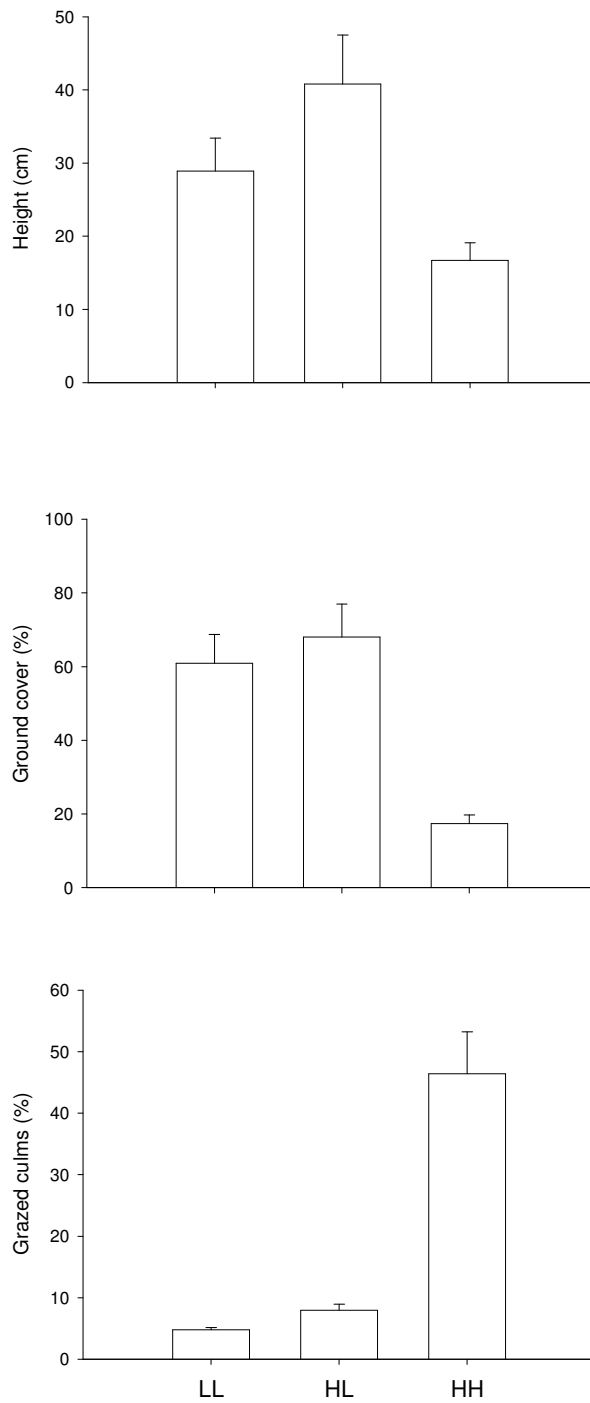
Fig. 3.1. Parameters related to grazing intensity measured in 288 quadrats (1 m² each) established within plots distributed along the browsing/grazing gradient in February 2003 (end of wet season). Browsing/grazing levels: LL = Low/Low, HL = High/Low, HH = High/High.

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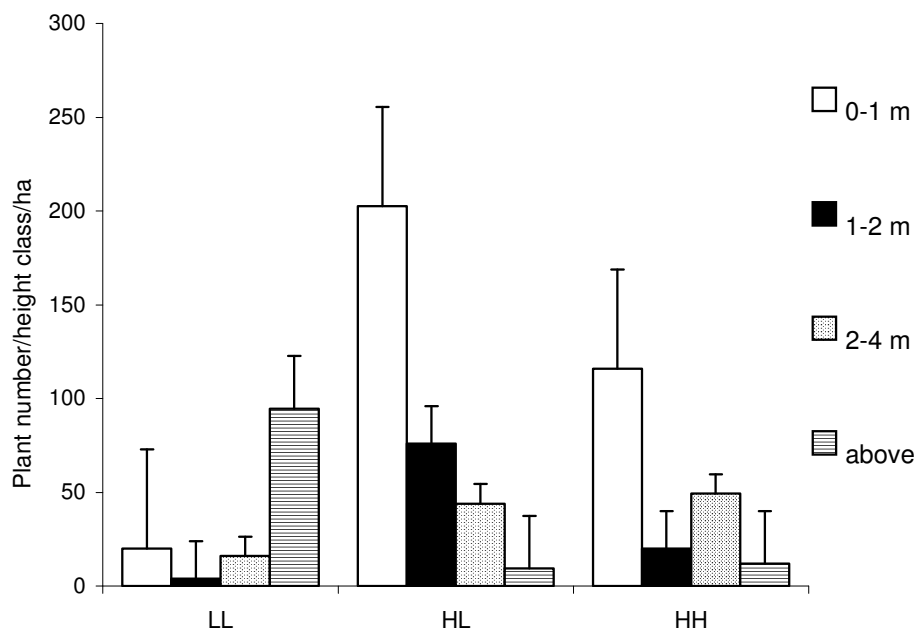
Fig. 3.2. Population structure of *Acacia nigrescens* along the browsing/grazing gradient. Abbreviations as for Fig. 3.1.

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

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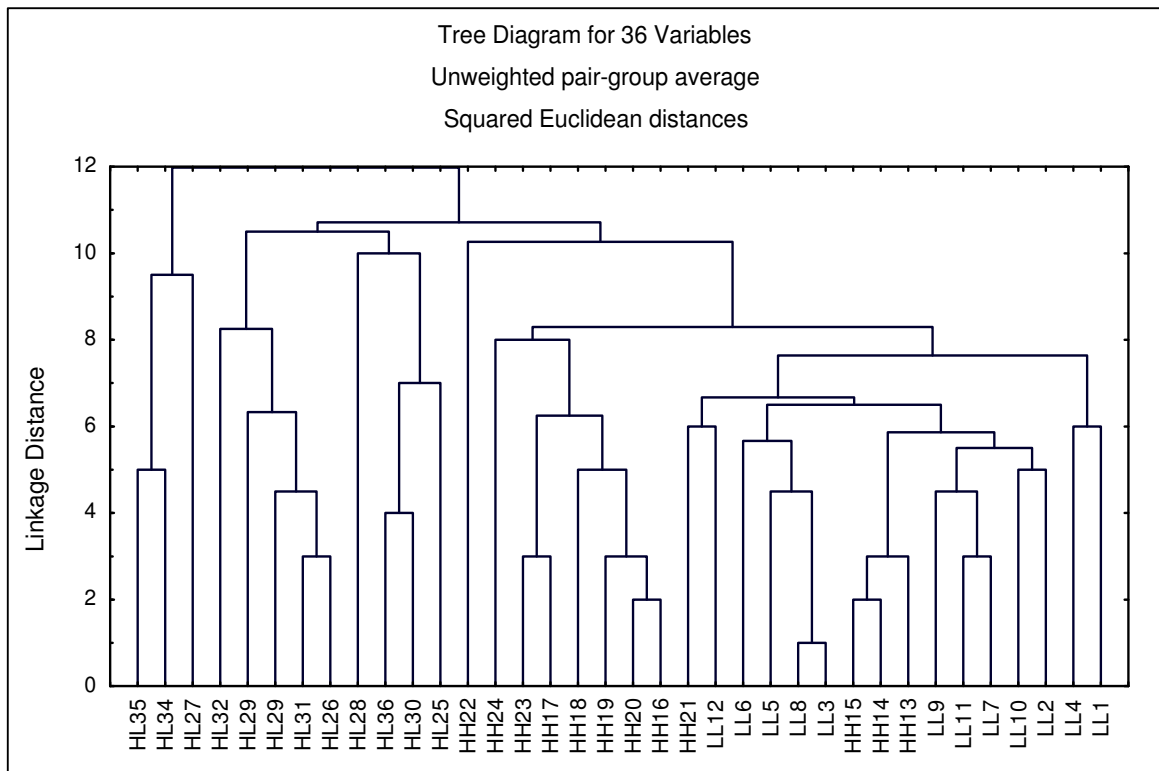
Fig. 3.3. Results from a cluster analysis (CA) based on data of species presence/absence among 36 plots along the browsing/grazing gradient. Abbreviations as for Fig. 3.1.

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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