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.*).

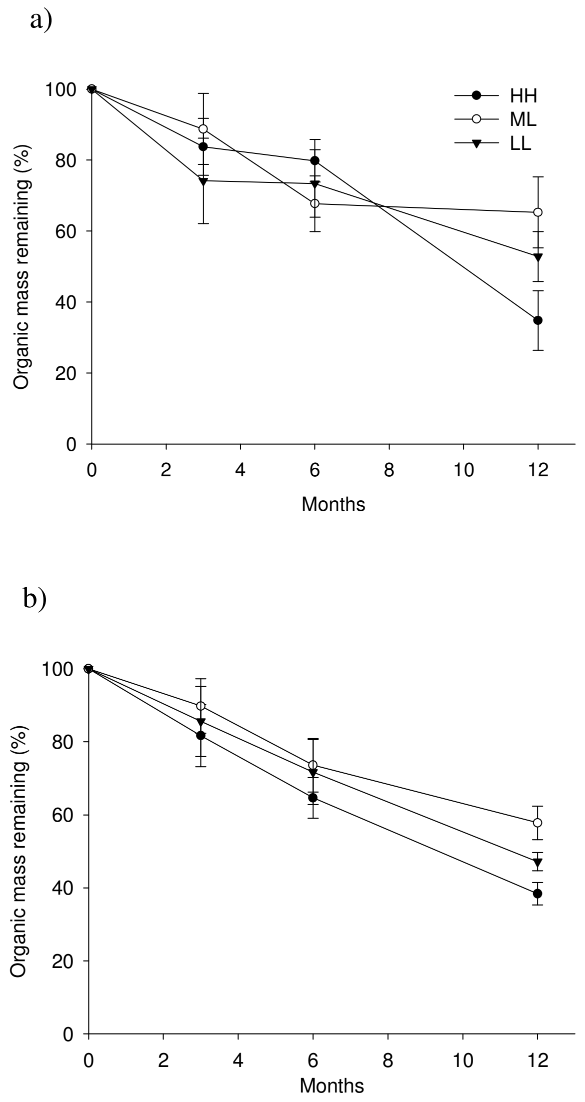
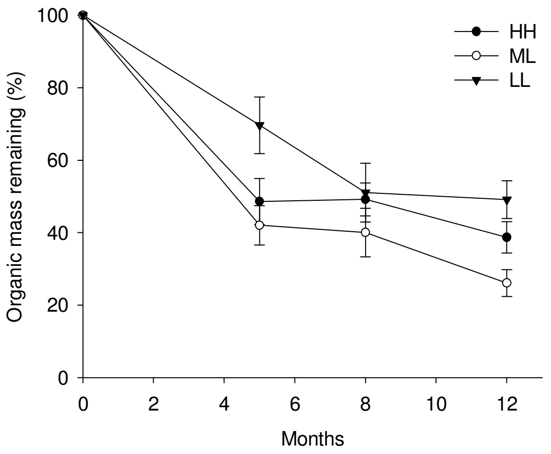


Fig. 4.1. Ash free litter mass remaining of samples collected from individual trees of *Acacia nigrescens* (a) and common straw (b), after 3, 6 and 12 months from August litterbag placement along different browsing/grazing levels. Browsing/grazing levels: HH = high/high; ML = medium-high, LL = low-low.

a)



b)

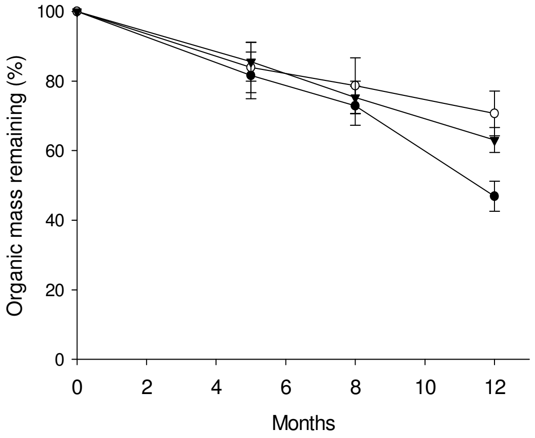


Fig. 4.2. Ash free litter mass remaining from mixed leaf samples of 10 *Acacia nigrescens* trees (a) and common straw collected (b), after 5, 8 and 12 months from June litterbag placement along the browsing/grazing levels. Browsing/grazing levels: HH = high/high; ML = medium-high, LL = low-low.

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

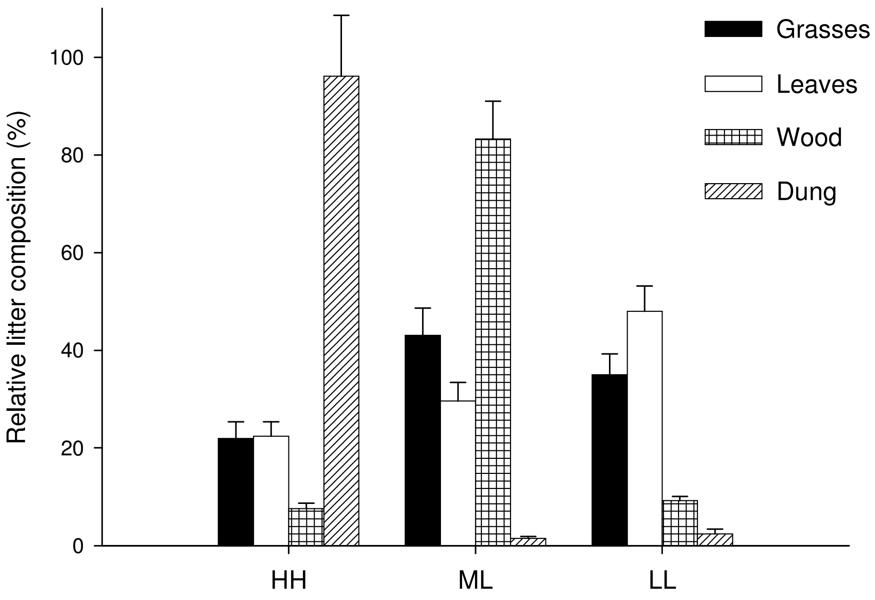


Fig. 4.3. Relative litter mass composition (%) established, along the browsing/grazing gradient (mean of 3 sites per browsing-grazing level). Abbreviations as for Table 4.1.

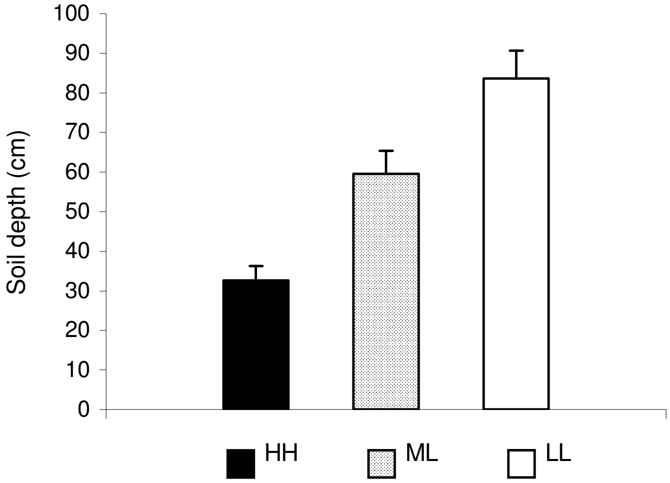


Fig. 4.4. Top-soil depth measured using a manual auger digging 30 cm away from the two places where soil and litter were collected. Abbreviations as for Table 4.1.

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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