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Browsing-induced Effects on Leaf Litter Quality and Decomposition in a Southern African Savanna

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Abstract

We investigated the linkages between leaf litter quality and decomposability in a savanna plant community dominated by palatable-spinescent tree species. We measured: (1) leaf litter decomposability across five woody species that differ in leaf chemistry; (2) mass decomposition, nitrogen (N); and carbon (C) dynamics in leaf litter of a staple browse species (*Acacia nigrescens*) as well as (3) variation in litter composition across six sites that experienced very different histories of attack from large herbivores. All decomposition trials included litter bags filled with chopped straw to control for variation in site effects. We found a positive relationship between litter quality and decomposability, but we also found that *Acacia* and straw litter mass remaining did not significantly vary between heavily and lightly browsed sites. This is despite the fact that both the quality and composition of litter returned to the soil were significantly different across sites. We observed greater N resorption from senescing *Acacia* leaves at heavily browsed sites, which in turn contributed to increase the C:N ratio of leaf litter and caused greater litter N immobilization over time. This, together with the significantly lower tree- and herb-leaf litter mass beneath heavily browsed trees, should negatively affect decomposition rates. However, estimated dung and urine N deposition from both browsers and grazers was significantly greater at high- than at low-herbivory sites. We hypothesize that N inputs from dung and urine boost litter N mineralization and decomposition (especially following seasonal rainfall events), and thereby offset the effects of poor leaf litter quality at chronically browsed sites.

Key words: *Acacia*; plant defences; ungulate herbivory; ecosystem functioning; nutrient cycling.

Introduction

Ungulate browsers 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 (Pastor and others 1988; Hobbs 1996; Wardle and others 2002; Bardgett and Wardle 2003). These linkages were well addressed in N-limited systems, such as many boreal and temperate forests, where the long-term consequences of intensive browsing (Naiman and others 1986; Pastor and others 1988) often provide a competitive advantage to chemically defended, unpalatable, slow-growing evergreens. Consequently, with slow nutrient uptake by slow-growing plants combined with reduced soil

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microbial activity and increased leaching, there is a net loss of available forms of soil nutrients (Bryant and others 1991; Pastor and Naiman 1992; Pastor and others 1993).

It is now clear that one of the mechanisms through which ungulate browsers can trigger shifts in the functional composition of the woody plant community (Kielland and others 1997; Bardgett and Wardle 2003) is by selectively removing fast-growing, highly preferred woody species that produce highly decomposable litter (but see Wardle and others 2002). However, for both woody species and grasses, it is also possible for large herbivores to promote the dominance of palatable herbivory-adapted species either by increasing compensatory growth abilities of preferred species (Augustine and McNaughton 1998; Fornara and du Toit 2007) or inducing a reallocation of nutrients within individual plants and indirectly stimulating soil mineralization processes (McNaughton 1984; Hamilton and Frank 2001; Stark and others 2007).

Such plant responses to herbivory are potentially significant at the ecosystem level, but unlike in boreal ecosystems, for example (Pastor and others 1988; Pastor and Naiman 1992; Pastor and others 1993; Persson and others 2005), browsing in savanna ecosystems has not been studied in the context of nutrient cycling. This despite the fact that many woody plant species of southern African savannas have eco-physiological adaptations to pruning, such as tolerance (that is, compensatory growth abilities) and resistance (that is, thorns, spines, and prickles) traits, which increase plant resilience to chronic browsing (Bryant and others 1989; du Toit and others 1990; Fornara and du Toit 2007) and possibly influence ecosystem nutrient cycling even in the absence of any significant change in plant species composition. A critical question is whether and how browsing affects the quantity and quality of litter produced in semi-arid, eutrophic savannas where tolerant-spinescent woody species are much more common than in temperate and boreal ecosystems. We consider the answer to this question as being crucial to understanding the top–down controls to those large herbivores exerts on ecosystem processes in African savannas (Scholes and others 2003).

In this study, the effects of browsing on litter quantity and quality were studied both within and among woody species. Within species, we investigated whether the decomposition rate of litter from a highly palatable-spinescent woody species (*Acacia nigrescens*) varied across stands with very different histories of attack from large herbivores. Among species, we reasoned that because savanna woody plant species vary widely in their palatability to browsing ungulates (Owen-Smith and Cooper 1987), the quality of their leaves as food for herbivores might covary with the decomposability of their leaf litter on the soil. We, therefore, investigated whether browse quality, as indicated by leaf N and condensed tannin content (Cooper and others 1988; Bryant and others 1989; Gallardo and Merino 1993; du Toit 2003), of five woody species with different adaptive defensive traits was positively related to litter decomposability.

We also tested if the decomposition of litter of standard quality (chopped straw) was influenced by its placement under canopies of plants producing either high or low quality browse. Finally, we considered how litter composition (that is, relative quantities of shed tree leaves, dead herb leaves and culms, woody debris and dung) and N inputs from animal wastes could affect nutrient cycling across sites with varying browsing–grazing intensities.

Study Site

The study was conducted in the Tshokwane section (24°47′ S, 31°52′ E) of the Kruger National Park, South Africa. Field experiments were set up in the Satara land system characterized by basaltic clay soil supporting a fine-leafed tree savanna dominated by *Acacia nigrescens*, *Sclerocarya birrea*, and *Dichrostachys cinerea* (Venter and others 2003). *Acacia nigrescens*, Miller, represents the staple food resource for the ungulate browsing guild, which is composed of giraffe (*Giraffa camelopardis*), kudu (*Tragelaphus strepsiceros*), steenbok (*Raphicerus campestris*), impala (*Aepyceros melampus*) and elephant (*Loxodonta africana*). Non-migrating herds of grazers such as zebras (*Equus burchellii*) and wildebeest (*Connochaetes gnou*) are also common in these open savanna woodlands.

The leaf characteristics of *A. nigrescens* are 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. Tree branches bear prickles and are usually leafless for 3–4 months during the dry season from June to September (see Coates Palgrave and others 2002). Rainfall in this area averages 560 mm per annum, with 80% of the precipitation concentrated in the wet season from October to March. On these semi-arid basaltic plains, water availability is a strong determinant of large herbivore distribution and a main source of heterogeneity at the landscape level (Redfern and others 2003). In the eastern part of the Tshokwane section, herbivore impact on woody vegetation is

particularly high less than 1 km from either temporary or permanent water sources, whereas woody vegetation is much less affected more than 7 km from watering points (du Toit and others 1990). Three sites were selected within a heavily grazed and trampled area vegetated by severely pruned *Acacia nigrescens* trees (hereafter refered to as HH sites). Ecological and demographic studies on the browsing guild (du Toit and Owen-Smith 1989; du Toit and others 1990; Owen-Smith 1990) indicate that woody vegetation in this area has experienced consistent browsing pressure presumably for centuries (see du Toit 2003). Three further sites (control sites) were selected among monospecific stands of mature, lightly browsed *Acacia* trees more than 7 km from permanent water sources and more than 3 km from a seasonal waterhole (LL sites, being lightly browsed and grazed). Sites were at least 1 km apart whereas the furthest distance between them was about 10 km, so rainfall differences were assumed to be negligible. Moreover, fire had not been recorded for 13 years among all study sites.

Methods

Litterbag Experiment of Five Woody Species and Straw at HH Sites

The leaves of five woody species, *Acacia nigrescens*, *Securinega virosa*, *Combretum hereroense*, *Euclea divinorum*, and *Maytenus senegalensis* were collected during two days in June 2002 from all around each shrub/tree canopy (Table 1). We collected only senescent leaves that fell into a previously stretched 1 m^2 nylon net (2 mm mesh size) from gently shaken randomly selected branches. *A. nigrescens* (tree) and *Securinega virosa* (deciduous shrub) are preferred browse species, have relatively high leaf N and P, and low concentrations of condensed tannins (du Toit 2003; Table 1). *Euclea divinorum* (evergreen shrub), *Combretum hereroense* (deciduous shrub-small tree) and *Maytenus senegalensis* (evergreen shrub) have high concentrations of condensed tannins, as well as total phenolics in their leaves, which decrease foliage acceptability (Table 1; for tree nomenclature see Coates Palgrave and others 2002). At each HH site we selected and tagged five individual trees per woody species. All leaf samples from each tagged trees, as well as common straw, were collected in one intensive two-day sampling session. Straw, comprising stalks of threshed, well-mixed native grasses, was collected at one site at the Tshokwane ranger station and used as a control to take into account

Table 1. Growth Form, Browse-related Plant Traits and Phenology of the Five Woody Species used in the Litterbag Experiments

Species	Growth form	Condensed tannins (% dry mass ± SE)	Leaf N (% dry mass ± SE)	Leaf P (% dry mass ± SE)	Foliage acceptability[1]	Physical defences[3]	Phenology
Acacia nigrescens	Tree	3.68 (0.33)	5.05 (0.08)	0.44 (0.0)	High	High	Deciduous
Securinega virosa	Shrub	1.44 (0.23)	3.06 (0.01)	0.23 (0.0)	High	Low	Deciduous
Combretum hereroense	Tree	14 (0.29)	1.73 (0.03)	0.11 (0.01)	Intermediate	Absent	Deciduous
Euclea divinorum	Shrub	[2]	[2]	[2]	Low	Absent	Evergreen
Maytenus senegalensis	Shrub	11.7 (0.33)	1.34 (0.03)	0.13 (0.0)	Low	Medium	Evergreen

[1] *Foliage acceptability was estimated from data of leaf chemistry (du Toit 2003) and studies on large browsers' feeding preferences (Cooper and others 1988; du Toit and others 1990).*
[2] *Foliage acceptability of Euclea divinorum was estimated from partial data on leaf and bark chemicals (van Grinsven and others 1999; see Holdo 2003) and from a review study (Scholes and others 2003).*
[3] *The presence of thorns, spines and prickles was used to estimate the efficiency of structural defences in reducing bite size by ungulate browsers (Cooper and Owen-Smith 1986; Gowda 1996). Branches of A. nigrescens bear pairs of strong recurved thorns and prickles. M. senegalensis bears sparsely long straight thorns. S. virosa, C. hereroense and E. divinorum do not have specialized forms of physical defence.*

across-site variations in decomposition rates of tree/shrub leaves that might be due to either variation in leaf chemistry or local microbial activity. Samples were kept separated and air-dried (3 days at ~25°C) until their mass no longer changed and were then used to fill steel mesh bags (15 cm × 15 cm; 2 mm mesh) each yielding 5 ± 1 g (mean ± SE). We prepared experimental units of six mesh bags consisting of three of common straw and three of leaves of a specific woody species. The experimental units were evenly fixed along a steel wire that was fastened around the tree trunk and carefully placed on the soil horizontally under each of the tree/shrub canopies from where leaves were collected. Litterbags were partially covered with dead litter found in place to decrease their chances of being investigated by large mammals. 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) × 3 collections × 5 species × 5 replicates of each species per site gave a total of 450 mesh bags. After retrieval the litterbags were carefully emptied, the contents oven dried at 70°C for 2 days and weighed to measure weight loss (dry matter). Since some of our litter samples had small particles (for example, dust, soil, debris left by termite activity, and so on) adhering to the leaves whereas other samples had not, to correct for such inorganic particulate matter, ash-free weights were obtained by igniting litter samples at 550°C for 4 h and subtracting the weight of the remaining ash from the dry mass of each litter sample. Ash-free weights were then used in all subsequent calculations.

Litterbag Experiment of *Acacia* Litter and Straw at HH and LL Sites

Leaf samples from each of 30 *A. nigrescens* trees (five trees in each HH and LL site) were collected in 2 days at the end of July 2002 during the peak period of leaf-fall, which for *Acacia nigrescens* occurs from June to August in the dry season (Coates Palgrave and others 2002). Leaves from each tree were kept separated and air-dried (3 days at ~25°C), weighed till constant mass and used to fill 90 (15 × 15 cm) steel mesh bags (2 mm mesh size). At the same time another 90 mesh bags were filled with common straw (collected and dried as above). The experimental design consisted of units of six mesh bags each (three of common straw and three of *Acacia* litter), evenly fixed along a steel wire that was fastened around the tree trunk of the tagged *Acacia* trees. Each pair of litterbags was then retrieved after 3, 6, and 12 months. Therefore, 2 litterbags (*Acacia* and straw) × 3 retrievals (November, February and August) × 30 trees gave a total of 180 litterbags. Initial sub-samples of *Acacia* leaves and all the litter samples retrieved during the year were analyzed for N and C. Nitrogen content was determined by the standard Kjeldahl method (Benton 1991) and carbon content by dry combustion.

Seasonal Variation in N Content of *Acacia* Leaves and Litter Composition Beneath *Acacia* Trees

Fresh leaf 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. Also litter samples (dead plant material) were collected from the soil surface inside three quadrats of 25 × 25 cm which were randomly positioned beneath each of the tagged *Acacia* trees within a radius of 1.5 m from the trunk. Standing dead biomass was not included in litter measurements. Litter samples were collected in June (early dry season), September (late dry season) and March (late rainy season). Litter was separated into wood, herbs, tree leaves, and dung (dung samples were also divided for each mammalian herbivore species), oven dried at 70°C for 2 days and weighed to give an estimate of total litter dry mass and relative composition around each of the 30 trees.

Estimate of N Inputs from Animal Dung and Urine

Since dung deposition rates can strongly influence nutrient cycling we also estimated N inputs from both animal dung and urine between heavily and lightly browsed sites. For dung N content we used data from the thorough study of Edwards (1991), which reported monthly variation of dung N content for common grazers and mixed feeders in the Mkuzi Game Reserve situated approximately 300 km SE of Kruger. Dung N content, expressed as % dry mass and averaged over 18 months, was 1.27% ± 0.19% for zebras, 1.59% ± 0.26% for wildebeest and 2.13% ± 0.29% for impalas. We used these values for the Tshokwane study site in Kruger to calculate dung N deposition (g N m^{-2}) at each sampling visit (March, June, and September). Urine deposition was calculated from dung deposition rates (see Frank and others 1994; Augustine and others 2003) using ratios of N excretion in dung versus urine for different ungulate herbivores measured in laboratory studies. For impala we used

a urine:dung N excretion ratio of 1.0 for the dry season (June and September measurements) and of 2.5 for the wet season (March measurement; see Augustine and others 2003). This assumes a diet containing 1.5% N in the dry winter months and 3% N in the wet summer months which actually agrees with leaf N content of the staple browse species, *Acacia nigrescens*, as measured in our study (see Results). We used the same N excretion ratios for wildebeest, which is similar to elk (*Cervus elaphus*) in body size, and for which N excretion ratios have been reported (see Augustine and others 2003 for review). For the non-ruminant zebra we used a dry season ratio of 1.2 and a wet season ratio of 2.1 derived from studies of horses, ponies and donkeys (see Augustine and others 2003). We finally estimated ammonia volatilization losses as 25% of urine deposition based on various studies on large herbivores that reported 20–30% of total N lost through volatilization (see Ruess and McNaughton 1988 for review).

Termite Activity

As termites are very common in arid, semi-arid savanna ecosystems and play a critical role in leaf-litter removal/decomposition (Bignell and Eggleton 2000), our litterbags were chosen as having 2 mm mesh size to allow termite access. In order to estimate frequencies of termite visits at our litterbag sites as well as signs of termite activity we recorded the presence of workers and soldiers during monthly inspections and/or earth debris left inside the mesh bags at the time of litterbag retrieval. Specimens were collected if found at the time of mesh bag retrieval, preserved in alcohol and sent off for identification.

Data Analysis

We compared remaining litterbag mass across five woody species (and associated straw) at the heavily browsed sites and we compared remaining *Acacia* litter (and associated straw) between heavily and lightly browsed sites. Since our aim was to compare treatment means and not decomposition rate constants we used the analysis of variance (ANOVA) as our statistical method (see Wieder and Lang 1982). Proportions of mass remaining in single litterbags either filled with leaf litter or straw (June incubation period) were arcsine transformed to meet assumptions of normality and homoscedasticity. In order to test for significant differences in litter biomass remaining after the 12-months-incubation period our ANOVA model had species identity as the treatment and site as block. The effects of species identity, time of litterbag retrieval and their interactions were further investigated using repeated measures ANOVA with site as a factor. Proportions of mass remaining in single *Acacia* and straw litterbags placed in August 2002 were also arcsine transformed. In order to test for the effects of ungulate browsing on litter biomass decomposition after the 12-month incubation period, we used ANOVA with ungulate browsing as the predictor variable and site as block. ANOVA was also used to test for significant changes in litter N and C concentrations measured after 12 months (values were expressed as proportions and arcsine transformed). We then performed repeated measures ANOVA to test for the effects of ungulate browsing, harvest time and their interactions (also including site as factor) on differences in biomass decomposition, as well as C and N concentrations (values were expressed as proportions and arcsine transformed). In order to reveal potential differences in onset rates of N immobilization and/or N mineralization between HH and LL sites, we calculated the nutrient accumulation index (NAI) for each *Acacia* litterbag for the August placement as follows (see Romero and others 2005): NAI $= (W_t X_t)/(W_0 X_0)$. Here W_t is the ash-free organic mass remaining in the litterbag at time t, X_t is the nitrogen concentration of the leaf litter at time t, W_0 is the initial leaf litter mass in the litterbag, and X_0 is the initial concentration of nitrogen in the leaf litter. If NAI = 1 then the ash-free organic mass remaining in the litterbag has the same mass of nitrogen as when the litterbag was placed; NAI less than 1 indicates net mineralization of nitrogen in the litterbag; and NAI greater than 1 indicates net immobilization (accumulation) of nitrogen. NAI values were calculated as the mean of five replicates (five separate *Acacia* trees) per site at each time of litterbag retrieval. A chi-squared test was performed to test for variation in frequencies of termite occurrence at the litterbag sites during the year of litter incubation.

Results

Effects of Species Identity on Mass of Woody Plant Litter and Straw Remaining at HH Sites

Woody species identity significantly affected the proportion of litter mass remaining after the 12-months-incubation period ($F_{4,44} = 43.03$, $P < 0.0001$). Specifically, the proportion of leaf mass remaining in the litterbags of the two species

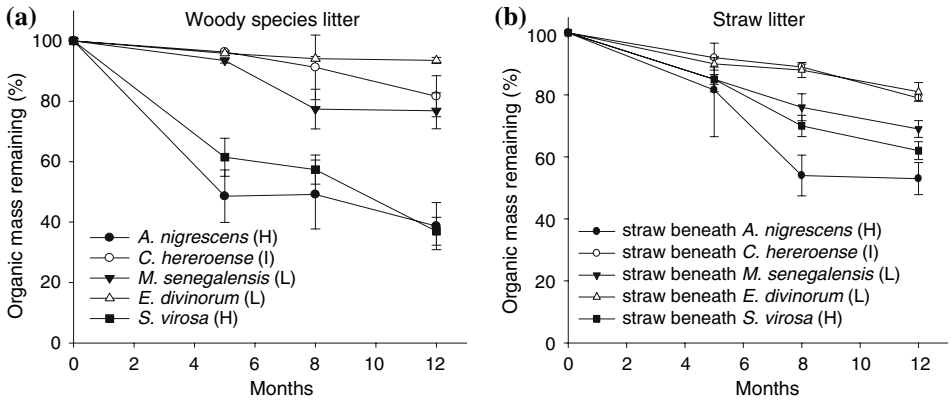

Figure 1. Ash-free mass remaining (mean ± SE) from (**A**) litter of five woody species and (**B**) straw placed beneath canopies of the same five woody species. Samples were collected at 5, 8 and 12 months following a June litterbag placement. Letters between brackets refer to foliage acceptability: H = high; I = intermediate; L = low.

Table 2. Results of Repeated Measures ANOVA Testing the Effects of Species Identity, Site and Litterbag Harvest Time (months) on Values of Mass Remaining (dependent variable) from Leaf Litter Samples of Five Woody Species and Straw Placed in June 2002

Source of variation	Leaf litter biomass			Straw biomass		
	df	*F*	*P*	df	*F*	*P*
Species identity	4,38	37.3	<0.0001	4,33	13.2	<0.0001
Site	2,38	2.12	NS	2,33	0.72	NS
Species × site	8,30	5.16	0.004	8,26	2.96	0.02
Time	2,37	11.8	0.0001	2,32	19.9	<0.0001
Time × species	8,74	2.56	0.01	8,64	1.78	NS
Time × site	4,74	0.66	NS	4,64	4.08	0.005

Note that five straw litterbags were not included in the analyses because were damaged during the incubation period.

with higher foliage acceptability, *Acacia nigrescens* (mass remaining = −0.30, $P < 0.0001$) and *Securinega virosa* (mass remaining = −0.29, $P < 0.0001$) was lower than that of the other species with lower foliage acceptability *Euclea divinorum* (mass remaining = 0.26, $P < 0.0001$), *Combretum hereroense* (mass remaining = 0.25, $P < 0.0001$) and *Maytenus senegalensis* (mass remaining = 0.09, $P = 0.045$; Figure 1a). Similarly, straw litterbags placed beneath the canopy of the most preferred browse species (*A. nigrescens* and *Securinega virosa*) for 12 months lost more biomass than when associated with the less preferred woody species ($F_{4,44} = 12.2$, $P < 0.0001$; see Figure 1b). These results suggest that leaf chemical composition might affect litter decomposition both directly and indirectly by affecting local conditions of decomposition beneath the tree canopy.

Repeated measures ANOVA showed the significant effects of species identity and time of litterbag retrieval on both straw litter (we lost five straw litterbags during the incubation period) and woody plant decomposition (Table 2; Figure 1a, b). The time × species interaction effect on biomass remaining was significant in the woody plant experimental trial (Table 2) and suggests that litter mass loss was different among species through time. We found no site effect on litter mass remaining but a significant interaction between species identity and site on litter mass decomposition in both woody plant and straw experimental trials (Table 2). This was mainly due to the higher mass decomposition of *Acacia* litter and related straw in one of the sites by the end of the incubation period.

Effect of Ungulate Browsing on Mass of *Acacia* and Straw Litter Remaining at HH vs. LL Sites

The proportion of ash-free organic mass remaining in both *Acacia* ($F_{1,29} = 3.84$, $P = 0.06$; $R^2 = 0.12$) and straw litterbags ($F_{1,29} = 1.91$, $P = 0.177$; $R^2 = 0.06$) after 12-months incubation was not significantly different between heavily and lightly browsed sites (Figure 2a, b). Repeated measures ANOVA also showed no effect of ungulate browsing or time × browsing interaction on both *Acacia* and straw litter mass decomposition (Table 3; note that three straw and three *Acacia* litterbags were not

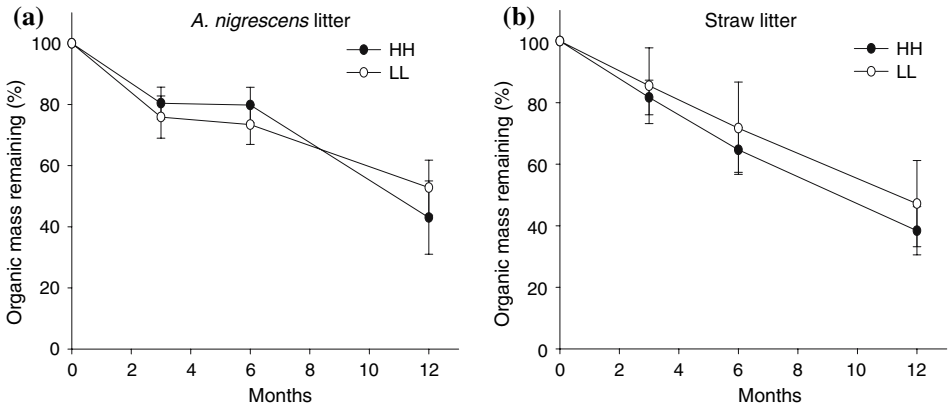

Figure 2. Ash-free mass remaining (mean ± SE) from litter samples of (**A**) *A. nigrescens* and (**B**) common straw after 3, 6 and 12 months following an August litterbag placement. HH = heavily browsed–grazed sites, LL = lightly browsed–grazed sites.

Table 3. Results of Repeated Measures ANOVA Testing the Effects of Browsing Intensity, Site and Litterbag Harvest Time on Values of Litter Mass Remaining (*Acacia* and straw) as well as *Acacia* Litter N and C Concentrations and C:N Ratio from Samples Placed in August 2002

Source of variation	*Acacia* biomass			Straw biomass			Litter N (*Acacia*)			Litter C (*Acacia*)			Litter C/N (*Acacia*)		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Browsing	1,26	0.44	NS	1,23	1.94	NS	1,23	4.08	0.039	1,23	1.02	NS	1,23	8.05	0.009
Site	2,26	3.97	0.031	2,23	0.98	NS	2,23	0.36	NS	2,23	0.13	NS	2,23	0.83	NS
Browsing × site	2,24	1.98	NS	2,23	2.94	NS	2,23	0.34	NS	2,23	0.45	NS	2,23	0.99	NS
Time	2,25	15.2	<0.0001	2,22	26.2	<0.0001	3,21	78	<0.0001	3,21	34.1	<0.0001	3,21	158	<0.0001
Time × browsing	2,25	2.05	NS	2,22	1.08	NS	3,21	14.2	<0.0001	3,21	1.05	NS	3,21	17.6	<0.0001
Time × site	4,50	0.14	NS	4,44	0.83	NS	6,42	2.70	0.02	6,42	0.46	NS	6,42	2.33	0.048

Note that three straw and three Acacia litterbags were not included in the analyses because of evidence of animal disturbance on them

included because of evidence of animal disturbance on them). There was, however, a site effect on litter mass remaining due to the high *Acacia* litter mass decomposition at one of the HH sites where litter mass remaining after 12 months was on average 20% of the original.

Changes in Litter N and C Between HH and LL Sites

We did not find significant effects of ungulate browsing on litter N concentration ($F_{1,29} = 3.32$, $P = 0.08$; see also Figure 3a), litter C concentration ($F_{1,29} = 3.8$, $P = 0.065$) and C:N ratio ($F_{1,29} = 0.04$, $P = 0.83$) as measured after the 12-month incubation period. However, repeated measures ANOVA showed that both browsing intensity and especially a browsing × time interaction did significantly affect N accumulation in the litterbags (Table 3). The significant effect was due to an increase of litter N content at heavily browsed sites (HH sites) through time (see Figure 3a). The litter N accrual at the HH sites partly explains the variation of the NAI index that we observed during the period of incubation and reveals a trend in litter N immobilization that was more pronounced at HH than at LL sites (Figure 3b). The higher N immobilization at the HH sites also supports the significant variation in litter C:N ratio (Table 3), which decreased more consistently through time at the HH than LL sites. The discrepancy between the final NAI value at LL sites in Figure 3b (which would suggest immobilization) and final litter N (g) in Figure 3c (which would suggest mineralization) was mainly due to a couple of initial N% values relatively low ($X_0 = 1.65$ and 1.5%) and two relatively high litter N% values measured after 12 months (that is, $X_t = 2.5$ and 2.6%). Leaf litter C:N ratio of *Acacia* trees at HH sites was 30.1 ± 2.91 at the peak period of leaf falling and 19.7 ± 2.2 after 12 months of litter incubation. At the LL sites litter C:N ratio was 25.7 ± 1.2 at leaf abscission and 20.1 ± 2.12 after 12 months of litter incubation. Moreover, the trend in seasonal variation of litter C:N is qualitatively similar to the change in litter N (%) shown in Figure 3a with a marked decrease in litter C:N ratio

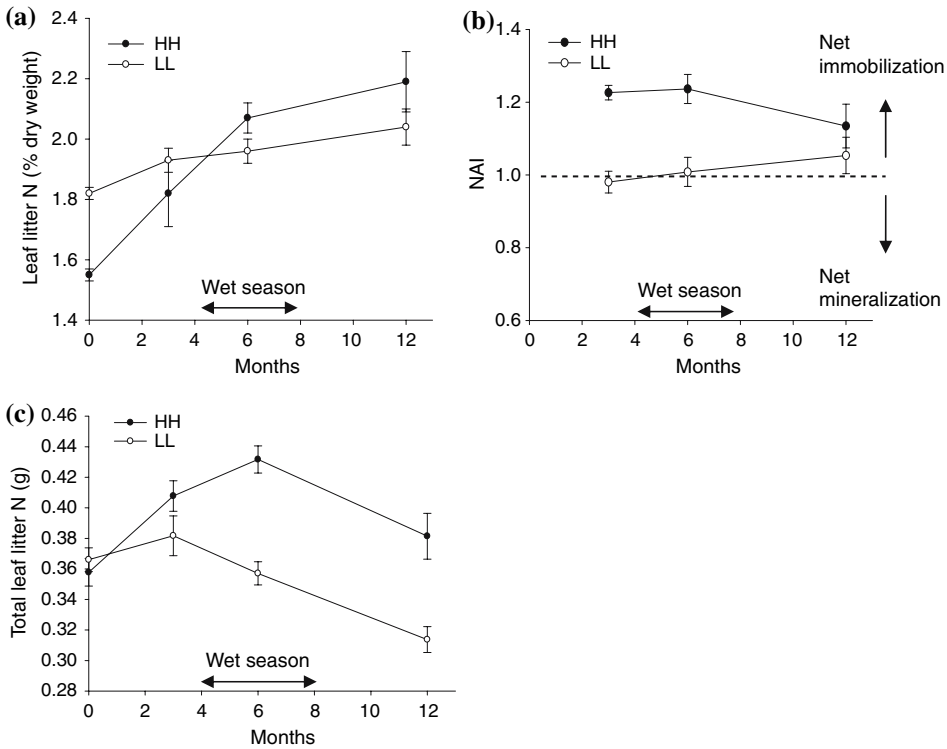

Figure 3. Percentage of N remaining (mean ± SE) in *Acacia* leaf litter (**A**), nutrient accumulation index (NAI; **B**), and total amount of N (g) in litter (**C**), all calculated during the period of litter incubation. HH = heavily browsed–grazed sites, LL = lightly browsed–grazed sites.

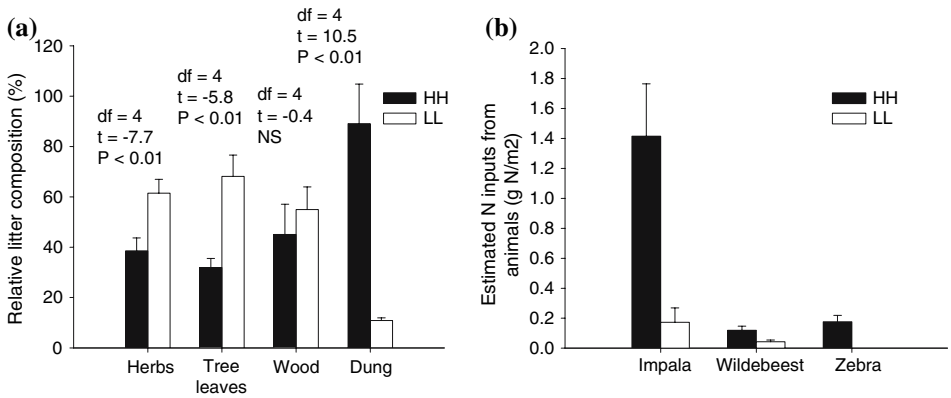

Figure 4. Relative litter mass composition (mean ± SE) measured across ungulate herbivory levels (**A**; note that bars represent the percentage litter of a particular type between the HH and LL sites) and estimated animal N inputs (g N m^{-2}; **B**) from both dung and urine deposition across the same sites. Abbreviations as for Figure 2.

during the first 6 months of incubation at HH sites. Finally repeated measures ANOVA showed significant differences in the total amount of N (g) in litter over time due to a browsing effect ($F_{1,28}$ = 15.5, P = 0.0005; Figure 3c) and a browsing × time effect ($F_{3,26}$ = 9.1, P = 0.0003; Figure 3c).

We found that total leaf N (%) for freshly collected *Acacia* leaves in the early rainy season (December), just after the main leaf flush, was significantly higher among *Acacia* trees at HH sites (2.9% ± 0.07%) than at LL sites (2.35% ± 0.09%; N = 15, P < 0.01). However, leaf N content was significantly lower at HH sites (1.55% ± 0.03%) than at LL sites (1.82% ± 0.02%) during the mid-dry season in June (N = 15, P < 0.0006). The leaf C:N ratio was significantly lower in heavily browsed than lightly browsed trees during the growing season (t = −2.28, df = 22, P < 0.03) whereas the opposite trend was observed in June during the peak of leaf abscission (t-test, t = 7.66, df = 28, P < 0.001).

A survey of litter composition throughout the year showed significantly higher proportions of dead herb leaves and culms as well as shed tree leaves at LL sites (Figure 4a) and a significantly higher proportion of dung at HH sites (Figure 4a). Herb dry weight was 507.4 ± 82.5 g m^2 at HH sites and 809 ± 88.8 g m^2 at LL sites, tree leaves dry weight was 140 ± 23.7 g m^2 at HH sites and 300 ± 68.2 g m^2 at LL sites, wood dry weight was 22.2 ± 17.4 g m^2 at

HH sites and 27.1 ± 19.4 g m^2 at LL sites, and dung dry weight was 43.6 ± 10.3 g m^2 at HH sites and 5.28 ± 2.4 g m^2 at LL sites. At the HH sites impalas accounted for 32.4 ± 7.8 g m^{-2} of dung dry mass whereas zebras and wildebeest were responsible for 7.6 ± 2.1 g m^{-2} and 3.53 ± 1.4 g m^{-2} respectively. Giraffe dung was often observed on the ground at the HH sites but never found within the randomly located quadrats. Total N inputs from animal dung and urine (dry + wet season for all herbivore species combined) were significantly higher at HH sites (1.71 ± 0.34 g N m^{-2}) than at LL sites (0.21 ± 0.08 g N m^{-2}; $t = 2.83$, df = 28, $P = 0.0083$). Impalas were responsible for 83% of total N dung and urine inputs at HH sites, whereas zebra and wildebeest contributed 10% and 7% respectively for overall N inputs at the same sites (Figure 4b). Finally, we did not find significant seasonal variations in animal N inputs ($F_{1,44} = 0.56$, $P = 0.456$) at the HH sites and LL sites.

Visitation of Termites to Litterbags

Termite activity varied according to litter type and period of litter placement. Litter samples of the June placement were visited at higher frequencies by foraging termites than those of the August placement. Frequencies at which litterbags were visited by termites during the year of incubation since June placement were statistically greater for straw at the HH sites than at the LL sites ($\chi^2 = 21.19$, df = 2, $P < 0.001$), but this was not true for *Acacia* litterbags ($\chi^2 = 2.73$, df = 2, $P < 0.24$). After one year's incubation since August placement, litterbag visitation by termites at HH and LL sites was neither significantly different for straw ($\chi^2 = 3.67$, df = 2, $P < 0.16$), nor for *Acacia* litter ($\chi^2 = 4.55$, df = 2, $P < 0.11$). Specimens of both workers and soldiers, collected at litterbag bait sites, were classified into the sub-families Termitinae (with one species: *Amitermes* sp.), and Macrotermitinae (with five species: *Macrotermes* sp., *Macrotermes ukuzii*, *Ancistrotermes latinotus*, *Microtermes* sp. and *Odontotermes* sp.).

Discussion

Our results show that the litter of preferred browse species (*Acacia nigrescens* and *Securinega virosa*) lost significantly more mass than the litter of the less preferred species (*Euclea divinorum*, *Maytenus senegalensis*, and *Combretum hereroense*) during the year of incubation. Moreover, the proportion of straw mass remaining in litterbags beneath trees of high palatability to browsers was significantly lower than under trees of less preferred species. These findings are consistent with studies from temperate and boreal systems, which demonstrated that traits governing plant responses to herbivores (for example, foliage acceptability) are positively related to litter quality and decomposability (Grime and others 1996; Wardle and others 2002; Stark and others 2007). However, although variation in leaf chemistry is linked to among-species variation in litter decomposition, there are also other factors related to large herbivores that appear to be particularly important in influencing within-species variation in litter decomposition and nutrient cycling in semi-arid, eutrophic African savannas.

We found that litterbag mass remaining (for both *Acacia* and straw litter) did not vary between heavily and lightly browsed *Acacia nigrescens* trees (Table 3; Figure 2a, b). We showed that heavily browsed trees had significantly higher N concentrations in freshly collected leaves (for example lower C:N ratio) than lightly browsed trees during the growing season, which likely contributed to attract further browsing. This, together with the high resprouting abilities observed for heavily browsed *Acacia* trees (Fornara and du Toit 2007), suggests that browsers induce changes in resource allocation within trees leading to the occurrence of 'browsing lawns' in African savannas. However, at the end of the growing season we also observed that heavily browsed trees withdrew N from their leaves more efficiently than lightly browsed trees. This resulted in leaf N concentrations being lower at leaf abscission (dry season), and so the leaf C:N ratio of leaf litter, a key indicator of litter quality, was higher beneath *Acacia* trees at heavily browsed sites. Hence, heavily browsed trees returned leaf litter to the soil with a higher C:N ratio than lightly browsed trees, which might partly explain the higher N immobilization that we found at heavily browsed sites (Figure 3a, b, c). It is well known that microbes tend to import N (and P) from the surrounding soil to compensate for an elevated C:N (and C:P) ratio in leaf litter (Aber and Melillo 1982).

The strong temporal variation in leaf N concentration at HH sites suggests that other important issues for the understanding of plant–browser interactions include the mechanisms of N storage and remobilization. These appear to be associated with *Acacia* tree responses to browsing and in turn affect litter quality, and therefore nutrient cycling. A crucial question for future research would then be how plant responses to browsing depend on plant components that store N (for example, roots, shoots, and so on) during the period of physiological inactivity (the dry season which coincides with

winter), as has been demonstrated in deciduous and evergreen temperate woody species (Millard and others 2001).

It is clear from our results (Figure 4a) that overall litter composition (dung included) was different between heavily and lightly browsed sites. Animal dung deposition was significantly higher at heavily browsed–grazed sites (43 ± 10.3 g m^{-2} at HH sites vs. 5.28 ± 2.4 g m^{-2} at LL sites) where large mammalian herbivores preferentially feed and rest, whereas tree leaves and herbs made up most of the litter mass at lightly browsed–grazed sites.

Our hypothesis is that the negative effects of browsers on leaf litter quality (increased C:N ratio of senescing leaves) and overall litter quantity (reduced biomass of herb and tree litter at high herbivory sites) can be offset by the positive effects of dung deposition and its local enhancement of litter decomposition rates. In our study the estimated N input from animal dung and urine was eight times higher at heavily browsed–grazed sites than at lightly browsed–grazed sites. We estimated the N deposition to the soil surface by large herbivores at HH sites to be approximately 17 kg ha^{-1} y^{-1} and at least part of that could readily become available for microbial mineralization in pulses after rainfall events. In our study we did not measure N mineralization rates at heavily browsed–grazed sites but previous studies provide evidence that mammalian herbivores enhance rates of N mineralization (McNaughton and others 1997; Tracy and Frank 1998; Garibaldi and others 2007; Stark and others 2007). Moreover, recent studies in a semi-arid eastern African savanna show that ungulate deposition of N in dung and urine contributed to increase the inorganic N pool available to plants on N-rich glades (Augustine and others 2003; Augustine and McNaughton 2006).

Our results suggest that despite the effect chronic intensive browsing has on enhancing leaf N in palatable trees during the growing season (the ''browsing lawn'' effect), such trees have an enhanced ability for leaf nutrient resorption before abscission. The resulting N-depleted leaf litter (that is, with high C:N ratio) at heavily browsed sites showed initially higher N immobilization (during the first 6 months of incubation) than the less N-depleted litter at the lightly browsed sites. However, between 6 and 12 months into the overall period of litter incubation, the trend in litter N immobilization changed dramatically at HH sites as compared with LL sites (see Figure 3a, b, and c), and this change coincided with the onset of the wet season. This is entirely consistent with straw litter decomposition under *A. nigrescens* trees in the first experiment (see Figure 1b) where we observed a marked change in decomposition after the wet season. Together such results suggest that pulsed N inputs from animal wastes during the wet season (November–March) compensated for the initial high litter C:N ratio and increased N mineralization rates (that is, stimulating microbial activity), which enhanced litter mass decomposition at heavily browsed–grazed sites. This also agrees with the significant browsing × time effect on both litter N (%) and litter C:N ratio (Table 3), as well as with the rapid loss of *Acacia* litter mass between 6 and 12 months just after the wet season months at HH sites (Figure 2a). Finally, these observations are consistent with previous findings that external N inputs increase litter mass loss (Berg and Matzner 1997) especially when initial litter N is comparatively low (Hobbie 2005), such as in the first dry months of incubation at the HH sites. However, despite a trend toward higher straw mass loss at HH sites in the second experiment (Figure 2b) there was no clear change in decomposition rate after the wet season. We attribute this anomaly to site factors including soil quality, the nature of the decomposer communities (termites included) at HH or LL sites, and the local availability of animal N inputs to our litterbags.

The potential implications of our results on the ecosystem nutrient cycling need further study. A parallel investigation carried out across the same study sites showed that the total soil N pool was significantly depleted at HH compared to LL sites (Fornara and du Toit, in press). This would suggest that although N inputs from animal wastes might speed up N cycling and litter decomposition rates through seasonal nutrient pulses at high herbivory sites, large herbivores are likely responsible for a net export of nutrients from sites exposed to chronic and intensive herbivory (see de Mazancourt and others 1999). Finally, other sources or sinks of nutrients, such as those related to termite or dung beetle activity as well as biological nitrogen fixation (Högberg 1992; Bignell and Eggleton 2000) must also influence plant–browser interactions in semi-arid eutrophic systems. Although our results show that termites visited *Acacia* litterbags with the same frequencies at both heavily and lightly browsed sites, we were unable to separate the litter removal effects of termites, microfauna and microbes.

Conclusion

Our findings indicate that *Acacia* trees exposed to a chronic browsing regime produce leaves of elevated quality during the growing season but then litter of

reduced quantity (due to consumption) and quality (due to enhanced resorption of nutrients) at the time of leaf abscission. The resulting reduction in the return of nutrients to the soil through litter is, however, offset by increased deposition of nutrients in dung and urine at high-herbivory sites. Such nutrients become available to plants in pulses following the onset of the rainy season, when litter decomposition also increases due to increased activity of the decomposer community. With the exceptionally high levels of ungulate herbivory in African savannas and the coevolved responses of palatable and resilient *Acacia* trees, it is becoming apparent that the woody plant community adapts to herbivory through adjustments in rates and pathways of nutrient flux. This represents an important difference from the community-level responses observed in other ecosystems, such as temperate and boreal forests, which undergo shifts in the functional composition of the woody plant community toward dominance by unpalatable and chemically defended species (for example, Naiman and others 1986; Pastor and others 1988).

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