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ORIGINAL PAPER

Tree size and herbivory determine below-canopy grass quality and species composition in savannahs

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Abstract Large single-standing trees are rapidly declining in savannahs, ecosystems supporting a high diversity of large herbivorous mammals. Savannah trees are important as they support both a unique flora and fauna. The herbaceous layer in particular responds to the structural and functional properties of a tree. As shrubland expands stem thickening occurs and large trees are replaced by smaller trees. Here we examine whether small trees are as effective in providing advantages for grasses growing beneath their crowns as large trees are. The role of herbivory in this positive tree-grass interaction is also investigated. We assessed soil and grass nutrient content, structural properties, and herbaceous species composition beneath trees of three size classes and under two grazing regimes in a South African savannah. We found that grass leaf content (N and P) beneath the crowns of particularly large (ca. 3.5 m) and very large trees (ca. 9 m) was as much as 40% greater than the same grass species not growing under a tree canopy, whereas nutrient contents of grasses did not differ beneath small trees (<2.3 m). Moderate herbivory enhanced these effects slightly. Grass species composition differed beneath and beyond the tree canopy but not between tree size classes. As large trees significantly improve the grass nutrient quality for grazers in contrast to smaller trees, the decline of the former should be halted. The presence of trees further increases grass species diversity and patchiness by favouring shade-tolerant species. Both grazing wildlife and livestock will benefit from the presence of large trees because of their structural and functional importance for savannahs.

Keywords Bush-encroachment · Grazing · Herb-layer · Nutrient content · Soil nutrients · South Africa

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Abbreviations

VLT	Very large tree
LT	Large tree
ST	Small tree
N	Nitrogen
P	Phosphorus

Introduction

African savannah systems are known for their spatial heterogeneity (du Toit et al. 2003), which is reflected in their specific vegetation structure and composition (Augustine 2003) as well as in the spatial distribution and composition of ungulate species (Adler et al. 2001). Savannahs are described as a continuous grass layer interspersed with trees (Sankaran et al. 2004), and their spatial heterogeneity strongly depends on the scale of observation (Adler et al. 2001). At a landscape scale, the patchiness in spatial nutrient distribution, vegetation structure, and tree species composition has been the focus of many studies (Vetaas 1992; Scholes and Archer 1997; Sankaran et al. 2004). This patchiness might be one important explanation for the high diversity of animals that inhabit these ecosystems. Large single-standing trees contribute to the structural diversity of savannahs as they strongly influence their immediate surroundings—soil (Belsky et al. 1993; Ludwig et al. 2004), plants (Belsky 1994; Treydte et al. 2007), and animals (Ash and McIvor 1998). The mechanisms by which trees affect grass quality beneath their crowns are manifold. Trees can improve the conditions for grass layer growth directly, for example, by providing shade and reducing evapo-transpiration, by accumulating soil nutrients close to their root systems (Belsky 1994; Dean et al. 1999), and by changing the micro-climate (Jackson et al. 1990; Belsky 1994; Ludwig et al. 2001; Power et al. 2003). Recent studies have shown that both soil and grass nitrogen (N) and phosphorus (P) contents were elevated beneath tree canopies compared to inter-canopy sites (Ludwig et al. 2004; Treydte et al. 2007, 2008) whereas some studies did not find any or only slight differences in soil properties between canopy and inter-canopy sites (Witkowski and Garner 2000).

Not only nutrient content but also species composition, grass layer structure, and biomass differed beneath and outside of tree canopies (Ludwig et al. 2004; Treydte et al. 2007). Grasses growing under the tree canopy contained more green leaf material and stayed green for longer into the dry season than grasses growing further away from trees (Treydte et al. 2008). Overall, trees contribute substantially to the grass species layer and to vertical and horizontal structural diversity in African savannah systems.

However, the number of large single-standing trees has declined due to wood harvesting activities or damage by elephants (Jacobs and Biggs 2002; Western and Maitumo 2004). Low recruitment rates of large tree species have also been reported by Holdo (2003) and Caro et al. (2005). In addition, open savannahs become denser due to bush encroachment which is often the result of landscapes being over-grazed (Jeltsch et al. 1997; Tobler et al. 2003) and because of poor fire management (Eckhardt et al. 2000). Since bush-encroached areas are mostly dominated by small and densely growing trees, tree size might be important in influencing grass quality and structure. While larger and older trees will have had more time to develop distinguished beneath-canopy grass patches, both nutrient-wise and structurally, through the mechanisms described earlier, smaller and younger trees

might show less strong effects on the grass layer. If the documented elevated soil and grass nutrients and differences in grass species composition scale up linearly with tree size one would expect the beneath-canopy soil and grass nutrients of smaller trees to be more similar to the inter-canopy grass sites, while those under larger trees would differ substantially from the inter-canopy grasses. This implies that grasses beneath canopies of larger trees would be qualitatively higher and, thus, a more attractive food source for grazers than those of smaller trees.

In addition, grazers can influence biomass and species composition of their fodder grasses (Alhamad and Alrababah 2008). Grazers decrease the grass biomass through removal but they also trigger enhanced productivity and fresh regrowth (du Toit and Cumming 1999). Dung deposition and constant grazing can also increase N and P contents of soil and grasses in feeding areas (McNaughton 1984). Grasses further benefit from grass tuft removal because the risk of fire and grass mortality through self-shading are reduced (Ong et al. 1978).

We therefore expect that the presence of grazers influences the amount by which a tree can increase the grass quality underneath its crown. If grazers are attracted to beneath canopy areas, they might add to the nutrient input of trees and, through grazing and defecating, enhance grass and soil nutrients below tree crowns. Hence, we would find the phenomenon of a “grazing lawn” (*sensu* McNaughton 1984) beneath canopy areas in areas of moderate grazing densities. Based on the previous assumptions, we propose:

1. The N and P contents of grasses and soils beneath large trees are more strongly enhanced than those beneath small trees when compared to grasses growing outside of trees.
2. Differences in the grass layer structure beneath and outside canopy plots will be more pronounced in areas of high grazing intensity compared to areas of low grazing intensity.
3. Beneath canopy soil and grass nutrients are higher in areas of high grazing intensity compared to areas of low grazing intensity.

We sampled soil and grass nutrients and structure beneath and beyond the canopies of differently sized trees and in areas of different grazing pressure in a South African savannah. Our aim was to examine the importance of tree size and herbivory to the patchy distribution of grass quality and forage for grazing ungulates in South African savannahs.

Materials and methods

Study site

Our study site was located in Kruger National Park, South Africa, receiving a mean annual rainfall of 515 mm. The study sites were two areas of different herbivore history but similar soils and rainfall regime. Both sites were mixed woodland savannahs; the abundant tree species were *Acacia nigrescens*, *Colophospermum mopane*, *Sclerocarya birrea*, *Combretum apiculatum*, and *Combretum hereroense*. The N’wathishumbwe Roan Enclosure (22°58’S, 31°26’E), an area of 301 ha, is situated on basaltic soils that have a high clay content (Venter et al. 2003). The enclosure was fenced off from all herbivores in 1967 (Levick and Rogers 2008). Large Marula (*S. birrea*) and Knobthorn (*A. nigrescens*) individuals dominated the tree community. A small Roan antelope population (*Hippotragus equinus*) has been kept inside the enclosure for further releases into the unfenced

Table 1 Biomass estimates (kg ha^{-1}) as cumulated body mass of the most common large herbivores around the Roan enclosure area, i.e., in the Northern plains, and in the Satara area of Kruger National Park (Grant et al. unpublished, census data 2006–2007)

Year	Northern plains		Satara area	
	2006	2007	2006	2007
Total biomass in kg ha^{-1}	17.37	34.4	31.33	27
% of total biomass				
Elephant <i>Loxodonta africana</i>	33	52	>1	45
Buffalo <i>Syncerus caffer</i>	37	31	34	23
Zebra <i>Equus burchelli</i>	13	7	23	20
White rhino <i>Ceratotherium simum</i>	6	5	12	11
Others	11	5	31	1

surroundings, ranging from 7 to 50 individuals between 1994 and 2008. The roan biomass in the camp was 18.9 kg ha^{-1} over the last 2 years, and grazing impact in the enclosure was minimal (personal observation) while outside of the enclosure herbivore densities were high (Table 1).

Data collection

We selected in total 39 trees of different sizes inside and outside the enclosure (Table 2) during the growing season in May 2008. We divided the trees into three different size categories: (1) Very large trees (VLT, average height 9 m): this category only occurred inside the Roan enclosure where four individuals were selected; (2) large trees (LT, average height 3.5 m): 16 trees were selected, eight of which grew inside the enclosure, eight outside; (3) small trees (ST, average height 2 m): 17 trees were selected, nine trees growing inside and nine trees outside of the enclosure. For each tree we recorded species, tree height, canopy radius, and the height at which branches occurred (Table 2). We established a $1 \times 1 \text{ m}$ quadrat beneath (within 50% of the respective canopy radius) and outside (150% of the respective canopy) of each tree crown. In every quadrat we assessed grass species composition using a modified Braun-Blanquet method (see Treydte et al. 2007). We also recorded average grass height (measured at ten random points within the quadrat), overall grass cover (visually estimated), and greenness (the overall state of the grass layer within the quadrat was assessed and separated into “green” or “dry”). Inside of these quadrats, we collected a soil sample (from 0 to 10 cm soil depth), and we clipped all plants to ground level within a $25 \times 25 \text{ cm}$ subsample-quadrat. Soil and plant samples were dried in a drying oven at 70°C for 48 h, plant samples were sorted into leaf and stem material and then weighed. A modified Kjeldahl method (Bradstreet 1965) was applied to ground leaf material and sieved (2 mm) soil samples. After digestion, nitrogen (N) and phosphorus (P) contents were determined colorimetrically using a continuous flow analyser (Skalar SA-4000).

In the Satara region of Kruger Park ($24^\circ 22' \text{S}$, $31^\circ 46' \text{E}$), an area influenced by high grazer densities (Table 1), we measured the change in grass species composition under grazing impact with increasing distance away from a tree. Here, we sampled 17 small, 24 large, and 14 very large trees. The woody vegetation was dominated by *A. nigrescens* and

Table 2 Tree species sampled in the Satara region and at the Northern Plains, inside and outside of the Roan enclosure (Inside Roan, Outside Roan, respectively)

	Satara			Northern plains					
	VLT	LT	ST	Inside Roan			Outside Roan		
VLT				LT	ST	VLT	LT	ST	
Tree size class	VLT	LT	ST	VLT	LT	ST	VLT	LT	ST
Number of trees sampled	14	24	17	4	8	9	0	9	9
Average height per class (m)	10.4	4.6	2.3	8.9	3.6	2.3		3.7	2.1
<i>Acacia</i> spp.	1	10	7	2	1	0		0	1
<i>Cassia abbreviata</i>	1	0	0	0	0	0		0	0
<i>Colophospermum mopane</i>	0	0	0	0	2	0		2	3
<i>Combretum</i> spp.	1	9	4	0	2	1		7	5
<i>Dichrostachys cinerea</i>	0	0	0	0	1	5		0	0
<i>Grewia villosa</i>	0	0	0	0	1	0		0	0
<i>Linnea schweinfurthii</i>	2	0	0	0	0	0		0	0
<i>Lonchocarpus carpassa</i>	0	0	6	0	0	0		0	0
<i>Sclerocarya birrea</i>	9	0	0	2	0	0		0	0
<i>Terminalia</i> spp.	0	5	0	0	0	0		0	0
<i>Zanthoxylum capense</i>	0	0	0	0	1	3		0	0

Size classification of trees: *VLT* very large tree (only found at Satara and inside the Roan enclosure), *LT* large tree, *ST* small tree. The number of trees that were sampled for each species is shown

C. apiculatum (Gertenbach 1983), and—in contrast to the area immediately adjacent to the Roan enclosure—also very large trees were present. We collected data for small, large, and very large trees along 20 m long transects. For each tree, transects radiated away from the trunk in N and S compass directions. Along all transects at 1 m intervals we recorded the grass species on the transect line.

Statistical analyses

We tested for normal distributions of residuals and transformed N and P data accordingly if the conditions were not met. Vegetation cover data were arcsin(sqrt)—transformed (Zar 1999). Leaf and stem biomass were calculated as leaf:stem ratio. We used a MANOVA to test the effect of “site”, “tree size”, and “canopy” (see below) on N and P levels in plants and soil. We then applied a nested ANOVA design for our model: The variables N and P content of soil and grasses, grass layer height, grass layer cover, and leaf:stem ratios were tested for their dependence on the fixed factors “site” (inside versus outside of the enclosure), nested within “tree size” (VLT, LT, ST), nested within “canopy” (beneath versus outside of tree canopies), and the random factor “tree”. LSD post hoc tests indicated differences between tree size class groups. We used multivariate analysis techniques such as principal component analysis (PCA) and one-way pairwise analysis of similarity (ANOSIM; Hammer et al. 2004) to identify distinct groups or patterns in grass species composition of our sample plots. We applied a Kruskal–Wallis test and a multiple comparison post-hoc test after Dunn (1964) for differences of the most common grass species growing inside and outside of the Roan enclosure beneath and outside canopies.

Results

Soil

Inside the Roan enclosure, soil N concentration was higher beneath canopies of very large trees (VLT) and lower beneath canopies of large trees (LT) than outside tree canopies, while small tree (ST) soil N levels did not differ between canopy locations (Fig. 1a). Outside the enclosure, beneath-canopy soil N concentrations were 20% higher compared to outside canopy soil for both ST and LT (VLT were absent; Fig. 1b). Similar patterns were found for soil P contents (Fig. 1c, d), with P levels being slightly higher beneath trees growing outside of the Roan enclosure. The MANOVA test did not show any significant effects of “enclosure” (*Pillai’s trace* = 0.33, $P = 0.16$, $n = 20$), “tree size” (*Pillai’s trace* = 0.36, $P = 0.39$, $n = 20$) or “canopy location” (*Pillai’s trace* = 0.15, $P = 0.48$, $n = 20$) on soil N and P levels. In our nested ANOVA model, “canopy location” influenced soil N ($F_{1,6} = 5.5$, $P = 0.06$) and for soil P levels there was a significant interaction in “enclosure” \times “canopy location” with P levels being lower outside of the enclosure and being slightly elevated beneath tree canopies ($F_{1,6} = 9.5$, $P = 0.02$).

Grass

The MANOVA model indicated that grass leaf N and P levels were significantly influenced by “tree size” (*Pillai’s trace* = 0.26, $P = 0.001$, $n = 76$) and “canopy location” (*Pillai’s trace* = 0.30, $P < 0.001$, $n = 76$) but not by “enclosure” (*Pillai’s trace* = 0.01, $P = 0.67$, $n = 76$). Nested ANOVA further indicated that N and P contents in grass were significantly affected by “tree size” and “canopy location” ($F_{2,33} = 4.1$, $P = 0.03$ and $F_{1,34} = 8.2$, $P = 0.01$, respectively, $n = 20$). Particularly grasses beneath VLT canopies had higher grass leaf N contents (40%) while grass leaf N content beneath LT was also higher (10%) but less so compared to grasses outside of tree canopies (Fig. 2a, b). In contrast, small trees had no effect on the N concentration in grass leaves. Phosphorus

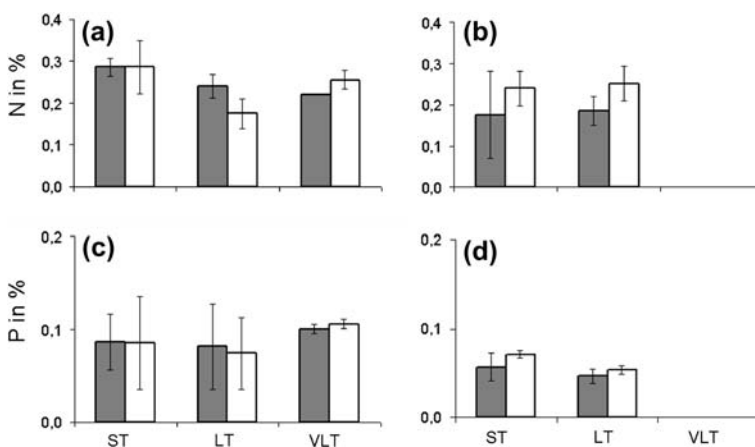


Fig. 1 Soil nutrient content (\pm SD) for different tree sizes. **a** Nitrogen content of soil inside the Roan enclosure and **b** outside of the enclosure. **c** Phosphorus content inside and **d** outside of the Roan enclosure. Grey bars indicate outside canopy soil and white bars beneath canopy soil N and P content. ST small trees, LT large trees, VLT very large trees

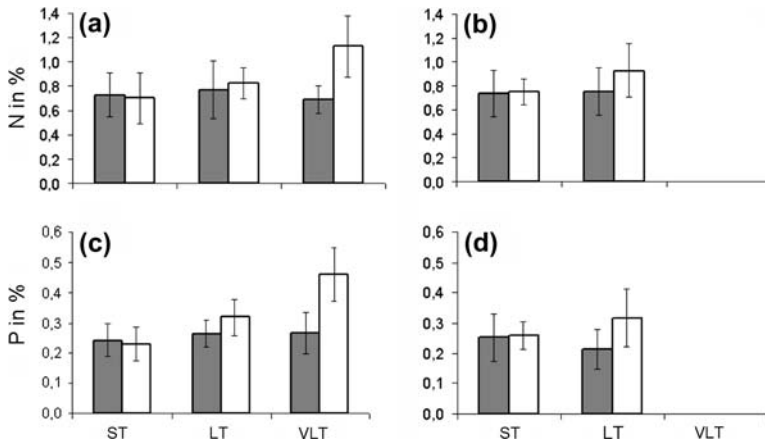


Fig. 2 Plant nutrient content (\pm SD) for different tree sizes. **a** Nitrogen content of soil inside the Roan enclosure, **b** outside of the enclosure. **c** Phosphorus content inside and outside **d** of the Roan enclosure. Grey bars indicate outside canopy soil and white bars beneath canopy soil samples. ST small trees, LT large trees, VLT very large trees

concentration in grass leaves was also significantly influenced by tree size ($F_{2,33} = 4.9$, $P = 0.01$) and canopy location ($F_{1,34} = 20.2$, $P < 0.01$) and there was a significant interaction between tree size and canopy location with P levels being highest beneath VLT ($F_{2,33} = 7.3$, $P < 0.01$). Phosphorus content was by 40% greater beneath VLT and by 33% beneath LT canopies (Fig. 2c, d); small trees had no effect on P concentrations in grass.

Grass structural analyses revealed no significant differences between canopy locations and tree sizes. However, certain trends were visible: differences in leaf-stem ratio, grass height, cover, and greenness were more pronounced beneath and outside of LT and VLT but less so for ST (Fig. 3a–h).

Discriminant analyses for pooled data in and around the Roan enclosure indicated that species composition was significantly different beneath and outside tree canopies ($\chi^2 = 44.5$, $P < 0.01$). ANOSIM indicated that grass species assemblages beneath LT differed significantly from assemblages outside of tree canopies (Bray–Curtis: $R = 0.57$, $P < 0.001$ inside the enclosure and $R = 0.90$, $P < 0.001$ outside the enclosure). However, differences between grass species composition beneath and outside ST canopies were not significantly different (Bray–Curtis: $R = -0.05$, $P = 0.7$ inside the enclosure and $R = 0.12$, $P = 0.06$ outside the enclosure). PCA indicated that the occurrence of particularly *Panicum maximum*, *Cenchrus ciliaris*, *Urochloa mosambicensis*, *Setaria spaelata*, *Digitaria eriantha*, and *Themeda tiandra* accounted for much of the variability in the data (Fig. 4). When testing for differences between the most abundant grass species beneath and outside canopy each for inside and outside the Roan enclosure, we found significant differences for *P. maximum* ($\chi^2 = 30.2$, $P < 0.001$, $n = 78$), *U. mosambicensis* ($\chi^2 = 9.2$, $P = 0.03$, $n = 78$), *Schmidia pappophoroides* ($\chi^2 = 15.1$, $P = 0.002$, $n = 78$) and *P. repens* ($\chi^2 = 22.5$, $P < 0.001$, $n = 78$). Post-hoc multiple comparisons indicated that *P. maximum* was more frequently found beneath tree canopies than outside of tree canopies, in contrast with *U. mosambicensis*, which showed the opposite distribution pattern (Fig. 5).

Transect counts at Satara indicated a decline in the frequency of *P. maximum* with increasing distance from a tree. This decline was steeper for LT ($y = -14.3 \ln(x) + 41$;

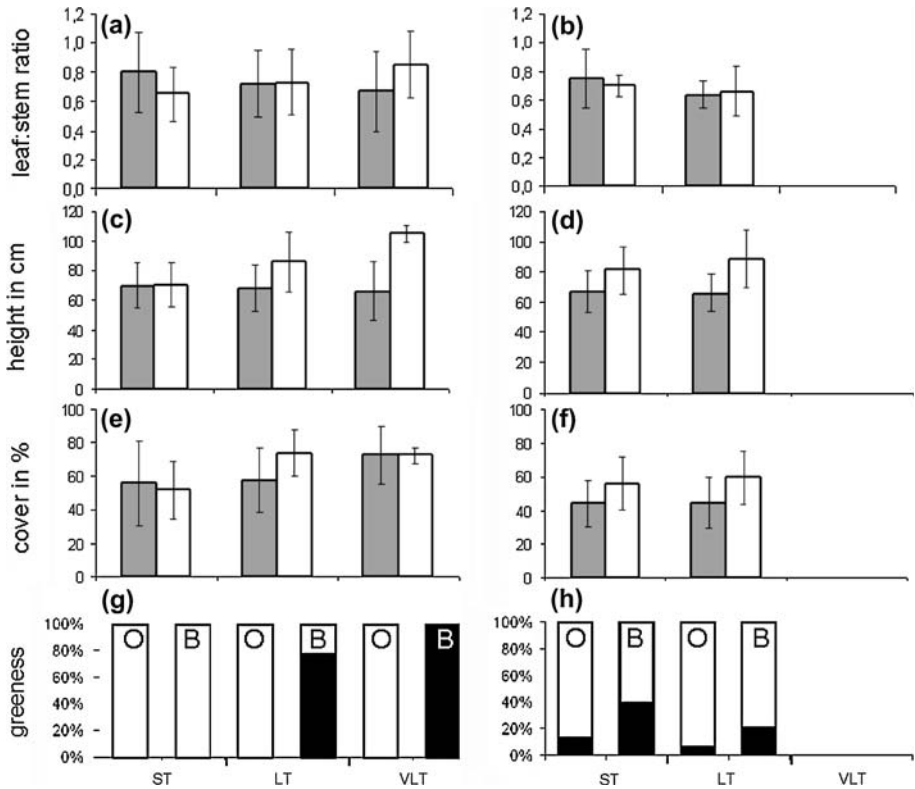


Fig. 3 Leaf:Stem ratio (\pm SD) of grasses growing beneath and outside of tree canopies for three size tree classes **a** inside the Roan enclosure, **b** outside of the Roan enclosure. Herbaceous layer height **c** inside and **d** outside the Roan enclosure and herbaceous layer cover **e** inside and **f** outside the enclosure for three tree size classes. Grey bars indicate outside canopy and white bars beneath canopy samples. Greenness of the grass layer in % of all plots **g** inside and **h** outside the Roan enclosure. White parts of the bars indicate dry, black parts indicate green condition of the grass layer; B beneath tree canopy, O outside tree canopy. ST small trees, LT large trees, VLT very large trees

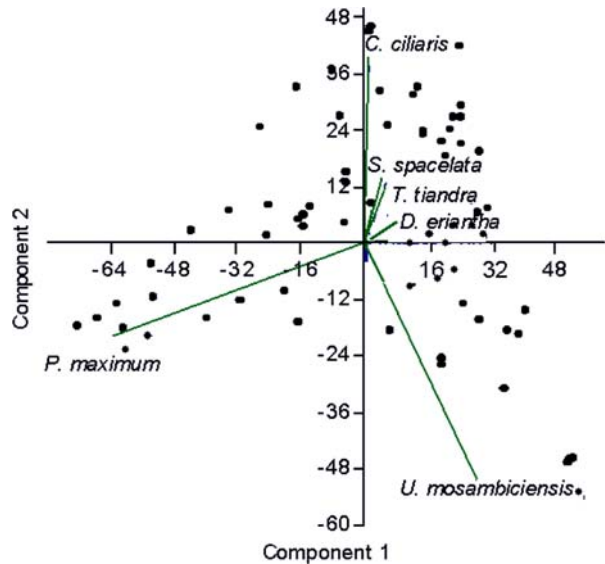
$R^2 = 0.82$) and VLT ($y = -8.8 \ln(x) + 25$; $R^2 = 0.85$) than for ST ($y = -4.1 \ln(x) + 13$; $R^2 = 0.59$). Other species such as *Bothriochloa insculpta* increased in abundance with proximity to a tree (e.g., for LT: $y = 3.7 \ln(x) + 0.3$; $R^2 = 0.62$).

Discussion

Tree size

Both soil and grass nutrient content were more strongly elevated beneath very large trees compared to large and small trees, confirming our first prediction that nutrient concentrations in forage and soil increase beneath the canopy with increasing tree size. While these trends were weaker for soil nutrients, grasses beneath very large tree canopies contained up to 40% more nutrients than grasses growing outside of canopies. Ludwig et al. (2004) also found that both soil and grass nitrogen content was higher beneath large trees than beneath

Fig. 4 Scatter plot generated through principal component analysis combined for all tree size classes inside and outside the Roan enclosure. The biplot rays indicate the strong discriminating character of the grass species *Panicum maximum*, *Cenchrus ciliaris*, *Urochloa mosambicensis*, *Setaria sphacelata*, *Digitaria eriantha*, and *Themeda tiandra*



small trees or bushes in an eastern African savannah. However, Witkowski and Garner (2000) did not detect differences in soil nutrients between beneath-canopy and inter-canopy sites. Witkowski and Garner (2000) sampled beneath trees, which might have been too small (>2 m) to detect any differences; the slightly higher P soil contents they found outside of tree canopies might be related to the fact that N-fixing trees such as *Acacia* spp. require high soil P content to fix atmospheric N (Hartwig 1998). The underlying mechanisms of a larger canopy improving grass nutrients more strongly compared to smaller canopies are that larger shady areas might be more beneficial because of a more favourable microclimate. Further, ongoing processes of defecation by attracted herbivores (Dean et al. 1999), hydraulic lift (Ludwig et al. 2003), nutrient accumulation through the tree's root system (Ludwig et al. 2004), and a higher amount of litter fall compared to smaller trees might have contributed to higher grass nutrients beneath larger trees. Our study shows that tree structure, such as size and canopy radius, are potentially important determinants of grass quality with respect to nutrient content and species composition; however, the underlying mechanisms still need to be experimentally tested. Treydte et al. (unpublished data) found that areas beneath and close to large and very large tree canopies were attractive to herbivores, and more dung was deposited at these sites compared to areas further away from tree canopies. The high accumulation of dung and grazing activity could lead to a positive feedback loop (McNaughton 1984), with herbivores further enhancing the nutrient quality of their feeding grounds beneath large tree canopies.

Besides tree size also tree species might be an important factor determining grass and soil characteristics beneath canopies. Belsky et al. (1993) found higher grass productivity and slightly different soil nutrients and organic matter beneath canopies of *Acacia tortilis* than beneath *Adansonia digitata* trees but found that overall the climatic condition, i.e., xeric versus mesic environment mainly determined differences in soil beneath and outside tree canopies rather than tree species. Treydte et al. (2007, 2008) compared the effect of N-fixing trees versus non-N-fixing trees on the grass and soil N contents beneath their canopies and did not find significant differences for these two species. In contrast, Power

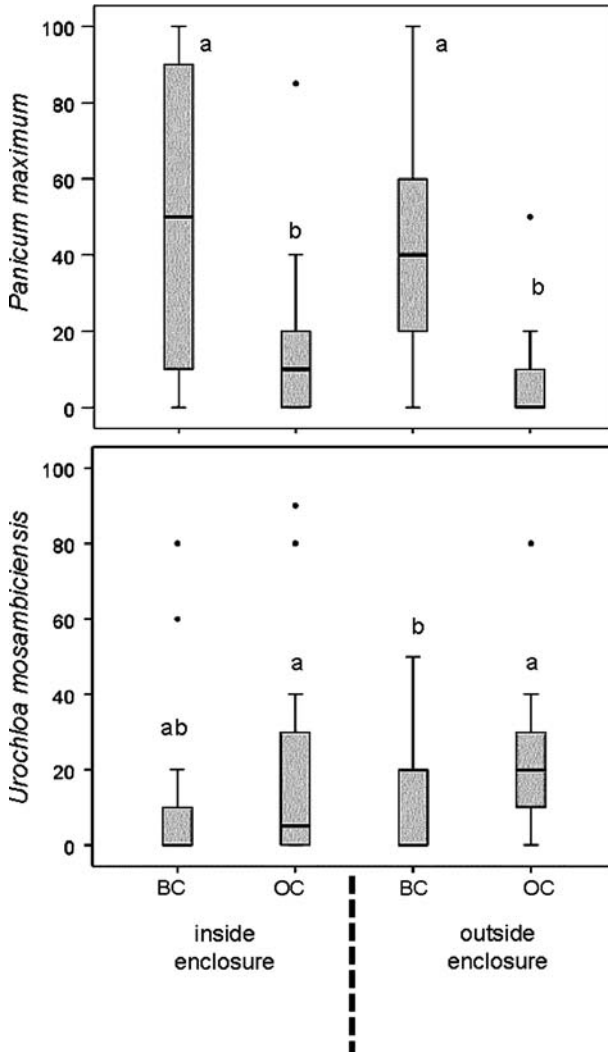


Fig. 5 Boxplot of *Panicum maximum* and *Urochloa mosambicensis* cover (in %) of beneath (BC) and outside (OC) tree canopies for trees growing inside and outside the Roan enclosure. Black bars, grey boxes, and whiskers indicate the median, quartiles, and extreme values, respectively. Letters denote significant differences after post-hoc multiple comparison tests

et al. (2003) found higher soil N and higher grass yield beneath *Acacia* trees, which they related to the *Acacia* tree's potential of fixing atmospheric N. However, as there are some constraints such as low P soil nutrients or very dry conditions (Hartwig 1998), under which N-fixation does not take place, actual measurements of N-fixing activities should be conducted before general conclusions can be drawn. Due to financial and time constraints and because our priority was to assess potential consequences of a threatening decline in large savannah trees we focused on the tree size rather than tree species effects in this study.

Herbivore impact

The nutrient concentration in the grass layer did not differ significantly between the inside and outside of the Roan enclosure, except for slightly higher proportions of leaves versus stems in areas beneath very large tree canopies. This was contrary to our expectation that more grass leaves should be eaten and grass height and cover would be reduced in areas that herbivores frequently used as feeding grounds. One of the main factors affecting these characteristics is seasonality influencing grass structure and nutrient contents (Treydte et al. 2008), which in turn influences the use of different nutrient patches. Herbivores tend to use patches such as termite mounds and sodic sites early in the growing season (Grant and Scholes 2006), thereafter they use the most nutritious vegetation under trees more heavily later in the growing season (personal observation). Fryxell (1991) also reported that in the late dry season food resources become scarce and grazing damage is focused on the few nutrient-rich patches. Hence, we expect the grass structure to differ more strongly between beneath and outside tree canopies further into the dry season than during the time when our study was conducted. Grasses beneath trees outside of the roan enclosure will then show strong structural differences compared to grasses inside the enclosure caused by a higher grazing intensity beneath canopies.

Grass species compositions beneath and outside LT canopies differed more strongly outside of the enclosure than inside the enclosure. Grazing can strongly alter grass species compositions (Vesk and Westoby 2001), and if grazing intensity is patchily distributed, i.e., in our study focused on beneath-canopy areas, the combination of herbivory and woody cover might lead to an often observed high spatial heterogeneity in semi-arid environments (Rietkerk et al. 2000).

In contrast to our predictions, soil and grass nutrients did not differ significantly inside and outside the Roan enclosure. Beneath canopy grass nutrients were slightly more elevated outside the enclosure than inside the enclosure. However, soil nutrients, particularly P content, were lower beneath and outside canopies at sites outside of the enclosure, i.e., with more intense grazing. Here, fire intensity might play a role as fires inside the enclosure are strictly controlled for safety reasons and tend to be cooler (Grant, unpublished data). P and N are lost with high intensity fires, which may explain the lower P concentration outside the enclosure.

Not only tree size but also tree density might play an important role in the choice of grass patch by herbivores. Areas where small trees are at high densities are relatively unattractive foraging sites for herbivores (Riginos and Grace 2008). Riginos and Grace (2008) reported a declining dung pile abundance of most herbivores with increasing tree densities and, hence, decreasing visibility with a concordant increase in predation risk. Riginos and Grace (2008) further argued that these areas were probably not being used by herbivores to avoid predators. By avoiding predators, prey species can shape the habitat vegetation structure of their refuge area (Ripple and Beschta 2004). Bush-encroached areas are usually composed of small trees at high densities (Jeltsch et al. 1997; Tobler et al. 2003). In addition to their structural disadvantage of poor visibility, our study showed that small trees do not contribute as much to the structural and nutritional quality of the beneath-crown grass layer as large trees do. Further, Smit (2005) argued that *Colophospermum mopane* trees even suppress grass productivity, more strongly so when trees grew in high densities. Hence, bush-encroached areas will become and remain poor feeding grounds for grazers.

Tree size also reflects the age of the grass patch beneath a tree canopy. Hence, the grass community assemblage around a growing tree will change over time as plants of higher

shade-tolerance or higher nutrient demands become more abundant. Differences in grass species composition beneath and outside tree canopies have been reported by Wong (1990), East and Felker (1993), and Treydte et al. (2007). In agreement with our study, they found that the shade-loving *Panicum* species dominated the grass layer beneath trees. *Panicum* spp., a grass of high nutritional value, was more abundant beneath large trees compared to small trees. As large trees are currently most threatened to disappear from certain savannah systems, we point out that they more strongly alter the species composition in their immediate surroundings compared to smaller trees. Large trees, thus, contribute to species diversity in savannah systems, in combination with smaller trees and open grassland. A high plant species diversity and heterogeneity on different spatial scales is an important feature in savannah systems and has probably caused the high abundance and diversity of herbivore species in these landscapes (Adler et al. 2001).

Conclusions

Large trees, and particularly very large trees, strongly enhance the grass layer quality for grazing ungulates: grasses high in nutrients (green, tall, high leaf proportions), and dominated by preferred species such as *Panicum* spp. grow beneath their crowns. The enhancement of nutrient concentration and favourable grass species and structure beneath the tree canopy appeared to scale up with increasing tree size. The loss of large and very large trees from the ecosystem may thus result not only in a decline in spatial heterogeneity but also in a loss of species diversity and functional diversity. The magnitude of this functional loss due to the declining numbers of large trees, and the lack of recruitment of these trees need to be addressed. To conserve biodiversity, large tree protection should become high priority in future management activities. This will foster the high structural and species diversity of the vegetation, generated by the woody cover of low, medium, and tall trees within open grassland areas. Consequently, as herbivores are dependent on this structural and functional vegetation diversity, protective action on vegetation will also support the future conservation of wild ungulates in savannah systems.

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