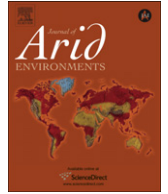




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Enhanced use of beneath-canopy vegetation by grazing ungulates in African savannahs

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ABSTRACT

The cover of large trees in African savannahs is rapidly declining, mainly due to human land-use practices. Trees improve grass nutrient quality and contribute to species and structural diversity of savannah vegetation. However, the response of herbivores to trees as habitat features is unknown. We quantified the habitat use of wild and domestic ungulates in two eastern and southern African savannahs. We assessed grazing intensities and quantified dung depositions beneath and around canopies of different sized trees. Grasses were eaten and dung was deposited twice as frequently beneath large (ca. 5 m in height) and very large trees (7–10 m) than in open grasslands. Small trees (<2.5 m) did not show this trend. Grazing intensity and dung deposition decreased with distance away from trees at both study sites. These results suggest that large trees represent essential habitat features for domestic and wild herbivores. Increased dung depositions beneath large trees may further promote the maintenance of a patchy nutrient distribution in savannahs. Small trees cannot provide the same structural and functional advantages as large trees do. We recommend that land-use practices be promoted which conserve large single-standing trees to benefit the flora and fauna of African savannahs.

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1. Introduction

Savannah ecosystems, defined by the co-existence of trees and grasses, are ecologically and economically important systems; they cover more than one fifth of the world's land surface and support some of the highest diversities and abundances of ungulate herbivores, both wild and domestic (Sankaran et al., 2005; Scholes and Archer, 1997). Isolated trees in savannahs can have a number of important consequences for ecosystem diversity, providing essential habitat structure and function for a wide variety of taxa. Browsing ungulates such as giraffe and kudu feed on tree leaves (Mapaure and Campbell, 2002; Ward and Young, 2002), birds perch and nest in tree crowns (Belsky, 1994; Dean et al., 1999; Ogada et al., 2008), ant species have symbiotic relationships with some tree species (Young et al., 1997), and predators such as leopards and lions use trees as hiding grounds (Schaller, 1972). Many plants can also profit from growing close to or beneath tree crowns. Sub-canopy areas often support grass and forb species that are not found in inter-canopy areas (Scholes and Archer, 1997). Additionally, the nutritional quality

of herbaceous species is often enhanced under tree canopies (Ludwig et al., 2004; Treydte et al., 2007). This is thought to benefit grazing ungulate herbivores. However, the extent to which these herbivores make use of the beneath-canopy habitat provided by trees has rarely been quantified.

Trees may benefit savannah herbivores both directly and indirectly. In addition to providing essential forage to browsing and mixed-feeding herbivores, large trees often appear to attract herbivores because of the shade they provide. In addition to these direct effects, trees may indirectly benefit herbivores via their effects on the herbaceous layer. Trees often improve the growing conditions for the herbaceous layer: they provide shade, thereby reducing evapotranspiration, and can accumulate soil nutrients close to their root systems (Belsky, 1994; Ludwig et al., 2004; Ries and Shugart, 2008). Litter fall can also increase soil nutrients and microbial activities (Belsky, 1994; Jackson et al., 1990) thus fertilizing the grasses and forbs growing close to tree canopies. Recent studies have shown that both soil and grass nutrient contents were elevated beneath tree canopies compared to inter-canopy sites (Ludwig et al., 2004; Treydte et al., 2007). In addition, grasses growing under tree canopies had higher biomass, more green leaf material and stayed green for longer into the dry season than grasses growing further away from trees (Treydte et al., 2008). It has therefore been hypothesized

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that grazing wildlife and livestock should preferentially select grasses growing beneath trees as a food source (Treydte et al., 2009) and that trees thus have important indirect effects on herbivore populations (Ludwig et al., 2008; Treydte et al., 2009).

In African savannahs, however, tree abundance and habitat structure are changing due to a variety of human land-use and management activities. In some areas, wood-harvesting (primarily for firewood and charcoal) and high densities of elephants are causing declines in tree cover and abundance (Goheen et al., 2007; Jacobs and Biggs, 2002; Luoga et al., 2002) – particularly among large, single-standing trees. In other areas, over-grazing and imprudent fire regimes appear to be causing woody or bush encroachment (Eckhardt et al., 2000; Jeltsch et al., 1998; Tobler et al., 2003) – an increase in tree density, particularly small and mono-specific trees or shrubs. These changes in savannah structure may have a variety of consequences for both wild and domestic herbivores. For example, if large rather than small trees provide essential shade and evoke the most enhanced grass quality compared to their surroundings, then large trees should be most frequently visited by grazers and most important to grazing and browsing herbivores alike. Additionally, if grazers improve their feeding grounds by depositing dung and constantly trimming the grasses we might expect a positive feedback loop, i.e., a “grazing lawn” effect (McNaughton, 1984) in areas beneath and close to trees (see also de Knegt et al., 2008). This effect might contribute to the maintenance or promotion of the areas under large trees as hotspots of high grass nutrient and structural quality in African savannahs.

To our knowledge, the extent to which trees attract herbivores and the extent to which the sub-canopy grass layer is eaten by grazing herbivores has not been quantified. Moreover the importance of tree size in affecting herbivore use of trees has not been examined. Here, we quantify the importance of trees and tree size for herbivore use in two African savannah systems. We test for herbivore activity patterns with respect to different tree sizes to quantify the importance of trees for herbivores. In doing this, we set out to test the following hypotheses:

1. Grazing intensity is higher for sub-canopy than for inter-canopy grasses.
2. Grazing and browsing ungulates are attracted to trees and, thus, leave more dung in close neighbourhood of trees than they do further away from tree canopies.

3. Tree structure modifies these effects: large trees are more attractive to grazers than small trees.
4. Cattle and wildlife behave similarly in their grazing preference for sub-canopy grasses.

2. Material and methods

Study area. Our study sites were located in South Africa and in Kenya, in savannahs that differed slightly in their rainfall, seasonality and underlying soil fertility. We investigated trees in the Satara area in Kruger National Park, South Africa (UTM grid: 36 J 0372496, 7300808) and at the Mpala Ranch, Laikipia district, Kenya (UTM grid: 37 N 263860, 35132). The Satara region in Kruger National Park is located on granitic sandy clay soils, with parts on basaltic soil. The average annual rainfall is about 550 mm (Eckhardt et al., 2000). At Mpala, our study area was underlain by both red sandy loams of granitic origin and “black cotton soils”, dark clay-rich soils of basaltic origin. The average annual rainfall is approximately 510 mm (Augustine et al., 2003). The woody vegetation at Satara is dominated by *Sclerocarya birrea*, *Acacia nigrescens*, *Combretum* spp., *Linnea schweinfurthii* and *A. tortilis*. The dominant tree species at Mpala are *Acacia drepanolobium*, *A. etbaica*, *A. mellifera*, *A. tortilis* and *Balanites aegyptiaca*. Both sites have rich native ungulate faunas, with about 30 large herbivore species present (Pienaar et al., 1987; Young et al., 1998). At Satara, the main grazer species are zebra *Equus burchelli*, buffalo *Syncherus caffer*, wildebeest *Connochaetes taurinus* and warthog *Phacochoerus africanus*, important browser species are Greater Kudu *Tragelaphus strepsiceros* and Giraffe *Giraffa camelopardis* and abundant mixed feeders are impala *Aepyperos melampus* and elephant *Loxodonta africana* (Pienaar et al., 1987). At Mpala, the main grazer species are zebra *E. bruchelli* and *E. grevyi*, hartebeest *Alcelaphus buselaphus*, warthog and buffalo, important browsers are giraffe *Giraffa reticulata* and dikdik *Madoqua kirki* and common mixed feeders are elephant, Grant’s gazelle *Gazella granti* and impala. The Mpala Ranch is also managed for cattle production (Young et al., 1998).

Data collection. We recorded evidence of herbivore activity beneath and around 131 isolated trees of different size and structure, each tree being about 30 m away from the nearest tree. We estimated individual tree heights visually, measured the canopy radius, i.e., the distance from the trunk to the canopy edge for three different compass directions (N, SE, SW) and recorded the height at

Table 1
Size characteristics (average in m ± SD) of trees sampled at the two study sites: Mpala, Kenya, and Satara, South Africa. Size classification of trees: VLT = very large tree, LT = large tree, ST = small tree. Species denotes the main tree species of which samples were taken.

	Class	N	Tree height	Canopy radius	Branching height	Species
Mpala	VLT	2	7.0 ± 1.4	3.0 ± 0.7	2.0 ± 0.0	<i>Acacia tortilis</i> <i>Ficus sycamorus</i>
	LT	41	4.5 ± 1.3	2.3 ± 0.9	1.3 ± 1.0	<i>Acacia mellifera</i> <i>Acacia drepanolobium</i> <i>Acacia tortilis</i> <i>Balanites aegyptiaca</i>
	ST	33	2.1 ± 0.4	1.2 ± 0.4	0.9 ± 0.4	<i>Acacia mellifera</i> <i>Acacia drepanolobium</i> <i>Acacia tortilis</i> <i>Balanites aegyptiaca</i>
Satara	VLT	14	10 ± 2.0	5.2 ± 1.5	6.4 ± 2.9	<i>Sclerocarya birrea</i> <i>Cassia abbreviata</i> <i>Acacia nigrescens</i>
	LT	24	4.6 ± 1.2	2.8 ± 1.3	1.4 ± 0.3	<i>Acacia nigrescens</i> <i>Combretum imberbe</i> <i>Terminalia pulmoides</i>
	ST	17	2.3 ± 0.3	1.1 ± 0.3	0.7 ± 0.4	<i>Acacia tortilis</i> <i>Lonchocarpus capassa</i> <i>Combretum apiculatum</i> <i>Combretum imberbe</i> <i>Acacia tortilis</i>

which the first branch diverted from the main trunk. We then classified the trees according to their height (\pm SD) into “very large trees” (8.5 ± 1.7 m), “large trees” (4.4 ± 1.2 m) and “small trees” (2.2 ± 0.3 m; Table 1). For each tree, we laid out two transects radiating away from the tree trunk in northern and southern compass directions, respectively. The length of each transect was three times the canopy radius (see Figs. 2 and 3). Every 1 m along the transect we recorded the grass species touching the transect measure tape and whether or not the grass had been grazed by an ungulate ($>$ 5 stems or leaves of the grass tuft bitten off at the same height level and cuts being planar). Recordings were grouped according to their distance away from the tree trunk: “beneath-canopy” (0 m away from trunk to the canopy edge), “outside canopy” (canopy edge to $2 \times$ canopy radius) and “open grassland” ($2 \times$ canopy radius to $3 \times$ canopy radius). Trees and grasses were identified using van Wyk and van Wyk (1997), and van Oudtshoorn (2004), respectively, for Satara and Beentje et al. (1994) and Ibrahim and Kabuye (1987) for Mpala and with the help of local expertise. Within a strip of 1 m each to the right and the left of the transect we recorded dung piles of ungulate herbivores. We noted location along the transect line, age and herbivore species of these dung piles according to Stuart and Stuart (2003).

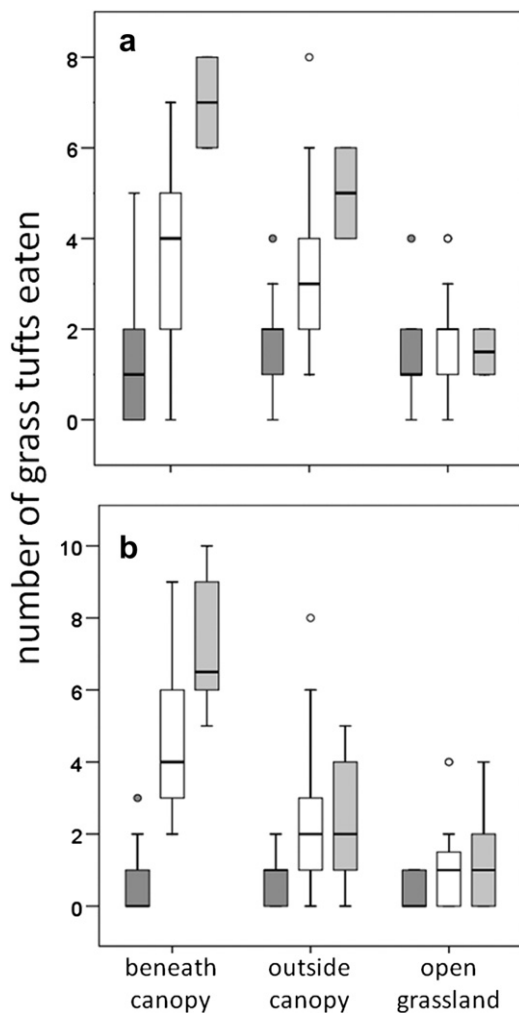


Fig. 1. Boxplot of the frequencies of the number of grass tufts eaten (touching the transect line at every metre) beneath tree canopies, outside of canopies, and in the open grassland for Mpala (a) and Satara (b). Median (black bar), inter-quartile range (boxes), outliers (whiskers) and extreme values (circles) are shown for small trees (dark grey boxes), large trees (white boxes) and very large trees (light grey boxes).

For most analyses, we used all dung piles of browsers and grazers pooled. However, to test whether cattle had similar feeding preferences as the wild herbivore guild, we used a slightly different study area and setup. As we could not properly discriminate between cattle and buffalo dung at Mpala, we surveyed cattle droppings inside the “cattle only” enclosures of the Kenya Long-term Exclusion Experiment (KLEE) (Young et al., 1998). This large-scale experiment is comprised of replicate plots, each 4-ha in area. The “cattle only” treatment has been grazed by cattle, but not wild herbivores, since 1995. The site is underlain by black cotton soil and the tree layer is essentially a mono-specific stand of *A. drepanolobium* (Young et al., 1998). We collected data in two of the enclosures immediately after a herd of 120 cattle had been grazing there for 2 h. Because tree cover in this area was high (2267 trees/ha (Young et al., 1998)) compared to the other sample sites (both around 200 trees/ha), we sampled grazing intensity with respect to tree canopies in a slightly different way. Here, we laid out eleven 40 m transects, parallel to and 10 m apart from each other. For every metre along the transect line we recorded the grass species touching the line, whether it was eaten and whether it was located directly beneath a tree canopy. Hence, in this controlled study area we were able to isolate the effect of cattle grazing on the grass layer both under and between tree canopies.

Data analysis. To model frequencies of dung depositions and of grass eaten with respect to the factors “canopy location” (beneath, outside of canopies and in the open grassland) and “tree size” we applied a Generalized Linear Model with a log-link (Schabenberger and Pierce, 2002). The model was applied separately to the Satara and Mpala sites. As we only sampled two very large trees at Mpala, we ran the model twice, once with and once without the “very large tree” class. For both sites and all tree classes pooled, we used an ordinal regression with a logit-link to test whether the frequency of dung deposition was positively correlated to that of eaten grasses. For the KLEE cattle enclosure data the location of every metre along each transect was located either beneath a tree canopy or outside of tree canopies, representing the “expected values”, i.e., the locations possibly occupied by dung depositions and grazing signs. These values were compared with the observed dung and grazing incidents found beneath and outside of tree canopies using a Pearson Chi-squared test. Analyses were done using SPSS 12.0.1. (Anon, 2003).

3. Results

At both study sites, our Generalized Linear Model significantly explained the occurrence of eaten grasses and dung depositions with respect to tree size, canopy location and the interaction of these factors (Table 2). For the occurrence of dung piles, interactions between “Tree size” and “Canopy locations” were not significant. The same results were achieved when we left the very large tree class out of the model at Mpala. On average, the frequency of grasses eaten was higher beneath canopies than outside of canopies or in the open grassland (Fig. 1); at Satara, grasses were eaten more than twice as frequently beneath canopies compared to the other canopy locations (Fig. 1b). The differences in the frequency of grass eaten between canopy locations were high for large and very large trees but not for small trees. The same pattern was visible for the spatial distribution of dung piles (data not shown).

Dung piles and grass eaten were about twice as frequently found beneath tree crowns of large and very large trees than outside of the canopy at Satara (Fig. 2a and b). In contrast, small trees did not show any patterns (Fig. 2). Differences were not as strong for Mpala, where about 25% more dung piles and grass eaten were found beneath large tree canopies (Fig. 3a and b). In line with these results, we also found that cattle foraged twice as much on grass beneath tree canopies than would have been expected, with 137

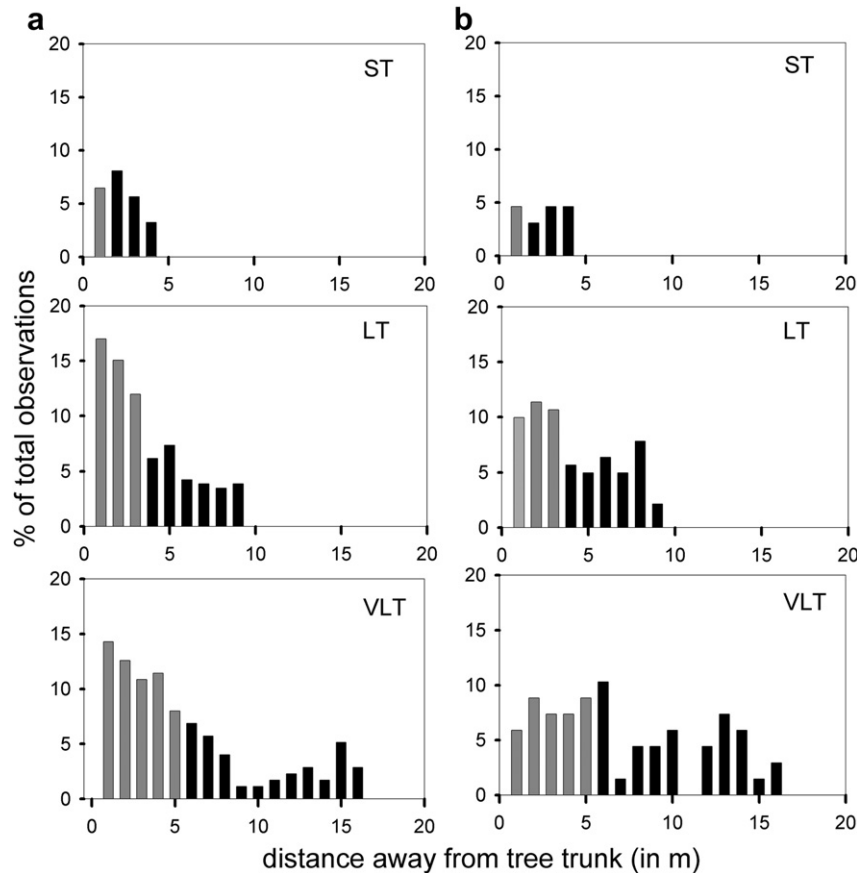


Fig. 2. Grasses eaten (a) and dung piles deposited (b) as a percentage of the total observations in relation to distance away from the tree trunk for Satara. Grey bars represent findings directly beneath the tree canopy, i.e., within the average canopy radius for each tree size class. Transect lengths extended to three times the canopy radius for each tree size class, i.e., small (ST), large (LT) and very large trees (VLT).

grazed grass tufts compared to 60 ungrazed tufts ($\chi^2 = 126.3$, $P < 0.0001$).

Regressing dung pile frequencies against grasses eaten in an Ordinal Regression Model with a logit-link revealed that both are correlated in their frequencies (Mpala: $X^2 = 30.2$, $df = 8$, $P < 0.001$, $n = 228$; Satara: $X^2 = 55.5$, $df = 10$, $P < 0.001$, $n = 165$). The frequency of dung depositions increased with an increase in grasses eaten at both study sites (Fig. 4). However, patterns were less clear at Mpala (Fig. 4a) than at Satara (Fig. 4b); at the latter site large and very large trees in particular contributed to the positive interaction. This was also true if we considered dung depositions of grazing herbivores only (Mpala: $X^2 = 55.5$, $df = 10$, $P < 0.001$; Satara: $X^2 = 30.3$, $df = 8$, $P < 0.001$).

4. Discussion

It has been suggested by several authors that trees are not only beneficial for browsing animals but can also indirectly benefit animals of other feeding guilds, particularly grazers (Ludwig et al., 2008; Treydte et al., 2008). Linear programming models have suggested that grazing ungulates can improve their forage intake significantly by feeding underneath large tree canopies (Ludwig et al., 2008; Treydte et al., 2009). Our study strongly demonstrates that herbivores use areas close to trees more often and respond to the enhanced forage beneath the canopies of savannah trees by feeding (and defecating) more at these microsites. This underscores the importance of trees, especially large trees, for grazing ungulate herbivores in savannah ecosystems.

We recorded higher rates of grass removal as well as dung piles beneath trees than outside of canopies or than even further away, in the open grassland. The indirect observation techniques of grazing impact used here allowed much larger sample sizes (and statistical power) than directly observing herbivore feeding behaviour. Dung droppings have proven to be good indicators for animal activity, reflecting feeding but also other kinds of presence such as resting in the shade (Treydte et al., 2006; Zavala and Holdo, 2005). As dung pellet groups can be assigned to species (Stuart and Stuart, 2003), we were able to discriminate among grazing and browsing herbivores. Even considering pure grazers alone, dung frequencies of both wild grazing herbivores and domestic cattle were higher than expected beneath tree canopies. Hence, it appears that grazers benefit indirectly from sub-canopy areas, in addition to browsers benefiting directly from the forage afforded by trees. Studies on wooded pasture grounds in Australia further support our findings as trees in pastures enhanced forage quality and promoted livestock body weight gain (Ash and McIvor, 1998).

The positive effects of trees on grazing herbivores may also extend beyond the canopy zone. Ludwig et al. (2008) showed that grass quality was higher in a “buffer zone” along tree canopy edges than further away in entirely open grassland, which might be related to soil nutrients distributed by extensive root systems. Our results also reflected this “tree-canopy-buffer” effect because, particularly at Mpala, grazing intensity was elevated not only directly underneath the tree canopy but also adjacent to the canopy edge (Fig. 3). This might indicate that grasses growing at the canopy edge are still higher in nutrients than those growing in open grasslands. It could

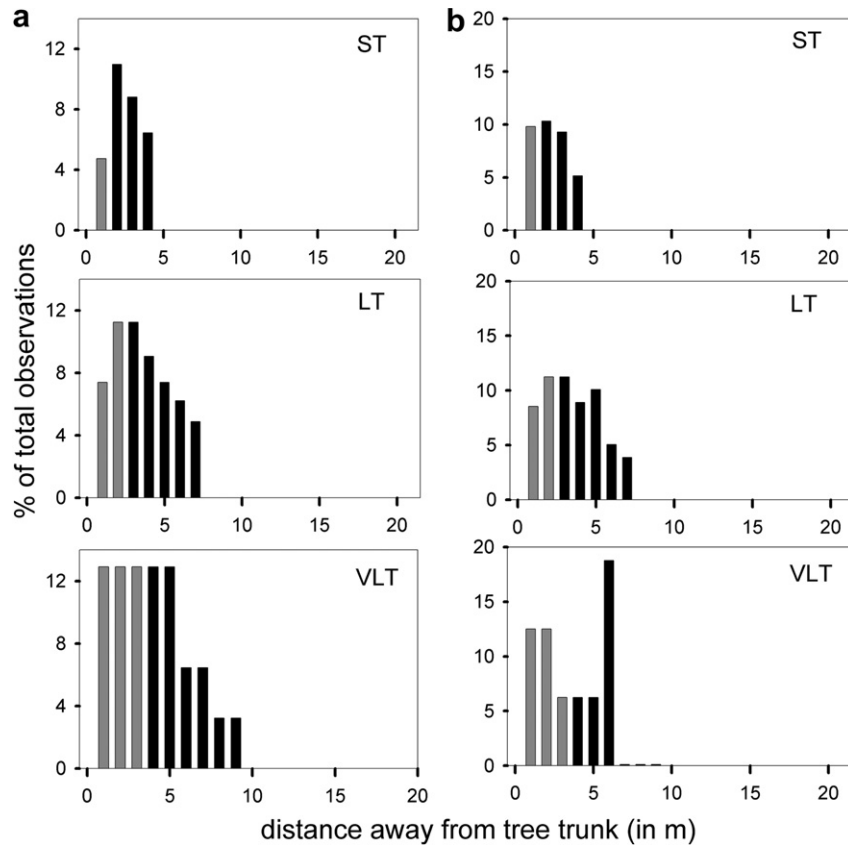


Fig. 3. Grasses eaten (a) and dung piles deposited (b) as a percentage of the total observations in relation to distance away from the tree trunk for Satara. Grey bars represent findings directly beneath the tree canopy, i.e., within the average canopy radius for each tree size class. Transect lengths extended to three times the canopy radius for each tree size class, i.e., small (ST), large (LT) and very large trees (VLT).

also reflect the less accessible structure of the Mpala trees: ungulates could not reach all grasses directly surrounding the trunk but also foraged in canopy edge zones as tree and branching height were lower and canopy areas were smaller compared to Satara trees (Table 1).

In addition to the indirect effects of trees on grazing herbivores via the grass layer, trees may also benefit herbivores (both grazers

and browsers) directly. Many ungulates seek shade during the heat of the day to cool their body system, particularly in warm savannahs, which has been thoroughly discussed in range literature (Roman-Ponce et al., 1977). At Satara, some very large trees produced shade up to 11 m away from their trunk (ACT, unpublished data). Hence, depending on the time of the day, a large canopy radius could provide essential shade to a variety of

Table 2

Statistical results of the Generalized Linear Model testing the effects of “Tree size” (very large trees = VLT, large trees = LT, small trees = ST), “Canopy location” (beneath tree canopy = trunk to canopy edge, outside canopy = canopy edge to $2 \times$ canopy radius and open grassland = $2 \times$ to $3 \times$ canopy radius) and an interaction between these two factors.

		N	Factors	χ^2	P
Grass eaten	Mpala	228	Tree size	46.2	<0.001
			Canopy location	9.8	0.007
			Tree size \times Canopy location	12.2	0.016
	Without VLT	222	Tree size	41.4	<0.001
			Canopy location	10.2	0.006
			Tree size \times Canopy location	9.2	0.010
Satara	165	Tree size	58.2	<0.001	
		Canopy location	32.8	<0.001	
		Tree size \times Canopy location	12.3	0.015	
Dung	Mpala	228	Tree size	22.1	<0.001
			Canopy location	14.5	0.001
			Tree size \times Canopy location	1.4	0.69
	Without VLT	222	Tree size	17.0	<0.001
			Canopy location	14.7	0.001
			Tree size \times Canopy location	1.0	0.61
Satara	165	Tree size	27.5	<0.001	
		Canopy location	6.1	0.047	
		Tree size \times Canopy location	1.6	0.81	

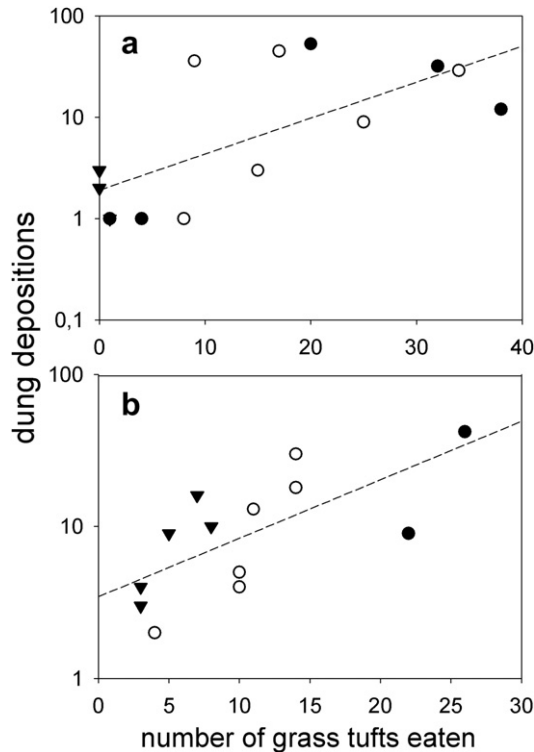


Fig. 4. Scatter plot on the frequency of dung pile depositions (found within the 2-m wide transect strips of various length) versus that of grasses eaten (i.e., eaten tufts touching the transect line at every m), for the Mpala (a) and Satara (b) study site. Data are shown separately for small trees (filled circles), large trees (empty circles) and very large trees (filled triangles). Dotted lines indicate best-fitting regression lines. Note the logarithmic y-axis scale.

herbivore species. This may be another mechanism underlying the elevated levels of dung deposition around tree canopies.

The positive effects of trees on herbivores, however, appear to depend on both tree size and tree architecture. Larger trees were, in general, more attractive to herbivores than smaller trees. There are at least three possible explanations for this pattern. First, larger trees generally enrich soil and grass nutrients more than smaller trees (Ludwig et al., 2004). Larger trees also cast deeper shadows, which may result in more green grass than under smaller trees and further lead to higher grass quality. Alternatively or concomitantly, herbivores, especially large-bodied species, may not be able to access sub-canopy areas of small trees or trees with very low branches. Trees at Mpala with a more bushy appearance than trees at Satara might attract fewer grazers; this may explain the less sharp decline in dung piles and grazing impact between beneath and outside canopy areas at Mpala compared to Satara (Figs. 2 and 3). Finally, the deeper and more extensive shade cast by larger trees may attract more herbivores, regardless of their foraging guild. This effect would again explain the relatively higher rates of dung deposition under less bushy trees at Satara than at Mpala.

Regardless of the mechanism, both grazers and browsers were consistently attracted to trees (especially large trees) and, thus, left more dung in the close neighbourhood of these trees relative to areas further away from tree canopies. Dung (and urine) can locally fertilize microsites (McNaughton et al., 1997; Powell and Mohamed-Saleem, 1987) as they contain macronutrients such as N and P (Arman et al., 1975; Stowe and Bonyongo, 2003). Dung deposited close to and beneath trees can enrich these patches and, thus, contribute to a “grazing lawn effect” (sensu McNaughton, 1984), where the already high grass quality beneath trees may be further improved by frequent grazing and by manure deposition, triggering

the production of new tillers and green leaves. Hence, in rather nutrient-poor savannahs, herbivore activity may contribute significantly to sub-canopy forage quality enhancement – in addition to the fertilizing and shading effect of the trees themselves. This may, in turn, promote the maintenance of the structurally and qualitatively diverse environments created by a mosaic of canopy and inter-canopy patches – to the benefit of a wide variety of floral and faunal taxa.

The positive effects of trees on ungulate herbivores may, however, be countered by some negative effects of trees. Predators also use trees and bushes for cover when approaching their prey, which might counteract a tree’s attractiveness for herbivores to a certain extent. Additionally, areas with high tree densities have been shown to be less attractive to herbivores because of impeded predator visibility in those areas (Riginos and Grace, 2008). We would particularly expect this to be the case in areas where many of the trees have low branching heights. Moreover, Riginos et al. (2009) have shown that the positive effects of individual trees on sub-canopy grass productivity and nutrient concentrations are also dampened in areas of high tree density. Thus, the overall attractiveness of individual trees may be reduced if those trees are surrounded by many other trees.

In general, areas of low to moderate tree density with few, large, single-standing trees seem to have the greatest positive effects on savannah herbivores, both wild and domestic. Yet, these habitats are quickly disappearing. Large trees are often the first to be targeted for harvesting for charcoal or other domestic uses. Charcoal demand continues to rise (Arnold et al., 2006), putting increasing pressure on unprotected land. At the same time, habitat fragmentation has constrained the movements of elephants, exposing trees in parks and other protected areas to increasing rates of elephant damage (Western and Maitumo, 2004). Many tree species coppice after being cut, broken, or burned, so that large trees are replaced by small, bushy trees. Heavy or prolonged cattle grazing, in combination with CO₂ fertilization, is also causing increases in woody cover in many savannah systems (Archer, 1995; Morgan et al., 2007; van Auken, 2000; Roques et al., 2001;). Such bush-encroached areas are often characterized by many, small, bushy trees. Thus, a suite of anthropogenic factors is contributing to the reduction in abundance of large, single-standing trees and an increase in abundance of small, dense, bushy trees.

The net effect of trees can be beneficial to the surrounding herbaceous layer and wild herbivores. These positive effects, however, may be diminished or even overturned in savannahs in which few, large trees have been replaced by many, small trees. Hence, the structural vegetation diversity might strongly influence the large herbivore distribution in African savannah landscapes. We therefore conclude that the protection of these trees should be a high priority in the management of African savannahs.

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