Original Investigation

Grazing ungulates select for grasses growing beneath trees in African savannas

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ABSTRACT

In savannas, isolated large trees can form 'islands of fertility', referring to their elevated soil nutrients and their effect on light and water availability in their direct surroundings. Consequently, a quality difference between understorey grasses and open grassland can develop, creating patches of highly nutritious forage for grazing ungulates. Grass species composition beneath and outside of tree canopies was determined in a savanna system of Kruger National Park, South Africa. Direct observations were used to test whether grazing ungulates, i.e., impala, Burchell's zebra and blue wildebeest graze relatively more often beneath than outside of large tree canopies. Additionally, it was investigated whether they selected feeding locations according to allometric scaling and to their sex, and if feeding behaviour was influenced by weather conditions. Instantaneous scan sampling showed that ungulates preferred beneath-canopy grasses, independently of weather conditions. Grass species composition differed beneath and outside tree canopies, and beneath-canopy grasses exhibited more bite marks than outside canopy grasses. Blue wildebeest grazed least often beneath canopies compared to the other species. Females of impala were found to feed on beneath-canopy forage more often than males. Thus, large isolated trees strongly influenced the feeding behaviour of grazing ungulates. The current decline in large savanna trees should therefore be retarded and protective measures should be taken.

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Introduction

Savannas amount to 12.5% of the earth's land surface and are found in the drier tropical and sub-tropical regions (Grant and Scholes 2006). The savanna biome consists of a heterogeneous landscape, characterised by a well-developed continuous grass layer and a distinct upper canopy layer of scattered to dense shrubs and trees (Grant and Scholes 2006; Low and Rebelo 1996). Despite a generally low nutrient quality and the high spatial and temporal heterogeneity of the herbaceous layer (Drescher et al. 2006), savannas host a high diversity of native grazing ungulates that have adapted to the prevalent feeding conditions (Du Toit and Cumming 1999). Vegetation heterogeneity is, amongst others, triggered by isolated savanna trees, affecting their immediate surroundings by changing resource availability (Anderson et al. 2001) as they improve growing conditions of the herbaceous layer, i.e., soil nutrients, the microclimate, light, and water availability (Ben-Shahar and Coe 1992; Ludwig et al. 2004; Reynolds et al. 1999; Scholes and Archer 1997; Weltzin and Coughenour 1990). Large isolated trees can even lead to an increase in grass productivity (Belsky 1994; Belsky et al. 1989, 1993; Ludwig et al. 2003) and nutrient quality, i.e., grass leaf nitrogen and phosphorus contents develops (Treydte et al. 2007). Hence, the understorey grass of isolated trees can become a patch of high quality food resources for mammalian herbivores that could even be essential in maintaining herbivore populations (Treydte et al. 2009b). These patches of highly nutritious food are thought to be the only areas where selective grazers can build up sufficient body reserves to carry them through the lean time of the dry period, as was found for termite mounds by Grant and Scholes (2006). Treydte et al. (2009b) proposed through linear modelling that large solitary trees fulfil such an important role for grazing ungulates. While studies have been conducted on plant-herbivore interactions in savanna ecosystems (Bell 1971; Cooper and Owen-Smith 1986; Lamprey 1964), the impact of large savanna trees on grazer species has only currently become a new field of interest (Treydte et al. in press). Facing the rapid decline in large tree cover in African savannas (Barnes 1983; Leuthold 1996; Lewis 1986), the importance of trees for wildlife needs to be assessed to quantify the consequences of tree loss. Knowledge about these trees as "islands of fertility" will enable predictions about future development of wild ungulate populations, and will have significant implications for conservation and monitoring design (Grant and Scholes 2006).

The main question of this research was therefore whether grazers forage relatively more often beneath canopies of large trees than

outside the canopy. Additionally, animals of different body size might show different preferences for sub-canopy grasses as they have characteristic energy requirements, i.e., in absolute terms, small herbivores need less energy and food than large ones (Kleiber 1961). However, small animals require more energy per unit weight as they have a higher metabolic turnover rate than large animals, which is known as "allometric scaling" (Kleiber 1961; Demment and Soest 1985; Mysterud 2000). To compensate for their larger energy requirements, small herbivores select food items of a higher quality and are therefore in general more selective than larger herbivores (Demment and Soest 1985; Du Toit and Cumming 1999; Okello et al. 2002; Mobæk et al. 2005). Partly due to allometric scaling, herbivores can be divided into separate feeding classes. Burchell's zebra (*Equus quagga burchelli* Gray), being the largest animal in this study, are assumed to be less selective grazers, while the smaller species, impala (*Aepyceros melampus* Lichtenstein) and blue wildebeest (*Connochaetes taurinus* Burchell), are classified as selective mixed feeder and grazer, respectively (Bothma et al. 2002). Therefore, we expected the latter to be more selective in their diet selection. We further expected that zebra, assumed to be able to sustain their metabolic requirements on a large amount of fibre-rich but relatively nutrient poor grass diet (Kingdon 2001; Okello et al. 2002; Mobæk et al. 2005), would select sub-canopy grass less often than the more selective feeders impala and wildebeest. Furthermore, a sex-determined difference in nutritional requirements are considered to exist within species (Ruckstuhl and Neuhaus 2002; Wronski 2002; Mobæk et al. 2005). Particularly females depend more strongly on highly nutritious diets as they need body resources during lactation and gestation periods (Main et al. 1996). It was, therefore, proposed that females would select sub-canopy grass more frequently than males, based on the 'sexual-dimorphism-body-size hypothesis' by Main et al. (1996). As weather conditions were expected to influence the selective behaviour in feeding locations by the animals it was also tested whether animals would feed in the sub-canopy area more often during rainy and sunny days, i.e., looking for cover and shade, than during overcast weather. Since it was expected that sub-canopy areas created highly nutritious grazing patches, the questions also rose whether attractive and nutrient-rich grass species occurred beneath compared to outside canopy, as found by Belsky et al. (1989) and Treydte et al. (2007, 2008), and whether more grasses with bite marks would be found in the sub-canopy area.

Material and methods

The research area was located in Kruger National Park (KNP), South Africa, situated in the semi-arid savanna biome (Grant and Scholes 2006). KNP has shown a strong decline in large solitary trees over the last couple of decades (Eckhardt et al. 2000). The park has a surface area of nearly 1.9 mill. ha and is divided both geologically and climatically. The western and eastern halves consist of granite and basaltic soils, respectively, and the southern part is wetter (mean annual rainfall between 500 and 700 mm) than the northern part (mean annual rainfall 300–500 mm) (Grant and Scholes 2006). The project was carried out in the south-eastern part of KNP, more specifically along the Salitjie road between Skukuza and Lower Sabie (24°59′42.1″S, 031°48′06.5″E; 25°00′06.3″S, 031°50′44.4″E). The area was classified as thornveld on gabbro (Gertenbach 1983) and is generally characterised by a higher altitude than the surrounding granite (between 550 and 600 m above sea level), flat to slightly undulating, and covering ca. 3.5% of the KNP (Gertenbach 1983). The average temperature during the observations, from mid-September until end of November, ranged from 20°C until 28°C. Rainfall in September, October, and November was 3 mm, 22 mm, and 88 mm, respectively (South African Weather Service, Climate

Information, station [0596179 3] – SKUKUZA). The dominant tree species were marula (*Sclerocarya birrea* (A. Rich.) Hochst.), followed by knobthorn (*Acacia nigrescens* Oliver), dominant grass species were Guinea grass (*Panicum maximum* Jacq.), bushveld signal grass (*Urochloa mosambicensis* (Hack.) Dandy) and finger grass (*Digitaria eriantha* Steudel). The most common animal species in the area were lion (*Panthera leo* Linnaeus), Burchell's zebra, blue wildebeest, impala, steenbok (*Raphicerus campestris* Thunberg), elephant (*Loxodonta Africana* Blumenbach), greater kudu (*Tragelaphus strepsiceros* Pallas), white rhinoceros (*Ceratotherium simum* Burchell) and giraffe (*Giraffa camelopardalis* Linnaeus).

The research site represented an openly wooded savanna consisting of solitary large (≥5 m tall) trees together with a fully developed grass layer, largely free of bush and thicket formations. This vegetation composition enabled an adequate number of observations distributed over sub-canopy and outside canopy areas. Additionally, the research area was characterised by little relief, a high homogeneity in vegetation, and was not located near open water. The site was stretched along a gravel road for 4 km, and all animal observations and vegetation assessments were recorded within a strip of 100 m wide on both sides of the road.

Behavioural observations were conducted by car to minimise disturbance for the vehicle-habituated animals. Observations were performed on impala, blue wildebeest and Burchell's zebra on a daily basis from sunrise until 10.00 am and during late afternoon (4:00 pm–6:00 pm) – to avoid the heat of the day when herbivorous ungulates are least active (Mobæk et al. 2005). Observations were conducted using an instantaneous scan sampling technique (Altmann 1974). Every 2 min, scans were executed starting with the animal seen on the outer left to the animal seen on the outer right within the field of view covered by the observer (Mitlöhner et al. 2001). Scan observations of feeding behaviour were conducted with binoculars if necessary until the observed animal moved out of sight or out of the research area. During each scan, animal species and sex were recorded together with the location of foraging. Feeding location was noted in two categories; (i) sub-canopy of a large isolated tree, (ii) outside canopy of a large isolated tree. To minimise observer effects, the categories of feeding location were made as unambiguous as possible: sub-canopy vegetation ended where the canopy ended, even though the influence of the tree can exceed the border of the canopy (Belsky et al. 1989). Feeding behaviour was defined as searching for or actually feeding (biting and swallowing) on grass (Baretto and Herrera 1998) with the head bent down. A total of 4028 observations were conducted, of which 3032 were for impala, 619 for zebra, and 377 for wildebeest. All observations were divided over 21 days and approximately 120 h.

In the study site a tree density of 6 trees/ha was calculated, with an average crown cover of 103 m^2. This resulted in an overall crown surface area of 627 m^2/ha. Consequently, the ratio between sub-canopy grass area and outside canopy grass area was 1:14.9. The position of observation from the road was selected so as to oversee the entire study area of a corresponding area of 1: 14.9 sub- and outside tree canopy area, respectively. If the observed animals selected their feeding locations randomly, the same ratio should be reflected in the number of feeding observations beneath and outside the tree canopy. Hence, we compared the observed location of impala, wildebeest, and zebra with the expected locations of 1: 14.9 sub- and outside tree canopy area, respectively, using a chi-square test. Observations were conducted by two observers, one recording while the other one was observing. Daily weather conditions were recorded; daily mean, minimum, and maximum temperature information was taken from the weather station at Skukuza while cloud cover and sunshine conditions were assessed by the observers during time of observation.

Additionally, 100 large isolated trees were selected within the study site, and their species, diameter at breast height (DBH), and
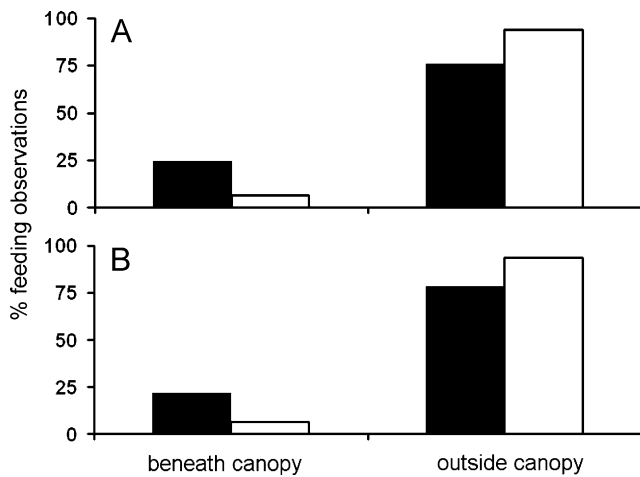
Fig. 1. Observed and expected percentages (black and white bars, respectively) of feeding observations beneath and outside the tree canopy area for impala, Burchell's zebra and blue wildebeest (A) at all observation days, i.e., during sunny, rainy and overcast weather and (B) during overcast weather only.

Fig. 2. Observed and expected percentages (black and white bars, respectively) of feeding observations beneath canopy only (A) comparing impala, Burchell's zebra and blue wildebeest and (B) comparing female and male impala. Data were collected during overcast weather only.

the longitudinal ($r1$) and lateral ($r2$) canopy radius were determined. Based on this information the surface area of the crown was calculated (Eq. (1)), adapted from Sandor (1987):

$$X = p \times (r1 - \tfrac{1}{2}\text{DBH}) \times (r2 - \tfrac{1}{2}\text{DBH}) \tag{1}$$

where X is surface area of the crown, and $r1$ and $r2$ are the longitudinal and lateral canopy radii, respectively. Subsequently, tree density of the research area was determined using the Ordered Distance Estimator for the 3rd nearest individual (Eq. (2)) (Pollard 1971; Engeman et al. 1994) according to (Picard *et al.* 2005):

$$\hat{\lambda}_{-2} = \frac{p-1}{\pi n} \sum_{i=1}^{n} \frac{1}{X_{pi}^2} \tag{2}$$

where p is the pth nearest tree, in this case p is the third nearest tree; n is the number of samples, and X_{pi} is the distance from the ith sampling point to the pth nearest tree.

Additionally, vegetation assessments were conducted on a 15 m line transect according to Treydte et al. (2006). For each of the 100 trees, one transect each was laid out starting at the trunk in alternating compass directions; north, east, south or west, avoiding sporadically distributed bushes. At every meter along the line, the touching grass species and forbs were recorded. Of all grasses recorded, we also noted their tuft height and whether they had been eaten, i.e., when >5 stems or leaves of the grass tuft were bitten off at the same height level and cuts were planar. Grass species were identified according to van Oudtshoorn (2004).

Mainly nominal data were gathered for both the animal observations, and the vegetation assessments. For vegetation structure we used *t*-tests with unequal variances to test for differences in grass height beneath and outside tree canopies. The nominal data were subjected to chi-square analyses in Excel and Kruskal–Wallis tests in SPSS to test for differences between observed and expected ratios, and the use of Scheffe's multiple comparison tests in SPSS.

Results

Animal observation analyses

The observed ratio between sub-canopy and outside canopy grazing, pooled for all grazer species observations, was 1:3.1 ($X^2 = 2123$, $P < 0.001$, $n = 4028$) indicating that sub-canopy grasses were selected more often (Fig. 1A).
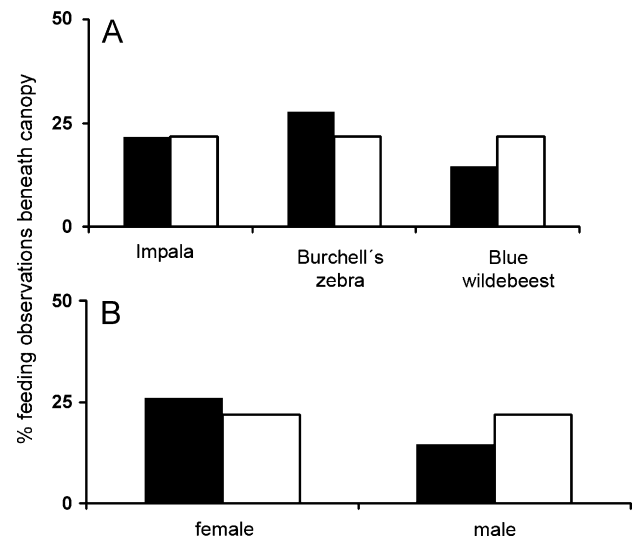
Weather conditions such as sunny, rainy, and overcast weather might have influenced the selective behaviour in feeding locations by the animals, i.e., looking for shade when sunshine is most intense. Even though observations were conducted outside the hottest period of the day, the animals behaved differently under different weather conditions ($X^2 = 21.5$, $P < 0.005$, $n = 4028$). The animals grazed significantly more often in the sub-canopy area during sunny and wet weather conditions compared to overcast weather conditions ($F = 10.8$, $P < 0.05$, $n = 4028$). Therefore, in all further analyses, only observations gathered during overcast weather were included to avoid the confounding weather factor. Again, the animals were more often observed feeding on sub-canopy than outside canopy vegetation ($X^2 = 1001$, $P < 0.001$, $n = 2562$). Instead of the expected ratio between selected sub-canopy grasses and outside canopy grasses of 1:14.9, an observed ratio of 1:3.6 was found (Fig. 1B).

Due to allometric scaling it was expected that impala and blue wildebeest would graze more often on sub-canopy grass than Burchell's zebra. Significant differences in selection of feeding location were found between the species ($X^2 = 18.5$, $P < 0.001$, $n = 2562$). While impala were feeding as frequently as expected beneath trees, zebra were feeding more than expected, and blue wildebeest significantly differed from the other two species, selecting sub-canopy grasses less frequently than did impala or zebra ($F = 9.3$, $P < 0.05$, $n = 2562$; Fig. 2A).

For impala, enough observations were available across all weather types to test for sex-specific differences in feeding choice. Females were expected to have higher nutritional requirements than males and thus were expected to select sub-canopy grasses more often than males, which was found to be true ($X^2 = 23.6$, $P < 0.001$, $n = 3032$; Fig. 2B).

Vegetation analyses

Grasses were with an average height of 66.8 cm significantly taller beneath trees than the grasses of 55.1 cm height outside of tree canopies ($t = 4.0$, $P < 0.001$, $df = 848$). In total, 25 species were encountered on all transects, of which *P. maximum*, *U. mosambicensis*, *D. eriantha*, *Themeda triandra* Forsk., *Panicum coloratum* L. and *Eragrostis superba* Peyr. were most abundant. Except for *D. eriantha*, these grasses showed the most bite marks of all grass
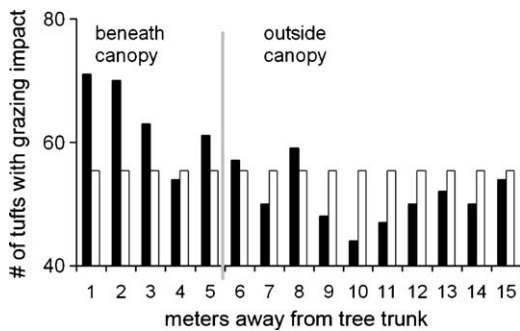
Fig. 3. The total observed and expected number of grass tufts (black and white bars, respectively) exhibiting bite marks with increasing distance away from the tree trunk. Data were collected along a 15 m transect line for 100 trees. Average crown radius was 5.4 m, as indicated by the vertical gray bar.

species recorded ($X^2 = 81.1$, $P = <0.001$, $n = 1500$). *Panicum maximum* occurred significantly more often under the crown compared to the other dominant species ($X^2 = 342.8$, $P < 0.001$, $n = 1206$), and in general grasses with bite marks occurred significantly more often in the sub-canopy area than outside the canopy area ($X^2 = 12.7$, $P < 0.001$, $n = 1310$; Fig. 3).

Discussion

The results on direct feeding observations indicate that sub-canopy grasses were more frequently eaten by grazing ungulate species compared to grasses outside of tree canopies. Even during overcast weather, i.e., when protection from sun in a tree's shade was not a reason for prevailing, animals used these feeding sites more often than expected. Our direct feeding observations were additionally supported by indirect observations, i.e., sub-canopy grasses exhibiting more bite marks than outside canopy grasses. This pattern of feeding patch selection agrees with predictions by Treydte et al. (2009b) who showed, based on linear programming, that grazing ungulates could benefit when feeding beneath tree canopies due to higher energy intake possibilities. Treydte et al. (2009b), however, stress that particularly during the dry season, digestible protein and phosphorus contents in grass leaves might not be enough for body maintenance if ungulates were exclusively feeding on sub-canopy grasses. Owen-Smith (2002) likewise termed high nutrient quality patches as "limited intake resource", providing highly nutritious food but only in limited abundance. A previous study in KNP indicated that grass leaf nitrogen contents were up to 40% higher beneath large trees compared to the same grass species growing outside of tree canopies (Treydte et al. 2009a). Higher nitrogen and phosphorus contents in grasses growing beneath trees compared to grasses growing outside of tree canopies were found in both dry and wet season in KNP (Treydte et al. 2008). Further, several studies reported that particularly *P. maximum*, a preferred forage grass species, grew significantly more often beneath tree canopies (East and Felker 1993; Treydte et al. 2009a), which could also be confirmed by our study. Moreover, Ben-Shahar and Coe (1992) found that zebra and blue wildebeest move to patches where the grass community contains a high proportion of nutritional species such as *P. maximum*. Hence, with respect to species composition and nutrient contents, beneath canopy grasses might contribute a significant part in the diet of grazing ungulates in savannas.

The hypothesis concerning allometric scaling predicted that impala would select sub-canopy grass most often and Burchell's zebra least often of the three species. Zebra, however, were found to feed most often beneath the canopy together with impala, and

blue wildebeest the least (Fig. 2A). These findings contradict the results by Ben-Shahar (1992) and Traill (2004), who both imply that zebra and blue wildebeest exploit similar habitats. They also contrast the findings by Mobæk et al. (2005), who found that impala grazed closer to nutrient rich grass on termitaria compared to zebra, and Ben-Shahar and Coe (1992), who conclude that wildebeest are more selective than zebra. Furthermore, literature indicates that zebra can deal efficiently with high fibre diets and coarser grass compared to ruminants of similar size (Mobæk et al. 2005), and thus can be a bulk and unselective feeder, whereas impala show a relatively selective foraging strategy (Okello et al. 2002). Additionally, Bothma et al. (2002) mention that zebra do not show a high selectivity for grass quality in their choice of grass species, except for a preference for grass shorter than 35 cm. Traill (2004) and Cromsigt et al. (2009) however, state that zebra can adapt to diverse habitats, foraging on both short and taller grass lawns, and is thus able to take advantage of the nutrient hot-spot situation. Additionally, grass preferences might also be triggered by the structure of the swards. Wilmshurst et al. (1999) mention that blue wildebeest need short grass swards with nutritious grass species to survive, a demand which might also be reflected in the wildebeests' mouth size and metabolic needs (Arsenault and Owen-Smith 2008). The average grass height beneath tree canopies was 67 cm, therefore the nutritious patches underneath trees could have been too tall for their selection, and the travel costs in between patches might have been too high, explaining why they were observed the least in the sub-canopy area. Hence, grass sward and mouth size will additionally play a role in sub-canopy feeding site selection by grazing ungulates (Drescher et al. 2006; Arsenault and Owen-Smith 2008).

As our observations were conducted at the end of the dry and beginning of the wet season, animals were probably not in a low nutritional status throughout the study period. One would expect that animals spread out into the surroundings at the onset of the rains and graze on the new green flush of grasses elsewhere, as was shown for Roan antelope in Nylsvley Nature Reserve, South Africa (Heitkönig and Owen-Smith 1998) and wildebeest in KNP (Ben-Shahar 1991). In contrast, we found that animals still used sub-canopy sites during the onset of the rains. This could be due to the fact that beneath-canopy grasses could have been still higher in nutrients than surrounding areas in the wet season as was found by Treydte et al. (2008). It might alternatively have been caused by social herding preferences as moving patterns can be strongly affected by group structure, predator avoidance, and vigilance in large groups (Kie 1999). However, our behavioural study of three months was too short to significantly detect any seasonal differences in feeding behaviour, and future long-term studies might provide insights into seasonal preferences of sub-canopy grasses by herbivores.

Direct observations clearly highlight that sub-canopy grasses were eaten more frequently than expected within a certain time span whereas indirect observations only indicated that sub-canopy grasses were eaten more frequently over an unknown period of time and by an unknown number of animals. While the latter suggest a frequent use by grazers, reasons for feeding remain unclear. With our study we could not test whether grazing happened as a "side effect" while seeking shade, or whether the animal grazed to overcome hunger. However, our direct observations were conducted during the morning and evening hours, i.e., not during the hottest times of the day, and data for overcast days only were used to avoid the confounding shade effect. Additional experimental studies are currently planned to separate the physical micro-climate and the nutritional herbaceous layer properties of sub-canopy feeding sites.

The assumption that female impalas would be found grazing in the sub-canopy area more often than males is confirmed by

the results, in agreement with similar findings by Ruckstuhl and Neuhaus (2002) and Mobæk et al. (2005). This difference was even more strongly apparent because of the high energy consuming period of gestation and lactation of the females (Wronski 2002), which occurred during the research.

A fact to take into consideration for impala observations is that impala are known to be mixed feeders, which also select for forbs during summer (Codron et al. 2009; Bothma et al. 2002; Traill 2004). In the study site, an average coverage of forbs with bite marks of 20% was found, which may imply that in 20% of impala observations, the animals could have been eating forbs instead of grass. However, no relation was found between forbs with bite marks and their position to the tree crown ($X^2 = 0.2$; $P > 0.5$). Therefore, we assumed that the relative distribution of utilised forbs was equal for beneath and outside the tree canopy.

This research was conducted in one vegetation type only and extrapolation of the results to other areas should be done with caution, unless those areas are characterised by a similar vegetation composition. Since the gabbros are known to be relatively nutrient rich areas (Venter 1986), one would expect even more pronounced preferences for sub-canopy grasses by grazers because the qualitative difference between sub- and outside canopy grasses was even more strongly developed in low nutrient savanna sites (Treydte et al. 2007).

In our study, the sub-canopy vegetation was defined to end where the canopy ended. However, if all grazing observations along or close to the canopy edge were included, the sub-canopy feeding observation numbers would have shown even larger numbers than expected (data not shown), strengthening the present conclusions. Further, to minimise the lack of independence effects when an individual's behaviour might be influenced by another individual, the data were collected on more than one day, on more than one species, and on many individuals divided over several herds. Moreover, because the scans were executed in 2-min intervals, the data can be seen as continuous sampling (Mitlöhner et al. 2001). Above measures give the results a high predictive validity, due to a small interval time coupled with a large number of observations (Kassilly 2002).

This study underpins the importance of large solitary trees to grazing ungulates in the savanna ecosystem based on feeding behaviour observations of wild ungulate species. Further research should investigate whether smaller trees have the same influence on their surroundings as large trees, and look at possible differences between selective behaviour in different seasons. The high nutrient and structural quality of beneath-canopy grasses (Treydte et al. 2007) that attract grazing ungulates need to be considered in future management strategies. Particularly in dry and dystrophic savannas, trees should be strictly protected to conserve the associated high-quality grass patches. Herbivores might more strongly depend on the tree presence than previously assumed, and certain species might suffer from nutrient deficiencies if tree losses continue.

Acknowledgements

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