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Elephant impact on shoot distribution on trees and on rebrowsing by smaller browsers

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ABSTRACT

In order to determine the effects of a megaherbivore, the African elephant (*Loxodonta africana*) on browse available for mesoherbivores, we assessed the vertical distribution of shoots (< 6 mm in diameter) on trees with different accumulated elephant impact. We also determined the foraging responses by a mixed feeder, impala (*Aepyceros melampus*) and a browser, greater kudu (*Tragelaphus strepsiceros*) which are mesoherbivores. The foraging responses by impala and kudu were in terms of preferences of trees with different accumulated elephant impact levels and whether animals browsed in different height sections in proportion to availability of shoots. We counted shoots in each 20 cm height section up to 2.6 m on trees in 25 m by 25 m plots and on trees observed to be browsed by impala and kudu. In most tree species, individuals with high accumulated elephant impact were shorter and had more shoots at low levels than tree individuals with either low or no accumulated elephant impact. Impala and kudu preferred to browse tree individuals with accumulated elephant impact over those without such impact. Impala and kudu browsed more than expected at height sections with many shoots and less than expected at height sections with fewer shoots indicating a non-linear overmatching foraging response. We suggest that increased shoot abundance at low levels in the canopy might explain part of the observed preferences. Elephants, therefore, seem to facilitate browsing by mesoherbivores by generating 'browsing lawns'. Such benefits need to be considered when making decisions on how to manage populations of megaherbivores like elephant.

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1. Introduction

Ecologically similar mammal species may directly or indirectly interfere with the food resources for each other and could alter each others' foraging behavior and population dynamics (Bell, 1971; McNaughton, 1976; Sinclair and Norton-Griffiths, 1982; Belovsky, 1984; De Boer and Prins, 1990; Wes-

tern and Gichohi, 1993; Putman, 1996; Prins and Olf, 1998; Makhabu et al., 2002). Interspecific competition (Belovsky, 1984; Putman, 1996; Hulbert and Andersen, 2001) and facilitation (McNaughton, 1976; Guy, 1981; Van de Koppel and Prins, 1998) has been reported, as well as indifference (De Boer and Prins, 1990). Competition and facilitation are not mutually exclusive, but may occur at the same time concerning different species or fluctuate over time (Van de Koppel and Prins, 1998; Taolo, 2003). Facilitation becomes possible when, first, consumption by a consumer produces a flow of resources into another consumer and, second, the latter consumer spe-

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cializes on consuming the produced resource (Farnsworth et al., 2002). In facilitation, often one consumer increases the accessibility to food for another (Guy, 1981; Van de Koppel and Prins, 1998), but also the quality of food may be enhanced (McNaughton, 1976). Body size has often been found important for food mediated interactions between small and large herbivore species. Relatively small species consume highly nutritious plant parts and survive on low food biomass, and may, thus, pre-empt food resources for larger species and outcompete them (Van de Koppel and Prins, 1998; Woolnough and du Toit, 2001; Taolo, 2003). Relatively large-bodied herbivores may, on the other hand, by consuming large amounts of relatively nutrient poor plant material, increase the production and/or availability of young nutritious plant tissue for smaller herbivores, thus facilitating their foraging (Bell, 1971; McNaughton, 1976, 1984; Guy, 1981; Van de Koppel and Prins, 1998; Taolo, 2003). For animals browsing on trees also the height distribution of nutritious regrowth is important for which herbivore species are able to use it.

Large herbivores have the potential to modify the architecture, physiology, biochemistry, productivity and phenology of plants they feed on (Laws, 1970; Bryant, 1981, 2003; Bergström and Danell, 1987; du Toit et al., 1990; Ben-Shahar, 1993; Prins and Olf, 1998). Such modification of plants by herbivores may include the activation of resistance traits, reducing subsequent herbivory (Bryant, 1981; Karban and Meyers, 1989; Hulbert and Andersen, 2001). More often it leads to increased palatability and probability for repeated foraging (Bell, 1971; McNaughton, 1976, 1984; Danell et al., 1985; du Toit et al., 1990; Duncan et al., 1998; Bergström et al., 2000). Thus a “feeding loop” can develop, where animal induced changes in plant morphology and physiology lead to further herbivory and further changes in the plants (McNaughton, 1984; du Toit et al., 1990; Bergqvist et al., 2003). Such “feeding loops” are, by definition, advantageous for the herbivore creating them, but may also facilitate foraging by other species, which, if smaller than the herbivore initiating the loop, may be more efficient harvesters of the nutritious regrowth biomass. While much of the fundamental studies of herbivore competition/facilitation is related to one-layered herbaceous vegetation or a theoretical single compartment vegetation (McNaughton, 1976, 1984; Prins and Olf, 1998; Van de Koppel and Prins, 1998; Farnsworth et al., 2002), the three-dimensional browsing system may be more complex (du Toit, 1990; Makhabu, 2005). In such systems not only quality and quantity of plant regrowth following (repeated) browsing, but also the height distribution of such regrowth in relation to possible foraging heights and foraging responses by members of the browsing guild, is essential. Browsing by megaherbivores, e.g. African elephant (*Loxodonta africana*) or giraffe (*Giraffa camelopardalis*) has been shown in savanna ecosystems to reduce the height of browsed trees (Pellew, 1983; Belovsky, 1984; Owen-Smith, 1988; Ben-Shahar, 1993) but the effect on shoot distribution within the canopy of these trees is little known. Foraging herbivores may respond differently to variation in food biomass or density, and linear (matching), and overmatching, when animals browse more than expected at height sections with many shoots and less than expected at height sections

with fewer shoots, relationships between intake rate and food availability have been described (Stephens and Krebs, 1986; Senft et al., 1987; Spalinger and Hobbs, 1992; Ginnett and Demment, 1995; Gordon, 2003). The response may be scale dependent as animals make foraging decisions at different scales, e.g. on the level of a tree stand, a tree or a height section of a tree (Senft et al., 1987; Danell et al., 1991; Spencer et al., 1995). Browsers have been shown to preferentially feed at about neck height (du Toit, 1990; Makhabu, 2005; Rutina et al., 2005), but differences in browse availability between different height levels may modify this pattern.

We studied the effects of accumulated elephant impact on trees on distribution of shoots and on browse utilization by the two most common smaller browsing, “mesoherbivore” species, the greater kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*) in order to assess competition/facilitation between elephant and the smaller herbivores. We predicted that:

- accumulated elephant impact has a negative effect on tree height;
- accumulated elephant impact has a positive effect on shoot numbers in lower levels of the tree canopy;
- feeding frequencies by mesoherbivores in different height sections is in proportion to the abundance of shoots present at those height sections (i.e. a linear response);
- browsing mesoherbivores prefer trees with accumulated elephant impact to such without.

2. Materials and methods

2.1. Study area

The research was conducted in the northern part of Chobe National Park (17°49′–17°55′S, 24°50′–24°59′E) in semi-arid northern Botswana. The study area stretches ca. 50 km along the south side of the Chobe River and being within 2 km of the river but excluding the riparian forest on the banks of the river. The rainfall is seasonal, with the wet season in summer mainly between November and April. Annual average rainfall is about 640 mm. Mean maximum and mean minimum monthly temperatures in October (the hottest month) are 39 and 14 °C, respectively and in July (the coldest month) 30 and 4 °C, respectively (Botswana Meteorological Service Department records).

The vegetation in the region of the study area is mainly a shrubland apart from floodplains and a narrow and in some places broken strip of riparian forest. The shrubland is dominated by *Capparis tomentosa* in some sections and by *Combretum mossambicense* in others (Mosugelo et al., 2002; Skarpe et al., 2004). The species composition in the shrubland farther from the river becomes mixed with small and medium sized tree species. The soils are Kalahari sands with a strip of alluvial soil along the river (Mosugelo et al., 2002; Skarpe et al., 2004). The area that is now shrubland on alluvial soil was open flats in the 1870s (Selous, 1881). After the 1870s a woodland established, which with time was dominated by large *Acacia* and *Combretum* trees. Subsequently in the 1960s the

woodland declined and was replaced by shrublands (Simpson, 1975; Skarpe et al., 2004). This change from open flats to woodland and then to shrublands has been attributed to the decline and later recovery of the populations of large herbivores, particularly elephant and impala (Rutina, 2004; Skarpe et al., 2004). Bushfires have been absent for some years in the area largely as a result of a major road ca. 10 km south of the river acting as a firebreak (Mosugelo et al., 2002; Taolo, 2003).

In the study area, browsing megaherbivores comprise the African elephant (*L. africana*) and giraffe (*G. camelopardalis*) while browsing mesoherbivores include greater kudu (*T. strepsiceros*), impala (*A. melampus*), steenbok (*Raphicerus campestris*) and bushbuck (*Tragelaphus scriptus*). Animal nomenclature follows Skinner and Smithers (1990). The elephant population is increasing at an annual rate of 6% and its density along the Chobe Riverfront during the dry season can be as high as 4 per km² (Gibson et al., 1998) or 8.5 per km² (DWNP, 2003) but during the wet season it can be reduced to 0.5 per km² (Gibson et al., 1998). Elephant densities above 0.6 per km² have been shown in some ecosystems to cause major vegetation changes (Jachmann and Croes, 1991). The elephant population of northern Botswana, unlike in many other ecosystems, remain little affected by either management culling or illegal hunting (Owen-Smith, 1989). However, that elephants and other herbivores have transformed the woodland fringing the Chobe River to shrubland is of great concern among some conservationist and members of the public (Owen-Smith, 1989; Cumming et al., 1997). One of the concerns is that elephants deplete food resources for other herbivores. The elephant, however, has also been identified as a 'keystone species' that play a disproportionately large role in the community structure (Owen-Smith, 1987, 1989). Owen-Smith (1987, 1989) argues that elimination of megaherbivores might negatively affect the population of some species.

2.2. Data collection

Data were collected during June–August 2004 and consisted of three datasets. These were: (a) food selection by impala and kudu in relation to shoot distribution and level of accumulated elephant impact, (b) proportions in the environment of woody plants (henceforth called 'trees') with different levels of accumulated elephant impact, and (c) shoot distributions on trees with different accumulated elephant impact levels.

To observe impala and kudu browsing, a car was driven on the dense net of tourist tracks taking care to cover different parts of the study area approximately evenly. The area is fairly open and during the months the data were collected, animals were visible at distances greater than 100 m. Whenever a kudu or impala was sighted browsing, the vehicle was stopped and the browsing animal was observed for 5 min. Afterwards the browsed tree was visited for identification and measurements. A frame, 3 × 1 m², marked with horizontal fish lines at every 20 cm along the vertical 3 m side was placed on the side where the animal browsed. In each 20 cm by 1 m section from ground level to a height of 2.6 m, the

number of shoots was counted. Shoots were defined as any current season twig-end < 6 mm in diameter. A calliper was used to check the diameter of shoots. The height browsed by the animal was measured with a measuring rod to the nearest cm. Accumulated elephant impact was visually determined and categorized into three levels according to the degree of change in tree growth form compared to "normal" growth of unaffected specimens of the species in question. Levels were: (0) no accumulated elephant impact, i.e. no obvious change in tree growth form (generally the main stem and main branches with no signs of old breaking and/or biting by elephant), (1) low accumulated elephant impact, i.e. growth form of tree obviously changed (generally signs of old breaking and/or biting by elephant on less than half of the total number of main branches and stems) and (2) high accumulated elephant impact, i.e. growth form of tree strongly changed (generally tree broken down or with old signs of breaking and/or biting by elephant on more than half the total number of main branches and stems).

In order to determine the overall proportions, within each tree species, with different accumulated elephant impact levels, sampling plots were distributed along four transects running ca. 5 km apart and perpendicular to the Chobe River. The plots were 25 × 25 m. Five plots were placed within the study area 400 m apart along each transect, starting 200 m from the river making a total of 20 plots. In each plot, all individuals of the selected tree species (see below) higher than 0.5 m were assessed for accumulated elephant impact levels and shoot distributions. The shoot distribution was assessed in the same way as was done on trees observed browsed by kudu and impala. The frame was placed on a randomly selected side of the tree and shoots were counted in each 20 cm height section.

Two species, *Combretum elaeagnoides* and *Flueggea virosa* were heavily impacted in the park. To increase sample sizes of low impacted individuals of these species, additional individuals were assessed for shoot distribution in shrubland areas with low elephant activity, also within 2 km of the Chobe River, at a nearby village. The tree individuals of these species near the village were not heavily browsed by small browsers.

A total of 1749 trees of seven species were assessed of which 193 were *C. tomentosa*, 254 *Combretum apiculatum*, 313 *C. elaeagnoides*, 516 *C. mossambicense*, 57 *Erythroxylum zambeziacum*, 128 *F. virosa* and 288 *Markhamia zanzibarica*. Plant names follow Coates Palgrave (2002).

2.3. Data analysis

Calculations were made separately for each tree species. We calculated the proportion of tree individuals within each accumulated elephant impact level based only on measurements in the plots. We also used measurements in the plots to calculate mean tree height of the three accumulated elephant impact levels. Differences in the mean tree heights in these three levels of accumulated elephant impact were tested using one-way ANOVA, after testing that the data met the required assumptions. Pair-wise contrasts with Tu-

key's HSD test were made when significant differences were found.

To estimate the vertical distribution of shoots on trees with different accumulated elephant impact level, we used both tree individuals in plots and those individuals observed browsed by impala and kudu. Also included in the calculations were the additional trees of *C. elaeagnoides* and *F. virosa* with low impact sampled near the village. In estimating the vertical distribution of shoots we used only the sampled portion of the tree (1 m wide and 2.6 m high) to represent the distribution on the tree. The number of shoots in each 20 cm height section was log transformed. The mean of log transformed number of shoots in each height section within an accumulated elephant impact level was calculated for each tree species. In calculating these means for *C. tomentosa*, *C. mossambicense* and *F. virosa*, which are shrubs to small trees, only individuals at least 2.2 m high were included. For *C. apiculatum*, *E. zambesiacum* and *M. zanzibarica*, which are small to medium sized trees, only individuals at least 2.6 m high, were included. To establish the relationship between height section and the mean number of shoots, a best fit regression curve was fitted.

To test whether accumulated elephant impact affects the number of shoots in each height section, a non-parametric multivariate analysis of variance (MANOVA) was done using DISTLM v.5 FORTRAN computer program (Anderson, 2004) which does the test by permutation (Anderson, 2001; McArdle and Anderson, 2001). XMATRIX FORTRAN computer program (Anderson, 2003) was used to generate design matrices corresponding to the factor in ANOVA design used in the DISTLM v.5 FORTRAN computer program. The non-parametric MANOVA was based on Bray-Curtis dissimilarities measured on $\log_{10}(x + 1)$ transformed shoot counts data. In conducting the test, the number of shoots in each 20 cm height section was the variable and accumulated elephant impact level was the only factor. The test was of ANOVA design and in all cases the *P*-values were obtained with 999 permutations. Both permutation and Monte Carlo *P*-values were obtained from the analysis. The number of tree individuals (sample sizes) in the three levels of accumulated elephant impact within the species was not equal, hence our tests were of an unbalanced ANOVA design. For species with individuals in all the three accumulated elephant impact levels, pair-wise contrasts of specific levels of the unbalanced design were made by the use of the DISTLM v.5 FORTRAN computer program. The *P*-values were then adjusted using the sequential Bonferroni (Holm, 1979) procedure (Quinn and Keough, 2002).

To test whether impala and kudu browsed in the different height sections in proportion to the number of shoots in the same height sections, the Chi-square test was applied. The mean number of shoots in each height section was calculated only from trees observed browsed. The number of observations of recorded browsing by an animal species in a height section was used as observed values while the expected values were the mean number of shoots in the height section. The height sections used were pooled to 40 cm intervals within heights reachable by each species, 1.6 m for impala and 2.2 m for kudu (Makhabu, 2005).

Preference index (P_{ijk}) for woody species *i* with accumulated elephant impact level *j* by herbivore species *k* was calculated as in Hunter (1962) and De Garine-Wichatitsky et al. (2004):

$$P_{ijk} = \frac{U_{ijk}}{A_{ij}}$$

where A_{ij} is the proportion of the woody species *i* with accumulated elephant impact *j* in the habitat and U_{ijk} is the proportion of the woody species *i* with accumulated impact *j* in the diet browsed by herbivore species *k*. Only trees assessed in the plots were used to calculate A_{ij} . U_{ijk} was calculated from trees observed browsed by the herbivores. The preference index ranges from 0 for species totally avoided to nearly infinity for highly preferred ones. Values > 1 are generally understood to indicate preference and values < 1 to indicate avoidance. The index is in this study used only for ranking, and the class of accumulated elephant impact with the highest preference index within a species was taken to be the most preferred.

All analyses except non-parametric MANOVA were carried out using SPSS for Windows (2004) (version 13.0) statistical package. Non-parametric MANOVA was done using DISTLM v.5 FORTRAN computer program (Anderson, 2004). All tests were considered significant at $P < 0.05$ level.

3. Results

3.1. Tree height and distribution of shoots on trees with different accumulated elephant impacts

A large percentage of the individuals of *C. apiculatum*, *C. elaeagnoides*, *E. zambesiacum* and *F. virosa* were affected by elephants either having low or high accumulated elephant impact (Fig. 1). *C. tomentosa* and *C. mossambicense* however, had most of their individuals not impacted by elephants. Almost half of the individuals of *M. zanzibarica* had no accumulated elephant impact (Fig. 1). *C. tomentosa* and *C. mossambicense* individuals with high accumulated elephant impact were very few hence this impact level is not used in further analysis for these species.

Trees with high accumulated elephant impact were significantly shorter than those with no accumulated elephant impact in all species (Fig. 2). The mean heights of trees with no accumulated elephant impact differed significantly from those with low accumulated elephant impact in *C. mossambicense* and *M. zanzibarica*, but not in the other species (Fig. 2). *M. zanzibarica* individuals with low accumulated elephant impact were significantly shorter than those with no accumulated elephant impact. *C. mossambicense* was the only species that showed individuals with low accumulated impact being significantly taller than those with no accumulated elephant impact (Fig. 2).

The interaction between accumulated elephant impact and tree species had an effect on the number of shoots in different height sections ($F_{2,593} = 50.23$; $P = 0.001$). Species were therefore analyzed separately. The results of the non-

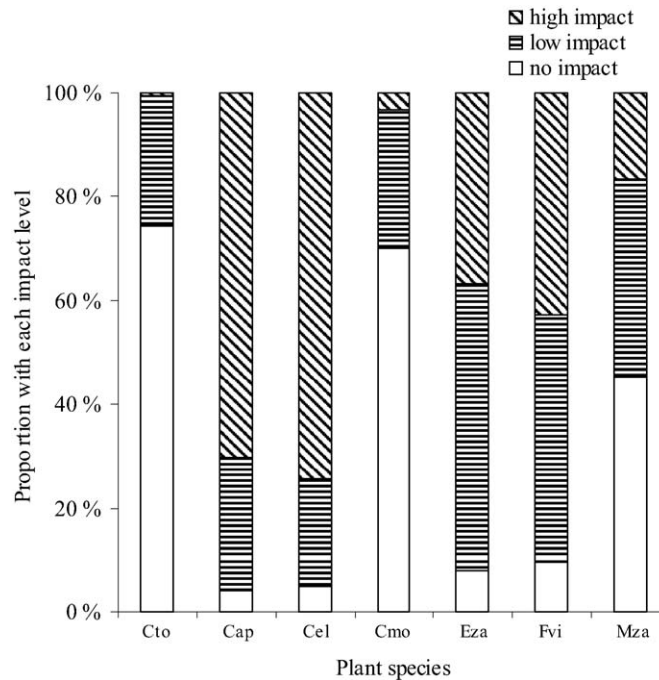


Fig. 1 – Percentage of tree/shrub individuals divided in three accumulated elephant impact levels as assessed in Chobe National Park, Botswana excluding trees sampled in a nearby village. Abbreviations are *C. tomentosa* (Cto), *C. apiculatum* (Cap), *C. elaeagnoides* (Cel), *C. mossambicense* (Cmo), *E. zambesiicum* (Eza), *F. virosa* (Fvi) and *M. zanzibarica* (Mza).

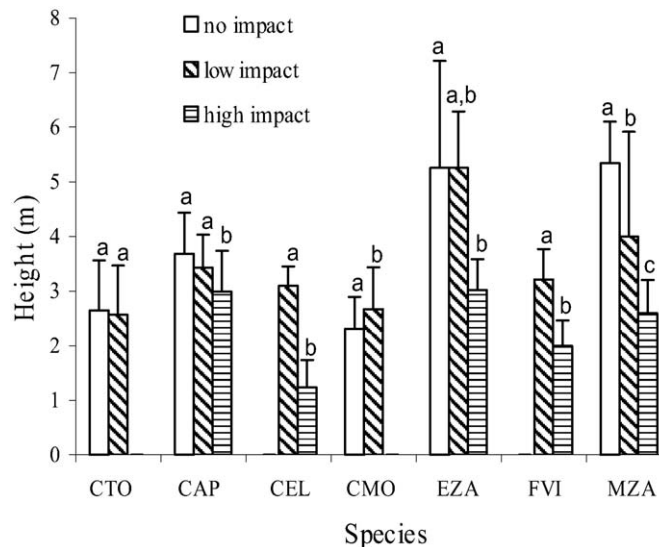


Fig. 2 – Mean (\pm S.D.) heights of trees divided in three different accumulated elephant impact levels. Within each species, different letters show significant differences ($P < 0.05$). The abbreviations of the plant species are as in Fig. 1.

parametric MANOVA test indicated that accumulated elephant impact level explained a significant proportion of the variation in the number of shoots in height sections of four of the six species (Table 1). This was indicated by a significant multivariate variation in number of shoots in different height sections in the overall comparison test for all species except for *C. apiculatum* and *C. mossambicense* (Table 1). The permutation and the Monte Carlo P -values were in all cases

in agreement for overall and some pair-wise comparisons. The pair-wise contrasts of the variation in the number of shoots in different height sections of no and high accumulated elephant impact levels were significant for *E. zambesiicum* and for *M. zanzibarica* (Table 1). The pair-wise contrasts of no and low accumulated elephant impact levels for *E. zambesiicum* and *M. zanzibarica* indicated no significant variation in the number of shoots in different height sections (Table 1).

Table 1 – Non-parametric MANOVA results of number of shoots within 20 cm height sections on trees with no accumulated elephant impact (0), low accumulated elephant impact (1) and high accumulated elephant impact (2). P-values are calculated by Monte Carlo randomization, and for pairs they have been adjusted using sequential Bonferroni procedure (Holm, 1979)

Species	All impact levels				Between pairs of accumulated elephant impact levels												
	df ₁	df ₂	F	P	0 and 1				0 and 2				1 and 2				
					df ₁	df ₂	F	P	df ₁	df ₂	F	P	df ₁	df ₂	F	P	
<i>C. tomentosa</i>	1	147	10.29	0.001													
<i>C. apiculatum</i>	2	102	1.01	0.432													
<i>C. mossambicense</i>	1	185	0.90	0.423													
<i>E. zambesiacum</i>	2	37	4.02	0.007	1	15	3.19	0.110	1	28	15.74	0.006	1	32	2.57	0.255	
<i>F. virosa</i>	1	53	4.09	0.004													
<i>M. zanzibarica</i>	2	57	5.71	0.001	1	44	0.95	0.822	1	36	7.52	0.003	1	35	6.33	0.012	

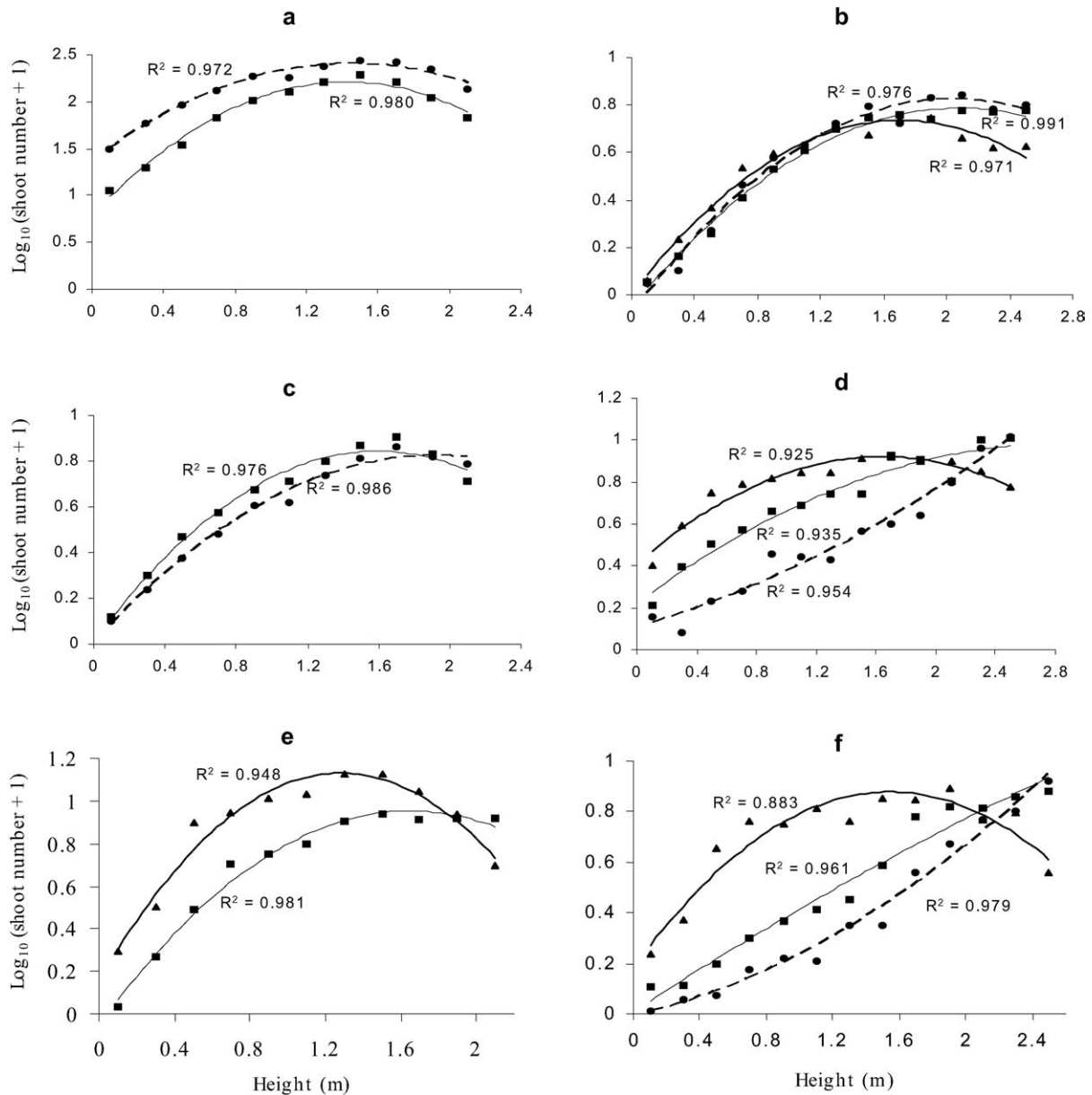


Fig. 3 – Relationships between tree height and number of shoots (log₁₀) available on tree individuals with no (●, dash curve), low (■, thin continuous curve) and high (▲, thick continuous curve) accumulated elephant impact on (a) *C. tomentosa* (b) *C. apiculatum*, (c) *C. mossambicense*, (d) *E. zambesiacum*, (e) *F. virosa* and (f) *M. zanzibarica*. Quadratic regression models have been fitted to the data and the R² presented is the adjusted value.

The pair-wise contrasts of low and high accumulated elephant impact levels for *E. zambesiacum* also indicated no significant variation in the number of shoots in different height sections whereas that of *M. zanzibarica* indicated a significant variation (Table 1).

The relationships between height sections and number of shoots in each height section were best fitted (adjusted $R^2 > 0.9$) by second-order polynomial (quadratic) regression models (Fig. 3). Few *C. elaeagnoides* with either low or high accumulated elephant impact levels were at least 2 m high and hence no comparisons of shoot numbers in different height sections across impact levels were made for this species. The fitted second-order polynomial (quadratic) regression curves give a general picture of the distribution of shoots in the different height sections for trees with different accumulated elephant impact levels (Fig. 3). *E. zambesiacum* and *M. zanzibarica* with high accumulated elephant impact had more shoots in lower height section than trees with no accumulated elephant impact level (Fig. 3d, f). *F. virosa* individuals with high impact had more shoots in lower height sections than trees with low accumulated elephant impact level (Fig. 3e). On *C. tomentosa* it was the reverse with more shoots at lower heights on trees with no accumulated elephant impact than on trees with low accumulated elephant impact (Fig. 3a). Number of shoots in different height sections of *C. apiculatum* (Fig. 3b) and *C. mossambicense* (Fig. 3c) trees did not differ between different accumulated elephant impact levels (Table 1).

3.2. *Mesoherbivores foraging patterns in relation to shoot abundance and elephant impact*

The observed frequencies of browsing by kudu and impala in different height sections differed from expected for all plant species (Table 2). The residuals obtained in the Chi-square test indicated that both kudu and impala browsed less than expected in height sections with few shoots (Table 2). Impala

browsed in height sections below 0.8 m less than expected. Impala browsed more than expected in height sections with high numbers of shoots, except that they browsed less than expected in the 1.2–1.6 m height section of *C. tomentosa* (Table 2). However, even if impala browsed more than expected in 1.2–1.6 m height sections of *C. mossambicense* and *F. virosa* the difference between observed and expected (residuals) was less than for 0.8–1.2 m height section (Table 2). Kudu browsed more than expected in height sections within 1.2–2.0 m but in the 1.6–2.0 m height section of *C. tomentosa* it was just above expected (Table 2). Due to that some height sections of some woody species had expected frequencies less than the minimum expected cell frequencies required in the Chi-square test; such woody species are not included in Table 2.

Both impala and kudu preferred trees with accumulated elephant impact over trees without accumulated elephant impact. This held for all species except *C. tomentosa* (Table 3).

Table 3 – Preference of trees of different accumulated elephant impact levels by impala (*A. melampus*) and greater kudu (*T. strepsiceros*). Bold faced indices indicate the most preferred impact level within a plant species

Animal species	Browsed plant species	Preference index		
		No impact	Low impact	High impact
Impala	<i>C. tomentosa</i>	1.216	0.263	
	<i>C. mossambicense</i>	0.546	2.307	
	<i>F. virosa</i>		0.263	2.042
Kudu	<i>M. zanzibarica</i>	0.158	1.678	1.732
	<i>C. tomentosa</i>	1.253	0.154	
	<i>C. elaeagnoides</i>		0.210	1.287
	<i>C. mossambicense</i>	0.856	1.499	
	<i>E. zambesiacum</i>	0.469	1.340	0.603
	<i>F. virosa</i>		0.447	1.837
	<i>M. zanzibarica</i>	0.130	1.997	1.070

Table 2 – Observed and expected frequencies of browsing in height sections 0–0.4, 0.41–0.8, 0.81–1.2, 1.21–1.6 and 1.61–2.0 m by (a) impala (*A. melampus*) and (b) greater kudu (*T. strepsiceros*)

Species	Height section (m)	Browsing frequency			χ^2	P
		Observed	Expected	Residual		
(a) Impala						
<i>C. tomentosa</i>	0.41–0.8	13	37.9	–24.9	44.656	< 0.001
	0.81–1.2	88	51.3	36.7		
	1.21–1.6	54	65.8	–11.8		
<i>C. mossambicense</i>	0–0.4	1	6.1	–5.1	23.383	< 0.001
	0.41–0.8	4	18.9	–14.9		
	0.81–1.2	39	26.9	12.1		
<i>F. virosa</i>	1.21–1.6	41	33.1	7.9	10.502	0.005
	0.41–0.8	5	15.2	–10.2		
	0.81–1.2	25	17.4	7.6		
	1.21–1.6	19	16.4	2.6		
(b) Kudu						
<i>C. tomentosa</i>	0.81–1.2	4	11.9	–7.9	8.233	0.016
	1.21–1.6	24	17.0	7.0		
	1.61–2.0	17	16.1	0.9		
<i>C. mossambicense</i>	0.41–0.8	1	8.8	–7.8	21.569	< 0.001
	0.81–1.2	3	13.1	–10.1		
	1.21–1.6	31	21.9	9.1		
	1.61–2.0	34	25.2	8.8		

The preferred accumulated elephant impact level for each tree species by either kudu or impala had more shoots in lower heights than trees at other accumulated elephant impact levels. However, *C. tomentosa* trees with no accumulated elephant impact were preferred by both impala and kudu (Table 3); these had more shoots than individuals with accumulated elephant impact (Fig. 3a). Further, impala preferentially browsed *C. mossambicense* with low accumulated elephant impact (Table 3), which was the highest impact level for this species. The number of shoots in height sections below 1.6 m on individuals of *C. mossambicense* with low accumulated elephant impact were slightly higher than on individuals with no accumulated elephant impact level (Fig. 3c) but not significantly different (Table 3). Impala preferentially browsed *F. virosa* and *M. zanzibarica* individuals with high accumulated elephant impact level (Table 3). *F. virosa* individuals with high accumulated elephant impact level had more shoots in height sections below 1.8 m than individuals with low accumulated elephant impact level (Fig. 3e). *M. zanzibarica* individuals with high accumulated elephant impact level had more shoots in height sections below 1.8 m high than individuals with no and with low accumulated elephant impact level (Fig. 3f). Kudu also preferentially browsed *F. virosa* individuals with high accumulated elephant impact level. Kudu further preferentially browsed *E. zambesiacum* and *M. zanzibarica* individuals with low accumulated elephant impact level (Table 3).

4. Discussion

4.1. Tree height and distribution of shoots on trees with different accumulated elephant impacts

In this study we found supporting evidence to our first two and the fourth hypotheses. This indicates that feeding and breakage of stems and branches by elephants promote what might be called “browsing lawns” (Owen-Smith, 2003), whereby tall trees are transformed to short trees (1–3 m tall). Such ‘browsing lawns’ are analogous to the ‘grazing lawns’ produced by wildebeest grazing in the Serengeti (McNaughton, 1976, 1984). Our results agree with those of Guy (1981) who found that in Sengwa Wildlife Research Area, Zimbabwe, elephant foraging resulted in more browse within reach of browsing mesoherbivores. *C. tomentosa* and *C. mossambicense* that did not agree with our first two hypotheses had few individuals with high accumulated elephant impact and the comparison was between trees with no impact and those with low impact. For the other species it could be argued that the difference in tree height depends on that elephant preferentially feeds on small/young trees. However, Makhabu (1994) found that elephant in neighboring Moremi Wildlife Reserve browse trees of the same species with stem diameters at breast height of 2–16 cm without preference.

Elephants use the study area mostly during the dry period and the majority of them move out of the area during the wet season (Gibson et al., 1998), which is the plants’ growing period. This gives coppiced and regrowth shoots time to

grow with minimal interruptions. The increase in the number of shoots at low height levels of trees with high accumulated elephant impact is explained by the activation of dormant lateral buds with reduced apical dominance following the removal of leading shoots (Järemo et al., 1996; Smit and Bolton, 1999). The resprout shoots then grow with minimal disturbance during the growing season when most elephants are absent being in their wet season ranges. In most situations elephants do not directly damage the tree’s root system (Makhabu, 1994). Trees might then grow in such a way as to re-establish the former root/shoot ratio (Bergström and Danell, 1987). Some plant species have been found to produce fewer but larger shoots that are more branched after real or simulated browsing (Danell et al., 1985; Bergström and Danell, 1987). In this study we counted twig ends < 6 mm, and the high numbers of shoots at low height levels we report here may be a combination of main current season’s shoots and branches on such shoots. The high capacity of these trees to resprout following browsing may be an adaptation evolved in response to browsing by large herbivores and/or to frequent fires (Bond and Midgley, 2001). Fewer shoots high in the canopies of trees with high accumulated elephant impact is more likely a consequence of changes in tree architecture following repeated elephant browsing than the result of elephants actually cropping the shoots at these levels. Elephant preferred browsing level in the area is 1.0–1.5 m (Stokke and du Toit, 2000).

The change in the distribution of the number of shoots on trees due to elephants’ browsing could be beneficial to mesoherbivores like impala and kudu, in that more shoots become available for them at low heights of tree canopies (Guy, 1981). Makhabu (2005) found that the woody species browsed by elephant do not significantly overlap with those browsed by impala and kudu, but there are some woody species like *F. virosa* and *M. zanzibarica* they both browse. Therefore the increase in shoot availability at lower heights in such woody species might benefit browsing mesoherbivores.

4.2. Mesoherbivores foraging patterns in relation to shoot abundance and elephant impact

Impala and kudu selected between height sections with different browse availability, seemingly treating them as separate patches (Senft et al., 1987; Spencer et al., 1995). Their browsing frequencies in different height sections were generally a non-linear function of the number of shoots, hence an “overmatch”. Thus, our third hypothesis is rejected. This finding may contradict the suggestion that browsers would show a linear relationship between the available biomass and intake rate (Renecker and Hudson, 1986; Spalinger and Hobbs, 1992). The difference could depend on the used scale and the measured variables. In this study, selection was between different height sections (patches) within a plant and the compared variables were number of shoots and frequency of browsing in height sections. Even with a linear response, browsers would spend more time browsing in height sections with high shoot densities, thus increasing the probability for observation. Thus, the overmatch response observed might to some extent be influenced by the method

used. In other studies selection was between plants or bushes and the variables being biomass and intake rate. The likely explanation to the pattern we observed is that animals select height sections (patches) with high number of shoots to optimize intake rate (Schoener, 1971; Stephens and Krebs, 1986). A complex interaction of several components such as mean bite rate, bite-size and movement rate determine the intake rate of food by herbivores (Renecker and Hudson, 1986; Spalinger and Hobbs, 1992). Renecker and Hudson (1986) suggested that for large herbivores to meet their daily requirements they must either occupy rich habitats (or at least those with dense forage patches) or reduce selectivity so that a greater proportion of available forage is selected as food. By selecting a height section with dense shoots, a browser might increase intake rate since it has an opportunity to take more bites without the need to move, but intake rate also depends on shoot size, which was not recorded. Food intake rate however, could be limited by the need to ruminate while bite rate and size are often dictated by vegetation characteristics (Renecker and Hudson, 1986). It could be argued that an animal could search for browse while it chews bites it has taken (Spalinger and Hobbs, 1992; Illius et al., 2002). However, some animal species like impala feed in a group (Fritz and de Garine-Wichatitsky, 1996) hence suitable sites might be occupied by other individuals. In this study we did not consider animal group size, which is vital in selection of patches by animals in a group (Fritz and de Garine-Wichatitsky, 1996). Fritz and de Garine-Wichatitsky (1996) reported that an impala in a group appears to adapt its 'prey' choice to minimize intraspecific competition.

It is not evident why impala browse less than expected in 1.2–1.6 m height section of *C. tomentosa* whereas they browse at the same height slightly more than expected on other species. Even for those species browsed as expected in 1.2–1.6 m height sections the residual was less than in the 0.8–1.2 m height section possibly because impala have difficulties reaching heights above 1.5 m. For *C. tomentosa*, the numerous sharp hooked spines it possesses possibly inhibit impala from leaning against the tree in order to reach the browse at high levels. The same tendency is observed for kudu in heights between 1.6 and 2 m of *C. tomentosa*. *F. virosa* does not have spines while *C. mossambicense* has spines (Coates Palgrave, 2002) but they are not hooked or as sharp and dense as those of *C. tomentosa*.

Impala and kudu mostly preferred plant individuals except of *C. tomentosa* with accumulated elephant impact to those without, supporting our fourth hypothesis. Preference for trees with accumulated elephant impacts by impala and kudu suggest that browsing by these species is facilitated by elephant. The browsing facilitation for impala and kudu by the impact of elephants appear to be by conversion of tall trees to short trees and a change in tree growth form. This leads to that in some species more shoots are produced in heights reachable by impala and kudu. Other studies have shown that browsed trees of some species produce shoots with increased biomass per shoot (Bergström and Danell, 1987; Molvar et al., 1993), increased nitrogen concentration and decreased concentration of secondary compounds like

tannins (du Toit et al., 1990) compared with unbrowsed individuals. If the tree species we studied respond to browsing in the same way, then it is likely that increased bite-size and nutrient advantages, besides availability of shoots, contributed to the observed preference for elephant impacted trees. However, large shoots might not benefit browsers if they are not branched, because their diameters may be larger than the maximum bite diameters of the twig biting ungulates (Makhabu et al., in press). More branching on regrowth shoots of trees previously browsed than on shoots of unbrowsed trees, as found in some species (Bergström and Danell, 1987), is likely to result in more shoot ends within the bite diameters of impala and kudu. The high density of shoots with preferred diameters (< 6 mm) recorded on elephant impacted trees is likely to contribute to the preference by impala and kudu for these trees. Rutina et al. (2005) reported that impala prefer elephant impacted habitats and we suggested that it might be due to the facilitation effect we report.

In here we also report that individuals of *C. tomentosa* with accumulated elephant impact were less browsed by impala and kudu than those without accumulate elephant impact. This might suggest that elephants have a negative impact on the use of this preferred woody species by impala and kudu. However, this might be mitigated by an increase in browse resource in other woody species leading to an overall positive effect.

Facilitation for impala and kudu by the modification of tall trees through the browsing activity by elephants to 'browsing lawns' probably is beneficial to them, but only if the rebrowsing of the elephants are not so intense as to deplete available shoots on those trees. Although elephant do not share many preferred woody food species with other browsing herbivores in the study area, the overlaps in resource use between elephants and other browsers do not significantly differ between seasons (Makhabu, 2005). This suggests that although elephants rebrowse trees, other browsing herbivores continue to browse tree species they share with elephants. However, the amount of browse taken by herbivores from trees elephant browse may differ between seasons, but was not recorded by Makhabu (2005). Browsers are not the only species facilitated by elephant in our study ecosystem. The African buffalo (*Syncerus caffer*) has been shown to prefer to graze on patches grazed more heavily than average by elephants 3–10 days before (Halley et al., 2003; Taolo, 2003). Gallinaceous birds prefer areas with high elephant impact (Motsumi, 2002).

This study has implications for management of coexisting megaherbivores and mesoherbivores. It highlights the need for a careful balanced assessment of the ecological role of major species in the ecosystem before decisions to manipulate population and distribution of any of them can be done. Elephant impact on vegetation has been indicated to be either detrimental (Cumming et al., 1997; Fritz et al., 2002) or beneficial (Owen-Smith, 1987, 1989; Skarpe et al., 2004) to other animal species. We found evidence that they might be beneficial for other species and thereby this study gives some support to the suggestion of Owen-Smith (1989) that elephant is a 'keystone herbivore'.

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