African Elephants *Loxodonta africana* Amplify Browse Heterogeneity in African Savanna

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ABSTRACT

There is a growing concern that the feeding habits of the African elephant, which include pushing over, uprooting and snapping trees, may have a negative impact on other herbivores. Browsed trees are known to respond by either increasing production (shoots and leaves) or defence (secondary compounds). It is not clear, however, what proportion of the browsed biomass can be made available at lower feeding heights after a tree is pushed over or snapped; thus, it is also unclear how the forage quality is affected. In a field survey in Kruger National Park, South Africa, 708 Mopane trees were measured over four elephant utilization categories: snapped trees, pushed-over trees, uprooted trees and control trees. The elephants' impact on the leaf biomass distribution was quantified, and the forage quality (Ca, P, K and Mg, N, digestibility and condensed tannin [CT] concentrations) were analyzed. Pushed-over and uprooted trees had the maximum leaf biomass at lower heights (< 1 m), snapped trees at medium heights (1–2 m) and control trees at higher heights (> 2 m). In all three utilization categories, the minimum leaf biomass was seven times higher than it was for control trees at a height of below 1 m. Leaf nitrogen content increased in all three categories and was significantly higher in snapped trees. CT concentrations increased slightly in all trees that were utilized by elephants, especially on granitic soils in the dry season. The results provide the insight that elephants facilitate the redistribution and availability of browse and improve the quality, which may positively affect small browsing herbivores.

Key words: browse amplification; browse biomass; condensed tannin; elephants' impact; green leaves; herbivore facilitation; nitrogen; vertical stratification.

The concept of facilitation in ecology has been an important aspect in explaining species co-existence through the broadening of resource availability (Bruno *et al.* 2003, Wegge *et al.* 2006) and enhancement of resource heterogeneity (Adler *et al.* 2001, Pretorius 2009) in both grazing (Belsky 1986) and browsing systems (Jager *et al.* 2009). Herbivores, particularly elephants, are classical facilitative examples in ecology that, through their feeding habits, cause a complex scale-dependent effect on habitat heterogeneity and suitability (Pringle 2008). Elephants are considered to be habitat modifiers or ecological engineers (Jones *et al.* 1994) that physically manipulate resources to cause cascading effects on other trophic levels (Smallie & O'Connor 2000, Calenge *et al.* 2002). The scale of this effect is relatively broad, as elephants are large animals that both graze and browse. Elephants push over, debark, break branches and stems and uproot trees (Barnes 1983b, Calenge *et al.* 2002). Such behaviors transform the vegetation structure through changes in tree height, canopy cover and species composition (Jachmann & Bell 1985, Smallie & O'Connor 2000). This process in turn has the potential to increase resource heterogeneity in the ecosystem (Levick *et al.* 2009). In addition, elephants remove a large amount of forage biomass (Shannon *et al.* 2006), which may then not be available for competing herbivores. Furthermore, woody plant species respond to browsing in a number of ways, first by producing a new flush of plant biomass to replace the removed parts (Bergström 1992), and second by increased antiherbivore de-

fences, such as tannins (Kohi *et al.* 2010) or thorns (Gowda 1997). Because elephants mainly push over or snap large trees, there is a growing concern that this behavior may have a negative effect on other herbivores (Ludwig *et al.* 2008). It is, however, unclear how much browsed biomass is made available after trees are pushed over, uprooted or snapped by elephants. Therefore, this study focuses on how the impact of elephants on the vegetation affects the availability and quality of browsable biomass. Particularly, we focus on the role of elephants in facilitating access to browsed biomass for smaller herbivores (Rutina *et al.* 2005). In this field study, trees under different elephant browsing pressures were selected to quantify the impact of elephants on the subsequent availability and quality of browsable biomass.

Trees that are pushed over or snapped by elephants are frequently reported in savanna systems (Gadd 2002, Mapaure & Moe 2009). Some of these trees resprout strongly and others do not, depending on the species, age, drought, fire and nutrients availability (McNaughton 1979, Kerley *et al.* 2008, Shannon *et al.* 2008). Increasing elephant densities are also associated with an increase in the number of trees that are pushed over, snapped or uprooted and subsequently killed (Jachmann & Croes 1991), although the numbers of killed trees are often not alarming (Shannon *et al.* 2008, Mapaure & Moe 2009) except for exceptional episodic events (reviewed by Kerley *et al.* 2008).

Tree stem breakage (pollarding) is known to stimulate trees to form multiple stems or bunches of resprouting shoots, which yields a higher amount of browsed materials (Jachmann & Bell 1985, Smit 2003, Rutina *et al.* 2005). Likewise, sprouting can be

stimulated when elephants push over trees, snap tree stems or remove tree branches. The heights at which sprouts are observed are influenced by the nature of the elephants' impacts on the trees (*i.e.*, pushed over, uprooted or snapped).

Field studies have indicated that elephant browsing plays a major role in the availability of browsed materials, especially during the season following the browsing activity (Jachmann & Bell 1985, Rutina *et al.* 2005). For instance, lightly browsed Mopane (*Colophospermum mopane*) trees were observed to have fewer flushing leaves than severely browsed trees (Smit 2003, Rutina *et al.* 2005). Jachmann and Bell (1985) found that the availability of browsed biomass in a Miombo woodland was relatively higher in pushed-over trees than it was in intact trees. Photosynthetic activity in browsed trees can be prolonged until late in the dry season (Sigurdsson 2001). The availability of these green leaves, provides crucial browsing materials for herbivores in the dry season where a browse 'bottleneck' is often experienced (Styles & Skinner 2000, Rutina *et al.* 2005).

Browsing can enhance the nutrient contents of foods in terms of proteins and essential minerals (Jachmann & Bell 1985, Holdo 2003). Nutrient concentrations of P, Na, Mg and K are normally higher in young leaves than all other leaves (Jachmann & Bell 1985, McNaughton 1988). Soil types and growing seasons also influence the foliar nutrient concentration and plant productivity. For example, foliar Ca, Na and K accumulate in mature leaves in the dry season but decrease in the wet season in relatively young leaves due the low retranslocation rate of senescing plant tissue from the previous season (McDowell *et al.* 1983, Tolsma *et al.* 1987). Soils that are rich in nutrients (*e.g.*, N, P or K) increase foliar production of a higher browse quality (Augustine & McNaughton 2006, van der Waal *et al.* 2009).

Besides responding by regrowth, trees may use other strategies to avoid future herbivore activities, such as increasing secondary plant compounds (Cooper & Owen-Smith 1985). For example, pruned Mopane trees were found to induce the production of secondary compounds (Wessels *et al.* 2007), while severe defoliation of Mopane trees was found to decrease condensed tannin (CT) concentrations (Kohi *et al.* 2010).

Therefore, in this study, we aimed to determine the extent to which elephant foraging behavior increases the availability of browsed materials in terms of quantity and quality at the feeding heights of smaller herbivores. We hypothesize that an increase in elephant browsing pressure: (1) decreases the height of the tree canopy and the height of the lowest leaves, amplifying the structural heterogeneity of the woody vegetation; (2) stimulates regrowth and increases the availability of leaf biomass at lower height classes; (3) causes trees to keep their photosynthetic leaves longer into the dry season; and (4) improves browsing quality through increased nitrogen concentrations, improves digestibility and generates higher mineral content (Na, P, K, Mg and Ca) through lower CT concentrations.

METHODS

The study site was located in the central section of the Kruger National Park (KNP) in the Phalaborwa, Mopani and Letaba sections between $31°9'43''$ E, $23°56'20''$ S; $31°24'59''$ E, $23°31'38''$ S; and $31°34'36''$ E, $23°51'3''$ S. The geology within the KNP changes from east to west with a subdivision of KNP roughly in half (north to south); granitic soils are in the west and basaltic soils in the east (Venter *et al.* 2003). In general, basaltic soils are relatively rich in nutrients, while granites are nutrient poor (Webb 1968, Brady 1987, Van Ranst *et al.* 1998). Basaltic soils are rich in iron and magnesium (Brady 1987, Van Ranst *et al.* 1998, Brady & Weil 2004) and can also store large amounts of anions, such as NO_3 and SO_4 in the subsoil (Van Ranst *et al.* 1998). The study sites receive approximately 450–600 mm/yr of rainfall and experience hot, wet seasons and cooler, dry seasons (Venter *et al.* 2003). The central and northern section of the KNP (north of Olifants River) is dominated by Mopane woodlands that cover approximately one-third of the park (Young *et al.* 2009). The Mopane tree is an important browse species for elephants and many other ungulate species, such as the Greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), giraffe (*Giraffa camelopardis*), common duiker (*Sylvicapra grimmia*) and steenbok (*Raphicerus campestris*) (Guy 1981, Timberlake 1995, Rutina *et al.* 2005). Unlike many savanna plant species, Mopane trees are known to withstand elephant utilization and rarely die unless they are totally uprooted (Guy 1981).

DATA COLLECTION.—Trees with stem diameters that were larger than 10 cm were selected using Barnes (1983b) and Jachmann and Bell's (1985) estimate of elephant utilization. Four groups of elephant utilization were distinguished: (1) snapped stems, (2) pushed-over trees, (3) uprooted trees, and (4) control (intact) trees. Each section (Phalaborwa, Letaba and Mopani) was researched for elephant-impacted trees. Because the KNP is broadly divided into basaltic and granite soils, the Phalaborwa and part of the Letaba section were used for surveying trees in granite soils, while the Mopani and another part of the Letaba section were used for surveying trees in basaltic soil. A survey was conducted from the beginning of May (end of the wet season for 2 wk) and again in October (end of the dry season for 2 wk) 2007. Tree measurements were taken based on the parameters that are required for estimating canopy volume: tree height (H_1), height at maximum canopy diameter (H_2), height at the lowest leaf (H_3), maximum canopy diameter at height H_2 (D) and canopy diameter at height H_3 (E). In total, 708 trees were sampled, of which 360 were sampled at the end of the wet season and 348 were sampled at the end of the dry season. Half were sampled on the granite and half on the basaltic soils. For each measured tree, a nonbrowsed control tree of similar diameter was located within 100 m. The 100 m maximum distance was chosen on the assumption that the variation in rainfall and soil type is minimal. The total leaf percentage and green leaf percentage of each tree were estimated visually.

LEAF BIOMASS ESTIMATION.—To estimate the browse biomass, trees were stratified vertically, based on the feeding heights of different browsing herbivores. The strata represent the browsing heights for a range of browser species, *i.e.*, steenbok (up to 0.9 m), impala (up to 1.45 m), Greater kudu (up to 2 m) (Du Toit 1990), elephant (Makhabu 2005) and giraffe (up to 5 m) (Pellew 1983).

Tree biomass was estimated using the relationship between the estimated canopy volume and the true leaf biomass (Smit 1996, van Essen *et al.* 2002). The tree volume was calculated using an ellipsoid formula. The tree was divided into two segments. The first segment represents the top part of the tree, is dome shaped, and is calculated using the formula for a half ellipsoid. The second segment represents either a cone frustum or a cylinder. Smit (1996) estimated the equations for coppiced trees and intact trees, and because our study also includes pushed-over trees, a new volume calculation was required to estimate the equation for pushed-over trees. For pushed-over trees and uprooted trees, the volume was also calculated with the 'two segments' approach. The dome-shaped segment was calculated following the ellipsoid formula for equal or unequal canopy diameter axes. The use of equal or unequal diameter axes was determined by the absolute difference between the diameter axes (D_1–D_2). If the difference between the axes was larger than 0.92 m (the upper 95% confidence interval of the mean absolute differences between the diameters axes of the control trees), then the formula for an unequal diameter axis was used. The use of a threshold on the formula choice was based on the fact that the canopy's shape changes when trees are pushed over, which affects the estimation of the canopy's volume.

BIOMASS EQUATION.—Tree volume was measured for pushed-over and uprooted trees. Thereafter, all of the leaves were handpicked, bagged and oven-dried at 70°C for 72 h. The measured total dry leaf biomass (g) was plotted against the calculated volume (cm^3) (see equation 1 and Fig. 1).

$$\text{Ln}(y) = -32.342 + 14.358\text{Ln}(x), R^2 = 0.82 \quad (1)$$
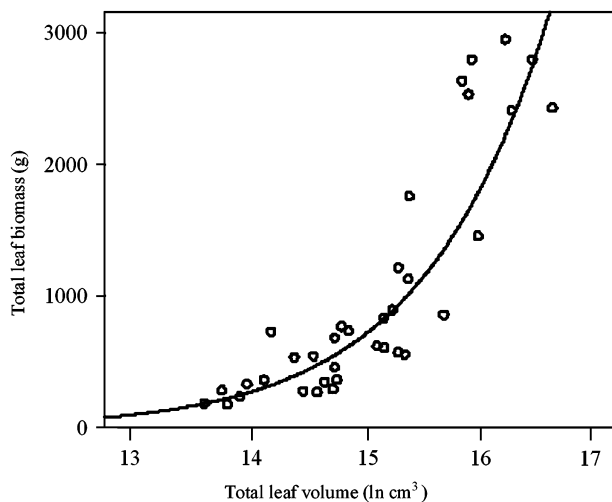$$\text{(uprooted/pushed-over trees)}.$$

FIGURE 1. The relationship between leaf biomass (g) and the measured canopy volume (cm^3) of uprooted or pushed-over trees. The power equation gave the best fit ($Y = 9 \times 10^{-15} \times X^{14.358}$, $R^2 = 0.82$, $N = 36$).

The snapped and intact tree equations were used from (Smit 1996, 2001):

$$\text{Ln}(y) = -3.196 + 0.728x, R^2 = 0.95 \quad \text{(coppiced trees).} \quad (2)$$

$$\text{Ln}(y) = -4.984 + 0.759x, R^2 = 0.92 \quad \text{(control trees).} \quad (3)$$

NUTRIENT ANALYSIS.—Leaf samples were collected from each of the sampled trees at the lowest height available. Sampled leaves were stored in paper bags and dried at 70°C for 48 h. The dried leaves were ground through a 1 mm sieve for nutrient analysis at the chemical laboratory of the Resource Ecology Group, Wageningen University (The Netherlands). The nutrient elements N, P, K, Na, Ca and Mg were measured after digestion in a mixture of sulfuric acid, salicylic acid and selenium (Novozamsky *et al.* 1983). N and P were measured with a Skalar San-plus auto-analyzer (Breda, The Netherlands), and Na, K, Ca and Mg were measured with an atomic absorption spectrometer (Varian AA600 analyzer, Varian Instruments, Walnut Creek, California, U.S.A.). The *in vitro* digestibility (IVD) was analyzed following the Tilley and Terry (1963) method in a Daisy incubator (AN-KOM Technology, Macedon, New York, U.S.A.). The CT concentrations were analyzed according to the proanthocyanidin method after extraction in acetone (50%) for 24 h (Waterman & Mole 1994).

DATA ANALYSIS.—An analysis of variance (ANOVA) was used to analyze the effects of the elephant utilization levels, browsing heights, soil types and seasons on the log (leaf biomass). Because the variances were not equal, Dunnett T3 was used to compare the biomass means against the control mean for each of the browsing heights for each elephant utilization level (Field 2009). The Games–Howell procedure was used to compare the biomass means for each browsing height across elephant utilization levels, as it is able to correct for the unequal sample sizes between different elephant utilization levels (Field 2009).

For the tree structure analysis, an ANOVA was used to test for differences in mean canopy heights (H_2) and lower leaf heights (H_3) (dependent variables) with elephant utilization categories (pushed-over, uprooted, snapped trees and control trees), soil types and seasons as independent variables. The Dunnett T3 test was used to compare mean canopy heights among categories. The Kruskal–Wallis test was used to test for differences in the lower leaf heights (dependent variables, deviating from normality) across the different elephant utilization categories (Quinn & Keough 2002, Field 2009). The Games–Howell procedure was used to compare mean lower leaf heights between the different categories (Field 2009). The green leaf percentages were arcsine-transformed before the ANOVA. Similarly, the Dunnett T3 test was used to compare the mean green leaf percentage with that of the control trees; thereafter, the Games–Howell procedure was used to compare the means among the elephants' utilization categories.

For the nutrients, CT and IVD analyzed using ANOVA to test for differences in each utilization category and its respective controls after an arcsine transformation had been carried out to

normalize the data. Data that did not follow a normal distribution after the transformation were analyzed using Mann–Whitney tests. An ANOVA was used to compare the means among the elephant utilization groups following the Games–Howell procedure.

RESULTS

LEAF BIOMASS.—The leaf biomass was significantly different among the different levels of elephant utilization (ANOVA, $F_{3, 2820} = 660.205$, $P < 0.001$) and was higher in the wet season (Games–Howell, $P < 0.001$) and for basaltic soils (Games–Howell, $P < 0.001$). The leaf biomass allocation at different heights was significantly influenced by the elephant utilization category (ANOVA, $F_{9, 2784} = 228.6$, $P < 0.001$). The foliar biomass was significantly higher in pushed-over (Dunnett T3, $P < 0.001$), uprooted (Dunnett T3, $P < 0.001$) and snapped trees (Dunnett T3, $P < 0.001$) than it was for the control trees at low heights. The foliar biomass decreased with increasing tree height for pushed-over and uprooted trees (Fig. 2). Among the utilized trees, pushed-over and uprooted trees had a higher leaf biomass than the snapped trees did at low heights (< 1 m) (Games–Howell, $P < 0.001$), with no difference between the 1 and 1.5 m heights. The snapped trees, however, had a significantly higher leaf biomass above 1.5 m than uprooted and pushed-over trees did (Games–Howell, $P < 0.001$). Generally, uprooted and pushed-over trees had a 60-fold higher leaf biomass than control trees below 1 m, but above 2 m the situation was reversed, and the factor decreased to 0.2-fold. Snapped trees had a sevenfold higher leaf biomass than control trees below 1 m, but the ratio decreased to 0.5-fold above 2 m (Fig. 2). Combining
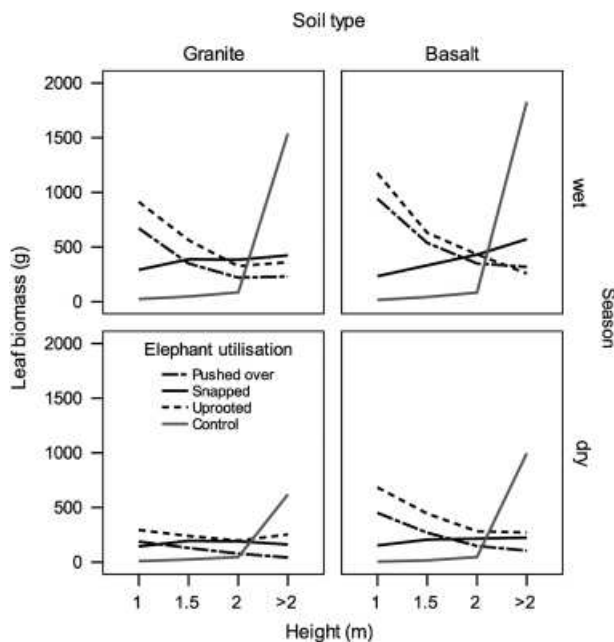

FIGURE 2. Total leaf biomass (g) against height (m) of trees from different elephant utilization categories. The panels indicate different soil types and seasons in which the trees were measured.

the three categories, however, leaf biomasses below 1 m were 30-fold larger for impacted trees than they were for the control trees.

TREE CANOPY HEIGHT (H_2).—Tree canopy heights were significantly affected by elephant utilization levels (ANOVA, $F_{3, 704} = 446.6$, $P < 0.00$). The heights of pushed-over trees (Dunnett T3, $P < 0.001$), uprooted trees (Dunnett T3, $P < 0.001$) and snapped trees (Dunnett T3, $P < 0.001$) were as expected or significantly lower than those of control trees. The mean canopy heights were 0.9 m for pushed-over and uprooted trees, 1.5 m for snapped trees and 3 m for intact trees. In general, the mean canopy heights of the control trees were 2 m higher than those of the pushed-over and uprooted trees and 1 m higher than those of the snapped trees. Soil types and the season did not affect tree canopy height (Fig. 3).

THE LOWEST LEAF HEIGHT (H_3).—As expected, the heights of the lowest leaves of elephant-utilized trees were significantly lower than those of the control trees (Kruskal–Wallis, $N = 708$, $\chi^2 = 465.6$, df = 3, $P < 0.01$). On average, the median height of the first leaves on elephant-impacted trees and control trees was 0.2 and 1.3 m, respectively. Among the elephant-utilized trees, however, the lower leaf heights were significantly higher on snapped trees than on pushed-over (Games–Howell, $P < 0.001$) and uprooted trees (Games–Howell, $P < 0.001$). Snapped trees, uprooted trees and pushed-over trees had median lower leaf heights of 0.4, 0.2 and 0.2 m, respectively (Fig. 4).

GREEN LEAF AVAILABILITY.—The availability of green leaves on Mopane trees differed among the four elephant utilization categories (ANOVA, $F_{3, 696} = 41.3$, $P < 0.001$) with a significant effect of soil types (ANOVA, $F_{3, 696} = 8.9$, $P < 0.001$) and seasons (ANOVA, $F_{3, 696} = 3.7$, $P < 0.01$). In the dry season, the elephant-utilized trees had a higher percentage of green leaves than the control trees did, especially on the granitic soils (Fig. 5). Pushed-over (Dunnett T3, $P < 0.01$), uprooted (Dunnett T3, $P < 0.01$) and snapped trees (Dunnett T3, $P < 0.01$) had a significantly higher proportion of green leaves than control trees did (Fig. 5), except in basaltic soil during the wet season. The estimated proportion of green leaves was not significantly different among the different categories of elephant utilization (Games–Howell, $P > 0.05$).

FORAGE QUALITY.—The foliar nitrogen concentrations of the pushed-over and uprooted trees did not differ from those of the respective control trees, but the leaves from snapped trees had significantly higher nitrogen concentrations than those of control trees (Table 1). The nitrogen concentration of the leaves in all three utilization categories was lower in the dry season than in the wet season (Fig. 6).

MINERAL ELEMENTS.—For mineral nutrients, Ca concentrations were significantly lower in uprooted and pushed-over trees than in control trees (Table 1). Among the snapped trees, no mineral nutrients (Ca, K, P, Na and Mg) showed significantly different levels from those of the control trees. In the pushed-over trees, K increased significantly while Mg decreased significantly, but both remained unchanged in uprooted trees (Table 1).
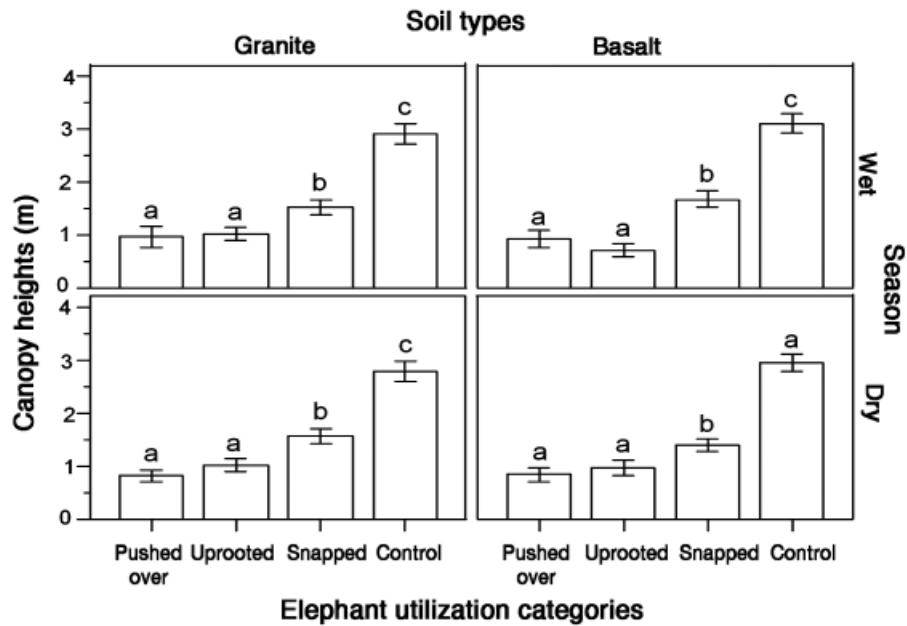
FIGURE 3. Mean canopy height (m ± 95% confidence interval) against different categories of elephant utilization. The panels indicate different soil types and seasons in which canopy height were measured. The letters indicate significant differences (Games–Howell, $P < 0.05$).

CONDENSED TANNINS.—CT concentrations were significantly higher in all of the elephant-utilized trees (Table 1). The CT concentrations increased substantially in trees that were utilized by elephants (Dunnett T3, $P < 0.05$), particularly on granitic soil during the dry season (Fig. 7), while the increase was not significant on basalt soil and in the wet season.
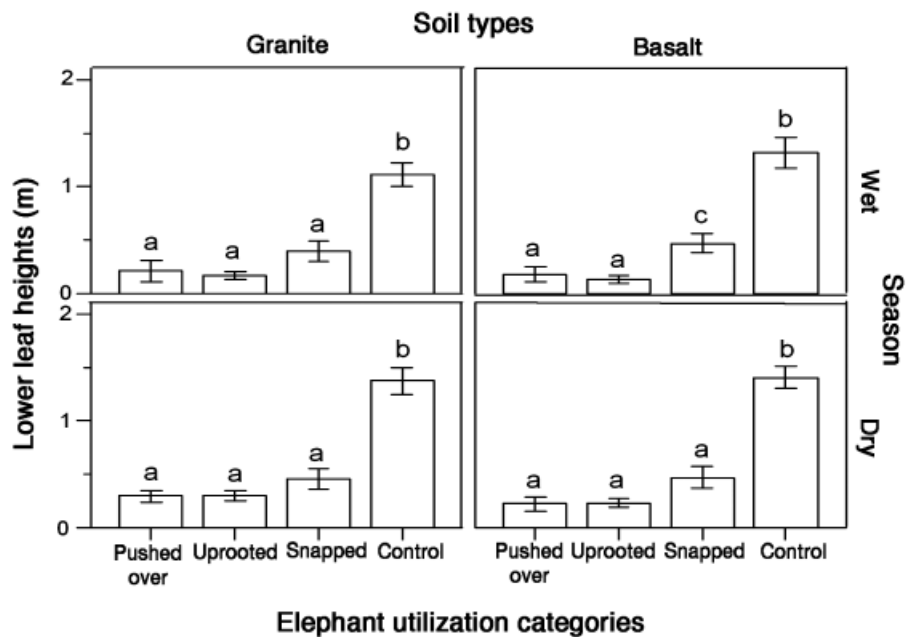

FIGURE 4. Lower leaf heights (m) against different categories of elephant utilization. The panels indicate soil types and seasons in which lower leaf heights were measured. The letters indicate significant differences (Games–Howell, $P < 0.05$).
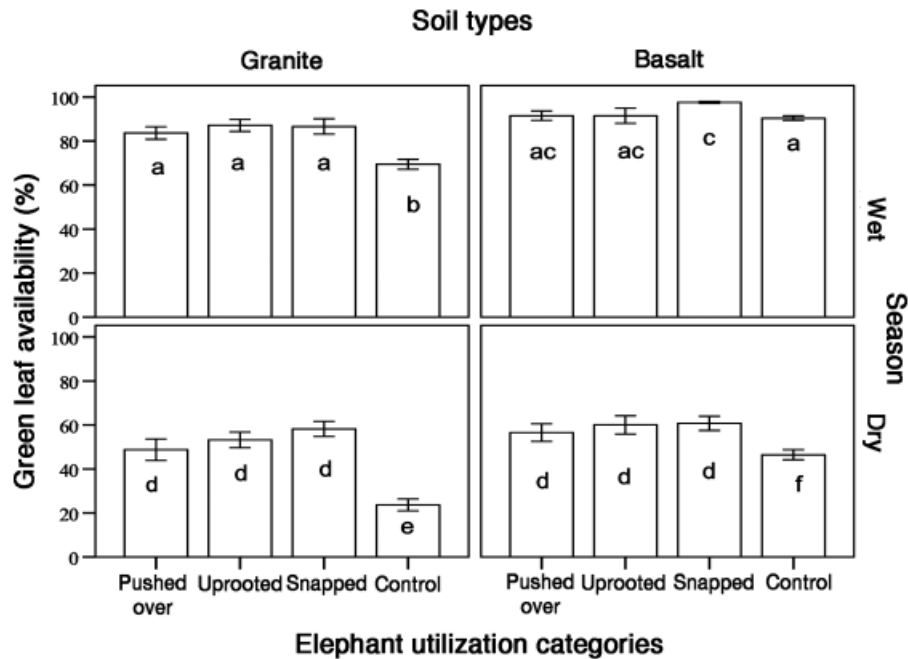
Soil types

FIGURE 5. The mean percentage of green leaves (± 95% confidence interval) for different categories of elephant utilization. The panels indicate soil types and seasons in which the leaves were measured. Control trees had a significantly lower percentage of green leaves than pushed-over, uprooted and snapped trees did in all four situations.

DIGESTIBILITY.—IVD was not affected by elephants' utilization patterns (Table 1), but it changed with the season and soil types. In the wet season, foliar IVD increased on granitic soil (ANOVA, $F_{1, 104} = 16.43$, $P < 0.001$), while in the dry season, the IVD was higher in basalt soil ($F_{1, 110} = 17.97$, $P < 0.001$). Pushed-over, uprooted and snapped trees had slightly higher IVD on granitic soil in the wet season than the control trees did, but the difference was not significant. Among utilized trees, snapped trees (Games–Howell, $P < 0.01$) and uprooted trees (Games–Howell, $P < 0.05$) had significantly higher IVD than uprooted trees did in the dry season. Nevertheless, the decrease in IVD in the dry season was not correlated to an increase in the CT concentration (Pearson $r = 0.27$, $P > 0.05$, $N = 238$). However, IVD percentages were positively correlated with N content (Pearson $r = 0.45$, $P < 0.05$, $N = 238$).

DISCUSSION

As the number of elephants increases, their role in ecosystem engineering becomes pivotal for not only increased forage availability but also habitat complexity that is advantageous to other organisms (Arsenault & Owen-Smith 2002, Pringle 2008, Campos-Arceiz 2009). Although elephants' feeding habits have gained more negative publicity due to their impact on large trees and 'perceived' habitat destruction (Barnes 1983, Shannon *et al.* 2008), this study demonstrated that elephants' feeding habits (*i.e.*, pushing over, uprooting and snapping of trees) in fact facilitates an increase in leaf biomass at lower heights (< 1 m) with a minimum increase of sevenfold when compared with intact trees. There is more evidence of

forage facilitation by mega-herbivores for small herbivores in grazing systems (McNaughton 1976, Arsenault & Owen-Smith 2002, Wegge *et al.* 2006) than in browsing systems, which is probably due to easier measurement arising from the simple structure and short growth period of grasses. As a result, Arsenault and Owen-Smith (2002) suggested that 'feeding facilitation arises mainly during the growing season, when grazing by larger species may stimulate vegetation regrowth'. Such a conclusion appears to be valid for grazing systems; however, in browsing systems, we observed an extended period of green leaf production in Mopane trees after utilization by elephants. This production provides short- to medium-term feeding facilitation that maintains food availability until late into the dry season. Similarly, Styles and Skinner (2000) observed that heavily utilized Mopane trees maintained green leaves until the beginning of the summer, while Rutina *et al.* (2005) showed that browse availability in the dry season increased in the heavily elephant-impacted *Capparis* shrub land.

Elephant browsing strategies, such as pushing over, uprooting and snapping of trees, influenced the quality of the resprouted leaves. In general, browsing pressure changes the foliar N content (Jachmann & Bell 1985, Bergström 1992) and CT concentration (Wessels *et al.* 2007, Kohi *et al.* 2010), which can affect the foliar digestibility (Jachmann 1989). The increase in N content is associated with increases in digestibility and thus forage quality. In our study, foliar N concentrations increased in all of the trees that were utilized by elephants, with significant increases in snapped trees (Table 1). This finding supports earlier studies, which showed that severe browsing caused an increase in N content in species such as

TABLE 1. *A comparison of foliar nutrient concentrations (N, P, K, Ca, Mg and Na as percentages of dry matter), condensed tannin (CT) concentrations (mg/g) and the in vitro digestibility (IVD) for three elephant utilization categories with their respective control trees. For each category, one-way analysis of variance (ANOVA) and Mann–Whitney (U) tests were used to test for differences in foliar nutrient concentrations. The positive (+) symbols show a significant increase of foliar nutrients and the negative (−) signs show a decrease of foliar nutrient concentrations. ns indicates no difference between the treatment and control trees. The number of trees that are pushed-over is N = 78, whereas N = 76 trees are uprooted and N = 84 trees are snapped. The asterisks (**) show medians, while other marks indicate means.*

Elephant utilization	Nutrient	Treatment mean concentration	Control mean concentration	Test	Test value	P	Significant value
Pushed-over	N	1.41	1.27	ANOVA	$F_{1,76} = 3.93$	0.051	ns
	P	0.11**	0.11**	U = 720	$Z = -0.405$	0.686	ns
	K (arcsine)	0.86	0.73	ANOVA	$F_{1,76} = 4.94$	0.029	+
	Ca	1.57	1.88	ANOVA	$F_{1,76} = 5.09$	0.027	−
	Mg	0.27	0.33	ANOVA	$F_{1,76} = 15.05$	0.0002	−
	IVD	51.18	50.21	ANOVA	$F_{1,76} = 1.37$	0.245	ns
	CT	981.58	866.31	ANOVA	$F_{1,76} = 8.77$	0.004	+
Snapped	N	1.38	1.19	ANOVA	$F_{1,74} = 5.83$	0.018	+
	P	0.13**	0.10**	U = 581	$Z = -1.46$	0.143	ns
	K	0.74**	0.58**	U = 651	$Z = -0.74$	0.461	ns
	Ca	1.79	1.92	ANOVA	$F_{1,74} = 0.89$	0.346	ns
	Mg	0.30	0.31	ANOVA	$F_{1,74} = 0.98$	0.326	ns
	IVD	53.26**	53.17**	U = 653	$Z = -0.72$	0.473	ns
	CT	943.52	865.95	ANOVA	$F_{1,74} = 6.39$	0.014	+
Uprooted	N	1.44	1.28	ANOVA	$F_{1,82} = 3.24$	0.076	ns
	P	0.12**	0.10**	U = 646	$Z = -2.11$	0.035	+
	K	0.68	0.61	ANOVA	$F_{1,82} = 1.58$	0.212	ns
	Ca	1.75	2.08	ANOVA	$F = 5.99$	0.017	−
	Mg	0.31**	0.34**	U = 751	$Z = -1.17$	0.241	ns
	IVD	52.813	51.353	ANOVA	$F_{1,82} = 3.92$	0.051	ns
	CT	968.71**	879.54**	U = 434	$Z = -4.01$	0.001	+

Acacia nigrescens in African savannas (Fornara & Du Toit 2007) and *Pinus sylvestris* in temperate forests (Edenius *et al.* 1993). The increase of N in browsed trees is associated with a compensation of lost tissue (Senock *et al.* 1991) and is facilitated by the large carbon reserves (Paula & Ojeda 2009) and high root-to-shoot ratios in browsed trees (Skarpe & Hester 2008). These factors increase the nutrient supply so as to maintain actively photosynthetic leaves with a high N content (Tolsma *et al.* 1987). Browse quality can, however, be reduced through an increase in the CT concentration (Foley *et al.* 1999). Our findings also show that elephant utilization induced increased CT concentrations in all categories (Table 1), which is in agreement with the results reported by Wessels *et al.* (2007). The CT increases contradict the notion that browsing always improves forage quality (Du Toit *et al.* 1990, Lehtila *et al.* 2000), but it should be noted that increases in CT content do not always decrease the nutritional quality of the browse, as the nutritional quality also depends on the level of CT concentrations (Foley *et al.* 1999). Increased CT concentrations are also associated with a reduction of forage digestibility through the binding of microbial enzymes, which inhibits the fermentation process and the breakdown of fiber (Jachmann 1989, Foley *et al.* 1999, Getachew *et al.* 2008), although in the present study no relationship was found between increased CT and decreased IVD. This finding

suggests that the increased CT concentrations were not large enough to influence foliar digestibility (Hervás *et al.* 2003, Getachew *et al.* 2008).

Mineral nutrients (*e.g.*, Ca, Mg) are reported to accumulate in older leaves, whereas P and K are transported from leaves to storage organs before abscission (Tolsma *et al.* 1987). This pattern reflects the observed mineral nutrient concentrations in control trees, which had relatively mature leaves (E. M. Kohi, pers. obs.) that nearly all turned yellow at the end of the dry season. Trees that were utilized by elephants, however, maintained their green leaves for longer during the dry season (Fig. 5). Our findings with regard to mineral nutrients were similar to those of Holdo (2003) for elephant-utilized trees in Mopane woodlands. The mineral nutrient concentrations of elephant-utilized trees were still high in terms of animal forage preference or requirements, even though they decreased relative to the control trees. Based on elephant browsing preferences as classified by Jachmann (1989), the mean nutrient levels of N, Ca and Mg were all in the preferred forage class, while P and K were in a less-preferred class. In addition, the Ca, K and Mg levels for all of the elephant utilization categories were above the nutrient requirements of the elephants, as reviewed by Rode *et al.* (2006). This finding suggests that elephant utilization improves browse quality in terms of increased N content.
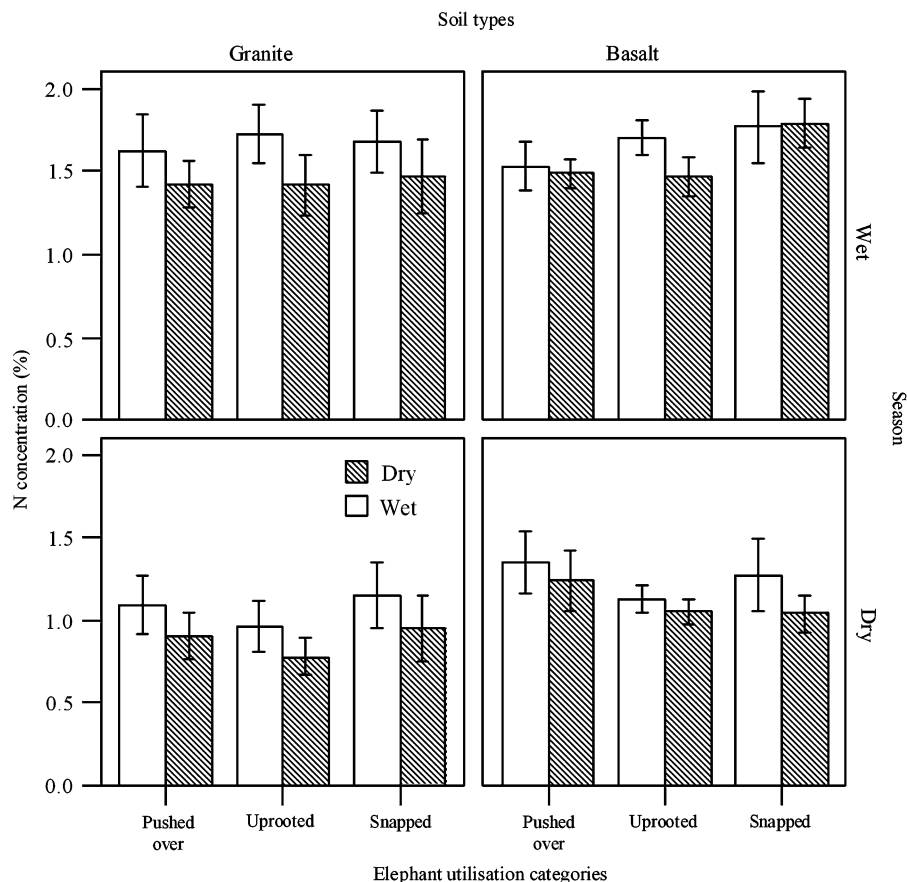
FIGURE 6. Mean N concentrations (% ± 95% confidence interval) for different categories of elephant utilization. The panels indicate soil types and seasons. The overlapping error bars are not significantly different (Games–Howell, $P < 0.05$).

This study provides a new insight for elephant impact modelling that should be included in management plans for elephants. Elephant feeding habits do not necessarily affect species diversity, but they can increase habitat complexity (Kerley & Landman 2006) and food availability, which results in the generation of suitable habitats for a variety of other organisms (Rutina *et al.* 2005, Kerley & Landman 2006, Pringle 2008). It is important to note that elephants that push over or snap large trees may improve and redistribute forage products rather than just removing them from the system (Jachmann & Bell 1985, Smallie & O'Connor 2000, Styles & Skinner 2000). This redistribution has an impact on the potential stocking rate of small herbivores, as reflected by recent increases in impala (Rutina *et al.* 2005) and kudu (Makhabu *et al.* 2006) in heavily browsed areas, and might decrease the browse availability for large herbivores such as giraffe.

CONCLUSION

This study provides evidence that elephant foraging amplifies habitat heterogeneity by creating a multilayer of canopy heights, thereby creating a continuum of leaf biomass availability from the ground layer (< 1 m) through the middle layer (1–2 m) to the

upper layer (> 2 m). The trees that are utilized by elephants maintained their green leaves until the end of the dry season, with improved forage quality through increased N content. The results also show the importance of elephants as a keystone species in savanna ecosystems because they improve and redistribute forage biomass and increase forage availability to animals feeding at lower heights. It is unfortunate that there is a preconceived idea that elephants are only agents of destruction, especially in terms of large trees. While not dismissing the potential destructive ability of elephants, this paper calls for an objective judgment of the impact of elephants on their habitat based on sound monitoring and research findings.
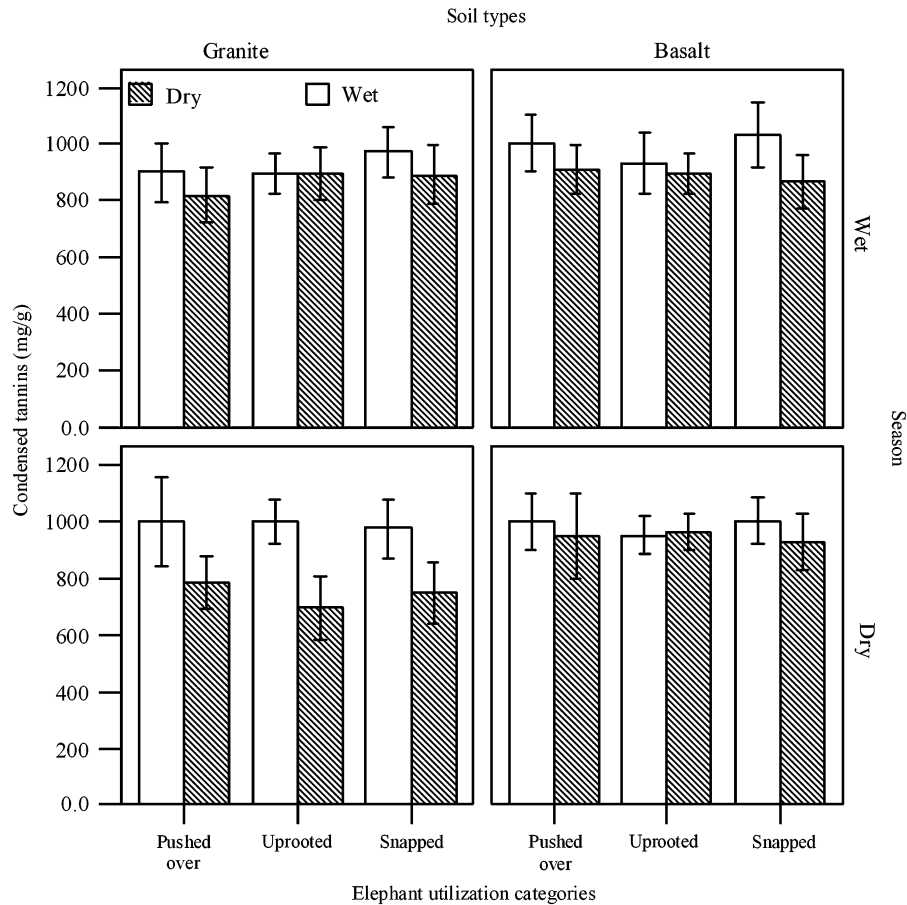
ACKNOWLEDGMENTS

Soil types

FIGURE 7. Mean condensed tannin concentrations (mg/g ± 95% confidence interval) of leaves from different elephant utilization categories. The panels indicate soil types and seasons. The overlapping error bars are not significantly different (Games–Howell, $P < 0.05$).

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