The Bulldozer Herbivore

How animals benefit from elephant modifying an African savanna

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The Bulldozer Herbivore: How Animals Benefit From Elephant Modifying an African Savanna

Edward Mtarima Kohi

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CHAPTER 1

General Introduction

Edward Mtarima Kohi

The African elephant (*Loxodonta africana*) as the largest terrestrial mammal has been important in structuring the dynamics of savanna vegetation through its feeding habits (Anderson and Walker 1974, Lewis 1991, Kerley and Landman 2006). Elephants, when feeding, use their trunk to pull off leaves and branches, snap trees, topple and uproot trees, and debark trees (Laws 1970, Caughley 1976, Barnes 1982, 1983a, Ben-Shahar 1993, Boundja and Midgley 2010). The negative effects of elephant feeding on tree abundance (Cowling et al. 2010) and plant species richness (Cumming et al. 1997, Kerley and Landman 2006, Landman et al. 2008) have been extensively reported. However, also positive responses have been reported, as damaged trees might regrow shoots after browsing with a higher browse density and improved foliar quality (Rutina et al. 2005, Makhabu et al. 2006). Nevertheless, positive feedback loops triggered by these positive tree responses, such as attracting browsing herbivores, are rarely reported.

In the 1960s through to 1990s elephant culling was advocated in different protected areas in Southern Africa (van Aarde et al. 1999a), but the decision to implement culling was drawn from lessons of studies conducted elsewhere while elephant effects are often site-specific (Guldemond and Van Aarde 2008). Several studies investigated the impact of elephants on the vegetation during the 1960s and referred to vegetation characteristics recorded in the beginning of the 20th century as the “natural situation”. These vegetation patterns reflected patterns at a period of very low elephant densities after excessive elephant hunting in the 1890s (Spinage 1973) and after the Rinderpest outbreak that killed many ungulate species in 1896s (Dublin et al. 1990). The introduction of culling in the 1960s and 70s were based on the assumption that elephant were a threat to their habitat and to other species. Studies carried out by Cumming and colleagues (1997) and Fritz and colleagues (2002) concluded that a growing elephant population might threaten biodiversity, with potentially negative impacts on insect and large herbivore species richness. These studies have been referred to frequently, even though they lack long-term observational data and are of a correlative nature (Cumming et al. 1997, Fritz et al. 2002). However, since the start of the culling operations, to my knowledge no study has shown a positive relationship between the numbers of elephant culled and the vegetation response, with positive effects on species biodiversity. Studies conducted so far on the elephant impact are mainly focussing on the general loss of the woody vegetation (Guldemond and Van Aarde 2008). While it is generally accepted that elephants can cause tremendous changes in vegetation structure, the conversion of woodland to grassland normally also need secondary factors, such as drought or fire (Shannon et al. 2008). The disturbance caused by elephant in the savanna woodlands (Prins and Van der Jeugd 1993, Mtui and Owen-Smith 2006) varies over different spatial scales, from plant parts, to whole plants, to a number of plants, and large clusters of plants, and as such its negative and positive (facilitative) effects might differ at these different spatial levels (Shannon et al. 2006b). For example, pushing over trees, uprooting and snapping trees can change the trees' structure and abundance in different ways (Ben-Shahar 1996b). This consequently can change the habitat heterogeneity (Makhabu et al. 2006, Pringle 2008, White and Goodman 2010, Nasseri et al. 2011), through differential shoot biomass distribution on re-sprouting trees. This resource modification might trigger facilitative, cascading effects for other herbivore species.

Facilitation in Ecology

Positive interaction or facilitation is not a new concept in ecology, however, it is rarely used in the formulation of new ecological theories (e.g., niche theory) (Hutchinson 1959, Bruno et al. 2003). For decades, plant-herbivore interactions of large herbivores, notably African elephant, were viewed largely as negative interactions (Laws 1970, Caughley 1976, Barnes et al. 1994, Calenge et al. 2002, Kerley and Landman 2006). Elephant feeding behaviour was mainly associated with tree damage, which in the 1970s was coined as the "elephant problem", i.e. the negative consequences of elephants to the ecosystem functioning and biodiversity (Laws 1970, Caughley 1976, Barnes 1983b). In a nutshell this is in line with the competitive exclusion thinking (Bruno et al 2003). However, positive interactions in ecology have been demonstrated both within species (intra-specific facilitation) and between species (inter-specific facilitation). These positive interactions often concern changes in community/habitat structure (e.g., biomass, space occupancy and productivity) that reduce negative interactions (e.g., predation, competition) (Huisman and Olff 1998, Van de Koppel and Prins 1998). Example of positive interactions include the hedging of mopane trees by elephant, (Smallie and O'Connor 2000, Styles and Skinner 2000) might attracts small browsing herbivores due to the increased new re-growth. Moreover, the open patches that are created by elephants can be used by small herbivores to watch predators (Hunter and Skinner 1998, Smith and Cain 2009). Another example of facilitation is described in papers on a number of facilitator organisms that shape our understanding of the interaction forces; for example, the salt marsh community experiment where manipulating key competitor and facilitator plants indicated that the presence of facilitator plants reduced the mortality of interacting species, and as such increased species diversity by more than 50% (Hacker and Gaines 1997). With the use of a plant-herbivore model Huisman and Olff (1998), showed that the presence of bulk feeding herbivores facilitated small, selective herbivore species by suppressing large plants that outcompete small plants which are consumed by selectively feeding herbivores. In the absence of bulk herbivores, small plants will be outcompeted by large plants through nutrient and light competition, reducing the forage availability for selective herbivore species.

Resource Heterogeneity

The niche concept was a large advancement in ecological sciences, improving our understanding of the role of resources on species richness (MacArthur and Lewontin 1968, August 1983), on the basis of resource partitioning and utilization mechanisms (Rotenberry and Wiens 1980, Huisman and Olff 1998, Prins and Olff 1998, Basset and de Angelis 2007). Resource heterogeneity has a temporal and/or a spatial component, indicating that the availability of a certain resource varies over time or over different locations. The main drivers governing the spatial and temporal variation of resources, particularly in African savannas, are rainfall, fire and herbivores (Barnes 2001, Van Langevelde et al. 2003, Boone et al. 2006, Moe et al. 2009). Herbivores manipulate their food resources through grazing and browsing and as such change the vegetation structure and forage availability (Calenge et al. 2002, Rutina et al. 2005, Moe et al. 2009, Valeix et al. 2011), and thereby influence the variation in the resource distribution. These changes resulting from grazing or browsing, lead to a diversification of forage availability, and hence amplify the resource heterogeneity. For example, since the Pleistocene period the presence of mega-herbivores in African savannas has been linked to the current high herbivore diversity as compared to North America, where due to the extinction of mega-herbivores, the extent of resource modification and thus habitat heterogeneity could not be maintained (Guthrie 1984, Owen-Smith 1987, Owen-Smith 1989). However, resource amplification as a positive feedback mechanism is rarely included in ecological predictions, even though it could be crucial in understanding community structure and species richness.

Thesis Focus and Outline

The aim of this thesis is to contribute to the understanding of species co- existence and community assemblage rules, through investigating herbivore-vegetation feedback loops, and their impacts on species diversity. The main hypothesis is that elephant amplify differences in existing resource heterogeneity through feedback loops, resulting in enhanced local species richness of the ungulate assemblage. This thesis focuses on the role of elephant feeding habits in enhancing herbivore species diversity through positive feedback mechanisms. The impact of elephant feeding habits as a facilitative mechanism of resources amplification has been investigated from the level of an individual plant (chapter 2-4) to a number of plants (plot). Secondly, the ecological consequences of this modification, how it affects the responses of various other large herbivore species in terms of microhabitat selection have been investigated in chapter 5. Resource modification in this thesis deals with the distribution of browse at different feeding height levels after elephants have pushed over, uprooted or snapped trees. Another studied aspect is how plants react to different browsing intensities and timing of defoliation, in terms of changing the quality and quantity of the re-growth.

Chapter 2 evaluates how the amount and the vertical stratification of leaf biomass is changed when trees are pushed over, uprooted, or snapped by elephants, by comparing them with intact control trees. The biomass-canopy volume relationship is used to estimate leaf biomass at different heights. Changes in tree structure and foliar nutrients concentration are also evaluated. In chapter 3 and 4 a simulated defoliation experiment (mimicking different intensity levels of browsing) is conducted to answer the question:

what are the plant response of the defoliated trees in reaction to various defoliation regimes (0 – 100%) and timing of defoliation in terms of the quantity (chapter 3) and quality of the regrowth (chapter 4). This knowledge will contribute towards a better understanding of the factors influencing the preference of browsers over areas previously browsed by elephants particularly in the dry season. Chapter 5 deals with the response of large herbivores to simulated plots of pushed over trees, snapped trees (tree cut at 50 cm from the base) and uprooted trees (tree removed). Herbivores' visitation frequencies (spoor counts) and dung deposition rates (dung counts) are used as a measure of plot utilization.

In summary, this thesis describes how trees respond to the feeding habits of elephants and how these responses affect habitat utilization of various large herbivore species. The thesis aims to contribute to our knowledge with regard to the impacts that elephants have on the vegetation with cascading effects on other herbivore species. These results will be useful in developing better elephant management strategies for African savanna.

Study area

The defoliation experiment was conducted in the central part of Kruger National Park (KNP) South Africa; and the simulated elephant feeding habit experiment was carried out in the Umbabati Private Nature Reserves. Umbabati is bordering KNP in the West, covering an area of around 195 km^2. The reserve constitutes several private farms. The reserve receives low annual rainfall with an average of 431mm, and annual mean temperature of 24°C (range 3.6-40.0°C). In KNP, the defoliation experiment was conducted in an area dominated by Mopane (*Colophospermum mopane*), which offers excellent opportunities to study resource modifications at different levels because mopane trees are highly browsed by elephants. Elephants were a good model herbivore species in this landscape as they dominate consumption in Mopane woodlands, and are known to modify the architecture and chemistry of Mopane trees, thereby enhancing resource quality and quantity (Smallie & O'Connor 2000, Styles & Skinner 2000).

CHAPTER 2

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). However, it is not clear 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 utilisation 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, Mg and N, digestibility and condensed tannin concentrations) were analysed. Pushed over and uprooted trees had maximum leaf biomass at lower heights (<1m), snapped trees at medium heights (1-2m) and control trees at higher heights (>2m). In all three utilisation 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. Condensed tannin concentrations increased slightly in all trees that were utilised 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: Elephants' impact; herbivore facilitation; browse amplification; vertical stratification; browse biomass; green leaves; nitrogen; condensed tannin.

INTRODUCTION

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 1986b) 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, Jones et al. 1997) that physically manipulate resources to cause cascading effects on other trophic levels (Smallie and 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 1983a, Calenge et al. 2002). Such behaviours transform the vegetation structure through changes in tree height, canopy cover and species composition (Jachmann and Bell 1985, Smallie and 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. 2006b), 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 anti-herbivore defences, such as tannins (Kohi et al. 2010) or thorns (Gowda 1996, Stapley 1998). Because elephants mainly push over or snap large trees, there is a growing concern that this behaviour may have a negative effect on other herbivores (Ludwig et al. 2008) and hence negatively affect biodiversity. 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 browseable 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 browseable biomass.

Trees that are pushed over or snapped by elephants are frequently reported in savannah systems (Gadd 2002, Mapaure and Moe 2009). Some of these trees re-sprout strongly and others do not, depending on the species, age (Bond and Midgley 2001) and influence of other ecosystem drivers, such as drought, fire and nutrients in particular (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 and Croes 1991), although the numbers of killed trees are often not alarming (Shannon et al. 2008, Mapaure and 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 re-sprouting shoots, which yields a higher amount of browsed materials (Jachmann and 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), which is mainly due to the differences in the angle at which the tree leans over after being pushed over or uprooted as well as the height at which the tree is snapped (E. Kohi, pers. obs). Such complexity has the potential to amplify browse heterogeneity in African savannahs.

Browsing can enhance the nutrient contents of foods in terms of proteins and essential minerals (Jachmann and Bell 1985, Holdo 2003). Nutrient concentrations of P, Na, Mg and K are normally higher in young leaves than all other leaves (Jachmann and Bell 1985, McNaughton 1988b). 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 re-translocation 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 and McNaughton 2006); this may in turn attract browsing herbivores (Jachmann and Bell 1985, Makhabu and Skarpe 2006, Fornara and Du Toit 2007). Elephants target particular species and plant parts at different times of the year (Woolley et al. 2009) and are capable of selecting trees with a higher nutrient level (Pretorius 2009).

Besides responding by re-growth, trees may employ other strategies to avoid future herbivore activities, such as increasing secondary plant compounds (Cooper and Owen-Smith 1985). For example, pruning and pollarding in 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 concentrations (Kohi et al. 2010). The presence of high concentrations of secondary compounds (*e.g.*, condensed tannins) in forage materials is known to deter animals from further food intake (Provenza et al. 1990, Foley et al. 1999).

Therefore, in this study, we aimed to determine the extent to which elephant foraging behaviour increases the availability of browsed materials in terms of quantity and quality at the feeding heights of smaller herbivores. We hypothesise 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 re-growth 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 N concentrations, improves digestibility and generates higher mineral content (Na, P, K, Mg, and Ca) through lower condensed tannin concentrations.

METHODS

Study areas

The study site was located in the central section of the Kruger National Park (KNP) in the Phalaborwa, Mopani and Letaba sections between 31º9´43´´E – 23º56´20´´S; 31º24´59´´E - 23º31´38´´S and 31º34´36´´E - 23º51´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). It is generally agreed upon that 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 and Weil 2004) and can also store large amounts of anions, such as $NO_3^{\square}$ and $SO_4^{2\square}$, in the subsoil (Van Ranst et al. 1998). The study sites receive approximately 450 to 600 mm/y 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 savannah plant species, Mopane trees are known to withstand elephant utilisation and rarely die unless they are totally uprooted (Guy 1981).

Data Collection

Trees with stem diameters that were larger than 10 cm and were two to four seasons since initial damage were selected. Using Barnes (1983c) and Jachmann and Bell’s (1985) elephant utilisation were distinguished into four groups: (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 two weeks) and again in October (end of the dry season for two weeks) 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) (Fig. 1). 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 non-browsed 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 (Pellew 1983) (up to 5 m).

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 (Fig. 1) 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 (D > E) or a cylinder (when D = E) (Fig. 1). 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; Fig. 1). If the difference between the axes was larger than 0.92 m (the upper 95 % Confidence Limit of the mean absolute differences between the diameter 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

1) 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. 2).

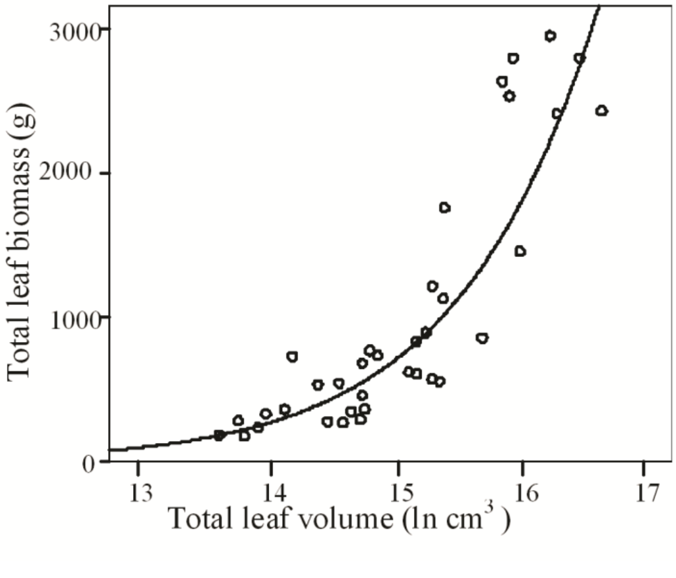

Figure 1. The relationship between leaf biomass (g) and the measured canopy volume (ln cm^3) of uprooted or pushed-over trees. The power equation gave the best fit ($Y = 9 \times 10^{-15} \times X^{14.358}$, R^2 = 0.82, N = 36).

1) $Ln(y) = -32.342 + 14.358Ln(x)$, $R^2 = 0.82$ - Uprooted/Pushed-over trees

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

2) $Ln(y) = -3.196 + 0.728x$, $R^2 = 0.95$ - Coppiced trees

3) $Ln(y) = -4.984 + 0.759x$, $R^2 = 0.92$ - Control trees

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 (total), P, K, Na, Ca and Mg were measured after digestion in a mixture of sulphuric acid (H_2SO_4), salicylic acid (H_2O_2) and selenium (Se) (Novozamsky et al. 1983). N and P were measured with a Skalar San-plus auto-analyser, and Na, K, Ca and Mg were measured with an atomic absorption spectrometer (Varian AA600 Analyser). The in-vitro digestibility (IVD) was analysed following the Tilley and Terry (1963) method in a Daisy incubator (ANKOM Technology). The condensed tannin concentrations (CT) were analysed according to the proanthocyanidin method after extraction in acetone (50 %) for 24 h (Waterman and Mole 1994).

Data Analysis

An analysis of variance (ANOVA) was used to analyse the effects of the elephant utilisation 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 utilisation level (Field 2009). The Games-Howell procedure was used to compare the biomass means for each browsing height across elephant utilisation levels to correct for the unequal sample sizes between different elephant utilisation levels (Field 2009).

For the tree structure analysis, an ANOVA was used to test for differences in mean canopy heights (H2) and lower leaf heights (H3) (dependent variables) with elephant utilisation categories (pushed-over, uprooted, snapped trees and control trees), soil types and seasons as independent variables. The Dunnet 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 utilisation categories (Quinn and Keough 2002, Field 2009). The Game-Howell procedure was used to compare mean lower leaf heights between the different categories (Field 2009). The green leaf percentages were arcsine-transformed prior to the ANOVA. Similarly, the Dunnet T3 test was used to compare the mean green leaf percentage with that of the control trees; thereafter, the Game – Howell procedure was used to compare the means among the elephants’ utilisation categories.

For the nutrients, CT and IVD analysed using ANOVA to test for differences in each utilisation category and its respective controls after an arcsine transformation had been carried out to normalise the data. Data that did not follow a normal distribution after the transformation were analysed using Mann-Whitney tests. An ANOVA was used to compare the means among the elephant utilisation groups following the Game-Howell procedure.

RESULTS

Leaf Biomass

The leaf biomass was significantly different among the different levels of elephant utilisation (ANOVA, $F_{3,\ 2820} = 660.205$, $P < 0.001$) and was higher in the wet season (Game-Howell, $P < 0.001$) and for basaltic soils (Game-Howell, $P < 0.001$). The leaf biomass allocation at different heights was significantly influenced by the elephant utilisation 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. 3). Among the utilised trees, pushed-over and uprooted trees had a higher leaf biomass than the snapped trees did at low heights (< 1 m) (Game-Howell, $P < 0.001$), with no difference between the 1-m and 1.5-m heights. However, the snapped trees had a significantly higher leaf biomass above 1.5 m than uprooted and pushed-over trees did (Game-Howell, $P < 0.001$). Generally, uprooted and pushed-over trees had a 60-fold higher leaf biomass than control trees below 1 m did, but above 2 m, the situation was reversed, and the factor decreased to 0.2 fold. Snapped trees had a 7-fold higher leaf biomass than control trees did below 1 m, but the ratio decreased to 0.5 fold above 2 m (Fig. 3). However, combining the three categories, leaf biomasses below 1 m were 30 fold larger for impacted trees than they were for the control trees.

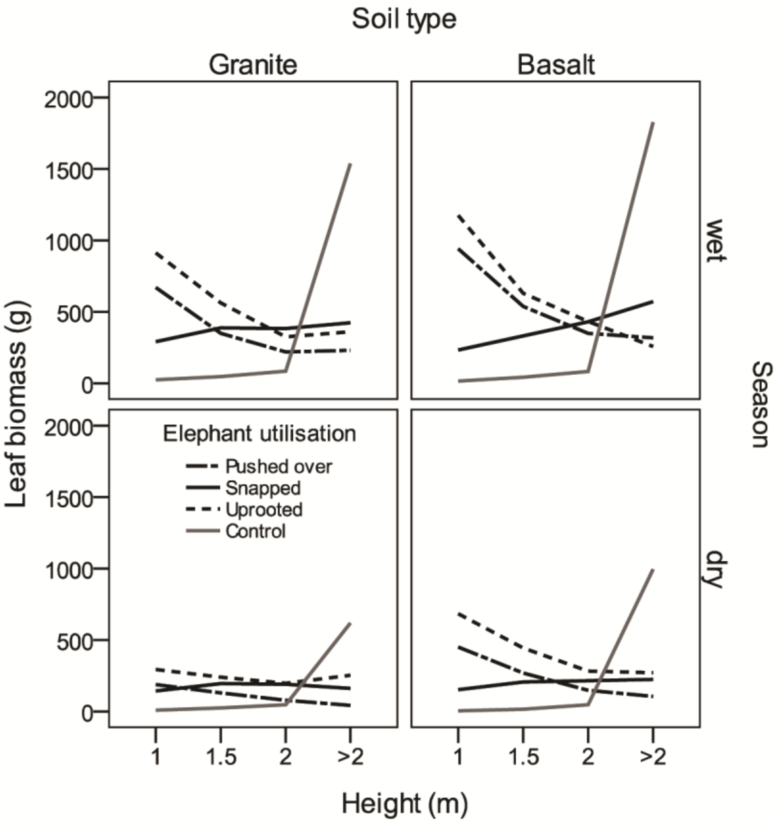

Figure 2. Total leaf biomass (g) against height (m) of trees from different elephant utilisation categories. The panels indicate different soil types and seasons in which the trees were measured.

Tree Canopy Height

Tree canopy heights were significantly affected by elephant utilisation 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).

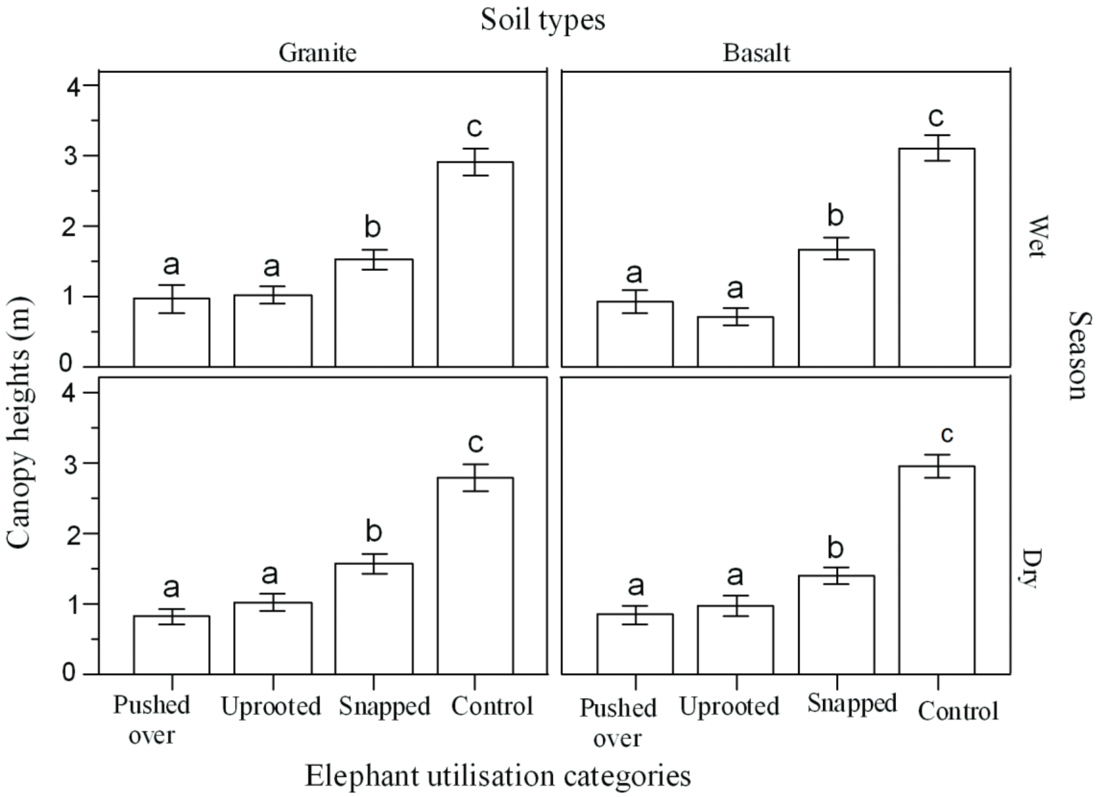

Figure 3. Mean canopy height (m ± 95% CI) against different categories of elephant utilisation. The panels indicate different soil types and seasons in which canopy height were measured. The letters indicate significant differences (Games-Howell, P<0.05)

The Lowest Leaf Height

As expected, the heights of the lowest leaves of elephant-utilised trees were significantly lower than those of the control trees (Kruskal Wallis, $n = 708$, Chi-square = 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 m and 1.3 m, respectively. However, among the elephant-utilised trees, the lower leaf heights were significantly higher on snapped trees than on pushed-over (Game-Howell, $P < 0.001$) and uprooted trees (Game-Howell, $P < 0.001$). Snapped trees, uprooted trees, and pushed-over trees had median lower leaf heights of 0.4 m, 0.2 m, and 0.2 m, respectively (Fig. 4).

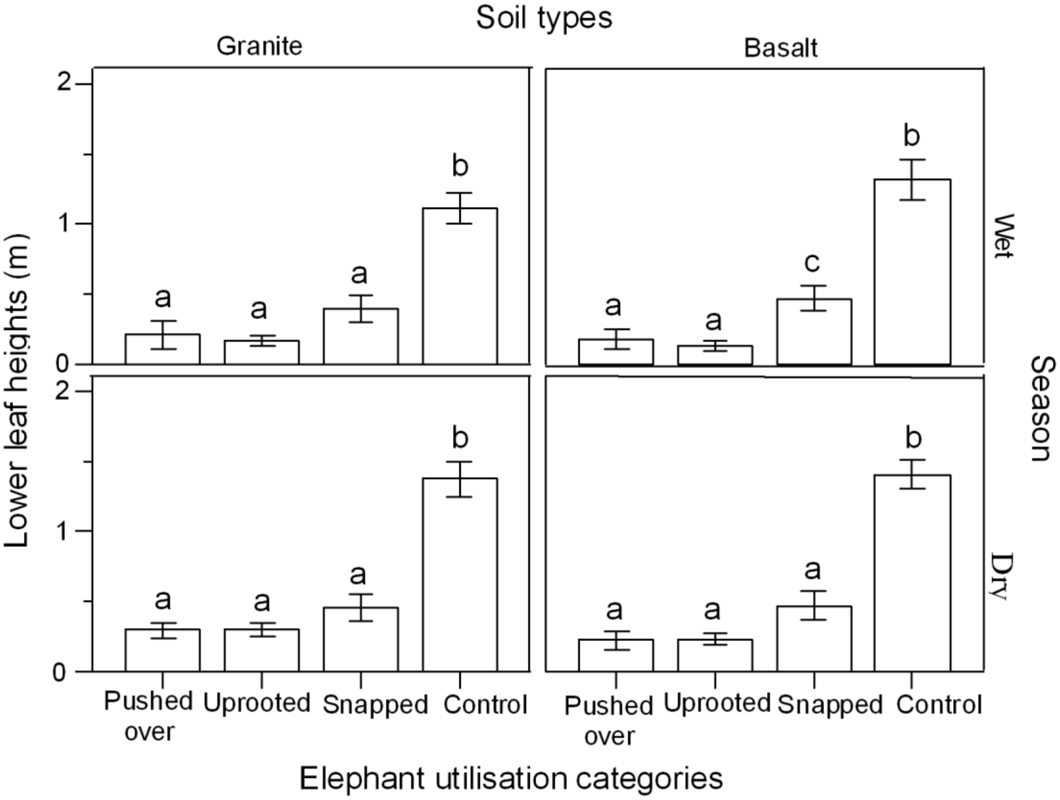

Figure 4. Lower leaf heights (m) against different categories of elephant utilization. The panels indicate soil types and seasons in which lower leaf heights were measured. The letters indicate significant differences (Games-Howell, P<0.05)

Green Leaf Availability

The availability of green leaves on Mopane trees differed among the four elephant utilisation 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-utilised trees had a higher percentage of green leaves than the control trees did, especially on the granitic soils (Fig. 6). 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 utilisation (Games-Howell, $P > 0.05$).

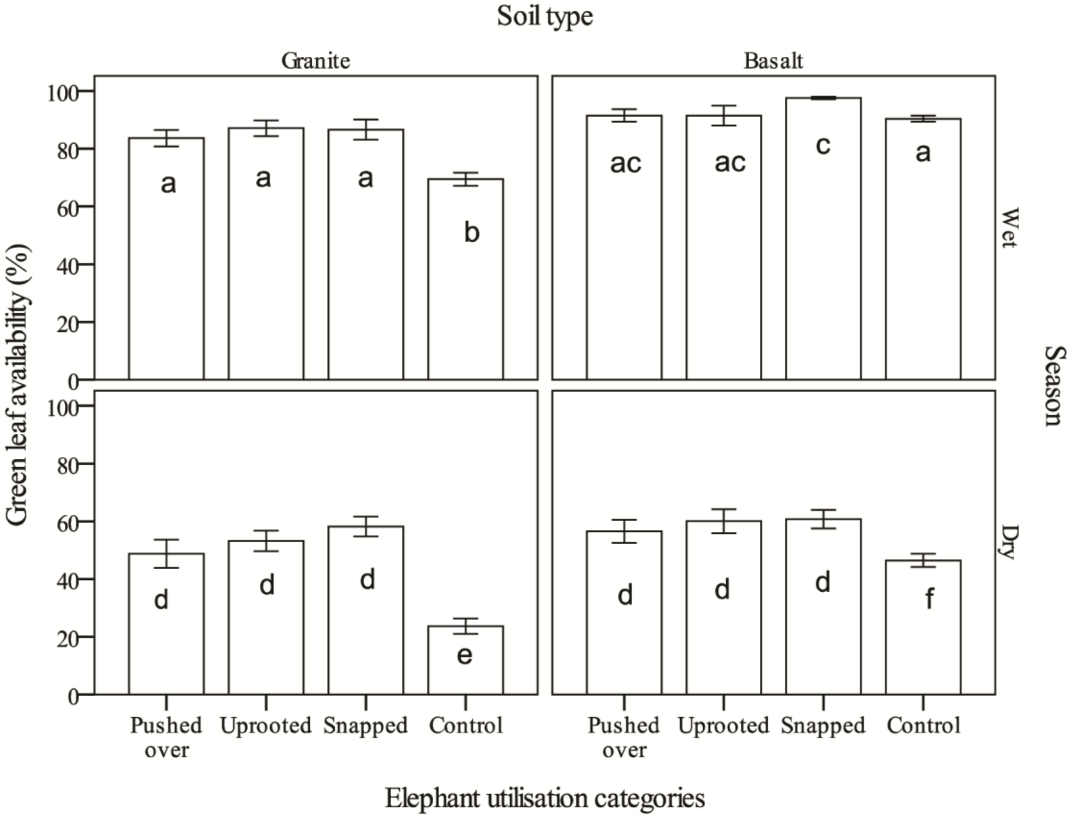

Figure 5. The mean percentage of green leaves (± 95% CI) for different categories of elephant utilisation. The panels indicate soil types and seasons in which the leaves were measured. Control trees had a significantly lower percentage of green leaves than pushed-over, uprooted and snapped trees did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

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 N concentration of the leaves in all three utilisation categories was lower in the dry season than in the wet season (Fig. 6).

Mineral Elements

For mineral nutrients, calcium (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).

Condensed Tannins

Condensed tannin concentrations were significantly higher in all of the elephant-utilised trees (Table 1). The CT concentrations increased substantially in trees that were utilised by elephants (Dunnet 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.

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 utilisation categories with their respective control trees. For each category, one-way 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 utilisation	*Nutrient*	*Treatment Mean conc.*	*Control Mean conc.*	*Test*	*Test value*	*P*	*Sig. 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	+

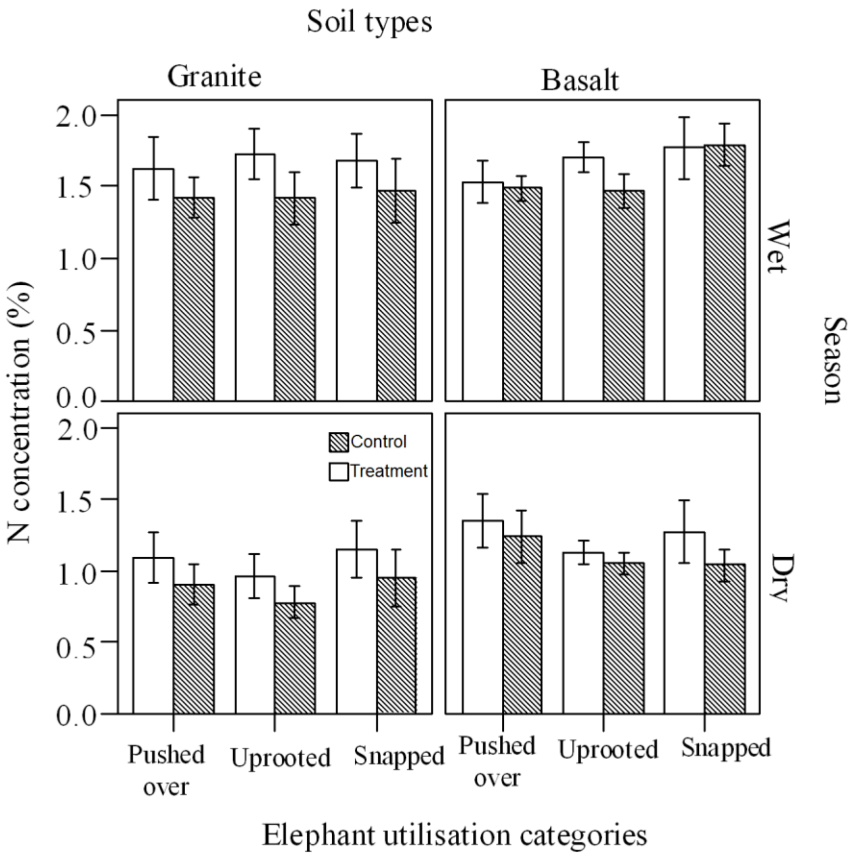

Figure 6. Mean N concentrations (% ± 95% CI) for different categories of elephant utilisation. The panels indicate soil types and seasons. The overlapping error bars are not significant different. (Games-Howell, P<0.05).

Digestibility

In-vitro digestibility (IVD) was not affected by elephants' utilisation 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 utilised trees, snapped trees (Game-Howell, $P < 0.01$) and uprooted trees (Game-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).

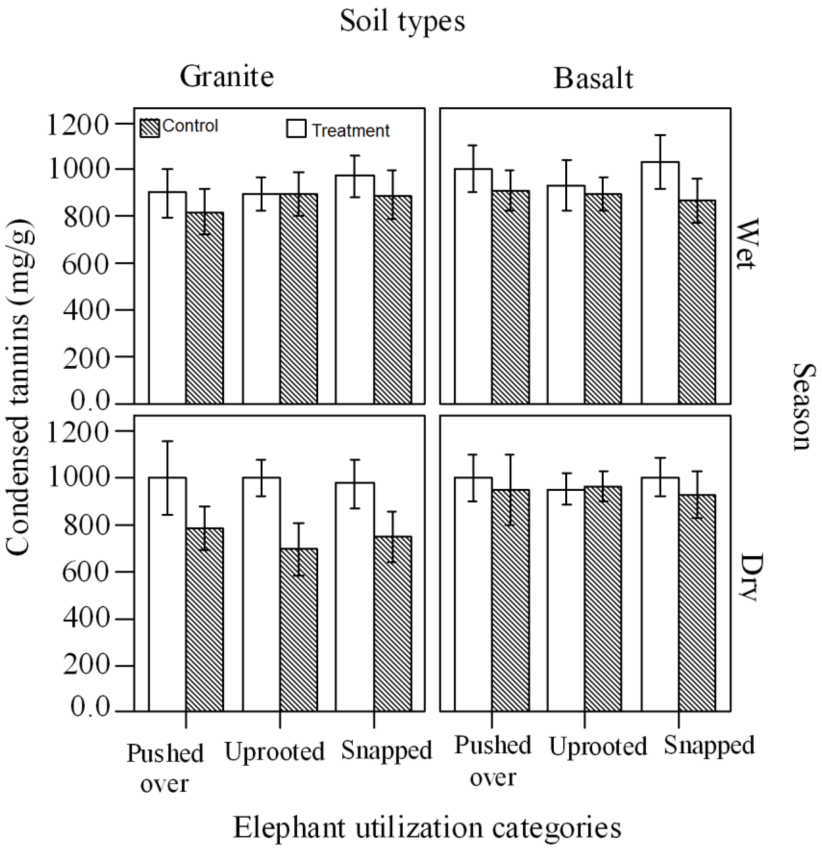

Figure 7. Mean condensed tannin concentrations (mg/g ± 95% CI) of leaves from different elephant utilisation categories. The panels indicate soil types and seasons. The letters indicate significant differences (Games-Howell, P<0.05)

DISCUSSION

As the number of elephants increases, their roles in ecosystem engineering become pivotal for not only increased forage availability but also habitat complexity that is advantageous to other organisms (Arsenault and 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 seven fold when compared to intact trees. There is more evidence of forage facilitation by mega-herbivores for small herbivores in grazing systems (Barnes 1983 , Arsenault and 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 & Owen-Smith (2002) suggested that 'feeding facilitation arises mainly during the growing season, when grazing by larger species may stimulate vegetation re-growth.' 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 utilisation 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-utilised 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 re-sprouted leaves. In general, browsing pressure changes the foliar N content (Jachmann and Bell 1985, Bergström 1992) and CT concentration (Wessels et al. 2007), 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 utilised 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 *Acacia nigrescens* in African savannahs (Fornara and 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 and Ojeda 2009) and high root-to-shoot ratios in browsed trees (Skarpe and 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 condensed tannin concentration (Foley et al. 1999). Our findings also show that elephant utilisation 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 fibre (Jachmann 1989, Foley et al. 1999, Getachew et al. 2008). However, 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 (Kohi, per. observation) that nearly all turned yellow at the end of the dry season. However, trees that were utilised by elephants maintained their green leaves for longer during the dry season (Fig. 6). Our findings with regard to mineral nutrients were similar to those of Holdo (2003) for elephant-utilised trees in Mopane woodlands. The mineral nutrient concentrations of elephant-utilised 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 utilisation categories were above the nutrient requirements of the elephants, as reviewed by Rode *et al.* (2006). This finding suggests that elephant utilisation improves browse quality in terms of increased N content.

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 and Landman 2006) and food availability, which results in the generation of suitable habitats for a variety of other organisms (Rutina et al. 2005, Kerley and 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 and Bell 1985, Smallie and O'Connor 2000, Styles and 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.

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 utilised 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 savannah 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.

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CHAPTER 3

Leaf compensatory growth of Mopane trees to simulated browsing

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Submitted OIKOS

ABSTRACT

Understanding the responses of trees after they have been browsed is an important aspect of herbivore ecology. Browsed trees by elephants have been reported to have leaf availability in the dry season when food resources are limited. While browsing intensity and frequency influence plant response, it is not clear yet how the extent and timing of browsing during the wet and the dry season improve the availability of forage to browsers particularly in the dry season. In a defoliation experiment conducted in Kruger National Park, South Africa, we varied the timing of simulated browsing (February, May and July 2007) at different browsing intensities (%) i.e., 25, 50, 75, and 100 to understand the responses of the trees in terms of leaf production over time. A total of 384 trees were defoliated. The leaves were collected during the wet and dry season. The results indicate that the timing of the initial browsing affected the food scarcity period by prolonging leaf availability in the dry season and initiating early leaf flush at the end of dry season. Trees that were defoliated in the dry season had high leaf biomass in the subsequent growing season and also extended their leaf availability in the subsequent dry season. The defoliated trees compensated for the leaf biomass in the same way regardless of the defoliation intensity and season. This suggests that heavy browsing is beneficial for browsers particularly in the dry season. These results contribute to better understanding the mechanisms of facilitation in plant-herbivore interactions.

Keywords: Defoliation intensity; leaf biomass; browse; timing; food scarcity; elephant

INTRODUCTION

Browsing by large herbivores has long been considered one of the main factors causing the suppression of woody vegetation in boreal (Edenius et al. 2002), temperate (Senn and Suter 2003) and tropical regions (Barnes 1983a, Mapaure and Mhlanga 1998) alike, preventing tree recruitment (Dublin et al. 1990, Nyengera and Sebata 2010) and possibly reducing plant species richness (Landman et al. 2008). In tropical regions, the conservation of elephants in particular are a cause of concern (Owen-Smith et al. 2006, van Aarde et al. 2006) due to their ability in changing vegetation structure (Ben-Shahar 1996a). However, in the Mopane woodland, one of the largest southern African biomes (Timberlake 1996) and one that is heavily browsed by elephants (Ben-Shahar 1996a), it is reported that browsing actually stimulates trees to prolong leaf availability during the dry season; it is also considered to be responsible for the early leaf flush on Mopane trees (Smallie and O'Connor 2000, Styles and Skinner 2000). The mechanisms behind the two main processes, i.e., prolonged leaf availability and early leaf flush, in relation to elephant browsing are not clearly understood.

Studies in herbivore ecology relate the trees' responses following browsing to its intensity and timing (Ouellet et al. 1994, Hobbs 1996, Stewart et al. 2006). Herbivory reduces the leaf surface area of a plant, which in turn reduces the photosynthetic rate (Raimondo et al. 2003). Therefore, certain browsed trees increase their leaf numbers and initiate a rapid expansion of leaves, increasing the leaves' photosynthetic area (Cerasoli et al. 2004) to compensate for the lost tissue and shift the photosynthate allocation to the apical region for regrowth (Prins et al. 1980, Bassman and Dickmann 1982). The increase in the amount of regrowth is linked to the browsing intensity (Prins et al. 1980, Belsky 1986a, Hobbs 1996, Rutina et al. 2005). The optimisation hypothesis predicts that biomass production follows a unimodal curve, with increasing browsing pressure reaching a maximum level during the intermediate browsing phase (McNaughton 1979, Prins et al. 1980, Stewart et al. 2006). Because elephants exhibit site fidelity (De Knegt et al. 2010a) and are bulk feeders, they can cause considerable browsing pressure on trees at their feeding sites (Calenge et al. 2002). The large home range of elephants (Shannon et al. 2006a) may thus be part of an evolved feeding strategy that allows trees to recover between visitations. Hence, the trees' responses in the form of leaf production and growth will differ among trees that are browsed at different feeding time intervals (Prins et al. 1980, Prins 1996). Hence, browsing events with a small time interval might not lead to large regrowth, whereas browsing events with a large time interval might allow competitors to forage. On the other hand, tree recovery from herbivory exhibits a time lag in mobilising resources (e.g., stored Carbon reserves) to initiate leaf production and soil moisture to allow nutrient uptake (Milla et al. 2005, Nord and Lynch 2009). Consequently, leaf growth and maturation may differ as a result of differences in the initiation of herbivory and the amount of time remaining in the growing season (Maschinski and Whitham 1989). The time lag between revisitations and tree recovery may be linked to prolonged leaf availability and early leaf flush during the dry season.

Animals may have adjusted their feeding strategies according to the time lag of tree recovery to ensure maximum food availability, especially during the dry season, when food is scarce by visiting areas where there is prolonged leaf retention and areas with an earlier leaf flush. Such an adjustment is not unheard of in animal behavioural science. For example, buffalo (Prins 1996), gorillas (Watts 1998) and birds (Henderson et al. 2006, Feeney et al. 2009) have been reported to revisit previous foraging sites, and estimate the time lag necessary for vegetation recovery (i.e., the revisitation interval) before making a second visit.

This paper focuses on understanding the timing and intensity of browsing, to prolong the availability of green leaves during the dry season, when food is scarce. We tested the following hypotheses: (1) An increase in defoliation intensity will increase leaf biomass compensation following a unimodal relation; (2) an increase in defoliation intensity in the growing season will prolong leaf availability in the dry season; (3) leaf biomass compensation will increase with early timing of the defoliation event.

METHODS

Study area

The experiment was conducted in the Mopani area of Kruger National Park, South Africa, (31º24´59´´E and 23º31´38´´S) on basaltic soils. The long-term average annual rainfall is 450–600 mm, with most of the rain falling between November and April (Venter et al. 2003). The defoliation experiment was conducted in the “Capricorn enclosure”, which was erected in 2002, with an area of 500 ha. The area was fenced to exclude all animals that are larger than hares. Only roan *Hippotragus equinus* and tsessebe *Damaliscus lunatus* occur inside the enclosure for breeding purposes; both are pure grazers. The experiment was carried out only in the middle block of the southern part of the enclosure because no fires have been reported in this block since the erection of the fence.

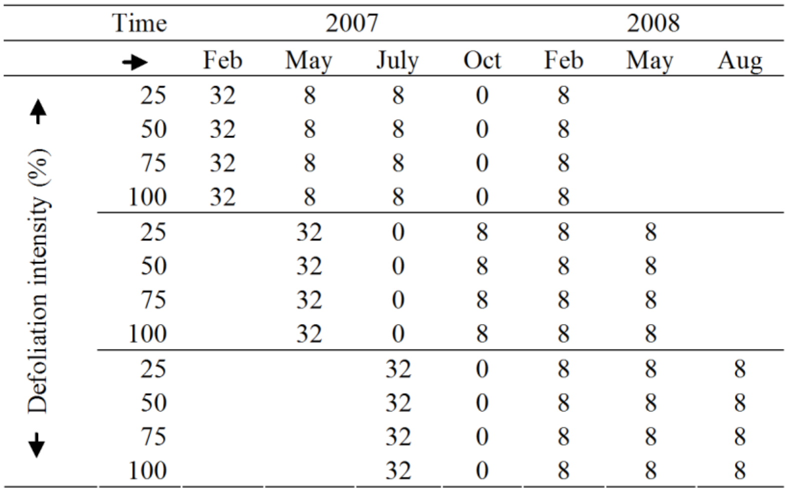
Simulated browsing by hand defoliation

Browsing was simulated by means of manual defoliation in which leaves were pulled off from shoots, similar to the way elephants use their trunks when browsing. The experiment was carried out on Mopane trees *Colophospermum mopane*, which within the distribution area of this species is a staple food of elephants (Ben-Shahar 1996a). The first initial defoliation was performed during the growing season in February 2007. At this time, all of the trees had fully-grown leaves. The second initial defoliation with a new set of trees was conducted in May 2007 at the end of the growing season. At this time, there was very little rainfall, but soil moisture was still available in the upper soil layer as evidenced by the fact that the grasses were still green. This was defined as late defoliation in the growing season. The final initial defoliation of a third set of trees was done in July 2007 in the dry season. The trees that were selected for defoliation were 1.75 ± 0.56 m (95 % CI) tall, with a mean stem diameter of 34 ± 2 mm (95 % CI, N = 384). The trees were defoliated in four categories of defoliation intensities; namely, 25 %, 50 %, 75%, or 100 % of all of the leaves on the trees were removed, except for the control trees (0 %). Each tree was tagged with an aluminium tag bearing a unique code. All of the defoliated branches were marked with binding wire to facilitate later identification. The trees were defoliated again according to the schedules presented in Table 1.

All of the harvested leaves were stored in paper bags, and air-dried. Subsequently, the leaves were oven-dried at 70^0C for 48 h and biomass was weighed at the SAEON laboratory in Phalaborwa, South Africa. After air-drying, twenty fully-grown leaves were selected from each tree and scanned with a scanner (HP Scanjet 3800) at a resolution of 300 dpi. On each scanned image, a reference square with an area of 4.0 cm^2 was scanned together with the leaves. Thereafter, the leaf surface area (cm^2) was calculated using

ArcGIS (ArcMap 9.3.1, ESRI Inc., Redlands, CA) based on the scanned reference square. The Specific Leaf Area (SLA) was calculated as the total leaf surface area per unit of oven-dried leaf weight (Ray et al. 2004). Leaf area was used as a proxy for photosynthetic rate (Raimondo et al. 2003). A high SLA means that the leaf has low weight in relation to its surface area (Skarpe and van der Wal 2002), which is an indication that the leaf has not matured (Cerasoli et al. 2004, Kruger and Volin 2006).

Table 1: The number of trees used in the defoliation experiments (initial numbers in bold) over the three periods of the year (middle wet = February 2007, late wet = May 2007 and dry season = July 2007). After the initial defoliation, eight trees were sampled from each treatment in each subsequent period. Each tree was harvested once. The zero values in the table indicate that there were no leaves on the tree to harvest because either the tree did not re-sprout or all of the leaves were dead.



	Time	2007				2008		
	→	Feb	May	July	Oct	Feb	May	Aug
↑ Defoliation intensity (%) ↓	25	32	8	8	0	8		
	50	32	8	8	0	8		
	75	32	8	8	0	8		
	100	32	8	8	0	8		
	25		32	0	8	8	8	
	50		32	0	8	8	8	
	75		32	0	8	8	8	
	100		32	0	8	8	8	
	25			32	0	8	8	8
	50			32	0	8	8	8
	75			32	0	8	8	8
	100			32	0	8	8	8

Leaf biomass compensation

Leaf biomass compensations of the resprouted trees were calculated based on the weights (g) of the initial defoliated leaves (x_i) plus the leaves harvested at the end of the experiment (x_f) and the control leaves (x_c).

$$C = \frac{x_i + x_f - x_c}{x_c} * 100$$

where C is the leaf biomass compensation (Belsky 1986a, Guillet and Bergstrom 2006). If the calculated value is 100% then is exact compensation, below 100% is under compensation and above 100% is over compensation.

Analysis

A general linear model was used to test the differences between defoliation intensities, the timing of defoliation (February 2007, May 2007 and July 2007) and the time interval between the defoliation events (see Table 1). The dependent variables were transformed to obtain normal distributions of the residuals. The SLA was log-transformed, and a double square root transformation was used for the leaf biomass compensation. For significant results from the independent variables or interactions, a post-hoc Tukey test was used for further analysis, and when the sample sizes were not equal, the Game-Howell test was used (Field 2009).

RESULTS

Leaf biomass compensation

All of the defoliated trees compensated their leaf biomass in the same way regardless of the defoliation intensity in each re-visitation time (Fig. 1). Therefore, we rejected our first hypothesis that when increasing the defoliation intensity, the leaf biomass compensation would exhibit a unimodal pattern.

The timing of the initial defoliation affected the leaf biomass compensation ($F_{2, 269} = 91.13$, $P < 0.001$).Trees that were defoliated early in the growing season (February 2007) compensated for less defoliated leaf biomass in comparison to trees that were defoliated late in the growing season (May 2007) and in the dry season (July 2007) (Fig. 2, Game-Howell, $P < 0.001$). The leaf biomass compensations for trees that were defoliated at the end of the growing season and at the beginning of the dry season did not differ (Fig. 2).

When the data were analysed separately according to the timing of the initial defoliation, the time interval between the initial defoliation and subsequent harvesting events influenced the leaf biomass compensation ($F_{8, 245} = 146.95$, $P < 0.001$). For trees that were initially defoliated early in the growing season (February 2007), the leaf biomass compensation increased as the time interval between harvesting events increased (Fig. 3).Trees that were harvested in the dry season in July 2007 (six months after the initial defoliation) did not differ in leaf biomass compensation from those that were harvested in the late growing season in May 2007 (three months after the initial defoliation), even though they showed an increasing trend over time. Trees that were harvested in February 2008 showed higher leaf biomass compensation than trees that were harvested in May 2007 and July 2007 (Game-Howell, $P < 0.01$, Fig. 3). The increasing trend in leaf biomass compensation in the dry season, i.e., from May 2007 to

July 2007, indicates that the leaves' growth rate increased, which was also shown by the decreases in the specific leaf area (SLA) from May 2007 to July 2007 (Game-Howell, P < 0.01; Fig. 4).

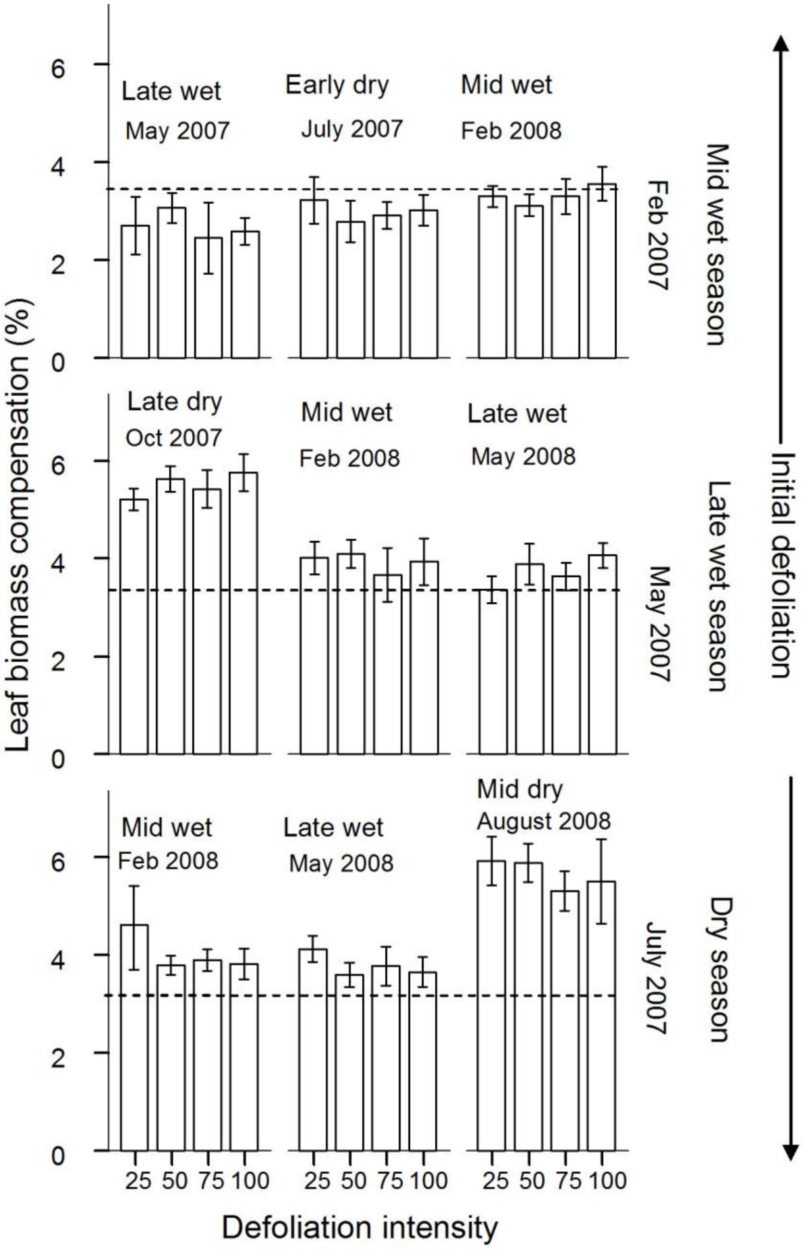


Figure 1. Mean leaf biomass compensation (%) for the different defoliation intensity at different timings of initial defoliation and re-visitation time. The broken lines indicate the exact compensation of amount of leaf biomass defoliated (100% ~ 3.5 of double square root transformed value); marks below the lines indicate under-compensation, and marks above the lines represent over-compensation. The overlapping bars of leaf biomass depicting the 95% CIs do not differ significantly within each sampling period.

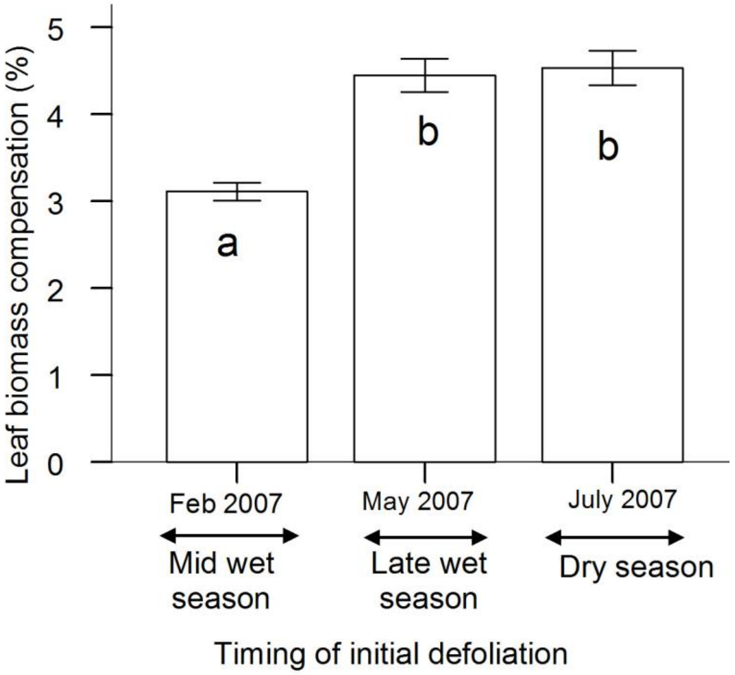


Figure 2. The mean leaf biomass compensation (%, double square root transformed value) for the different timing of the initial defoliation. Different letters indicate significant differences according to the Game-Howell test ($P < 0.01$).

In addition, we examined the trees that were initially defoliated late in the growing season in May 2007. For the first three months, i.e., until July 2007, in the dry season, there were no leaves to harvest because the trees did not respond after defoliation. Only a few buds were observed. In the late dry season in October 2007 (six months after the initial defoliation), all of the defoliated trees showed a high response rate for the early leaf flush that resulted in over-compensation for defoliated leaf biomass. The early leaf flush exhibited significantly higher leaf biomass compensation in these trees than in trees that were defoliated later in February 2008 (nine months after the initial defoliation) or in May 2008 (one year after the initial defoliation) (Tukey, $P < 0.01$; Fig. 3).

Finally, we considered trees that were initially defoliated in the dry season (July 2007). In the late dry season, i.e., October 2007 (three months after the initial defoliation), defoliated trees had buds only; therefore, we could not collect leaves (pers. obs). In the subsequent growing season, in the middle of the wet season (February 2007) and late wet season (May 2008), the leaf biomass compensations did not differ (Fig. 3). However, in the dry season (August 2008), defoliated trees had significantly increased their leaf biomass compensation when compared to trees that were harvested in May 2008 and February 2008 (Game-Howell, $P < 0.01$; Fig. 3).The increase in the leaf biomass compensation in the dry season suggests that the control trees had a sharp decrease in their leaf biomass in the dry season, while defoliated trees maintained their leaves.

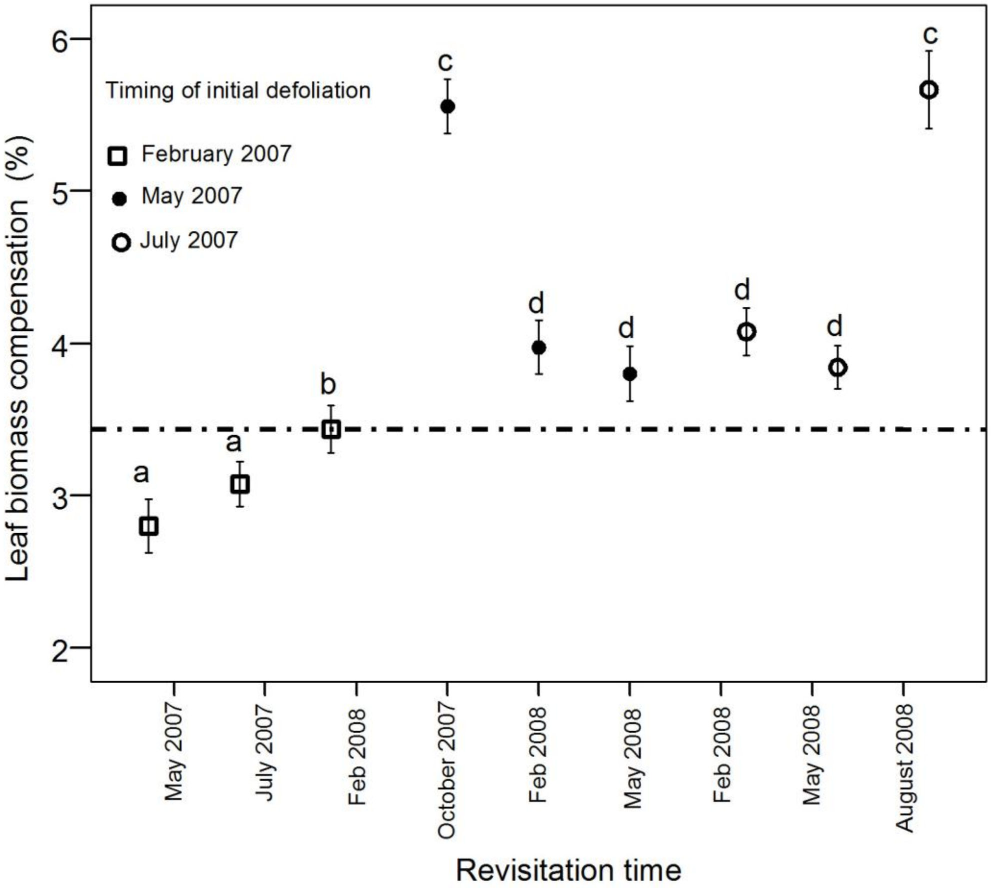


Figure 3. Leaf biomass compensation (%, double square root transformed value) for the different time intervals between the defoliation events. The letters illustrate significant differences (Game-Howell test, $P < 0.01$). The broken lines indicate the exact compensation of amount of leaf biomass defoliated (100% ~ 3.5 of double square root transformed value); marks below the lines indicate under-compensation, and marks above the lines represent over-compensation.

Specific Leaf Area

The timing of defoliation ($F_{2,\ 556} = 16.325$, $P < 0.01$) affected the specific leaf areas of trees that were defoliated at the end of the growing season (May 2007) in comparison to those defoliated earlier in the growing season (February 2007) and early in the dry season (July 2007; Game-Howell, $P < 0.01$, Fig. 4). In addition, earlier leaf harvesting event resulted in higher SLA for all occasions ($P < 0.01$) (Fig. 4).

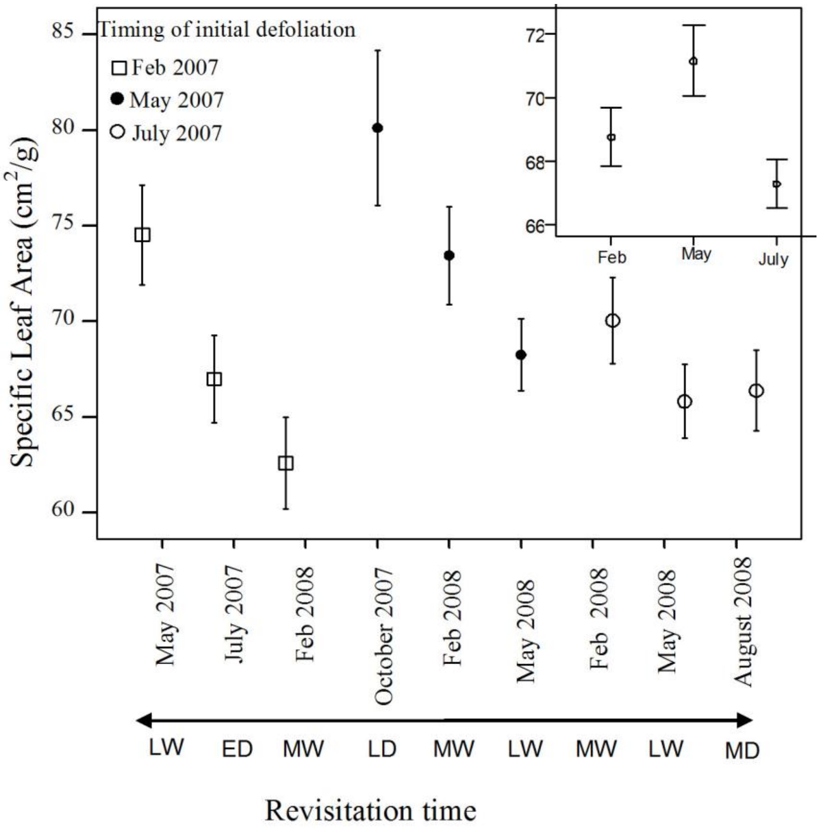


Figure 4. The mean specific leaf area (SLA) for different revisitation time. The inset graph shows the mean SLA (y-axis) in relation to the timing of the initial defoliation (x-axis) in 2007. Different letters indicate significant differences (Game-Howell, $P < 0.01$). MW = mid-wet season, LW = late wet season, ED = early dry season, MD = mid-dry season, and LD = late dry season.

DISCUSSION

So far, theory on facilitation in plant-herbivore interactions is emerging in ecology (Van de Koppel and Prins 1998, Arsenault and Owen-Smith 2002, van Langevelde et al. 2008). Facilitation due to browsing; particularly when and how much to browse to prolong the availability of green leaves in the dry season, has however received little attention (Styles and Skinner 1997). Insight in the mechanisms of this facilitation is crucial for understanding animal movements and distributions. Animal migration in times of food scarcity is a well-known phenomenon in animal behavioural science (Fryxell and Sinclair 1988, Wright et al. 2010). Some animals (e.g., elephants and impala) instead of migrating adjusted by switching their diets from grazing to browsing to overcome the forage scarcity constraint (Beekman and Prins 1989, Kos and Hoetmer 2006). Our results show that early browsing during the growing season (February 2007), regardless of browsing intensity, sustained leaf availability longer in the dry season, while late browsing in the growing season (May 2007) stimulated the early leaf flush at the end of the dry season (Plate 1).

Plate 1. This photo was taken outside of the experimental plot on 28 October 2007; it shows the early flush of Mopane trees previously browsed by an elephant. The flush reflects our results, wherein the period of food scarcity is shortened by an early flush from browsed trees. The tree in front showing bursting buds was also browsed. Photo credit: E. M. Kohi.

These disparate mechanisms of shortening the dry season forage scarcity employ forward (prolong) and backward (early flush) effects, respectively. While the trees defoliated in the dry season had only bursting buds in October 2007, they may have had fully opened leaves only two weeks later (ca. early November), which could have increased forage availability. Browsed trees have been shown to sustain green leaves longer in the dry season (Styles and Skinner 2000, Rutina et al. 2005), a phenomenon that may be an adaptation of browsing animals to time the initiation of browsing to ensure the availability of food in the dry season. This pattern is not new in animal behaviour science. For example, birds feeding on nectar have been shown to time the emptying of the nectar from the flowers to a particular interval that triggers the plant to refill the flowers (Gill 1988, Henderson et al. 2006). Elephants are also known to revisit previously visited sites (De Knegt et al. 2010a); their behaviour might have been adapted to the time needed for the new regrowth. We showed that short revisitation between feeding interval provides younger regrowth (as demonstrated by a high SLA) (Veneklaas et al. 2002, Kruger and Volin 2006), while a long revisitation interval yields a large amount of leaf biomass; with the exception of the early leaf flush (in October 2007).

For compensatory production to occur, plants have to overcome physiological constraints and environmental stress (Maschinski and Whitham 1989, Nord and Lynch 2009). When trees are defoliated in the dormant period, their leaves are normally already old, and the photo-assimilates have been transported from the leaves to the buds (Milla et al. 2005). Earlier defoliation could deprive the plants of these photo-assimilates (Tuomi et al. 1989). Without this early defoliation, the reserved resources will be available for earlier flush under late defoliation (Tuomi et al. 1989, Milla et al. 2005). This explains why the trees that were defoliated at the end of the growing season (May 2007) had significantly larger flush at the end of the dry season (October 2007) versus trees defoliated at other times of year.

Defoliation intensity did not affect the compensatory response of leaf production. Our result does not support our initial prediction that foliar biomass compensation would follow a unimodal relation with increasing defoliation intensity (McNaughton 1979, Stewart et al. 2006). Field studies have reported an increase in the availability of leaf biomass in heavily browsed trees in the dry season (Jachmann and Croes 1991, Styles and Skinner 1997, Smallie and O'Connor 2000, Rutina et al. 2005). Because, in our study, no compensatory differences between defoliation intensities were observed, this means that a constant proportion of the amount of leaves that were removed was replaced. Hence, heavy browsing induced a higher biomass production tan light browsing. These results confirm findings from other field studies (Ydenberg and Prins 1981, Styles and Skinner 2000, Rutina et al. 2005, Fornara and Du Toit 2007) stating that heavy browsing increases browsing availability more than light browsing does.

While trees defoliated during the dormant period had overcompensated for the defoliated leaf biomass after one year in our study, Scogings et al. (2005) found no effect of defoliation on the availability of browseable shoots one year later when *Acacia karroo* was defoliated during the dormant period. Similarly, in an arboreal forest, the total biomass of the clipped birch (*Betula pendula*) did not differ between the clipping treatment and control samples (Hester et al. 2004). Possible explanations for this difference include the unit of measurement that is used and the studied plant species. We used Mopane, which is a browse-tolerant species. In the present study, we measured absolute leaf weight, while in prior studies; browseable shoot values and the total biomass of the shoot were measured. In most savanna trees, leaf mass varies between ca.

5% (Pretorius 2009) and ca. 8% (Bergström 1992) of the total twig mass, which could reduce or inflate the leaf weight.

Forage quantity and availability are among the factors that influence herbivore choices at a small spatial scale (Bailey et al. 1996, Iason et al. 1996, Pretorius et al. 2009), and revisiting a patch can be influenced by either previous knowledge about the patch or the attractiveness of the patch (Searle and Shipley 2008). Because browsing stimulates the production of new shoots and leaves (Hester et al. 2004, Fornara and Du Toit 2007), it also creates attractive patches (so called browsing lawns) that can easily be revisited. For example, kudu and impala were observed spending more time browsing in patches with higher shoot abundance than in those with fewer shoots (Makhabu et al. 2006).

The response of trees to browsing has a major implication for the management of browsers' populations in protected areas. Trees that are tolerant to browsing are important in times of food scarcity (Styles and Skinner 2000). Mopane woodland in our study supports large herds of elephants (Ben-Shahar 1996a, Makhabu et al. 2006), elands and kudu (Styles and Skinner 2000) in times of food scarcity that are thought to have negative impacts on the woodland due to heavy browsing (Guldemond and Van Aarde 2008). Our result, however, suggests that the congregation of elephants in the Mopane woodlands during the dry season may have a long-term facilitative effect on increasing browsing availability in the subsequent growing season and may even extend the effect to the following dry season, thereby shortening the food scarcity period (Fig. 4).

The long-term effects of this facilitative mechanism for tree survival and recruitment are crucial for maintaining suitable habitat. Resistant species to browsing such as Mopane might actually redistribute forage availability over time rather than reduce it (Kohi et al. 2011) and the majority of trees resprout successfully after heavy browsing. Also, we cannot ignore the fact that, when heavy browsing coincides with an extended dry season, the system may collapse, as appears to have been the case for Tsavo National Park in Kenya in the early 1970s as reported by (Myers 1973).

In conclusion, the timing of defoliation played a major role in stimulating leaf productivity and shortening the duration of food scarcity, while the time interval between the browsing events defined how much biomass would be available. Hence, revisiting a patch at the correct time seems pivotal for the survival of browsing herbivores, especially during stressful periods. The timing of browsing in the growing season will prolong the lifespan of photosynthetic leaves during the dry season, while late defoliation will stimulate earlier flush as compared to non-browsed trees, thus shortening the duration of forage scarcity during the dry season. These results contribute to better understanding the mechanisms of facilitation in plant-herbivore interactions.

ACKNOWLEDGEMENTS

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CHAPTER 4

Timing of browsing amplifies browse quality in the dry season

Edward M. Kohi, Willem F. de Boer, Herbert H. T. Prins

ABSTRACT

Trees that are browsed by African elephant (*Loxodonta africana*) are observed to maintain green leaves with improved quality longer in the dry season relative to non-browsed trees, thereby shortening the period of nutrient shortage. However, knowledge about specific herbivore behaviours or strategies that shorten this bottleneck period is lacking. We investigated how the timing and intensity of browsing influence forage quality in an African savanna. A defoliation experiment was conducted in the Kruger National Park, South Africa, wherein Mopane trees were defoliated by hand, simulating different extents of browsing and revisitation intervals. The first defoliation was conducted in February 2007 (early growing season), then in May 2007 (late growing season) and July 2007 (early dry season). Five defoliation intensity categories were applied: 0 %, 25 %, 50 %, 75 %, and 100 %. Leaf samples were collected three times during the year after the initial defoliation. Nutrient concentrations (N, P, K, Ca, and Mg), fibre and condensed tannins content, and digestibility were analysed. The results indicate that the timing of initial browsing can significantly improve forage quality in the dry season in two ways. First, the early defoliated trees showed delayed leaf senescence, resulting in higher nutrient concentrations as compared to the control trees. Second, the trees defoliated later in the growing season had an early leaf flush in October (late dry season), with leaves with higher nitrogen content, improved digestibility and a lower fibre content (NDF) relative to the control trees. Calcium and phosphorus concentrations decreased in the defoliated trees. Hence, the timing of browsing has important repercussions for large herbivores because it affects forage quality positively in times of nutritional stress. With this finding, this study contributes to the emerging theory of facilitation by animals and the mechanisms driving this facilitation.

INTRODUCTION

The impacts of elephant on vegetation have been well documented (Barnes 1982, 1983b, Mtui and Owen-Smith 2006). Although elephants can largely damage trees (Caughley 1976, Barnes 1983b, Calenge et al. 2002, Jacobs and Biggs 2002, Druce et al. 2008), increasing evidence of the facilitative role of elephants has been documented for various taxa, from insects (Kerley et al. 2008, Banks et al. 2010), amphibians (Campos-Arceiz 2009) and reptiles (Pringle 2008) to large mammals (Rutina et al. 2005, Makhabu et al. 2006). Yet less emphasis has been placed on what determines the elephant' facilitative effect on increasing the availability of higher quality forage, particularly in the dry season. Browsed trees, especially those browsed by elephant, have been reported to have better forage quality in the dry season (Styles and Skinner 1997, Smallie and O'Connor 2000, Styles and Skinner 2000). In addition, early leaf flush with high-quality forage in the late dry season has also been linked to elephant browsing (Styles and Skinner 1997, Holdo 2003). The late dry season is considered as the nutritional bottleneck period that can lead animals to become emaciated or die (Karasov 1989, Moss 2001). For example, Greater kudu *Tragelaphus strepsiceros* (Van der Waal and Smit 2001) and African elephant (Dudley et al. 2001) mortality has been correlated with nutritional stress in the dry season. The availability of high-quality forage during such a period is essential for the survival of many herbivores through the dry season. However, knowledge is lacking on how the timing of browsing, browsing intensity and time of revisitation influence forage quality during the nutritional bottleneck period.

The quality of forage decreases from wet season to dry season (Chapin 1980, Prins 1988, Karasov 1989, Prins and Beekman 1989, Owen-Smith 1997). Herbivores have evolved various strategies for overcoming low-quality forage through adjusting their habitat selection (Heitkönig and Owen-Smith 1998), changing their diet (Beekman and Prins 1989, De Boer et al. 2000) and increasing their daily food intake time (Owen-Smith 1997). Revisitation (Prins et al. 1980, Prins 1996) or returning to previously browsed trees (De Knegt et al. 2010a), may also be an adaptation to increase nutritional intake (Bailey et al. 1996, Owen-Smith 2008). Site revisitation may increase browsing pressure on vegetation during the wet season (Smallie and O'Connor 2000) and in the dry seasons (Ben-Shahar 1993). It has been suggested that browsing increases the availability of green-leaved biomass for the dry season (Rutina et al. 2005), but the best time to browse to stimulate an early leaf flush in the late dry season is not yet known (Styles and Skinner 2000, Holdo 2003). Because tree growth has a time lag (Milla et al. 2005), the timing of browsing influences leaf age nutrient content (Styles and Skinner 1997, Cerasoli et al. 2004). Therefore, the time lag between the time of first browsing and revisitation is expected to influence leaf biomass and nutrient content and may therefore be especially important during the dry season, when forage quality is limited. One can even hypothesise that by increasing the variation in the timing of the first browsing and revisitation events, the bottleneck period could be shortened through the availability of high-quality forage at different points in time, assuring a steady supply of leaf nutrients through the availability of leaves that differ in their growth phases. The prolonged nutrient availability in forage may explain the observation that many large herbivore species (re)visit such sites in times of nutritional stress (Styles and Skinner 2000).

Browsing causes resource depletion (Tuomi et al. 1989, Watts 1998), and trees can grow vigorously to compensate for these lost tissues (Fornara and Du Toit 2007, Skarpe and Hester 2008). Browsing can trigger trees to respond by remobilising stored nutrients from old leaves to support the growth of meristem and young leaves and by expanding new leaves to increase their photosynthetic area (Skarpe and Hester 2008). Because new leaves are rich in protein and minerals, such a response can trigger a positive feedback loop (Du Toit et al. 1990). This increase in leaf nutrient content (e.g., N) has been demonstrated to delay leaf senescence in the dormant period (Silvola and Ahlholm 1993, Sigurdsson 2001, Cooke and Weih 2005); as a result, leaves that are rich in nutrients will be available longer during the dry season. The early leaf flush before the onset of rainfall is also stimulated by stored resources (Tuomi et al. 1989, Chapin et al. 1990, Skarpe and Hester 2008).

Besides compensation for consumed leaf material, trees may also select to defend new leaves through the production of secondary compounds (Kohi et al. 2010) causing reduced further herbivory. The production of these secondary compounds depends on the intensity of browsing (Kohi et al. 2010) and soil nutrient availability (Bryant et al. 1992, Ferwerda et al. 2006b), which decreases with the onset of the dry season (Nord and Lynch 2009). Because trees are known to increase their production of secondary compounds in nutrient-poor soil (Bryant et al. 1992, Ferwerda et al. 2006a), they might strengthen their chemical defences when defoliated late in the growing season.

Nutrient re-translocation is well known in deciduous trees in times of leaf senescence as a strategy for saving scarce nutrients (Chapin 1980). In this process, trees withdraw inorganic N, P and K from old leaves to store in their storage organs (Chapin 1980, Chapin et al. 1990). Other minerals, such as Ca and Mg, have very low translocation rates from senescing plant tissue during the dry season (Chapin 1980, McNaughton 1988a). The decline in the availability of mineral nutrients in plants reduces forage quality, which has a direct effect on animal habitat use and animal survival in the dry season(Karasov 1989, Van der Waal and Smit 2001, Van der Waal et al. 2003, Foley et al. 2008). In this study, we experimentally investigated the effects of the timing of initial browsing, the revisitation time since the initial browsing, and browsing intensity on ameliorating forage quality, particularly in the dry season.

METHODS

Study area

The research was conducted in the central part of Kruger National park (31º24´59´´E and 23º31´38´´S), South Africa. The site lies on basaltic soils (Venter et al. 2003). The long-term mean annual rainfall ranges between 450 and 600 mm, with most of the rain falling between November and April. The defoliation experiment was carried out in the "Capricorn enclosure" in Mopani section. The enclosure has an area of 500ha and was erected in 2002 for a roan antelope breeding programme. The area was fenced to exclude all animals that are larger than hares. Only roan and tsessebe antelopes occur inside the enclosure for breeding purposes; both are pure grazers. The experiment was carried out in the middle block of the southern part of the enclosure because no fire management has ever been applied in this block since the erection of the fence.

Simulated browsing by hand defoliation

Browsing was simulated by means of manual defoliation in which leaves were pulled off from shoots, similar to the way elephant use their trunks when browsing. The experiment was carried out on *Colophospermum mopane*, a preferred tree by elephant within the range of mopane trees (Smallie and O'Connor 2000). Defoliation was done as described in chapter 3. The trees were defoliated again according to the schedules presented in Table 1.

Table 1: Defoliation scheme showing the initial defoliations (February 2007, May 2007 and July 2007) and the follow up defoliation. The defoliation intensity was estimated to the nearest % (e.g., 25%) after counting all leaves on a tree. The zero values in the table indicate that there was no tree response or all of the leaves were dead before the sampling date.

	Time	2007				2008		
	→	Feb	May	July	October	Feb	May	August
Defoliation intensity	25	32	8	8	0	8		
	50	32	8	8	0	8		
	75	32	8	8	0	8		
	100	32	8	8	0	8		
	25		32	0	8	8	8	
	50		32	0	8	8	8	
	75		32	0	8	8	8	
	100		32	0	8	8	8	
	25			32	0	8	8	8
	50			32	0	8	8	8
	75			32	0	8	8	8
	100			32	0	8	8	8

Nutrient Analysis

Leaf samples were collected from each sampled tree following the design of the experiment (Table 1). Sampled leaves were stored in paper bags and dried at 70˚C for 48 hrs. The dried leaves were ground in a cyclone analytic grinder to 1 mm of particle size at the SAEON facility in Phalaborwa, South Africa. The nutrient analysis was performed at the chemical laboratory of the Resource Ecology Group, Wageningen University, (The Netherlands). The nutrient elements, N (total), P, K, Na, Ca and Mg, were measured after digestion in a mixture of sulphuric acid (H_2SO_4), salicylic acid (H_2O_2) and selenium (Se) following Novozamsky et al. (1983). N and P were measured with a Skalar San-plus auto-analyser (Breda, The Netherlands), whereas 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 analysed following the Tilley and Terry (1963) method in a Daisy incubator (ANKOM Technology, Macedon, New York, U.S.A.). The condensed tannin concentrations (CT) were analysed according to the proanthocyanidin method after extraction in acetone (50 %) for 24 h (Waterman and Mole 1994). Given the problems involved in applying an appropriate standard for the proanthocyanidin method (Waterman and Mole 1994), the data are presented as final absorbance values at 540 nm. The neutral detergent fibre (NDF) was analysed using an ANKOM fibre analyser and an added commercial neutral detergent solution (alpha-amylase was not added); the solution and fibre were agitated for 75 min at 100ºC (Van Soest et al. 1991, Udén et al. 2005).

Data analysis

The measurements of the forage quality were analysed using general linear models. The dependent variables used for the forage quality test were N, P, K, Ca, CT, NDF and IVD. N, P, K and Ca were arcsine transformed to approach normality of the residues. The differences in the forage quality were tested for the differences in the timing of the initial defoliation, the defoliation intensity and the revisitation interval. For significant results of the independent variables or their interactions, a post-hoc Tukey test was used for further analysis, and, in case sample size was not equal, the Game-Howell test was used (Field 2009). In some cases, we used independent samples t-tests to test for differences between the control and defoliated trees.

RESULTS

The timing of defoliation had a significant effect on nutrient concentrations, digestibility and fibre content (Table 2). Early defoliation in the growing season was associated with an increase in total potassium availability, whereas total nitrogen was higher in trees that were defoliated late in the growing season (Fig. 1). Foliar calcium was high in trees that were defoliated in the dry season, whereas total phosphorus was low in all of the defoliated trees (Table 2). Leaf digestibility (IVD) was high for trees that were defoliated late in the growing season, a finding similar to the increase in total nitrogen. The condensed tannins content (CT), however, was higher in trees that were defoliated early in the growing season (Table 2).

The nutrient contents depended on the defoliation intensity (Table 2). However, most of the observed differences were between the control trees (0 % defoliation) and the defoliated trees (25 %, 50 %, 75 %, 100 %; Appendix 1). There was no directional influence of defoliation intensity on nutrients, fibre, IVD and CT (Appendix 1). Therefore, we focus on the effects of the timing of the first browsing and revisitation and compare all of the defoliated trees to the control trees.

Foliar Nitrogen

The timing of defoliation had an effect on the availability of foliar nitrogen ($F_{2,\ 336} = 30.78$, $P < 0.01$) especially in the dry season (Fig. 1, Table 3 and 4). The foliar nitrogen content of trees that were initially defoliated during the early growing season (February 2007) was lower than that of the control trees when they were revisited in the late growing season (May 2007, Fig. 1a). However, the nitrogen concentration in the defoliated trees remained unchanged for a longer period during the dry season, whereas in the control trees, the nitrogen content decreased sharply during the dry season (Fig. 1a, Table 4). Trees that were initially defoliated at the end of the growing season (May 2007) had a strong foliar nitrogen flush in the late dry season (October 2007), with about three times more nitrogen than the control trees had (Fig. 1b). However, in the following wet season (February 2008 and May 2008), the foliar nitrogen concentrations of both defoliated and control trees were similar. The trees that were defoliated in the dry season did not have an early flush in the late dry season (October 2007). However, they increased their foliar nitrogen in the following dry season (August 2008, Fig. 1c). Regardless of the timing of the initial defoliation, foliar N was high in the dry season (July, August and October), which is a period of nutritional stress in most of the wildlife areas in the southern African savanna (Fig. 1).

Foliar Potassium

Potassium concentrations increased in the defoliated trees when the trees were revisited at short intervals but also decreased toward the beginning of the dry season. The leaves of the trees defoliated early in the growing season had higher potassium concentrations in the late growing season (May 2007) than control trees did, and the concentrations decreased in the dry season (July 2007, Table 3). This finding suggests that as the leaves matured, the trees withdrew potassium from the leaves (Fig. 2a). In the following growing season (February 2008), new leaves were observed on both the control and defoliated trees, and their potassium levels did not differ. The trees that were initially defoliated in the late growing season (May 2007) had higher potassium concentrations during the early leaf flush, with about three times more potassium than the control trees had. However, in the growing season, the defoliated trees did not differ from the control trees (Fig. 2b). For the trees that were initially defoliated in the dry season (i.e., July

2007), the potassium concentrations did not differ during the growing season (February 2008 and May 2008).

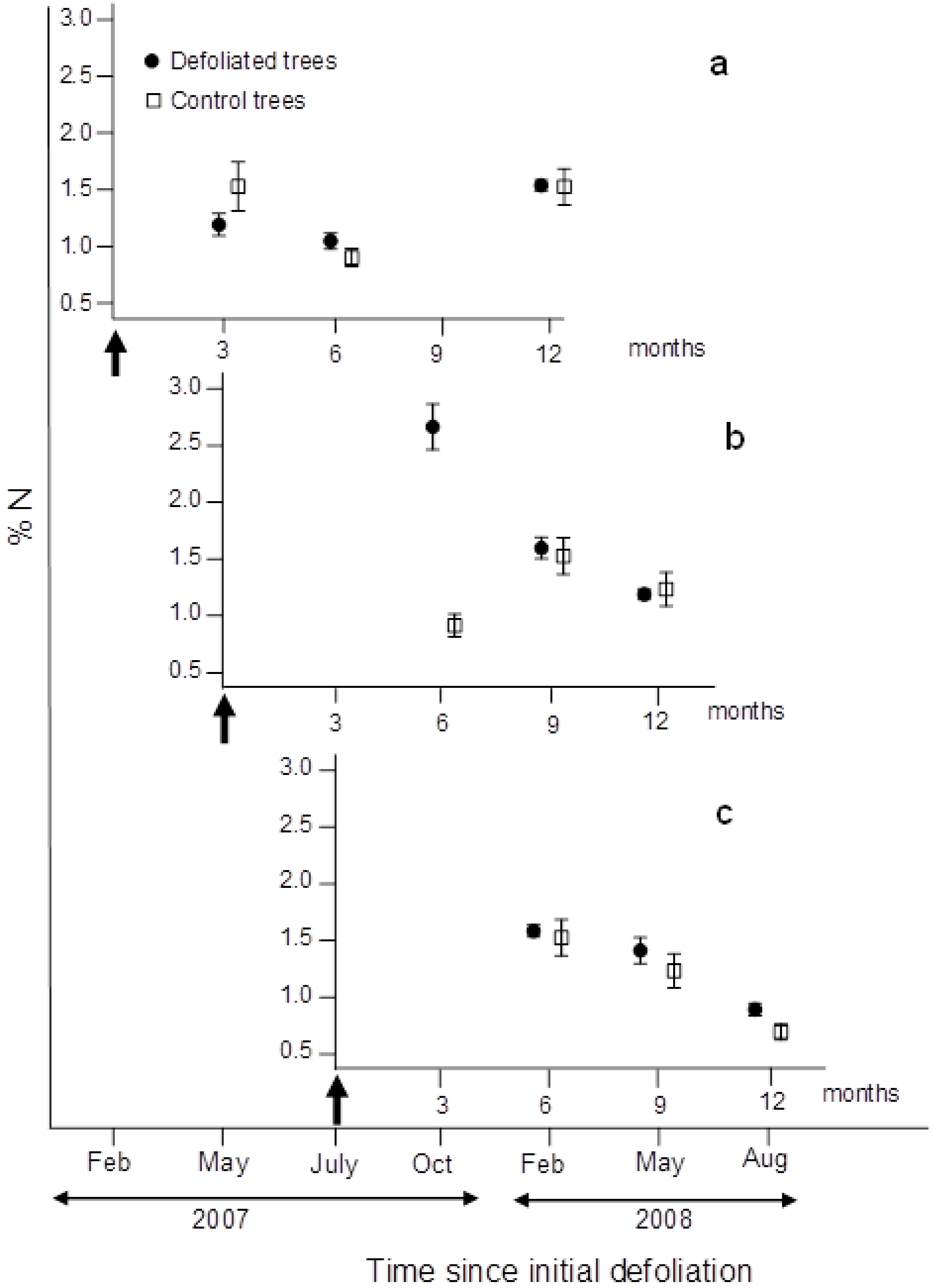


Figure 1: Mean (95% CI) nitrogen (N) concentration of leaves of previously defoliated and control trees measured at different intervals for a period of one year. (a) Defoliated in February 2007, (b) defoliated in May 2007, and (c) defoliated in July 2007. The overlapping error bars of the defoliated and control trees indicate no significant differences.

Table 2: Comparisons of mean leaf nutrient concentrations (N, P, K, Ca, and Mg), NDF, IVD (all expressed in % DM) and CT (540 nm) in relation to the timing of the initial defoliation (TID) event and defoliation intensity (DI), with ANOVA-F values and the percentage of explained variance (R^2). The values between brackets are the mean values of the control trees. Asterisks indicate ANOVA P-values: * = P < 0.05 and ** = P < 0.001. The letter “t” indicates a significant difference between the treatment and control (t-test). Letters “a”, “b” and “c” indicate Game-Howell significant group differences in relation to the timing of defoliation; ns = not significant.

Nutrients	Feb. 2007	May 2007	July 2007	DI	TID	DI*TID	R^2
% N	1.26^{a} [1.32]	1.82^{b} [1.25] ^{t}	1.29^{a} [1.15]	$F_{4, 336} = 2.67*$	$F_{2, 336} = 30.78**$	$F_{8, 336} = 1.39$	0.20
% P	0.37^{ns} [0.45] ^{t}	0.41^{ns} [0.46]	0.39^{ns} [0.46] ^{t}	$F_{4, 336} = 5.89**$	$F_{2, 336} = 1.92$	$F_{8, 336} = 1.45$	0.10
% K	1.43^{a} [0.94] ^{t}	1.37^{a} [0.97] ^{t}	0.92^{b} [0.83]	$F_{4, 336} = 14.1**$	$F_{2, 336} = 52.82**$	$F_{8, 336} = 1.17$	0.34
% Ca	0.75^{a} [1.85] ^{t}	1.09^{b} [1.8] ^{t}	1.63^{c} [1.83]	$F_{4, 336} = 20.19**$	$F_{2, 336} = 52.48**$	$F_{8, 336} = 3.6**$	0.39
% Mg	0.29^{a} [0.25] ^{t}	0.22^{b} [0.24]	0.26^{a} [0.26]	$F_{4, 336} = 3.9*$	$F_{2, 336} = 25.38**$	$F_{8, 336} = 4.51**$	0.24
% IVD	54.52^{a} [52.55]	51.83^{b} [50.31]	54.79^{a} [53.33]	$F_{4, 336} = 3.69*$	$F_{2, 336} = 17.22**$	$F_{8, 336} = 0.9$	0.11
% NDF	35.35^{a} [35.23]	35.64^{a} [36.29]	33.41^{b} [35.35] ^{t}	$F_{4, 336} = 2.89*$	$F_{2, 336} = 9.79**$	$F_{8, 336} = 3.66**$	0.15
CT (nm)	1.27^{a} [1.00] ^{t}	1.16^{b} [1.08]	1.04^{c} [1.12] ^{t}	$F_{4, 336} = 10.15**$	$F_{2, 336} = 25.46**$	$F_{8, 336} = 5.76**$	0.29

Table 3: Comparisons of mean leaf nutrient concentrations (N, P, K, Ca, and Mg), NDF, IVD (all expressed in % DM) and CT (540 nm) in relation to the timing of revisitation (RevT) and defoliation intensity (DI), with ANOVA-F values and the percentage of explained variance (R^2). Asterisks indicate P-values: ** = $P < 0.001$ and ns = not significant.

Variables	RevT	DI	RevT*DI	R^2
% N	$F_{8,306}$ = 124.29**	$F_{4, 306}$ = 10.59**	$F_{32, 306}$ = 7.45**	0.81
% P	$F_{8,306}$ = 3.75**	$F_{4, 306}$ = 6.48**	$F_{32, 306}$ = 1.46^{ns}	0.25
% K	$F_{8,306}$ = 82.18**	$F_{4, 306}$ = 41.59**	$F_{32, 306}$ = 8.33**	0.78
% Ca	$F_{8,306}$ = 98.43**	$F_{4, 306}$ = 65.65**	$F_{32, 306}$ = 10.56**	0.82
% Mg	$F_{8,306}$ = 12.45**	$F_{4, 306}$ = 4.9**	$F_{32, 306}$ = 3.15**	0.42
% Na	$F_{8,306}$ = 39.27**	$F_{4, 306}$ = 11.56**	$F_{32, 306}$ = 6.31**	0.65
IVD (% DM)	$F_{8,306}$ = 16.88**	$F_{4, 306}$ = 6.02**	$F_{32, 306}$ = 2.79**	0.44
NDF (% DM)	$F_{8,306}$ = 12.11**	$F_{4, 305}$ = 3.84**	$F_{32, 306}$ = 3.28**	0.42
CT (540 nm)	$F_{8,306}$ = 13.24**	$F_{4, 305}$ = 13.55**	$F_{32, 306}$ = 4.3**	0.50

In the dry season (August 2008), potassium was significantly higher in the defoliated trees than it was in the control trees (Fig. 2c). Again, defoliated trees showed increased foliar potassium in the late dry season (July, August and October) in relation to the control trees (Fig. 2).

Tables 4: Mean (±SE) nutrients (N, P, K, Ca, Mg, and Na), IVD, NDF and condensed tannins (CT) at different revisitation intervals. The ▼ arrow symbol indicates the month of the initial defoliation. Letters show significant differences among groups of revisited defoliated trees (Game-Howell, $P < 0.05$).

▼	Revisitation	Treatment	% N	% P	% K	% Ca	% Mg	% IVD	% NDF	CT (540 nm)
February 2007	May 2007	Defoliated	1.19 (0.05)^{ab}	0.36 (0.01)^{a}	1.83 (0.04)^{a}	0.45 (0.02)^{a}	0.29 (0.01)^{ade}	55.2 (0.49)^{ab}	35.63 (0.55)^{abd}	1.33 (0.04)^{ad}
		Control	1.53 (0.09)	0.41 (0.03)	0.9 (0.09)	1.65 (0.07)	0.25 (0.02)	48.82 (1.55)	35.71 (1.26)	0.92 (0.04)
	July 2007	Defoliated	1.05 (0.03)^{b}	0.34 (0.01)^{a}	1.11 (0.04)^{b}	0.64 (0.05)^{b}	0.26 (0.01)^{abde}	55.55 (0.56)^{b}	34.13 (0.41)^{bc}	1.22 (0.02)^{abd}
		Control	0.9 (0.03)	0.5 (0.06)	0.7 (0.11)	2.53 (0.24)	0.29 (0.02)	55.55 (1.09)	34.3 (0.74)	0.95 (0.11)
	Feb 2008	Defoliated	1.54 (0.02)^{c}	0.41 (0.02)^{ab}	1.36 (0.04)^{c}	1.12 (0.05)^{c}	0.3 (0.01)^{ae}	52.93 (0.53)^{a}	36.25 (0.62)^{abd}	1.25 (0.02)^{d}
		Control	1.52 (0.07)	0.45 (0.04)	1.22 (0.04)	1.36 (0.09)	0.22 (0.02)	53.27 (1.49)	35.66 (0.78)	1.14 (0.05)
May 2007	Oct 2007	Defoliated	2.66 (0.1)^{d}	0.46 (0.01)^{b}	1.85 (0.05)^{a}	0.34 (0.04)^{d}	0.17 (0.004)^{c}	50.58 (1.17)^{c}	31.93 (0.85)^{abc}	1.31 (0.04)^{ade}
		Control	0.91 (0.04)	0.48 (0.07)	0.59 (0.11)	2.41 (0.41)	0.22 (0.04)	41.87 (0.78)	39.02 (1.05)	0.9 (0.06)
	Feb 2008	Defoliated	1.59 (0.05)^{c}	0.39 (0.02)^{a}	1.2 (0.03)^{b}	1.24 (0.04)^{c}	0.26 (0.01)^{ed}	49.87 (0.53)^{cd}	38.02 (0.68)^{d}	1.09 (0.02)^{abe}
		Control	1.52 (0.07)	0.45 (0.04)	1.22 (0.04)	1.36 (0.09)	0.22 (0.02)	53.27 (1.49)	35.66 (0.78)	1.14 (0.05)
	May 2008	Defoliated	1.19 (0.02)^{a}	0.36 (0.02)^{a}	1.06 (0.03)^{b}	1.71 (0.06)^{e}	0.21 (0.01)^{bcd}	55.15 (0.57)^{ab}	36.39 (0.44)^{d}	1.07 (0.02)^{be}
		Control	1.23 (0.06)	0.47 (0.05)	1 (0.06)	1.79 (0.14)	0.27 (0.02)	53.69 (0.87)	34.88 (0.86)	1.16 (0.02)
July 2007	Feb 2008	Defoliated	1.58 (0.03)^{c}	0.36 (0.02)^{a}	1.12 (0.03)^{b}	1.14 (0.04)^{c}	0.3 (0.01)^{a}	55.84 (0.5)^{ab}	32.79 (0.42)^{c}	1.09 (0.03)^{abe}
		Control	1.52 (0.07)	0.45 (0.04)	1.22 (0.04)	1.36 (0.09)	0.22 (0.02)	53.27 (1.49)	35.66 (0.78)	1.14 (0.05)
	May 2008	Defoliated	1.41 (0.06)^{c}	0.42 (0.02)^{ab}	0.9 (0.04)^{d}	1.9 (0.08)^{e}	0.26 (0.01)^{ade}	56.08 (0.51)^{b}	31.89 (0.49)^{c}	1.06 (0.02)^{bc}
		Control	1.23 (0.06)	0.47 (0.05)	1.0 (0.06)	1.79 (0.14)	0.27 (0.02)	53.69 (0.87)	34.88 (0.86)	1.16 (0.02)
	Aug 2008	Defoliated	0.89 (0.03)^{e}	0.38 (0.02)^{a}	0.74 (0.04)^{d}	1.86 (0.1)^{e}	0.23 (0.01)^{d}	52.53 (0.79)^{ad}	35.48 (0.62)^{abd}	0.97 (0.03)^{c}
		Control	0.69 (0.03)	0.48 (0.03)	0.28 (0.03)	2.33 (0.14)	0.28 (0.03)	53.02 (1.18)	35.52 (1.14)	1.06 (0.01)

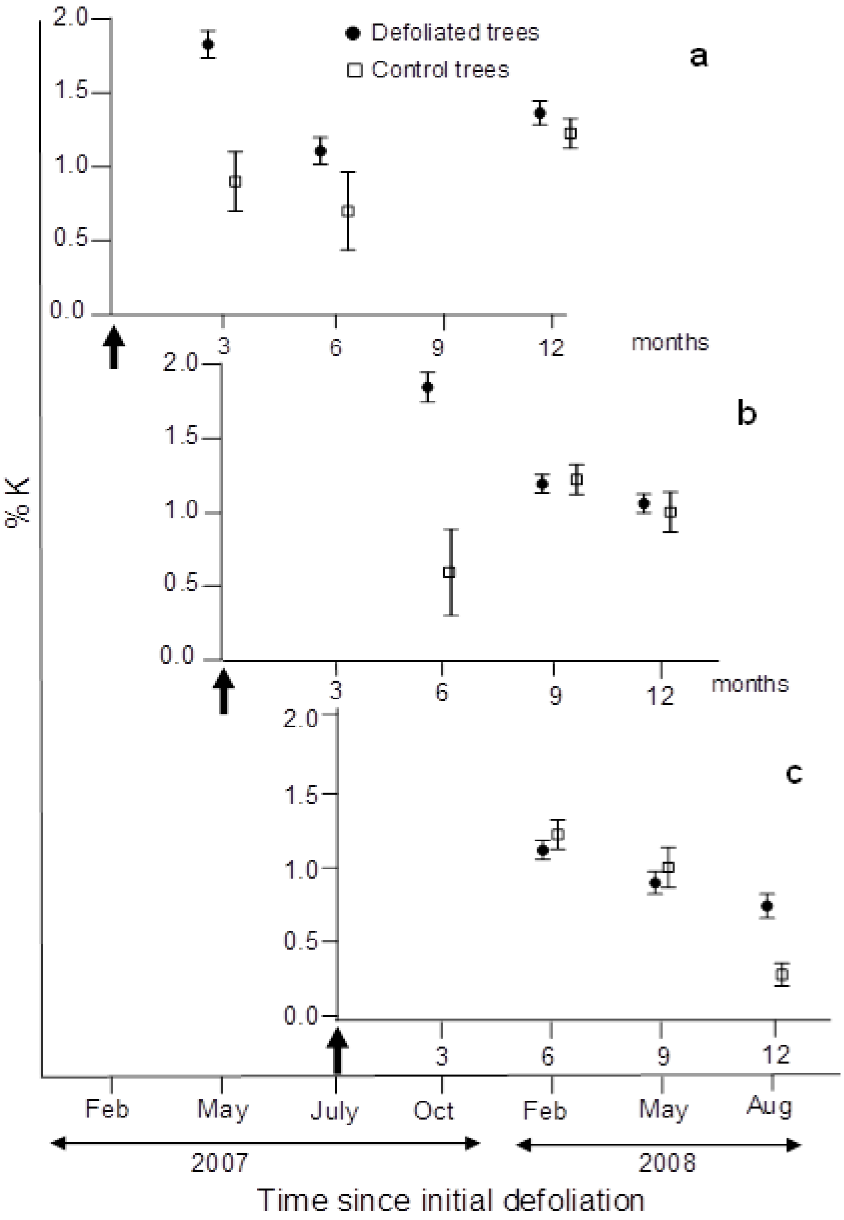


Figure 2: Mean (95%CI) potassium (K) concentration of leaves of previously defoliated and control trees measured at different intervals for a period of one year. (a) Defoliated in February 2007, (b) defoliated in May 2007, and (c) defoliated in July 2007. The overlapping error bars of the defoliated and control trees indicate no significant differences.

Foliar Phosphorus (P)

The concentrations of phosphorus were consistently reduced in the defoliated trees in all treatments (Table 2). The phosphorus concentration depended on the time of revisitation (Tables 3 & 4). Early defoliation in the growing season resulted in the lowest phosphorus concentration in the dry season (July 2007, Fig. 3a). In the late dry season, trees that were initially defoliated at the end of the growing season had the highest phosphorus concentration of all defoliated trees (Table 4, Fig. 3b). Defoliation in the dry season resulted in a relatively constant concentration of phosphorus for the whole year (Fig. 3c). In general, phosphorus was low in the leaves of trees that were defoliated early in the dry season but increased in the early flush (Fig. 3). Defoliation intensity reduced the phosphorus concentration in the remaining leaves ($F_{4,\ 336} = 5.89$, $P < 0.01$), but these differences were mainly found between the control trees and the defoliated trees (25, 50, 75 and 100 %; Game-Howell, $P < 0.01$). There were no differences between the 25 % and 100 % defoliation intensities. This finding suggests that defoliation itself, rather than the intensity of defoliation, reduced leaf phosphorus concentration.

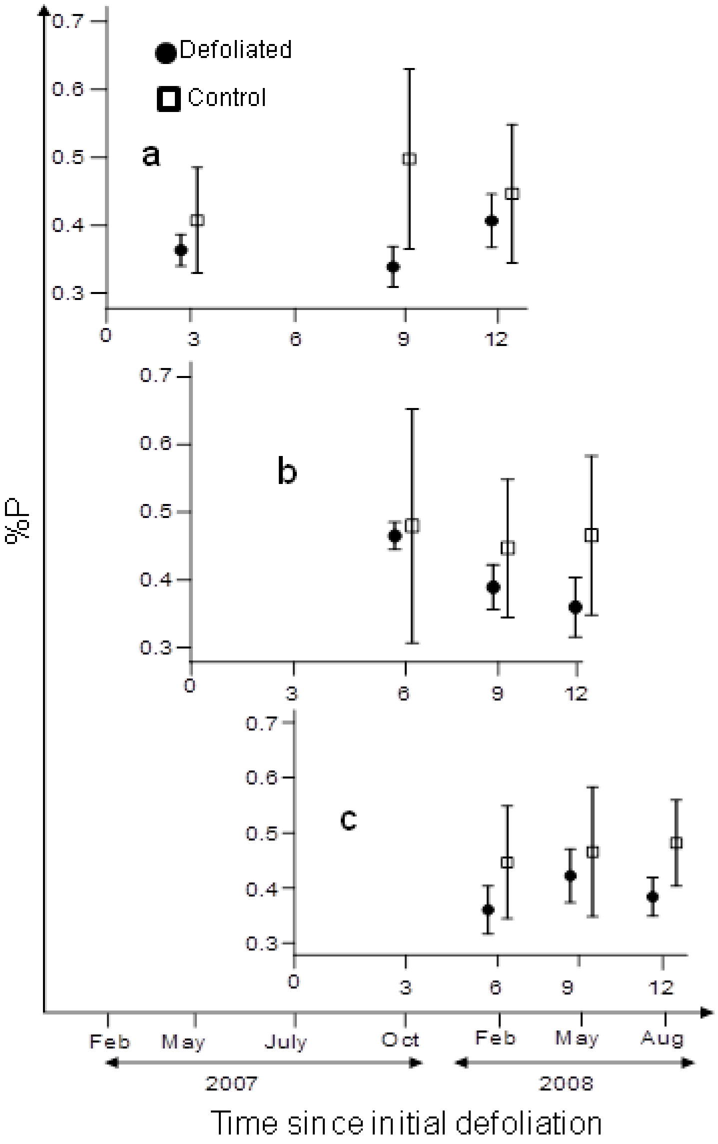


Figure 3: Mean (95%CI) leaf phosphorus (P) concentration of previously defoliated and control trees measured at different intervals for a period of one year. (a) Defoliated in February 2007, (b) defoliated in May 2007, and (c) defoliated in July 2007. The overlapping error bars of defoliated and control trees indicate no significant differences.

Foliar Calcium (Ca)

The timing of initial defoliation affected the total calcium (Ca) concentrations in the leaves ($F_{2,\,336} = 52.48$, $P < 0.001$) in the dry season. Leaves of trees defoliated early in the growing season had significantly lower calcium concentrations in May 2007 and July 2007 in comparison to those of the control trees (Fig. 4a, Table 2). Compared to trees defoliated in February 2007, the calcium leaf concentration in the control trees was three times higher at the end of the growing season (May 2007), and this value increased to about four times during the dry season (July 2007, Table 4). However, in the following growing season (February 2008), leaves of the defoliated trees did not differ from the control trees. The young leaves had lower calcium concentrations, which increased as the leaves matured (Fig. 4).

Neutral Detergent Fibre (NDF)

The fibre content (NDF) in the leaves varied in response to differences in the timing of initial defoliation ($F_{2,\,336} = 19.89$, $P < 0.01$) and the revisitation time (Table 3). The fibre contents were similar in the leaves of trees that were initially defoliated in the early growing season when visited in May 2007, July 2007 and February 2008 (Fig. 5a). However, early flushed leaves in the late dry season (October 2007) had significantly lower fibre values (Fig. 5b). The increase in leaf fibre content in the growing seasons of February 2008 and May 2008 may be related to the maturity of the leaves. Surprisingly, the NDF was low in the growing season for leaves of trees that were initially defoliated in the dry season, while this was not the case for trees that were defoliated late in the growing season (Fig. 5b c).

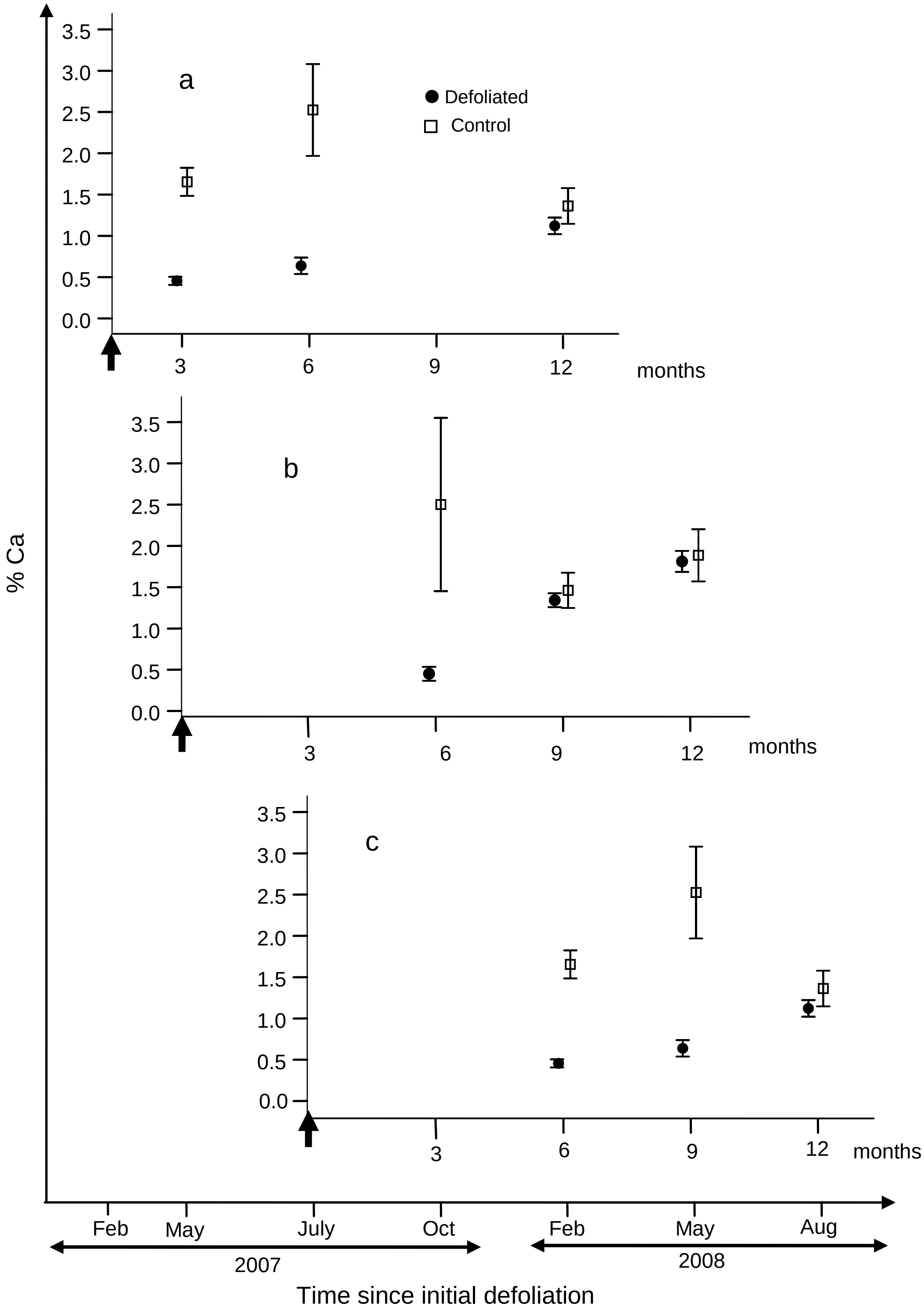


Figure 4: Mean (95%CI) calcium (Ca) concentration of leaves of previously defoliated and control trees measured at different intervals for a period of one year. (a) Defoliated in February 2007, (b) defoliated in May 2007, and (c) defoliated in July 2007. The overlapping error bars of defoliated and control trees indicate no significant differences.

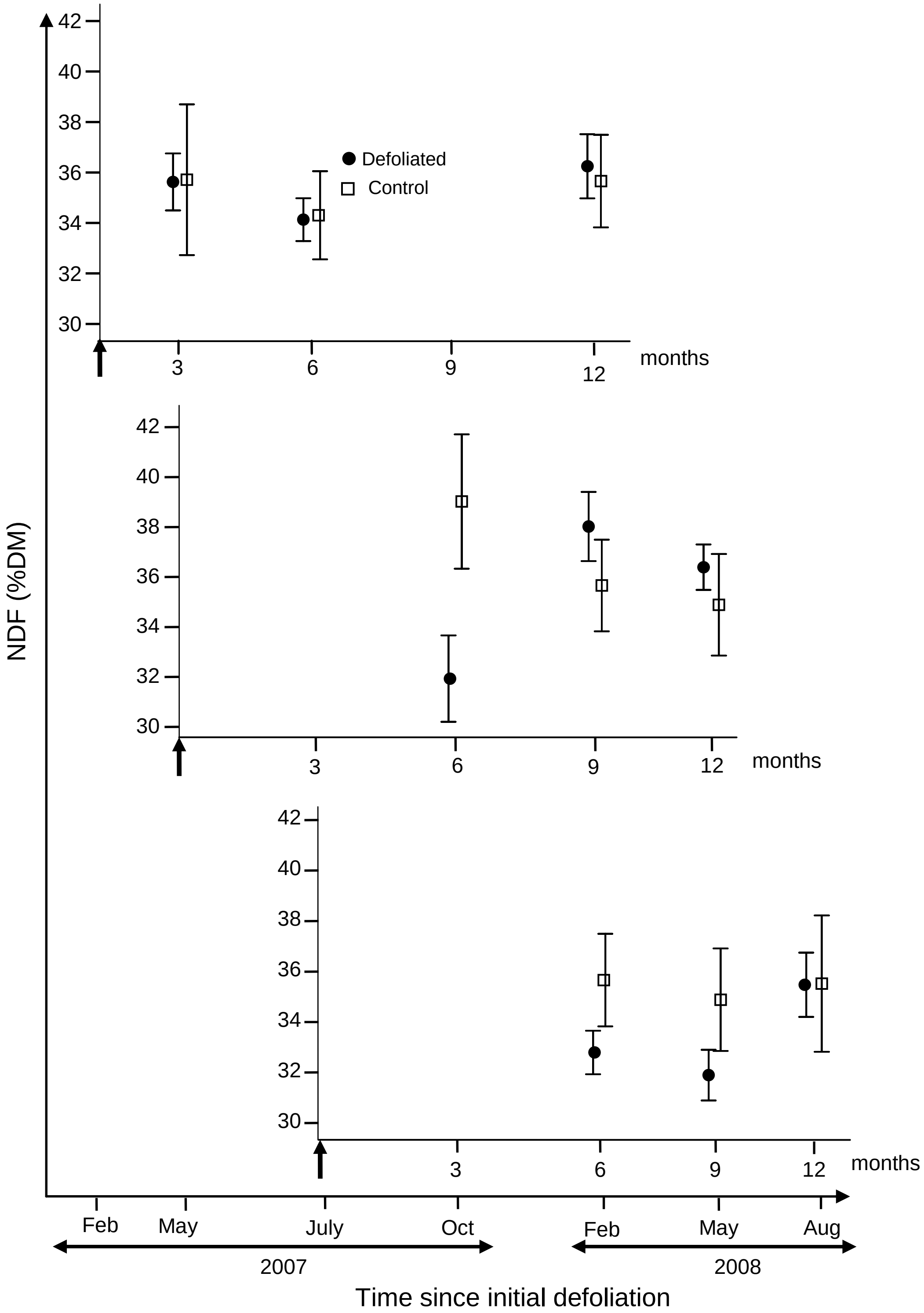


Figure 5: Mean (95%CI) NDF concentration in leaves of previously defoliated and control trees measured at different intervals for a period of one year. (a) Defoliated in February 2007, (b) defoliated in May 2007, and (c) defoliated in July 2007. The overlapping error bars of defoliated and control trees indicate no significant differences.

In Vitro Digestibility (IVD)

The young regrowth had higher leaf digestibility, which decreased as the leaf matured (Table 2, Fig. 6a b). The defoliation early in the growing season resulted in an increase in leaf digestibility in May 2007 ($t_{36} = 5.153$, $P < 0.01$), which remained similar in July 2007 (Fig. 6a). Similarly, early flushing leaves had higher leaf digestibility than control leaves did ($T_{36} = 3.37$, $P < 0.001$) in the late dry season (October 2007) for trees that were defoliated late in the growing season (Fig. 6b). In the wet season, (i.e., February), and in July and August (dry season), the leaf digestibility was similar in all treatments (Fig. 6). However, in the late dry season (October), the digestibility was higher in defoliated trees than it was in control trees (Fig. 6c). Defoliation intensity increased leaf digestibility in heavily defoliated trees (75 % and 100 %) only in the early leaf flushes (Game-Howell, $P < 0.01$).

Condensed tannin (CT)

The timing of the initial defoliation affected the condensed tannin content of the leaves ($F_{2,\ 336} = 25.46$, $P < 0.01$). However, the tannin content also depended on the time of revisitation (Tables 3 & 4). Leaves of trees that were defoliated in the dry season had the lowest tannin content, while the highest tannin content occurred in those of trees that were defoliated earlier in the growing season (Game-Howell, $P < 0.01$, Table 3), contrary to our prediction. Leaves from trees defoliated in the dry season had a lower condensed tannin content in comparison to those of the control trees ($t_{116} = -2.54$, $P < 0.01$), while early in the growing season, leaves from defoliated trees had higher condensed tannin contents than control leaves did ($t_{114} = 6.19$, $P < 0.001$; Fig. 7a). No differences between the control and defoliated trees were found when the trees were defoliated at the end of the growing season (Table 3, Fig. 7b).

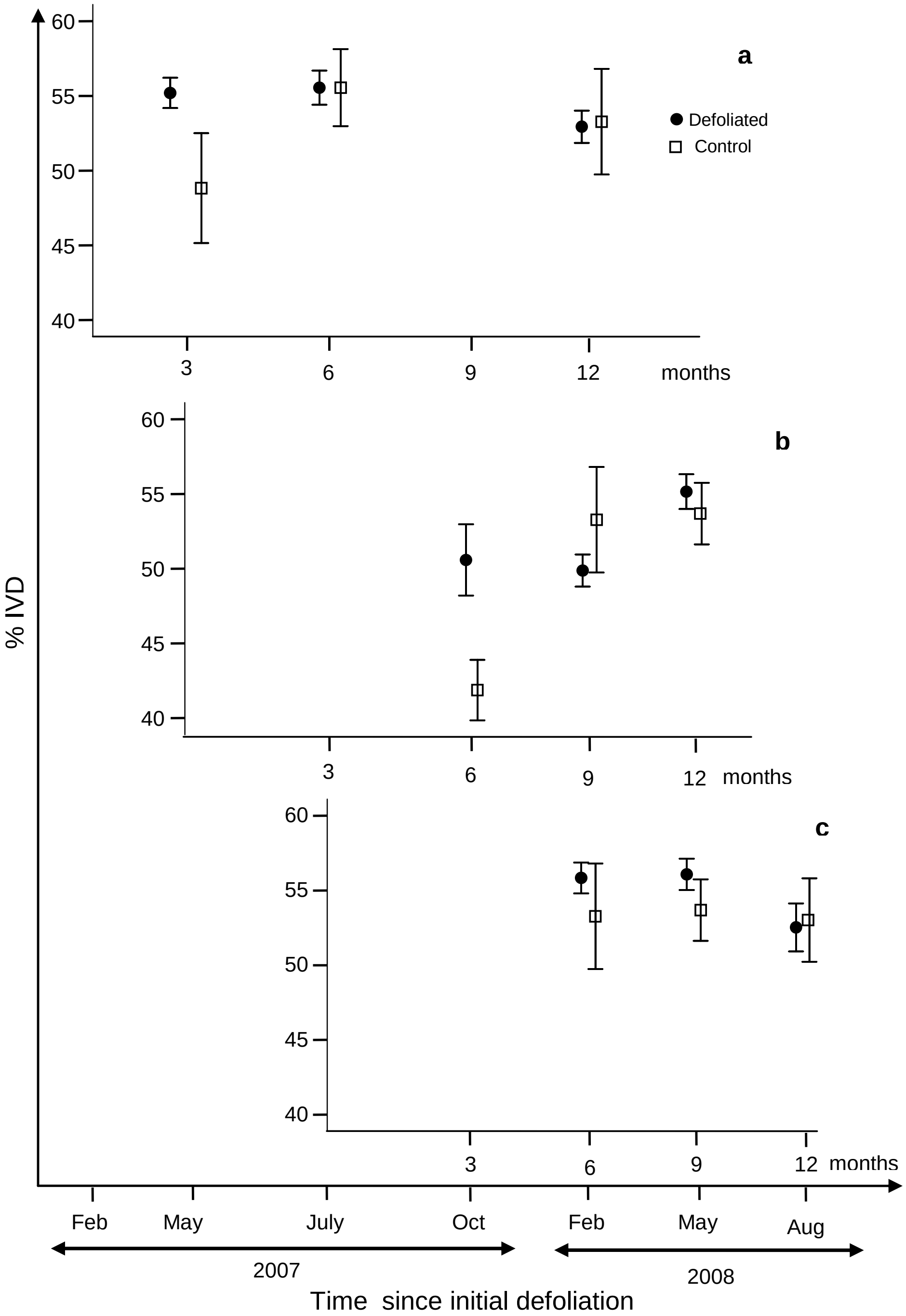


Figure 6: Mean (95%CI) IVD percentage of leaves of previously defoliated and control trees measured at different intervals for a period of one year. (a) Defoliated in February 2007, (b) defoliated in May 2007, and (c) defoliated in July 2007. The overlapping error bars of defoliated and control trees indicate no significant differences.

The interaction of defoliation intensity and the timing of the initial defoliation significantly influenced the condensed tannin content ($F_{8, 336} = 5.76$, $P < 0.01$). In leaves of trees defoliated early in the growing season (February 2007) the tannin content was increased when they were defoliated heavily (Fig. 7a), whereas, for trees that were defoliated late in the growing season (May 2007), the defoliation intensity had no effect on the tannin content (Fig. 7b). For trees that were defoliated in the dry season, the leaves of trees that were defoliated earlier had decreased tannin levels only in the case of the lightly defoliated trees (Fig. 7c). When all of the defoliated trees were combined in the analysis, regardless of the time of initial browsing, the defoliation intensity increased the tannin content in the leaves ($F_{4, 345} = 8.21$, $P < 0.01$). Leaves from the 0 % and 25 % defoliation intensities did not differ, but had lower condensed tannin contents than did trees in the 75 % and 100 % defoliation intensity categories (Game-Howell, $P < 0.01$, Fig. 7d). Leaves from trees that were defoliated by 50 % had similar tannin contents to all other levels of defoliation.

The condensed tannin content was higher in leaves of previously defoliated trees shortly after defoliation occurred (8a) and during the early leaf flushes (8b) but decreased as the revisitation interval increased. The leaves in May 2007 were new regrowth for trees that were initially defoliated in February 2007, whereas the leaves in October 2007 were from the early flush in the late dry season. This result suggests that defoliation in Mopane trees triggered the production of condensed tannin in young leaves. However, as the growing season progressed, the condensed tannin content decreased.

The increase in CT levels in young leaves did not affect foliar digestibility. There was no correlation between CT and IVD. However, the digestibility significantly decreased with increases in the fibre content for all treatments ($R^2 = 0.53$, $F_{1,\ 338} = 106.3$, $P < 0.01$, Fig. 9).

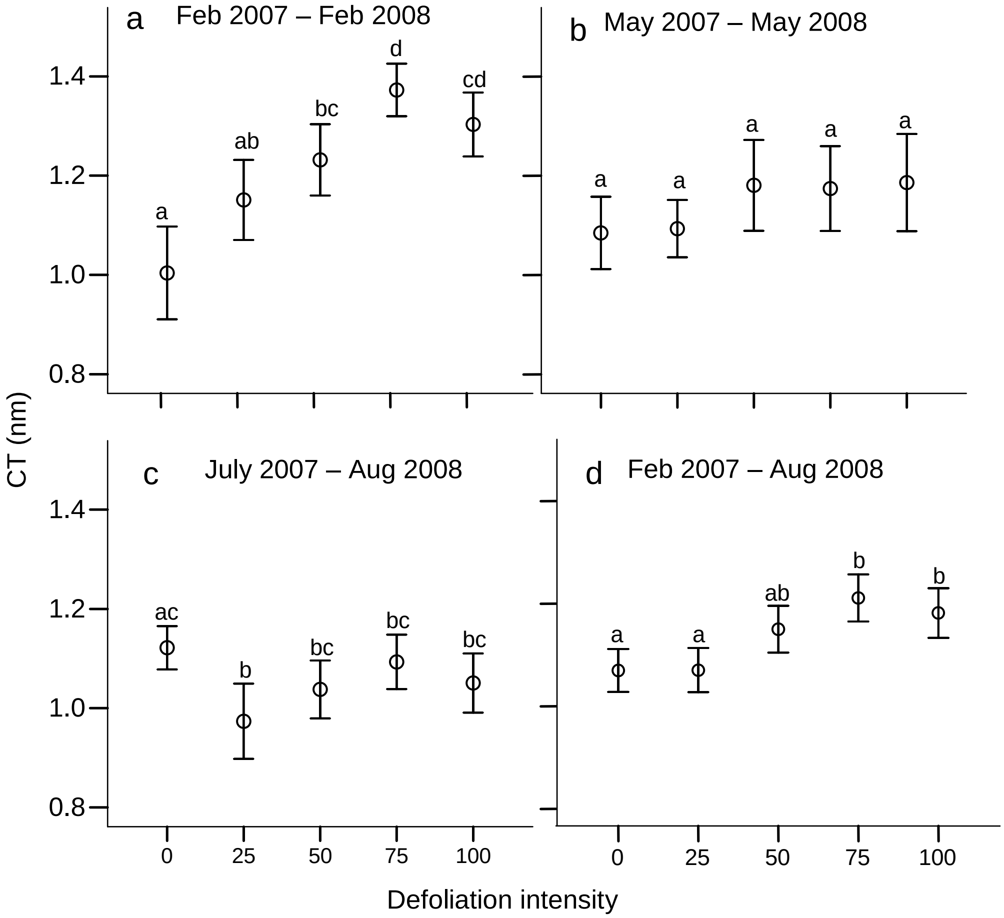


Figure 7: Mean (95%CI) condensed tannin contents in leaves in relation to defoliation intensity and timing of initial defoliation. (a) Defoliation early in the growing season, (b) Defoliation late in the growing season, (c) Defoliation early in the dry season, and (d) a combination of all three times of initial defoliation. Letters indicate differences between groups (Game-Howell group differences at P < 0.05).

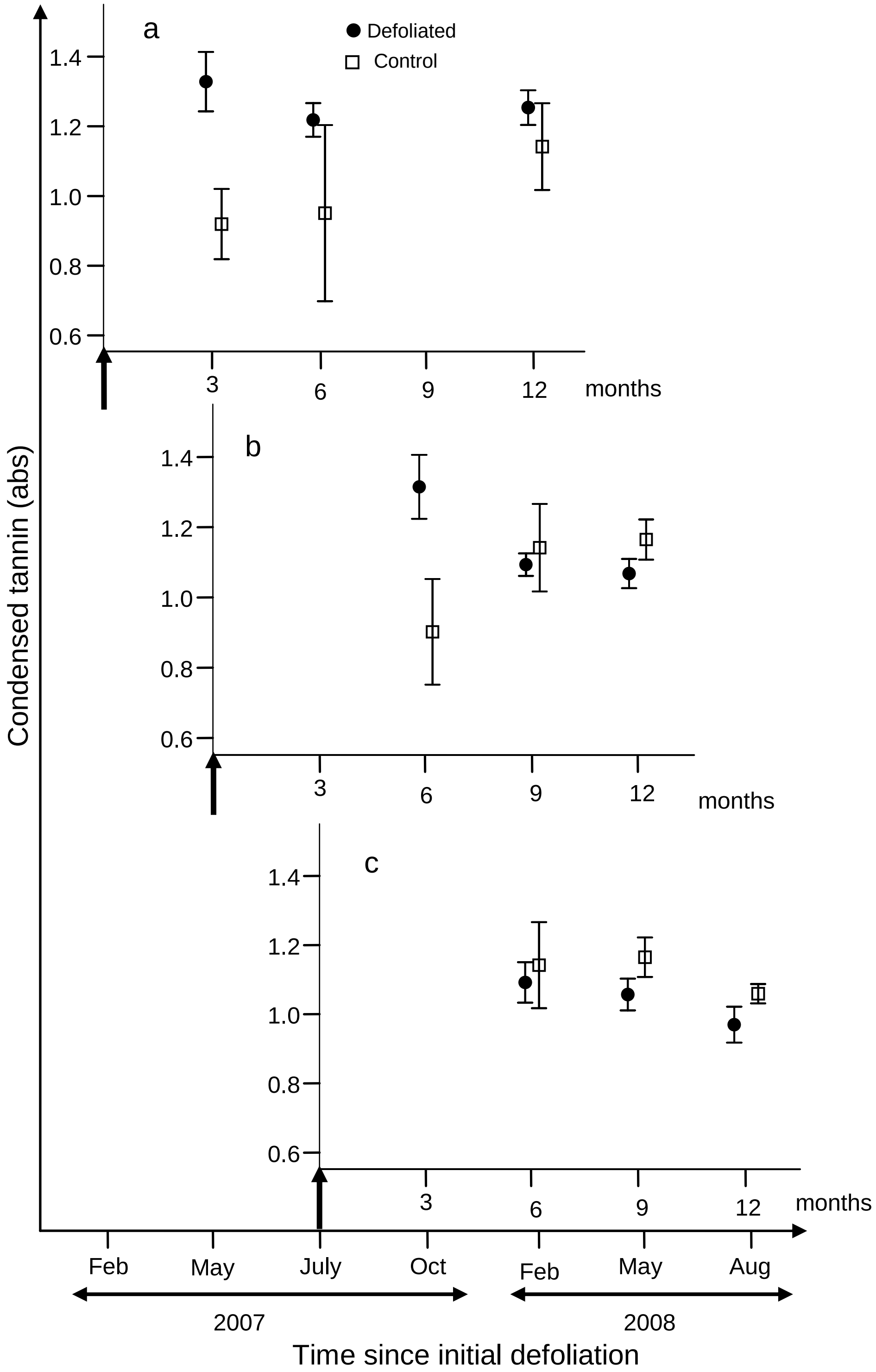


Fig. 8: The mean (95%CI) condensed tannin content (absorption, nm) measured in Mopane leaves in relation to the revisitation interval and the timing of the initial defoliation. Letters represent the timing of initial defoliation, where a (2007 – 2008), b (May 2007 – May 2008), and c (July 2007 – August 2008). The overlapping confidence intervals of measurements in defoliated and control trees indicate no significant differences.

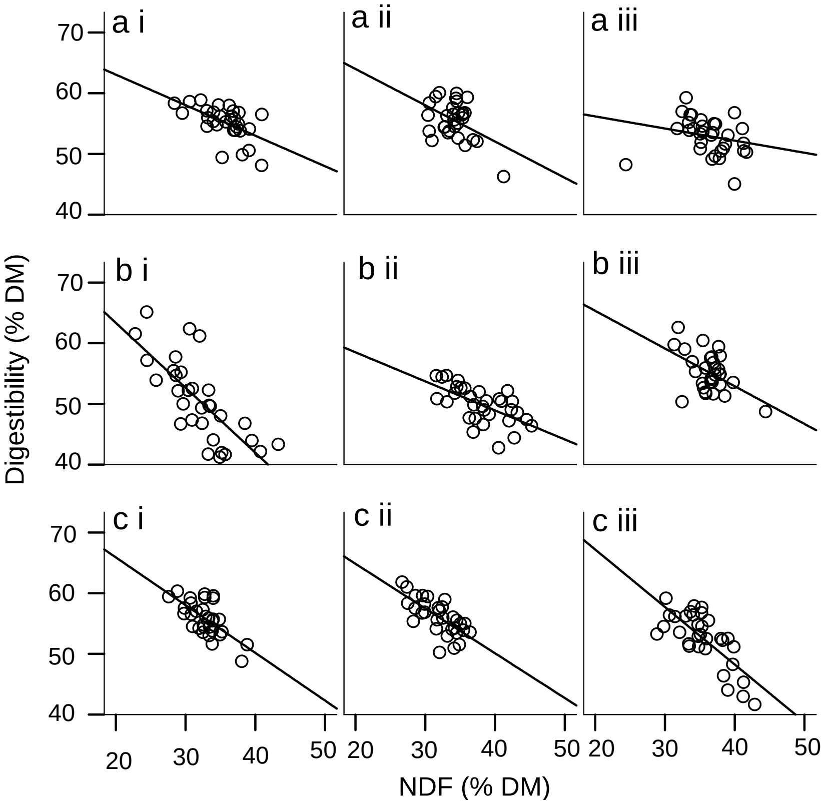


Figure 9: Relationships between leaf digestibility and leaf fibre content (NDF) of the defoliated trees. Letters indicate the timing of initial defoliation in (a) February 2007, (b) May 2007, and (c) July 2007. The Roman numerals beside the letters indicate the revisitation intervals with respect to the timing of initial defoliation, where (a i) represents May 2007, (a ii) July 2007, (a iii) February 2008, (b i) October 2007, (b ii) February 2008, (b iii) May 2008, (c i) February 2008, (c ii) May 2008, and (c iii) August 2008.

DISCUSSION

A puzzling question for many ecologists is how animals assemble their diets in times of nutritional stress and whether they can promote food availability and quality during these times. Not surprisingly, there are a range of possible answers, namely, that animals broaden their diet choices, increase their foraging time (Owen-Smith 1997), or alter their diets (Beekman and Prins 1989, De Boer et al. 2000). This paper, explores a less acknowledged mechanism of the timing of browsing as a food quality enhancement mechanism in times of nutritional stress. Human beings have the ability to plan ahead, for example, by collecting and preserving food that can be used in times of food scarcity. Certain insects (Kalshoven 1956, Cameron et al. 2008), arachnids (Dippenaar-Schoeman and Harris 2005) and small mammals (Jensen 1985, Shimada 2001) are also known to store food, which they use in times of food scarcity. Even though no such organised plan is followed by large herbivores, we show that the timing of browsing by large herbivores shortens the nutritional stress period by inducing changes in plant physiology. Mopane trees experimentally defoliated by us early during the growing season increased their potassium and maintained their nitrogen levels during the dry season, whereas defoliation late in the growing season increased leaf digestibility, nitrogen and potassium during the late dry season whereas the fibre content in the leaves was low. Such an increase in energy, protein and nutrients in browsed trees is a response of plant that enabling large herbivores to expand their dry-season feeding period by increasing the availability of high-quality resources. While we are not claiming that elephant manipulate their food supplies consciously or that this is a co-evolved mechanism, we emphasize that site revisitation during the dry season might be related to the timing of initial browsing as a forage facilitation mechanism that enables animals to estimate where regrowth of high-quality foods can be found (De Knegt et al. 2010a). Revisitation strategies in relation to energy gain have also been reported for birds (Ydenberg and Prins 1981, Henderson et al. 2006), African buffalo *Syncerus caffer* (Prins 1996) and gorillas *Gorilla gorilla* (Watts 1998).

In the dry season, calcium and phosphorus contents were low in all of the new regrowth. The deficiency of calcium in young leaves can be explained by the low ability of trees to reabsorb calcium from leaves to the storage organ during the senescence period (Chapin 1980, Lal et al. 2001) and by the fact that calcium is mostly transported by mass flow and so requires fully expanded leaves (Lal et al. 2001). As a result, calcium concentrations were high in mature leaves. The low phosphorus concentrations in the regrowth indicates that phosphorus might be limited in basaltic soils (e.g., 0.1 – 0.25 % P, as shown by Venter et al. 2003). However, because, during the dry season, forage quantity is also limited, the deficit in phosphorus and calcium in the new regrowth can be compensated for by eating old leaves (Prins et al. 2006).

Nutritional Bottleneck Period

The temporal distribution of forage quality and quantity in the African savanna is governed by spatio-temporal variation in rainfall (McNaughton 1990). In the wet season, resource abundance for herbivores is not limiting and is of high quality, but the quality deteriorates already during the wet season as the dry season approaches (Drent and Prins 1987, Owen-Smith 1997, Styles and Skinner 1997). In the dry season, herbivores face difficulties in assembling their diets because of the limited choices they have for high-quality forage products (Owen-Smith 1994, Prins and van Langevelde 2008). In the late dry period, herbivores are vulnerable to loss of condition, starvation, and even death (Dudley et al. 2001, Moss 2001). Many game reserves in southern Africa are fenced, preventing animals from moving to better areas in times of food scarcity. In East Africa, large ungulate migration is linked to nutritional stress periods (Sinclair et al. 1985, McNaughton 1990, Holdo et al. 2009a). Therefore, regrowth of heavily browsed vegetation (e.g., by elephant) is important in enhancing forage quality, which could benefit elephant and other browsing species. We argue that the timing of browsing by elephant can ameliorate nutrient availability during the early and late dry seasons. This, we think, explains the frequent observations of other herbivore species in elephant-browsed areas throughout the dry season (Styles and Skinner 2000, Rutina et al. 2005, Makhabu et al. 2006). Our results show that leaves of Mopane trees have low fibre content within the tolerable range (< 40 % NDF) of small ruminants (e.g., duikers, whose diet contains 10 % - 50 % NDF) (Conklin-Brittan and Dierenfeld 1996, Shipley and Felicetti 2002), with the lowest values (31 %) found in leaves of previously defoliated trees and the highest values found in the control trees (39 %) in the late dry season (October).

Conceptual Model of Browsing Facilitation

We have shown that the timing of defoliation can improve the availability of nutrients in the dry season. Bruno et al. (2003) stated that the inclusion of facilitation in ecological theory will increase our understanding of how nature works. We demonstrate that trees respond differently to herbivore activities in the growing season as compared to the dry season. In the growing season, browsed and control trees both exhibited increases in nutrient concentrations. However, from the end of the growing season to the beginning of the dry season (when leaves are old), trees start reabsorbing nutrients from mature leaves to their storage organs (Fig. 9c; Chapin 1980, Skarpe and Hester 2008). During this period, the leaves that were replaced after defoliated in the growing season were not yet mature(Fig. 9c, dash line).; a period (dry season) at which tree start to re-absorb nutrients from the leaves. As the dry season advances, the previously defoliated trees also began to return nutrients from replacement leaves to storage organs (Fig. 9d), but the forage quality remained relatively higher in the defoliated trees than it was in the control trees. In the late dry season, all defoliated trees parts flushed earlier than non-defoliated trees. The leaf flushed trees showed higher protein and energy contents than the non-browsed trees (Fig. 9d).

In conclusion, improved forage quality in the dry season is crucial to herbivores' survival. The timing of removal of plant parts by either elephant or other browsers creates a growth window further in the dry season and stimulates early leaf flushing, which increases nutrient concentrations in the dry season. The increased nutrient concentrations subsequently shorten the nutritional bottleneck period. The presence of large herbivores (e.g., elephant) therefore plays a major role in creating habitat heterogeneity not only from a nutritional perspective but also in terms of forage biomass (Chapter 3). Therefore, timing of browsing influences changes in forage quality that are exploited by large herbivores particularly in dry season period.

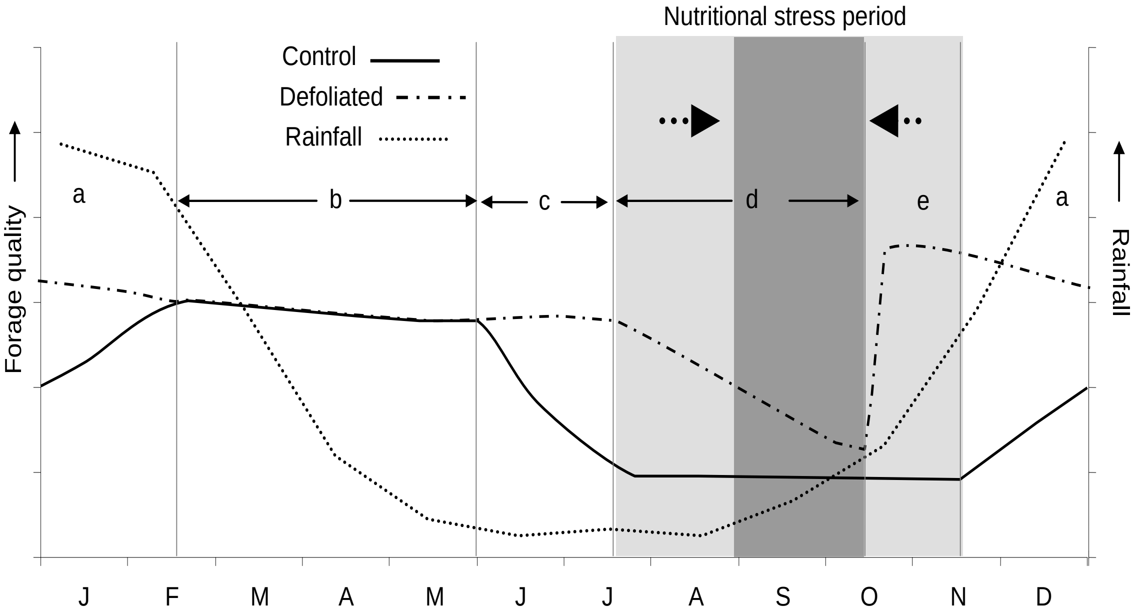


Fig. 9: A conceptual model indicating how nutrients respond to the timing of browsing. The solid line represents the control trees, whereas the broken line represents the defoliated trees. Letter “a” shows the period that is early in the growing season, “b” shows the growing period, “c” shows the senescence period, and “d” shows the dormant period (dry season). Letter “e” indicates the early leaf flush in the late dry season. The light grey area indicates the period when forage nutrients decline, which is referred to as the nutritional stress period. The dark grey colour indicates the extent to which the nutritional stress period is shortened as a result of the timing of browsing. The arrows with thick heads indicate the reduction of the nutritional stress period.

CHAPTER 5

The role of elephant feeding habits on the habitat use of large herbivores: An experimental approach

Edward M. Kohi, Willem F. de Boer, Cornelis van der Waal, Hendrick J. de Knegt, Frank van Langevelde, Herbert H. T. Prins

ABSTRACT

Our knowledge of how elephant feeding affects the habitat use of other herbivorous species is limited. This study investigated the microhabitat choice of herbivorous species in response to the uprooting, pushing over or coppicing of trees by African elephants. We hypothesised that grazers will frequently visit the areas opened by these activities, browsers will visit areas with pushed-over or coppiced trees, and mixed feeders will visit both open areas and areas with pushed-over and coppiced trees. This study was carried out in a Mopane-dominated woodland savanna in South Africa, and the following three vegetation treatments were created to mimic different elephant feeding habits: 1) complete tree removal; 2) pushing trees over and 3) tree snapping or coppicing. Each treatment was replicated three times, and a paired control plot was assigned to each treatment plot. The herbaceous biomass was measured monthly for two years, and the browse biomass was measured at its peak annual production in 2008 and 2009. Dung and spoor counts were measured at intervals of 12 days from June 2007 to April 2009. The results indicated that the total number of animal species identified increased in the treatment plots. The microhabitat selection differed among the small and large herbivorous species as a combined response to increased visibility (thereby providing a greater chance to detect predators on manipulated plots) and an increase in the browse availability at lower feeding heights. Therefore, small predation-sensitive herbivore species (i.e., steenbok, impala and common duiker) preferred the opened plots, whereas the habitat preference of the larger herbivores was less affected by the elephant activity. We found that elephant feeding habits create new habitats that attract small herbivores, which could create a positive feedback loop by increasing soil nutrients through increased dung deposition, thereby attracting grazers and browsers that feed on the promoted plant growth.

INTRODUCTION

Although the conservation of biological diversity has become a common agenda worldwide (Tylianakis et al. 2008), there is an increasing debate among ecologists on the effects that elephants have on species diversity (Fritz et al. 2002, Makhabu 2005, Rutina et al. 2005, Valeix et al. 2007, Valeix et al. 2008). The increases in elephant populations pose a major challenge to conservation managers, who often resort to culling elephants to avert the expected adverse effects of these animals on other species (van Aarde et al. 1999a, Gillson and Lindsay 2003, Owen-Smith et al. 2006, Bode and Possingham 2007). Since the early 1970s, a great deal of research has been conducted on the intense episodic or localised utilisation of trees by elephants (Laws 1970, Caughley 1976, Ben-Shahar 1993, Calenge et al. 2002, Kerley and Landman 2006, Kerley et al. 2008), and this is sometimes referred to as “the elephant problem” (Caughley 1976, Barnes 1982, 1983b). Elephants may push over, topple, snap or uproot large trees, and these behaviours are linked to a decrease in tree density (Jachmann and Bell 1985, Jachmann and Croes 1991, Mapaure and Moe 2009), habitat loss, and the potential decline of meso-browser populations (Fritz et al. 2002). Although the effect of elephant feeding habits on other large herbivorous species, particularly browsers, remains unclear (Fritz et al. 2002, Valeix et al. 2008), there is a limited body of scientific data showing how browsers and grazers change their habitat selection as a result of the impacts of elephant feeding.

Large herbivores are important drivers that structure the heterogeneity of African savanna (Kerley et al. 2008, Kohi et al. 2011, van der Waal et al. 2011). Elephants, in particular, are well documented for their ability to change vegetation structure through breaking tree branches and pushing over, toppling, snapping, and even uprooting trees

(Barnes 1983b, Mtui and Owen-Smith 2006, Sankaran et al. 2008), thereby enhancing the habitat heterogeneity (Kohi et al. 2011). These opened areas facilitate the development of the herbaceous layer (Jachmann and Bell 1985, Jachmann and Croes 1991), and the re-sprouting of browsed shoots increases leaf biomass at heights accessible to small browsers (Kohi et al. 2011). Hence, the distribution of herbivorous species can be affected by elephants given that their habitat use is related to energy and nutrient gain and is, therefore, dependent on, for example, the availability and quality of food (Beekman and Prins 1989, McNaughton 1990, Prins 1996, Dussault et al. 2005). Moreover, the ability of a species to avoid energy loss (e.g., through minimising predation risk) (Riginos and Grace 2008, Briand et al. 2009) or extreme environmental conditions (e.g., high and low temperatures) (Dussault et al. 2005, De Knegt et al. 2010b) are also influenced by tree cover and are, therefore, indirectly determined by the impacts of elephants.

Habitat selection differs between large and small herbivorous species due to differences in body size-related nutrient requirements and variations in their risk of predation (Riginos and Grace 2008). Elephant feeding habits create openings in woodlands (Barnes 1983), and small herbivores may prefer these clearings, as they allow them to feed and detect predators easily (Riginos and Grace 2008). We expect an increase in the herbaceous biomass of opened areas, thus, we hypothesise that grazers will frequent these areas, whereas browsers will visit areas with pushed-over or coppiced trees more frequently, given that these areas have a larger availability of browse at lower feeding heights. We tested these hypotheses in an experiment that simulated elephant feeding impacts in a South African savanna system.

METHODS

Study area

This study was conducted on a wildlife farm situated in the Associated Private Nature Reserves (APNR), bordering the Kruger National Park (1 km to the east) in South Africa. The area is not fenced, and wildlife move freely between the Kruger National Park and the APNR. The area is characterised by a granitic soil, and the vegetation is dominated by mopane (*Colophospermum mopane*) woodlands. A mixture of mopane trees and red bush willow (*Combretum apiculatum*) dominate hilltop areas of the woodlands, whereas the valleys and slopes of this region primarily consist of mopane trees. The long-term mean annual rainfall for 1983–2009 was 431 mm. The mean maximum temperature during 1992–2009 was 40.1ºC in October, and the mean minimum temperature was 3.6ºC in June (Ingwelala weather station, 7 km from the study site).

Experimental setup

We applied a randomised block design, with three blocks that were similar in fire history (all had burned 3 years prior the experiment) and position in the landscape (all are located 0.5 km from a seasonal river and on hilltops). The block effect accounted for the differences in the landscape heterogeneity and, thus, for differences in the wildlife densities. The distance between the plots within a block was 100 m, whereas the distance between the blocks was at least 1 km. The following three treatments were applied to the plots: complete tree removal, tree cutting (resulting in coppiced trees), and pushing trees over. The plots were circular in shape to minimise edge effects and had an area of 900 m^2. The treatments simulated the effects of elephant feeding, such as uprooting and killing trees (complete tree removal), breaking trees close to the ground (tree coppicing) and pushing trees over (some roots remained attached, and the trees survived).

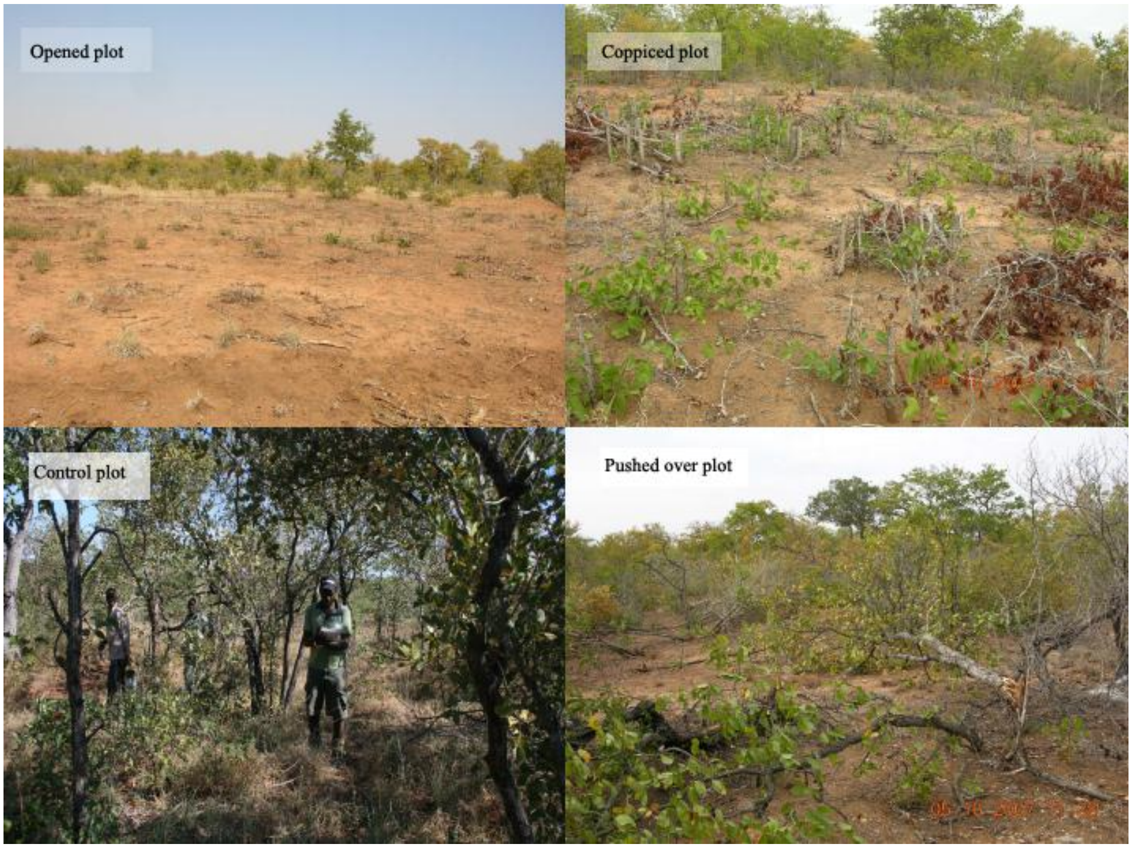


Figure 1. the pictures illustrate the changes in vegetation structure on the experimental plots after applying the treatment

Tree removal (opened plot): Trees were cut close to the ground with a chain saw and treated with a target-specific arboricide (Access, 2%) to prevent re-sprouting. All of the cut parts of the trees were removed from the plots. The overall treatment success was 98%. The recurring shoots of the trees that were not killed were repeatedly removed.

Tree cutting (coppiced plot): Trees were cut at 50 cm above the ground using a chain saw without chemical treatment to allow re-sprouting. All of the cut parts of the trees were removed from the plots.

Pushed-over tree plot: Trees were pulled over using a 2 ton Magnum hand winch to mimic how elephants push trees over. To accomplish this, the winch was anchored to large trees with a cable, and the trees in the plots were subsequently pulled down. Because we intended to imitate the effects of elephants, we pulled the trees into different directions within a plot by hauling from different angles; indeed, a windfall would result in the trees resting in a similar manner. All of the pushed-over trees re-sprouted in the following growing season.

These treatments were carried out between April and May of 2007. Each treatment was replicated in blocks and paired with a control plot (at a distance of 100 m between the plots), yielding a total of eighteen plots, nine of which were control plots. For clarity, the control plots were named after their treatment (i.e., opened control, coppiced control and pushed-over control). At the border of each treatment and control plot, four 1x10 m strips (spoor beds) were created for counting animal spoors. Herbaceous plants in spoor beds were removed, and the soil surface was softened to facilitate spoor recognition and identification.

Spoor count: A trial of spoor disappearance rates was conducted for two weeks on steenboks and elephants. During this period, the test sites were visited five times, every three days. The elephant spoor was difficult to detect after day 15; although elephants are large and heavy, their feet do not leave deep tracks. The steenbok tracks were still detectable on day 15 by an experienced field ranger because of their sharp hooves. From these observations, we decided to set the spoor-observation interval (the time between raking the spoor plot and the observation) to 12 days. The spoor identification at a species level was performed by two experienced field rangers (>30 years of work). The number of individual animals that had crossed the spoor beds was counted, and the species count per plot was documented. Spoor and dung were sampled and counted every 12 days from June 2007 to March 2009.

Dung count: All of the dung piles were counted in each plot and recorded per species. The dung piles that were recorded were marked with coloured pebbles to avoid double counting, with each sampling day represented by a different coloured pebble. The dung counts were carried out at similar intervals as spoor counts.

Vegetation measurement: At the end of the growing season (April 2008 and April 2009), the leaf biomass of the trees was estimated following the BECVOL method (Smit 1996, Kohi et al. 2011), which uses canopy volume to estimate the leaf biomass. The number of trees that had flushed leaves in the late dry season (November 2008) was counted, and the proportion of flushed trees was calculated per treatment. The combined biomass of grass and herbal dicots was measured monthly (January 2008 to April 2009) using a calibrated disc pasture metre (Trollope and Potgieter 1986, Zambatis et al. 2006), taking twenty readings per plot.

Data Analyses

We tested for differences in the herbaceous biomass between the seasons (early to middle growing period – December to February; middle to late growing period – March to June; dry season – July to November) using an ANOVA followed by a Game-Howell test. To test for differences in the browse biomass production and the vertical distribution of the browse biomass among the treated plots, we also applied an ANOVA, followed by Tukey post-hoc tests to differentiate between the treatments and the control. We used a Kruskal-Wallis test followed by Scheffé's post-hoc test to determine the differences in the proportion of trees that had flushed leaves late in the dry season among the treatment groups.

The dung and spoor count data were first used to estimate the species richness following the Abundance-based Coverage Estimate (ACE) method (Magurran 2004) using EstimateS software version 7.5.1. The differences in species richness for (1) dung count-derived estimates and (2) spoor count-derived estimates were then tested using a general linear model. In this model, the species richness estimate was the dependent variable, the treatments and control were the fixed factors, the time (sampling date) was used as a covariate, and the blocks were random variables. Sidak post-hoc tests were used to test for differences between the treatment areas and control plots.

The daily visitation rate was calculated from the total number of individuals per species crossings divided by the sampling interval (12 days). A general linear model was used to test for differences in the visitation rates among the treatment areas and was followed by a Sidak post-hoc test. The dependent variable was the accumulated visitation rate per plot, the block was used as a random factor, and the sampling date was used as a covariate. The data from giraffes, warthogs, and wildebeest were not analysed because of their low sample sizes.

The dung counts were accumulated over time per plot and per species from June 2007 to April 2009. A general linear model was used to test for differences in the accumulated dung deposition rates. The differences between the treatment areas and control plots were analysed using a Sidak test. Each species was modelled independently. The data from white rhino, giraffes, warthogs and wildebeest were not analysed due to low dung counts or non-random defecation behaviour (i.e., latrine use by white rhino).

Spoor and dung ratio

To test for differences among the treatment groups, we considered the local spatial differences. Therefore, for each species *i*, we calculated a ratio, P_i, that expresses the relative difference between the quantity of spoor or dung counted on a treatment plot and that counted on its paired control plot. The formula is as follows:

$$Pi = \frac{\left(Aci_{Tp} - Aci_{Cp}\right)}{Aci_{Tp}}$$

P*i* = proportion for species *i*;

Ac = accumulated dung or spoor density

Tp = treatment plot

Cp = control plot

Differences in the dung or visitation rates between the treatments were analysed using a general linear model, as described above, where P*i* is the dependent variable correcting for local differences in the visitation rates.

RESULTS

Forage availability

Herbaceous biomass – The herbaceous biomass was the highest in the opened plots (1200 kg/ha) in the growing season (February) and the lowest (400 kg/ha) in the coppiced plots in the dry season (October). The herbaceous biomass differed between the three periods, i.e., early to middle growing season (December-February), middle to late growing season (March-June), and the dry season (July-November; $F_{2,180}$=19.433, P<0.001, Fig. 2). As expected, the lowest biomass values occurred during the dry season (Game-Howell, P=0.01, Fig. 2). The herbaceous biomass did not differ among treatments ($F_{2,180}$=1.585, P=0.167).

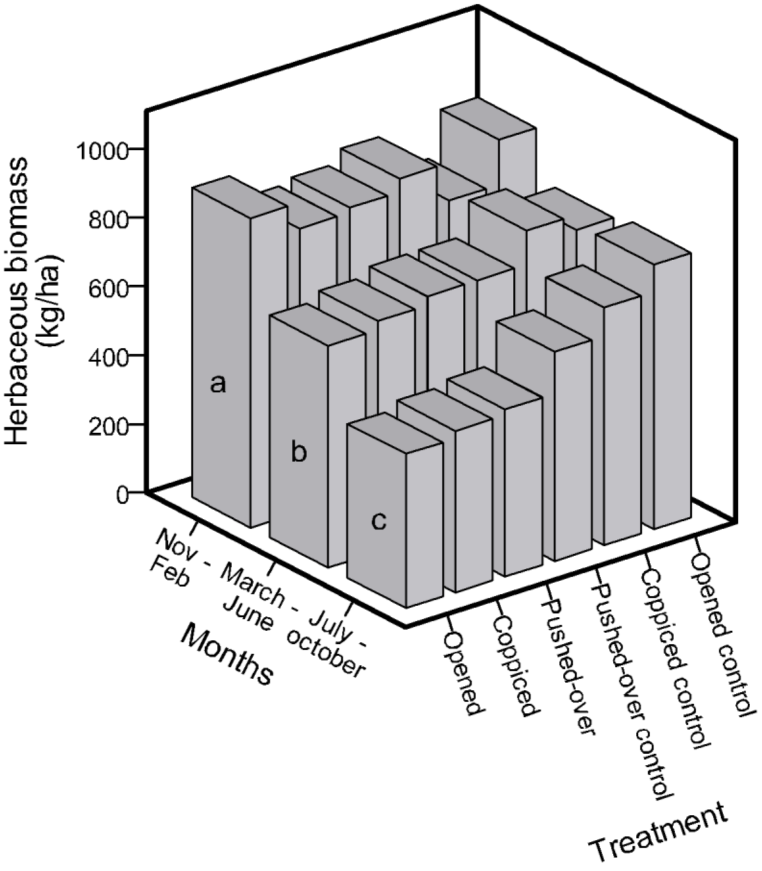


Figure 2. Estimated mean herbaceous biomass in kg/ha in all treatments from January 2008 to March 2009.
The letters indicate significant differences calculated (Game-Howell post-hoc test, P<0.001) among the three seasonal periods

Browse biomass – The treatments significantly affected the leaf biomass of the trees ($F_{2,60}$=29.487, P<0.001), and there was a significant interaction between the treatment and the vertical distribution of the leaf biomass ($F_{8,60}$=73.302, P<0.001). Pushed-over trees had a significantly higher total leaf biomass (Tukey, P<0.01) than the coppiced and control trees. The leaf biomass increased at lower heights (<1.5 m) for the pushed-over and coppiced trees (Tukey, P<0.05, Fig. 3), whereas the control trees had more leaf biomass above 1.5 m. Taken together, the treatment and height variables explained the majority of the variation observed in the leaf biomass (R^2_{adj}=0.91).

Early leaf sprouting – One week after the first rain, we found that the coppiced trees had a significantly higher proportion of new leaves, followed by the pushed-over trees, whereas the lowest proportion was found in the control plots (Chi-Square=9.689, df=2, P<0.01, Scheffé's, P<0.05; Fig. 4).

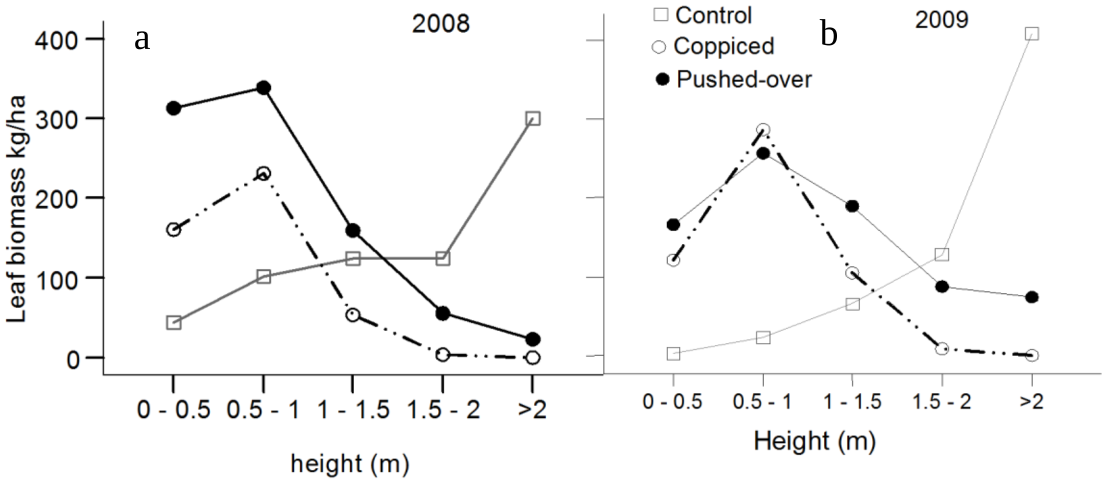


Figure 3. Mean tree leaf biomass (kg/ha) on coppiced, pushed-over, and control trees measured in April 2008 (3a) and April 2009 (3b). The graphs illustrate the increase in leaf biomass at lower heights when trees are pushed-over or coppiced compared to control trees.

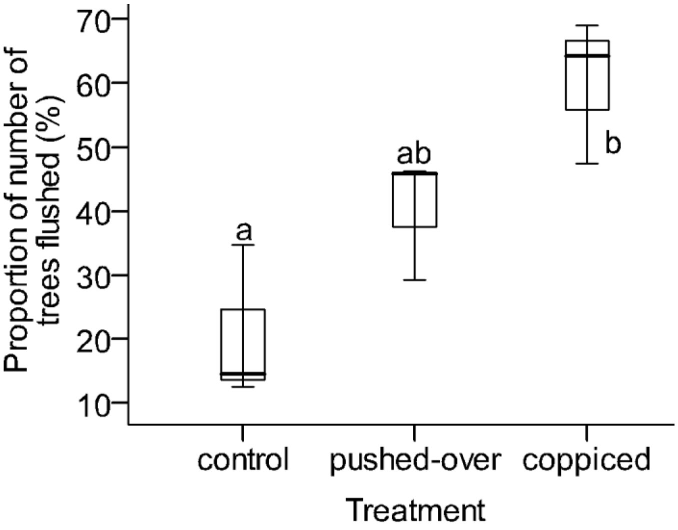


Figure 4. Box plot showing median, 25% and 75 % quartiles (boxes) and minimum and maximum values (whiskers) of the proportions of early flushed leaves among the three treatments at the beginning of the growing season in November 2008.

Species diversity

Using spoor and dung counts, 24 large mammalian species were identified as having visited the plots (Appendix 1), fifteen of which were herbivores and nine of which were carnivores. The simulated elephant feeding habits influenced the estimated animal species richness, as measured by dung count ($F_{5,682}$=173.2, P<0.001) and spoor count ($F_{5,233}$=12.887, P<0.001). Based on the dung and spoor counts, the opened plots had a higher species richness than the control plots (Sidak, P<0.001). The dung counts indicated a higher animal species richness in the coppiced plots than in the control plots (Sidak, P<0.01, Fig. 5a), whereas the spoor counts indicated that the animal species richness was similar between the coppiced and control plots (Fig. 5a). Based on the spoor counts, the pushed-over plots were used by more animal species than the control plots (Sidak, P<0.001), whereas no differences were detected from the dung count data (Fig. 5b).

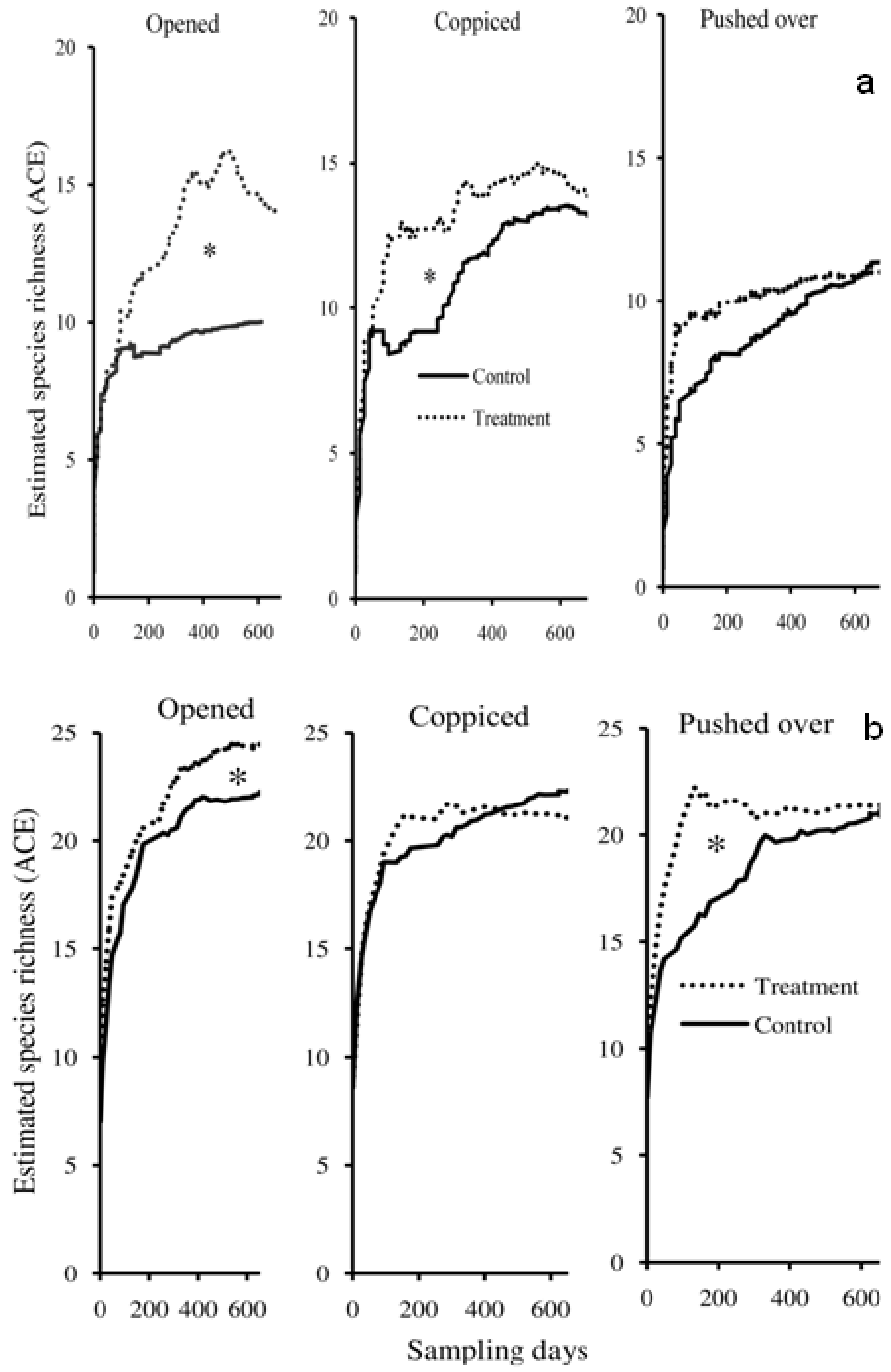


Figure 5. Estimated animal species richness over time (sampling days) from June 2007 to April 2009 in three treatments and their respective control for spoor (a) and dung counts (b). The asterisk indicates significant differences between treatment and control (Sidak, P<0.01).

Visitation rates based on spoor count

Browsers – Vegetation manipulation had a significant influence on the visitation rate of browsers (steenbok: $F_{5,639}$=34.211, P=0.0001; greater kudu: $F_{5,639}$=84.214, P=0.001; common duiker: $F_{5,639}$=22.943, P=0.0001; Fig. 6a). Steenbok visited the opened-up and coppiced plots more frequently than their respective control plots (Sidak, P<0.001), but they did not differentiate between the pushed-over plots and the control plots (Sidak, P>0.05). Common duiker visited the opened plots more than the corresponding control plots (Sidak, P<0.001) but did not differentiate between the pushed-over plots, coppiced plots and control plots (Sidak, P>0.05). When comparing the treatment plots (i.e., opened-up, coppiced, and pushed-over plots), the steenbok and common duiker visited the opened plots more than the coppiced and pushed-over plots (Table 1). Greater kudu rarely visited the opened plots, and the visitation rates were higher in the pushed-over and coppiced plots (Table 1). The kudu visitation frequency did not differ between the control plots and pushed over plots (Sidak, P>0.05), but the kudu were found to visit the control plots more than the coppiced (Sidak, P<0.01) and opened plots (Sidak, P<0.01; Fig. 6a).

Table 1. Results of the ANOVA analysis used to test for differences in visitation rates among the three categories (opened, coppiced and pushed over plots), with F, P and R^2_{adj} values. The dependent variable was expressed as the relative differences between observed and control values. Letters indicate significant differences (Game-Howell, P=0.01) among the treatments. A higher numbers of plus symbols indicates relatively higher visitation rates.

Species	Statistics	P values	R^2_{adj}	Treatment comparison		
				opened	coppiced	Pushed over
Steenbok	$F_{2, 321}$=14.543	<0.0001	7.7	+++a	++b	+c
Common duiker	$F_{2, 321}$=19.276	0.0001	10.2	+++a	+b	++b
Greater kudu	$F_{2, 321}$=39.438	0.0001	19.2	+a	++b	+++c
Common zebra	$F_{2, 321}$=13.379	0.0001	7.1	+++a	++b	+b
African buffalo	$F_{2, 321}$=39.780	0.0001	19.4	+++a	++b	+c
White rhino	$F_{2, 200}$=64.685	0.001	40.4	+++a	+b	++b
Impala	$F_{2, 321}$=34.152	0.0001	17	+++a	+b	++c
African elephant	$F_{2, 221}$=37.005	0.001	49.3	++a	+++b	+a

Grazers – The visitation rates of grazers differed between the treatments and their corresponding control plots for buffalo ($F_{5,639}$=39.144, P<0.01) and white rhino ($F_{5,639}$=39.265, P<0.01) but not for zebra (Fig. 6b); the visitation rates for zebra were similar between the treatments and their control areas (Fig. 6b). The buffalo visited the control plots more than the pushed-over plots (Sidak, P<0.001) and did not visit the opened plots (Sidak, P>0.05), coppiced plots (Sidak, P>0.05) or their control areas. The white rhino visited the opened plots (Sidak, P<0.001) and pushed-over plots (Sidak, P<0.001) more than the control plots but visited the coppiced plots and their controls at similar rates (Sidak, P>0.05). When comparing the treatments (i.e., opened, coppiced and pushed-over), all three of the grazer species registered the highest visitation rates in the opened plots (Table 1).

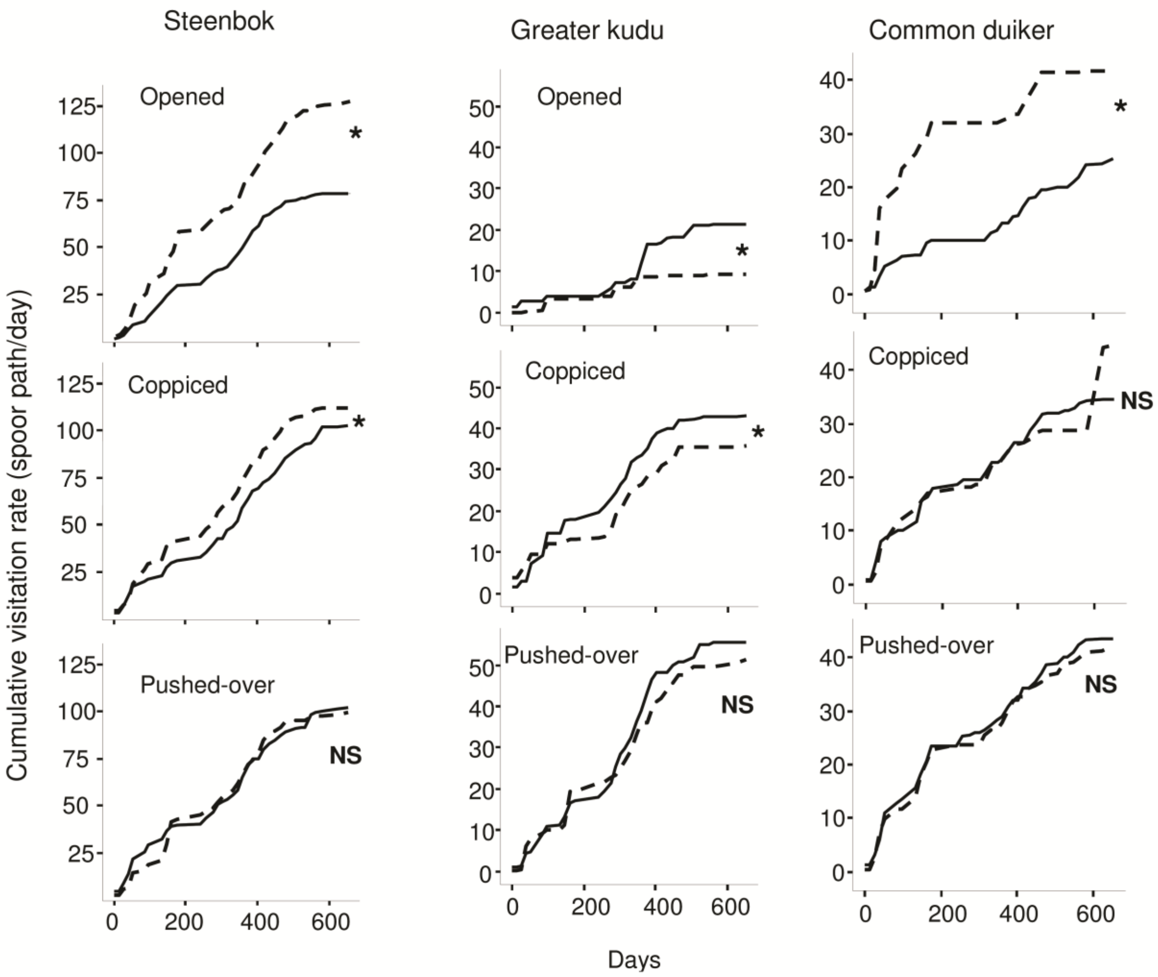


Figure 6a Browsers' cumulative visitation rates on plots with three different treatments that simulated elephant feeding impact (opened plots and plots with coppiced and pushed over trees) and control plots for a period of two years in a mixed mopane woodland. The dashed lines indicate the treatments and the solid lines the controls. NS indicates no significant difference between treatment and control while asterisk indicate a significant difference at $P<0.05$.

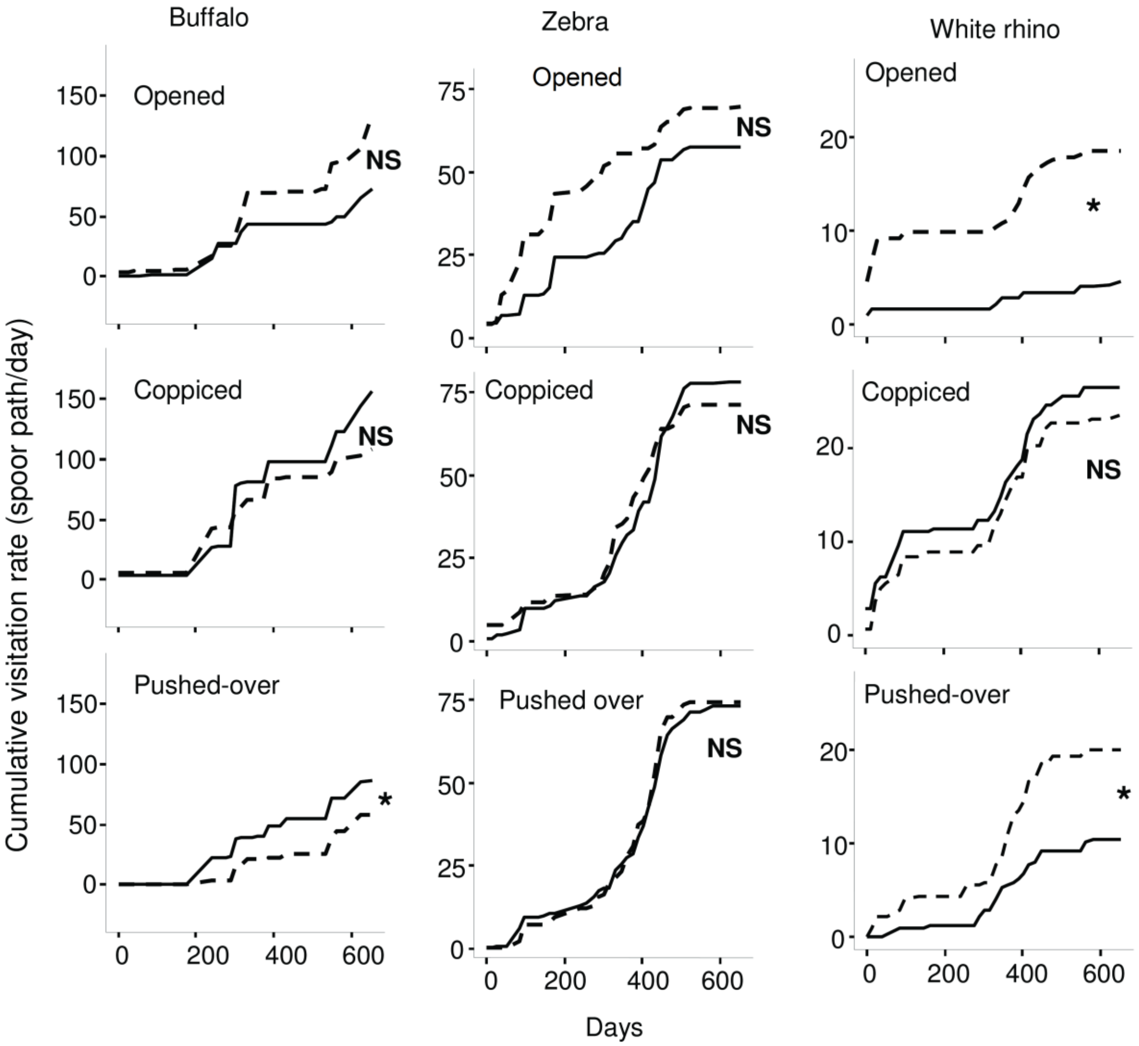


Figure 6b Grazers' cumulative visitation rates on plots with three different treatments that simulated elephant feeding impact (opened plots and plots with coppiced and pushed over trees) and control plots for a period of two years in a mixed mopane woodland. The dashed lines indicate the treatments and the solid lines the controls. NS indicates no significant difference between treatment and control while asterisk indicate a significant difference at P<0.05.

Mixed feeders – The manipulation of vegetation also influenced the visitation rate of the mixed feeders (impala: $F_{5,639}$=50.981, P<0.01; elephant: $F_{5,639}$=97.468, P<0.001, Fig. 6c). The impala had higher visitation rates in the opened plots than in the control plots (Sidak, P<0.001), but their visitation rates in the coppiced (Sidak, P>0.05) and pushed-over

(Sidak, P>0.05) plots were similar to those for the control plots. Among the treatment groups, the impala visited the opened plots most frequently, followed by the pushed-over plots (Table 1).

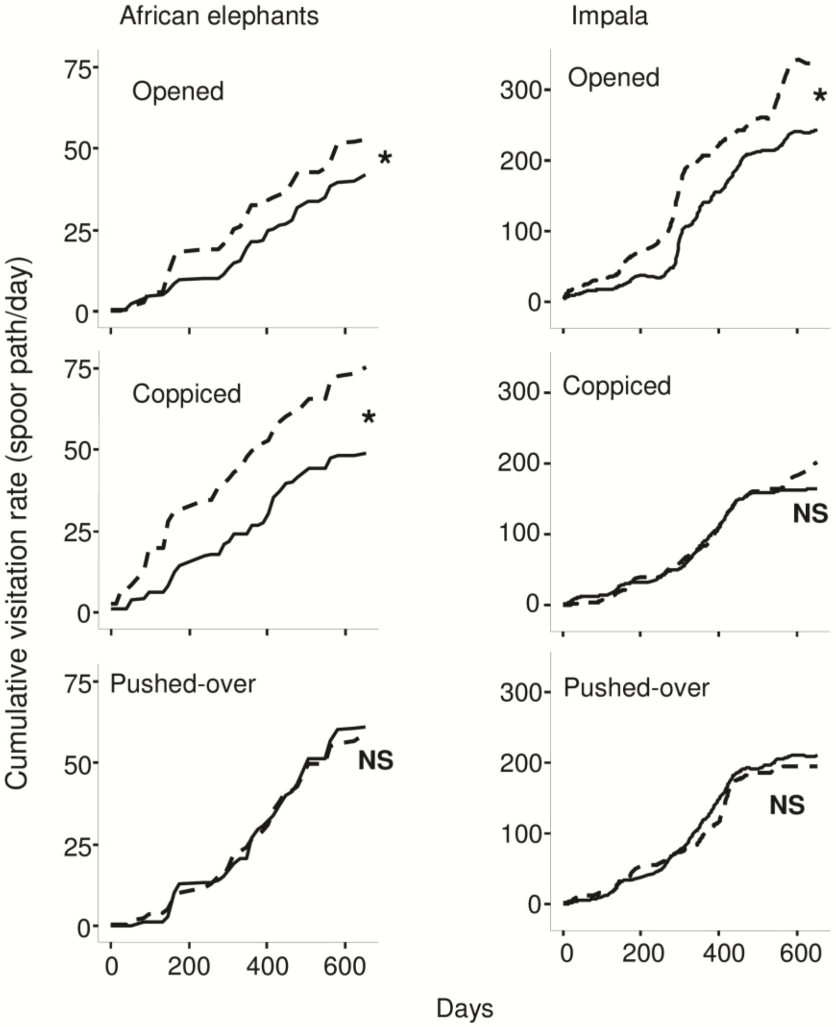


Figure 6c Mixed feeders' cumulative visitation rates on plots with three different treatments that simulated elephant feeding impact (opened plots and plots with coppiced and pushed over trees) and control plots for a period of two years in a mixed mopane woodland. The dashed lines indicate the treatments and the solid lines the controls. NS indicates no significant difference between treatment and control while asterisk indicate a significant difference at P<0.05.

The visitation rates of elephants were higher in the opened (Sidak, $P<0.001$) and coppiced plots (Sidak, $P<0.001$) than in their corresponding control areas, whereas the elephant visitation rates in the pushed-over plots were similar to those of the control plots (Sidak, $P>0.05$). By comparing the visitation rates among the treatment groups, we found that elephants visited the coppiced plots the most, followed by the opened-up plots, and with the pushed-over plots having the lowest visitation rates (Table 1).

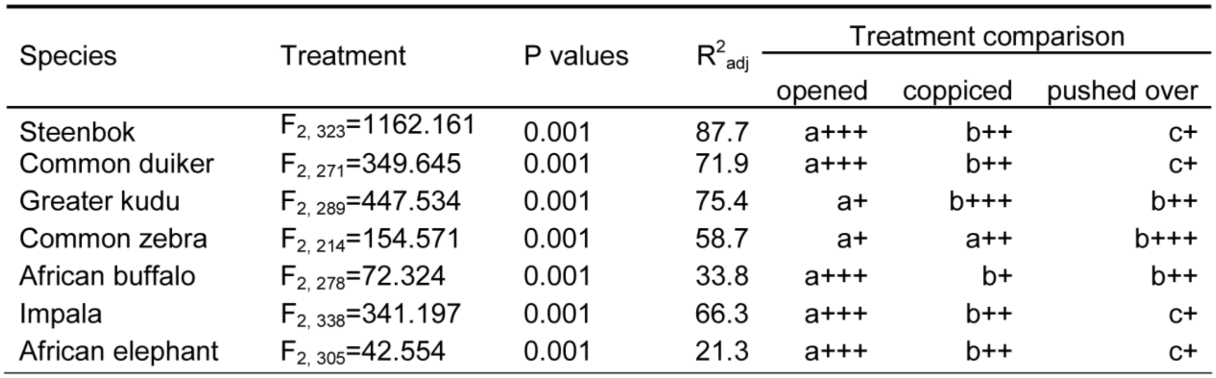
Dung deposition rates

Browsers – The simulation of elephant feeding impacts influenced the habitat use of browsing species, as measured by their dung deposition (steenbok: $F_{5,680}=74.69$, $P<0.01$; common duiker: $F_{5,680}=84.481$, $P<0.01$; greater kudu: $F_{5,680}=30.706$, $P<0.01$; Fig. 7a). The small browsers (common duiker and steenbok) deposited more dung in the opened plots than in their control plots (Sidak, $P<0.01$) but also deposited less dung in the pushed-over plots than in the control plots (Sidak, $P<0.01$). The medium-sized browsers (Greater kudu) deposited less dung in the opened plots than in the control plots (Sidak, $P<0.001$) but did not use the control plots differently from the coppiced (Sidak, $P>0.05$) or pushed-over plots (Sidak, $P>0.05$). The kudu deposited more dung in the coppiced plots than in the opened plots (Table 2), and the common duiker and steenbok deposited more dung in the opened plots than in the coppiced and pushed over plots (Table 2).

Grazers – Our vegetation manipulation also affected the dung deposition rates of grazers (zebra: $F_{5,680}=70.592$, $P<0.001$; buffalo: $F_{5,680}=24.488$, $P<0.01$; Fig. 7b). Zebra droppings were rarely found in the opened or coppiced plots, and this was contrary to our expectations that grazers would visit these plots more frequently (Table 2). The zebras had significantly higher dung accumulation rates in the control plots than in the opened

(Sidak, $P<0.001$) or coppiced plots (Sidak, $P<0.001$) and apparently did not discriminate between the pushed-over plots and their control areas (Sidak, $P>0.05$). The buffalo had a higher dung accumulation rate in the plots that were opened up (Sidak, $P<0.001$) and deposited less dung in the coppiced and pushed-over plots compared to their control plots (Sidak, $P<0.001$).

Table. 2 A comparison of proportion of dung deposition in different simulated elephant feeding categories. ANOVA analysis used to differentiate high dung deposition among the three categories (opened, coppiced and pushed over plots). Letters indicate significant differences (Game-Howell, P=0.01) among the treatments. A higher number of plus symbols indicates higher dung deposition.



Species	Treatment	P values	R^2_{adj}	Treatment comparison		
				opened	coppiced	pushed over
Steenbok	$F_{2,\,323}=1162.161$	0.001	87.7	a+++	b++	c+
Common duiker	$F_{2,\,271}=349.645$	0.001	71.9	a+++	b++	c+
Greater kudu	$F_{2,\,289}=447.534$	0.001	75.4	a+	b+++	b++
Common zebra	$F_{2,\,214}=154.571$	0.001	58.7	a+	a++	b+++
African buffalo	$F_{2,\,278}=72.324$	0.001	33.8	a+++	b+	b++
Impala	$F_{2,\,338}=341.197$	0.001	66.3	a+++	b++	c+
African elephant	$F_{2,\,305}=42.554$	0.001	21.3	a+++	b++	c+

Mixed feeders – The dung accumulation rates of the mixed feeders were influenced by the vegetation manipulation (African elephant: $F_{5,680}=57.613$, $P<0.001$; impala: $F_{5,680}=86.213$, $P<0.001$; Fig. 7c). The impala had a higher dung deposition in the opened plots than in the control plots (Sidak, $P<0.001$), whereas in the plots that had been coppiced (Sidak, $P>0.05$) or where the trees were pushed-over (Sidak, $P>0.05$), the dung accumulation rates were not different from the control plots. Impala also deposited more dung in the opened compared to the coppiced and pushed-over plots (Table 2). In contrast, the elephants had relatively high levels of dung deposition in the open and pushed-over plots compared to the coppiced plots (Table 2). The elephant dung piles in the pushed-over (Sidak, P>0.05) and opened plots (Sidak, P>0.05) were similar in volume to those in the corresponding control plots, whereas the dung accumulation in the coppiced plots was lower than that found in the control plots (Sidak, P<0.001).

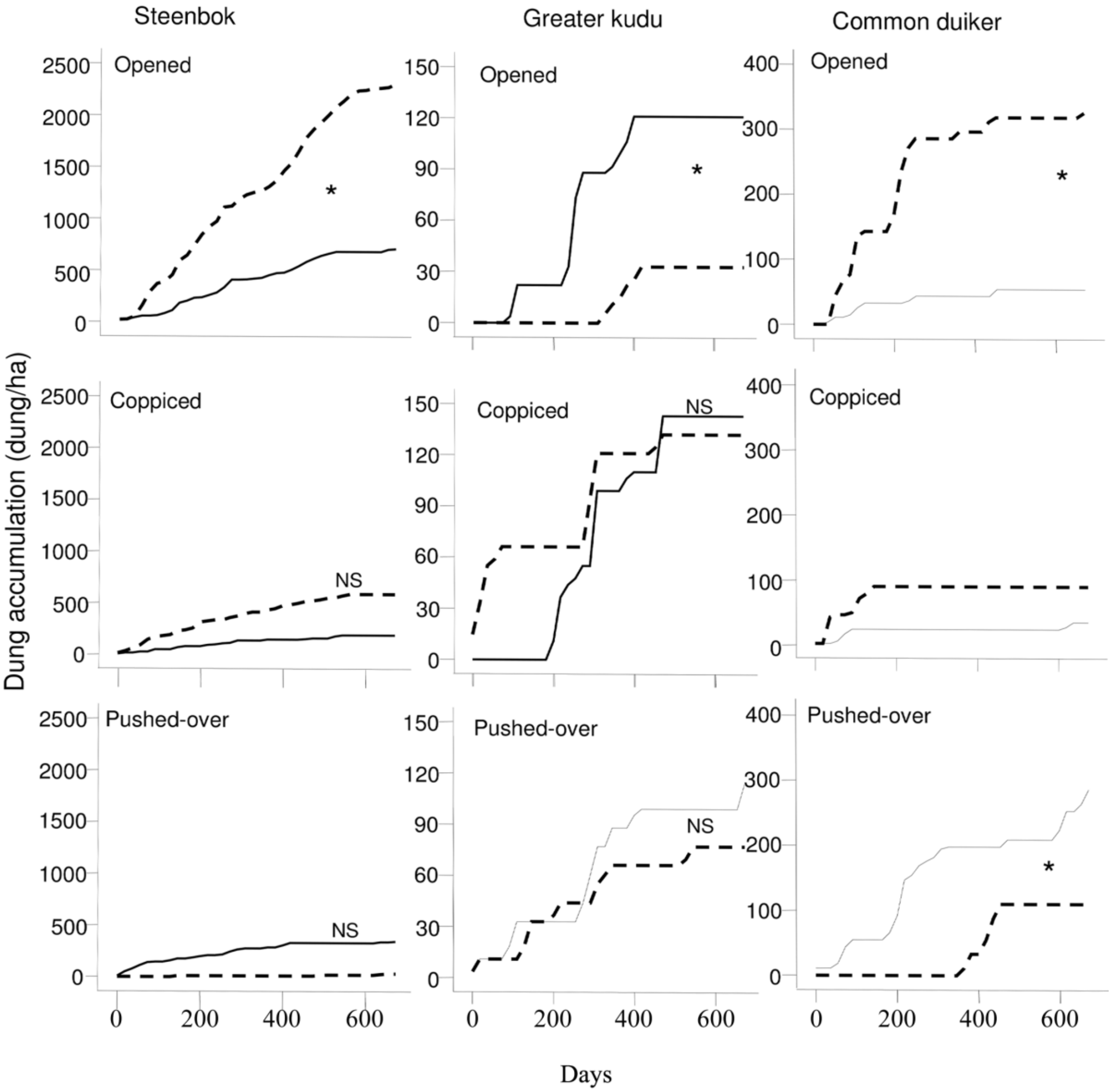


Figure 7a. Browsers' cumulative dung accumulation rates on plots with three different treatments that simulated elephant feeding impact (opened plots and plots with coppiced and pushed over trees) and control plots for a period of two years in a mixed Mopane woodland. The dashed lines indicate the treatments and the solid lines the controls. NS indicates no significant difference between treatment and control while asterisk indicate a significant difference at P<0.05.

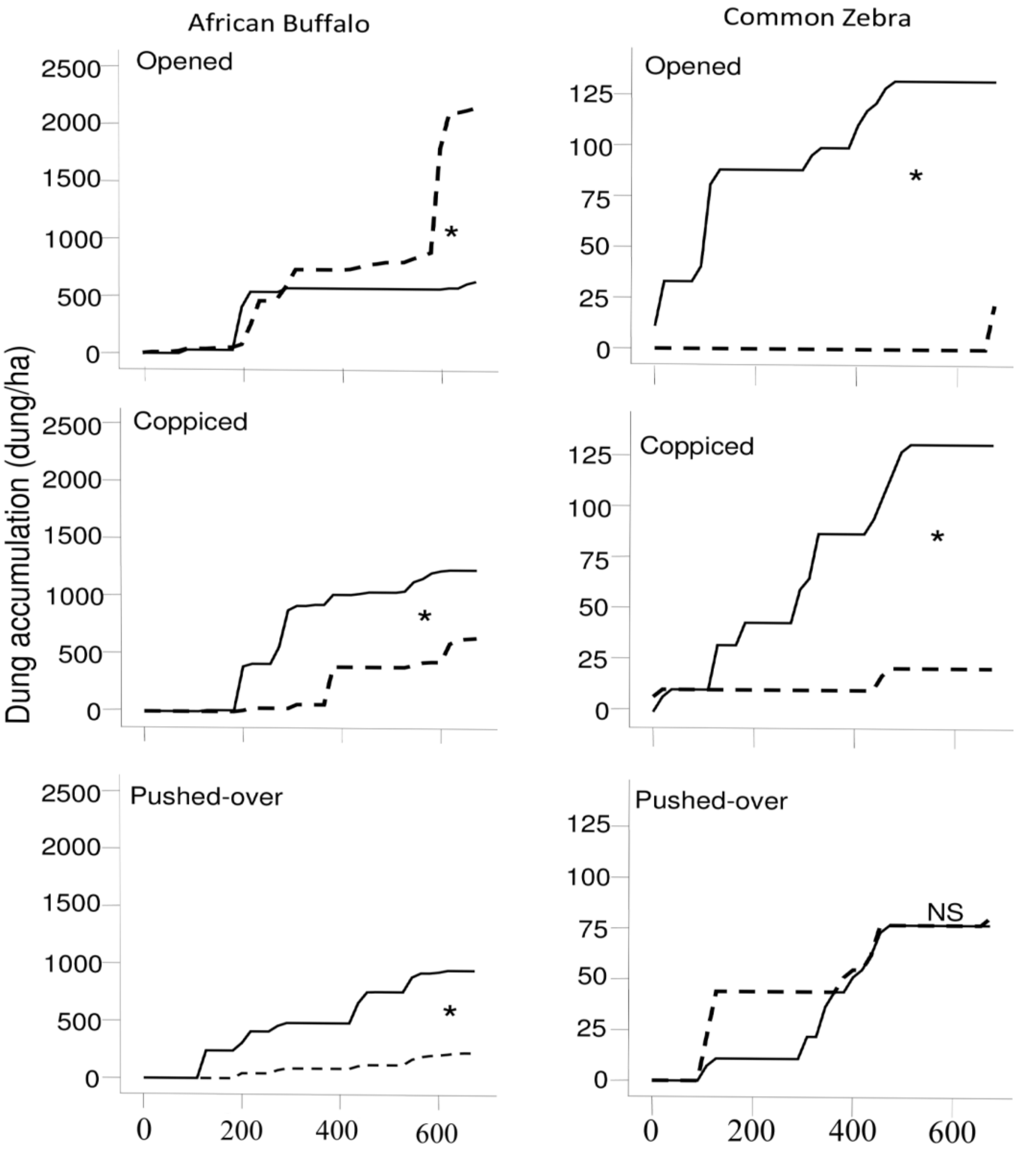


Fig. 7b. Grazers' cumulative dung accumulation rates on plots with three different treatments that simulated elephant feeding impact (opened plots and plots with coppiced and pushed over trees) and control plots for a period of two years in a mixed Mopane woodland. The dashed lines indicate the treatments and the solid lines the controls. NS indicates no significant difference between treatment and control while asterisk indicate a significant difference at P<0.05.

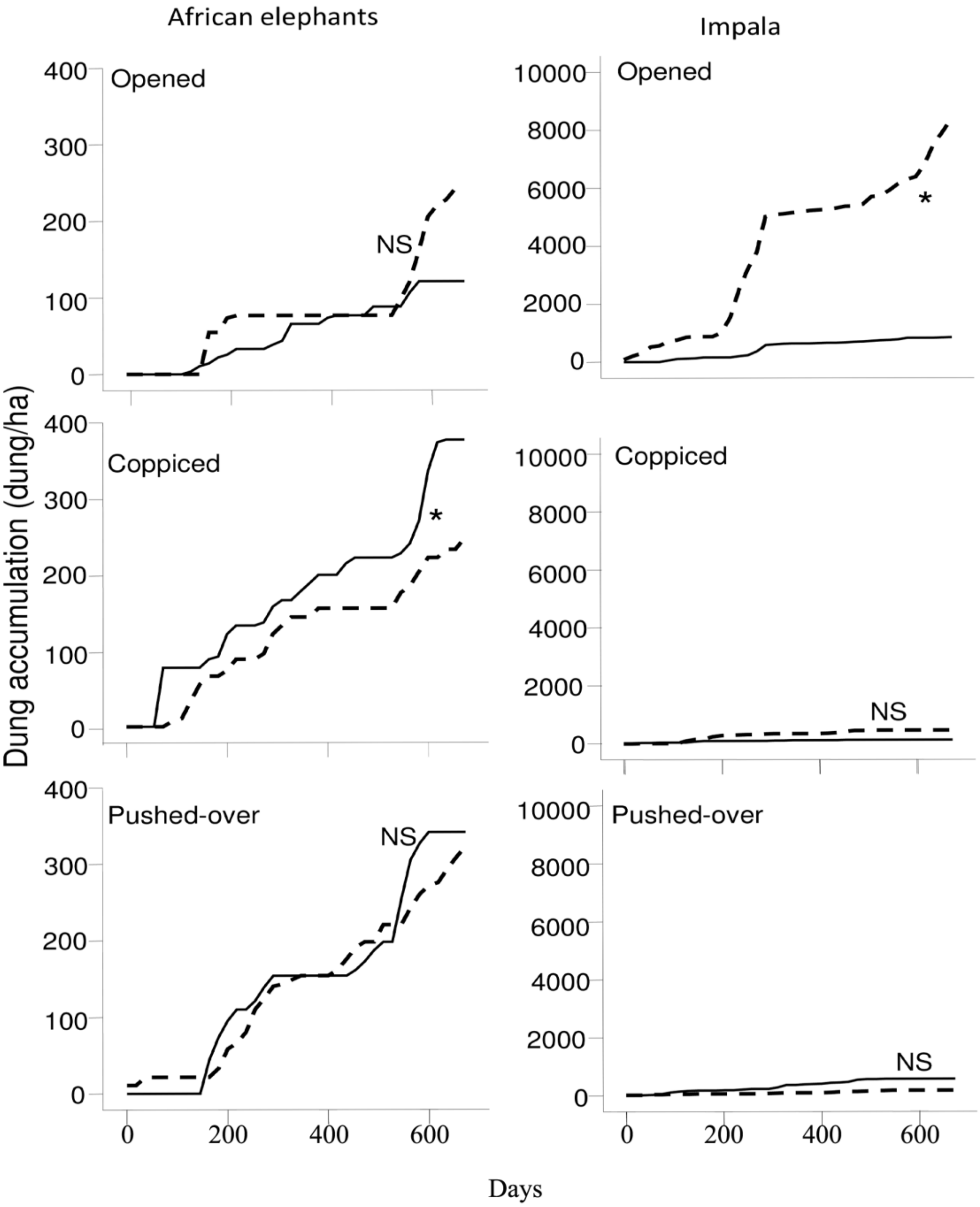


Fig. 7c. Mixed feeders’ cumulative dung accumulation rates on plots with three different treatments that simulated elephant feeding impact (opened plots and plots with coppiced and pushed over trees) and control plots for a period of two years in a mixed Mopane woodland. The dashed lines indicate the treatments and the solid lines the controls. NS indicates no significant difference between treatment and control while asterisk indicate a significant difference at P<0.05.

DISCUSSION

The effect of elephant feeding habits on vegetation and animal species richness has been a widely debated topic, but these discussions and their corresponding evidence have generally been based on correlative or short-term studies (Cumming et al. 1997, Fritz et al. 2002, Valeix et al. 2008). Jacobs and Biggs (2002) showed that large trees might be lost as a consequence of elephant feeding, triggering a decrease in browse availability. However, in this study we showed that all trees that were simulated elephant feeding were recovered in the following growing season and hence changed the dynamic of browse availability and its effect to various herbivorous species and probably of carnivore too.

Habitat selection involves a trade-off between maximising gains (e.g., increased forage) and minimising losses (e.g., higher predation risk) (Masse and Cote 2009) such that species avoid areas with scarce resources or high predation risks (Dussault et al. 2005). Our visitation and dung data suggest that the creation of open patches in woodlands due to simulated elephant impacts benefited certain species, such as steenbok, common duiker and impala, thereby indicating that the loss of trees due to elephant foraging can have positive cascading effects on these species.

For decades, the management of elephants has focused on culling and translocating certain populations (van Aarde et al. 1999b, Slotow et al. 2008) and contraceptive use (Pimm and van Aarde 2001, Bertschinger et al. 2008) in an effort to minimise the negative effects of elephant foraging on vegetation. Although it has been suggested that herbivore diversity can be negatively affected by elephant feeding impacts (Fritz et al. 2002, Valeix et al. 2008), the effects of elephant feeding behaviour on the habitat use and species diversity of other animal species remains poorly understood. The findings from our two year field experiment indicated that estimated animal species richness was higher in plots with manipulated vegetation than in the control plots. Other studies have also indicated that trees browsed by elephants attract other herbivorous species, such as greater kudu (Makhabu 2005), impala (Rutina et al. 2005) and eland (Styles and Skinner 2000), due to increases in forage availability and quality. Small herbivorous species (i.e., steenbok, impala and common duiker) showed a strong preference for the opened plots. In contrast, the kudu avoided the opened plots and selected the pushed-over plots. On a landscape scale, Fritz *et al*. (2002) suggested that elephants had negative impacts on meso-browsers. However, in our study, we found that small browser species benefited from the simulated elephant feeding habits on a finer spatial scale (900 m^2 plot), as these meso-browsers showed a preference for open areas over plots with increased food availability. One explanation for this attraction to these opened plots is that species differ in their predator avoidance strategies. For example, impala use vigilance to detect predators (Smith and Cain 2009, Valeix et al. 2009), whereas kudu prefer to hide in the bush as a means to avoid predators (Estes 1991). Hence, these different anti-predation strategies might determine the impact that elephants have on other herbivorous species.

The grazers in our study sites were all large herbivores (zebra, buffalo and white rhino) and had dissimilar habitat-use patterns. For example, the buffalo had a higher dung accumulation rate in areas that had been opened-up than in the control plots, but their visitation rates, as indexed by the spoor counts, were similar in both of these sites. Contrary to our expectations, the zebra had a higher dung accumulation in the control plots compared to the opened-up plots, but the control and opened plots had similar spoor counts for this species. White rhino normally defecate in middens, therefore only the spoor counts were analysed. As expected, these were higher in the opened plots. These patterns suggest that large grazers might not be strongly affected by elephant feeding habits on the spatial scale of manipulation covered in this study and that other factors, such as competition and social behaviour, might be more influential. For instance, buffalo graze in large social herds (Prins 1996).

The herbaceous biomass of opened plots was similar to that of the other treatments, even though the opened plots were visited more frequently by herbivores, as evidenced by the higher dung densities recorded in these plots. Hence, we could not illustrate a possible higher offtake by herbivores by measuring the aboveground biomass. However, we expect that the herbaceous layer in these opened plots had a higher net production capable of sustaining higher offtake rates (De Mazancourt et al. 1999). A study by van der Waal et al. (2011) showed that, in open areas, small herbivores eliminated competing trees and increased nutrient cycling through dung deposition and that this facilitated the production of high-quality grasses. This contrasts with the suggestion that the predilection of elephants to push over trees will lead to a lower grass quality as a consequence of the observed positive effects of trees on sub-canopy grasses through providing nutrient pumping or shade (Treydte et al. 2007, Treydte et al. 2009). Hence, areas opened up by elephant activity can attract smaller herbivores, possibly due to improved possibilities for predation detection, and these higher densities of smaller herbivores can lead to increased dung accumulation, thereby benefiting the productivity and quality of the herbaceous layer and triggering a feedback loop (van der Waal et al. 2011).

Elephants are ecosystem engineers that modulate their environment, triggering cascading effects that affect several other species (Jones et al. 1994, Jones et al. 1997). This modulation enhances resource heterogeneity (Pringle et al. 2010) and species diversity (Tylianakis et al. 2008). In nature, ecosystem engineering has been demonstrated in a number of other systems. For example, beaver dams create new habitats with multiple niches that are capable of attracting a variety of plant and animal species (Bartel et al. 2010), and cyanobacteria and shrubs in the desert accumulate soil and water (Shachak et al. 1998), thus initiating the formation of a new habitat for other organisms. Elephants transform the architecture of savanna trees (Rutina et al. 2005, Sankaran et al. 2008, Guldemond and van Aarde 2010) by affecting the forage availability at different feeding heights and creating open patches, thereby influencing the availability of habitats for other species. This study shows that the composition of herbivore communities is influenced by elephant-modulated changes in the vegetation.

In conclusion, our experimental manipulation of the vegetation structure in a savanna woodland simulated different elephant feeding modes, affected habitat heterogeneity, and changed the availability of grass and browse. As such influencing the habitat choices of various herbivorous species and increasing animal species richness. An increase in vegetation openness positively influenced the visitation rates of small, but not large, herbivorous species. These results pose a challenging new question to ecologists, namely whether the positive effects of elephants on the habitat selection by smaller species also leads to population density effects. The findings of this study, thus, function as an original contribution to the existing theories on the facilitation of plant-animal interactions.

ACKNOWLEDGEMENTS

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Appendix 1.

A list of animal species that were identified in the study area. The first column is common name, and then scientific name, family name and the last column is the mode of feeding.

No	Common name	Scientific name	Family	Feeding type
1	Common duiker	*Sylvicapra grimmia*	Bovidae	Browser
2	Giraffe	*Giraffa camelopardalis*	Giraffidae	Browser
3	Greater kudu	*Tragelaphus strepsiceros*	Bovidae	Browser
4	Steenbok	*Raphicerus campestris*	Bovidae	Browser
5	African civet	*Civettictis civetta*	Viverridae	Carnivore
6	Caracal	*Caracal caracal*	Felidae	Carnivore
7	Honey badger	*Mellivora capensis*	Mustelidae	Carnivore
8	Jackal	*Canis adustus, and C. mesomelas*	Canidae	Carnivore
9	African leopard	*Panthera pardus pardus*	Felidae	Carnivore
10	Lion	*Panthera leo*	Felidae	Carnivore
11	Common genet	*Genetta genetta*	Viverridae	Carnivore
12	Wild dog	*Lycaon pictus*	Canidae	Carnivore
13	African wild cat	*Felis libyca*	Felidae	Carnivore
14	African buffalo	*Syncerus caffer*	Bovidae	Grazer
15	Hippopotamus	*Hippopotamus amphibius*	Hippopotamidae	Grazer
16	African savanna hare	*Lepus microtis*	Leporidae	Grazer
17	Warthog	*Phacochoerus aethiopicus*	Suidae	Grazer
18	White rhino	*Ceratotherium simum*	Rhinocerotidae	Grazer
19	Blue wildebeest	*Connochaetes taurinus*	Bovidae	Grazer
20	Common zebra	*Equus burchellii*	Bovidae	Grazer
21	African elephant	*Loxodonta africana*	Elephantidae	Mixed feeder
22	Impala	*Aepyceros malampus*	Bovidae	Mixed feeder
23	Cape porcupine	*Hystrix Africaeaustralis*	Hystricidae	Mixed feeders
24	Spotted hyaena	*Crocuta crocuta*	Hyaenidae	Omnivores

CHAPTER 6

The impact of elephant feeding in enhancing species diversity: A synthesis

Edward Mtarima Kohi

INTRODUCTION

The central question in this thesis is to what extent does elephant feeding amplify resource heterogeneity in terms of vegetation structure, and forage biomass and quality, and thereby affect herbivore species diversity? The question aimed to contribute to a long debate since the 1960s (Laws 1970, Caughley 1976), Barnes (1983c), (Owen-Smith et al. 2006, van Aarde et al. 2006) whether elephant populations should be regulated in protected areas to avoid adverse effects of elephants (e.g., by culling, translocation or immunocontraception), or to allow disturbance being part of the ecological processes in savanna (Gillson and Lindsay 2003). In this thesis a number of insights have emerged that contribute to our understanding of the role of elephant feeding as a major process in structuring savanna ecosystem heterogeneity and thereby enhancing herbivore species diversity.

FACILITATION THEORY

Recent ecological experiments (Bruno 2000, Palmer et al. 2008, Pringle 2008) have increased the appreciation of the facilitation concept in shaping the science of community ecology. Resource modulation and/or ecosystem engineering concepts have increased our understanding of various ecological phenomena and have changed the way ecologists approach fundamental ecological questions on species distribution, community assemblage structure and species coexistence. It is arguable that competition has been at the forefront in explaining certain ecological patterns and distributions of species, backed-up by the niche theory and the carrying-capacity concept. However, unexplained patterns in studies of competitive exclusion (Wilson et al. 1999, Bruno et al. 2003), such as species coexistence, may be better understood when including facilitation mechanisms, and considering how certain species are able to partition resources and modulate resource availability. In this thesis experimental manipulation of browse resources, mimicking elephant feeding behaviour, from plant parts, to trees, to small scale systems ($900m^2$ plots), indicated that:

(1) Browse resources availability increased on the short to medium term (up to the second season ~ almost 1 year)

(2) Browse resources improved in terms of quality i.e., higher nutrient content

(3) Resource modulation changed the habitat structure (i.e., creating open areas and multiple canopy layers) and;

(4) The spatial distribution of browse biomass, i.e. the vertical distribution of the browse resources, changed.

Again, the change in resource allocation and spatial distribution will influence the way herbivores will interact and select their feeding sites. The conceptual model below (Fig.1) indicates how the elephant feeding behaviour triggers a chain of events that creates habitat heterogeneity. The model has two main components i.e., herbivores (elephants and other herbivore species) and vegetation; and there are three links of herbivores impacting vegetation (III, & III) and vegetation impacting herbivores (IV). The herbivore has a direct link i.e., modifying vegetation structure (I&II) and an indirect link through improving soil nutrients (III). Among the herbivore links, elephant is the leading link in modifying the vegetation. The other herbivore link (II) follows after foraging on the regrowth has occurred; further modifying vegetation structure. The nutrient link is based on the frequent visitations and re-visitations of the sites; the animals spend more time at these sites due to attractiveness of the patch and as a result, they deposit more dung and urine. The nutrient link affects the vegetation positively through adding nutrients into the soil. The vegetation link (IV) affect herbivores (elephants and other herbivore species) in three ways; first, the regrowth improves forage quality (positive effect for quality limited herbivores), second, it increases forage availability at reachable height (positive effect for quantity limited and browsing height limited herbivores) and third, the increased visibility positively affect herbivores that depends on their vision to avoid predators.

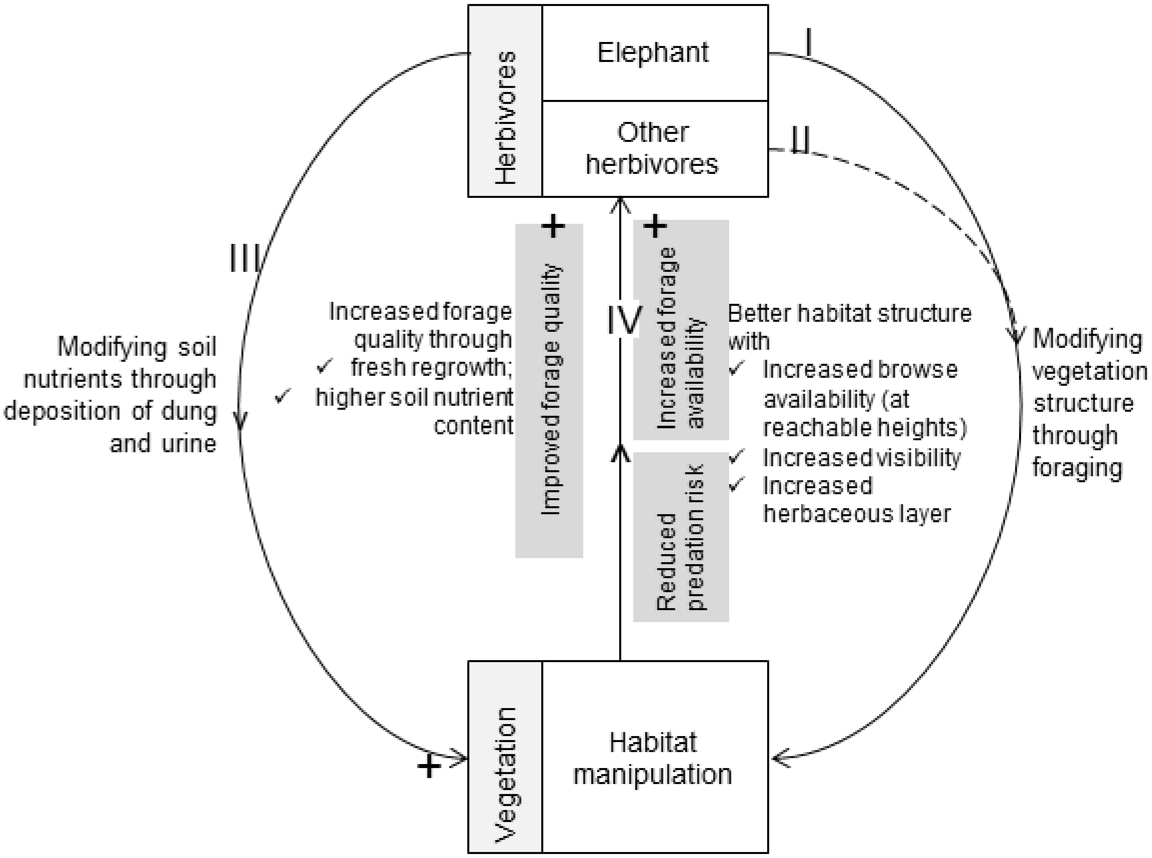

Fig. 1 Conceptual model of the impact of elephant feeding, showing the interactions of plant-elephants and their feedbacks. The modified vegetation structure (I) is exploited differently by different herbivore species and elephants themselves through re-browsing on high quality re-growth (IV). Further foraging creates a cycle of vegetation structure modifications (II), and at the same time improves soil nutrients by depositing dung and urine in the foraging patch (III). The positive sign indicates positive effect.

CHANGE OF RESOURCES IN TIME AND SPACE: WHO BENEFITS?

Resource partitioning, is increasingly used in explaining species co-existence (Makhabu 2005, Kleynhans et al. 2011). The differential distribution of resources in space and time is therefore governing the way resources are exploited by the consumers. Thus, the spatio-temporal differences in resource responses determine the type and nature of the consumers (Olff et al. 2002, Holdo et al. 2009b). Understanding how resources are distributed and the mechanisms that influence the resource distribution is crucial to understand differences in species distribution in community ecology.

Forage Availability Impacts**:** This thesis underlines the role of elephant feeding on affecting the vertical distribution of foliar biomass and its temporal availability. The reported increase in browse availability in response to elephant feeding habits likely will influences the spatial distribution of browsers as a consequence of differences in forage accessibility. The reasoning is that tall browsers such as giraffe can access browse without the help of elephant at any height. Kudu and eland (intermediate sized browsers) have less access to leaves in high canopies compared to giraffe but they have a larger range of access to leaves at intermediate heights compared to steenbok or duikers (small sized browsers). A conceptual model in Fig. 2 indicates two scenarios (i) low - high impact where trees do not die off and; (ii) where trees die off (tree removal in chapter 5). On figure 2a-b; the accessible height of available leaves shows that elephant impacts increase accessibility of browsable resources which will first impact intermediate browsers followed by small browsers (Fig. 2a-b). The intermediate browsers will be the first to benefit because the reduction of tree height through elephant feeding (which influences the accessible leaf height) can be in a range that is not accessible to small browsers. The amplification of leaf accessibility on the other hand, will have a negative impact on grazers. Again the increase in elephant impact will open up areas (scenario 2, Fig. 2c-d) that will favour the growth of herbaceous layer i.e., grass and forbs (Smit 2005), which in turn may attract grazers and certain browsers for forbs. The increase in herbaceous layer due to opening up areas by elephant feeding will favour grazers positively (Fig. 2c-d).

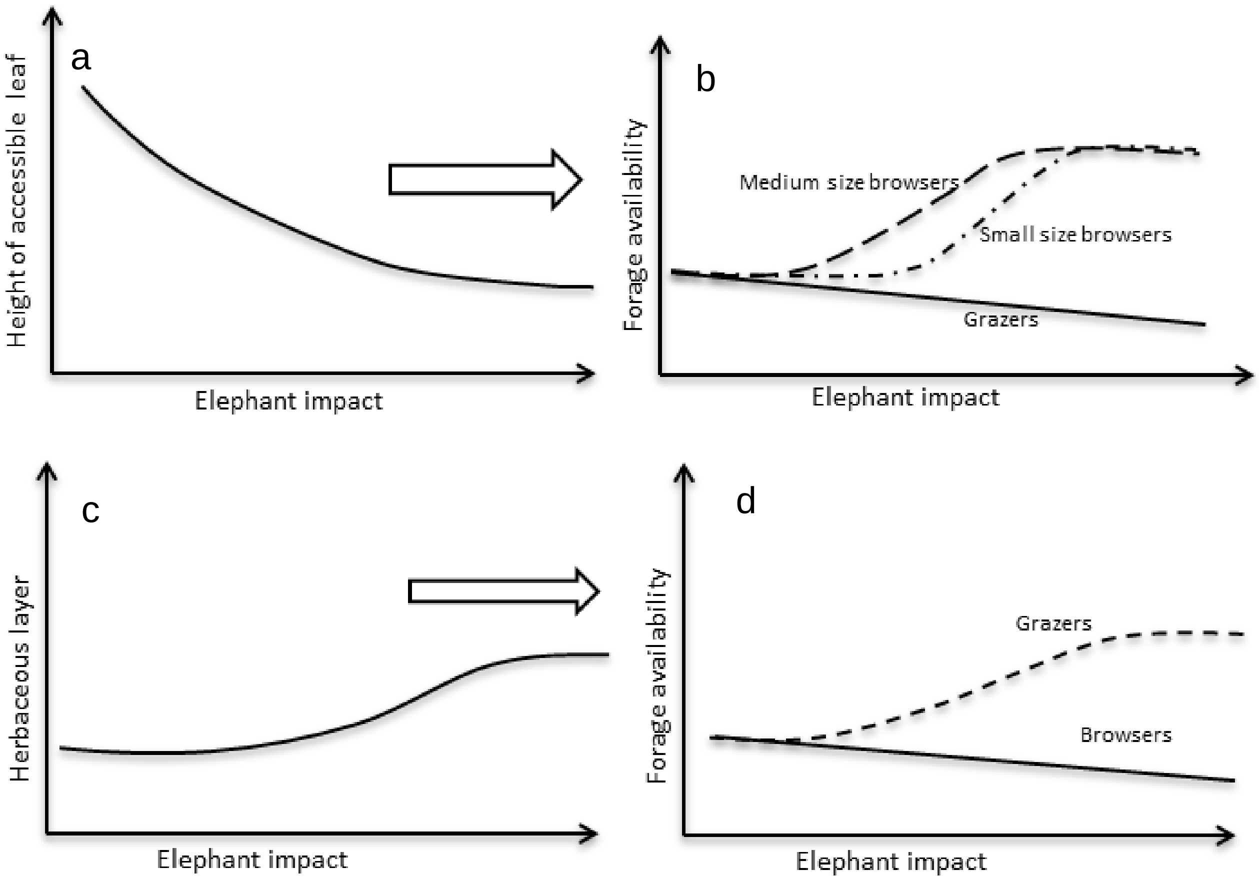

Fig. 2 The conceptual model here indicates that elephant influences the forage availability. Fig 2a shows that increasing elephant impact lowers the feeding height of accessible leaves (see chapter 2 & 5) that benefits browsers (2b). In 2b medium sized browsers are expected to first benefit more than small sized browsers because they can exploit a larger range of feeding heights. In fig 2c, opening up of woodlands by decreasing tree density will increase areas for herbaceous growth, thus, increasing forage availability for grazers. Fig 2d indicates that the increase in availability of herbaceous forage will benefit grazers more than browsers.

Forage Quality Impacts: An increase in forage quality can attract browsers and grazers. Herbivores' site revisitation has also been linked to forage quality changes (Skarpe and Hester 2008). The selection of a patch of high quality forage is associated with the animal's body size (Olff et al. 2002) i.e. small herbivores are more selective than large herbivores. Amplification of browse quality in a feeding patch will therefore be crucial for small and intermediate browsers. Several studies have reported that heavily browsed trees provided forage that is used by meso-herbivores and elephants themselves, i.e. self-facilitation (Jachmann and Bell 1985, Jachmann and Croes 1991, Styles and Skinner 1997, 2000). Kudu, impala and eland are the frequently cited species to benefit from previously browsed trees by elephants (Styles and Skinner 2000, Rutina et al. 2005, Makhabu et al. 2006). Most of the cited animals are meso-herbivores. Conceptually, meso-herbivores are expected to benefit more from these forage quality increases (Fig. 3 a and b) due to their relatively higher demand of high quality forage than mega-herbivores. The induced vegetation changes by elephants improve the quality of the regrowth (Chapter 2 & 4) and thereby the forage conditions for these meso-herbivores.

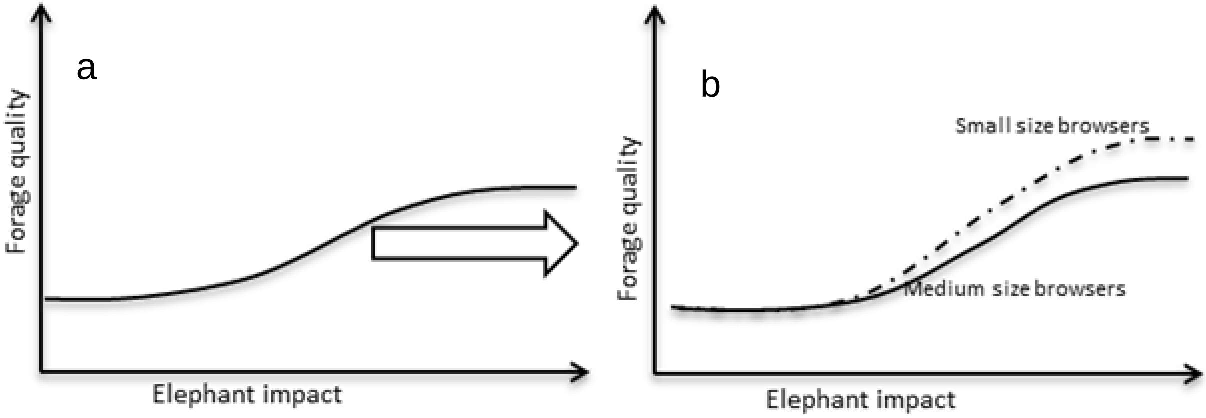

Fig 3. Elephant feeding improves the browse quality, and small sized browsers will benefit more than medium sized browsers due to their relatively higher nutrient requirements.

The Role of Opened up Patches: Tree removal, which mimics the uprooting of trees, attracts grazers (white rhino), mixed feeders (impala) and small browsers that prefer forbs, such as steenbok and common duiker. However, also a reduction of bush cover to better detect predators is important. In one of our observations at the cleared plot where impala used to deposit a lot of dung, the appearance of a lion in the area was accompanied by an almost total absence of impala dung in a number of days thereafter. However, Impala reappeared in the plot again. This suggests that cleared plots were important not only for the foraging on herbaceous vegetation but also for predator detection. The reduction of tree density will influence the choices of foraging sites, especially for meso-herbivore species because they are more sensitive to predation than larger herbivores (de Boer et al. 2010). Theoretically, the reduction in tree density will reduce the vulnerability of meso-herbivores from ambush predators (e.g., lions, leopards), which are common in the study area, but could also increase the vulnerability of being hunted by cursorial predators such as cheetah (Fig. 4). However, selecting open areas where it is easier to detect predators is more advantageous for most small herbivores than selecting areas with a high tree density where it is difficult to detect predators (Pays et al. 2012, Périquet et al. 2012).

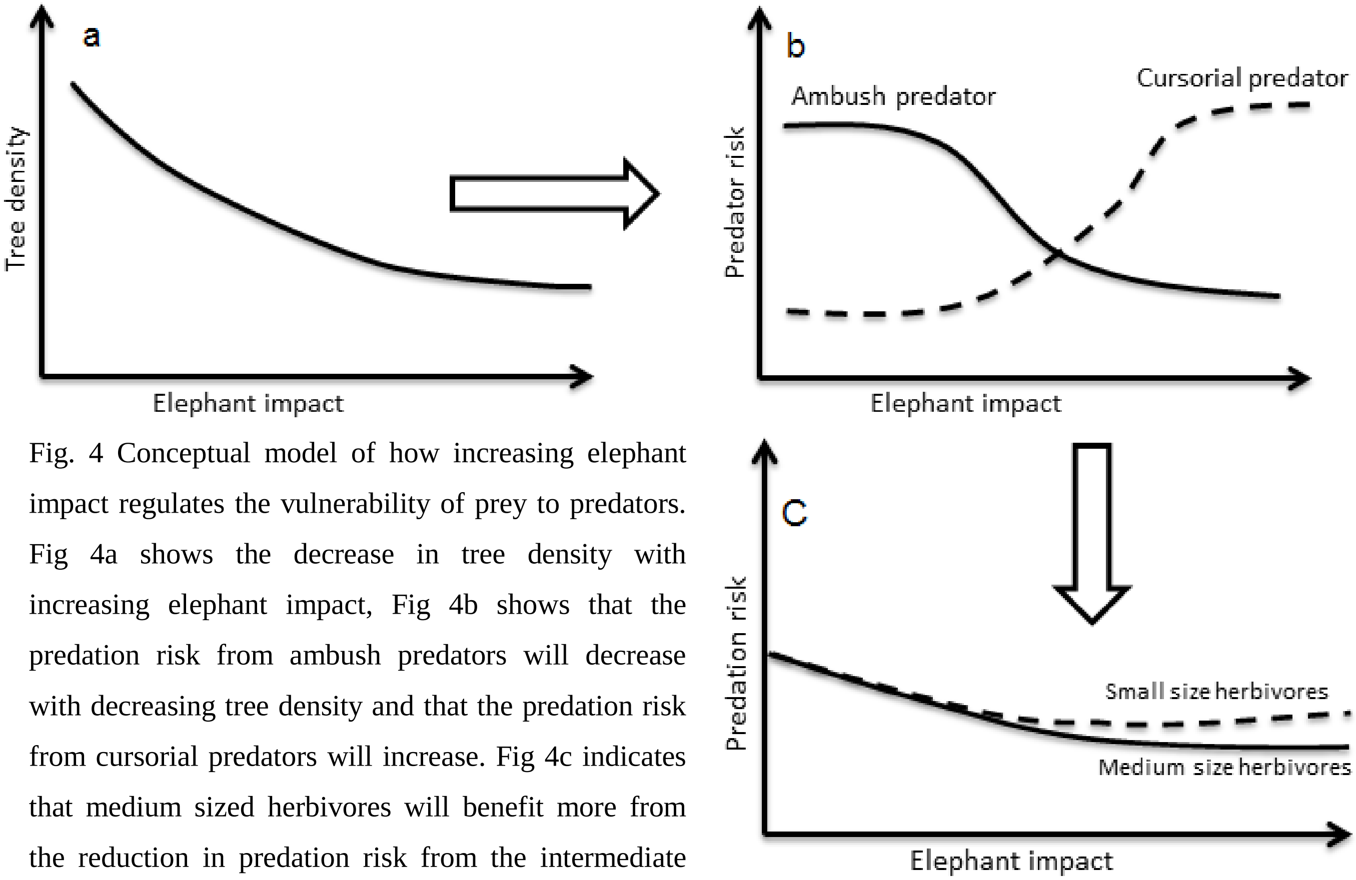

Fig. 4 Conceptual model of how increasing elephant impact regulates the vulnerability of prey to predators. Fig 4a shows the decrease in tree density with increasing elephant impact, Fig 4b shows that the predation risk from ambush predators will decrease with decreasing tree density and that the predation risk from cursorial predators will increase. Fig 4c indicates that medium sized herbivores will benefit more from the reduction in predation risk from the intermediate levels of elephant impact. Most cursorial predators are preying on small herbivores.

Buffering Dry Season Effect: Dry seasonal forage is always limited in most of the foraging range of savanna herbivores, which sometimes triggers animals to migrate to other areas, such as river systems, or wetlands. Other herbivore species resort in changing their forage selection. In the defoliation experiment (Chapter 3 & 4) I showed that the timing of browsing can facilitate the availability of green leaves longer in the dry season, but also induce early leaf flush, which acts as a buffer in situations of forage scarcity. In addition, the intensity of browsing can increase the amount of available browse during the dry season. Studies carried out in Mopane woodlands (Styles and Skinner 2000), Capparis woodlands (Rutina et al. 2005) and Brachystegia woodlands (Jachmann and Bell 1985) have showed that heavily utilized browsed trees significantly influenced the availability of browse of high quality, particularly in the dry season. However, these studies did not capture how the variation in timing of browsing promoted the availability of green leaf in the dry season and triggered an early leaf flush, which is addressed in this study (Chapter 3 & 4). It is therefore reasonable to state that by increasing the variation in the timing of browsing and revisitation events, the bottleneck period for browsers could be shortened through increasing the availability of high-quality forage at different points in time, assuring a more steady supply of leaf nutrients from leaves that differ in their growth phases. Field studies have reported that browser species visited previously elephant foraging trails in the dry season where the regrowth is plenty and of high quality (Skarpe et al. 2004, Skarpe and Hester 2008). For species like duikers, steenbok and kudu which are not long distance migratory species, the vegetation changes induced by elephant foraging might be critical for their food security during periods of food scarcity. This study indicates that a positive feedback simulated by defoliation (mimicking elephant feeding habits) could have positive effects on the foraging success of the different herbivore species through maintaining green leaves longer in the dry season and hence shortening the food scarcity period (Fig 5a-b). The browsers will likely benefit more from this effect than the grazers with a greater impact to small browsers (Fig 5c).

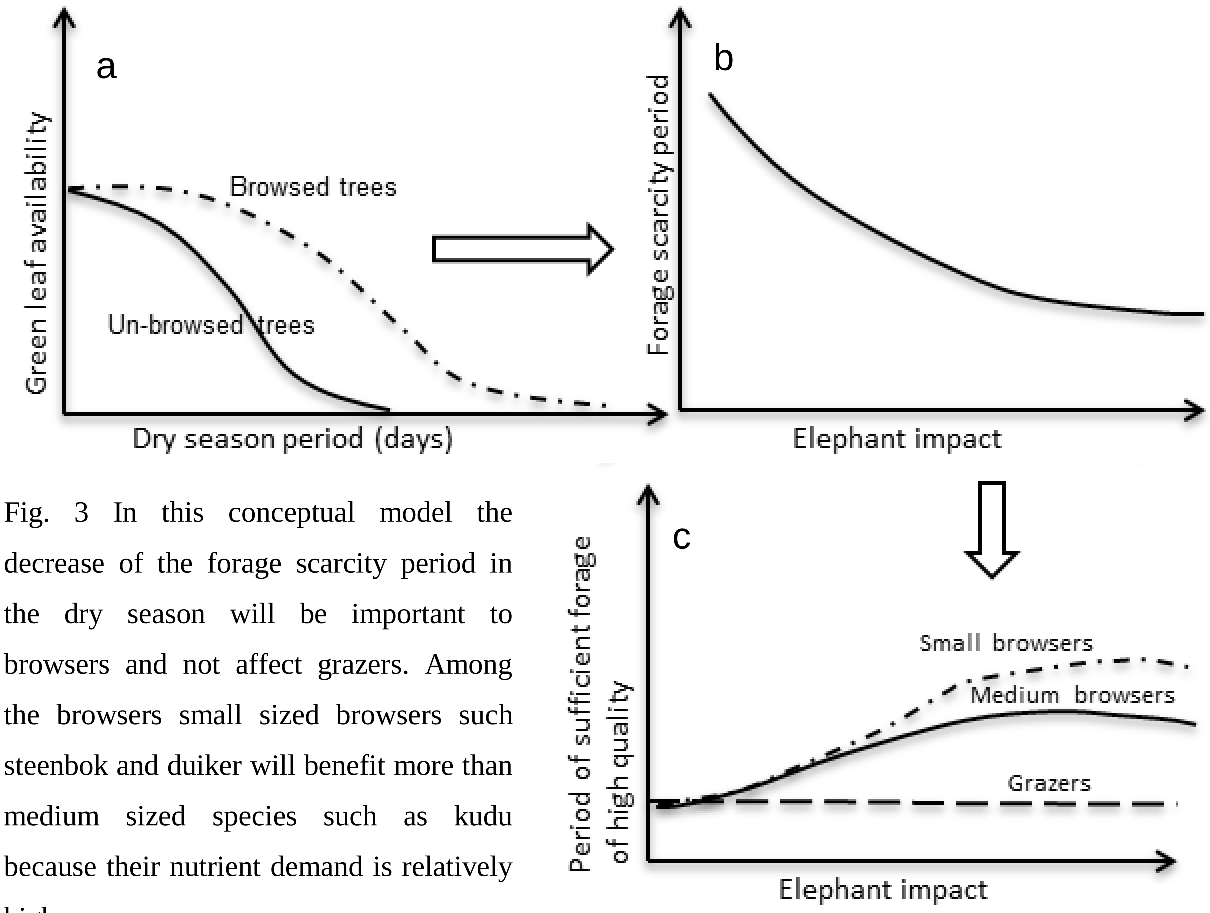

Fig. 3 In this conceptual model the decrease of the forage scarcity period in the dry season will be important to browsers and not affect grazers. Among the browsers small sized browsers such steenbok and duiker will benefit more than medium sized species such as kudu because their nutrient demand is relatively higher.

Inducing Selection of Long Term Foraging Spots: The selection of a foraging spot by an animal is determined by a number of factors including attractiveness of the patch and security (predation risk) of the spot. The experimentally simulated elephant feeding habits (Chapter 5) changed the resource distribution (browsable biomass) and created spatial (over both the vertical and horizontal axis) and temporal patterns of resource availability that indirectly influenced the soil nutrient cycling (Pastor et al. 2006). For example, opened up plots (mimicking uprooting) attracted a high number of impala and steenbok that deposited dung and urine in these plots (Chapter 5). On average, small herbivores' dung had higher N contents (Kohi unpublished data: impala=2.1%, steenbok=2.2%, common duiker=2.4%) than larger herbivores (buffalo=1.9%, giraffe =1.8%, elephants = 0.9%). This should increase plant available nutrients and indirectly make these plots more attractive for browsers and grazers; this effect is known to persist for several years (Pastor et al. 2006, van der Waal et al. 2011). Studies on former cattle kraals indicated that once nutrients hotspots are formed, herbivores are able to maintain them through grazing and further depositing dung and urine in these areas (Augustine 2003, van der Waal et al. 2011). As such, the induced vegetation changes can trigger selection of long term foraging spots.

SPECIES DIVERSITY: A RESPONSE TO RESOURCE AMPLIFICATION

The results of the simulated elephant feeding habit experiment i.e., pushing over trees, removing trees, and snapping trees, is the first experiment where elephant vegetation impacts have been experimentally simulated at the appropriate scale, and shed some light on the positive effects of mega-herbivores on meso-herbivores (Chapter 5). Vegetation manipulation can influence the habitat choices, particularly those of meso-herbivores. I evaluated the vegetation responses to elephant feeding habits from an individual tree to a plot level ($900m^2$), where the changes in browse availability was intensively studied. Based on the defoliation experiments, field sampling and a large vegetation manipulation experiment where herbivore response were recorded, the following findings were observed on the vegetation response:

1. available leaf biomass increased, mostly below 1.5m;
2. Foliar quality increased in the regrowth; and
3. The regrowth retained their leaves longer in the dry season.

Herbivore species responded to this manipulation, with the smaller herbivore species (impala, steenbok and duikers) reacting stronger in plots with a higher visibility i.e., cleared and coppiced plot, kudu responded well in pushed over plots, while the grazing white rhino responded to cleared plots as predicted.

The understanding of elephant feeding impacts and its feedback to the herbivore communities is still inconclusive. At a small scale analysis, i.e., field experiment (this thesis), meso-browsers are benefiting from previously browsed trees by elephant, which is confirmed by field observation studies (Rutina et al. 2005, Makhabu and Skarpe 2006), and meso-herbivores revisit such areas (Skarpe and Hester 2008). At a large scale analysis, mega-herbivores can negatively affect meso-herbivores, as Fritz et al. (2002) showed that mega-herbivores, (African elephant in particular) were negatively correlated to the abundance of meso-browsers probably via competition for food or habitat alterations. In their analysis Fritz et al. (2002) found that elephant were positively correlated to rainfall, which normally results in high forage production but of low quality (Olff et al. 2002). If you consider that in Africa censuses are generally carried out in the dry season, then it might be that the elephants that were used in the analysis of Fritz et al. (2002) selected water and forage at high rainfall areas while meso-browsers, that are generally less water dependent, were benefiting from the impacts of elephant on the vegetation. Therefore, the effect of elephant feeding observed at a local scale might be better observed at the ecosystem scale if the spatial-temporal bias in distribution and the bias in detection of small herbivores under woody cover are also accounted for in the analysis.

In summary (see table 1) the elephant feeding impact at a local scale could have big influences on habitat choice of meso-browsers. At intermediate elephant impact, medium browsers will benefit more from increased availability of browse biomass while small browsers will benefit more from an increase in forage quality (a limiting factor) and a reduction in predation risk.

Grazers will be benefit from an increase in the herbaceous layers. At high elephant feeding impacts small browsers will probably benefit more than medium and large browsers. At this point the amount of browse is decreasing but the remaining part is of high quality; in addition forbs also become numerous which are consumed mostly by small browsers. The elephant browsing reduces the period of forage scarcity for browsers. Also here, small browsers will probably benefit more because they are more limited by forage quality than the medium and large browsers.

In conclusion, this study has expanded our ecological thinking on how elephant feeding habit plays a role in resource modification and thereby on structuring the savanna communities. This thesis provides base-line information which is important in modeling elephant-plant-herbivore population dynamics and feedbacks, and therefore for the development of elephant management plans.

Table 1 indicates the benefits of elephant feeding habit on small, medium and large browser and grazer species over different categories of elephant impact.

Elephant Impact	Intermediate Impact						High Impact					
	Browsers			Grazers			Browsers			Grazers		
	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
Height of accessible leaf	+	++	+	-	-	-	++	+	-	-	-	-
Herbaceous layer	+-	-	-	++	+	+	+-	--	--	+	++	++
Browse quality	++	+	+-	-	-	-	++	+	+-	-	-	-
Reduction of predation risk	+	+-	+-	+	+	+-	+	-	+-	+	+	+-
Availability of high quality forage in a period of forage scarcity	++	+	+-	-	-	-	++	+	+-	-	-	-
Total Score (++=2, +=1, +-=0, -=-1, --=-2)	6	3	0	0	-1	-2	7	0	-3	-1	0	-1

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SUMMARY

Herbivore-vegetation interactions are important structuring forces in savanna that modify the availability and quality of forage resources. Elephant for example, are known for their ability to change the vegetation structure through toppling trees, uprooting, snapping, debarking and breaking branches. Controlling the number of elephant is a common response of wildlife managers who think that the increase of elephant will further destroy the habitat and hence cause loss of biodiversity. However, our knowledge on how elephant feeding habits affect other large herbivore species in habit use is limited. Therefore, the question in this thesis is: What is the impact of elephant feeding habits on species diversity of large herbivores in African savanna? To answer this question, it is important to understand the responses of trees when impacted by elephant. What proportion of the browsed biomass is made available after a tree is pushed over or snapped by elephant? How is the forage quality affected? Is the seasonal and intensity of browsing affecting forage availability? Field experiments and field surveys were used to investigate the tree's response and herbivore species responses to elephant impact. These experiments were (1) simulation of timing and intensity of browsing (hand defoliation) and (2) manipulation of vegetation i.e. simulated pushed over trees, uprooted trees (tree removal) and snapped trees (tree cut at the stem). The field survey involved measuring impacted trees by elephant. Leaf biomass and quality of pushed over, snapped and uprooted trees were measured. The defoliation experiment was conducted in the roan antelope enclosure in Kruger National Park South Africa, and the vegetation

manipulation experiment was conducted in the Umbabati Private Nature Reserve, South Africa.

The results indicate that elephant foraging habits change the distribution of forage, increasing the forage availability at lower feeding heights, which means that accessibility of forage to medium and small herbivores increases. Elephant browsing also improved forage quality and availability in the dry season, which is very important to browsing animals. A high intensity of browsing by elephant in the wet season increased the dry season forage, because the amount of new regrowth (leave compensation) is proportional to the amount of leaves that was removed. Elephant therefore initiate inter and intra-species facilitation processes. Inter-species facilitation occurs when other herbivores species utilize the regrowth stimulated by elephant, whereas intra-species facilitation occurs when the browse resource is exploited by other elephants. The herbivore responses to elephant browsing clearly indicated that facilitation effects occur, especially for certain guilds when selecting their habitat. For example, small predation-sensitive herbivore species (steenbok, impala and common duiker) preferred completely opened up areas, whereas large herbivores were less affected in their habitat preference by elephant impact. Greater kudu selected pushed over and control plots and rarely visited opened up areas. These differential response of herbivores species to elephant impact resulted in a high species richness of large mammals in elephant impacted areas. In conclusion, elephant feeding habits play a major role in structuring the herbivore assemblage/community through modifying the vegetation. Resource heterogeneity increased under the influence of elephant feeding, in particular through increasing the accessibility of leaf biomass at lower feeding heights, increasing green leaf availability in the dry season, and improving the nutrient content in re-growth. Moreover, habitat selection, especially that of small herbivores was positively influenced by elephant impact. With these findings, this study contributes to a better understanding of the role of elephant feeding habits and its cascading effects to other herbivore species.

SAMENVATTING

In savannes vormen herbivoorvegetatie-interacties belangrijke sturende krachten die de beschikbaarheid en kwaliteit van voedselbronnen beïnvloeden. Olifanten bijvoorbeeld staan erom bekend dat ze de vegetatiestructuur veranderen door het breken van takken en het ontwortelen, knappen en omverwerpen van bomen. Als antwoord hierop controleren veel wildbeheerders de populatieomvang, met de gedachte dat anders een te grote vernietiging van het habitat zal plaatsvinden met een verlies aan biodiversiteit als gevolg. Onze kennis van hoe het foerageergedrag van olifanten andere herbivorensoorten beïnvloedt is echter beperkt. De hoofdvraag van deze dissertatie is daarom: Wat is het effect van het foerageergedrag van olifanten op de soortendiversiteit van grote herbivoren van de Afrikaanse savanne? Om deze vraag te beantwoorden is het belangrijk om te begrijpen hoe bomen reageren op beïnvloeding door olifanten. Hoe verandert de beschikbare voedselbiomassa voor andere herbivoren na het omverduwen of breken van bomen door olifanten? Wat is het effect op de kwaliteit van het voedselaanbod? Verandert het moment waarop olifanten de bomen gebruiken en de intensiteit van hun gebruik de voedselbeschikbaarheid? Veldexperimenten en correlatieve studies zijn gebruikt om de reactie van bomen en herbivoorsoorten op het foerageergedrag van olifanten te onderzoeken. De veldexperimenten waren (1) simulatie van timing en intensiteit van bladconsumptie (handmatige ontbladering) en (2) manipulatie van de vegetatie doormiddel van simulatie van omvergeduwde bomen, ontwortelde bomen (verwijdering van bomen) en afgeknapte bomen (boom omgezaagd bij de stam). De correlatieve studie betrof metingen aan de door olifanten gebruikte bomen. Hierbij werd de bladbiomassa en kwaliteit van omgeduwde, geknapte en ontwortelde bomen bepaald. Het ontbladeringsexperiment is uitgevoerd in Kruger Nationaal Park te Zuid-Afrika. Het vegetatiemanipulatie-experiment is gedaan in Umbabati Private Nature Reserve, ook gelegen in Zuid-Afrika.

De resultaten wijzen erop dat het foerageergedrag van olifanten de verdeling van het voedselaanbod verandert op zo’n manier dat de beschikbaarheid ervan toeneemt op lagere foerageerhoogten. Dit betekent dat de voedseltoegankelijkheid toeneemt voor kleine en middelgrote herbivoren. Ook bevorderde het foerageergedrag van olifanten de voedselkwaliteit en –beschikbaarheid in het droge seizoen, wat erg belangrijk is voor browsers. Een hoge intensiteit van ontbladering door olifanten in het natte seizoen zorgde voor een toename in het voedselaanbod in het droge seizoen, omdat de hoeveelheid hergroei (bladcompensatie) zich evenredig verhield tot de hoeveelheid verwijderd blad. Olifanten initiëren derhalve inter- en intraspecifieke facilitatieprocessen. Interspecifieke facilitatie heeft plaats wanneer andere herbivorensoorten de hergroei van de bomen en struiken consumeren die veroorzaakt is door olifanten. Intraspecifieke facilitatie, daarentegen, gebeurt wanneer de voedselbronnen worden benut door andere olifanten. De reacties van herbivoren op ontbladering door olifanten gaven duidelijk aan dat facilitatie-effecten plaatsvinden, vooral voor bepaalde soorten herbivoren tijdens habitatselectie. Kleine, predatie-gevoelige herbivorensoorten bijvoorbeeld (zoals steenbokantilope, impala en gewone duiker) prefereerden volledig geopende gebieden, daar waar grote herbivoren minder beïnvloed waren in hun habitatselectie. De grote koedoe selecteerde gebieden met omvergeduwde bomen en controlegebieden, maar bezocht nauwelijks gebieden waar alle bomen waren weggehaald. Deze verschillende reacties van herbivoorsoorten op verstoringen door olifanten resulteerde in een grotere soortenrijkdom van grote zoogdieren. Concluderend speelt via een veranderde vegetatie het foerageergedrag van olifanten een grote rol in the structurering van de herbivorengemeenschap. De heterogeniteit in voedselbronnen nam toe onder invloed van het foerageergedrag van olifanten. Dit werd vooral veroorzaakt door een grotere beschikbaarheid van bladbiomassa op lagere foerageerhoogten, een toegenomen beschikbaarheid van groene bladeren en door het verbeteren van het nutriëntengehalte in de hergroei. Bovendien was habitatselectie, met name dat van kleine herbivoren, positief beïnvloed door de voedselconsumptie van olifanten. Met deze bevindingen draagt dit onderzoek bij aan een beter begrip van de rol van het foerageergedrag van olifanten en de effecten hiervan op andere herbivoorsoorten.

MUHTASARI

Uhusiano kati ya mimea na wanyamapori walao majani (hebivora) ni jambo muhimu kwa muonekano, upatikanaji na ubora wa malisho katika nyanda za malisho za savanna. Kwa mfano tembo, wanafahamika kwa uwezo wao wa kubadilisha muonekano wa uoto wa mimea katika nyanda za malisho. Hii inatokana na tabia yao ya kula majani yaliyo juu ya miti, kung’oa na kukata miti, kubandua magome ya miti, na kuvunja matawi ya miti ya malisho. Wahifadhi wa wanyamapori wamekuwa wakififikiri kwamba ni muhimu kudhibiti idadi ya tembo ili wasisababishe uharibifu mkubwa wa mazingira na upotevu wa bioanuwai. Hata hivyo, uelewa bado ni mdogo kuhusu tabia ya ulaji malisho wa tembo unvyoathiri tabia ya wanyamapori hasa walao majani. Kwa hiyo swali muhimu katika andiko hili ni kutaka kujua tabia ya ulaji malisho wa tembo unavyoathiri tabia ya wanyamapori wengine ambao wanaishi katika nyanda za savanna za Afrika. Ili kupata jibu la swali hili ni muhimu kuelewa miti inavyoweza kujihami wakati inapoliwa na tembo. Ni kiasi gani cha majani ya malisho kinakuwepo baada miti kusukumwa au kuvunjwa na tembo? Je, ubora wa malisho unaathiriwa kwa kiwango gani? Je, majira ya mwaka na kiwango cha ulaji wa miti ya malisho unaofanywa na tembo vina madhara kwa upatikanaji wa malisho kwa wanyama wengine? Ili kupata ufumbuzi wa maswali haya, utafiti ulifanyika kwa kuandaa majaribio na kudodosa ili kuchunguza miti na wanyamapori wengine wanavyojihami kutokana na matokeo ya ulaji malisho wa tembo. Majaribio yalikuwa kama ifuatavyo:

1. Kuigiza wakati na kiwango cha ulaji malisho wa tembo kwa kukata majani ya miti ya malisho kwa mikono.

2. Kubadilisha uoto wa mimea kwa kuangusha, kung’oa na kukata miti katika mashina mithili ya tembo wafanyavyo.

Vile vile utafiti porini ulifanyika kwa kupima miti ilivyoathiriwa na tembo katika nyanda za malisho. Wingi na ubora wa majani katika miti iliyoangushwa, iliyong’olewa na iliyokatwa ulipimwa. Jaribio la ulaji malisho katika miti ya malisho ulifanyika katika Uzio wa mnyama korongo kwenye hifadhi ya Taifa ya Kruger Afrika ya Kusini. Jaribio la kubadilisha uoto wa mimea lilifanyika kwenye pori la akiba la binafsi la Umbabati Afrika ya Kusini.

Matokeo yalionyesha kuwa, tabia ya ulaji wa tembo hubadilisha mtawanyiko wa majani malisho kwenye miti. Majani mengi kwa kawaida huwa yako juu lakini tembo anaposukuma miti majani ya malisho hupatikana kwenye kima kifupi, hii inamaanisha kuwa inasaidia kuongezeka kwa upatikanaji wa malisho kwa wanyama wadogo na wa kati. Tabia ya ulaji malisho wa tembo umeonesha kuongeza ubora na upatikanaji wa malisho wakati wa kiangazi jambo ambalo ni muhimu kwa wanyama wanaotegemea majani kwa chakula. Kiwango kikubwa cha ulaji malisho wa tembo kwa wakati wa masika husaidia upatikanaji wa malisho ya kutosha kwa wanyama wengine wakati wa kiangazi. Hii inatokana na tabia ya mimea iliyoliwa kutoa vichipukizi na majani zaidi ili kufidia majani yaliyoliwa. Hivyo, tembo wanawezesha upatikanaji wa malisho kwa ajili yao na kwa ajili ya wanyama wengine (huwezesha spishi nyingine). Matokeo ya tabia ya ulaji malisho wa tembo yameonekana bayana kwa wanyama wa jamii ya swala kupendelea zaidi kukusanyika ili kupata malisho kwenye maeneo yaliyofanywa wazi kutokana na tabia ya ulaji malisho wa tembo. Hata hivyo, tabia ya ulaji malisho wa tembo haikuonyesha athari kubwa kwa wanyama walao majani wenye umbo kubwa. Hitimsho la utafiti huu ni kwamba tabia ya ulaji malisho wa tembo inachangia mkusanyiko wa wanyama walao majani katika maeneo ya malisho ya tembo. Tabia ya ulaji malisho wa tembo huchangia upatikanaji wa aina mbalimbali za malisho yenye kimo kifupi, upatikanaji wa majani mabichi wakati wa kiangazi na ongezeko la ubora wa malisho kwa wakati wa kiangazi kutokana na majani yaliyochipua. Utafiti umeonesha kuwa wanyama walao majani wenye umbo dogo hupendelea kupata malisho kwenye maeneo ya malisho ya tembo. Kutokana na matokeo haya, utafiti huu umeongeza ufahamu kuhusu jukumu la tabia ya ulaji malisho wa tembo katika upatkanaji wa malisho na matokeo yake kwa wanyama wengine hasa walo majani walioko kwenye nyanda za savanna za Afrika.

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CURRICULUM VITAE

Edward Mtarima Kohi was born on August 4, 1975 in Musoma, Tanzania. In 2000 he started his BSc. in Wildlife Management at Sokoine University of Agriculture, Morogoro, Tanzania and thereafter joined Tanzania Wildlife Research Institute in 2003 as a research officer III. In 2004 he started his MSc. Forest and Nature Conservation at Wageningen University where he was supervised by Ignas Heitkonig and Fred de Boer at the Resource Ecology Group. During his MSc. He worked on recovering of herbivore diet from faecal sample and chemical response of trees on browsing pressure.

In August 2006 he started his PhD at the Resource Ecology Group under the TEMBO (The Elephant Movements and Bio-economic Optimality) integrated program. He was supervised by Herbert Prins and Fred de Boer. His research was focused on the role elephant feeding behaviour and how other herbivore species benefit on modified resource by elephant.

Currently he still works with Tanzania Wildlife Research Institute in Tanzania and he is appointed as centre director of Mahale and Gombe Wildlife Research Centres in the Western Tanzania. The western Tanzania is a less research area in Tanzania yet is situated in high biodiversity regions such as the Albertine rift valley and convergence of Congo and Zambezian eco-regions.

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PE&RC PhD Training Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)

- The impact of elephants feeding on enhancement of large herbivore species diversity

Writing of project proposal (4.5 ECTS)

- The impact of elephants feeding on enhancement of large herbivore species

Post-graduate courses (4.8 ECTS)

- The art of modeling; PE&RC (2006)
- Consumer resource interaction; PE&RC/SENSE (2006)
- Bayesian statistics; PE&RC (2009)
- Introduction to R for statistics; PE&RC (2009)
- Generalized linear models; PE&RC (2010)

Laboratory training and working visits (2.5 ECTS)

- Fieldwork experiment: simulated browsing; Kruger National Park and Southern Africa Environmental Observation Network (SAOEN), South Africa (2007/2008)
- Nutrient analysis (N,P); Agricultural Research Council, South Africa (2009)

Invited review of (unpublished) journal manuscript (2 ECTS)

- African Journal of Range & Forage Science; forage quality (2007)
- Tropical Conservation Science: elephant impact on vegetation (2011)

Deficiency, refresh, brush-up courses (3.5 ECTS)

- Academic writing (2006)
- Advanced statistics (2007)

Competence strengthening / skills courses (1.5 ECTS)

- The art of writing; WUR (2006)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.2 ECTS)

- PE&RC Day (2006)
- PE&RC Weekend (2008)

Discussion groups / local seminars / other scientific meetings (5 ECTS)

- Discussion group on Forest and Conservation Ecology (2006-2010)
- SAEON and SANPARK research presentations and discussion; South Africa (2007-2009)
- APNR Joint management meetings: research session; South Africa (2007-2009)
- Elephant Management and Owner's Association (EMOA) Meetings: research & management presentation (2009)

International symposia, workshops and conferences (6 ECTS)

- 5th Annual Kruger National Park science network meeting; Sukukuza, South Africa (2007)
- 6th Annual Kruger National Park science network meeting; Sukukuza, South Africa (2008)
- 7th Annual Kruger National Park science network meeting; Sukukuza, South Africa (2009)
- 48th Annual ATBC and the 2nd SCB Africa Conference; Arusha, Tanzania (2011)

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