

Woody plant damage by African elephants in relation to leaf nutrients in western Zimbabwe

Ricardo M. Holdo¹

Department of Zoology, University of Florida, Gainesville, FL 32611, USA
(Accepted 18 January 2002)

Abstract: The relationship between elephant damage and leaf nutrient concentration across tree species was investigated in a semi-arid savanna in western Zimbabwe with the purpose of investigating possible nutritional factors influencing elephant feeding preferences in Kalahari sand woodlands. The presence of elephant damage was recorded in all trees above 1 m in height, and leaf samples were collected from all tree species encountered in 12 vegetation plots during the late dry season. Elephant damage was positively correlated with leaf calcium, magnesium, potassium and protein concentration, but not with sodium, phosphorus or fibre. Tree species associated with sandy soils appeared to be less preferred by elephants and to have lower nutrient concentrations than species occurring on more fertile soils, such as species associated with termite mounds. Elephant damage may suppress recruitment in preferred tree species in these woodlands. This notion was supported by (1) the fact that 44% of all trees surveyed had had their main stems broken by elephants, a situation that leads to a multi-stemmed growth form with limited vertical growth; and (2) the negative correlation between the height of damaged trees and elephant damage across species.

Key Words: elephants, food selection, Kalahari sand, *Loxodonta africana*, mineral nutrients, woodlands, Zimbabwe

INTRODUCTION

African savanna elephants (*Loxodonta africana africana* Blumenbach) can have profound effects on the structure and composition of woodlands (Barnes 1985, Guy 1989, Jachmann & Croes 1991, Laws 1970, Laws *et al.* 1975). Elephant suppression of woody vegetation can lead to changes in the tree/grass balance of savannas (Caughley 1976, Dublin *et al.* 1990, Laws *et al.* 1975) and woodland structure (Barnes 1985, Guy 1989, Jachmann & Bell 1985, Laws 1970). Despite this impact, relatively little is known about the factors, nutritional or otherwise, that influence food and habitat selection in elephants. Knowledge of these factors can help determine the role of elephant–tree interactions in shaping savanna structure and species composition, and may assist managers seeking to address problems associated with overexploitation of certain tree species by elephants.

Research conducted in African savannas has shown that browsers favour woody species with high concentrations of protein and minerals, and low concentrations of fibre, lignin and condensed tannins (Cooper *et al.* 1988, Cooper & Owen-Smith 1985, Owen-Smith & Cooper 1987). Few studies have investigated the importance of interspecific variation in plant nutrient concentration for

elephant food selection. One study conducted in miombo woodlands in Kasungu National Park, Malawi, found that elephant feeding preferences across species were positively correlated with leaf cations such as sodium and magnesium and crude protein (Jachmann & Bell 1985). Further research at the same site found a positive correlation between utilization by elephants and sugar concentration, and a negative correlation with lignin (Jachmann 1989). Elephants also appeared to avoid tree species with high levels of total phenols (Jachmann 1989). Other studies conducted in miombo woodlands in Zimbabwe have failed to detect associations between elephant feeding preferences and plant nutritional concentration (Anderson & Walker 1974, Thomson 1975). Thus, although there is some evidence to suggest that elephant food selection in miombo woodlands is driven by some of the same factors that influence preferences in other browsers, further research is required for a more general pattern to emerge. Furthermore, no studies of this type have been conducted in the Kalahari sand woodlands of Zimbabwe and Botswana. Kalahari sands are deficient in plant nutrients (Frost 1997, IGBP 1997), and there is evidence to suggest that Kalahari sand browse may be inadequate to meet elephant sodium requirements during the dry season (Holdo *et al.*, 2002, Weir 1972). It might therefore be expected that elephants would select species with high sodium concentration in this habitat, as reported in the Kasungu study (Jachmann & Bell 1985).

¹ Present address: Department of Ecology and Evolutionary Biology, Princeton, NJ 08544–1003, USA.

The woodlands of western Zimbabwe are home to one of the largest concentrations of elephants in Africa (Douglas-Hamilton & Michelmore 1996, Said *et al.* 1995, Verlinden & Gavor 1998). The extent of the damage caused by elephants to many tree species in these woodlands has raised concerns among managers (Campbell *et al.* 1996, Martin *et al.* 1992), yet the factors underlying differences in species utilization have not been investigated. The primary aim of this study was to determine whether nutritional factors are associated with a preference by elephants for certain tree species in the woodlands of western Zimbabwe, and to determine whether elephants lead to the suppression and/or decline of nutrient-rich species. A second objective was to investigate the potential role of sodium in driving food choice by elephants.

METHODS

Study area

The study was conducted in October and November 1997 in Farm 41 (18°38'S, 26°55'E), a 2300-ha private game-viewing area of wooded bushland adjacent to Hwange National Park, Matabeleland North Province, Zimbabwe. The area receives a mean annual rainfall of 650 mm, most of it falling during a single rainy season between November and March (Childes & Walker 1987, Rogers 1993), and the vegetation can be classified as semi-arid woodland. Farm 41 is part of a continuous area of protected elephant habitat that extends from the Bulawayo–Victoria Falls highway 20 km east of Farm 41 up to the Botswana border in the west. During the first part of this century much of the property was logged, but this type of activity was abandoned in the 1950s, and since that time the natural bush has regenerated (J. Foster, pers. comm.). Trees up to 5 m in height dominate in most areas, and the canopy cover is sparse. Before the logging that took place on either side of the railway line in the early part of the century, much of the property was dominated by mature trees of the commercially important *Baikiaea plurijuga* Harms, which are typical of the Kalahari sands that predominate in Western Zimbabwe (Childes & Walker 1987). *Baikiaea plurijuga* is a common species in Farm 41 and young trees of this species occur throughout the property. Farm 41 soils are dominated to a large extent by Kalahari sands, which have a low (< 10%) clay and silt fraction, and very low levels of organic matter and weatherable minerals (Childes & Walker 1987, IGBP 1997). The vegetation is dominated by open *Baikiaea plurijuga* woodlands, *Terminalia–Combretum* bushland and *Acacia* spp. bushland. Soils derived from the Basement Complex (Rogers 1993) intrude on the north-western edge of the property, and this is reflected by the presence of *Colophospermum mopane* Kirk ex J. Leonard and *Brachystegia* spp. in that area. Termite mounds are conspicuous

in the latter habitat types. These mounds are often associated with particular suites of plant species (Frost 1997, pers. obs.) and are a prominent feature in *Brachystegia*-dominated miombo woodlands (Dangerfield 1990, Frost 1997).

Vegetation survey and analysis

To study elephant damage to the vegetation, six landmarks were identified on a map of Farm 41. The landmarks served as starting points for plot placement. One-km lines were set up along the tracks that limit the border of the property, and two 10 × 10-m plots were randomly located along each of these lines, within 100 m of the nearest track. Plots were not set up less than 10 m from the tracks because of edge effects caused by the presence of the tracks. Logistical considerations limited the study to peripheral areas of the property, so it is unclear to what extent the survey reflects average vegetation patterns and elephant damage to trees in Farm 41. Elephants were free to move across the property boundaries into surrounding areas of similar habitat, and the tracks were only infrequently used by authorized vehicles. Therefore the results of the study may be reasonably extrapolated to the entire area.

Elephant feeding patterns were quantified by recording damage to trees in the plots. Elephant damage is distinctive and therefore easy to distinguish from damage caused by other browsers, fire or frost (Jachmann & Bell 1985). Feeding elephants tear off entire branches with their trunks, leaving characteristic scars on the sides and ends of damaged stems. Within each plot, the species, presence of elephant damage, and height class were recorded for each individual stem. Broken main ramets or stems were distinguished from broken side branches or secondary ramets, but for the purposes of this study the presence of either type of damage was sufficient to classify a tree as damaged. Only trees taller than 1 m were included in the survey. In many cases, plants that would otherwise have been > 1 m in height had been reduced in height by elephant browsing, and these were therefore included in the survey. To estimate which trees would have been > 1 m in height before elephant browsing, the basal diameter that corresponded to a cutoff point for the 1-m height class was determined by measuring several stems < 1 m and several > 1 m in height for each species.

Leaf samples were collected from at least three trees of each species within or near each plot for analysis of calcium (Ca), magnesium (Mg), potassium (K), sodium (Na), phosphorus (P), crude protein (CP) and neutral detergent fibre (NDF) concentration. Although elephants feed on many plant items besides leaves, such as bark, twigs and roots, only one type of sample was collected in this study. Leaves were chosen because they were considered to be more likely to influence food selection than other plant

parts, given that leaves are often higher in protein and cations (Holdo & McDowell, unpubl. data), and have lower concentrations of fibre and lignin than bark or twigs. Other studies of food selection by elephants have also focused on leaves rather than other plant parts (Jachmann 1989, Jachmann & Bell 1985). A single sample was created for each species by combining the samples from all the plots in which that species occurred. Surgical gloves were used for all collections to minimize Na contamination (Weeks & Kirkpatrick 1976). Samples were air-dried prior to transport to Gainesville, USA, where they were oven dried for 48 h at 50 °C. Leaves were ground with a Wiley Mill, and 1–2-g subsamples were taken from each sample for elemental analysis following a standard procedure (Fick *et al.* 1979). Samples were analysed for Na, Ca, K and Mg concentration with a Perkin–Elmer Model 5000 Atomic Absorption Spectrophotometer. For total N and total P analysis, samples were digested using a modification of the aluminium-block digestion procedure of Gallaher *et al.* (1975). Sample weight was 0.25 g, catalyst used was 1.5 g of 9:1 K₂SO₄:CuSO₄, and digestion was conducted for at least 4 h at 375 °C using 6 ml of H₂SO₄ and 2 ml of H₂O₂. N and P in the digestate were determined by semi-automated colorimetry. CP was calculated by multiplying total N by 6.25. NDF was determined using the procedure of Golding *et al.* (1985).

Within each plot, a preference or selection ratio d_i/n_i was calculated for each species *i*, where d_i is the proportion of damaged plants represented by species *i*, and n_i is the proportion of *i* in the plot (Crawley 1983). The overall selection ratio for a species was given by its median selection ratio across all plots in which it occurred. Only species with a minimum of two individuals per plot were included in the analysis because the inclusion of cases in which a single individual occurred resulted in damage proportions of 0 or 100%. Rare species thus have the potential to unduly influence the analysis of associations between nutritional variables and selection ratio. Spearman rank correlations were used to test for associations between selection ratios and nutritional concentration across all species. To investigate whether elephants selectively suppress Farm 41 trees, the median height of damaged individuals was tested for a significant correlation with selection ratio across species.

A preliminary inspection of nutritional patterns across species suggested an association between certain habitat types and leaf nutrient concentration. To investigate this graphically, species were plotted along nutritional concentration axes. Collinearity was observed among variables, and therefore a principal components analysis (PCA) was used to reduce the variance in nutritional concentration into one or two dimensions (Legendre & Legendre 1998). The PCA was conducted on the correlation matrix of nutrient concentrations with SAS for Windows 6.12 (SAS

Institute 1996). Only variables that explained a significant or marginally significant amount of variance in selection ratio were included in the analysis.

RESULTS

One thousand and thirty-three trees of 39 species were identified in the 12 plots. Of these, 1015 individuals of 30 species were used in the analysis after rare species (< 4 individuals) were dropped. One species, *Commiphora africana* Engl., had seven individuals, but all were leafless at the time of the survey. It was therefore excluded from the nutritional analysis but included in the analysis of plant height. *Baphia massaiensis* Taub. and *Bauhinia petersiana* Bolle accounted for approximately 40% of all woody plants in the survey. The total proportion of damaged trees was 53%, and 44% of all trees (or 83% of those damaged) had broken main stems or ramets. Species with high selection ratios included *Colophospermum mopane*, *Acacia* spp., *Markhamia acuminata* K. Schum. and *Pterocarpus* spp. (Table 1). Species that were largely avoided included *Baikiaea plurijuga*, *Erythrophleum africanum* Harms, *Brachystegia spiciformes* Benth. and *Burkea africana* Hook. (Table 1). The selection ratio was positively correlated with leaf Ca, K, Mg and crude protein (Table 2), but not with Na, fibre or phosphorus, although the correlation coefficients were in the expected directions for the latter three variables (Table 2).

The first axis of the PCA accounted for 60% of the total variance in mineral concentration, and all variables had positive loadings on this axis (Figure 1). The first principal axis was positively correlated with selection ratio ($r_s = 0.65$, $n = 27$, $P < 0.0005$), as expected from the positive associations between elephant damage and the variables included in the PCA. Species with negative values along PC1 were primarily species associated with nutrient-poor sandy habitats, e.g. *Baikiaea plurijuga*, *Burkea africana*, *Erythrophleum africanum* and *Ochna pulchra* Hook. Species with positive values along this axis tended to be species associated with more fertile soils, e.g. *Acacia* spp. and *Grewia flavescens* Juss. A subset of species often associated with termite mounds, e.g. *Euclea divinorum* Hiern, *Pterocarpus rotundifolius* Druce and *Grewia monticola* Sonder (pers. obs.), also had positive values along PC1 (Figure 1).

The median height of damaged trees was negatively correlated with selection ratio across species ($r_s = -0.52$, $n = 28$, $P < 0.005$).

DISCUSSION

Elephant damage is generally associated with leaf mineral concentration, and to a lesser extent with crude protein, across species in Kalahari sand woodlands. Other studies have found a similar relationship between

Table 1. Selection ratio and leaf nutrient concentration of trees damaged by elephants in Farm 41. Nutrient concentration is expressed on a dry matter basis. CP, crude protein; NDF, neutral detergent fibre.

Species	Family	Selection ratio		Mineral content (%)					CP (%)	NDF (%)
		Median	Range	Na	Mg	K	Ca	P		
<i>Acacia ataxacantha</i>	Mimosaceae	0.7	0.6–0.8	0.01	0.29	1.17	0.78	0.18	26.1	47.4
<i>Acacia erioloba</i>	Mimosaceae	1.4	1.4–1.4	0.02	0.14	0.90	0.62	–	–	–
<i>Acacia fleckii</i>	Mimosaceae	1.1	1.0–1.1	0.06	0.29	1.09	0.80	0.19	30.4	46.5
<i>Acacia luederitzii</i>	Mimosaceae	0.3	0.3–0.3	0.05	0.25	1.38	0.49	–	–	–
<i>Baikiaea plurijuga</i>	Caesalpinaceae	0.0	0.0–2.0	0.03	0.16	0.89	0.19	0.23	21.0	70.8
<i>Baphia massaiensis</i>	Fabaceae	1.1	0.4–2.2	0.01	0.17	0.99	0.47	0.20	26.6	48.3
<i>Bauhinia petersiana</i>	Caesalpinaceae	1.4	0.0–2.2	0.02	0.19	1.16	0.45	0.19	20.8	49.7
<i>Brachystegia spiciformes</i>	Caesalpinaceae	0.3	0.0–1.0	0.02	0.20	1.33	0.60	0.24	17.1	56.5
<i>Burkea africana</i>	Caesalpinaceae	0.0	0.0–0.0	0.02	0.10	0.56	0.08	0.09	11.7	45.2
<i>Canthium huillense</i>	Rubiaceae	0.0	0.0–0.0	0.03	0.16	0.67	0.24	0.16	16.3	18.4
<i>Colophospermum mopane</i>	Caesalpinaceae	1.6	1.1–2.0	0.04	0.20	1.09	0.93	0.16	13.6	42.3
<i>Combretum apiculatum</i>	Combretaceae	0.9	0.9–0.9	0.01	0.42	1.55	0.89	0.18	15.0	30.9
<i>Combretum collinum</i>	Combretaceae	1.8	1.1–2.2	0.03	0.28	1.09	0.81	0.17	19.3	36.9
<i>Combretum hereroense</i>	Combretaceae	0.3	0.3–0.3	0.04	0.21	1.08	0.73	0.16	17.9	54
<i>Combretum zeyheri</i>	Combretaceae	0.3	0.0–3.3	0.02	0.21	1.11	0.37	0.16	18.4	33.9
<i>Commiphora africana</i>	Burseraceae	1.4	1.4–1.4	–	–	–	–	–	–	–
<i>Dichrostachys cinerea</i>	Mimosaceae	1.1	0.8–1.3	0.02	0.21	1.32	0.67	0.15	23.5	56.9
<i>Erythrophleum africanum</i>	Caesalpinaceae	0.0	0.0–0.0	0.01	0.13	0.78	0.07	0.25	25.6	57.2
<i>Euclea divinorum</i>	Ebenaceae	1.0	1.0–1.0	0.03	0.34	1.35	1.05	0.17	13.6	52.7
<i>Grewia flavescens</i>	Tiliaceae	0.9	0.2–1.0	0.02	0.25	1.54	1.18	0.19	22.5	50.2
<i>Grewia monticola</i>	Tiliaceae	1.3	1.1–1.4	0.03	0.19	1.55	1.71	0.20	17.5	53.7
<i>Hippocratea buchamanii</i>	Celastraceae	1.7	1.7–1.7	0.04	0.46	2.22	1.23	0.21	33.1	–
<i>Lonchocarpus nelsii</i>	Fabaceae	1.2	0.2–2.1	0.02	0.19	1.50	0.57	0.23	36.4	53.6
<i>Markhamia acuminata</i>	Bignoniaceae	2.0	1.1–2.2	0.02	0.24	1.30	0.47	0.25	24.7	64.4
<i>Ochna pulchra</i>	Ochnaceae	0.0	0.0–0.0	0.01	0.15	0.70	0.28	0.12	11.2	70.3
<i>Pseudolachnostylis maprouneifolia</i>	Euphorbiaceae	0.0	0.0–0.0	0.03	0.12	1.04	0.15	–	–	–
<i>Pterocarpus angolensis</i>	Fabaceae	3.8	1.0–6.6	0.04	0.33	2.10	0.55	0.19	26.2	56.1
<i>Pterocarpus rotundifolius</i>	Fabaceae	1.2	1.2–1.2	0.05	0.21	1.91	0.74	0.30	27.3	34.1
<i>Rhus tenuinervis</i>	Anacardiaceae	1.5	1.3–1.7	0.03	0.31	1.48	0.86	0.20	25.4	52.8
<i>Terminalia brachystemma</i>	Combretaceae	0.7	0.7–0.7	0.02	0.29	0.99	0.95	0.13	10.7	61.1
<i>Terminalia sericea</i>	Combretaceae	1.4	1.1–3.4	0.02	0.24	0.64	0.64	0.12	12.3	52.7

Table 2. Spearman correlation coefficients between selection ratio and leaf nutrient concentration in Kalahari sand woodland vegetation in Farm 41, Zimbabwe.

Variable	r_s	P
Na	0.26	0.2
Mg	0.51	0.004
K	0.52	0.003
Ca	0.56	0.002
NDF	–0.09	0.7
CP	0.37	0.06
P	0.25	0.2

feeding preferences by large herbivores and minerals (Cooper *et al.* 1988, Jachmann 1989, Jachmann & Bell 1985, McNaughton 1988). The hypothesis that elephants select Na-rich species was not supported. A possible explanation for this is that in this habitat elephants often have access to licks with Na concentrations that are orders of magnitude higher than those in plant tissues (Holdo *et al.*, 2002), and elephants may therefore have little need to select Na-rich species.

The research conducted by Cooper *et al.* (1988) and Cooper & Owen-Smith (1985) in South African savannas underscores the importance of conducting year-round

studies that take phenological patterns into account when investigating food selection in relation to plant nutrient concentration. Since leaf nutrient concentration may vary throughout leaf development, short-term data on nutrient content may be misleading if a high degree of asynchrony in leaf development occurs across species. However, unlike the case of less markedly seasonal habitats, leaf emergence during the dry season in southern African woodlands is temporally predictable and shows quite a high degree of synchrony among species (Rutherford & Panagos 1982, *pers. obs.*). A second potential concern associated with the short duration of the study is that whereas the elephant feeding patterns measured in this study were based on plant damage occurring over more than one season, leaf chemistry was measured over a short time period. This study was designed to be conducted at a time when elephants rely the most on woody vegetation, i.e. late in the dry season, when the population density and impact of elephants on the vegetation is at a peak in Farm 41. At this time of the year elephants congregate around artificial water sources in the eastern sector of Hwange National Park and surrounding areas, and their diet consists almost exclusively of browse (Williamson

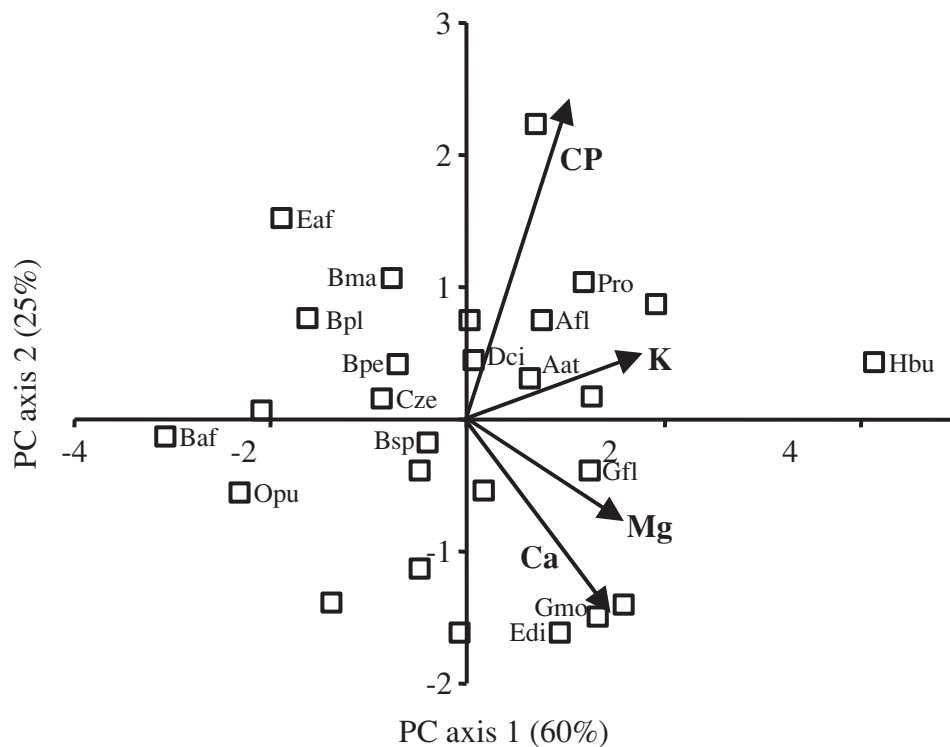


Figure 1. Principal components analysis based on leaf mineral and crude protein concentration of 27 tree species in Farm 41. Each object in the figure represents one species. Species referred to in the text are labelled. The loadings for the original variables (multiplied by 3 to improve visual display) are represented by vectors (CP, crude protein). Key to species: Aat, *Acacia ataxacantha*; Afl, *Acacia fleckii*; Baf, *Burkea africana*; Bma, *Baphia massaiensis*; Bpe, *Bauhinia petersiana*; Bpl, *Baikiaea plurijuga*; Bsp, *Brachystegia spiciformes*; Cze, *Combretum zeyheri*; Dci, *Dichrostachys cinerea*; Edi, *Euclea divinorum*; Eaf, *Erythrophleum africanum*; Gfl, *Grewia flavescens*; Gmo, *Grewia monticola*; Hbu, *Hippocratea buchannanii*; Opu, *Ochna pulchra*; Pro, *Pterocarpus rotundifolius*.

1975a, b). During the wet season their diet is dominated by grasses and they occur in lower numbers in Farm 41 and the eastern portion of HNP, and their impact on the woody vegetation is therefore less severe (Williamson 1975a, b). Since elephants feed on woody vegetation mostly in the dry season, it is reasonable to assume that their feeding choices are influenced by leaf chemistry at this time.

Still, even within the dry season, important changes in leaf chemistry occur as nutrients are reabsorbed from senescing leaves and new leaves are produced (Salisbury & Ross 1992). For example, the crude protein levels measured in this study were 26% higher on average than those recorded by Williamson (1975b) for 22 tree species in neighbouring Hwange National Park, and 55% higher than composite values measured in 24 vegetation plots in a subsequent study conducted in Farm 41 (Holdo & McDowell, unpubl. data). In the latter case, samples were collected in July, when leaves are mature or senescing, whereas in the present study leaves were collected in October, when leaves are young.

Leaf samples were used to quantify plant nutrient concentration in this study, but elephants also feed extens-

ively on the bark, twigs, and roots of woody plants. In Hwange National Park, elephants have been observed to feed on the bark of young stems of *Guibourtia coleosperma* J. Leonard, but never on leaves of this species (*pers. obs.*). Other species appear to be targeted for specific parts at particular times of the year, for example the bark of *Acacia fleckii* and *Brachystegia spiciformes* and the roots of *Combretum zeyheri* during the dry season (*pers. obs.*). To fully understand the nutritional factors driving elephant feeding preferences, a more comprehensive study that takes into account plant phenology, temporal variation in chemistry among plant species and parts, and seasonal patterns of elephant selection for particular species and parts might be desirable.

The association between elephant damage and leaf mineral concentration does not necessarily imply a causal link between mineral concentration and species preferences, which may be influenced by other nutritional factors, such as sugar concentration or plant secondary compounds. These other factors could be correlated with mineral concentration, or could influence selection in conjunction with minerals (*cf.* Cooper *et al.* 1988). Secondary compounds play an important role in determining food

selection by browsing ungulates in African savannas (Cooper *et al.* 1988, Furstenburg & van Hoven 1994). Condensed tannins in particular appear to deter feeding by giraffe (Furstenburg & van Hoven 1994), impala and kudu (Cooper & Owen-Smith 1985). Unpalatable tree species with high levels of constitutive secondary compounds (e.g. tannins) tend to occur on nutrient-poor soils (Bryant *et al.* 1989, Coley *et al.* 1985, Owen-Smith & Cooper 1987). Since plants obtain minerals largely from the soil (McDowell 1985), a negative correlation between leaf minerals and constitutive secondary compounds might be expected across soil nutrient gradients (cf. Cooper *et al.* 1988). Kalahari sands are particularly poor in mineral nutrients (Frost 1997, IGBP 1997), and therefore the low palatability of many tree species associated with these soils (e.g. *Baikiaea plurijuga*) may be driven by high levels of condensed tannins rather than by low concentrations of minerals in plant tissues. This hypothesis is supported by the fact that the nutrients that might be most expected to influence food selection by elephants (protein and sodium) showed only a weak or no association with elephant damage, unlike calcium, magnesium and potassium, which are less likely to be limiting for elephants in this ecosystem (Holdo *et al.*, 2002), but are important for plant growth (Salisbury & Ross 1992).

The savannas of southern Africa have been divided into nutrient-poor 'broad-leaved' savanna and nutrient-rich 'fine-leaved' savanna (Scholes & Walker 1993). Many of the woody species in the former type occur on poor, sandy soils and are relatively unpalatable and avoided by large herbivores such as kudu and impala (Bryant *et al.* 1989, Owen-Smith & Cooper 1987). In contrast, fine-leaved savanna species such as *Acacia* spp. occur on richer soils and tend to be more palatable (Cooper & Owen-Smith 1985, Scholes & Walker 1993). The nutritional differences that might be expected between these two types in Farm 41 were supported by the ordination of species by principal components. A third vegetation type comprises species that are often associated with termite mounds. Termite mounds have higher clay concentrations than surrounding soils because the mound-building termites of the Kalahari region are clay specialists that tend to concentrate clay particles (Dangerfield *et al.* 1998). In an ecosystem of sand-dominated soils, these clay mounds become fertile islands (Dangerfield *et al.* 1998, Frost 1997) associated with a particular suite of plant species (Dangerfield 1990, Frost 1997). The presence of these mounds creates spatial heterogeneity in plant species composition and this may in turn affect the pattern of elephant habitat use.

The identification of ecological associations of species with similar nutritional characteristics and levels of elephant use suggests that the relationship between elephant feeding preference and leaf mineral composition may be better interpreted at the scale of vegetation types rather than species. Since the distribution of vegetation types is

largely determined by edaphic factors (Childes & Walker 1987, Rogers 1993, Scholes & Walker 1993), soil composition may be a primary underlying factor determining patterns of habitat use by elephants. The P-values obtained in the correlation analyses should be treated with some caution because the use of species as independent units of observation is questionable (Felsenstein 1985). The lack of independence (ecological rather than phylogenetic) among species in the present analysis suggests that they may constitute less than ideal units for statistical treatment. Species were selected as units of observation both because elephants appear to show strong discrimination at the species level in Kalahari sand woodlands (*pers. obs.*), and because many ecological and management questions dealing with the effects of herbivores on their environment focus on changes in populations at the species level.

The selective suppression of plant species by elephants has been well documented (Anderson & Walker 1974, Barnes 1985, Guy 1989). Elephants frequently break the main stems of trees, resulting in the release of apical dominance and a stunted multi-stemmed growth form (Jachmann & Bell 1985, Lewis 1991). Repeated browsing can prevent trees from recruiting into larger size classes and 'escaping' the elephant feeding stratum (Caughley 1976, Jachmann & Bell 1985). As a result, some palatable species have few individuals that reach these size classes, and this may result in decreased reproductive output for species in which reproduction is height-dependent, as has been suggested for *Colophospermum mopane* (Caughley 1976). Elephants may suppress recruitment into mature size classes in some species in Farm 41, as suggested by the negative correlation between selection ratio and median height across species, and the fact that 44% of trees sampled had had their main stems or trunks broken. For example, stems of *Pterocarpus angolensis*, which normally occurs as a tree in this type of woodland, had been damaged to such an extent by elephant browsing that under existing conditions they appeared unlikely to escape the smaller size classes. Elephant damage in *Baikiaea* woodlands in Hwange National Park is selective (Williamson 1975b) and appears to affect regenerating classes rather than mature trees (Childes & Walker 1987, Conybeare 1991). Despite the high incidence of elephant damage in the Farm 41 plots, it is difficult to determine the extent to which elephants drive woodland change in this ecosystem without estimates of tree growth, mortality and seedling establishment.

The impact of elephants on vegetation is strongly dependent on elephant population density (Jachmann & Croes 1991), which may vary considerably over distances of a few km depending on the distribution of water supplies (Ben-Shahar 1993, Conybeare 1991). Based on past estimates of elephant numbers in Hwange National Park and population growth rates estimated over a couple of

decades (Martin *et al.* 1992), the average elephant population density of elephants in HNP was probably of the order of 2.8 animals km⁻² at the time of the study. This value is probably considerably higher during the dry season in the eastern sector of HNP and Farm 41, where none of the vegetation plots was located more than a few km from permanent water sources. This population density is considerably higher than the maximum of 0.5 animals km⁻² recommended for the long-term maintenance of *Terminalia-Combretum* woodlands in West Africa (Jachmann & Croes 1991), but may still not result in the destruction of the less palatable *Baikiaea*-dominated habitat.

The index of elephant damage used in this study – the proportion of damaged trees per species – measures the probability that a tree of a given species will be damaged, but does not reflect the magnitude of this damage. This suggests that taking into account only the proportion of trees damaged as an index of elephant damage underestimates true differences in biomass removal among species. For example, only 6% of *Baikiaea plurijuga* trees were damaged, as opposed to 100% of *Colophospermum mopane* trees, but this difference is probably even greater if it is considered that most of the former had only slight damage whereas most of the latter had extensive and repeated damage. To quantify inter-specific differences in elephant selectivity more accurately, within-tree variation in biomass removal should be quantified.

In conclusion, the pattern of elephant damage encountered in Farm 41 indicates that elephants are selective feeders in Kalahari sand woodlands, and this selectivity may be driven by nutritional differences among species and/or vegetation types. As has been reported for other sites (Barnes 1985, Guy 1989, Jachmann & Bell 1985, Jachmann & Croes 1991), elephants may selectively suppress certain tree species in Farm 41, resulting in changes in vegetation structure and composition.

ACKNOWLEDGEMENTS

Lionel Reynolds and Touch The Wild (Pvt.) Ltd. kindly provided permission for research to be conducted in Farm 41. The research was funded by a Grinter Fellowship from the Department of Zoology, University of Florida. The following people generously provided field and laboratory support: Joseph Dudley, Lee McDowell, John Foster, Felix Banda, Nancy Wilkinson and Nariman Heshmati. John Eisenberg, Lee McDowell, Colin Chapman, Daphne Onderdonk and three reviewers provided helpful comments on earlier drafts of the manuscript.

LITERATURE CITED

ANDERSON, G. D. & WALKER, B. H. 1974. Vegetation composition and elephant damage in the Sengwa Wildlife Research Area, Rhode-

sia. *Journal of the South African Wildlife Management Association* 4:1–14.

BARNES, R. F. W. 1985. Woodland changes in Ruaha National Park (Tanzania) between 1976 and 1982. *African Journal of Ecology* 23:215–222.

BEN-SHAHAR, R. 1993. Patterns of elephant damage to vegetation in northern Botswana. *Biological Conservation* 65:249–256.

BRYANT, J. P., KUROPAT, P. J., COOPER, S. M., FRISBY, K. & OWEN-SMITH, N. 1989. Resource availability hypothesis of plant antiherbivore defense tested in a South African savanna ecosystem. *Nature* 340:227–229.

CAMPBELL, B. M., BUTLER, J. R. A., MAPAURE, I., VERMEULEN, S. J. & MASHOVE, P. 1996. Elephant damage and safari hunting in *Pterocarpus angolensis* woodland in northwestern Matabeleland, Zimbabwe. *African Journal of Ecology* 34:380–388.

CAUGHLEY, G. 1976. The elephant problem: an alternative hypothesis. *East African Wildlife Journal* 14:265–283.

CHILDES, S. L. & WALKER, B. H. 1987. Ecology and dynamics of the woody vegetation on the Kalahari sands in Hwange National Park, Zimbabwe. *Vegetatio* 72:111–128.

COLEY, P. D., BRYANT, J. P. & CHAPIN, F. S. 1985. Resource availability and plant antiherbivore defense. *Science* 230:895–899.

CONYBEARE, A. M. 1991. *Elephant occupancy and vegetation change in relation to artificial water points in a Kalahari sand area of Hwange National Park*. Ph.D. thesis, University of Zimbabwe, Harare.

COOPER, S. M. & OWEN-SMITH, N. 1985. Condensed tannins deter feeding by browsing ruminants in a South African savanna. *Oecologia* 67:142–146.

COOPER, S. M., OWEN-SMITH, N. & BRYANT, J. P. 1988. Foliage acceptability to browsing ruminants in relation to seasonal changes in the leaf chemistry of woody plants in a South African savanna. *Oecologia* 75:336–342.

CRAWLEY, M. J. 1983. *Herbivory: the dynamics of animal-plant interactions*. University of California Press, Berkeley. 437 pp.

DANGERFIELD, J. M. 1990. The distribution and abundance of *Cubitermes sankurensis* (Wassmann) (Isoptera; Termitidae) within a miombo woodland site in Zimbabwe. *African Journal of Ecology* 28:15–20.

DANGERFIELD, J. M., MCCARTHY, T. S. & ELLERY, W. N. 1998. The mound-building termite *Macrotermes michaelsoni* as an ecosystem engineer. *Journal of Tropical Ecology* 14:507–520.

DOUGLAS-HAMILTON, I. & MICHELMORE, F. 1996. *Loxodonta africana*: range and distribution, past and present. Pp. 321–326 in Shoshani, J. & Tassy, P. (eds). *The proboscidea: evolution and paleoecology of elephants and their relatives*. Oxford University Press, Oxford.

DUBLIN, H. T., SINCLAIR, A. R. E. & MCGLADE, J. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara Woodlands. *Journal of Animal Ecology* 59:1147–1164.

FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.

FICK, K. R., MCDOWELL, L. R., MILES, P. H., WILKINSON, N. S., FUNK, J. D. & CONRAD, J. H. 1979. *Methods of mineral analysis for plant and animal tissues*. (Second edition). Animal Science Department, University of Florida, Gainesville. 80 pp.

- FROST, P. G. H. 1997. The ecology of miombo woodlands. Pp. 11–57 in Campbell, B. M. (ed.). *Woodlands and welfare in Africa: miombo woodlands in transition*. Center for International Forestry Research, Bogor.
- FURSTENBURG, D. & VAN HOVEN, W. 1994. Condensed tannin as anti-defoliate agent against browsing by giraffe (*Giraffa camelopardalis*) in the Kruger National Park. *Comparative Biochemistry and Physiology* 107A:425–431.
- GALLAHER, R. N., WELDON, C. O. & FUTRAL, J. G. 1975. An aluminum block digester for plant and soil analysis. *Soil Science Society of America Journal* 39:803–806.
- GOLDING, E. J., CARTER, M. F. & MOORE, J. E. 1985. Modification of the neutral detergent fiber procedure for hay. *Journal of Dairy Science* 68:2732–2736.
- GUY, P. R. 1989. The influence of elephants and fire on a *Brachystegia–Julbernardia* woodland in Zimbabwe. *Journal of Tropical Ecology* 5:215–226.
- HOLDO, R. M., DUDLEY, J. P. & McDOWELL, L. R. 2002. The role of sodium in the ecology of the African elephant *Loxodonta africana* in a semi-arid woodland. *Journal of Mammalogy* 83: 652–664.
- IGBP 1997. *The Kalahari transect: research on global change and sustainable development in Southern Africa*. Scholes, R. J. & Parsons, D. A. B. (eds). International Geosphere-Biosphere Programme, Stockholm. 61 pp.
- JACHMANN, H. 1989. Food selection by elephants in the miombo biome, in relation to leaf chemistry. *Biochemical Ecology and Systematics* 17:15–24.
- JACHMANN, H. & BELL, R. H. V. 1985. Utilization by elephants of the *Brachystegia* woodlands of the Kasungu National Park, Malawi. *African Journal of Ecology* 23:245–258.
- JACHMANN, H. & CROES, T. 1991. Effects of browsing by elephants on *Combretum/Terminalia* woodland at the Nazinga Game Ranch, Burkina Faso, West Africa. *Biological Conservation* 57:13–24.
- LAWS, R. M. 1970. Elephants as agents of habitat and landscape change in East Africa. *Oikos* 21:1–15.
- LAWS, R. M., PARKER, I. S. C. & JOHNSTONE, R. C. B. 1975. *Elephants and their habitats: the ecology of elephants in North Bunyoro, Uganda*. Clarendon Press, Oxford. 376 pp.
- LEGENDRE, P. & LEGENDRE, L. 1998. *Numerical ecology*. (Second edition). Elsevier, Amsterdam. 853 pp.
- LEWIS, D. M. 1991. Observations of tree growth, woodland structure and elephant damage on *Colophospermum mopane* in Luangwa Valley, Zambia. *African Journal of Ecology* 29:207–221.
- MARTIN, R. B., CRAIG, G. C. & BOOTH, V. R. 1992. *Elephant management in Zimbabwe: a review*. Department of National Parks and Wild Life Management, Harare. 124 pp.
- MCDOWELL, L. R. 1985. Contribution of tropical forages and soil toward meeting mineral requirements in grazing ruminants. Pp. 165–188 in McDowell, L. R. (ed.). *Nutrition of grazing ruminants in warm climates*. Academic Press, Orlando. 443 pp.
- MCNAUGHTON, S. J. 1988. Mineral nutrition and spatial concentrations of African ungulates. *Nature* 334:343–345.
- OWEN-SMITH, N. & COOPER, S. M. 1987. Palatability of woody plants to browsing ruminants in a South African savanna. *Ecology* 68:319–331.
- ROGERS, C. M. L. 1993. *A woody vegetation survey of Hwange National Park*. Department of National Parks and Wild Life Management, Harare. 176 pp.
- RUTHERFORD, M. C. & PANAGOS, M. D. 1982. Seasonal woody plant shoot growth in *Burkea africana* – *Ochna pulchra* savanna. *South African Journal of Botany* 1:104–116.
- SAID, M. Y., CHUNGE, R. N., THOULESS, C. R., BARNES, R. F. W. & DUBLIN, H. T. 1995. *African elephant database*. IUCN/SSC Occasional Paper No. 11. IUCN, Gland. 225 pp.
- SALISBURY, F. B. & ROSS, C. W. 1992. *Plant physiology*. (Fourth edition). Wadsworth Publishing Co, Belmont. 682 pp.
- SAS INSTITUTE. 1996. SAS for Windows 6.12. SAS Institute, Cary.
- SCHOLES, R. J. & WALKER, B. H. 1993. *An African savanna: synthesis of the Nylsvley study*. Cambridge University Press, Cambridge. 306 pp.
- THOMSON, P. J. 1975. The role of elephants, fire and other agents in the decline of a *Brachystegia boehmii* woodland. *Journal of the South African Wildlife Management Association* 5:11–18.
- VERLINDEN, A. & GAVOR, I. K. N. 1998. Satellite tracking of elephants in northern Botswana. *African Journal of Ecology* 36:105–116.
- WEEKS, H. P. & KIRKPATRICK, C. M. 1976. Adaptations of white-tailed deer to naturally occurring Na deficiencies. *Journal of Wildlife Management* 40:610–625.
- WEIR, J. S. 1972. Spatial distribution of elephants in an African National Park in relation to environmental sodium. *Oikos* 23:1–13.
- WILLIAMSON, B. R. 1975a. Seasonal distribution of elephant in Wankie National Park. *Arnoldia (Rhodesia)* 7:1–16.
- WILLIAMSON, B. R. 1975b. The condition and nutrition of elephant in Wankie National Park. *Arnoldia (Rhodesia)* 7:1–20.