Termitaria as browsing hotspots for African megaherbivores in miombo woodland

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Abstract: Thirteen termite mounds and 13 similar-sized control plots were surveyed in central Zimbabwe in order to study large mammalian browsing and vegetation characteristics. The mounds supported almost twice as many tree species as the control plots and the woody vegetation was denser on mounds compared with the woodland plots. Species of woody plants were recorded along with the percentage of branches browsed (cumulative browsing score) by black rhino, *Diceros bicornis*, elephant, *Loxodonta africana* and other browsers combined. In addition we measured how the cumulative browsing score on three woody plant species, *Acacia nilotica*, *Colophospermum mopane* and *Dichrostachys cinerea*, which were common both on and off mounds, was related to the distance from mound centre. Both black rhino and elephant cumulative browsing scores were significantly higher on the mound plants compared with the woodland plots. Cumulative browsing score was negatively related to distance from the mound centre for *Dichrostachys cinerea*, *Colophospermum mopane* and *Acacia nilotica*. We propose that termite mound construction in miombo woodland contributes to sustaining populations of megaherbivores and perhaps some woody species in these areas.

Key Words: browsing ecology, *Diceros bicornis*, elephant, *Loxodonta africana*, miombo, rhinoceros, termitaria, Zimbabwe

INTRODUCTION

Large, sometimes vegetated, termite mounds (termitaries or termitaria) are a feature of many tropical savanna landscapes (Lee & Wood 1971). They are prominent in miombo (*Brachystegia*/*Julbernardia*), *Acacia*, mixed riverine and *Colophospermum mopane* woodland, which covers large parts of the southern African region. Individual termite mounds may be formed over as much as 700 y (Watson 1967) by various species of the fungus-growing termites (Isoptera; Macrotermitinae), occur at densities from 2–7 ha^{-1}, and may be as large as 9 m high and 20–30 m in diameter at the base (Lee & Wood 1971). At least for granite-derived soils in Zimbabwe, it has long been known that termitaria soils are composed of a finer fraction and have more mineral nitrogen and available phosphorus than the soils of the surrounding woodland (Watson 1977). Thus it has been stated (Frost 1996) that these termitaria represent

nutrient hotspots in the otherwise nutrient-poor miombo woodland. Furthermore, Wild (1952) observed that large termitaria in Zimbabwe supported a different flora than the surrounding woodland. These observations were amplified by Malaisse (1978) working in miombo of the Shaba Province (formerly Katanga) of the Democratic Republic of the Congo. It is evident that these differences in vegetation between termitaria and surrounds are just as marked in some African grasslands (Glover *et al.* 1964).

Armstrong & Siegfried (1990) showed that in the succulent karoo, South Africa, domestic sheep spent more time feeding on heuweltjie mounds, thought to be formed by termites and mole-rats, than on inter-mound vegetation. Some studies have shown that woody plants growing on nutrient-poor savanna soil are generally less preferred by browsers than plants from nutrient-rich areas because plants growing on nutrient-poor soils are more effectively chemically defended (Bryant *et al.* 1983, 1989). The naturally occurring eutrophic islands, represented by termitaria within a nutrient-poor miombo landscape, not only provide an opportunity to test browsing differences between plant species, but also

an opportunity to test intraspecific differences in browsing between plants growing both on and off mounds.

This research was directed to discover whether termite mounds in miombo woodland support woody vegetation that is used more by browsing herbivores than the plants in the more nutrient-poor parts of the environment.

STUDY SITE

The study was conducted in June 1999 in central Zimbabwe at the 10 000-ha Iwaba wildlife estate (18°44′S, 30°05′E, altitude 1130–1230 m). The 40-y mean annual rainfall is 697 mm (range of 333–1128 mm) with a coefficient of variability (Torrance 1981) of 30%. The single rainy season usually starts at the beginning of November, ending around mid-March, lasting on average 128 d with 59 ± 16 rainy days. Mean annual maximum and minimum air temperatures at Kwekwe (1215 m) between 1956 and 1986 were 27.4 and 12.5 °C, respectively. The hottest month is October (mean maximum 31.4 °C), and the coolest July (mean minimum 5.7 °C) (Torrance 1981). The soils on Iwaba are generally poor, sandy and leached, derived mainly from granite. There are sodic patches (Thompson 1965) along drainage lines, as well as some areas with more nutrient-rich red soil derived from amphibolite and ultramafic schists (Stowe 1979). The area supports *Brachystegia spiciformis* woodland (Wild & Barbosa 1967; Table 1 lists common species) locally called miombo woodland. Observation on the ground shows the miombo woodland on ridges to be dominated by *B. spiciformis/ Julbernardia globiflora* (Benth.) Troupin, but *Burkea africana*, *Brachystegia boehmii* Taub. and *Terminalia sericea* can be locally important. On the margins of seasonally waterlogged drainage lines (dambos or vleis) the grass is frequently invaded by *T. sericea*. On the sodic soils, commonly associated with dambos, mopane woodland dominated by *Colophospermum mopane*, often associated with *Combretum apiculatum*, is present, but nowhere extensive.

Apart from the African buffalo, *Syncerus caffer* (Sparrman), most of the native African savanna large mammalian herbivores are found on Iwaba. At the time of study there were 12 black rhino, *Diceros bicornis* (L.), 20 white rhino, *Ceratotherium simum* (Burchell) and seven elephants, *Loxodonta africana* (Blumenbach) at Iwaba as well as substantial populations of common African antelopes like impala, *Aepyceros melampus* (Lichtenstein), greater kudu, *Tragelaphus strepsiceros* (Pallas) and eland, *Taurotragus oryx* (Pallas). In total 54 mammal species have been recorded.

The mounds we studied in the area were constructed by termites of the genus *Macrotermes*. Earlier workers (Coaton 1962, Dejean *et al.* 1997, Josens 1983) have

shown that mounds previously occupied by one termite species may later be recolonized by other species. Thus, the present species of termites occupying the mound may not have been the main agent shaping the physical and chemical environment of the mounds.

METHODS

Thirteen termitaria were selected within the areas of granite-derived soil at Iwaba. Woodland plots (n = 13) in the adjacent woodland were randomly sited in relation to the centre of each termite mound using a table of random numbers for a compass bearing (in the range 1–360°) and distance (in the range 20–80 m). Careful inspection ensured that each woodland plot was not closer than 20 m to any other termite mound centre. On each mound four mound radii were measured to estimate the mound area and the mean radius determined the radius of the circular woodland plot. This distance was measured from the centre in the direction of the random bearing and at right angles to it, thus determining the boundary of the plot. Thus, each woodland plot was of exactly the same size as the adjacent termite mound.

At each site, both mound and control, tallest tree height (using a Suunto tree height meter) and basal area of woody plants (using a relascope) were measured. Mound height was measured on each mound.

Shrubs were defined as woody plants with stem diameters at 15 cm height > 1.0 cm and < 6.0 cm. Trees had a stem diameter at 15 cm > 6.0 cm. Shrubs, as defined here, therefore include tree seedlings of the given stem diameter range. The shrub subsample comprised the first 10 shrubs encountered starting along the line of the random bearing and progressing clockwise; the angle in which they were sampled was measured in order to estimate the number of shrubs on the mound or in the control plot. On each woody plant we counted the number of terminal branches and determined whether the branch had previously been browsed by black rhino, elephant, other browsers (combined) or if the branch was unbrowsed. A cumulative browsing score (a form of quantified non-mass browse data – Rutherford 1979) was then calculated representing the % browsed branches by a particular animal species on a particular woody plant. To standardise the sampling, only shoots below a height of 2.5 m from the ground were assessed (Rutherford 1979). Elephant browsing can easily be separated from black rhino feeding because the latter species is characteristic in the way it clips shoots and leaves to leave a scissor-like cut stump (Oloo *et al.* 1994, Ritchie 1963), while elephants leave browsed twigs with a shredded appearance (Dierenfeld *et al.* 1995). When comparing mound and woodland plots the distributions of variables were highly skewed.

Accordingly non-parametric statistics have been used to compare medians.

Woody species diversity was analysed for trees only according to the recommendations of Ludwig & Reynolds (1988). Hill's diversity numbers (N0, N1 and N2) and the modified Hill's evenness ratio (E5) were calculated. The shrubs were not analysed as only a proportion of these were sampled for each plot (because of time constraints), and it was therefore not appropriate to use these data in diversity calculations. Three species of woody plants (*Dichrostachys cinerea, Colophospermum mopane* and *Acacia nilotica*) were selected to study the relationship between cumulative browsing of individual species and distance to mound centre. These species were commonly found both on and off mounds. Both cumulative browsing for each plant as well as distance to mound centre for the 13 study mounds and a number of other mounds nearby were recorded.

RESULTS

Both black rhino and elephant browsing of woody plants on termitaria were significantly higher on termite mound plants compared with woodland plants (Wilcoxon Rank Sum Tests, P < 0.0001 and P = 0.002, respectively) (Figure 1). There were no significant differences between the use of termitaria and control plots by the other unidentified browsers, although the P-value was low (Wilcoxon Rank Sum Test, P = 0.08).

Only a few woody species had enough replicates (> 5 plants in both termitaria and woodland plots), both on mounds and in woodland plots, for statistical analysis to be performed at species level (Table 1). Both *Acacia nilotica* and *Colophospermum mopane* were significantly more browsed on termite mounds compared with individuals of these species in woodland (Table 1). *Dichrostachys cinerea*, which was also commonly found both on mounds and in the woodlands, showed this pattern only weakly (Table 1). For all the investigated species *Dichrostachys cinerea, Colophospermum mopane* and *Acacia nilotica* the cumulative browsing score was linearly related to the distance from mound centre (Figure 2). No species had a significantly higher cumulative browsing score in the control plots compared with mounds (Table 1). The most heavily browsed species, *Catunaregam spinosa*, was common in some of the woodland plots, though never recorded on mounds (Table 1).

The 13 termite mounds had a mean (± SD) height of 1.58 ± 0.50 m, and mean area of 83.7 ± 32.3 m^2; 11 of them showing signs of recent termite activity. The woody vegetation on the mounds was significantly taller (as judged by the tallest tree), and supported a significantly greater woody basal cover than the woodland plots (Table 2). Tree densities on termite mounds were twice
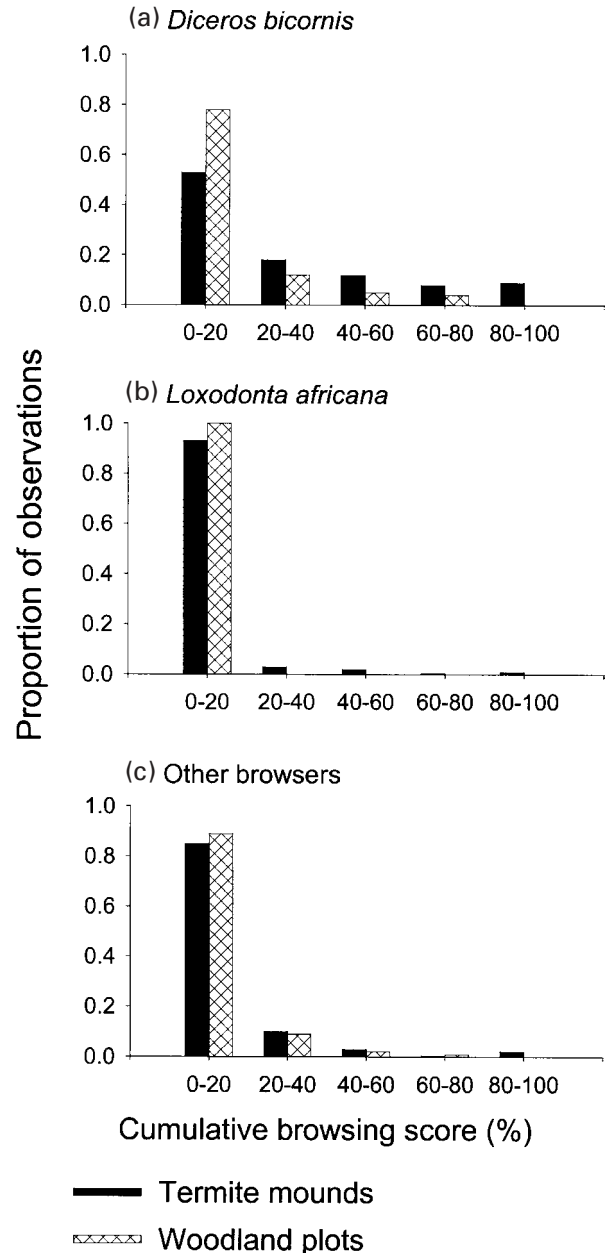

Figure 1. Proportion of observations in different cumulative browsing score groups on termite mounds and woodland plots for (a) black rhino (Wilcoxon Rank Sum Test, P < 0.0001), (b) elephant (Wilcoxon Rank Sum Test, P = 0.002) and (c) other browsers (Wilcoxon Rank Sum Test, P = 0.08). The survey included 13 mounds (259 plants) and 13 woodland plots (185 plants).

those in the woodland plots, but shrub densities were not significantly higher on the termite mounds than those in the woodland (Table 2).

The total number of tree species (N0) on the 13 termitaria was 24, as compared to 13 in the woodland plots. The number of abundant species (N1) was 14.1 and 7.0, and the number of very abundant species (N2) (Ludwig & Reynolds 1988) was 9.5 and 5.4 on termitaria and in the

Table 1. Browsing (median % browse and 25%, 75% percentiles in parentheses) on some woody species found on termitaria and in woodland at Iwaba. The criterion for inclusion is that the species occurred in two or more plots. Statistical analysis (Mann–Whitney U test) was only performed when at least 10 plants were recorded in both groups.

Species	Termite mounds			Woodland plots			P
	No. of mounds	Median % browse	No. of plants	No. of plots	Median % browse	No. of plants	
Acacia nilotica (L.) Willd. ex Delile	10	18.4 (10.8, 45.8)	25	9	2.9 (0.7, 11.8)	22	0.0001
Albizia harveyi Fourn.	2	34.5 (0, 48.2)	15	0	– –	0	
Brachystegia spiciformis Benth.	1	28.0	2	2	0.0 *	1	
Burkea africana Hook.	0	– –	0	2	37.5	2	
Cassia abbreviata Oliver	2	0.0 *	2	0	– –	0	
Catunaregam spinosa (Thunb.) Tirveng.	0	– –	0	5	69.1 (57.1, 82.3)	16	
Colophospermum mopane (Kirk ex Benth.) Kirk ex J. Léonard	9	28.9 (14.6, 83.3)	54	8	4.8 (0, 7.18)	33	< 0.0001
Combretum apiculatum Sonder	2	61.0 (53.8, 69.7)	4	10	9.4 (3.7, 16.4)	35	
Combretum hereroense Schinz	1	9.7	1	4	6.8 (3.7, 22.3)	5	
Combretum imberbe Wawra	0	– –	0	2	6.1 *	1	
Combretum molle R. Br. ex G. Don	2	24.7 (12.3, 27.9)	3	3	14.3 (6.5, 39.4)	3	
Commiphora mollis (Oliver) Engl.	2	45.5 (40.9, 53.8)	3	0	– –	0	
Dichrostachys cinerea (L.) Wight & Arn.	8	39.2 (27.0, 62.3)	21	6	22.9 (13.6, 47.3)	16	0.1178
Euclea divinorum Hiern	2	9.7 (8.6, 14.3)	6	2	14.1	2	
Flueggia virosa (Roxb. ex Willd.) Pax & K. Hoffm.	4	59.1 (43.0, 69.9)	9	0	– –	0	
Gardenia volkensii K. Schum.	0	– –	0	2	6.1 (5.4, 57.8)	3	
Grewia flavescens Juss.	9	51.2 (43.8, 60.0)	22	3	33.3 (23.7, 48.5)	3	
Grewia monticola Sonder	7	22.7 (17.5, 30.1)	9	3	8.2 (4.6, 16.0)	3	
Lannea schweinfurthii (Engl.) Engl.	3	49.4 (30.0, 81.0)	14	0	– –	0	
Ormocarpum trichocarpum (Taub.) Engl.	3	47.4 (9.3, 86.5)	10	1	20.2 (18.9, 21.2)	3	
Peltophorum africanum Sonder	1	13.2	1	2	3.9	2	
Rhus tenuinervis Engl.	7	55.0 (44.6, 65.1)	9	0	– –	0	
Sclerocarya birrea (A. Rich.) Hochst.	3	50.0 *	1	0	– –	0	
Terminalia sericea Burch ex DC.	0	– –	0	10	5.6 (0, 11.6)	25	
Ziziphus mucronata Willd.	9	23.2 (14.4, 35.2)	20	1	12.6	1	

* One or more of the plants had no available browse below 2.5 m height.

Table 2. Median (25% and 75% percentiles) tree heights, basal area, tree and shrub densities and cumulative browsing score of woody plants (all animals included) on termite mounds and in nearby miombo woodland.

	Termite mounds (n = 13)	Woodland plots (n = 13)	Wilcoxon Rank Sum Test P-value
Height of tallest tree (m)	9.25 (7.56, 10.19)	5.50 (4.69, 8.94)	0.007
Basal area ($m^2\,ha^{-1}$)	16.50 (15.50, 19.50)	6.00 (4.00, 7.50)	< 0.0001
Tree density (trees m^{-2})	0.12 (0.10, 0.17)	0.04 (0.03, 0.08)	< 0.0001
Shrub density (shrubs m^{-2})	0.58 (0.33, 0.70)	0.32 (0.26, 0.76)	0.644
Cumulative browsing score (%)	36.2 (32.4, 44.4)	17.0 (11.9, 24.9)	< 0.0001

woodland, respectively. The evenness index (E5) was 0.65 and 0.74 for trees on the termitaria and in the woodland, respectively.

DISCUSSION

This study clearly documents that woody vegetation growing on termite mounds is preferred by black rhino and elephants, when compared with woody vegetation growing in adjacent miombo woodland. The browsing on *Acacia nilotica*, *Colophospermum mopane* and *Dichrostachys cinerea* decreased with distance to mound centre (Figure 2).

Acacia nilotica, which is generally regarded as a highly palatable species in southern African savannas (Owen-Smith & Cooper 1987), has a relatively high browsing score (29%) when growing on termitaria. The same species in the woodland has a browsing score of only 7%, which is slightly lower than *Terminalia sericea* (8%), one of the least-palatable species to ungulate browsers in the woodland (Owen-Smith & Cooper 1987).

Bell (1982, 1986) hypothesized that the moist dystrophic (nutrient-poor) African savannas should be dominated by large mammalian herbivores with wide dietary tolerance, while smaller selective feeders should dominate
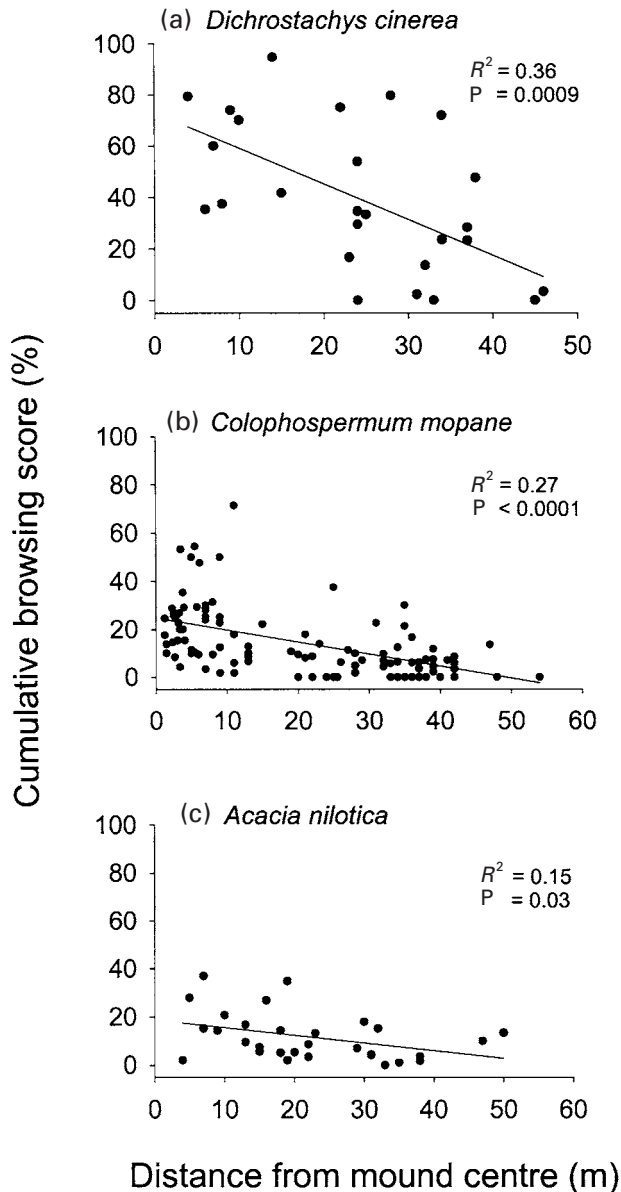
Figure 2. Cumulative browsing score as a function of distance from termite mound centre for (a) *Dichrostachys cinerea* (Y = 73.0 − 1.39X), (b) *Colophospermum mopane* (Y = 24.7 − 0.50X) and (c) *Acacia nilotica* (Y = 18.7 − 0.32X).

arid eutrophic (nutrient-rich) savannas. This general pattern has been confirmed by later studies (East 1984, Owen-Smith 1988). Our study suggests that termite activities contribute significantly in increasing the available food for browsing mammals in a nutrient-poor miombo system. Using the average mound size found in this study and earlier reported densities of up to 7 mounds ha⁻¹ (Lee & Wood 1971), termite mounds may cover 5–6% of the area in miombo woodland. In addition, the mounds in our study supported twice the density of trees and had almost three times the basal area as adjacent woodland plots.

Although the presence of termitaria does not change the general pattern described by Bell (1982, 1986) termitaria may contribute to sustaining higher population densities of African megaherbivores than would otherwise have been predicted in these nutrient-poor woodlands.

It is not yet clear why megaherbivores prefer mound vegetation. Earlier studies have shown that termite-mound soils have a higher level of soil nutrients than surrounding woodland (Lee & Wood 1971, Watson 1977). Armstrong & Siegfried (1990) have shown that for a short period of the afternoon after rains, sheep (*Ovis aries* L.) a domestic grazer, preferred heuweltjie mound vegetation in the succulent karoo in South Africa. In Kenya, Young *et al.* (1995) found that anthropogenic glades attracted wild mammals, possibly because of higher-quality food or as part of an anti-predator strategy.

A recent study in Kenya has shown that the black rhino, the main browser in our study area, feed selectively on plants with low phenol and alkaloid contents and high fibre values (Muya & Oguge 2000). The black rhino is also known to prefer dense bushland habitat (Tatman *et al.* 2000). The densely vegetated mounds provide such habitat where the black rhino may find both shade and cover while feeding. Longer occupancy of mounds for feeding and shelter will probably result in dung and urine deposition there, thus accentuating the differences in soil nutrients between mounds and miombo woodland. Eutrophic soils may increase the nutrient content of plants growing on termitaria and hence affect the browsers' food selection pattern. Further studies are needed to investigate any differences in plant nutrient content between woody plants growing on mounds and plants growing in the surrounding woodland, and possible feedback loops.

The termite mounds had a higher diversity of trees than the surrounding woodland. Diverse vegetation has been mentioned as a key habitat factor for black rhino (Muya & Oguge 2000). Species like *Albizia harveyi*, *Commiphora mollis*, *Flueggia virosa*, *Lannea schweinfurthii* and *Rhus ten-uinervis* were all recorded on mounds only and they all had a relatively high cumulative browsing score (more than 30% of terminal shoots browsed – Table 1). *Terminalia sericea*, *Gardenia volkensii*, *Catunaregam spinosa* and *Burkea africana* were found in the woodland plots only. *Terminalia sericea*, which is common in these miombo woodlands, is generally unpalatable (Owen-Smith & Cooper 1987).

Our data do not indicate that mound-growing woody plant species are consistently more palatable than woodland species. *Catunaregam spinosa*, found in the woodland plots only, is the most heavily browsed species recorded in this study with an average of 69% terminal shoots browsed. Also, species like *Dichrostachys cinerea* and *Acacia nilotica*, both generally palatable browse species in southern Africa (Owen-Smith & Cooper 1987), were

common both on the mounds and in the woodland plots.

Although the cumulative browsing by megaherbivores (black rhino and elephant) on the mound vegetation was higher than in the woodland, no such significant pattern was found for other browsers combined. When food is scattered in small units in the miombo woodland, animals with smaller body size are probably more effective than megaherbivores in choosing higher-quality diet. Thus, the discrete, large mounds with food of both high quality and quantity are probably most beneficial for the bulk-feeding megaherbivores.

In summary, we have shown that termitaria are browsing hotspots for African megaherbivores in nutrient-poor miombo woodland. Termite mound construction may therefore be important in sustaining populations of megaherbivores in these woodlands. Both densities and diversity of plants are higher on mounds compared to adjacent woodland. Earlier studies of soil nutrient content (Watson 1977) and of plant response to resource availability (Bryant *et al.* 1989) suggest that plants growing on mounds may be less defended and have a higher nutrient content than plants growing in the woodland. Further studies of plant chemistry are needed to confirm this.

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