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Do the large termite mounds of *Macrotermes* concentrate micronutrients in addition to macronutrients in nutrient-poor African savannas?



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ABSTRACT

The influence of soil organisms on the availability of nutrients to other biota within ecosystems can be context-dependent. Fungus-culturing termites, for example, are known to concentrate nutrients by building large mounds in nutrient-poor savannas, but several factors determine the nutritional value of the mounds – whether by geophagy or consumption of forage – for large herbivores. Such factors include the limitations of the local edaphic environment and the degree of nutritional enrichment of plants growing on these mounds. We investigated, in nutrient-poor miombo vegetation in Zimbabwe, how the surrounding soils and maturity of the mounds affected concentrations of macro- and micronutrients in mounds and the woody plant foliage growing on them. All macro- and micronutrients save ammonium, extractable P, Zn and Se were enriched in large mounds relative to matrix soils, but none was significantly enriched in incipient mounds, suggesting that the full nutritional value of mounds is only expressed in large mounds. Concentrations of macronutrients, other than extractable P, in large mounds varied independently of concentrations in the matrix of surrounding topsoils. However, six (Mo, Cu, Fe, Zn, Se and Mn) of the nine micronutrient elements tested showed correlation with surrounding topsoils. Although foliar concentrations of N and P in mound species of woody plants did not differ significantly from those of matrix species, they reached maxima in mound species (5.7% for N and 0.4% for P, exceeding maxima of 4.3% and 0.24% in matrix species). Similarly, foliar concentrations of 75% of the micronutrients tested did not differ between mound and matrix species; but mound species contained maxima for 75% of these elements. Since herbivory is affected by soil nutrients, herbivores might meet their nutrient requirements in this nutrient-poor system by including mound plant species in their diets. © 2013 Elsevier Ltd. All rights reserved.

1. Introduction

Patches of high quality resources can be particularly important in nutrient-poor ecosystems, influencing nutrient cycling, plant dispersal and recruitment, mammalian carrying capacity, and disturbance regimes, as exemplified by roosting sites (Ellsworth and McComb, 2003), earth licks (Mills and Milewski, 2007), savanna trees (Dean et al., 1999; Seymour and Huyser, 2008), and former cattle enclosures (Young et al., 1995). Soil organisms, and termites in particular, can produce patchiness in the distribution of nutrients. The largest fungus-culturing termites in the subfamily Macrotermitinae (Isoptera: Termitidae), namely *Macrotermes*, are recognized as ecosystem engineers (Jones et al., 1994) because they redistribute soil particles on scales of tens of metres, ultimately influencing mineral composition, hydrology, drainage, topography, and fluxes of nutrients in landscapes (Mills et al., 2009; Sileshi et al., 2010). These changes in turn influence plant (Fanshawe, 1968; Moe et al., 2009) and animal species composition (Fleming and Loveridge, 2003; Joseph et al., 2011), and can influence productivity of the entire biome (Pringle et al., 2010).

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Macrotermes falciger occurs in miombo savanna woodlands (dominated by broad-leaved deciduous members of the family Fabaceae, subfamily Caesalpinioideae) in south-central Africa (Fig. 1). The mounds of *M. falciger* can be large, rising up to 9 m high with basal diameters of up to 30 m (Malaisse, 1978), and may be ancient by virtue of successive recolonisation, usually by *M. falciger*, but sometimes by other termite species (e.g., *Ancistrotermes latinotus*, subfamily Macrotermitinae), each colony living approximately 15–20 years. Large mounds (defined here as having diameter >10 m, Fig. 2) built by *M. falciger* constitute patches of crusted loam in the sandy matrix of miombo savanna woodlands, and support stands of shrubs and trees which differ in species composition from

the surrounding matrix (Joseph et al., 2012; Traoré et al., 2008). Although large mounds only represent a minor proportion of the landscape, they have marked effects on disturbance regimes, attracting herbivores (Levick et al., 2010; Sileshi et al., 2010) but excluding fires (Joseph et al., 2013). Large mounds typically contain greater concentrations of N (nitrogen), P (phosphorus), and major cations (Grant and Scholes, 2006; Holdo and McDowell, 2004; López-Hernández et al., 1989; Watson, 1977) than are found in soils in the surrounding matrix. A preliminary study found that large mounds may also concentrate micronutrients (Mills et al., 2009). Vegetation growing on mounds can represent foraging hotspots for herbivores (Brody et al., 2010; Mobæk et al., 2005), and

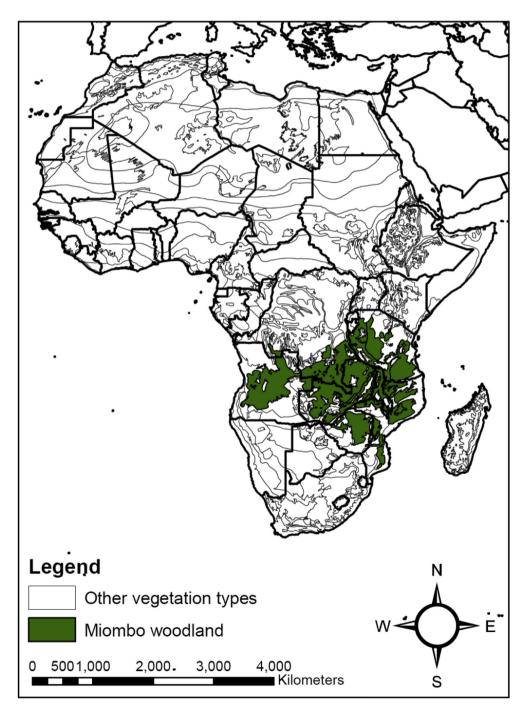


Fig. 1. Map showing the extent of miombo woodlands in southern and central Africa, based on White's vegetation map (1983).

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