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Original article

Nutrient dynamics and plant assemblages of *Macrotermes falciger* mounds in a savanna ecosystem

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ABSTRACT

Termites through mound construction and foraging activities contribute significantly to carbon and nutrient fluxes in nutrient-poor savannas. Despite this recognition, studies on the influence of termite mounds on carbon and nitrogen dynamics in sub-tropical savannas are limited. In this regard, we examined soil nutrient concentrations, organic carbon and nitrogen mineralization in incubation experiments in mounds of *Macrotermes falciger* and surrounding soils of sub-tropical savanna, northeast Zimbabwe. We also addressed whether termite mounds altered the plant community and if effects were similar across functional groups i.e. grasses, forbs or woody plants. Mound soils had significantly higher silt and clay content, pH and concentrations of calcium (Ca), magnesium (Mg), potassium (K), organic carbon (C), ammonium (NH_4^+) and nitrate (NO_3^-) than surrounding soils, with marginal differences in phosphorus (P) and sodium (Na) between mounds and matrix soils. Nutrient enrichment increased by a factor ranging from 1.5 for C, 4.9 for Mg up to 10.3 for Ca. Although C mineralization, nitrification and nitrification fraction were similar between mounds and matrix soils, nitrogen mineralization was elevated on mounds relative to surrounding matrix soils. As a result, termite mounds supported unique plant communities rich and abundant in woody species but less diverse in grasses and forbs than the surrounding savanna matrix in response to mound-induced shifts in soil parameters specifically increased clay content, drainage and water availability, nutrient status and base cation (mainly Ca, Mg and Na) concentration. In conclusion, by altering soil properties such as texture, moisture content and nutrient status, termite mounds can alter the structure and composition of sub-tropical savanna plant communities, and these results are consistent with findings in other savanna systems suggesting that increase in soil clay content, nutrient status and associated changes in the plant community assemblage may be a general property of mound building termites.

1. Introduction

Epigeous termite mounds are a prominent feature in tropical and subtropical savannas. They are major sources of ecosystem spatial heterogeneity through their influence on soil physical and chemical properties such as topography, water status, decomposition rates and nutrient cycling (Lee and Wood, 1971; Sileshi et al., 2010). Termites process and redistribute considerable quantities of organic material and soil particles during mound construction, and therefore strongly modify soil properties on mounds relative to the surrounding intermound matrix. These changes to soil properties influence the composition, spatial distribution and dynamics of plants (Dangerfield et al., 1998; Joseph et al., 2012, 2013; Moe et al., 2009; Seymour et al., 2014), plant nutrient status (Grant and Scholes, 2006; Holdo and McDowell, 2004; Joseph et al., 2014) and animal landscape choices (Loveridge and Moe, 2004; Mobæk et al., 2005; Muvengwi et al., 2014). Thus, by modulating the availability of resources to other organism, termites act as ecosystem engineers in environments where they occur (Dangerfield et al., 1998; Jones et al., 1994).

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Mounds receive large quantities of organic material and nutrients which are essential for the function of the soil decomposer community such as bacteria, fungi or arthropods. Additionally, through nest architecture, mounds create favourable conditions in terms of temperature and soil moisture (Holt, 1987). As a result, biological activity from termites and their associated microbial populations is greater on mounds than the surrounding surface soils, and consequently decomposition and mineralization rates (Collins, 1981). Mineralization of organic matter is a key process regulating the cycling of nutrients in soil, and elevated mineralization rates are associated with high soil fertility. Indeed, consistently higher soil nutrient concentrations on mounds compared to intermound matrix soils have been reported in many studies (e.g. Holdo and McDowell, 2004; Ndiaye et al., 2004; Sileshi et al., 2010). Although several studies have shown termite mounds to contain elevated soil nutrients, few studies have examined mineralization rates and temporal dynamics of soil nutrients on termitaria relative to the surrounding matrix (e.g., Jiménez et al., 2008; López-Hernández, 2001). Where mineralization has been examined, studies were carried out over short periods which limits our understanding of the role of termites in nutrient cycling over long periods. Additionally, the existing short term studies have focused on *Cubitermes*, *Trinervitermes*, *Spinetermes* and *Nasutitermes* (Ji and Brune, 2006; Jiménez et al., 2008; Ndiaye et al., 2004) despite the importance of other termites such as *Macrotermes* in many ecosystem processes.

Modifications to soil properties such as increased soil nutrients and moisture, due to termite building activities, have a great impact on the spatial and temporal characteristics of vegetation. Generally, termitaria contain a diverse assemblage of plant species and maintain evergreen vegetation compared to the inter-mound vegetation matrix (Muvengwi et al., 2013, 2014; Sileshi et al., 2010), which influences patch utilization by small and large mammalian herbivores (Mobæk et al., 2005; Muvengwi et al., 2014). The effect of changes in resources on mounds should depend largely on the equality with which these resources benefit individual plant species and functional groups. Considering the relationship between resource (e.g. nutrients) supply and plant performance is rarely equal across all species, some species or groups of species may benefit more from these resources, and are therefore likely to be more prominent than others. Which functional group may benefit from modified mound properties partially depends on the functional characteristics of that group. The assemblage of plant communities on mounds and the surrounding intermound matrix have been examined in many savanna habitats, and findings have been varied between studies (Davies et al., 2014; Holdo and McDowell, 2004; Moe et al., 2009; Muvengwi et al., 2013). However, many of these studies have examined functional groups separately focusing on either grasses (Arshad, 1982; Davies et al., 2014), woody plants (Davies et al., 2016a) or forbs (Okullo and Moe, 2012). We are aware of only one study which has explicitly considered all the three taxa in their study (Moe et al., 2009), which limits our understanding of the effect of altered mound soil properties on the characteristics of different functional groups.

Species of the Macrotermitinae family construct the largest and most conspicuous mounds in African savannas. During mound and subterranean gallery construction, these termites redistribute soil particles improving permeability and soil water storage (Konate et al., 1999). The improved hydrology together with nest architecture maintain constant temperature and high humidity essential for the cultivation of exosymbiotic *Termitomyces* fungi (Korb, 2000), which decomposes organic material that is conveyed into the mound. These activities lead to accumulation of end-products of mineralization in the centre of the nest (Watson, 1975), altering soil nutrient concentrations which can ultimately influence local plant and animal assemblages (Dangerfield et al., 1998; Joseph et al., 2013; Muvengwi et al., 2014; Seymour et al., 2014). Despite their significant influence on soil nutrients, nutrient dynamics of *Macrotermes* mounds have never been studied in great detail and over longer periods. Therefore, we investigated soil nutrient concentrations, nitrogen dynamics and carbon and nitrogen mineralization rates on *Macrotermes falciger* mounds and their surrounding surface soils. Since plants differ in their response to changes in nutrient concentrations on mounds, the composition of vegetation and plant assemblages are also expected to vary. Thus, we also examined the assemblage and size characteristics of plants on termitaria and their surrounding matrix.

Specifically, we asked whether: a) soil nutrient concentrations, nitrogen dynamics and nitrogen and carbon mineralization on termitaria were similar to surrounding soils? b) changes to the soils were reflected in changes to plant assemblages, and if so, is change similar across functional groups i.e. grass, forb or woody?

2. Methods

2.1. Description of study area

The study was conducted in Seke communal lands (18° 02′ 15.50″ S and 31° 05′ 40.65″ E) 40 km south east of Harare, Zimbabwe. The altitude of the area ranges between 1470 and 1490 m above sea level, receiving an annual precipitation of 750 mm (range: 650 and 850 mm) and an average temperature of 22 °C. The soils of the study area show a catenary association, with moderately well-drained sands (>50 cm thickness) over bedrock or coarse-grained sandy loams in the upper slopes to pale brown coarse sand (>100 cm) in the bottom slopes, some of which are sodic (Anderson et al., 1993). The study site is dominated by *Parinari curatellifolia*, but also includes other trees such as *Uapaca kirkiana*, *Colophospermum mopane*, *Brachystegia spiciformis* and *Strychnos* spp. with *Cynodon dactylon*, *Urochloa mosambicensis* and *Hyparrhenia dissoluta* dominating the herbaceous layer.

2.2. Field methods

We examined soil and vegetation attributes on seven pairs of mound and intermound matrix plots in a 5 ha piece of land. A transect 400 m long and 100 m wide was constructed from the southern side running through the centre of the study area in a northerly direction. Then two mounds were selected at 100 m intervals on either side of the transect, except on the last sampling point where one mound was sampled. Only mounds with surface area at least 100 m^2 and height ≥1 m were selected because they have a stable soil chemistry and contain a variety of plant

Table 1
Mean ± SE of soil variables measured on and off termites mounds compared using a paired *t*-test.

Variable	On	Off	*t* value	*p* value
Clay (%)	24.8 ± 1.21	15.3 ± 1.19	−2.88	0.03
Silt (%)	25.4 ± 1.30	19.3 ± 1.14	−8.18	<0.001
Sand (%)	53.0 ± 1.12	64.8 ± 1.00	7.94	<0.001
SOC (%)	1.13 ± 0.14	0.71 ± 0.13	−4.04	0.01
pH	6.83 ± 0.18	5.51 ± 0.24	−3.62	0.01
Ca (mg/100 g)	11.2 ± 2.70	1.22 ± 0.23	−3.65	0.01
Mg (mg/100 g)	1.85 ± 0.37	0.44 ± 0.11	4.88	0.003
Na (mg/100 g)	0.12 ± 0.03	0.08 ± 0.01	−2.47	0.049
K (mg/100 g)	0.48 ± 0.11	0.13 ± 0.02	−2.81	0.031
P (ppm)	24.3 ± 2.60	18.0 ± 1.84	−2.38	0.054
NH_4^+ (ppm)	11.9 ± 0.92	7.90 ± 0.91	−3.19	0.019
NO_3^- (ppm)	21.1 ± 1.80	12.2 ± 1.09	−7.22	<0.001