2016-08-08

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Muvengwi, J. et al. (2016). Nutrient dynamics and plant assemblages of Macrotermes falciger mounds in a savanna ecosystem
http://ir.nust.ac.zw/xmlui/handle/123456789/729

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

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**A R T I C L E   I N F O**

Article history:
Received 1 March 2016
Received in revised form 30 July 2016
Accepted 8 August 2016

Keywords:
Diversity
*Macrotermes falciger*
Mineralization
Nitrogen
Savanna
Termite

**A B S T R A C T**

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.

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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 organisms, termites act as ecosystem engineers in environments where they occur (Dangerfield et al., 1998; Jones et al., 1994).
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., Jimenez et al., 2008; Lopez-Hernandez, 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 the genera Macrotermes, Termes, Spinotermes and Nasutitermes (Li and Brune, 2006; Jimenez 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 (Mobak 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 Macrotermiteinae 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 kirkiiana, Colophospermum mopane, Brachystegia spiciformis and Strychnos spp. with Cynodon dactylon, Hyparrhenia rufa and Urochloa mosambicensis and Hyparrhenia rufa 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 m² and height >1 m were selected because they have a stable soil chemistry and contain a variety of plant species of the Macrotermiteinae 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.

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### Table 1

<table>
<thead>
<tr>
<th>Variable</th>
<th>On</th>
<th>Off</th>
<th>t value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clay (%)</td>
<td>24.8 ± 1.21</td>
<td>15.3 ± 1.19</td>
<td>-2.88</td>
<td>0.03</td>
</tr>
<tr>
<td>Silt (%)</td>
<td>25.4 ± 1.30</td>
<td>19.3 ± 1.14</td>
<td>-8.18</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Sand (%)</td>
<td>53.0 ± 1.12</td>
<td>64.8 ± 1.00</td>
<td>7.94</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>pH</td>
<td>6.83 ± 0.18</td>
<td>5.51 ± 0.24</td>
<td>-3.62</td>
<td>0.01</td>
</tr>
<tr>
<td>Ca (mg/100 g)</td>
<td>11.2 ± 2.70</td>
<td>1.22 ± 0.23</td>
<td>-3.65</td>
<td>0.01</td>
</tr>
<tr>
<td>Mg (mg/100 g)</td>
<td>1.85 ± 0.37</td>
<td>0.44 ± 0.11</td>
<td>4.88</td>
<td>0.003</td>
</tr>
<tr>
<td>Na (mg/100 g)</td>
<td>0.12 ± 0.03</td>
<td>0.08 ± 0.01</td>
<td>-2.47</td>
<td>0.049</td>
</tr>
<tr>
<td>K (mg/100 g)</td>
<td>0.48 ± 0.11</td>
<td>0.13 ± 0.02</td>
<td>-2.81</td>
<td>0.031</td>
</tr>
<tr>
<td>P (ppm)</td>
<td>24.3 ± 2.60</td>
<td>18.0 ± 1.84</td>
<td>-2.38</td>
<td>0.054</td>
</tr>
<tr>
<td>NH₄ (ppm)</td>
<td>11.9 ± 0.92</td>
<td>7.90 ± 0.91</td>
<td>-3.19</td>
<td>0.019</td>
</tr>
<tr>
<td>NO₃ (ppm)</td>
<td>21.1 ± 1.80</td>
<td>12.2 ± 1.09</td>
<td>-7.22</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Mean ± SE of soil variables measured on and off termites mounds compared using a paired t-test.
assemblages (Joseph et al., 2012; Seymour et al., 2014). The long and short diameter of each termite mound was measured at right angles using a tape measure. The mean ± SE termite mound surface area was $122.9 \pm 8.86$ m$^2$ and height was $2.10 \pm 0.14$ m. All mounds were assumed to be purely conical and the area of the control plots were calculated following procedures in Muvengwi et al. (2013). A circular intermound matrix control plot was marked in a random compass direction at least 30 m from the mound in order to avoid the influence of the mound (Davies et al., 2016a; Levick et al., 2010). A new bearing was only chosen when the control plot was less than 20 m from any other mound in the vicinity.

Soil cores were extracted from two random locations on the middle section of the mound in the top 10 cm using a soil auger (Mills et al., 2009; Seymour et al., 2014). The soil cores within each mound were then mixed thoroughly and a composite sample was drawn for laboratory analysis. The soils were then passed through a 2-mm mesh sieve discarding the fine roots and rocks >2 mm in size before air-drying. Nitrogen (N) and carbon (C) mineralization rates were measured using the buried bag technique (Eno, 1960). At each sampling, we sealed 20 g of soil in polythene bags and buried the bags for 30 d. The same procedure was repeated on control plots marked in the inter-mound matrix. Soil samples were collected in the dry season, March to October.

Vegetation was surveyed on paired mounds and matrix control plots. Since all the mounds were >100 m$^2$, we compared vegetation attributes in 100 m$^2$ mound surface area and adjacent inter-mound control plots of similar area (Joseph et al., 2013). To assess plant species composition and abundance, all plants were recorded. Plants were identified to the lowest category possible such as genus or species using taxonomic guides for southern African plants (Coates-Palgrave, 2002; Van Oudtshoorn, 2014). The plants were then separated into three functional groups i.e. grass, forb or woody. We also assessed basal cover and aerial cover for grasses and forbs and for woody species we assessed the density, canopy cover, height and basal area. Tree basal diameter, canopy long and short diameters and height were measured using a forest calliper, tape measure and a 10 m graduated pole, respectively. For multi-stemmed woody plants, basal diameters were measured separately for basal area estimation, and expressed per hectare (Moe et al., 2009). Tree density and canopy cover were estimated following procedures in Muvengwi et al. (2013, 2014).

### 2.3. Soil chemical analysis

Soils were tested for texture (clay: < 0.002 mm, silt: 0.02–0.002 mm, sand: 0.02–2 mm), pH, total nitrogen (N), resin-extractable phosphorus (P) and exchangeable calcium (Ca), magnesium (Mg), sodium (Na) and potassium (K) at the Department of Research and Specialist Services, Chemistry and Soil Research Institute in Harare, Zimbabwe. In the laboratory, soil samples were air dried at room temperature before analysis. Soil texture and pH were obtained using the hydrometer and CaCl2 method, respectively (Okalebo et al., 2002). Total N was determined using the Kjeldahl method (Okalebo et al., 2002). Available P was estimated by colorimetry using the ascorbic acid–molybdate method. Exchangeable bases were extracted using the aqua regia digestion method (Anderson and Ingram, 1993). Soil samples were dissolved using aqua regia and the mixture dried under ultraviolet light. The resulting compound was then dissolved in concentrated HCl, filtered and diluted with distilled water. Total Ca and Mg were determined using a spectrophotometer at 0.460 nm and 0.595 nm, respectively, and flame emission was used for K and Na.

Nitrogen mineralization was derived by subtracting initial extractable N (NH$_4^+$–N + NO$_3^-$–N) from the final N concentration divided by incubation days (Robertson et al., 1999; Ndagurwa et al., 2013). Nitrification was calculated as the difference between initial NO$_3$–N and incubated NO$_3$–N. The nitrification fraction which shows the percentage of mineralized N that was nitrified was calculated as nitrification/mineralization. Carbon mineralization was calculated as initial carbon content less final carbon content divided by incubation days. The net N mineralization, C mineralization and net nitrification were multiplied by the bulk density of the 0–10 cm soil layer to obtain results per unit area (Robertson et al., 1999).

### 2.4. Data analysis

Data were tested for normality and homogeneity of variance before analysis. All percentage data followed a binomial distribution and were arcsine square root transformed before analysis. Soil variables were compared between mounds and matrix plots using paired t-test. A repeated measures analysis of variance (ANOVA) was used to analyse the effect of month, location and interaction of month and location on ammonium N, nitrate N, N mineralization, nitrification, nitrification fraction, and C mineralization. Where the assumption of sphericity was not met, significance values followed the Greenhouse-Geisser correction. When a significant interaction was detected, values were compared separately for each month with an independent student t-test. All the analyses were carried out in R software v 2.13.1 (R Foundation for Statistical Computing, Vienna, AT).

Species richness, species evenness (e.g. Hill’s numbers and
evenness), species accumulation curves and diversity indices (e.g. Fisher’s, Shannon and Simpson) were calculated using EstimateS. We used $-\ln \lambda$ of Simpson’s index (Williams et al., 2005). A one-way analysis of similarity (ANOSIM) was used to test for significant differences in plant species composition between mound and matrix plots (Clarke and Warwick, 2001). The R-statistic is a measure of similarity of assemblages, with values ranging between −1 and 1, and values closer to 1 indicate dissimilarity between assemblages. In order to visualise differences in grass, forb and woody species composition between termite mounds and matrix plots, non-metric multidimensional scaling (nMDS) iterated fifteen times in order to achieve a global optimum was applied. The ANOSIM and nMDS analyses were carried out using Primer software v 6.1.13 (Clarke and Warwick, 2001).

3. Results

3.1. Soil physical and chemical variables

Silt and clay content were significantly higher on termite mounds, while sand was higher on control plots (Table 1). Soil pH was elevated on mound than off mounds (Table 1). Soil on termite mounds had significantly higher concentrations of Ca, Mg, K, NH$_4$+, NO$_3$− and organic C compared to soils from the savanna matrix (Table 1; Fig. 1). There were marginal differences in soil P and Na concentrations between termite and savanna matrix. Enrichment was highest in Ca, Mg and K with factors of 10.3, 4.8 and 3.9, respectively. Sodium, NO$_3$−, NH$_4$+, C, P and clay had a similar enrichment factor of −1.8 (Fig. 1).

Month and location had a significant influence on ammonium N, nitrate N and N mineralization (Table 2) with significantly higher
concentrations on mounds compared to control plots across the sampling period (Fig. 2a, b, c). The interaction of month and location was significant for N mineralization (Table 2) with higher mineralization rates on mounds than off mounds across months except in October. Nitrification differed significantly between months but was not influenced by location and the interaction between location and month (Table 2; Fig. 2e). The nitrification fraction and C mineralization did not differ with month, location and their interaction (Table 2). Ammonium production was generally lower than nitrate production both in matrix soils and on mounds (Fig. 2b, c).

3.2. Vegetation attributes

Species accumulation curves showed that sampling was sufficient after sampling seven termite mounds and their intermound control plots (Fig. 3). Species asymptotic richness was obtained for graminoids and forbs (Fig. 3). Woody plants only levelled off on intermound control plots but still showed an increasing trend on mounds (Fig. 3). A total of 54 plant species were found in the study area, and of these, 36 species occurred on termite mounds, 33 species occurred on control plots and 13 species were common on and off termitaria. We recorded a total of 17 grass species, 5 species occurred on mounds, 12 species occurred on control plots and 5 species occurred on both termite mounds and control plots. The most frequent grass species on termite mounds were Cynodon dactylon, Sporobolus pyramidalis and Urochloa mosambicensis while Hyparrhenia dissoluta and Pogonanthra squarrosa were frequent on matrix habitats (Fig. 4). Two of the grass species Cynodon niem-fluensis and Dyschoriste matopensis were unique to termite mounds while six species were unique to control plots (Fig. 4). A total of 25 woody species were recorded with 22 species occurring on mounds, 8 species on control plots and 5 were common at both sites (Fig. 4). The most frequent woody species on mounds were Ethretia obtusifolia, Securinega virosa, Lantana camara and Diospyros lycoides (Fig. 4). Of the 19 forb species recorded, 13 species occurred on control plots, 6 species occurred on mounds and 14 were common on and off termitaria (Fig. 4). While seven of the seven forb species occurred exclusively on matrix habitats, only one forb species Commelina africana was exclusively associated with termite mounds (Fig. 4).

The diversity and species richness of forbs and graminoids was greater on intermound control plots than on termite mounds, as reflected by higher values of $H'$, -ln $\lambda$ and Fisher's $\alpha$ (Table 3). In contrast, woody species diversity was greater on mounds than on intermound control plots (Table 3). Evenness was higher on intermound control plots than on termite mounds for all the functional groups (Table 3). Analysis of similarity revealed significant differences in the plant community assemblage of forbs ($R = 0.20$, $p = 0.04$), graminoids ($R = 0.43$, $p = 0.002$) and woody species ($R = 0.44$, $p = 0.002$) between termite mounds and intermound control plots. Indeed, the nMDS showed that mounds and the savanna matrix harbour different species of forbs, graminoids and woody species (Fig. 5).

The aerial and basal cover of grasses was greater in the surrounding matrix than on mounds (Table 4). In contrast, aerial cover of forbs was greater on termitaria than off termitaria but basal cover was similar between sites (Table 4). Woody vegetation was denser, with greater canopy cover and basal area on mounds than in the surrounding matrix (Table 4). However, tree height did not differ between mounds and matrix habitats (Table 4).

3.3. Relationship between soil and plant variables

In grasses, Mg was positively correlated with basal cover and aerial cover on and off mounds, respectively (Table 5). The basal cover of grasses was negatively correlated to Ca on mounds (Table 5). Na was positively correlated with grass aerial cover off mounds (Table 5). On mounds, forb abundance was negatively correlated with Ca, Mg and Na (Table 5). On mounds, forb basal cover was negatively correlated with Mg but positively correlated with nitrate off mounds (Table 5). On mounds, Ca was positively correlated to woody species diversity while off mounds positively correlated with canopy cover, density and abundance (Table 6). Woody height was negatively correlated with Na on mounds (Table 6). Phosphorus and pH had significant positive correlations with all woody plant variables except height off mounds (Table 6).

4. Discussion

Termites are a source of spatial heterogeneity in African savannas via their influence on soil properties and plant assemblages (Dangerfield et al., 1998; Joseph et al., 2012, 2013; Moe et al., 2009; Muvengwi et al., 2014; 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 Moore, 2004; Mobâk et al., 2005; Muvengwi et al., 2014). Consistent with these studies, we show that termite mounds have high clay and soil nutrient concentrations, nitrogen cycling attributes, and contain plant community rich in woody species but less diverse in grasses and forbs than the surrounding savanna vegetation. Additionally, by correlating soil and vegetation parameters, this study has been the first to find the connections among changes in soil physical and chemical properties (e.g., soil pH), nutrient status and plant community structure.

We found that termite mounds supported unique plant communities, which were rich and abundant in woody species but less diverse in grasses and forbs than the surrounding savanna matrix consistent with findings in other savanna environments (Joseph et al., 2012, 2013; Moe et al., 2009; Muvengwi et al., 2013, 2014). These changes to the plant community are related to mound-induced shifts in soil parameters specifically increased clay content (and associated increase in soil water availability), nutrient status and base cation concentration. Termites select and transport fine soil particles from deep to upper soil layers (Sileshi et al., 2010), and in the process mounds are enriched in fine soil particles, which increases soil water availability (Konate et al., 1999; Turner, 2006). Considering tree and shrub density tends to increase with...
increasing soil water availability in savanna habitats (Scholes and Archer, 1997), the increased water availability could have contributed to elevated dominance of woody plants on mounds. Indeed, most of the woody species such as Diospyros lycioides, Ehretia obtusifolia, Grewia spp., and Rhus longipes that were found on mounds have an affinity for damp soils, and most are found on riparian habitats (Coates-Palgrave, 2002). Similarly, standing out as mound grass species were Cynodon dactylon, Sporobolus pyramidalis, Urochloa mosambicensis and Cynodon nlemfuensis, species which favour soils with high soil moisture content (Van Oudtshoorn, 2014). Thus, plant species occurring on mounds are likely less adapted to drought than plant species in the surrounding savanna as also suggested by other authors (Joseph et al., 2012; Van der Plas et al., 2013).

The most contrasting difference of nutrient concentration between mounds and surrounding savanna soil was the Ca concentration, with approximately 10 times more the concentration of Ca on mounds than surrounding savanna soil. Further, correlation analysis showed that Ca was negatively correlated to forb abundance and grass basal cover but was positively correlated to woody

![Fig. 4. Species richness of forb (a), grass (b) and woody (c) species occurring on mounds and matrix plots.](image-url)
species abundance, canopy cover, density and species diversity. The most likely explanation is that a greater proportion of soil clay increased the soil water content, reduced leaching of exchangeable bases (Lal, 1988; Dangerfield et al., 1998; Konate et al., 1999), and thus increased the Ca concentration which likely altered the plant community structure probably due to its negative effects on forb and grass species (Bui, 2013) and its positive effects on tree species (Geiger et al., 1991; Lautner and Fromm, 2010). Calcium regulates many processes related to both growth and responses to environmental stresses in trees (Lautner and Fromm, 2010), and thus increased calcium supplies may strongly influence growth of woody species. Pioneer studies on termitaria-induced heterogeneity in savanna vegetation also suggested that, due to the high Ca concentration associated with termitaria, plant communities on mounds are often dominated by plant species that are calciphilous (Hesse, 1955; Wild, 1952), and is an area open to future research. Furthermore, because of a high available Ca content, mounds can be suggested to be calcareous. In this regard, it can be inferred that surrounding soils are poorly drained or seasonally waterlogged, and thus the plants (e.g., woody species in this study) confined to the termite mound may be intolerant of poorly drained soils (Hesse, 1955). However, since correlations merely describe relationships between variables without cause and effect, we remain conservative in our interpretation of the positive correlation between woody species and Ca concentrations, and further research is required to establish the mechanisms with which increased Ca concentrations influence mound vegetation.

Mineralization rates were higher on mounds relative to surrounding soils possibly due to the elevated soil moisture content and abundant cellulose decomposers, ammonifiers and denitrifiers associated with termite mounds (Collins, 1981). As a result, mounds were enriched in the most common limiting nutrients N (measured as ammonium N, nitrate N and N mineralization rates) and P compared to the surrounding savanna matrix similar to findings elsewhere (Jiménez et al., 2008; Ndiaye et al., 2004). The increase in N and P is expected to alter the competitive dominance of plants and may also enable the coexistence of nutrient demanding plants. We suggest that woody species likely outcompeted grasses and forbs for nutrients on mounds possibly due to a well-developed root system (Belsky, 1994), which led to elevated tree diversity, density and canopy cover on mounds relative to intermound matrix. However, woody plant height was not different between mounds and matrix plots probably, as indicated by the negative correlation between Na and woody height, because of the negative effects of Na on woody plants (Belsky, 1990). Alternatively, it may also indicate that effects on vegetation structure such as herbivory (e.g. from livestock in the study area) were likely similar between mound and intermound matrix. Further, because forbs are highly competitive in nutrient-enriched habitats (Gusewell, 2004), we also suggest that they likely outcompeted grasses resulting in a greater aerial cover on the nutrient-rich mound soils relative to the

![Fig. 5. Non-metric multi-dimensional scaling (nMDS) ordination of graminoid (a), forb (b) and woody (c) assemblages occurring on mounds and their control plots at the study site.](image-url)
The richness of forbs and graminoids was greater in the surrounding matrix. These results accord with findings by Joseph et al. (2014) showing that mounds contain greater response to soil nutrients with nutrient uptake strategy accounting for a greater proportion of differences in species traits between mound and matrix habitats.

Contrary to our initial prediction, the diversity and species richness of forbs and graminoids was greater in the surrounding savanna matrix. These results accord with findings by Davies et al. (2014; Joseph et al., 2013; Konate et al., 1999). Because the species richness for these species groups peaks at intermediate nutrient levels on mounds (Van der Plas et al., 2013); therefore, in the mound environment, due to competition for light and other resources with mound communities compared with nutrient-poor intermound matrix, we suggest that the species richness for these species groups peaks at relatively low productivity levels (sensi Tilman, 1988). Therefore, it is possible that there is competitive exclusion within the grass and forb communities leading to lower species richness on the nutrient-rich mounds (Gusewell, 2004; Moe et al., 2009). Also, the concentration of trees and a more closed canopy cover on termite mounds suggests that less light penetrates lower parts of mounds (Van der Plas et al., 2013); therefore, in the mound environment, due to competition for light and other resources with woody plants, understory plant growth is suppressed (Belsky, 1994), explaining the relatively low forb and grass species richness on mounds. Alternatively, our findings that forbs were negatively influenced by Mg and Na concentrations suggest that these plants are less adapted to the high concentrations of base cations on mounds than those in the surrounding savanna soils. As expected, the presence of Ca, Na, Mg and K, even at low levels, is an abiotic stress factor that influences vegetation patterns and diversification (Bui, 2013). In addition, mounds had low grass cover than surrounding matrix habitats, likely due to foraging by termites (Dangerfield et al., 1998) or animals seeking nutrient-rich mound vegetation (Davies et al., 2016b; Mobák et al., 2005; Muvengwi et al., 2014). Consequently, the reduced grass cover along with higher soil moisture content and elevation of termitaria above the surrounding matrix protects mound vegetation from fire (Joseph et al., 2013; Moe et al., 2009; Sileshi et al., 2010), and thus allows the persistence of woody species on termitaria. Indeed, seventeen (or 68%) woody species including fire sensitive species like Grewia spp. were solely found on termite mounds supporting the notion that termitaria act as fire refugia for woody species (Moe et al., 2009; Joseph et al., 2013). Further, establishment of woody species may also be facilitated by seed deposited in dung from the many animals visiting mounds for the nutrient-rich vegetation, shade, shelter or roosting sites (Joseph et al., 2012, 2013; Muvengwi et al., 2014).

In conclusion, soil clay content, pH, nutrient (Ca, Mg, K, Na, Mg and K) concentrations and N mineralization rates were elevated on mounds than surrounding matrix habitats further confirming termite mounds as nutrient hotspots. Increase in clay content also likely led to improved drainage and soil water availability. As a result of these changes to the soil properties, the plant communities on termite mounds were more abundant and diverse in woody plants while the surrounding savanna matrix was dominated by grasses and forbs. These findings indicate that, by

| pH | 0.25 | 0.55 | 0.14 | 0.63 | 0.41 | 0.15 | 0.22 | 0.13 | 0.56 | 0.32 |
| Ca | 0.19 | 0.83* | 0.17 | 0.49 | 0.29 | 0.54 | 0.40 | 0.16 | 0.65 | 0.33 |
| Mg | 0.25 | 0.90* | 0.06 | 0.09 | 0.04 | 0.81* | 0.62 | 0.12 | 0.15 | 0.05 |
| Na | 0.03 | 0.63 | 0.61 | 0.25 | 0.47 | 0.87* | 0.07 | 0.02 | 0.01 | 0.01 |
| K  | 0.19 | 0.58 | 0.53 | 0.07 | 0.38 | 0.60 | 0.13 | 0.13 | 0.37 | 0.08 |
| P  | 0.50 | 0.17 | 0.49 | 0.70 | 0.56 | 0.43 | 0.21 | 0.31 | 0.34 | 0.12 |
| NH4 | 0.44 | 0.01 | 0.10 | 0.53 | 0.38 | 0.47 | 0.54 | 0.20 | 0.31 | 0.20 |
| NO3 | 0.43 | 0.02 | 0.01 | 0.53 | 0.30 | 0.39 | 0.08 | 0.38 | 0.58 | 0.44 |

| pH | 0.15 | 0.32 | 0.07 | 0.43 | 0.18 | 0.22 | 0.13 | 0.49 | 0.42 | 0.36 |
| Ca | 0.52 | 0.66 | 0.37 | 0.75* | 0.11 | 0.43 | 0.06 | 0.28 | 0.46 | 0.10 |
| Mg | 0.70 | 0.79* | 0.16 | 0.82** | 0.22 | 0.08 | 0.24 | 0.33 | 0.21 | 0.73 |
| Na | 0.71 | 0.73 | 0.54 | 0.79* | 0.40 | 0.06 | 0.53 | 0.12 | 0.26 | 0.03 |
| K  | 0.42 | 0.43 | 0.05 | 0.45 | 0.36 | 0.19 | 0.35 | 0.30 | 0.37 | 0.14 |
| P  | 0.12 | 0.14 | 0.36 | 0.01 | 0.37 | 0.14 | 0.21 | 0.40 | 0.57 | 0.13 |
| NH4 | 0.53 | 0.39 | 0.52 | 0.11 | 0.43 | 0.26 | 0.41 | 0.24 | 0.44 | 0.27 |
| NO3 | 0.52 | 0.37 | 0.49 | 0.13 | 0.33 | 0.62 | 0.75* | 0.23 | 0.03 | 0.38 |

| pH | 0.07 | 0.13 | 0.21 | 0.10 | 0.29 | 0.15 | 0.69 | 0.22 | 0.95*** | 0.97*** | 0.97*** | 0.95*** | 0.97*** |
| Ca | 0.19 | 0.39 | 0.32 | 0.34 | 0.56 | 0.33 | 0.78* | 0.03 | 0.73 | 0.77* | 0.79* | 0.75 | 0.80* | 0.74 |
| Mg | 0.30 | 0.58 | 0.51 | 0.50 | 0.62 | 0.52 | 0.51 | 0.45 | 0.08 | 0.04 | 0.04 | 0.06 | 0.07 | 0.02 |
| Na | 0.79* | 0.31 | 0.33 | 0.54 | 0.24 | 0.26 | 0.19 | 0.14 | 0.64 | 0.66 | 0.62 | 0.62 | 0.60 | 0.70 |
| K  | 0.31 | 0.50 | 0.37 | 0.12 | 0.63 | 0.47 | 0.62 | 0.20 | 0.56 | 0.57 | 0.53 | 0.52 | 0.51 | 0.62 |
| P  | 0.01 | 0.09 | 0.17 | 0.32 | 0.39 | 0.04 | 0.49 | 0.26 | 0.82* | 0.84* | 0.83* | 0.84* | 0.84* | 0.84* |
| NH4 | 0.42 | 0.11 | 0.17 | 0.15 | 0.33 | 0.01 | 0.62 | 0.05 | 0.03 | 0.08 | 0.09 | 0.01 | 0.04 | 0.03 |
| NO3 | 0.12 | 0.04 | 0.05 | 0.17 | 0.12 | 0.12 | 0.65 | 0.14 | 0.29 | 0.31 | 0.35 | 0.33 | 0.33 | 0.30 |

Table 5: Pearson product moment coefficients for correlations between grass and forb variables and possible controlling soil physical and chemical variables on and off termite mounds. *, p < 0.05; **, p < 0.01.

Table 6: Pearson product moment coefficients for correlations between woody variables and possible controlling soil physical and chemical variables on and off termite mounds. *, p < 0.05; **, p < 0.001.
providing better drainage, increased water holding capacity and increased nutrients as well as protection from fire, termite mounds influence the structure and composition of plant assemblages potentially increasing the spatial heterogeneity of savanna ecosystems.

References


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