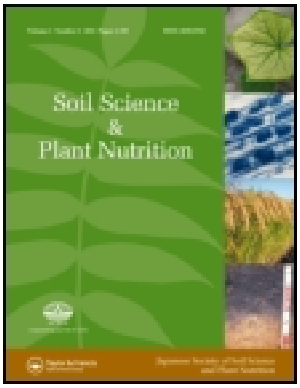

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Nutrient storage in termite (*Macrotermes bellicosus*) mounds and the implications for nutrient dynamics in a tropical savanna Ultisol

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ORIGINAL ARTICLE

Nutrient storage in termite (*Macrotermes bellicosus*) mounds and the implications for nutrient dynamics in a tropical savanna Ultisol

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Abstract

The role of mounds of the fungus-growing termite *Macrotermes bellicosus* (Smeathman) in nutrient recycling in a highly weathered and nutrient-depleted tropical red earth (Ultisol) of the Nigerian savanna was examined by measuring stored amounts of selected nutrients and estimating their rates of turnover via the mounds. A study plot (4 ha) with a representative termite population density (1.5 mounds ha^{-1}) and size (3.7 ± 0.4 m in height, 2.4 ± 0.2 m in basal diameter) of *M. bellicosus* mounds was selected. The mounds were found to contain soil mass of $9249 \pm 2371\ \mathrm{kg\ ha^{-1}}$, composed of $7502 \pm 1934\ \mathrm{kg\ ha^{-1}}$ of mound wall and $1747 \pm 440\ \mathrm{kg\ ha^{-1}}$ of nest body. Significant nutrient enrichment, compared to the neighboring topmost soil (Ap1 horizon: 0–16 cm), was observed in the nest body for total nitrogen (N) and exchangeable calcium (Ca), magnesium (Mg) and potassium (K), and in the mound wall for exchangeable K only. In contrast, available (Bray-1) phosphorus (P) content was found to be lower in both the mound wall and the nest body than in the adjacent topmost soil horizon. Consequently, the mounds formed by *M. bellicosus* contained $1.71 \pm 0.62\ \mathrm{kg\ ha^{-1}}$ of total N, $0.004 \pm 0.003\ \mathrm{kg\ ha^{-1}}$ of available P, $3.23 \pm 0.81\ \mathrm{kg\ ha^{-1}}$ of exchangeable Ca, $1.11 \pm 0.22\ \mathrm{kg\ ha^{-1}}$ of exchangeable Mg and $0.79 \pm 0.21\ \mathrm{kg\ ha^{-1}}$ of exchangeable K. However, with the exception of exchangeable K (1.2%), these nutrients amounted to less than 0.5% of those found in the topmost soil horizon. The soil nutrient turnover rate via *M. bellicosus* mounds was indeed limited, being estimated at $1.72\ \mathrm{kg\ ha^{-1}}$ for organic carbon (C), $0.15\ \mathrm{kg\ ha^{-1}}$ for total N, $0.0004\ \mathrm{kg\ ha^{-1}}$ for available P, $0.15\ \mathrm{kg\ ha^{-1}}$ for exchangeable Ca, $0.05\ \mathrm{kg\ ha^{-1}}$ for exchangeable Mg, and $0.06\ \mathrm{kg\ ha^{-1}}$ for exchangeable K per annum. These findings suggest that the mounds of *M. bellicosus,* while being enriched with some nutrients to create hot spots of soil nutrients in the vicinity of the mounds, are not a significant reservoir of soil nutrients and are therefore of minor importance for nutrient cycling at the ecosystem scale in the tropical savanna.

Key words: ecological engineer, *Macrotermes bellicosus*, nutrient accumulation, soil nutrient turnover, termite mound.

INTRODUCTION

Soil particle transportation and soil composition modification by mound-building termites have implications for resource mobilization by ecosystem engineers (Jouquet *et al.* 2006). A comparison with surrounding surface soils (Lobry de Bruyn and Conacher, 1990; Black and Okwakol, 1997) shows that the soil material that constitutes termite mounds often accumulates some nutrients along with clay particles. This association of nutrients with large mounds of *Macrotermes* termites is why some researchers have suggested that subsistence farmers use termite mound debris as soil amendments in low-input cropping systems (Watson 1977; Dangerfield *et al.* 1998; Duponnois *et al.* 2005). From an ecological point of view, termite mounds and the eroded material from these mounds often create nutrient patchiness that

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leads to ecological hot spots in nutrient-depleted tropical savanna soils (Salick *et al.* 1983; Obi and Ogunkun 2009). In fact, some field observations in various regions have reported higher plant production associated with increased content of some nutrients on dead and eroded termite nest structures than on surrounding land (Arshad 1982; Spain and Mclvor 1988; Ackerman *et al.* 2007). It is therefore considered likely that soil nutrients are accumulated in termite mounds and that their turnover plays a crucial role in ecosystem functions and ecological diversity in the tropics and subtropics.

The subject of soil nutrient storage in termite mounds and nutrient turnover via termite mounds have, however, been little explored. Major constraints are that (1) most previous work has focused on quality assessment without quantitative measurement of mound soils (Lobry de Bruyn and Conacher 1990; Black and Okwakol 1997), and (2) the lack of accurate data on the dynamics and equilibrium of the termite community over time and on the rate of mound renewal has made valid estimation of soil (and thus nutrient) turnover impossible (Lepage and Darlington 2000). Furthermore, soil modification in termite mounds and the fluxes in the life cycles of mounds vary to a considerable extent, depending on the termites' feeding behavior and materials utilized in nest building under the influence of local environments (Black and Okwakol 1997; Duponnois *et al.* 2005; Jouquet *et al.* 2006; López-Hernández *et al.* 2006).

The objectives of the present study were to examine nutrient storage in termite mounds and to estimate the nutrient turnover rate via termite mounds in a Nigerian tropical savanna. To this end, we assessed nutrient amounts preserved in the mound structures of *Macrotermes bellicosus* (Smeathman), a fungus-growing termite in a tropical savanna plateau of central Nigeria. In addition, soil nutrient turnover rates via *M. bellicosus* mounds were estimated using mound nutrient stock data from this study and complementary information on soil turnover obtained from a literature survey. *M. bellicosus* was selected for this study because it is a major termite species in the study region and because the lifespan renewal and longevity of the mound nests have been studied more than those of other termite species.

MATERIALS AND METHODS

Site description

The study site is located on a flat (1–2% gradient) plateau of gently undulating peneplain at about 150 m above sea level in Gaba Doko (Bida), Niger state, central Nigeria (8°56'N, 6°05'E). This area is situated in the Guinea savanna agro-ecological zone and has a mean annual rainfall of about 1100 mm and a mean daily temperature of approximately 23°C. A deeply weathered tropical red earth originating from Nupe Sandstone (Cretaceous sedimentary rock) widely covers the study area. This soil is comprised of predominantly kaolinite and quartz in the clay and fine-sand fractions, respectively (Abe *et al.* 2006, 2007), and is classified in the order Ultisols or sandy, kaolinitic, isohyperthermic Typic Kandiustults in detail (Soil Survey Staff 2006). *M. bellicosus*, the target species of this study, is one of the dominant termite species in the study region and often builds large epigeal mounds that display various types of cathedral shape (Collins 1979, 1981; Korb 2003; Abe *et al.* 2009a, 2009b).

Study plot

The study plot (200 m x 200 m) was situated in a farmer's field where pearl millet (*Pennisetum americanum* (L.) Leeke) and groundnut (*Arachis hypogaea* L.) and/or Egusi melon (*Colocynthis citrullus* L.) had been predominantly inter-cropped for the past five years. This plot was chosen as representative of the study area in terms of size (3.7 ± 0.4 m in height, 2.4 ± 0.2 m in basal diameter, 5.7 ± 1.5 m^3 estimated volume) and density (1.5 mounds ha^{-1}) of *M. bellicosus* mounds (Abe *et al.* 2012). All mounds of *M. bellicosus* at the study plot appeared to have reached their maximum size (based on the state of nest mutuality observed) (Abe *et al.* 2012). Few epigeal mounds of any termite species other than *M. bellicosus* were observed in the plot.

Field sampling

In the study plot, three neighboring *M. bellicosus* mounds of average size were destroyed to measure the soil mass constituting the mound structures and to collect soil samples from the mounds for laboratory analysis. These mounds displayed a cathedral shape with a spiral baseplate, as described by Collins (1979), and were partially infested by millipedes, as described by Mwabvu (2005). Within each sampled mound, the nest body and mound wall were sampled separately, referring to Collins (1979). Nest body indicates the main body of the hive (including the royal chamber and baseplate) but does not include the pillars. This demarcation of the mound structures is reasonable, because soil characteristics vary considerably between the mound wall and the nest body (Abe *et al.* 2009a, 2009b; Abe and Wakatsuki 2010; Abe *et al.* 2012). The mound wall and nest body were individually weighed using a counterbalance prior to sampling. These *M. bellicosus* mounds contained a total soil mass of 6166 ± 1581 kg $mound^{-1}$, of which the mound wall and nest body accounted for 5002 ± 1289 and 1164 ± 293 kg $mound^{-1}$, respectively (Abe *et al.* 2012). The soil mass accumulated in *M bellicosus* mounds amounted to 0.26% of that stored in the topmost (Ap1) horizon (Abe *et al.* 2012). Undisturbed soil samples were collected in triplicate using a stainless-steel cylinder ($V = 100$ cm^3) in addition to disturbed bulk samples that were composited by mixing of several parts of each mound structure.

In addition, three soil pits were dug at least 10 m from their nearest termite mound to sample reference soils. In each soil profile, we distinguished four soil horizons, i.e., two plow layers (Ap1: 0–16 cm; Ap2: 16–32 cm) and two subsoil layers with clay illuviation (Bt1: 32–68 cm; Bt2: 68–150+ cm) (Abe *et al.* 2012). The distance of more than 10 m between the mounds and reference soils is optimal to ensure the quality of the control soils (Arshad 1982; Ackerman *et al.* 2007). Both undisturbed and disturbed soil samples were taken from each natural horizon at each soil pit using the same method as that used for sampling the termite mound structures.

Laboratory analysis

The data on soil mass and bulk density were obtained by correcting for the moisture content, which was determined on sub-samples after drying at 105°C for 48 h. Soil physicochemical analysis was done according to the routine method (IITA 1977). Soil pH was determined with a glass electrode (AP-50, A&D Company, Ltd., Tokyo) at a soil : liquid ratio of 1:1 in deionized water and 1 mol L^{-1} potassium chloride (KCl) solution, respectively. The ΔpH was calculated by the subtraction of pH value in 1 mol L^{-1} KCl solution (pH$_{\text{KCl}}$) from that in water (pH$_{\text{water}}$). Soil electrical conductivity (EC) was measured by an EC meter (Cond Meter D-54 equipped with 9382-10D, Horiba Ltd., Kyoto) at a soil:liquid ratio of 1:1. Total carbon (C) and nitrogen (N) were simultaneously determined by the dry combustion method (Smigraph NC-22A, Sumika Ltd., Tokyo). Exchangeable cations, i.e., calcium (Ca), magnesium (Mg), potassium (K), and sodium (Na), were leached with 1 mol L^{-1} neutral ammonium acetate, and their concentrations in leachates were determined by Zeeman polarized atomic adsorption spectroscopy (Z-1600, Hitachi Co., Tokyo). Available phosphorus (P) was extracted by the Bray No. 1 method and was spectrophotometrically determined by a molybdenum blue method.

Data analysis

Statistical analysis was performed by StatView Ver. 5.0.1. (SAS Inst., Cary, NC, USA). The means of three replications were separated by Fisher's protected least significant difference test. Correlation coefficients of selected soil parameters were calculated for the mound structures and for the natural soil horizons. For both statistical analyses, probability of less than 0.05 was considered to be significant.

The nutrient enrichment coefficient was calculated by the division of [nutrient content in a mound structure – nutrient content in the soil horizon] by [nutrient content in the soil horizon]. The respective enrichment coefficients of mound structures against the Ap1 and Bt2 horizons are given in this paper.

RESULTS

Soil characteristics in natural soil horizons

Soil pH values with 1 mol L^{-1} KCl solution (pH$_{\text{KCl}}$) as well as with water (pH$_{\text{water}}$) indicated acidic reactions throughout the soil profile; both types of pH values represented a decreasing trend with increasing soil depth with significant differences between the topmost (Ap1) and subsoil (Bt1 and Bt2) horizons. The ΔpH value increased with soil depth, though there was no significant difference between the soil horizons. Soil EC was highest in the topmost horizon and gradually decreased down the soil profile without any significant difference. Both the organic C and total N contents, which were correlated strongly with one another (Table 2), decreased with increasing soil depth, while a significant difference was only found for organic C between the uppermost horizon and the other underlying horizons. The C/N ratio decreased downward through the soil profile, with a significant difference between the topmost and subsoil horizons. Available P content showed a descending trend with increasing soil depth. Available P was positively correlated with pH$_{\text{water}}$, EC, and organic C but negatively correlated with clay content to significant degrees. Exchangeable Ca content was relatively high in both the topmost and subsoil horizons, and the subsurface (Ap2) horizon had the lowest amount of exchangeable Ca content. Exchangeable Mg showed a similar trend in the profile distribution to that of exchangeable Ca, although there was a significant difference between the subsurface and lowest (Bt2) horizons. Exchangeable K content was found to be very low and to be relatively constant over the soil horizons without any significant difference among soil horizons. Exchangeable Na content was lower in the upper (Ap1 and Ap2) horizons than in either the Bt1 or Bt2 horizon, although significant differences were only found between the former two and the Bt2 horizon. The sum of the exchangeable bases (Ca, Mg, K and Na) was lowest in the subsurface horizon and highest in the lowest horizon with a significant difference between the two horizon. Moreover, bulk density significantly increased from the topmost horizon to the lowest horizon. The clay content was significantly higher in the subsoil horizons than in the upper horizons.

Soil properties in termite mounds

The mound structures (mound wall and nest body) had a significantly higher value of $\mathrm{pH}_{\mathrm{water}}$ than that of the adjacent subsoil horizons but showed no significant difference from that of the upper horizons (Table 1). The mound wall showed no significant difference in $\mathrm{pH}_{\mathrm{KCl}}$ value from any neighboring soli horizons, whereas the nest body had a significantly higher value than those of the subsoil horizons. The ΔpH value showed no significant difference either among the mound structures or between the mound structures and soil horizons. The soil EC value was significantly higher in the nest body than in the mound wall and in the neighboring soil horizons, while the mound wall had a significantly higher soil EC value than those of the subsoil horizons only.

Organic C content in the mound structures was similar to that of the adjacent topmost horizon but significantly higher than those of the other underlying horizons. Total N content was significantly higher in the nest body than in the mound wall and in the surrounding soil horizons. There was no significant difference in total N content between the mound wall and the surrounding soil horizons. Total N was positively correlated with soil EC, organic C and clay in the mound structures (Table 2). Available P content didn't show any significant difference between the mound wall and nest body.

Table 1 Selected physicochemical properties of mound structures of *Macrotermes bellicosus* (Smeathman) in comparison with those of surrounding natural soil horizons

		Mound structures		Natural horizons			
Property	Unit	Wall	Nest	Ap1	Ap2	Bt1	Bt2
$\mathrm{pH}_{\mathrm{water}}$	–	6.77a (0.52)	6.96a (0.12)	6.58a (0.21)	6.20ab (0.19)	5.84b (0.18)	5.84b (0.17)
$\mathrm{pH}_{\mathrm{KCl}}$	–	5.31ab (0.52)	5.69a (0.22)	5.64a (0.78)	5.04ab (0.43)	4.62b (0.16)	4.60b (0.27)
ΔpH	–	1.47ns (1.03)	1.27ns (0.28)	0.94ns (0.64)	1.15ns (0.25)	1.21ns (0.15)	1.23ns (0.30)
EC	mmoh m-1	2.57b (1.41)	4.74a (2.03)	1.17bc (0.52)	0.83bc (0.16)	0.47c (0.06)	0.38c (0.06)
Organic C	g kg^{-1}	2.76ab (0.30)	3.51a (1.28)	3.24a (0.87)	1.76b (0.26)	1.62b (0.24)	1.70b (0.20)
Total N	g kg^{-1}	0.24b (0.01)	0.40a (0.12)	0.23b (0.04)	0.16b (0.03)	0.19b (0.05)	0.19b (0.05)
C/N ratio	–	11.3ab (0.79)	8.68b (0.49)	14.1a (1.54)	11.3ab (0.72)	8.94b (1.84)	9.55b (2.99)
Avail. P	mg kg^{-1}	0.69bc (0.24)	0.70bc (0.40)	1.33a (0.31)	0.91ab (0.09)	0.40c (0.17)	0.27c (0.09)
Exch. Ca	cmolc kg^{-1}	1.12b (0.19)	2.16a (0.39)	1.08bc (0.44)	0.53c (0.10)	0.97bc (0.43)	1.06bc (0.15)
Exch. Mg	cmolc kg^{-1}	0.58b (0.16)	1.52a (0.36)	0.30bc (0.15)	0.16c (0.07)	0.45bc (0.27)	0.62b (0.26)
Exch. K	cmolc kg^{-1}	0.21b (0.05)	0.85a (0.08)	0.03c (0.01)	0.03c (0.01)	0.03c (0.01)	0.03c (0.01)
Exch. Na	cmolc kg^{-1}	0.01ab (0.00)	0.02a (0.00)	0.01b (0.00)	0.01b (0.00)	0.01ab (0.00)	0.02a (0.01)
Σ	cmolc kg^{-1}	1.92b (0.38)	4.54a (0.81)	1.41bc (0.59)	0.73c (0.17)	1.46bc (0.69)	1.72b (0.40)
Bulk density	g cm−3	1.68ab (0.03)	1.64ab (0.05)	1.51c (0.04)	1.49c (0.06)	1.63b (0.05)	1.71a (0.03)
Clay	g kg^{-1}	252b (9.97)	559a (51.0)	46.4c (12.8)	72.7c (13.5)	189b (71.9)	248b (75.3)
Texture	–	sandy clay loam	clay	loamy sand	loamy sand	sandy loam	sandy clay loam

Number shows a mean of three replications followed by a standard deviation in parentheses
Different letters following the means within a row show a significant difference at a probability of less than 0.05
ns following the means within a row indicates no significant difference at a probability of less than 0.05
"Σ" denotes sum of exchangeable bases (Ca, Mg, K & Na)
KCl, potassium chloride; EC, soil electrical conductivity; C, carbon; N, nitrogen; P, phosphorus; Ca, calcium; Mg, magnesium; K, potassium; Na, sodium

Table 2 Correlation matrix of selected physicochemical properties of mound structures of *Macrotermes bellicosus* (Smeathman) and adjacent natural soil horizons, respectively

	Mound structures				Soil horizons			
	$\mathrm{pH}_{\mathrm{water}}$	EC	Org. C	Clay	$\mathrm{pH}_{\mathrm{water}}$	EC	Org. C	Clay
Total N	0.23	0.86^{*}	0.92^{**}	0.81	0.37	0.41	0.67^{*}	0.13
Avail. P	0.45	0.37	0.76	0.10	0.88^{***}	0.93^{***}	0.83^{***}	-0.86^{***}
Exch. Ca	0.04	0.85^{*}	0.67	0.96^{***}	0.15	0.19	0.49	0.40
Exch. Mg	0.14	0.86^{*}	0.67	0.96^{***}	−0.34	−0.3	−0.01	0.84^{***}
Exch. K	0.21	0.73	0.56	0.98^{***}	0.23	0.24	0.19	−0.13
Σ	0.12	0.83^{*}	0.65	0.97^{***}	−0.06	−0.01	0.30	0.62^{*}

***, ** and * indicates a significant correlation at the probability of less than 0.001, 0.01 and 0.05, respectively
Termite mound structure, n = 6; Natural soil horizon, n = 12
"Σ" denotes sum of exchangeable bases (Ca, Mg, K & Na)
EC, soil electrical conductivity; Org. C, organic carbon; N, nitrogen; P, phosphorus; Ca, calcium; Mg, magnesium; K, potassium; Na, sodium

The mound structures had a significantly lower content of available P than that of the adjacent topmost horizon. Available P was positively correlated with organic C in the mound structures but was little correlated with pH_{water}, EC, or clay.

Exchangeable Ca and Mg were significantly higher in the nest body than in all neighboring soil horizons, while the mound wall didn't show any significant difference from the surrounding soil horizons, except for the subsurface horizon. The mound wall showed no significant difference in exchangeable Na from the neighboring soil horizons, though the nest body had a significantly higher content than that of the surrounding upper horizons. Meanwhile, exchangeable K was significantly higher in the mound structures, in particular in the nest body, than in the adjacent soil horizons. As a result, the sum of exchangeable bases had a significantly higher value in the nest body than in all the surrounding natural horizons. The mound wall, however, showed a significantly higher value than the subsurface horizon only. Exchangeable Ca, Mg, and K and the sum of exchangeable bases were positively correlated with EC, organic C, and clay. The mound wall had a significantly higher value of bulk density and clay content than that of the upper horizons but didn't show any significant difference from the subsoil horizons. The nest body contained more clay than did any of the neighboring soil horizons.

Nutrient accumulation in termite mounds

The nutrient enrichment coefficients gave positive values except for available P, and organic C when comparing the mound wall with the topmost horizon (Table 3). The enrichment coefficients of the mound wall for organic C, total N, available P, and exchangeable K showed more positive values against the lowest horizon than those against the top horizon. In contrast the individual exchangeable bases and their summation indicated lower enrichment coefficients against the lowest horizon than against the topmost horizon, except for exchangeable K, which showed similar values in both cases. The nest body indicated much higher positive values of enrichment coefficients against the topmost and lowest horizons than did the mound wall. As an exception, available P gave similar enrichment coefficients for each mound structure against the topmost horizon and lowest horizon.

The mounds of *M. bellicosus* accumulated 18.2, 1.71, 3.23 1.11, and 0.79 kg ha^{-1} for organic C, total N, and exchangeable Ca, Mg, and K, respectively (Table 4). Irrespective of the substantial disparity in soil mass, mound wall, and nest body, each contained almost the same amount of exchangeable K. In contrast, available P and exchangeable Na were stored at 0.004 and 0.018 kg ha^{-1} in the mounds, respectively. These nutrient amounts accumulated in *M. bellicosus* mounds accounted only for <0.01% to 0.33% of the amounts in the topmost soil horizon. Exchangeable K was preserved in *M. bellicosus* mounds at an exceptionally high level, corresponding to 1.20% of the amount in the topmost horizon.

DISCUSSION

Soil characteristics in natural soil horizons

The topmost soil horizon at the study site showed an acidic reaction and low contents of organic C, total N, available P, and exchangeable bases (Ca, Mg, K, and Na). The subsoil horizons had a stronger acidic reaction and lower contents of organic C, total N, and available P but a larger amount of exchangeable bases than those of the topmost horizons. Although these soil characteristics with poor fertility status originate from Nupe sandstone, they are also very common in tropical savanna soils derived from Basement Complex (metamorphic rocks of Precambrian origin) in West Africa (Windmeijer and Andriesse 1993; Abe *et al.* 2010). Leaching of basic cations and clay eluviation from the surface soils and their

Table 3 Enrichment coefficients of soil nutrients in mound structures of *Macrotermes bellicosus* (Smeathman) against those in surrounding natural soil horizons

Property	Wall vs Ap1	Nest vs Ap1	Wall vs Bt2	Nest vs Bt2
Organic C	−0.10 (0.30)	0.23 (0.85)	0.65 (0.38)	1.05 (0.61)
Total N	0.10 (0.25)	0.88 (0.97)	0.37 (0.40)	1.34 (1.32)
Avail. P	−0.42 (0.37)	−0.39 (0.52)	1.64 (0.63)	1.54 (0.79)
Exch. Ca	0.15 (0.39)	1.49 (1.77)	0.06 (0.09)	1.11 (0.67)
Exch. Mg	1.21 (0.94)	5.95 (5.78)	−0.02 (0.23)	1.81 (1.30)
Exch. K	6.62 (1.93)	31.2 (11.2)	6.94 (1.13)	32.7 (11.1)
Exch. Na	0.63 (0.74)	1.11 (0.69)	−0.18 (0.20)	0.26 (0.93)
Σ	0.50 (0.51)	3.03 (2.90)	0.13 (0.15)	1.79 (0.97)

Number shows a mean of three replications followed by a standard deviation in parentheses

"Σ" indicates sum of exchangeable bases (Ca, Mg, K & Na)

C, carbon; N, nitrogen; P, phosphorus; Ca, calcium; Mg, magnesium; K, potassium; Na, sodium

Table 4 Nutrient storage in mound structures of *Macrotermes bellicosus* (Smeathman) (kg ha^{-1}) in comparison with that of the surrounding surface (Ap1) horizon

Property	Mound structures: Wall	Mound structures: Nest	Mound Total	Ap1 horizon	Percentage of Mound/Ap1
Organic C	13.97 (4.51)	4.27 (2.52)	18.2 (7.03)	8037 (2358)	0.26 (0.17)
Total N	1.23 (0.36)	0.48 (0.26)	1.71 (0.62)	562 (122)	0.33 (0.19)
Avail. P	0.004 (0.002)	0.001 (0.001)	0.004 (0.003)	3.30 (0.89)	0.16 (0.15)
Exch. Ca	2.19 (0.38)	1.04 (0.43)	3.23 (0.81)	2683 (1177)	0.15 (0.11)
Exch. Mg	0.67 (0.01)	0.45 (0.21)	1.11 (0.22)	743 (375)	0.21 (0.17)
Exch. K	0.40 (0.08)	0.39 (0.13)	0.79 (0.21)	70.4 (24.9)	1.20 (0.46)
Exch. Na	0.013 (0.002)	0.004 (0.002)	0.018 (0.004)	19.4 (4.12)	0.09 (0.01)
Σ	3.27 (0.46)	1.88 (0.77)	5.14 (1.05)	3515 (1550)	0.56 (0.14)

Number shows a mean of three replications followed by a standard deviation in parentheses
"Σ" indicates sum of exchangeable bases (Ca, Mg, K & Na)
C, carbon; N, nitrogen; P, phosphorus; Ca, calcium; Mg, magnesium; K, potassium; Na, sodium

illuviation in the subsoils are among major soil-forming processes in this region (Abe *et al*. 2009a, 2009b, 2012). Moreover, soil organic matter loss and nutrient depletion are widespread under low-input subsistence farming systems in the tropics such as traditional swidden agriculture and shifting cultivation (e.g., Kyuma and Pairintra 1983). Although the topmost horizon is relatively rich in soil nutrients thanks to organic matter accumulation, the subsurface horizon generally had the poorest soil fertility status among the soil horizons in the examined pedons due to nutrient leaching and clay eluviations, implying its low nutrient holding capacity and susceptibility to nutrient loss. The subsoil horizons with clay illuviation (argillic horizons) that often accumulate free iron oxides strongly fix soil P (Juo *et al*. 1974; Abe and Wakatsuki 2010), as suggested by negative correlation of available P content with clay amount. By contrast, a positive correlation of available P with organic C suggests that organic matter enhances P availability in the soil.

Soil properties in termite mounds

The soil properties of the mound wall showed many similarities to those of the subsoil horizons, while the nest body showed much more modified properties of the soil than those of the mound wall. Soil composition modification by termites is dependent on termites' feeding behavior and materials utilized during mound (nest) construction (Black and Okwakol 1997; López-Hernández *et al*. 2006). *M. bellicosus* feeds on plant debris and builds mound nests mainly using soil material from deeper soil layers (Abe *et al*. 2009a, 2009b, 2012; Abe and Wakatsuki 2010). This would be a primary reason why the soil characteristics of *M. bellicosus* mounds basically reflect those of the neighboring subsoils and why they show less soil fertility than the adjacent surface soils (Miedema and Van Vuure 1977; Maduakor *et al*. 1995; López-Hernández *et al*. 2006; Abe *et al*. 2009a). In particular, the subsoil material had low availability of P, resulting in the significantly lower content of available P in the mound structures than in the adjacent topmost soil horizon. Higher P sorption and lower P availability in the mounds of *M. bellicosus* than in the adjacent topsoils have been reported elsewhere (López-Hernández *et al*. 2006; Abe *et al*. 2009a). Accumulated free iron oxides associated with clay enrichment in *M. bellicosus* mounds would increase soil P fixation while lowering P availability (Abe and Wakatsuki 2010). By contrast, preferential use of the subsoil material with illuviation of basic cations would result in higher levels of exchangeable bases in the mound structures than in the neighboring topsoil.

The increased soil pH and EC values along with an increase in exchangeable cations content in the mound structures of *M. bellicosus* compared to those in adjacent soils have been reported elsewhere (Pomeroy 1976b; Miedema and van Vuure 1977; Lobry de Bruyn and Conacher 1990; Abe *et al*. 2009a). Although some researchers (Miedema and van Vuure 1977; Lobry de Bruyn and Conacher 1990) have attributed the higher soil pH value in the mound soils to increased contents of exchangeable bases and decreased base saturation, we did not find any significant correlation between soil pH and exchangeable base contents in the mound structures. On the other hand, it is likely that the increased contents of exchangeable bases resulted in the enhanced soil EC value, as indicated by a significant correlation between these parameters (Table 2). As *M. bellicosus* preferentially use subsoil material for mound construction, the accumulation of soil nutrients caused by *M. bellicosus* would be indicated by positive values of the enrichment coefficients for the mound structures against the lowest horizon (Table 3). In particular, *M. bellicosus* preferentially collects clay particles among susbsoil materials that hold exchangeable bases, resulting in enrichment of the bases in the mound structure as compared with the surface soil horizons. Some nutrients would also accumulate while *M. bellicosus* manipulates soil particles and lives in the mounds after mound construction. This was suggested by the finding that the modification of soil nutrients apart from available P was much more prominent in the nest body, where *M. bellicosus* mainly lives, than in the mound wall. *M. bellicosus* accumulated exchangeable K and Mg in the mound structures to a greater extent, as indicated by their enrichment coefficients being higher than those of the other nutrients examined in this study. This suggests that major parts of exchangeable K and Mg accumulated in the mound structures originate from plant debris decomposition and the deposit of termite feces and dead termite bodies in addition to the incorporation of termite saliva during the mound building (Miedema and van Vuure 1977). Moreover, both the mound wall and nest body gave positive enrichment coefficients for organic C, total N, and available P against the lowest horizon. A modest accumulation of organic C with the lower C/N ratio in the termite mounds than that in the adjacent topsoils has been reported in regard to Macrotermitinae termites, especially *Macrotermes* (Lobry de Bruyn and Conacher 1990; Black and Okwakol 1997).

In general, the fungus-growing termites such as *Macrotermes* spp. use their saliva to bind soil particles, resulting in a subtle increase in organic C in the mound structures. This is in contrast to the soil-feeding termites such as *Cubitermes* spp. that use their feces, of plant origin, to aggregate soil particles, resulting in substantial enrichment of organic C in the mound structures compared with that in the surrounding topsoils (Contour-Ansel *et al.* 2000). The higher organic C content but lower C/N ratio in the nest body than the mound wall may result from deposition of N-rich feces and dead termite bodies in the nest body. Meanwhile, the similar enrichment coefficient of available P against the lowest horizon found between the mound wall and nest body would deny biological accumulation of available P in the mound structures. The enhanced P availability found in the mound structures compared with the subsoil horizon may arise from increased soil pH value and organic C content. However, no significant correlation of available P with soil pH and organic C was observed in the mound structures in contrast with that in the natural horizons (Table 2). These findings suggest complex mechanisms of P sorption and availability in the soil as increased organic matter content and soil pH would reduce P sorption and increase P availability (López-Hernández *et al.* 2006), whereas free iron oxides associated with clay accumulation in the mounds would have an adverse effect (Abe and Wakatsuki 2010).

Our results clearly indicated enrichment of some nutrients in the mound structures, as compared to the adjacent topsoils. It therefore seems possible for local farmers to use the mound debris, especially the nest body parts, as a soil amendment, as proposed by Watson (1977), Dangerfield *et al.* (1998) and Duponnois *et al.* (2005). In particular, the use of termite debris would have a beneficial effect on crop growth in K-deficient soils and sandy soils such as savanna soils in the Basement Complex area of West Africa (e.g., Abe *et al.* 2010), since they have very high levels of exchangeable K and clay. Enriched clay in the mound debris can enhance the soil nutrient-holding capacity as well as its water retention capacity. However, the users may have to look out for strong P fixation and low P availability of the mound debris of *M. bellicosus* upon agricultural use of the termite debris (López-Hernández *et al.* 2006). Application of fertilizer P combined with termite debris would be a possible solution to this constraint. In fact, Duponnois *et al.* (2005) documented that combined application of mound debris of *M. subhyalinus* with rock phosphate improved the growth of *Acacia seyal* in a sandy soil of Burkina Faso. However, mound debris of other termites such as *Cubitermes* sp. (a soil-feeder) and *Trinervitermes* sp. (a grass-feeder) stimulated *A. seyal* growth much more than those of *M. subhyalinus* even though the amendments were applied individually without a supplemental P source (Duponnois *et al.* 2005). This disparity of efficiency of the termite mound amendment on plant growth would arise from the differing nutrient enrichment sustained by the termite feeding groups.

Nutrient storage in termite mounds

Nutrient amounts conserved in the mounds of *M. bellicosus* were very low, accounting only for <0.01% to 0.33% of those in the topmost horizon, except for exchangeable K (1.20%) (Table 4). These nutrient stock percentages in the termite mounds as compared to those in the surrounding surface soil are much lower than those in the previous studies: up to 2.3% of organic matter, 1.8% of Ca, 1.5% of Mg, and 7.4% of K in the mounds of *T. geminatus*, a harvesting grass-feeder in a savanna area of central Burkina Faso (Brossard *et al.* 2007), and 1.7% of organic C, 2.5% of NO_3-N, 2.0% of NH_4-N, 0.3% of P, and 1.0% of K in the mounds of *Drepanotermes tamminensis* (Hill), a litter-harvesting termite in the Western Australian wheatbelt shrubland (Park *et al.* 1994). Soil (mass) stock in *M. bellicosus* mounds, i.e., $9249 \pm 2372\,\mathrm{kg\,ha^{-1}}$, in this study was similar to or even higher than that in *T. geminatus* mounds, i.e., 6000–9000 kg ha^{-1} (Roose 1981 cited by Brossard *et al.* 2007) and 7800 kg ha^{-1} (Park *et al.* 1994). This lower nutrient stock in *M. bellicosus* mounds would arise from the lower enrichment coefficients of the nutrients in the mound structures of *M. bellicosus* when compared with those of *T. geminatus* and *D. tamminensis*. In general, the grass- and litter-feeding termites collect and accumulate live and dead plant debris, respectively, in their mounds, and they feed on organic matter mixed with soil particles collected mainly from the topsoil, resulting in enrichment of organic matter and associated nutrients in mound structures (Brossard *et al.* 2007). In contrast, the fungus-growing termites obtain most of their mound construction material from deeper layers, aggregate soil particles with termite saliva, and enrich it modestly with soil organic matter and nutrients (Maduakor *et al.* 1995).

Implications for soil nutrient dynamics

It is possible to estimate nutrient turnover rates associated with *M. bellicosus* mounds using our data in this study in conjunction with complementary information from the literature. The nutrient turnover rate (R_T) (kg mound^{-1} year^{-1}) can be estimated using the following equation:

$$R_T = \frac{R_E \times M_W \times T_L + W_M}{T_L + T_D}$$

where R_E is the annual soil erosion rate from a termite mound (kg mound^{-1} yr^{-1}) while the nest is alive, M_w is the concentration of a specific nutrient in the mound wall, T_L is the time (in years) of nest longevity, T_D is the time (in years) needed for complete erosion of the mound, and W_M is the stock amount of the specific nutrient (kg mound^{-1}) in the mound (mound wall + nest body) at maturity. As stated in our previous paper (Abe *et al.* 2012), we consider the annual soil erosion rate from a *M. bellicosus* mound, the life span of *M. bellicosus* colonies, and complete disappearance of the mound after the colony death to be 538 kg mound^{-1} yr^{-1}, 15 years, and 20 years, respectively, based on our data and the literature information (Nye 1955; Pomeroy 1976a, 1976b; Collins 1981; Lepage 1984).

Considering the mound density (1.5 mounds ha^{-1}) at the study site, we calculated the soil turnover rate as 610 kg ha^{-1} yr^{-1} and the nutrient turnover rates as 1.72 kg ha^{-1} yr^{-1} for organic C, 0.15 kg ha^{-1} yr^{-1} for total N, 0.0004 kg ha^{-1} yr^{-1} for available P, 0.15 kg ha^{-1} yr^{-1} for exchangeable Ca, 0.05 kg ha^{-1} yr^{-1} for exchangeable Mg, and 0.06 kg ha^{-1} yr^{-1} for exchangeable K in the study site. These nutrient turnover rates are substantially lower than those estimated by previous studies (Coventry *et al.* 1988; Black and Okwakol 1997). Black and Okwakol (1997) suggested that up to 800 kg ha^{-1} of annually eroded soil from termite mounds includes up to 24 kg ha^{-1} for organic C, 1.8 kg ha^{-1} for N, and 0.0015 kg ha^{-1} for P; Coventry *et al.* (1988) suggested that some mound-building termites (*Amitermes vitiosus*, *Drepanotermes perniger* and *Tumulitermes pastinator*) can turn over 300–400 kg ha^{-1} of soil material annually with nutrient levels 2–7 times higher than those of the surface soil horizon in Australia. The low nutrient turnover rates estimated in this study can be attributed to low nutrient enrichment coefficients in *M. bellicosus* mounds rather than a difference in soil turnover rate associated with the mounds. These findings suggest that the fungus-growing termites may have less impact on soil nutrient dynamics than the soil feeders because of the lower nutrient enrichment in the mounds constructed by the former than by the latter. In contrast, soil mass associated with the mounds is usually higher for the fungus-grower than for the soil-feeder, suggesting that the former has more impact on the dynamics of soil particles, especially clay, than the latter in the African savanna ecosystems (Abe *et al.* 2012).

Conclusion

The mounds of *M. bellicosus*, especially the nest body, were significantly enriched with nutrients such as exchangeable Ca, Mg and K and total N regardless of the dilution of available P, as compared to the adjacent topmost soil horizon. This result confirms that termite mounds create hot spots of soil nutrients in tropical savanna ecosystems. However, the actual amounts of the soil nutrients associated with *M. bellicosus* mounds were very low, accounting for only 1.2% or less of the amounts in the topmost soil horizon. In addition, estimated nutrient turnover rates via *M. bellicosus* mounds were very low. These findings suggest that nutrient cycling via *M. bellicosus* mounds is of minor importance in a full tropical savanna ecosystem.

In effect it would be impractical for local farmers to use mound debris of *M. bellicosus* as a soil amendment unless supplemental P was additionally applied. However, the higher clay content in *M. bellicosus* mound debris would be beneficial for clay incorporation into the sandy topsoil, which can enhance the capacity for retaining water and nutrients in the surface soil.

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