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Soil particle accumulation in termite (*Macrotermes bellicosus*) mounds and the implications for soil particle dynamics in a tropical savanna Ultisol

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Abstract This study investigated the influence of mound-building termites on soil particle dynamics on the land surface and in soil-forming processes by examining the amount of soil particles in mound structures of *Macrotermes bellicosus* in a highly weathered Ultisol of tropical savanna. Soil particle turnover via the mounds was estimated using particle stock data and soil turnover data from previous studies. A 4-ha study plot with six mounds of relatively uniform shape and size was investigated. Soil mass constituting the mounds was 6,166 ± 1,581 kg mound^{-1} within which the mound wall and nest body accounted for 5,002 ± 1,289 and 1,164 ± 293 kg, respectively. The mound wall contained a significantly larger amount of clay (252 ± 9.97 g kg^{-1}) balanced with a lower sand content (676 ± 26.5 g kg^{-1}) than in the adjacent surface (Ap1) horizon, (46.4 ± 12.8 g clay kg^{-1}; 866 ± 83.2 g sand kg^{-1}); the nest body had much higher clay content (559 ± 51.0 g kg^{-1}) but less sand (285 ± 79.2 g kg^{-1}) than the mound wall. As a result, the mounds of *M. bellicosus* accumulated clay of 2,874 ± 781 kg ha^{-1} (corresponding to 2.52% of clay stock in the Ap1 horizon) along with an estimated clay turnover rate of 169 kg ha^{-1} year^{-1}. These findings suggest a positive feedback effect from termite mound-building activity on soil particle dynamics in tropical savanna ecosystems: *M. bellicosus* preferentially use subsoil material for mound construction, resulting in relocation of illuvial clay in the subsoil to the land surface where clay eluviation from the surface soil and its illuviation in the subsoil are major soil-forming processes.

Keywords Clay turnover · Ecosystem engineer · *Macrotermes bellicosus* · Soil particle redistribution · Termite mounds

Introduction

Resource mobilization by ecosystem engineers is increasingly viewed as a key component of ecosystem function and ecological diversity (Jones et al. 1994). Termites (Isoptera) are a major example of ecosystem engineers in the tropics and sub-tropics. They influence resource availability to other organisms (Dangerfield et al. 1998; Jouquet et al. 2006) by collecting and processing live and dead plant material to feed themselves (Collins 1981b; Ohiagu 1979) as well as by manipulation and translocation of soil particles to build (mound) nests and sheetings/galleries (Bagine 1984; Jouquet et al. 2002). Species of the genus *Macrotermes* (Macrotermitinae) cultivate symbiotic basidiomycete fungi of the genus *Termitomyces* that digest plant-derived persistent ingredients such as lignin and tannin (Collins 1981b). *Macrotermes* species construct nests with epigeal mounds and extensive underground gallery systems (Collins 1979) by soil composition modification due to non-random selection of soil particles (Dangerfield et al. 1998; Jouquet et al. 2002; Abe et al. 2009b).

In the southern Guinea savanna zone of Nigeria, large epigeal nests of *Macrotermes bellicosus* (Smeathman) are dominant and diagnostic features of the landscape (Wood et al. 1977, 1982; Collins 1979, 1981a). The nest of *M. bellicosus* is often covered by a cathedral-shaped mound with many ridges (Collins 1979) and functions as a homoeostatic regulator of the internal microclimate (Noirot and Darlington 2000; Korb 2003). *M. bellicosus*

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preferentially select fine soil particles during mound construction to improve structural stability and water-holding capacity (Jouquet et al. 2002, 2004), resulting in the subsequent enrichment of clay and silt in the mounds (Miedema and van Vuure 1977; Abe et al. 2009a, b). The mound soil is subjected to erosion during rainfall events, especially after a colony dies and eroded material with fine particles accumulates in the nest surroundings (Bonell et al. 1986; Lavelle et al. 1992). Dead mounds and their surroundings become favored locations for plant growth because of the higher water-holding capacity and nutrients availability than in the adjacent non-affected sites (Arshad 1982; Salick et al. 1983; Konaté et al. 1999; Ackerman et al. 2007; Brossard et al. 2007; Obi and Ogunkun 2009). Moreover, some termites preferentially use clay-enriched subsoil (argillic) material for the mound construction (Lobry de Bruyn and Conacher 1990); soil turnover via these mounds may have substantial influence on soil particle dynamics in the tropics where clay eluviations from the surface soils and its illuviation in the subsoils are predominant soil-forming processes (Abe et al. 2009a, b; Abe and Wakatsuki 2010). Enriched clay in the dead and eroded termite mounds would improve soil nutrient holding capacity, which implies substantial effects of the termite engineering on soil fertility and the plant community in infertile soils of the tropics.

The intensity of soil particle selection and transport during mound construction and maintenance has implications for soil particle (mineral) redistribution. It is hypothesized that the influence of termite mound-building activity on soil particle dynamics is primarily determined by the quality and quantity of soil material in the mound structures at mutuality. Although there has been extensive qualitative assessment of termite mounds (Lobry de Bruyn and Conacher 1990; Black and Okwakol 1997), few studies have been concerned with soil quantity (mass) incorporated into mounds of Macrotermitinae. Furthermore, the combined effects of qualitative and quantitative alteration of mound soil have been very little explored.

The objective of the present study was to assess the integrated effects of quantity (soil mass) and physical quality (particle-size distribution) of *M. bellicosus* mounds by comparing them with surrounding soils as a way to examine the impact of termite mound-building habits on the soil particle dynamics and soil-forming processes in a tropical savanna soil.

Materials and methods

Site description

A field survey was carried out in Gaba Doko (Bida), Niger state, central Nigeria (8°56′N, 6°05′E), at the beginning of the dry season (December) 2008. The study area belongs to the southern Guinea savanna agro-ecological zone, which has a mean annual rainfall of about 1,100 mm and a mean daily temperature of approximately 23°C. The research site is located on a flat (1–2% in gradient) plateau in a peneplain underlain by Nupe Sandstone (Cretaceous sedimentary rock). This area is widely covered by deeply weathered tropical soils that are generally classified into Ultisols or Typic Kandiustults in detail (Soil Survey Staff 2006). These soils are often referred to as low-activity clay soils because the clay and primary minerals of the soils consist predominantly of kaolinite and quartz, respectively (Abe et al. 2006, 2007). *Macrotermes bellicosus* (Smeathman), the target species of this study, is one of the dominant termite species in this region. *M. bellicosus* is a fungus-growing Macrotermitinae that often builds a large epigeal mound displaying various types of cathedral shape (Collins 1979, 1981a; Abe et al. 2009a, b).

Study plot

A study plot of 4 ha including six mounds of *M. bellicosus* (mound density = 1.5 mound ha^{-1}) was set up in a farmer's field where the primary crop cultivated had been pearl millet (*Pennisetum americanum* (L.) Leeke), mainly in combination with groundnut (*Arachis hypogaea* L.) and/or Egusi melon (*Colocynthis citrullus* L.) during the past five years (Fig. 1). We selected this plot because it represents the study area in terms of mound size and density. The low frequency of *M. bellicosus* mounds in the study area may be explained as follows: (1) the mound density correlates with the mound size becoming less than two mound ha^{-1} when the mound becomes over 2 m tall (Collins 1981a), and (2) anthropogenic disturbance such as bush clearing and subsequent farming reduces the mound density (Hullugale and Ndi 1993; Ekundayo and Aghatise 1997). Moreover, our preliminary survey by means of field observation and farmer interview revealed that the majority

Fig. 1 A view of the study site. There are two mounds of *M. bellicosus*; harvested pearl millet on the ground in the front part; pre-harvested pearl millet, neem (*Azadirachta indica*) and Shea butter trees (*Parkia biglobosa*) at the rear

of *M. bellicosus* mounds in the study region were over 2 m tall, and that the savanna plateau is increasingly over-exploited due to lengthened cultivation periods and shortened fallow duration driven by the demands of a rapidly growing population. Our plot selection was therefore an adequate representation of the study area. The aboveground mounds of termite species other than *M. bellicosus* in the plot were merely observed.

Termite mound characterization and soil sampling

All mounds built by *M. bellicosus* in the study plot were mapped by a global positioning system receiver (eTrex Venture HC, Garmin, KS, USA) (Fig. 2). The size of each mound (height and basal diameter) was determined in duplicate using a measuring tape, and the mound volume was estimated according to the formula given by Collins (1979): $V = \pi{\cdot}D^2/4{\cdot}H/3$ where V is mound volume, D is diameter at the base, and H is mound height. To measure soil mass that constitutes the termite mounds and to take soil samples from the nest body inside the mound, we destroyed three mounds of *M. bellicosus* neighboring each other (see mounds no. I, II, and III in Fig. 2), and made three soil pits at least 10 m away from the mounds to examine reference pedons (marked with crosses in Fig. 2). This distance (>10 m) between the mounds and pedons would be optimal to ensure the quality of the control soils (Arshad 1982; Ackerman et al. 2007). The selected mounds exhibited a cathedral shape with a spiral baseplate, as reported by Collins (1979), and were partially infested by millipedes, as reported by Mwabvu (2005).

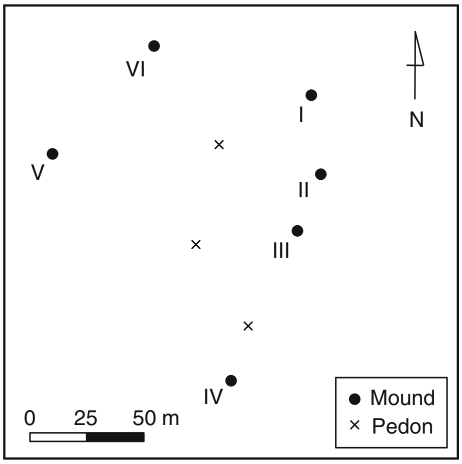

Fig. 2 Mound distribution at the study plot. The mound nos. I, II, and III were sampled for soil mass measurement and particle size analysis, while the mound nos. IV, V, and VI were used only for the size measurement. On the other hand, all three pedons shown here were sampled and analyzed for particle-size distribution

In each mound, the nest body was distinguished from the mound wall by referring to Collins (1979) and Abe et al. (2009a). Herein, nest body indicates the hive, including royal chamber and baseplate with the exception of organic structures, i.e., termite body, fungus combs and stored food; the mound wall indicates the rest of the mound structures made by soil. Exceptionally, the pillars that consist of soil were not considered for this study because *M. bellicosus* constructs the pillars underground (up to 2–3 m below the ground) and this is beyond the scope of this study that focuses on soil particle dynamics in the land surface. This demarcation is reasonable, because soil characteristics differ considerably between mound wall and nest body (Abe et al. 2009a, b). The mound wall and nest body were weighed separately in situ using a counterbalance. In the prepared soil pits, soil profile characteristics were investigated according to the Japanese Society of Pedology (1997), and soil color was determined by the Munsell color system (Table 1). Undisturbed soil samples were collected in triplicates from each mound structure or each soil horizon using a 100-cm^3 stainless-steel cylinder. In addition, disturbed bulk samples were taken by aggregating at least five different parts of each structure in each mound or each horizon in each soil profile. The soil mass and bulk density were calculated by correcting for the moisture content, which was determined on subsamples after drying at 105°C for 48 h.

Laboratory analysis

Soil samples were air-dried, gently ground, and screened by a mesh sieve (2 mm). Gravel (>2 mm) content was

Table 1 Soil profile description at the study site

Horizon	Ap1	Ap2	Bt1	Bt2
Depth	16.3 (0.58)	31.7 (0.58)	68.3 (1.5)	150+
Color	6.25YR4/3.5	5YR4/5	1.25YR4/5.5	1.25YR4/6
Structure	Plumbling Weak, medium	Subangular blocky Weak, coarse	Subangular blocky Moderate, medium	Subangular blocky Moderate, coarse
Consistency	Non-sticky Non-plastic Soft, very friable	Non-sticky Non-plastic Soft, very friable	Slightly sticky Slightly plastic Hard, friable	Slightly sticky Plastic Hard, friable
Boundary	Smooth, gradual	Smooth, clear	Smooth, gradual	–
Other notes	–	–	Clay cutan, few	Clay cutan, common

Numbers in parentheses are standard deviations of means for $n = 3$. Soil description was given according to Japanese Society of Pedology (1997) determined when preparing fine earth samples. Particle-size distribution was determined by the combination of sieving and pipetting (Gee and Or 2002). Pretreatment was made by the decomposition of organic matter with hydrogen peroxide (10%, w/w) on a hot plate. Five sand fractions, i.e., very coarse sand, 2–1 mm; coarse sand, 1–0.5 μm; medium sand, 500–250 μm; fine sand, 250–100 μm; very fine sand, 100–53 μm, were differentiated by multiple passes of wet sieving. The content of two silt fractions, i.e., coarse silt (53–20 μm) and fine silt (20–2 μm), and the clay fraction (< 2 μm) were obtained by pipetting, and particle dispersion was optimized in 0.1 N sodium hexametaphosphate solution followed by ultrasonic treatment (40 kHz, 240 W, 15 min). The particle-size distribution was calculated based on an oven-dry basis (105°C for 24 h). Total sand and total silt were obtained by the summation of the sub-fractions, respectively.

Data analysis

The clay enrichment coefficient was calculated by the division of [clay content in mound structure − clay content in natural horizon] by [clay content in natural horizon]. Means of three replications were separated by Fisher's protected LSD test (StatView Ver. 5.0.1., SAS Inst., Cary, NC, USA) and a difference at a probability of less than 0.05 was considered to be significant.

Results

Termite mound characterization

The distribution of *M. bellicosus* mounds in the study plot is shown in Fig. 2. The mean mound height and basal diameter were 3.7 ± 0.4 and 2.4 ± 0.2 m, respectively (Table 2). The mean volume of the mound was estimated as 5.7 ± 1.5 m^3. Total soil mass stored in the mound was 6,166 ± 1,581 kg $mound^{-1}$, within which nest body and mound wall accounted for 1,164 ± 293 (18.9 ± 0.5%) and 5,002 ± 1,289 kg $mound^{-1}$. *M. bellicosus* mounds occupied 0.07% of the land surface area and constituted a stored soil mass of 9,249 ± 2,371 kg ha^{-1}. This storage amount was comparable to 0.25% of the soil mass in the uppermost (Ap1) horizon.

Particle-size distribution

In the examined pedons, soil particles were dominated by sand (Table 3). The content of total sand was the highest in the uppermost horizon, i.e., the Ap1 horizon, followed by the Ap2, Bt1, and Bt2 horizons. Variation of total sand content increased with soil depth, as indicated by an increase in the value of coefficient of variance from Ap1 horizon to Bt2 horizon. By the same token, the total silt content was higher in the surface horizons (Ap1 and Ap2

Table 2 Size, estimated volume, and soil mass of *M. bellicosus* mounds

Parameters (unit)	Mound no.						Average	SD	CV
	I	II	III	IV	V	VI			
Height (m)	3.4	4.1	4.1	3.3	4.1	3.4	3.7	0.4	10.8
Diameter (m)	2.4	2.8	2.4	2.1	2.2	2.5	2.4	0.2	10.2
Circumference (m)	8.9	10.1	8.1	6.3	8.2	8.4	8.3	1.2	14.8
Basal area (m^2)	7.5	8.8	7.5	6.6	6.9	7.9	7.5	0.8	10.2
Volume (m^3)	5.1	8.4	6.2	3.8	5.2	5.6	5.7	1.5	26.9
Mound mass (kg)	3,561	5,396	6,047	ND	ND	ND	5,002	1,289	25.8
Nest mass (kg)	851	1,211	1,432	ND	ND	ND	1,164	293	25.2
Total mass (kg)	4,412	6,607	7,479	ND	ND	ND	6,166	1,581	25.6
Nest mass/mound mass (%)	23.9	22.4	23.7	NA	NA	NA	23.3	0.8	3.4
Nest mass/total mass (%)	19.3	18.3	19.1	NA	NA	NA	18.9	0.5	2.7

Mound no. corresponds to that in Fig. 2

SD standard deviation, *CV* coefficient of variance, *ND* not determined, *NA* not applicable

Table 3 Comparison of particle-size distribution (g kg^{-1}) of mound structures and neighboring natural horizons

Particle size	Mound		Natural horizon			
	Wall	Nest	Ap1	Ap2	Bt1	Bt2
Sand (total)	676^{b} (±26.5)	285^{c} (±79.2)	866^{a} (±83.2)	833^{a} (±78.4)	741^{b} (±146)	693^{b} (±226)
Silt (total)	71.9^{bc} (±2.66)	156^{a} (±30.2)	87.6^{bc} (±20.9)	94.3^{b} (±9.84)	69.9^{bc} (±22.0)	58.9^{c} (±16.7)
Clay	252^{b} (±9.97)	559^{a} (±51.0)	46.4^{c} (±12.8)	72.7^{c} (±13.5)	189^{b} (±71.9)	248^{b} (±75.3)

Numbers in parentheses are standard deviations of means for $n = 3$. *Different letters* show a significant difference at $p < 0.05$

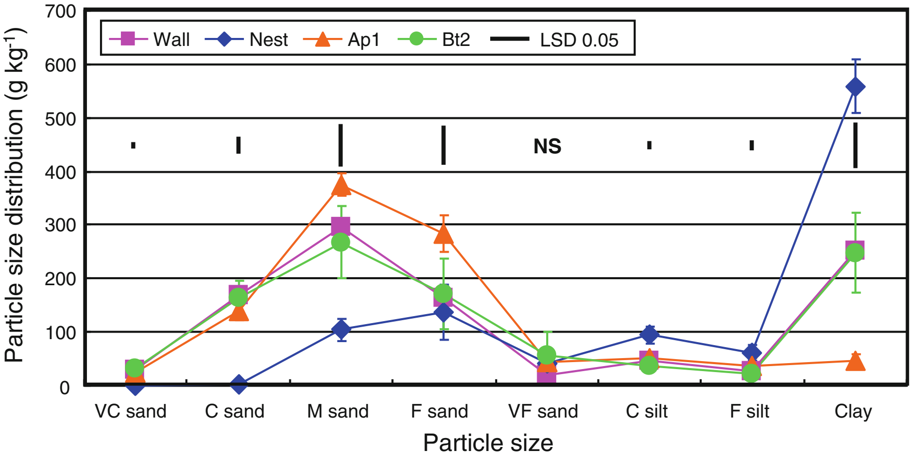

Fig. 3 Comparison of soil particle-size distribution of mound structures and selected natural horizons at adjacent pedons. *Error bars* show standard deviation. *Bars* (LSD 0.05) indicate a range of the least significant difference at $p < 0.05$; NS means an insignificant difference at $p < 0.05$

horizons) than the subsoil horizons (Bt1 and Bt2 horizons). In contrast, the opposite trend was observed in the clay fraction: the clay content increased with soil depth from Ap1 horizon to Bt2 horizon. There was no significant difference in particle-size distribution between the Ap1 and Ap2 horizons and between the Bt1 and Bt2 horizons, respectively. Both the Ap1 and Ap2 horizons were categorized as loamy sand, while the Bt1 and Bt2 horizons were classified respectively as sandy loam and sandy clay loam according to the USDA soil texture classification system (Soil Survey Staff 2006).

Particle-size distribution of the mound wall was very similar to that of subsoil (Bt2) horizons, and was thus classified as having a sandy clay loam texture (Table 3). The nest body contained a significantly lower quantity of total sand but a higher content of total silt and clay than mound wall and was categorized as having a clay texture. Comparing mound structures with adjacent natural horizons, we found that the soil texture of mound wall was the same as that of the neighboring subsoil (Bt1 and Bt2) horizon but had a finer texture than those of the upper (Ap1 and Ap2) horizons. Moreover, nest body showed a finer texture than the subsoil (Bt1 and Bt2) horizon and thus mound wall.

Figure 3 shows the results of further fractionation of sand and silt fractions. Data on the Ap2 and Bt1 horizons are not given, since they did not show any significant difference from those on the Ap1 and Bt2 horizons in the adjacent pedon, respectively. The particle-size distribution was quite similar between mound wall and the neighboring subsoil (Bt2) horizon; there was no significant difference between mound wall and the Bt2 horizon over the particle-size fractions. The mound wall and the Bt2 horizon showed a significantly lower amount of medium sand and/or fine sand, but higher content of clay from the Ap1 horizon. The nest body contained a significantly lower amount of fine sand and/or coarser fractions but higher content of coarse silt and finer fractions than mound wall and the adjacent surface (Ap1) and subsoil (Bt2) horizons. A considerable enrichment of clay in the mound structures was indicated by a high clay enrichment coefficient against the Ap1 horizon in spite of a low clay enrichment coefficient against the Bt1 (Table 4). In addition, the nest body was free of very coarse sand and had a negligible amount of coarse sand in contrast to mound wall which had a similar content of very coarse sand and coarse sand to those of the Ap1 and Bt2 horizons. There was no significant difference in very fine sand content among the mound soils and natural soil horizons.

Soil particle stock

The soil particle mass accumulated per mound of *M. bellicosus* is illustrated in Fig. 4 according to the particle size. The biggest stock was clay (1,916 ± 521 kg mound^{-1}), which accounted for 31.1 ± 0.86% of the total particle stock. This was followed by medium sand (1,604 ± 408 kg mound^{-1}; 26.0 ± 0.02%), fine sand (968 ± 215 kg mound^{-1}; 15.8 ± 0.63%) and coarse sand (850 ± 241 kg mound^{-1}; 13.7 ± 0.64%). In addition, the mound contained coarse silt (342 ± 96.4 kg mound^{-1}; 5.54 ± 0.40%) and fine silt (200 ± 51.9 kg mound^{-1}; 3.25 ± 0.16%), together with very fine sand (144 ± 27.9 kg mound^{-1}; 2.37 ± 0.21%) and very coarse sand (141 ± 32.4 kg mound^{-1};

Table 4 Clay enrichment coefficient of *M. bellicosus* mounds against adjacent natural soil horizons

Mound structure	Natural horizon	
	Ap1	Bt2
Mound wall	4.70 (±1.53)	0.07 (±0.27)
Nest body	11.5 (±2.29)	1.42 (±0.80)

Numbers in parentheses are standard deviations of means for $n = 3$

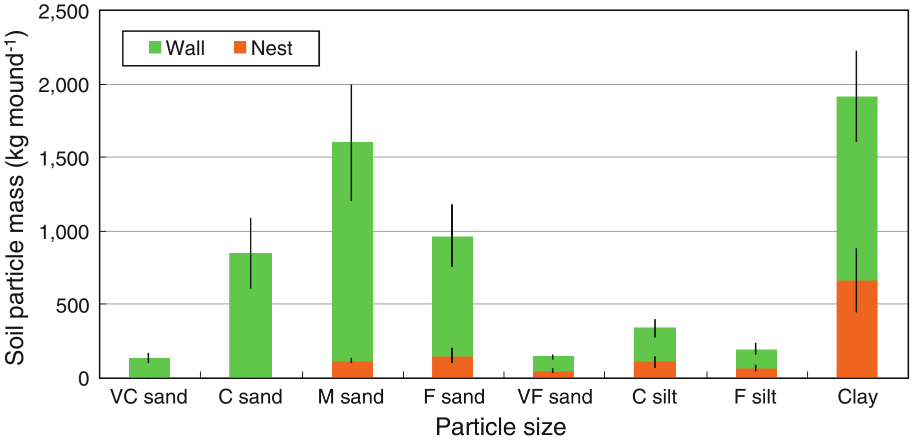

Fig. 4 Soil particle stock per mound of *Macrotermes bellicosus*. *Error bars* show standard deviation

Table 5 Estimated soil particle stock (kg ha^{-1}) in *M. bellicosus* mounds

Particle size	Mound wall	Nest body	Total
Sand	5,078 (±1,333)	483 (±67.0)	5,561 (±1,377)
Silt	542 (±149)	272 (±90.4)	814 (±222)
Clay	1,883 (±462)	992 (±328)	2,874 (±781)

Numbers in parentheses are standard deviations of means for $n = 3$

2.32 ± 0.32%) to a minor extent. Clay stock in nest body accounted for a considerable portion (34.1 ± 2.64%) of the total clay stock (mound wall + nest body) in the mound. The nest body comprised a substantial part of the total particle stock for fine silt (35.4 ± 7.63%), coarse silt (32.4 ± 4.00%), and very fine sand (33.0 ± 5.41%). In contrast, the remaining sand fractions of nest body occupied only a minor part (0.00–16.3%) of the total particle stock.

The soil particle stock per unit of ground area is shown in Table 5. The total clay stock in *M. bellicosus* mounds was estimated to be 2,874 ± 781 kg ha^{-1} at the study site, of which 1,883 ± 462 and 992 ± 328 kg ha^{-1} were stored in mound wall and nest body, respectively. This stock accounted for only 2.52% of clay mass in the surface (Ap1) horizon (1.14×10^5 kg clay ha^{-1}). The mounds also contained 814 ± 222 kg ha^{-1} (mound wall, 542 ± 149 kg ha^{-1}; nest body, 272 ± 90.4 kg ha^{-1}) of total silt and 5,561 ± 1,377 kg ha^{-1} (mound wall, 5,078 ± 1,333 kg ha^{-1}; nest body, 483 ± 67.0 kg ha^{-1}) of total sand, which accounted for 0.38 and 0.26%, respectively, compared to that of the surface soil (Ap1) horizon (2.16×10^5 kg silt ha^{-1}; 21.3×10^5 kg sand ha^{-1}).

Discussion

Natural soil characteristics and soil formation processes

Soils in the study site had a sandy texture, which was inherited through the nature of the parent material, i.e., Nupe Sandstone. The increase in clay content with increasing soil depth and presence of clay film (cutan) on the ped surface in the subsoil (Bt1 and Bt2) horizons (Table 1) suggests the downward movement and subsoil illuviation of clay particles and thus the formation of argillic horizons. Correspondingly, the surface horizons had very little clay content. The larger variability of sand-size distribution with a higher value of standard deviation found in the subsoil (Bt1 and Bt2) horizons than the surface (Ap1 and Ap2) horizons may indicate homogenization of surface soils by farming tillage and varied amounts of sedimentation in the Cretaceous era. A medium and moderate subangular blocky structure has developed in the surface horizons regardless of the sandy texture and low organic matter content due to a seasonal cycle of wet and dry conditions. In contrast, the mounds are structureless (massive) in terms of soil structural development (Abe et al. 2009a), indicating dense packing of soil particles by termites (Sleeman and Brewer 1972; Mermut et al. 1984; Sarcinelli et al. 2009).

Termite mound characteristics

The ranges of mound height (3.3–4.1 m) and basal diameter (2.1–2.8 m) observed in this study suggest that all mounds in the study plot have almost reached a maximum size (mutuality) as the previous reports (Collins 1981a; Lepage 1984) indicate that maximum size of mounds of *M. bellicosus* is often found at about 3.5 m in height and 2.5 m in basal diameter in the savanna of Nigeria and Ivory Coast. In spite of considerable variability in the soil mass constituting the mound wall and nest body, the ratios of soil mass in the nest body to that in the mound wall as well as to that in the whole mound were relatively constant. This suggests that a sound soil mass balance exists between the nest body and mound wall in the matured mounds of *M. bellicosus*.

Soil particle selection by termites

The mound wall showed very similar particle-size distribution to that of the subsoil (Bt2) horizon in the adjacent pedon. Meanwhile, mound wall had higher levels of clay but a lower level of total sand than the surface (Ap1) horizon by a significant amount (Fig. 3; Table 3). In addition to these results, a high clay enrichment coefficient against the Ap1 horizon but a low clay enrichment coefficient against the Bt2 horizon (Table 4) suggests that *M. bellicosus* enrich their mound structures with clay particles by predominantly collecting soil material from clay-rich subsoil (argillic) horizons in a Typic Kandiustult. One can also speculate on the source of soil material used by termites based on the soil color of the mound structures (Abe et al. 2009a). In this study, similarity of the Munsell color index was observed between the mound structures (2.5YR4/6) and surrounding subsoil (Bt1 and Bt2) horizons (1.25YR4/6) (Table 1). Termites' preferential use of subsoil material and subsequent clay enrichment in the mound structures have been reported elsewhere (e.g., Miedema and van Vuure 1977; Abe et al. 2009b). Clay particles accumulated in the mound structure enhance its structural stability and water-holding capacity (Jouquet et al. 2003, 2004).

On the other hand, a contrasting particle-size distribution found between mound wall and nest body suggests that termites can manipulate soil properties according to their ecological requirements, as reported by Jouquet et al. (2002, 2006). The enhanced water-holding capacity in nest body suggested by its higher contents of clay and silt than mound wall would be crucial for fungus culture and larvae growth. The particles in the fine sand and coarser fractions were attenuated, but those in the coarse silt and finer fractions were enriched in the mound structures (Fig. 3). In addition, there was no significant difference in very fine sand between the mound structures and adjacent natural soil horizons. These results are well consistent with those by Abe et al. (2009b), suggesting that very fine sand is a criterion of soil particle selection by *M. bellicosus*.

Implications for soil particle dynamics

Figure 5 illustrates the soil particle dynamics associated with termite mounds, based on our survey results and the limited available literature. To estimate soil turnover rate via termite mounds, this study took two factors into account, i.e., soil erosion from the living mound and soil turnover of the mound material after the mound death. Only a few data have been so far available for soil erosion rate from a living *M. bellicosus* mound: 0.27 m^3 mound^{-1} year^{-1} in Uganda (Pomeroy 1976a) and 0.37 m^3 mound^{-1} year^{-1} in Ivory Coast (Lepage 1984). We consider the erosion rate in this study to be 0.32 m^3 year^{-1}, a median value of those of Pomeroy (1976a) and Lepage (1984). The soil erosion rate from living mounds of *M. bellicosus* is estimated at 538 kg soil mound^{-1} year^{-1} or 135 kg clay mound^{-1} year^{-1} using the bulk density (1.68 g cm^{-3}) and clay content (25.2%) data for the mound wall in this study since the erosion occurs only in the mound surface. On the other hand, soil turnover rate can be estimated as the function of longevity of the mound and soil turnover time

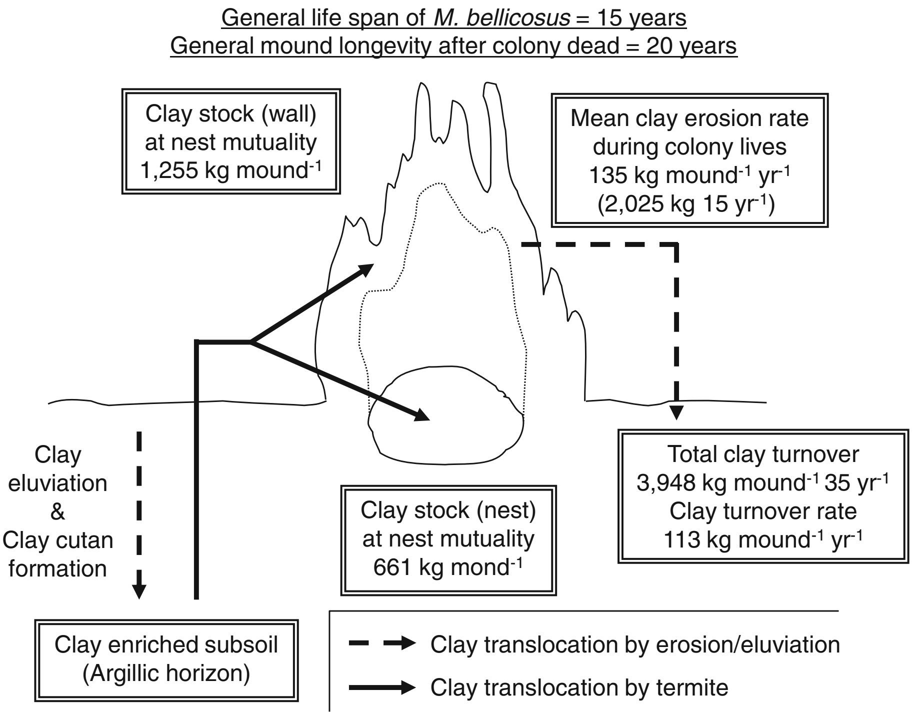

Fig. 5 Schematic diagrams of soil particle dynamics via mounds of *Macrotermes bellicosus*

after the mound death. The life span of *M. bellicosus* colonies was previously estimated as ranging from 4 to 10 years (Nye 1955; Pomeroy 1976a) and from 15 to 20 years at maximum, based on mound growth measurement (Collins 1981a). The mound reaches the biggest size (mutuality) by 10–15 years (Collins 1981a) and rapidly breaks down after the death of the nest (Pomeroy 1976b). There is an estimation that a 4-m^3 mound would lose 20% of its volume in 2 years and 40% in 5 years and erode completely within 20 years (Pomeroy 1976a). Herein, we assume the nest longevity of 15 years followed by complete disappearance 20 years after colony death. Finally, the clay turnover rate (R_T) was calculated as follows:

$$R_T = \frac{R_E \times T_L + W_S}{T_L + T_E}$$

where R_E is the mean annual clay erosion rate (kg mound^{-1} year^{-1}) while the nest survives, T_L is the time (in years) of nest longevity, T_E is the time (in years) needed for complete erosion of the mound, and W_S is the amount of clay stock (kg mound^{-1}) in the mound (mound wall + nest body) at maturity [1,916 kg mound^{-1} (data from this study)]. We considered the *M. bellicosus* mound to be at maturity when the mound reaches a particular size: 3.5 m in height and 2.5 m in basal diameter in the study area. Using the given equation, the mean annual clay turnover rate was estimated as 113 kg mound^{-1} year^{-1} and thus 169 kg ha^{-1} year^{-1} at the study site (mound density = 1.5 mound ha^{-1}).

The amount of clay accumulated in *M. bellicosus* mounds (2,874 ± 781 kg clay ha^{-1}), which was equivalent to 2.52% of clay stock in the surface (Ap1) horizon, and the estimated clay turnover rate via the mounds (169 kg clay ha^{-1} year^{-1}) suggest a substantial impact of termite mound-building activity on soil particle dynamics in a tropical savanna. Clay eluviation from the surface soil and its illuviation in the subsoil are often major soil-forming processes in tropical ecosystems. *M. bellicosus* causes a contrasting (upward) movement of clay due to preferential use of subsoil material for mound construction. The mounds enriched with clay are subject to erosion, especially after the mound death, resulting in the formation of new soil layer having more clay than surrounding soil. Soil turnover via termite mounds may occur heterogeneously in the ecosystems and clay particles would be concentrated in the vicinity of the mounds. This suggests soil turnover via termite mounds is a key component of ecosystem diversity in tropical ecosystems due to not only nutrient cycling that creates nutritional hotspots in the ecosystems (Abe et al. 2009a, 2011) but also soil particle dynamics via termite mounds.

Conclusions

Resource mobilization by ecosystem engineers is increasingly viewed as a key part of ecosystem function and ecological diversity. In a rare opportunity to gather quantitative information on termite soil particle mobilization, the mounds in this study had a total clay stock of 2,874 ± 781 kg ha^{-1}, which was equivalent to 2.52% of that in the surface soil (Ap1 horizon), along with an estimated clay turnover rate of 169 kg ha^{-1} yr^{-1} on a highly weathered tropical Ultisol of Nigerian savanna. These findings did suggest that the mound-building termite plays an important role in soil particle dynamics: *M. bellicosus* preferentially use subsoil material for mound construction resulting in relocation of illuvial clay in the subsoil to the land surface where clay eluviation from the surface soil and its illuviation in the subsoil are major soil-forming processes.

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