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# Possible influence of termites (*Macrotermes bellicosus*) on forms and composition of free sesquioxides in tropical soils

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ABSTRACT

There has been less concern about soil mineralogical alteration than about soil physical, chemical and biological changes induced by termite nest-building activity. Furthermore, much less attention has been paid to free sesquioxides than to phyllosilicate minerals. In the present study, we conducted field morphological observations and selective dissolution analysis to characterize free sesquioxides in termite (*Macrotermes bellicosus*) mounds as compared with surrounding pedons in different toposequence positions, i.e., seasonally flooded valley bottom, hydromorphic fringe and well-drained upland sites. Distinctive redoximorphic features, such as surface yellowish layers on mound structures from the fringe site, indicate possible alteration of iron sesquioxide forms in the mounds due to the transportation of soil from reductive (aquic subsoil) to oxidative (epigeal mound) environments by the nest-building activity of *M. bellicosus*. On the other hand, the iron-soluble content in the dithionite–citrate–bicarbonate (DCB) system ($Fe_d$) was generally higher in the mound structures than at the adjacent sub-surface (Ap2) horizon at each toposequence position, while there was less difference in the content of acid ammonium oxalate (AAO) extractable iron ($Fe_o$) as compared to $Fe_d$. As a consequence, the iron activity index ($Fe_d/Fe_o$ ratio) was found for the most part to be lower in the mound structures than in the neighboring Ap2 horizon. In addition, the content of $Fe_d$, AAO-soluble Al ($Al_o$) and DCB-extractable Al ($Al_d$) was significantly correlated with clay content in these soils. These findings suggest that *M. bellicosus* preferentially collects clay particles, probably from the clay-rich subsoils, such as the argillic horizon, which has been formed by the co-migration of phyllosilicate minerals and relatively crystalline sesquioxides. The species then likely incorporates them into the mounds, which induces an increase in the $Fe_d$ content relative to that of $Fe_o$, resulting in a decreased iron activity index in the mound structures.



## Introduction

Termites (Isoptera) are regarded as one of the major ecosystem engineers that modulate the availability of natural resources to other organisms (Jones et al., 1994; Lavelle et al., 1997; Jouquet et al., 2006). Some species of termites build their nest in an epigeal mound using soil material, and the mound has direct and positive feedback effects on the termite colonies through the maintenance of humidity and protection of the population from enemies (Korb, 2003; Noirot and Darlington, 2000). Termite nest-building activity inevitably influences soil functions and processes and preserves soil and ecosystem diversity (Lavelle et al., 1992; Lavelle, 1997; Obi and Ogunkun, 2009) because termites cause modification and redistribution of material soils (Lobry de Bruyn and Conacher, 1990; Lavelle et al., 1992) due to selection of fine particles, i.e., clay and silt (Jouquet et al., 2002a, 2007; Abe et al., 2009a) and the addition of saliva and/or feces during nest construction (Fall et al., 2001).

The physical, chemical and biological alteration of soils caused by the nest-building or soil-feeding of termites have been extensively explored (Lobry de Bruyn and Conacher, 1990; Black and Okwakol, 1997). However, much less attention has been paid to soil mineralogical alteration. Leprun and Roy-Noël (1976) reported that mound distribution of *Macrotermes* spp. was substantially influenced by soil clay mineralogy. Boyer (1982) and Mahaney et al. (1999) found that the clay mineralogical composition of termite (Macrotermitinae) mounds was somewhat different from that of adjacent surface soils. More recently, Jouquet et al. (2002b, 2007) demonstrated subtle alteration of clay minerals in the soils handled by *Odontotermes* nr. *Pauperans* and *Pseudacanthotermes spiniger* in laboratory experiments. This qualitative alteration was described as the transformation of

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well-crystallized illite to poorly crystallized illite with smectite layers to a minor extent, which suggested the partial removal of non-exchangeable potassium in illite interlayers. These previous studies suggested that the termite mound-building activity caused the qualitative and quantitative alteration (redistribution) of soil clay minerals by such processes as (i) the transportation of fine particles with different mineralogical clays into the nest, and (ii) direct or indirect modification of clay properties by the termite saliva/excreta and associated organisms.

On the other hand, the authors of previous studies examined the influence of termites on soil phyllosilicate minerals only and did not take any free sesquioxides into account. However, formation of secondary phyllosilicate minerals occurs in parallel to that of pedogenetic sesquioxides in soil (Schwertmann, 1985). In particular, tropical soils at an advanced weathering stage, e.g., Oxisols, Ultisols and Alfisols, often contain free sesquioxides as major components of the mineral phase (Schwertmann and Taylor, 1989). We hypothesized that termites have the influence on soil-free sesquioxides in addition to phyllosilicate minerals.

The objective of the present study therefore was to examine our hypothesis. To this end, we investigated the forms and composition of free sesquioxides in structures of termite mounds by selective dissolution analysis and compared them with those of pedogenetic horizons in adjacent pedons.

## Materials and methods

### *Study site*

The study site (08°98′N, 06°00′E) was 10 km south of the Bida town, central Nigeria, about 200 km west of the capital, Abuja. The site is composed of nearly level to gently undulating peneplains of a benchmark inland valley watershed of the Emikpata River in the Guinea savanna agroecological zone (Hirose and Wakatsuki, 2002). This area has a mean annual rainfall of about 1100 mm and a mean annual daily temperature of approximately 23 °C. The soils in this region are predominantly sandy loam and kaolinitic or siliceous at an advanced weathering stage (Abe et al., 2006, 2007), underlain by Cretaceous sediment rocks that are generally known as Nupe Sandstone (Esu, 1986). The soils are classified into Fluvaquentic Epiaquepts, Fluvaquentic Epiaqualf and Typic Kandiustalf at the bottom, fringe and upland site, respectively (Soil Survey Staff, 2006).

A more detailed site description has been reported elsewhere (Hirose and Wakatsuki, 2002; Abe et al., 2009b).

### *Field survey and soil sampling*

Representative mounds constructed by *Macrotermes bellicosus* (Isoptera, Macrotermitinae) were selected at different toposequence positions of the inland valley, including the valley bottom, hydromorphic fringe and well-drained upland plateau. The mound on the upland plateau had a cathedral shape with many ridges (estimated mound volume $V$=5.4 m$^3$), while the others exhibited a dome shape and did not have any ridges ($V$=2.9 and 1.8 m$^3$ at the bottom and fringe, respectively) (Abe et al., 2009b). The mound density (number of mounds per hectare) varied with possible anthropogenic disturbance from 3 to 10 in the upland site and from 0 to 2 in the bottom and fringe sites (Abe et al., 2009b).

Soil profiles (without termite activity), used for sampling reference soils, were exposed approximately 2 m away from the mounds. Morphological characteristics of the examined soils of the mounds and pedons were described according to the Japanese Society of Pedology (1997), and soil color was identified using the Muncell notation (Research Council for Agriculture, Forestry and Fisheries, 1967) prior to soil sampling. The samples were collected from various structures of the termite mounds because soil properties of termite mounds vary considerably according to structural units within the mound (Jouquet et al., 2003; Abe et al., 2009a, 2009b). Also, termites select materials not only from topsoils but also from subsoils (Jouquet et al., 2002a; Abe et al., 2009a, 2009b), so the reference samples were taken from both types of soil according to natural horizons.

Further information on the soil sampling method employed as well as toposequential soil characteristics has been given by Abe et al. (2009b).

### *Laboratory analysis*

Soil samples were air-dried, gently ground and sieved (2 mm mesh) prior to the laboratory analysis. Soil pH was recorded at a soil:water ratio of 1:5 with a glass electrode. Total C content was measured by the dry combustion method. Clay content was determined by the pipette method. These routine methods of soil analysis have been previously described in detail (Abe et al., 2009b).

Subsamples of the fine-earth samples were subsequently ball-milled and passed through a 0.5-mm sieve for selective dissolution analysis, which was performed according to Nagatsuka (1993). This procedure is primarily based on the acid ammonium oxalate (AAO) method (Tamm, 1922) and the dithionite–citrate–bicarbonate (DCB) method (Mehra and Jackson, 1960). Using the AAO method, one can dissolve relatively amorphous (poorly crystalline or short-range ordered) iron sesquioxides such as ferrihydrite in a dark place, while the DCB method is used to extract all secondary iron sesquioxides (Borggaard, 1985; Schwertmann and Taylor, 1989). The concentration of Al, Fe and Mn in the extracts was simultaneously determined by an inductively coupled plasma spectroscopy (CIROS, Rigaku, Co., Tokyo). In the following description, Fe, Al and Mn soluble by the AAO method are referred to as $Fe_o$, $Al_o$ and $Mn_o$, respectively, whereas Fe, Al and Mn extractable by the DCB method are referred to as $Fe_d$, $Al_d$ and $Mn_d$, respectively. The iron activity index was calculated as the ratio of the content of $Fe_o$ to that of $Fe_d$ (Schwertmann, 1964).

### *Statistical analysis*

The analysis of variance (ANOVA) was carried out using the StatView software (Ver. 5.0.1. SAS Inst., Cary, NC, USA). Fisher's protected probability test was applied to differentiate mean scores between the mound structure and pedogenetic horizon. Correlation analysis was made among the components examined in this study and between them. Selected physicochemical properties were reported in the previous study (Abe et al., 2009b). A two-way ANOVA was applied to determine the influence of toposequence and termites as well as their interactive effect on the examined components. The toposequence factor includes three positions – the bottom, fringe and upland – while the termite influence factor indicates whether the material includes termite mound structure or not (natural soil horizons). These groups and their sample sizes are shown in Table 1.

**Table 1**
Comparison of selectively extractable Fe, Al and Mn between the mound structures of *Macrotermes bellicosus* and surrounding pedogenetic horizons at each toposequence position.

| Structure | Clay (%) | pH ($H_2O$) | Total C (g kg$^{-1}$) | $Fe_o$ (g kg$^{-1}$) | $Al_o$ (g kg$^{-1}$) | $Mn_o$ (g kg$^{-1}$) | $Fe_d$ (g kg$^{-1}$) | $Al_d$ (g kg$^{-1}$) | $Mn_d$ (g kg$^{-1}$) | Fe activity ($Fe_o/Fe_d$) |
|---|---|---|---|---|---|---|---|---|---|---|
| **Bottom mound** | | | | | | | | | | |
| External wall | 9.6 | 5.9 | 5.3 | 0.81 | 0.21 | 0.11 | 1.82 | 0.24 | 0.08 | 0.44 |
| Internal wall | 12.3 | 6.5 | 13.5 | 0.76 | 0.22 | 0.20 | 2.32 | 0.24 | 0.14 | 0.33 |
| Hives | 15.3 | 6.2 | 7.6 | 1.21 | 0.20 | 0.14 | 2.92 | 0.26 | 0.10 | 0.42 |
| Below nest | 14.9 | 8.7 | 6.4 | 0.54 | 0.27 | 0.28 | 1.97 | 0.19 | 0.21 | 0.27 |
| **Mean** | **13.0**$^{***}$ | **6.8** | **8.2** | **0.83** | **0.23** | **0.18**$^{*}$ | **2.26** | **0.23** | **0.13** | **0.37**$^{*}$ |
| **S.D.** | **2.7** | **1.3** | **3.6** | **0.28** | **0.03** | **0.08** | **0.49** | **0.03** | **0.06** | **0.08** |
| **Fringe mound** | | | | | | | | | | |
| External wall | 19.3 | 5.7 | 7.7 | 0.88 | 0.27 | 0.10 | 3.13 | 0.32 | 0.09 | 0.28 |
| Internal wall | 27.5 | 6.0 | 6.8 | 2.12 | 0.32 | 0.08 | 5.17 | 0.36 | 0.06 | 0.41 |
| Hives | 27.2 | 5.6 | 6.6 | 1.56 | 0.31 | 0.08 | 5.01 | 0.36 | 0.06 | 0.31 |
| Royal chamber | 30.6 | 5.7 | 6.6 | 2.03 | 0.37 | 0.09 | 5.84 | 0.40 | 0.07 | 0.35 |
| Below nest | 15.6 | 6.1 | 9.4 | 1.51 | 0.25 | 0.12 | 2.68 | 0.32 | 0.09 | 0.56 |
| **Mean** | **24.0**$^{*}$ | **5.8** | **7.4** | **1.62**$^{*}$ | **0.30** | **0.09** | **4.37**$^{**}$ | **0.35**$^{*}$ | **0.07** | **0.38** |
| **S.D.** | **6.3** | **0.2** | **1.2** | **0.50** | **0.05** | **0.02** | **1.38** | **0.03** | **0.02** | **0.11** |
| **Upland mound** | | | | | | | | | | |
| External wall | 22.5 | 7.6 | 6.5 | 0.22 | 0.59 | 0.17 | 10.36 | 0.88 | 0.16 | 0.02 |
| Internal wall | 21.0 | 6.9 | 4.8 | 0.19 | 0.51 | 0.14 | 9.73 | 0.79 | 0.14 | 0.02 |
| Hives | 48.2 | 6.7 | 6.7 | 0.22 | 0.59 | 0.05 | 13.96 | 1.08 | 0.10 | 0.02 |
| Royal chamber | 48.2 | 7.3 | 5.5 | 0.28 | 0.69 | 0.08 | 13.66 | 1.10 | 0.10 | 0.02 |
| Base-plate | 46.5 | 7.5 | 5.5 | 0.27 | 0.64 | 0.12 | 13.76 | 1.05 | 0.14 | 0.02 |
| Pillars | 21.4 | 7.6 | 5.1 | 0.19 | 0.56 | 0.16 | 5.68 | 0.54 | 0.09 | 0.03 |
| **Mean** | **34.6**$^{*}$ | **7.2**$^{**}$ | **5.7** | **0.23** | **0.60** | **0.12** | **11.19** | **0.91** | **0.12**$^{*}$ | **0.02**$^{*}$ |
| **S.D.** | **14.3** | **0.4** | **0.8** | **0.04** | **0.06** | **0.05** | **3.27** | **0.22** | **0.03** | **0.00** |

| Horizon | Depth (cm) | Clay (%) | pH ($H_2O$) | Total C (g kg$^{-1}$) | $Fe_o$ (g kg$^{-1}$) | $Al_o$ (g kg$^{-1}$) | $Mn_o$ (g kg$^{-1}$) | $Fe_d$ (g kg$^{-1}$) | $Al_d$ (g kg$^{-1}$) | $Mn_d$ (g kg$^{-1}$) | Fe activity ($Fe_o/Fe_d$) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Bottom pedon (Fluvaquentic Epiaquept)** | | | | | | | | | | | |
| Ap1 | 0-8 | 5.8 | 5.4 | 11.0 | 0.79 | 0.22 | 0.15 | 1.53 | 0.26 | 0.10 | 0.52 |
| Ap2 | 8-19 | 5.1 | 5.7 | 5.2 | 0.72 | 0.22 | 0.07 | 1.36 | 0.26 | 0.05 | 0.53 |
| Bwg1 | 19-37 | 5.5 | 6.3 | 3.3 | 1.26 | 0.11 | 0.09 | 1.40 | 0.17 | 0.06 | 0.90 |
| Bwg2 | 37–58 | 7.1 | 6.5 | 3.5 | 1.65 | 0.11 | 0.09 | 2.96 | 0.15 | 0.08 | 0.56 |
| Bwg3 | 58–80+ | 6.5 | 5.0 | 2.0 | 0.74 | 0.19 | 0.00 | 0.81 | 0.16 | 0.00 | 0.91 |
| **Mean** | | **6.0**$^{***}$ | **5.8** | **5.0** | **1.03** | **0.17** | **0.08**$^{*}$ | **1.61** | **0.20** | **0.06** | **0.68**$^{*}$ |
| **S.D.** | | **0.8** | **0.6** | **3.5** | **0.41** | **0.06** | **0.05** | **0.80** | **0.06** | **0.04** | **0.20** |
| **Fringe pedon (Fluvaquentic Epiaqualf)** | | | | | | | | | | | |
| Ap1 | 0-10 | 12.4 | 5.9 | 17.1 | 0.80 | 0.38 | 0.23 | 2.07 | 0.34 | 0.15 | 0.39 |
| Ap2 | 10-27 | 10.7 | 6.1 | 9.6 | 0.82 | 0.27 | 0.18 | 2.08 | 0.33 | 0.14 | 0.39 |
| Btg1 | 27–45 | 17.7 | 7.5 | 8.5 | 0.96 | 0.25 | 0.20 | 2.29 | 0.28 | 0.15 | 0.42 |
| Btg2 | 45–71 | 20.4 | 7.3 | 6.4 | 1.29 | 0.29 | 0.06 | 2.62 | 0.14 | 0.04 | 0.49 |
| 2Bwg | 71–86 | 3.6 | 5.1 | 2.6 | 0.25 | 0.25 | 0.00 | 0.42 | 0.19 | 0.00 | 0.59 |
| 2BC | 86–100+ | 0.4 | 5.6 | 0.3 | 0.05 | 0.18 | 0.00 | 0.09 | 0.11 | 0.00 | 0.58 |
| **Mean** | | **10.9**$^{*}$ | **6.2** | **7.4** | **0.70**$^{*}$ | **0.27** | **0.11** | **1.60**$^{**}$ | **0.23**$^{*}$ | **0.08** | **0.48** |
| **S.D.** | | **7.8** | **0.9** | **5.9** | **0.46** | **0.07** | **0.10** | **1.06** | **0.10** | **0.08** | **0.09** |
| **Upland pedon (Typic Kandiustalf)** | | | | | | | | | | | |
| Ap1 | 0–7 | 5.5 | 6.6 | 10.8 | 0.16 | 0.52 | 0.30 | 3.76 | 0.42 | 0.19 | 0.04 |
| Ap2 | 7–33 | 5.4 | 6.6 | 4.4 | 0.16 | 0.47 | 0.29 | 3.65 | 0.44 | 0.19 | 0.04 |
| Bw | 33–62 | 6.0 | 6.4 | 2.1 | 0.15 | 0.38 | 0.21 | 4.14 | 0.45 | 0.15 | 0.04 |
| Bt | 62–120+ | 34.0 | 5.8 | 2.7 | 0.32 | 0.83 | 0.09 | 14.40 | 1.20 | 0.14 | 0.02 |
| **Mean** | | **12.7**$^{*}$ | **6.3**$^{**}$ | **5.0** | **0.20** | **0.55** | **0.22** | **6.49** | **0.63** | **0.17**$^{*}$ | **0.04**$^{*}$ |
| **S.D.** | | **14.2** | **0.4** | **4.0** | **0.08** | **0.20** | **0.10** | **5.28** | **0.38** | **0.03** | **0.01** |

$Fe_o$, $Al_o$, $Mn_o$=acid ammonium oxalate extractable iron, aluminum and manganese; $Fe_d$, $Al_d$, $Mn_d$=dithionite–citrate–bicarbonate extractable iron, aluminum and manganese.
$^{*}$, $^{**}$ and $^{***}$ represent a significant difference at the level of $P<0.05$, 0.01 and 0.001, respectively, between the mound structures and pedogenetic horizons at each toposequence position.

# Results

## *Field observations*

Our field survey found distinctive redoximorphic features in a cross-section of the mound structures at the fringe site (Fig. 1). The structures, with particular attention to the hives, exhibited a matrix color of grayish yellow (10YR6/2), while their surface was more yellowish with a higher chroma (10YR6/6–10YR7/8) (Fig. 1a). The surface yellowish layers were morphologically different from yellowish brown mottles in the subsurface pedogenetic horizons of the adjacent pedon. We also found a tubular-like mottle (7.5YR4/6) in a cross-section of the mound structures (Fig. 1b). Further information on soil morphological features has been reported previously (Abe et al., 2009b).

## *Selective dissolution analysis*

The results of the selective dissolution analysis are shown in Table 1. The pedon at the lower slope had a high level of $Fe_o$, but low levels of $Fe_d$, $Al_o$, $Al_d$ $Mn_o$, and $Mn_d$. The iron activity index showed higher values in the lower slope that generally increased with soil depth. The levels of the given components and the iron activity index were generally parallel to those in the mounds, except for $Mn_o$ and $Mn_d$. Among the mound structures, the nest body consisting of the hives, royal chamber and base-plate, showed relatively higher levels of $Fe_d$, $Fe_o$, $Al_d$, and $Al_o$ than those of the other structures.

The level of $Fe_d$ in the mound structures (bottom, 1.82–2.92 g kg$^{-1}$; fringe, 2.68–5.84 g kg$^{-1}$; upland, 5.68–13.96 g kg$^{-1}$) was generally higher than that of the subsurface (Ap2) horizon of the adjacent pedon (bottom, 1.36 g kg$^{-1}$; fringe, 2.08 g kg$^{-1}$; upland, 3.65 g kg$^{-1}$). In addition, there was a significant difference ($P<0.01$) when comparing the mean $Fe_d$ content between the mound structures ($4.37 \pm 1.38$ g kg$^{-1}$) and pedogenetic horizons ($1.60 \pm 1.06$ g kg$^{-1}$) at the fringe site. There was less difference in the $Fe_o$ content as compared with $Fe_d$ between the mound constructions (bottom, 0.54–1.21 g kg$^{-1}$; fringe, 0.88–2.12 g kg$^{-1}$; upland, 0.19–0.28 g kg$^{-1}$) and adjacent Ap2 horizon (bottom, 0.72 g kg$^{-1}$; fringe, 0.82 g kg$^{-1}$; upland, 0.16 g kg$^{-1}$) at each toposequence position although a significant difference ($P<0.05$) was observed in the mean value of $Fe_o$ between the mound structures and the pedogenetic horizons at the fringe site. As a result, the mound structures tended to have a lower index of iron activity (bottom, 0.27–0.44; fringe, 0.28–0.56; upland, 0.02–0.03) than that of the surrounding Ap2 horizon (bottom, 0.53; fringe, 0.39; upland, 0.04) at each toposequence position. Moreover, the mean of the iron activity index was significantly ($P<0.05$) higher in the mound structures (bottom, $0.37 \pm 0.08$; upland, $0.02 \pm 0.00$) than that in the pedogenetic horizons (bottom, $0.68 \pm 0.20$; upland, $0.04 \pm 0.01$) at the bottom and upland sites. On the other hand, in the upland site, the levels of $Fe_d$, $Fe_o$ and $Al_d$ in the termite nest body, i.e., hives, royal cell and base-plate, were similar to those of the argillic (Bt) horizon of the surrounding pedon, while the other mound constructions such as the external wall, internal wall and pillars showed intermediate values between those of the Bt horizon and the upper horizons (Ap1, Ap2 and Bw). The $Mn_o$ and $Mn_d$ content were generally higher in the mound structures than in the natural horizons at the bottom site, while an opposite tendency was observed at the fringe and in upland sites. In contrast, the levels of $Al_o$ and $Al_d$ showed little difference between the mound structures and natural horizons.

The correlation analysis revealed a significant correlation between the $Fe_d$ and clay contents (Fig. 1 and Table 2). The clay content was also significantly correlated with the content of $Al_d$ and $Al_o$ content. In contrast, these components were not significantly correlated with the other selected physicochemical properties such as soil pH and total C content.


**Fig. 1.** A cross section of a mound structure (hives) of *Macrotermes bellicosus* at the fringe: (a) surface yellowish layers and (b) tubular-like mottle.

# Discussion

The presence of distinctive redoximorphic features, i.e., yellowish surface layers observed on the mound structures at the fringed site is simple but robust evidence of qualitative alteration of free sesquioxides, especially iron sesquioxides, in a termite mound. It seems likely that *M. bellicosus* brought up subsoil material into the epigeal nest during mound building, which resulted in changes in the soil oxidation–reduction environment. This is supported by the result of the selective dissolution analysis showing a higher level of $Fe_d$ relative to $Fe_o$ and the resultant lower index of iron activity in the mound structures than that of the neighboring soil horizons. These results suggest changes in forms and/or composition of free iron sesquioxides, from active non-crystalline iron forms under reduced conditions to non-active crystalline iron forms in oxidation state, by the termites' mound-building activity. The redox alteration of soil-free sesquioxides in the termite mound seems to occur only in the lowland with aquic moisture regime (valley bottom and fringe) because the soil sesquioxides are generally susceptible to oxidation–reduction status as affected by hydrological disparity due to the toposequence positions (Veneman et al., 1976; Franzmeier et al., 1983). The significant effect of toposequence on the content of the examined components was apparent except for $Mn_o$ (Table 3). On the other hand, the tuber-like shaped, brown mottle in the cross section of the mound structures (Fig. 1b) is attributable to plant tissues buried in the mound which act as electron donors.

More interestingly, the nest body, i.e., hives, royal cell and base-plate, represented more intensive modification of the given components than did the other mound constructions such as the walls and pillars. This modifying trend was similar to that of other physicochemical properties (Abe et al., 2009b), suggesting that *M. bellicosus* can manipulate pedogenetic iron sesquioxides due to their ecological requirements, such as structural stability of the mound constructions

**Table 2**
Correlation matrix among selectively dissolved components (Fe, Al and Mn) and selected physicochemical properties of the mound structures *Macrotermes bellicosus* and surrounding pedogenetic horizons.

| | pH ($H_2O$) | Total C | $Fe_o$ | $Al_o$ | $Mn_o$ | $Fe_d$ | $Al_d$ | $Mn_d$ | $Fe_o/Fe_d$ |
|---|---|---|---|---|---|---|---|---|---|
| Clay | 0.36 | 0.03 | 0.01 | 0.70*** | −0.19 | 0.87*** | 0.80*** | 0.13 | −0.55** |
| pH ($H_2O$) | | 0.07 | −0.26 | 0.37* | 0.50** | 0.36 | 0.32 | 0.60*** | −0.51** |
| Total C | | | 0.21 | −0.04 | 0.51** | −0.13 | −0.09 | 0.43* | −0.08 |
| $Fe_o$ | | | | −0.50** | −0.22 | −0.30 | −0.44* | −0.33 | 0.51** |
| $Al_o$ | | | | | 0.17 | 0.89*** | 0.93*** | 0.44* | −0.84*** |
| $Mn_o$ | | | | | | −0.07 | 0.00 | 0.91*** | −0.46* |
| $Fe_d$ | | | | | | | 0.98*** | 0.30 | −0.73*** |
| $Al_d$ | | | | | | | | 0.36 | −0.76*** |
| $Mn_d$ | | | | | | | | | −0.66*** |

$n=30$ (including both mound structures and natural horizons).*, ** and *** represent significant levels at $P<0.05$, 0.01 and 0.001, respectively.

**Table 3**
Analysis of variance of the influence of toposequence and *Macrotermes bellicosus* on selected physicochemical properties.

| Entry | Topo-sequence (d.f.=2) | Termite influence (d.f.=1) | Toposequence X Termite influence (d.f.=5) |
|---|---|---|---|
| | *F*-value | | |
| Clay | 5.29* | 16.39*** | 1.48 |
| pH | 3.03 | 3.71 | 3.33 |
| Total C | 0.83 | 0.92 | 0.50 |
| $Fe_o$ | 19.49*** | 3.71 | 7.24** |
| $Al_o$ | 48.63*** | 1.99 | 0.04 |
| $Mn_o$ | 2.34 | 0.05 | 4.76* |
| $Fe_d$ | 20.63*** | 8.35** | 1.48 |
| $Al_d$ | 27.55*** | 4.89* | 1.18 |
| $Mn_d$ | 5.81** | 0.2 | 4.11* |
| $Fe_o/Fe_d$ | 57.69*** | 12.95** | 5.05* |

*, ** and *** represents $P<0.05$, 0.01 and 0.001, respectively.

(Jouquet et al., 2002a, 2007). Iron sesquioxides play an important role in the stabilization of soil structure due to the formation of aggregates and the cementation of other major soil components (Schwertmann and Taylor, 1989). Soil structural stability in relation to the levels of $Fe_d$, $Al_o$ and $Al_d$ has been reported previously (Pinheiro-Dick and Schwertmann, 1996; Barthés et al., 2008).

On the other hand, correlation analysis revealed a significant and positive correlation between the clay and $Fe_d$ content with the former also correlated to the levels of $Al_o$ and $Al_d$, respectively. Moreover, ANOVA results indicated the significant influence of termites on the levels of $Fe_d$ and $Al_d$ (Table 3). These findings suggest that preferential selection of clay particles ($<2$ μm) by *M. bellicosus* (Jouquet et al., 2004; Abe et al., 2009a, 2009b) leads to the enrichment of secondary (DCB-soluble) iron and aluminum sesquioxides during mound construction. The secondary iron sesquioxides occur as very fine particles and thus, predominantly exist in the clay-sized ($<2$ μm) fraction of the soil (Schwertmann and Taylor, 1989). While they often co-migrate with phyllosilicate clay minerals due to lessivage during pedogenesis (Blume and Schwertmann, 1969; Stonehouse and St. Arnaud, 1971; Juo et al., 1974), our findings indicate that termite nest-building activity is important for the redistribution of soil-free sesquioxides in tropical ecosystems.

The selective dissolution analysis provided additional evidence of preferential manipulation of the Bt horizon by *M. bellicosus* in addition to soil matrix color, soil texture and contents of clay and organic C (Abe et al., 2009a, 2009b). Assuming practically no effect of termites on the quality of sesquioxides in the well-drained upland, the contents of the examined components were very similar between the mound structure and the adjacent subsoils (Bt1 and Bt2 horizons) (Table 1). However, this assumption would not be applicable to the lowland soils with aquic moisture regimes because of redox alteration of free sesquioxides during and after termite mound building, as suggested by Fig. 1 and Table 1.

## Conclusions

The present study provided the first evidence of the influence of termites on free sesquioxides in the soil. On the basis of the findings described in this paper, we conclude that *M. bellicosus* can influence the form and composition of free sesquioxides (especially iron) in the soil due to the direct effect of the enrichment of fine (clay-sized) soil particles in the mound and/or due to the indirect effect of changes in soil redox conditions caused by the soil transportation from reductive (aquic subsoil) to oxidative (epigeal mound) environments. The termite nest-building activity can affect spatial distribution of soil-free sesquioxides thereby contributing to soil and ecosystem diversity. Further research should include a detailed mineralogical analysis and should examine other termite species having different feeding and/or dwelling habitats. The influence of free sesquioxides on the structural stability of termite mounds is also an interesting topic for exploration.

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