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SHORT COMMUNICATION

Soil-particle selection by the mound-building termite *Macrotermes bellicosus* on a sandy loam soil catena in a Nigerian tropical savanna

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Many species of termite (Isoptera) build their nests inside mounds because a mound has direct and positive feedback effects on the termite colonies through the maintenance of humidity and protection of the population from enemies, e.g. ants (Jouquet *et al.* 2006, Korb 2003, Noirot & Darlington 2000). Soil manipulation by termites (Isoptera) for mound construction is of particular interest for many researchers in terms of pedogenesis of the tropics (Lavelle *et al.* 1992, Lobry de Bruyn & Conacher 1990). The termites select soil particles according to ecological requirements such as water availability (Jouquet *et al.* 2002, 2007) and improve soil structural stability by means of application of clay particles and saliva/excreta (Fall *et al.* 2001, Jouquet *et al.* 2004). The nest-building activity of the termites inevitably causes regional translocation of soils (Bagine 1984, Holt & Lepage 2000) and distinctive patches in local ecosystems, which contributes to ecological diversity (Lavelle *et al.* 1992). This is the reason why termites are regarded as an ecological engineer (Jouquet *et al.* 2006). Soil-particle selection by the termites, however, has not been fully explored in relation to diverse ecologies and landscapes in Africa.

Inland valleys are an important geological component in West Africa supporting biological or ecological diversity. In the inland valleys, soil characteristics are often affected by toposequence position (Windmeijer & Andriesse 1993). We hypothesize that toposequence influences termite nest-building activity. In fact, number and volume of termite mounds are often found to be lower in the lowlands than the uplands (Abe *et al.* 2009, Kang 1978). The objective of this paper, therefore, was to examine effects of toposequence on soil-particle selection by *Macrotermes bellicosus*, a dominant species in Nigerian tropical savanna. To achieve this aim, we assessed principal mound structures as compared with natural horizons of surrounding pedons (smallest volume of a representative soil for description and sampling) on a sandy loam catena by measuring particle size distribution with five sand and two silt fractions. Most previous studies considered the mound as a whole and compared it with adjacent topsoil only (Lobry de Bruyn & Conacher 1990). However, other studies have shown that termites use subsoil to build a mound and that soil properties may vary according to the different structures built within the mound, such as walls, hives and pillars (Jouquet *et al.* 2004, Lavelle *et al.* 1992).

A field survey was conducted in an inland valley in Bida, about 165 km west of the capital Abuja, Nigeria, during the dry season (February 2005). This location is part of the Guinea savanna agro-ecological zone with mean annual rainfall of about 1100 mm and mean annual daily temperature of approximately 23° C. The soil in this region is underlain by Nupe sandstone, a Cretaceous mixture of coarse grits, conglomerates, fine-grained sandstones, siltstones and shales, and thus is sandy, kaolinitic and/or siliceous (Abe *et al.* 2006, 2007). In the inland valley, we investigated three different toposequence positions, i.e. valley bottom, hydromorphic fringe and upland plateau,

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and selected a representative mound constructed by *M. bellicosus* Smethman (Isoptera: Macrotermitinae) at each position. Soil samples were collected from identifiable biogenic structures i.e. external wall, internal wall, hives, royal cell, base-plate and pillars, in mounds and soils below the nest. The bottom and fringe mounds were less developed and thus provided fewer samples than the upland mound (Abe *et al.* 2009). Soils were also sampled from natural horizons of pedons 2 m away from the mounds. Soil morphological alterations by the termites were not visible in the pedons.

The gravel (>2 mm) content was obtained by dry-sieving. The particle-size distribution was measured after decomposition of the organic matter and removal of free sesquioxides (when necessary), as described by Gee & Or (2002). The sand fractions, i.e. very coarse (VC) sand (1–2 mm), coarse (C) sand (0.5–1 mm), medium (M) sand (0.25–0.5 mm), fine (F) sand (0.10–0.25 mm) and very fine (VF) sand (0.05–0.10 mm) were separated by wet-sieving. The silt, i.e. C silt (20–53 μm) and F silt (2–20 μm), and clay (<2 μm) fractions were separated by means of the pipette method ensuring optimal dispersion in 0.5% sodium hexametaphosphate solution. The particle-size distribution was expressed on an oven-dry basis at 105 °C.

Data were statistically examined by analysis of variance using the StatView software (Version 5.0.1., SAS Inst., Cary, NC, USA) and means were separated between mound structures and natural horizons at each toposequence position by Fisher's protected probability test.

Particle size distribution varied widely among structural units of the mounds (Figure 1), which indicated the methodological weakness of many previous reports (Ekundayo & Aghatise 1997, Sheikh & Kayani 1982) that assessed the mound as a whole and adjacent topsoil only. In particular, structural units in the nest body (i.e. hives, royal cells and base plates) contained finer particles than the other mound constituents (i.e. walls and pillars) and soils below the mound, except for the fringe mound, where nest body and other mound constituents had similar particle size distribution. Combination of silt and sand distribution differentiates nest bodies from the other mound structures at any location on the toposequence. This suggests that *M. bellicosus* will use different soil particles depending on the function of each mound structure or ecological requirement for their livelihood. Jouquet *et al.* (2002, 2007) also pointed out that the termites (*Odontotermes* nr. *pauperans* and *Pseudacanthotermes spiniger*) used soils having contrasting particle size distribution by selection to various extents in response to ecological requirements such as structural stability and water-holding capacity.

Table 1. Analysis of variance of the influence of toposequence and *Macrotermes bellicosus* on particle-size distribution.*, ** and *** represent $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively. T = total; VC = very coarse; C = coarse; M = medium; F = fine; VF = very fine.

Particle-size fractions	Toposequence	Termite influence	Toposequence × Termite influence
Gravel	1.81	14.2**	1.68
T sand	4.15*	15.5***	0.88
VC sand	10.1***	8.55**	1.03
C sand	7.09**	10.7**	1.55
M sand	5.94**	7.88*	0.89
F sand	3.78*	8.09**	0.80
VF sand	51.4***	0.36	0.41
T silt	50.8***	6.57*	0.29
C silt	55.1***	3.65	0.05
F silt	35.9***	8.27**	0.77
Clay	5.50*	14.7***	1.62

In spite of considerable variability in the mounds, the mound structures, particularly the upland mounds, apparently had finer particles than the upper horizons of the adjacent pedons (Figure 1). Setting the subsurface horizon (Ap2) fraction to 100%, fractions that were depleted in the mound as compared with the subsurface horizon were: VC sand (average bottom mound (M_B), 58%; fringe mound (M_F), 33%; upland mound (M_U), 49%), C sand (average M_B, 54%; M_F, 38%; M_U, 39%), M sand (average M_B, 71%; M_F, 66%; M_U, 60%) and F sand (average M_B, 79%; M_F, 81%; M_U, 84%). Fractions that were enriched in the mound as compared with the subsurface horizon were: C silt (average M_B, 130%; M_F, 103%; M_U, 130%), F silt (average M_B, 145%; M_F, 124%; M_U, 116%) and clay (average M_B, 254%; M_F, 224%; M_U, 636%). The limit for particle size selection by *M. bellicosus* was VF sand because there were no clear differences observed in VF sand content between the mound and the pedon at each toposequence position. In addition, the mound structures were gravel-free in contrast to the surrounding pedons which contained gravel in the range 0.39–7.61 g kg^{-1}. These results were supported by analysis of variance which showed influence of *M. bellicosus* on various sizes of particles except for VF sand and C silt (Table 1). Furthermore, the Fisher's protected probability test indicated significant differences in the contents of gravel, total (T) sand and clay between the mound and pedon at each toposequence position (Table 2). This indicates that *M. bellicosus* preferentially uses finer soil particles and intentionally excludes gravel in building mounds. This is in agreement with many previous studies (Jouquet *et al.* 2002, 2004, 2007; Lobry de Bruyn & Conacher 1990). *Macrotermes bellicosus* manipulated clay most among the different particle size fractions because clay accumulated in the mounds plays a significant role in stabilization of the mound structure or in enhancement of water-holding capacity (Jouquet *et al.* 2002, 2004).

It is noticeable from Figure 1, that the upland mound contained more clay but less C and F silts and VF sand than the fringe and bottom. The particle size distribution

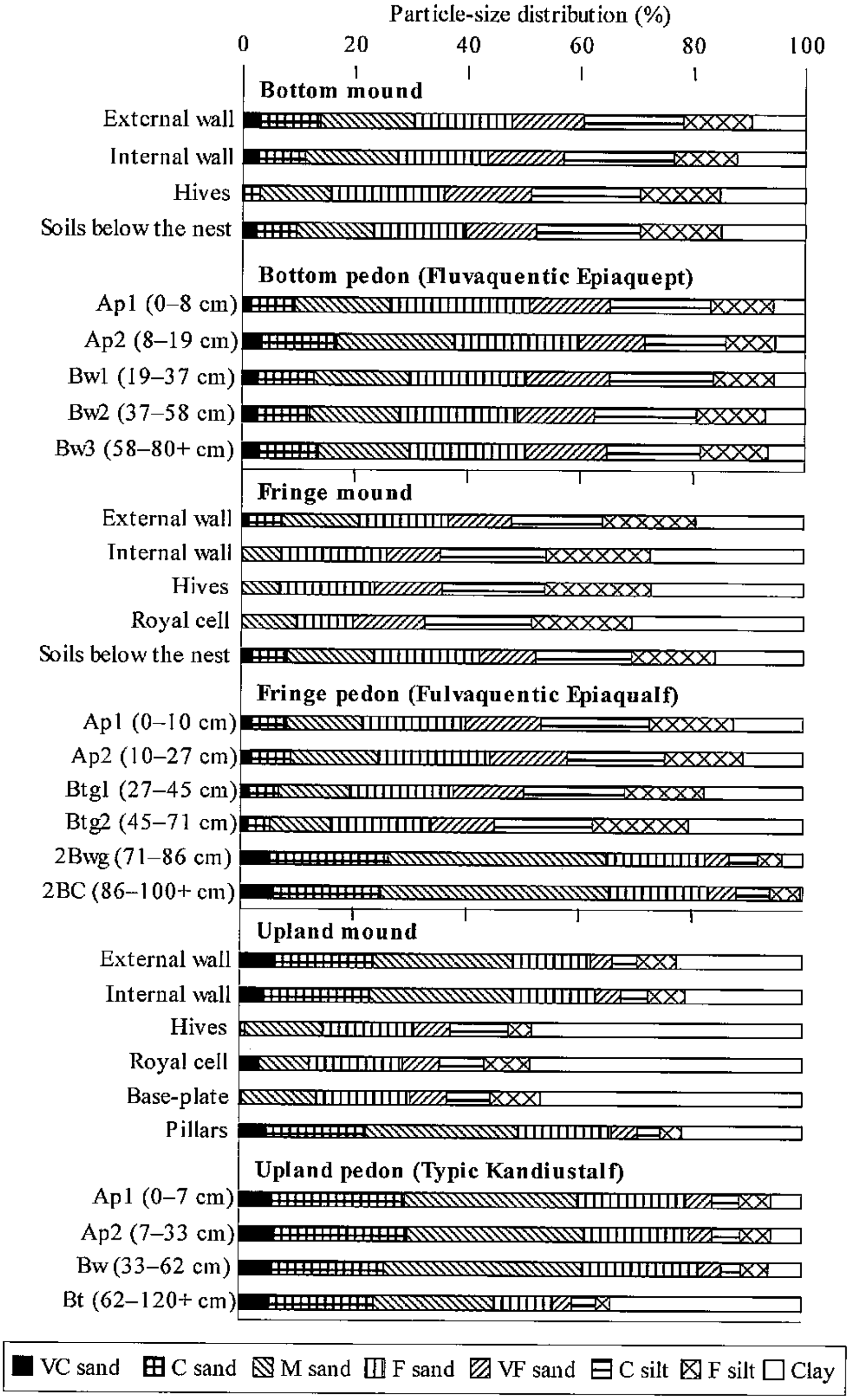

Figure 1. Particle-size distribution of *Macrotermes bellicosus* mounds and surrounding pedons on a toposequence at the study site. A = mineral surface horizon with organic matter accumulation; B = subsurface soil structure; C = little or no pedogenic alteration. g = greyish colour with redoximorphic features; p = plough layer or other artificial disturbance; t = illuvial accumulation of silicate clay; w = weak colour or structure development.

Table 2. Comparison of particle-size distribution between the *Macrotermes bellicosus* mound and surrounding pedon at each toposequence position at the study site. The value represents mean ± SD. The *t*-test represents not significant (ns), significant $P < 0.05$ (*), $P < 0.01$ (**) or $P < 0.001$ (***) between the mound structures and adjacent natural horizons at each toposequence position. Gravel in the fringe pedon exceptionally has $n = 5$. T = total; VC = very coarse; C = coarse; M = medium; F = fine; VF = very fine.

Particle-size fractions	Bottom (Fluvaquentic Epiaquept)			Fringe (Fluvaquentic Epiaqualf)			Upland (Typic Kandiustalf)		
	Mound (n = 4)	Pedon (n = 5)	*t*-test	Mound (n = 5)	Pedon (n = 6)	*t*-test	Mound (n = 6)	Pedon (n = 4)	*t*-test
Gravel	0.0 ± 0.0	0.6 ± 0.2	***	0.1 ± 0.2	2.8 ± 3.4^{b}	**	0.0 ± 0.0	2.8 ± 0.9	**
T sand	55.3 ± 2.1	65.9 ± 1.5	**	40.9 ± 3.9	63.6 ± 7.7	*	52.5 ± 7.1	78.3 ± 6.4	*
VC sand	1.9 ± 1.2	2.5 ± 0.7	ns	0.6 ± 0.8	2.8 ± 2.0	*	3.0 ± 2.5	5.7 ± 0.4	ns
C sand	7.4 ± 3.4	10.4 ± 2.1	ns	2.7 ± 3.3	10.6 ± 7.6	ns	9.4 ± 9.7	21.7 ± 2.5	*
M sand	14.8 ± 2.0	17.3 ± 2.0	ns	10.4 ± 4.0	22.0 ± 13.8	ns	18.8 ± 7.7	29.5 ± 5.9	*
F sand	17.6 ± 1.9	21.9 ± 1.7	**	16.1 ± 3.5	18.3 ± 0.9	ns	15.9 ± 1.3	17.4 ± 4.6	ns
VF sand	13.5 ± 1.3	13.7 ± 1.3	ns	11.1 ± 1.3	10.0 ± 4.3	ns	5.4 ± 1.3	4.0 ± 0.5	ns
T silt	31.8 ± 0.8	28.1 ± 1.2	ns	35.1 ± 1.2	25.5 ± 4.8	ns	12.9 ± 1.4	9.0 ± 0.9	ns
C silt	18.7 ± 0.9	17.1 ± 1.7	ns	17.8 ± 1.3	13.8 ± 6.4	ns	6.6 ± 2.6	4.5 ± 0.6	ns
F silt	13.1 ± 1.6	11.0 ± 1.3	ns	17.3 ± 1.6	11.7 ± 5.4	ns	6.4 ± 2.1	4.6 ± 1.4	ns
Clay	13.0 ± 2.6	6.0 ± 0.8	***	24.0 ± 6.3	10.9 ± 7.8	*	34.6 ± 14.3	12.7 ± 14.2	*

of the mounds apparently reflects that of the surrounding pedons. It is widely agreed that termites preferentially use subsoil material to build their mounds (Lee & Wood 1971, Lobry de Bruyn & Conacher 1990). The findings of this study suggest that *M. bellicosus* mainly used argillic horizons (a subsurface horizon with clay illuviation), i.e. Btg1 and Btg2 at the fringe, and Bt2 at the upland, for building their mounds. This assumption is also supported by soil organic carbon distribution and forms and contents of iron oxides (Abe & Wakatsuki unpubl. data, Abe *et al.* 2009). The limited number and relatively small volume of *M. bellicosus* mounds in the lowlands (Abe *et al.* 2009, Kang 1978) is probably due to interference with a shallow water table in poorly drained soils. However, limited access to a clay-rich subsoil may be another constraint for mound construction. This might be endorsed by field observation that well-developed mound nests with a cathedral shape and base plate were found only in well-drained upland sites (Abe *et al.* 2009).

Our findings showed (1) *M. bellicosus* generally selected the same particle size whatever the local soil along the toposequence, but (2) clay content in the subsoil and accessibility to clay-rich soil horizons may define nest-building capacity.

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