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ORIGINAL ARTICLE

Physicochemical and morphological properties of termite (*Macrotermes bellicosus*) mounds and surrounding pedons on a toposequence of an inland valley in the southern Guinea savanna zone of Nigeria

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Abstract

Termites play a significant role in soil-forming processes of the tropics. The influence of termites on pedogenesis as affected by the toposequence, however, has rarely been explored. We investigated the soil physicochemical and morphological characteristics of epigeal mounds constructed by *Macrotermes bellicosus* (Smethman) compared with those of surrounding pedons along a toposequence (bottom, fringe and upland sites) of an inland valley in central Nigeria. The physicochemical and morphological properties of the mound soils varied according to structural units but were generally different from those of the adjacent pedons. The differences included finer texture, higher electrical conductivity, total N, exchangeable bases (Ca, Mg and K) and effective cation exchange capacity and lower C/N ratio and exchange acidity in the mound than the pedon at each toposequence position. This tendency to modify the soil properties was more prominent in the nest body where the termites actually live, that is, in the hives, royal cell and base-plate, than in the soils below the nest and the other mound parts, that is, the external wall, internal wall and pillars. We found this trend to a greater or lesser degree at all toposequence positions. Our findings suggest that: (1) *M. bellicosus* can manipulate the mound soils according to functional applications of structure units or environmental requirements for its livelihood, regardless of local soils; (2) *M. bellicosus* makes ecological patches (hot spots) at all toposequence positions in the same measure; (3) the influence of *M. bellicosus* on the pedogenesis is reduced in the lowlands compared with the uplands because the number and volume of the mounds were substantially lower in the bottom and fringe sites compared with the upland site.

Key words: *Macrotermes bellicosus*, pedogenesis, termite mounds, toposequence.

INTRODUCTION

Soil fauna are one of the essential factors determining pedogenesis. In tropical ecosystems, termites (Isoptera) play an important role in soil-forming processes because of their manipulation of mineral particles and collection of plant fragments (Collins 1981b; Lobry de Bruyn and Conacher 1990; Lavelle *et al.* 1992) and many researchers have paid particular attention to the nest-building activity of termites (e.g., Hesse 1955; Lee and Wood 1971; Pomeroy 1976a; Collins 1979; Arshad 1981; Ezenwa 1985). Mound-building termites substantially affect earth-surface processes by transporting soil materials from various depths to epigeal mound structures (Lavelle *et al.* 1992; Jouquet *et al.* 2002). On the African continent, mound nests can occupy up to 10% of the land surface area in tropical savanna or forest regions (Lavelle 1997). Mound longevity is generally believed to be a few years to decades and the soil turnover rate can be 1–10 t ha^{-1} $year^{-1}$; both mound longevity and soil turnover rate depend on the termite species, soil material, climate and other biophysical conditions (Lobry de Bruyn and Conacher 1990). These figures indicate a significant impact of termite nest-building activity on soil formation and land-surface processes. Termites hoard nutrients in the mounds because of their digestion of collected plants and their deposition or application of excreta/saliva to the mounds (Contour-Ansel

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et al. 2000; Fall *et al.* 2001; Sall *et al.* 2002; López-Hernández *et al.* 2006; Brossard *et al.* 2007). Surface structures continuously erode after abandonment, leading to a redistribution of soil materials in the landscape, which creates nutrient patchiness and preserves ecological diversity (Bonell *et al.* 1986; Lavelle *et al.* 1992).

The authors of many previous reports have described a simple comparison of mounds and neighboring soils (Lobry de Bruyn and Conacher 1990). In these studies, the authors often considered mounds as a whole (sometimes without description) and simply compared them with adjacent topsoils (e.g., Hesse 1955; Lee and Wood 1971; Sheikh and Kayani 1982; Wood *et al.* 1983; Ezenwa 1985; López-Hernández *et al.* 1989, 1990). This methodology, however, has major weaknesses because: (1) termites select materials not only from topsoils, but also from subsoils (Jouquet *et al.* 2002; (2) the soil properties of termite mounds vary significantly according to structural units within the mound (Arshad 1981; Jouquet *et al.* 2003), (3) mound soils are subjected to rainfall and thus eroded materials may affect the surface soils surrounding the mounds (Arshad 1982; Lavelle *et al.* 1992). In contrast, our review of the relevant literature indicated that little is known about the effect of termites on pedogenesis as influenced by toposequence. In general, there are many more termite mounds in the uplands than in the lowlands (Pomeroy 1976b; Kang 1978). This is one possible reason why only a few studies have focused on wetland regions. However, termites can also affect soil-forming processes in the lowlands, and determining the differences in soil characteristics of mounds compared with the surrounding soils along a toposequence is needed to shed more light on this issue. In the present study, we investigated the physicochemical and morphological properties of the principal structures of termite mounds and compared them with the properties of the pedogenic horizons of the surrounding soils on a representative toposequence of an inland valley in central Nigeria.

MATERIALS AND METHODS

Study site

The inland valley is a widespread topography in West Africa and displays a significant potential for agricultural development (Windmeijer and Andriesse 1993). In the present study, a typical inland valley was selected from a suburb of Bida (08°N, 06°E), central Nigeria. A general description of the inland valley in this region has been reported elsewhere (Smaling *et al.* 1985; Oyediran 1990; Ishida 1998; Hirose and Wakatsuki 2002). This area lies on the southern edge of the Guinea savanna agro-ecological zone. The mean annual rainfall is approximately 1100 mm, and the mean annual daily temperature is 23°C. Soils in this region are underlain by Nupe sandstone that mainly consists of Cretaceous sediments made up of semi-consolidated coarse grits, conglomerates, fine-grained sandstones, siltstones and locally occurring shales (Esu 1986). The clay and primary minerals of the soils consist predominantly of kaolinite and quartz, respectively (Abe *et al.* 2006, 2007). Faunal pedo-turbation as a result of the activities of termites is one of the dominant soil-forming processes in the region (Wood *et al.* 1977, 1983; Collins 1979, 1981a,b; Esu 1986). *Macrotermes bellicosus* (Smethman) is one of the predominant species of Macorotermitinae (Termitidae), a mound builder/fungus grower, in the study region (Wood *et al.* 1977, 1983; Collins 1979, 1981a,b) and builds impressive cathedral-shaped mounds with many ridges (Korb 2003). The traditional Nupe farming system prevails in this area coupled with cattle grazing by Fulani nomads (Hirose and Wakatsuki 2002). The toposequential soil characteristics in the inland valley investigated in this study were previously described by Smaling *et al.* (1985), Oyediran (1990) and Ishida (1998).

Field survey and soil sampling

The field survey for the present study was carried out in February 2005 during the dry season. Soil samples were collected from both termite mounds and adjacent pedons. A representative mound constructed by *M. bellicosus* was chosen at the upper slope (upland), footslope (hydromorphic fringe) and bottom of the inland valley, respectively. The mound distribution of *M. bellicosus* was checked in some locations (each area was 5–10 ha) around Bida using a receiver for a global positioning system (eTrex, Garmin, Inc., Kansas, USA). Mound density was expressed as the range of the *M. bellicosus* population per hectare. Parameters giving the size of an individual mound, that is, the north–south diameter, the east–west diameter and the height, were recorded according to Pomeroy (1976b). The volume of the mound was estimated by $V = kdh$, where k is a constant set to 0.668, d is the mean diameter and h is the height (Pomeroy 1976b). Soil pits were dug approximately 2 m away from the mounds. Soil morphological alterations by termites were not visible in these pedons. Before sampling, morphological features (soil color, field texture, structure, consistence and boundary) of the soil profiles were described according to the Japanese Society of Pedology (1997). We also described the morphology of material constituents in the termite mounds. Samples were collected from various parts of the termite mounds (i.e., the base plate, external wall, hives, internal wall, pillars, royal chambers and soils below the nest) and from natural horizons in the surrounding soil profiles. The soil samples were air-dried and passed through a 2-mm mesh sieve for laboratory analysis.

Laboratory analysis

Undisturbed core samples were used for the determination of bulk density after oven-drying at 110°C for 72 h. The pipette method was used to measure particle-size distribution after separation of the sand fraction by wet sieving. Prior to the particle-size analysis, the organic matter was digested using 10% hydrogen peroxide on a hot plate. In addition, Fe oxides in the samples from the upland site were removed with 3% hydrochloric acid. Optimal dispersion of the mineral particles was obtained with 0.1% sodium hexametaphosphate. The electrical conductivity (EC) was recorded in deionized water at a soil : water ratio of 1:5, and the soil pH was measured using a glass-electrode at a soil : water ratio of 1:2.5. Total C and N were simultaneously determined by the dry combustion method (SumiGraph NCH-21, Sumika Chemical Analysis Service, Tokyo, Japan). Available P was extracted by the Bray No. 1 method followed by spectrophotometric determination with molybdate and ascorbic acid. Exchangeable cations (Ca, Mg, K, and Na) were extracted with 1.0 mol L^{-1} ammonium acetate (pH 7), and the content of the bases in the extract was examined using a polarized Zeeman atomic absorption spectrophotometer (Z-2300; Hitachi, Tokyo, Japan). Exchangeable Al and H were obtained using a titration method after extraction with 1.0 mol L^{-1} KCl. The effective cation exchange capacity (ECEC) was calculated by the summation of exchangeable bases and exchange acidity. All analytical methods are described by the International Institute of Tropical Agriculture (1979) or the Japanese Society of Soil Science and Plant Nutrition (1997).

RESULTS AND DISCUSSION

Mound description

Our field observation indicated that the population of *M. bellicosus* mounds varied from 3 to 10 per hectare in the upland and from zero to two in the lowland (valley bottom and fringe) at the study site. The mound density in the lowland was comparable to that described in previous studies (Pomeroy 1976b; Kang 1978), whereas that in the upland was relatively lower than that described in previous works (Collins 1981a; Lepage 1984), probably because of anthropogenic disturbance. The mound on the upland site (M_U) had a well-developed structure with a spiral base plate, as reported by Collins (1979), whereas the mounds at the bottom (M_B) and the fringe (M_F) had a far less developed structure and were smaller than M_U (Table 1 and Fig. 1). The estimated aboveground volumes of M_B and M_F were 2.94 and 1.83 m^3, accounting for 54% and 34% of that of M_U ($V = 5.41$ m^3), respectively. In contrast, the royal cell of M_U was situated approximately 15 cm belowground, whereas that of M_F was observed approximately 20 cm aboveground. Although unfortunately the royal cell was not identified in M_B, we observed this tendency, that is, the royal cell was located above ground in the lowlands, but below ground in the uplands, in other mounds during the reconnaissance. These findings suggest that *M. bellicosus* would prevent the royal cell from seasonal submergence at the lower positions of the valley slope and indicate a possible interruption of the mound development in poorly drained soils because of hydrological interference. As stated above, the authors of previous studies found that the effects of termites on soil formation were substantially less in the lowlands than in the uplands (Pomeroy 1976b; Kang 1978). Our findings regarding the number and volume of mounds also suggested much less impact by *M. bellicosus* on land-surface processes in the bottom and fringe areas compared with the upland areas.

Morphological features

Table 2 shows selected morphological characteristics of the soils in the mounds and pedons. The soil matrix color of the pedons at the valley bottom (P_B) and fringe (P_F) ranged from grayish brown to light brownish in hue with

Table 1 Brief description of the sampling sites, *Macrotermes bellicosus* mounds and surrounding pedons

Position	Bottom	Fringe	Upland
Latitude	08°98′89″N	08°98′96″N	08°99′52″N
Longitude	06°00′02″E	06°00′15″E	06°00′37″E
Topography	Very gently sloping	Gently sloping	Very gently sloping
Land use	Bush fallow (burned)	Bush with shrubs	Bush fallow (burned)
Soil taxonomy†	Fluvaquentic Epiaquept	Fluvaquentic Epiaqualf	Typic Kandiustalf
World Reference Base‡	Lixic Stagnosols	Lixic Planosols	Cutanic Lixisols
Mound size (m^3) §	2.94	1.83	5.41
d_{NS}, d_{EW}, h (m)	3.03, 3.17, 1.42	2.03, 1.74, 1.45	2.44, 2.32, 3.40
Note	Beside *Parkia biglobosa* nearby an irrigation canal	Near *Mangifera Indica* on a farmer-resting place	Beside *Vitellaria paradoxa*

†Soil Survey Staff (2006). ‡IUSS Working Group World Reference Base (2006). §Mound size estimated according to Pomeroy (1976b). d_{NS}, the north–south diameter; d_{EW}, the east–west diameter; h, height; V, volume.

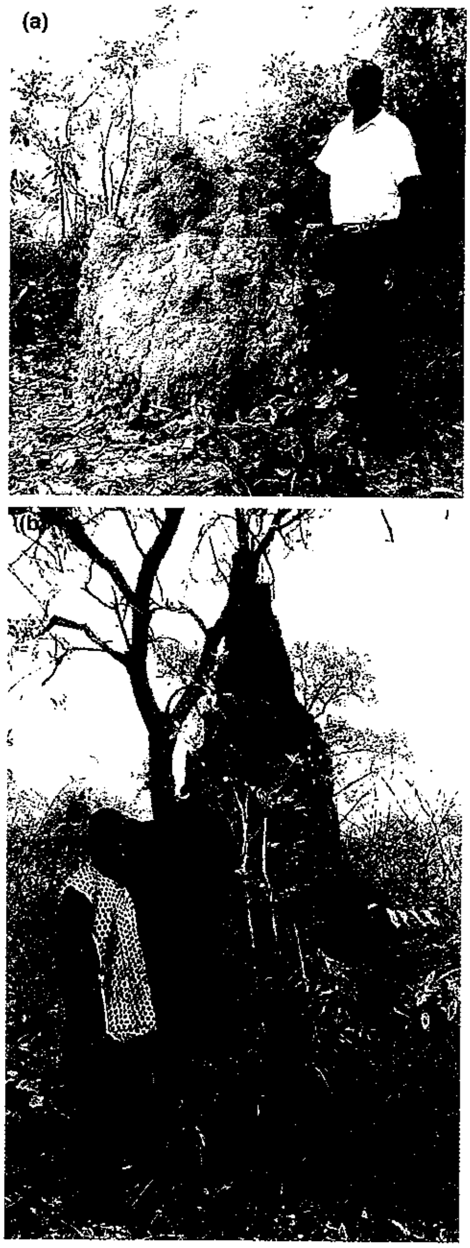

Figure 1 *Macrotermes bellicosus* mounds (a) at the fringe and (b) upland.

low chroma. Some subsurface horizons in these pedons displayed yellowish brown mottles and/or concretions (Bwg2 horizon of P_B). These descriptions signify seasonal development of reductive conditions at the bottom and fringe sites. In contrast, the pedon at the upland site (P_U) had a reddish brown hue with high value and chroma, reflecting intensive weathering under well-drained conditions. The matrix color of the mound constituents was well associated with that of the adjacent pedons under the influence of toposequence positions. This indicates that *M. bellicosus* uses soil material from the vicinity of the mounds.

The mounds showed markedly different characteristics in terms of soil structure and consistence compared with the neighboring pedons. The mound constituents were structureless (massive) because the termites preferentially transport finer particles and repack them very tightly (Sleeman and Brewer 1972; Arshad 1981; Mermut *et al.* 1984) by incorporation of saliva or excreta (Contour-Ansel *et al.* 2000; Fall *et al.* 2001; Sall *et al.* 2002) during the mound building. In contrast, the pedons were dominated by a weak to moderate subangular blocky structure. In addition, the mounds were generally firmer and harder than the adjacent topsoils. In particular, external or internal walls had very firm consistency and extremely hard compactness. The mound walls are the interface between the termitaria and the external environment. Thus, the mound walls need to be firm and strong enough to protect the nest from rainfall as well as invaders and have massive structure to control the climate inside the mound (Noirot and Darlington 2000; Korb 2003). The soil material used in the mounds was also stickier and more plastic after wetting than was the soil of the adjacent pedons, reflecting clay enrichment in the mounds, which was easily detectable by a field texture test. The 2Bwg and 2BC horizons of P_F had a sandy texture, derived from the nature of the parent materials of the soils (sandstones) in the study region. We also found reddish iron mottles with specific features in some parts of the hives and royal cells of M_F. The subsoil material, which was situated under seasonally reduced conditions at the lower slope, was preferentially incorporated into the epigeal mound, causing changes in the soil redox potential and the formation of unique redoximorphic features (S. Abe and T. Wakatsuki, unpubl. data).

Physical characteristics

Selected physical characteristics of the mounds and pedons are shown in Table 2. In general, the nest body inside the mound, that is, the hives, royal chamber and base plate where *M. bellicosus* actually dwell, contained higher moisture content than the other mound structures at all toposequence positions. In addition, the moisture content of the nest body was higher than that of the adjacent pedons, except for some subsoil horizons in P_F and P_B. This trend in moisture distribution was more prominent for the upland site than for the other two positions, which suggests a certain environmental control inside the well-developed mound. Korb (2003) found that *M. bellicosus* made a larger mound to modulate the environment inside the mound and to render it more comfortable in response to conditions outside the mound.

The bulk density of the mound walls varied from 1.5 to 1.7 g cm^{-3}. These values were closer to the values obtained for the surrounding subsoils (1.4–1.7 g cm^{-3})

Table 2 Selected physical and morphological characteristics of *Macrotermes bellicosus* mounds and surrounding pedons on a toposequence of the inland valley investigated in the present study

Part/horizon	Depth (cm)	Matrix color (Dry)	Consistence			Moisture (g kg^{-1})	BD (g cm^{-3})	PSD (%)			Texture[¶] (USDA)
								Sand	Silt	Clay	
Bottom mound											
External wall	—	10YR4.5/2	ss[†]	sp[‡]	eh[§]	16.7	1.5	60.5	29.9	9.6	SL
Internal wall	—	10YR7.5/2	ss	p	eh	42.6	1.6	56.9	30.8	12.3	SL
Hives	—	2.5Y5.5/2	ss	p	eh	—	—	51.3	33.5	15.3	L
Below nest	—	10YR5.5/2	ss	p	vh	77.1	—	52.3	32.8	14.9	SL
Bottom pedon											
Ap1	0–8	10YR5/2	ss	sp	l	23.7	1.4	65.3	29.0	5.8	SL
Ap2	8–19	10YR5.5/2	ss	sp	h	28.0	1.5	71.5	23.4	5.1	SL
Bwg1	19–37	10YR6/2	ss	sp	h	34.6	1.5	65.2	29.3	5.5	SL
Bwg2	37–58	10YR5.5/2	ss	sp	h	49.1	1.5	62.6	30.2	7.1	SL
Bwg3	58–80+	10YR4.5/2	ss	sp	h	112.9	1.4	64.9	28.6	6.5	SL
Fringe mound											
External wall	—	10YR4.5/2	s	p	eh	20.3	1.6	48.0	32.6	19.3	L
Internal wall	—	2.5Y4/2	s	vp	eh	62.0	—	35.4	37.1	27.5	CL
Hives	—	2.5Y4/2	s	vp	eh	74.6	—	35.9	36.9	27.2	CL
Royal chamber	—	2.5Y4/2	s	vp	eh	104.7	—	32.6	36.9	30.6	CL
Below nest	—	2.5Y5/3	ss	p	h	78.7	—	52.4	32.0	15.6	SL
Fringe pedon											
Ap1	0–10	10YR4.5/1.5	s	p	l	69.0	1.2	53.3	34.3	12.4	SL
Ap2	10–27	10YR4.5/2	ss	sp	h	58.6	1.5	58.0	31.2	10.7	SL
Btg1	27–45	10YR5/2	s	p	h	78.4	1.5	50.4	31.9	17.7	L
Btg2	45–71	10YR5/2	s	p	h	86.5	1.5	45.1	34.5	20.4	L
2Bwg	71–86	10YR6/2	ns	np	h	27.9	1.5	86.8	9.6	3.6	S
2BC	86–100+	10YR7/2.5	ns	np	h	83.4	1.7	88.2	11.4	0.4	S
Upland mound											
External wall	—	2.5YR3/6	ss	p	eh	9.2	1.7	66.1	11.4	22.5	SCL
Internal wall	—	2.5YR5/6	ss	p	eh	51.6	—	67.7	11.3	21.0	SCL
Hives	—	2.5YR3.5/6	s	p	eh	127.5	—	37.5	14.4	48.2	C
Royal chamber	—	2.5YR4/7	s	p	eh	135.4	—	35.7	16.1	48.2	C
Base-plate	—	2.5YR4/4	s	p	eh	125.3	—	37.0	16.5	46.5	C
Pillars	—	2.5YR4.5/6	ss	sp	eh	42.6	—	70.7	7.9	21.4	SCL
Upland pedon											
Ap1	0–7	5YR4.5/4	ss	sp	h	12.1	1.5	84.2	10.3	5.5	LS
Ap2	7–33	5YR4/3.5	ss	sp	vh	16.1	1.6	84.0	10.5	5.4	LS
Bw	33–62	2.5YR5/4	ss	p	eh	18.0	1.5	85.6	8.4	6.0	LS
Bt	62–120+	10R3.5/6	s	vp	eh	84.0	1.5	59.2	6.7	34.0	SCL

[†]Stickiness: ns, non-sticky; ss, slightly sticky; s, sticky. [‡]Plasticity: np, non-plastic; sp, slightly plastic; p, plastic; vp, very plastic. [§]Hardness: l, loose; s, soft, h, hard; vh, very hard; eh, extremely hard. [¶]C, clay; CL, clay loam; L, loam; LS, loamy sand; SCL, sandy clay loam; SL, sandy loam. BD, bulk density; PSD, particle-size distribution; —, not applicable or not determined.

than for the surrounding surface soils (1.2–1.5 g cm^{-3}). As indicated by the morphological features of the mounds, *M. bellicosus* packs soil grains very tightly by adding clay particles to soil material, which would increase the bulk density. Although only a limited number of reports are available that describe the bulk density of termite mounds, in most cases, termites increase the bulk density compared with the surrounding topsoils (Lobry de Bruyn and Conacher 1990; Ekundayo and Aghatise 1997). The magnitude of the modification of bulk density may depend on the termite species (Omo Malaka 1977).

The analysis of particle-size distribution revealed that the soils handled by *M. bellicosus* became more enriched in clay and more depleted in sand compared with the adjacent pedons. In addition, the mound soils had a slightly higher amount of silt than did the pedons. In particular, the clay and silt contents were found to be higher in the hives, royal chambers and base plate than in the other structures. This indicates that *M. bellicosus* selectively uses soil particles to respond to ecological requirements, such as the water-holding capacity (Jouquet *et al.* 2002), which was well demonstrated by the finer texture and greater moisture content in the nest body. According to our study and to an earlier report (Jouquet *et al.* 2004), the accumulated clay also plays a significant role in the structural stability of the termite mounds. In contrast, the particle-size distribution of the mound soils apparently reflects the soils around the mound. The M_U contained more clay and less sand than did M_B or M_F, corresponding to the particle-size distribution of the surrounding subsoils. This suggests that *M. bellicosus* used neighboring subsoils for mound construction.

Chemical properties

Selected chemical properties of the mounds and pedons are presented in Table 3. The total C contents of the mound constructions were less than that of the neighboring surface horizon at all toposequence positions, except for the internal wall of M_B, which had an exceptionally high C content. In general, organic C distribution in termite mounds is related to termite feeding habits and the type of materials used for nest building (Contour-Ansel *et al.* 2000; Fall *et al.* 2001; Sall *et al.* 2002). Fall *et al.* (2001) reported that fungus-growing *M. bellicosus* made use of saliva to get soil particles to adhere to one another, but did not affect the organic C content of the soil material, whereas soil-feeding *Cubitermes niokoloensis* incorporated feces into the soil material during mound construction, resulting in enrichment of organic C in the mound. This indicates that the organic C content in *M. bellicosus* mounds is a useful index for speculating about the soil material. The C content of the mound was similar to the subsurface soils rather than the surface horizons. This result is comparable to the results described in many previous studies (Hesse 1955; Lee and Wood 1971; Pomeroy 1976a) and supports the idea that *M. bellicosus* mainly uses subsoil material for mound building, as previously suggested by the particle-size distribution. There was no clear trend of difference in the Bray-1 P content between the mound and the pedon at all toposequence positions, although the internal walls and soil below the nest of M_B and the external wall of M_F did have a relatively higher Bray-1 P content than the corresponding pedon.

As stated previously regarding the organic C content, the P availability of mound soils is likely to be affected by termite feeding habit and the nature of the soil material (López-Hernández *et al.* 2006). *Macrotermes bellicosus* either does not affect or sometimes even decreases P availability in the mound soil in comparison with the adjacent surface soil (Ezenwa 1985; Lobry de Bruyn and Conacher 1990; López-Hernández *et al.* 2006) because *M. bellicosus* uses subsoils that usually contain less available P than the topsoil. In contrast to C and P, a relatively higher amount of total N was observed in some mound constructions compared with the pedon N contents at each toposequence position. As a result, the C/N ratio was generally found to be lower in the mound structures than in the pedon. These results are in agreement with the results of previous studies (Pomeroy 1976a; Fall *et al.* 2001). In particular, N enrichment was prominent in nest bodies, except for the hives of M_U. The nest body includes the royal cell, the most significant structure in which organic components ingested by the termites are stored and/or sequestered, resulting in relative N enrichment and a decreased soil C/N ratio in the mounds.

The pedon soils at the study site were generally acidic and low in EC. The mound soils generally had higher values of pH and EC than the neighboring pedon, corresponding to higher values of exchangeable bases. Exceptions were found in some horizons of P_F, which had relatively higher values of pH and EC and a higher number of exchangeable bases than M_F. These chemical properties of M_F, however, were somewhat different from those of normal pedons (Smaling *et al.* 1985; Oyediran 1990; Ishida 1998), which suggests anthropogenic contamination at the place where farmers take a break during their working day. Otherwise, the relationship between the mound and the adjacent pedon at the fringe shows the same trend as that at the valley bottom and upland sites. It is noteworthy that, among the exchangeable bases, the content of exchangeable K was markedly higher in the mound than in the pedon at all toposequence positions.

We also found that some mound structures contained relatively higher amounts of exchangeable Ca and Mg than the natural horizons, whereas there was no difference in exchangeable Na between the mounds and pedons. This indicates an accumulation of bases of biogenic origin, such as plant digestion and dead termites (Lobry de Bruyn and Conacher 1990). Clay increments can increase the nutrient-holding capacity of mound soils and allow them to have a higher ECEC value. The soil below the nest of M_B accumulated a substantial number of exchangeable bases; this result was also observed by Watson (1962). In contrast, M_F did not show much accumulation of exchangeable bases below the nest. This contradiction might be explained by different hydrological conditions, which were suggested by differences in the moisture content, which was lower in the upper horizons (Ap1, Ap2, Bwg1 and Bwg2) of P_B than in the upper horizons (Ap1, Ap2, Btg1 and Btg2) of P_F, and the presence of concretions (Bwg2 horizon of P_B) between these two pedons (Table 2). In contrast to higher pH and EC values and exchangeable bases in the mounds than the pedons, exchange acidity was lower in the former than in the latter. This might indicate that termite nest-building activity can ease soil acidification in the tropics.

Table 3 Selected chemical properties of *Macrotermesbellicosus* mounds and surrounding pedons on a toposequence of the inland valley investigated in the present study

Part/horizon	Depth (cm)	pH (H_2O)	EC (mS m^{-1})	Total C (g kg^{-1})	Total N (g kg^{-1})	C/N ratio	Bray-1 P (mg kg^{-1})	Exch. bases (cmol$_c$ kg^{-1})				Exch. acidity (cmol$_c$ kg^{-1})	ECEC (cmol$_c$ kg^{-1})
								Ca	Mg	K	Na		
Bottom mound													
External wall		5.9	3.2	5.3	0.52	10.3	9.7	1.41	0.32	0.38	0.31	0.17	2.60
Internal wall		6.5	6.7	13.5	1.19	11.3	17.0	4.62	1.20	0.42	0.39	0.11	6.74
Hives		6.2	3.1	7.6	0.85	8.9	6.0	2.31	0.43	0.75	0.28	0.15	3.93
Below nest		8.7	8.6	6.4	0.67	9.5	11.2	10.35	1.03	0.19	0.38		11.95
Bottom pedon													
Ap1	0–8	5.4	2.8	11.0	0.91	12.1	9.8	1.09	0.42	0.22	0.30	0.39	2.42
Ap2	8–19	5.7	1.9	5.2	0.48	10.8	6.3	0.42	0.12	0.14	0.47	0.48	1.63
Bwg1	19–37	6.3	1.3	3.3	0.34	9.7	8.9	0.70	0.12	0.12	0.49	0.18	1.61
Bwg2	37–58	6.5	1.7	3.5	0.34	10.4	4.4	1.48	0.17	0.14	0.33	0.13	2.25
Bwg3	58–80+	5.0	0.8	2.0	0.22	8.9	3.8	0.28	0.05	0.12	0.24	0.57	1.26
Fringe mound													
External wall		5.7	2.8	7.7	0.69	11.1	12.8	2.01	0.80	0.61	0.26	0.21	3.90
Internal wall		6.0	3.2	6.8	0.75	9.1	5.9	2.65	1.17	1.00	0.25	0.15	5.22
Hives		5.6	3.1	6.6	0.74	9.0	4.3	2.47	1.10	0.73	0.24	0.31	4.85
Royal chamber		5.7	2.3	6.6	0.77	8.6	5.1	2.69	1.12	0.83	0.26	0.33	5.23
Below nest		6.1	3.7	9.4	0.88	10.6	9.8	2.47	0.92	0.24	0.39	0.14	4.16
Fringe pedon													
Ap1	0–10	5.9	2.7	17.1	1.44	11.9	9.4	2.78	1.03	0.30	0.26	0.11	4.49
Ap2	10–27	6.1	2.8	9.6	0.83	11.6	6.7	2.31	0.82	0.21	0.28	0.10	3.71
Btg1	27–45	7.5	5.2	8.5	0.81	10.5	8.7	4.09	1.27	0.23	0.37		5.95
Btg2	45–71	7.3	4.3	6.4	0.65	9.9	9.1	4.68	1.55	0.23	0.35		6.80
2Bwg	71–86	5.1	1.5	2.6	0.25	10.4	6.7	0.29	0.13	0.13	0.26	0.31	1.13
2BC	86–100+	5.6	0.4	0.3	0.03	10.1	2.2	0.05	0.02	0.09	0.24	0.11	0.51
Upland mound													
External wall		7.6	5.2	6.5	0.60	10.8	4.3	2.30	0.88	0.47	0.24		3.90
Internal wall		6.9	1.8	4.8	0.41	11.8	3.3	1.50	0.68	0.50	0.26	0.08	3.03
Hives		6.7	5.0	6.7	0.43	15.4	2.7	1.54	1.03	1.39	0.23	0.12	4.32
Royal chamber		7.3	3.9	5.5	0.63	8.7	1.9	1.62	1.25	1.11	0.25		4.23
Base-plate		7.5	4.6	5.5	0.53	10.4	2.7	2.15	1.62	0.79	0.28		4.84
Pillars		7.6	4.7	5.1	0.40	12.7	3.6	2.00	0.90	0.51	0.25		3.66
Upland pedon													
Ap1	0–7	6.6	1.6	10.8	0.82	13.2	5.5	1.74	0.60	0.22	0.24	0.01	2.80
Ap2	7–33	6.6	1.0	4.4	0.30	14.6	3.7	0.98	0.47	0.16	0.25	0.07	1.93
Bw	33–62	6.4	0.6	2.1	0.15	14.0	8.1	0.48	0.33	0.13	0.24	0.08	1.27
Bt	62–120+	5.8	0.7	2.7	0.33	8.1	2.2	0.99	0.62	0.19	0.25	0.16	2.21

Conclusions

The present study investigated typical mounds constructed by *M. bellicosus* along a toposequence of an inland valley in central Nigeria. The mound soils were physicochemically and morphologically distinct from the soil material in surrounding pedons, although they still reflected the nature of the soil material (mainly subsoils) in the surrounding pedons. We found finer texture, higher EC, total N, exchangeable bases (Ca, Mg and K) and ECEC, but lower C/N ratio and exchange acidity in the mound than the pedon at each toposequence position. The elements of the nest body, that is, the hives, royal cells and base plate, which are the dwelling places of *M. bellicosus*, were modified more intensively than were the other mound structures, that is, the walls and pillars. These results suggest that *M.bellicosus* can create soil ecological patches (hot spots) at all toposequence positions in the same measure, and the impact of this species is substantially reduced in the lowlands compared with the uplands, as indicated by the number and volume of the mounds.

Ecological and environmental characterization of inland valley bottoms is becoming increasingly important because of their potential for agricultural use and intensification (Windmeijer and Andriesse 1993; Hirose and Wakatsuki 2002). In contrast, much less attention has been paid to the ecological traits of termites in the lowlands, regardless of their significant impact as ecosystem engineers in wetland ecosystems. Further research should be carried out to determine the influence of termites on soil characteristics in relation to vegetation distribution and water dynamics in the lowlands compared with the uplands. This approach would be useful to address the role of termites in sustainable agricultural development and environmental conservation in wetland ecosystems.

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