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Comparative distribution of organic matter in particle and aggregate size fractions in the mounds of termites with different feeding habits in Senegal: *Cubitermes niokoloensis* and *Macrotermes bellicosus*

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Abstract

The comparative distribution of organic components in different soil fractions as a result of the activities of two of the most representative species of termites (*Cubitermes niokoloensis* and *Macrotermes bellicosus*) in the semi-arid savanna of Senegal was assessed by physical fractionation. The impact of these two species on soil organic matter (SOM) differed. For the soil feeding *C. niokoloensis*, the internal and external wall of the mound contained five times higher carbon and 10 times higher nitrogen concentrations than the reference soil. In contrast, the mounds of the fungus-growing *M. bellicosus* had lower C content than the reference soil. Although both species select fine soil particles for mound construction, their strategy differs. Particle-size fractions finer than 50 μm represented 75% of the total mass of soil sampled from the internal and external walls of the mound of soil feeding termites, while clay size particles were the most abundant fraction of these compartments of the fungus growing mound. For the soil feeding species, the particle-size fractions contained 3–10 times higher C concentrations than the fractions isolated from the reference soil, the enrichment being the highest for clay fractions. About 60% of these clay particles remained aggregated within the coarser structures of the silt (2–50 μm) and the sand size particles (50–200 μm). The latter represented 60% of the total soil mass and contained 50% of the total carbon. No impact of *M. bellicosus* on soil aggregation was recorded.

These results clearly reveal the contrasting effects (positive for soil feeding, negative for fungus feeder) of these two species on SOM dynamics. The use of the aggregate fraction of the coarse silt size (20–50 μm) as an indicator of the activity of soil feeding termites is suggested. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Termite effects; Physical fractionation; Organic matter; Soil properties

1. Introduction

In tropical regions soil invertebrate macrofauna plays a key role in organic matter cycling (Lavelle, 1997; Lavelle et al., 1994). The invertebrate macrofauna is dominated by termites in terms of density. The impact of termites is mainly due to their building activity where the mounds represent the most spectacular biogenic structures. Organic components, digested by the termite during the gut transit, are stored and/or sequestered in these structures (Brauman et al., 2000). The mound density can be very high, with soil surface occupied by these structures corresponding with up to 10% of land area of the African

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continent (Lavelle, 1997). Therefore, termite mounds represent a major functional compartment of tropical soils. Despite this ecological importance, the impact of these biogenic structures on soil organic matter (SOM) remains poorly documented.

The mounds and their associated biogenic structures (galleries, sheeting, and fungus combs) have a significant impact on the physico-chemical features of the soil, such as the soil morphology, i.e. soil translocation and formation of subsurface horizons (Wood, 1988), the soil structure, i.e. aeration, porosity and structural stability (Garnier-Sillam, 1990; Garnier-Sillam et al., 1991), and chemical properties, i.e. enrichment in cations, P, and N (Lobry de Bruyn and Conacher, 1990). Although the impact on SOM has often been mentioned, very few studies have taken into account the importance of the various modes of mound construction resulting from different feeding habit. Amongst the two dominant African feeding habits (Wood, 1988), the fungus growing termites mix soil particles with their saliva to build their nests (Grassé, 1984), whereas nests of soil feeding termites are built with soil particles glued with their feces (Wood et al., 1983). Consequently, SOM content and soil structure differ between these two biogenic constructions (Wood, 1988). However, these studies were conducted considering the nest as a whole, without any consideration of possible heterogeneity within the nest (Garnier-Sillam and Harry, 1995). Different location of SOM within the nest compartments (external and internal wall) and its distribution within the particle-size fractions were not addressed. In fact, SOM cycling and microbial activity rely mostly on SOM location. Gupta and Germida (1988) reported a higher mineralization potential in aggregates >300 μm compared to those recorded in aggregates of a smaller size. Chotte et al. (1998) observed different turn-over rates for soil microorganisms depending on their location within the soil matrix.

There is an abundant literature dealing with the usefulness of physical soil fractionation methods for the characterization of SOM dynamics in relation to soil texture and structure (Christensen, 1992; Feller and Beare, 1997). Termites have a selective effect on SOM content and soil mineral particles (Anderson and Wood, 1984). The purpose of the present study was to describe and quantify the impact of the two most representative feeding habits observed in the tropical semi-arid region of Senegal (Sarr et al., 1998) on the distribution of organic components within the different particle-size and aggregate-size fractions. The study was conducted on two different compartments of the mound, reflecting possible different patterns of SOM dynamics within the mound (Fall et al., 1999). Particle and aggregate size fractions were obtained by two physical methods of soil fractionation (Gavinelli et al., 1995; Jocteur Monrozier et al., 1991). The impact of the feeding habits of termites on the dynamics of SOM and the roles of the mound's different compartments are discussed.

2. Material and methods

2.1. Site characteristics

The study was conducted in a field site located in the village of Sare Yorobana (12°49′N and 14°53′W) about 700 km south of Dakar. Over the past 20 years, annual rainfall has ranged between 570 and 1320 mm. The climate is tropical dry, with a unique rainy season from June to October. Slash-and-burn agriculture is carried out on the up-slope plateau. There are still large areas of woodland. Combretacea (mostly *Combretum geitonophyllum* Diels, *C. glutinosum* Pen.) form the major component of the woody vegetation. Bush fields are restricted to the edge of the plateau, with biennial groundnut millet crop rotation being the main practice.

The soil is described to as a ferruginous soil or a Lixisol (FAO, 1998).

2.2. Termite mounds

Two species constructing epigeal mounds that belong to the two most abundant feeding groups of termites (Sarr et al., 1998) were investigated in this area, i.e. *Cubitermes niokoloensis* (a soil feeding termite) and *Macrotermes bellicosus* (a fungus growing termite). Their mounds were sampled in a 10-year-old fallow. Each mound was separated into two different compartments: the external wall corresponding to the external layer and the internal wall corresponding to the internal part of the mound. For each mound, a reference soil sample, composed of 10 sub-samples pooled together, was taken at least 10 m away from the mound, from the 0–10 cm soil layer for the

Table 1
Physico-chemical characteristics of the two termites mounds

	Cubitermes niokoloensis			*Macrotermus bellicosus*		
	Internal wall	External wall	Reference soil	Internal wall	External wall	Reference soil
pH (water)	6.2	6.2	6.0	5.5	4	6.1
Texture (% dry soil)						
Coarse sand	9.6	9.0	66.1	10.5	32.7	48.5
Fine sand	10.7	9.8	17.6	18.5	19.5	21.0
Coarse silt	24.9	28.8	6.8	10.8	8.8	9.7
Fine silt	27.1	25.4	3.6	8.7	5.3	8.3
Clay	23.7	22.8	5.8	48.5	31.8	13.1

Cubitermes mound and from the 0–20 cm layer for the *Macrotermes* mound. The soils were stored air dried and kept at 4°C pending analysis. The characteristics of these mounds are shown in Table 1.

2.3. Particle-size fractionation

A sub-sample (equivalent to 30 g oven-dried soil) was taken from each compartment. The soil was fractionated according to the procedure described by Gavinelli et al. (1995). Briefly, the soil was suspended in distilled water (200 ml) for 16 h in the presence of sodium hexametaphosphate (40 g l^{-1} final concentration). The soil was rolled end-over-end (50 rpm) for 2 h with five agate marbles. The suspension was successively sieved to yield coarse and fine sand-size fractions (>200 and 50–200 μm, respectively), and the coarse silt fraction (20–50 μm). Particles of 2–20 μm were separated from the clay-size fraction (<2 μm) by sedimentation. The 0–2 μm fraction was concentrated by centrifugation (2500 × *g* for 10 min) and the addition of $CaCl_2$ (0.1 M final concentration). The fractions were oven dried (at 60°C for 2 days). Three replicates of each mound's distinct compartment were processed. The fractionation schedule required 5 days for a complete set of six samples.

2.4. Aggregate-size fractionation

The procedure is very similar to the previous one except for the dispersion and shaking processes. No chemical (sodium hexametaphosphate) was used and the soil sub-samples were rolled for 16 h in order to disrupt macro-aggregates (Jocteur Monrozier et al., 1991). Similarly, the procedure resulted in five aggregate-size fractions (>200, 50–200, 20–50, 2–20 and 0–2 μm).

2.5. Soil texture

The mass of the fractions obtained by these procedures was compared to that of the same fractions isolated by mechanical analyses, that is after total destruction of SOM with hydrogen peroxide and the total dispersion of mineral particles in a NH_4Cl solution (1 M concentration). The mineral particles were isolated by the same sieving and sedimentation procedure.

2.6. C and N determination

Sub-samples of unfractionated soils and fractions were thoroughly grounded to 200 μm. Total carbon and nitrogen were determined by the Walkey and Black, and Kjeldhal methods, respectively (Bremner, 1965).

3. Results and discussion

Physical fractionation is a powerful tool to characterize the relationship between the SOM and the soil matrix (Christensen, 1992). Of the two different approaches used in the present study, one aims at the entire dispersion of the mineral particles to reach a mass distribution of particle-size fractions similar to that obtained by mechanical analysis (Christensen, 1992), while in the second approach the energy

involved in the procedure is meant to limit the disaggregation and the dispersion of soil particles. This method has been used to evaluate the distribution and the stability of organo-mineral aggregates (Henin et al., 1958). These two approaches are complementary, particle-size fractionation giving access to the "primary organo-mineral complex", aggregate size fractionation giving access to "secondary organo-mineral complex" (Christensen, 1992; Feller et al., 1996). Results obtained from both approaches are discussed here, complementing the information on total carbon content.

3.1. Organic matter content in the different compartments

The results of carbon and nitrogen content analysis (Table 2) indicated that the mound of the soil feeding termite, *C. niokoloensis*, was outstanding in the level of its organic matter enrichment. The concentrations of carbon and nitrogen in the internal and external wall of the mound were, respectively, 5–10 times higher than those of the reference soil. In contrast, carbon and nitrogen contents in the compartments of the *M. bellicosus* mound were similar or slightly lower (for the internal wall) than those of the reference soil (Table 2). The impact of the two termite species on the organic matter concentration of their mounds varied greatly according to the origin of the construction materials. Soil feeding termites build their mound with their very rich feces (Garnier-Sillam and Harry, 1995). In contrast, deeply sampled soil material, mixed with saliva, is used by the fungus feeders, and their feces contribute only to mound construction to a very limited extent (Grassé, 1984). These results confirm prior studies (Anderson and Wood, 1984; Garnier-Sillam and Harry, 1995). However, the assumption that soil feeding termites have a positive impact on the concentration of organic compounds within their mounds should be taken with caution (Garnier-Sillam and Harry, 1995). This effect relies very much upon the quality of the surrounding soil. In rich forest soils, no or slight differences were noticed, while significant increases were recorded for mounds built from poor savanna soils (Anderson and Wood, 1984). While our results confirm those in the literature, the difference between the C content of the reference soil and the mound of *C. niokoloensis* is the highest ever documented. According to Anderson and Wood (1984), such nutrient enrichment reveals the capacity of soil feeding termites to select organic particles from a poor medium. This capacity may be responsible for the geographical distribution of different soil feeding termites species, along with SOM richness (Yapi, 1991). However other authors deny the possibility of such a level of selection (Bignell et al., 1980).

This enrichment in the mound of *C. niokoloensis* seems also to affect the C/N ratio, being lower for SOM of the internal and external wall (12 and 16, respectively) than that of the reference soil (24). This change in the SOM quality may have resulted from a higher activity of soil microorganisms, which were particularly abundant in that mound compartment (Fall et al., 1999). For the fungus feeding species, the C/N ratios were generally lower in both compartments, as a result of the very important contribution of clay particles to their construction (Garnier-Sillam and Harry, 1995).

3.2. Particle-size fractions

3.2.1. Mass distribution

The total mass of the particle-size fractions amounted close to 100%, indicating that no loss occurred during the fractionation procedure. For each compartment, the mass distribution of the particle-size

Table 2
Carbon and nitrogen concentration in the soil of the two termite mounds (mean of three replicates ± standard error)

Compartments	*Cubitermes niokoloensis*			*Macrotermus bellicosus*		
	Total C ($mg\,C\,g^{-1}$ soil)	Total N ($mg\,N\,g^{-1}$ soil)	C/N	Total C ($mg\,C\,g^{-1}$ soil)	Total N ($mg\,N\,g^{-1}$ soil)	C/N
Internal wall	37.7 ± 0.6	3.1 ± 0.2	12	4.9 ± 0.1	0.6 ± 0.1	8
External wall	40.3 ± 0.5	2.5 ± 0.2	16	6.0 ± 0.2	0.6 ± 0.2	10
Reference soil	7.1 ± 0.5	0.3 ± 0.1	24	7.0 ± 0.2	0.7 ± 0.1	10

Table 3
Mass distribution, carbon concentration and C/N ratio of the particle-size fractions (mean of three replicates ± standard error)

	Cubitermes niokoloensis				*Macrotermes bellicosus*			
		Carbon				Carbon		
	Mass g 100 g^{-1} soil	mg C g^{-1} fraction	% of Ct[a]	C/N	Mass g 100 g^{-1} soil	mg C g^{-1} fraction	% of Ct[a]	C/N
Internal wall (μm)								
>200	11.37 ± 1.13	41.5 ± 1.25	12.5	33	10.56 ± 1.03	0.3 ± 0.20	0.7	nd
50–200	11.12 ± 1.21	45.5 ± 1.03	13.4	12	20.18 ± 1.07	0.4 ± 0.14	1.6	51
20–50	26.10 ± 1.53	18.7 ± 0.85	13.0	12	11.65 ± 1.41	1.5 ± 0.35	3.7	22
2–20	25.50 ± 1.16	35.3 ± 0.90	23.9	13	7.24 ± 1.14	5.4 ± 0.20	7.1	13
0–2	25.90 ± 1.02	49.3 ± 0.59	33.9	9	50.37 ± 0.91	8.6 ± 0.82	88.4	10
Recovery (%)	100		97		100		102	
External wall (μm)								
>200	10.46 ± 1.80	61.6 ± 1.06	16.0	18	34.26 ± 1.39	2.4 ± 1.05	13.7	16
50–200	11.52 ± 1.54	23.0 ± 0.99	6.6	15	19.77 ± 0.82	2.7 ± 0.48	8.7	18
20–50	27.13 ± 1.53	18.9 ± 0.56	12.7	18	8.2 ± 0.87	4.8 ± 0.76	6.5	10
2–20	26.13 ± 1.52	51.0 ± 1.03	33.1	13	4.39 ± 1.28	13.2 ± 1.31	9.6	11
0–2	24.72 ± 1.41	48.9 ± 1.10	30.1	10	33.37 ± 1.30	10.7 ± 1.46	59.1	9
Recovery (%)	100		99		100		98	
Reference soil (μm)								
>200	67.17 ± 1.44	4.1 ± 1.36	38.9	nd	50.37 ± 1.65	2.3 ± 0.41	17.0	18
50–200	16.22 ± 1.25	3.0 ± 1.03	7.0	51	20.7 ± 0.73	4.1 ± 0.79	12.4	15
20–50	6.31 ± 1.61	5.5 ± 0.90	4.9	22	8.69 ± 1.54	2.6 ± 0.55	3.3	18
2–20	3.95 ± 0.95	21.3 ± 0.58	12.0	13	6.98 ± 1.31	8.8 ± 0.33	9.0	13
0–2	6.41 ± 1.30	35.8 ± 0.66	32.3	10	13.45 ± 1.64	26.9 ± 0.75	53.1	10
Recovery (%)	96		95		100		95	

[a] Calculated as ((fraction mass × C mg g^{-1})/(C total of unfractionated soil)).

fractions was not different from that obtained by the mechanical analysis (Tables 1 and 3).

The mass distribution of the particles isolated from the two compartments of the two mounds differed significantly (ANOVA, $P < 0.05$) from that of the fractions obtained in the reference soil (Table 3). For the soil feeding termites, the clay and the coarse size fractions represented about 25 and 10% of the total soil mass, respectively, whereas they amounted to 5 and 70% of the total mass of the reference soil, respectively. Although a similar pattern was recorded for *M. bellicosus*, the concentration of clays and coarse sands varied between the two compartments. These differences in the mass distribution of the particle-size fractions confirmed the selective impact of termites on the material used for their construction (Wood, 1988; Garnier-Sillam and Harry, 1995). Nonetheless, the selection pattern was restricted to clays for the fungus-growing termites, whereas it affected the fractions <50 μm for the soil feeding termites. This may be explained by the various particle sampling strategies developed by these two species. Soil feeding termites explore the superficial soil layer near the mound (Anderson and Wood, 1984). In contrast, deeper soils and a wider zone around the construction (10–20 m) are subject to the influence of fungus growing termites (Wood, 1988). Thus, fungus growing termites sharply affect soil texture and structural stability over a large zone, while the influence of soil feeding termites is restricted to the surroundings of the mound, which results in less damage to soil properties (Anderson and Wood, 1984; Garnier-Sillam, 1990). However, this conclusion may be reconsidered considering the high density of the mounds of soil feeding termites and the fact that most of these species are subterranean termites (Grassé, 1984).

3.2.2. C concentrations

The sum of organic C amounts in the particle-size fractions was close to 100% (from 95 to 103%). Any loss of the organic components was recorded (Table 3).

For the soil feeding termites, the C concentrations (mg C g^{-1} fraction) of the different particle-size fractions were higher than those of the fractions isolated from the reference soil (Table 3). The difference was particularly high for the fractions >50 μm, which showed a C concentration 10 times higher than that in the reference soil. However, C concentrations of particle-size fractions, expressed as a percentage of the unfractionated soil C, indicated that about 70% of the total C was associated with the finer fractions (0–50 μm) in the internal wall. In contrast, these fractions concentrated 50% of the total C of the reference soil (Table 3). This result confirms the hypothesis that the protection of organic matter induced by the soil feeding termites originates from the increase in the percentage and amount of the organic matter bound to the clay particles (Garnier-Sillam and Harry, 1995).

Values of C/N ratio varied (from 9 to 51) between the compartments and the particle-size fractions. The highest differences between fractions were recorded in the fractions >50 μm. These variations in organic quality and quantity within the fractions isolated from the mound of *C. niokoloensis* cannot be attributed solely to the mechanism of substrate selection (Anderson and Wood, 1984; Garnier-Sillam and Harry, 1995). It is likely that they can be partially explained by the profound transformation of the ingested organic matter during gut transit. A drastic chemical environment, which characterizes the soil feeding gut transit (Brune, 1998) leads to the extraction of the humic components from the mineral soil matrix, followed by their dissolution and their partial biodegradation by the digestive microorganisms (Kappler and Brune, 1999). Therefore, microbial biomass and metabolites could replace hydrosoluble components and/or organic matter with high C/N ratio present in the ingested material (Kappler and Brune, 1999). In the feces, these components are bound to the clay particles in organo-mineral complexes, and are therefore protected from further biodegradation (Garnier-Sillam, 1990).

In contrast to the soil feeding termites, the C concentrations of the fractions separated from the mounds of the fungus growing termites were lower than that of the corresponding fractions obtained from the reference soil. This was particularly obvious for the >50 μm fractions, where the C contents were 7.5 to 10 times lower than those in the reference soil. This result shows depletion (internal wall) or relative stability (external wall) of carbon concentrations in the particle-size fractions compared to those from the reference soil. The SOM decrease can be attributed either to the selection of soil material sampled in deep and poor soil layers, or to the partial degradation of organic substrates by the termite enzymatic salivary secretions (Rouland et al., 1988).

3.3. Aggregate-size fractions

3.3.1. Mass distribution

No loss occurred during the fractionation procedure since the sum of the mass of the aggregate-size fraction amounted to 100% (Table 4). The contribution of the different aggregate size fractions to the total soil mass differed sharply between the two mounds and their compartments. The comparative distribution of the fractions isolated by the two fractionation procedures revealed that the mass distribution of the aggregate-size fractions differed from that of the particle-size fractions (Tables 3 and 4). The mass of the aggregate-size fractions 20–50 and 50–200 μm in the internal wall of the soil feeding termites' mound were higher than those of the corresponding particle-size fractions, while the opposite was the case for the clay size fraction. This fraction isolated by the aggregate fractionation procedure (10.3 g 100 g^{-1}, Table 4), accounted at most for 40% of the clay mineral particles (25.9 g 100 g^{-1}, Table 3). Therefore, 60% of these particles remained associated with larger aggregates (i.e. the 20–50 and 50–200 μm fractions), the gain in mass of these fractions corresponding to the mass of non-dispersed clays. No significant impact of the two methods was observed on the mass of the >200 and 2–20 μm fractions. In contrast to the internal wall, the non-dispersed clays (15.9 g 100 g^{-1} soil, Table 5) of the external compartment contribute to all other fractions. However, this contribution was bimodally distributed in the fine and coarse-sand size fractions (+8.8 and +3.5 g 100 g^{-1} soil, respectively, Table 5). For the reference soil, the extent to which the fractionation procedure affected the mass distribution of the fractions was less than that for the mound materials. Nevertheless, the mass of the 2–20 and 50–200 μm fractions estimated by aggregate fractionation, increased slightly, while that of the clay size decreased by almost 5%. For the fungus growing termites, the results between the

Table 4
Mass distribution, carbon concentration and C/N ratio of the aggregate-size fractions (mean of three replicates ± standard error)

	Cubitermes niokoloensis				*Macrotermes bellicosus*			
		Carbon				Carbon		
	Mass g 100 g^{-1} soil	mg g^{-1} fraction	% of Ct[a]	C/N	Mass g 100 g^{-1} soil	mg g^{-1} fraction	% of Ct[a]	C/N
Internal wall (μm)								
>200	11.8 ± 1.08	46.7 ± 1.67	14.6	29	9.7 ± 1.4	0.6 ± 0.19	1.2	11
50–200	18.7 ± 0.93	39.9 ± 1.49	19.9	12	19.0 ± 1.1	1.2 ± 0.27	4.8	12
20–50	33.8 ± 1.19	24.4 ± 0.89	21.9	13	11.9 ± 1.4	2.3 ± 0.48	5.6	12
2–20	25.4 ± 1.14	35.1 ± 1.21	23.7	17	15.9 ± 1.0	6.8 ± 0.24	22.3	16
0–2	10.3 ± 1.45	61.7 ± 0.50	16.9	7	43.5 ± 0.7	7.4 ± 1.31	66.1	8
Recovery (%)	100		99.8		100.0		99.8	
External wall (μm)								
>200	13.0 ± 1.41	36.9 ± 1.48	12.8	22	33.3 ± 0.9	1.9 ± 1.1	10.7	11
50–200	20.3 ± 1.44	44.8	22.6	18	19.9 ± 1.5	2.0 ± 0.9	6.7	12
20–50	28.7 ± 1.23	29.0	20.7	16	8.9 ± 0.6	6.3 ± 0.7	9.3	12
2–20	28.1 ± 1.08	44.4 ± 1.57	31.0	17	7.3 ± 1.2	19.1 ± 07	28.0	16
0–2	8.9 ± 0.99	55.8 ± 1.20	12.3	12	30.6 ± 1.3	8.3 ± 1.5	42.3	8
Recovery (%)	99		96.9		99.9		96.9	
Reference soil (μm)								
>200	67.9 ± 1.51	4.1 ± 1.36	39.4	51	49.6 ± 1.1	2.5 ± 0.66	18.3	12
50–200	18.2 ± 1.20	3.0 ± 1.03	13.2	36	20.8 ± 1.4	3.0 ± 0.76	9.2	11
20–50	6.6 ± 1.10	5.5 ± 0.90	8.2	23	10.8 ± 1.0	5.0 ± 0.62	7.9	12
2–20	5.6 ± 1.34	21.3 ± 0.58	25.6	15	8.3 ± 0.9	12.8 ± 1.37	17.6	14
0–2	1.6 ± 0.51	35.8 ± 0.66	8.3	12	10.6 ± 1.4	26.9 ± 0.64	42.0	12
Recovery (%)	99.9		95.1		100.0		95.1	

[a] Calculated as ((fraction mass × C mg g^{-1})/(C total of unfractionated soil)).

different soil fractionation procedures did not reveal any significant difference for the compartments.

3.3.2. C concentration

No loss of organic C occurred after soil fractionation (96 to 99.8% of C recovery, Table 4). In the *C. niokoloensis* mound, the C concentration (mg C g^{-1} fraction) of each aggregate-size fraction was higher than that of the reference soil (Table 4). The difference was particularly obvious for the 20–50 and 50–200 μm fractions, where the C concentration was, respectively, 4.5 and 13 times higher in the internal wall than that in the same aggregate size fractions obtained from the reference soil.

For the fungus growing termites, all aggregate fractions, except for the 2–20 μm of the external wall, showed lower C concentrations than those in the reference soil. Regardless of the origin of the soil, most of the C expressed as a percentage of the total soil C, was concentrated in the fractions <20 μm (i.e. 2–20 and 0–2 μm). The general C distribution within aggregate-size fractions was similar in the two compartments of the soil feeding termite mound. Carbon associated with the aggregate-size fractions <2 and >200 μm amounted, respectively, to 66 and 1% of the total C in the internal wall, and 42 and 10% of the total C in the external wall.

For the soil feeding termite mound, values of the C/N ratio in the aggregate fractions of the mound compartments were at most equal to those of the reference soil. No difference in C/N ratio was recorded for the fungus growing termites.

It is possible to calculate the quantity of material kept aggregated in structures of larger size by comparing the C concentrations of the fractions obtained with the two procedures (Table 5). This calculation concerned only the soil feeding termites, as for the fungus growing species, no significant difference was recorded in term of mass distribution between the two fractionation procedures (Tables 3 and 4). The

Table 5
Differences (aggregate-size fractions–particle-size fractions) in the mass and carbon concentrations within the fractions isolated from the different compartments of a *C. niokoloensis* mound[a]

Compartments	Fraction (μm)	Mass[b]	Carbon	
		g 100 g^{-1} soil	mg 100 g^{-1} soil[c]	mg g^{-1} fraction[d]
Internal wall	>200	0.4	0.7	1.8
	50–200	7.6	2.4	0.3
	20–50	7.7	3.4	0.4
	2–20	−0.1	−0.1	0.8
	0–2	−15.6	−6.4	0.4
External wall	>200	3.5	−3.2	n.c.
	50–200	8.8	16.0	0.7
	20–50	1.6	8.0	2.0
	2–20	1.9	−2.1	n.c.
	0–2	−15.9	−17.8	0.4
Reference soil	>200	−0.8	0.5	n.c.
	50–200	2.0	6.2	0.04
	20–50	0.3	3.3	0.03
	2–20	1.6	13.6	0.21
	0–2	−4.8	−24.3	0.36

[a] ASF: aggregate size fraction; PSF: particle-size fraction; n.c.: not calculable.
[b] Calculated as (ΔMass = mass of ASF − mass of PSF).
[c] A calculated as [ΔC = ((mass of ASF × C mg g^{-1})/100) − ((mass of PSF × C mg g^{-1})/100)].
[d] ΔC/ΔMass.

comparison of carbon concentration in clay fractions clearly indicated that the clay should not be considered as a homogeneous entity. For the internal wall, C concentration obtained after the total dispersion represented 49 mg C g^{-1} fraction, while after the less disruptive method it amounted to 61 mg C g^{-1}, the difference being significant (ANOVA, $P < 0.05$). For the other compartments, the differences were less pronounced, being nil for the reference soil. For the internal wall, carbon associated with the non dispersed clay particles amounted to 6.4 mg C 100 g^{-1} soil, representing (Table 5) almost 20% of the C of the unfractionated soil (Table 2). The C concentration of this non-dispersed material (0.4 mg C g^{-1} fraction) was very similar to the concentration of the fraction responsible for gain of mass of the aggregate-size 20–50 and 50–200 μm. Therefore, these fractions were likely to be composed of aggregated clays. As for the internal and external walls, the C associated with the non-dispersed material accounted for 20% of the C of the unfractionated soil. Moreover, its C concentration was similar to that recorded for the internal wall (0.4 mg C g^{-1} fraction). Nevertheless, some difference might be pointed out. While a direct transfer of non-dispersed material to aggregate-fraction might be hypothesized for the internal wall, no direct relationship between the C concentration of the non-dispersed clay particles and that of the material gained by the other fractions could be identified for the external wall (Table 5). Therefore, it is likely that clay particles of that compartment are confined to fine aggregates (2–50 μm) and that the 50–200 μm aggregates might have resulted from the association of particles of the silt size. This different model in aggregate hierarchy (Oades and Waters, 1991) might be explained by different turn-over patterns of organic components responsible for the stability of the aggregates (Hassink, 1997). These two different fractionation procedures allow us to distinguish an interesting characteristic of the termite aggregation pattern. Compared to the reference soil, soil feeding termites seemed likely to be responsible for the formation of aggregates of the coarse-silt size (i.e. 20–50 μm). This result, which needs to be confirmed for other species, could indicates that the 20–50 μm aggregates could serve as a "signature" of soil feeding termite activity in soil, as already pointed out by Eschenbrenner (1986).

4. Conclusions

This comparative study based on two complementary fractionation procedures yielded useful insights on the impact of tropical termites on SOM. This work provides the first evidence at the fraction level, of the negative impact of a fungus growing termite species on SOM. These termites depleted SOM content accumulated within their mounds and had little effect on soil structure. Conversely, soil-feeding termites tended to concentrate SOM in each particle-size fraction of their mounds. This study confirmed that a significant part of SOM (60%) is protected from active mineralization due to its distribution within the fine soil fractions. The differential physical fractionation approaches provided for the first time evidence for an aggregate size fraction (20–50 μm) specific for soil feeding species constructions. This result remains to be confirmed for other species in order to determine whether this aggregate could be used as an indication of soil feeding termite activity in tropical soils. The SOM enrichment of the mound soil may indicate that this structure should not be considered as just a termite shelter. The ecological significance of soil feeding termite mounds in terms of termite nutrition and SOM cycling are currently under investigation.

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