Modulated Effect of the Termite *Ancistrotermes cavithorax* (Isoptera, Macrotermitinae) on Soil Properties According to the Internal Mound Structures

by

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ABSTRACT

Structures built by fungus-growing (Isoptera, Macrotermitinae) termites could be considered as an extended phenotype linked to the optimization of a climatic homeostasis and to a better protection against predators. Most of the literature regarding the impact of termites on soil properties refers to termite epigeous mounds. In spite of their abundance in African savannas, few studies deal with the properties of underground fungus-comb chambers and galleries. In this study we compare the physical and chemical properties of fungus-comb chamber wall and interconnecting gallery wall from *Ancistrotermes cavithorax* and relate these properties to the termite ecological requirements (soil structural stability and moisture regime).

The termite workers increased the proportion of fine particles and the soil organic matter content in their constructions, as compared to the control soil. No difference was observed in C content between nest and gallery walls, but the nitrogen content was greater in the chamber wall. C:N ratio also decreased significantly from control soil to gallery wall and to chamber wall. These changes could help explain the increase in structural stability of the termite modified soil material. Soil water retention was also improved in termite constructions, and exhibited its greatest values in the chamber wall.

Both termite constructions, chamber and gallery walls were very stable. Therefore, we suggested that both types of construction increased the protection against environmental hazards, such as dryness and water flow, and indirectly against predators. Despite similar data in fine particles and carbon content, chamber wall was a better buffer than the gallery wall for maintaining adequate moisture within

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the nest. We concluded that termite building activities vary according to the type of structure edified.

Key words: Termites, Macrotermitinae, building activity, soil properties, biological requirements

INTRODUCTION

In tropical savannas, two main termite feeding groups are recognized: "soil-feeders" and "litter-feeders" (Lavelle *et al.* 1997, Bignell & Eggleton 2000). Among the litter-feeder group, the Macrotermitinae subfamily is of particular interest because of its specialized exo-symbiosis with the fungus *Termitomyces*. This termite-fungus relationship has resulted in the evolution of unique features in environmental microclimatic regulation within the nest (Noirot & Darlington 2000). Macrotermitinae achieve control over the microclimate of their nest by adapting nest architecture (Noirot & Darlington 2000). Such structures are the main facilitator of the role of Macroterminae as ecosystem engineers (Dangerfield *et al.* 1998). It has been suggested that the structures built by termites could be considered as extended phenotype (Dawkins 1982). The nest architecture and the properties of the soils modified by termites are supposed to optimize the climatic homeostasis for both the colony and the exosymbiotic fungus, and to protect the colonies against predators (Collins 1977, Lepage 1983, Noirot & Darlington 2000). Recently, Korb and Linsenmair (1998a,b, 2000) showed that *Macrotermes bellicosus* modifies the architecture of its epigeous nests according to environmental conditions, in order to ensure a constant temperature within the nest. The results suggest that fungus-growing termites are able to modulate their buildings depending on their ecological requirements.

Jouquet *et al.* (2002) evidenced that the subterranean fungus-growing termites *Odontotermes* nr. *pauperans* supplied more or less organic matter and selected more or less fine particles according to the purpose for which the constructions were intended. In their paper, Jouquet *et al.* (2002) differentiated two types of structures: the foraging galleries and the fungus-comb chamber walls. The galleries are temporary structures utilized for exploring the outside environment while the chamber walls are perennial structures protecting the colony and ensuring the maintenance of an adequate moisture regime for the termite-fungus symbiosis.

The influence of fungus-growing termites on soil properties is usually related to the impact of epigeous mound material and few studies have investigated the impact of below-ground structures, such as fungus-comb chambers and galleries. However, these structures probably play a significant role in the functioning of many tropical ecosystems. Josens (1971) observed that the density of fungus-comb chambers in a Guinean savanna can reach a density of 10.2 units m^{-2}. Abbadie and Lepage (1989) suggested that the underground galleries interconnecting such nest units or the galleries connected to the above-ground foraging area could certainly play a major, but unknown, role in the ecosystem.

Comparative studies of the properties of underground nest structures and connecting galleries of fungus-growing termites are very rare. The aim of this study, therefore, is to assess whether the fungus-growing termite workers could modulate soil material properties according to the structures they built, either nest wall chambers or galleries. Physical and chemical properties of both structures are compared and related to some of the ecological requirements (moisture requirements and protection against predators) of Macrotermitinae termites.

METHODS AND MATERIALS

Study site and species studied

Termite materials were collected at the Lamto Ecological Station in Côte d'Ivoire (West Africa, 6°13' N, 5°02' W), at the margin of the rain forest (Menaut and César 1979), in the Guinean bioclimatic zone (rainfall ≈ 1200mm.yr-1). The species chosen, *Ancistrotermes cavithorax,* is one of the dominant Macrotermitinae species in the Lamto savanna ecosystem (Josens 1977). This species builds underground nests consisting of several fungus-comb chambers and elaborates connecting galleries plus galleries connecting the fungus-comb chambers to forage zones on the soil surface (Abbadie *et al.* 1992, Josens 1977). Both the fungus-comb chamber walls and the galleries were collected and their physical and chemical properties compared to surrounding soil without visible termite activity (the control). Nests were excavated to approximately 20-30 cm deep and chamber wall material was collected in addition to galleries from the same depth. In the laboratory, the finer reddish material covering the inner layer of the chamber wall and galleries was carefully separated from the rest of the chamber wall and gallery material (described in Abbadie & Lepage 1989) and its properties analyzed.

Measurements

Soil structural stability was determined according to the Le Bissonnais (1996) test. The resistance of soil aggregates to water is measured using three methods, each having a different treatment for altering the structural stability of 3- to 5- mm soil aggregates: (1) a breakdown test (fast wetting), (2) a slow capillary restoration test (slow wetting) and (3) a desegregation test (mechanical breakdown). Results are expressed by the Mean Weight Diameter (MWD) as an estimate of the structural stability. A higher MWD implies stronger cohesive forces between the soil particles resulting in a more stable structure. Eighteen replicate measurements were conducted on each type of soil (control, gallery and chamber wall).

Particle size analysis on four replicates of each type of soil was determined after sieving and weighing (AFNOR, NFX 31107): 2000-200 µm (coarse sands), 200-50 µm (fine sands), 50-20 µm (coarse silts), 20-2 µm (fine silts) and 2-0 µm (clays).

The percentage total organic C and N and the C:N ratio of nine replicates of each soil was measured with an elemental analyzer (NA 1500 Series 2, Fisons).

The kinetics of soil water retention was determined after rising the soil to the maximum water holding capacity and then heating at 105°C. Samples were weighed each 15 mn during 105 mn and water content was determined at each time (Jouquet *et al.* 2002). Measurements were replicated 12 times.

Statistical analyses

Statistical analyses were carried out using Statistica for Windows. Differences of means between soils were tested by analysis of variance and subsequent post hoc comparisons (Tukey HSD test). The comparison of the water-loss kinetics was tested using a covariance analysis with time as covariant. All tests were performed at the 0.05 significance level.

RESULTS

Stability

All three methods gave similar results (Table 1). Therefore, we present the mean of the three treatments for each type of soil (control, gallery and chamber wall) (Fig. 1). No significant difference occurred between the two types of termite structures (P=0.916), which showed better structural stability than the control soil (P< 0.001). Results are 0.46 (Standard Error, SE: 0.04), 2.67 (SE: 0.39) and 2.57 (SE: 0.59) mm, respectively for the control soil, the chamber wall and the gallery.

Texture

The proportion of clay, silt and sand are shown in Table 2. The percentage of clay, fine and coarse silts were significantly greater in the termite structures (P< 0.001), with no statistical difference between them (P> 0.05). Termite constructions had a greater proportion of finer particles (more than 30% clays and fine silts) than the control soil (16.3 %).

Carbon content and C:N ratio

Termite activity has resulted in a significant increase in the C and N contents of their structures (Table 3). The carbon concentration was similar between gallery and chamber walls (P= 0.789) while nitrogen content in the chamber wall was significantly greater than in the gallery (P= 0.020). Results of the C:N ratio are shown in the same table. Soils could be ranked according to the C:N ratio as follows: control > gallery > chamber wall (P< 0.05).

Kinetics of water retention

Whatever the type of structures, the soil handled by termites exhibited a better water holding capacity (Fig. 2) (P< 0.001). In

Table 1. Results of the 2-way ANOVA on the effect of the factors 'soil' and 'treatment' on MWD values.

	df	MS effect	F	P level
Soil (1)	2	29.10	49.39	< 0.001
Treatment (2)	2	1.15	1.94	0.151
Interaction (1×2)	4	0.19	0.32	0.860

Table 2. Textures of the different soils: control soil, gallery and chamber walls. (n = 4, standard error in brackets).

	clay	fine silts	coarse silts	fine sands	coarse sands
Control	9.3 (SE: 0.3)	7.0 (SE: 0.3)	5.0 (SE: 0.4)	19.2 (SE: 1.5)	59.6 (SE: 1.7)
Gallery wall	22.0 (SE: 0.6)	10.7 (SE: 0.1)	9.1 (SE: 0.6)	25.8 (SE: 0.5)	32.4 (SE: 0.5)
Chamber wall	22.4 (SE: 3.1)	9.9 (SE: 1.3)	8.3 (SE: 0.8)	23.1 (SE: 1.4)	36.4 (SE: 5.8)

Table 3. C, N content and C:N ratio in the control soil, gallery and chamber walls. (n = 9, standard error in brackets).

	C (mg g^{-1} soil)	N ($\times 10^{-2}$ mg g^{-1} soil)	C:N
Control	0.63 (SE: 0.03)	3.5 (SE: 0.2)	17.8 (SE: 0.7)
Gallery wall	0.79 (SE: 0.01)	5.8 (SE: 0.2)	13.7 (SE: 0.2)
Chamber wall	0.79 (SE: 0.05)	6.6 (SE: 0.6)	12.2 (SE: 0.7)

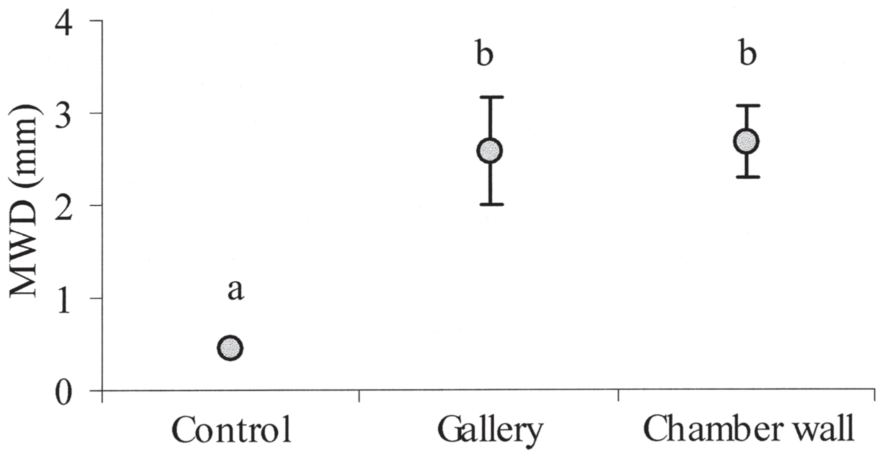

Fig. 1. Soil aggregate stability was assessed using the MWD index (mm). Samples were control soil (in white), gallery (in grey) and chamber wall (in black). Standard errors are represented as vertical bar (n=18); histograms with the same letter are not different at *P*=0.05.

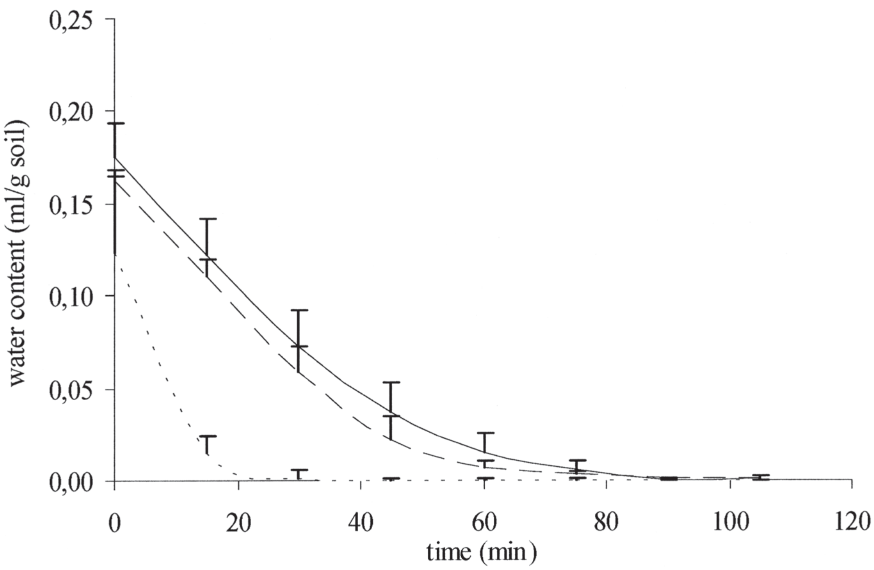

Fig. 2. Kinetics of water retention for the different soils: control soil (dashed line), gallery (broken line) and chamber wall (solid line). Standard errors are represented as vertical bar (n=12).

comparison, the control soil looses all its water content in the first 30 mn, while the soil handled by termites looses its water after 90 mn. Over the time of the experiment, the water content was always significantly greater in the chamber wall than in the gallery wall (P< 0.001).

DISCUSSION

Soil properties

Fungus-growing termite nest structures are often enriched in fine particles (Arshad 1981, Bagine 1984, Holt & Lepage, 2000) as also recorded in the present study. Soil from Macrotermes spp. mounds has a lower soil organic matter (SOM) content than the surrounding control soil (Garnier-Sillam *et al.* 1988, 1991, Brauman *et al.* 2000). However, our study showed that structures built by the subterranean fungus-growing termite Ancistrotermes contained greater amounts of SOM than the surrounding soil. This result is in accordance with Abbadie and Lepage (1989), working on the same species. *Ancistrotermes cavithorax* selected in the same way soil particles for building chamber walls and connecting galleries. The quantity of organic carbon incorporated was also similar in both types of structures. But the quality of the organic matter differed between the chamber and gallery walls, as expressed by the C:N ratios, it was lesser for the chamber wall compared to the gallery wall.

On the other hand, soil aggregates from Macrotermitinae termite nests are usually considered to have a low structural stability. Contour-Ansel *et al.* (2000) found respectively a value of MWD = 0.32 mm for *Macrotermes subhyalinus* mound soil and MWD = 0.19 mm for the control surrounding soil. Using the same test (Le Bissonnais 1996) with *Ancistrotermes cavithorax,* we found MWD values almost 6 times higher in the termite structures than in the surrounding soil (Fig. 1). Consequently, *Ancistrotermes cavithorax* structures are much more stable than the control soil. This illustrates differences in soil properties between *Macrotermes* sp. and *Ancistrotermes cavithorax* and emphasizes the necessity to take into account differences in biology between termite species (epigeous or underground nests, concentrated or diffuse nests) to determine more precisely their role in the ecosystem, as stressed by Lavelle *et al.* (1997).

Soil modifications as related to the termite ecological requirements

Moisture is one of the main environmental parameters termites need to control (Korb & Linsenmair 1998a,b, 2000). Jouquet *et al.* (2002) demonstrated that soil utilized to protect the fungus-comb of a related species, *Odontotermes* near pauperans, had a better buffering effect for maintaining a suitable relative humidity than the soil utilized to built the foraging galleries. Also, the gallery material collected was different: in the laboratory experiment, the soil for running galleries on the surface was clearly different from the soil utilized to built the fungus-comb chamber while in the field, the underground gallery structures, with the interior covered by a fine layer of reddish soil material, were similar to the interior of the fungus-comb chamber (Josens 1972, Abbadie & Lepage 1989). The present results indicated that the soils (chamber and gallery walls) handled by the termite *Ancistrotermes cavithorax* had a better water-holding capacity than the control soil and thus improved the soil capacity to buffer the moisture within the termite nest even if the surrounding soil was dry. The wall of the fungus-comb chamber was more effective in holding water, and thus in the protection against temporary dryness, than the wall of the connecting gallery. Since, the two constructions had the same texture, the increase of the soil water retention was probably caused by the change in SOM quality (Chenu *et al.* 2000). This result is consistent with those obtained by Jouquet *et al.* (2002) in laboratory controlled conditions, where termites can adjust the quantity and quality of organic matter supplied according to the type of structure.

According to the classification of Le Bissonnais and Le Souder (1995), the control soil is "very unstable" whereas soil aggregates rehandled by termites were "very stable"., i.e. were more firmly bound together. A higher structural stability may confer a better protection for the colony against environmental hazards, such as water flows in soil. As Noirot and Darlington (2000) postulated, termite constructions can also be seen as shelters against predators. By improving soil structural stability, termites effectively limit the rate of soil weathering. In addition, the enhancement of the cohesive forces between soil particles can impede the burrowing activities of subterranean invertebrate predators such as ants.

These differences between chamber and gallery walls could be partially explained by their role in termite biology. Fungus-comb chambers are more or less permanent structures over time for maintaining suitable climatic conditions within the nest and protecting the symbiotic fungus and the termites, whereas galleries are more temporary structures utilized for travelling between the nest chambers and for foraging the outside environment. Therefore, termites can adjust the quantity of organic matter supplied in the structure edified according to their requirements.

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