

Properties and functional impact of termite sheetings

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Abstract Termites are considered soil engineers and key bioturbators in tropical and subtropical soils. A large number of studies have described the specific properties of the above-ground mounds that termites construct to protect their colonies from environmental hazards. However, there is a paucity of information on properties of soil sheetings; more temporary but often extensive structures are covering over or inserted within substrates on the ground such as leaves and woody materials or components of arboreal runways. Such sheetings are conspicuously produced not only by the Macrotermitinae but also by many other unrelated taxa. Here, we review the available literature and discuss (i) the relationship between rainfall and soil sheeting production and (ii) how termites affect the clay and C contents in soil sheetings. This reveals that sheeting production is highly variable and site specific. We also found that soil sheetings are always enriched in clay, but their impacts on soil C content are variable and related to the C content of the parent soil and to the quality of the substrates consumed by termites.

Keywords Termites · Soil sheeting · Soil engineers · Bioturbation · Carbon and clay

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Introduction

Soil bioturbation is the process in which soil aggregates are modified and/or displaced in the soil profile by soil fauna (Wilkinson et al. 2009; Bottinelli et al. 2015). This process is of primary importance in the soil system (sensu Ponge 2015) because it regulates key ecological functions such as nutrient cycling, infiltration and diffusion of water in soil, resistance of soil to erosion, and quality of runoff water (Jones et al. 2006; Ali et al. 2013). In many tropical soils, bioturbation is mainly carried out by termites and, to a lesser extent, by earthworms, ants, or beetles (Lavelle 1997; Bignell 2006; Jouquet et al. 2016c).

As bioturbators, termites mediate soil properties at different spatial and temporal scales, which range from modifying clay mineralogy, driving aggregate dynamics, and inducing physical stability to enhancing and sustaining porosity at the profile scale and generating nutrient-rich patches at landscape level (e.g., Hedde et al. 2005; Jouquet et al. 2011, 2016b; Bonachela et al. 2015). Most termite activity occurs below ground and involves the creation of subterranean nests and galleries (Holt and Lepage 2000). At the soil surface, termite activity leads to the production or epigeal structures such as mounds, and soil sheetings covering prospective substrates for consumption. But, while there is abundant bibliography describing the specific biological, physical, and chemical properties of termite mound soils compared to the surrounding environment (e.g. Holt and Lepage 2000; Jouquet et al. 2011, 2016a), much less information is available on the properties of soil sheetings. For instance, the number of articles identified by ISI Web of Science on 09 May 2017 was 731 for termite mounds as a keyword, 137 for termitaria and just 24 for soil sheetings. Sheetings are soil aggregates which have been partially or extensively reconstituted by termites and have different physical, chemical, and microbial properties

compared to the surrounding environments (Lamoureux and O’kane 2012). The sheetings cover the organic materials the termites are consuming, and recent studies also suggest that their properties vary with the type of substrates being eaten (Diouf et al. 2005, 2006a, b; Jouquet et al. 2015; Harit et al. 2017). Regarding the ecological importance of soil sheetings for termites and their potential impact on soil dynamics, a contemporary dedicated review describing the influence of termites on the properties of soil sheetings and the impact of these biogenic structures (sensu Bullock et al. 1985) on ecosystem functioning is now therefore appropriate. Using the literature available from various sources such as the Web of Science, Scopus, and unpublished data from several PhD theses from the University of Agricultural Science (UAS GKVK, Bangalore, India), the aim of this article was therefore to review the impact of termites on soil surface properties when they produce soil sheetings. We also discuss the potential impact of these structures on soil and ecosystem functioning.

Soil sheeting production: why, where and who?

The ecological needs of termites and their impact on soil functioning are two closely related concepts (Jouquet et al. 2016c). This close dependence between termite fitness and soil properties is stressed by the “extended phenotype engineering” concept (Jones et al. 1994) which states that termites are “intended engineers” (in contrast to “accidental engineers”) that modify the soil properties with purpose according to their ecological needs (Turner 2004; Jouquet et al. 2006). Although understanding how and why termites produce soil sheetings seems to be a simple question, it is however far from trivial. From an ecological point of view, the translocation of soil and the formation of sheetings by termites can be seen as a huge investment in terms of energy. In this context, why should termites spend so much energy producing soil sheetings? To date, three different scenarios have been suggested. First, termites are weak and relatively fragile invertebrates and sheetings are used for protection against predators and desiccation (Bagine 1984; Jouquet et al. 2002, 2015; Oberst et al. 2016; Kaiser et al. 2017). Second, termites produce sheetings when they excavate soil to construct belowground galleries and nest chambers (Harit et al. 2017). Finally, filling stems or logs with soil is a way to support the weight of plants, and thus avoid that they collapse while being eaten (Oberst et al. 2016).

In total, 29 articles were found which specifically studied termite sheetings (Table 1). Most of these studies were carried out in Africa (13), followed by Asia (6) and America and Australia (2 for each), whereas only one reported study was from Europe. Sheetings are generally constructed on dry grass, leaf litter, wooden logs and twigs, bark on living trees, and also on animal dung pads. Since termite sheetings are, by definition, covering organic substrates on the ground, it is unsurprising to see that most studies on sheetings have

Table 1 List of studies on soil sheetings and referenced in the Web of science, Scopus, and unpublished data from several PhD theses from the University of Agricultural Science (UAS GKVK, Bangalore, India)

| References | Termite species (functional group) | Location | Habitat |
|-------------------------|---|-------------------------|------------------------------|
| Kaiser et al. (2017) | <i>Odontotermes</i> sp. ^a , <i>Macrotermes</i> sp. ^a , <i>Trinervitermes</i> sp. ^b (FGT) | Burkina Faso, Africa | Sub-sahel zone |
| Harit et al. (2017) | <i>Hypotermes obscuriceps</i> ^a (FGT) | India | Laboratory |
| Oberst et al. (2016) | <i>Coptotermes acinaciformis</i> ^c (WFT) | Canberra, Australia | Laboratory |
| Jouquet et al. (2015) | <i>Odontotermes feae</i> ^a and <i>Odontotermes obesus</i> ^a (FGT) | India | Natural forest |
| Kihara et al. (2015) | – | Nyabeda, Kenya, Africa | Subhumid |
| Vlieghe et al. (2015) | <i>Psammotermes allocerus</i> ^d (GFT) | Namibia, Africa | Nature desert |
| Jouquet et al. (2012) | Unknown sp. (FGT) | Vietnam | Grassland |
| Killgore et al. (2009) | Unknown sp. | Mexico, USA | Chihuahuan Desert, Grassland |
| Villenave et al. (2009) | <i>Ancistrotermes guineensis</i> ^a , <i>Odontotermes nilensis</i> ^a , <i>Macrotermes subhyalinus</i> ^a (FGT) | Senegal, Africa | Savanna |
| Jouquet et al. (2007) | <i>Pseudacanthotermes spiniger</i> ^a (FGT) | France | Laboratory |
| Diouf et al. (2006a) | <i>Macrotermes subhyalinus</i> ^a , <i>Odontotermes nilensis</i> ^a , <i>Ancistrotermes guineensis</i> ^a (FGT) | Senegal, Africa | Sahelian savannah |
| Mora et al. (2006) | <i>Odontotermes nilensis</i> ^a , <i>Ancistrotermes guineensis</i> ^a (FGT) | Senegal, Africa | Mango orchard |
| Mora et al. (2005) | <i>Spinitermes</i> sp. ^e , <i>Ruptitermes</i> sp. ^f . (SFT) | Colombia, South America | Savanna |
| Diouf et al. (2005) | <i>Ancistrotermes guineensis</i> ^a , <i>Macrotermes subhyalinus</i> ^a , <i>Odontotermes nilensis</i> ^a (FGT) | Senegal, Africa | Savanna |
| Ndiaye et al. (2004) | <i>Macrotermes subhyalinus</i> ^a , <i>Odontotermes nilensis</i> ^a (FGT) | Senegal, Africa | Semi-arid savanna |
| Rouland et al. (2003) | <i>Macrotermes subhyalinus</i> ^a , <i>Odontotermes nilensis</i> ^a , | Senegal, Africa | Semi-arid savanna |

Table 1 (continued)

| References | Termite species (functional group) | Location | Habitat |
|------------------------------|---|---------------------------|---------------------------------|
| Mora et al. (2003) | <i>Ancistrotermes guineensis</i> ^a , <i>Microtermes</i> sp ^a (FGT) <i>Odontotermes nilensis</i> ^a , <i>Ancistrotermes guineensis</i> ^a (FGT) | Senegal, Africa | Mango orchard |
| Mando and Brussaard (1999) | <i>Odontotermes smeathmani</i> ^a , <i>Microtermes lepidus</i> ^a (FGT) | Burkina Faso, Africa | Sahelian-Sudanian |
| Mando and Miedema (1997) | <i>Odontotermes smeathmani</i> ^a , <i>Microtermes lepidus</i> ^a (FGT) | Burkina Faso, Africa | Sahelian-Sudanian |
| Debruyne and Conacher (1995) | <i>Amitermes neogermanus</i> ^c , <i>Tumulitermes</i> sp ^b (WFT) | Australia | Durokoppin Reserve and Farmland |
| Kumar (1991) | <i>Odontotermes</i> spp ^a (FGT) | India | Green house |
| Kalidash (1986) | <i>Odontotermes</i> spp ^a (FGT) | India | Farmland |
| Basappa (1984) | <i>Odontotermes</i> spp ^a (FGT) | India | Farmland |
| Bagine (1984) | <i>Odontotermes latericius</i> ^a , <i>O. boranicus</i> ^a (FGT) | Northern Kenya, Africa | Arid shrub land area |

FGT fungus-growing termites, WFT wood feeding termites, SFT soil feeding termite and GFT grass feeding termite

^a Termitidae, Macrotermitinae

^b Termitidae, Nasutitermitinae

^c Rhinotermitidae, Coptotermitinae

^d Rhinotermitinae, Psammotermitinae

^e Termitidae, Termitinae

^f Termitidae, Apicotermitinae

focused on litter-feeding termites (Table 1). Indeed, from the 21 species identified, most belonged to the fungus-growing termite subfamily (Termitinae, Macrotermitinae). Only two studies have focused on lower termites, *Coptotermes acinaciformis* and *Psammotermes allocerus* (Rhinotermitidae, see Table 1). Thus, there is clearly a lack of information on how the other termite families influence soil dynamics when they produce soil sheetings.

Soil sheeting production and properties

Sheetings are temporary structures, removed by rain and the activities of other animals, including potential predators of termites. Consequently, and despite the fact that the sheetings contain much less soil than termite-nest structures, their turnover is quicker and their impact on ecosystem functioning can be considered to be more important in terms of soil and

nutrient dynamics. The rate of soil translocation obviously varies from species to species and according to the soil type and climatic conditions. For example, several studies suggest that termites produce more sheetings during the dry season than during the rainy season (Mora et al. 2006; Kaiser et al. 2017). Similarly, Bagine (1984) stated that soil sheeting production decreased with increasing rainfall amounts or, in other words, that termites have a more pronounced effect on soil dynamics in drier and hotter habitats than in more humid environments because termite activity does not depend on soil moisture, which is not the case of earthworms and microbes (Lavelle 1997). However, this assumption is contradicted by the absence of a linear relationship ($R^2 = 0.18$, $P = 0.285$) between rainfall level and sheeting production obtained from the limited number of articles ($n = 8$) which measured the annual soil sheeting production rate (Fig. 1). Conversely, this distribution rather suggests a peak of production in environments with ~ 500 mm year⁻¹ and a rather low production before and after. Although our conclusion should be considered carefully due to the low number of data points, Fig. 1 shows that the amount of soil translocated in the form of soil sheeting is highly variable and site specific, in addition to be highly seasonal. In Africa, 300 to 4000 kg soil ha⁻¹ year⁻¹ are translocated on the ground in the form of sheetings (Lepage 1974; Wood and Sands 1978; Aloni et al. 1983; Bagine 1984; Kooyman and Onck 1987). In Senegal, Rouland et al. (2003) reported a quantity of soil sheetings of nearly 47,000 kg ha⁻¹ after 5 months, while Mando (1997) measured 3900 kg soil ha⁻¹ in Burkina Faso within 2 weeks. In the Chihuahu desert (North America), Mackay and Whitford (1988) reported up to 2600 kg ha⁻¹ year⁻¹.

The source of soil that termites use to produce sheetings appears to be the top centimeter of the profile, where foraging galleries are also most commonly found (Diouf et al. 2006a; Jouquet et al. 2015; Harit et al. 2017). The properties of soil sheetings vary depending on the species, type of feed, and soil type (Lee and Wood 1971; Konaté et al. 1999; Grohmann 2010). The C and clay content are the two variables most commonly used to characterize sheetings, but these are very variable, even within the same termite species. For example, although some studies found higher clay and C contents in termite sheeting than in the control surrounding soil (Bagine 1984; Basappa 1984; Kalidash 1986; Nutting et al. 1987; Ndiaye et al. 2004; Harit et al. 2017), others reported less C in sheetings than the control soil (Kumar 1991; Mora et al. 2003; Jouquet et al. 2007, 2015). Figure 2 shows that these contrasting findings can be explained by a logarithmic relationship between the C content in the sheetings and the surrounding soil ($y = 0.27 \log(x) + 0.95$, $n = 23$, $R^2 = 0.23$, $P = 0.022$). Indeed, Fig. 2 shows that, in soil with a low C content, termite sheetings are slightly enriched in C whereas they are impoverished in C in soil with a higher C content. The logarithmic regression suggests that this threshold value is

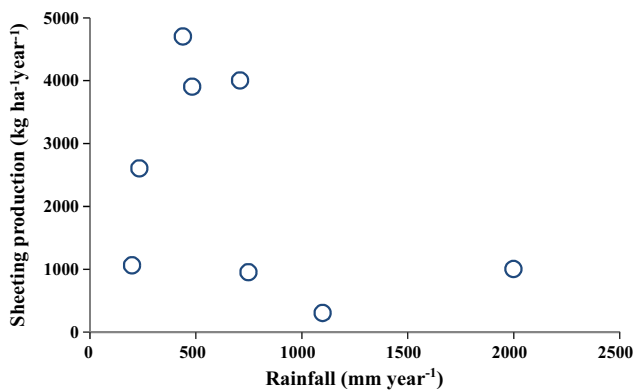


Fig. 1 Termite sheeting production (in kg ha⁻¹ year⁻¹) according to the annual rainfall amount (mm year⁻¹) ($n = 8$)

reached for soils with approximately 1% C. A significant enrichment in clay content was also measured in termite sheetings compared to the surrounding soil environment (Fig. 3). The enrichment in clay followed a linear regression with values always above the bisecting line ($y = 1.41x + 4.07$, $n = 16$, $R^2 = 0.80$, $P < 0.001$). Consequently, although more data is clearly needed to confirm these results, they suggest that termites have a different impact on the clay and C contents in their constructions depending on the soil. While in poor soils termites tend to enrich their sheetings in C and decrease their C content in soil with C content $> 1\%$, they are always enriched in clay compared to the surrounding surface soil.

The ratio of C or clay contents in soil sheetings to the C or clay contents in the surrounding soil provides information about the strategy termites use to cover their food (Fig. 4). In this example, *Odontotermes nilensis*, *O. wallonensis*, *O. horni*, *O. obesus*, and *Hypotermes obscuriceps* (all fungus-growing termite species) have a direct impact on these ratios (data obtained from Basappa 1984; Kalidash 1986; Kumar 1991; Mora et al. 2003; Ndiaye et al. 2004; Harit et al. 2017). Interestingly, a linear relationship was obtained from *O. nilensis*, which increases the C content the most in

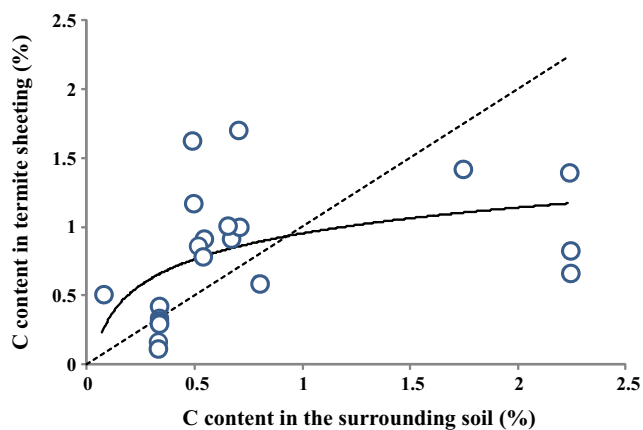


Fig. 2 C content (%) in termite sheetings and the surrounding soil environment. The logarithmic regression is shown ($n = 32$). The dashed line corresponds to the bisecting line ($y = x$)

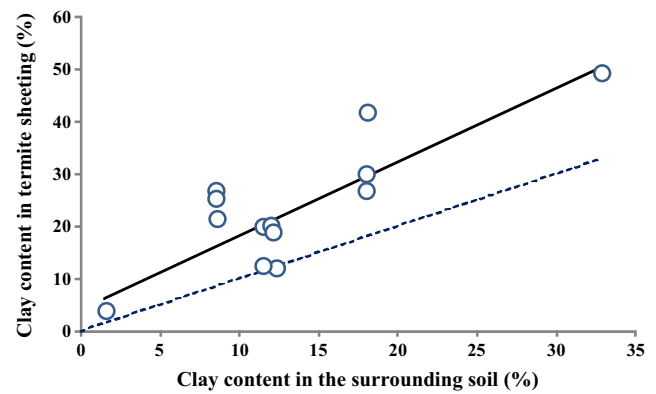


Fig. 3 Clay content (%) in termite sheetings and the surrounding soil environment. The linear regression is shown ($n = 16$). The dashed line corresponds to the bisecting line ($y = x$)

soil (highest $C_{\text{sheeting}}:C_{\text{soil}}$) and has the smallest impact on the soil clay content ($\text{Clay}_{\text{sheeting}}:\text{Clay}_{\text{soil}} \sim 1$). On the contrary, *O. obesus* reduces the soil C content but enriches the soil the most with clay (highest $\text{Clay}_{\text{sheeting}}:\text{Clay}_{\text{soil}}$ value). Therefore, these results suggest a gradient from species enriching soil sheetings with clay particles to species that do not modify soil texture but incorporate organic matter in the form of saliva and/or organic residues, most likely for ensuring their stability and resistance to environmental hazards.

Similarly, the influence of the substrate quality on sheeting properties was reviewed from 16 articles. Organic substrates were grouped into five categories, namely manure, straw, fallen log on the ground, bark, and wood from living trees (Fig. 5). Non-parametric statistical analysis (pairwise comparisons using a Wilcoxon rank sum test) failed to show an influence of the substrate quality on clay enrichment in termite sheetings (ratio of clay content in sheeting to the clay content in soil, $P > 0.05$). In contrast, a significant impact of the substrate

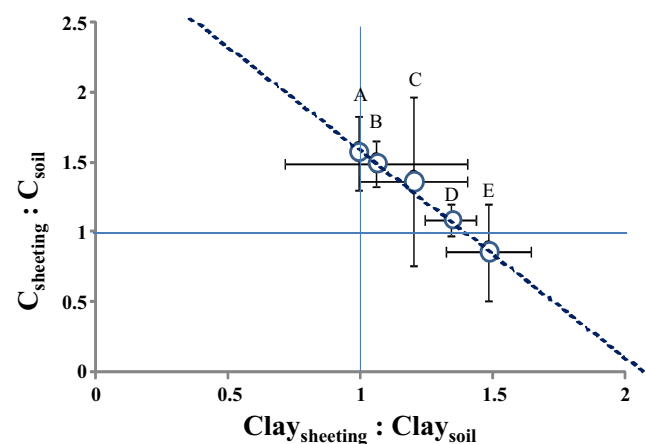


Fig. 4 Relationship between the ratios of the C and clay contents in termite sheetings and the control surrounding environments ($C_{\text{sheeting}}:C_{\text{soil}}$ and $\text{Clay}_{\text{sheeting}}:\text{Clay}_{\text{soil}}$) for different fungus-growing termite species: *Odontotermes nilensis* (A), *Hypotermes obscuriceps* (B), *O. wallonensis* (C), *O. horni* (D), and *O. obesus* (E). The linear regression is shown

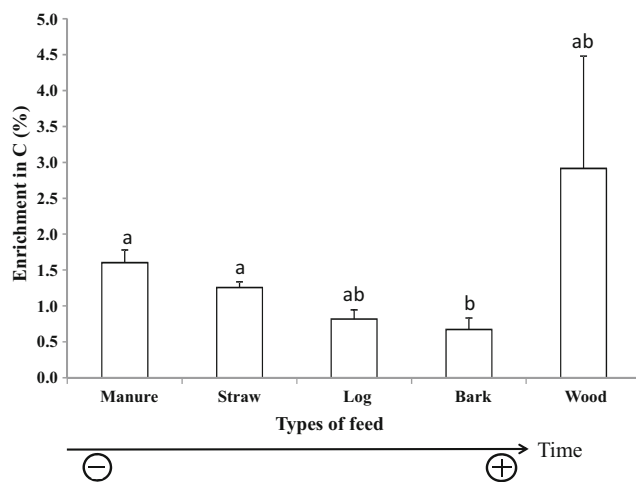


Fig. 5 Enrichment in C (percentage of the C content in the surrounding soil to the C content in the termite sheeting) for different types of food resources (manure, straw, log, bark, and wood). The arrow represents the time needed for termites to consume the different substrates, from rapidly consumed manure substrates to slowly consumed bark and wood substrates

Histograms with similar letters are not significantly different at $P = 0.05$.

quality on C enrichment was observed in sheetings (ratio of C content in sheeting to the C content in soil, $P = 0.009$). The higher enrichment in C was measured in the sheetings that covered the manure and straw substrates ($P > 0.05$ between both), and the lowest values were measured in sheetings covering the bark ($P < 0.05$). Intermediate values were measured for sheetings that covered the log substrates ($P > 0.05$ in all cases). Although it is possible that foreign particles from the substrates were glued with the termite saliva during the molding of sheetings, especially in the case of dung and straw materials, these results suggest that termites incorporate more C within their sheetings when they cover more fibrous and less compact substrates (dung > straw > log > bark). Finally, the C content in the wood was very high but it varied considerably making it difficult to distinguish this substrate from the others ($P > 0.05$ in all cases). Unfortunately, further information about the tree species and their properties (e.g., wood density and C:N ratio) are not available and we could not test whether this high variability is due to the diversity of trees and the quality of their wood.

The redistribution of termite sheetings on the ground is likely to influence the properties of the soil surface, such as their resistance to erosion and water infiltration rate (Jouquet et al. 2012). The higher clay and C content in sheetings may also contribute to improve soil fertility, especially in sandy soils with low C and nutrient contents, while their erosion can be associated with a significant loss of nutrients in water runoff (Mando 1997; Mando and Stroosnijder 1999; Léonard and Rajot 2001; Kaschuk et al. 2006; Jouquet et al. 2012; Harit et al. 2017). As evidenced by several authors, the accumulation of sheetings over time can also contribute to

the formation of stone lines in Africa and Australia (Nye 1955; Watson 1960; Williams 1968; Lee and Wood 1971). However, as yet, the importance of termites in stone line formation has never been specifically investigated and more research is therefore clearly needed for determining how the rain and animal trampling impact soil sheetings lifetime and then soil functioning.

Conclusion

The importance of soil sheetings in soil dynamics is highly variable but this review showed that there are both general patterns as well as key questions that remain to be studied. Termite sheetings clearly have different C and clay contents in comparison with the surrounding topsoil. However, more research is clearly needed to determine if a relationship exists between sheeting production and pedoclimatic conditions. We also showed that the clay content in sheetings is directly related to the clay content in the surrounding topsoil. On the other hand, the C content follows a logarithmic regression, leading to either an enrichment or impoverishment in C compared to the surrounding environment.

The influence of sheetings on soil functioning remains also poorly studied, especially compared to termite mounds which have received a lot of attention. For example, the lifetime and fate of termite sheetings, as well as the fate of their specific microbial populations and how they impact soil nutrient cycling, soil erosion, and soil profile, are unknown and should be the subject of further research.

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