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Nematodes, indicators of the origin of the soil used by termites to construct biostructures

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Summary

In Sahelian savannas, fungus-growing termites form biogenic structures made of soil or sheetings, on the soil surface and inside the soil, to protect themselves against heat, desiccation and predators while collecting food. The purpose of this study was to determine if analysis of the nematofauna can show differences in the way termites construct sheetings according to termite species or organic material harvested. In this study, soil nematodes, which were inactive during the experiment, were passively transported in soil pellets by termites when they built sheetings. Composition of the soil nematofauna was analyzed in sheetings produced when harvesting the four different types of different organic matter and in the soil around which these structures were produced. Three of the four organic materials were applied on soil as mulch whereas wood logs were inserted in the soil. Nematode density and diversity in sheetings produced by the three different termite species present (*Ancistrotermes guineensis*, *Ondontotermes nilensis* and *Macrotermes subhyalinus)* were similar in the four organic treatments except for sheetings constructed within the wood by *A. guineensis*. Nematode densities in sheetings were about ten-fold lower than in the 0–10 cm upper soil layer. Moreover, the composition of the nematofauna in sheetings was very different from that of the upper 10 cm, except for the sheetings built on wood. A finer comparison of the soil nematofauna in the top 7 cm of soil (separated in 0–0.25, 0.25–3.0 and 3.0–7.5 cm), and of fresh surface sheetings (produced within 24 h) showed that nematode composition of sheetings was very similar to that of the soil in the superficial strata (0–3 cm).
Analysis of the nematofauna led us to conclude that the soil used by termites to construct biogenic structures when harvesting organic matter originates from soil layers as close as possible to the area where the organic resource is located.

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Moreover, there were no differences in the soil or the three type of surface-applied organic matter used for the three fungus-growing termites.
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Introduction

In tropical areas, termites and earthworms are the main actors in soil functioning (Lavelle and Spain, 2001) and influence physico-chemical properties such as structure (Gutierrez and Jones, 2006; Jouquet et al., 2007), carbon and nitrogen cycles (Barrios, 2007). This impact is mainly the result of the soil differentiation induced by their building activities. Due to their large size, most of the studies concerning the biogenic structures built by termites, focus on the above-ground nest (Holt and Lepage, 2000). However, in dry areas like the Sahelian savannas, mound-building and subterranean termites that forage on the soil surface construct extensive protective soil sheetings in order to shield themselves against heat, desiccation and predators. Sheetings are made of soil pellets moistened with termite saliva that are deposited onto or inside plant materials. This behaviour involves the transport of soil to the surface thereby increasing the total amount of soil translocated by termites activities (Holt and Lepage, 2000). In fact, the net contribution of surface sheetings to soil translocation may, in many situations exceed the contribution of mound construction. The amount of soil moved by fungus-growing termites for the construction of this type of biostructure can be substantial, reaching 950 kg to 47 t ha^{-1} to in Senegal (Lepage, 1974; Rouland et al., 2003), or 2600 kg ha^{-1} in a Chihuahuan desert ecosystem (Brown and Whitford, 2003). Thus, soil sheetings represent one of the most significant types of biogenic structures constructed by ''ecological engineers'' (Jones et al., 1994). Because of the low resistance of crop sheetings to erosion, they are more rapidly recycled than termite nests and consequently can have a more immediate effect on soil processes. Despite their ecological importance, studies on soil sheeting built by termites remain sparse. Previous studies done in the Senegal dry savanna, demonstrated that, compared with the surrounding soil, (sampled between 0 and 20 cm) sheetings were slightly enriched in organic matter (C, N, phenol and proteins) while their physical characteristics were not significantly different (Mora et al., 2003). Soil sheeting characteristics also differ among various termite species. Ndiaye et al. (2004) reported a significant increase of ammonium in soil sheeting of only one termite species (*Macrotermes subhyalinus*) resulting presumably from an inhibition of nitrification in this species. Like Bagine (1984), this author hypothesised that these differences between soil sheetings within various termite species originated from their methods to build structures. Therefore, the aim of this work is to test this hypothesis using the nematodes structures as soil bio-indicators.

Nematodes have thus been used as soil indicators for the last decade (Freckman and Ettema, 1993; Bongers and Ferris, 1999; Yeates, 2003). These properties arise from different nematode specificities including (i) their abundance in soil – nematodes are the most abundant metazoa in soils, with densities of up to 3 million individuals m^{-2}, and soil assemblages are diverse, with up to 200 species found at some sites (Ettema, 1998; Neher, 2001) – and (ii) their functional diversity – nematodes belong to several trophic levels, namely, plant feeders, bacterial feeders, fungal feeders, omnivores and predators (Yeates et al., 1993). Interestingly species composition of nematode assemblages in a soil sample reflect the influence of agricultural practices such as use of mineral or organic fertilizers and anthropogenic disturbances (Bongers and Ferris, 1999). In Senegal, the nematode fauna is abundant and diverse throughout the year (Pate et al., 2000; Villenave et al., 2001). Nematodes mostly survive during the dry season in a state of anhydrobiosis and are reactivated very rapidly when soil humidity increases.

The purpose of this study was to determine if the comparison of the nematofauna of sheetings and soils can show differences in the way termites construct sheetings and whether organic material harvested by termites can help in understanding their mode of construction. In this study, soil nematodes, which were inactive at the time of the experiment, were used as ''inert'' components of the soil. They were passively transported in soil pellets by termites when they built sheetings.

Materials and methods

Study site and soil sampling

Initial study

Experimental plots were established at the Ecole Nationale Supérieure d'Agriculture (ENSA) of Thiès

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