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Influence of soil pedological properties on termite mound stability

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ABSTRACT

This study investigated the influence of soil properties on the density and shape of epigeous fungus-growing termite nests in a dry deciduous forest in Karnataka, India. In this environment, *Odontotermes obesus* produces cathedral shaped mounds. Their density, shape (height and volume) and soil physicochemical properties were analyzed in ferralsol and vertisol environments. No significant difference was observed in *O. obesus* mound density ($n = 2.7$ mound ha^{-1} on average in the vertisol and ferralsol areas). This study also showed that *O. obesus* has a limited effect on soil physical properties. No differences in soil particle size, pH, or the C:N ratio and base saturation were measured whereas the C and N contents were reduced and CEC was higher in termite nest soils in both environments. Clay mineralogical composition was also measured, and showed the presence of higher amounts of smectite clays in termite nest soils, which thus explained the increasing CEC despite the reduced C and N content. However, the main difference was the shape of the termite mounds. The degradation of the nests created a hillock of eroded soil at the base of termite mounds in the vertisol while only a thin layer of eroded soil was observed in the ferralsol. The increased degradation of termite mounds in the vertisol is explained by the presence of smectites (2:1 swelling clays), which confer macroscopic swelling and shrinking characteristics to the soil. Soil shrinkage during the dry season leads to the formation of deep cracks in the termite mounds that allow rain to rapidly penetrate inside the mound wall and then breakdown unstable aggregates. In conclusion, it appears that despite a similar abundance, termite mound properties depend to a large extent on the soil properties of their environments.

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1. Introduction

Bioturbation is the modification of soil structure by animals or plants. In tropical ecosystems, termites are some of the most important soil bioturbators (Lavelle et al., 1997). Also named 'soil engineers', 'soil aggregate reorganizers' or 'weathering agents' (Dangerfield et al., 1998; Jouquet et al., 2011; Bottinelli et al., 2015), termites create galleries, build organo-mineral structures with specific soil physical, chemical and biological properties, and modify the mineralogical properties of clays in some circumstances (Jouquet et al., 2002, 2005, 2007). These 'biogenic' structures have a large impact on the regulation of major biogeochemical processes in most tropical ecosystems (Lavelle et al., 1997).

Termite mounds or termitaries built by fungus-growing termite species (Termitidae, Macrotermitinae subfamily) are conspicuous features of many landscapes in tropical ecosystems and undoubtedly some of the most impressive structures in the animal world (Smeathman, 1781). Termites use these biogenic structures to protect the colony, and their symbiotic fungus against predators, environmental hazards, such as variation in temperature and humidity, and/or pathogens (Fuller et al., 2011). Whether termites adapt the shape and properties of their biogenic mounds to their ecological needs and to the properties of their environment has long been debated (Lüscher, 1955). For example, *Macrotermes* sp. termite mounds in Africa have been described as extended phenotypes because they protect the colony, act as buffers against the environment and power the ventilation of the nest (Noirot, 1990; Turner, 2000). As an 'extended-phenotype', termite mound structures would therefore take a variety of shapes and have different properties resulting from the equilibrium between termite behavior and their environment. However, this hypothesis is mainly based on studies carried out in Africa with the genus *Macrotermes*, and especially the species *Macrotermes bellicosus*, and by comparing the shape and densities of termite mounds in open savanna or forest environments (Korb and Linsenmair, 1998a, 1998b, 2001). Further studies are therefore needed to determine whether the ability of termites to adapt the properties of nest structures according to their environments is also a characteristic of other termite species from the same genus and similar building strategy but from other continents. In addition, the abovementioned studies focused on the influence of vegetation cover on termite mound density and properties (i.e., termite mound shape and ventilation inside the

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nest), and little is known about how soil properties influence termite mound properties.

In Southern India, *Odontotermes obesus* (Termitidae, Macrotermitinae subfamily) produces large mounds. These biogenic structures are usually less than 2 m high with many circumvolutions and have many similarities in shape to those produced by the African termite species *M. bellicosus*. Thus these mounds are an interesting model on which to test whether results obtained with *Macrotermes* sp. are also found with other species from the Macrotermitiane sub-family. The aims of this study were therefore to determine the influence of pedological parameters (i.e. particle size distribution, physical and chemical properties, mineralogical composition) on the distribution and properties of *O. obesus* mounds. The main questions raised by this study are: (i) How do soil properties influence the mound area number density of termite mounds? (ii) Are the soil chemical and physical properties and shape of termite mounds independent of the soil types?

2. Material and methods

2.1. Study site and study model

The mound area number density and properties of *O. obesus* mounds were studied in the Mule Hole experimental watershed (4.1 km^2). This dry deciduous forest is located in the Bandipur Tiger reserve in South India at 11°44′N and 76°26′E (Karnataka state, Chamarajanagar district). The Mule Hole watershed is located in the subhumid zone of the sharp climatic gradient induced by the Western Ghats. As a result of the short-term variability of the south-west monsoon, Mule Hole experimental watershed is characterized by rainfall ranging from 700 to 1500 mm yr^{-1}, with an average over the last thirty years of 1100 mm yr^{-1}. The elevation of the watershed ranges from 820 to 910 m a.s.l. The relief is mostly undulating with gentle slopes. The soil is mainly composed of well-drained ferralsols and of impervious vertisols (Barbiéro et al., 2007; Braun et al., 2009). Ferralsol and vertisol areas cover 88% and 12% of the watershed, respectively. Ferralsols are developed on granite-gneiss on the hillslopes. Vertisols are developed in the lower part of the slope and the flat valley bottoms, on gneiss and mafic rocks.

In this environment, *O. obesus* builds abundant cathedral mound nests with several ridges and conical turrets that are very similar to those made by *Macrotermes* sp. in Africa (Roonwal, 1970, 1978; Ferry, 1992). These mounds are usually less than 2 m high but can reach almost 3 m high in some circumstances. Rain degrades the mounds leading to an accumulation of soil in their vicinity, which forms a hillock at the base of the mounds.

2.2. Termite mound nest density and volume of soil mobilized in the nests

O. obesus mound area number density was recorded from GIS-based analyses with Q-Gis-2.4.0. Termite mound densities were recorded in five plots of 1.1 ha on average for the ferralsol areas, and in three plots of 1.3 ha on average for the vertisol areas. In this study, only active termite mounds (i.e. mounds hosting living colonies) were considered. Termite mound dimensions were recorded in the field. The volume of soil that termites used to produce their nests was assessed by comparing termite mounds as cones with the following equation: volume $= [\pi \times R^2 \times h] / 3$ where R is the average radius and h the height of the termite mound. The volume of soil eroded at the base of the termite mounds and forming a hillock was assumed to be dome shaped and the equation used to measure it was: volume $= [\pi \times h \times (3R^2 + h^2)] / 6$.

2.3. Soil physical and chemical properties

Three active termite mounds (size > 1 m) were randomly selected in the vertisol and ferralsol areas. Soil samples were collected from the mound walls and the surrounding soil surface environment (control, 0–10 cm deep, distance to termite mound: ~5 m). Soil pH was determined in 1:25 soil:water suspensions and soil organic matter (SOM) was assessed from C and N concentrations using an elemental analyzer Flash 2000 HT. The particle-size distribution was assessed after destruction of SOM and dispersion with sodium hexametaphosphate (AFNOR, NFX 31 107): clay (<2 μm) and silts (2–50 μm) were obtained by sedimentation and sand (50–2000 μm) by sieving. The cationic exchange capacity was determined at soil pH by exchange with cobaltihexamine (AFNOR, NF ISO 23470). Base saturation (BS) was determined from the CEC value and the content of exchangeable cations (Ca, Mg, Na, K, Fe, Mn and Al) (AFNOR, NF ISO 23470). Soil aggregate stability was assessed using the mean weight diameter (MWD) according to Le Bissonnais (1996), which measures the resistance of soil aggregates to water after three types of alteration (fast wetting, slow wetting and mechanical breakdown). Aggregate wettability was assessed with the water drop penetration time (WDPT) test (Chenu et al., 2000) which measures the time for a water drop to penetrate into a soil aggregate.

Clay mineralogical composition was determined after extraction of the clay size fraction (particles <2 μm) from the bulk soil samples. The <50 μm fractions were obtained by wet sieving and then dispersed into mol L^{-1} NaCl (five saturations) and ultrasonication. The <2 μm fractions were obtained by sedimentation and were subsequently flocculated and saturated with 0.5 mol L^{-1} $CaCl_2$ (Caner et al., 2014). XRD patterns of oriented preparations were recorded in the air-dried state (Ca-AD) and after saturation with ethylene glycol (Ca-EG) to identify the clay minerals (Caner et al., 2014).

2.4. Statistical analyses

Residues were tested for normality of variance using the Shapiro–Wilk test and log10-transformed if required. Soil chemical and physical properties were analyzed by analysis of variance (ANOVA) with treatments as independent variables. LSD tests were then performed to assess differences between means. Post-hoc planned pairwise comparisons were performed by Wilcoxon–Mann–Whitney U tests when parametric ANOVA was impossible to use, even after data transformation. Linear regressions were used to assess the relationships between the volume of soil eroded from termite mounds and the height of the termite mounds. All statistical calculations were carried out using R (R Development Core Team, 2008). Differences among treatments were declared significant at the <0.05 probability level unless stated otherwise.

3. Results

3.1. Mound density and shape

There was no significant difference in *O. obesus* mound density in the vertisol and ferralsol areas ($n = 1.96$ mound ha^{-1}, Standard error SE: 0.89, and $n = 3.40$ mounds ha^{-1}, SE: 3.39, for the ferralsol and vertisol, respectively).

Fig. 1 shows the relationship between the height of termite mounds and the volume of soil eroded at the base of the mounds. Linear relationships were measured in both the ferralsol and vertisol conditions ($y = 1.55x$, $R^2 = 0.49$, $P = 0.003$, and $y = 0.087x$, $R^2 = 0.33$, $P = 0.026$, for the vertisol and ferralsol, respectively).

3.2. Soil physical and chemical properties

Soil chemical properties are shown in Table 1 and results of the two-way ANOVA shown in Table 2. The pH, C and N contents and clay content were higher in the vertisol than in the ferralsol. However, no significant difference in pH or particle size fractions was observed between termite mound nests and the surrounding control environment. Lower C and N contents were measured in the termite mound wall than in the surrounding environment for both the ferralsol and vertisol. No significant differences between treatments were observed

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