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Fungus-growing termite foraging activity increases water infiltration but only slightly and temporally impacts soil physical properties in southern Indian woodlands

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ABSTRACT

In the tropics, termites are known to be key litter decomposers and soil bioturbators. Their foraging activity in the soil leads to the production of galleries with specific soil physical, chemical and biological properties. This study investigates the influence of these foraging galleries on water infiltration and soil properties in south-Indian woodlands. A significant increase in water infiltration (× 3 that of control plots) was measured in soil as a result of *Odontotermes* spp. activities, likely because of the production of galleries in the first cm of the soil. Termite foraging activity was also associated with a significantly greater amount of clay in soil, probably because termites cover the wall of their galleries with fine-size particles, resulting in an increased saturated soil water content. Conversely, no differences in C content, CO_2 emission and soil bulk density were measured in comparison with the surrounding soil. Consequently, this study confirms the beneficial impact of termites on water infiltration in soil but suggests a rather low local impact on soil chemical and biological functioning.

1. Introduction

A substantial body of literature suggests that human societies derive many essential environmental goods and services from biodiversity [1–3]. In this context, the study of the ecological impacts of soil biodiversity has become a priority for the definition of sustainable agricultural practices [4]. This challenge is particularly exacerbated in various tropical regions of the world by the fact that many species remain unknown and/or endangered by the degradation of natural habitat [2,5,6].

In the tropics, arthropods, particularly insects, make up the majority of known biodiversity [5,6]. In these environments, termites (Isoptera) are considered key soil physical engineers or bioturbators (*sensu* [7,8]) because they influence many ecological processes such as the decomposition of litter on the ground, the regulation of soil organic matter (SOM) and nutrient cycling, the infiltration and storage of water in the soil, the erosion of soil, and the regulation of plant growth and diversity [7,9–12]. Thus, because of their large abundance and their impact on a large number of ecological functions, termites are considered to play a role similar to that of earthworms in arid and sub-arid tropical ecosystems [13]. However, this comparison between earthworms and termites remains speculative in most of the cases and there is a paucity of information on the influence of termite on soil biostructures (sheetings, mound nests) and biopores (galleries, subterranean chambers) in most tropical ecosystems, especially if we compare to the large amount of information available on the impact of earthworms on soil porosity and water dynamic in temperate ecosystems (e.g. [14,15]).

In Southern Indian forests, fungus-growing termites (Macrotermitiane subfamily) are key actors of litter decomposition [16,17]. They produce above- and below-ground nest structures and sheetings covering the litter that is consumed with specific soil physical and chemical properties in comparison with the surrounding soil environment, then impacting soil fertility and erosion at the ecosystem scale [18–20]. Fungus-growing termites also produce galleries in soil that are used for foraging and bringing the litter from the ground to their nests. However, although the properties of their soil sheetings have been described (e.g. Refs. [21,22]), the influence of their galleries on soil functioning, and especially water and SOM dynamics, remains limited to studies carried out in Sahelian soils where they increase soil porosity, water infiltration and water storage, and reduce crust

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formation, water runoff and soil erosion [23–26]. Consequently, the aim of this study was to determine if termites also influence water infiltration and soil properties in south Indian woodlands through the production of galleries, as observed in African savannas. Our hypothesis was that the foraging activity of termites is associated to a modification of the soil biological, chemical and physical properties in comparison with the surrounding soil, and especially a higher water infiltration rate.

2. Materials and methods

2.1. Study site and soil sampling

This study was carried out during the dry season (February–March) in 2016 in the forest of the Jubilee Garden in the Indian Institute of Science (IISc, 13°01′18″N and 77°34′14″E) in Bangalore city, Karnataka state, India. The vegetation is a planted deciduous forest dominated by Acacia trees, mainly *Acacia auriculiformis*. This ecosystem has a tropical savannah climate with distinct wet and dry seasons, and the annual rainfall ranges from 900 to 1100 mm yr^{-1} [27]. The soil is described as Alfisol in the US Soil Taxonomy (USDA) or Luvisol according to FAO classification. The clay fraction is mainly kaolinite and soil pH is 5.7.

In this study site, litter-feeding termites are mainly *Odontotermes feae*, *O. obesus* and *O. feoides* [27]. These species are commonly found in South India [28]. Their activity is associated to the presence of soil sheeting on wood logs or fallen leaves on the ground. Hence, the influence of termites on soil properties was assessed in comparing the properties of the soil sampled from 0 to 5 cm depth without visible recent activity of termites (CTRL) to the soil below logs covered by termite sheeting (T). A differentiation was made between samples where termites were observed feeding on the wood (T_{new}) and samples where termites were not observed and then considered to be old or unused (T_{old}).

2.2. Soil hydraulic conductivity

Water infiltration was measured with the beerkan method [29] with a cylinder having an inner diameter of 11 cm. The surface litter was gently removed over an area slightly larger than the cylinder diameter, while the soil was untouched. The cylinder was positioned at the soil surface and inserted to a depth of 2–3 cm to prevent lateral losses of water. A fixed volume of water (100 mL, corresponding to a water depth of 1 cm) was initially poured into the cylinder, and the time needed for the water to infiltrate was recorded. As soon as the first volume had completely infiltrated, another equal volume of water was added to the cylinder and the time for this volume to infiltrate (cumulative time) was recorded. The procedure was repeated until reaching steady state conditions, usually after 12 to 15 consecutive infiltration times. In this way, a cumulative infiltration, I (mm), versus time, t (sec), relationship including N_i discrete points (t_i, I_i) was determined. This value was used to derive field-saturated hydraulic conductivity (K_{fs} in mm s^{-1}) using the formula described by Ref. [30]:

$$K_{fs} = \frac{b_1}{0.467\left(\frac{2.92}{r \times \alpha^*} + 1\right)}$$

Where b_1 corresponds to the slope of the linear relation $\frac{I}{t^{0.5}} = f(t^{0.5})$ (in mm s^{-1}) and r to the ring radius (in mm). A value of $\alpha^* = 0.012\,mm^{-1}$ was chosen as suggested by Ref. [31] for soils with intermediate clay values.

Once the steady state was reached, a volume of 300 mL of water dyed with methylene blue (~0.3 g L^{-1}) was poured in the cylinder for measuring the functional porosity and investigate water pathways [32]. The soil in the centre of the cylinder was then sampled using a smaller cylinder (5.7 diam x 5 cm high). Samples were weighted humid and air-died during 2–3 days. The first mm of the soil samples were gently scratched in order to assess the preferential flow paths that were dyed in blue. Soil samples were thereafter carefully cut at 1, 2.5 and 4 cm depth and a picture was taken for each of these depths (see supplementary file for an illustration). The surface of the soil dyed in blue was then manually delimited and measured (in %) at 0, 1, 2.5, 4 and 5 cm depth using Image J software. Soil water content after the infiltration experiment was measured in weighting soil samples after sampling and after drying them at 110 °C during 48 h and considered thereafter as saturated soil water content. The number of replicates was n = 10.

2.3. Soil analyses

Soils were sampled outside of the cylinder for measuring their physical and chemical properties. SOM was assessed from carbon concentration with a TOC analyzer (model SSM-5000A) using a SHIMADZU TOC V_{CSH} analyzer. Soil particle size distribution was measured after destruction of organic matter using H_2O_2 and complete soil dispersion with Na-hexametaphosphate (20 g L^{-1}, AFNOR, NFX 31107) in an ultrasonic bath during 15 min. Particles were then wet-sieved and particles < 20 µm were determined using a laser particle size analyzer. Soil bulk density was measured using cylinders (5.7 cm diam x 5 cm high) and after drying at 105 °C during 2 days. Undisturbed soil samples were also collected using the same cylinders and incubated in the dark in hermetic boxes (13 cm diameter x 14 cm high) at 28–30 °C and 80% of the water holding capacity during 44 days. C-CO_2 emission was measured after 1, 4, 7, 14, 21, 29, 37 and 44 days through a vial containing 5 mL aqueous NaOH solution (0.5 M) to trap the CO_2 emitted. The C-CO_2 produced was determined by back titration (HCl 0.2 M; pH 8.6) of the NaOH trap with excess $BaCl_2$ (1.5 M) using a DL 50 – potentiometric titrator. The numbers of replicates was n = 5, except for the measure of the soil bulk density where 10 replicates were considered.

2.4. Statistical analyses

The normal distribution of residues was tested using the Shapiro-Wilk test. Analysis of variance (ANOVA) and LSD tests were performed to assess differences between means. Kruskal-Wallis Chi-squared and Wilcoxon-Mann-Whitney U tests post-hoc planned pairwise comparisons were performed with a false discovery rate correction when parametric analysis of variance was impossible to use, even after data transformation. All statistical calculations were carried out using R and RStudio (version i386 3.2.5). Differences among treatments were declared significant at the < 0.05 probability level.

3. Results

3.1. Soil properties

Results concerning the influence of termites on soil physical and chemical properties are shown in Table 1. No significant difference in bulk density, respiration and C concentration was measured between

Table 1
Results of the ANOVA testing the influence of termite foraging activity (CTRL, T_{new} or T_{old}) on the sand, clay and C contents (%); soil respiration (amount of C-CO_2 emitted over 44 days, in µg g $soil^{-1}$) and saturated soil water content (in %) (n = 5 in all cases) as well as on soil bulk density (g cm^{-3}, n = 10).

	F	*P*-value
Sand	$F_{2,12} = 6.96$	0.010
Clay	$F_{2,12} = 6.06$	0.015
C content	$F_{2,12} = 0.18$	0.834
Soil bulk density	$F_{2,26} = 0.42$	0.663
Soil respiration	$F_{2,12} = 1.10$	0.364
Saturated soil water content	$F_{2,12} = 76.94$	< 0.001