



RESEARCH ARTICLE - TERMITES

Litter Quality Affects Termite Sheeting Production and Water Infiltration in the Soil

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Abstract

This study aimed to understand the relationship between termite foraging activity and the ecological benefits derived from their activity in soil dynamics and water infiltration. A field study was carried out for six months, between pre-wet and wet seasons, with different food baits (elephant dung, *Acacia auriculiformis* leaves, twigs and leaves of *Lantana camara* as well as *Ficus religiosa*, *Pterocarpus marsupium*, *Prosopis juliflora*, *Michelia champaca*, *Azadirachta indica* and *Hevea brasiliensis* wood stakes) installed on the soil surface in a semi-deciduous forest in southern India. At the end of the experiment we determined bait consumption, water infiltration rate in soil, and the amount of soil sheetings covering the different baits. The initial infiltration rates under the baits were compared to those at the end of the experiment. Three termite species, *Odontotermes obesus*, *O. feae* and *Microtermes obesi*, were found associated with some of the baits in the study area. Among the different baits, elephant dung and Acacia leaves were the most preferred and a positive relationship was observed between the quantity of soil sheetings and the bait consumption rate. Termite preference for elephant dung and Acacia leaves was also associated with higher water infiltration rates. However, this difference was only significant at the beginning of the experiment and no significant difference was measured once the steady state was reached. In conclusion, we showed that resource quality was of primary importance for soil sheeting production but that the influence of termites on water infiltration remained limited, most likely because of the low stability of their tunnels in the soil.

Introduction

In terrestrial ecosystems, bioturbation by soil physical engineers (*sensu* Jones et al., 1994) regulate several important ecological processes, such as those influencing soil fertility and water dynamic in soil (Lavelle et al., 2006; Bottinelli et al., 2015). In temperate and tropical humid ecosystems this role is mainly carried out by earthworms (Lavelle et al., 1997). However, in tropical African and Asian drylands, termites, and

especially fungus-growing termites (Macrotermitinae sub-family) are the key bioturbation agents (Jouquet et al., 2016). In these environments, they directly or indirectly influence the availability of nutrient and water resources to “subordinate organisms” (*sensu* Jouquet et al., 2006) from microorganisms to plants (e.g., Wood & Sands, 1978; Schaefer & Whitford, 1981; Konaté et al., 1999; Harry et al., 2001; Jouquet et al., 2005; Bignell, 2006; Sileshi et al., 2010). The influence of termites on ecosystem functioning relies on their ability to



act as key decomposers of organic residues (Collins, 1981; Freyman et al., 2008, 2010; Fatondji et al., 2009) and in the formation of biostructures (termite mounds and sheetings) and biopores (tunnels and below-ground chambers) which have specific physical, chemical and biological properties differing from the surrounding soil environment (Holt & Lepage, 2000; Jouquet et al., 2011).

Termite mounds are often conspicuous features of tropical landscapes and, for this reason, their specific properties and abundance have been extensively studied (e.g., Moe et al., 2009; Horiuchi et al., 2014; Joseph et al., 2014; Sujada et al., 2014; Jouquet et al., 2017; Shanbhag et al., 2017; Muvengwi et al., 2018). Comparatively, the specific properties and abundance of soil sheetings have received much less attention, although it has been suggested that they represent several tons of soil ha⁻¹ year⁻¹ in some situations (Rouland et al., 2003; Ali et al., 2013; Harit et al., 2017a). Termites also influence soil functioning through the formation of foraging galleries which increase soil porosity (e.g., Lee & Wood, 1971; Bottinelli et al., 2015) and consequently water infiltration (Elkins et al., 1986; Mando et al., 1996, 1999; Léonard & Rajot, 2001; Mettrop et al., 2013) and water storage (Lobry & Conacher, 1990; Ouédraogo et al., 2006; Pringle et al., 2010). As a consequence, this impact of termites on soil porosity and water dynamics makes them important agents of agro-ecosystem functioning (Mando & Miedema, 1997; Evans et al., 2011; Jouquet et al., 2018).

Termites are considered “intended” or “extended soil engineers” since they manipulate soil functioning to protect themselves against desiccation and predators, to maintain a micro-climate within their constructions and/or to favor the growth of the vegetation they prefer to consume (Jouquet et al., 2006). The close relationship between the ecological impacts of termites and their ecological needs has mainly been demonstrated in the context of termite nest constructions (mounds and fungus-growing chambers) (Dangerfield et al., 1998; Jouquet et al., 2002, 2003; Turner, 2004). However, termites also adapt the amount and the properties of their sheetings depending on substrate physical and chemical properties and feeding preferences, with relatively long-lasting structures being most different to the parent soil material (Harit et al., 2017b). For example, non-fungus growing termites prefer mammalian dung over alternative food items because of its higher C/N ratio (Freyman et al., 2008) and consequently use a larger amount of soil to cover dung pats than plant litter (Herrick & Lal, 1996). As another example, a positive relationship was also measured in Senegal between the quantity of sheetings and the amount of substrate consumed by fungus-growing termites as well as the number of pores on the surface (Rouland et al., 2003). Consequently, the relationship between food preference, bioturbation (i.e., the formation of sheeting and galleries) and water infiltration in soil remains unexplored, especially in Asia where the influence of fungus-growing termites on soil dynamic is poorly documented (Jouquet et al., 2016).

Therefore, the aim of this study was to examine the links between termite feeding preferences and the production of sheetings and galleries in a tropical forest in Southern India. We then investigated the relationship between resource quality, termite foraging activity and water infiltration in soil. Our hypotheses were that (i) the more termites prefer a type of resource and the more they produce sheetings above-ground and galleries below-ground, and (ii) that higher resource consumption is associated to greater water infiltration in soil.

Materials and Methods

Study site and experimental design

The study was carried out in a park at the Institute of Wood Science and Technology (IWST), Bangalore (13.0112° N, 77.5702° E) from February to August 2016. The study site is dominated by teak trees, which represent one of the major types of tree plantation in South India. The climate in the area is semi-arid with an average annual rainfall of 900 mm year⁻¹, a mean annual temperature of 23.6 °C and a wet (July-October), a dry (November-April) and pre-wet season (May-June) (Jouquet et al., 2015; Cheik et al., 2018). Situated at an elevation of 900 to 1000 m above sea level, the soil in the area is described as Luvisol by FAO (Soil Survey Staff, 2014). The soil is reddish brown in color and has a loamy texture with ~19 and 36% of clay and sand, respectively, and a bulk density of ~0.9 g cm⁻³ and it is characterized by a good drainage (Soil Survey Staff, 2014). It is moderately acidic with low organic carbon content (~1.3%) (Cheik et al., 2018).

The experiment consisted in the utilization of organic baits that were placed on the soil surface to attract termites. Ten different substrates were used. Elephant dung (‘ED’) was chosen for its attractiveness because termites are often observed below elephant dung in South Indian forests (Chaudhary and Jouquet, com. pers.). *Lantana camara* twigs (‘LT’) and leaves (‘LL’) were also used because *Lantana* sp. is known to have secondary metabolites which act as feeding deterrents for termites (Sousa & Costa, 2012). This plant is also an invasive species in India and how termites participate to its degradation remains unknown (Ramaswami & Sukumar, 2014) and therefore an important question in this environment. *Acacia auriculiformis* leaves (‘AC’) and different wood stakes (*Ficus religiosa* (‘FI’), *Michelia champaca* (‘MI’), *Hevea brasiliensis* (‘HB’), *Prosopis juliflora* (‘PJ’), *Pterocarpus marsupium* (‘PT’) and *Azadirachta indica* (‘AZ’)) were also used because they constituted gradients of high quality resources, with higher N contents in leaves than in wood, and less to high density wood materials (d ~ 0.39, 0.43, 0.53, 0.63, 0.67 and 0.93 g cm⁻³, respectively) (Shanbhag & Sundararaj, 2013a,b). Recently produced ED (< 2 days), recently fallen and non-decayed AC collected on the ground and cut pieces of lantana (LT, ~10 cm in length, and LL) were air-dried during 10 days before being placed on the soil surface while wood stakes (15 cm in length x 3.5 x 3.5 cm) were dried at 80 °C during 2 days.

All baits were weighed before the experiment (~200 g bait¹ in average). Since termite mounds were not visible in the study field, substrates were randomly distributed with a minimum distance between bait ~ 2 m. Baits were also covered by plastic boxes (23 cm long x 17 cm wide x 8 cm height) performed with 2 mm holes on their sides. Boxes were covered on their top to protect them from the rain but they were open on the ground to allow soil fauna to have access to the baits. Five replicates were used per treatment and 5 boxes without baits were also installed on the soil surface for the control treatment.

Biodiversity and litter consumption

At the end of the experiment, all baits were carefully removed. Baits with termite activity were recorded. All active soil macrofauna under the baits but above the soil surface, including termites, were sampled and kept in vials containing 80% alcohol and further identified at the species or taxon level. Soil fauna diversity was described by the number of species and morpho-species (taxon richness, R) and the Shannon index (H').

Soil sheetings covering the substrates were collected and placed in separate plastic bags along with the residual organic bait. Both sheetings and bait materials, except wood samples, were dried at room temperature (~30°C) until they reached a constant weight, and then weighed and expressed as g soil sheeting g bait⁻¹. Wood stakes were dried at 80°C for two days. Termite feeding preferences were evaluated by comparing the weight of the baits before and after the experiment. Values were then converted to percentage weight loss. The amounts of soil translocated over the individual baits were also calculated.

Soil physical properties

Water infiltration rates were measured under the baits following the Beerkan method (Haverkamp et al., 1994; Braud et al., 2005). A cylinder (diam 11 cm) was positioned at the soil surface and inserted to a depth of 1 cm to prevent lateral water loss. 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 steady state conditions were reached. A distinction was made between the infiltration rate at the beginning and end of the experiment. The first three recordings were considered as starting points and the average infiltration rate of the last three readings were considered for the last points. Undisturbed soil cores were also sampled in the surrounding top-soil environment (0-5 cm depth) to confirm that initial water content, θ_i (m³ m⁻³), was similar for all the treatments. The soil in the center of the cylinder was also sampled using a smaller cylinder (5.7 diam x 5 cm high). Samples were weighed humid and after drying at 110°C for 48 hours. These values were used to measure soil bulk density and gravimetric water content at saturation.

Statistical analyses

All statistics were calculated using R studio and R version 3.2.1. (R development Core Team, 2008). Residues were tested for normality using the Shapiro-Wilk test and the homogeneity of variance was tested using Levene's test. A one-way analysis of variance (ANOVA) was performed on normally distributed data sets and differences between means were tested with Fischer least significant (LSD) tests. Data were analyzed using Kruskal-Wallis Chi-squared tests when residues failed to show normal distribution even after log-transformation. Differences were considered significant at $P < 0.05$.

Results

Soil biodiversity

The influence of the feeding baits on soil macrofauna biodiversity is shown in Table 1. No significant difference in taxon richness and Shannon index could be measured (Kruskal-Wallis test, $p = 0.235$ and 0.388 for R and H', respectively). Three termite species were found (*Odontotermes obesus*, *O. feae* and *Microtermes obesi*) in AC and ED but with a low occurrence (Table 2). Along with termites many different organisms were also found below all the baits, such as pseudo scorpions ($n = 66$), centipedes ($n = 23$), Coleoptera ($n = 16$), as well as ants ($n = 3$), millipedes ($n = 2$) and snails ($n = 2$).

Bait preferences and soil sheeting production

The bait consumption rates highlighted a clear preference for ED and to a lesser extent for leaves (no significant difference between AC and LL, $p = 0.219$),

Table 1. Diversity indices (taxon richness R and Shannon index H') of the soil macrofauna for each treatment (elephant dung = ED, *Acacia auriculiformis* leaves = AC, *Lantana camara* twigs = LT and leaves = LL, and wood stakes of *Ficus religiosa* = FI, *Pterocarpus marsupium* = PT, *Prosopis juliflora* = PJ, *Michelia champaca* = MI, *Azadirachta indica* = AZ and *Hevea brasiliensis* = HB). Values in parenthesis are standard deviations ($n = 5$).

Treatments	Control	ED	AC	LL	LT	FI	PT	PJ	MI	AZ	HB
R	0.40 (0.55)	1.20 (0.84)	1.60 (1.14)	1.60 (0.55)	1.20 (0.84)	0.80 (0.84)	0.60 (0.55)	0.60 (0.89)	0.60 (0.89)	0.60 (0.55)	0.60 (0.89)
H'	0.00 (0.00)	0.27 (0.37)	0.36 (0.39)	0.28 (0.27)	0.21 (0.30)	0.14 (0.31)	0.00 (0.00)	0.14 (0.31)	0.14 (0.31)	0.00 (0.00)	0.14 (0.31)

Table 2. Soil macrofauna (total number of individuals or occurrence for termites and ants) found on the soil surface and below the baits at the end of the experiment. Baits were elephant dung ('ED'), *Acacia auriculiformis* leaves ('AC'), *Lantana camara* twigs ('LT') and leaves ('LL'), and wood stakes of *Ficus religiosa* ('FI'), *Pterocarpus marsupium* ('PT'), *Prosopis juliflora* ('PJ'), *Michelia champaca* ('MI'), *Azadirachta indica* ('AZ') and *Hevea brasiliensis* ('HB') and in the surrounding soil without bait (CTRL). Taxon meanings: Isoptera (sp.1 = *Odontotermes obesus*; sp.2 = *O. feae*; sp.3 = *Microtermes obesi*). Coleoptera (sp.1 = *Platypodidae* sp.; sp.2 = *Bostrychidae* sp.; sp.3 = *Cerambycidae* sp.). Hymenoptera (sp.1 = *Camponotus pennsylvanicus*; sp.2 = *Monomorium minimum*). Diplopoda (sp.1 = Millipedes). Chilopoda (sp.1 = Centipedes). Arachnida (sp.1 = *Cheliferoides* sp.). Mollusca (sp.1 = snail).

Bait types	Number of individuals or occurrence of soil macrofauna											
	Isoptera			Coleoptera			Hymenoptera		Diplopoda	Chilopoda	Arachnida	Mollusca
	sp.1	sp.2	sp.3	sp.1	sp.2	sp.3	sp.1	sp.2	sp.1	sp.1	sp.1	sp.1
ED			1			3	1			6		
AC	1	1				2				2	14	
LT								1	1	3	9	
LL						2	1			2	37	
FI				3						2	2	
PT										2		
PJ					2					1	1	
MI						1				1		
AZ						1				2		
HB						2			1	2	3	
CTRL												2

that were consumed at a rate of 98.8% and 58%, respectively (ANOVA, $F_{9,40} = 23.34$, $p < 0.001$) (Figure 1). Conversely, the amounts of bait consumed were very low for the different wood substrates (no significant difference between FI, PT, PJ, MI, AZ and HB, $p > 0.05$). The consumption rates of LT were

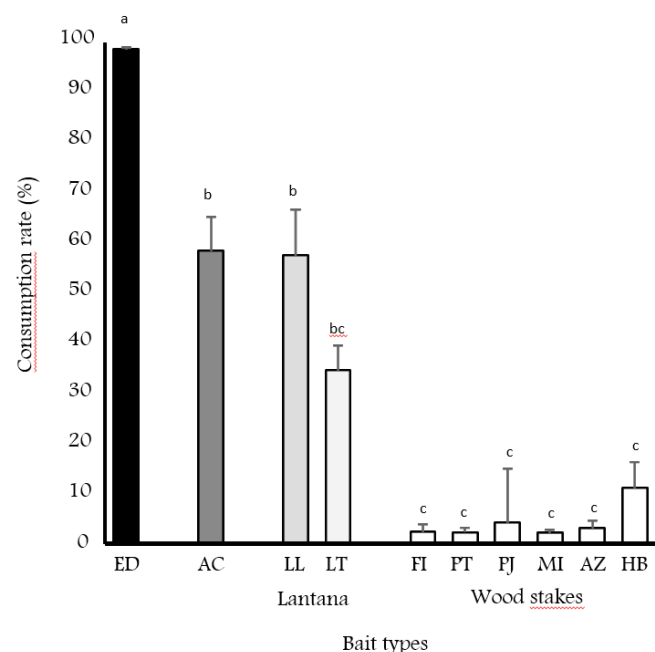


Figure 1. Baits preference and consumption by soil macrofauna, in % weight loss of the initial bait materials (elephant dung ('ED'), *Acacia auriculiformis* leaves ('AC'), *Lantana camara* twigs ('LT') and leaves ('LL'), wood stakes of *Ficus religiosa* ('FI'), *Pterocarpus marsupium* ('PT'), *Prosopis juliflora* ('PJ'), *Michelia champaca* ('MI'), *Azadirachta indica* ('AZ') and *Hevea brasiliensis* ('HB')). Vertical bars are standard errors. Histograms with the same letter are not significantly different at $p = 0.05$ ($n = 5$).

intermediate between those of LL and AC on one side and those for the wood substrates on the other side ($p < 0.05$ in all cases).

The quantity of soil sheetings also varied between substrates (Kruskal-Wallis Chi Squared = 34.33, $df = 9$, $p < 0.001$; Figure 2). ED, LT and LL were covered with 2.18 g soil $g\text{ bait}^{-1}$, while the wood substrates were covered with only 0.09 g soil $g\text{ bait}^{-1}$. Intermediate values were measured for AC with 0.9 g soil $g\text{ bait}^{-1}$ ($p > 0.05$ in all cases, except with ED where $p = 0.041$). A positive relationship was found between the total amount of soil sheetings (in grams) and the bait consumption rate (in %) ($y = 9.69x$; $R^2 = 0.75$; $p < 0.001$; Figure 3).

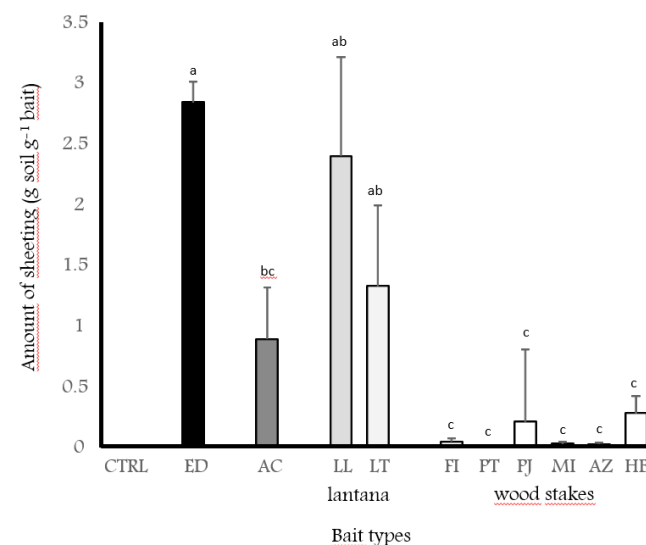


Figure 2. Amount of soil sheetings (in grams) produced by termites on the different bait types (see legend of Figure 1 for more details concerning the treatments). Vertical bars are standard errors. Histograms with the same letter are not significantly different at $p = 0.05$ ($n = 5$).

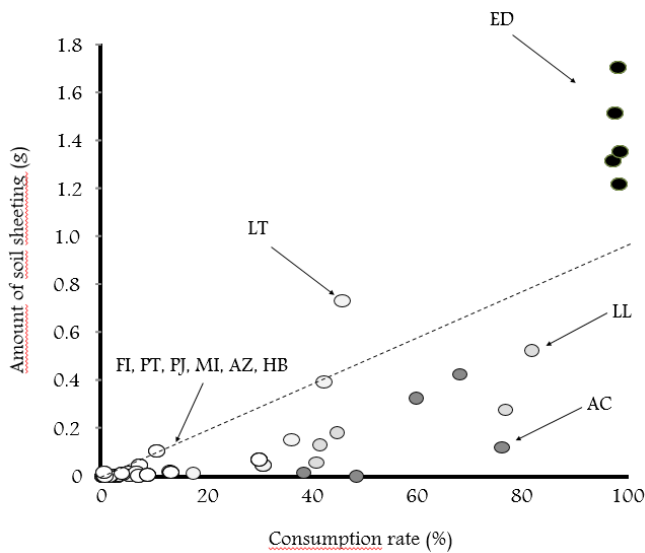


Figure 3. Relationship between termite feeding preference (in % bait consumption) and the amount of soil translocated (in grams). See legend of Figure 1 for more details concerning the treatments. The dashed line corresponds to the linear regression.

Soil belowground properties

Termite activity did not have a significant effect on soil bulk density (0.93 g cm^{-3} in average; ANOVA test, $F_{10,44} = 1.47$, $p = 0.183$) or soil moisture at saturation ($F_{10,44} = 0.79$, $p = 0.637$). However, water infiltration below the baits during the three first consecutive trials showed significant differences between treatments ($F_{10,43} = 6.54$, $p < 0.001$, Figure 4). The highest infiltration rate was measured for ED with an infiltration rate of 26.8 mL sec^{-1} ($p < 0.05$ in all cases). No difference occurred between the other substrates with an average water infiltration rate of 4.5 mL sec^{-1} ($p > 0.05$ in all cases), except for AC with intermediate average values of

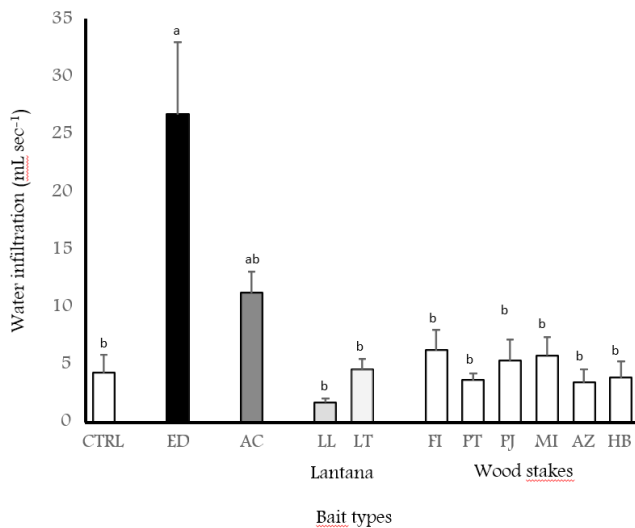


Figure 4. Water infiltration rates of the soil below of the baits (mL water sec^{-1}) at the beginning of the Beerkan experiment. Vertical bars are standard errors. Histograms with the same letter are not significantly different at $P = 0.05$ ($n = 5$). See legend of Figure 1 for more details concerning the treatments.

11.3 mL sec^{-1} . Figures 5a, b show that the infiltration rate at the beginning of the experiment was linearly related to the consumption rate and the amount of soil sheetings ($y = 0.18x + 3.02$, $R^2 = 0.46$, $p < 0.001$; $y = 0.01x + 4.52$, $R^2 = 0.55$, $p < 0.001$, for the consumption rate and the quantity of soil sheeting, respectively). However, the baits did not significantly influence the steady state infiltration rate ($\sim 0.96 \text{ mL sec}^{-1}$ on average; Kruskal-Wallis Chi-squared test = 8.76, $df = 10$, $p = 0.555$).

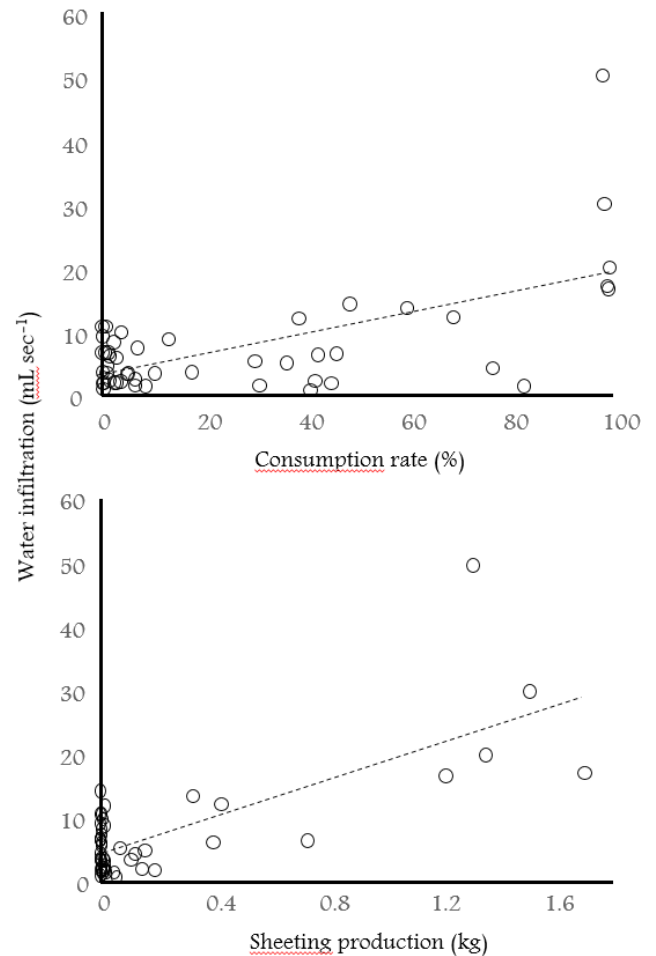


Figure 5a, b. Relationships between water infiltration rate of the soil below of the baits at the beginning of the Beerkan experiment (in mm sec^{-1}) and soil macrofauna feeding preference (in % bait consumption) or the amount of soil sheetings (in kg soil). Linear regressions are displayed.

Discussion

Impact of the baits on soil biodiversity

In total, three termite species were identified (Table 2). Along with termites, several soil macrofauna were observed below the baits. Some could be associated with litter degradation (e.g., snails, millipedes) while others were predators (e.g., ants, chilopods). Unfortunately, due to the overall low number of soil macrofauna individuals and number of repetition ($n = 5$) we could not determine if some of the baits were more attractive than others (i.e. no significant

difference in R and H'). In addition, termites were not sampled with most the baits, although the presence of sheetings showed that ED, AC, LL and LT baits were attractive to them. Since samples were collected only once after a period of six months, it is also possible that other termite species and/or other soil invertebrates were also involved in earlier decomposition stages of the baits but were no longer active when samples were collected (Sundararaj et al., 2015). Similarly, six months is a short period for wood decomposition (van Geffen et al., 2010) and it is also possible that other termite species would have been found associated with wood baits if the experiment had lasted longer.

Termite feeding preference and soil translocation

Termites produce sheetings mainly to protect themselves from direct sunlight and predation while they forage (Jouquet et al., 2006, 2015; Harit et al., 2017b), and to excavate soil to construct below-ground galleries and nest chambers (Harit et al., 2017a). Termites do not always cover the food material on which they feed with sheetings but in this study a clear relationship was measured between the amount of sheetings produced over the feeding substrate and the amount of substrate that was consumed. This result therefore confirms the study of Rouland et al. (2003) who found a positive relationship between the amount of millet cane consumed by termites and the quantity of soil sheetings. It is also in agreement with Jouquet et al. (2015) and Harit et al. (2017a) who showed that when termites prefer a food they invest more energy in the production of soil sheetings.

Soil translocation levels were the highest for ED samples since all the elephant dung was covered and filled in with sheetings. Termites clearly preferred ED over the other baits, most likely because of its high C and N contents (~40 and 1 % in South Indian woodlands, respectively; Chaudhary com. pers.) (Freyman et al., 2008). ED was also perhaps more attractive to termites because it is a mechanically and biochemically "preprocessed" substrate, after its passage through the elephant gut. Indeed, it is likely that its high mass per volume ratio in comparison reduced the energy needed for termites, and their symbiotic fungi, to mechanically and biochemically break it down (He, 2013). Termites then preferred feeding on leaves and to a lesser extent twigs but wooden baits were almost left untouched by termites during this experiment. This preference can easily be explained by the fact that leaves are less dense and enriched in N compared with twigs and wood (e.g. 2.4% and 0.62% of N in leaves and wood of *Acacia*, respectively; Snowden et al., 2005). Due to the low consumption of wood we could not confirm the results of Shanbhag and Sundararaj (2013a, b) who showed that *Odontotermes* spp. termites prefer less dense wood over denser wood types. Finally, this study also showed that termites can consume *Lantana camara*, which is an invasive species in India where it is becoming a threat to biodiversity (Priyanka & Joshi, 2013). Therefore, this study

confirms the key role played by termites in the decomposition of litter and herbivore dung in tropical ecosystems (Collins, 1981; Freyman et al., 2008). It also suggests that *L. camara* is likely to be degraded by termites in South Indian forests, despite the fact that it contains secondary metabolites that are used for biological control of forest pests, including termites (Verma et al., 2009; Yuan & Hu, 2012).

Effects of termites on water infiltration

In our experiment, the consumption rate and amount of soil sheetings were linearly related to the water infiltration rate at the beginning of the Beerkan measurements. It is likely that the higher water infiltration in soil for the ED treatment resulted from the higher foraging activity of termites below ED. Hence a larger number and/or diameter of galleries may have been produced in the area, as shown by the greater excavation of soil in the form of sheetings. Our study confirmed the higher water infiltration rate associated with termite foraging activity (Mando & Miedema, 1997; Léonard & Rajot, 2001; Léonard et al., 2004; Kaiser et al., 2017). However, this higher water infiltration rate was only significant for the initial stages of the experiment and no significant differences were found in the later stages. Consequently, this result suggests that the macropores produced by termites were unstable. It is likely that galleries were initially playing the role of preferential flow paths, improving water infiltration in the soil, but that they did not resist the successive applications of water on the soil and collapsed, leading to similar soil porosity for all the treatments. This scenario would explain why no difference in soil bulk density and soil humidity at saturation was measured at the end of the experiment. It also suggests that termite foraging activity has a rather limited impact on soil porosity after prolonged rains. These conclusions are, however, in contradiction with results found in Africa where fungus-growing termites increased soil porosity and water infiltration and retention (Mando & Miedema, 1997; Konaté et al., 1999; Léonard & Rajot, 2001; Léonard et al., 2004; Kaiser et al., 2017). Different soil properties between our study site and the study sites in Africa could explain these differences. In Africa, soils were mainly sandy with a high bulk density (> 1.5-2), while in our study site the soil was characterized by a very low bulk density (~ 0.9, Shanbhag, pers. obs.) and a good water drainage, which is a characteristic of Luvisol (Soil Survey Staff, 2014). More research is therefore clearly needed to examine how the impact of termites, and especially the stability of their foraging galleries, vary with soil properties.

Conclusion

The aim of this study was to gain a better understanding of the relationship between termite food preferences and the ecological benefits derived from their activity in terms of soil dynamics and water infiltration. A clear relationship was found between termite feeding preference, soil sheeting

production and water infiltration, at least in the initial stages of the experiment. Thus, this confirms the need for new data concerning the link between plot-scale termite ecology and their impacts on ecosystem processes. The lack of evidence in the present study that termites affect water infiltration raises questions about the stability of termite foraging galleries and their overall role in regulating soil bulk density in Luvisol. Therefore, a perspective of this study would be to test the generality of this result in other soil pedological contexts (e.g., in compacted or poorly draining soils). Finally, another key conclusion of this study is the ability of termites to consume *Lantana camara* residues, which cannot be eaten by most other forest insects in India.

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