Food preferences and foraging strategies of wood-feeding termites in a West African savanna

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The feeding preferences of termites in a Guinean savanna (Lamto, Côte d'Ivoire) were studied in the field to better understand the incidence of termite damages observed on adult trees, which, on interaction with fire, affect the dynamics of the tree community. Two separate multiple-choice test experiments were conducted on the six dominant tree species, aiming at determining preferences for the species and for wood conditions naturally encountered and likely to affect termite consumption behaviour. The preferences of termites were determined by their occurrence on standard-sized wood pieces and their behaviour during the first attack. Two fungus-growing termites, *Ancistrotermes* and *Microtermes* were frequently encountered on wood pieces, whereas wood feeders were absent. The two genera have different preferences, and they do not compete for the same food. Wood density and water content did not explain termite preference. Holes in the bark seem to facilitate termite entry into pieces of wood, whereas the action of fire on wood apparently makes it less attractive to termites. In the field, the decision by termites to forage on a given tree species seems to be more driven by habitat and accessibility differences than real food quality differences.

Keywords: Food preference, foraging strategies, tree species, wood-feeding termites.

ABOUT 2600 species belonging to 281 genera of termites (Isoptera) have been described[1]. Termites are abundant in tropical ecosystems. They affect the decay of plants debris in soil, playing an important role in soil nutrients cycling and fertility[2]. Many species are known to move organic matter from the surface to deeper layers of the soil, improving and maintaining its porosity and aeration[3,4]. Their negative impact on crops and houses is relatively well understood[5–8]. Recently, they have been proven to affect the mechanical resistance of living trees in fire-prone savanna ecosystems[9], and the population dynamics of trees through their mortality rate[10]. It is therefore of key importance to understand what drives termites towards feeding on and colonizing the trunks of particular tree species. Termite food preferences might, in the end, be responsible for the whole savanna physiognomy through their impacts on tree population dynamics, as suggested by Gould *et al.*[11].

We tested the feeding preferences of termites through field experiments in order to understand their impact on the adult tree populations. Termites interact with fire to cause external openings on trees[9]. This has population-level consequences, trees with external openings reach smaller sizes both in height and basal diameter[9]. It also affects adult mortality of some dominant tree species[10]. Although a plausible scenario of termite–fire interaction has been proposed, the precise mechanisms of interaction are unknown. In particular, we do not know which are the termite genera responsible for the impacts observed on trees; which tree species are more suitable for termites; how are trees entered, and in particular, whether holes caused by fire on trees allow termites to enter them. Our experiments address these questions. Experiment 1 was a multiple-choice test designed to test relative preferences among tree species, whereas experiment 2 was a multiple-choice test designed to test relative preferences among five different wood conditions. In order to better understand the tree–termite interactions, we identified (1) termite genera responsible for tree damage, (2) tree species more suitable to termites and (3) condition of the wood preferred by termites.

Materials and methods

Study site

The experiments were conducted at the Lamto Research Station in Côte d'Ivoire (6°13′N, 5°02′W). The major tree species are shrubby and usually <10 m, high, and more than 90% of the woody layer is composed of four species: *Bridelia ferruginea* Benth. (Phyllantaceae), *Crossopteryx febrifuga* (Afzel. ex G. Don) Benth. (Rubiaceae), *Cussonia barteri* A. Rich. (Araliaceae), and *Piliostigma thonningii* (Schum.) Milne-Redhead (Caesalpiniaceae)[12]. Shoots of woody species such as *Annona senengalensis*

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Pers. (Annonaceae) grow in the grass layer, whereas in the upper stratum we find *Terminalia schimperiana* Hochst. (Combretaceae).

With biomass reaching 3.4–19.6 g m^{-2} (fresh weight), termites are one of the major animal components of the Lamto ecosystem[13,14]. The main trophic groups are the fungus-growing (from 1.15 to 5.93 g m^{-2}), humivorous (from 2.14 to 11.65 g m^{-2}), and xylophageous and grass-foraging (from 0.17 to 1.98 g m^{-2}) termites[14–16]. Their activities result in the formation of biogenic structures which are frequently encountered in all savanna types[17]: above-ground termitaria; below-ground nests; comb chambers; sheetings and galleries. The latter two are built by workers, generally using soil-impregnated saliva covering the food supply or termite pathway. Also, termite mounds which are very large, complex biogenic structures grouping below-ground nests of different termite species, are frequently encountered in all savanna types[13,18]. All Lamto savannas are subject to annual fires[19,20]. Termites, which are known to consume only dead material[21], have recently been observed to use the burned parts of trees to enter the trunk[9]. Experiments were conducted in two burned shrubby savanna habitats (the most frequent savanna type in Lamto), replicated twice in each area. Experimental plots were selected as far as possible from termite mounds, nests and trees, which could bias the sampling because they favour the presence of one species of termite.

Termite sampling methods on experimental plots

To estimate the overall termite diversity of an experimental habitat, the whole experimental plot was searched for termites. A modified standardized method of the protocol for rapid assessment of termite diversity by Jones and Eggleton[22] was used[9]. Sampled termites were identified to the genus level using standard determination keys[23–26] and species descriptions[27]. Following Josens[15], Deligne[28] and Sands[29], they were classified into fungus-growers, soil-feeders, wood-feeders and grass-feeders. Wood-feeders and fungus-growers were expected to be actively feeding on wood.

Tree species and experimental procedures

A total of six dominant tree species of the Lamto reserve were used as potential food for termites: *A. senegalensis*; *B. ferruginea*; *C. febrifuga*; *Cussonia arborea*; *P. thonningii* and *T. schimperiana*.

Five wood blocks (~10 cm in length) were cut from living (around 6 cm dia) branches of each of the six species and additional treatments were applied to the blocks to mimic the possible conditions of wood debris that could be encountered by termites in the field. The fresh wood with holes (FH) was obtained by making holes with nails through the bark of wood blocks to simulate the

holes left by fire and broken branches on the living trees as a test of the 'access point' hypothesis[30,31], as observed in N'Dri *et al.*[9]. According to N'Dri *et al.*[9], termites are better able to consume parts of trees impacted by fire than fresh ones and use them to get into the trees. These observations were tested using burned (B) and charred (C) pieces of wood in order to simulate the impact of fire on living trees. To standardize their water content, the dry, burned and charred wood blocks were oven-dried at 100°C for 72 h. Burned and charred treatment was obtained by placing blocks in dry grass (cropped in the field and drying) fires, until char appeared on the block surface for 'C' and less than 2 min, for 'B', according to the description of savanna fire behaviour in the literature[32–34]. Dry wood (D) was added to test whether dead wood was preferred over fresh (F) wood by termites, as suggested by Josens[15] and Grassé[35]. All the wood blocks (FH, B, C, D, F) were tagged and placed on each of the two plots.

Our first experiment focused on termite preference for wood of a particular tree species (species preference test, SPT). Wood blocks of the six species in the same condition were grouped at one field location, directly on the soil and 10 cm apart (distance chosen to give the same probability for a wood block to be consumed by foraging termites) from each other. Five groups of wood blocks, one for each wood condition, were randomly placed 35 m apart from each other, which corresponds to the approximate range of termite prospection (S.K., pers. commun.). The second experiment focused on termite preference for a particular wood condition (condition preference test, CPT). It was setup like the first experiment, but reversing the role of species and wood conditions. Each of these experiments was replicated twice in each shrubby savanna (four replicates overall).

Wood blocks were visited daily for termite impacts, to determine the attack order of different tree species. A block was considered impacted by termites when it was covered by biogenic structures (sheetings or/and tunnel-galleries). Biogenic structure type (gallery or sheeting) was recorded to determine the use of wood blocks by termites, tunnel-galleries being built for prospection and sheetings for feeding[36]. When termite attacks were found on all wood blocks, observations were done every second week from April 2009 to January 2010. F and FH wood blocks were changed at each sample. Termites and their biogenic structures were systematically searched in order to determine the termite genera. When termites were found, representative (~10) individuals of the soldier caste and/or worker were collected and preserved in 75% alcohol and later identified to the genus level.

Measurement of wood species density

According to Behr *et al.*[37], termites preferentially consume lower density wood. To test this, we estimated the

wood density of five of the dominant tree species of the Lamto reserve (*B. ferruginea*, *C. febrifuga*, *C. arborea*, *P. thonningii* and *T. shimperiana*) in two different conditions (fresh and dry). One wood block was cut from living branches of five different trees for each species, then each wood block was weighed and its volume determined by immersion in water in a 1 litre beaker graduated to the nearest cubic centimetre, density being then obtained as the ratio of sample mass over its volume. The average humidity content of each wood species was determined simultaneously by weighing the samples after oven-drying at 100°C during 72 h. The impact of average water content of each tree species on the feeding preference of termite genera was then tested.

Statistical analyses

All analyses were performed using the R software (http://www.r-project.org/). The distribution of different termite genera on wood blocks, and of sheetings and galleries on wood blocks during the first termite attack were compared using χ^2 tests. Linear models (LM) with logit transformation were used to analyse the effect of tree species, wood condition and experiment design on: (1) the feeding preference of two termite genera (i.e. *Ancistrotermes* and *Microtermes*) and (2) the occurrence of biogenic structures (galleries and sheetings) on tree species and wood condition during the first attack. Linear models were also used for analysing the wood humidity and density according to wood species and condition. Post-hoc Tukey's HSD test was used to identify (1) the more preferred tree species and wood condition by termites and (2) the wood block conditions and species presenting the highest density and humidity. Generalized linear models (GLM) were used for analysing the occurrence of biogenic structures during the first attack.

Results

Termite diversity in the study site

At the experiment sites, 10 termite genera distributed into four functional groups were collected. Five fungus-growers (*Ancistrotermes*, *Macrotermes*, *Microtermes*, *Pseudacanthotermes* and *Odontotermes*), two soil-feeders (*Adaiphrotermes* and *Amitermes*), two wood-feeders (*Microcerotermes* and *Fulleritermes*) and one grass-feeder (*Trinervitermes*) were found.

Termite genera on the wood baits

Ancistrotermes and *Microtermes* were the only genera frequently found on wood blocks for statistical analyses to be performed (Figure 1). The occurrence of termites on

wood blocks significantly differed with termite genus ($\chi^2 = 5530.69$, d$f = 7$, $P < 0.001$).

Ancistrotermes and Microtermes feeding

The occurrence of termites on different tree species changed according to their genera (ANOVA, $F_{1,10} = 45.61$; $P < 0.001$; Figure 2).

Occurrence of the *Ancistrotermes* on wood blocks varied according to tree species (ANOVA with logit transformation, $F_{5,60} = 4.91$; $P = 0.001$). No experiment-type
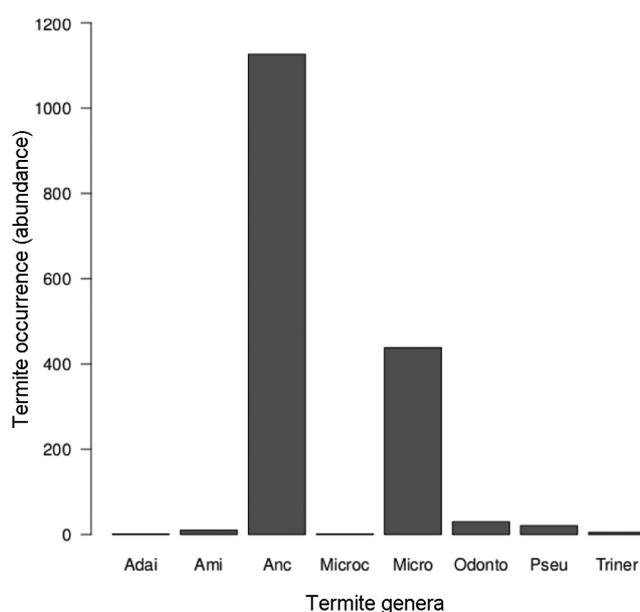

Figure 1. Occurrence of different termite genera on wood blocks. Adai, *Adaiphrotermes*; Ami, *Amitermes*; Anc, *Ancistrotermes*; Microc, *Microcerotermes*; Micro, *Microtermes*; Odonto, *Odontotermes*; Pseu, *Pseudacanthotermes* and Triner, *Trinervitermes*.
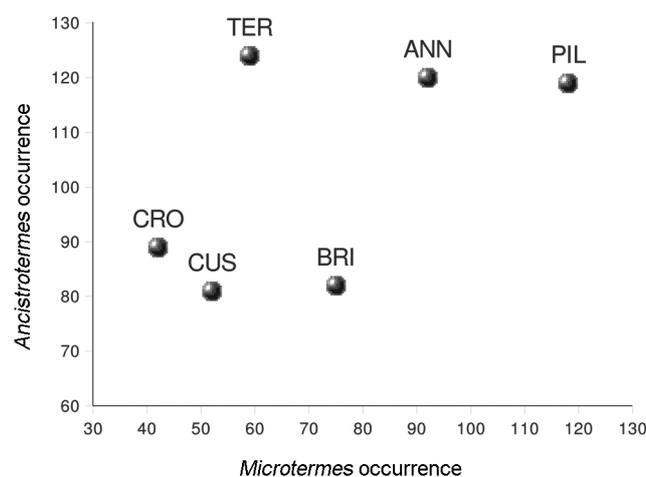

Figure 2. Absence of competition between *Ancistrotermes* and *Microtermes* for tree species preferences. ANN, *Annona senegalensis*; BRI, *Bridelia ferruginea*; CRO, *Crossopteryx febrifuga*; CUS, *Cussonia arborea*; PIL, *Piliostigma thonningii* and TER, *Terminalia schimperiana*.

effect was observed on their occurrence (ANOVA with logit transformation, $F_{1,60} = 1.40$; $P = 0.24$). The most preferred wood species was *T. schimperiana* and the least preferred was *B. ferruginea* (Figure 3).

The occurrence of *Microtermes* also varied with tree species (ANOVA with logit transformation, $F_{5,180} = 8.61$; $P < 0.001$); the most preferred species was *P. thonningii* and the least preferred were *C. febrifuga* and *C. arborea* (Figure 3). Experiment type did not influence *Microtermes* consumption (ANOVA with logit transformation, $F_{1,180} = 0.007$; $P = 0.93$).

The interaction between wood condition and experiment type was statistically significant (ANOVA with logit transformation, $F_{4,180} = 4.35$; $P = 0.002$). When individuals of *Microtermes* had to choose between several wood conditions (CPT), fresh wood with holes (FH) was the most preferred and the least preferred was charred wood (C; ANOVA with logit transformation, $F_{4,15} = 3.86$; $P = 0.024$, post hoc Tukey's HSD test, 95% confidence interval; Figure 4).

Foraging behaviour of termites according to tree species and wood condition

The occurrence of galleries and sheetings during the first attack of termites changed according to experiment type (ANOVA with logit transformation, $F_{1,117} = 5.24$; $P = 0.02$). The occurrence of this biogenic structure changed significantly according to tree species in SPT (binomial GLM model with logit link; deviance = 12.95, d$f = 5$, $\chi^2 = 136.53$, $P = 0.023$, Figure 5). In addition,

more sheetings (67%) were built than galleries (33%) during the first attack of termites in SPT ($\chi^2 = 13$, d$f = 1$, $P \leq 0.001$).

CPT did not reveal any termite preference for a specific wood condition during the first attack. No significant difference was noted on the occurrence of sheetings and galleries (binomial GLM model with logit link; deviance = 3.055, d$f = 4$, $\chi^2 = 159.38$, $P = 0.55$; Figure 5). Termites built nearly as many galleries (46%) as sheetings (54%) during their first attack ($\chi^2 = 0.68$, d$f = 1$, $P = 0.41$).

Wood density and humidity per species

Wood block density varied with tree species and condition (ANOVA, $F_{4,40} = 14.53$; $P < 0.001$ and $F_{3,40} = 118.28$; $P < 0.001$). Highest densities were observed in dry woods of *C. febrifuga*, *B. ferruginea* *P. thonningii* and *T. schimperiana*, whereas *C. arborea* presented the lowest value. Intermediate density was observed in fresh woods of *T. schimperiana* (Figure 6). Wood humidity averaged ~30%, but varied according to species (ANOVA, $F_{4,20} = 3.12$; $P = 0.04$). *C. arborea* presented the highest water content, whereas *B. ferruginea* presented the lowest value (Figure 7).

Discussion

Among the eight termite genera collected in this work, only *Ancistrotermes* and *Microtermes* were significantly abundant. As wood-feeders were frequently found in living trees[9], we expected to collect more of them on wood
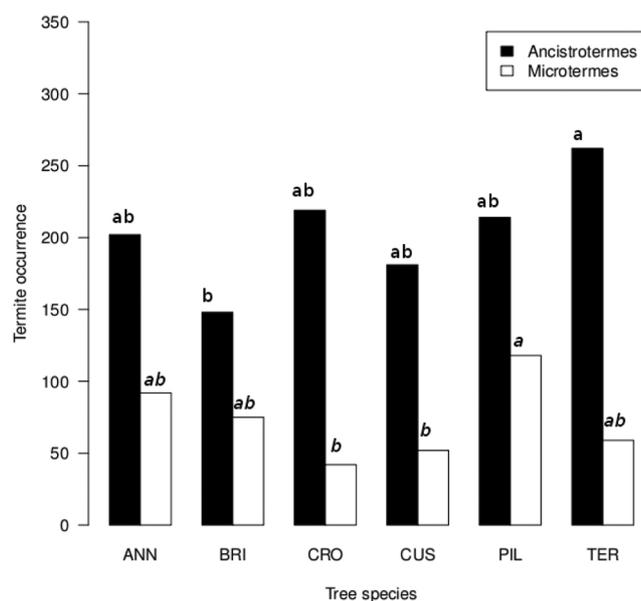

Figure 3. Tree species preferences of *Ancistrotermes* and *Microtermes*. Letters indicate groups of non-significantly different values at the 95% level according to per-termite genus Tukey's HSD post-hoc tests. Species codes as in Figure 2.
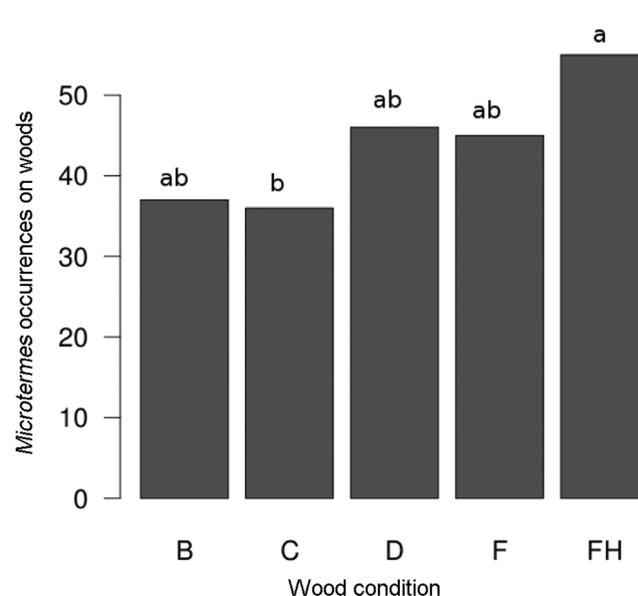

Figure 4. *Microtermes* preferences in the wood condition preference test. Letters indicate groups of non-significantly different values at the 95% level according to Tukey's HSD post-hoc tests. B, Burned; C, Charred; D, Dry; F, Fresh; FH, Fresh with holes.

blocks, but found fungus-growing termites instead, as observed by Basu[38] in Lamto on food preference of fungus-growing termites. Fungus-growers (Termitidae : Macrotermitinae) need plant material for the establishment of their fungus combs, known as the substratum of their symbiotic fungi[39]. In addition, termites of these two genera have been classified as pests in many studies in human-managed ecosystems[40–43] and naturals ones[44]. Together with the fact that *Ancistrotermes* and *Microtermes* are known as the most common fungus-growing termites[15,38,44] in Lamto, their habit of digging galleries into living trees was also revealed in natural ecosystems[9,15,45,46].

The absence of wood-feeders on wood samples could be due to the preference for higher quantity of wood found on a whole tree: wood-feeders often build arboreal nests on living trees[9,47] and would therefore preferably exploit the trees they live on rather than risk exploration in the open to search for smaller wood quantities. For wood-feeders, wood is not only a food, but also a habitat.

As suggested by Stewart and Zalucki[48], aggregation or occurrence on different wood blocks was used as a measure of preference. The ability of termites to be attracted by one wood species or condition during their first attack was also used to measure preference.

The occurrence of termites on wood samples changed according to tree species. They also built directly more feeding sheetings than prospection galleries on wood during their first attack when presented with different wood species, suggesting that the termites are able to choose their food. Indeed, food preference of termites has been reported in several studies[38,49–51].

Among the many factors which could explain this preference of termites, we tested a possible effect of wood density and wood average humidity. Inta *et al.*[49] studied the material properties on termite food choice. According to Behr *et al.*[37], termites prefer lower density wood because wood density affects the fragmentation process by termites[52]. According to our density measurements, wood densities were remarkably similar among species, except for *C. arborea* which had low density and high water content. The uniformity in density prevents any explanation of preferences based on this factor alone.
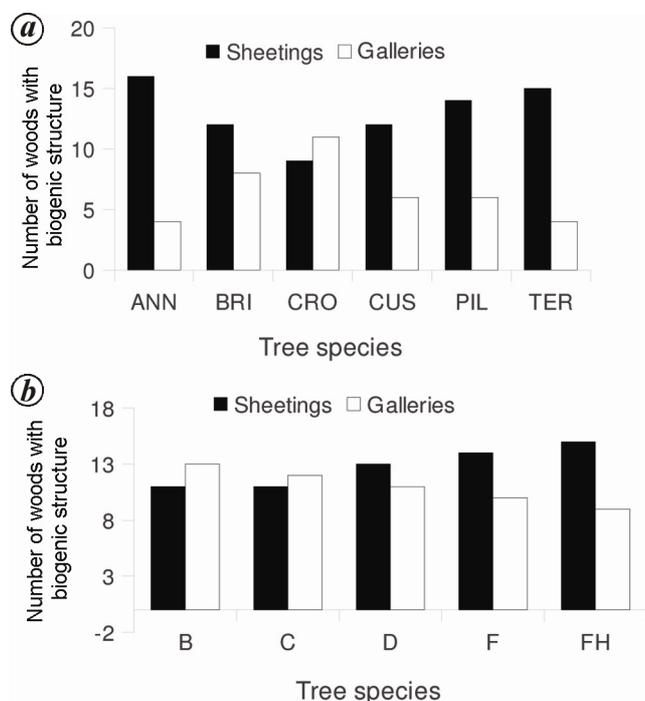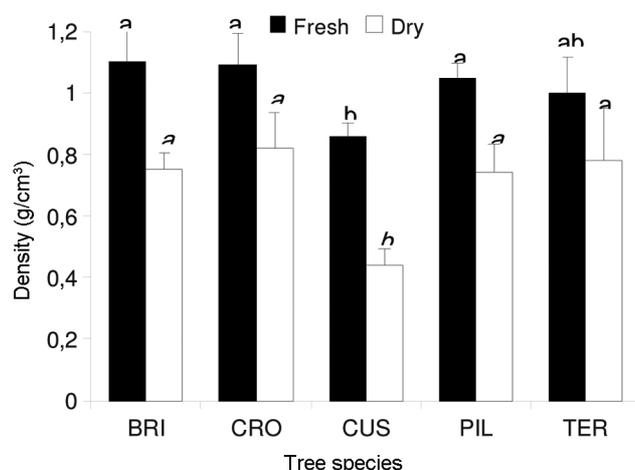

Figure 6. Density according to wood species and condition. Species codes as in Figure 2. Letters indicate groups of non-significantly different values at the 95% level according to per-wood density Tukey's HSD post-hoc tests.

Figure 5. Biogenic structures build by termites on wood during the first attack on (*a*) SPT and (*b*) CPT. Species and wood conditions codes as in Figures 2 and 4.
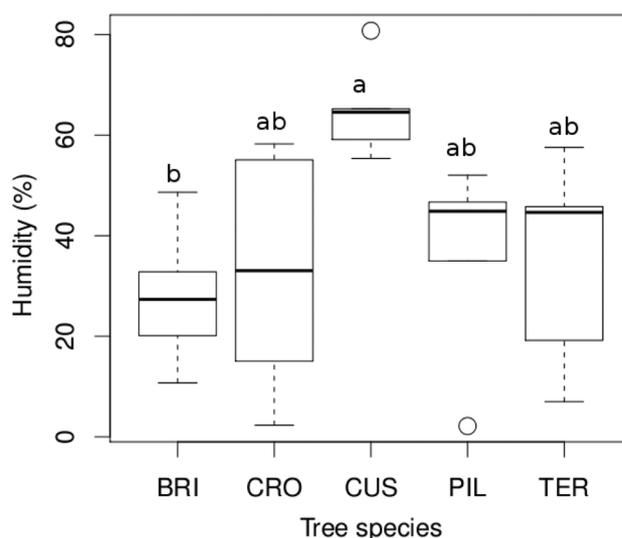

Figure 7. Water content of different wood species. Species codes as in Figure 2. Letters indicate groups of non-significantly different values at the 95% level according to per-wood humidity Tukey's HSD post-hoc tests.

Termite foraging has been shown to depend on moisture in some cases[53,54]. As in case of humidity, the pattern of variations of wood humidity did not match the preferences of the studied termite genera (Figure 7). According to Wong and Lee[55], several factors could explain the food preference of termites. In a laboratory experiment, these authors studied up to ten factors to explain the feeding behaviour of *Micorcerotermes crassus*. In field experiments, many other factors could further complicate the patterns. Any tree species did not seem attractive for termites since they did not compete for the same tree species.

Fresh wood with holes was preferred by termites than the other wood conditions, probably due to the fact that holes constitute easy entry points into the wood[9]. Charred wood blocks were the least preferred, suggesting that the positive effect of fire on termite trunk-digging activity is more related to the creation of entry points and exposure of dead wood by fire than by an improvement in food quality.

Food preferences at the wood block level did not match observations on adult trees[9]. These authors[9] observed that *C. febrifuga* was a preferred target for termites, most individuals of this species being entirely piped, while in the present study *T. schimperiana* and *P. thonningii* were the two most preferred species. However, N'Dri et al.[10] have observed that *P. thonningii* (more preferred in this field experiment) suffered a higher mortality as a result of termite and fire impact.

Our results show that (1) wood-feeders are not interested in small pieces of wood, while fungus-growers are; (2) the two different genera studied have different preferences, but they do not seem to compete for the same food; (3) neither wood density nor water content is correlated with preferences; (4) holes in the bark seem to facilitate termite entry into pieces of wood; (5) the action of fire on wood apparently makes it less attractive to termites. These results tend to show that, in the field, the decision of termites to forage on a given tree species is driven by habitat and accessibility differences (points (1) and (4)) than real food quality differences (point (3)). From points (4) and (5) above, it is clear that fire improves the access of termites to dead wood, but that its direct effect on wood (charring and probably hardening) makes it less attractive to termites, thus confirming the hypothesis of N'Dri et al.[9].

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