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Association between subterranean termites and grasses in a West African savanna: spatial pattern analysis shows a significant role for *Odontotermes* n. *pauperans*

P. Jouquet[a,*], N. Boulain[a], J. Gignoux[a], M. Lepage[b]

[a] *Laboratoire d'Ecologie, UMR 7625, Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris 05, France*
[b] *IRD, 01 BP 182 Ouagadougou 01, Burkina Faso, France*

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Abstract

Fungus-growing termites (Isoptera, Macrotermitinae) play an important role in tropical ecosystems: they modify soil physical properties and thereby make food available for other organisms. These impacts justify considering the fungus-growing termites as ecosystem engineers. Fungus-growing termites have been classified in the same group because of their influence on soil properties. The aim of this work was to compare the influence of three fungus-growing termite species on the spatial pattern of some savanna grass species in a Guinean savanna (Côte d'Ivoire). Our study illustrates differences in the relationship between termite-built structures (fungus-comb chambers and lenticular mounds) and grasses. We suggest that *Odontotermes* n. *pauperans* can strongly influence the pattern of some grass species. Conversely, *Microtermes toumodiensis* and *Ancistrotermes cavithorax* appear to have no or little influences on grass species distribution, at the scale studied. Consequently, fungus-growing termites should not be regarded as a single functional group when considering their influence on grass communities.

Keywords: Functional group; Grasses; Heterogeneity; Macrotermitinae termites; Nutrients

1. Introduction

Among the soil macrofauna, many species exert a profound influence on their environment. In modifying the physico-chemical properties of the soil to a great extent, such species, called *ecosystem engineers* (sensu Jones et al., 1994), modulate the availability of resources (e.g., physical space and food) for other species such as microorganisms or plants (Lavelle, 1997). Earthworms and termites have been identified amongst the main soil engineers.

Fungus-growing termites (Isoptera, Macrotermitinae) constitute a major component of African savanna ecosystems (Bignell and Eggleton, 2000). They have significant effects on soil physico-chemical properties, which include the promotion of microbial metabolism in nest materials and increased mobilisation of ammonium and nitrate in the vicinity of the nest (e.g., Abbadie and Lepage, 1989; Brauman et al., 2000). Therefore, termite-built structures might constitute patches in the landscape where the availability of soil nutrients for plants should be improved (Konaté et al., 1999; Jouquet, 2002). This enrichment in mineral

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[*] Corresponding author. Tel.: +33 1 69 15 56 92; fax: +33 1 59 15 56 96.
E-mail address: jouquet@biologie.ens.fr (P. Jouquet).

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nitrogen could be particularly important in the savanna ecosystems where nitrogen is considered to be a limiting factor for plant productivity (Medina, 1996). In the Lamto Savanna ecosystem (Côte d'Ivoire), the three species, *Ancistrotermes cavithorax*, *Microtermes toumodiensis* and *Odontotermes* n. *pauperans* are dominant within the fungus-growing trophic group (Josens, 1972). All have below-ground nests from 5 to 25 cm depth, consisting of several units, called "fungus-comb chambers", interconnected with galleries. *Ancistrotermes* and *Microtermes* build diffuse nests in the various savanna environments, while chambers of *Odontotermes* are mostly concentrated in space and constitute huge lenticular mounds of various size (Josens, 1972; Konaté, 1998). These mounds are scattered in the Lamto savanna ecosystem. They range from 2 to 20 m in diameter and from 0 to 2 m high (Abbadie et al., 1992) and their density varies from 8.1 to 12.2 ha^{-1} (Konaté, 1998). The occurrence of such mounds is a characteristic feature of the Lamto Savanna (Abbadie et al., 1992; Konaté, 1998). The fertile "islands" created by termites may therefore be differentiated according to their size: fungus-comb chambers (scale of 1–100 cm^2; Abbadie and Lepage, 1989) and lenticular mounds (scale of 1–100 m^2; Abbadie et al., 1992; Konaté et al., 1999). At these two scales, the structures are often enriched in small particles, organic matter and mineral nitrogen in comparison with the control soil (Abbadie and Lepage, 1989; Jouquet et al., 2002).

Very few studies have analysed the influence of termite-built structures on savanna grasses (mounds and fungus-comb chambers) although the spatial pattern and diversity of plants could be indirectly influenced by them. The presence of mounds may modify the grass environment through the abundance of trees (and therefore shading effects), the abundance of litter or the point-scale change in soil properties. Moreover, an impact at the very small spatial scale of fungus-comb chambers is also possible: Jouquet (2002) pointed out grass root proliferation, taking advantage of the nutrients present in the wall of the fungus-comb chambers. This relationship is probably related both to the type of grass and the termite species.

This paper aims at describing the relationships between grasses and termite-built structures. For these purposes, we analysed (i) the abundance of dominant grasses from control savanna soils to the centre of lenticular mounds, (ii) the spatial pattern of the fungus-comb chambers, and (iii) the spatial relationships between grasses and fungus-comb chambers.

2. Materials and methods

2.1. Study site and species studied

Field data were collected at the Lamto Research Station in Côte d'Ivoire (West Africa, 6°13′N, 5°02′W) at the edge of the rain forest domain (Menaut and César, 1979), in the Guinean bioclimatic zone (rainfall $\approx$ 1200 mm year^{-1}). The study site is a shrubby savanna with dominant grasses from the Andropogonae tribe. The four dominant grass species are: *Andropogon canaliculatus*, *Andropogon schirensis*, *Hyparrhenia diplandra* and *Imperata cylindrica*. Except for the latter, all grass species form dense, unconnected, clearly identifiable tussocks. *Imperata* produces isolated or small groups of tillers connected by deep belowground rhizomes (Monnier, 1968). The species chosen, *A. cavithorax*, *M. toumodiensis* and *O.* n. *pauperans*, are the dominant Macrotermitinae species in the Lamto Savanna ecosystem and represent about 70% of the total trophic group biomass (Josens, 1972). It was impossible to delimit separate colonies and nests in the field, because the sets of interconnected chambers are impossible to track.

2.2. Data analysis and statistical methods

Data were collected at the beginning of the rainy season (April, May 2000). In three different randomly selected plots, all free of trees, two quadrats were sampled along a transect from the control savanna to the centre of the termite lenticular mound (Fig. 1): (i) the control open savanna, (ii) the mound; within the mound, two types of 1 m^2 sub-quadrats were classified as 'mound slope' or 'mound top' according to their topography (same classification as Konaté et al., 1999). Quadrat size was adapted to mound size, i.e. 4 m × 5 m for all quadrats on one transect, and 3 m × 3 m on the two other transects. Mound slope sub-quadrats represented 8/20, 3/9 and 3/9 m^2 in the three transects. All grass tussocks and fungus-comb chambers found in the first 25 cm of soil were mapped. The density of fungus-comb chambers and grasses

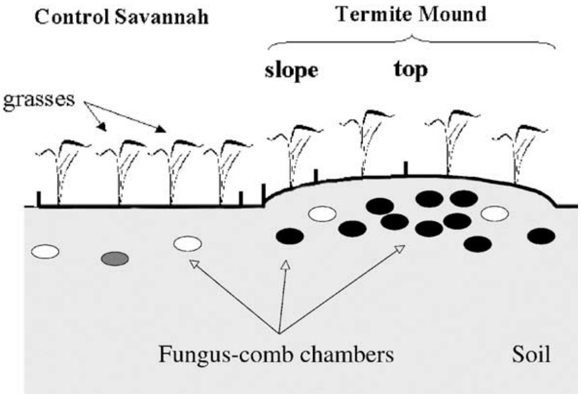

Fig. 1. Location of sampling quadrats (in bold) along a transect from the top of lenticular mounds to the surrounding savanna. The termite species were *A. cavithorax* (fungus-comb chambers are in white), *M. toumodiensis* (in grey) and *O.* n. *pauperans* (in black), and the four dominant grass species were *A. canaliculatus*, *H. diplandra*, *A. schirensis* and *I. cylindrica*.

were computed per 1 m^2-sub-quadrat. Densities were analysed by two-way analysis of variance (ANOVA) with transects and locations within the transect (control, slope and top of the mound) as factors. All tests were performed at the $P < 0.05$ significance level.

The spatial distribution of fungus-comb chambers and associated grasses was analysed using a method adapted to spatial point processes, based on Diggle's nearest neighbour functions *F(x)* and *G(w)* and Ripley's *K(d)* function (Ripley, 1981; Diggle, 1983; Barot et al., 1999). Analyses were carried out for the control savanna and on the top of the mound. The spatial distribution and association between grasses and fungus-comb chambers were not analysed in the case of the slope of the mound because not enough data were available. *G*, *F* and *K* functions analysed the spatial pattern whereas the spatial interactions were analysed by $G_{1\text{-}2}$, $G_{2\text{-}1}$ and *K* functions in accordance with Barot et al. (1999). Observed functions for the measured samples were compared to the theoretical functions under the null hypothesis of a complete spatial randomness (or independence in the spatial association test) (Fig. 2). The method enables testing of (i) whether the observed samples are regularly, randomly or aggregatedly distributed and (ii) whether the relationships between two types of sampled points are positive (association), negative (repulsion) or neutral (independence). Statistical analyses were performed with SPASTAT (Barot et al., 1999) and the SAS statistical software (Statistical Analysis System, SAS Institute 1989). Samples lower than 10 points per quadrat were not analysed and Monte Carlo tests were computed with 999 simulations. All tests were performed at the $P < 0.05$ significance level.

3. Results

3.1. Spatial relationships between lenticular mounds and grass community

The densities of grass species among the sampled quadrats are shown in Fig. 3a. Results of the two-way ANOVA show significant differences amongst transects for all grass species (Table 1a). The density of all grasses as well as the specific densities of *H. diplandra* and *A. schirensis* decreased significantly along the transect from the control soil to the top of the lenticular mounds while the densities of *I. cylindrica* increased from the control savanna to the top of the lenticular mounds (Table 1a). No significant difference occurred with *A. canaliculatus*. Although weakly represented in the control soil, *I. cylindrica* became the dominant species on the top of lenticular mounds. Conversely, although *H. diplandra* and *A. schirensis* were dominant grass species in the control savanna, they were rarely present on the mounds.

3.2. Distribution and density of fungus-comb chambers

The pattern of fungus-comb chamber distribution in the different sites is described in Table 2. Fungus-comb chambers were aggregated in all cases.

Densities of fungus-comb chambers are shown in Fig. 3b. The density of all fungus-comb chambers increased significantly from the control soil to the top of the mounds (Table 1b). However, results were different according to termite species: *Odontotermes* fungus-comb chambers were very rare in the control soil and their density increased significantly from the slope to the top of the mounds; the density of *Ancistrotermes* fungus-comb chambers did not change significantly and the densities of *Microtermes* fungus-comb chambers decreased along the transect.

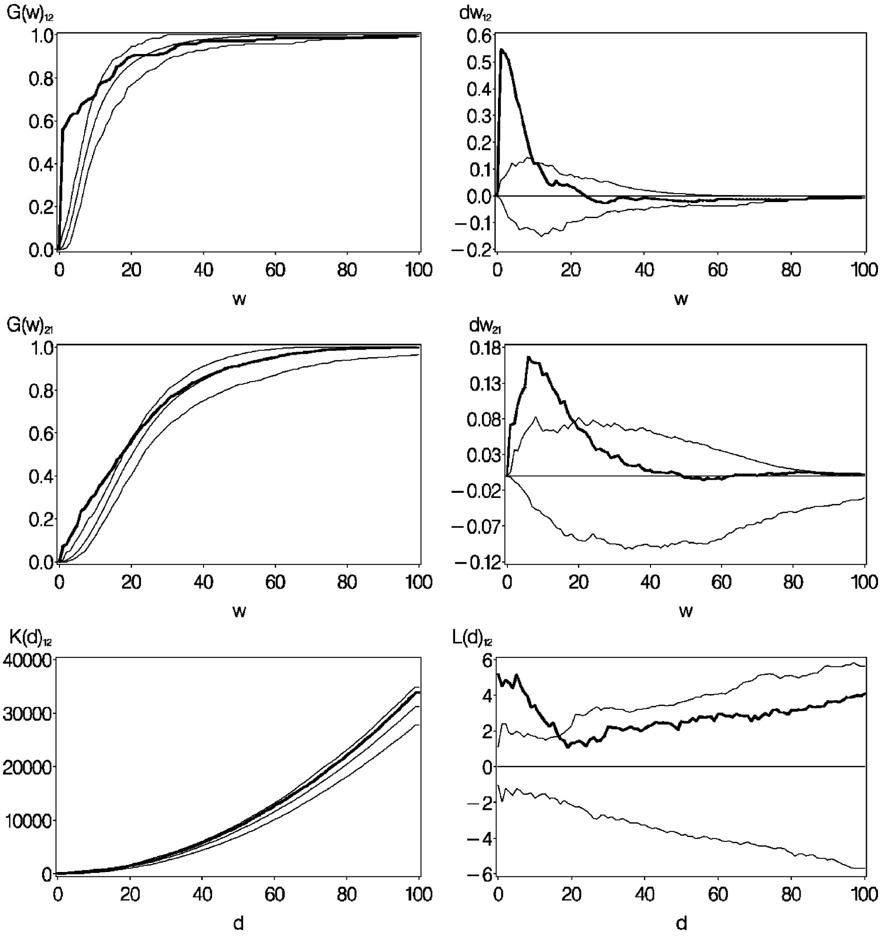

Fig. 2. Example of spatial association analysis. Graphs of the functions $G_{1\text{-}2}$, $G_{2\text{-}1}$ and K and the corresponding test statistics $dw_{1\text{-}2}$, $dw_{2\text{-}1}$ and L between Macrotermitinae termites ($n = 1132$) and *A. canaliculatus* ($n = 150$) on the top of the mound. The variable w denotes the distance between a point of the sample and its nearest neighbour whereas d is the distance between any two points of the sample. Black line: function for the observed point patterns; Grey line: theoretical function for a random spatial pattern (middle curve) and envelope of 999 simulations as a confidence interval (extreme curves). Test results are $dw_{1\text{-}2} = 0.55$, $P < 0.001$; $dw_{2\text{-}1} = 0.17$, $P < 0.001$; $L = 5.17$, $P = 0.006$.

The densities of *Microtermes* and *Ancistrotermes* fungus-comb chambers were similar amongst the quadrats while significant differences occurred with the density of *Odontotermes* chambers. Similarly, considering termite species as a whole, we found a significant transect effect.

3.3. Spatial relationships between grasses and fungus-comb chambers

When Macrotermitinae are considered as belonging to the same functional group, there was no relationship evident with grass species on the control soil, while associations were found on the top of the mounds (Table 3).

The association pattern of Macrotermitinae as a whole to *A. canaliculatus* changed between the open savanna and the top of the mounds from independence to association. This pattern was not visible for *H. diplandra* and *A. schirensis,* present in both sites, but this may be due to their low density on the top of the mound (Fig. 3a). As for *A. canaliculatus* these species were independent of fungus-comb chambers in the open savanna. *I. cylindrica*, which was present

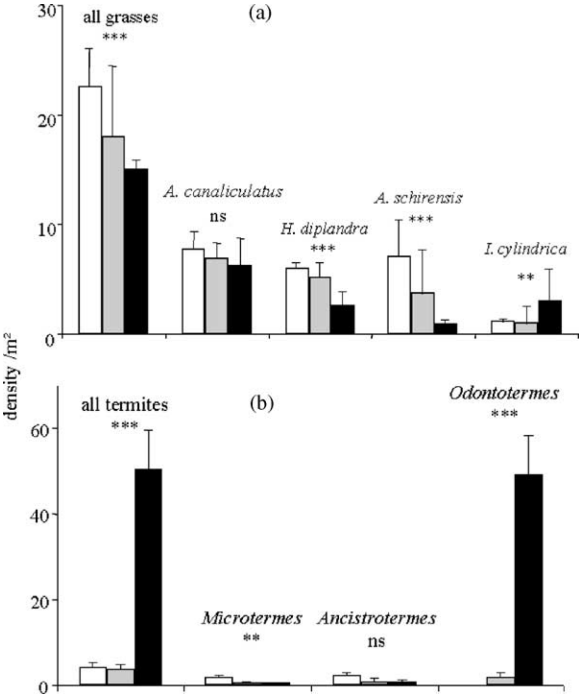

Fig. 3. Density of tussock grasses (a) and fungus-comb chambers (b) along the transect from the control soil to the top of the mound (control, in white; slope, in grey and top of the mound, in black). Significance of the location effect on density: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; ns $P \geq 0.05$.

Table 1
Results of the two-way ANOVA on the effect of the factors 'transect' and 'within transect location' on the density of grasses (a) and termite fungus-comb chambers (b)

	d.f.	*F*	*P*-level
(a)			
Grasses			
Transect (1)	2	11.57	<0.001
Location within transect (2)	2	8.15	<0.001
Interaction (1, 2)	4	3.34	0.015
A. canaliculatus			
Transect (1)	2	7.24	0.001
Location within transect (2)	2	1.14	0.326
Interaction (1, 2)	4	3.73	0.008
H. diplandra			
Transect (1)	2	3.95	0.024
Location within transect (2)	2	12.10	<0.001
Interaction (1, 2)	4	3.09	0.021
A. schirensis			
Transect (1)	2	30.52	<0.001
Location within transect (2)	2	27.39	<0.001
Interaction (1, 2)	4	7.00	<0.001
I. Cylindrica			
Transect (1)	2	20.38	<0.001
Location within transect (2)	2	6.96	0.002
Interaction (1, 2)	4	4.38	0.003
Termites			
Transect (1)	2	5.52	0.006
Location within transect (2)	2	90.85	<0.001
Interaction (1, 2)	4	4.46	0.003
(b)			
Microtermes			
Transect (1)	2	0.34	0.710
Location within transect (2)	2	6.10	0.003
Interaction (1, 2)	4	0.35	0.84
Ancistrotermes			
Transect (1)	2	0.83	0.441
Location within transect (2)	2	2.61	0.080
Interaction (1, 2)	4	0.39	0.813
Odontotermes			
Transect (1)	2	6.42	0.003
Location within transect (2)	2	104.02	<0.001
Interaction (1, 2)	4	4.42	0.003

only on the top of mound was significantly associated with fungus-comb chambers.

Considering grass species as a whole, no relationship was found between *Ancistrotermes* or *Microtermes* fungus-comb chambers and grasses. Conversely, *Odontotermes* and grasses were directly associated on the top of the mounds.

Almost all the species by species tests were consistent with these general patterns: on the top of the mounds, *Odontotermes* and grasses tended to be associated (except for *A. schirensis*); all the other tests resulted in independence (except *A. canaliculatus* and *Ancistrotermes* on the mound).

4. Discussion

4.1. Termite spatial distribution

Our results are consistent with Konaté (1998) who studied the distribution of fungus-comb chambers in the Lamto savanna ecosystem. The fungus-comb chambers were aggregated in all the quadrats. We found a higher density of fungus-comb chambers on the mounds (15.5 times higher) than in the control soil and 96% came from *Odontotermes* spp. Conversely,

Table 2
Analysis of spatial pattern of termite fungus-comb chambers using *G(w), F(x)* and *K(d)* tests of spatial distribution (see Section 2.2)

Distribution	Tests	Control	Top of the mound
Macrotermitinae	$G(w)$	A ($P < 0.001$)	A ($P < 0.001$)
	$F(x)$	A ($P < 0.001$)	A ($P < 0.001$)
	$K(d)$	A ($P < 0.001$)	A ($P < 0.001$)
		$n = 182$	$n = 1133$
Odontotermes	$G(w)$	$n < 10$	A ($P < 0.001$)
	$F(x)$		A ($P < 0.001$)
	$K(d)$		A ($P < 0.001$)
			$n = 1096$
Ancistrotermes	$G(w)$	A ($P < 0.001$)	A ($P = 0.002$)
	$F(x)$	A ($P = 0.007$)	A ($P < 0.001$)
	$K(d)$	A ($P < 0.001$)	A ($P < 0.001$)
		$n = 102$	$n = 19$
Microtermes	$G(w)$	A ($P = 0.035$)	$n < 10$
	$F(x)$	A ($P = 0.001$)	
	$K(d)$	A ($P < 0.001$)	
		$n = 75$	

A = aggregated pattern. *P*-values test the null hypothesis, H_0 of random distribution. n = number of fungus-comb chambers in the three sites. For $n < 10$ per site, the power of tests is too weak to perform analysis.

Microtermes was very rare on the mounds whereas the density of *Ancistrotermes* fungus-comb chambers was similar whatever the site. Our results are consistent with those of Sheppe (1970) and Konaté (1998) who considered *Odontotermes* as the main agent responsible for mound dynamics.

It is well-known that the soil worked by termites is enriched in fine particles, cations, and mineral nitrogen and has a better water holding capacity than the control unworked soil (Holt and Lepage, 2000; Jouquet, 2002). Consequently, the aggregation of fungus-comb chambers leads to the concentration of nutrients in the savanna and to the increase in the heterogeneity of nutrient availability for plants. Our results suggest that, in building the mounds, *O.* n. *pauperans* plays a greater role in the maintenance of the heterogeneity in the savanna than *M. toumodiensis* and *A. cavithorax*.

4.2. Spatial relationships between termite-built structures and grasses

The lenticular mound density varies from 8.1 to 12.2 ha^{-1} (Konaté, 1998) and could represent up to 9% of the area in the Lamto savanna (Abbadie et al., 1992; Konaté et al., 1999). Such mounds can be considered as fertile “islands” in the savanna maintaining factors (such as resistance to fire, shade, mineral nutrients and water availability) necessary for the development of some grass species to the detriment of others. For instance, the density of *I. cylindrica* increased and it became dominant on the top of mounds. Inversely, *H. diplandra* and *A. schirensis* were frequently observed in the control savanna whereas they had very low densities on mounds. Because *Odontotermes* is supposed to be responsible for the mound construction, it can also be considered as responsible for the change in the grass community and, in other words, as a keystone species because the presence and abundance of *I. cylindrica* seems to be directly linked to its activity.

Spatial association analyses demonstrated that *Odontotermes* n. *pauperans* is a key species in grass–Macrotermitinae relations: where it is present, spatial association with grass tussocks occurred, while the other termite species are not involved in any associations (except for a few particular association patterns). Fungus-comb chambers are enriched in fine particles such as clay, soil organic matter and mineral nitrogen as compared to the control savanna soil (Abbadie and Lepage, 1989). At a smaller scale than lenticular mounds, fungus-comb chambers can be considered as nutrient-rich patches in the savanna ecosystem. Two opposite mechanisms could be suggested to explain the relationship between grasses and termite fungus-comb chambers: first, if there was a termite food preference towards some grass species, the fungus-comb chambers could be built in the vicinity of these to optimise building and foraging effort. Analyses done in the laboratory by Konaté (1998) illustrated that fungus-growing termite species forage mostly on ground litter from shrub or herbaceous species. Although the termites feed on both grasses and wood litter, *Ancistotermes* feeds preferentially on wood while *Odontotermes* feeds preferentially on herbaceous material (Konaté, 1998). Concurrently, this author has shown that *Odontotermes* n. *pauperans* prefers *I. cylindrica* as compared to *A. schirensis*. Therefore, there is a clear agreement between the *Odontotermes* food preferences and their relationships with *I. cylindrica* (association) and *A. schirensis* (repulsion), and between the absence of association and the food preference of *Ancistrotermes*. Secondly,

Table 3
Relationships between grasses (1) and fungus-comb chambers (2)

Associations	Control				Top of the Mound			
	n	$G_{2\text{-}1}$	$G_{1\text{-}2}$	K	n	$G_{2\text{-}1}$	$G_{1\text{-}2}$	K
Grasses (1) ×	897	$P = 0.351$	$P = 0.273$	$P = 0.324$	291	$P < 0.001$	$P < 0.001$	$P = 0.002$
Macrotermitinae (2)	183	Ind	Ind	Ind	1132	A	A	A
A. canaliculatus (1) ×	321	$P = 0.420$	$P = 0.679$	$P = 0.339$	143	$P < 0.001$	$P < 0.001$	$P = 0.006$
Macrotermitinae (2)	183	Ind	Ind	Ind	1132	A	A	A
A. schirensis (1) ×	332	$P = 0.019$	$P = 0.717$	$P = 0.815$	26	$P = 0.408$	$P = 0.047$	$P = 0.117$
Macrotermitinae (2)	183	A	Ind	Ind	1132	Ind	R	Ind
I. cylindrica (1) ×	16 183				69	$P < 0.001$	$P = 0.030$	$P = 0.278$
Macrotermitinae (2)					1132	A	A	Ind
H. diplandra (1) ×	228	$P = 0.009$	$P = 0.520$	$P = 0.519$	53	$P < 0.001$	$P = 0.814$	$P = 0.308$
Macrotermitinae (2)	183	R	Ind	Ind	1132	A	Ind	Ind
Grasses (1) ×	897	$P = 0.413$	$P = 0.629$	$P = 0.763$	291	$P = 0.408$	$P = 0.383$	$P = 0.985$
Ancistrotermes (2)	102	Ind	Ind	Ind	19	Ind	Ind	Ind
Grasses (1) ×	897	$P = 0.769$	$P = 0.674$	$P = 0.241$	291			
Microtermes (2)	76	Ind	Ind	Ind	8			
Grasses (1) ×	897				291	$P < 0.001$	$P < 0.001$	$P = 0.016$
Odontotermes (2)	5				1095	A	A	A
A. canaliculatus (1) ×	321	$P =0.375$	$P = 0.833$	$P = 0.515$	143	$P = 0.154$	$P = 0.104$	$P = 0.024$
Ancistrotermes (2)	102	Ind	Ind	Ind	19	Ind	Ind	R
A. schirensis (1) ×	332	$P = 0.103$	$P = 0.995$	$P = 0.781$	26	$P = 0.188$	$P = 0.080$	$P = 0.083$
Ancistrotermes (2)	102	Ind	Ind	Ind	19	Ind	Ind	Ind
I. cylindrica (1) ×	16				69	$P = 0.706$	$P = 0.804$	$P = 0.466$
Ancistrotermes (2)	102				19	Ind	Ind	Ind
H. diplandra (1) ×	228	$P = 0.718$	$P = 0.602$	$P = 0.774$	53	$P = 0.570$	$P = 0.302$	$P = 0.414$
Ancistrotermes (2)	102	Ind	Ind	Ind	19	Ind	Ind	Ind
A. canaliculatus (1) ×	321	$P = 0.890$	$P = 0.657$	$P = 0.890$	143			
Microtermes (2)	76	Ind	Ind	Ind	18			
A. schirensis (1) ×	332	$P = 0.424$	$P = 0.534$	$P = 0.862$	26			
Microtermes (2)	76	Ind	Ind	Ind	18			
I. cylindrica (1) ×	16				69			
Microtermes (2)	76				18			
H. diplandra (1) ×	228	$P = 0.214$	$P = 0.870$	$P = 0.311$	53			
Microtermes (2)	76	Ind	Ind	Ind	18			
A. canaliculatus (1) ×	321				143	$P = 0.001$	$P = 0.001$	$P = 0.001$
Odontotermes (2)	5				1095	A	A	A
A. schirensis (1) ×	332				26	$P = 0.070$	$P = 0.001$	$P = 0.016$
Odontotermes (2)	5				1095	Ind	R	R
I. cylindrica (1) ×	16				69	$P = 0.001$	$P = 0.030$	$P = 0.278$
Odontotermes (2)	5				1095	A	A	Ind
H. diplandra (1) ×	228				53	$P = 0.001$	$P = 0.586$	$P = 0.180$
Odontotermes (2)	5				1095	A	Ind	Ind

The number of individuals per group (n) is given in the first column; G, F and K are tests of spatial distribution. The probabilities are testing the null hypothesis of pattern independence between fungus-comb chambers and grasses. For each test, the first line is the P-value estimated from Monte Carlo simulations, and the second is the results of the $G_{2\text{-}1}$, $G_{1\text{-}2}$ and K tests: ‘A’ for association, ‘R’ for repulsion and ‘Ind’ for independence. For $n < 10$ per quadrat, the power of tests is too weak to perform analysis.

if grasses were able to take advantage of the nutrients available from the wall of the fungus-comb chambers by developing more roots in these areas, there could be a spatial association, with grass tussocks growing close to fungus-comb chambers having a competitive advantage. The fungus-comb chambers of *Microtermes* and *Ancistrotermes* are temporary structures depending on the season and the local food (Josens, 1972) and their density was less in the open savanna. Therefore, a permanent spatial association between termite structures and grass roots was not likely to be established in this case. Thus, structures built by *Microtermes* and *Ancistrotermes* in the savanna had no or little impact on grass distribution. On the other hand, the density of *Odontotermes* fungus-comb chambers was greater on the mounds and these structures are more permanent throughout the season (Josens, 1972). The nutrients from the wall of such structures may therefore be available for grasses.

One may question whether the repulsion evident between grasses and termite structures is responsible for the negative relationship found between *Odontotermes* chambers and *A. schirensis* on the top of mounds. As suggested by Rogers et al. (1999), we hypothesise that termites could reduce plant growth by pruning the roots that invade the termite chambers. Another explanation could be related to the ecology of *A. schirensis* and the hydraulic properties of the mounds. This grass species may prefer a slightly moister soil than that which would be present on the tops of convex mound surfaces.

4.3. Relevance of the functional group concept

When Macrotermitinae are considered as a functional group, two sites are clearly differentiated. First, the soil outside the lenticular mound with few fungus-comb chambers where no relationship was found between their spatial distributions and those of grasses. Therefore, the direct effect of Macrotermitinae on grasses is assumed to be very weak. The second site corresponds to the mound where the fungus-comb chamber density was greater and where we found associations between fungus-comb chambers and grasses. Taking into account the termite species, *Odontotermes* species appeared as a keystone species and ecosystem engineer because of its building activity and its influence on the distribution and abundance of grasses in the savanna. Conversely, *Ancistrotermes* and *Microtermes*, although well-represented in the whole savanna, did not seem to have a significant impact on the grass pattern at the scale we studied. In conclusion, this study illustrates the complexity of the functional group concept when applied to Macrotermitinae termites. Distinguishing between the different termite species within the subfamilly Macrotermitinae results in a better understanding of the influence of fungus-growing termites on the savanna vegetation than when using the functional group concept. When applied to fungus-growing termites, the biological attributes of each species (pattern of the fungus-comb chamber, food preference . . .) should be taken into account to assess their exact role in ecosystem functioning.

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