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Influence of large termitaria on soil characteristics, soil water regime, and tree leaf shedding pattern in a West African savanna

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Abstract

Termitaria are major sites of functional heterogeneity in tropical ecosystems, through their strong influence on soil characteristics, in particular soil physico-chemical properties and water status. These factors have important consequences on nutrient availability for plants, plant spatial distribution, and vegetation dynamics. However, comprehensive information about the influence of termite-rehandled soil on soil water regime is lacking. In a humid shrubby savanna, we characterized the spatial variations in soil texture, soil structure and maximum soil water content available for plants (AWC_{max}) induced by a large termite mound, at three deepths (0–0.10, 0.20–0.30 and 0.50–0.60 m). In addition, during a three month period at the end of the rainy season, soil water potential was surveyed by matrix sensors located on the termite mound and in the surrounding soil at the same depths and for the 80–90 cm layer. Concurrently, the leaf shedding patterns of two coexisting deciduous shrub species exhibiting contrasted soil water uptake patterns were compared for individuals located on termite mounds and in undisturbed control areas. For all the soil layers studied, clay and silt contents were higher for the mound soil. Total soil clods porosity was higher on the mound than in control areas, particularly in the 0.20-0.60 m layer, and mound soil exhibited a high shrinking/swelling capacity. AWC_{max} of the 0-0.60 m soil layer was substantially higher on the termite mound (112 mm) than in the surroundings (84 mm). Furthermore, during the beginning of the dry season, soil water potential measured *in situ* for the 0.20-0.90 m soil layer was higher on the mound than in the control soil. In contrast, soil water potential of the 0-0.10 m soil layer was similar on the mound and in the control soil. In the middle of the dry season, the leaf shedding pattern of *Crossopteryx febrifuga* shrubs (which have limited access to soil layers below 0.60 m) located on mounds was less pronounced than that of individuals located on control soil. In contrast, the leaf shedding pattern of the shrub *Cussonia barteri* (which has a good access to deep soil layers) was not influenced by the termite mound. We conclude that in this savanna ecosystem, termite mounds appear as peculiar sites which exhibit improved soil water availability for plants in upper soil layers, and significantly influence aspects of plant function. Implications of these results for understanding and modelling savanna function and dynamics, and particularly competitive interactions between plant species, are discussed.

Introduction

Termite mounds are among the most conspicuous figures of many tropical ecosystems, especially in African savanna landscapes. Termites process considerable quantities of material in their building activities, strongly influencing the soil properties as compared to surrounding soils (reviewed in Lee and Wood, 1971 and Lobry de Bruyn and Cornacher, 1990; see also Arshad, 1982; Maduakor et al., 1995; Pomeroy, 1976, 1983). These modifications have a great impact on the vegetation, through spatial and temporal effects, even when the termite colony is dead and the mound material subject to erosion (Belsky et al., 1983; Glover et

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al., 1964; Kang, 1978; Soyer 1983; Troll, 1936). Thus termites have been referred to as large soil builders and ecosystem engineers (Dangerfield et al., 1998; Jones et al., 1994).

Many studies emphasized the role of termites on soil texture and chemical properties (Badawi et al., 1982; Hesse, 1955; Laker et al., 1982; Pomeroy, 1983; Wood et al., 1983), soil nutrient cycling and soil metabolism (Abbadie and Lepage, 1989; Arshad et al., 1982; Meiklejohn, 1965; Menaut et al., 1985). Other studies focused on termites influence on the spatial distribution and dynamics of vegetation (Aubreville, 1957; Belskyet al., 1983; Fanshawe, 1968; Malaisse and Anastassiou-Socquet., 1977; Morison et al., 1948; Myers, 1936; Wild, 1952). However, very few studies focused on the causal link between the modifications of soil properties and the consequences for the vegetation growing on termitaria. In particular, information on the role of termitaria on soil water balance is scarce (Elkins et al., 1986; Janeau and Valentin, 1987; Ouédraogo, 1997). This is a major deterrent for understanding the role of termitaria on soil nutrient cycling, primary production or vegetation dynamics because soil water availability is a key determinant of all these aspects of savanna function (Frost et al., 1986; Walker and Noy-Meir, 1982). In a humid preforest savanna (Lamto, Côte d'Ivoire), termite mounds represent a major source of heterogeneity in the landscape, occupying up to 9% of the area in some biotopes (Abbadie et al., 1992). These termitaria are sites of intense and permanent activity of soil fauna, mainly three sympatric species of fungus growing termites (*Odontotermes* sp, *Ancistrotermes cavithorax* and *Microtermes toumodiensis*) (Josens, 1972). The termitaria are also characterized by peculiar soil microbial activities (Le Roux et al., 1995a) and a peculiar vegetation pattern, as compared to the surrounding savanna (César and Menaut, 1974). In particular, the density of both mature and young individuals of woody species is 2 to 3 times higher on termitaria than in surrounding areas in open shrubby ecosystems (Abbadie et al., 1992). The work presented here focused on the impact of termites on soil texture, structure and water regime, as a potential explanation for this termitaria-vegetation relationship. We studied the soil texture, structure and the soil water regime at different depths in a termite mound and in comparable surrounding savanna areas. In a previous study (Le Roux and Bariac, 1998) performed at our experimental site, the two deciduous shrubs *Cussonia barteri* and *Crossopteryx febrifuga* were found to have different access to soil water below 60 cm depth. The timing of abscission of leaves on mounds and savanna areas was investigated.

Materials and methods

Site description and mound studied

The study was carried out at the Lamto Reserve (6°13′ N, 5°02′ W), in a typical Guinea (i.e. humid) savanna of the Côte d'Ivoire. The Guinea savanna domain is defined as a zone of dense and high grass layer dominated by scattered trees where the annual precipitations exceed 1,000 mm and where the dry season remains less than two months (Menaut, 1983). In Lamto, annual precipitations average 1,210 mm (Lamotte and Tireford., 1988). Well-defined precipitation periods occur: a long rainy season from February to November, usually interrupted by a short dry season in August, and a long dry season in December and January. Temperatures (annual mean 27 °C) are quite constant all year long.

Like in many other savannas, termitaria are a conspicuous component of the ecosystem. In Lamto, three main genus of fungus-growing termites (*Odontotermes*, *Ancistrotermes* and *Microtermes*) are associated with these mounds. *Odontotermes* is suspected to be the main contributor in the building of such large mounds of varied sizes (2–20 m in diameter and 0.10 m^{-2} m in height). Large variations in mound density (9.3–22.4 ha^{-1}) are observed between savanna biotopes (Lepage, personal communication). At a particular shrubby savanna site, Abbadie et al. (1992) showed that mounds (12.9 ha^{-1}) represented 9% of the total area and an above ground soil volume around 300 m^3 ha^{-1}.

The present study took place in an open shrubby savanna. The herbaceous layer consisted mainly of C_4 grasses dominated by *Andropogon* sp. and *Hyparrhenia* sp. The woody layer (2 <height< 6 m) was dominated by *Cussonia barteri*, *Crossopteryx febrifuga* and *Bridelia ferruginea*, altogether covering about 15% of the test site. At this site, termitaria density was 16.0 ha^{-1} and represented 3.3% of the total area (Lepage, personal communication). Tree leaf shedding experiments were made on five different termite mounds. However, a single termite mound (basal diameter = 7 m, height = 0.3 m: see Figure 1) was selected for survey of the soil water potential due to the limited number of moisture probes available. In contrast to surrounding areas, the grass cover was sparse

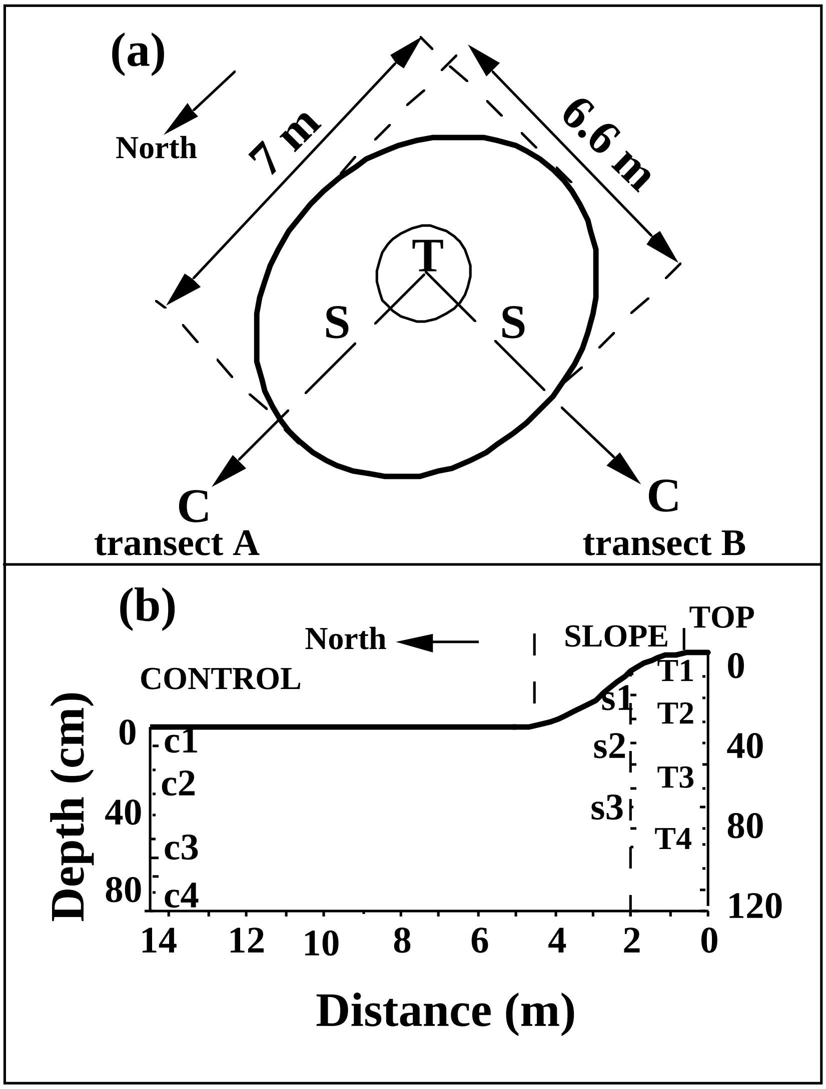

Figure 1. (a) Schematic map of the termite mound studied. The two transects instrumented and the location of the soil moisture sensors are indicated (T:Top; S:Slope; C:Control). (b) Schematic cross-section of the termite mound studied along transect A. The location of the soil moisture sensors is indicated (C, S, T) with the numbers referring to the depth (1: 0–0.10 m; 2: 0.20–0.30 m; 3: 0.50–0.60 m; 4: 0.80–0.90 m).

and the woody cover (*Anona senegalensis, Borassus aethiopum, Crossopteryx febrifuga* and *Cussonia barteri*) was dense on the selected mound.

Surveys of soil water potential in the field

To provide a continuous survey of soil water potential on mound and in control areas, eighteen soil moisture probes (Watermark model 200, Irrometer Co., Riverside, CA, USA) were used (Figure 1). These probes consist of two concentric electrodes buried in a reference matrix material which is protected by a synthetic membrane. At a given temperature, the resistance of the sensor is related to the soil water potential. The Watermark-200 probes were initially shown to be adequate for assessing soil water potential in the 0 to -0.1 MPa range (Eldredge *et al.*, 1993; Thomson and Armstrong, 1987). When used with caution and when individual calibration curves are performed *in situ*, these probes can provide reliable estimates of soil water potential down to -0.2 or -0.3 MPa (Jovanovic and Annandale, 1997; Kastanek, 1996).

The probes were installed in March, i.e. at the beginning of the long rainy season. As recommended, the sensors went through several wet and dry cycles before installation. During installation, a slurry of soil (of the layer studied) and water was used to ensure uniform soil contact. Since the moisture sensor signal is influenced by temperature (Jovanovic and Annandale, 1997; Thomson and Armstrong, 1987), a Cu/Cst thermocouple was located near each soil moisture sensor. In order to ensure satisfying soil-probe equilibration, data were only collected from mid July to the end of October. The soil moisture sensors were located on the mound top and the control areas at four depths (0.05 m, 0.25 m, 0.55 m, 0.85 m) and on the mound slope just in the three first depths, along two transects (Figure 1). The moisture probes (Campbell Scientific, 1993) and thermocouples were connected to a datalogger (CR10 and relay multiplexer AM416, Campbell Scientific, Shepshed, UK). Measurements performed at 15 min intervals provided hourly means. Since the soil water potential sensors cannot give reliable estimates of low Ψ, measurements obtained for potentials lower than -0.3 MPa were discarded. In order to test the probe curve calibration, in October, during a rainy period and a short dry period, soil samples were collected near each moisture probe for determination of soil moisture by the gravimetric method. Given the water retention curve of each soil layer, these data were used to check the probe calibration curve proposed by Thomson and Armstrong (1987):

$$\Psi = R/[0.01306(1.062(34.21 - T + 0.0106T^2) - R)] \tag{1}$$

where Ψ is the soil water potential (kPa), R is the actual sensor resistance (kΩ), and T is the actual soil temperature (°C).

Measurements of soil texture and water retention curves

At the end of the field experiment, in October, the soil moisture probes were removed and undisturbed soil samples of 152 cm^3 were collected near each probe site. The samples were collected during the rainy period and they were sealed in order to prevent them from drying. In the laboratory, soil clods of ca. 10 cm^3 were taken from these samples and brought to saturation. The relationship between the soil water potential Ψ and the soil volumetric water content θ (i.e. the soil water retention curve WRC) was documented for Ψ values ranging from -3.2 to 1600 kPa. Four pressure steps were used: 3.2, 10, 320, and 1600 kPa. For the first three pressure values, a filtration device was used as detailed in Tessier and Berrier (1979). For the lower pressure value, cells of Richards (1941) were used. At every pressure step, the clod volumes were determined by measuring buoyancy in kerosene (Monnier et al., 1973) to account for potential changes due to swelling or shrinking. Weight loss was measured by gravimetry after drying at 105 °C during 48 h. The soil volumetric water content corresponding to each pressure step was thus determined considering the measured specific bulk density of each sample at every step. Because we are dealing with a swelling soil, we used as variables the soil water ratio (or volumetric water content) (θ) and air ratio (e) computed as:

$$\theta = V_w/V_s \tag{2}$$

$$e = V_a/V_s \tag{3}$$

where V_w, V_a and V_s are the water, the air and the solid volumes of the soil clod, respectively (i.e. the total soil volume of the soil clod is given as $V_t = V_w + V_a + V_s$) (Baize, 1993). Soil water retention curves (WRC) were not determined for the 0.80–0.90 m soil layers for all the locations, and for 0.50–0.60 m layers at the mound slope. For each soil sample and at each water potential value, 3 replicates were performed. Based on the soil water retention curves, the maximum water content available for plants was computed as the difference between the values of volumetric water content measured for Ψ equal to -3.2 and -1600 kPa. Values for unstudied soil layers (i.e. 0.10–0.20 m for the three locations and 0.30–0.50 m on mound top and in control areas) were inferred by linear extrapolation.

After collecting and preparing the soil clods for WRC analysis, soil texture was determined on the remaining material for each soil sample. Organic matter was destroyed by adding 200 mL of H_2O_2 to 20 g of soil, held at 20 °C for 6 h and then 60 °C for 16 h. Distilled water (300 mL) and 25 mL hexametaphosphate (40 g L^{-1}) were then added and samples were shaken for 16 h at 175 rev min^{-1}. The aqueous suspension was sieved at 250, 100 and 50 μm. The 0-50 μm fraction was sonicated at 100 J mL^{-1} (Branson Sonifier 450) and passed throught 20 μm sieve in water. The 0–20 μm fraction was centrifugated (Sorvall RC 3B Plus, Du Pont De Nemours) to isolate a 2–20 μm fraction and a 0.05–2 μm fraction. Centrifugation speed and time were calculated according to Tanner and Jackson (1948). The resulting six fractions were dried at 40 °C: 250–2000 μm (coarse sand), 100–250 μm (fine sand), 50–100 μm (very fine sand), 20–50 μm (coarse silt), 2–20 μm (fine silt), and 0–2 μm (clay).

Table 1. Comparison of the soil texture on termite mound top and in control areas for the 0–0.1 m (Table 1a), 0.2–0.3 m (Table 1b) and 0.5–0.6 m (Table 1c) layers. Means are presented with standard errors. In each table and for each column, values with the same letter are not significantly different at the p = 0.05 level

(1a)	Clay (%)	Silt (%)		Sand (%)		
	0–2 μm	2–20 μm	20–50 μm	50–100 μ	100–250 μm	250–2000 μm
0–0.10 m	22.9^a	22.0^a	8.8^a	$10.2\ ^a$	15.7^a	20.4^a
Mound	(0.6)	(0.8)	(0.6)	(1.2)	(1.8)	(2)
0–0.10 m	8.2^b	10.4^b	6.5^b	8.5^a	19.4^b	47.0^b
Control	(0.4)	(1)	(1.1)	0.8)	(1.3)	(1.4)

(1b)	Clay (%)	Silt (%)		Sand (%)		
	0–2 μm	2–20 μm	20–50 μm	50–100 μm	100–250 μm	250–2000 μm
0.20–0.30 m	28.9^a	22.4^a	7.8^a	7.5^a	11.4^a	22.0^a
Mound	(0.6)	(0.5)	(0.5)	(1.8)	(1.7)	(1.9)
0.20–0.30 m	9.9^b	9.4^b	4.7^b	7.5^a	18.1^b	50.5^b
Control	(0.5)	(1.2)	(1.2)	(1.2)	(1.1)	(1.2)

(1c)	Clay (%)	Silt (%)		Sand (%)		
	0–2 μm	2–20 μm	20–50 μm	50–100 μm	100–250 μm	250–2000 μm
0.50–0.60 m	31.0^a	16.8^a	6.7^a	6.5^a	9.0^a	30.0^a
Mound	(1.2)	(1)	(0.9)	(0.8)	(1.1)	(1.6)
0.50–0.60 m	16.1^b	9.8^b	4.3^b	6.4^a	14.4^b	49^b
Control	(1)	(1.3)	(1.3)	(0.6)	(1.8)	(2)

Measurements of tree leaf-shedding patterns

During the end of the dry season (21/12/96 to 11/01/97), the leaf shedding patterns of the two deciduous shrubs *Cussonia barteri* and *Crossopteryx febrifuga* were surveyed on termite mounds and in control areas at this site. For both *C. barteri* and *C. febrifuga*, 10 individuals were selected: 5 trees located on 5 different termite mounds and 5 trees located in control areas. For each tree, 3 shoots were arbitrarily chosen and the number of leaves beared by each shoot was surveyed from 21 December 1996 to 11 January 1997, i.e. during the leaf shedding phase associated to the long dry season. Initially, the number of leaves per shoot surveyed was around 270 for *C. febrifuga* and 16 for *C. barteri*, with no significant differences between trees located on mounds or in control areas. Fire occurred on 15 January 1997.

Results

Textural composition of the termite mound

The comparison of the soil texture on mound and in control areas showed that the proportion of finest soil particles (i.e. 0–20 μm) was higher on the mound than in the surroundings, particularly for the upper soil layers (Table 1). For instance, clay content of the 0–0.10 m soil layer was three times higher on the mound (23%) than in the control area (8%). Clay content was similar on the mound top and in the mound slope (Figure 2). In contrast, on the mound, silt proportions decreased and sand proportions increased as a function of the distance to mound top. Soil texture observed at the boundary of the mound was close to that in the control areas (Figure 2).

Influence of the termite mound on soil air and soil water ratios, and soil water retention curves

The soil air ratio (e) determined on clods was higher on the mound than in control areas, particularly in the deeper layers (Figure 3). This means a high total soil clods porosity (p = e / [1+e]). For instance, for a soil water potential equal to -3.2 kPa, total soil clods porosity was around 46% for mound soil and only 33% for control soil in the 0.20–0.30 m layer. For each soil layer, at a given soil water potential, soil water ratio θ was always higher for mound soil than for control soil (Figure 3). In control areas, θ values at a given soil

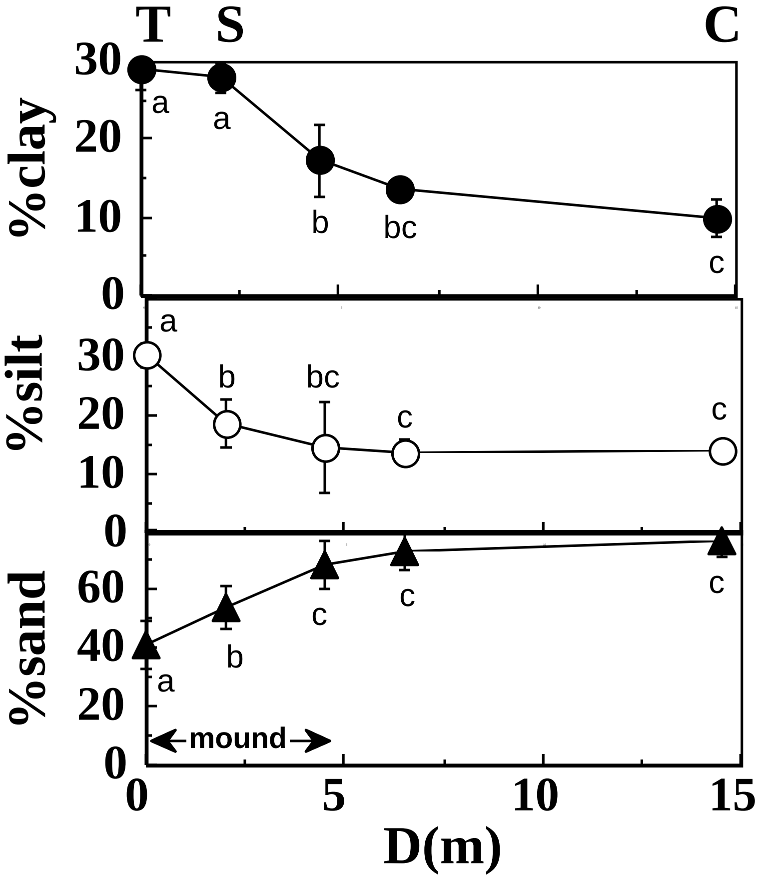

Figure 2. Spatial variations in the clay (l), silt (m), and sand (s) contents of the 0.20–0.30 m soil layer as a function of the distance to the mound top (D) (T:Top; S:Slope; C:Control). Bars are confidence intervals (p = 0.05). For each panel, values with the same letter are not significantly different at the p = 0.05 level.

Table 2. Values of the maximum water content available to plants AWC_{max} computed for the 0–30 cm and 0–60 cm soil layers on termite mound and in control areas

	AWCmax (mm)		
Soil layer	Mound (Top)	Mound (Slope)	Control areas
0–0.30 m	54	51	50
0.30–0.60 m	58	–	34
0–0.60 m	112	–	84

water potential decreased with depth. In contrast, θ values at a given soil water potential slightly increased with depth on the termite mound according to the clay proportion. The porosity open to air (difference between the void ratio and the water ratio) decreased with depth for control soil.

Figure 4 shows the shrinking curves obtained for soils sampled on mound or in control areas. The control soil exhibited a low degree of shrinking, and its porosity was saturated with a low increase in water volume. In contrast, the soil on the mound was not a fully rigid medium, and the volume of a sample significantly varied over the range of potential encompassed by the water retention curve. Thus, the mound soil exhibited an important shrinking/swelling capacity, i.e. the decrease of water volume lead to a similar change in the soil volume.

The maximum soil water content available for plants (AWC_{max}) on the mound was close to that observed in control areas for the 0–0.30 m layer (Table 2). In contrast, the maximum soil water content available for plants in the 0.30–0.60 m layer was much higher on the mound (58 mm) than in control areas (34 mm). Thus, the difference of water storage capacity in the 0–0.60 m layer between mound and control soil was 28 mm (Table 2).

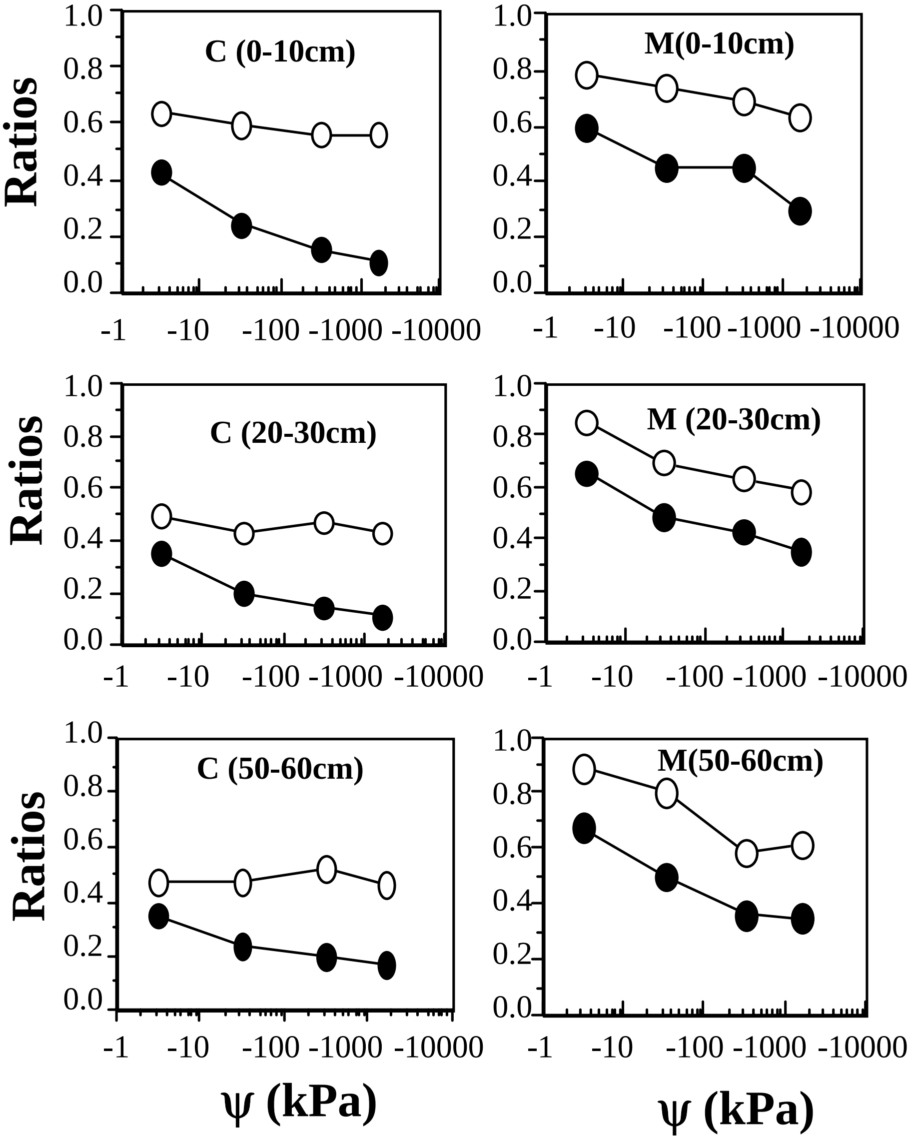

Figure 3. Spatial variation in the soil void ratio (m) and water ratio (l) as a function of the soil water potential Ψ (absolute values). Results are presented for (upper panel) the 0–0.10 m soil layer, (middle panel) the 0.20–0.30 m soil layer, and (lower panel) the 0.50–0.60 m soil layer, for control areas (C) and termite mound (M).

Effect of the termite mound on soil water regime

Whatever the depth and location, concurrent *in situ* measurements of (i) soil volumetric water content θ and (ii) soil water potential Ψ deduced from moisture sensor data by applying the calibration curve proposed by Thompson and Armstrong (1987) were consistent with the soil water retention curves determined in the laboratory (Figure 5). Thus, the proposed calibration curve (Equation 1) was retained for all the soil moisture sensors.

The temporal variations in the soil water potential were strongly correlated to the rainfall pattern in the upper soil layer, with a more rapid response than in the lower soil layer (Figure 6). During rainy periods, soil water potential remained higher than ca. -100 kPa whatever the depth, indicating that soil moisture was near the water retention upper limit (i.e. -32 kPa). During dry periods, soil water potential markedly decreased in the 0–0.10 m layer after less than one week without rainfall, while changes in Ψ were very weak in the 0.50–0.60 m and 0.80–0.90 m layers even after the

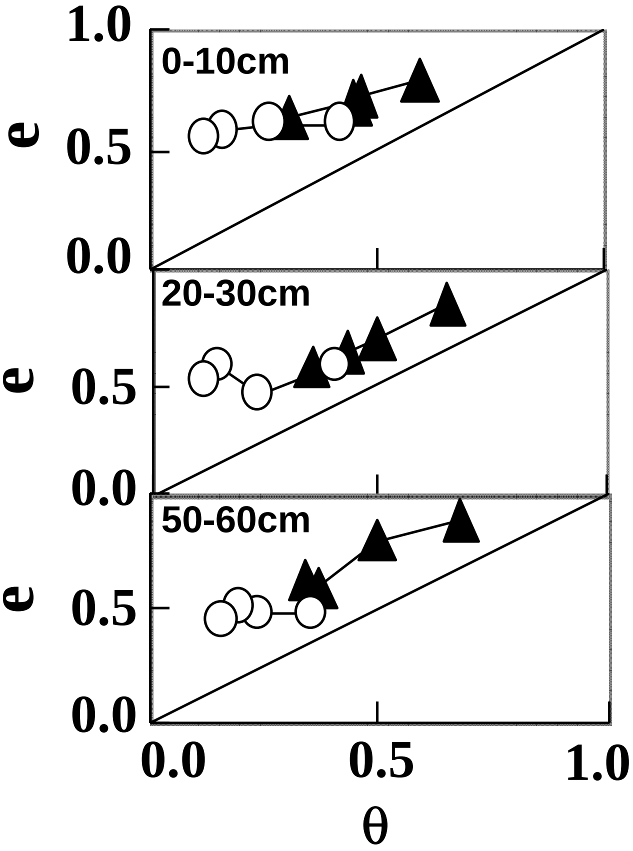

Figure 4. Variation in the soil void ratio (e) as a function of the soil water ratio (*θ*) (i.e. shrinkage curve). Results are presented for soil from the termite mound (s) and soil from control areas (m) at three depths.

12 day dry period (days of year 201 to 213). In the 0–0.10 m soil layer, variations in soil water potential on mound and in control areas were very close (Figure 6). In contrast, soil water potential in the 0.20–0.30 and moreover 0.50–0.60 m layers decreased more rapidly in control areas than on the mound during dry spells. For instance, in the 0.50–0.60 m soil layer, Ψ reached −300 kPa on day of year 262 and 273 in control areas and on the mound, respectively. In the 80–90 cm soil layer, decrease in Ψ was slightly more rapid in control areas. However, during the study period, Ψ in this layer remained always higher than -220 and -130 kPa in control areas and in the mound, respectively. Full re-hydration of this deeper soil layer was observed around days of year 278 on the control areas but not on the mound.

Influence of the termite mound on tree leaf shedding patterns

On 21 December 1996, defoliation has not begun for both *Crossopteryx febrifuga* and *Cussonia barteri*. During the three week period studied, the leaf shedding pattern of *Crossopteryx febrifuga* shrubs located on mounds was less pronounced than that of individuals located on control soil (Figure 7). In particular, on 11 January, 78% of the leaves were lost by individuals located in control areas whereas individuals located on mounds had only lost 17% of their leaves. In contrast, the leaf shedding pattern of the shrub *Cussonia barteri* was not significantly influenced by the termite mound (Figure 7). The survey of the leaf shedding pattern was interrupted in mid January since fire occurred on 15 January and induced the fall of nearly all the remaining leaves.

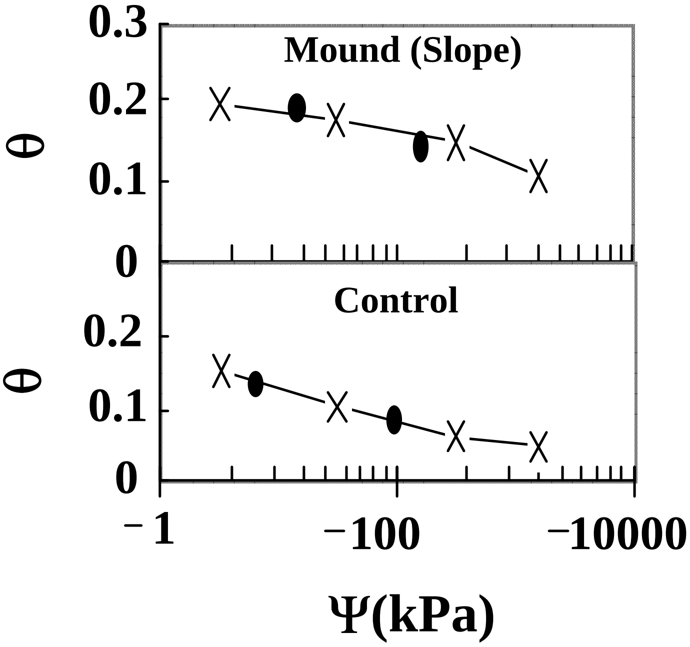

Figure 5. Comparison of the soil water retention curve determined in the laboratory (-x-), and it in situ measurements of soil volumetric water content (θ) and soil water potential Ψ deduced from moisture sensor data by applying the calibration curve proposed by Thompson and Armstrong (1987). Sample results are presented for the 0–10 cm soil layer on the termite mound slope and in control areas.

Discussion and conclusion

Impact of termite mound on soil texture and structure

Soil texture and structure were strongly modified on the termite mound as compared to the surrounding control soil. The soil on termite mound exhibited a higher proportion of fine particles (Table 1 and Figure 2). In particular, a threefold and twofold increase in clay content was observed in the 0–0.30 m and 0.50–0.60 m soil layers, respectively. Such an enrichment in fine soil particles on mounds has been reported in other tropical savanna environments (Abbadie et al., 1992; Arshad, 1982; Hesse, 1955; Lee and Wood, 1971; Lobry de Bruyn and Cornacher, 1990; Maduakor et al., 1995; Pomeroy, 1976, 1983; Wood, 1983). Soil rehandling by termites (i.e. selection and importation of finest soil particles from deep to upper soil horizons) was shown to be the main source of modification of soil texture on mounds (Grassé, 1984; Lee and Wood, 1971).

Concurrently to changes in soil texture, soil structure was deeply modified on the mound. Soil clods porosity was higher on the mound than in control areas, particularly for the deeper layers studied. Furthermore, mound soil exhibited an important shrinking/swelling capacity as found by other authors for clay-rich soils (Bruand and Prost, 1987; Tavares-Filho and Tessier, 1998). This shrinking capacity could induce soil cracking on mound and thus could increase the water infiltration rate in dry conditions, and the deeper percolation of water. This could also improve the spatial distribution of roots by the effects of cracks due to the wet-dry soil cycles. Such a change in soil structure on termite mounds were reported by Maldague (1959) and Garnier-Sillam (1991).

It should be noted that soil physical characteristics (i.e. soil water content and soil porosity) were only measured on clods. These small samples do not take in to account the soil macroporosity (e.g. termite and earthworm galleries), but they represent the best scale for observation to study the soil shrinking/swelling capacity (Chrétien et al., 1988). Furthermore, water available for plants is essentially retained in soil micropores.

Impact of termite mound on soil water availability for plants

Soil water balance is controlled by (i) the soil water storage capacity, and (ii) the different processes driving water flux in the soil-plant-atmosphere continuum, namely precipitation interception, surface runoff, soil evaporation, plant transpiration and

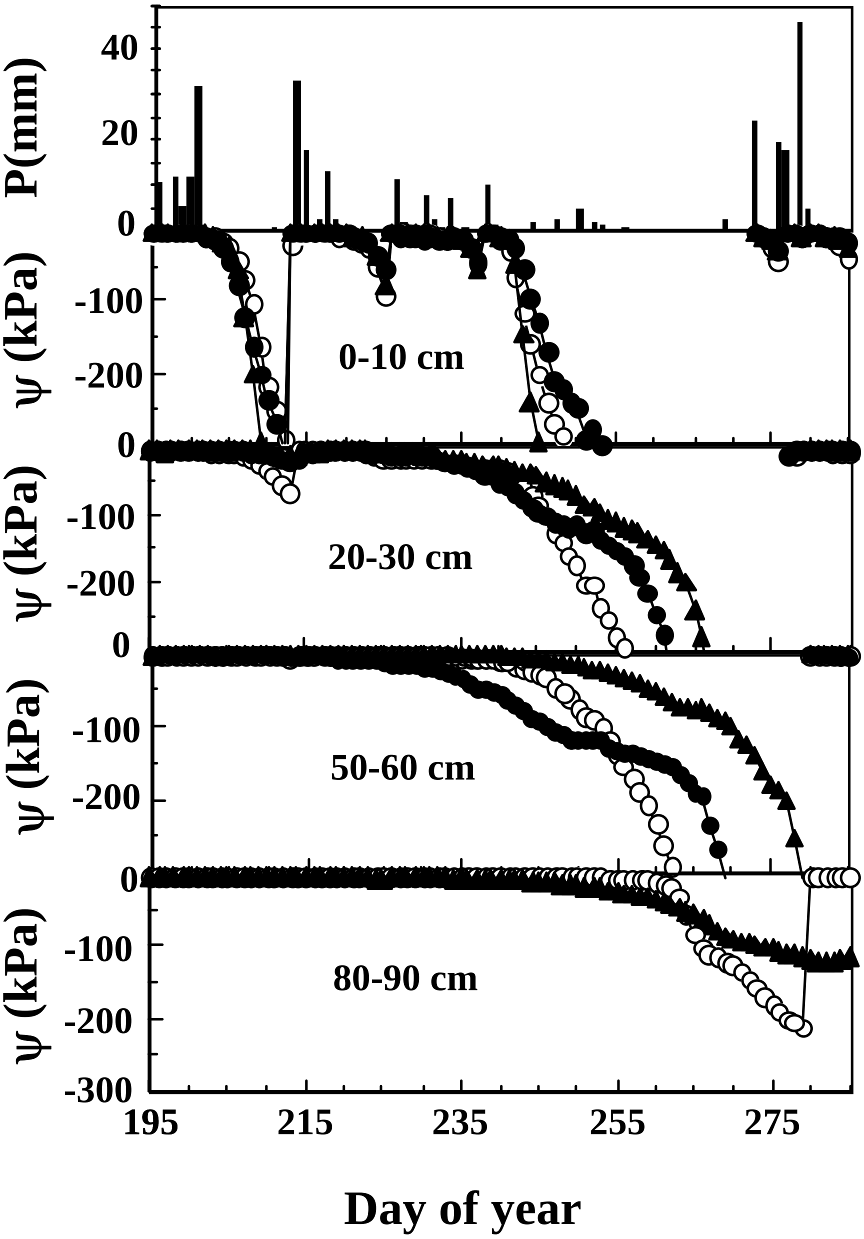

Figure 6. Temporal variations in the soil water potential Ψ at three depths (0–0.10 m, 0.20–0.30 m and 0.50–0.60 m) for the control areas (m), the mound slope (l) and the mound top (s), and at 0.80–0.90 m soil layer for the control areas (m) and the mound top (s). Daily precipitations P are indicated.

drainage below the rooting zone. However, documenting the effect of the termite mound on all these processes would have been prohibitive. Thus, only soil water potential was surveyed. This variable results from the complex interactions between the different components of the soil water balance and determines soil water availability for plants.

In this study, both soil water storage capacity and the seasonal trends in soil water potential differed on the mound as compared to control areas. As a result of the changes in soil structure, the maximum soil water content available for plants in the 0–0.60 m layer was higher on the mound (112 mm) than in control areas (84 mm) (Table 2). The value obtained in control areas is slightly higher than values previ-

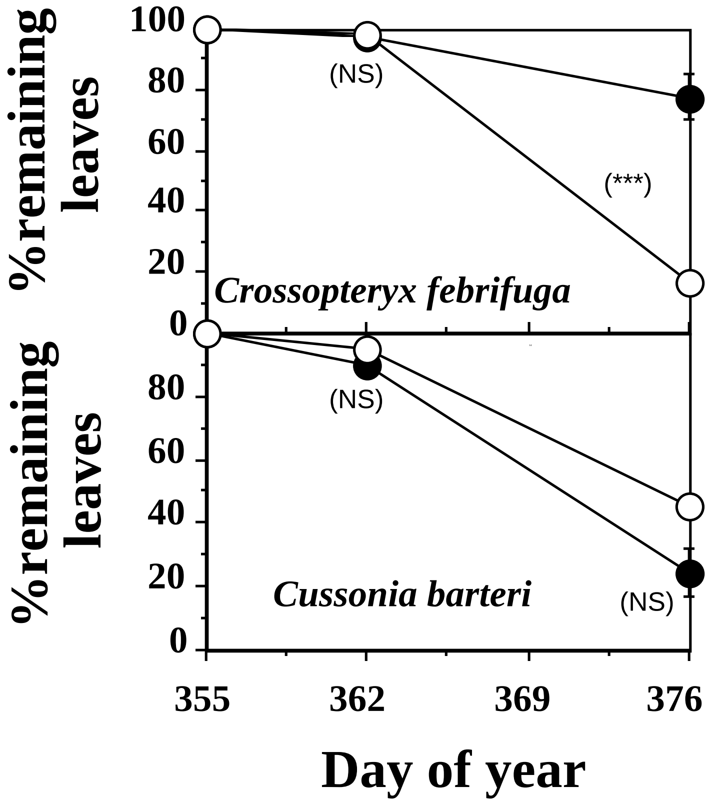

Figure 7. Leaf shedding pattern of the two shrub species *Crossopteryx febrifuga* and *Cussonia barteri* for individuals located either on termite mounds (l) or in control areas (m). Bars are standard errors. For each panel and each date, mean comparisons were performed (NS: non significant; ***: significantly different at the it p = 0.001 level).

ously reported for open areas at Lamto (74 mm, Le Roux and Bariac, 1998). The increased AWC$_{max}$ of the 0–0.60 m soil layer on mound as compared to surrounding areas was probably due to the increased clay content because clay enrichment has been shown to improve AWC$_{max}$ for sandy soils (e.g. Bousnina and Mhiri, 1997). The difference of water storage capacity in this layer between mound and control soil (28 mm) was great enough to be considered as a major feature which could improve soil water availability for vegetation throughout the year on the termite mound. Indeed, micrometeorological measurements showed that measured daily evapotranspiration rates are around 4 mm day^{-1} during the wet season at Lamto (Le Roux, 1998).

In the 0–10 cm soil layer, the temporal variations in water potential recorded on the mound and in control areas were close. In contrast, soil water potential in the 0.20–0.30, 0.50–0.60 and 0.80–0.90 m layers decreased more rapidly in control areas than on the mound during dry spells (Figure 6). This implies that during dry periods, water availability for plants was, at least transiently, better in the 0.20–0.90 m soil layer on mound than in the surroundings. Interpreting such different seasonal trends in soil water potential in the 0.20–0.90 m layer is beyond the scope of this paper. Indeed, the specific microtopography, vegetation cover, and soil surface infiltrability associated to mounds can potentially influence water input to the soil by affecting precipitation interception and runoff. For instance, soil surface crusts associated with eroded termite mounds were found to increase surface runoff while termite foraging areas exhibited high infiltration rates in mesic savannas in Ivory Coast (Janeau and Valentin, 1987), Chihuahua (Elkins et al. 1986), and dry Sahelian savannas (Ouédraogo, 1997). In addition, water losses from the soil can also be modified on mounds since leaf area index and specific composition (i.e. tree/grass ratio) influence soil evaporation and transpiration rates.

It should be argued that improved soil moisture in the 0.20–0.60 m layer during dry spells on the mound essentially resulted from the fact that the mound was associated to a specific vegetation cover, similar to shrub clumps encountered in control areas. However, the seasonal variations in soil moisture observed in open (i.e. grassy) areas and under shrub clumps for a same plot (i.e. same soil) at Lamto were found to be very close (Le Roux and Bariac, 1998). Mordelet et al. (1993a) even found that soil moisture was slightly lower under shrub clumps than in open areas. Thus, the woody vegetation cover probably not explained the higher soil water potential observed during dry spells on mounds. In order to better understand these differences in soil water potential, complementary experiments determining water infiltration, soil evaporation and plant transpiration rates are warranted.

Effect on shrub leaf shedding patterns

Whatever the reason explaining the higher soil water potential observed on the mound during dry spells, this improved soil water availability could be expected to influence vegetation phenology. Indeed, plant water status is suspected to partly control tropical tree leaf shedding patterns (e.g. Duff et al., 1997; Reich and Borchert, 1984; Williams et al., 1997). However, some authors pointed out that atmospheric factors (i.e. air water vapour pressure deficit, air temperature, incident radiation and/or photoperiod) could also strongly influence leaf fall of tropical trees (Wright and Cornejo, 1990).

In the present study, the leaf shedding pattern of *Crossopteryx febrifuga* was found to be less pronounced on mounds than in control areas. In contrast, the leaf shedding pattern of the shrub *Cussonia barteri* was not influenced by termite mounds. At Lamto, savanna shrubs are shallow rooted (Le Roux et al., 1995b; Mordelet et al., 1993b). However, in a previous study carried out at the same site (Le Roux and Bariac, 1998), *C. febrifuga* and *C. barteri* were found to have a limited and good access to soil layers below 0.60 m during dry conditions, respectively. Atmospheric conditions were the same for shrubs located either on mounds or in control areas. Furthermore, soil temperatures on the mound and in the surroundings were very close (Konaté, personal communication). Thus, soil water status was probably the major factor discriminating mounds and control areas during the dry season. Hence, the influence of termite mound on the leaf shedding pattern of *C. febrifuga* could be explained by a better water status in the 0.20–0.60 m soil layer and an ensuing improved shrub water status, since *C. febrifuga* has a limited access to deep soil layers. In contrast, the similar leaf shedding patterns exhibited by *C. barteri* on mounds and in control areas were consistent with the fact that this shrub has a good access to soil layers below 0.60 m where water availability remains high throughout the year. Our results do not imply that soil water status is the major determinant of leaf shedding for the shrub species studied. However, our results show that soil water status substantially modulated the leaf shedding pattern of *C. febrifuga*.

Potential effect of mounds on vegetation structure and function

The improved soil water status exhibited on termite mounds in Lamto savannas could strongly influence the vegetation structure and function. In particular, soil water availability is a key determinant of vegetation structure and dynamics in savanna ecosystems (e.g. Frost et al., 1986; Walker and Noy-Meir, 1982).

At Lamto, the density of both mature and young individuals of woody species is 2 to 3 times higher on mounds than in surrounding areas (Abbadie et al., 1992; Josens, 1972). Similarly, woody plant density was found to increase on mounds in different savanna environments (Burtt, 1942; Glover, 1937; Glover et al, 1964; Goodland, 1965; Wild, 1952). Moreover, forest tree species e.g. *Securinega virosa, Albizia zygia* and *Ficus sur* were found on termite mounds located in savanna biotopes close to gallery or riparian forests at Lamto (Konaté and Le Roux, unpublished). In the light of the present study, the better water availability encountered on mounds could be identified as an important factor explaining this change in vegetation structure and specific composition. Indeed, tree or shrub density generally increases with increasing soil water availability both at the local or regional scales in savanna-like environments (e.g. Williams et al., 1996). Furthermore, tropical moist forest tree species are known to be restricted to environments characterized by high soil water availability. However, other constraints such as soil nutrient availability or the impact of fire on tree recruitment and mortality probably also influence the vegetation pattern on mounds.

In conclusion, termite mounds appear as a major source of functional heterogeneity in this humid savanna ecosystem. Due to their specific soil texture and structure, they represent sites of high water and possibly nutrient availability for plants which can deeply influence (directly or indirectly) vegetation function, and particularly competitive interactions between plant species. As a result, vegetation structure is strongly modified by termite mounds which exhibit high shrub densities and sometimes moist forest tree species which are never encountered in savanna biotopes. Thus, accounting for these hot spots of high resource availability is needed to improve our understanding and modelling of savanna function and dynamics.

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