Research article

Termite soil preferences and particle selections: strategies related to ecological requirements

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Summary. At the Lamto Savanna Ecological Station (Côte d'Ivoire), *Odontotermes* nr. *pauperans* (Termitidae, Macrotermitinae) was observed to build mounds enriched with fine particles. Using laboratory experiments we studied the selection of building materials by worker termites offered soil from two contrasting horizons: superficial soil (15–20 cm) and a deeper layer (70–80 cm). The physical and chemical properties of the unused soil and subsequent termite constructions (foraging galleries and fungus-comb chambers) were compared in each case.

When presented with a single soil type, the termites modified soil texture for different parts of their structure. Termite building activity increased when presented with both soil types and a notable selection was observed in the use of a given soil type for a specific part of the structure built.

We conclude that termites utilise soil particles selectively, favouring finer particles and making constructions which match ecological, physiological, and behavioural needs. Compared with material from deeper horizons, less energy was expended when surface soil was used as a resource for gallery building and less C and N supplementation was needed. In contrast, termites preferred deeper soil for constructing fungus-comb chamber walls because this material has greater water-holding capacity.

Key words: Termites, Macrotermitinae, building, soil preferences.

Introduction

Among the soil macrofauna, fungus-growing termites play a primary role in savanna ecosystem functioning. They significantly modify their environment by increasing the content of fine soil particles, thereby stimulating microbial activity and raising the amount of soil water available to plants (Lee and Wood, 1971; Abbadie and Lepage, 1989; Ouedraogo, 1997; Konaté et al., 1999; Holt and Lepage, 2000).

A purely descriptive approach to termite effects on soil properties, however is not enough to understand why termites have to modify the material for their own needs (Black and Okwakol, 1997). The Macrotermitinae subfamily, for example, is characterised by exosymbiosis with a fungus (*Termitomyces*). This relationship has well-defined temperature and humidity optima (Collins, 1977), and hence a complex nest structure is necessary within which conditions remain constant (Grassé, 1986) or are actively controlled via mound architecture (Korb and Linsenmair, 1998). The success of the symbiosis, together with the ability to retrieve water from moist horizons deep in the soil, allows many Macrotermitinae to dominate semi-arid and arid environments (Lepage et al., 1974).

In the Lamto Savanna ecosystem (Côte d'Ivoire), *Odontotermes* nr. *pauperans* (Silvestri) cultivates its fungus in interconnected chambers, concentrated in space and constituting a termitarium (Josens, 1972; Konaté, 1998). These termites also construct covered runways (sheetings or galleries) on the soil surface in order to collect plant litter (Bagine, 1984). The termitaria density varies from 8.1 to 12.2 ha^{-1} (Konaté, 1998), occupying up to 9% of the soil surface and representing a soil volume of 300 m^2 in some biotopes (Abbadie et al., 1992; Konaté et al., 1999). Termite workers bring and handle fine particles to the soil surface, which enriches the nest surroundings with fine particles and other incorporated substrates. One of the consequences is an increase in the amount of the water available to plants (Konaté et al., 1999).

The impact of termites on soils is closely related to their construction activities and these, in turn, reflect their ecological needs. Most published work on soil modification, however, is descriptive, consisting of comparisons of in situ constructions and putative parent soils without an experimental component. In a new approach to study and understand the

impact of termites on soil particles, we conducted experiments in controlled situations. The questions asked were threefold: (i) what are the effects of *Odontotermes* nr. *pauperans* on the properties of two different soils (a top-soil and a deep-soil collected in the Lamto Savanna ecosystem); (ii) do termites select deeper soils for building activities; and (iii) what are the consequences in terms of termite activity.

Materials and methods

Termite models and study site

Termites were collected at the Lamto Research Station in Côte d'Ivoire (West Africa, 6°13′N, 5°02′W) at the margin of the rain forest (Menaut and César, 1979) in the Guinean bioclimatic zone (rainfall ≈ 1200 mm · yr⁻¹). The study site was a shrubby savanna dominated by Andropogonae grasses. The species chosen, *Odontotermes* nr. *pauperans*, is one of the dominant Macrotermitinae species in the Lamto Savanna ecosystem (Josens, 1972). This species has an aggregated distribution and termitaria are a conspicuous component of its ecosystem (Abbadie et al., 1992; Konaté, 1998; Konaté et al., 1999).

Experiments in the laboratory

Manipulations were carried out in a rearing room at the Lamto station: 170 termite workers were put in boxes (17.5 * 11.5 cm, 6.5 cm high). The soils we utilised came from the topsoil (15−20 cm deep) and from the deeper horizons (75−80 cm deep). They were chosen because of their contrasting texture, organic matter content, and maximum water content available to plants (Konaté, 1998; Konaté et al., 1999). The soils were sieved at 800 μm and spread to cover the bottom of the boxes at a depth of about 3 mm. Approximately 2 g of fungus-comb was placed in the middle of the box. Food (100 mg dried palm leaves, *Borassus aethiopum*) was supplied on the second day.

There were three experimental designs, all based on incubating fresh fungus-comb (with termites present) with an exact quantity (100 g) of a defined soil horizon or combination of two horizons. After incubation, termite constructions were sampled and analysed, and then compared with control samples from the original soils. Top-soil and deep-soil were offered to termites separately and, in the third experiment, together in the incubation box (50 g on each side of the container). Each treatment was replicated 8 times.

The experiments ran for 20 days in January 2000. At the end of the experiments, the fungus-comb wall and vertical foraging galleries along the sides of the box were collected and the following parameters were determined: (i) texture, incorporation of organic matter, and water-holding capacity (top-soil and deeper soil experiments only); and (ii) the proportion of each soil type used in the fungus-comb chamber wall, termite activity, quantity of soil handled, and the number of exploratory galleries made (all experiments).

Measurements

(i) Soil properties
Soil texture was determined for each soil type and after exposure to termites, using the Feller method (1979). Distilled water and sodium hexametaphosphate (40 g × l⁻¹) were added to disperse the aggregates. The samples were shaken for 16 h at 175 rpm. The soil particles were sieved at 250 μm and 100 μm. The 0−50 μm fraction was sonicated at 100 J × m⁻¹ (Branson Sonifier 450) and passed through a 20-μm sieve in water in order to split microaggregates. The 0−20 μm fraction was centrifuged (Sorvall RC 3B Plus, Du Pont De Nemours) at 500 t × min⁻¹ during 3 * 9 min and at 2500 t × min⁻¹ during 3 * 2 h to separate the 2−20 μm and the 0−2 μm fractions, respectively. The resulting 5 fractions were dried at 60 °C and weighed: 800−250 μm (coarse sands), 250−100 μm (fine sands), 100−20 μm (coarse silts), 20−2 μm (fine silts) and 2−0 μm (clay). The percentage of organic substrates incorporated in the soils was assessed by the total organic C and N content, using an elemental analyser (NA 1500 Series 2, Fisons).

The kinetics of water retention is a synthetic index of soil properties altered by the termites. The different structures were brought to their maximum watert-holding capacities and then placed in a desiccator box with perlite previously heated at 130 °C. The samples were weighed regularly. The water content (w_t) was determined by the following equation:

$$w_t = (W_t − W_{dry}) / (W_{dry} − W_{pot})$$

Where W_t is the sample weighed at time t, W_{dry} the sample weighed without any water, and W_{pot} the pot weighed without soil.

(ii) Termite preferences
The quantity of each soil type utilised in building the fungus-comb wall was determined using an arbitrary index by means of X-ray diffraction of the clay fraction: the two soil types could be differentiated by their kaolin/mica-illite-smectite ratio (K/MIS). The K/MIS values were obtained by X-ray diffraction (XRD) using an INEL position-sensitive curved detector system (Co-Kα radiation). Samples were scanned at a speed of 2° (2θ) min⁻¹ in the range of 2 to 15°. Samples were prepared routinely by Sr saturation and X-rayed in the air dried state. The relative clay-mineral abundance was determined after estimating the peak surface of the different soils derived using peak decomposition methods (Lanson and Besson, 1992). This method is only relative and should gives changes in the abundance of clay species present for similar materials (Lanson and Velde, 1992; Velde, 1995). Because of the shortage of samples needed to determine all soil parameters, only three replicates were used for the control soils and chambers. Eight replicates were used for the soil handled by termites when they had a choice between the two soils.

(iii) Termite activities
Termite movement (flux) in each soil was used as an index of soil preference for building and or exploring the outside environment. The number of workers passing a random point during 5 s was counted 20 times for each soil type.

The proportion of the arena covered by reprocessed soil was determined by observation through the transparent bottom of the boxes. Handled areas could be clearly distinguished by their textural aspect. These handled areas were outlined on paper and their surface scanned using Photoshop 4.0 and quantified with Scion Image software (1998).

The number of vertical galleries on the walls of the boxes used by termites for forage prospection was also recorded.

Statistical analyses
Data were tested using SAS® (Statistical Analysis System, SAS institute Inc. 1990). Repeated measure analyses of variance were performed according to the SAS statistical GLM procedure and CONTRAST option to determine if there were statistical differences between the treatments. All tests were performed at the 0.05 significance level.

Results

a) Soil properties from single horizon experiments

(i) Variation in soil texture
The deep-soil contained more coarse sands and clay particles and had less fine sands and coarse silts than the top-soil (P < 0.05) (Table 1).

Although the texture of the constructions did not differ from the control top-soil (P > 0.05), there was a marked

Table 1. Textures of the different soils and constructions: fungus-comb chamber (wall) and galleries created with either topsoil or deep soil (n = 3, standard error in brackets)

Top or deep soils	Coarse sands	Fine sands	Coarse silts	Fine silts	Clays
Wall (*top-soil*)	57.063 (± 4.589)	17.866 (± 2.929)	9.717 (± 1.837)	9.162 (± 0.237)	6.192 (± 0.060)
Galleries (*top-soil*)	54.242 (± 1.829)	19.967 (± 1.166)	10.903 (± 0.853)	8.962 (± 0.054)	5.925 (± 0.136)
Control (*top-soil*)	54.643 (± 7.0737)	19.626 (± 5.891)	10.512 (± 1.357)	9.240 (± 0.305)	5.979 (± 0.093)
Wall (*deep-soil*)	42.900 (± 3.257)	17.450 (± 2.098)	9.965 (± 0.169)	11.591 (± 0.839)	18.094 (± 0.490)
Galleries (*deep-soil*)	36.236 (± 2.737)	21.298 (± 1.475)	13.731 (± 0.190)	10.828 (± 0.573)	17.906 (± 0.356)
Control (*deep-soil*)	60.606 (± 0.945)	9.369 (± 0.979)	6.421 (± 0.236)	8.575 (± 0.185)	15.029 (± 0.455)

particle selection when the deeper horizon was offered ($P < 0.05$). In the latter case, both types of construction contained less coarse sands and more fine sands, coarse and fine silts, and clays than the control deep-soil ($P < 0.05$). The chamber walls contained more coarse sands and less fine sands and coarse silts than the galleries ($P < 0.05$).

Figure 1. C and N supplementation of the two different soil horizons when offered separately to termites (mean content ± SE; n = 6)

(ii) Carbon and nitrogen in gallery and chamber materials
Whatever the soil type, termites enriched the C and N levels in the material used for construction (Fig. 1). When top-soil was offered, there was more C and N in the fungus-comb chamber walls, but little of either in the foraging galleries. In contrast, when deep-soil was offered, there were more C and N supplies in the galleries than in the chamber walls.

The incorporation of carbon and nitrogen in the chamber walls in the top-soil experiments was similar to that in the galleries with the deeper soil type ($P > 0.05$).

(iii) Kinetics of water retention
Whatever the constructions, the soils from the deeper horizon exhibited better water retention than the topsoils ($P < 0.05$, Fig. 2).

The galleries and chamber walls built by termites using top-soil had better water retention than control top-soil ($P < 0.05$). Moreover, these two constructions had similar kinetics of water retention ($P > 0.05$). The control top-soil and the constructions established from top-soil did show the same slope of water retention curve for $t < 40$ h ($P > 0.05$). At $t = 70$ h, both constructions and the control surface soils had the same kinetics of water retention ($P > 0.05$).
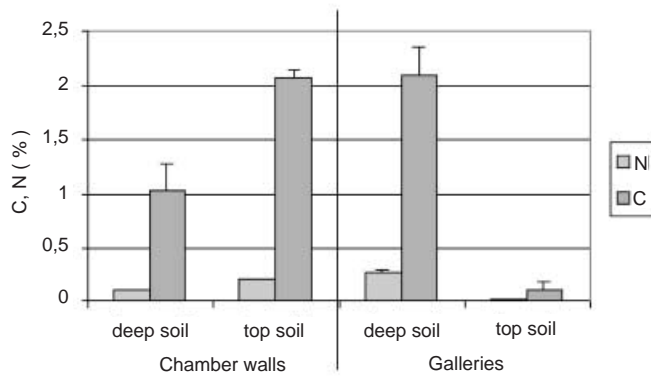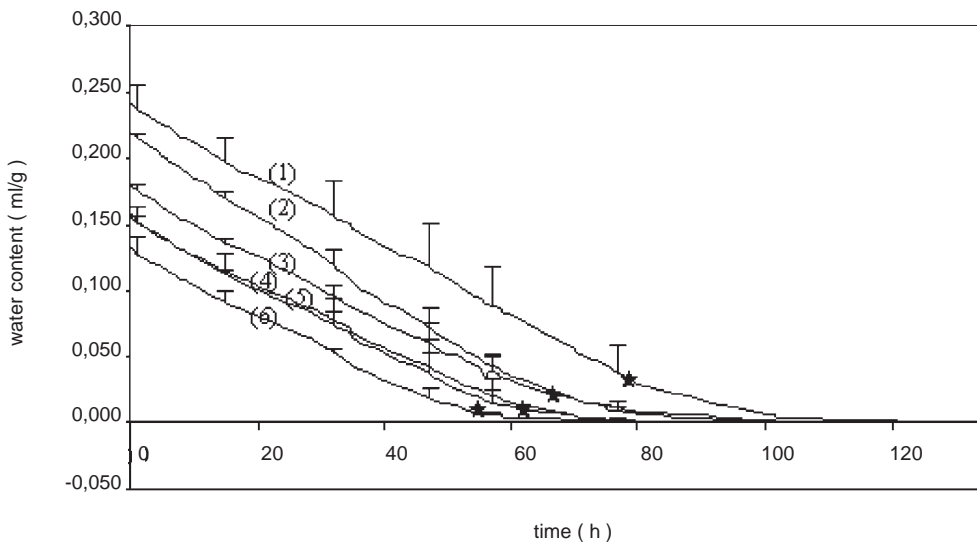

Figure 2. Kinetics of water retention for the different soils. Walls of the fungus comb chamber with the top-soil (4) or deep-soil (1) alone; galleries created with top-soil (5) or deep-soil (2) alone; top-soil (6) and deep-soil (3) controls (mean water content ± SE; n = 3). (★: time of the change in the slope magnitude of the curve)
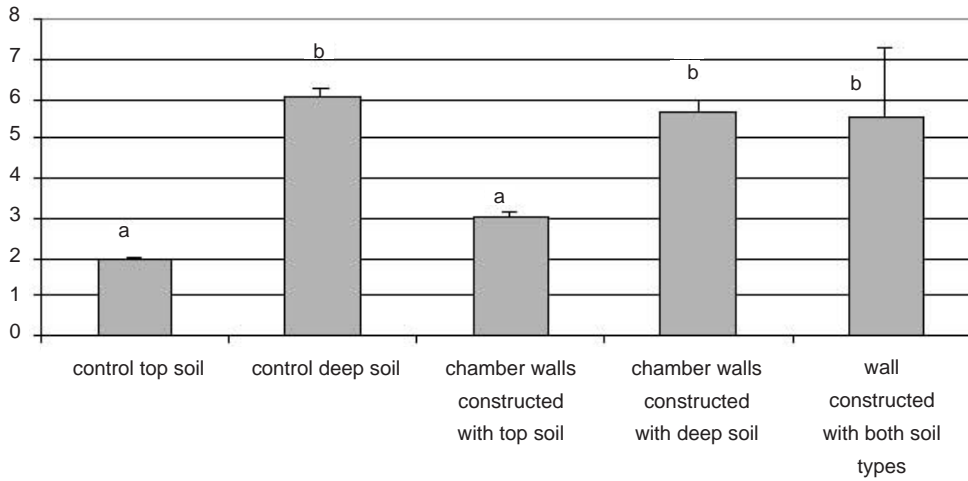
Figure 3. K/MIS ratio for the different soils. n = 3 for the simple soil experiment and n = 8 for the chambers with a soil choice; standard error are represented as vertical bar; histograms with the same letter are not different at P = 0.05

The galleries and chamber walls built from deep-soil exhibited better water retention than the control deep-soil for t < 60 h (P < 0.05). The slope of the water retention kinetic curve of the control deep-soil at t < 60 h was different from that of the galleries (P < 0.05), but similar to that of the chamber walls and the control deep-soil (P > 0.05). At longer times, the galleries had water retention properties similar to those of the control soil (P > 0.05), while the chambers showed better water retention up to t = 120 h (P < 0.05).

b) Soil selection by termites
Since top-soil and deep-soil are significantly different mineralogically (P < 0.05), the K/MIS ratio was a good index to determine the soil utilised by termites to cover the fungus-comb.

The analysis (Fig. 3) showed that termites have no influence on the K/MIS ratio when each soil type was used alone (P > 0.05). When termites had a choice between the two soil types, however, the K/MIS ratio of the chamber wall was very similar to that of the deep-soil type (P > 0.05).

c) Termite activity
(i) The number of termites crossing a random point of the box per second (termite flux) did not differ between the three experiments (P > 0.05). As can be seen in Table 2, the level of termite activity was independent of the soil type.

Table 2. Termite activity in different soil types (n = 20, standard error in brackets)

	Experiment 1	Experiment 2	Experiment 3	
	Top-soil alone	Deep-soil alone	Top-soil (with deep-soil)	Deep-soil (with top-soil)
Number. sec^{-1}	1.613 (± 0.738)	1.270 (± 0.701)	1.363 (± 0.750)	1.578 (± 0.825)

Table 3. Surface of soil handled by termites (n = 8, standard error in brackets)

	Experiment 1	Experiment 2	Experiment 3	
	Top-soil alone	Deep-soil alone	Top-soil (with deep-soil)	Deep-soil (with top-soil)
Area (cm²)	22.23 (± 5.88)	21.04 (± 3.95)	27.32 (± 6.24)	35.26 (± 4.01)

Table 4. Number of vertical galleries (n = 8, standard error in brackets)

	Experiment 1	Experiment 2	Experiment 3	
	Top-soil alone	Deep-soil alone	Top-soil (with deep-soil)	Deep-soil (with top-soil)
Number of vertical galleries/g soil	0.017 (± 0.011)	0.007 (± 0.004)	0.027 (± 0.015)	0.030 (± 0.018)

(ii) There was no difference in the surface of the handled soil (Table 3) when each soil was given separately (P > 0.05). Top-soil and deep-soil given alone were handled less than the same soils given together (P < 0.05). When offered together, deep soil was more handled than top-soil (P < 0.05).

(iii) There was a significant difference in the number of vertical galleries built (Table 4) when the soils were offered separately (P < 0.05): the termites constructed more galleries with top-soil. In contrast, there was no significant difference between the two soil-types when they were given together (P > 0.05). However, the number of vertical foraging galleries in the experiment with the combined soil-types was greater than when the soils were given alone and the total was four times that of the deep soil.

Discussion

Particle selection and organic matter supply by termites

We found no evidence of particle selection when termites used only the top-soil. When deeper soil was offered, however, the constructions contained less coarse sands and more fine particles. Thus, particle selection by termites depends on the control soil and on the constructions built.

Carbon and nitrogen were enhanced in the handled soil; however, the termites incorporated less C and N in the galleries than in the chamber walls built with topsoil and *vice versa* in the case of the deeper soil horizon. This shows that termites can modulate the incorporation of supplementary material according to the type of construction and the nature of the soil used.

This study demonstrates the importance, in fieldwork, of making a distinction between different constructions and of identifying the parent horizon from which the constructions are derived. Comparisons with field observations are difficult however, because most previous studies were made between mound materials (undifferentiated) and top-soil only (Black and Okwakol, 1997).

Properties of the soil handled and the termite-fungus symbiosis

In order to maintain a microclimatic condition optimum for *Termitomyces* (Lüscher, 1961; Korb and Linsenmair, 1998), the exosymbiosis inside the termite nest requires the construction of special structures (Grassé, 1986; Collins, 1977). Therefore, it was particularly interesting to note the water-retention capacity of the materials in the different structures. The kinetics of water retention reveals the ability of each soil to hold and to exchange water with the outside environment. Regardless of the type of construction (comb wall or foraging gallery), soils from the deep horizon retained more water than the surface soil. This can probably be explained by the larger clay and organic matter contents of the deep soil (Schlosser, 1988; Sala and Tessier, 1994; Chenu, 1993). The two slopes observed in the curves (Fig. 2)

correspond to the two states of soil water: free water (pF < 4.7) and adsorbed water (pF > 4.7). The first slope corresponds to the loss of free water in the macroporosity and the second slope to the loss of adsorbed water in the microporosity. The binding forces between water and soil increase drastically after the maximum hydroscopic point (pF 4.7) is reached, thus accounting for the different slopes. In the two cases, there are hygroscopic equilibriums between soil and atmosphere. However, atmospheric relative humidity is maintained nearly constant before pF 4.7 whereas it decreases drastically after this point (Vannier, 1971). All of the soils have the same slopes and thus the same capacity to lose water, while the changes in the magnitude of the slopes are different depending on the capacity of the soils to hold water (Fig. 2). Only those galleries built with deep-soil had a different behaviour, leading to a more rapid loss of water, which would permit a better exchange with the outside environment. Chamber walls built with deep-soil exhibited the smallest slope change and zero water content value, suggesting that this soil acts as the best buffer for maintaining the atmospheric relative humidity in the chamber.

Since control and handled top-soils had the same texture, the increase in the water-holding capacity was caused by the enrichment in organic matter (saliva?), despite the difference in content supplies between the constructions. In contrast, the variations water-holding capacities of the deeper soils can be explained by the texture and organic matter content shifts.

Termite soil preferences

When comparing termite activity between the three experiments, we conclude that there was no influence on soil quality. If the termites were offered a choice between the two soil types, there was much more activity in both vertical foraging gallery construction and soil handling. These results mean that although termites are active whatever the soil type, building activity is more stimulated when both top-soil and deep-soil are present.

Although the number of vertical foraging galleries was similar regardless of the soils used, the termites altered the texture of the deep soil much more when soils were offered together. When given the choice of soil types, termites exhibited no preference when establishing vertical foraging galleries, but preferentially utilised the deepest soil for building their fungus-comb chamber walls. Deep-soil seems to provide the main construction material, while top-soil is utilised when termites have no choice. It has been proposed that termites probably prefer to use the finer particles from deeper soil horizons than to top-soil material to built their constructions (e.g. Lee and Wood, 1971; Bagine, 1984; Lal, 1987; Lobry de Bruyn and Conacher, 1990; Lavelle et al., 1992; Holt and Lepage, 2000). At the Lamto site, termites probably utilise deep soil material to build their nest (fungus-comb chambers), while foraging galleries, outside the nest, can be built from top-soil.

The more the termites preferred a soil for construction, the less they incorporated carbon and nitrogen. These adjust-
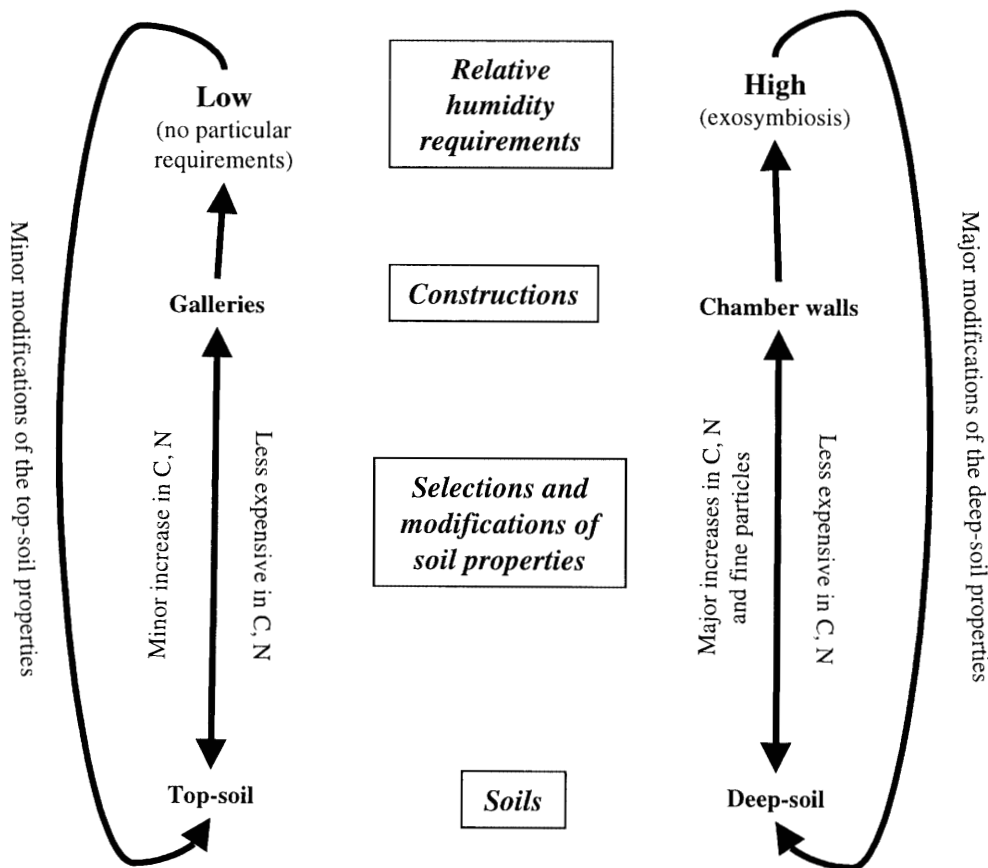
Figure 4. Hypothetical diagram of soil preferences in *Odontotermes*, according to the type of building activity. Termites are able to utilise both top and deep soil when building galleries, but they prefer the less costly top-soil. The special needs of the exosymbiosis with *Termitomyces* explains the preferential utilisation of deep soil when building chamber walls

ments can be explained by economic principles, since it will probably be less costly for termites to utilise soil that needs less carbon and nitrogen to be incorporated. Therefore, deeper soil appears more suitable for termites to establish the fungus-comb chambers because it needs less supplementation with C and N than top-soil. A similar reasoning could be applied in the case of top-soil and vertical foraging galleries. The selection of the deeper soil for creating the fungus-comb chamber walls could also occur because termites can work it, more easily.

It was observed that termites incorporated more carbon and nitrogen in the chamber walls with the deeper soil than in the galleries formed from top-soil. These two constructions have different roles. Chamber walls are permanent structures and have the important function of maintaining humidity and protecting fungus and termites, while galleries constitute only conduit structures used for foraging. A schematic diagram of the building activities of termites, their ecological needs, and the consequent influences on soil properties is shown in Fig. 4.

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