Chemical variations in the biostructures produced by soil ecosystem engineers – Examples from the Neotropical savannas

Juan J. Jiménez[1, *], Thibaud Decaëns[2]

[1] *Laboratoire d'Ecologie des Sols Tropicaux, IRD, 32 Av. H. Varagnat, F-93143 Bondy, France*

[2] *Laboratoire d'Ecologie. UPRES-EA 1293. UFR Sciences. Université de Rouen. F-76821 Mont Saint Aignan Cedex, France*

[1] Address during the study

[*] Corresponding author (current address):

Carbon Management and Sequestration Center
School of Environment and Natural Resources
The Ohio State University
2021 Coffey Road
Columbus, OH-43210
USA
Tel: +614 292 2298
Fax: +614 292 7432
E-mail address: jimenez.58@osu.edu

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Abstract

“Ecosystem engineers” are those organisms capable to modify physically the environment by producing “biogenic” structures (BS). Termites, earthworms, ants and other large macroinvertebrates produce BS with varying properties. In this study, our objective was to quantify total C_{org} (g kg dry soil^{-1}), NH_4^+ and NO_3^- concentrations (µg g dry soil^{-1}) in different parts of the BS produced by termites and ants to test the hypothesis that higher concentrations are found where new building material is deposited, i.e. at the top of the BS. The study was carried out in a natural savanna (NS), an introduced grass-legume pasture (IP) and a gallery forest (GF) at the Carimagua Research Station in the Eastern Plains of Colombia. Progressive sampling distances across the BS were used, i.e. from the top to the base of the BS by using proportional distances, i.e. 20-100% for large BS and 50-100% for the smallest BS, and these were compared with two types of control soil, 120% or 150% in the case of large and small BS, respectively, and soil sampled 1 m away from the BS. All the BS analysed had, in general, higher concentrations of nutrients than the control soil. There were differences in the variables measured in the BS according to the organism that produced them. The lowest values of C_{org} were observed in the BS (surface dumps) deposited by fungus-growing ants (*Trachymyrmex* sp. in the NS, and *Atta laevigata* in the GF), while the highest concentrations were found in the BS produced by termites in the GF, where a high N concentration was also observed. Nutrient concentrations were higher in general in the BS than in the control soil in all cases. However, other BS seemed not to have any influence in the surrounding soil. We concluded that the activity of soil ecosystem engineers increased the spatial variability of chemical parameters measured in this study. The ecological significance of these differences is discussed.

Keywords: Soil macrofauna / Ecosystem engineers / Soil ecology / Termites / Ants / Savanna

1. Introduction

By definition “ecosystem engineers” or “ecological engineers” (*sensu* [12,25]) are those organisms that modify physically the environment in which they live. The engineer organisms do so by producing “biogenic” structures or biostructures (BS) that impact in some soil processes and affect the spatial and trophic resources for one, or generally more, organisms. The peculiarity of the BS is that such processes continue in the absence of the organisms that created them [12,1,14]. As a result the abundance and community structure of other organisms are modified without establishing any direct trophic relationship [12,13].

Ants and termites are important regulators of soil aggregate structure as they remove (ants) or ingest (termites) large amounts of soil that can be either remove it from the bottom to the top soil (fungus growing ants) or egest it above or in the soil profile (termites). In doing so, they form BS with constituting aggregates of different sizes and characteristics, i.e. ant hills, termite mounds. These BS have varying characteristics according to the species and the soil where they carry their activities [17,5]. These various effects upon habitat structure are part of the numerous sources of soil ecosystem heterogeneity and hence may affect soil biota diversity with important functional consequences [6].

The BS may sometimes cover a large proportion of the soil surface. Nonetheless, there is a lack of studies dealing with a description and characterization of the BS produced by these invertebrates. Their description can be used to establish a functional classification of these organisms in order to assess their contribution to soil processes and ecosystem function. The morphology, size, abundance and physico-chemical properties of BS are a previous step to evaluate their indirect effects´ type and wideness in the surrounding environment at a given scale [12,13]. Thus, it is necessary to describe the dynamics and phenomena that occur in the BS [20]. The BS may reflect functional attributes of the species producing them that are linked to the definition of ecosystem engineers. These structures and the specific environment associated to them have been given the name of "functional domain" [15]. These are places where specific soil processes occur at certain spatial and temporal scales, so that the effects of ecosystem engineers in the ecosystem through their functional domain can be quite significant [14,15]. The functional domain is then a part of the soil that is influenced by a regulator that can be either biotic or abiotic.

The BS can be separated from the soil due to its different physico-chemical properties. Decaëns et al. [9] set up a classification of engineer organisms (macroinvertebrates) in the savannas from Carimagua. They demonstrated the rich diversity of BS produced by ecological engineers in the soil surface of the natural savanna, i.e. i) compact structures, rich in organic matter (earthworm casts), ii) soft structures, rich in organic matter (termite mounds), and iii) soft granular structures poor in organic matter (ant nests). In this study, however, our objective was to quantify the organic C (C_{org}), NH_4^+ and NO_3^- concentrations in different parts of the BS produced by termites and ants to test the hypothesis that higher concentrations are found where new building material is deposited, i.e. at the top of the BS. The criterion was set up “a priori” since differences in concentration of these nutrients are supposed to occur owing to the age, with the oldest part located at the bottom of the BS, since these structures are normally constructed upwards.

2. Materials and Methods

2.1. Study site

The study was carried out in a natural savanna (NS), an introduced grass-legume pasture (IP) and a gallery forest (GF) at the CORPOICA – CIAT Carimagua research station (Figure 1), in the well-drained isohyperthermic savannas of the Eastern Plains of Colombia (4° 37’ N, 71°19’ W and 175 m altitude). Average annual rainfall and temperature are about 2,280 mm and 26 °C respectively with a dry season from December to March. Soils at the study site are oxisols characterized by their acidity (pH [H_2O] = 4.5) and a high Al saturation (>90%).

In the NS *Trachypogon vestitus* Anderss, *Paspalum pectinatum* Nees, *Axonopus aureus* Beauv., *Schyzachyrium hirtiflorum* Ness, *Gymnopogon foliosus* Nees and *Hiptis conferta* Pohl ex Benth. (Labiatae) are the most frequent grass species. The IP was an association of *Brachiaria humidicola* Rendle with three different legumes, *Arachis pintoi* Krap & Greg, *Desmodium ovalifolium* Wall. and *Stylosanthes capitata* Vog. Pasture was sown in 1993 and legume resown in 1996. Stocking rates for the pasture were 1 cattle ha^{-1} (1 animal unit [AU] = 250 kg live weight) in the dry season and 2 AU ha^{-1} in the rainy period.

The GF where the BS were sampled was in an site called “La Reserva”, very close to the Carimagua Lake (Figure 1). The dominant vegetation in the GF is constituted by several tree species such as *Ficus* spp., *Dendropanax arboreux*, *Enterolobium* sp., *Jacaranda copaia*, *Copernicia tectorum*, *Cecropia* sp. and palm forests of *Mauritia flexuosa* and *M. minor*.

2.2. Identification of BS and morphological descriptions

The different plots studied were thoroughly checked and all BS found were described, and the macroinvertebrates responsible for their construction identified as precisely as possible (family, genus, or species). We restricted this study to the BS produced by termites and ants, and did not include earthworm casts, since these were intensively studied, at least for one anecic species [8,9].

2.3. Sampling procedure

The study was conducted in the middle of the rainy season of 1999 (August). Complete BS produced by ecosystem engineers in the area were sampled. The protocol of sampling procedure is indicated in Figure 2. For those BS of large size, i.e. more than 80 cm height we sampled at 0, 20, 40, 60, 80 and 100% of the distance from the top to the base; due to size reasons only 0, 50, and 100% sampling distance was used for the smallest BS. Two types of control soil were used, (1) soil taken aside the BS, i.e.., 120% and 150% for large and small BS, respectively, and (2) soil taken 1 m away from the BS. A small metal cylinder (5 cm Ø) was used to sample at 0-5 and 5-10 cm (Figure 2).

Four replicates, i.e. four BS produced by the same organism, were sampled at each site. Each sample taken at different distances, i.e., 0, 20, etc., was introduced separately in plastic bags and put in an ice chest to preserve further mineralisation processes and carried to the laboratory. We only sampled those BS that were sufficiently represented to permit the collection of enough material for laboratory determinations. The ants and termites that might be found in the samples were carefully removed before preserving the samples at 4 °C prior to analysis. In total 380 samples were analysed.

2.4. Chemical analysis

Chemical analysis were carried out at the “Centro Internacional de Agricultura Tropical” (CIAT) headquarters in Cali, so samples were sent from Carimagua in an ice chest and all the samples inside plastic bags to avoid direct contact with ice. NH_4^+ and NO_3^- concentrations were determined following standard techniques recommended by the Tropical Soil Biology and Fertility Programme (TSBF) [2]. We used a colorimetric method after acid digestion to measure total C concentrations [11] in samples that were dried at 75 °C for 48 h.

2.5. Statistical treatments

Data were transformed before analysis to reduce the asymmetry of the frequency distribution. Normalisation of data was obtained using the Shapiro-Wilks test for normality. Mean comparisons were performed with one-way ANOVA.

3. Results

3.1 Diversity and description of BS

Decaëns et al. [9] described fourteen types of BS and the invertebrates responsible for their construction on the soil surface in the NS. Out of 14 BS we collected eight types of BS (Table I), three epigeic ant nests (Plates 1a-c) and five types of epigeic termite domes (one located above trees) (Plates 2a-c). Table II lists those macroinvertebrates identified and the size of the BS, including those listed in [9]. In this paper only the two termite BS sampled in the GF are described:

- *Nasutitermes* sp.1 (unidentified species)

  The BS constructed by this termite species is an epigeic conic mound of large size (60 cm height x 50 cm Ø). The surface of the mound is rough, with cemented material and with colour similar to the surrounding soil (Plate 3a, from J.J. Jiménez).

- *Nasutitermes* sp. 2 (unidentified species)

  This termite constructs an arboreal BS which is located in the range of 1.70 – 3.70 m above soil surface. The BS is a spheric, pasteboard-like structure, and generally some decomposed leaves are visible throughout the surface. There seems to be some kind of specificity between this termite and the tree where nests are built. All BS were found in trees belonging to the same species with about the same dimensions, i.e. 5-8 cm Ø (arboreal termite mound, Plate 3b, from J.J. Jiménez).

3.2. C_{org}, NH_4^+, and NO_3^- in BS and control soil

Concentrations of C_{org} were lowest in the BS structures produced by ants, especially those deposited by *A. laevigata* and *Trachymyrmex* sp. in the NS (Figure 3a, b). In the GF values of C_{org} were also rather low in the BS of *A. laevigata*, although higher than the control soil (only significant for 5-10 cm in control soil 1 and for both 0-5 and 5-10 cm of control soil 2). In the case of termites, similar values were obtained for *Spinitermes* sp. (Figure 3a) (ca. 6, considering the BS from the NS and IP) and *Velocitermes* sp. (Figure 3b) (mean values ranging from 5 to 9 throughout the BS). The highest C_{org} concentrations were observed in the BS of *Nasutitermes* sp.1 in the GF (15 – 22), *Microcerotermes* sp. in the NS (20 – 31), and *Nasutitermes* sp2 in the GF (37– 54).

Regarding NH_4^+ concentrations in the large BS the highest values were obtained in *Spinitermes* sp. (Figure 4a). High NH_4^+ concentration was also obtained in the BS produced by *Nasutitermes* sp1. in the GF, although these values were on average three times lower than those obtained for *Spinitermes* sp. Regarding the BS produced by *A. laevigata*, NH_4^+ concentrations were the lowest (below 10 µg g dry soil^{-1} in all cases and distances). However, when considering the entire set of BS analysed, the highest NH_4^+ concentrations were obtained in the arboreal pasteboard-like BS produced by *Nasutitermes* sp2 in the GF (between 1,200 and 1,600 µg g dry soil^{-1}, depending on the sampling distance) (Figure 4b). There were significant differences between the BS and both types of control soil for the BS produced by termites in the GF (ANOVA, $P<0.01$).

Regarding NO_3^- the highest values were found in the BS produced by *Nasutitermes* sp1 and *Nasutitermes* sp2 (Figure 5a, b). In general these values were ten times higher (above 1,000 µg g dry soil^{-1}) than those obtained for the rest of BS. Rather high values of

NO_3^- were also obtained in the BS produced by *A. laevigata* in the GF. The BS constructed by *Spinitermes* sp. had the lowest concentrations of NO_3^-.

In general it was observed a decrease in all variables measured as a function of sampling distance, thus revealing that the most recent material deposited in the BS corresponded to the distance 0%, unless an area in the BS had to be repaired that might lead to higher values in other sampling distances. The highest concentration of NH_4^+ was obtained in the first sampling distance, i.e. 0% (Figure 4). Regarding NO_3^- concentrations these were rather low for the entire set of small BS (Figure 5b).

When comparing the entire set of BS, there were significant differences in the 0% sampling distance for NH_4^+ concentrations (ANOVA, F = 37.70; d.f. = 6; $p < 0.001$), and C_{org} concentrations (ANOVA, F = 10.14; d.f. = 6; $p < 0.001$), but not for NO_3^- concentrations (F = 2.27; d.f. = 6; $p > 0.05$).

When comparing both types of control soil, i.e. the sampling distance beside the BS, 120% or 150% and control soil (0-5 and 5-10 cm) only statistically significant differences were found for C_{org} in the BS produced by *Microcerotermes* sp. in the NS, and *Spinitermes* in both NS and IP systems(ANOVA, $P<0.05$).

3.3. Effects of sampling site

Only for two species, *A. laevigata* (NS, GF and IP) and *Spinitermes* sp. (NS, IP) statistical analysis between systems could be performed. No significant differences were found between both NH_4^+ (ANOVA, F = 0.09; d.f. = 1; $p>0.05$) and NO_3^- (ANOVA, F = 0.29; d.f. = 1; $p>0.05$) concentrations in the BS produced by *Spinitermes* sp. However, significant differences appeared regarding total C_{org} concentrations (ANOVA, F = 10.12; d.f. = 1; $p<0.005$).

In the case of *A. laevigata* all systems studied could be compared. There was no significant differences for NH_4^+ (ANOVA, F = 2.92; d.f. = 2; $p>0.05$) but differences were highly significant for NO_3^- concentrations (ANOVA, F = 321.58; d.f. = 2; $p<0.001$) and total C_{org} (ANOVA, F = 8.90; d.f. = 2; $p<0.001$).

4. Discussion

The activities of soil ecosystem engineers contribute to the variability of chemical concentrations in the BS they produce, and sometimes in the surrounding environment. Our results seemed to confirm the presence of a mosaic of areas with different C and N concentrations. Attention must be paid when sampling these structures and preliminary characterizations of chemical properties are sought.

The comparison of our results with those reported in other studies seems difficult since the sampling methodology employed here has not been used before. However, some general considerations can be taken into account. In a study conducted in the Brazilian Cerrados it was found that soil organic carbon was enriched by a factor of 3.5 (90.2 g/kg C_{org} in clayey Oxisols) and 11.5 (109 g/kg C_{org} in the loamy Oxisols) in the tops of the epigeic mounds of termites of the genera *Armitermes* and *Dihoplotermes* [27]; these termites selected fresh and partly decomposed organic matter. In our study, C_{org}, NH_4^+ and NO_3^- concentrations were also higher in the BS compared to the control soil, except in the BS produced by *Nasutitermes* sp2 in the gallery forest (Figure 4b), since here we compared an arboreal carton-type BS with control soil, showing the differences in the composition of microbial population in both types of substrates.

Differences in total C_{org}, NH_4^+, and NO_3^- concentrations observed between BS and the control soil are due to several reasons depending on the species and how these BS were built. For instance, higher amounts of organic matter are found in faeces and salivary excretions of termites [4,19]. Epigeic termite mounds are normally cemented with soil particles that contain variable quantities of salivary secretions and excrements [17,18]. In certain cases, the walls of the termite mounds are made of a pasteboard-like material that is very rich in C_{org}, e.g. *Microcerotermes* sp. in the savanna and the arboreal nests constructed by *Nasutitermes* sp2. in the GF.

The epigeic domes built by ants, in contrast to the structures built by termites were in this study pale yellow or light orange. It is worth noticing that the BS produced by *A. laevigata* in the pasture was of smaller size and the one from the GF was the biggest. In the pasture the presence of cattle and also de control of ant populations are factors responsible of this size, otherwise these BS can be quite big as usually seen in the natural ecosystems. Fungus growing ants bring their depositions (soil plus fungi residues) up from the deeper horizons of the soil profile (B horizon begins at 26 cm depth in these soils). Ants accumulate all these residues on the soil surface. Despite the high amount of soil removed by foraging ants the BS are poor in organic matter concentration and this soil does not undergo significant modifications [9].

The highest values of NO_3^- were obtained in the BS produced by *Nasutitermes* sp1 in the GF. This BS is very compacted and not only salivary secretions and faeces of termites but also hydrosoluble carbohydrates of microbial origin [26] could be responsible of its compact nature. This must be further tested since no correlation between the structural stability of biogenic aggregates and hydrosoluble carbohydrates for the same BS has been found [9]. In our case it was also common to observe green areas over the surface of the BS indicating the presence of other microorganisms such as algae that may have contributed to the great values of C_{org} (Figure 3d). This was also confirmed by analysing the organic matter concentrations of this structure by Near Infrared Reflectance Spectroscopy (NIRS) [10] and enzymology analyses [21].

Owing to the sampling distance 0% or the zone of the BS where the “most recently” deposited material is found (confirmed by the results obtained in this study), NH_4^+ values were in general highest in the BS produced by *Spinitermes* sp. (in the savanna) and *Nasutitermes* sp1 and *Nasutitermes* sp2 (from the GF). These values were higher than those obtained in the BS produced by another soil ecosystem engineer (an anecic earthworm) in the same area [9].

High NH_4^+ concentration probably indicated that N mineralization was high in the recently deposited material in these BS. Nitrifying microorganisms would be greatly activated in the BS produced by *A. laevigata* and *Nasutitermes* sp1 in the GF. These BS are the biggest found at the study site and the values obtained in this study were higher than those reported by [9]. A detailed study on the role of which microbial populations are enhanced or inhibited in these BS merits further efforts.

Termites are the most important decomposers of all invertebrates in tropical forests [3]. Termites strongly influence soil organic matter and nutrient dynamics [16]. Total C_{org} concentrations in this study were different according to the BS and were in general higher than reported in other studies, for example, the termite mounds of *Microcerotermes* *nervosus* Hill 1942 from northern Australia (5-15% organic C) [18]. In another species, *Amitermes laurensis* Mjoerberg C_{org} (%) ranged from 6.9 in the upper part of the termite mound to 3.9 and 1.7 in the central and lower parts, respectively [22]. In our study the highest values were obtained in the termite structures produced in the GF by *Nasutitermes* sp1 (ranging from 15 to 22) and *Nasutitermes* sp2 (from 37 to 54).

Termite effect of total soil respiration results from direct CO_2 emissions from respiration of live tissues (termite and fungal tissues) and from the additional soil respiration due to the stimulation of soil microbial metabolism in the processed material. The high concentration of C_{org}, and NO_3^- observed in the BS produced by *Nasutitermes* sp1 in the GF may enhance the activity of micro-organisms in a similar way to that described for ants [7].

In the natural savannas, fire and termites cause emissions of CO_2, CO, CH_4, NO, N_2O to the atmosphere [10]. It has been shown that the only contribution to net emissions of CH_4 is made by *Spinitermes* sp., and it is much lesser than the emissions from cattle (0.10 Tg yr^{-1}) or direct emissions from biomass burning (0.06 Tg yr^{-1}) [23]. All CH_4 generated by subterranean termites is oxidized by soils before escaping into the atmosphere. Estimated fluxes due to termites were reported as 7.2 g CH_4 ha^{-1} yr^{-1} in the NS. The integrated annual CH_4 flux coming from termite mounds in the Llanos is 76 Mg CH_4 yr^{-1}. This value is only about 0.0004% of the total global emissions of 19.7 Tg CH_4 attributed to termites [24].

Our results also highlighted the evidence that the activities of some ecosystem engineers affect the surrounding soil by significantly increasing the concentration of some nutrients compared to the control soil. For example, some termites are accumulating C_{org} aside the BS which is an area that would correspond to the "functional domain" of the ecosystem engineer [15], although more studies are needed. A further study should be considered to assess the microbial communities in different termite mounds under the hypothesis of different microbial community composition within the same functional domain, and whether this is the result of BS building or habitat preferences by these organisms, as suggested by [7]. Besides it remains unknown which taxa of the microbial community are activated in the mounds of termites in both savanna ecosystem and GF from the Colombian Llanos.

Finally, we conclude that the activity of soil ecosystem engineers increased the spatial variability of chemical parameters measured in this study. Other BS, however seemed not to have any influence in the surrounding soil. Nutrient concentrations were higher in general in the BS than in the control soil in all cases. This shows the fact of a nutrient variability in the systems studied that may affect ecosystem processes and functional diversity of micro-organisms and plants at certain scales. A model of the dynamics of nutrients in the BS in these savannas and gallery forests of the Colombian “Llanos” and how above-ground plant communities are affected by the activities of soil ecosystem engineers should be further addressed. Besides, some unanswered questions remain, e.g. which proportion of C in the mounds of leaf-foraging ants is of plant or soil-derived origin? A further assessment with recently available techniques like Near Infrared Spectroscopy (NIRS) can help answer these questions. It would also be necessary to initiate studies about the lifespan and dynamics of break-down of these BS [8] in different environments to test the hypothesis of higher functional diversity of soil ecosystem engineers and soil processes, and also the dynamics of BS when the organisms that produce them are no longer present.

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Tables

Table I

Taxonomic position of macroinvertebrates together with a brief description of the BS produced

Macroinvertebrates				**Structures**				
Order	Family	Species	Feeding regime	Type	Colour	Shape	Aspect	
Ants								
Hymenoptera	Formicidae	*Atta laevigata* (F. Smith, 1858)	Fungi growers	Dome	orange	truncated cone	Mobile rubbish (loose aggregates)	Plate 1a
Hymenoptera	Formicidae	*Acromyrmex landolti* (Forel, 1885)	Fungi growers	Dome	orange	cone	Mobile rubbish	Plate 1b
Hymenoptera	Formicidae	*Trachymyrmex* sp. Forel	Fungi growers	Dome	orange	cone	Mobile rubbish	Plate 1c
Termites								
Isoptera	Termitidae	*Microcerotermes* sp. Silvestri 1901	Soil feeder	Dome	black	cylinder	Pasteboard-like material	Plate 2a
Isoptera	Termitidae	*Spinitermes* sp. Wasmann 1867	Soil feeder	Dome	black	cone	cemented material	Plate 2b
Isoptera	Termitidae	*Velocitermes* sp. Holmgren 1912	Litter feeder	Dome	grey	cone	cemented material	Plate 2c
Isoptera	Termitidae	*Nasutitermes* Dudley 1890 sp1.	Soil feeder?	Dome	grey	cone	cemented material	Plate 3a
Isoptera	Termitidae	*Nasutitermes* Dudley sp.2	Soil-litter feeder?	Arboreal	Dark brown	Sphere	Pasteboard-like material	Plate 3b

Table II

Size of the biogenic structures sampled (mean and standard deviation)

		Dimensions (cm)	
Species	Site	Height	Radius
Atta laevigata	NS	17.75 ± 8.26	50 ± 34.64
	GF	50 ± 16.33	33.75 ± 24.28
	IP	11 ± 8.76	29.75 ± 20.60
Acromyrmex landolti	NS	4 ± 0.82	27 ± 10.13
Trachymyrmex sp.	NS	6 ± 1.6	14.5 ± 4.4
Microcerotermes sp.	NS	12.5 ± 2.1	5.5 ± 0.6
Spinitermes sp.	NS	49.25 ± 14.2	19.75 ± 3.9
	IP	50 ±16.8	27.25 ±9.3
Velocitermes sp.	NS	13.25 ± 2.4	6.5 ± 1.3
Nasutitermes sp1	GF	57.5 ± 22.5	18.9 ±8.5
Nasutitermes sp2	GF	57.5 ± 9.6	25 ± 5.8

Figure legends

Figure 1. A map of the Carimagua research station (adapted from G. Escobar)

Figure 2. Illustration of the sampling location along the distance (expressed as %) from the top (0) to the base (100) of the BS. Large BS allowed the collection of more samples to be taken (left) than small ones (right).

Figure 3. Concentration of C_{org} in large (a) and small (b) BS produced by some ants and termites in the different systems studied. The distance from the top to the base of the BS is given as percentage(100%); 120% and 150% indicate the distance outside the BS (control soil 1) and CS indicates the control soil 2 (0-5 cm).

Figure 4. Concentration of NH_4^+ in large (a) and small (b) BS produced by some ants and termites in the different systems studied. The distance from the top to the base of the BS is given as percentage(100%); 120% and 150% indicate the distance outside the BS (control soil 1) and CS indicates the control soil 2 (0-5 cm).

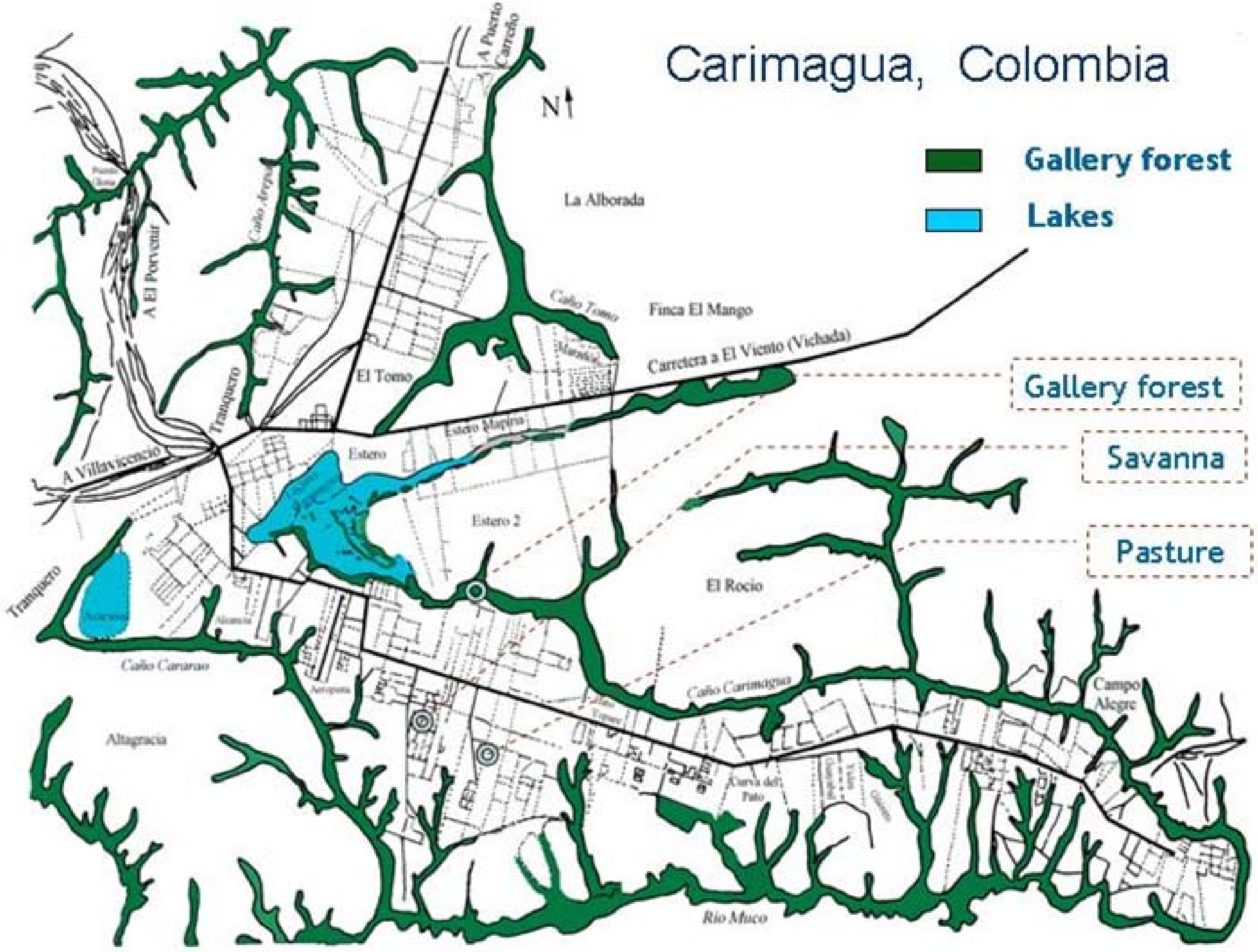
Figure 5. Concentration of NO_3^- in large (a) and small (b) BS produced by some ants and termites in the different systems studied. The distance from the top to the base of the BS is given as percentage(100%); 120% and 150% indicate the distance outside the BS (control soil 1) and CS indicates the control soil 2 (0-5 cm).

List of plates

Plate 1. Biogenic structures produced by ants in the savanna that were analysed; a) *Atta laevigata* Smith nest (Picture from J.J. Jiménez), b) *Acromyrmex landolti* Forel nest (Picture from J.J. Jiménez), c) *Trachymyrmex* sp. (picture from T. Decaëns)

Plate 2. Biogenic structures produced by termites in the savanna that were analysed a) *Microcerotermes* sp., b) *Spinitermes* sp., c) *Velocitermes* sp. (all pictures from T. Decaëns).

Plate 3. Biogenic structures produced by termites in the GF that were analysed a) *Nasutitermes* sp1, b) *Nasutitermes* sp2 (pictures by Jiménez).


Carimagua, Colombia
N
Gallery forest
Lakes
Gallery forest
Savanna
Pasture
La Alborada
Finca El Mango
Carretera a El Viento (Vichada)
Caño Tomo
El Tomo
A Puerto Carreño
A El Porvenir
Transquero
A Villavicencio
Estero
Estero Mapira
Estero 2
El Rocio
Caño Carimagua
Campo Alegre
Caño Cararao
Altagracia
Curva del Pato
Río Muco

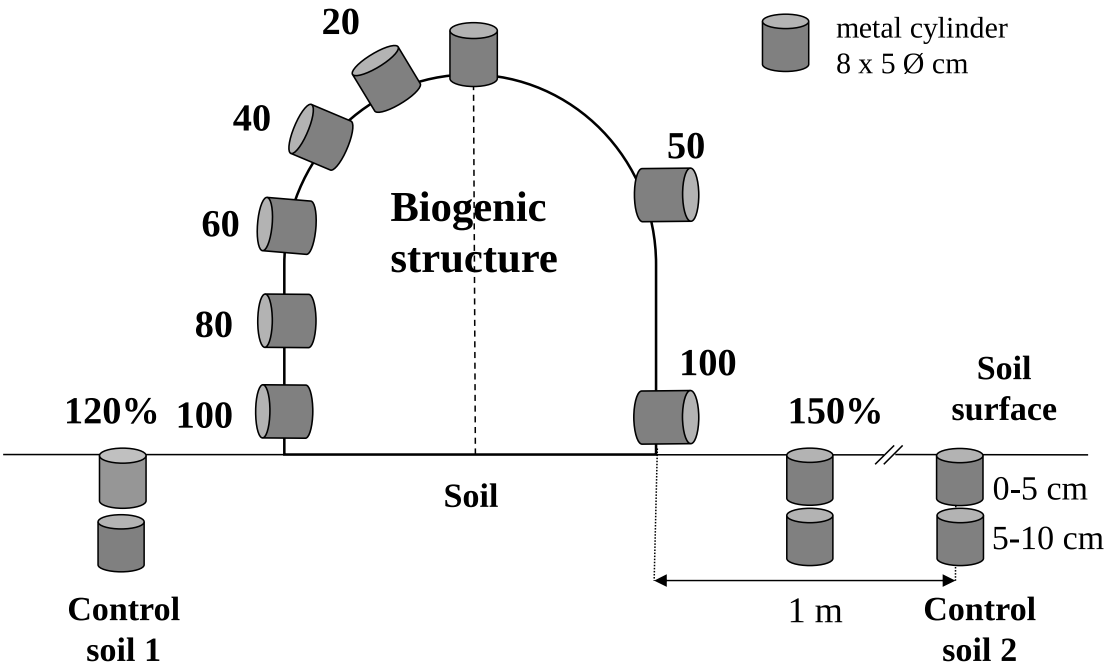

20
40
60
80
100
120%
50
100
150%
metal cylinder
8 x 5 Ø cm
Biogenic structure
Soil surface
Soil
0-5 cm
5-10 cm
1 m
Control soil 1
Control soil 2

Figure 2.

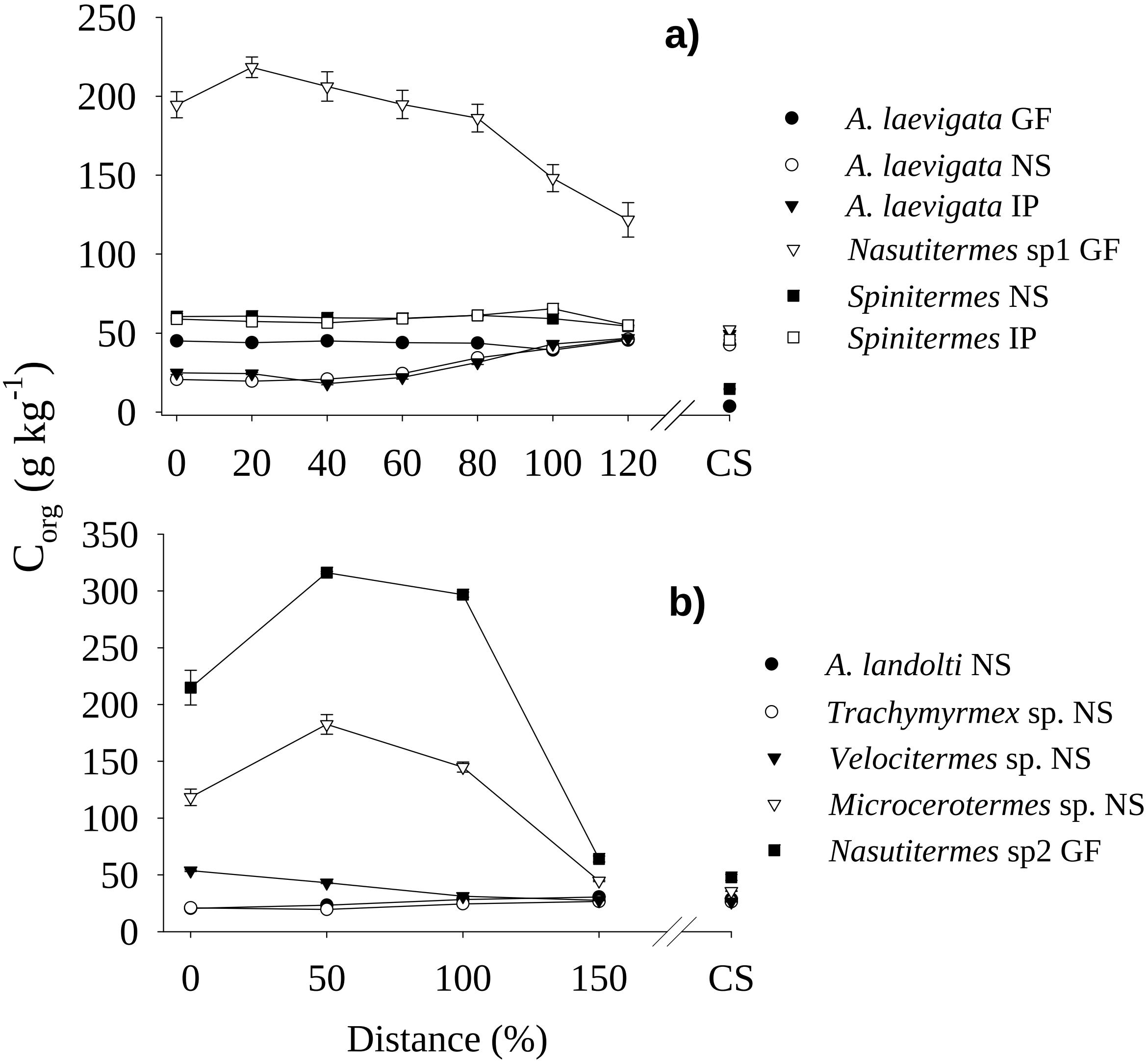

a)
250
200
150
100
50
0
0
20
40
60
80
100
120
CS
● A. laevigata GF
○ A. laevigata NS
▼ A. laevigata IP
▽ Nasutitermes sp1 GF
■ Spinitermes NS
□ Spinitermes IP
C_{org} (g kg^{-1})
b)
350
300
250
200
150
100
50
0
0
50
100
150
CS
● A. landolti NS
○ Trachymyrmex sp. NS
▼ Velocitermes sp. NS
▽ Microcerotermes sp. NS
■ Nasutitermes sp2 GF
Distance (%)

Figure 3.

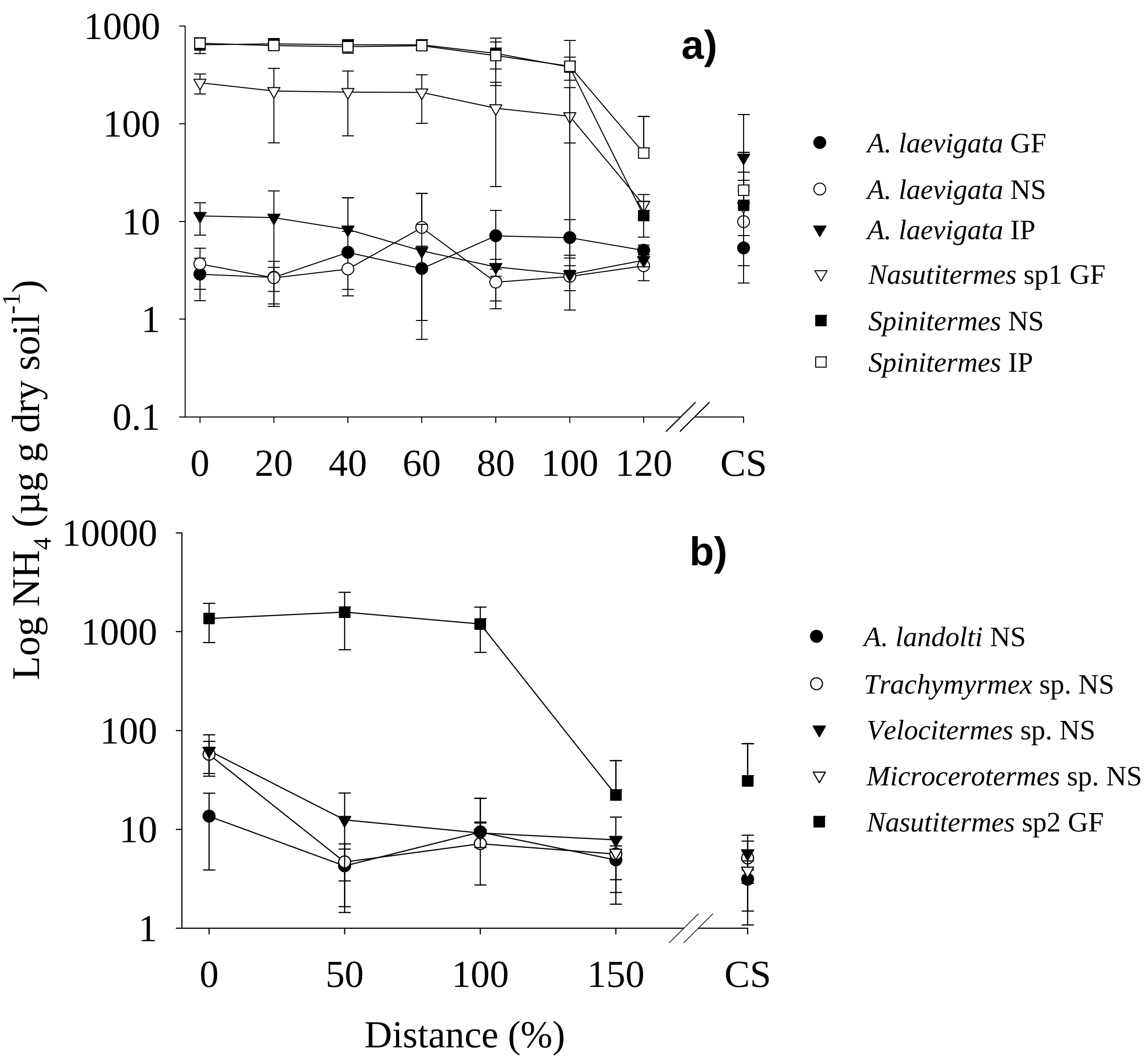

a)
1000
100
10
1
0.1
0
20
40
60
80
100
120
CS
● *A. laevigata* GF
○ *A. laevigata* NS
▼ *A. laevigata* IP
▽ *Nasutitermes* sp1 GF
■ *Spinitermes* NS
□ *Spinitermes* IP
Log NH$_4$ (µg g dry soil^{-1})
b)
10000
1000
100
10
1
0
50
100
150
CS
Distance (%)
● *A. landolti* NS
○ *Trachymyrmex* sp. NS
▼ *Velocitermes* sp. NS
▽ *Microcerotermes* sp. NS
■ *Nasutitermes* sp2 GF

Figure 4.

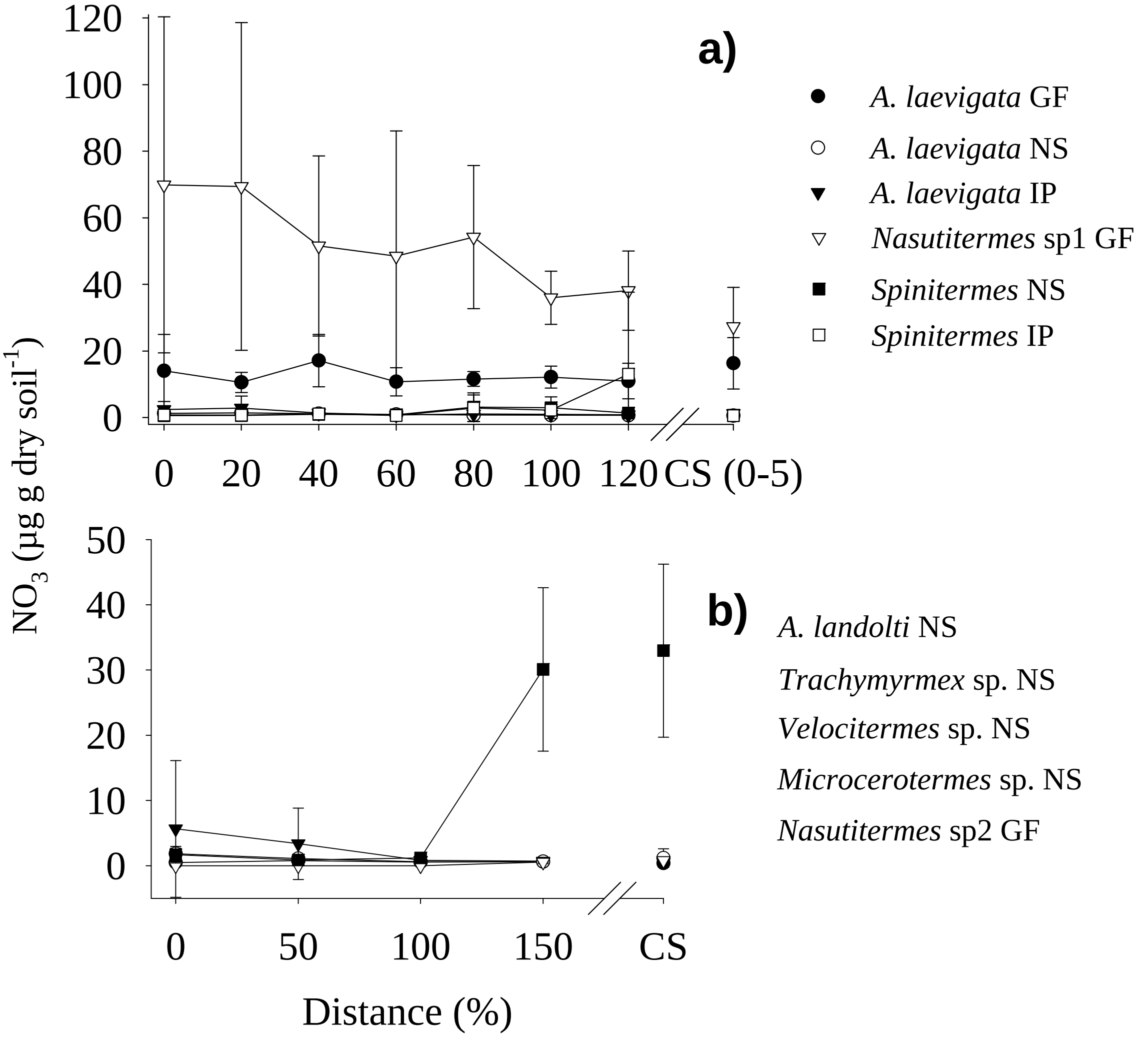

a)
120
100
80
60
40
20
0
0
20
40
60
80
100
120
CS (0-5)
● *A. laevigata* GF
○ *A. laevigata* NS
▼ *A. laevigata* IP
▽ *Nasutitermes* sp1 GF
■ *Spinitermes* NS
□ *Spinitermes* IP
NO3 (µg g dry soil-1)
b)
50
40
30
20
10
0
0
50
100
150
CS
A. landolti NS
Trachymyrmex sp. NS
Velocitermes sp. NS
Microcerotermes sp. NS
Nasutitermes sp2 GF
Distance (%)

Figure 5.

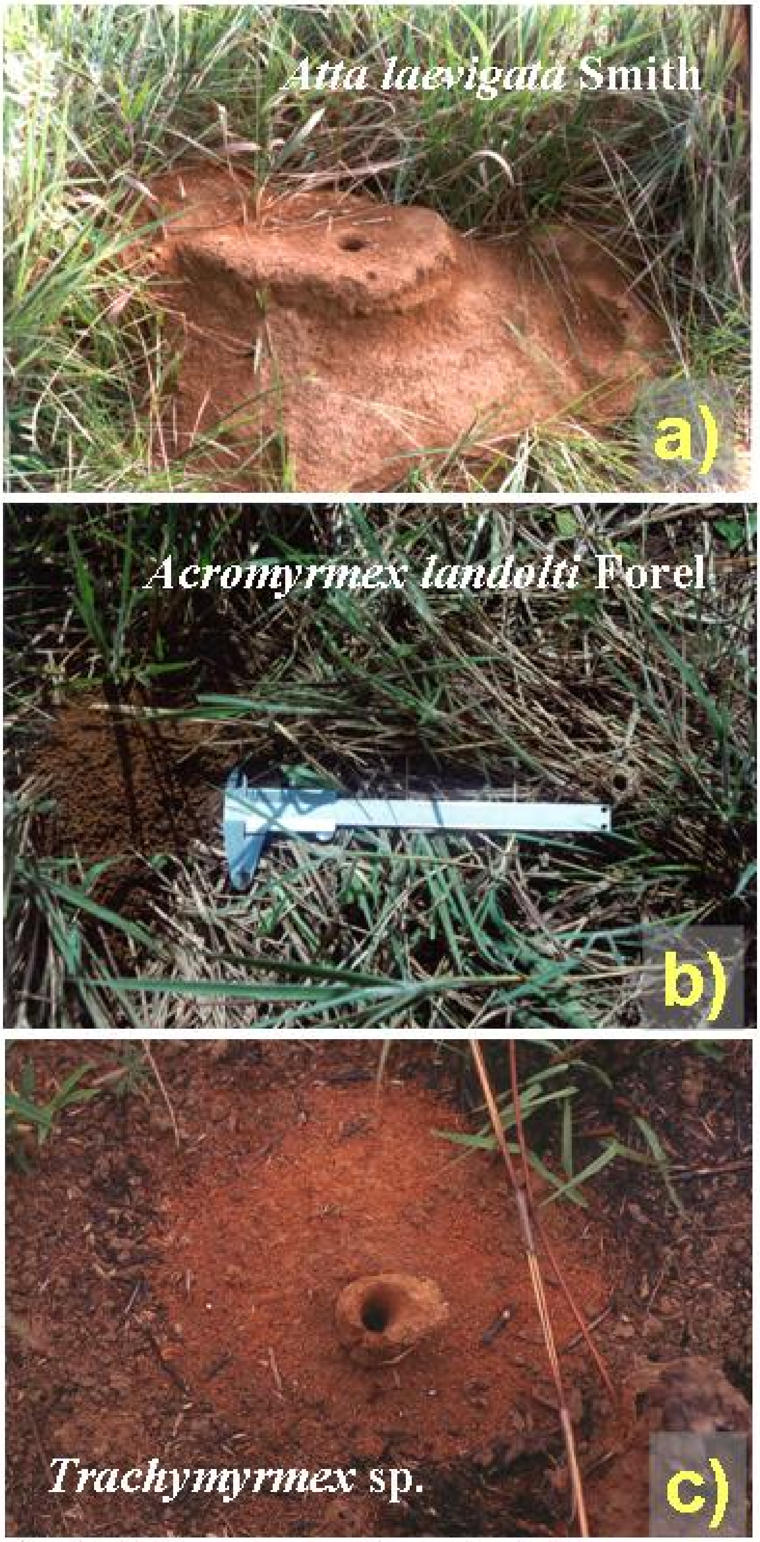


Plate 1. BS produced by ants in the savanna.

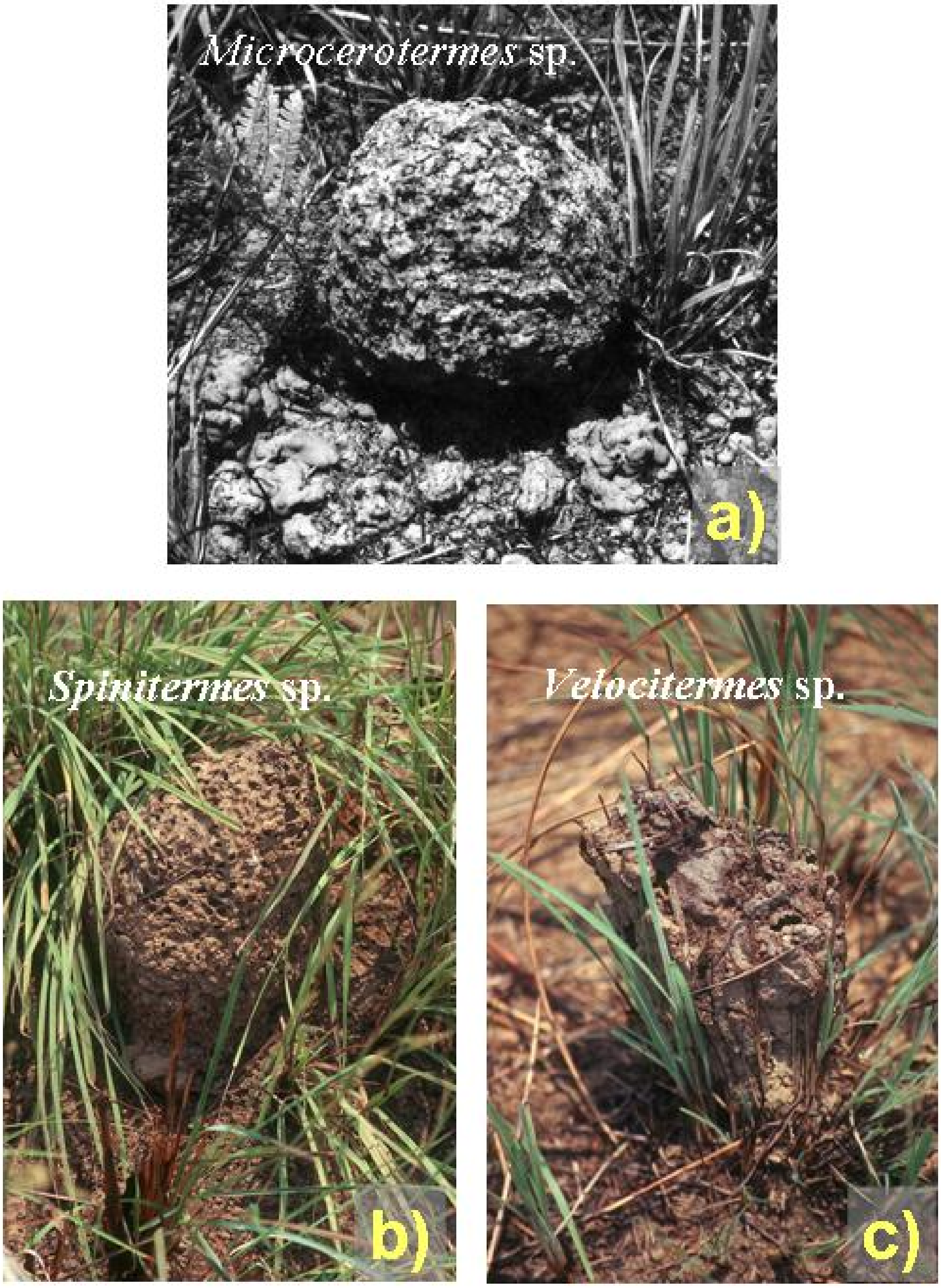


Plate 2. BS produced by termites in the savanna (Decaëns et al. 2001).

Plate 3. BS produced by termites in the gallery forest.