Nutrient spatial variability in biogenic structures of Nasutitermes
(Termitinae; Isoptera) in a gallery forest of the Colombian “Llanos”

Juan J. Jiménez^{a,*}, Thibaud Decaëns^b, Patrick Lavelle^a

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

^b *Laboratoire d'Ecologie. UPRES-EA 1293. UFR Sciences. Université de Rouen. F-76821 Mont St. Aignan
Cedex, France*

* Corresponding author (present address):

Carbon Management and Sequestration Center

School of Natural Resources

2021 Coffey Road

The Ohio State University

Columbus, OH-43210

USA

Tel: +614 292 2298

Fax: +614 292 7432

E-mail address: jimenez.58@osu.edu; juanjo_jimenezj@yahoo.com

Abstract

By definition “ecosystem engineers” are those organisms capable to modify physically the environment by producing “biogenic” structures (BS). Large macroinvertebrates like termites, earthworms and ants produce BS with distinguishable physico-chemical properties. We measured total C_{org} , NH_4^+ and NO_3^- contents in the BS produced by two species of Neotropical termites (subfamily Nasutitermitinae) in a gallery forest (GF) of the Eastern Plains of Colombia. We sampled from the top of the BS to the edge at proportional distances, i.e. 20-100% for the largest BS in the soil surface and 50-100% for the smallest arboricole BS. Control soil was sampled 1 m apart from the BS. Values of total C_{org} were high in the BS produced by Nasutitermes sp1 (epigeic mound), while a high N mineralization process was observed in the same BS and in the Nasutitermes sp2 arboreal nest. The role of these two ecosystem engineers in nutrient cycling is discussed.

Keywords: Nutrient dynamics; Termites; Carbon; Soil ecology; Ecosystem engineers; Gallery forest; Savanna

1. Introduction

Many types of disturbances determine spatial and temporal heterogeneity, i.e. the spatial structure of a given variable in soils (Wiens 2000). Disturbances also affect processes that may control ecosystem productivity, such as nutrient cycling, organic matter dynamics and soil development (Borman and Likens 1979).

Disturbances in ecosystems can be also the result of organisms' activities. For instance, soil ecosystem engineers (*sensu* Jones et al. 1994) are those organisms that modify physically the environment in which they live through the creation of biogenic structures (BS) with different physico-chemical properties according to the species and the soil where they carry their activities (Lee and Foster, 1991; Blanchart et al., 1997). This has detectable effects on habitat structure and constitutes an important source of soil heterogeneity with relevant consequences in soil function (Brussaard et al., 1997). In fact, they are an important component of tropical soils since BS may cover a large area of the soil surface, although this has rarely been quantified.

In the study of functional impact of soil engineers "soft" biological traits can be easily measured and enable prediction of "hard" traits, i.e. those characters that have direct functional implications but are difficult or not possible to measure (Díaz et al., 1999). The properties of the BS can be considered as soft traits that relate to hard traits. For this reason, it is necessary to describe the dynamics and processes that occur in the BS and how these are linked to important soil processes and function. The size and morphology of the BS, its abundance and the assessment of their physico-chemical properties are necessary steps to evaluate the indirect

effects´ in the environment at different spatial and temporal scales (Anderson, 1995, Jones et al., 1994, 1997; Lavelle, 1997). By so doing, the functional impact of soil ecosystem engineers can be investigated.

A preliminary study on the description of the main BS produced by 14 soil ecosystem engineers in a natural savanna served to establish a typology of the BS (Decaëns et al., 2001). This classification clearly discriminated the BS from their physical and chemical properties according to the soil engineer that produced them, i.e. termites, earthworms and ants. The use of Near Infrared Spectroscopy (NIRS) and enzymology analysis confirmed later this typology (Hedde et al., 2005; Mora et al., 2005).

In soil-feeding termites the soil organic matter is strongly modified forming organo-mineral complexes with clay. The soil organic matter ingested is further included as faeces in the BS and the galleries (termitosphere), which is more stable and protected from the intense mineralization that occurs in tropical soils. Soil-feeding termite BS are built with materials coming mainly from the topsoil (Anderson & Wood 1988). Faeces and salivary excretions are cemented with soil and this has important consequences on the chemical nest environment (Brauman 2000).

Termites are not only an important key group in the natural savannas but also in the gallery forests of the Colombian “Llanos”. There is a lack of empirical studies that address the description and characterization of nutrient dynamics in the BS produced by termites, and in particular in the Neotropical savannas and gallery forests. Studies on termites have not been conducted in these vegetation strips associated to the water streams and rivers in the eastern region of Colombia. Some pioneer work regarding the role of termite mounds of Nasutitermes ephratae (Holmgren) in phosphorous dynamics

has been done in the savannas of Venezuela by López-Hernández et al., (1989) and more recently on C and N contents (López-Hernández, 2001).

These studies have generally focused on the BS as a whole, rather than analyzing different areas within the BS. In this study, we assessed the spatial and temporal variability of the nutrient contents in one termite mound and one arboreal termite nest. Our main objective was to assess the spatial variability of C_{org} , NH_4^+ and NO_3^- contents within the BS. Two hypotheses were tested in this study: i) that there is a spatial variability in the amount of nutrients owing to the area of the BS, so revealing a nutrient variability in the BS according to the time of deposition, and ii) that differences in the BS construction due to distinct feeding habits will result in different chemical properties in the BS. This approach may reveal new insights in nutrient availability within these structures that may affect important ecosystem processes, like nutrient cycling and organic matter dynamics.

2. Materials and methods

2.1. Study site

The study was carried out in a gallery forest (GF) at the 22,000 ha CORPOICA – CIAT Carimagua research station (4° 37' N, 71°19' W and 175 m altitude), 320 km east from Villavicencio (Meta) in the well-drained savannas of the Eastern Plains of Colombia. Mean annual temperature and precipitation are 26 °C and 2,280 mm, respectively, with a marked four-month dry season (from December to March). Soils at the study site are isohyperthermic Oxisols in the upland savanna and Ultisols in the

lowland areas associated to gallery forests. Both soil types are characterized by their high acidity ($\text{pH} [\text{H}_2\text{O}] = 4.5$) and a high Al saturation ($>90\%$).

Soils in the GF are classified as Ultisols and the most abundant plant species were tree species like Dendropanax arboretum (Araliaceae), Enterolobium sp. (Leguminosae), Ficus spp. (Moraceae), Jacaranda copaia (Bignoniaceae), Copernicia tectorum (Caesalpinaceae), Cecropia sp. (Cecropiaceae), and palm trees like Mauritia flexuosa and M. minor (Palmaceae).

2.2. Sampling of biogenic structures

Two types of BS produced by two species of Nasutitermes Dudley were collected and sampled in this study (Plate 1a, b).

a) Nasutitermes n. sp.1

The BS constructed by this termite species was an epigeic conic mound of large size (average size of 57.5 ± 22.5 cm height x 37.8 ± 9.0 cm Ø; $n=4$). The mound was built with cemented material and the surface was rough with similar colour to the surrounding soil (Plate 1a).

b) Nasutitermes n. sp.2

The BS was an arboreal nest rather large (average size of 57.5 ± 9.6 cm height x 50.0 ± 11.0 Ø; $n=4$) which was located at 1.70-3.70 m height above the soil surface. The BS was a dark-brown coloured pasteboard-like structure that broke easily when

touching (Plate 1b). Some leaves in different stages of decomposition were normally observed in the surface of this BS.

We collected material from both BS in the middle of the rainy season of 1999. Those BS that had some part destroyed or affected by a recent deposition of material (moist) were not considered. The sampling procedure is indicated in Figure 1. Samples from the BS were taken from the center of the BS and at proportional distances, i.e. 0, 20, 40, 60, 80, 100 and 120% (control soil 1) for the large epigeic mound and 0, 50, 100 and 150% (control soil 1) for the arboreal nest. Another soil core was taken 1 m apart from the BS (control soil 2) with a small metal cylinder (5 cm Ø) to sample at two depths, 0-5 and 5-10 cm. In total 68 samples were analysed, 40 for the BS built by Nasutitermes n. sp1. and 28 for the arboreal nest produced by Nasutitermes n. sp2.

Four samples (repetitions) on each different BS were used in each site. Each sample was split in two subsamples, one for C analysis and the other for N analysis, and introduced separately in identifiable plastic bags. These were then put in an ice chest to halt possible further mineralisation processes and carried to the laboratory. Termites that were found in the samples were carefully removed before preserving the samples at 4 °C prior to analysis.

2.3. Chemical analyses

Colorimetric methods were used to determine NH_4^+ and NO_3^- contents (Anderson and Ingram 1993). Total C contents were measured with the colorimetric method after acid digestion (Houba et al. 1988) in samples that were oven-dried at 75 °C for 48 h.

2.4. Statistical analyses

Significant differences for each distance class of both BS were tested with ANOVA. The F-test was used for comparisons between distances when significant differences were found. The “R” package (version 2.1.0) was used to perform the analyses and the Sigmaplot software for graph representation.

• 3. Results

3.1. Nutrient contents in the BS and control soil

Values of NH_4^+ in the BS built by Nasutitermes n. sp1 decreased along the BS and ranged from 262.5 to 119.4 $\mu\text{g g dry soil}^{-1}$, for the 0 and 100% distance, respectively (Figure 2a); however, no significant differences were detected. Contents of NH_4^+ were much higher in the arboreal BS compared with the epigeic mound (Figure 3a) (Table 1). In general, these values were higher than 1,000 $\mu\text{g N g dry soil}^{-1}$ for all sampling distance classes (0, 50 and 100%).

Regarding NO_3^- high values were obtained in the BS built by Nasutitermes sp1, i.e. 69.9 to 36.0 $\mu\text{g g dry soil}^{-1}$ in the 0% and 100% distance, respectively, (Figure 4b). This might indicate that nitrification processes are more important in the epigeic termite mound compared to the arboreal termite nest (Figure 3b), where microbial populations may have inhibited nitrification.

Total C_{org} contents in the BS built by Nasutitermes sp1 ranged from 14.8 (distance 0) to 21.8% (distance 20%), whereas in Nasutitermes sp2 values were slightly higher, i.e. 21.5 (distance 0) to 31.6% (distance 50%).

No significant differences were found between distances 120% (Nasutitermes sp1) and 150% (Nasutitermes sp2) and control soil for 0-5 and 5-10 cm depths in all variables analyzed (Figures 3 and 4).

3.2. Effect of sampling distance

In general, a decrease in the nutrient contents as a function of the sampling distance was observed for the epigeic mound built by Nasutitermes sp1, although this decrease was not significant (Figure 3a). This means that our *a priori* assumption was correct, and that the most recent material deposited in the BS corresponded to the distance 0%, unless an area in the BS needed to be repaired that might lead to higher values in other sampling distances.

No significant differences were detected in NH_4^+ , NO_3^- and total C_{org} contents for the BS built by Nasutitermes sp1; however, values throughout the BS were significantly different to those obtained for the control soil (Figure 2a, b).

We compared values obtained for distances 0, 50 and 100% between both types of BS. In order to establish valid comparisons we used the average value of distances 40 and 60% in the case of Nasutitermes sp1. Significant differences were found for all variables, except for total C_{org} in distances 0 and 100%, respectively (Table 1).

4. Discussion

Our results showed a significant spatial variability in nutrient contents throughout the BS, e.g. regarding C_{org} contents in the BS produced by Nasutitermes n. sp2, and in NO_3^-

contents in the one produced by Nasutitermes n. sp1. Our results also highlighted a significant spatial variability regarding nutrient contents between the BS and both types of control soil. Hence, attention must be paid when sampling these structures and characterization of chemical properties are sought, since the activities of soil ecosystem engineers contribute to the heterogeneity of important processes, e.g., nutrient cycling, in the BS.

The comparison of our results with those reported in other studies is difficult since the sampling methodology used here has seldom 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 C_{org} was enriched by a factor of 3.5 ($90.2 \text{ g kg}^{-1} C_{org}$ in clayey Oxisols) and 11.5 ($109 \text{ g kg}^{-1} C_{org}$ in the loamy Oxisols) in the top of the epigeic mounds of Armitermes and Dihoplotermes (Zech et al., 1999). In our study, C_{org} , NH_4^+ and NO_3^- contents were also higher in the BS compared to the control soil, except in the BS produced by Nasutitermes sp2 (Figure 3), since here we compared an arboreal carton-type termite structure with soil.

In the mounds of the Venezuelan savanna termite N. ephratae (Holmgren) López-Hernández (2001) reported NH_4^+ values of $1528 \text{ } \mu\text{g g}^{-1}$, whereas in the savanna soil these ranged from 20.4 to $39.9 \text{ } \mu\text{g g}^{-1}$. This means that as much as 20% of the total nitrogen was found as inorganic nitrogen within this BS. On the other hand, NO_3^- production was negligible in both soils and mound, so that the nitrification rate seemed to be not limited by NH_4^+ production (López-Hernández, 2001).

In a study conducted in a semi-arid savanna of Senegal (West Africa) Ndiaye et al. (2004) assessed the N content in the BS of Cubitermes niokoloensis Roy-Noel, a

representative species of the soil-feeding guild from a dry savanna, and they found that the BS was a hot spot of mineral N (100-times NH_4^+ and 50-times NO_3^-) representing 25% of the total N content of the mound, compared with only 2% in the savanna soil. This increase was due to the presence of large population of denitrifying bacteria. In our study, the BS built by the soil feeding termite had higher contents in C_{org} , but less NH_4^+ and NO_3^- (Table 2).

The highest values of NO_3^- were obtained in the BS produced by Nasutitermes sp1. These values were nearly ten times greater than the values obtained in a set of BS produced by other soil ecosystem engineers in the savannas of Carimagua (Jiménez and Decaëns, 2005). Compared to other BS where nitrification seems to be inhibited, with values in the external wall of the mound 10 times lower to those found in the soil (Garnier-Sillam and Harry, 1995), in our study a high mineralization process is probably occurring. Nitrifying micro-organisms seem to be activated in the BS produced by Nasutitermes sp1 in the GF. A detailed study on which microbial populations are enhanced or inhibited in these BS merits further investigation.

Termites are the most important decomposers of all invertebrates in tropical forests (Bignell and Eggleton, 2000). They strongly influence soil organic matter and nutrient dynamics. Differences in nutrient contents observed between BS and the control soil are due to several reasons depending on the species and how these BS were built. Soil feeding termite mounds are constructed with materials from the surface horizon (Anderson and Wood, 1984). Epigeic termite mounds are normally cemented with soil particles that contain variable quantities of salivary secretions and excrements (Lee and Wood, 1971; Lee and Foster, 1991; Black and Okwakol, 1997; Lobry-de-Bruyn and

Conacher, 2000). Nasutitermes n. sp2, on the other hand, builds an arboreal nest 3 m above the soil surface. It is probably a plant-feeder termite since significant differences were found between this easily breakable pasteboard-like BS and the control soil, in contrast to the BS built by Nasutitermes n. sp1, which likely cement soil particles with salivary secretions and faeces (Wood, 1988).

In our case it was also common to observe green areas over the surface of the BS of Nasutitermes n. sp1 indicating the presence of algae and other micro-organisms that might have contributed to the high values of C_{org} observed due to CO_2 fixation processes (Figure 3d). Total C_{org} contents 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% C_{org}). 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 (Okello-Oloya and Spain, 1985). López-Hernández (2001) found that in termite mounds of the species N. ephratae soil microbial metabolisms was significantly stimulated due to the accumulation of C_{org} (9.3%).

Fall et al. (2001) addressed the concentration of C in different fractions within the mound, providing useful insights to the dynamics of SOM in these structures. They found that a significant part of SOM (60%) was protected in fine particle-size fractions from active mineralization. Since the BS produced by Nasutitermes sp1 had a high content of C_{org} , it is also expected that there is a high concentration of C in the different particle-size fractions. Fall et al. (2001) found that soil feeding termites seem to be responsible for the formation of aggregates of the coarse-silt size (i.e. 20–50 μm). This

opens the questions for analyzing other BS produced by different species to test the hypothesis of specific signature of soil feeding termite activity in soils, as suggested by Eschenbrenner (1986). Specific signatures for different BS produced by large invertebrates can be analyzed with NIRS as shown by Hedde et al. (2005).

Termite effect on total soil respiration results from direct CO₂ emission 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. Our results indicated that the activities of termites may result in the accumulation of C_{org} aside the BS, an area that may correspond to the “functional domain” hypothesis (Lavelle, 2002). One further study should be considered to assess the composition of 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 (Dauber and Wolters, 2000). Cultures of these BS under lab conditions and fingerprinting studies are also necessary to answer these questions.

Finally, the activity of these soil ecosystem engineers in the gallery forest of the Colombian Llanos increased the spatial variability of soil parameters measured in this study. In general, nutrient concentrations were higher in the BS than in the control soil, except for NO₃⁻ in the arboreal BS. This indicates the existence of hotspots of nutrients that may affect subsequently ecosystem processes at certain spatial and temporal scales. In our study we have observed that there seems to be three different areas throughout the BS of Nasutitermes sp1 regarding the dynamics of NH₄⁺ (0%, 20-60% and 80-100%) and NO₃⁻ (0-20%, 40-80% and 100-120%), whereas C_{org} fluctuated around 20% in almost all

distance classes. A model of nutrient dynamics and flow within the BS and through the surrounding environment in these savannas and gallery forests deserves more attention, as well as the quantification of the amount of C that can be stored in these structures at larger scales of observation and the fate and dynamics of C when these BS are destroyed by abiotic or biotic factors.

Acknowledgements

Financial support was provided by the Soil, Water and Nutrient Management systemwide programme of the CGIAR and through the IBOY-DIVERSITAS programme. We would like to thank R. Thomas and E. Amézquita (CIAT), N. Asakawa for N-NH_4^+ and N-NO_3^- and P. Pinto for her help in C determinations at CIAT lab facilities. Thanks to P. Eggleton (Natural History Museum, London) for a preliminar identification of termite genus.

References

- Anderson, J. M., 1995. Soil organisms as engineers: microsite modulation of macroscale processes. In: Jones, C. G., Lawton, J. H. (Eds.), *Linking Species and Ecosystems*, Chapman and Hall, London. pp. 94-106.
- Anderson, J. M., Ingram, J., (Eds), 1993. *Tropical soil biology and fertility program, a handbook of methods*. CAB International, Oxford.
- Anderson, J. M., Wood, T. G., 1988. Mound composition and soil modification by two soil-feeding termites (Termitinae, Termitidae) in a riparian Nigerian forest. *Pedobiologia* 26, 77-82.

- Bignell, D. E., Eggleton, P., 2000. Termites in ecosystems. In: Abe, T., Higashi, M., Bignell, D. E. (Eds.), *Termites: Evolution, Sociality, Symbiosis, Ecology*. Kluwer Academic Press, Dordrecht.
- Black, H. I. J., Okwakol, M. J. N., 1997. Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of termites. *Applied Soil Ecology* 6, 37–53.
- Blanchart, E., Lavelle, P., Braudeau, E., Bissonais, Y. L., Valentin, C., 1997. Regulation of soil structure by geophagous earthworm activities in humid savannas of Côte d'Ivoire. *Soil Biology & Biochemistry* 29, 431-439.
- Borman, F. H., Likens, G. E., 1979. *Patterns and processes in a forested ecosystem*. Springer-Verlag, New York.
- Braumann, A. 2000. Effect of gut transit and mound deposit on soil organic matter transformations in the soil feeding termite: A review. *European Journal of Soil Biology* 36, 117-125.
- Brussaard, L. J., Behan-Pelletier, V. M., Bignell, D. E., Brown, V. K., Didden, W., Folgarait, P., Fragoso, C., Freckman, D. W., Gupta, V. S. R., Hattori, T., Hawksworth, D. L., Klopatek, C., Lavelle, P., Malloch, D. W., Rusek, J., Söderström, B., Tiedje, J. M., Virginia, R. A., 1997. Biodiversity and ecosystem functioning in the soil. *Ambio* 26(8), 563-570.
- Dauber, J., Wolters, V., 2000. Microbial activity and functional diversity in the mounds of three different ant species. *Soil Biology & Biochemistry* 32, 93-99.

- Decaëns, T., Galvis, J. H., Amézquita, E., 2001. Propriétés des structures produites par les ingénieurs écologiques à la surface du sol d'une savane colombienne. Comptes Rendus de l'Académie des Sciences Paris 324, 465-478.
- Díaz, S., Cabido, M., Zak, M., Carretero, E. M., Aranibar, J., 1999. Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. *Journal of Vegetation Science* 10, 651-660.
- Eschenbrenner, V., 1986. Contribution des termites à la microagrégation des sols tropicaux. Cahier ORSTOM, serie Pedologie XXII, pp. 397-408.
- Fall, S., Braumann, A., Chotte, J.-L., 2001. Comparative distribution of organic matter in particle and aggregate size fractions in the mounds of termites with different feeding habits in Senegal: Cubitermes niokoloensis and Macrotermes bellicosus. *Applied Soil Ecology* 17, 131-140.
- Garnier-Sillam, E., Harry, M., 1995. Distribution of humic compounds in mounds of soil-feeding termites: its influence on soil structural stability. *Insectes Sociaux* 42, 167-185.
- Hedde, M., Lavelle, P., Joffre, R., Jiménez, J. J., Decaëns, T., 2005. Specific functional signatures in soil macro-invertebrate biostructures. *Functional Ecology* 19(5), (in press).
- Houba, V.J.C., van der Lee, J. J., Novozamsky, I., Walinga, J., 1988. Soil and plant analysis. In: Department of Soil Science and Plant Nutrition, (Ed.), *Soil analysis procedures*, 4th ed., Agricultural University, Wageningen, The Netherlands. pp. 4-14.

- Jiménez, J.J., Decaëns, T., 2005. Spatio-temporal dynamics of chemical properties in the biostructures produced by soil ecosystem engineers – A synchronical approach in the Neotropical savannas. *European Journal of Soil Biology* (in press).
- Jones, C. G., Lawton, J. H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Jones, C. G., Lawton, J. H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78, 1946-1657.
- Lavelle, P., 1997. Faunal activities and soil processes: adaptive strategies that determine ecosystem function. *Advances in Ecological Research* 27, 93-132.
- Lavelle, P., 2002. Functional domains in soils. *Ecological Research* 17, 441-450.
- Lee, K., Foster, R.C., 1991. Soil fauna and soil structure, *Australian Journal of Soil Research* 29, 745–775.
- Lee, K., Wood, T. G., 1971. Physical and chemical effects on soils of some Australian termites, and their pedological significance. *Pedobiologia* 11, 376–409.
- Lobry-de-Bruyn, L. A., Conacher A J., 1990. The role of termites and ants in soil modification: a review, *Australian Journal of Soil Research* 28, 55–93.
- López-Hernández, D., 2001. Nutrient dynamics (C, N and P) in termite mounds of Nasutitermes ephratae from savannas of the Orinoco Llanos (Venezuela). *Soil Biology & Biochemistry* 33, 747-753.
- López-Hernández, D., Fardeau, J. C., Niño, M., Nannipieri, P., Chacón, P., 1989. Phosphorous accumulation in savanna termite mounds in Venezuela. *Journal of Soil Science* 40, 635-640.

- Mora, P., Miambi, E., Jiménez, J.J., Decaëns, T., Rouland, C., 2005. Functional complement of biogenic structures produced by earthworms, termites and ants in the Neotropical savannas. *Soil Biology & Biochemistry* 37(6), 1043-1048.
- Ndiaye, D., Lepage, M., Sall, C. E., Brauman, A., 2004. Nitrogen transformations associated with termite biogenic structures in a dry savanna ecosystem. *Plant and Soil* 265, 189-196.
- Okello-Oloya, T. Spain, A., John, R. D., 1985. Selected chemical characteristics of the mounds of two species of Amitermes (Isoptera, Termitinae) and their adjacent surface soils from northeastern Australia. *Revue d'Ecologie et Biologie du Sol* 22, 291-311.
- Wiens, J. A., 2000. Ecological heterogeneity: an ontogeny of concepts and approaches. In: Hutchings, M. J., John, E. A. and Stewart, A. J. (Eds.), *Ecological consequences of environmental heterogeneity*. Blackwell Science, Oxford, pp. 8-30.
- Wood, T. G., 1988. Termites and the soil environment. *Biology & Fertility of Soils* 6, 228-236.
- Zech, W., Amelung, W., Neufedt, H., 1999. Organic matter in termite mounds of the Brazilian Cerrados. In: Thomas, R. J., Ayarza, M. A. (Eds.) *Sustainable Land Management for the Oxisols of the Latin American Savannas*, CIAT publication no. 312, 231 p.

Table 1. Statistical comparison between sampling distances 0, 50 and 100% in two BS in a gallery forest from the Colombian “Llanos”.

Variable	Sampling distance (%)		
	0	50 ¹	100
NH ₄ ⁺	**	**	*
NO ₃ ⁻	***	***	***
TotalC _{org}	n.s.	*	n.s.

*P<0.05, **P<0.01, ***P<0.001, n.s. = not significant.

¹ average value of 40 and 60% distances for the larger BS

Table 2. Total C_{org} , NH_4^+ and NO_3^- in the BS produced by two soil-feeding termites and the control soil (0-5 cm depth). Different letters indicate significant differences at $P < 0.05$. Standard deviation is in brackets. BS = Biogenic structure (external wall); CS = Control soil.

Species		C (%)	NH_4^+ ¹	NO_3^-	Moisture (%) w/w	Reference
<u>Cubitermes</u> <u>niokoloensis</u>	BS	3.20 (0.14) b	507.8 (193.6) b	181.8 (17.6) b	2.37 (0.96) b	Ndiaye et al. 2004
	CS	0.57 (0.12) a	6.4 (3.1) a	1.4 (1.2) a	0.49 (0.22) a	
<u>Nasutitermes</u> n. sp1.	BS ²	19.14 (2.39) b	193.7 (52.4) b	54.9 (13.1) a	25.5 (6.9) a	This study
	CS	8.7 (3.5) a	14.6 (0.2) a	32.7 (5.4) a	29.9 (2.9) a	

¹ $\mu\text{g N g}^{-1}$ dry

² Average value of all distance classes (from 0 to 100%)

Figure legends

Plate 1. Biogenic structures analysed in this study a) epigeic termite mound built by Nasutitermes sp1. and b) arboreal termite nest of Nasutitermes sp2. (Pictures from J.J. Jiménez).

Figure 1. Sampling methodology to collect material from the biogenic structures constructed by soil ecosystem engineers at Carimagua (Colombia). The distance employed for both biogenic structures, expressed as percentage of size, is represented on the left- and right-hand sides, respectively.

Figure 2. Nutrient contents a) NH_4^+ , b) NO_3^- , and c) $Total\ C_{org}$ in the BS built by Nasutitermes sp1 (epigeic mound) and in the two distances used for control soil at 0-5 and 5-10 cm depths.

Figure 3. Nutrient contents a) NH_4^+ , b) NO_3^- , and c) $Total\ C_{org}$ in the BS built by Nasutitermes sp2 (arboreal nest) and in the two distances used for control soil at 0-5 and 5-10 cm depths.

Plate 1.

Figure 1. Jiménez, J.J., Decaëns, T. and Lavelle, P.

Figure 2. Jiménez, J.J., Decaëns, T. and Lavelle, P.

Figure 3. Jiménez, J.J., Decaëns, T. and Lavelle, P.