TERMITES IN ECOSYSTEMS OF CENTRAL AMAZONIA: SPECIES COMPOSITION, SOIL PROPERTIES, AND NUTRIENT CYCLING

A Dissertation
Presented to the Faculty of the Graduate School
of Cornell University
in Partial Fulfillment of the Requirements for the Degree of
Doctor of Philosophy

by
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August 2006

TERMITES IN ECOSYSTEMS OF CENTRAL AMAZONIA:
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Cornell University 2006

We investigated how termite species composition differed between primary forest and agroecosystems, and the impact of mound-building termites on soil properties and nutrient cycling in a secondary forest. In Chapter 1, we compared the termite assemblage of a primary forest with that of low- and high-diversity agroforests using a rapid biodiversity assessment protocol. The agroforests maintained the same percentages of termite species across feeding guild and taxonomic classes as primary forest, indicating that agroforests may be able to support the same suite of termite functions as primary forest. The palm-based, low-diversity agroforest hosted a termite assemblage more similar to the primary forest than the high-diversity agroforest, indicating that specific plant attributes may be more important drivers of termite diversity than plant diversity alone. An unusually high percentage of soil-feeding termite species was found in all land uses.

In Chapter 2 we investigated chemical, physical, and hydraulic properties of termite mounds in secondary forest to determine the most important constraints on plant establishment. Termite mounds were found at a density of 760 ha^{-1} in the study site, covering 3% of the area. Root biomass was 50% lower in the surface of these mounds than in the soil surface. The physical strength of the termite mounds (13.5 MPa resistance) and their hydraulic characteristics (higher

infiltration rate (16 mm s^{-1}), lower water retention, and lower rates of water absorption) were found to be the most important constraints to plants.

In Chapter 3, we looked at the role of termite mounds in carbon and nitrogen storage in a secondary forest site. Termite mounds stored 80% and 20% more carbon and nitrogen per mass soil than the surrounding soils. Carbon mineralizes at the same rate as the control soil, but nitrogen mineralizes 30% more slowly, at 0.14 mg $(g\ N)^{-1}\ d^{-1}$. Microbial carbon in termite mounds was 50% lower than in control soils, at 0.5 and 1%, respectively. Neither moisture nor physical protection in termite-mound aggregates were constraints to nitrogen mineralization. We inferred that low-quality organic matter used in mound construction (post-digestion) is responsible for the lower rates of nitrogen mineralization.

BIOGRAPHICAL SKETCH

Ilse grew up in Virginia and Africa. She expressed an affinity for soil fauna early on, first with earthworm collections, later with an ant hospital. At nine, she unwittingly betrayed the objects of her fancy by helping a visiting entomologist in his searches.

Her undergraduate studies started with psychobiology at Wellesley College and biogeography at The School for Field Studies - Australia, and she graduated in environmental sciences from Antioch College. Never having outgrown her interest in soil fauna, her senior thesis was on the effect of earthworms on bacteria in sewage sludge. She was an aerospace research fellow at NASA, worked on a carbon cycling study at The Woods Hole Research Center, and in research at Kentucky's Appalachia—Science in the Public Interest's organic farm.

After college, she received a National Institute for Global Environmental Change Fellowship to start a soil respiration study at Harvard Forest, and from there went to work as a research assistant for The Woods Hole Research Center on a study of trace gas emissions from different land uses in eastern Amazonia. She did her Master's in the Soil, Crop, and Atmospheric Sciences department at Cornell, modeling the effects of fungus-growing ants and termites on carbon pools in tropical ecosystems.

In memory of my grandfather, Lauren Aquilla Yoder, whose curiosity and appreciation for orchards, fields, creatures, and distant lands shaped my own; and to my grandmother, Nina Viola Yoder, who has looked after the soil and plants of a single acre of land for over fifty years.

ACKNOWLEDGMENTS

While specific acknowledgements follow each article, some more general thank-you's are also due. First to my advisor, Erick Fernandes, for his generosity with knowledge and opportunities, and for supporting my directions. To Elisa Wandelli for facilitating the work of our team and giving us a broader vision. To my committee members Susan Riha, Johannes Lehmann, Mike Villani, and J. M. Anderson, and collaborators Wenceslau Teixeira, Reginaldo Constantino, Marco Rondon, and Hugh Gauch, for their valued input and advice. And to the lab groups of Erick Fernandes, Susan Riha, and Johannes Lehmann for their feedback, advice, and support.

…To the LBA ND-04 lab group, including Juliete Moraes, Rosana Palheta, Lucerina Trujillo, Guilherme da Silva, Ivan Cortez, and Jorge Gallardo, for sharing the field experience and limited resources with good spirits. Rubenildo Lima gave us wonderful logistical support. Seu João sustained our work at kilometer 54 with his inspired cooking.

In field work, I'm heavily indebted to Osmar Barbosa Ferreira for his conscientiousness, and the knowledge of the creatures and plants of Amazonia which added much to my research. I enjoyed the opportunity to work with Juliete Queiroz Moraes, who brought an inquisitive mind, high energy, and contagious research interest to the field. Thank you to Dênis Valente Leite and technicians Paulo da Silva and Orlando Ferreira da Cruz Jr for their assistance in the field and lab.

In Ithaca: special friends and officemates in Bradfield Hall who helped my work, my transitions between Virginia and Ithaca, and my school-work-life balance: Stefan Jirka, Jijy Sooksa-nguan, Steve Culman, Steve Welch, Brendan O'Neill, Ted Feldpausch, Luis Duque, and André Gonçalves,.

Robby and Susan Ackerman, parents, in many ways assisted with my doctoral studies, from loaned vehicles to brave Ithaca cold, to relieving me of home responsibilities (cat rescue!), to actually pitching in and doing article filing! Other notable family are Jim and Connie Lehman (checking on my progress!), Anita Yoder and Anje Cassel (encouragement), Hans Ackerman (sage advice), and Dorothy Baxter (prayers!)!

Friends Nicole Yoder, LaDene King, Angie Showalter, Tswakai Tsomondo, and Michael Weaver have all supported me in many ways. Special thanks to Yamily, Carly, and Ylimay Zavala, for always being my home away from home.

Housemates deserve a special category of recognition, for covering for me on pet and home care on school absences and putting up with dissertation-dictated needs, such as space and quiet! Thank you to those housemates who in varying mixes put up with/suffered through/supported me through data collection, analysis, and writing: on *Rua das Seringas*: Suzana Ketelhut, Ingrid Quintero, Carlos da Costa, Carol Schwendener, and Christoph Steiner. On Old Furnace Road: Esther Kang, Melody Mast, Anje Cassel, and on Wolfe Street: Amy Potter, Gretchen and Ella Werner, Nicole Yoder, Jen Graber, and Stacy and Martin Vlasits.

To the folks at Fairfield Language Technologies, for unusual flexibility and extraordinary accommodations in making room for me to write my dissertation while employed. Thanks go especially to Robert Bland, Marion Bittinger, Melissa Ritter, Jack Marmorstein, and Greg Keim.

To my friends on the Daily Board of pHinished.org for their shared experiences and encouragement.

For the institutional support of Embrapa-CPAA, INPA, NASA-LBA, and the Department of Crop and Soil Sciences at Cornell.

And finally, “to the little ones who run the world!” (E. O. Wilson) for all the amazement and wonder they’ve brought me.

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CHAPTER 1

TERMITE (INSECTA: ISOPTERA) ASSEMBLAGES IN PRIMARY RAIN FOREST AND AGROFORESTS IN CENTRAL AMAZONIA

ABSTRACT

Termites play an important role in organic matter decomposition, nutrient cycling, and soil structure in tropical forests. Little is known about how primary forests and other land covers in Amazonia may differ in terms of termite species composition and function. We compared the termite assemblage of a primary forest with that of a low-plant-diversity, palm-based agroforest (5 plant spp.) and a high-plant-diversity, home-garden agroforest (10 plant spp.) using a rapid biodiversity assessment protocol. Unexpectedly, the palm-based agroforest, despite its lower plant diversity, was closer to primary forest in termite species composition than was the home-garden agroforest, suggesting that the presence of particular plant attributes may be a more important determinant of the termite assemblage than plant diversity in these agroecosystems.

The agroforests maintained the same proportions of termite species across feeding guild and taxonomic class as primary forest. Insomuch as feeding guild is a proxy for function, this indicates that these closed-canopy agroforests may be able to sustain the same termite functions as primary forest.

Across land uses at the site, we found an unusually high percentage of species in the soil-feeding guild, at 57%. In terms of abundance, Apicotermitinae and soil feeders in general were proportionally more abundant in agroforests than primary forest (22% and 11% higher,

respectively). The ability of the agroforests to support populations of soil feeders has a potentially positive effect on soil fertility in these agroecosystems.

Introduction

Termites are an integral part of tropical rain forest ecosystems. Though not easily observed due to their cryptic nature, they are ubiquitous in the soil, leaf litter, and dead woody debris of the forest, and are often the dominant arthropod detritivore (Jones and Eggleton, 2000). A diverse range of termite species processes plant organic matter at all stages of decomposition, from leaf litter, to rotten wood, to humus throughout the soil. With tropical rainforest associated with low-fertility soils (Jordan, 1985), the termites' cycling of organic matter is important for the efficient return of nutrients to the vegetation.

While Amazonia contains the largest continuous rain forest in the world (Leopoldo et al., 1987), the ecology of its termite fauna is little known compared to that of the rainforests of the Old World Tropics (Martius, 1994). Only a handful of surveys of termite species have been conducted in Amazonia ((Snyder, 1926), (Mill, 1982), (Bandeira and Torres, 1985), (Bandeira, 1989), (Apolinário, 1993), (Constantino, 1992), and (De Souza and Brown, 1994)).

In extensive areas of Amazonia, the rainforest ecosystem has been replaced with agriculture. Pasture, crops, and fallows now occupy over 500,000 km^2 (INPE, 2004) of the original extent of the forest. While the information about primary forest termite assemblages is sparse, data on how those assemblages change with conversion of forest to agroecosystems is even scarcer (Okwakol, 2000). The loss of termite diversity on converting tropical forest to agriculture has been shown in Africa by Collins (1980), Eggleton et al. (1996), and Okwakol (2000), and in Asia by Abe and Watanabe (1983), Watanabe et al. (1984), and Abe and Matsumoto (1979). At an African site, Okwakol (2000) found 60% of termite species to be eliminated upon forest clearance, and only two species survived cultivation. In eastern Amazonia, Bandeira (1983) found the termite species richness reduced by half (from 63 to 32 species) when primary forest was converted to pasture.

The maintenance of active soil fauna communities improves the sustainability of cropping systems through regulations of soil processes at various temporal and spatial scales (Lavelle et al., 2001). To maintain these soil communities, Lavelle et al. (2001) propose agricultural practices that maintain plant cover with diverse types of vegetation. Agroforestry is one such promising agricultural strategy in the Amazon Basin (Fernandes and Matos, 1995), maintaining a structural diversity that imitates the native forest better than do pasture or crops. While such practices exist, their interaction with soil fauna has been little studied (Lavelle et al., 2001). When the derived system is similar in structure to the primary vegetation, such as tree-based systems in forest areas, these communities are apparently best conserved ((Decaëns et al., 1994), (Decaëns et al., 2002), (Fragoso et al., 97), and (Barros, 1999) in Lavelle et al. (2001)). More research is needed to confirm this relationship (Barros et al., 2002), especially in agroforestry systems that have not been investigated using comparable sampling protocols ((Vohland and Schroth, 1999) and (Lavelle et al., 2002)). Beare et al. (1997) similarly concluded from a review of the literature that more research needs to focus on how multicropping management practices influence the biodiversity and function of tropical soils.

In this study, we compared the termite species composition of a primary forest in Central Amazonia to that of two agroforestry systems: a low-plant-diversity palm-based agroforest and a high-plant-diversity home-garden agroforest. We expected the home-garden agroforest to be closer in termite species composition to the primary forest than the palm-based agroforest, due to its greater plant diversity (Table 1.1).

Because termite species have a wide variety of feeding and nesting habits, the impact of termites on decomposition is likely to depend largely on the composition of the termite assemblage (Lawton et al., 1996). We hypothesized that the distribution of termite species among feeding guilds in agroforests would differ from their distribution in primary forest.

Methods

Study site

The study site was located at 02° 31′ 04″ S and 60° 01′ 48″ W at the Empresa Brasileira de Pesquisa Agropecuaria research station, at km 54 of the highway BR-174 north of Manaus, Amazonas, Brazil. Soils on the plateau where this study was conducted are classified as dystrophic, isohyperthermic, clayey, kaolinitic Xanthic Hapludox. The climate is tropical humid. Mean annual precipitation is 2400-2500 mm, with an average maximum in

Table 5.1. Species composition and spacing of the agroforests at the study site in Central Amazonia (after (McCaffery, 2003)).

High-diversity agroforest	Low-diversity agroforest	Use	Abundance (plants ha^{-1})	Spacing (m)
Gliricidia sepium Jacq.	*Gliricidia sepium*	green manure	375	2 x 2
Theobroma grandiflorum Willd. ex Spreng	*Theobroma grandiflorum*	fruit	83	6 x 6
Bertholletia excelsa Berg.		nut	79	10 x 10
Eugenia stipitata McVaugh		fruit	79	6 x 6
Genipa americana Linn.		fruit	144	6 x 6
Inga edulis Mart.		green manure	120	2 x 6
Malpighia glabra Linn.		fruit	194	2 x 6
Musa paradisiaca L.		fruit	300	2 x 6
Swietenia macrophylla King		timber	40	6 x 8
Tectona grandis Linn.		timber	90	6 x 8
	Colubrina glandulosa Perkins	timber	125	6 x 12
	Bactris gasipaes H. B. K.	fruit, palm heart	650	2 x 6
	Euterpe oleracea Mart.	fruit, palm heart	596	2 x 6

February-March of around 320 mm and an average minimum in August-September of around 80 mm ((Marques et al., 1981), (de Paiva, 1996)). Mean annual air temperature is 26 C, and atmospheric humidity is around 84% (Vose et al., 1992).

Three land uses were chosen for this study: a primary forest, a home-garden agroforest, and a palm-based agroforest. The agroforests had been established on pastureland abandoned ten years prior to the experiment, and had accumulated 34 and 42 Mg aboveground C ha^{-1} respectively (McCaffery, 2003). Each plot measured 50 x 60 m. The agroforests were replicated on three blocks according to their land-use history: blocks one, two, and three had been in fallow for three, four, and five years respectively and in pasture for four, five, and eight years previously. These sites occurred on the plateau of the study site, and were surrounded by primary forest on the surrounding slopes. The primary forest site sampled was 3500 m away, chosen as the nearest accessible primary forest also on plateau soils of the study site. The primary forest was part of continuous, closed-canopy, dense, evergreen non-flooding forest (Veloso et al., 1991), as occupies about 90% of the Amazon Basin (Schubart, 1983). Canopy height was 20-30 m, with an open understory dominated by stemless palms (De Souza and Brown, 1994).

Sampling

We assessed termite species composition using the protocol recommended by Bignell and Eggleton (2000). This protocol has been shown to provide unbiased samples of the total termite species assemblage other than drywood termites (Jones and Eggleton, 2000), and it standardizes effort across sampling sites. The method employs a belt transect with ten 2 x 5 m sections sampled sequentially. We halved the transect length to 50 m to correspond to the perpendicular dimension of the agroforest plots. We established transect through the middle of each plot, amounting to three in each land use, nine in total. A team of two collectors sampled as many species as possible in 30 minutes in each 2 x 5 m section. We collected in soil, litter, dead wood, mounds, nests, soil to 5 cm depth, and runways to 2 m height in the vegetation. The presence of a species in each section was considered an encounter and used as a surrogate for relative abundance. Observations on feeding substrates and nesting locations were recorded simultaneously.

Termites were preserved in vials of 80% ethanol and labeled with section number for later identification to species or morphospecies by the second author. The collection was deposited in the Entomological Museum of the National Institute for Amazonian Research (INPA), Brazil.

Genera were assigned to feeding guilds based on known feeding habits ((Roisin and Leponce, 2004), (De Souza and Brown, 1994), (Constantino, 1999), (Hanne, 2001), (Apolinário, 1993), (Davies et al., 2003)) and the first author's personal observations in the field. These groups were (1) soil feeders: species that feed on mineral soil and humus, (2) litter feeders: species that feed on leaf and small woody litter, (3) soil/wood interface feeders: species that feed on very decayed wood that has become soil-like, and (4) wood feeders: species that feed on dead wood, and (5) pest species, i.e., species that feed on living plant tissue (Constantino, 2002).

Statistical analysis

We used reciprocal averaging (Gauch, 1982) to ordinate the species and samples of the dataset, using FORTRAN code (H. G. Gauch, Jr., pers. comm.).

Reciprocal averaging is also called correspondence analysis, weighting species abundance by location. Species that were encountered rarely in the survey (3 times or less) were not included in this analysis, as they did not provide enough information to place them along an ecological gradient.

The similarity in the species composition of the three land uses was evaluated using Bray-Curtis cluster analysis (Biodiversity Professional, Version 2, The Natural History Museum and the Scottish Association for Marine Science). To determine if species had preferences among the land uses studied, we used the additive main effects and multiplicative interactions (AMMI) model to evaluate the species by environment interaction. This model uses principal component analysis to partition the multiplicative structure within the interaction, where interaction is the residual from the ANOVA (Gauch, 1992). The AMMI model was run in the software MATMODEL (Microcomputer Power, Ithaca, NY).

Chi-square tests of independence were used to test for differences in both functional and taxonomic composition of the termite species between the three land uses. Both numbers of species as well as number of species encounters were tested. The chi-square test was also used to compare the proportions of unique species among the land uses.

Results

A graph of the average number of species over the three transects in each land use is displayed in Figure 1.1. The rate of new species discovery was higher in primary forest than in the agroforests (Figure 1.1), though not significantly higher at this sample size. The palm-based agroforest was intermediate to the primary forest and the home-garden agroforest in its rate of species accumulation (Figure 1.1). The rate of accumulation appeared to be approaching zero in the home-garden agroforest after 100 m^2 of sampling, but continued to be positive in the primary forest and palm-based agroforest (Figure 1.1).

The termites collected belonged to two families (Rhinotermitidae and Termitidae), three Termitidae subfamilies (Apicotermitinae, Nasutitermitinae, and Termitinae), 32 genera, and 67 species (Table 1.2). Of these, 52, 30, and 19 species were collected in primary forest, palm-based agroforest, and home-garden agroforest these, 52, 30, and 19 species were collected in primary forest, palm-based agroforest, and home-garden agroforest respectively (Table 1.2). In the primary forest, 32 species were collected that were unique to that environment, while only six and four unique species were collected in the palm-based and home-garden agroforests, respectively. There was no block effect (land-use history) on termite species richness in the agroforests.

Very rare species (encountered only once) made up a significantly higher percentage ($P < 0.01$) of the primary

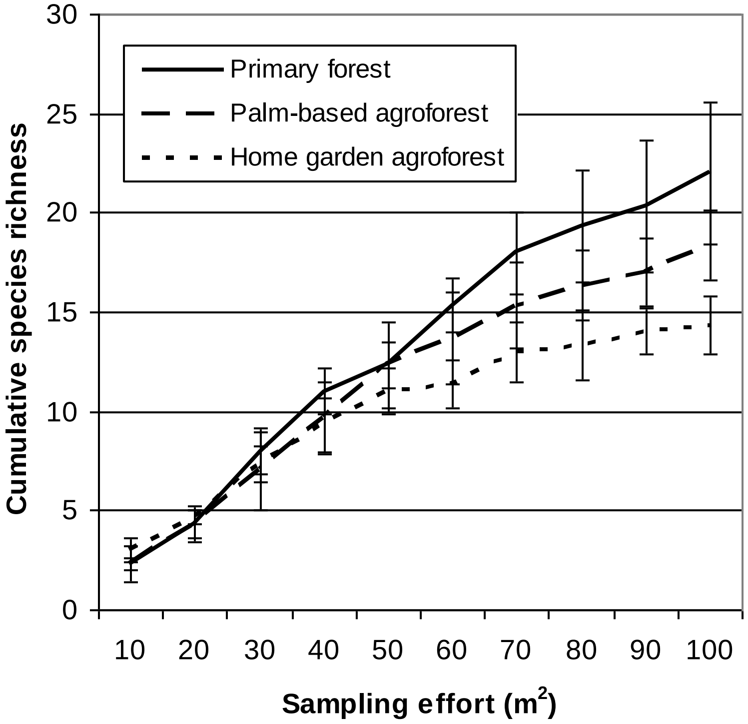

Figure 8.1. Cumulative species richness over sampling effort for each land use, Central Amazonia, Brazil. Each series of values is in the real sampling order. Each point is a mean of three transects. Bars are standard errors of the mean. Each 10 m^2 of sampling effort is also equivalent to one person-hour of sampling.

Table 1.7. Number of termite species encounters (unique species in parentheses) in primary forest, palm agroforest, and home-garden agroforests in Central Amazonia, Brazil. A dash indicates absence of that species.

Taxonomic group		Species encounters		
	Feeding guild	Primary forest	Palm-based agroforest	Home-garden agroforest
RHINOTERMITIDAE				
Coptotermes testaceus (Linnaeus)	wood	2	-	-
Dolichorhinotermes cf. *longilabius* (Emerson)	wood	1	-	-
Heterotermes tenuis (Hagen)	wood	10	11	6
Rhinotermes marginalis (Linnaeus)	wood	-	1	1
Total		13 (3)	12 (2)	7 (2)
TERMITIDAE: APICOTERMITINAE				
Anoplotermes banksi Emerson	soil	1	-	-
Anoplotermes sp. 1	soil	2	5	5
Anoplotermes sp. 2	soil	2	7	4
Anoplotermes sp. 3	soil	5	6	7
Anoplotermes sp. 4	soil	-	2	3
Anoplotermes sp. 5	soil	-	2	-
Anoplotermes sp. 6	soil	-	1	-
Anoplotermes sp. 7	soil	1	-	-
Anoplotermes sp. 9	soil	1	-	-
Anoplotermes sp. 10	soil	3	-	-

Table 1.2 (CONTINUED)

Taxonomic group		Species encounters		
	Feeding guild	Primary forest	Palm-based agroforest	Home-garden agroforest
TERMITIDAE: APICOTERMITINAE				
Anoplotermes sp. 11	soil	2	6	4
Anoplotermes sp. 12	soil	3	6	1
Anoplotermes sp. 13	soil	5	-	-
Anoplotermes sp. 14	soil	5	11	6
Anoplotermes sp. 15	soil	-	1	3
Anoplotermes sp. 16	soil	1	1	-
Anoplotermes sp. 17	soil	2	5	9
Anoplotermes sp. 18	soil	-	-	1
Anoplotermes sp. 19	soil	4	1	-
Anoplotermes sp. 20	soil	4	1	-
Ruptitermes sp. 1	litter	1	-	-
Ruptitermes sp. 2	litter	1	-	-
Total		43 (17)	55 (14)	43 (10)
TERMITIDAE: NASUTITERMITINAE				
Agnathotermes glaber (Snyder)	soil	1	-	-
Amitermes excellens (Silvestri)	interface	1	-	-
Angularitermes sp.	soil	1	-	-
Anhangatermes macarthuri Constantino	soil	-	1	-
Araujotermes parvellus (Silvestri)	soil	1	-	1

Table 1.2 (CONTINUED)

Taxonomic group		Species encounters		
	Feeding guild	Primary forest	Palm-based agroforest	Home-garden agroforest
TERMITIDAE: NASUTITERMITINAE				
Armitermes holmgreni Snyder	interface	1	-	-
Armitermes peruanus Holmgren	interface	1	5	-
Atlantitermes snyderi (Emerson)	soil	1	-	-
Atlantitermes sp.	soil	3	1	-
Paraconvexitermes sp.	soil	3	-	-
Cornitermes pugnax Emerson	litter	3	9	1
Cyrilliotermes angulariceps (Mathews)	soil	2	4	-
Embiratermes cf. *brevinasus* (Emerson & Banks)	soil	-	2	-
Labiotermes pelliceus Emerson & Banks	soil	2	-	-
Nasutitermes sp.	wood	-	-	-
Nasutitermes acangassu Bandeira & Fontes	wood	-	2	-
Nasutitermes guayanae (Holmgren)	wood	1	1	-
Nasutitermes macrocephalus (Silvestri)	wood	-	2	-
Nasutitermes major (Holmgren)	wood	1	-	-
Nasutitermes similis Emerson	wood	1	2	1
Nasutitermes surinamensis (Holmgren)	wood	-	-	1

Table 1.2 (CONTINUED)

Taxonomic group		Species encounters		
	Feeding guild	Primary forest	Palm-based agroforest	Home-garden agroforest
TERMITIDAE: NASUTITERMITINAE				
Rotunditermes bragantinus (Roonwal & Rathore)	wood	1	-	-
Syntermes molestus (Burmeister)	litter	3	5	-
Velocitermes sp.	litter	3	-	-
Total		30 (18)	34 (11)	4 (4)
TERMITIDAE: TERMITINAE				
Cornicapritermes mucronatus Emerson	soil	1	-	-
Crepititermes verruculosus (Emerson)	soil	1	-	-
Cylindrotermes parvignathus Emerson	wood	1	-	-
Dihoplotermes sp.	soil	1	-	-
Genuotermes spinifer Emerson	soil	1	-	-
Neocapritermes angusticeps (Emerson)	interface	3	1	-
Neocapritermes braziliensis (Snyder)	interface	2	-	-
Neocapritermes pumilis Constantino	interface	2	-	-
Neocapritermes talpa (Holmgren)	interface	1	-	-
Neocapritermes taracua Krishna & Araujo	interface	2	-	3

Table 1.2 (CONTINUED)

Taxonomic group		Species encounters		
	Feeding guild	Primary forest	Palm-based agroforest	Home-garden agroforest
TERMITIDAE: TERMITINAE				
Neocapritermes unicornis Constantino	interface	-	-	-
Orthognathotermes cf. *brevipilosus* Snyder	soil	4	2	2
Orthognathotermes humilis Constantino	soil	-	-	1
Planicapritermes planiceps (Emerson)	interface	4	-	-
Spinitermes trispinosus (Hagen & Bates)	soil	1	-	-
Termes fatalis Linnaeus	interface	-	1	-
Termes medioculatus (Emerson)	interface	1	-	-
Total		25 (14)	4 (3)	6 (3)
Grand total		111 (52)	105 (30)	60 (19)

forest samples than of the agroforest samples (40%, 13%, and 13% of species, respectively). The most commonly encountered species was *Heterotermes tenuis* (Hagen), found in a third of all sections.

Similarity

The cluster analysis of termite species composition showed a low similarity between the primary forest and agroforest species composition (21%)(Figure 1.2). The greatest similarities occurred among transects of the agroforests, while transects of the primary forest themselves were not similar to each other; they fell in a range of similarity of 40 to 70% (Figure 1.2).

Ordination

In reciprocal averaging, similar species are brought together and dissimilar species far apart; likewise for similar and dissimilar samples. The scores of the first axis in this ordination technique maximize the correlation of the samples and species (Gauch, 1982).

Arranging the samples in a rank order of their first-axis ordination scores will have their largest values concentrated along the matrix diagonal (Gauch, 1982).

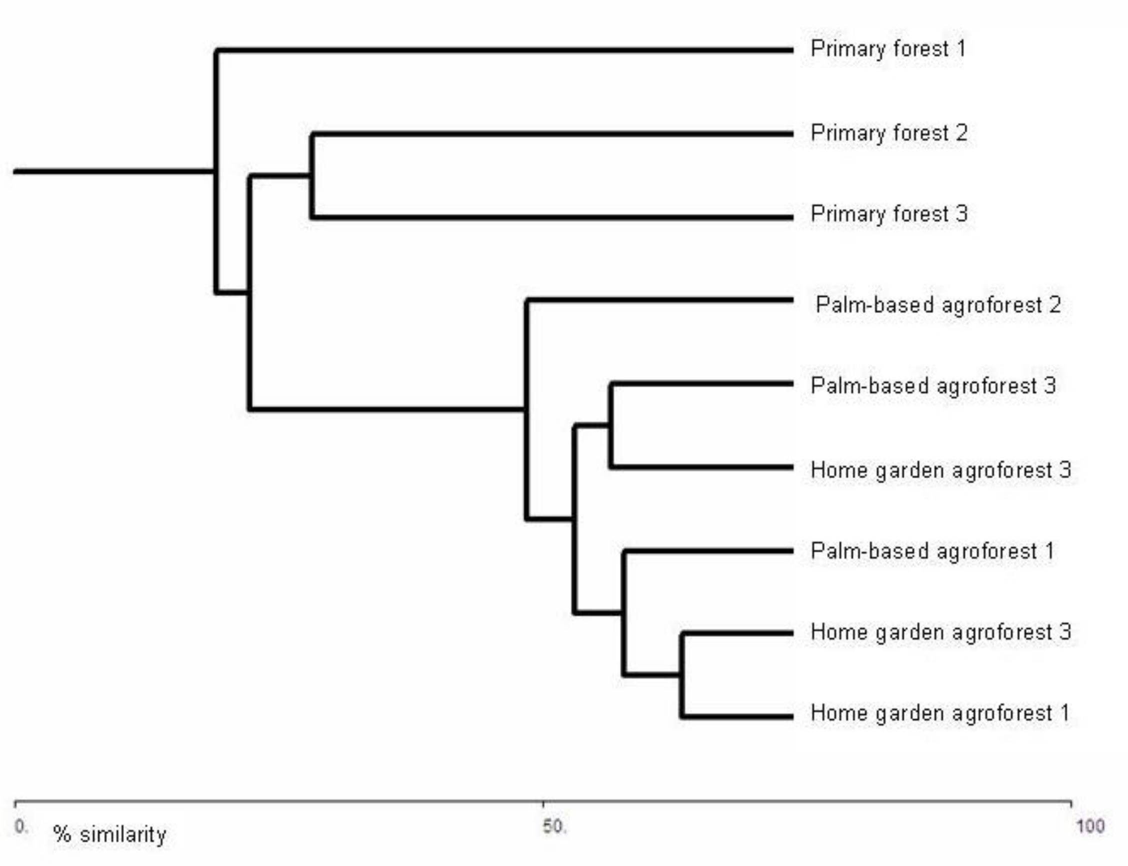

Figure 1.9. Cluster analysis (Bray-Curtis similarity index) of termite species assemblages in primary forest and agroforests, Central Amazonia, Brazil

This ordination demonstrated a gradient from primary forest to home-garden agroforest, with the palm-based agroforest intermediate to the two (Table 1.3). *Rhinotermes marginalis* exhibited complete preference for the home-garden agroforest, while *Anoplotermes* sp. 13, had the most extreme preference for the primary forest environment. Only two species showed intermediate preference, with reciprocal analysis scores in the range of 25 to 75%. These were the two undescribed *Anoplotermes* species 16 and 20.

Land use/species interaction

The AMMI model demonstrated a strong interaction between species and land use (Table 1.4). Early IPCAs selectively recover signal, whereas late IPCAs selectively recover noise (Gauch, 1992). The signal in the species by environment interaction had an estimated sum of squares of 20.2, which nearly equaled that of the first two IPCAs (13.7 + 8.9 = 22.6). Therefore, IPCA1 and IPCA2 captured mostly signal, whereas higher components captured mostly noise and hence were discarded and ignored (Figure 1.3). The first IPCA corresponded to an opposition between the primary forest and the agroforests in terms of termite species preference (Figure 1.3). The second IPCA discriminated among the

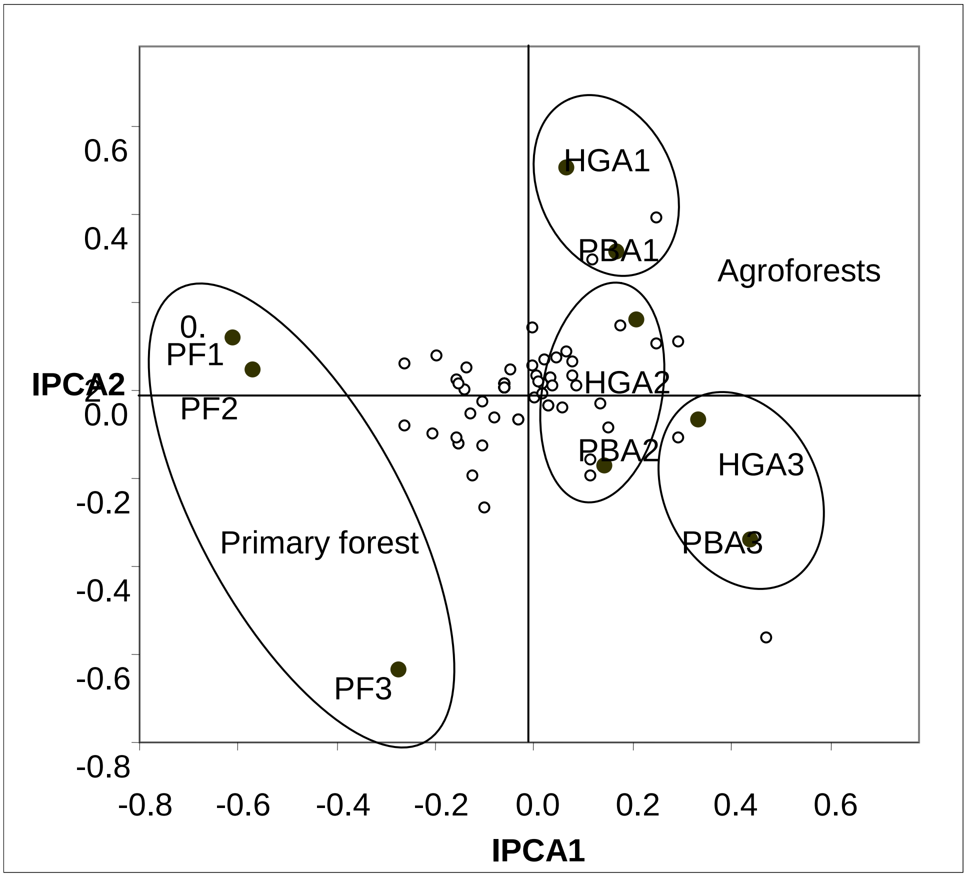

Figure 1.10. AMMI1 biplot of termite species and land uses, Central Amazonia, Brazil. Species are open circles, land uses solid circles. HGA = Home-garden agroforest, PBA = palm-based agroforest, PF = primary forest. The number following the land use is the transect number. Any two sites or species are highly correlated if they are at nearly the same angle from the center of the plot, negatively correlated if opposing, and nearly uncorrelated if the angle between them is close to 90 degrees. The first and second IPCAs account for 32% and 21% of the interaction, that is, the differential response of species to environments. The remaining variation is merely noise.

Table 1.8. Arranged data matrix of reciprocally averaged termite species and land use for species that were found in two or more transects. The number at the top of each column is the number of transect. The values within the matrix are the number of encounters of a species within transect out of a possible 10 encounters. Zeroes in the matrix were substituted by periods, to make the absence of a species encounter easier to see.

Species name	Homegarden agroforest	Palm-based agroforest	Primary forest
	123	123	312
Rhinotermes marginalis	1.1	...	...
Anoplotermes sp. 4	211	.1.	...
Anoplotermes sp. 15	21.	.1.	...
Anoplotermes sp. 2	225	2.2	...
Anoplotermes sp. 17	45.	214	...
Anoplotermes sp. 11	223	212	...
Nasutitermes guayanae	..1	1..	...
Embiratermes brevinasus	..1	..1	...
Nasutitermes major	..1	..1	...
Cornitermes pugnax	1.3	342	...
Nasutitermes similis	.1.	1.2	...
Anoplotermes sp. 5	...	.11	...
Orthognathotermes brevipilosus	2.1	3.1	..1
Cyrilliotermes angulariceps	..1	23.	1..
Heterotermes tenuis	414	952	41.
Anoplotermes sp. 3	342	213	.21
Anoplotermes sp. 14	244	243	121
Syntermes molestus	...	223	..1
Neocapritermes taracua	.3.	1..	..1
Anoplotermes sp. 1	322	2.3	4..
Armitermes peruanus	..4	1.1	2..
Anoplotermes sp. 12	1.3	112	.11
Anoplotermes sp. 16	...	..1	..1
Anoplotermes sp. 20	...	11	.21
Neocapritermes angusticeps	...	.1.	.3.

Table 1.3 (CONTINUED)

Species name	Homegarden agroforest	Palm-based agroforest	Primary forest
	123	123	312
Atlantitermes sp.	...	..1	.3.
Anoplotermes sp. 19	...	..1	.13
Araujotermes parvellus	...	...	21.
Crepititermes verruculosus	...	...	21.
Spinitermes trispinosus	...	...	11.
Coptotermes testaceus	...	...	22.
Labiotermes pelliceus	...	...	22.
Neocapritermes braziliensis	...	...	2.2
Anoplotermes sp. 10	...	...	212
Neocapritermes pumilis	...	...	120
Planicapritermes planiceps	...	...	2.4
Convexitermes nigricornis	...	...	021
Anoplotermes sp. 13	...	...	014

Table 1.9. Analysis of variance associated with the additive main effects and multiplicative interaction (AMMI) model. Species refers to termite species and environment to primary forest, palm-based agroforest, and home-garden agroforest. The species by environment interaction is estimated to contain sums of squares of 20.2 for signal and 22.0 for noise.

Source	Degrees of freedom	Sum of squares
Total	6029	293.2
Treatment	602	66.5
Species	66	23.9
Environment	8	0.4
Species x environment	528	42.2
IPCA 1	73	13.7
IPCA 2	71	8.9
IPCA 3	69	5.4
Residual	315	14.2
Error	5427	226.7

blocks of the agroforestry systems and between one transect and the other two in the primary forest (Figure 1.3).

Taxonomic composition

The proportion of termite species in the four taxonomic groups did not differ significantly between the primary forest and agroforests (Figure 1.4). However, the agroforests had a significantly higher proportion of encounters ($P = 0.000$) of the Apicotermitinae subfamily than the primary forest, and correspondingly lower proportions of Nasutitermitinae and Termitinae encounters (Figure 1.5).

Functional composition

Likewise, the feeding guild composition by species did not differ significantly across the different land uses (Figure 1.6). By encounter, however, there was a marked difference ($P = 0.000$). The proportion of soil/wood interface feeders was much reduced in the agroforests (Figure 1.7). None of the species encountered in the study are known to be pest termites of the plant species in the agroecosystems studied, according to Constantino (2002), except for *Rhinotermes*

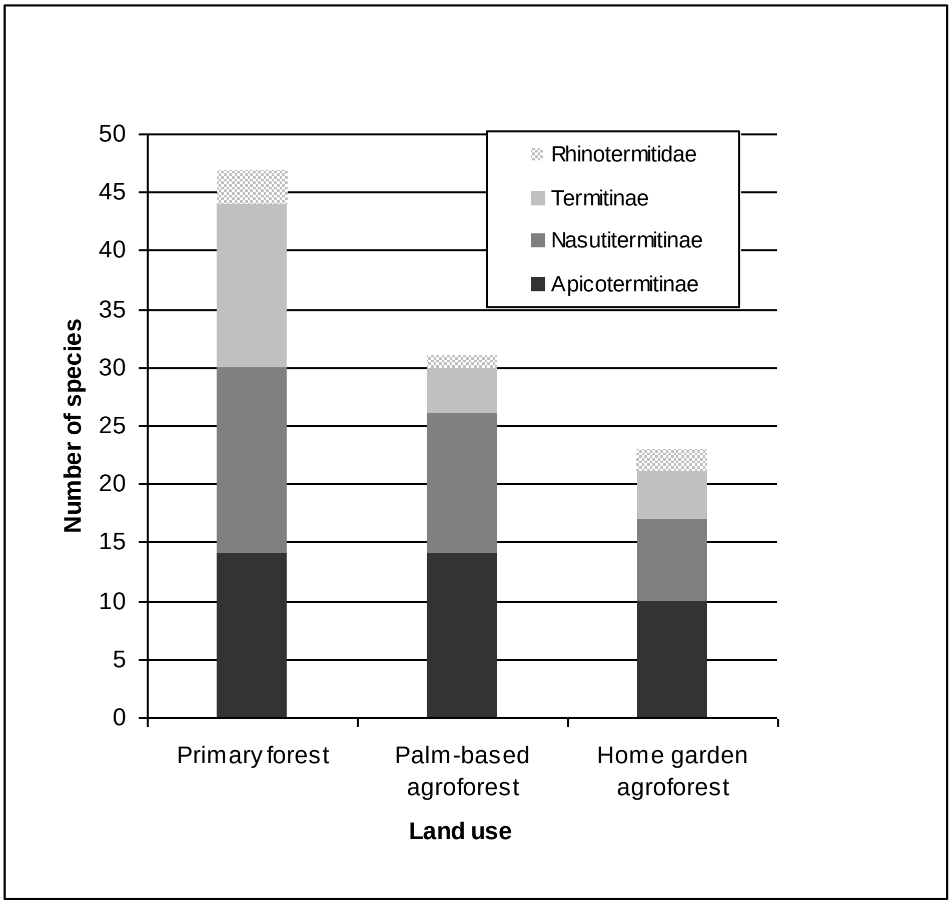

Figure 1.11. Taxonomic composition of termite species in primary forest and agroforests, Central Amazonia, Brazil. Values are pooled over all three transects in each land use.

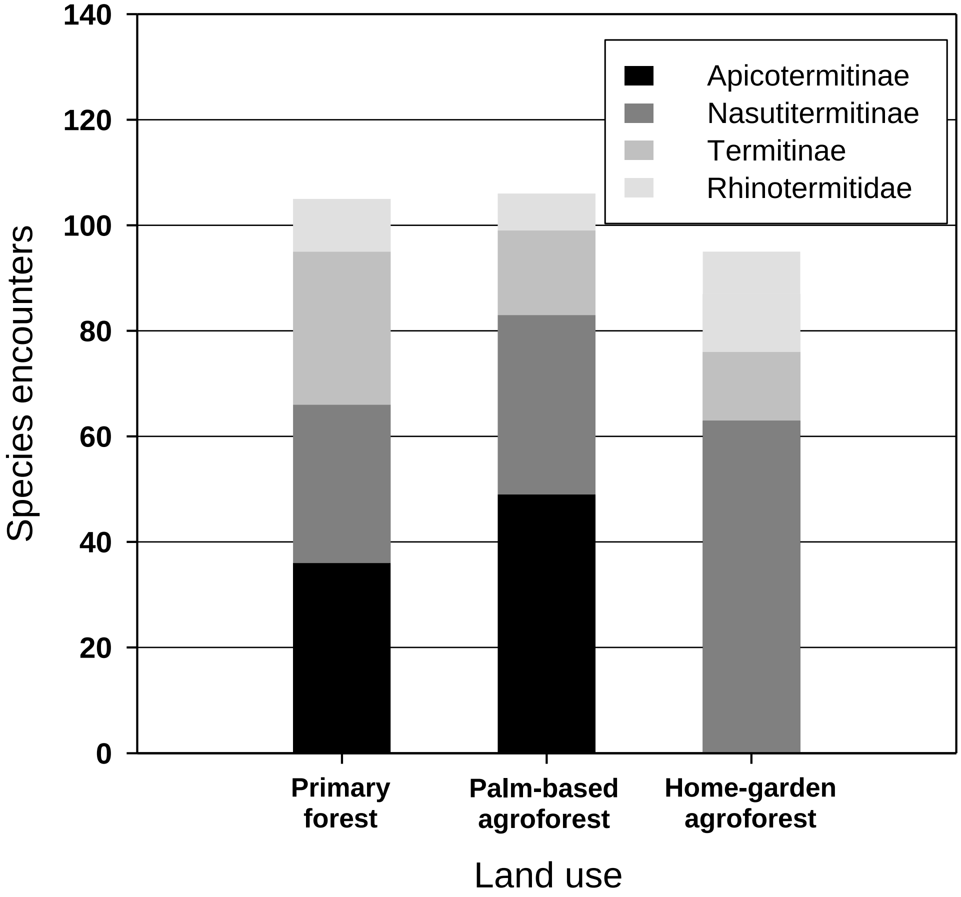

Figure 1.12. Taxonomic composition of termite species abundance (encounters) in primary forest, palm-based agroforest, and home-garden agroforest. Values are numbers of encounters in the survey.

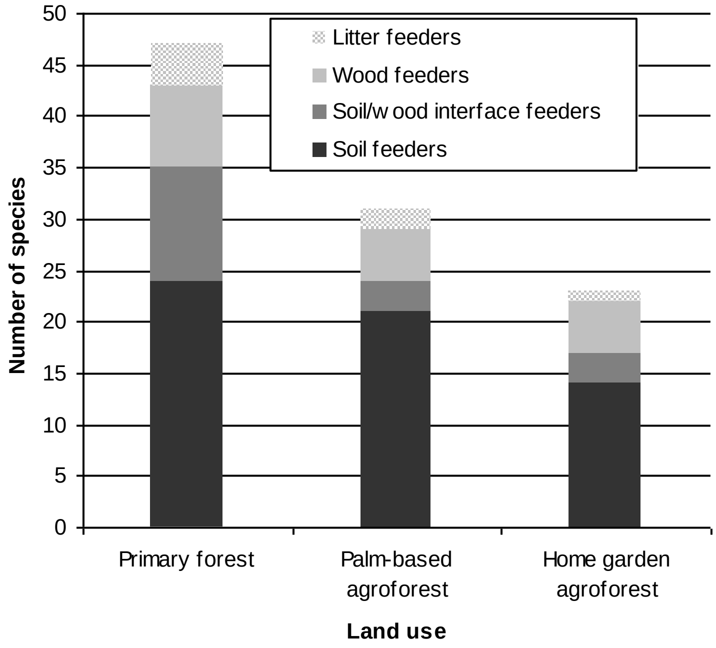

Figure 1.13. Functional composition of termite species in primary forest and agroforests, Central Amazonia, Brazil. Values are pooled over all three transects in each land use.

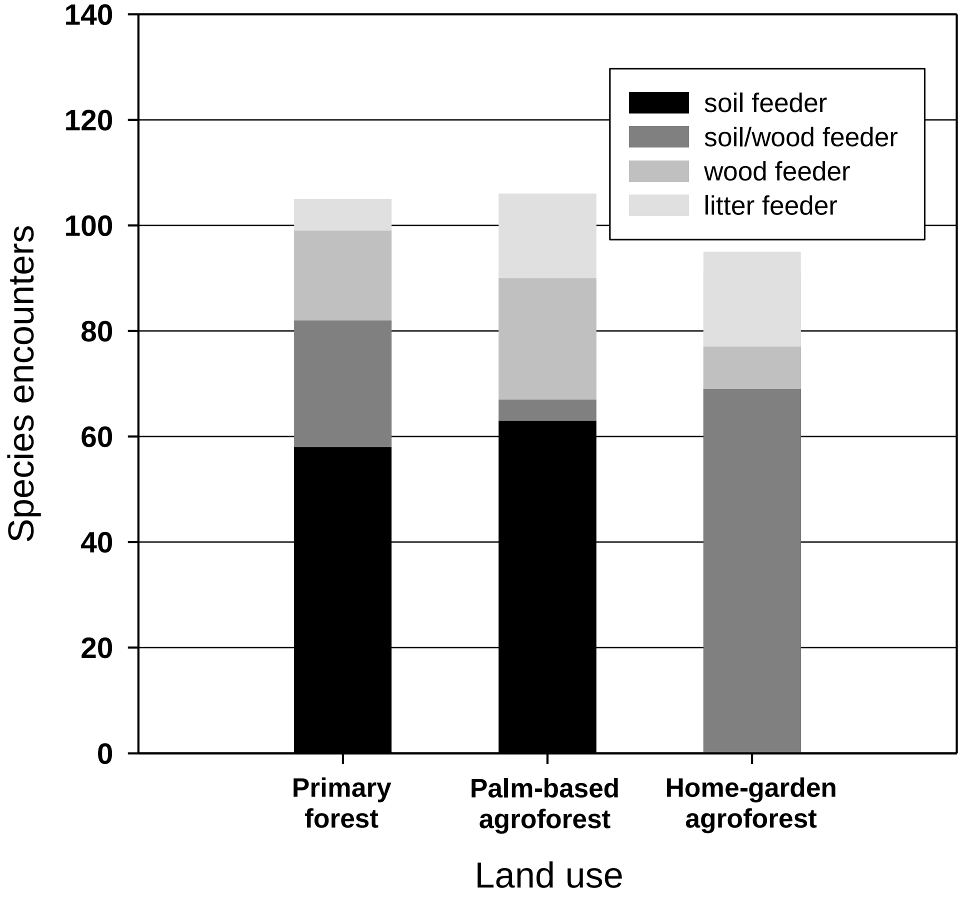

Figure 1.14. Functional composition of termite species abundance (encounters) in primary forest, palm-based agroforest, and home-garden agroforest. Values are numbers of encounters in the survey.

marginalis (Linnaeus), considered to be a minor agricultural pest in Amazonia (Constantino, 2002).

Discussion

Of the studies in non-flooding primary forests of Amazonia, Mill (1982), Apolinario (1993), Bandeira (1989), Bandeira and Macambira (1988), Bandeira (1979), and Bandeira and Torres (1985) each sampled plots of the same size (1 hectare), and observed from 30 to 90 species. The total number of species found in the primary forest fell in this range, at 52 spp. The termite assemblage in this study differed from previous studies in the region, however ((Snyder, 1926), (Mill, 1982), (Bandeira and Torres, 1985), (Bandeira, 1989), (Apolinário, 1993), (Constantino, 1992), and (De Souza and Brown, 1994)). In terms of taxonomic composition, we found the Nasutitermitinae subfamily and the Nasutitermes genus to be less dominant than in other areas. Martius (1994)'s review of the literature found that the Nasutitermitinae family usually accounts for about 50% of the species, and the Nasutitermes genus for 25%. We found 35% and 14%, respectively. In terms of feeding guild, we found the majority of species to be soil feeders (57%), while the South American termite fauna has been characterized to be dominated by wood-feeding species (Bignell and Eggleton, 2000).

Several factors may contribute to the difference in results between this study and others: (1) real differences between these proportions among sites, (3) the classification of feeding habits may be ambiguous, or (3) the sampling methods may emphasize particular substrates over another. (Eggleton et al. (2002) likewise found an extremely high species richness of soil-feeding termites through transect sampling that explicitly sampled soil.)

The rapid biodiversity assessment protocol (Jones and Eggleton, 2000) provided an efficient means of maximizing the number of species returned per amount of effort while returning information on relative abundance. Where intersite comparison is the primary objective, the rapid biodiversity assessment protocol is useful by standardizing for effort (both labor and sampling area) and sampling with equal intensity across substrates. A caveat: this method, like most, underrepresents the dry-wood termites (Kalotermitidae), which inhabit primarily dead wood in the forest canopy.

The cluster analysis, AMMI model, and reciprocal averaging offered complementary information in interpreting the results of the survey. The cluster analysis neatly differentiated the species composition between primary forest and the agroforests. It also illustrated that there was greater termite species turnover between primary forest transects than between agroforest transects, as would be expected. The AMMI model demonstrated a strong preference of individual termite species for particular land uses, contrasting the primary forest transects with those of the agroforests, and even showing some discrimination by termite species based on the land-use history of the agroforests.

Although we had expected the termite species composition of the home-garden agroforest to be the most similar to the primary forest, we found that the palm-based agroforest more closely imitated the forest. Reciprocal averaging demonstrated a gradient in termite species composition from primary forest to home-garden agroforest, with the palm-based agroforest intermediate to the two.

Likewise, it was the palm-based agroforest that more closely imitated the makeup of the primary forest in terms of the proportion of abundance of termites in different feeding classes, with more soil feeders. Davies et al. (2003) found that the termite assemblage in a primary forest in Guiana, and that of soil feeders in particular, was influenced by palm density. Barros et al. (2003) found termite density under peach palm to be significantly higher in general than soil under the non-palm species cupuassu. The authors above attributed these findings to greater litter inputs around palms, but root turnover and quality may also be contributing factors. In support of this explanation, the palm species in the agroforests had significantly higher root densities than the other principal agroforestry species measured by Gallardo-Ordinola (2005), at 6 and 7 Mg ha^{-1} for *açaí* and peachpalm, respectively. Turnover of fine roots was also significantly higher than that of other principal agroforestry species, at 3 Mg ha^{-1} y^{-1}. Peachpalm roots had the lowest lignin content of the species measured (Gallardo-Ordinola, 2005). Palm litter, in the rainy season, had significantly lower polyphenol content than the home-garden agroforest litter (da Silva, 2005). Canopy cover has been shown to be an important factor in determining termite abundance (Dibog et al., 1999), and the leaf area index of the palm-based agroforest was slightly higher than the home-garden agroforest (3.1 and 3.0) (S. Welch, in prep.). These results indicate that particular plant functional attributes (Gillison et al., 2003) could be more important drivers of termite species richness than plant species richness alone.

The agroforests maintained the same distribution of species among taxonomic classes and feeding guilds as primary forest. In terms of the distribution of termite *abundance* among taxonomic classes and feeding guilds, however, the agroforests did distinguish themselves from primary forest. Both agroforestry systems had higher abundances of soil feeders than the primary forest. A possible role of soil feeders in soil fertility is indicated by the increased exchangeable cations and other nutrients after passage of soil through the termite gut (Anderson and Swift, 1983). Dibog et al. (1999) found that crop yield was positively correlated with abundance of soil-feeding termites. Soil feeders are strongly affected by disturbance and drying of the soil (Dibog et al., 1999), so the capability of the agroforests to create favorable conditions for soil feeders is likely a positive feedback for the fertility of those agroecosystems.

Feeding guild was used as a crude surrogate for function in this study. For more sophisticated analysis of the relationships between termite community composition and agroecosystem function, many additional dimensions of insect function beyond feeding guild need to be explored. In the same way that plant functional attributes have been related to ecosystem function, termite functional attributes could also. These could go beyond feeding preference to include nitrogen fixation ability, body width, fungus cultivation ability, mouthpart design, type of digestion, type of nest construction, and building material. To facilitate this, more taxonomic work in the Apicotermitinae, and species-level biological research to support it will be needed.

CONCLUSIONS

Although we had expected the termite species composition of the high-diversity, home-garden agroforest to be more similar to primary forest, we found the palm-based agroforest assemblage more similar instead. The palm-based agroforest was also closer in species richness to the primary forest than was the home-garden agroforest. Greater root turnover and root and litter quality by the palms may support the greater diversity and abundance of termite species in the palm-based system. These results indicate that plant attributes may be more important than plant diversity in determining termite species composition in these agroecosystems.

All land uses in this study had an unusually high proportion of soil feeders in comparison to other studies in Amazonia. In addition, soil feeders and Apicotermitinae were proportionally more abundant in agroforests than in primary forest. The ability of the agroforests to maintain populations of soil feeders may have positive feedbacks for the fertility of their soil. The agroforests maintained the same proportions of termite species across feeding guild and taxonomic class as primary forest. Insomuch as feeding guild is a proxy for function, this result supports the assertion that closed-canopy agroforests may be able to sustain the same termite functions as primary forest. Further research in species-level characterization of the functional attributes of termites is needed to improve our understanding of how termite community composition contributes to agroecosystem function.

Acknowledgments

This study was funded by NASA LBA-ECO Project ND-04. We thank Elisa Wandelli (Embrapa-CPAA) for her guidance and support throughout this research. Osmar Barbosa Ferreira provided excellent field assistance throughout this study. We thank Rubenildo Lima, Sabino Neto, and Embrapa-CPAA for the logistical support, and Eleusa Barros (National Institute for Amazonian Research (INPA)) for lab space for identifications. J. M. Anderson (University of Exeter) provided valuable feedback on a draft of this paper. Steve Culman (Cornell University) assisted in the application and interpretation of the AMMI model. We appreciate Augusto Henrique's (INPA) assistance in the loan of this study's termite collection from the INPA Entomology Museum to the University of Brasilia.

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CHAPTER 2

THE IMPACT OF MOUND-BUILDING TERMITES ON SURFACE SOIL PROPERTIES IN A SECONDARY FOREST OF CENTRAL AMAZONIA

ABSTRACT

Termites are important components of biologically mediated feedback to land-use change in the tropics. In central Amazonia, termite mounds are prevalent in post-clearing landscapes and appear to constrain the re-colonization of the landscape by vegetation. To determine the most important constraints imposed by the termite mounds on plant establishment, we investigated chemical, physical, and hydraulic properties of termite mounds at an eight-year-old secondary forest site, and their effects on the development of native plant species. Termite mounds were found at a density of 760 ha^{-1} in the study site, covering 3% of the area. Mounds contained only half of the root biomass found in neighboring soil in the surface 0.05 m. Carbon, nitrogen, and iron levels in the termite mounds were significantly elevated, by 33, 28, and 4%, respectively (44 g kg^{-1}, 2.5 g kg^{-1}, and 320mg kg^{-1}), while no significant difference in phosphorus, potassium, magnesium, or zinc concentrations was observed. Calcium was depleted by 27% in the termite mounds, at 0.026 g kg^{-1}. Aluminum concentrations and acidity were significantly higher in the termite-mound material (0.23 g kg^{-1}, pH 4.3) than surrounding soils (0.15 g kg^{-1}, pH 4.4). Resistance to penetration was significantly higher in termite mounds, at 13.5 MPa. Termite mounds were on average 5 mm drier than the control soil in the surface 0.05 m, with a significantly higher median water infiltration rate through the termite mound than the adjacent soil (16 mm s^{-1} vs. 3 mm s^{-1}). Termite mound material retained significantly less water than control soil under the same suction. Termite mound clods absorbed water

significantly more slowly than control soil. Plant assays ruled out an effect of aluminum toxicity on seed germination and seedling development in termite mounds over control soil. Water availability and mechanical impedance were the most important constraints for seed germination and seedling development. Understanding the impact of mound-building termites on vegetation dynamics will be important in predicting the rates at which aboveground biomass will accumulate in the ever-increasing areas of secondary forest in Amazonia.

Introduction

Land-use change alters resource availability and environmental conditions and can cause dramatic changes in the abundance and species composition of the soil biota. The role of the soil biota is often not apparent until the natural ecosystem is disrupted, but then the fauna may act as driving variables determining the rate of change and the new equilibrium state of soil processes (Anderson, 1988). These soil processes can in turn determine vegetation dynamics.

In the old-growth forests of Amazonia, termites are an integral component of soil processes. Highly diverse in their feeding habits, they decompose virtually all types of dead plant material, from dead logs and tree bark to fallen leaves, soil humus, and tree lichen. The complex architecture of the old-growth forest ecosystem offers termites protection within hollow trees, inside logs, between buttress roots, under tree bark, and around the stems of spiny palm species. High temperatures and rainfall impact are mediated by the intercepting leaves of the forest canopy. In this setting termites are able to maintain large populations, around 1900 individuals/m^2 (Bandeira and Torres, 1985), accelerating the return of nutrients immobilized in dead wood and other litter to the soil and to plant roots.

When forest is cleared for pasture or agriculture, the type and abundance of substrates available for termite consumption change abruptly, environmental conditions become more extreme, and exposure of termites to predators increases. In a typical clearing scenario in Central Amazonia, logs and stumps are left on the soil surface and endure a partial burning. Dead wood availability rises initially, while leaf litter nearly disappears. The soil surface is exposed to direct sunlight and high temperatures, and humidity is reduced. Rainfall impact is no longer mediated by intervening vegetation. In this modified habitat, wood-feeding termite species which have the ability to mediate their environment by constructing protective mounds are able to thrive and to use the new stocks of dead woody biomass as a resource. Some species exhibit plastic nesting habits. *Cornitermes ovatus,* for example, inhabits tree trunks in primary forest, yet within a cleared environment, constructs earth mounds (Bandeira, 1989), presumably for the control of microclimate (Bandeira, 1983).

In central Amazonia, typical land use in the last decades has involved forest felling, burning, and pasture implementation in the late 1970's, and land abandonment in the 1980's. The landscape in the vicinity of roads is now a mosaic of successional forest, pasture, small-holder agriculture, and logged and old-growth forests. In these land uses, termite mounds become an abundant and prominent feature of the landscape. Bandeira (1979) found twice the number of termite mounds in a five-year-old pasture on clayey soils than in the neighboring primary forest. These mounds, constructed of soil and digested organic matter, may stand alone or surround logs or stumps. While these structures allow termites to continue their important ecosystem role of decomposing dead woody biomass, the mounds themselves are inhospitable to colonization by vegetation. Where the mounds are numerous, this phenomenon creates a marked patchiness of the vegetation in the landscape and reduces the area suitable for plantations, crops, forage grasses, or successional species. As the longevity of the mounds is unknown, and further cycles of clearing could increase their abundance, this phenomenon may become of only increasing concern to land managers in the future.

Very little information is published on the response of termites to the clearing and cultivation of tropical rain forests (Okwakol, 2000). Most of those studies ((Abe and Matsumoto, 1979), (Abe and Watanabe, 1983) and (Watanabe et al., 1984)) were conducted in Asia. In Australia, the increase in availability of dead and decomposing wood after clearing has been shown to cause a temporary increase in the abundance of wood-eating termites (Abensperg-Traun and Steven, 1996). They observed that mound-building wood-eating termites may be more resilient to clearing, as they maintain an active subterranean gallery system for foraging on wood on the soil surface. In Africa, macrotermitine termites are known to survive land clearing, and this is attributed to their nest-building ability (Noirot, 1970).

Termite mounds in the Neotropics have been investigated even less in comparison to other parts of the Tropics (Bignell and Eggleton, 2000). In Venezuela, López-Hernández (2001; 1989) evaluated C, N, and P dynamics in savanna termite mounds, and Salick et al. (1983) analyzed rain forest termite mounds for nutrient contents. In Brazil, Filho et al. (1990) analyzed a single mound of *Cornitermes cumulans* in São Paulo for nutrient content and particle-size distribution. In eastern Amazonia, Bandeira (1983) analyzed eight mounds each of *Cornitermes* cf. *ovatus, Armitermes neotenicus*, and *Nasutitermes minimus*, and in central Amazonia, Amelung et al. (2002) analyzed the organic matter of two mounds of *Embiratermes* aff. *neotenicus* and *Termes fatalis*.

No studies on the physical or hydraulic properties of termite mounds were found for Amazonia. Holt and Lepage (2000) cite a general lack of studies on the effects of termites on the hydraulic properties of soils. A single published study, in Australia, was found that experimented with termite mound constraints for plant growth (Rogers et al., 1999). The authors found that plant growth suppression was not chemically mediated, but was due to the impenetrable nature of the mound surface.

The objectives of our study were (1) to quantify the area covered by termite mounds in a central Amazonian successional forest site, (2) to determine the mounds' effect on secondary forest species, (3) to characterize the chemical, physical, and hydraulic properties of the surface of the termite mounds, and (4) to determine which of these properties constrain the development of plant species on termite mounds. We hypothesized that plant development would be impeded by the termite mounds, and that the primary constraint for plants would be mechanical resistance to exploitation by plant roots.

MATERIALS AND METHODS

Site description

The study was conducted at the *Empresa Brasileira de Pesquisa Agropecuária* (*Embrapa Amazonia Ocidental*) research station located at km 54 of the federal highway BR-174 north of Manaus, Amazonas, Brazil. Soils on the plateau of the study site are classified as dystrophic, isohyperthermic, clayey kaolinitic Hapludox. The climate is tropical humid. Mean annual precipitation is 2400-2500 mm, with an average maximum in February-March of around 320 mm and an average minimum in August-September of around 80 mm ((Marques et al., 1981), (de Paiva, 1996)). Precipitation often occurs as heavy rains of short duration. Mean air temperature is 26.6 C, and atmospheric humidity is around 84% (Vose et al., 1992). The native vegetation of the region is closed-canopy, dense, evergreen *terra firme* (non-flooding) forest (Veloso et al., 1991).

The study site was located at 02° 30' 56"S and 60° 01' 28" W, a seven to eight year-old secondary forest dominated by *Vismia* spp. This site was originally cleared for pasture in the late 1970's, grazed, and then abandoned. In 1993, the successional vegetation was cleared, burned, and left fallow once again. This study was conducted from 2000 to 2002.

Methods

To fulfill the study objectives, we (1) surveyed and mapped the extent of coverage of termite mounds at the study site, (2) compared belowground biomass of secondary forest plant species in the termite mounds and in the surrounding soil, (3) assessed the chemical, physical, and hydraulic properties of the termite mounds using a battery of laboratory and field tests, and (4) used plant bioassays to determine the primary constraints to vegetation development on termite-mound material.

Termite mound survey

To determine percent coverage and density of termite mounds, 8 transects through the secondary forest study site were mapped. Transects were 2 m in width, 40 to 80 m in length as circumscribed by the edge of the plateau, and 20 meters apart, a total of 1040 m^2. All litter in these transects was removed by raking to expose the soil surface and all mounds. A portion of each mound was cut away and color and internal structure examined to distinguish termite mounds from earth mounds of other origins. Termite mounds that fell within the transects were mapped, counted, and measured. Where mounds occurred on the border of the transect, only the basal area of the mound within the transect was included in the total.

Termite species collection

To identify the termite species inhabiting the mounds in the study area, 17 mounds were excavated. The mounds were broken with a heavy soil implement, and the mound material was transferred to a plastic sheet. Termites were hand-collected with forceps and transferred to vials containing 80% ethyl alcohol for preservation and subsequent identification under magnification. R. Constantino (University of Brasilia, Brazil) identified the species collected.

Root biomass

To compare belowground plant biomass between termite mounds and control soil, volumetric soil samples in 100-cm^3 stainless steel cylinders were taken from the surface 0.05 m of 19 randomly chosen termite mounds and adjacent soil. The sampling point for the control area was 1.5 m from the border of the termite mound in a randomly chosen cardinal direction. If the point fell within a 1.5 m radius of another termite mound, a different location was chosen by randomly selecting a second direction. This sampling procedure was used for comparisons of termite mound and adjacent soil characteristics throughout this study. The raw data was not distributed normally and was therefore log-transformed to reach a normal distribution. A paired t-test was then performed on the transformed data (Minitab 13.1, Minitab, Inc., State College, PA, USA).

Soil chemical analyses

Twenty-one termite mound sites were selected randomly and sampled along with their corresponding control soil sites. Evaluations of soil properties throughout this study were made using the surface soil in order to best approximate the microsite conditions encountered by a seed or seedling. In this sampling, an auger was used to sample the surface 0.1 m of soil, and at each sampling point three samples were taken and pooled in the field. Soil samples were air-dried, and roots and other non-soil components were removed by hand-sorting. Subsamples were analyzed for pH, carbon (C), soil macro- and micronutrients, and aluminum (Al). Carbon was determined by the Walkley-Black method, and total soil nitrogen (N) by the Kjeldahl technique.

Available phosphorus (P) and exchangeable potassium (K) were extracted using a double-acid solution of 0.05 N hydrochloric acid and 0.025 N sulfuric acid. Phosphorus was determined by photocolorimetry, and K was determined on a flame photometer (Micronal B, São Paulo, Brazil). Exchangeable calcium (Ca), magnesium (Mg), and Al were extracted with 1 N potassium chloride. Iron (Fe), zinc (Zn), manganese (Mn), and copper (Cu) were extracted with a Mehlich 1 solution in a 1:5 ratio and determined on an atomic absorption spectrophotometer (AA-1475, Varian Associates, Palo Alto, CA). For non-normally distributed data for which an appropriate transformation was not found, the non-parametric equivalent of a paired t-test, the Mann-Whitney test, was used to assess the significance of the difference between the two experimental categories (Minitab 13.1, Minitab, Inc., State College, PA, USA).

Effective cation exchange capacity (eCEC) was calculated as the sum of K^+, Ca^{2+}, Mg^{2+}, Al^{3+}, and H^+. Aluminum saturation was calculated as Al^{3+} divided by the eCEC. Base saturation was calculated as the sum of K^+, Ca^{2+}, and Mg^{2+}. The contribution of Na^+ was assumed to be negligible in this acid, highly weathered Oxisol.

Soil physical analyses

Particle-size fractionation

Twenty termite mounds and 20 soil control areas were sampled. Each sample consisted of a composite of three 0.10 m surface samples. The sand fractions were separated by wet sieving, and clay and silt fractions were determined using the sieve-pipette sedimentation method for clay (EMBRAPA, 1997). Dispersion was carried out using 1 N NaOH and mechanical agitation. The

Brazilian classification system was used to determine the particle-size classes (EMBRAPA, 1997).

Water content and bulk density

Soil water content and bulk density were measured by sampling the surface 0.05 m of soil using 100 cm^3 stainless steel cylinders. Three samples were taken from each mound and adjacent area. Nine termite mounds and 9 adjacent control areas were sampled in the secondary forest. The samples were weighed in the field and later oven-dried and re-weighed in the laboratory to determine their original water content and to obtain the mass of dry soil to calculate bulk density.

Resistance to penetration

Measurements of resistance to penetration were made using a cone penetrometer (Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands), as prescribed by Bradford (1986). A cone of 2 cm^2 surface area and a penetration depth of 0.05 m was selected after a pilot study. Ten termite mounds and 10 adjacent control areas were tested. The average of five readings on each mound and on each corresponding control area was taken.

Infiltration rate

The rate of infiltration of water into the soil was measured using a constant head method. A stainless steel cylinder 0.20 m in diameter was inserted 0.10 m into the soil or termite mound surface (n = 9) and the amount of water needed to maintain the cylinder full for 10 minutes was measured.

Aggregate-size fractionation

To compare aggregate size fractions, 20 termite mound and 20 adjacent soil samples were collected. Each sample was composed of two 0.10-m auger samples. Roots and charcoal were manually removed from the samples with forceps, and the samples were sieved to a size between 2 and 4 mm. Out of each sample of 2-4 mm aggregates, 10 g were used to determine moisture content, and 25 g were agitated mechanically in water for ten minutes through sieves of 2-mm, 1-mm, 0.5-mm, and 0.25-mm mesh. The soil aggregates in each resulting category were recovered, oven-dried at 105 C for at least 24 h, and weighed.

Water retention curve and porosity

The water retention curve of termite mound and adjacent soil was evaluated by the tension table method as well. Cores from six termite mounds and control sites were collected, and a fine mesh fabric was secured across the bottom of each core by a rubber band. The cores were placed on a bed of fine wet sand and left saturating with the water level midway up the side of the core. A sample was considered saturated when the surface glistened. The weight of each core was determined at 0, 4, 10, 25, 30, 63, and 80 cm of water of tension. The samples were then transferred to a pressure-plate apparatus and weighed after equilibrating at pressures equivalent to columns of 100 and 1000 cm of water. Oven-dry weights were determined after the experiment.

The pore-size distribution was determined using Jurin's law, below, where d_{eq} is the equivalent diameter of the largest soil pore which remains filled with water after a tension h has been applied to the soil. This approach represents the soil pore space in the form of capillaries of varying sizes, and relates the capillary pressure (P_C) to the equivalent diameter of the water-filled pore space (d_{eq}) at each equilibrium state using the following equation:

$$P_c = P_O - P_W = \frac{4 y \cos a}{d_{eq}} = - h \qquad \textbf{Eq. 1}$$

where P_O = atmospheric pressure, P_W = water pressure, v = the surface tension of water, and α = the contact angle of water with the pore walls, assumed to be 0 (Grimaldi et al., 2003). The water tensions listed above corresponded to pore diameters of >745, 298-745, 119-298, 74-119, 47-74, 38-47, 30-38, and 3-30 μm via Eq. 1.

The non-parametric version of the t-test, the Mann-Whitney test, was used to compare water contents and volume of pores in termite mound and control soil at each pressure level in the experiment.

Soil water repellency

Sandbox method

To compare the water repellency of termite mound and control soil clods, an absorption curve method was devised. A tray of washed sand was saturated with water. Ten soil clods of each treatment category (termite mound, control soil, and termite mound that had been exposed to fire) were dried and weighed. Each clod was re-weighed after every 5 seconds in contact with the bed of sand. The clod was re-exposed and re-weighed until its weight no longer increased, and its weight was recorded at each interval.

A segmented regression with unknown point of segmentation was fitted to the absorption curve of each of the three treatments (SAS 8.02, SAS Institute Inc., Cary, NC, USA). A quadratic polynomial (Eq. 2) was fitted to the first segment of the curve, and a line (Eq. 3) was fitted to the second segment of the curve, the plateau at which the water content reached saturation. The time at which the curve leveled out was estimated by Eq. 4 below.

$$i = a + bt + ct^2 \qquad \textbf{Eq. 2}$$

$$i = a + bt_0 + ct_0^2 \qquad \textbf{Eq. 3}$$

$$t_s = -\ 0.5\,\frac{b}{c} \qquad \textbf{Eq. 4}$$

An ANOVA was used to test for differences in the time to saturation (t_s) and saturation level (θ) among the three treatments.

Droplet method

The molarity of ethanol droplet test was used as another assessment of soil water repellency. The protocol suggested by Roy and McGill (2002) was modified slightly. Five samples from termite mounds and 5 samples from corresponding control soils were sieved to 1-mm mesh size, and test solutions were made using 95% ethyl alcohol.

Bioassays

Allelopathy

To test for the presence of allelopathic substances in the termite mounds responsible for inhibiting germination, a bioassay was set up using cucumber seeds (*Cucumis sativus*), a species used to test for allelopathic effects due to its sensitivity (e.g. (Muller et al., 1963), (Gondim, 1982), (Fletcher, 1991)). Based on a pilot experiment, three repetitions from five termite mound and five control sites were agitated with distilled water for 30 minutes on a mechanical shaker. Blanks of distilled water were agitated simultaneously. From each bottle, 10 mL of the resulting liquid was pipetted onto sterile gauze in a Petri dish. Twenty-five cucumber seeds were placed on the moist gauze, covered, and incubated in the dark for 48 hours. The number of germinated seeds in each repetition was counted at 24 and 48 hours. The non-parametric version of the ANOVA, the Kruskal-Wallis test, was used to test for differences between the germination count of the two treatment categories, as the raw data were not normally distributed.

Seed bank

To examine the effect of termite mounds on the germination of the soil seed bank, two 0.05-m soil scrapes were collected from the surface of five termite mounds and corresponding soils, mixed with sand, and watered while monitoring germination for seven weeks. An ANOVA was conducted to compare the number of seeds germinated at the end of the experiment between termite-mound and control soil.

Factorial experiment

Based on the results of the previous experiments, a bioassay was designed to discriminate between mechanical, chemical, and allelopathic suppression of seedling germination and development in termite mounds. Soil cores from 40 termite mounds and 40 control soil points were collected in 100 cm^3 stainless steel cylinders. Based on a pilot bioassay, a 2 x 2 x 2 x 2 factorial experiment was set up to evaluate the effect of termites, mechanical impedance, allelopathy, and acidity on seed germination and seedling development. To remove mechanical barriers to germination, the material was ground to a texture favorable to seedling development. Autoclaving was used to denature any allelopathic organic substances, as in Rogers et al. (1999). Soil acidity, a potential barrier to germination and seedling development, was corrected by amendment with lime.

Sesbania exasperata was chosen for the test species, a native plant with a known pre-germination treatment and described growth pattern. To stimulate germination, the *S. exasperata* seeds were subjected to thermal shock by submersion in boiling water and subsequent cooling. Seeds were then soaked overnight in water, and only those which imbibed water were planted.

Litter and charcoal on the surface of the soil cores were manually removed with forceps before initiating the experiment. Six seeds were planted per cylinder.

Each factorial combination of the experiment had five cylinder repetitions, for a total of 480 seeds. Each of the 80 100-cm^3 cylinders received 10 mL of water daily as needed. Germination was recorded daily for nine days. Seedling height, number of leaves, and leaf color were recorded for seedlings over 0.01 m in height each day for five days. The emergence velocity index (EVI) of the planted seeds was calculated, which weights the germination data by dividing by the number of days until germination, giving early-germinating seeds a higher EVI. The height of seedlings four days after planting was compared among treatments. A 2 x 2 x 2 x 2 factorial analysis of variance was performed on the data (Minitab 13.1, Minitab, Inc., State College, PA, USA).

RESULTS

Termite mound survey

In the 1040 m^2 of transects exposed in the survey, 79 termite mounds were observed, equivalent to a density of 760 mounds per hectare. The mounds ranged from 0.01 to 2.8 m^2 in area. The geometric mean basal area of the mounds was 0.29 m^2, and their coverage of the study area amounted to 3%. The surface of the mounds was gray in color, slightly pitted, and gently sloping. The mounds appeared eroded, with no evidence of recent building on the surface of the mound.

Eighteen termite species were found in the mounds sampled from the study site (Table 2.1). More than half of the mounds in this study hosted multiple species, and from a single mound four species were collected (*Cornicapritermes mucronatus* (Emerson), *Nasutitermes guayanae* (Holmgren), *Neocapritermes angusticeps* (Emerson), and *Subulitermes microsoma* (Silvestri). Eleven species only occurred in a single sample (*Anoplotermes* spp. 5, 8, 10, 11, 13, and 20, *Crepititermes verruculosus* (Emerson), *Glossotermes oculatus* (Emerson), *Nasutitermes similis* (Emerson),

Table 2.10. Ecology of termite species collected in termite mounds at study site

Termite species	**Distribution**	**Ecosystem**	**Feeding habit**	**Nesting habit**	**Mound-building habit**
Anhangatermes macarthuri Constantino	Brazilian Amazonia[i,vi]	Forest[i]	Humivorous[i]	Intermediate[ii] Subterranean[i]	unknown[ii]
Anoplotermes spp. 5, 8, 10, 11, 12, 13, 20	Neotropical[i]	Forest[v] Pasture[v] secondary forest[v]	Humivorous[ii,v] Intermediate[ii]	few arboreal[i] some epigeic[i,iii] subterranean[i]	inquilines[iii] some spp. of genus are mound-builders[i]
Cornicapritermes mucronatus Emerson	Brazilian Amazonia[vi] Guyana[vi]	Forest[i,iv,v]	Humivorous[v]	epigeic[v] probably subterranean[i]	unknown
Crepititermes verruculosus (Emerson)	Guyana[vi] Brazilian Amazonia[vi] Trinidad[vi]	Forests[i] other habitats[i]	Humivorous[I,II,V]	Arboreal[ii] Epigeic[ii,3,7] Intermediate[ii] Wood[ii]	Inquilines[i,iii] sometimes appears to be small mound-builder[i]
Glossotermes oculatus Emerson	Guyana[i] one known collection in Brazil[i]	Forest[i]	Xylophagous[ii]	Epigeic[ii] Intermediate[ii]	not a mound-builder[ii]
Nasutitermes guayanae (Holmgren)	Costa Rica to Amazonia[vi] Guyanas[vu] Trinidad and Tobago[vi]	primary forest[v] secondary forest[v]	Xylophagous[ii,v]	Arboreal[v] in wood[ii]	not a mound-builder[ii]
Nasutitermes similis Emerson	Brazilian Amazonia[iv] Guyana[vi]	unknown	unknown	unknown	unknown

Table 2.1 (Continued)

Neocapritermes angusticeps (Emerson)	Brazilian Amazonia[vi] Guyanas[vi] Trinidad[vi]	primary forest[v]	Intermedi-ate[ii,v] Xylophagous[ii,v]	Arboreal[ii] Epigeic[ii,v] Intermediate[ii] in wood[ii,v]	variable habit[ii]
Orthognathotermes cf. *brevipilosus* Snyder	genus Neotropical[i,iii]	genus in various eco-systems[i,iii]	genus humivorous[i,iii]	genus: epigeic[ii] intermediate[ii] subterranean[ii]	inquilines[iii] two spp. of genus not mound-builders[ii]
Subulitermes microsoma Silvestri	Argentina[vi] Bolivia[vi] central, southern Brazil[vi] Peru[vi] Paraguay[vi]	genus in forests[iii,v] pasture[iv] secondary forest[iv]	other *Subulitermes* spp. Humivorous[i,ii,v]	genus: arboreal[ii] epigeic[i,ii,iii] intermediate[ii] subterranean[i] in wood[iii]	two spp. of genus not mound-builders[ii]
Termes fatalis Linnaeus	Guyanas[vi] Brazilian Amazonia[vi] Trinidad[vi]	Forest[v] Pasture[v] secondary forest[v]	Generalist[ii] Humivorous[v] Xylophagous[v]	Epigeic[v]	variable habit, including mound-building[ii]

Orthognathotermes cf. *brevipilosus* (Snyder), and *Termes fatalis* (Linnaeus).

The mean root biomass in the surface of termite mounds was significantly lower ($P \leq 0.05$) than that of the adjacent soil (0.0019 g cm^{-3} and 0.0034 g cm^{-3}, respectively). Plant roots in the termite mound samples were 87% *Vismia* spp. by dry weight.

Soil chemical analyses

Carbon and N (g/kg) concentrations in the termite mounds were significantly elevated (by 33 and 28%, respectively, $P \leq 0.001$) (Table 2.2). The C:N ratio and median P and Mg concentrations did not differ significantly between termite mound and control soil, but K was elevated, and Ca was depleted (Table 2.2). pH was slightly lower in the termite mound ($P \leq 0.05$), at 4.3, compared to 4.4 in the neighboring soil. Aluminum concentrations were significantly elevated in the mound, by 47% ($P \leq 0.0001$). Micronutrients (Zn, Mn, Cu, Fe) did not differ significantly between the mound and control soil, with the exception of Mn ($P \leq 0.05$), which was 42% depleted in the mound soil (Table 2.2). Al saturation was significantly higher in termite mound material (91%) than in the neighboring soil (86%)

Table 2.2. Mean element concentrations of termite mounds and adjacent soils (standard errors in parentheses below). Values are reported as means for normally distributed data, and as medians for non-normally distributed data. Columns in bold indicate a significant difference at $P \leq 0.05$.

Location	**C**	**N**	P	**K**	**Ca**	Mg	**Al**	Fe	Zn	**Mn**	Cu
	(g/kg)		(mg/kg)		(g/kg)			(mg/kg)			
Termite mound	**43.8**	**2.47**	3.30	**33.3**	**0.0256**	0.007	**0.227**	324	0.916	**2.048**	0.288
	(2.02)	(0.06)			(0.004)		(0.007)	(10.7)			
Control soil	**32.9**	**1.93**	3.11	**24.1**	**0.0350**	0.007	**0.145**	312	0.800	**2.741**	0.271
	(1.85)	(0.05)			(0.006)		(0.003)	(17.0)			

Table 3. 11 Physical properties of termite mound and adjacent control soil. Values are reported as means for normally distributed data, and as medians for non-normally distributed data. Where the mean is given, the standard error of the mean is given in parentheses directly below. Column titles in bold indicate a significant difference at $P \leq 0.05$.

Location	Particle-size distribution				Bulk density	**Soil water content**		**Penetration resistance**	**Infiltration**
	Coarse sand	**Fine sand**	**Silt**	**Clay**					
	(%)				(g/cm^3)	(g/g)	(cm^3/cm^3)	(MPa)	(mm/s)
Termite mound	**7**	2	**20**	**72**	0.92	**0.37**	**0.34**	**13.5**	**15.8**
	(0.4)	(0.1)	(0.7)	(1.0)	(0.02)	(0.01)	(0.01)		
Control soil	**6**	2	**17**	**76**	0.92	**0.49**	**0.44**	**4.1**	**2.8**
	(0.3)	(0.1)	(0.7)	(0.8)	(0.02)	(0.02)	(0.01)		

Soil physical analyses

The distribution of clay, silt, and sand differed only slightly between the termite mound and adjacent soils, although these differences were significant. Slightly less clay and more silt and sand were found in the termite mounds than in the adjacent soil (Table 2.4).

Gravimetrically determined soil water content was 25% lower in the termite mound than in the adjacent soil (Table 2.4). The mean bulk density of the termite mound and the soil were equal, at 0.92 Mg/m^3. The resistance to penetration of the termite mound surface was around three times greater than that of the soil (Table 2.4).

The rate of water infiltrating under a constant head of pressure was five to six times greater in the termite mound than in the soil ($P \leq 0.05$). The mass of water-stable aggregates differed significantly between termite mound and control soil in each of the four size categories ($P \leq 0.0001$). There was a greater mass of large (2–4 mm) water-stable aggregates and fewer aggregates of the smaller size categories in the termite-mound material than in control soil (Figure 2.2).

The termite-mound material retained significantly lower water content than the termite-mound material over the entire pressure range of 0.0 to 1.9 pF (Figure 2.4).

Table 2.4. Soil chemistry of termite mounds and adjacent soils. Values are reported as means, and values in parentheses are standard errors of the mean. All values were significantly different between treatments, at $P \leq 0.05$.

Location	**pH** **(H_2O)**	**eCEC** **($cmol^+/kg$)**	**Al saturation**	**Base saturation**
			(%)	
Termite mound	**4.28**	**12.9**	**90.8**	**1.75**
	(0.02)	(0.420)	(0.568)	(0.106)
Control soil	**4.36**	**8.96**	**85.8**	**2.80**
	(0.03)	(0.258)	(0.946)	(0.199)

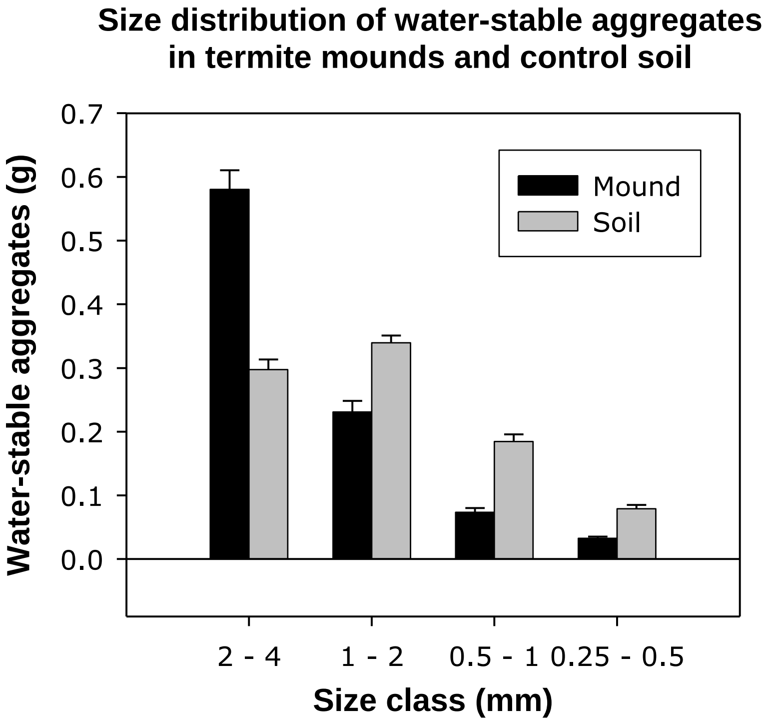

Figure 2.15.Mass of water-stable aggregates in different size categories from termite mounds and control soil at study site in Central Amazonia. Columns represent means for each treatment. All differences between termite mound and control soil are significant. n = 20.

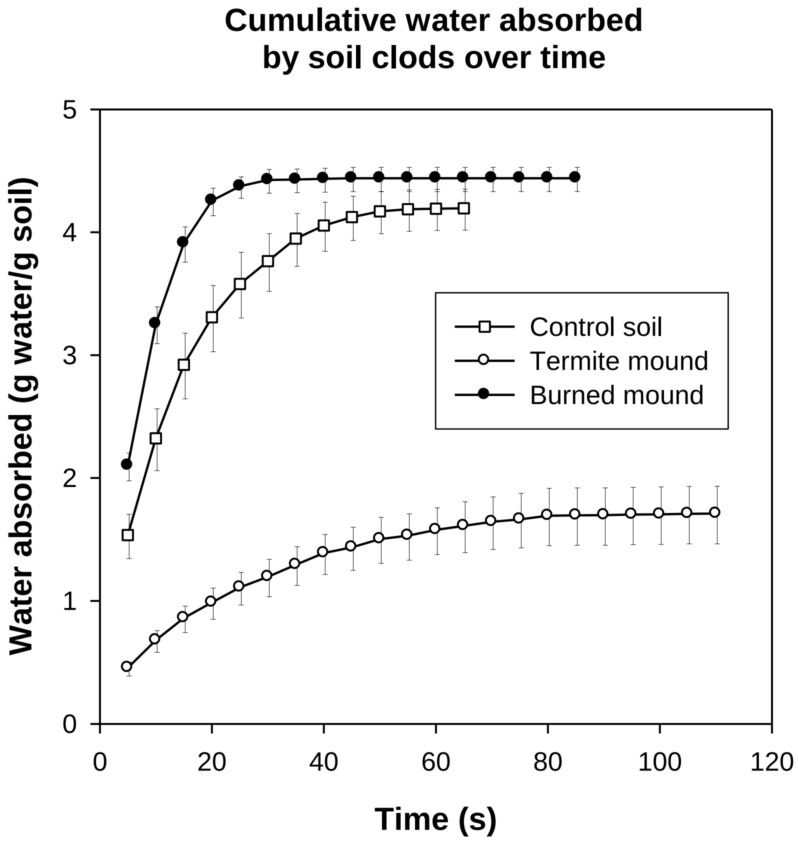

Figure 2.16 Cumulative water absorbed by soil clods over time. Termite mound and soil samples from study site in Central Amazonia. Bars indicate standard error of the mean. n = 10.

No significant difference in the pore-size distribution between the two materials was observed.

Time to saturation differed significantly between the termite mound, burned mound, and control soil (Figure 2.3). Time to saturation was 80% greater for termite mound material than control soil (Table 2.5). Termite mound material that had been exposed to fire reached saturation more than three times as quickly as termite mound material (Table 2.5). The water content of the termite mound material at saturation was 60% lower than that of the control or burned soil (Table 2.5). The water content of the burned mound material was not significantly different than that of the control soil (Table 2.5). Neither the soil nor the termite-mound material showed any degree of water repellency as measured by the molarity of an ethanol droplet test.

Bioassays

In the seed bank study, the number of seeds germinating was 78% lower in the termite mound material than in the control soil after 45 days ($P \leq 0.000$) (Figure 2.4). A higher proportion of emergent seedlings were dicots in the termite mound than in the control soil.

Table 2.5. Least squares means from segmented regressions of water absorption curves, where T_s is time to saturation, and θ is water content at saturation. Superscripts of different letters indicate a significant difference ($P < 0.01$).

	T_s (s)	**θ** (g water/g soil)
Termite mound	74.5^a	0.14^a
Control soil	42.2^b	0.35^b
Burned mound	23.8^c	0.37^b

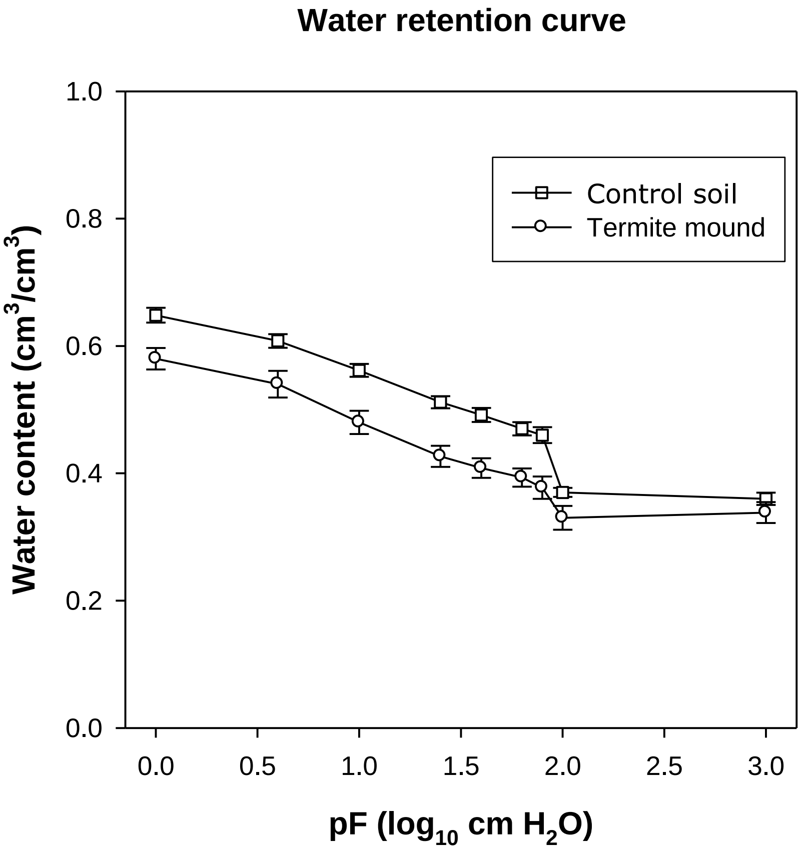

Figure 2.17.Water retention curve of termite mound and control soil with increased pressure. Termite mound and soil samples from study site in Central Amazonia. Bars indicate standard error of the mean. n = 15.

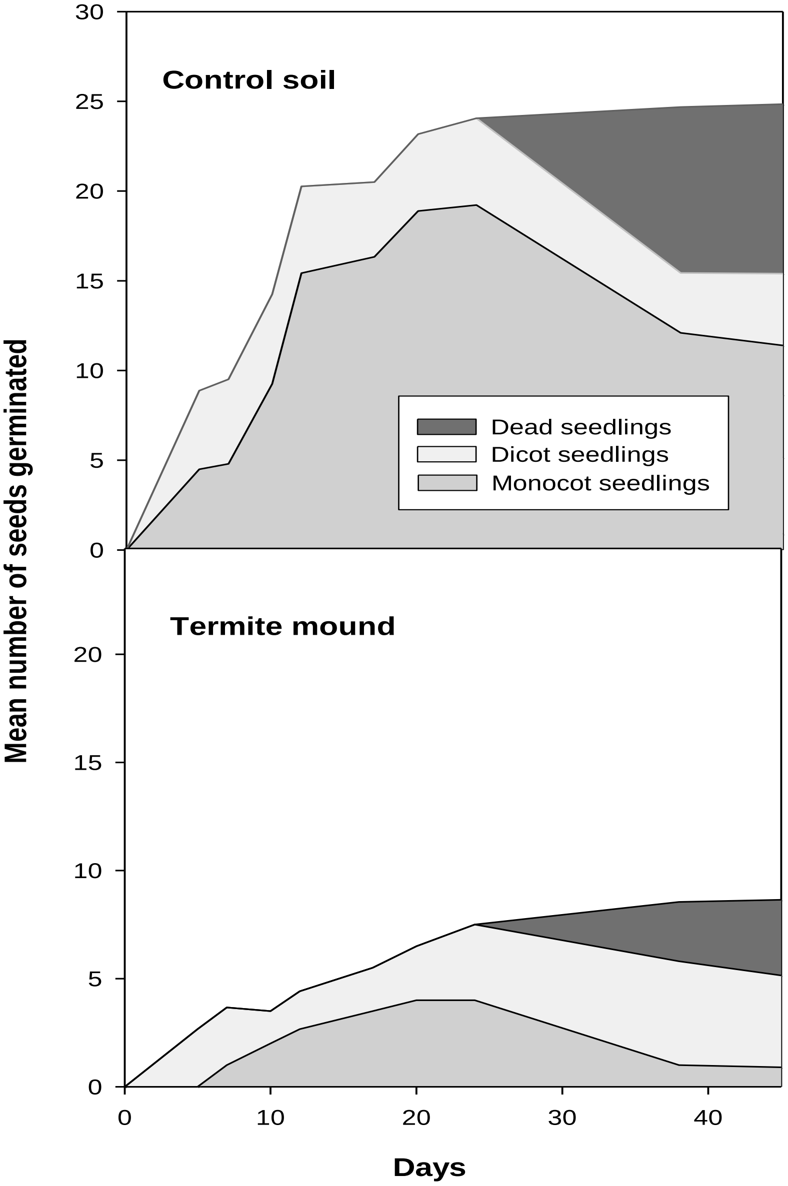

Figure 2.18. Mean number of seeds germinated from the seed bank in termite mound material and control soil. Termite mound and soil samples from study site in Central Amazonia.

In the factorial experiment, there were significant interaction effects of termite mound and impedance ($P \leq 0.0005$) and termites and autoclaving ($P \leq 0.05$) on the emergence velocity index (EVI) (Figure 2.5). Reducing the impedance of the soil had a positive effect, increasing the EVI in termite-mound material more than in soil material (Figure 2.5). While the EVI was equal for non-autoclaved termite-mound and soil material, autoclaving increased the EVI in the termite-mound material (Figure 2.5). Alleviating the acidity constraint increased the EVI similarly in termite mound and control soil (Figure 2.5).

Seedling height showed a greater increase in termite mounds that had been ground than in soil that had been ground ($P \leq 0.0005$), suggesting that the impedance of the termite mound is a constraint for seedling development. Although seedling height increased significantly in response to the acidity alleviation ($P \leq 0.005$), seedling height did not respond differently to the allelopathy or acidity levels between termite mound and control soil categories. No difference in the germination of seeds in termite mound or soil solution was observed in the allelopathy assay.

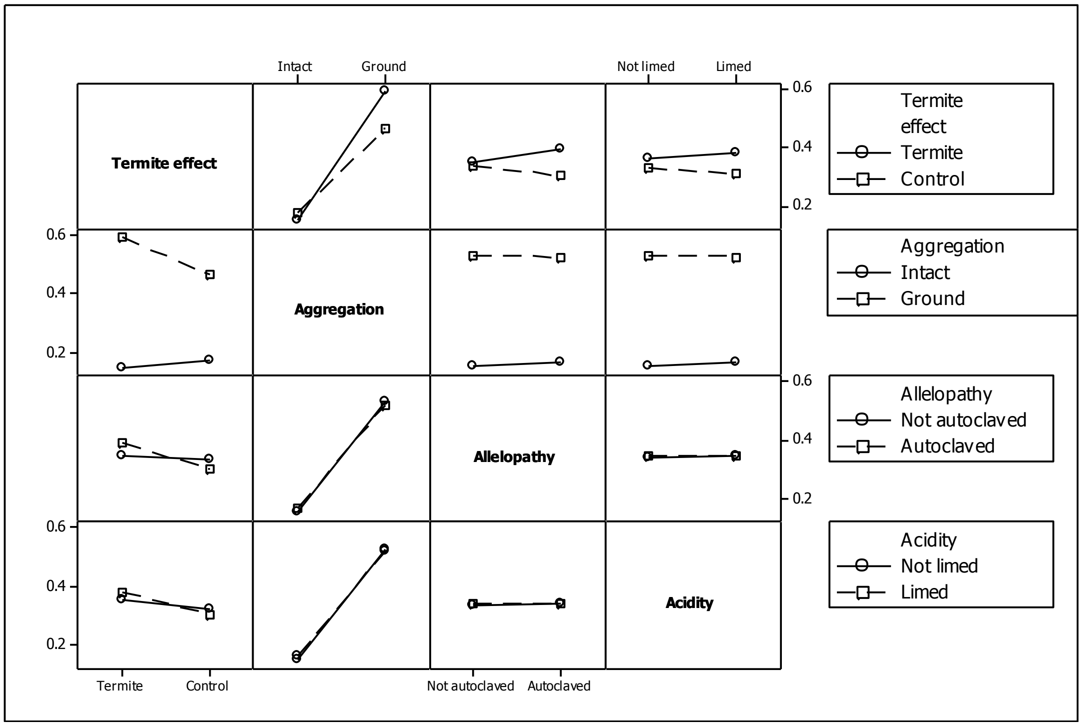

Figure 2.5.Interaction effects of four factors on the emergence velocity index of *Sesbania exasperata* seeds. Termite mound and soil samples from study site in Central Amazonia.

Discussion

The termite mound density at the study site, equivalent to 760 mounds per hectare, was higher than all but one of the values reported in the 22 studies found in the literature. Only Akamigbo (1984)'s survey of termite mounds in Nigeria reported a higher value (933 ha^{-1}). The most similar value was that of Domingos and Gontijo (1996), at 605 mounds per hectare, in the savanna of south-eastern Brazil. In terms of percent coverage of the area, the present study was second only to (though much lower than) Boyer (1969)'s survey of *Bellicositermes bellicosus rex* abundance in central Africa.

To determine which species found in the mounds was responsible for their construction, the literature on the ecology of the termite species found in this study was reviewed (Table 1). Of the five species collected which have known building habits, two are known not to be mound-builders, while the other three (*Neocapritermes angusticeps* (Emerson), *Crepititermes verruculosus* (Emerson), and *Termes fatalis* (Linnaeus)) exhibit variable habits. Of these, *N. angusticeps* was only collected twice, and *C. verruculosus* and *T. fatalis* were each collected in only a single mound. Of the seven species collected which have known feeding habits, three are considered to be humus-feeders, three are considered to be wood-feeders, and one is a generalist (Table 1).

From the information available and the results of the termite survey, no species was unequivocally responsible for the construction of the mounds in the study. Mound-building habits of Neotropical termite species are little described in the literature (Apolinário, 1993), and mound-building and inquiline species may cohabit and succeed each other in a single mound (Apolinário, 1993), making tracing the original builder of the mound difficult. Despite the variety of species likely to be involved in the building of the termite mounds in this study, the chemical, physical, and hydraulic profiles of the termite mounds were consistent across mounds, and exhibited much less variability between mounds than between mounds and control soil.

The root biomass results demonstrated a strong limitation for plant root exploitation of the termite mounds in the study area. These data are the first published that compare root biomass in termite mounds to the surrounding soil. This difference in belowground biomass falls within the range of the difference in aboveground biomass on and off termite mounds described by J. M. T. de Queiroz et al. (unpub. data) at a neighboring secondary forest site.

Eighty-seven percent of the plant root samples in the termite mound consisted entirely of *Vismia* spp., the predominant secondary forest genus at the site, which can propagate by sprouting from lateral roots (Williamson et al., 1998). These species may have an advantage over species which rely on seed germination for propagation and must survive the conditions at the termite mound surface to exploit the nutrients in the interior of the termite mound.

The elevated C and N concentrations in termite mounds were expected, due to the feeding and building habits of Neotropical termites that concentrate organic matter in the mound material. Low nitrogen concentrations in the soil can be limiting to plant biomass accumulation, as in Gehring et al. (1999), so conceivably the higher N concentrations of the termite mound could relax the N constraints where limiting. None of the other nutrients appears to be limiting factors for plant development on termite mounds, and although Al saturation was significantly higher in termite mound material (91%) than in the neighboring soil (86%) (Table 2.4), the bioassay did not show that it caused greater toxicity for *S. exasperata* growing on termite mounds than on control soil.

The finding of slightly less clay in the termite mounds differs from the majority of studies in the literature, which find an elevated clay content in the structure of the termite mounds (Black and Okwakol, 1997). This phenomenon is usually attributed to the termites' use of subsoil in the construction of their nests, or particle selection by termites. In this case, the percent clay is originally so high that termites may not need to preferentially select clay particles in their construction activities. The soil profile of the plateau soils has only a minimal texture gradient, so this may also explain the small textural difference.

Mechanical resistance to penetration was significantly higher on the termite mounds, and the bioassay confirmed this characteristic as a constraint to plant growth on termite mounds. Termite saliva and fecal matter used in mound construction have cementing properties (Adepegba et al., 1974), and the drier conditions of the termite mound material would similarly contribute, as resistance to penetration increases with lower water content (Spain et al., 1990). The results from the indicated that limitations to seed germination and seedling growth can in part be overcome by grinding the termite-mound material into finer particles. While mechanically crushing a termite mound may be a solution for land-use managers in cases of abandoned termite mounds, it is not appropriate for mounds with active colonies (as all mounds were in this study), as multiple colonies can result.

Although mechanical impedance was demonstrated to be an important factor for plants in this study, similar to the results of Rogers et al. (1999), this study also identified an important constraint in water availability to plants. Termite mound water content was lower, and appears to be related to several factors quantified in this study. (1) The greater water infiltration rate in termite mounds over soil applies to such saturated conditions as might occur during heavy rainfall. During such an event, the greater infiltration rate may in part be responsible for the lower water content of the termite mounds, as seen in the results of the soil water content analysis after a heavy rain. (2) The sandbox water absorption curves demonstrated a degree of water repellency in termite-mound material not found in control soil. The water-absorption behavior of burned termite-mound material suggests that the hydrophobicity of termite-mound material is due to an organic substance that combusts under high temperature. This supposition is supported by the greatly reduced carbon content of termite mound material that had been exposed to fire over termite mound material that showed no sign of having burned (3.8 and 36.9 g kg^{-1}, respectively). While the results of the molarity of an ethanol droplet test did not demonstrate any degree of water repellency, this may perhaps be explained by the difference in the scale of the experimental unit. Since the sandbox method used intact soil clods, and the droplet test used sieved soil, the water repellency may be a feature of the soil bonds rather than an intrinsic characteristic of the soil. This also suggests that the water repellency may be alleviated by grinding the termite mound material. (3) Both the tension table and column water retention curves demonstrated lower water retention capacity of termite mound material. Although the mean termite mound water content may be sufficient for vegetation growth, the lower moisture conditions in the termite mound may mean fewer seeds successfully germinating relative to the adjacent soil.

The allelopathy assay did not indicate the presence of a water-extractable allelopathic substance in termite mounds, but the factorial experiment did suggest the presence of a constraint that is relieved by autoclaving.

The number of seedlings in the termite-mound material was lower than in the control soil. Although the 45-day length of the present study was not sufficient to determine the absolute number of viable seeds in the samples, it was appropriate for a comparison of the relative quantity of viable seeds in termite mounds and surrounding soil. The lower number of seedlings in the termite-mound material may be due to (1) poor conditions for germination, (2) poor conditions for the plant between germinating and breaking the soil surface, or (3) lower seed stocks in the termite mound due to seed erosion or predation from the surface of the termite mound. No previous studies have been published assessing the seed banks of termite mounds, although rodents were found to cache seeds in abandoned termite mounds at a site in Africa (Bationo et al., 2002). That phenomenon was not observed at the site in this study.

To prevent this phenomenon in newly cleared areas, land management practices that encourage soil-nesting termites over mound-building termites should be employed. Land uses such as agroforestry systems or tree plantations that provide shade, as opposed to open pasture or crops, may be able to provide more environmental protection to termites and reduce the incidence of mound building. Making use of the logs and stumps in cleared areas instead of leaving them on the soil surface should also make the area less vulnerable to termite mound proliferation. These should be able to keep land in crop, forage, or successional productivity, accumulating aboveground biomass at a higher rate.

CONCLUSIONS

The abundance of termite mounds in a secondary forest in central Amazonia is surprisingly high, greater than some of the more famous termite mound-dotted savannas of Africa. The total area covered by termite mounds amounts to 3% of the study site, and the physical and chemical characteristics of these numerous microsites are substantially different from the surrounding soil and impede plant growth and development.

Fewer seeds germinated from the seed bank in termite-mound material, and termite mounds reduced seed germination and seedling growth of planted seeds. Neither nutrient availability nor aluminum saturation were limiting factors for plant growth in termite mounds over control soils. The physical strength of the termite mounds, their hydraulic characteristics that discourage water absorption and retention, and a potential allelopathic effect on seed germination are responsible for the mounds' constraints to colonization by plants.

Further research should attempt to determine how the heterogeneity imposed on the landscape by the surface properties of termite mounds affects the overall productivity of the ecosystem; how long the phenomenon persists; and what land management practices could prevent this phenomenon. Understanding the impact of mound-building termites on vegetation dynamics will be important in predicting the rates at which aboveground biomass will accumulate in the ever-increasing areas of secondary forest in Amazonia.

Acknowledgments

Michael Villani contributed ideas and advice at the initiation of this study, and his continuing contribution is greatly missed. We thank Elisa Wandelli for her guidance and support throughout this study. Marco Rondon, Luiz Augusto Gomes da Souza, Götz Schroth, Philippe Baveye, Carol Schwendener, and Risonei Assis provided valuable discussions on study methodology. We thank Reginaldo Constantino (University of Brasilia) for his identification of the termite species. We thank Emanoel dos Santos Alencar and Edilza da Silva Rocha for soil nutrient analyses, and Estevão Oliveira dos Santos for the soil texture analyses at the *Laboratório de Solos e Plantas–Embrapa Amazonia Ocidental*. Maria de Rosário (*Laboratório de Solos e Plantas—Embrapa*), Eleusa Barros (*Laboratório Temático de Solos e Plantas—INPA*) and the personnel of the *Laboratório de Sementes—INPA* graciously allowed the use of laboratory space and equipment. Rubenildo Lima da Silva, Antonio Sabino Neto da Costa Rocha, and Embrapa-CPAA provided essential logistical support. In data collection we are indebted to Osmar Barbosa Ferreira for his energy and dedication in both the field and laboratory. This study benefited from the assistance of Orlando Ferreira Cruz Junior and Carlos Lúcio Araujo Pimentel in the laboratory. The manuscript benefited from reviews by Profs. J. M. Anderson (University of Exeter) and Armand van Wambeke (Cornell University). Funding for this study was provided by the NASA Long-term Biosphere-Atmosphere Experiment in Amazonia (LBA-ECO) project ND-04 “Carbon and Nutrient Stocks, Soil Water Dynamics, and Trace Gas Fluxes in Abandoned Pastures and Agroforestry Systems in the Central Amazon.”

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CHAPTER 3

TERMITE MOUNDS SEQUESTER CARBON AND NITROGEN IN A SECONDARY FOREST IN CENTRAL AMAZONIA

ABSTRACT

We investigated the role of termite mounds in carbon and nitrogen storage and cycling at a secondary forest site in Central Amazonia. Termite mounds are prevalent at this study site (760 ha^{-1}) and sequester 80% and 20% more carbon and nitrogen per mass soil than the surrounding soils. We found that the carbon mineralizes at the same rate as the control soil, but that the nitrogen mineralizes 30% more slowly than in the surrounding soils (0.14 mg g N^{-1} d^{-1}). Microbial carbon in termite mounds was 50% lower than in control soils, at 0.5 and 1%, respectively. Neither moisture nor physical protection in aggregates were shown to be constraints to nitrogen mineralization. Disrupting termite mound aggregates actually reduced mineralization rates, suggesting that the C:N ratio of this material resulted in immobilization. The C:N ratio of termite mounds was 40% higher than the neighboring soils, at 17:1 versus 12:1. We infer that poor quality of organic matter used in mound construction, post termite digestion, is responsible for the lower rates of nitrogen mineralization.

INTRODUCTION

Land-use change alters resource availability and environmental conditions and can cause dramatic changes in the soil biota. Over 500 000 km^2 of closed-canopy forest in Amazonia have been cleared and clearing continues at a rate of 24000 km^2 per year (INPE, 2004). Forest clearing more than doubled termite mound abundance at a site in central Amazonia (Bandeira, 1978). At the site of the present study, a secondary forest which has undergone two clearings since its original vegetation twenty-five years ago, termite mounds occur at a high density of 760 ha^{-1} (Ackerman et al., in prep.).

The significance of the effects of soil macrofauna is often not apparent until natural systems are disrupted, but then the fauna may be one of the factors determining the rate of change and the new equilibrium state of soil processes (Anderson, 1988a). Invertebrates contribute directly and indirectly to carbon and nitrogen fluxes in soils: directly, though feeding excretion, respiration, and turnover of tissue production. Indirectly, through activities which alter the physicochemical environment for other soil organisms (Anderson, 1988). Soil fauna can influence turnover of microbial populations and affect net nitrogen mineralization through their effects on microsite conditions for microorganisms (Anderson, 1988b).

The effects of the changing populations of soil macrofauna in the landscapes of Amazonia on nutrient stocks and rates are only beginning to be investigated. In eastern Amazonia, (Moutinho et al., 2003) found elevated calcium, magnesium, and potassium stocks in the nests of leaf-cutting ants associated with secondary forest, and (Verchot et al., 2003) found elevated inorganic nitrogen stocks in the same. (Martius et al., 1996) estimated the change in methane emissions from Amazonia due to termite population change with deforestation. Most of the information on nitrogen in termite mounds has been on total organic nitrogen (Holt and Lepage, 2000).

For termites, carbon resources are not likely to be limiting, but nitrogen likely is (Lee, 1983). The C:N ratio of undecomposed wood is 350-500:1, and termites are 9-11% nitrogen by dry weight (Lee, 1983). The mound-building termites at this site use their feces in constructing their mounds. Termites exhibit many nitrogen-conserving behaviors, e.g. (Collins, 1983), and their feces have been shown to have very low nitrogen content, less than 1% (Lee, 1983).

The objective of this study was to further our understanding of the carbon and nitrogen dynamics in the prevalent termite-modified patches of the study site. We knew from previous studies that these termite mounds had higher carbon and nitrogen content, lower water content, and a greater proportion of large (2-4 mm) aggregates than the surrounding soil (Ackerman et al., in prep.). We postulated that the lower water content and the larger aggregates create less hospitable conditions for microbial decomposition of the organic matter found in termite mounds. We tested the hypotheses that (1) carbon and nitrogen mineralization are slower in termite mounds than the surrounding soils, and (2) that aggregation and moisture are the primary constraints.

MATERIALS AND METHODS

Site description

The study was conducted at the *Empresa Brasileira de Pesquisa Agropecuária* (Embrapa Amazônia Ocidental) research station located at km 54 of the federal highway BR-174 north of Manaus, Amazonas, Brazil. Soils on the plateau of the study site are classified as dystrophic, isohyperthermic, clayey kaolinitic Hapludox. The climate is tropical humid. Mean annual precipitation is 2400-2500 mm, with an average maximum in February or March of around 320 mm and an average minimum in August or September of around 80 mm ((Marques et al., 1981), (de Paiva, 1996)). The precipitation often occurs as heavy rains of short duration. Mean air temperature is 27 C, and atmospheric humidity is around

84% (Vose et al., 1992). The native vegetation of the region is closed-canopy, dense, evergreen *terra firme* (non-flooding) forest (Veloso et al., 1991).

The soil in this study was collected from a 10-year-old secondary forest site dominated by *Vismia* spp, located at 02° 30' 56"S and 60° 01' 28" W. The site was originally cleared for pasture in the late 1970's, grazed, and later abandoned to secondary vegetation. In 1993, the successional vegetation was cleared, burned, and left fallow once again.

A survey of some of the termite mounds in the study area found *Anhangatermes macarthuri* Constantino, *Cornicapritermes mucronatus* Emerson, *Crepititermes verruculosus* (Emerson), *Glossotermes oculatus* Emerson, *Nasutitermes guayanae* (Holmgren), *Nasutitermes similis* Emerson, *Neocapritermes angusticeps* (Emerson), *Orthognathotermes* cf. *brevipilosus* Snyder, *Subulitermes microsoma* Silvestri, *Termes fatalis* Linnaeus, and seven undescribed species of the *Anoplotermes* genus (Ackerman et al., in prep.). These species were not necessarily the original builders of the mounds, as successive species may colonize and/or cohabit in a single mound ((Apolinário, 1993) (Mill, 1984)). However the chemical, physical, and hydraulic profiles of the termite mounds were consistent across mounds, and exhibited much less variability between mounds than between mounds and control soil (Ackerman, I.L., in prep.).

Carbon

Soil respiration in situ

Most estimates of termite CO_2 production have been calculated from laboratory testing (Black, 1997). We decided to measure soil respiration in situ, as field assays provide more accurate information on termites' role at the ecosystem level (Bignell, 1997). Eight termite mounds were selected randomly from the termite mounds at the study site. A 20-cm polyvinyl chloride (PVC) ring 10 cm in height was pushed into the soil to a depth of 2-3 cm in each sampling location. Two corresponding rings were likewise installed at 1.5 m from the termite mound in the control soil to comprise the two control treatments. All litter was removed from the surface of the soil in one of the control treatments, as the termite mounds were devoid of litter themselves.

At sampling an open tin of soda lime was placed inside a covered chamber for 24 hours, then capped and re-weighed. A blank was used at each sampling session. The increase in dry mass of the soda lime was converted to carbon dioxide (CO_2) using the factor 1.69 to correct for the chemical formation of water (Grogan, 1998). Respiration was measured at three sampling events. During each event, four of the eight sites were measured the first day, and the other four sites the next. All sampling was done in June of 2002.

An ANOVA was conducted on the data of two sampling events, and the non-parametric version of the ANOVA, the Kruskal-Wallis test, was used for the non-normal data from the third sampling event.

Soil respiration *in vitro*

Soil was collected from six termite mounds and six corresponding control sites by auger, in June of 2002. Water content was determined from a subsample of each sample. The soil samples were sieved to a size of 2 mm.

Soil microbial respiration was measured by an infrared gas analyzer (HCM-1000, Heinz Walz GmbH, Effeltrich, Germany). The instrument was run in open flow mode using ambient air from outdoors. Temperature during the experiment ranged from 17 to 23 C. Twelve cuvettes were filled with fresh soil equivalent to 40 g dry weight.

Basal respiration (BR) was measured for 4.5 h. BR was calculated as follows:

$$BR = \frac{(F(C_1 - C_0))}{S}$$

where C_1 was the CO_2 value in parts per million (ppm) of the air leaving the sample cuvette, C_0 was the CO_2 concentration of the air before the cuvette, F was the flow rate of the air flushing the cuvette in mL min^{-1}, and S was the dry weight of the soil in grams.

Substrate-induced respiration (SIR) was subsequently measured. A mixture of 240 mg glucose monohydrate and 500 mg talc was added to each tube and mixed with soil. The new respiration rate after one hour was considered the substrate-induced respiration rate.

Microbial biomass carbon (C_{mic}) was calculated using the relationship determined by (Anderson and Domsch, 1978):

$$C_{mic} = 40.04R + 0.37$$

where R = increase in respiration rate after glucose addition, in μL h^{-1} (g soil)$^{-1}$. The activation quotient (QR) was calculated from the ratio BR to SIR. The population density independent from carbon content was calculated by the ratio of C_{mic} to C_{org}. The metabolic quotient was calculated as the BR divided by the C_{mic}.

A paired t-test was used to test for significant difference between the treatments. For non-normal data, the Mann-Whitney test was used.

Cellulose decomposer populations

Twenty termite mounds were randomly selected from the study site for sampling. Three 10-cm surface samples from each mound were collected with an auger and bulked into a composite sample. The adjacent soil (1.5 m in distance in a random direction) was likewise sampled. Each sample was shaken with sterilized water and glass beads for ten minutes and a dilution series was made from 10^{-3} to 10^{-7}.

40 g of soil from each sample were dried at 105 C for 24 h and the loss in weight measured. The method described in Meiklejohn (1965) was followed. A strip of Whatman No. 1 filter paper was added to a vial containing 10 mL of Jensen's medium (Jensen, 1940). The cellulose medium was composed of 1.0 g $(NH_4)_2SO_4$, 1.0 g K_2HPO_4, 0.5 g $MgSO_4 \cdot 7H2O$, 0.2 g NaCl, 2.0 g $CaCO_3$, and 1000 mL tap water. The vials were incubated for seven days and counted as positive if microbial growth or break-up of the paper strip was observed. This experiment occurred in June of 2002. A paired t-test was used on these data.

Nitrogen

Nitrogen mineralization

An aerobic incubation was set up in a shadehouse as a 2 x 2 x 2 factorial. The three experimental factors were termite mound effect, aggregation, and moisture, each consisting of two levels (termite mound and control soil, intact and broken soil, and normal and elevated moisture levels). Five repetitions were used, for a total of 40 experimental units.

Five termite mounds were chosen randomly for sampling. Termite-mound material was collected from the upper 10 cm of the mound surface with an auger in four places, and bulked into a composite sample. Control soil was collected in the same manner at 1.5 m from the border of the termite mound. This sampling was done in the rainy season.

Moisture content of each sample was determined in the laboratory by oven-drying a subsample for 24 h at 105 C. In the broken treatment, large aggregates were broken manually to a consistent size. For the elevated moisture treatment, gravimetric water content was increased to a moisture level 10% higher than field content. Water was added three times a week to maintain the desired water content in both treatment and control samples. The soil was incubated in closed containers with a large headspace and a hole in the lid to permit gas exchange.

A subsample was taken on day zero and analyzed for nitrogen by Kjeldahl extraction (Bremmer, 1982). At 0, 8, 43, and 66 days, 25 g subsamples from the incubations were extracted with 75 mL KCl by shaking for 30 minutes and then allowing the soil to settle overnight. These incubations were done from February to May of 2002. NH_4^+ and NO_3^- determinations were made on a continuous flow analyzer (Skalar, Brenda, The Netherlands). Net ammonification and net nitrification were calculated as the difference in NH_4^+-N and NO_3^--N before and after the incubation. Net mineralization was calculated as the difference in (NO_3-N + NH_4^+-N) before and after the incubation. These values were calculated on a per-mass-total-N basis. Non-linear regression equations were used to attempt to fit the data to models of net nitrogen mineralization potential, for example, (Cabrera, 1993):

$$N_t = N_i + N_0 (1 - e^{-kt}),$$

where N_t = inorganic N concentration (mg N kg^{-1} soil) at time t (d), N_i = initial inorganic N concentration (mg N kg^{-1} soil), N_0 = N mineralization potential (mg N kg^{-1} soil), and k = non-linear mineralization constant (d^{-1}).

A 2 x 2 x 2 factorial analysis of variance was performed on the data. The data were re-analyzed after dropping terms that were not significant. Minitab was used for all the statistical analyses in this study (Minitab 14, Minitab, Inc., State College, PA, USA).

Ammonifier populations

The same dilutions used for determining populations of cellulose-decomposing microorganisms above were used in an experiment to compare ammonifier populations. This experiment was conducted in June of 2002. Methods for estimating the population of ammonifying microorganisms were followed according to (Andrade et al., 1994). Vials with orange coloration were counted as negative for ammonifying microorganisms and vials with pink or yellow coloration were counted as positive. The most probable number of microorganisms was calculated using the DOS application MPNES (Woomer et al., 1990). A paired t-test was performed on these data.

RESULTS

Carbon

Soil respiration *in situ*

CO_2 flux from the surface did not differ significantly between the termite mound and the control treatments at any sampling event (Table 3.1).

Soil respiration *in vitro*

Organic C was significantly enriched in the termite mound. Substrate-induced respiration was significantly depressed (Table 3.3). A linear regression of this ratio for the termite-mound material against the control soil material yielded the relationship

$$\left(\frac{C_{mic}}{C_{org}}\right)_{Termite} = 0.0 + 0.5 \cdot \left(\frac{C_{mic}}{C_{org}}\right)_{Soil}$$

with an R^2 value of 91.5% ($P < 0.005$). Basal respiration, C_{mic}, the activation quotient, and the metabolic quotient did not differ significantly between termite and control soil, but the C:N ratio was significantly higher in the termite-mound material (Table 3.2, Table 3.3).

Cellulose decomposer populations

The population of cellulose-decomposing microorganisms did not differ significantly between termite-mound material and control soil (Table 3.4).

Table 3.12. Mean soil respiration values (n = 8) for termite mound and control soil from a secondary forest in Central Amazonia, using the soda lime method, *in situ*. Standard errors in parentheses. Values are not significantly different between termite mound and control soils at $P < 0.05$.

Sampling date	Soil respiration (g CO_2-C m^{-2} d^{-1})		
	Termite	Control	Control plus litter
June 4-6	28.3 (1.6)	26.7 (2.4)	29.6 (1.0)
June 17-19	23.0 (1.1)	24.5 (1.5)	23.5 (1.0)
June 24-26	24.6 (0.9)	25.5 (1.9)	24.5 (1.2)

Table 3.13. Mean carbon values (n = 6) for termite mound and control soil from a secondary forest in Central Amazonia, using the subtrate-induced respiration method and IRGA *in vitro*. Standard errors in parentheses. Column titles in bold indicate a significant difference at $P < 0.05$.

Treatments	**Potential respiration (μL CO_2 (g C)$^{-1}$ h^{-1})**	C_{mic} (mg (kg soil)$^{-1}$)	**C_{org} (g (kg soil)$^{-1}$)**	**C_{mic}:C_{org}**	Activation quotient	Metabolic quotient	**C:N**
Termite mound	**150**	180	**37**	**0.0049**	0.20	0.0075	**17**
	(24)	(35)	(3)	(0.0010)	(0.07)	(0.0032)	(1)
Control soil	**260**	200	**21**	**0.0092**	0.16	0.0052	**12**
	(43)	(44)	(1)	(0.0019)	(0.05)	(0.0017)	(1)

Table 3.14. Mean basal respiration values (n = 6) for termite mound and control soil from a secondary forest in Central Amazonia. Values expressed on a per g C basis and on a per g soil basis. Standard errors in parentheses. Values are not significantly different between termite mound and control soil at $P < 0.05$.

Treatments	Basal respiration (μL CO_2 (g C)$^{-1}$ h^{-1})		Basal respiration (μL CO_2 (g soil)$^{-1}$ h^{-1})	
	Whole	aggregates only	whole soil	aggregates only
Termite mound	26 (6)	21 (3)	0.90 (0.21)	5.4 (0.7)
Control soil	35 (7)	34 (4)	0.76 (0.16)	5.6 (1.0)

Table 3.15. Most probable number of ammonifiers and cellulose decomposers. Standard errors in parentheses. No significant differences between treatments.

	Ammonifiers	Cellulose decomposers	
Termite mound	29339 (16730)	19578	(9384)
Control soil	82611 (53119)	7343	(2061)

Table 3.16. Mean nitrogen values (n = 20) in termite mound and control soil from a secondary forest site in Central Amazonia. Initial nitrogen values were determined on day zero of a 66-day incubation. Rates are calculated over a 66-day aerobic incubation. Values are given on a dry weight basis. Standard errors in parentheses. Column titles in bold indicate a significant difference at $P < 0.05$.

Treatments	Initial NH4+-N	Initial NO3-N	**Initial Total N**	Net ammonification	**Net nitrification**	**Net mineralization**
	----- (g N (kg soil)$^{-1}$) -----			----- (mg g N^{-1} d^{-1}) -----		
Termite mound	3.3 (0.4)	1.7 (1.0)	**2.4** (0.1)	-0.0018 (0.0061)	**0.15** (0.01)	**0.14** (0.01)
Control soil	3.2 (0.3)	0.75 (0.20)	**2.0** (0.1)	0.0075 (0.0059)	**0.19** (0.01)	**0.20** (0.01)

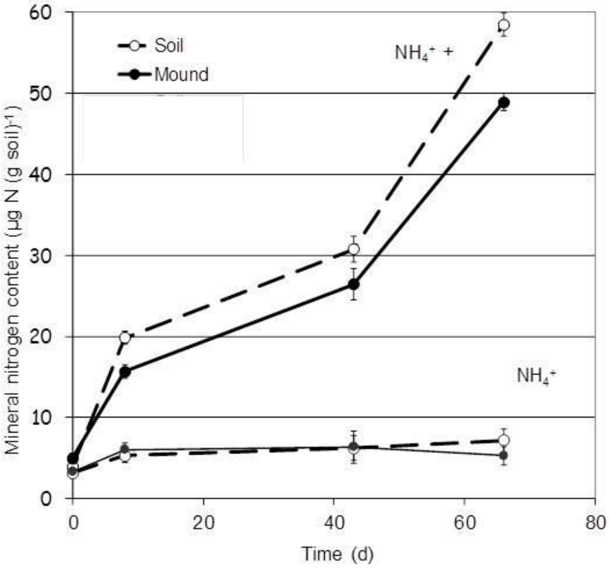

Figure 3.19. Mean mineral nitrogen concentrations (n = 20) over the course of an aerobic incubation of termite mound and control soil from a secondary forest site in central Amazonia. Bars indicate standard errors of the mean. Values are given on a dry weight basis.

Nitrogen

Nitrogen mineralization

At the onset of the experiment, total nitrogen was significantly higher in the termite mound than in the control soil ($P < 0.005$), while NH_4^+-N and NO_3^--N individually were not significantly different (Table 3.5).

The termite-mound material had significantly lower net nitrification and mineralization ($P = 0.005$) rates across treatments (Table 3.5). Traditional models of net nitrogen mineralization potential did not fit the data, and so we've graphed the empirical data instead (Figure 3.1). No significant interactions between the effect of termite mounds and the levels of moisture or aggregation on nitrogen mineralization rates were observed. Breaking aggregates significantly decreased net ammonification and mineralization ($P < 0.001$ and $P < 0.05$) in all treatments.

Ammonifier populations

Populations of ammonifying microorganisms did not differ significantly between termite mound and control soil (Table 3.4).

DISCUSSION

Our first hypothesis was partially confirmed. Nitrogen mineralization was indeed slower in termite mounds than the surrounding soils, while carbon mineralization rates were no slower than the control soil. Our test of whether the slower nitrogen mineralization in termite mounds was due to protection in aggregates and moisture limitations found neither to be the case. These findings suggest that it is the composition of the termite-mound organic matter itself that is particularly refractory. (Amelung, 1998) found lignin contents of termite mounds in the same region as this study to be higher than those of wood, suggesting that lignin may be accumulated in preference to other organic compounds in nest-building. Termites are able to assimilate up to >90% of the carbon in cellulose, and only up to 15-25% of the carbon in lignin (Lee, 1983). (Lee, 1971a; Lee, 1971b) found termite nests with 0.095-0.14% nitrogen to have extremely slow microbial breakdown due to lack of carbohydrate substrate and to the presence of humic acids.

Another result in support of this explanation is that the ratio of microbial carbon to total soil organic carbon in termite mounds in this study was about half that of neighboring soils. Microbial carbon usually males up about 1-3% of total organic carbon (Jenkinson and Ladd, 1981) under equilibrium conditions. While the control soil in this study fell within this range (1%), the termite-mound material fell below, at 0.5% (Table 3.2).

The fact that nitrogen mineralization in fact decreased significantly upon breaking aggregates may point to immobilization of nitrogen. (Glaser, 2001) also inferred an immobilization of nitrogen in termite mounds from their study of carbon and nitrogen dynamics in East Africa.

No significant differences in populations of cellulose decomposers or nitrifiers were found between termite mounds and soil in this study. In contrast, (Holt, 1998) found mound soils to have higher microbial biomass than nearby surface soils. (Meiklejohn, 1965) found more cellulose decomposers and nitrifiers in *Macrotermes* mounds than control soils. (López-Hernández, 2001) found that microbial activity was elevated in the mounds of the termite *Nasutitermes ephratae* in Venezuela, with higher CO_2 and ammonium production than in the surrounding savanna soils. These contrasting findings confirm the importance of not generalizing termite mound characteristics across termite species (Black, 1997).

Using a conservative estimate of 0.05 m^3 for the volume of a termite mound, a bulk density of 0.9 g cm^{-3} (Ackerman et al., in prep.), a mound density of 760 ha^{-1} (Ackerman et al., in prep.), and the nitrogen concentration from this study, we estimate the size of this slower termite-mound nitrogen pool to be 84 kg N ha^{-1}. We estimate the amount of carbon in termite mounds at the study site to be equivalent to 1.3 Mg C ha^{-1}. Yet it also appears that the termite mounds are not important sources of heterogeneity in CO_2 emissions on a landscape scale at the study site.

It should be noted that the comparison in this study is between termite mounds and neighboring soil, not between termite-modified and non-termite-modified soil. Soil-dwelling termites are present in the surrounding soil (I. L. Ackerman, pers. obs.) and presumably affect its characteristics as well.

CONCLUSIONS

Termite mounds at this site store more carbon and nitrogen than the surrounding soils, sequestering 80% and 20% more per mass soil. Carbon does not mineralize any faster, and nitrogen mineralizes more slowly than in the surrounding soils. Neither moisture nor physical protection in aggregates were shown to be constraints to nitrogen mineralization in this study, rather we infer that the low quality of organic matter post termite digestion reduces its rate of mineralization.

An interesting direction for further study would be in determining whether this phenomenon amounts to simply a redistribution of recalcitrant organic matter from other parts of the ecosystem, or whether the termites have a role in stabilizing organic matter. Additional research on the source of the mound-derived organic matter (whether coarse woody debris, leaf litter, soil organic matter, or symbiotic biological nitrogen fixation), would help elucidate the termite-mediated flows of carbon and nitrogen in the ecosystem.

ACKNOWLEDGMENTS

This study was funded by LBA-Ecology Project ND-04 “Carbon and nutrient stocks, soil water dynamics, and trace gas fluxes in abandoned pastures and agroforestry systems in the Central Amazon” and a grant from the Program in Biogeochemistry and Environmental Change at Cornell University. Elisa Wandelli of Embrapa-CPAA facilitated this work. Luis Antonio de Oliveira, Christoph Steiner, Carol Schwendener, Marcos Garcia, and Janice Thies provided valuable input on study methodology. Márcia Pereira de Almeida did the mineral N analyses and Osmar Ferreira Barbosa provided invaluable assistance in the field, laboratory, and greenhouse. We thank Rubenildo Lima, Sabino Neto, and Embrapa-CPAA for excellent logistical support. We thank SHIFT (Studies of Human Impact on Floodplains and Forests in the Tropics) and Embrapa-CPAA for the use of the continuous flow analyzer and the IRGA. The *Laboratório Temático de Solo e Plantas* of *INPA-Agronomia* kindly accommodated several of the experiments in this study.

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APPENDIX A

Figure A1. An unusual observation: the alcohol in some of the vials after termite preservation turned bright red. After some investigation, the phenomenon appeared to be the product of teak leaves in the termite gut. The photograph below illustrates this: top vial contains shredded teak leaves, bottom vial contains teak leaves in alcohol. A new low-tech tracer method!

Figure A2. An image of an undescribed member of the Apicotermitinae family collected in one of the agroforestry systems. An unusually large species for the *Anoplotermes* genus.

Figure A3. An image of an individual of an undescribed species of the *Velocitermes* genus collected in one of the primary forest transects.

APPENDIX B

Table B1. Germination on Day 2 of allelopathy experiment.

Number of *Cucumis sativus* seeds germinated out of 20.

		Block		
Location	Mound no.	2	3	4
Termite	A13	20	19	17
	A174	19	18	17
	A5_	15	18	18
	A54	19	17	17
	A6	18	20	19
Soil	A13	19	19	19
	A174	19	19	18
	A5_	17	19	15
	A54	7	8	9
	A6	5	8	7
Blank		6	0	7

Table B2. Bulk density and water content in the surface 5 cm of nine termite mounds and adjacent control areas in a secondary forest in July of 2000. 3 replicates were taken from each mound and treatment. One missing value.

Mound no.	Location	Rep	Bulk density ($g\ cm^{-3}$)	Gravimetric water content (g H2O g^{-1} soil)	Volmetric water content ($g\ H_2O\ cm^{-3}$ solo)
A36	Termite mound	1	1.07	0.36	0.39
		2	0.93	0.35	0.32
		3	0.91	0.32	0.29
	Control soil	1	0.97	0.38	0.37
		2	0.77	0.39	0.30
		3	0.96	0.45	0.43
A8	Termite mound	1	0.87	0.38	0.33
		2	0.92	0.34	0.31
		3	0.79	0.59	0.47
	Control soil	1	0.94	0.49	0.46
		2	0.87	0.49	0.43
		3	0.86	0.50	0.43
A17	Termite mound	1	0.79	0.35	0.28
		2	0.72	0.40	0.29

		3	0.90	0.33	0.30
	Control soil	1	0.98	0.45	0.45
		2	0.98	0.45	0.45
		3	0.89	0.49	0.43
A13	Termite mound	1	0.89	0.36	0.32
		2	0.98	0.33	0.33
		3	1.08	0.32	0.35
	Control soil	1	0.86	0.57	0.49
		2	0.78	0.67	0.52
		3	1.00	0.25	0.26

Table B2. (Continued)

Mound no.	Location	Rep	Bulk density (g cm^{-3})	Gravimetric water content (g H2O g^{-1} soil)	Volmetric water content (g H_2O cm^{-3} solo)
A32	Termite mound	1	0.96	0.42	0.41
		2	0.96	0.38	0.37
		3	1.04	0.34	0.35
	Control soil	1	0.89	0.50	0.45
		2	0.91	0.54	0.49
		3	0.99	0.46	0.46
A89	Termite mound	1	0.94	0.39	0.36
		2	0.93	0.44	0.41
		3	0.92	0.37	0.34
	Control soil	1	0.89	0.57	0.51
		2	0.97	0.56	0.54
		3	0.77	0.66	0.51
A91	Termite mound	1	0.77	0.42	0.32
		2	0.99	0.34	0.34
		3	0.90	0.39	0.35
	Control soil	1	1.05	0.44	0.46
		2	0.80	0.50	0.40
		3	0.95	0.52	0.49
A1	Termite mound	1	1.05	0.29	0.30

		2	0.93	0.28	0.26
		3	0.97	0.32	0.31
	Control soil	1	1.12	0.37	0.42
		2	1.09	0.40	0.44
		3	1.02	0.42	0.43
A65	Termite mound	1	0.98	0.38	0.37
		2	0.83	0.45	0.37
		3	0.84	0.41	0.35
	Control soil	1	0.86	0.58	0.50
		2	0.61	0.62	0.38
		3	0.97	0.48	0.47

Table B3. Number of termite species found per mound in the secondary forest site.

Mound No.	Number of species
A139	5
A20	3
A138	2
A142	2
A150	2
A191	2
A69	2
A9	2
A148	1
A156	1
A16	1
A176	1
A55	1
A79	1
A8	1

Table B4. Rate of infiltration in termite mounds and control soil.

Mound No.	Infiltration (mL min^{-1})	
	Termite mound	Control soil
A-32	36	25
A-89	44	48
A-91	283	106
A-36	198	135
A-75	430	18
A-8	263	35
A-17	1350	50
A-13	1100	160
A-1	1063	250

Table B5. Descriptions of features (termite mounds, logs, and stumps) found along study transects. Termite mounds covered the same amount of total area as logs. Average mound area = 0.5 m^2.

Mapping						Area						Description			
Transect	Feature	Mound No.	Dist. (m)	Direction	Dist. to high pt. (cm)	Shape	Length (cm)	Width (cm)	Within transect (%)	Area (m2)	Area in transect (m2)	Color	No. of burrows	Burned?	Associated with
B	mound	126	10.16	West	46	circ	64	52	100	0.26	0.26	gray	0	no	burnt stump
	mound	127	13.38	West	143	rect	87	35	50	0.30	0.15	lt. gray	0	no	burnt log
	mound	16	18.06	East	83	rect	120	48	100	0.58	0.58	gray	0	no	-
	mound	128	18.67	West	87	oval	56	31	100	0.17	0.17	gray	0	no	-
	mound	129	19.56	West	62	circ	20	13	100	0.02	0.02	gray	0	no	-
	mound	130	20.10	East	81	circ	30	23	100	0.06	0.06	gray	0	no	-
	mound	131	21.42	East	49	circ	43	52	100	0.18	0.18	gray	0	no	-
	mound	14	23.10	East	98	circ	125	107	70	1.06	0.74	gray	?	yes	stump
	stump		23.84	East	13	circ	14	12	100	0.01	0.01	-		?	-

mound	132	24.10	West	41	oval	47	50	100	0.24	0.24	gray	0	no	stump
log		35.36	East	81	rect	243	15	100	0.36	0.36	-		yes	-
log		37.22	East	42	rect	220	18	100	0.40	0.40	-		yes	-
log		35.50	East	22	rect	122	15	100	0.18	0.18	-		yes	-

Table B.5 (Continued)

Mapping						Area						Description			
Transect	Feature	Mound No.	Dist. (m)	Direction	Dist. to high pt. (cm)	Shape	Length (cm)	Width (cm)	Within transect (%)	Area (m2)	Area in transect (m2)	Color	No. of burrows	Burned?	Associated with
C	mound	133	58.27	West	63	circ	75	27	100	0.20	0.20	gray	0		-
	log		56.39	West	20	rect	210	7	100	0.15	0.15	-	-	yes	-
	log		55.30	East	99	rect	176	16	50	0.28	0.14	-	-	yes	-
	mound	134	55.57	West	47	circ	37	22	100	0.07	0.07	gray	0		stump
	stump		55.51	West	51	circ	20	15	100	0.02	0.02	-	-	yes	-
	mound	135	57.14	West	105	circ	40	36	50	0.11	0.06	gray	0	no	-
	mound	136	54.14	West	56	oval	95	89	100	0.85	0.85	lt. gray	0	no	stump
	log		53.51	West	0	rect	119	7	100	0.08	0.08	-	-	yes	-
	log		45.63	West	28	rect	364	19	100	0.69	0.69	-	-	yes	-
	mound	19	43.90	East	90	circ	92	45	80	0.37	0.29	gray	0	no	stump
	mound	137	20.66	West	54	circ	23	15	100	0.03	0.03	gray	0	no	-
D	log		5.32	West	98	rect	594	17	40	1.01	0.40	-	-	-	-

stump		3.23	West	81	circ	18	12	100	0.02	0.02	-	-	-	-
stump		6.66	East	11	circ	10	6	100	0.01	0.01	-	-	-	-
log		12.62	West	114	rect	118	12	90	0.14	0.13	-	-	-	-
log		12.11	East	40	oval	65	20	100	0.13	0.13	lt. Gray	-	no	-
mound	138	21.07	East	72	circ	32	25	100	0.06	0.06	lt. Gray	0	no	stump
log		22.03	East	42	rect	650	17	15	1.11	0.17	-	-	-	-
mound	139	22.26	East	50	circ	78	43	100	0.29	0.29	gray	0	no	stump

Table B.5 (Continued)

Mapping						Area						Description			
Transect	Feature	Mound No.	Dist. (m)	Direction	Dist. to high pt. (cm)	Shape	Length (cm)	Width (cm)	Within transect (%)	Area (m2)	Area in transect (m2)	Color	No. of burrows	Burned?	Associated with
	mound	140	23.93	West	32	circ	73	68	100	0.39	0.39	lt. gray	-		
	mound	69	30.00	East	115	tri	90	43	30	0.19	0.06	gray	0	yes	
	log		31.10	West	45	sqre	37	32	100	0.12	0.12	-	-	-	
	mound	141	39.18	West	30	rect	134	22	100	0.29	0.29	lt. gray	0	no	log
	mound	142	40.45	West	35	oval	74	50	100	0.37	0.37	gray	0	no	-
	stump		42.36	West	92	circ	13	12	100	0.01	0.01	-	-	?	-
	mound	143	45.10	East	121	oval	102	80	10	0.82	0.08	gray	0	no	-
	mound	144	47.39	West	27	oval	27	24	100	0.06	0.06	gray	0	no	-
	mound	145	54.23	East	42	circ	34	27	100	0.07	0.07	gray	0	no	-
	mound	146	55.12	East	14	circ	55	43	100	0.19	0.19	gray	0	no	-
	mound	147	56.88	East	95	circ	30	18	100	0.05	0.05	gray	0	no	stump
E	mound	148	40.22	East	32	circ	74	37	100	0.24	0.24	lt. gray	0	no	-

mound	149	7.07	West	135	oval	212	114	5	2.42	0.12	gray	0	no	-
mound	150	11.07	West	54	circ	54	50	100	0.21	0.21	gray	0	no	log
mound	151	20.18	East	38	circ	60	42	100	0.20	0.20	gray	0	no	-
mound	152	29.71	West	60	circ	45	38	100	0.14	0.14	gray	0	no	-
mound	153	31.90	East	72	circ	37	30	100	0.09	0.09	gray	0	no	-
mound	154	33.16	West	79	circ	43	34	100	0.12	0.12	gray	0	no	-
mound	155	34.36	East	18	circ	55	37	100	0.17	0.17	gray	0	no	-
mound	156	36.24	East	112	circ	63	48	10	0.24	0.02	gray	0	no	wood

Table B.5 (Continued)

Mapping						Area						Description			
Transect	Feature	Mound No.	Dist. (m)	Direction	Dist. to high pt. (cm)	Shape	Length (cm)	Width (cm)	Within transect (%)	Area (m2)	Area in transect (m2)	Color	No. of burrows	Burned?	Associated with
	mound	157	36.04	West	85	circ	65	64	50	0.33	0.16	gray	0	no	trunk
	mound	172	79.76	West	42	circ	75	59	100	0.35	0.35	gray	0	no	charcoal
	log		78.62	West	66	rect	568	15	30	0.85	0.26				
	mound	173	73.69	East	60	circ	26	22	100	0.05	0.05	gray	0	no	stump
	log		71.65	East	18	rect	1627	38	15	6.18	0.93				
	stump		69.93	West	48	circ	13	10	100	0.01	0.01				
	mound	174	66.35	West	98	circ	93	122	10	0.91	0.09	gray	0	yes	stump
	mound	175	58.06	West	65	rect	96	26	100	0.25	0.25	gray	0	no	log
	mound	176	57.64	West	64	circ	50	38	100	0.15	0.15	gray	0	no	log
	mound	177	52.70	West	83	circ	30	25	100	0.06	0.06	gray	0	no	
	log		50.48	East	29	rect	132	16	100	0.21	0.21				
	mound	178	46.18	West	104	circ	67	63	70	0.33	0.23	gray	0	no	

mound	179	40.36	West	35	oval	104	46	52	0.48	0.25	lt. gray	0	no	
mound	180	55.92	East	87	circ	70	58	50	0.32	0.16	gray	0	no	stump
mound	181	56.06	East	115	circ	85	50	20	0.36	0.07	gray	0	no	
mound	182	54.35	East	26	circ	60	20	100	0.13	0.13	gray	0	no	
mound	183	53.16	West	76	circ	47	100	100	0.42	0.42	gray	0	no	
mound	184	51.87	East	74	circ	38	100	100	0.37	0.37	gray	0	no	
mound	185	49.67	West	58	circ	54	100	100	0.47	0.47	gray	0	no	
mound	187	44.94	East	28	circ	26	100	100	0.31	0.31	gray	0	no	

Table B.5 (Continued)

Mapping						Area						Description			
Transect	Feature	Mound No.	Dist. (m)	Direction	Dist. to high pt. (cm)	Shape	Length (cm)	Width (cm)	Within transect (%)	Area (m2)	Area in transect (m2)	Color	No. of burrows	Burned?	Associated with
F	mound	158	4.20	East	90	circ	20	18	100	0.03	0.03	gray	0	no	-
	mound	159	5.69	East	101	circ	54	57	80	0.24	0.19	lt. gray	1	no	-
	mound	25	8.81	West	35	oval	156	80	90	1.25	1.12	gray	0	yes	-
	stump		9.52	East	100	circ	8	8	50	0.01	0.00	-	-	-	-
	mound	160	11.76	East	59	circ	84	74	90	0.49	0.44	gray	0	no	Vismia
	mound	161	21.96	West	42	oval	32	20	100	0.06	0.06	gray	0	no	-
	log		24.05	East	94	rect	109	9	50	0.10	0.05	-	-	-	-
	log		24.64	East	18	rect	121	9	100	0.11	0.11	-	-	-	-
	log		24.81	West	19	rect	107	16	100	0.17	0.17	-	-	-	-
	log		25.84	East	74	rect	194	13	95	0.25	0.24	-	-	-	-
	log		25.59	East	50	rect	90	8	100	0.07	0.07	-	-	-	-
	mound	162	26.22	East	77	oval	76	59	95	0.45	0.43	gray	0	no	-

mound	163	47.40	West	13	oval	66	47	100	0.31	0.31	mixed	1	no	
mound	A50	57.62	West	87	oval	80	42	95	0.34	0.32	dark	0	yes	-
mound	164	58.5	West	13	oval	46	29	100	0.13	0.13	dark	0	yes	log
log		58.48	West	5	rect	60	13	100	0.08	0.08	-	-	-	-
log&mound	165	59.62	West	70	rect	80	8	100	0.06	0.06	gray	0	no	log
mound	166	61.69	East	108	circ	32	17	50	0.05	0.02	gray	0	no	Vismia
mound	167	61.71	West	64	oval	68	50	100.00	0.34	0.34	Intri-cate	0	no	Vismia
mound	51	66.45	West	113	rect	246	70	70.00	1.72	1.21	gray	0	no	-

Table B.5 (Continued)

Mapping						Area						Description			
Transect	Feature	Mound No.	Dist. (m)	Direction	Dist. to high pt. (cm)	Shape	Length (cm)	Width (cm)	Within transect (%)	Area (m2)	Area in transect (m2)	Color	No. of burrows	Burned?	Associated with
	stump		66.28	West	13	circ	16	10	100.00	0.01	0.01	-	-	-	-
	mound	168	68.52	East	120	circ	62	58	60.00	0.28	0.17	gray	1	no	
	mound	52	71.88	East	96	oval	132	94	90.00	1.24	1.12	gray	1	no	
	stump		72.13	East	97	circ	18	14	50.00	0.02	0.01	-	-	-	-
	mound	170	73.46	West	46	rect	70	40	100.00	0.28	0.28	gray	0	no	-
	mound	171	77.94	West	102	circ	35	27	60.00	0.08	0.05	gray	1	no	
G	mound	A101	4.45	West	84	oval	32	16	100	0.01	0.01		0	no	
	log		6.64	East	91	y cylnd	98	42	100	0.41	0.41		0	yes	
	log		8.90	West	100	cylnd	195	43	100	0.84	0.84		0	yes	
	mound	A102	13.88	West	28	circ	105	93	100	0.77	0.77		0	no	
	mound	A103	15.71	East	50	linea	190	45	100	0.86	0.86		0	no	
	log		17.64	East	100	cylnd	26	29	100	0.08	0.08		0	yes	

log		20.47	West	100	rect	33	8	100	0.03	0.03		0	yes
mound	A104	22.09	East	176	circ	154	122	5	1.50	0.07		7	yes
log		24.79	East	83	rect	40	8	100	0.03	0.03		0	yes
mound	A105	27.86	East	106	circ	85	66	50	0.45	0.22		1	no
stump		30.15	East	73	circ	13	10	100	0.01	0.01		0	no
mound	A106	30.40	East	81	circ	22	22	100	0.04	0.04		0	no
mound	A107	32.02	East	10	circ	100	103	100	0.81	0.81		0	no
stump		36.46	West	77	circ	15	8	100	0.01	0.01		0	yes
mound	A108	36.03	East	60	circ	220	158	90	2.81	2.52		3	no

Table B.5 (Continued)

Mapping						Area						Description			
Transect	Feature	Mound No.	Dist. (m)	Direction	Dist. to high pt. (cm)	Shape	Length (cm)	Width (cm)	Within transect (%)	Area (m2)	Area in transect (m2)	Color	No. of burrows	Burned?	Associated with
	mound	A109	37.56	West	90	circ	100	92	80	0.72	0.58		0	no	
	mound	A110	38.29	East	77	squr	77	90	75	0.69	0.52		0	no	
	mound	A111	39.50	West	19	rect	41	22	100	0.09	0.09		0	no	
	mound	A112	42.38	East	9	line	183	42	50	0.77	0.38		0	yes	
	mound	A113	47.52	West	86	circ	160	190	80	2.41	1.92		0	yes	
	mound	A114	50.10	East	32	oval	130	20	95	0.26	0.25		0		
	mound	A115	60.16	West	87	circ	70	68	70	0.37	0.26		0	no	
	mound	A116	61.63	East	10	line	386	40	65	1.54	1.00		0	no	
	mound	A117	62.71	East	163	circ	150	107	5	1.30	0.06		3	no	
	mound	A118	63.52	East	10	oval	92	60	100	0.14	0.14		1	yes	
	stump		63.52	East	10	circ	15	9	100	0.01	0.01		0	yes	
	mound	A119	64.88	East	43	oval	47	33	100	0.16	0.16		0	no	

stump		64.88	East	43	circ	10	8	100	0.01	0.01		0	no
mound	A120	66.91	West	63	trng	121	87	97	0.53	0.51		0	no
mound	A121	69.52	West	5	oval	107	100	100	1.07	1.07		0	no
mound	A122	70.86	West	113	rect	95	60	15	0.57	0.09		0	no
mound	A123	70.96	East	69	circ	84	80	100	0.53	0.53		0	no
stump		70.77	East	70	circ	8	8	100	0.01	0.01		0	no
mound	A97	71.07	West	166	circ	120	110	5	1.04	0.05		1	yes
mound	A124	72.36	East	20	oval	100	74	100	0.74	0.74		0	no
stump		76.87	West	42	circ	9	10	100	0.01	0.01		0	no

Table B.5 (Continued)

Mapping						Area						Description			
Transect	Feature	Mound No.	Dist. (m)	Direction	Dist. to high pt. (cm)	Shape	Length (cm)	Width (cm)	Within transect (%)	Area (m2)	Area in transect (m2)	Color	No. of burrows	Burned?	Associated with
	mound	A125	79.20	West	11	circ	125	116	100	1.14	1.14		0	no	
H	mound	195	5.73	West	78	oval	108	50	90	0.54	0.49				
	stump		5.19	West	87	circ	21	20	100	0.03	0.03			yes	
	log		8.22	East	82	trng	36	24	100	0.04	0.04			yes	
	stump		9.11	West	40	circ	16	15	100	0.02	0.02			yes	
			14.73	West	26	oval	267	170	95	4.54	4.31				
			16.00		0	circ	69	70	100	0.38	0.38				
			16.94	West	71	oval	90	78	80	0.70	0.56				
	log		18.36	East	49	cyln	80	27	100	0.22	0.22			yes	
	log		19.09	East	59	cyln	55	22	100	0.12	0.12			yes	
	log		19.66	East	91	cyln	152	26	100	0.40	0.40			yes	
	log		19.62	East	96	cyln	44	21	100	0.09	0.09			yes	

log		20.28	East	49	cyln	77	39	100	0.30	0.30		yes
log		20.90	East	101	cyln	167	25	95	0.42	0.40		yes
log		23.60	East	30	cyln	104	16	100	0.17	0.17		yes
log		24.17	West	81	cyln	99	18	100	0.18	0.18		yes
mound	196	23.30	West	146	circ	132	112	10	1.17	0.12		yes
mound	197	25.84	East	70	oval	130	100	60	1.30	0.78		n
log		28.71	East	85	cyln	233	20	100	0.47	0.47		yes
mound	198	30.08	West	163	circ	433	300	10	10.55	1.05	1	n
stump			West	92	circ	22	14		0.03	0.00		

Table B.5 (Continued)

Mapping						Area						Description			
Transect	Feature	Mound No.	Dist. (m)	Direction	Dist. To high pt. (cm)	Shape	Length (cm)	Width (cm)	Within transect (%)	Area (m2)	Area in transect (m2)	Color	No. of burrows	Burned?	Associated with
	stump		34.95	West	93	sqre	14	15	90	0.02	0.02		0	no	
	stump		37.50	East	106	circ	17	14	50	0.02	0.01		3	yes	
	stump		46.87	East	39	circ	16	21	100	0.03	0.03		-	yes	
	mound	187	46.87	East	39	sqre	46	40	100	0.18	0.18		1	no	
	log		47.83	East	19	circ	330	26	80	2.49	1.99		-	yes	
	mound	188	54.94	East	112	rect	83	66	60	0.55	0.33		1	no	
	stump		57.10	East	20	circ	11	11	100	0.01	0.01		-	yes	
	mound	189	63.43	West	81	circ	80	16	100	0.18	0.18		0	no	
	log		66.29	East	34	rect	218	33	100	0.72	0.72		-	yes	
	log& mound	190	73.03	West	64	rect	209	19	85	0.40	0.34		2	yes	
	log		71.53	East	65	rect	139	17	40	0.24	0.09		-	no	

stump		72.19	East	100	circ	42	43	30	0.14	0.04		-	yes
mound	191	72.19	East	100	circ	84	94	50	0.62	0.31		-	
stump		73.63	West	57	circ	31	25	100	0.06	0.06		-	yes
mound	192	73.63	West	57	circ	95	93	90	0.69	0.62		2	no
log		75.66	West	80	rect	150	20	100	0.30	0.30			yes
log		76.30	West	91	rect	146	15	70	0.22	0.15			yes
mound	193	75.80	West	40	circ	45	25	100	0.10	0.10		1	no
mound	194	78.34	West	49	rect	159	46	50	0.73	0.37		0	no

Table B.5 (Continued)

Mapping						Area						Description			
Transect	Feature	Mound No.	Dist. (m)	Direction	Dist. to high pt. (cm)	Shape	Length (cm)	Width (cm)	Within transect (%)	Area (m2)	Area in transect (m2)	Color	No. of burrows	Burned?	Associated with
I	stump		4.48	West	94	circ	20	18	100	0.03	0.03			yes	
	mound	199	11.23	East	26	circ	80	70	100	0.44	0.44		1	no	
	mound	200	14.73	West	26	circ	100	102	100	0.80	0.80		3	no	
	mound	179	16.53	East	102	circ	117	112	50	1.03	0.51		0	yes	stump
	stump& mound	185	24.54	East	24	circ	29	29	100	0.07	0.07		0	yes	
	mound	181	48.27	West	98	oval	70	32	95	0.22	0.21		0		
	mound	182	54.70	West	82	oval	185	24	50	0.44	0.22		0	no	
	mound	183	53.95	East	106	oval	35	28	50	0.10	0.05		0	yes	stump
	stump			West		circ	18	16	100	0.02	0.02				

Table B6. The percent coverage of termite mounds at the study site.

Transect	Area		Coverage
	mounds (m^2)	total (m^2)	(%)
B	2.4	80	3.0
C	1.5	120	1.2
D	1.9	120	1.6
E	2.4	120	2.0
F	3.4	160	2.1
G	14.8	160	9.3
H	4.9	160	3.0
I	2.3	120	1.9
Total	33.6	1040.0	3.2

Table B7. The density of termite mounds per hectare at the study site.

Transect	Mounds (no.)	Area (m^2)	Mound density (no. ha^{-1})
B	8.2	80	1025
C	5.3	120	442
D	9.4	120	783
E	12.8	120	1063
F	10.0	160	625
G	19.8	160	1239
H	8.1	160	503
I	5.5	120	454
Total	79.1	1040	761

Table B8. Percent coverage and density of termite mounds in the literature

Location	Region	Ecosystem	Species	Surface area (%)	Mound density (ha^{-1})	Reference
Australia	Australia		*Drepanotermes perniger* *Drepanotermes rubiceps*	20		(Watson & Gay 1970)
Australia	Australia		*Amitermes* spp.	1.2		(Lee & Wood 1971a)
Uganda	Africa	various	*Macrotermes subhyalinus* *Macrotermes bellicosus*		1 – 4	(Pomeroy 1977)
Cameroon	Africa	agriculture	*Microtermes* spp.		2	(Hulugalle & Ndi 1993)
Congo	Africa	savanna	*Bellicositermes bellicosus rex*		2.3 – 2.9	(Bouillon & Kidieri 1964)
	Africa		*Macrotermes* spp.		2.5 – 25	(Sands 1965) in (Pomeroy 1977)
	Africa		*Macrotermes* spp.		2 – 3	(Bouillon & Kidieri 1964) in (Pomeroy 1977)
	Africa		*Macrotermes* spp.		3 – 10	(Bouillon 1970)
Cameroon	Africa	secondary forest	*Microtermes* spp.		4	(Hulugalle & Ndi 1993)
Cameroon	Africa	humid forest	*Microtermes* spp.		6	(Hulugalle & Ndi 1993)
Australia	Australia		*Nasutitermes triodiae*		10	(Lee & Wood 1971a) in (Coventry et al. 1988)
Brazil	Neotropical	pasture			11	(Bandeira 1983)
Brazil	Neotropical	pasture	*Cornitermes* cf. *ovatus*	0.12	17	(Bandeira 1983)
Australia	Australia	mixed heath	*Drepanotermes tamminensis* *Amitermes obeuntis*	0.004	20	(De Bruyn & Conacher 1995)

Table B.8 (Continued)

Location	Region	Ecosystem	Species	Surface area	Mound density	Reference
Australia	Africa	savanna	*Trinervitermes trinervius* *Trinervitermes occidentalis* *Bellicositermes natalensis* *Odontotermes pauperans* *Amitermes evuncifer*		20 - 25	(Bodot 1967)
Brazil	Neotropical	pasture			"dozens"	(Rezende et al. 1999)
Brazil	Neotropical	primary forest	*Anoplotermes banksi* *Cornitermes* cf. *ovatus* *Cornitermes* cf. *weberi* *Nasutitermes minimus* *Nasutitermes* sp. J *Rotunditermes bragantinus*		26	(Bandeira 1983)
Ivory Coast	Africa	gallery forest	*Macrotermes bellicosus*		< 30	(Korb & Linsenmair 2001)
Senegal	Africa		*Trinervitermes* spp. *Macrotermes* spp.		27 – 63	(Roy-Nöel 1978)
Central African Republic	Africa	savanna	*Bellicositermes bellicosus rex* *Bellicositermes natalensis*	73	40	(Boyer 1969)
Brazil	Neotropical	rain forest			64	(Bandeira 1978) in (Martius et al. 1996)
Australia	Australia	open woodland	*Drepanotermes tamminensis* *Amitermes obeuntis*	0.003	70	(De Bruyn & Conacher 1995)
Ghana	Africa	northern guinea savanna	*Trinervitermes geminatus* *Trinervitermes oeconomus* *Trinervitermes occidentalis* *Cubitermes curtatus* *Macrotermes bellicosus*		70 ± 9	(Benzie 1986)

Table B.8 (Continued)

Location	Region	Ecosystem	Species	Surface area	Mound density	Reference
Ghana	Africa	grassland	*Cubitermes curtatus* *Trinervitermes geminatus* *Trinervitermes oeconomus* *Trinervitermes togoensis*		89 ± 16	(Benzie 1986)
Ivory Coast	Africa	gallery forest	*Macrotermes bellicosus*		< 100	(Korb & Linsenmair 2001)
Nigeria	Africa	secondary forest	*Nasutitermes* spp.	0.07[1]	112	(Asawalam et al. 1999)
	Africa	Detarium woodland	*Trinervitermes geminatus* *Cubitermes curtatus* *Trinervitermes occidentalis* *Trinervitermes togoensis* *Fulleritermes tenebricus* *Trinervitermes trinervius*		118 ± 13	(Benzie 1986)
Cameroon	Africa	rain forest	*Cubitermes fungifaber* *Cubitermes banksi*		124.5 ± 13.6	(Dejean et al. 1996)
Brazil	Neotropical	pasture			152	(Bandeira 1978) in (Martius et al. 1996)
Australia	Australia	open forest or woddland	various species	0.09 – 1.35[2]	105 – 287	(Spain et al. 1986)

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[1] Calculated from basal circumference and mound density data given in (Asawalam et al. 1999).

[2] Calculated from mound basal area and mound density data in (Spain et al. 1986).

Table B.8 (Continued)

Location	Region	Ecosystem	Species	Surface area	Mound density	Reference
Ivory Coast	Africa	gallery forest	*Macrotermes bellicosus*		< 100	(Korb & Linsenmair 2001)
Nigeria	Africa	secondary forest	*Nasutitermes* spp.	0.07[3]	112	(Asawalam et al. 1999)
	Africa	Detarium woodland	*Trinervitermes geminatus* *Cubitermes curtatus* *Trinervitermes occidentalis* *Trinervitermes togoensis* *Fulleritermes tenebricus* *Trinervitermes trinervius*		118 ± 13	(Benzie 1986)
Cameroon	Africa	rain forest	*Cubitermes fungifaber* *Cubitermes banksi*		124.5 ± 13.6	(Dejean et al. 1996)
Brazil	Neotropical	pasture			152	(Bandeira 1978) in (Martius et al. 1996)
Australia	Australia	open forest or woodland	various species	0.09 – 1.35[4]	105 – 287	(Spain et al. 1986)
Nigeria	Africa	northern Guinea savanna	*Trinervitermes* spp.		109 – 531	(Sands 1965)
Australia	Australia		*Amitermes vitiosus*	0.6	173	(Holt & Coventry 1982) in (Coventry et al. 1988)

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[3] Calculated from basal circumference and mound density data given in (Asawalam et al. 1999).

[4] Calculated from mound basal area and mound density data in (Spain et al. 1986).

Table B.8 (Continued)

Location	Region	Ecosystem	Species	Surface area	Mound density	Reference
Australia	Australia		*Amitermes laurensis* *Nasutitermes longipennis* & others	0.8	230	(Okello-Oloya et al. 1985) in (Coventry et al. 1988)
Malaysia	Asia	rain forest	*Macrotermes carbonarius* *Dicuspiditermes nemorosus* *Homallotermes foraminifer*		231 – 411	(Matsumoto 1976)
Brazil	Neotropical	campina baixa "short-grass savanna"	*Nasutitermes minimus* and *Termes* spp.	0.06	254	(Bandeira 1983)
Ivory Coast	Africa	savanna	*Cubitermes severus* *Cubitermes subcrenulatus* *Trinervitermes trinervius* *Trinervitermes occidentalis* *Bellicositermes natalensis* *Odontotermes pauperans* *Amitermes evuncifer*		260	(Bodot 1967)
Australia	Australia	woodland	*Amitermes vitiosus* *Drepanotermes perniger* *Drepanotermes rubriceps* *Tumulitermes pastinator*	0.9	283	(Coventry et al. 1988)
Brazil	Neotropical	open grassland	*Cornitermes cumulans* *Velocitermes heteropterus* *Armitermes euamignathus* *Syntermes dirus* *Orthognathotermes gibberorum*		323	(Redford 1984)

Table B.8 (Continued)

Location	Region	Ecosystem	Species	Surface area	Mound density	Reference
Malaysia	Asia	undisturbed lowland rain forest	*Homallotermes foraminifer* *Dicuspiditermes nemorosus* B *Dicuspiditermes nemorosus* A *Macrotermes carbonarius*		231 – 390	(Matsumoto 1976)
Brazil	Neotropical	cerrado	*Nasutitermes* sp. *Velocitermes* sp. *Armitermes euamignathus* and others		605[5]	(Domingos & Gontijo 1996)
Australia	Australia		*Amitermes vitiosus* *Drepanotermes* spp. and others	0.9	643	(Okello-Oloya et al. 1985) in (Coventry et al. 1988)
Brazil	Neotropics	secondary forest	Various species	3	760	this study
Nigeria	Africa	derived savanna	*Nasutitermes* spp.	0.17[6]	933	(Akamigbo 1984)
Congo	Africa		*Macrotermes* spp. and associated species	30		(Meyer 1960) in (Wood 1988)
				0.1 – 10		(Lee & Wood 1971b)
Australia	Australia		*Amitermes vitiosus* *Drepanotermes* spp. *Tumulitermes hastilis*	1.7	1108	(Lee & Wood 1971a) in (Coventry et al. 1988)

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[5] Calculated from survey area given (Domingos & Gontijo 1996).

[6] Calculated from basal circumference and mound density data in (Akamigbo 1984).

Figure B9. Histogram of the mound area of the mounds surveyed at the study site.

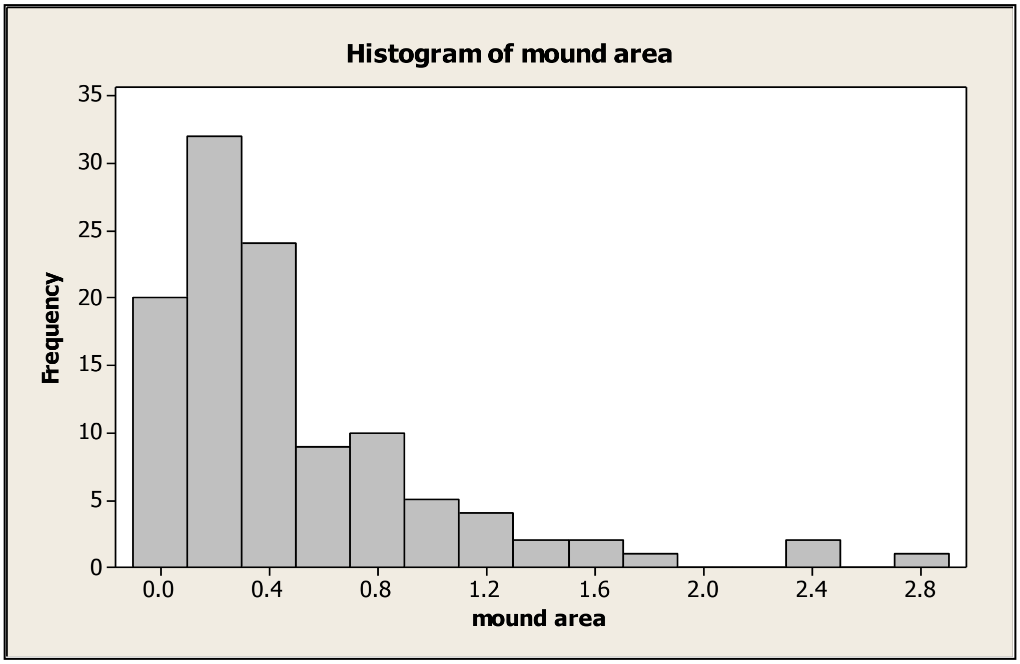

Table B10. Root biomass in termite mounds and control soil in the secondary forest site. Samples were taken in 100-cm3 cylinders. Roots were identified as Vismia spp. or other.

Mound (No.)	Root biomass (g/cm3)		Plant genus	
	Termite mound	Control soil	Termite mound	Control soil
A6	0.0015	0.0020	*Vismia*	*Vismia*
A25	0.0002	0.0023	other	*Vismia*
A69	0.0009	0.0023	*Vismia*	*Vismia*
A105	0.0006	0.0023	*Vismia*	*Vismia*
A108	0.0004	0.0008	other	other
A116	0.0002	0.0008	*Vismia*	*Vismia*
A125	0.0053	0.0035	*Vismia*	*Vismia*
A134	0.0024	0.0028	*Vismia*	*Vismia*
A136	0.0041	0.0043	*Vismia*	*Vismia*
A138	0.0017	0.0013	*Vismia*	*Vismia*
A140	0.0012	0.0032	*Vismia*	*Vismia*
A141	0.0029	0.0016	*Vismia*	*Vismia*

A146	0.0012	0.0011	*Vismia*	*Vismia*
A147	0.0021	0.0013	*Vismia*	*Vismia*
A156	0.0011	0.0079	other	*Vismia*
A159	0.0029	0.0034	*Vismia*	other
A168	0.0028	0.0107	*Vismia*	*Vismia*
A169	0.0017	0.0058	*Vismia*	*Vismia*
A170	0.0032	0.0068	*Vismia*	*Vismia*

Table B11. Number of seeds germinated from the soil seed bank in termite mound and control soil (5 samples, 2 blocks, 11 dates)

Category	Mound	Block	Date										
			6-Mar-2002	8-Mar-2002	11-Mar-2002	13-Mar-2002	18-Mar-2002	21-Mar-2002	25-Mar-2002	28-Mar-2002	1-Apr-2002	8-Apr-2002	15-Apr-2002
Termite mound	A13	1	0	0	0	0	0	0	0	0	0	0	0
		3	0	0	0	0	0	0	0	0	0	0	0
	A174	1	4	3	0	0	0	0	7	12	12	13	13
		3	0	0	1	1	1	1	1	2	2	2	3
	A5_	1	0	0	0	1	1	1	3	3	4	3	5
		3	3	4	0	2	3	5	6	10	10	12	12
	A54	1	0	0	0	0	0	0	0	0	0	0	0
		3	1	2	4	8	8	9	9	11	11	11	10
	A6	1	0	0	0	1	0	0	0	0	0	0	0
		3	0	0	0	2	2	2	0	1	1	4	4
Total			8	9	5	15	15	18	26	39	40	45	47
Control soil	A13	1	1	1	0		1	3	5	5	3	5	5
		3	1	1	1	0	1	3	3	2	3	3	4
	A174	1	18	12	8	24	35	36	36	36	35	38	38
		3	13	25	23	34	37	45	45	49	51	52	52
	A5_	1	5	6	7	7	12	12	12	12	12	12	12
		3	8	7	12	9	10	10	10	11	11	11	11
	A54	1	11	1	21	30	36	49	48	48	45	49	47

		3	4	17	29	28	33	34	35	36	36	37	37
	A6	1	2	2	0		0	0	0	0	0	0	1
		3	8	9	3	5	7	8	8	8	8	8	8
Total			71	81	104	137	172	200	202	207	204	215	215

Figure B12. Results from a pilot study of the effects of termite mound texture on seedling survivorship (not discussed in chapter).

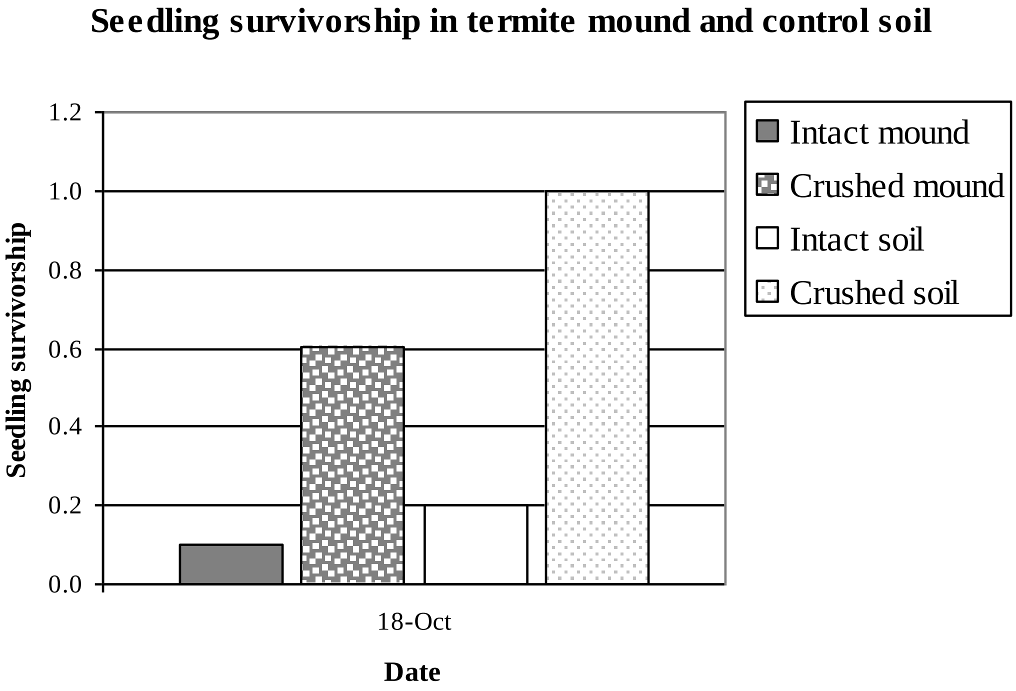

Figure B13. Results from a pilot study of the effects of termite mound texture on seedling germination (not discussed in chapter).

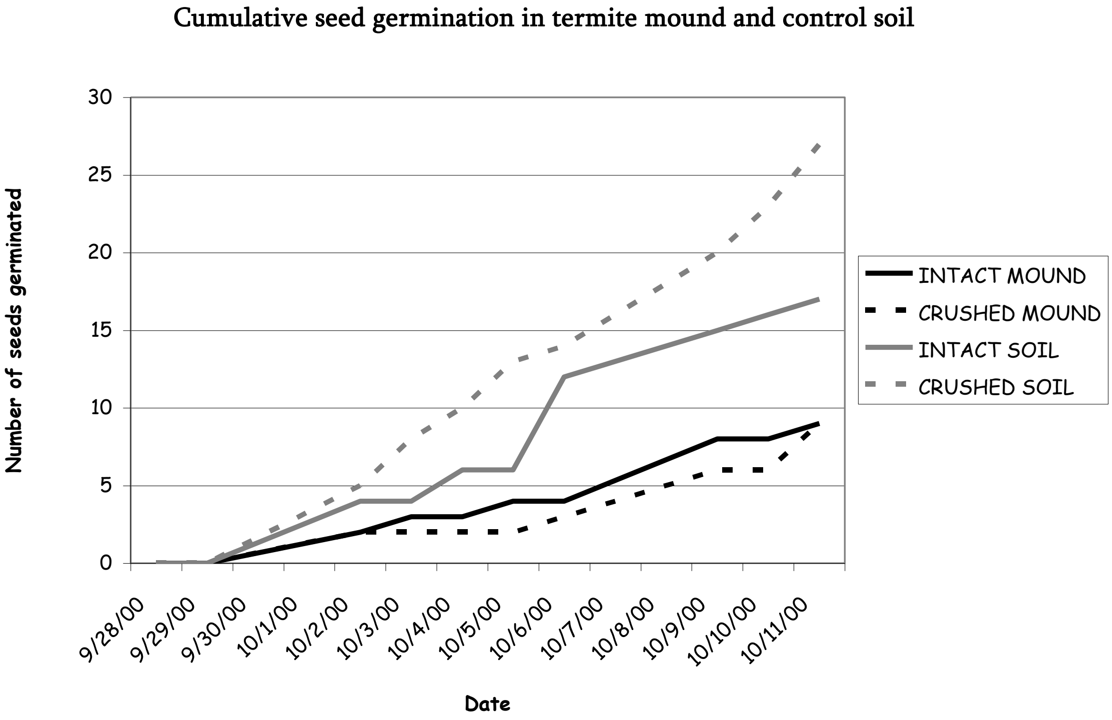

Figure B14. Photo showing contrast in germination rates between termite mound (left) and control soil (right).

18-Oct

Date

Table B15. Emergence velocity indices of the seeds in the factorial germination experiment.

Rep	Treatment				Seed						Mean
	Location	Texture	Autoclaved	Amended	1	2	3	4	5	6	
1	termite mound	intact	yes	yes	0.25	0.25	0.25	0.25	0.25	0.25	0.25
				no	0.25	0.11	0.11	0.25	0.25	0.25	0.20
			no	yes	0.00	0.17	0.00	0.11	0.14	0.00	0.07
				no	0.20	0.17	0.20	0.20	0.20	0.17	0.19
		crushed	yes	yes	0.50	0.50	0.50	0.20	0.50	0.50	0.45
				no	0.25	0.50	0.50	0.50	0.50	0.50	0.46
			no	yes	1.00	1.00	1.00	1.00	1.00	1.00	1.00
				no	0.33	0.50	0.50	0.50	0.50	0.33	0.44
	control soil	intact	yes	yes	0.14	0.17	0.00	0.00	0.14	0.14	0.10
				no	0.00	0.25	0.25	0.25	0.25	0.25	0.21
			no	yes	0.00	0.11	0.00	0.00	0.14	0.17	0.07

				no	0.11	0.14	0.00	0.00	0.14	0.14	0.09
		crushed	yes	yes	0.33	0.33	0.33	0.33	0.33	0.33	0.33
				no	0.50	0.50	0.50	0.50	0.50	0.33	0.47
			no	yes	0.50	0.50	0.50	0.33	0.33	0.33	0.42
				no	0.50	1.00	1.00	1.00	0.25	0.50	0.71
2	termite mound	intact	yes	yes	0.14	0.17	0.00	0.00	0.00	0.00	0.05
				no	0.20	0.25	0.25	0.25	0.00	0.20	0.19

Table B15 (Continued)

Rep	Treatment				Seed						Mean
	Location	Texture	Autoclaved	Amended	1	2	3	4	5	6	
			no	yes	0.20	0.17	0.20	0.20	0.17	0.20	0.19
				no	0.00	0.00	0.17	0.17	0.17	0.00	0.08
		crushed	yes	yes	1.00	0.50	1.00	0.50	0.50	0.50	0.67
				no	0.25	0.50	0.33	0.50	0.33	0.50	0.40
			no	yes	0.50	0.50	0.50	0.50	0.50	0.50	0.50
				no	0.50	0.50	0.50	0.50	0.50	0.20	0.45
	control soil	intact	yes	yes	0.25	0.25	0.25	0.14	0.14	0.25	0.21
				no	0.25	0.20	0.33	0.25	0.17	0.00	0.20
			no	yes	0.25	0.25	0.25	0.25	0.25	0.25	0.25
				no	0.14	0.11	0.11	0.00	0.00	0.00	0.06
		crushed	yes	yes	1.00	0.50	1.00	1.00	0.50	1.00	0.83
				no	0.00	0.25	0.25	0.25	0.25	0.25	0.21
			no	yes	0.25	0.33	0.33	0.33	0.33	0.50	0.35
				no	0.50	0.50	0.50	0.50	0.33	0.50	0.47

3	termite mound	intact	yes	yes	0.25	0.33	0.33	0.00	0.25	0.25	0.24
				no	0.00	0.11	0.00	0.00	0.00	0.00	0.02
			no	yes	0.25	0.25	0.00	0.33	0.33	0.25	0.24
				no	0.17	0.25	0.33	0.25	0.25	0.25	0.25
		crushed	yes	yes	1.00	1.00	1.00	1.00	1.00	1.00	1.00
				no	1.00	1.00	1.00	1.00	1.00	1.00	1.00
			no	yes	0.50	0.00	0.20	0.50	0.50	0.50	0.37
				no	0.25	0.25	0.25	0.17	0.25	0.25	0.24

Table B15 (Continued)

Rep	Treatment				Seed						Mean
	Location	Texture	Autoclaved	Amended	1	2	3	4	5	6	
	control soil	intact	yes	yes	0.20	0.25	0.20	0.20	0.17	0.25	0.21
				no	0.33	0.33	0.33	0.33	0.33	0.33	0.33
			no	yes	0.33	0.33	0.33	0.33	0.25	0.20	0.30
				no	0.17	0.20	0.17	0.17	0.20	0.20	0.18
		crushed	yes	yes	0.33	0.33	0.33	0.33	0.33	0.33	0.33
				no	0.25	0.33	0.33	0.33	0.50	0.33	0.35
			no	yes	0.33	0.50	0.50	0.50	0.50	0.33	0.44
				no	1.00	1.00	1.00	1.00	1.00	1.00	1.00
4	termite mound	intact	yes	yes	0.00	0.13	0.17	0.17	0.14	0.00	0.10
				no	0.25	0.00	0.25	0.13	0.00	0.00	0.10
			no	yes	0.13	0.25	0.33	0.25	0.33	0.00	0.22
				no	0.33	0.25	0.33	0.25	0.00	0.25	0.24
		crushed	yes	yes	0.50	0.50	0.50	0.50	0.50	0.50	0.50
				no	1.00	0.50	0.50	0.50	0.50	1.00	0.67

		no	yes	1.00	1.00	1.00	1.00	1.00	0.50	0.92
			no	0.50	1.00	0.00	1.00	0.50	0.50	0.58
control soil	intact	yes	yes	0.14	0.25	0.25	0.14	0.14	0.25	0.20
			no	0.17	0.25	0.17	0.25	0.17	0.25	0.21
		no	yes	0.13	0.13	0.13	0.25	0.13	0.13	0.15
			no	0.13	0.13	0.13	0.13	0.00	0.13	0.10
	crushed	yes	yes	0.50	0.33	0.33	0.33	0.33	0.25	0.35
			no	0.50	0.50	0.50	0.50	0.50	0.50	0.50

Table B15 (Continued)

Rep	Treatment				Seed						Mean
	Location	Texture	Autoclaved	Amended	1	2	3	4	5	6	
			no	yes	0.50	0.50	0.50	0.50	0.50	0.33	0.47
				no	1.00	0.50	1.00	0.00	0.50	0.50	0.58
5	termite mound	intact	yes	yes	0.00	0.14	0.25	0.00	0.25	0.14	0.13
				no	0.00	0.00	0.00	0.25	0.00	0.00	0.04
			no	yes	0.00	0.00	0.00	0.00	0.00	0.00	0.00
				no	0.17	0.17	0.17	0.17	0.17	0.17	0.17
		crushed	yes	yes	0.50	0.50	0.50	0.50	0.00	0.50	0.42
				no	0.50	1.00	1.00	1.00	1.00	1.00	0.92
			no	yes	0.33	0.33	0.33	0.33	0.50	0.33	0.36
				no	0.50	0.50	0.50	0.50	0.50	0.50	0.50
	control soil	intact	yes	yes	0.25	0.17	0.17	0.25	0.25	0.17	0.21
				no	0.17	0.17	0.00	0.17	0.17	0.17	0.14
			no	yes	0.17	0.00	0.17	0.25	0.17	0.17	0.15

		no	0.17	0.17	0.00	0.00	0.14	0.00	0.08
crushed	yes	yes	0.14	0.33	0.50	0.33	0.33	0.33	0.33
		no	0.20	0.00	0.25	0.50	0.50	0.50	0.33
	no	yes	0.50	0.50	0.50	0.50	0.50	0.50	0.50
		no	0.50	0.33	0.33	0.33	0.25	0.25	0.33

Table B16. Height of the seedlings in the factorial germination experiment at the end of the experiment.

Rep	Treatment				Seed						Mean
	Location	Texture	Autoclaved	Amended	1	2	3	4	5	6	
1	termite mound	intact	yes	yes	2.9	0.0	2.7	2.0	2.7	2.9	2.2
				no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
			no	yes	0.0	0.0	0.0	0.0	0.0	0.0	0.0
				no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		crushed	yes	yes	0.0	5.5	3.4	0.0	4.9	4.4	3.0
				no	0.0	2.4	2.9	4.3	3.2	4.2	2.8
			no	yes	0.0	4.4	4.0	4.5	4.0	4.3	3.5
				no	4.3	3.6	2.8	4.1	4.4	5.1	4.1
	control soil	intact	yes	yes	0.0	0.0	0.0	0.0	3.0	0.0	0.5
				no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
			no	yes	0.0	0.0	0.0	0.0	0.0	0.0	0.0

		no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
crushed	yes	yes	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	no	yes	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		no	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table B16 (Continued)

Rep	Treatment				Seed						Mean
	Location	Texture	Autoclaved	Amended	1	2	3	4	5	6	
2	termite mound	intact	yes	yes	0.0	0.0	0.0	0.0	0.0	0.0	0.0
				no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
			no	yes	2.6	0.0	0.0	1.4	0.0	2.4	1.1
				no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		crushed	yes	yes	0.0	6.2	5.6	5.7	5.6	5.7	4.8
				no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
			no	yes	4.1	5.0	4.3	3.3	4.8	5.6	4.5
				no	4.1	0.0	0.0	0.0	4.2	0.0	1.4
	control soil	intact	yes	yes	0.0	0.0	0.0	0.0	0.0	0.0	0.0
				no	0.0	0.0	0.0	1.5	0.0	0.0	0.3
			no	yes	2.7	2.7	0.0	0.0	0.0	3.4	1.5
				no	0.0	0.0	0.0	0.0	0.0	0.0	0.0

		crushed	yes	yes	0.0	5.0	3.5	4.2	5.6	5.2	3.9
				no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
			no	yes	0.0	4.3	2.9	3.6	4.0	3.5	3.1
				no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3	termite mound	intact	yes	yes	0.0	0.0	0.0	0.0	0.0	0.0	0.0
				no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
			no	yes	1.2	2.3	0.0	1.9	1.3	1.6	1.4
				no	0.0	2.7	0.0	0.0	0.0	2.3	0.8

Table B16 (Continued)

Rep	Treatment				Seed						Mean
	Location	Texture	Autoclaved	Amended	1	2	3	4	5	6	
		crushed	yes	yes	4.9	0.0	4.4	5.6	5.2	4.6	4.1
				no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
			no	yes	4.3	0.0	5.2	5.0	5.3	3.6	3.9
				no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	control soil	intact	yes	yes	0.0	0.0	0.0	2.8	0.0	0.0	0.5
				no	0.0	0.0	2.4	0.0	0.0	0.0	0.4
			no	yes	4.7	0.0	3.4	2.5	3.5	0.0	2.4
				no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		crushed	yes	yes	0.0	4.0	3.8	3.7	4.0	4.0	3.3
				no	0.0	0.0	0.0	0.0	3.4	0.0	0.6
			no	yes	4.2	3.7	3.7	0.0	4.3	0.0	2.7
				no	4.2	4.8	4.0	3.6	4.2	4.4	4.2

4	termite mound	intact	yes	yes	0.0	0.0	0.0	0.0	0.0	0.0	0.0
				no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
			no	yes	0.0	3.0	3.0	0.0	2.9	0.0	1.5
				no	0.0	2.5	0.0	0.0	0.0	2.9	0.9
		crushed	yes	yes	0.0	5.5	5.8	5.2	4.9	5.6	4.5
				no	5.2	4.6	3.9	4.5	3.2	4.6	4.3
			no	yes	0.0	0.0	0.0	4.5	0.0	0.0	0.8
				no	5.7	4.3	0.0	2.9	0.0	4.6	2.9

Table B16 (Continued)

Rep	Treatment				Seed						Mean
	Location	Texture	Autoclaved	Amended	1	2	3	4	5	6	
	control soil	intact	yes	yes	0.0	0.0	0.0	0.0	0.0	3.1	0.5
				no	0.0	0.0	3.2	1.2	0.0	2.5	1.2
			no	yes	0.0	0.0	0.0	0.0	0.0	0.0	0.0
				no	0.0	0.0	0.0	0.0	0.0	2.0	0.3
		crushed	yes	yes	4.5	3.5	4.1	3.6	4.0	4.1	4.0
				no	3.9	2.5	3.7	4.3	4.9	4.5	4.0
			no	yes	3.8	3.4	3.6	3.7	4.3	4.4	3.9
				no	4.2	0.0	0.0	0.0	4.8	4.5	2.3
5	termite mound	intact	yes	yes	0.0	0.0	0.0	0.0	0.0	0.0	0.0
				no	0.0	0.0	1.7	2.5	0.0	2.0	1.0
			no	yes	0.0	0.0	0.0	0.0	0.0	0.0	0.0
				no	0.0	0.0	0.0	0.0	0.0	0.0	0.0

	crushed	yes	yes	4.2	4.9	4.2	5.0	0.0	4.9	3.9
			no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		no	yes	4.3	2.9	0.0	3.2	0.0	0.0	1.7
			no	0.0	0.0	3.8	0.0	0.0	0.0	0.6
control soil	intact	yes	yes	1.7	0.0	1.5	0.0	3.7	1.4	1.4
			no	0.0	1.7	0.0	0.0	0.0	0.0	0.3
		no	yes	0.0	0.0	1.6	2.2	0.0	0.0	0.6
			no	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table B16 (Continued)

Rep	Treatment				Seed						Mean
	Location	Texture	Autoclaved	Amended	1	2	3	4	5	6	
5	termite mound	crushed	yes	yes	4.2	4.9	4.2	5.0	0.0	4.9	3.9
				no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
			no	yes	4.3	2.9	0.0	3.2	0.0	0.0	1.7
				no	0.0	0.0	3.8	0.0	0.0	0.0	0.6
	control soil	intact	yes	yes	1.7	0.0	1.5	0.0	3.7	1.4	1.4
				no	0.0	1.7	0.0	0.0	0.0	0.0	0.3
			no	yes	0.0	0.0	1.6	2.2	0.0	0.0	0.6
				no	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		crushed	yes	yes	0.0	0.0	0.0	0.0	0.0	0.0	0.0
				no	0.0	0.0	0.0	0.0	3.3	0.0	0.6

no	yes	3.2	1.9	4.3	4.2	4.4	3.8	3.6
	no	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table B17. Number of leaves of the seedlings at the end of the factorial germination experiment.

Rep	Treatment				Seed						Mean
	Location	Texture	Autoclaved	Amended	1	2	3	4	5	6	
1	termite mound	intact	yes	yes			2	2			2.0
				no							
			no	yes							
				no			2				2.0
		crushed	yes	yes		3	3		3	3	3.0
				no		2	2	2		2	2.0
			no	yes		3	3	3		3	3.0
				no		2		1	3	3	2.3
	control soil	intact	yes	yes							
				no					2		2.0
			no	yes							

		no							
crushed	yes	yes		2	2	3	3	2	2.4
		no		2	2	2	2	2	2.0
	no	yes	3		1		3	1	2.0
		no	2	2			2	2	2.0

Table B17 (Continued)

Rep	Treatment				Seed						Mean
	Location	Texture	Autoclaved	Amended	1	2	3	4	5	6	
2	termite mound	intact	yes	yes							
				no							
			no	yes				1			1.0
				no							
		crushed	yes	yes		3	3	4	3	3	3.2
				no	2			3	2	2	2.3
			no	yes	3	3	3		4	3	3.2
				no	2		2	2	2		2.0
	control soil	intact	yes	yes							
				no							
			no	yes	2					2	2.0
				no							

crushed	yes	yes	1	3	4	3	3	2.8
		no						
	no	yes	3	3		3	3	3.0
		no	2			2	2	2.0

Table B17 (Continued)

Rep	Treatment				Seed						Mean
	Location	Texture	Autoclaved	Amended	1	2	3	4	5	6	
3	termite mound	intact	yes	yes							
				no							
			no	yes						2	2.0
				no		2					2.0
		crushed	yes	yes	1		3	3	3	1	2.2
				no		2					2.0
			no	yes	2		3	3	3	1	2.4
				no							
	control soil	intact	yes	yes			2	2			2.0
				no							
			no	yes	3				2		2.5
				no							

crushed	yes	yes		2	2	3	3	3	2.6
		no					2		2.0
	no	yes		2	4		3		3.0
		no	3	4	2	2	3	1	2.5

Table B17 (Continued)

Rep	Treatment				Seed						Mean
	Location	Texture	Autoclaved	Amended	1	2	3	4	5	6	
4	termite mound	intact	yes	yes							
				no							
			no	yes		2			2		2.0
				no							
		crushed	yes	yes		3	3	3	3	3	3.0
				no	3	3	2	3	2	3	2.7
			no	yes				3			3.0
				no	3	3		2		3	2.8
	control soil	intact	yes	yes							
				no						2	2.0
			no	yes				2	2		2.0
				no						2	2.0

crushed	yes	yes	3	1	3	3	1	3	2.3
		no	3	2	3	3	3	3	2.8
	no	yes	2	3			3	3	2.8
		no	3		2		2	3	2.5

Table B17 (Continued)

Rep	Treatment				Seed						Mean
	Location	Texture	Autoclaved	Amended	1	2	3	4	5	6	
5	termite mound	intact	yes	yes							
				no			2	2			2.0
			no	yes							0.0
				no							
		crushed	yes	yes	1	3	3	3		3	2.6
				no	2	3			3		2.7
			no	yes	2	2		3			2.3
				no	3		3	2	1	3	2.4
	control soil	intact	yes	yes					2		2.0
				no		2					2.0
			no	yes				2		2	2.0
				no							

crushed	yes	yes		3	3	3	3	2	2.8
		no					2		2.0
	no	yes	3		3	3	3	1	2.6
		no					2	2	2.0

Table B18. Sample calculation of emergence velocity index per experimental unit.

Date	Days elapsed	Cumulative no. of seeds germinated	No. of seeds germinated per day	Ratio
21-Nov-01	1	0	0	0.00
22-Nov-01	2	0	0	0.00
23-Nov-01	3	0	0	0.00
24-Nov-01	4	0	0	0.00
25-Nov-01	5	0	0	0.00
26-Nov-01	6	2	2	0.33
27-Nov-01	7	3	1	0.14
28-Nov-01	8	4	1	0.13
29-Nov-01	9	4	0	0.00
30-Nov-01	10	4	0	0.00

Emergence velocity index (total)	0.60
Number of days to first emergence	6
Percent germination	0.67

Table B19. Soil chemical analyses of termite mound and control soil from secondary forest site. Samples are paired.

Location	pH	mg/dm^3		c.mol$_c$/dm^3				g/Kg			mg/dm^3			
	H_20	P	K	Ca	Mg	Al	H+Al	C	OM	N	Fe	Zn	Mn	Cu
Termite mound	4.21	1.93	24	0.02	0.05	2.2	13	37	63	2.4	318	0.30	0.41	0.26
Control soil	4.24	1.29	18	0.02	0.05	1.5	8	32	56	1.7	226	0.36	1.01	0.25
Termite mound	4.16	1.93	26	0.08	0.06	2.2	13	41	71	2.4	258	0.63	1.68	0.32
Control soil	4.35	1.29	20	0.26	0.10	1.6	10	36	62	2.1	199	0.91	4.40	0.29
Termite mound	4.33	3.22	32	0.07	0.06	2.8	16	55	95	2.6	232	0.89	0.86	0.20
Control soil	4.27	1.93	18	0.04	0.05	1.4	8	27	46	1.7	418	0.47	2.06	0.19
Termite mound	4.21	2.58	34	0.07	0.06	2.4	14	48	82	2.8	276	0.80	2.35	0.15
Control soil	4.44	1.29	20	0.07	0.05	1.5	8	57	98	1.8	242	0.42	1.51	0.19
Termite mound	4.40	1.93	20	0.05	0.04	1.7	10	35	60	2.1	172	0.53	1.07	0.38
Control soil	4.25	1.29	18	0.02	0.05	1.6	8	31	54	2.0	340	0.79	2.27	0.22
Termite mound	4.24	1.93	26	0.05	0.05	2.2	12	38	65	2.3	264	0.40	0.58	0.2
Control soil	4.42	1.29	20	0.06	0.05	1.5	8	55	94	1.8	326	0.39	1.34	0.22

Termite mound	4.23	1.93	24	0.07	0.04	2.7	15	50	86	2.6	288	1.40	0.57	0.19
Control soil	4.13	2.58	16	0.13	0.07	1.7	9	32	55	2.0	254	0.76	1.56	0.23
Termite mound	4.21	2.58	24	0.12	0.05	2.8	16	58	99	2.6	227	1.54	0.60	0.14
Control soil	4.21	1.93	18	0.11	0.05	1.5	8	30	52	1.9	245	0.86	1.63	0.21
Termite mound	4.23	1.93	20	0.12	0.05	1.9	9	29	50	1.7	215	0.55	1.11	0.22
Control soil	4.62	2.58	16	0.14	0.05	1.4	8	27	46	1.8	190	0.88	2.34	0.14
Termite mound	4.21	1.93	24	0.11	0.05	2.0	11	32	56	2.1	259	0.37	1.04	0.24

Table B19 (Continued)

Location	pH	mg/dm^3		c.mol$_c$/dm^3				g/Kg			mg/dm^3			
	H$_2$0	P	K	Ca	Mg	Al	H+Al	C	OM	N	Fe	Zn	Mn	Cu
Control soil	4.57	1.29	18	0.10	0.05	1.3	7	26	44	1.7	274	0.46	1.33	0.24
Termite mound	4.27	1.93	24	0.20	0.07	2.3	14	60	103	2.9	325	0.84	4.17	0.29
Control soil	4.27	8.37	20	0.29	0.06	1.5	9	33	56	1.9	233	0.53	1.50	0.24
Termite mound	4.40	7.09	32	0.15	0.06	2.0	13	46	79	2.7	226	0.46	0.80	0.24
Control soil	4.22	4.51	20	0.18	0.06	1.7	11	32	55	2.2	304	0.48	1.79	0.30
Termite mound	4.39	3.22	24	0.17	0.07	1.8	11	38	65	2.5	299	0.53	1.54	0.24
Control soil	4.38	1.29	24	0.16	0.07	1.4	8	28	47	2.1	339	0.43	2.22	0.22
Termite mound	4.20	1.93	32	0.06	0.06	2.0	11	37	63	2.3	265	0.43	0.61	0.17
Control soil	4.36	3.87	20	0.17	0.05	1.2	8	24	41	1.8	172	0.46	1.57	0.21
Termite mound	4.21	2.58	26	0.15	0.06	1.9	11	38	66	2.2	248	0.55	2.20	0.26
Control soil	4.35	3.87	18	0.24	0.10	1.4	8	27	47	2.1	306	0.48	1.52	0.14
Termite mound	4.24	5.80	34	0.13	0.06	2.3	14	49	85	2.7	211	1.44	6.29	0.24
Control soil	4.62	6.44	20	0.60	0.24	1.4	9	36	62	2.3	168	1.34	5.32	0.26
Termite mound	4.37	4.51	34	0.38	0.12	1.9	12	36	62	2.6	289	0.97	2.06	0.23

Control soil	4.32	1.93	22	0.16	0.08	1.5	9	31	54	1.8	282	0.66	2.07	0.17
Termite mound	4.47	3.22	34	0.12	0.05	2.4	14	47	81	2.8	223	0.57	2.46	0.20
Control soil	4.34	2.58	22	0.14	0.06	1.5	8	29	50	1.8	249	0.40	1.65	0.33
Termite mound	4.28	3.22	30	0.05	0.04	2.6	14	53	92	2.5	214	0.79	0.52	0.18
Control soil	4.4	7.09	20	0.14	0.05	1.6	10	32	55	1.9	234	0.97	1.90	0.18
Termite mound	4.36	5.80	24	0.07	0.04	2.0	11	37	64	2.3	236	0.54	0.88	0.23
Control soil	4.37	5.80	22	0.14	0.07	1.5	9	27	47	1.9	266	1.01	2.23	0.36
Termite mound	4.20	5.15	36	0.11	0.04	2.0	13	57	99	2.7	256	0.47	1.75	0.14
Control soil	4.42	7.09	24	0.24	0.07	1.8	11	38	65	2.5	166	0.88	6.54	0.14

Table B20. Soil resistance of termite mounds and control soils in the secondary forest site. Penetrometer readings were taking to a depth of 5 cm. The surface area of the cone was 2 cm. The maximum reading of the manometer was 500 kgf.

No.	Treatment	Manometer	Resistance		
		(kgf)	(kgf/cm2)	(kgf/m2)	(Mpa)
A34	termite mound	270	135	1350000	13
		150	75	750000	7
		220	110	1100000	11
		270	135	1350000	13
		310	155	1550000	15
	control soil	50	25	250000	2
		40	20	200000	2
		30	15	150000	1
		70	35	350000	3
		230	115	1150000	11
A1	termite mound	320	160	1600000	16
		320	160	1600000	16
		500	250	2500000	25
		230	115	1150000	11
		500	250	2500000	25
	control soil	120	60	600000	6
		80	40	400000	4
		30	15	150000	1

		50	25	250000	2
		60	30	300000	3
A2	termite mound	290	145	1450000	14
		100	50	500000	5
		240	120	1200000	12
		150	75	750000	7
		270	135	1350000	13

Table B20 (Continued)

No.	Treatment	Manometer	Resistance		
		(kgf)	(kgf/cm2)	(kgf/m2)	(Mpa)
A2	control soil	80	40	400000	4
		60	30	300000	3
		40	20	200000	2
		70	35	350000	3
		100	50	500000	5
A3	termite mound	500	250	2500000	25
		500	250	2500000	25
		500	250	2500000	25
		500	250	2500000	25
		500	250	2500000	25
	control soil	245	123	1225000	12
		210	105	1050000	10
		70	35	350000	3
		125	63	625000	6
		180	90	900000	9
A72	termite mound	200	100	1000000	10
		20	10	100000	1
		180	90	900000	9
		450	225	2250000	22
		90	45	450000	4
	control soil	140	70	700000	7

		215	108	1075000	11
		225	113	1125000	11
		225	113	1125000	11
		220	110	1100000	11
A59	termite mound	220	110	1100000	11
		230	115	1150000	11
		240	120	1200000	12
		290	145	1450000	14
		230	115	1150000	11

Table B20 (Continued)

No.	Treatment	Manometer		Resistance	
		(kgf)	(kgf/cm2)	(kgf/m2)	(Mpa)
A59	control soil	130	65	650000	6
		50	25	250000	2
		30	15	150000	1
		80	40	400000	4
		75	38	375000	4
A4	termite mound	500	250	2500000	25
		230	115	1150000	11
		320	160	1600000	16
		410	205	2050000	20
		210	105	1050000	10
	control soil	120	60	600000	6
		150	75	750000	7
		80	40	400000	4
		60	30	300000	3
		120	60	600000	6
A53	termite mound	500	250	2500000	25
		260	130	1300000	13
		255	128	1275000	13
		345	173	1725000	17
		160	80	800000	8
	control soil	50	25	250000	2
		100	50	500000	5

		40	20	200000	2
		110	55	550000	5
		80	40	400000	4
A5	termite mound	210	105	1050000	10
		210	105	1050000	10
		240	120	1200000	12
		220	110	1100000	11
		230	115	1150000	11
	control soil	30	15	150000	1
		60	30	300000	3

Table B20 (Continued)

No.	Treatment	Manometer	Resistance		
		(kgf)	(kgf/cm2)	(kgf/m2)	(Mpa)
A5		110	55	550000	5
		100	50	500000	5
		110	55	550000	5
A6	termite mound	500	250	2500000	25
		500	250	2500000	25
		500	250	2500000	25
		500	250	2500000	25
		500	250	2500000	25
	control soil	130	65	650000	6
		70	35	350000	3
		90	45	450000	4
		150	75	750000	7
		10	5	50000	0

Table B21. Soil texture of paired samples of termite mound and control soil in the secondary forest site.

Treatment	Sample no.	Sand coarse (%)	Sand fine (%)	Sand total (%)	Silt (%)	Clay (%)
Termite mound	1	4.4	1.5	5.9	14.6	79.5
	2	3.6	1.7	5.3	14.5	80.2
	3	2.8	1.2	3.9	15.0	81.1
	4	5.3	1.9	7.2	15.4	77.5
	5	8.0	2.7	10.7	18.0	71.3
	6	6.5	1.8	8.3	21.0	70.7
	7	6.6	1.8	8.3	23.4	68.3
	8	7.3	1.8	9.1	24.8	66.2
	9	6.7	1.9	8.6	19.3	72.2
	10	7.4	2.0	9.4	20.9	69.7
	11	12.0	1.5	13.5	19.0	67.5
	12	6.2	1.0	7.2	22.7	70.1
	13	6.8	0.7	7.5	22.8	69.7
	14	7.6	3.0	10.7	12.6	76.8
	15	7.7	1.9	9.5	21.2	69.3
	16	9.2	1.4	10.6	20.4	69.0
	17	8.8	2.5	11.4	20.8	67.8
	18	8.2	2.1	10.3	23.1	66.7

	19	8.6	1.8	10.3	21.1	68.6
	20	7.9	2.2	10.1	17.6	72.3
Control soil	1	3.6	1.4	5.1	21.3	73.7
	2	7.4	1.7	9.1	22.1	68.9
	3	5.5	1.8	7.2	19.1	73.7
	4	6.0	1.7	7.7	24.2	68.2
	5	4.9	1.5	6.4	15.4	78.3
	6	5.0	1.7	6.6	13.9	79.5
	7	5.8	1.6	7.4	13.8	78.8
	8	6.0	2.0	8.0	15.2	76.8

Table B21 (Continued)

Treatment	Sample no.	Sand coarse (%)	Sand fine (%)	Sand total (%)	Silt (%)	Clay (%)
Control soil	9	5.4	1.8	7.2	15.4	77.5
	10	5.2	1.4	6.6	18.2	75.2
	11	2.7	1.0	3.7	14.3	82.0
	12	5.6	1.5	7.0	18.3	74.7
	13	5.4	0.8	6.2	13.1	80.7
	14	6.8	1.8	8.6	19.5	71.9
	15	7.6	1.8	9.4	16.9	73.8
	16	7.1	1.8	8.9	19.5	71.7
	17	7.7	1.7	9.4	16.6	74.0
	18	4.3	1.5	5.8	15.5	78.7
	19	4.8	1.7	6.4	16.6	77.0
	20	3.4	1.3	4.6	16.4	79.0

Table B22. Pilot soil hydrophobicity experiment (results not shown in chapter). Values compare the absorption of water by termite mound soil clods with control soils and termite mounds that have undergone burning.

Treatment	Rep.	Original weight (g)	Weight 15 s (g)	Weight 30 s (g)	Water 15 s (g)	Water 30 s (g)	Water absorbed 15 s (g/min)	Water absorbed 30 s (g/min)
Termite mound	1	9.022	9.088	9.155	0.07	0.13	0.26	0.18
	2	12.324	12.404	12.468	0.08	0.14	0.32	0.19
	3	9.899	9.930	9.986	0.03	0.09	0.12	0.12
	4	8.464	8.571	8.628	0.11	0.16	0.43	0.22
	5		8.490	8.540				
	6	11.666	12.159	12.414	0.49	0.75	1.97	1.00
	7	10.334	10.404	10.450	0.07	0.12	0.28	0.15
	8	7.686	7.749	7.779	0.06	0.09	0.25	0.12
	9	11.175	11.217	11.259	0.04	0.08	0.17	0.11
	10	10.174	10.290	10.367	0.12	0.19	0.46	0.26

	11	11.988	12.177	12.334	0.19	0.35	0.76	0.46
	12	9.530	9.623	9.702	0.09	0.17	0.37	0.23
	13	8.770	8.974	9.115	0.20	0.35	0.82	0.46
	14	10.954	11.127	11.261	0.17	0.31	0.69	0.41
	15	8.810	8.961	9.161	0.15	0.35	0.60	0.47
	16	6.251	6.319	6.372	0.07	0.12	0.27	0.16
Mean							0.52	0.30

Table B22 (Continued)

Treatment	Rep.	Original weight (g)	Weight 15 s (g)	Weight 30 s (g)	Water 15 s (g)	Water 30 s (g)	Water absorbed 15 s (g/min)	Water absorbed 30 s (g/min)
Control soil	1	7.544	7.921	8.786	0.38	1.24	1.51	1.66
	2	10.783	10.911	11.349	0.13	0.57	0.51	0.75
	3	6.666	6.797	7.931	0.13	1.27	0.52	1.69
	4	10.868	11.232	12.551	0.36	1.68	1.46	2.24
	5	6.802	7.015	7.112	0.21	0.31	0.85	0.41
	6	8.822	9.453	10.282	0.63	1.46	2.52	1.95
	7	7.787	8.889	9.316	1.10	1.53	4.41	2.04
	8	8.839	9.737	10.320	0.90	1.48	3.59	1.97
	9	10.786	11.405	11.919	0.62	1.13	2.48	1.51
	10	6.405	6.922	7.296	0.52	0.89	2.07	1.19
	11	8.266	8.452	9.400	0.19	1.13	0.74	1.51
	12	9.001	9.329	9.839	0.33	0.84	1.31	1.12

	13	7.276	8.045	8.936	0.77	1.66	3.08	2.21
	14	6.799	7.753	8.158	0.95	1.36	3.82	1.81
	15	9.252	11.417	12.272	2.17	3.02	8.66	4.03
	16	6.829	7.920	8.231	1.09	1.40	4.36	1.87
Mean							2.62	1.75

Table B22 (Continued)

Treatment	Rep.	Original weight (g)	Weight 15 s (g)	Weight 30 s (g)	Water 15 s (g)	Water 30 s (g)	Water absorbed 15 s (g/min)	Water absorbed 30 s (g/min)
Burnt mound	1	6.876	7.689	8.634	0.81	1.76	3.25	2.34
	2	6.135		7.040				
	3	6.463	7.302					
	4	4.877	5.118					
	5	6.641	6.927	7.173	0.29	0.53	1.14	0.71
	6	6.939	7.094	7.321	0.16	0.38	0.62	0.51
	7	8.880	9.322	10.140	0.44	1.26	1.77	1.68
	8	8.053	8.637	9.730	0.58	1.68	2.34	2.24
	9	5.948	6.654	7.390	0.71	1.44	2.82	1.92
	10	8.120	8.649	9.330	0.53	1.21	2.12	1.61
	11	6.267	6.512	7.025	0.24	0.76	0.98	1.01
	12	9.152	10.594	11.354	1.44	2.20	5.77	2.94

	13	8.513	9.163	9.560	0.65	1.05	2.60	1.40
	14	9.231	10.102	10.884	0.87	1.65	3.48	2.20
	15	8.217	8.984	9.834	0.77	1.62	3.07	2.16
	16	5.446	6.380	7.377	0.93	1.93	3.74	2.57
Mean							2.59	1.79

APPENDIX C

Table C.1 Summary

Field treatment	Replicate	Lab treatment	Basal respiration		S.I. respiration		C_{mic}	C_{mic}/C_{org}
			(µl/h/g soil)	(µl/h/g C)	(ul/h/g soil)	(µl/h/g C)	(ug C/g soil)	
Termite	14	normal	0.70	19.5	4.10	114	137	0.0038
Termite	16	normal	1.06	30.1	3.84	109	112	0.0032
Termite	6	normal	1.73	48.3	3.64	102	77	0.0021
Termite	75	normal	0.60	16.7	7.94	222	294	0.0082
Termite	76	normal	1.07	34.4	6.98	225	237	0.0077
Termite	13	normal	0.25	5.1	5.89	121	226	0.0046
Mean			0.90	25.7	5.40	149	180	0.0049
S.E.			0.21	6.2	0.74	23.9	34.5	0.0010
Soil	14	normal	1.24	47.8	5.00	193	151	0.0058
Soil	16	normal	0.98	48.9	4.38	219	137	0.0068
Soil	6	normal	1.06	53.4	3.44	173	95	0.0048

Soil	75	normal	0.56	25.6	8.05	371	300	0.0139
Soil	76	normal	0.50	22.7	9.42	425	357	0.0161
Soil	13	normal	0.21	12.5	3.40	207	128	0.0078
Mean			0.76	35.1	5.61	265	195	0.0092
S.E.			0.16	6.9	1.03	43.2	43.7	0.0019

Table C1 (Continued)

Field Treatment	QR	metabolic quotient (Q)BR	metabolic quotient (Q)SIR	C:N	pH H2O	P	K	Na	Ca	Mg	Al	H+Al	N	C g/kg soil	Fe	Zn	Mn	Cu
Termite	0.17	0.0051	0.030	16.9	4.4	4.8	22	4	0.08	0.04	2.2	12.8	2.1	36.0	200	34	0.53	0.17
Termite	0.28	0.0095	0.034	16.8	4.4	5.5	22	4	0.01	0.04	1.9	10.5	2.1	35.2	233	20	0.43	0.24
Termite	0.48	0.0225	0.047	12.4	4.5	3.4	22	5	0.08	0.04	2.0	11.7	2.9	35.8	256	23	0.68	0.20
Termite	0.08	0.0020	0.027	19.5	4.5	4.8	30	6	0.05	0.05	2.0	11.0	1.8	35.7	375	37	3.19	0.29
Termite	0.15	0.0045	0.029	14.0	4.3	3.4	24	5	0.07	0.05	1.6	9.3	2.2	31.0	155	16	1.05	0.27
Termite	0.04	0.0011	0.026	20.2	4.4	5.5	28	4	0.07	0.05	2.3	13.1	2.4	48.9	253	23	0.66	0.24
Mean	0.20	0.0075	0.032	16.6	4.4	4.6	25	4.7	0.06	0.05	2.0	11.4	2.3	37.1	245	26	1.09	0.24
S.E.	0.06	0.0032	0.003	1.2	0.0	0.38	1.4	0.3	0.01	0.00	0.1	0.6	0.1	2.5	30	3	0.43	0.02
Soil	0.25	0.0082	0.033	14.3	4.5	2.1	20	5	0.12	0.09	1.2	7.4	1.8	25.9	206	30	1.84	0.44
Soil	0.22	0.0072	0.032	14.4	4.3	2.7	14	4	0.05	0.05	1.1	6.3	1.4	20.0	172	24	0.84	0.31
Soil	0.31	0.0111	0.036	13.7	4.3	2.1	14	4	0.16	0.06	1.2	6.6	1.5	19.9	230	4	1.53	0.13

Soil	0.07	0.0018	0.027	7.3	4.3	3.4	14	4	0.02	0.04	1.1	6.9	3.0	21.7	175	29	1.50	0.45
Soil	0.05	0.0014	0.026	9.3	4.4	2.7	24	6	0.02	0.05	1.2	6.9	2.4	22.2	206	24	0.98	1.22
Soil	0.06	0.0016	0.027	12.8	4.4	2.1	14	4	0.20	0.05	0.9	5.4	1.3	16.4	241	34	1.43	0.27
Mean	0.16	0.0052	0.030	12.0	4.4	2.5	17	4.5	0.10	0.06	1.1	6.6	1.9	21.0	205	24	1.35	0.47
S.E.	0.05	0.0017	0.002	1.2	0.0	0.2	1.8	0.3	0.03	0.01	0.0	0.3	0.3	1.3	11	4	0.15	0.16

Table C1 (Continued)

Field treatment	Replicate	Lab treatment	Basal respiration (µl/h/g soil)	Basal respiration (µl/h/g C)	S.I. respiration (ul/h/g soil)	S.I. respiration (µl/h/g C)	C_{mic} (ug C/g soil)	C_{mic}/C_{org}
Termite	14	aggregates	0.64	17.9				
Termite	16	aggregates	0.57	16.1				
Termite	6	aggregates	0.59	16.5				
Termite	75	aggregates	0.79	22.2				
Termite	76	aggregates	1.01	32.6				
Termite	13	aggregates	0.89	18.3				
Average			0.75	20.6				
S.E.			0.07	2.6				
Soil	14	aggregates	0.65	24.9				
Soil	16	aggregates	0.46	22.8				
Soil	6	aggregates	0.79	39.6				
Soil	75	aggregates	0.89	41.2				

Soil	76	aggregates	1.01	45.5
Soil	13	aggregates	0.47	28.5
Average			0.71	33.8
S.E.			0.09	3.9

Table C1 (Continued)

	QR	metabolic	metabolic	C:N	pH	P	K	Na	Ca	Mg	Al	H+Al	N	C	Fe	Zn	Mn	Cu
Field		quotient	quotient		H2O									g/kg soil				
Treatment		(Q)BR	(Q)SIR															
Termite					4.4	4.8	22	4	0.08	0.04	2.2	12.8	2.1	36.0	200	34	0.53	0.17
Termite					4.4	5.5	22	4	0.01	0.04	1.9	10.5	2.1	35.2	233	20	0.43	0.24
Termite					4.5	3.4	22	5	0.08	0.04	2.0	11.7	2.9	35.8	256	23	0.68	0.20
Termite					4.5	4.8	30	6	0.05	0.05	2.0	11.0	1.8	35.7	375	37	3.19	0.29
Termite					4.3	3.4	24	5	0.07	0.05	1.6	9.3	2.2	31.0	155	16	1.05	0.27
Termite					4.4	5.5	28	4	0.07	0.05	2.3	13.1	2.4	48.9	253	23	0.66	0.24
Average					4.4	4.6	25	4.7	0.06	0.05	2.0	11.4	2.3	37.1	245	26	1.09	0.24
S.E.					0.0	0.38	1.4	0.3	0.01	0.00	0.1	0.6	0.1	2.5	30	3	0.43	0.02
Soil					4.5	2.1	20	5	0.12	0.09	1.2	7.4	1.8	25.9	206	30	1.84	0.44
Soil					4.3	2.7	14	4	0.05	0.05	1.1	6.3	1.4	20.0	172	24	0.84	0.31
Soil					4.3	2.1	14	4	0.16	0.06	1.2	6.6	1.5	19.9	230	4	1.53	0.13
Soil					4.3	3.4	14	4	0.02	0.04	1.1	6.9	3.0	21.7	175	29	1.50	0.45

Soil	4.4	2.7	24	6	0.02	0.05	1.2	6.9	2.4	22.2	206	24	0.98	1.22
Soil	4.4	2.1	14	4	0.20	0.05	0.9	5.4	1.3	16.4	241	34	1.43	0.27
Average	4.4	2.5	17	4.5	0.10	0.06	1.1	6.6	1.9	21.0	205	24	1.35	0.47
S.E.	0.0	0.23	1.8	0.3	0.03	0.01	0.0	0.3	0.3	1.3	11	4	0.15	0.16

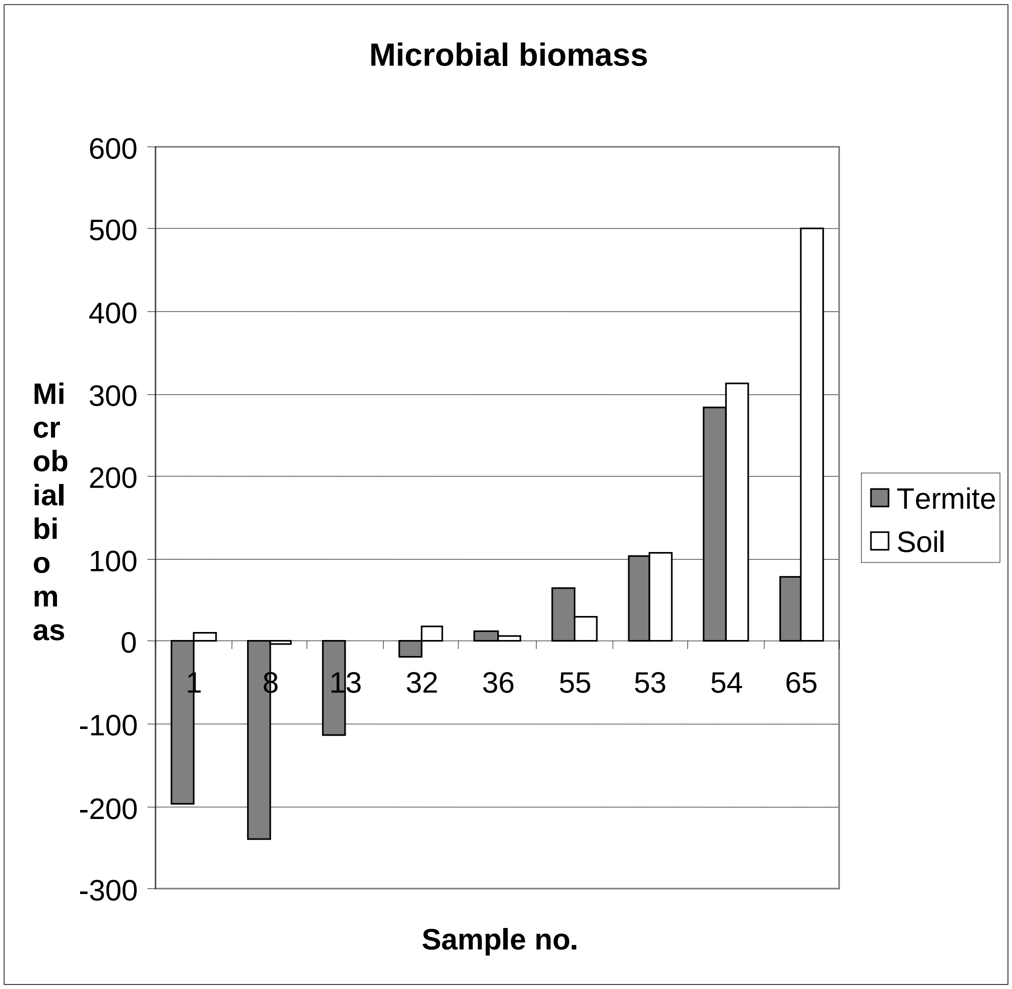

Figure C2. Microbial biomass as measured by fumigation-extraction. Values are plotted over sample order to show that there was an experimental error causing a change in values over time. Each data point is the mean of three replicates. While the data aren't useful statistically because of this drift, they do show qualitatively that the soil has consistently higher microbial biomass C values over termite-mound material, which is in line with our findings using the substrate-induced respiration method.

Table C3. Total and mineral nitrogen contents and rates over the course of the nitrogen mineralization experiment.

Day	Mound	Treatment			N	NO_3^-	NH_4^+	NO_3^-	NH_4^+-N
	No.	Termite	Moisture	Aggregation	(g/kg)	(µg/g soil)	(µg/g soil)	(µg/g N/d)	(µg/g N/d)
0	A6	Mound	Normal	Intact	2.26	3.06	2.50	1.35	3.38
				Broken	2.34	3.88	2.80	1.66	3.50
			Elevated	Intact	2.22	11.64	1.73	5.25	3.26
				Broken	2.35	1.48	2.05	0.63	3.36
		Soil	Normal	Intact	1.97	0.34	4.15	0.17	3.95
				Broken	1.98	0.31	3.83	0.15	3.99
			Elevated	Intact	1.91	0.39	3.19	0.20	3.90
				Broken	1.89	0.39	3.66	0.21	3.97
	A13	Mound	Normal	Intact	2.41	0.29	3.13	0.12	3.72
				Broken	2.41	0.33	2.79	0.14	3.67
			Elevated	Intact	2.40	0.37	3.43	0.16	3.77
				Broken	2.59	0.24	2.70	0.09	3.60

Soil	Normal	Intact	1.89	0.33	2.39	0.18	3.62
		Broken	1.87	0.42	2.48	0.23	3.69
	Elevated	Intact	1.78	0.59	2.21	0.33	3.62
		Broken	1.74	0.51	1.58	0.29	3.44

Table C3 (Continued)

Day	Mound No.	Treatment Termite	Moisture	Aggregation	N (g/kg)	NO_3^- (μg/g soil)	NH_4^+ (μg/g soil)	NO_3^- (μg/g N/d)	NH_4^+-N (μg/g N/d)
	A54	Mound	Normal	Intact	2.27	0.04	2.36	0.02	3.58
				Broken	2.23	0.04	2.40	0.02	3.58
			Elevated	Intact	1.98	0.04	3.10	0.02	3.68
				Broken	2.07	0.08	2.82	0.04	3.70
		Soil	Normal	Intact	1.86	0.64	3.50	0.34	3.85
				Broken	1.91	0.26	4.16	0.14	4.00
			Elevated	Intact	1.86	0.59	3.45	0.32	3.83
				Broken	1.86	0.64	4.14	0.35	3.94
	A5_	Mound	Normal	Intact	2.62	1.14	4.53	0.43	3.77
				Broken	2.56	1.06	4.06	0.41	3.76
			Elevated	Intact	2.52	4.19	3.40	1.66	3.66
				Broken	2.57	3.65	5.43	1.42	3.77
		Soil	Normal	Intact	2.09	1.27	4.39	0.60	4.03

	Broken	2.09	1.39	4.14	0.66	3.98
Elevated	Intact	2.10	1.59	2.28	0.76	3.80
	Broken	2.22	1.34	2.67	0.61	3.81

Table C3 (Continued)

Day	Mound		Treatment		N	NO_3^-	NH_4^+	NO_3^-	NH_4^+-N
	No.	Termite	Moisture	Aggregation	(g/kg)	(µg/g soil)	(µg/g soil)	(µg/g N/d)	(µg/g N/d)
	A174	Mound	Normal	Intact	3.09	0.57	4.02	0.18	3.72
				Broken	3.06	0.32	4.16	0.10	3.68
			Elevated	Intact	2.75	0.04	2.24	0.01	3.45
				Broken	1.98	0.50	6.75	0.25	3.92
		Soil	Normal	Intact	2.27	0.87	2.37	0.38	3.76
				Broken	2.72	1.03	3.84	0.38	3.91
			Elevated	Intact	2.06	1.00	2.80	0.48	3.83
				Broken	2.06	1.12	2.09	0.54	3.66
8	A6	Mound	Normal	Intact	2.26	-0.36	5.92	-0.16	3.52
				Broken	2.34	8.80	6.95	3.76	3.48
			Elevated	Intact	2.22	8.64	7.52	3.90	3.67
				Broken	2.35	7.70	2.49	3.28	3.07
		Soil	Normal	Intact	1.97	8.42	4.31	4.27	3.19

	Broken	1.98	3.45	10.64	1.74	3.56
Elevated	Intact	1.91	11.22	11.45	5.87	3.87
	Broken	1.89	7.24	11.17	3.83	3.81

Table C3 (Continued)

Day	Mound No.	Treatment Termite	Moisture	Aggregation	N (g/kg)	NO_3^- (µg/g soil)	NH_4^+ (µg/g soil)	NO_3^- (µg/g N/d)	NH_4^+-N (µg/g N/d)
	A13	Mound	Normal	Intact	2.41	10.27	6.80	4.26	3.45
				Broken	2.41	12.94	10.36	5.36	3.59
			Elevated	Intact	2.40	8.94	9.46	3.73	3.82
				Broken	2.59	*	*	*	*
		Soil	Normal	Intact	1.89	10.23	4.86	5.41	3.31
				Broken	1.87	11.71	3.86	6.27	3.16
			Elevated	Intact	1.78	23.91	7.88	13.42	3.67
				Broken	1.74	18.10	1.68	10.43	2.71
	A54	Mound	Normal	Intact	2.27	9.68	1.07	4.27	2.19
				Broken	2.23	12.95	3.31	5.80	3.10
			Elevated	Intact	1.98	7.98	1.98	4.04	2.88
				Broken	2.07	10.86	2.61	5.26	3.01
		Soil	Normal	Intact	1.86	10.43	7.20	5.62	3.43

	Broken	1.91	16.23	11.83	8.51	3.59
Elevated	Intact	1.86	16.19	2.52	8.72	3.08
	Broken	1.86	16.76	2.67	9.01	3.18

Table C3 (Continued)

Day	Mound No.	Termite	Treatment Moisture	Aggregation	N (g/kg)	NO_3^- (µg/g soil)	NH_4^+ (µg/g soil)	NO_3^- (µg/g N/d)	NH_4^+-N (µg/g N/d)
	A5_	Mound	Normal	Intact	2.62	17.01	8.64	6.48	3.50
				Broken	2.56	16.68	8.85	6.51	3.47
			Elevated	Intact	2.52	11.72	1.58	4.65	2.64
				Broken	2.57	12.57	2.21	4.89	2.95
		Soil	Normal	Intact	2.09	16.92	2.31	8.08	2.86
				Broken	2.09	21.09	3.13	10.08	3.10
			Elevated	Intact	2.10	23.56	2.17	11.20	2.89
				Broken	2.22	16.88	1.69	7.61	2.77
	A174	Mound	Normal	Intact	3.09	6.41	11.50	2.08	3.60
				Broken	3.06	6.91	11.65	2.26	3.64
			Elevated	Intact	2.75	6.10	3.03	2.22	3.19
				Broken	1.98	7.11	8.85	3.59	3.72
		Soil	Normal	Intact	2.27	15.86	7.13	6.99	3.40

		Broken	2.72	17.11	4.58	6.28	3.25
	Elevated	Intact	2.06	13.83	2.70	6.72	3.13
		Broken	2.06	11.66	2.08	5.65	2.92

Table C3 (Continued)

Day	Mound No.	Treatment Termite	Moisture	Aggregation	N (g/kg)	NO_3^- (µg/g soil)	NH_4^+ (µg/g soil)	NO_3^- (µg/g N/d)	NH_4^+-N (µg/g N/d)
43	A6	Mound	Normal	Intact	2.26	13.43	4.76	5.94	3.15
				Broken	2.34	16.36	4.52	6.99	2.97
			Elevated	Intact	2.22	10.67	2.38	4.81	2.62
				Broken	2.35	15.14	11.42	6.45	3.62
		Soil	Normal	Intact	1.97	15.08	12.58	7.64	3.61
				Broken	1.98	17.23	17.57	8.69	3.67
			Elevated	Intact	1.91	23.37	9.09	12.22	3.58
				Broken	1.89	16.79	18.50	8.88	3.91
	A13	Mound	Normal	Intact	2.41	17.24	1.10	7.16	1.77
				Broken	2.41	25.77	3.80	10.67	2.90
			Elevated	Intact	2.40	16.81	1.11	7.02	1.83
				Broken	2.59	20.52	0.82	7.93	1.53
		Soil	Normal	Intact	1.89	25.64	2.18	13.56	2.45

	Broken	1.87	28.62	1.75	15.32	2.24
Elevated	Intact	1.78	26.33	1.15	14.77	1.86
	Broken	1.74	27.99	0.63	16.13	1.29

Table C3 (Continued)

Day	Mound	Treatment			N	NO_3^-	NH_4^+	NO_3^-	NH_4^+-N
	No.	Termite	Moisture	Aggregation	(g/kg)	(µg/g soil)	(µg/g soil)	(µg/g N/d)	(µg/g N/d)
	A54	Mound	Normal	Intact	2.27	20.22	1.53	8.92	2.10
				Broken	2.23	26.00	1.31	11.64	1.93
			Elevated	Intact	1.98	25.94	1.61	13.12	2.20
				Broken	2.07	26.01	1.20	12.59	1.88
		Soil	Normal	Intact	1.86	26.93	7.57	14.51	3.39
				Broken	1.91	20.75	24.21	10.87	3.79
			Elevated	Intact	1.86	32.12	1.86	17.29	2.41
				Broken	1.86	28.26	7.23	15.20	3.62
	A5_	Mound	Normal	Intact	2.62	21.05	2.13	8.02	2.40
				Broken	2.56	20.84	2.77	8.14	2.64
			Elevated	Intact	2.52	25.77	1.59	10.21	2.24
				Broken	2.57	24.78	4.39	9.64	3.11
		Soil	Normal	Intact	2.09	27.22	2.32	12.99	2.49

	Broken	2.09	23.63	1.00	11.29	1.70
Elevated	Intact	2.10	25.29	0.86	12.03	1.56
	Broken	2.22	27.05	1.38	12.20	2.09

Table C3 (Continued)

Day	Mound No.	Termite	Treatment Moisture	Aggregation	N (g/kg)	NO_3^- (µg/g soil)	NH_4^+ (µg/g soil)	NO_3^- (µg/g N/d)	NH_4^+-N (µg/g N/d)
	A174	Mound	Normal	Intact	3.09	24.65	29.79	7.99	3.80
				Broken	3.06	17.16	21.11	5.60	3.66
			Elevated	Intact	2.75	17.58	4.10	6.39	3.10
				Broken	1.98	15.37	26.07	7.75	3.86
		Soil	Normal	Intact	2.27	25.13	5.57	11.09	3.17
				Broken	2.72	26.27	5.65	9.65	3.19
			Elevated	Intact	2.06	21.25	1.31	10.33	2.02
				Broken	2.06	25.83	2.15	12.51	2.53
66	A6	Mound	Normal	Intact	2.26	38.15	13.31	16.86	3.73
				Broken	2.34	36.49	7.67	15.60	3.34
			Elevated	Intact	2.22	33.06	2.57	14.90	2.82
				Broken	2.35	33.50	9.45	14.27	3.61
		Soil	Normal	Intact	1.97	34.91	13.76	17.69	3.69

	Broken	1.98	30.46	13.72	15.36	3.64
Elevated	Intact	1.91	38.92	14.53	20.34	3.81
	Broken	1.89	37.86	14.98	20.02	3.89

Table C3 (Continued)

Day	Mound No.	Treatment Termite	Moisture	Aggregation	N (g/kg)	NO_3^- (µg/g soil)	NH_4^+ (µg/g soil)	NO_3^- (µg/g N/d)	NH_4^+-N (µg/g N/d)
	A13	Mound	Normal	Intact	2.41	48.20	1.12	20.01	1.92
				Broken	2.41	38.73	1.23	16.04	2.02
			Elevated	Intact	2.40	41.60	2.25	17.36	2.68
				Broken	2.59	43.04	0.97	16.64	1.83
		Soil	Normal	Intact	1.89	59.41	2.36	31.42	2.66
				Broken	1.87	61.55	1.33	32.95	2.11
			Elevated	Intact	1.78	50.95	0.80	28.59	1.64
				Broken	1.74	46.77	0.78	26.95	1.63
	A54	Mound	Normal	Intact	2.27	52.80	2.06	23.29	2.51
				Broken	2.23	42.79	1.79	19.16	2.36
			Elevated	Intact	1.98	46.01	1.96	23.27	2.54
				Broken	2.07	48.32	1.82	23.39	2.43
		Soil	Normal	Intact	1.86	54.71	14.79	29.49	3.71

	Broken	1.91	32.63	15.18	17.10	3.71
Elevated	Intact	1.86	57.36	1.49	30.88	2.33
	Broken	1.86	59.55	8.48	32.02	3.78

Table C3 (Continued)

Day	Mound		Treatment		N	NO_3^-	NH_4^+	NO_3^-	NH_4^+-N
	No.	Termite	Moisture	Aggregation	(g/kg)	(µg/g soil)	(µg/g soil)	(µg/g N/d)	(µg/g N/d)
	A5_	Mound	Normal	Intact	2.62	52.97	3.05	20.18	2.82
				Broken	2.56	51.92	2.51	20.27	2.68
			Elevated	Intact	2.52	53.67	2.05	21.27	2.66
				Broken	2.57	51.15	1.70	19.90	2.40
		Soil	Normal	Intact	2.09	50.37	13.93	24.04	3.63
				Broken	2.09	49.74	1.75	23.77	2.39
			Elevated	Intact	2.10	48.97	1.74	23.29	2.41
				Broken	2.22	62.34	2.35	28.12	2.79
	A174	Mound	Normal	Intact	3.09	43.80	13.53	14.20	3.66
				Broken	3.06	36.01	13.34	11.76	3.59
			Elevated	Intact	2.75	44.33	9.18	16.12	3.68
				Broken	1.98	35.79	14.11	18.06	3.74
		Soil	Normal	Intact	2.27	53.97	13.71	23.81	3.62

		Broken	2.72	53.70	3.38	19.72	2.94
	Elevated	Intact	2.06	51.95	2.22	25.24	2.71
		Broken	2.06	55.09	1.75	26.68	2.46

APPENDIX D

Table D1. A comparison of bryophyte species on termite mounds and surrounding surfaces at two secondary forest sites. Only three of the bryophyte species colonized termite mounds, and the only one to be collected multiple times was *Fissidens prionodes. Vitalianthus urubuensis* Zartman and Ackerman was a new species. Zartman, C.E., and I.L. Ackerman. 2002. A New Species of *Vitalianthus* (Lejeuneaceae, Hepaticae) from the Brazilian Amazon. The Bryologist 105:267-269.

Location	Category	Live plant?	Burned?	Category	Genus or scientific name
Block I	mound	--	not burnt	moss	*Fissidens prionodes*
	mound	--	not burnt	moss	*Octoblepheram ampullaceum*
	mound	--	not burnt	moss	*Fissidens prionodes*
	mound	--	not burnt	moss	*Fissidens prionodes*
	mound	--	not burnt	moss	*Fissidens prionodes*
	mound	--	not burnt	moss	*Fissidens prionodes*
	mound	--	not burnt	moss	*Fissidens prionodes*
	mound	--	not burnt	moss	*Fissidens prionodes*
	mound	--	not burnt	moss	*Fissidens prionodes*
	mound	--	not burnt	moss	*Arachniopsis*

mound	--	not burnt	moss	*Fissidens prionodes*
wood	dead	burnt	moss	*Syrrhopodon rigidus*
wood	dead	burnt	moss	*Octoblepheram ampullaceum*

Table D1 (Continued)

Location	Category	Live plant?	Burned?	Category	Genus or scientific name
Block I	wood	dead	burnt	liverwort	ARCHILEJEUNEA FUSCESCENS
	wood	dead	burnt	moss	*Octoblepheram ampullaceum*
	wood	dead	burnt	moss	*Sematophyllum subsimplex*
	wood	dead	burnt	liverwort	*Octoblepheram ampullaceum*
	wood	dead	burnt	liverwort	*Archilejeunea fuscescens*
	wood	dead	burnt	moss	*Syrrhopodon rigidus*
	wood	dead	burnt	moss	*Octoblepheram ampullaceum*
	wood	dead	burnt	moss	*Octoblepheram ampullaceum*
	wood	dead	burnt	moss	*Sematophyllum subsimplex*
	wood	dead	burnt	moss	*Syrrhopodon rigidus*
	wood	dead	burnt	moss	*Octoblepheram ampullaceum*
	wood	dead	burnt	moss	*Octoblepheram ampullaceum*
	wood	dead	burnt		*Trichosteleum fluviale*
	wood	dead	burnt	moss	*Sematophyllum subsimplex*
	wood	dead	burnt		*Leucobryum crispum*

wood	dead	burnt	moss	*Octoblepheram ampullaceum*
wood	dead	burnt	liverwort	*Archilejeunea fuscescens*
wood	dead	burnt	liverwort	*Trachylejeunea sp.*
wood	dead	burnt	moss	*Octoblepheram ampullaceum*

Table D1 (Continued)

Location	Category	Live plant?	Burned?	Category	Genus or scientific name
Block I	wood	dead	burnt	moss	SEMATOPHYLLUM SUBSIMPLEX
	wood	dead	burnt	moss	*Syrrhopodon rigidus*
	wood	dead	not burnt	moss	*Sematophyllum subsimplex*
	wood	dead	not burnt	moss	*Octoblepheram ampullaceum*
	wood	dead	not burnt	moss	*Syrrhopodon rigidus*
	wood	dead	not burnt	moss	*Fissidens prionodes*
	wood	dead	not burnt	liverwort	*Trachylejeunea*
	wood	dead	not burnt	liverwort	*Cheilolejeunea+H61*
	wood	dead	not burnt	liverwort	*Rectolejeunea berteroana*
	wood	dead	not burnt	liverwort	*Ceratolejeunea cubensis*
	wood	dead	not burnt	liverwort	*Archilejeunea fuscescens*
	wood	dead	not burnt	moss	*Sematophyllum subsimplex*
	wood	dead	not burnt	moss	*Sematophyllum subsimplex*
	wood	dead	not burnt	liverwort	*Archilejeunea fuscescens*
	wood	dead	not burnt	liverwort	*Archilejeunea fuscescens*

wood	dead	not burnt	liverwort	*Acrolejeunea torulosa*
wood	dead	not burnt	liverwort	*Trachylejeunea*
wood	dead	not burnt	liverwort	*Archilejeunea fuscescens*
wood	dead	not burnt	liverwort	*Trachylejeunea*

Table D1 (Continued)

Location	Category	Live plant?	Burned?	Category	Genus or scientific name
Block I	wood	dead	not burnt	moss	*Sematophyllum subsimplex*
	wood	dead	not burnt	moss	*Sematophyllum subsimplex*
	wood	dead	not burnt	liverwort	*Pycnolejeunea cf. callosa*
	wood	dead	not burnt	?	*Zoopsidella*
	wood	dead	not burnt	liverwort	*Ceratolejeunea cubensis*
	wood	dead	not burnt	liverwort	*Archilejeunea fuscescens*
	wood	dead	not burnt	liverwort	*Trachylejeunea*
	wood	live	not burnt	liverwort	*Leptolejeunea elliptica*
	wood	live	not burnt	liverwort	*Vitalianthus urubuensis sp.*
	wood	live	not burnt	liverwort	*Microlejeunea cf. ulicina*
	wood	live	not burnt	liverwort	*Pycnolejeunea cf. callosa*
	wood	live	not burnt	liverwort	*Cheilolejeunea sp.*
	wood	live	not burnt	liverwort	*Trachylejeunea sp.*
	wood	live	not burnt	liverwort	*Aphanolejeunea sicaefolia*
	wood	live	not burnt	liverwort	*Pycnolejeunea cf. callosa*

wood	live	not burnt	liverwort	*Archilejeunea fuscescens*
wood	live	not burnt	liverwort	*Microlejeunea cf. ulicina*
wood	live	not burnt	?	*Verdoorniathus griffinii*
wood	live	not burnt	liverwort	*Cyclolejeunea convexistipa*

Table D1 (Continued)

Location	Category	Live plant?	Burned?	Category	Genus or scientific name
Block I	wood	live	not burnt	liverwort	*Ceratolejeunea cubensis*
	wood	live	not burnt	moss	OCTOBLEPHERAM AMPULLACEUM
	wood	live	not burnt	moss	*Syrrhopodon ligulatus*
	wood	live	not burnt	liverwort	*Rectolejeunea*
	wood	live	not burnt	liverwort	*Pycnolejeunea*
	wood	live	not burnt	liverwort	*Archilejeunea fuscescens*
	wood	live	not burnt	liverwort	*Vitalianthus urubuensis*
	wood	live	not burnt	liverwort	*Trachylejeunea sp.*
	wood	live	not burnt	liverwort	*Vitalianthus urubuensis*
	wood	live	not burnt	liverwort	*Microlejeunea*
	wood	live	not burnt	liverwort	*Ceratolejeunea*
	wood	live	not burnt	liverwort	*Acrolejeunea*
	wood	live	not burnt	liverwort	*Pycnolejeunea*
	wood	live	not burnt	liverwort	*Ceratolejeunea*

wood	live	not burnt	liverwort	*Archilejeunea fuscescens*
wood	live	not burnt	liverwort	*Trachylejeunea sp.*
wood	live	not burnt	liverwort	*Pycnolejeunea*
wood	live	not burnt	liverwort	*Archilejeunea fuscescens*
wood	live	not burnt	liverwort	*Cheilolejeunea*

Table D1 (Continued)

Location	Category	Live plant?	Burned?	Category	Genus or scientific name
Block I	wood	live	not burnt	liverwort	*Pycnolejeunea*
	wood	live	not burnt	liverwort	*Trachylejeunea sp.*
	wood	live	not burnt	liverwort	LEPTOLEJEUNEA
	wood	live	not burnt	liverwort	*Rectolejeunea*
	wood	live	not burnt		*Frullania*
	wood	live	not burnt	moss	*Octoblepheram ampullaceum*
	wood	live	not burnt	liverwort	*Vitalianthus urubuensis*
	wood	live	not burnt	liverwort	*Trachylejeunea sp.*
	wood	live	not burnt	liverwort	*Archilejeunea fuscescens*
	wood	live	not burnt	liverwort	*Pycnolejeunea*
	wood	live	not burnt	liverwort	*Vitalianthus urubuensis*
	wood	live	not burnt	liverwort	*Pycnolejeunea*
	wood	live	not burnt	liverwort	*Cheilolejeunea*
Block IV	wood	live	not burnt	liverwort	*Pycnolejeunea*
	wood	live	not burnt	moss	*Octoblepheram*

wood	live	not burnt	liverwort	*Ceratolejeunea coarina*
wood	live	not burnt	liverwort	*Trachylejeunea*
wood	dead	burnt	moss	*Calymperes*
wood	dead	burnt	moss	*Sematophyllum*

Table D1 (Continued)

Location	Category	Live plant?	Burned?	Category	Genus or scientific name
Block IV	wood	dead	burnt	liverwort	*Archilejeunea* cf. *fuscescens*
	wood	dead	burnt	moss	*Octoblepheram*
	mound		not burnt	moss	FISSIDENS
	mound		not burnt	moss	*Fissidens*
	mound		not burnt	moss	*Campylopus surinamensis*
	mound		not burnt	liverwort	*Calypogeia*
	wood	dead	not burnt	moss	*Octoblepheram* sp.
	wood	dead	not burnt	moss	*Sematophyllum* sp.
	wood	dead	not burnt	liverwort	Genus B
	wood	dead	not burnt	moss	Genus C
	wood	dead	not burnt	moss	*Leucodon* H5
	wood	dead	not burnt	moss	*Sematophyllum*
	mound		not burnt	moss	*Fissidens*
	mound		not burnt	moss	*Fissidens*
	mound		burnt	moss	*Sematophyllum*

mound		not burnt	liverwort	*Calypogeia*
mound		not burnt	moss	*Fissidens*
mound		not burnt	moss	*Fissidens*
mound		not burnt	liverwort	*Calypogeia*

Table D1 (Continued)

Location	Category	Live plant?	Burned?	Category	Genus or scientific name
Block IV	mound		not burnt	moss	*Fissidens*
	mound		not burnt	moss	FISSIDENS
	mound		not burnt	liverwort	*Calypogeia*
	mound		not burnt	moss	*Fissidens*
	mound		not burnt	moss	*Fissidens*
	mound		not burnt	moss	*Fissidens*
	mound		not burnt	moss	*Fissidens*
	mound		not burnt	liverwort	*Calypogeia*
	mound		not burnt	moss	*Fissidens*
	mound		not burnt	moss	*Campylopus surinamensis*
	mound		not burnt	moss	*Fissidens prionodes*
	wood	dead	burnt	moss	*Sematophyllum subsimplex*
	wood	dead	burnt	moss	*Octoblepheram ampullaceum*
	wood	dead	not burnt	moss	*Campylopus surinamensis*
	wood	dead	not burnt	moss	*Octoblepheram ampullaceum*

mound		not burnt	moss	*Fissidens prionodes*
mound		not burnt	liverwort	*Calypogeia* sp.
wood	dead	not burnt	moss	*Verdoorniathus griffinii*
wood	dead	not burnt	moss	*Verdoorniathus griffinii*
mound			moss	*Fissidens prionodes*

Figure D2. Photograph of an unidentified saprophyte found growing from a termite mound.

Figure D3. Photograph of an unidentified plant (known locally as uru'a) with an ant-plant association growing directly out of a termite mound.

Table D4. Soil chemical analyses of termite mound and control soil from pasture site. Samples are paired.

Location	Mound	pH	mg/dm^3		c.mol$_c$/dm^3				g/Kg		mg/dm^3			
	No.	H$_2$0	P	K	Ca	Mg	Al	H+Al	C	OM	Fe	Zn	Mn	Cu
Termite mound	C26	4.70	10.4	56	1.70	0.40	1.07	21.39	43.94	75.57	274	1.70	15.49	0.32
	C27	4.20	4.9	32	0.93	0.34	1.21	27.70	33.49	57.61	361	1.70	10.59	0.28
	C35	4.62	10.4	62	1.96	0.39	1.58	28.09	57.71	99.27	279	2.79	8.37	0.28
	C37	4.55	5.6	26	0.65	0.14	1.57	30.75	37.18	63.96	293	1.48	1.43	0.20
	C49	4.15	3.5	32	0.28	0.17	1.78	29.77	36.00	61.92	273	1.92	1.63	0.13
	C52	4.09	2.8	24	0.05	0.07	1.80	24.52	29.65	51.00	234	0.82	0.71	0.11
	C53	4.25	2.8	26	0.22	0.16	1.51	24.27	29.34	50.47	277	0.89	1.53	0.15
	C54	4.44	2.8	28	0.31	0.27	1.26	23.62	28.56	49.12	279	1.40	2.19	0.15
Control soil	C26	4.55	5.6	32	0.23	0.19	1.24	22.23	26.88	46.24	224	1.08	2.89	0.11
	C27	4.95	2.8	22	0.50	0.33	0.61	19.94	24.11	41.48	370	0.54	4.23	0.23
	C35	4.41	3.5	24	0.13	0.09	1.08	18.13	21.92	37.71	296	0.55	1.65	0.05

C37	4.36	3.5	24	0.43	0.20	1.36	25.49	30.82	53.00	402	1.84	2.63	0.14
C49	4.02	2.8	28	0.09	0.10	1.62	22.40	27.09	46.59	239	0.61	0.54	0.05
C52	4.26	2.1	24	0.06	0.07	1.24	17.27	20.88	35.91	439	0.79	1.4	0.05
C53	4.36	2.1	18	0.04	0.06	1.33	25.54	30.88	53.11	329	0.82	0.82	0.11
C54	4.57	2.8	22	0.25	0.20	1.48	21.73	26.27	45.19	518	0.90	2.29	0.18

Table D5. Soil resistance of termite mounds and control soils in the pasture site. Penetrometer readings were taking to a depth of 5 cm. The surface area of the cone was 2 cm. The maximum reading of the manometer was 500 kgf. Three replicates were taken per location.

No.	Treatment	Manometer	Resistance		
		(kgf)	(kgf/cm2)	(kgf/m2)	(Mpa)
C26	termite mound	500	500	5000000	49
		500	500	5000000	49
		500	500	5000000	49
	control soil	450	450	4500000	44
		500	500	5000000	49
		500	500	5000000	49
C27	termite mound	500	500	5000000	49
		440	440	4400000	43
		500	500	5000000	49
	control soil	500	500	5000000	49
		500	500	5000000	49
		500	500	5000000	49
C49	termite mound	185	185	1850000	18
		245	245	2450000	24
		240	240	2400000	24
	control soil	220	220	2200000	22
		190	190	1900000	19

	230	230	2300000	23
C52 termite mound	215	215	2150000	21
	210	210	2100000	21
	240	240	2400000	24
control soil	240	240	2400000	24
	255	255	2550000	25
	250	250	2500000	25
C53 termite mound	500	500	5000000	49
	225	225	2250000	22
	200	200	2000000	20
control soil	270	270	2700000	26

Table D5 (Continued)

No.	Treatment	Manometer	Resistance		
		(kgf)	(kgf/cm2)	(kgf/m2)	(Mpa)
	Control soil	240	240	2400000	24
		240	240	2400000	24
C54	termite mound	300	300	3000000	29
		320	320	3200000	31
		410	410	4100000	40
	control soil	260	260	2600000	25
		260	260	2600000	25
		270	270	2700000	26
C37	termite mound	255	255	2550000	25
		250	250	2500000	25
		200	200	2000000	20
	control soil	420	420	4200000	41
		250	250	2500000	25
		250	250	2500000	25

Table D6. Soil texture of paired samples of termite mound and control soil in the pasture site to 10 cm.

Treatment	Sample no.	Sand coarse (%)	Sand fine (%)	Sand total (%)	Silt (%)	Clay (%)
Termite mound	c26	7.2	1.0	8.2	21.0	70.8
	C27	10.7	2.5	13.2	17.8	68.9
	C35	9.0	3.3	12.3	16.7	71.0
	C37	9.2	2.2	11.3	21.0	67.6
	C49	9.6	2.7	12.3	23.8	63.9
	C52	10.3	3.2	13.5	21.5	64.9
	C53	10.5	2.7	13.2	23.0	63.8
	C54	11.1	3.1	14.2	22.1	63.7
Control soil	C26	11.0	2.7	13.7	19.1	67.2
	C27	10.1	2.5	12.5	20.2	67.2
	C35	11.6	2.8	14.4	25.8	59.7
	C37	10.3	2.7	13.0	21.9	65.1
	C49	14.8	3.4	18.2	22.5	59.3
	C52	9.1	2.5	11.6	25.8	62.7
	C53	11.9	2.3	14.3	27.0	58.7
	C54	9.4	2.7	12.1	21.9	66.0

Table D7. A comparison of root density in termite mounds and control soils between secondary forest and agroforest (paired data shown.)

Block	Treatment	Root density (g root/g soil)	
		Termite mound	Control soil
I	Agroforestry	0.0029	0.0066
		0.0009	0.0060
		0.0001	0.0014
		0.0036	0.0111
			0.0214
		0.0003	0.0118
		0.0006	0.0063
			0.0402
	Secondary forest	0.0021	0.0040
		0.0008	0.0025
		0.0015	0.0027
		0.0033	0.0086
		0.0023	0.0026
		0.0007	0.0072
		0.0011	0.0017
		0.0015	0.0015
II	Agroforestry	0.0024	0.0377

0.0005	0.0000
0.0108	0.0000
0.0020	0.0430
0.0029	0.0283

Table D7 (Continued)

Block	Treatment	Root density (g root/g soil)	
		Termite mound	Control soil
		0.0003	
		0.0008	0.0163
	Secondary forest	0.0017	0.0019
		0.0008	0.0044
		0.0004	0.0021
		0.0028	0.0024
		0.0011	0.0012
			0.0050
		0.0030	
III	Agroforestry	0.0068	0.0112
		0.0011	0.0115
		0.0018	0.0251
		0.0010	0.0212
		0.0202	0.0095
		0.0001	0.0035
		0.0003	0.0092
		0.0003	0.0313
	Secondary forest	0.0009	0.0048
		0.0032	0.0005

0.0022	0.0032
0.0017	0.0030
0.0062	0.0091
0.0040	0.0020
0.0024	0.0079
0.0023	0.0022

Table D8. A comparison of soil chemical characteristics between termite mound and control soil in agroforest and secondary forest

				pH	mg/dm^3			c.mol$_c$/dm^3				g/kg	mg/dm^3			
Block	Land use	Category	No.	H2O	P	K	Na	Ca	Mg	Al	H+Al	C	Fe	Zn	Mn	Cu
I	AS1	Termite mound	6	4.70	6.9	36	9	0.76	0.24	1.31	12.0	51	400	91	2.3	0.41
		Control soil	6	4.98	6.2	40	9	1.41	0.24	0.66	10.2	39	481	31	6.1	0.31
		Termite mound	25	4.53	12.4	48	16	1.46	0.26	1.73	13.2	67	372	127	5.2	1.84
		Control soil	25	4.84	13.7	48	15	1.06	0.41	0.88	11.6	59	430	157	7.1	0.94
		Termite mound	40	4.76	10.3	56	12	0.72	0.34	1.22	10.9	45	393	136	5.3	0.43
		Control soil	40	4.76	7.5	40	11	0.80	0.22	0.63	8.6	37	304	181	4.3	0.54
		Control soil	41	5.11	8.2	50	14	1.92	0.62	0.24	8.1	51	318	212	5.4	0.62
		Termite mound	41	5.14	8.2	56	10	1.41	0.66	0.58	10.9	49	312	112	3.4	0.42
		Termite mound	44	4.87	11.0	48	10	0.86	0.33	0.92	10.6	51	379	176	14.2	3.03
		Control soil	44	5.09	6.9	44	11	1.26	0.68	0.26	6.8	32	492	235	5.2	0.54

	Termite mound	48	4.74	7.5	34	6	0.44	0.18	1.07	9.2	37	366	55	2.4	0.30
	Control soil	48	5.09	6.9	36	9	0.89	0.40	0.40	7.2	34	260	206	3.0	0.33
	Termite mound	54	4.65	12.4	50	12	0.46	0.19	1.52	13.1	49	460	170	3.9	1.13
	Control soil	54	4.88	11.0	62	14	1.10	0.51	0.56	8.7	43	529	239	4.2	0.51
Cap	Termite mound	2	4.53	4.1	28	7	0.10	0.08	1.06	9.6	34	323	211	2.6	0.27
	Control soil	2	4.64	3.4	30	8	0.28	0.09	1.02	9.3	34	244	126	2.0	0.48
	Termite mound	4	4.75	5.5	40	9	0.47	0.16	0.96	8.3	38	413	194	8.5	0.29
	Control soil	4	4.93	4.1	32	12	0.60	0.20	0.88	9.4	38	459	185	2.9	0.62

Table D8 (Continued)

				pH	mg/dm^3				c.mol$_c$/dm^3			g/kg	mg/dm^3			
Block	Land use	Category	No.	H2O	P	K	Na	Ca	Mg	Al	H+Al	C	Fe	Zn	Mn	Cu
	Cap	Termite mound	8	4.59	5.5	42	10	0.54	0.16	1.30	10.1	39	408	169	3.7	0.24
		Control soil	8	4.43	5.5	34	11	0.62	0.17	1.41	12.1	49	641	168	3.1	0.32
		Termite mound	11	4.64	3.4	30	9	0.19	0.08	1.16	10.7	43	229	83	4.8	0.21
		Control soil	11	4.45	4.1	32	12	0.27	0.13	1.28	10.4	47	639	167	3.1	0.34
		Termite mound	28	4.60	6.2	32	9	0.13	0.08	1.46	10.5	37	337	100	3.5	0.33
		Termite mound	37	4.63	4.8	36	7	0.20	0.15	0.53	8.3	35	301	213	5.3	0.30
		Control soil	37	4.65	2.7	34	8	0.29	0.15	0.98	7.9	33	291	148	4.5	0.37
		Termite mound	47	4.59	5.5	34	8	0.16	0.09	1.33	10.8	49	323	184	6.5	0.28
		Control soil	47	4.68	3.4	30	10	0.14	0.20	1.28	13.2	51	242	253	2.8	0.20
		Termite mound	49	4.45	5.5	36	9	0.15	0.09	1.48	12.4	55	409	286	4.7	0.24
		Control soil	49	4.30	4.1	28	9	0.10	0.06	1.54	11.4	38	265	119	1.9	0.32
II	AS1	Termite mound	4	4.73	8.9	48	11	0.31	0.13	1.25	10.3	35	320	163	5.8	0.78
		Control soil	4	5.04	4.8	42	13	1.48	0.51	0.27	7.0	31	327	201	5.7	0.27

Control soil	6	4.74	7.5	42	10	0.74	0.28	1.08	9.5	39	335	164	4.0	0.25
Termite mound	6	4.97	7.5	50	12	1.41	0.63	0.37	8.1	59	374	166	5.7	0.49
Control soil	8	5.05	45.3	66	14	2.61	0.64	0.44	10.7	55	369	59	17.3	0.83
Termite mound	8	5.47	9.6	40	11	1.14	0.62	0.16	8.1	47	277	176	7.4	0.29
Control soil	9	4.73	10.3	50	12	0.85	0.28	0.73	10.1	39	424	274	7.8	0.27
Termite mound	9	4.65	17.2	76	15	0.96	0.32	1.10	13.2	57	320	82	15.8	2.08
Termite mound	10	4.68	13.0	66	9	0.69	0.24	1.31	12.5	57	344	115	5.1	0.25

Table D8 (Continued)

				pH	mg/dm^3			c.mol$_c$/dm^3				g/kg	mg/dm^3			
Block	Land use	Category	No.	H2O	P	K	Na	Ca	Mg	Al	H+Al	C	Fe	Zn	Mn	Cu
II	AS1	Control soil	10	4.71	9.6	46	11	0.31	0.16	1.14	11.7	53	312	122	5.4	0.21
		Control soil	20	4.83	7.5	40	8	0.94	0.34	1.11	11.0	49	356	151	5.5	0.56
		Control soil	s/n	4.69	11.0	46	8	0.18	0.13	1.36	10.9	38	428	182	8.6	0.28
		Termite mound	s/n	5.31	8.9	44	12	1.74	0.84	0.08	7.9	234	261	440	8.9	0.25
	Cap	Termite mound	36	4.52	5.5	52	9	0.59	0.17	1.37	12.0	43	514	127	10.1	0.56
		Control soil	36	4.48	3.4	38	13	0.31	0.18	0.98	8.4	35	491	121	4.0	0.48
		Termite mound	55	4.67	6.2	76	12	0.82	0.24	1.12	12.4	63	517	258	14.7	0.49
		Control soil	55	4.63	3.4	52	10	0.59	0.27	0.95	10.3	45	548	220	6.5	0.30
		Control soil	58	4.56	3.4	38	15	0.32	0.17	0.85	7.4	29	443	96	4.2	0.67
		Termite mound	61	4.63	6.9	76	24	1.63	0.73	1.05	13.1	77	615	111	11.2	0.59
		Control soil	61	4.74	3.4	40	10	1.38	0.21	0.71	8.5	33	550	246	3.2	0.36
		Termite mound	70	4.99	3.4	70	16	1.68	0.44	0.30	6.8	36	547	303	13.5	0.45
		Control soil	70	4.50	2.7	42	13	0.59	0.29	0.80	7.8	31	411	105	6.2	0.45
		Termite mound	71	4.61	3.4	34	8	0.40	0.25	0.70	7.3	31	318	183	5.3	0.41

Control soil	71	4.61	2.7	32	10	0.53	0.25	0.73	7.6	31	431	163	4.6	0.48
Termite mound	72	4.77	4.8	36	9	0.54	0.23	0.52	7.7	32	525	352	5.1	0.32
Control soil	72	4.50	3.4	32	8	0.52	0.20	0.86	7.8	32	442	108	3.6	0.41

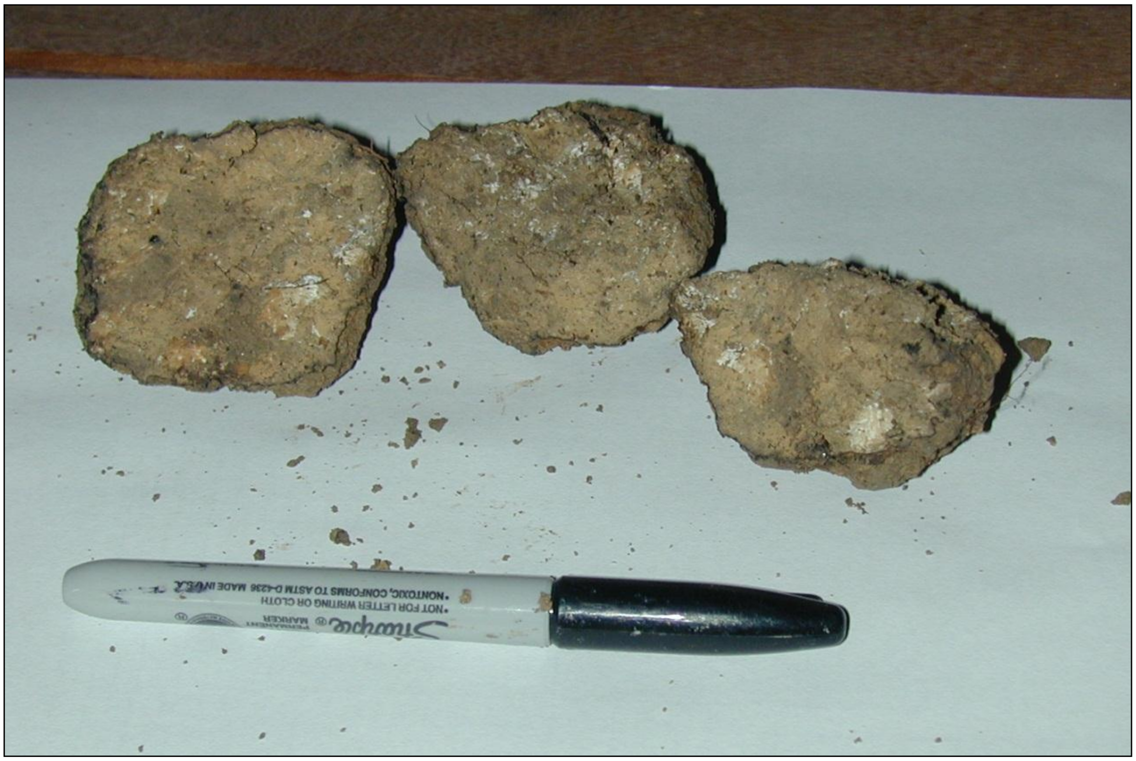

Figure D9. This photograph depicts an unusual feature, found in a termite mound, only seen on one occasion. It was a spherical unit of soil, that when broken open, showed white fungus. The edges of the sphere had a black line, as can be seen on the lower edges of the cross-sections.

Table D10. Summary of comparison of termite mounds and paired control soils in the pasture site.

		Termite mound	Control soil
pH	Mean	4.38	4.44
	S.E.	0.08	0.10
N (g/kg)	Mean	2.40	1.74
	S.E.	0.22	0.08
C (g/kg)	Mean	37.0	26.1
	S.E.	3.5	1.3
Ca (c.mol$_c$/dm^3)	Mean	0.76	0.22
	S.E.	0.25	0.06
Mg (c.molc/dm^3)	Mean	0.24	0.16
	S.E.	0.04	0.03
Al (c.molc/dm^3)	Mean	1.47	1.25
	S.E.	0.09	0.11
H + Al (c.molc/dm^3)	Mean	26.3	21.6
	S.E.	1.2	1.1
P (mg/dm^3)	Mean	5.38	3.13
	S.E.	1.08	0.44
K (mg/dm^3)	Mean	36	24
	S.E.	5.2	1.5
Fe (mg/dm^3)	Mean	284	352
	S.E.	12.6	35.5

Zn (mg/dm^3)	Mean	1.59	0.89
	S.E.	0.22	0.15
Mn (mg/dm^3)	Mean	5.24	2.06
	S.E.	1.96	0.43
Cu (mg/dm^3)	Mean	0.20	0.12
	S.E.	0.03	0.02

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