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The impact of mound-building termites on surface soil properties in a secondary forest of Central Amazonia

Ilse L. Ackerman^{a,*}, Wenceslau G. Teixeira^b, Susan J. Riha^c,
Johannes Lehmann^a, Erick C.M. Fernandes^{a,1}

^aDepartment of Crop and Soil Sciences, Cornell University, Ithaca, NY 14853, USA

^bEmbrapa Amazônia Ocidental, Caixa Postal 319, Manaus, AM 69.011-970, Brazil

^cDepartment of Earth and Atmospheric Sciences, Cornell University, Ithaca, NY 14853, USA

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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 re-colonization of the landscape by vegetation. To determine the most important constraints imposed by termite mounds on plant establishment, we investigated chemical, physical, and hydraulic properties of termite mounds at an 8-year-old secondary forest site, and their effects on the development of native plant species. Mounds contained only half of the root biomass found in neighboring soil in the surface 0.05 m. Carbon, nitrogen, and potassium levels in the termite mounds were significantly elevated, by 33, 28, and 38%, respectively (44 g kg^{-1} , 2.5 g kg^{-1} , and 33 mg kg^{-1}), while no significant difference in phosphorus, magnesium, iron, zinc, or copper 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}). Although drainage through the mounds *in situ* was faster, termite mound samples absorbed water significantly more slowly than control soil. Termite mound material retained significantly less water than control soil under the same suction. 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. The abundance of termite mounds was 760 ha^{-1} in the study site, but covered only 3% of the area. Complementing the results from this study with investigations of termite mounds and nutrient cycling, carbon storage, and biodiversity will further our understanding of the effects of mound-building termites in the pastures and secondary forests of Amazonia.

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* Corresponding author at: 441 East Wolfe St., Harrisonburg, VA 22802, USA. Tel.: +1 540 578 3074; fax: +1 678 669 0961.
E-mail address: ilse.ackerman@gmail.com (I.L. Ackerman).

¹ Present address: The World Bank, ESSD-ARD, 1818 H Street, WA 20433, USA.
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1. Introduction

Forest clearing and other land-use changes in Amazonia alter the population dynamics and composition of soil fauna communities (e.g. Bandeira, 1989; Barros et al., 2002, 2004; Lavelle and Pashanasi, 1989; Mathieu et al., 2005; Nepstad et al., 1995; Souza, 1989; De Souza and Brown, 1994; Teixeira and Schubart, 1988; Vasconcelos and Cherrett, 1995; Vasconcelos, 1999). These modified soil communities in turn impact their ecosystems in ways we are beginning to observe and describe (e.g. Barros et al., 2001; Höfer et al., 2001; Martius et al., 1996; Moutinho et al., 2003; Vasconcelos, 1997; Verchot et al., 2003). North of Manaus, in Central Amazonia, one such impact is that of mound-building termites in post-clearing landscapes. Highly visible in many of the roadside pastures of the AM-010 highway or in the secondary forests of the region, are mounds bare of vegetation, creating a marked visual patchiness to the landscape (Ackerman, personal observation).

In other regions, rather than a paucity of vegetation, we find trees preferentially colonizing termite mounds over the surrounding soils (de Oliveira Filho, 1992; Ponce and Cunha, 1993; de Araujo Neto et al., 1986). Salick et al. (1983), in the neighboring Venezuelan Amazonia, found termite mounds to be nutrient-rich microsites for seedling establishment. What properties of the mounds at our study site constrain vegetation establishment instead? Only a handful of studies exist describing chemical properties of termite mounds in Amazonia (Richard et al., 2006; Bandeira, 1983; Filho et al., 1990). No studies on the physical or hydraulic properties of termite mounds were found for Amazonia, and 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 was found experimented with termite mound constraints for plant growth (Rogers et al., 1999). The authors of this Australian study found that plant growth suppression was not chemically but mechanically mediated.

In this study, we (1) quantified the area covered by termite mounds in Central Amazonian successional forest site, (2) characterized chemical, physical, and hydraulic properties of the mounds, and (3) determined which of these properties constrain the development of plant species on termite mounds. We hypothesized that the constraint for plants would be mechanical resistance to exploitation by plant roots.

2. Materials and methods

2.1. Site description

The study was conducted at the *Embrapa Amazonia Ocidental* research station located at 54 km of the federal highway BR-174 north of Manaus, Amazonas, Brazil. The study site was located at 02°30'56"S and 60°01'28"W, a 7–8 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.

Soils on the plateau of the study site are classified as dystrophic, isohyperthermic, clayey kaolinitic Hapludox

(Demattê and Demattê, 1993). 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 27 °C, and atmospheric humidity is around 84% (Vose et al., 1992). The native vegetation of the region is closed-canopy, dense, evergreen, non-flooding forest (Veloso et al., 1991).

2.2. Methods

To fulfill the study objectives, we (1) surveyed the extent of coverage of termite mounds at the study site, (2) measured root biomass as an indicator of termite mound impact on vegetation, (3) assessed chemical, physical, and hydraulic properties of the termite mounds, and (4) used plant bioassays to determine the primary constraints to vegetation development on termite mound material.

2.3. Termite mound survey

To determine percent coverage and density of termite mounds, eight transects through the secondary forest study site were surveyed. Transects were 2 m in width, 40–80 m in length as circumscribed by the edge of the plateau, and 20 m apart, a total of 1040 m².

2.4. Termite species collection

Seventeen mounds were sampled for termite species. Termites were hand-collected with forceps and transferred to vials containing 80% ethyl alcohol for preservation and subsequent identification. The collected termites were deposited in the entomology collection at INPA, Manaus.

2.5. Root biomass

To compare root biomass between termite mounds and control soil, volumetric soil samples in 100-cm³ stainless steel cylinders were taken from the surface 0.05 m of 19 randomly chosen termite mounds and control areas. The sampling point for the control soil was 1.5 m from the border of the termite mound in a randomly chosen cardinal direction, for this sampling and for all other comparisons throughout this study. Roots were washed, identified where possible, and dried.

2.6. Soil chemical analyses

Twenty-one termite mound and control sites were randomly selected and sampled. 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 repetitions were collected and pooled in the field. 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 photocolourimetry, 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).

Effective cation exchange capacity (e_{CEC}) 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 e_{CEC} . Base saturation was calculated as the sum of K^+ , Ca^{2+} , and Mg^{2+} .

2.7. Soil physical analyses

2.7.1. Particle-size fractionation

Twenty termite mounds and 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 1N NaOH and mechanical agitation.

2.7.2. Water content and bulk density

Soil water content and bulk density were measured by sampling the surface 0–0.05 m of soil using 100 cm³ stainless steel cylinders ($n = 9$). Three samples were taken from each mound and adjacent area. The samples were oven-dried at 105 °C.

2.7.3. Resistance to penetration

Resistance to penetration was measured using a cone penetrometer (Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands), following Bradford (1986). A cone of 2 cm² surface area and a penetration depth of 0.05 m were selected. The average of five readings on each mound and on each corresponding control area was taken ($n = 10$).

2.7.4. 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 min was measured.

2.7.5. Water retention curve and porosity

The water retention curve of termite mound and control soil cores ($n = 6$) was evaluated by the tension table method (Reeve and Carter, 1991). Cores were saturated and then re-weighed at 0, 4, 10, 25, 30, 63, and 80 cm of water of tension. After 80 cm of tension, the samples were 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:

$$P_C = P_O - P_W = \frac{4\gamma \cos a}{d_{eq}} = -h \quad (1)$$

where P_O is the atmospheric pressure, P_W the water pressure, γ the surface tension of water, and a the contact angle of water with the pore walls, assumed to be 0 (Grimaldi et al., 2003).

2.8. Soil water repellency

2.8.1. 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 s in contact with the bed of sand until it ceased to gain mass.

To compare the absorption curves, a segmented regression with unknown point of segmentation was fitted to the 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.

$$i = a + bt + ct^2 \quad (2)$$

$$i = a + bt_0 + ct_0^2 \quad (3)$$

$$t_s = -0.5 \frac{b}{c} \quad (4)$$

2.8.2. Droplet method

The molarity of ethanol droplet test (Roy and McGill, 2002 (modified)) was used as another assessment of soil water repellency. Samples ($n = 5$) were sieved to 1-mm mesh size. Test solutions were made using 95% ethyl alcohol.

2.9. Bioassays

2.9.1. Allelopathy

To test for the presence of allelopathic substances in the termite mounds responsible for inhibiting germination, a bioassay was set up using *Cucumis sativus*, a species used for allelopathic assays due to its sensitivity (Fletcher, 1991). Three repetitions from five termite mound and five control soils, as well as blanks, were agitated with distilled water for 30 min on a mechanical shaker. From each bottle, 10 mL of the resulting liquid was pipetted onto sterile gauze in a Petri dish, and 25 seeds placed. Seeds were incubated in the dark for 48 h.

2.9.2. 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 control soils, mixed with sand, and watered while monitoring germination for 7 weeks.

2.9.3. Factorial experiment

Based on the results of the previous experiments, a 2 × 2 × 2 × 2 factorial bioassay was designed to discriminate between mechanical, chemical, and allelopathic suppression of seedling germination and development in termite mounds versus control soils. Soil cores (n = 40) were collected in 100-cm³ stainless steel cylinders. 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 (20 and 12 mg of lime per cylinder in the ground and intact treatments, respectively).

Six seeds of the native *Sesbania exasperata* were planted per experimental unit. Each factorial combination of the experiment had five experimental units, for a total of 480 seeds. Each of the eighty 100-cm³ cylinders received 10 mL of water daily as needed. Germination was recorded daily for nine days. The emergence velocity index (EVI) (Mendonça, 1997) of the seeds was calculated.

2.9.4. Statistical analyses

The root biomass data was log-normally distributed and was therefore log-transformed. To compare means, a paired t-test was then performed on the transformed data. For the water retention curve, and for non-normally distributed soil chemistry data for which an appropriate transformation was not found, the Mann-Whitney test was used. In the sandbox experiment and in the seed bank experiment, an ANOVA was used to test for significant differences among the treatments. In the allelopathy experiment, the Kruskal-Wallis test was used to test for significant differences between the treatment categories. The data from the factorial experiment were analyzed using a 2 × 2 × 2 × 2 factorial analysis of variance. Where not indicated above, a t-test was used for comparing the two experimental treatments. Minitab 13.1 (Minitab, Inc., State College, PA, USA) was used for these analyses.

3. Results

3.1. Termite mound survey

In the 1040 m² of transects exposed in the survey, 79 termite mounds were observed, equivalent to a density of 760 mounds per hectare. The geometric mean basal area of the mounds was 0.29 m², and their coverage of the study area amounted to 3%. The surface of the mounds was gray in color, slightly pitted, and gently sloping. Although the mounds appeared eroded, with no evidence of recent building on the surface of the mound, all were found to be inhabited by termites.

Table 1 – Mean or median element concentration of termite mounds and adjacent soils

Location	C (g/kg)	N (g/kg)	P (mg/kg)	K (mg/kg)	Ca (g/kg)	Mg (g/kg)	Al (g/kg)	Fe (mg/kg)	Zn (mg/kg)	Mn (mg/kg)	Cu (mg/kg)	pH (H ₂ O)	e _{CFC} (cmol ⁺ /kg)	Al saturation (%)	Base saturation (%)
Termite mound	43.8 [*] (2.02)	2.47 [*] (0.06)	3.30	33.3 [*]	0.0256 [*] (0.004)	0.007	0.227 [*] (0.007)	324 (10.7)	0.916	2.048 [*]	0.288	324 [*] (10.7)	0.916 [*]	2.048 [*]	0.288 [*]
Control soil	32.9 [*] (1.85)	1.93 [*] (0.05)	3.11	24.1 [*]	0.0350 [*] (0.006)	0.007	0.145 [*] (0.003)	312 (17.0)	0.800	2.741 [*]	0.271	312 [*] (17.0)	0.800 [*]	2.741 [*]	0.271 [*]

Standard errors are given in parentheses. An asterisk indicates a significant difference (P ≤ 0.05) between mound and control soil.

Table 2 – Mean or median physical properties of termite mounds and adjacent control soil

Location	Particle-size distribution				Bulk density (g/cm ³)	Soil water content		Penetration resistance (MPa)	Infiltration (mm/s)
	Coarse sand (g/kg)	Fine sand (g/kg)	Silt (g/kg)	Clay (g/kg)		(g/g)	(m ³ /m ³)		
Termite mound	0.7 [*] (0.04)	0.2 (0.01)	2.0 [*] (0.07)	7.2 [*] (0.10)	0.92 (0.02)	0.37 [*] (0.01)	0.34 [*] (0.01)	13.5 [*]	15.8 [*]
Control soil	0.6 [*] (0.03)	0.2 (0.01)	1.7 [*] (0.07)	7.6 [*] (0.08)	0.92 (0.02)	0.49 [*] (0.02)	0.44 [*] (0.01)	4.1 [*]	2.8 [*]

Standard errors are given in parentheses. Asterisks indicate a significant difference at $P \leq 0.05$.

3.2. Termite species collection

Eighteen termite species were found in the mounds sampled from the study site. The most commonly encountered species were *Subulitermes microsoma* (Silvestri) (in four mounds) and *Anhangatermes macarthuri* Constantino (in three mounds). Eight of the 15 mounds in this study hosted 2 or more species, and from a single mound 4 species were collected: *Cornicapritermes mucronatus* Emerson, *Nasutitermes guayanae* (Holmgren), *Neocapratermes 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, *Orthognathotermes* cf. *brevipilosus* Snyder, and *Termes fatalis* Linnaeus). The termite mounds were also found to host many other non-termite species of soil fauna, including ants, centipedes, earthworms, spiders.

3.3. Root biomass

The mean root biomass in the surface of termite mounds was significantly lower ($P \leq 0.05$) than that of the adjacent soil (1.9 and 3.4 mg cm⁻³, respectively). The 90% of plant roots by dry weight in the termite mound samples belonged to the common secondary forest genus *Vismia*.

3.4. Soil chemical analyses

The results of the chemical analyses of termite mounds and adjacent soil (Table 1) show that C and N (g/kg) concentrations in the termite mounds were significantly elevated (by 33 and 28%, respectively, $P \leq 0.001$). The C:N ratio and median P and Mg concentrations did not differ significantly, but K was elevated, and Ca was depleted. 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 mounds, by 47% ($P < 0.001$). Zn, Mn, Cu, and 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. Al saturation was significantly higher in termite mound material (91%) than in the neighboring soil (86%) (Table 1).

3.5. Soil physical analyses

Soil texture differed only slightly between the termite mound and adjacent soils, although these differences were significant (Table 2). Slightly less clay and more silt and sand were found in the termite mounds than in the adjacent soil.

Soil water content was 25% lower in the termite mound than in the adjacent soil (Table 2). The mean bulk density of the termite mound and the soil were equal, at 0.92 Mg/m³. The resistance to penetration of the termite mound surface was around three times greater than that of the soil (Table 2). 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 termite mound material retained a significantly lower water content than the control soil over the entire pressure range of 0.0–1.9 pF (Fig. 1). No significant difference in the pore-size distribution of the two materials was observed.

Time to saturation differed significantly between the termite mound, burned mound, and control soil treatments (Fig. 2). Time to saturation was 80% greater for termite mound material than control soil (Table 3). Furthermore, termite mound material that had been exposed to fire reached saturation more than three times as quickly as the unburnt termite mound material. The water content of the termite mound material at saturation was 60% lower than that of the control or burned soil, but the water content of the burned mound material was not significantly different than that of the control soil (Table 3). Neither the soil nor the termite mound material showed any degree of water repellency as measured by the molarity of an ethanol droplet test.

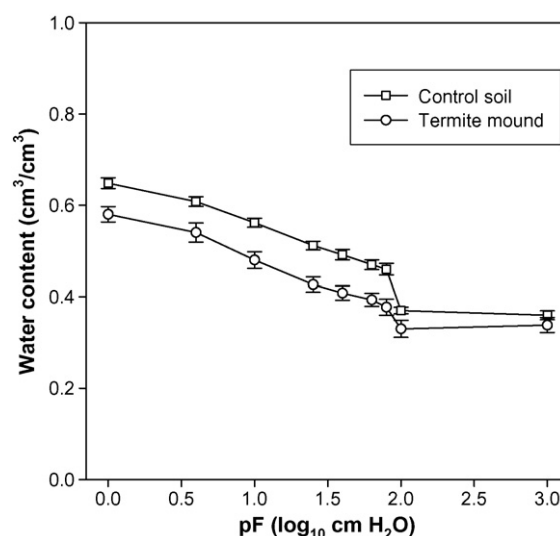


Fig. 1 – Water retention curve of termite mound and control soil from a secondary forest north of Manaus, Central Amazonia. Bars indicate standard error of the mean; n = 15.

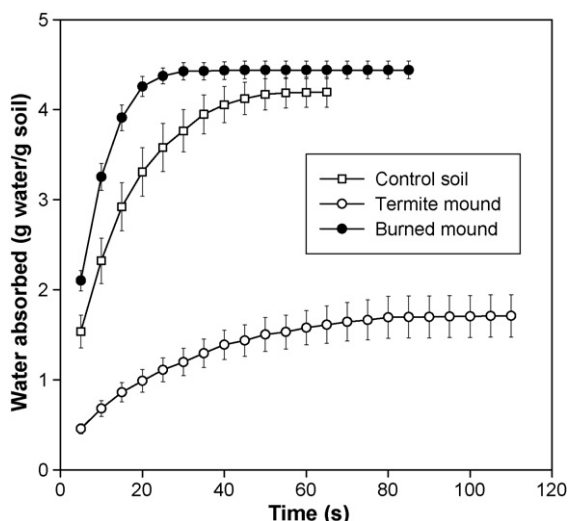


Fig. 2 – Cumulative water absorbed by soil clods over time. Termite mound and soil samples from a secondary forest north of Manaus, Central Amazonia. Bars indicate standard error of the mean; n = 10.

3.6. 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 ($P \leq 0.000$) (Fig. 3). A higher proportion of emergent seedlings were dicots in the termite mound than in the control soil (Fig. 3).

In the factorial experiment, there were significant interaction effects of termite mound and impedance ($P < 0.001$) and termites and autoclaving ($P \leq 0.05$) on the emergence velocity index (EVI) (Fig. 4). Reducing the impedance of the soil had a positive effect, increasing the EVI in termite mound material more than in soil material (Fig. 4). Alleviating the acidity constraint increased the EVI similarly in termite mound and control soil (Fig. 4). Autoclaving increased the EVI slightly in the termite mound material over the control soil (Fig. 4).

The grinding treatment produced a greater response in seedling height in termite mounds than in control soil ($P < 0.001$). Although seedling height increased significantly in response to the acidity alleviation ($P \leq 0.005$), the response was not dependent on the termite mound effect. Seedling height was not affected by the autoclaving treatment. Likewise, no difference in the germination of seeds in termite mound or soil solution was observed in the allelopathy assay.

Table 3 – Least squares means from segmented regressions of water absorption curves, where T_s is time to saturation, and θ is water content at saturation

	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

Superscripts of different letters indicate a significant difference ($P < 0.01$).

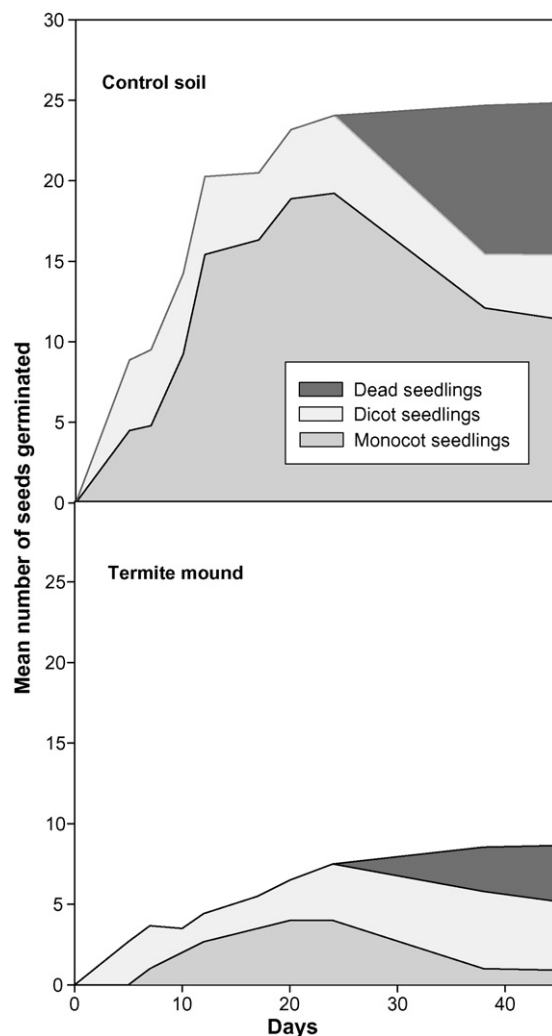


Fig. 3 – Mean number of seeds germinated from the seed bank in termite mound material and control soil from a secondary forest near Manaus, Central Amazonia.

4. Discussion

Five of the termite species collected had known mound-building habits: two are known not to be mound-builders, while the other three (*N. angusticeps*, *C. verruculosus*, and *T. fatalis*) exhibit variable habits (Constantino, 1999; Apolinário, 1993). Of these, *N. angusticeps* was only collected twice, and *C. verruculosus* and *T. fatalis* were each collected in only a single mound. So, from the results of the survey, no particular species was unequivocally responsible for construction of the mounds of the study site. Mound-building habits of Neotropical termite species are little described in the literature, and mound-building and inquiline species may cohabit and succeed each other in a single mound, making tracing the original builder of the mound difficult (Apolinário, 1993). Despite the variety of species likely to be involved in the building and maintenance 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 among mounds than between mounds and control soil.

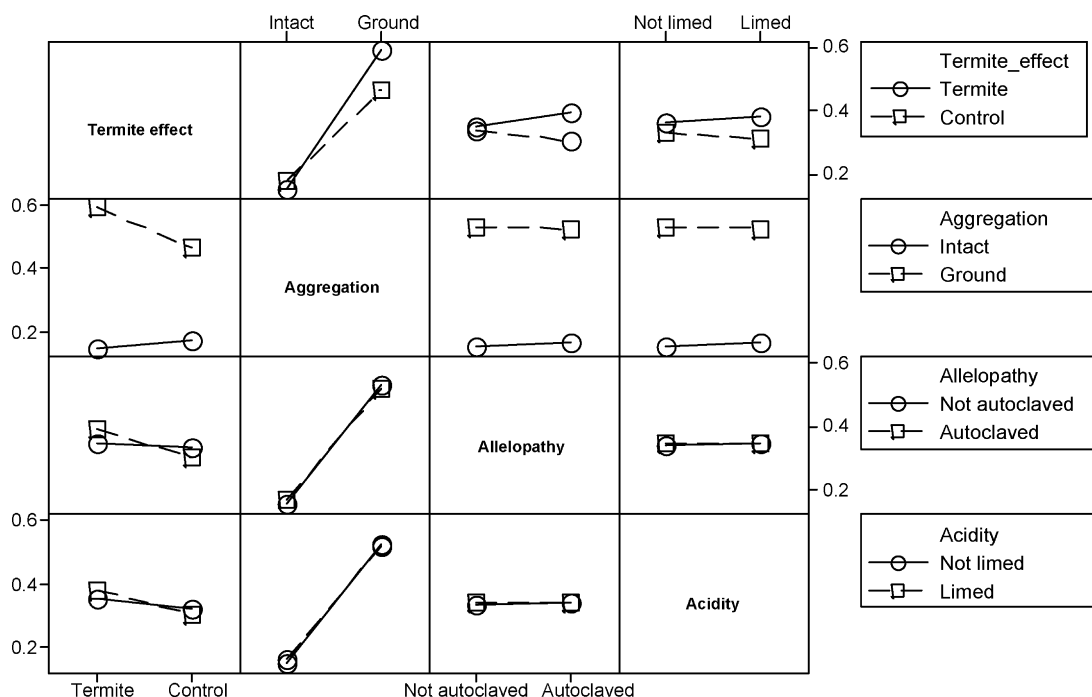


Fig. 4 – Interaction effects of four factors on the emergence velocity index (EVI) of *Sesbania exasperata* seeds ($n = 30$). Termite mound and soil samples from a secondary forest near Manaus, Central Amazonia, were subjected to various mechanical (grinding), chemical (liming), and heat (autoclaving) treatments to assess suppression of seedling germination and growth (see details in text).

The root biomass results demonstrated strong constraints 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 de Queiroz Moraes et al. (unpublished data) at a neighboring secondary forest site.

Ninety 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). Such 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 termite mound nutrients.

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 N constraints where limiting. None of the other nutrients appear 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 1), 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 show an elevated termite mound clay content (Holt and Lepage, 2000). This phenomenon is usually attributed to the termites' use of subsoil in the construction of their nests, or to 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. Also, the soil profile of the plateau soils has only a minimal texture gradient with depth.

Mechanical resistance to penetration was significantly higher on the termite mounds, and the bioassay confirmed this characteristic as a constraint for plant growth. Termite saliva and fecal matter used in mound construction have cementing properties (Adepegba and Adegoke, 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 indicate 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 managers in cases of abandoned termite mounds, it is not appropriate for mounds with active colonies, as multiple colonies can result (Krishna and Weesner, 1969).

As hypothesized, mechanical impedance was demonstrated to be an important factor for plants in this study, similar to the results of Rogers et al. (1999). However, this study also identified an important constraint of water availability in termite mounds. Termite mound water content was lower,

and appeared to be related to several factors. (1) The greater water infiltration rate observed in termite mounds 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 burned termite mound category had a greatly reduced water repellency and a greatly reduced carbon content (from 37 to 4 g kg⁻¹ C). Although fire is known for inducing water repellency in Amazonian pasture soils (Johnson et al., 2005). Doerr et al. (2003) found that at a particular range of high temperatures in other soils, water repellency is eliminated. While there was no burned control soil category, the results are congruent with the interpretation that the water repellency in termite mound material is due to an organic substance that combusts under high temperature. (3) 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 finely grinding the termite mound material. (4) The water retention curve demonstrated a lower water retention capacity of termite mound material. Under the heavy rainfall events of this region, swift drainage, water repellency, and low water retention would certainly be adaptive characteristics for termite colonies in cleared areas lacking canopy protection. Although the mean termite water content may be sufficient for vegetation growth, the relatively lower moisture conditions in the termite mound may mean a lower percentage of seeds successfully germinating relative to the adjacent soil.

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

The number of seedlings that grew in the termite mound material was lower than in the control soil. Although the 45-day length of this 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 germination and emergence from the soil, or (3) lower seed stocks in the termite mound due to seed erosion or predation from the surface of the termite mound. No 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). This phenomenon was not observed at our study site.

The termite mound density at the study site was higher than all but one of the values found in a 23-study literature search. 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) in the savanna of south-eastern Brazil, at 605 ha⁻¹. Although the mound abundance at our site was high, and the patchiness created in the landscape visually striking, the percent coverage amounted to only 3% of the area, equal to the area unavailable to plants due to dead wood remaining from clearing (unpublished data). The question of whether termite mounds are a real threat to productivity, or just a "visual" pest has been treated in literature (Constantino, 2002; Fernandes et al., 1998; Macedo, 1999), and these results may be further confirmation that the visual impact may not translate into actual impact on land availability.

Constraints to vegetation by termite mounds may not be the only matter of consideration to land managers. The elevated C, N, and K contents observed in this study, the ubiquitous populations of other soil fauna inhabiting the mounds, and the large stocks of dead wood in the landscape, beg the question as to what benefits the mound-building termites may provide in carbon storage, nutrient cycling, biodiversity, and nutrient cycling.

If land managers do find the extent of termite mound presence unacceptable, management practices to discourage mound building could be investigated. While as yet little is known about how specific land management practices affect termites in these ecosystems, Bandeira (1979) found the number of termite mounds to double between primary forest and pasture. Some species exhibit variable 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). It may be worth investigating whether land uses such as agroforestry systems or tree plantations that provide shade, as opposed to open pasture, may be able to reduce the incidence of mound building by providing a more tempered microclimate.

If mound-building termites are determined to be primarily wood-feeders, investigating management practices that encourage populations of soil-feeders over wood-feeders may be an interesting direction. Wood-feeders are found to predominate in disturbed areas (Filho, 2005). Dibog et al. (1999) found agricultural yield to be positively correlated with soil-feeding termite abundance, but not to termite abundance in general. Leaving less wood on the ground in cleared areas could be experimented with to make an area less vulnerable to termite mound proliferation, yet preserve the benefits of soil feeding termites. Both of these strategies could double as ways to increase agricultural productivity or aboveground biomass accumulation in succession.

5. Conclusions

Termite mounds at this secondary forest site constrain plant establishment through the physical strength of the mounds and their hydraulic characteristics that discourage water absorption and retention. Although the density of termite mounds per hectare was unusually high on this site compared to sites described in the literature, the actual percent land area occupied by the mounds was only 3%, a percentage which may

not necessarily be of concern to land managers in this region. Furthermore, this percentage loss in land area to productive vegetation may be offset by other services. Interesting topics for future investigation would be the role of mound-building termites in carbon storage, nutrient cycling, decomposition of standing dead wood stocks, and biodiversity in these landscapes.

Further studies to see how representative this study site is of other areas are warranted. Other areas for further research could include the longevity of the termite mounds, the fate of their nutrient stocks after abandonment, how additional cycles of clearing would affect their abundance, and how the landscape heterogeneity induced by the termite mounds affects the overall productivity of the ecosystem. Understanding the impact of mound-building termites on soil properties and nutrient cycling may be important in predicting vegetation dynamics in the ever-increasing areas of secondary forest in Amazonia.

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