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INFLUENCE OF LEAF-CUTTING ANT NESTS ON SECONDARY FOREST GROWTH AND SOIL PROPERTIES IN AMAZONIA

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Abstract. Leaf-cutting ants (*Atta* spp.) often increase in abundance following deforestation and may have an important effect on forest succession on abandoned land. In this study, we evaluated the effects of leaf-cutting ant (*Atta sexdens*) activity on physical and chemical properties of soil, root distribution, and tree growth in a 17-yr-old secondary forest in eastern Amazonia, Brazil. We compared the soil properties and root distribution in shafts excavated into five mature nests and at 15 m distanced from each nest mound. We evaluated the nest effects on vegetation measuring the stem diameter growth of nine tree species and predawn leaf water potential of the tree species, *Banara guianensis*, along a gradient of increasing distance from the nest mounds. The growth of seedlings (*Cecropia* sp.) in pots containing different proportions of mineral soil and organic matter removed from nest refuse chambers was also compared. The deep soil beneath *A. sexdens* nests at different depths (100, 200, and 300 cm) presented a low (fivefold, $P < 0.01$) resistance to penetration and was rich in Ca (three- to fourfold, $P = 0.06–0.02$), K (7–14-fold, $P < 0.05$), and Mg (two- to threefold, $P = 0.09$ for 200 cm depth) when compared to non-nest soil. These changes in nest soil properties were accompanied by increases in coarse root biomass (>2 mm diameter, three- to fourfold) and fine root biomass (<2 mm, 10–50 fold). However, stem diameter growth was generally not affected by distance from the nest. The growth of *Cecropia* sp. seedlings in a pot experiment was favored by the addition of organic matter from the refuse chambers. *Banara guianensis* trees experienced greater water stress (low predawn water potential) close to the nest mound, perhaps indicating increased competition for soil water that may have accompanied the proliferation of roots of several species in the nest. The competing *Atta* effects of defoliation vs. deep soil tillage and nutrient enrichment upon secondary forest growth are difficult to compare. *Atta*'s modification of soil physical and chemical properties point to its potential role in facilitating the rapid recovery of deep root systems and soil water uptake previously observed in this secondary forest.

Key words: *Amazon basin; bioturbation; forest succession; tropical forest; tropical soil.*

Introduction

In the Brazilian Amazon, more than 500 000 km^2 of closed-canopy tropical forest have been converted into cattle pastures and agricultural fields (Fearnside 1997, Houghton et al. 2000, Instituto Nacional de Pesquisas Espaciais [INPE] 2000). Approximately one-third of this converted land has been abandoned and now supports regrowth forests (Houghton et al. 2000) that remove large amounts of carbon from the atmosphere (Fearnside and Guimarães 1996), restore evapotranspiration and related hydrological functions of the mature forest (Hölscher et al. 1997, Jipp et al. 1998), reduce flammability of agricultural landscapes (Uhl and Kauffman 1990, Nepstad et al. 2001), and allow many native species of plants and animals to expand beyond residual fragments of mature forests (Nepstad et al. 1996, Gascon and Moutinho 1998). Regrowth forests have been observed to reestablish evapotranspiration rates similar to those of mature forests in 10–15 years following agricultural abandonment (Nepstad et al. 1995, Hölscher et al. 1997, Jipp et al. 1998). An important aspect of this recovery is the reestablishment of deep root systems (to 8 m depth) that supply the forest's evapotranspirational demands during the dry season (Jipp et al. 1998).

The rate at which forest recovery occurs on abandoned Amazon pastures is highly variable, and depends upon the intensity of land use prior to abandonment (Uhl et al. 1988). The initial stages of forest recovery on abandoned pastures can be limited by low rates of tree seed dispersal, seed and seedling predation by ants and rodents, soil moisture stress, and fire (Nepstad et al. 1995, 1996, Vasconcelos and Cherrett 1997, Moutinho 1998*a*). Little is known, however, about the factors that determine the rate of forest regrowth once trees are established. Leaf-cutting ants may slow forest regrowth by harvesting 12–17% of annual forest leaf production (Cherrett 1986). This presumably negative effect on forest regrowth may be counteracted, how-

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ever, by the positive effect of leaf-cutting ant nests on soil properties. Leaf-cutting ants excavate underground nests to 6 m or more (Hölldobler and Wilson 1990) creating specialized chambers in which they cultivate fungus. They then eat the fungus that they have cultivated on the harvested leaf and flower material. Additional chambers are also excavated for disposing of organic refuse. The nest mounds frequently cover 50–100 m^2. The density of *Atta* nests can increase 30-fold when primary forests are converted to pasture and crop land, and then abandoned to regrowth forest (Vasconcelos and Cherrett 1995).

Beyond the conspicuous effect that *Atta* species have on trees through leaf cutting and seedling predation, the nests that they excavate in the soil exert a potentially large but poorly understood effect on forests (Weber 1972, Farji-Brener and Illes 2000). The soil (0–2 m depth) beneath the nests of *A. cephalotes*, in Costa Rica, for example, was lower in density and higher in porosity than neighboring soils (Alvarado et al. 1981). Soil nutrient concentrations were higher beneath soil-surface refuse piles (0–20, 50–70 cm of depth) of *A. colombica*, where root density was also higher (Haines 1978, 1975). In Venezuela, soil nutrient concentration (0–20 cm depth) was higher beneath nests of *A. laevigata* (Farji-Brener and Silva 1995*a*). However, studies documenting both the effect of cutter ant nests on deep soils (>1 m) and the influence of these soil changes on the vegetation are rare (Farji-Brener and Illes 2000)

In this study, we examined the effects of leaf-cutting ant (*A. sexdens*) nest mounds on deep soil physical and chemical properties, soil water content, root distribution, and the growth of aboveground vegetation in a regrowth forest in eastern Amazonia. These field measurements were designed to test five hypotheses. *A. sexdens* (1) reduces soil resistance to penetration as a result of its excavation activities and its transport of organic matter into underground chambers; and (2) increases the concentration and stocks of plant-available nutrients through the deposition and subsequent decomposition of organic matter. If these predictions prove to be true, then *A. sexdens* should (3) stimulate root growth, thus increasing root biomass, root length density, and penetration; (4) reduce plant water stress by facilitating access to deep soil water through increased root biomass; and (5) increase the growth rates of plants growing near the nest.

METHODS

Study area

The study was conducted at Vitória Ranch (2°59′ S, 47°31′ W), located 6.5 km northwest of Paragominas, in the eastern Amazonian state of Pará. Paragominas is a regional logging and ranching center that was established in the 1960s (Nepstad et al. 1991). One-third of the forests surrounding this town had been converted to cattle pasture and approximately one-half of these pastures had been abandoned and overgrown with forest at the time of the study (Nepstad et al. 1999). Rainfall is highly seasonal, with monthly means of <55 mm from July through November and a mean annual total of 1830 mm (1969–1994, Jipp et al. 1998). Monthly weather station means for maximum daily air temperature ranged from 32 to 34°C and minimum temperatures from 20 to 21°C. Fazenda Vitoria is located on a Pleistocene terrace (Sombroek 1966), which is part of the Belterra clay formation (Clapperton 1993). The Oxisol (Haplustox) is 75–90% clay, mostly kaolinite, with moderate acidity (pH 5.0 in water at soil surface, range: 4.7–5.1). A layer of iron-oxide concretions occurs in the soil at depths from 6 to 12 m.

A 17-yr-old, 60-ha regrowth forest was chosen for study. The primary forest that once occupied this site was converted to pasture in 1969, planted with the forage grass *Panicum maximum*, and grazed at high densities (>1 head/ha). It was burned two or three times prior to abandonment in 1976. Cattle had access to the site through 1984. At the time of the study (1994–1995), live aboveground biomass of the regrowth forest was 51 Mg/ha (Moutinho 1998*b*), which is 15% of the biomass measured in primary forest (Nepstad 1989). The study forest supported a mean of 12 tree species (dbh > 5 cm) per 100 m^2 (Moutinho 1998*b*). Of the 42 tree species identified in the regrowth forest, nine (21%) were frequently harvested by *Atta sexdens* (Moutinho 1998*b*).

Identification and nest excavation

In a 25-ha plot of the regrowth forest, all of the identified *Atta sexdens* nests were mapped. Voucher specimens of ants were deposited in collections of the Museu Paraense Emílio Goeldi, in Belém, Brazil. We determined the influence of leaf-cutting ants on the secondary forest by comparing the soil and vegetation close to and far from *A. sexdens* nests. A total of 10 mature nests among those identified during the nest mapping were selected for the study of nest effects on soil and were identified by letters (A, C, D, E, G, I, L, P, Q, and R). For five nests (A, C, E, G, and I), we manually excavated a shaft (0.8 × 1.8 × 3 to 4 m deep) at the center of the nest mound (usually the highest point of the mound) and another shaft 15 m from the edge of the mound, in a randomly selected direction (Fig. 1). For each shaft dug at the nest center, we measured the area of intersection between the shaft wall and the subterranean chambers of the nests, and classified them as fungal garden, refuse chamber, loose soil chamber, or empty chamber. We used the five unexcavated nests (D, L, P, Q, and R) to expand our study of nest effects on tree growth and water stress.

Soil physical analyses

Soil resistance to penetration was measured in 10 shafts (at the center of the nests and 15 m away from

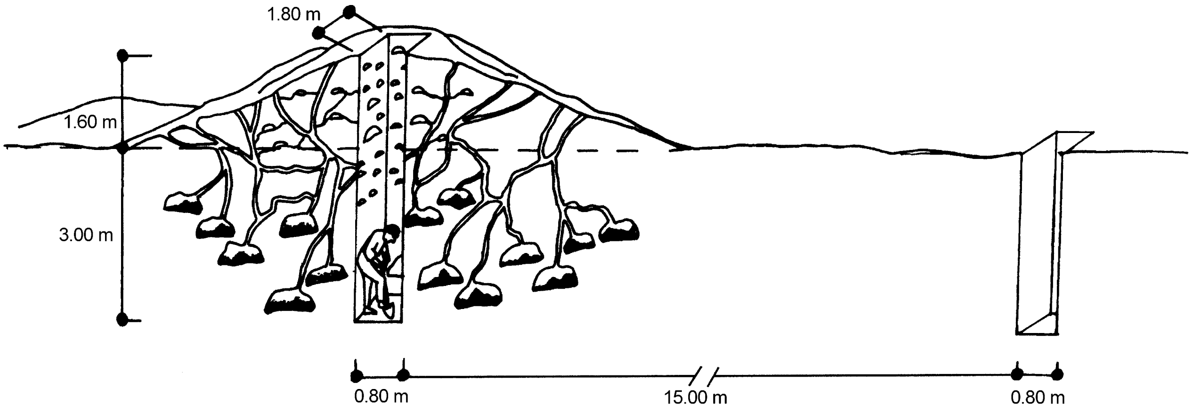

FIG. 1. Schematic design regarding the methodology employed in the excavation of the shafts in the nests and in their respective adjacent areas. The chamber filled with black dots represents the refuse chambers. The others are the fungus chambers. The shape of refuse and fungus chambers do not correspond necessarily to those found during the nest excavation.

nests A, C, E, G, and I) at depths of 10, 50, 100, 200, and 300 cm. Resistance was also measured at two depths in the nest mounds. At each randomly selected measurement location on the shaft wall, a 1-cm layer of soil was removed to reduce soil compaction that may have been caused by the shaft excavation. The measurement position was sprayed with water to reduce the effects of moisture content on resistance to penetration, which we measured using an Eijelkamp penetrometer (Giesbeek, The Netherlands). Five measurements were made per depth in each shaft.

Water retention curves were determined for four intact soil cores at each sampling depth in nest C and in the adjacent non-nest soil shaft using soil moisture pressure plates of the Empresa Brasileira de Pesquisa Agropecuária EMBRAPA Amazônia Oriental. Soil bulk density was measured for these cores and total porosity was calculated from bulk density, assuming a mean soil particle density of 2.5 g/cm^3. Soil microporosity was estimated as being equal to the volumetric soil water content at −6 kPa soil water tension. Macroporosity was estimated as the difference between total porosity and microporosity.

Soil water analyses

Volumetric water content (in cubic centimeters of water per cubic centimeter of soil) of the soils was

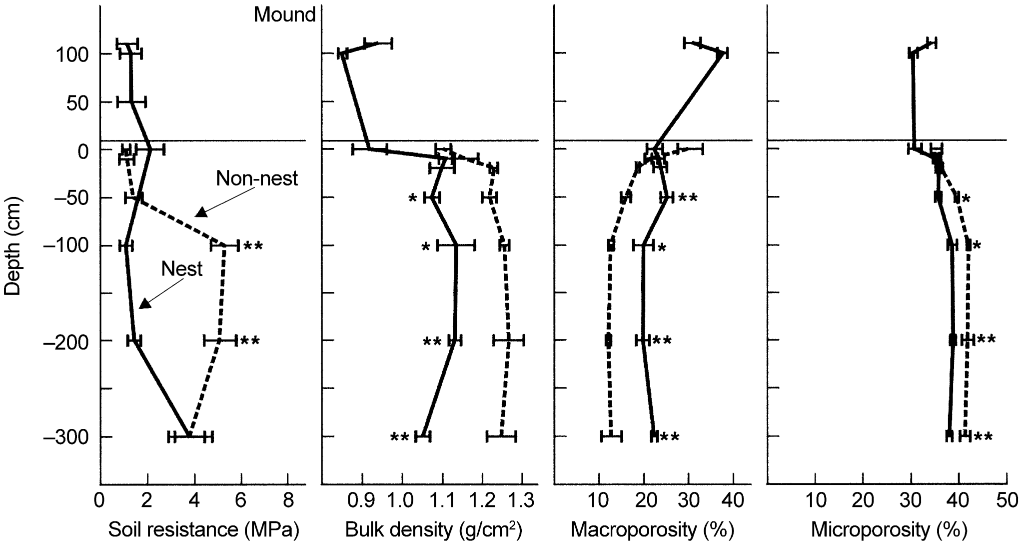

FIG. 2. Physical parameters of the soil. (A) The values of soil resistance to penetration are means of the means of the resistance values recorded (four recordings per depth interval per nest) in 10 nests and 10 non-nest soil samples in the secondary forest of Vitoria Ranch. (B) The soil bulk density and the soil porosity for one *Atta sexdens* nest soil sample and one non-nest soil sample in the secondary forest. The values are means of four measurements per depth interval. The horizontal bars represent the standard error for means of soil resistance, soil bulk density, and porosity across replicate samples of a single pit. The continuous horizontal line indicates the original surface of the soil under the nest mound. Presence of statistical differences at significance levels of $P < 0.05$ and $P < 0.01$ (one-way ANOVA) between nest soil and non-nest soil for each depth are indicated by * and **, respectively.

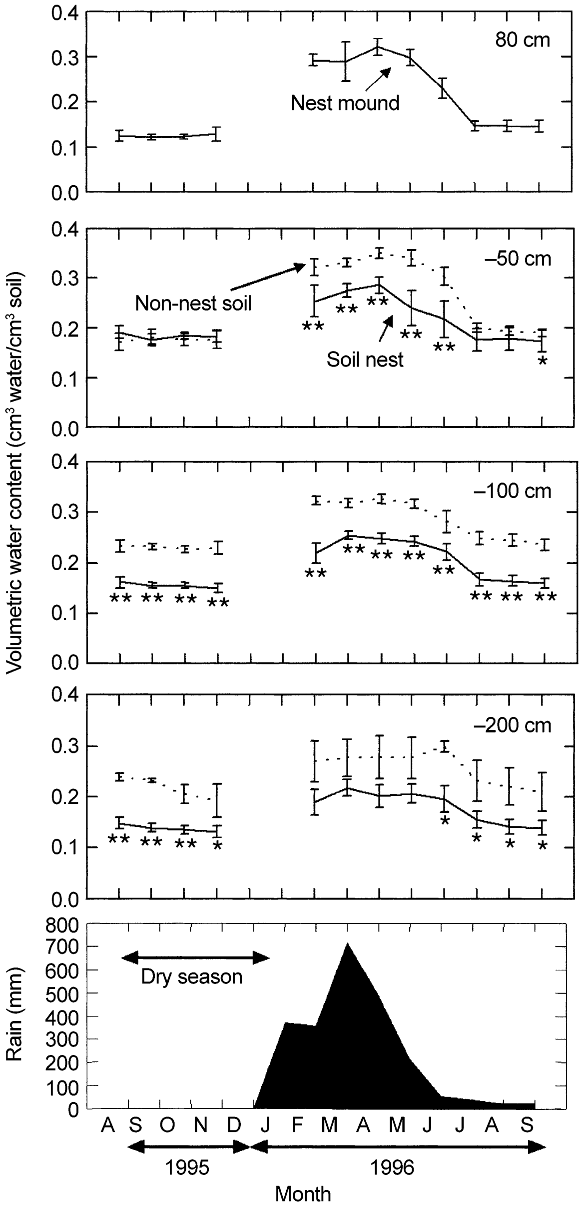

FIG. 3. Means of volumetric water content in the nest mound (+80 cm) and at 50, 100, and 200 cm depths in the nest and non-nest soil ($n = 5$) at Vitória Ranch, Paragominas, Pará, Brazil. The vertical bars represent ±1 SE. Monthly rainfall is presented in the bottom panel. Data are missing for December 1995 and January 1996. The presence of statistical differences at significance levels of $P < 0.05$ and $P < 0.01$ (one-way ANOVA) between nests soil and non-nest soil for each TDR sensor depth are indicated by ★ and ★★, respectively.

measured monthly in 10 shafts (at the center of nests A, C, D, E, and G and 15 m away from each of these) using time domain reflectometry (TDR; Topp et al. 1980, Topp and Davis 1985) with probes that we designed and calibrated at the study site in an earlier study (Jipp et al. 1998). In each shaft, one TDR sensor was installed at 50, 100, and 200 cm depth; one additional sensor was installed in the mounds of each of the nest shafts at 30 cm depth. To avoid shaft influence on soil water, the sensors were installed at the ends of 1.5-m holes excavated horizontally into the shaft walls, which were then refilled with soil.

Soil chemical analyses

We measured nest influence on soil chemical characteristics by comparing soil samples taken from six shafts (at the centers of nests C, G, and I and 15 m away from these). In each shaft, four 150–200 g soil samples were taken at 10, 50, 100, 200, and 300 cm depths. Two additional sets of samples were taken in the nest mound (10 and 50 cm depth). In the nest shafts, samples were taken from intact soil that had not been excavated by ants. Two to five samples were also taken from each of the refuse and loose soil chambers that intersected the shaft walls. Soil samples were dried at 60°C for a minimum of 24 h, manually ground and stored in plastic bags. Soil chemical analysis included soil pH in water in a 1:25 soil mass solution volume ratio, potassium (K) and phosphorus (P) extracted in Mehlich I solution, and exchangeable calcium (Ca) and magnesium (Mg) extracted with 1 mol/L KCl solution (5 g soil : 50 mL of solution) (Empresa Brasileira de Pesquisa Agropecuária [EMBRAPA Amazônia Oriental] 1979, Van Raij 1994). P, Ca, and Mg in the extracts were determined using an inductively coupled plasma source mass spectrometer (ICP-MS; Durrant 1992). Potassium was determined by atomic absorption. Total carbon was quantified with a Leco CR 12 analyzer (St. Joseph, Michigan, USA) which first combusts samples in an oxygen environment followed by quantification of CO_2 in its infrared gas analyzer. Total N was measured using the Kjeldahl method. Finally, nitrate (NO_3^-) was determined from field-moist soil samples (15 g) extracted in 100 mL of 2 mol/L KCl. The soil–KCl solution was shaken for one hour on an orbital shaker and allowed to settle overnight. A 20-mL aliquot of the supernatant was removed, filtered through a 45-μm polysulfone membrane, and frozen for later analysis. The analysis was done on an Alpkem autoanalyzer (Saskatoon, Saskatchewan, Canada) using a modified Griess-Illosvay procedure for determination of NO_3^- (Bundy and Meisinger 1994). To estimate nutrient stocks, soil concentrations were multiplied by bulk density and depth increment.

Root biomass, distribution, and diversity

We measured the mass and vertical distribution of coarse roots (diameter >2 mm) in four nests (A, C, G, and I) by separating roots during shaft excavation at depth intervals of 0–10, 11–50, 51–100, 101–200, and 201–300 cm and nest mound. Roots were washed, dried to constant mass at 60°C, and weighed. These coarse roots were also sorted into morphospecies following Restom (1998).

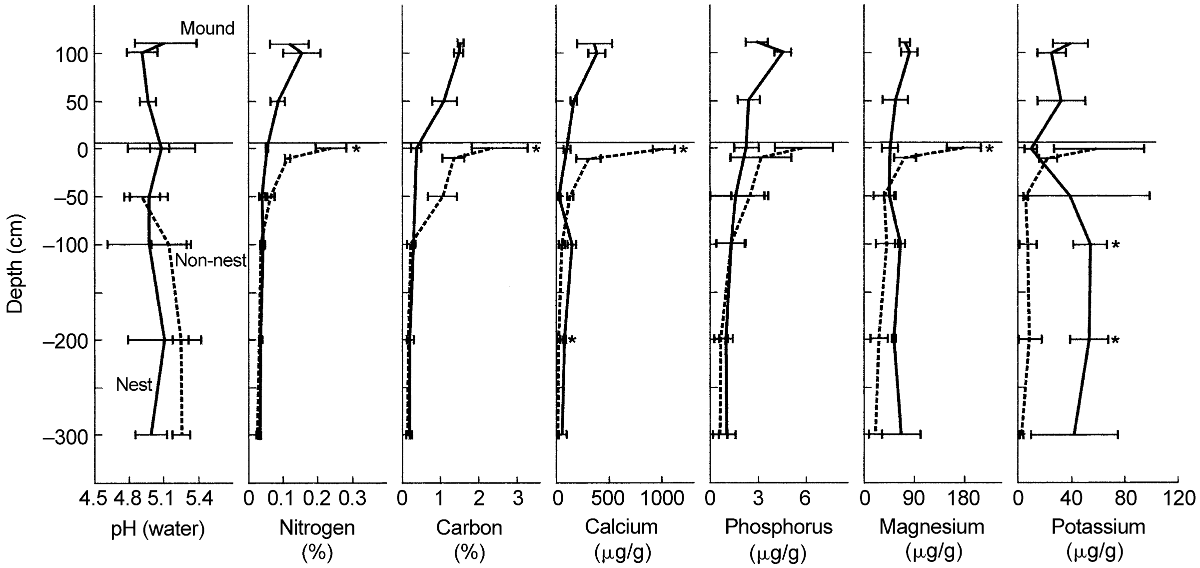

FIG. 4. Extractable nutrients and pH in the soil of three *Atta sexdens* nests and three non-nest areas ($n = 4$ soil samples per depth interval per shaft) at Vitória Ranch, Paragominas, Pará, Brazil. The continuous horizontal line indicates the original surface of the soil under the nest mound. Presence of statistical difference ($P < 0.05$, one-way ANOVA) between nests soil and non-nest soil for each depth is indicated by *.

In the same shafts, and at the same depth intervals, we measured fine root (<2 mm diameter) biomass and vertical distribution. In each shaft, four 1-kg (800 cm^3) samples per depth interval were taken in the shaft wall using an auger. We also took two or three samples of 800 cm^3 from each of the refuse and loose soil chambers intersected by the shaft wall. Soil samples were stored at 2–5°C until processed for root removal. Each sample was placed in a bucket with 10 L of water and mixed for 30 min. All roots that floated to the water surface were stored in 50% ethanol. The water and suspended soil were poured through a 0.3 mm mesh sieve to collect suspended roots. This mixing and sieving was repeated three times, at which point >90% of the soil sample had gone into suspension and passed through the sieve, with roots retained in the sieve. Roots were then removed from the remaining soil through visual inspection. All roots were stored in 50% ethanol.

Using a 10× dissecting microscope, we separated the fine roots in each sample into small (0–1.0 mm diameter) and large (1.1–2.0 mm) categories. Sorted samples were dried at 65°C and weighed. We determined the root length density (root length per soil volume) multiplying the live, fine root dry mass by the ratio of fine root length to dry mass calculated by Nepstad (1989).

Tree growth and water stress

We tested the hypothesis that ant nests enhance tree growth by measuring changes in diameters of stems >2 cm within a 40-m radius of five nests (3.5 ha). Stem diameter was measured at 6-mo intervals at marked positions on the stems of nine tree species (*Banara guianensis*, *Chameacrista* sp., *Cecropia palmata*, *Rollinia exsucca*, *Poecillanthe effusa*, *Visma guianensis*, *Zanthoxylum rhoifolia*, *Ocotea grandifolia*, and *Casearia grandifolia*).

We also examined nest influence on tree growth by comparing seedling growth in soil containing varying ratios of mineral soil and organic refuse from nest chambers. Seedlings of *Cecropia* sp., a common species in our study site, were established from seeds in 60 pots (one seedling per pot), divided into groups of 15 pots per treatment. The four treatments consisted of 1:9, 1:1, 9:1, and 1:0 proportions of mineral soil to organic refuse and associated loose soil from eight refuse chambers from three nests used as the potting medium. The mineral soil was excavated from the walls of a soil shaft far from nest influence, at a depth of 4 m. Seedling height was measured at 15-d intervals for a total of 115 d. Pots were watered every 2 d with deep (~50 m) well water. This experiment was conducted in a shade house (27% of full sun) at the study site.

Finally, we tested the hypothesis that ant nests influence tree water stress by measuring pre-dawn leaf water potential of *Banara guianensis* trees established on and outside nest mounds. We measured the water stress on leaves of three small branches per tree, cut about 1 hour before sunrise, during the 1995 dry season (August through November), using a pressure chamber.

Statistical analyses

We used one-way ANOVA to assess statistical differences in soil physical and chemical parameters and soil water content between nest and non-nest soils. The effect of nests on tree growth was tested for each tree

TABLE 1. Comparison of nutrient concentrations and pH among refuse chambers, deep soil of nests of *Atta sexdens* (n = 3 nests), and soil without nest influence (non-nest soil) in a secondary forest on the Vitória Ranch, Paragominas, Para, Brazil.

	pH		Total (%)		
Source	H_2O	KCL	N	C	Ca
Refuse chamber	4.40 ± 0.08	4.70 ± 0.08	2.60 ± 0.12[a]	19.5 ± 5.91[a]	2179 ± 246[a]
Nest soil	4.97 ± 0.48	4.69 ± 0.25	0.034 ± 0.003[b]	0.223 ± 0.039[b]	95.4 ± 14.2[b]
Non-nest soil	5.15 ± 0.20	4.67 ± 0.27	0.031 ± 0.002[b]	0.178 ± 0.047[b]	27.7 ± 12.9[b]

Notes: Means (± 1 SE) were calculated for each nest soil and non-nest soil from four soil samples collected at each depth (100, 200, and 300 cm) totaling 12 samples per nest. Nutrient concentration means from refuse chambers were calculated from a total of 20 samples (2–5 samples per refuse chamber, 3–13 cavities sampled per nest) of refuse chamber material collected in three nests. The superscript letters a and b indicate the statistical comparison between the nest and non-nest means for each season. Different letters indicate the presence of statistical difference (one-way ANOVA, $P < 0.05$).

species by a simple linear regression between stem growth rate (dependent variable) and distance (independent variable) from the edge of the nest mound. The same regression test was used for predawn leaf water potential (dependent variable) of *Banara guianensis* trees. The differences in seedling growth among soil mixture treatments in the pot study were analyzed by one-way ANOVA. All analyses were accomplished with SYSTAT (SPSS, Chicago, Illinois, USA).

RESULTS

Nest density, size, and structure

Nest density in the 25-ha secondary forest of Vitoria Ranch was 2.5 nests/ha, and the mean mound area of the 10 nests selected for this study was 73 ± 23 m^2 (mean ± 1 SE). Hence, nest mounds covered ~200 m^2/ha, or 2% of the secondary forest soil surface.

The portion of shaft walls that intersected nest chambers was highly variable, ranging from <1% of the shaft wall surface (nests E and I) to 30% (nest A). Chambers intersected 3–7% of the shaft wall surface of the remaining two nests excavated (nests C and G). Fungal garden chambers were restricted to the upper 1 m of soil, and also occurred in the nest mound. Refuse chambers were encountered primarily at depths of 1–3 m. We did not find chambers on walls of non-nest shafts.

Nest effects on soil properties

Soil resistance (mean ± 1 SE) to penetration was significantly lower in the nest soil (1.2 ± 0.3 MPa and 1.3 ± 0.2 MPa at depth of 100 and 200 cm, respectively) than in the non-nest soil of secondary forest (5.0 ± 0.5 MPa and 4.9 ± 0.3 MPa; $n = 5$, $P = 0.001$; Fig. 2). Resistance to penetration, however, was similar in nest and non-nest soils at 0–50 and 300 cm ($P > 0.30$) depths, and was low (1.5 MPa) in the nest mound (Fig. 2).

The lowest bulk density (~0.8 to 0.9 g/cm^3) was encountered in the nest mound. Consistent with this lower bulk density, the ant nest soil also had higher macroporosity than non-nest soil (Fig. 2). In contrast, microporosity of nest soil was lower than that of non-nest soil (Fig. 2).

Volumetric soil water content was significantly ($P < 0.05$) lower in nest soil profile during the dry season (range of means 0.13–0.18 cm^3/cm^3) and wet season (0.21–0.24 cm^3/cm^3) than in the soil profile away from the nest in the dry and wet seasons (0.19–0.23 cm^3/cm^3 and 0.28–0.34 cm^3/cm^3, respectively, Fig. 3). The means (±1 SE) of volumetric soil water content of nest mound soil was 0.12 (±0.03) cm^3/cm^3 during the dry season and 0.29 (±0.03) cm^3/cm^3 in the wet season (Fig. 3).

At 50 cm soil depth and above (including the nest mound), the pH of soil in nests was similar to the pH of adjacent non-nest soil. Below 50 cm depth, however, where the refuse chambers occurred in the nests, the nest soil tended to have lower pH than the non-nest soil (Fig. 4), but these differences were not statistically significant ($P = 0.80$). However, at 300 m depth the differences was nearly significant ($P = 0.09$). The availability of some soil nutrients to plants in soil samples collected from 100 to 200 cm was higher in the nest soil, such as Ca (three- to fourfold; $P = 0.065$, 100 cm and $P = 0.019$, 200 cm depth), Mg (two- to threefold; $P = 0.095$, 200 cm depth), P (1.5- to twofold; $P = 0.41$, 100 cm depth) and K (3–14-fold; $P = 0.012$, 100 cm and $P = 0.025$, 200 cm depth; Fig. 4). Nitrate was highly variable among nests but was more abundant in deep nest soil. The means (±1 SE) of nitrate concentration at 200 and 300 m of depth in the soil nest were 67 (±36) mg/g and 107 (±86) mg/g, respectively, compared to 0 mg/g at 200 m and 0.48 (±0.48) mg/g at 300 cm in soil without nest influence. The differences between nest soil and non-nest soil concentrations of nitrate were statistically significant at 200 m (Mann-Whitney Test, $U = 9$, $n = 3$, $P = 0.037$) and nearly statistically significant at 300 m ($U = 6$, $P = 0.076$). At the other depths the nitrate concentration was relatively low (<3.0 mg/g) and not different between nest soil and non-nest soil.

The nutrient concentration inside the refuse chambers found between 100 and 300 cm depth was higher for all elements analyzed when compared with the nest soil (i.e., soil beside the refuse chambers) and soil of adjacent secondary forest (Table 1). There was a trend for higher nutrient stocks in nest soil than non-nest

TABLE 1. Extended.

Exchangeable (μg/g)		
Mg	P	K
892.1 ± 50.1^{a}	252.9 ± 37.6^{a}	602.6 ± 60.9^{a}
61.6 ± 6.4^{b}	1.1 ± 0.46^{b}	49.6 ± 14.3^{b}
30.4 ± 9.8^{b}	0.84 ± 0.43^{b}	6.3 ± 3.9^{b}

soils for K ($P = 0.02$), Ca ($P = 0.05$), and Mg ($P = 0.06$), but not for N, C, or P (Table 2).

Nest effects on plant

The mean (±1 SE) of cumulative coarse root biomass in the nest soil profile (1.04 ± 0.2 kg/m^2) was significantly higher than in non-nest soil (0.34 ± 0.05 kg/m^2, $P = 0.044$, Table 3). Sixty-six percent (0.69 kg/m^2) of total coarse root biomass was concentrated in the soil mound. Only in nest soil did coarse roots appear below 200 cm depth, representing 3% of the total biomass (Table 3). The mean number (±1 SE) of coarse root species was larger in nest soil (4 ± 1 species/m^3, $n = 3$) than non-nest soil (3 ± 1 species/m^3; $P = 0.091$).

The total fine root biomass and fine root length density is length per unit volume and was higher in the nest soil than in non-nest soil for several of the depth increments (Table 4). The mean (±1 SE) of integrated values (in kilograms per cubic meter for each depth multiplied by the height of the depth interval in meters) of root biomass from 0 to 4 m depth (including nest mound) for nest soil and non-nest soil were 2.34 (±0.19) kg/m^2 and 0.57 (±0.09) kg/m^2, respectively ($P = 0.001$). The total integrated root length of nest soil (42.4 ± 4.36 km/m^2) and non-nest soil (9.7 ± 1.45 km/m^2) were also statistically different ($P = 0.03$; Table 4). Thirty percent of the total length and biomass of fine roots in nest soil occurred at depth >100 cm, compared to only 10% of the fine root biomass and length occurring below 100 cm in soil of non-nest soil (Table 4). The contribution of refuse chambers to total fine-root biomass, however, was dependent on the soil volume occupied by these chambers, which is highly variable (between 1 and 30% of total soil volume under the ants' influence) and represented <3% of total fine root biomass in the nest soil.

A total of 1227 trees distributed among nine species, established on and near the nests, were monitored for stem diameter growth. *Rollinia exsucca* was the most abundant, followed by *Banara guianensis*, *Poecilanthe effusa*, and *Casearia grandiflora*. *R. exsucca* had the highest stem diameter growth rate (1.03 ± 0.88 cm/yr), followed by *Oecotea laxiflora* (1.01 ± 0.94 cm/yr), *Vismia guianensis* (1.01 ± 1.13 cm/yr), and *Cecropia* sp. (0.93 ± 0.75 cm/yr). The other tree species presented growth rates between 0.23 and 0.58 cm/yr. For most tree species, the stem growth rates had no significant relationship with distance from the nest centers. For the two species that showed significant relationships between growth and distance from the next, the relationship was negative for *Chamaecrista* sp. and positive for *O. grandifolia* (Table 5).

The predawn water potential of *B. guianensis* trees established on nest mounds (within a 10 m radius) was lower (−0.51 ± 0.03 MPa, mean ± 1 SE) than those that of trees occurring outside (−0.32 ± 0.02 MPa, $n = 25$, $P = 0.012$) of the nest. The regression of water potential and distance from the nest centers was statistically significant but very weak ($n = 73$, $r^2 = 0.07$ $P = 0.022$, analyses of log-log transformed data; Fig. 5).

After 115 d of growth in pots, the seedlings of *Cecropia* sp. planted in soil of 50 and 90% material from nest refuse chambers were five times taller than those planted in pots with low (10% and 0%) chamber refuse additions (Fig. 6).

DISCUSSION

Various effects of *Atta* nests on soil and plant processes have been previously shown (see Farji-Brener and Illes 2000). Most of these studies have reported positive effects of *Atta* nests on soil physical properties and fertility, but they were limited to analyses only of near-surface soil (0–50 cm). Our results extend the influences of *Atta* nests to deep soils (2–3 m), indicating that *Atta sexdens* plays a very important role in bioturbation, changing properties of enormous soil volumes.

TABLE 2. Extractable nutrient stocks (in kilograms per hectare) in nest soil of *Atta sexdens* and in soil without nest influence ($n = 3$) in a secondary forest.

	Nest soil				
Element	Nest mound (height 1.6 m)	(depth 0–4 m)	Total	Non-nest soil (depth 0–4 m)	*P*
Nitrogen (N)	9960 ± 3200	15 000 ± 1200	25 700 ± 3000	21 650 ± 1300	0.30
Carbon (C)	11 200 ± 230	101 500 ± 34 000	216 000 ± 31 000	200 000 ± 43 000	0.78
Calcium (Ca)	2400 ± 600	4000 ± 1000	6400 ± 700	3500 ± 780	0.05
Magnesium (Mg)	600 ± 180	2500 ± 450	3000 ± 200	1800 ± 460	0.06
Phosphorus (P)	2.8 ± 0.6	5.3 ± 3.6	8.2 ± 2.0	6.0 ± 3.0	0.59
Potassium (K)	230 ± 12	1850 ± 80	2700 ± 400	400 ± 200	0.02

Notes: The nutrient stocks were integrated to 4 m soil depth and nest mound (mean ± 1 SE). *P* values from the one-way ANOVA comparisons between total nutrient stocks for nests and non-nest soil are given. Total nutrient stocks were integrated to 4 m using the soil bulk density by depth increment (0–10, 10–50, 50–100, 100–200, 200–300, and 300–400 m).

TABLE 3. Means (±1 SE) of coarse root biomass in nests of *Atta sexdens* ($n = 4$) and in soil without nest effect in a secondary forest.

Depth interval (cm)	Biomass (kg/m^2)†		Cumulative total (kg/m^2)	
	Nest soil	Non-nest soil	Nest soil	Non-nest soil
Nest mound (height)				
101–110	0.18 ± 0.06	···	0.18	···
51–100	0.36 ± 0.21	···	0.54	···
0–50	0.15 ± 0.05	···	0.69	···
Below ground (depth)				
0–50	0.14 ± 0.07	0.30 ± 0.06	0.83	0.30
51–100	0.08 ± 0.03	0.03 ± 0.01	0.91	0.33
101–200	0.06 ± 0.02^{a}	0.005 ± 0.01^{b}	0.97	0.34
201–300	0.03 ± 0.02	0	1.00	0.34
301–400	0.04 ± 0.01	0	1.04 ± 0.25^{a}	0.34 ± 0.05^{b}

Notes: The superscript letters a and b indicate the statistical comparison between the nest and non-nest means. Different letters indicate the presence of statistical difference (one-way ANOVA, $P < 0.05$).

† Calculated by multiplying values in kilograms per cubic meter by the depth interval (in meters).

The ants of our study area excavated chambers in the soil to depths of more than 4 m, comprising 1–30% of the soil volume, and deposited excavated soil in mounds of ~1 m height above the original soil surface. We found newly deposited red soil (2.5 YR 5/8; Munsell Color Charts, Macbeth Division of Kollmorgen Instruments Corporation, Baltimore, Maryland, USA) on the nest mounds that matched the color of soil beneath 5 m depth in the soil shafts, as soil of the upper horizons (0–5 m) was yellow (10 YR 7/8) or reddish yellow (7.5 YR 7/8). The ants introduced clipped leaves, flowers and fruits into the fungal garden chambers that they excavated near the soil surface (0–1 m depth), and they moved the nest organic debris and loose soil into refuse chambers deeper in the soil (1–3 m depth).

The soil of the ant nests had lower resistance to penetration, lower bulk density, and higher concentrations of some plant available nutrients (Ca, Mg, K, and nitrate) than nearby soil with little nest influence. Both the reduction in resistance to penetration and the increase in macropore volume in the nest soil may be the result of aggregation of clay particles induced by diffusion of organic acids and cations into this ''intact'' soil from fungal garden and refuse chambers. Organic matter can increase the aggregation of soil, thereby decreasing resistance to penetration and increasing soil macroporosity (Uehara and Gilman 1981, Oades et al. 1989). Cations can also form bridges between soil particles, further aggregating the soil (Paul and Clark 1996).

Also, our study supports the hypothesis that detritus deposited in subterraneous chambers by *Atta sexdans* increases the concentrations of available nutrients. Lower resistance to penetration and increased nutrient availability may explain the observed proliferation of fine roots in the nest soil. A similar result was observed for *A. colombica* in Costa Rica (Haines 1975, 1978), but that species deposits detritus on the soil surface, not in buried chambers. Other *Atta* species, such as *A.*

TABLE 4. Mean (±1 SE) of fine root biomass and length in nest soil of *Atta sexdens* and non-nest soil ($n = 3$) in a secondary forest and presence of statistical differences between pairs of means for $P < 0.05$ (one-way ANOVA).

Depth interval (cm)	Mean of biomass (kg/m^2)			Mean of total length (km/m^2)†		
	Nest soil	Non-nest soil	*P*	Nest soil	Non-nest soil	*P*
Nest mound (height)						
110	0.06 ± 0.01			10.52 ± 2.41		
100	0.27 ± 0.05			11.55 ± 1.93		
50	0.32 ± 0.07			11.62 ± 2.70		
Below ground (depth)						
0–50	0.14 ± 0.03	0.31 ± 0.04	0.030	5.30 ± 1.23	4.31 ± 0.46	0.105
51–100	0.12 ± 0.02	0.18 ± 0.05	0.365	4.31 ± 0.53	2.84 ± 0.81	0.466
101–200	0.68 ± 0.20	0.04 ± 0.02	0.033	12.42 ± 4.00	1.79 ± 0.72	0.059
201–300	0.25 ± 0.06	0.03 ± 0.01	0.027	4.52 ± 1.20	0.58 ± 0.21	0.025
301–400	0.49 ± 0.22	0.01 ± 0.00	0.101	9.22 ± 4.23	0.23 ± 0.07	0.101

† Values in kilometers per square meter calculated by the relationship between root mass (in grams) and root length (in kilometers) according to Nepstad (1989; 1.895 km : 1 g for roots of diameter <1 mm and 0.155 km : 1 g for root diameters between 1 and 2 mm) and multiplying the results by depth interval (in meters).

TABLE 5. Mean (±1 SD) stem diameter growth rates (in centimeters per year) for nine tree species growing within a 40 m radius (total ~3.5 ha) of seven *Atta sexdens* nests and summary of regression analyses showing relationship between distance (in meters) from nest center and stem growth rates.

Tree species	Stem growth rate (range)	n	Results of regression analyses: Equation	r^2	P
Chamecrista sp.	0.41 ± 0.41 (0–2.3)	83	$y = -0.01x + 0.62$	0.07	0.015
Cecropia sp.	0.93 ± 0.75 (0–3.4)	60	$y = 0.01x + 0.71$	0.03	0.209
Rolinea exsucca	1.03 ± 0.88 (0–3.9)	144	$y = -0.00x + 1.12$	0.00	0.524
Poecilanthe effusa	0.25 ± 0.38 (0–3.2)	318	$y = -0.00x + 0.27$	0.00	0.557
Vismia guianensis	1.01 ± 1.13 (0–3.9)	44	$y = 0.00x + 0.95$	0.00	0.888
Oecatea laxiflora	1.01 ± 0.94 (0–3.1)	85	$y = 0.04x + 0.33$	0.11	0.002
Banara guianensis	0.43 ± 0.59 (0–3.8)	314	$y = -0.00x + 0.46$	0.00	0.735
Casearia grandifolia	0.58 ± 0.46 (0–3.4)	204	$y = -0.00x + 0.63$	0.06	0.355
Zanthoxylum rhoifolia	0.23 ± 0.19 (0–0.8)	25	$y = -0.01x + 0.38$	0.13	0.073

cephalotes, do not appear to affect fine root growth (Farji-Brener and Medina 2000). Cecropia seedlings grew significantly faster in a pot study when grown in a medium with at least 50% material from the detritus chambers of the nests that we studied, which is consistent with exceptional root proliferation in the refuse chambers of nests in the field.

The volumetric soil water content was consistently lower in the nest soil and always below field capacity (i.e., always less than the volumetric water content when all micropores are filled with water). The differences in water content between nest and non-nest soils are larger than differences in porosity between nest and non-nest soil, so the effect cannot be explained by changes in soil water holding properties alone. Roots proliferated in the relatively penetrable, nutrient-rich nest soil, with 2–12 times more coarse roots (>2 mm diameter) and 10–50 times more fine roots than in nearby non-nest soil. This dense network of fine roots in the nest soil may absorb a disproportional amount of water from nest soil vs. non-nest soil to supply the forest's transpirational water demand, thereby preventing soil water content from reaching field capacity in the nests. It is also possible that water inputs to the nest are lower than water inputs to the non-nest soil. The domed mound above the soil may direct some throughfall away from the nest. The channels in the nest may also drain incoming water before the intact

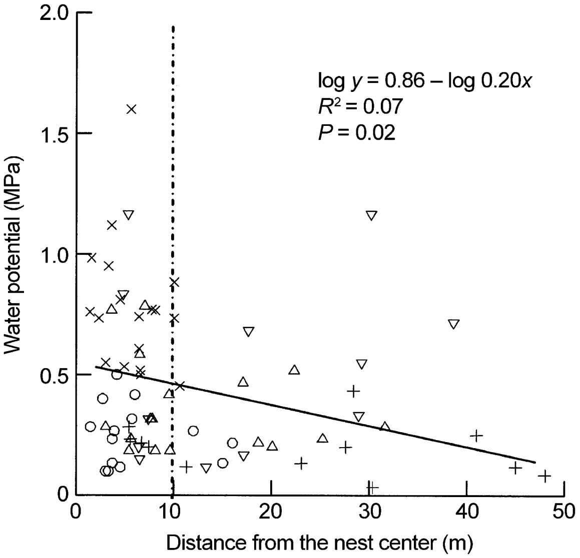

FIG. 5. Predawn leaf water potential (MPa) of *Banara guianensis* trees established at different distance from the nest center of five nests of *A. sexdens* at Vitória Ranch, Paragominas, Pará, Brazil. The symbols identify the different nests. The vertical dashed line delimits the area covered by nest mounds. The relationship is statistically significant ($n = 73$, $r = -0.26$, $P < 0.05$; analyses on log-log transformed data).

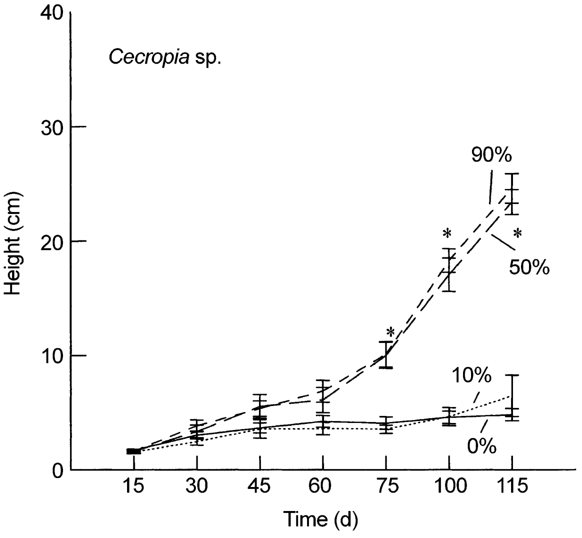

FIG. 6. Means (±1 SD) of height of *Cecropia* sp. seedlings planted in pots containing different proportions of mineral soil (excavated from 4 m depth at secondary forest of Vitória Ranch and without nest influence) and organic refuse and soil from subterranean chambers of *Atta sexdens* nests. The asterisks indicate statistically significant differences (one-way ANOVA, $P < 0.05$) between treatments 0–10% and 50–90% on the same date. The sample size (number of pots) ranged from 11 to 15 for the height measurements made on days 15, 30, 45, and 60; and from 8 to 9 for the measurements made on days 75, 100, and 115.

soil of the nest has reached field capacity (Jipp et al. 1998).

Contrary to the pattern observed for root growth, tree stem growth showed no spatial correlation with the nest for seven of the nine species studied and weak and inconsistent relationships for the other two species. We cannot explain these two weak correlations of opposite sign, and suggest that they may be due to chance. The lack of a clear and consistent relationship between tree growth and distance from the nest has several possible explanations. First, the nests may stimulate tree growth, but trees may be capable of tapping the nest from large distances. In other words, the lateral distance of the rooting zone of trees in the secondary forest may be large enough to obfuscate the spatial correlation between nests and aboveground tree growth. We know that at least one of the roots identified in the nests (*Memora flava*) had grown at least 15 m to access the nest, because the nearest individual of that species was that far from the nest center. Roots that extend laterally for 10–70 m have been demonstrated for 27 Amazonian tree species (L. Carvalho and D. Nepstad, *unpublished data*).

Second, the changes in nest soil properties may be small relative to other potentially limiting resources for the trees in the size categories studied (>2 cm diameter). The nest influence may be apparent in the early stages of establishment, but disappear as competition for light and soil water becomes more severe. The mobility of most nutrients in the soil is a function of soil moisture content, which is consistently lower in the nest than in non-nest soil. The dramatic growth response of *Cecropia* sp. seedlings in the pot experiment to amendments from nest chambers may not translate into enhanced growth of older trees in situ because of this interaction with soil water depletion.

The reported effects of *Atta* nest on soil and roots could have a positive effect on vegetation dynamics at earlier stages of succession than the 17-yr-old forest that we studied. For example, *Atta* nests provided an appropriate place for tree seedling establishment in open woodland in Paraguay (Jonkman 1978) and in savannas in Venezuela (Farji-Brenner and Silva 1995*b*). In Brazilian savannas, nests of *A. laevigata* are favorable for grass invasion (Coutinho 1982). In our Amazonian study area, *Atta* nests could be propitious places for development of vegetation islands on abandoned pastures, such as nearby areas at Vitoria Ranch that were abandoned <5 yr ago and where pioneer successional species (*Solanun* spp. and *Cordia multispicata*) are commonly found on *Atta* nests (P. Moutinho, *unpublished data*). These pioneer plant species attract seed-carrying birds and bats to abandoned pasture and ameliorate local microclimatic and soil condition for plant growth and forest recovery (Vieira et al. 1994, Nepstad et al. 1996, Silva et al. 1996). The negative effects of *Atta*-induced seed predation and seedling herbivory on forest recovery are also likely to be more important during the first few years after pasture abandonment (Nepstad et al. 1996, Vasconcelos and Cherrett 1997, Moutinho 1998*b*).

In the secondary forest of our study site, *Atta sexdens* harvested 9 of 42 tree species (dbh > 5 cm). They chose trees >15m from the nest and seldom harvested trees established on nest mound (P. Moutinho, *unpublished data*). Hence, any negative impacts of harvesting on tree growth, vigor, or carbon allocation would not be important on or near the nest area.

The influence of the cutter ants that we studied on the forest may extend well beyond the 2% of the area that is covered by the nest mounds. For example, if trees within a 10 m radius of the nest mounds are affected by the nest, either through lateral root extension, or through the chamber excavation activities that take place beyond the mound, then the nests affect almost 20% of the forest. Nest effects may also accumulate over time. The balance between nest establishment (natality) and nest mortality could affect a large area of forest (Perfecto and Vandermeer 1993). For example, at our study site the nest density increases to seven nests per hectare if dead colonies are included in the density estimate, thus directly affecting ~6% of the secondary forest area. Additional evidence of the effect of *A. sexdens* on soil may be revealed by the occurrence of soil soft spots and hollow chambers to 8 m depth in secondary and primary forest at our study site, far from the nearest active cutter ant nest (Carvalheiro and Nepstad 1996). Based on physical appearance and the presence of organic debris, these authors suggested that these chambers and soil soft spots are vestiges of old *Atta* nests. These soft spots and chambers occupied only 0.8–1.2% of the total soil volume, but contained two to three times more fine roots than adjacent intact soil. Thus, the bioturbation associated with cutter ant excavations may last for centuries, facilitating root penetration and proliferation in deep soil well beyond the lifetime of the ant colony. The magnitude of this long-lasting effect of *Atta* is difficult to demonstrate quantitatively, but our results provide evidence that this source of bioturbation in tropic forest soils is worthy of more study.

In summary, the leaf-cutting ant *Atta sexdens* clearly modified the soil of their nests in a 17-yr-old secondary forest of Amazonia, supporting our first three hypotheses: (1) resistance to penetration declined; (2) concentrations of plant nutrients increased; and (3) significant root proliferation was observed within the soil of these ant nests. However, our fourth and fifth hypotheses were not supported: (4) water stress did not decrease closer to the nest; and (5) tree diameter growth did not increase in the nest areas. The abundant root proliferation in the nest soil may have depleted soil water storage, provoking the observed drought stress closer to the nest. Stem growth may have shown little relationship with distance to the nest because of root competition for nest resources and because of long lateral extension of tree root systems. Trees may also have been limited by resources other than nutrients, such as light and water, at this stage of the successional process.

The competing effects of defoliation vs. deep soil tillage and nutrient enrichment on secondary forest growth are difficult to compare, but these results point to a potential role of a soil-excavating insect in explaining recovery of deep root functions by native vegetation in abandoned cattle pastures. Although the direct effects of this modification of soil properties on aboveground tree growth remain unclear, the observed bioturbation and its effects on physical and chemical properties of the soil should be recognized in secondary succession processes affecting the tropical forested habitats and forest regrowth on degraded pastures of Amazonia.

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