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Effect of leaf-cutting ant nests on plant growth in an oligotrophic Amazon rain forest

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Abstract: This study examined whether high nutrient concentrations associated with leaf-cutting ant nests influence plant growth and plant water relations in Amazon rain forests. Three nests of *Atta cephalotes* were selected along with 31 *Amaioua guianensis* and *Protium* sp. trees that were grouped into trees near and distant (>10 m) from nests. A ^{15}N leaf-labelling experiment confirmed that trees located near nests accessed nutrients from nests. Trees near nests exhibited higher relative growth rates (based on stem diameter increases) on average compared with trees further away; however this was significant for *A. guianensis* (near nest 0.224 y^{-1} and far from nest 0.036 y^{-1}) but not so for *Protium* sp. (0.146 y^{-1} and 0.114 y^{-1} respectively). Water relations were similarly species-specific; for *A. guianensis*, near-nest individuals showed significantly higher sap flow rates (16 vs. 5 cm h^{-1}), higher predawn/midday water potentials (−0.66 vs. −0.98 MPa) and lower foliar δ^{13}C than trees further away indicating greater water uptake in proximity to the nests while the *Protium* sp. showed no significant difference except for carbon isotopes. This study thus shows that plant response to high nutrient concentrations in an oligotrophic ecosystem varies with species. Lower seedling abundance and species richness on nests as compared with further away suggests that while adult plants access subterranean nutrient pools, the nest surfaces themselves do not encourage plant establishment and growth.

Key Words: *Amaioua guianensis*, Amazon, *Atta cephalotes*, leaf-cutting ant nest, nutrient concentrations, nutrient uptake, plant–water relations, *Protium*, sap flow, stable isotopes

INTRODUCTION

Leaf-cutting ants of the genus *Atta* are prominent herbivores in the neotropics (Cherrett 1986). These social insects collect and transport large quantities of fresh leaves into their nests that are subsequently degraded by a mutualistic fungus (Hölldobler & Wilson 1990) thereby increasing organic matter in the soil. Leaf-cutting ants mix soil horizons and concentrate nutrients locally (Alvarado *et al.* 1981, Bucher 1982, Coutinho 1982, Jonkman 1978, Jukubczyk *et al.* 1972, Petal 1978, Wagner & Jones 2004, Weber 1972). This has been observed in forests (Hudson *et al.* 2009, Moutinho *et al.* 2003, Wirth *et al.* 2003), savannas (Farji-Brener & Silva 1995, Souza-Souto *et al.* 2007) and semi-arid regions (Farji-Brener & Ghermandi 2000) throughout the neotropics.

High nutrient availability in the soil of leaf-cutting ant nests can, among other factors, locally increase plant abundance and diversity as well as accelerate nutrient cycling in otherwise oligotrophic tropical forest soils (Farji-Brener & Medina 2000, Garrettson *et al.* 1998, Haines 1978, Lugo *et al.* 1973). Using leaves labelled with ^{15}N that were transported by ants into their nests, and by subsequently tracing the ^{15}N label in leaves of trees surrounding the nests, Sternberg *et al.* (2007) demonstrated that plants near nests did access nutrients from the nests. However, field studies examining the actual response of vegetation to the supposed benefits of the nests in terms of growth and reproduction are few and with varied results. Schoereder & Howse (1998) found no effect of leaf cutter ant nests on plant community structure in a savanna in southeastern Brazil. In the eastern Amazon, Moutinho *et al.* (2003) reported higher

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root density in nest soil and lower predawn leaf water potential values in trees near nests than in trees far away, an indication of possible water stress in near-nest trees arising from increased water uptake. However they also mentioned that most species did not show any significant linear relationships between stem diameter increase and nest proximity, thereby suggesting that other factors apart from nutrient availability influence growth.

This study looked at the influence of leaf-cutting ant nests on plant growth and water relations in an oligotrophic forest to examine whether high nutrient availability results in greater growth and water uptake, the latter as nutrient uptake happens in the dissolved form. Sap flow velocity, leaf water potential and carbon stable isotope ratio were measured as proxies for photosynthetic activity since it is expected that plants accessing high nutrient concentrations would have high levels of photosynthesis. Trees growing near leaf-cutting ant nests were compared with trees far away from nests. The study hypothesized that plants near the nests would exhibit: (1) higher relative growth rates as measured by stem diameter increases; (2) higher sap flow velocities accompanying increased photosynthesis; and (3) lower dry season water stress as measured by less enriched foliar δ^{13}C and higher leaf water potential, as long as water is not limiting. In addition, as water/nutrient uptake and light availability can differ between adult and sapling stages, naturally occurring saplings near and far from nests were counted to examine if the supposedly higher nutrient availability in nest soil would positively influence sapling growth.

METHODS

Study site

The study was conducted between October 2005 and November 2007 at Fazenda Tanguro in the municipality of Querência (13°04′35.39″S, 52°23′08.85″W), Mato Grosso, Brazil. The site lies in a short-stature lowland Amazon rain forest bordering savanna (cerrado) woodlands. The annual average temperature is 23.5 °C with a rainfall ranging from 1800 to 2000 mm. The dry season occurs between May and September and the rainy season between October and April. Soils are oxisols (Balch *et al.* 2008). Three active leaf-cutting ant nests of *Atta cephalotes* (L.) (Hymenoptera: Formicidae) were chosen; they were located several hundred metres apart, about 100 m from the forest edge and were representative of leaf-cutting ant nests in the area. The percentage of canopy cover at the nests and forest sites without nests were calculated from digital photographs taken at ground level that were converted in Adobe Paintshop Pro to high-contrast black-and-white images from which the proportion of cover (black pixels) was obtained.

Nutrient uptake from nests

^{15}N was used as a tracer to ascertain plant nutrient uptake from leaf-cutting ant nests. Leaves of *Citrus aurantifolia* (Christm.) Swingle (Rutaceae) and *Mangifera indica* L. (Anacardiaceae) impregnated with ^{15}N in the form of potassium nitrate (2.5%) were offered to the ants in September 2005 who were observed transporting the leaves to their nests (three nests). Foliar ^{15}N levels in selected trees (14 near nests, 14 far from nests for each species) were observed in samples taken every 2 mo (2005–2006) and analysed by isotope ratio mass spectrometry in the Nuclear Energy Center for Agriculture in Sao Paulo, Brazil and in the Laboratory of Stable Isotope Ecology in Tropical Ecosystems at the University of Miami, USA (Autorização IBAMA; Licença de Exportação: 07BR000346/DF) Nitrogen isotope ratios are expressed as δ^{15}N in ‰ where

$$\delta^{15}\text{N} = ((\text{R}_{\text{sample}}/\text{R}_{\text{std}}) - 1) \times 1000$$

R_{sample} and R_{std} represent the ratio of the heavier to lighter nitrogen isotope in the sample and in the standard. Atmospheric nitrogen was the standard for δ^{15}N values. The precision of analysis was ± 0.1‰.

Plant growth

We tested whether plants closer to leaf-cutting nests have higher relative growth rates than those farther from nests. Thirty-one trees established near and far from three leaf-cutting ant nests with diameters (at breast height) ranging from 20 to 25 cm were randomly selected. These trees belonged to the two most common genera within the study area and were *Amaioua guianensis* Aubl. (Rubiaceae) and *Protium* sp. (Burseraceae). Individuals occurring up to 10 m from the edge of a nest were considered part of the near-nest group while those further than 10 m from the nest that were also exempt from the influence of any other leaf-cutting ant nests formed the far-from-nest group; an earlier investigation by Moutinho (unpubl. data) found that on average trees up to 10 m away from a nest had their roots in the nest area. A clumped approach was chosen instead of examining growth relationships with nest distance, in order to sidestep other potentially confounding factors that influence growth. Monitoring of the stem diameter of trees was carried out every 2 mo between October 2005 and November 2007, by using an electronic caliper to measure changes in dendrometers (stainless steel bands with a spring attached to the ends) encircling the main trunk at breast height. The dendrometers were installed in September 2005 and adjusted weekly to allow time for them to settle in over the tree bark. Relative growth rate (RGR) over the study period, expressed on a per year basis, was calculated as:

$$\mathrm{RGR} = \frac{\ln(\text{diameter at time 2}) - \ln(\text{diameter at time 1})}{\text{time 2} - \text{time 1}}$$

Plant–water relations

Higher photosynthesis is accompanied by increased stomatal conductance that in turn leads to higher transpiration, sap flow velocities, lower leaf water potential (Larcher 2006) under water-limiting conditions and lower foliar carbon isotope ratios (Farquhar *et al.* 1982).

Sap flow velocities were measured by the thermal dissipation method (Granier *et al.* 1992) in the dry season (July 2007) for a period of seven consecutive days in a subset of the trees selected for growth measurements: 10 *Protium* sp. trees and six *A. guianensis* trees that had similar diameters. Five of the ten *Protium* sp. trees were near one nest, while the other five were located further away (>10 m away) from the nest. Similarly, three *A. guianensis* trees were near the same nest while the other three were further away. The 2-cm-long probes of a copper-constantan thermocouple were coated with heat-conducting paste and inserted in holes drilled 10 cm apart at breast height along the longitudinal axis of the tree trunk after bark removal. The heated probe was placed in the upper hole while the unheated needle (reference probe) was placed in the lower hole. Sap flow velocity was calculated from the temperature difference-induced voltage as:

$$J = 119\ (\Delta \mathrm{Tmax} - \Delta \mathrm{Tmin})\,|\,(\Delta \mathrm{Tact})$$

Glasswool insulation was placed around the probes and covered in reflective aluminium foil to minimize ambient heat sources and sinks. A CR10× datalogger linked to an AM16/32 multiplexer (Campbell Scientific, Utah, USA) to accommodate 16 probes measured the voltage difference every 30 s and stored the average over a 10-min interval. The probe heater circuits and the datalogger were powered by a 12-V battery charged by a solar panel, with battery voltage monitored at dawn and dusk to guard against voltage dropping below 11 V. Power was supplied at a standard 0.2 W per heater circuit, for which a resistor-based power strip was used. The entire probe and cable assembly was also monitored twice a day along with the data to check for circuit malfunctions due to animal movements tripping cables, moisture accumulation and ants that often chewed cable insulation.

Carbon stable isotopic analysis. For each species, mature leaves were collected from a set of 13 trees near three nests and 13 trees far from these three nests as the growth study on six occasions over 14 mo spanning the wet and dry seasons, dried at 50 °C and ground in preparation for isotopic analysis. Foliar δ^{13}C was analysed by isotope mass spectrometry in the Laboratory of Stable Isotope Ecology in Tropical Ecosystems at the University of Miami, USA. Carbon isotope ratios are expressed as δ^{13}C in parts per thousand (‰) where:

$$\delta^{13}\mathrm{C} = ((\mathrm{R}_{\mathrm{sample}}/\mathrm{R}_{\mathrm{std}}) - 1) \times 1000$$

$\mathrm{R}_{\mathrm{sample}}$ and $\mathrm{R}_{\mathrm{std}}$ represent the ratio of the heavier to lighter carbon isotope in the sample and a standard. We used Vienna Pee Dee Belemnite (vPDB) with a precision of analysis ± 0.1‰.

Leaf water potential. For each species, predawn and midday leaf water potential were measured in leaves from eight trees near one nest and from eight trees far from the nest in the dry season (July 2007) as per Scholander *et al.* (1964) using a Scholander Pressure Chamber (PMS Instruments, Corvallis, Oregon, USA). The difference between predawn and midday leaf water potentials (typically more negative values at midday indicating some degree of water stress) indicates the extent of transpiration-caused water stress in the tree. Three branches per tree were cut 1 h before dawn and around midday, bagged and kept in a cooler and transported back to the laboratory for immediate measurement of leaf water potential.

Recruitment

Species composition and abundance of saplings (diameter <5 cm) in the vicinity of the nests were noted in January 2007 at 23 locations on the three nests and 23 locations situated >10 m away from these nests. At each location, three 1-m^2 plots were randomly selected and counted.

Data analysis

Relative growth rates (RGR) for the two groups of trees (near nest and far from nest) were compared for each species separately using ANOVA with leaf-cutting ant nests as randomized blocks and the two groups of trees (near and far from nests) as the main effect, to test if RGR was influenced by within-nest and/or by distance from the nest. Sap flow velocity values for each tree were averaged over 7 d (after removing erroneous data when cables were shorted out by ants) to obtain a daily average for each tree. A daily group average (near nest or far from nest for a species) was then obtained by averaging the daily averages for individual trees in the group; sapflow studies were performed around only one nest. The group averages for a species were then compared using the Student's t-test. Foliar δ^{13}C values of near-nest trees were analysed for within-nest variation for each one of six sampling events by ANOVA. Thereafter a repeated-measures ANOVA was carried out to examine the variation of foliar δ^{13}C within six sampling events in a year (as the within-subjects factor) as well as whether this variation of distance from the leaf-cutting ant nests (between-subjects factor). Predawn leaf water potential and midday leaf water potential between near- and far-from-nest groups for each species were compared using Student's t-test, since only one nest was involved. All statistical analyses were performed using SPSS version 13.0 (Chicago, USA).

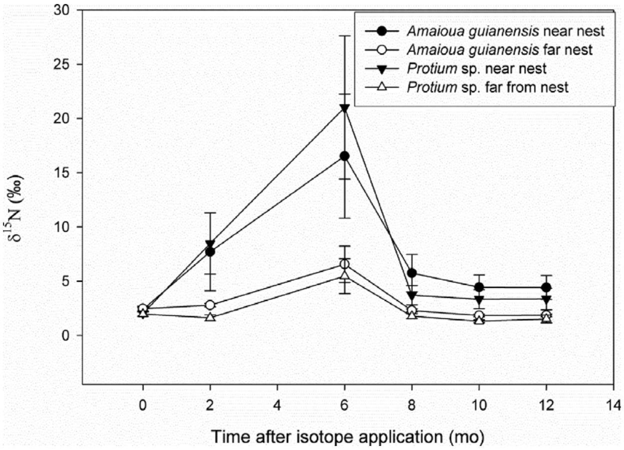

Figure 1 Foliar δ^{15}N measured from the time of isotopic label application until 1 y thereafter. Filled symbols (▼, ●) refer to trees near leaf-cutting ant nests while unfilled symbols refer to trees far away from the nest. Error bars indicate 1 SE.

RESULTS

Plant nutrient uptake from nests

For both the species considered, trees situated near nests had significantly higher foliar δ^{15}N than trees far from nests (Figure 1). For instance, 6 mo after label introduction, near-nest *A. guianensis* trees had a mean (± SD) foliar δ^{15}N value of 16.5‰ ± 5.7‰ while trees far away had a mean value of 6.6‰ ± 1.7‰ ($t = 1.67$, $n = 14$, $P < 0.05$). Similarly near-nest trees of *Protium* sp. had a mean value of 21.0‰ ± 6.6‰ while trees far away from nests had 5.5‰ ± 1.6‰ ($t = 2.27$, $n = 12$, $P = 0.017$). Foliar δ^{15}N values in near-nest trees increased approximately 2 mo after label introduction with a peak in 6 mo. Trees far away from nests also exhibited a peak that was smaller in magnitude as compared with near-nest trees.

Plant growth

The effect of proximity to leaf-cutting ant nests on plant growth was significant for *A. guianensis* ($F_{1,15} = 10.8$, $P = 0.034$) with trees near leaf-cutting ant nests exhibiting significantly higher growth rates (0.224 y^{-1}) as compared with 0.036 y^{-1} for trees far from nests (Figure 2). There was no significant difference in growth amongst the three nests for near-nest *A. guianensis* trees ($F_{2,13} = 0.996$, $P = 0.375$). For *Protium* sp., neither the nests ($F_{2,13} = 0.493$, $P = 0.685$) nor distance from the nests ($F_{1,17} = 0.730$, $P = 0.432$) had a significant effect on relative growth rate. There was no significant linear or non-linear relationship between distance to the nest and stem diameter increase for either species.

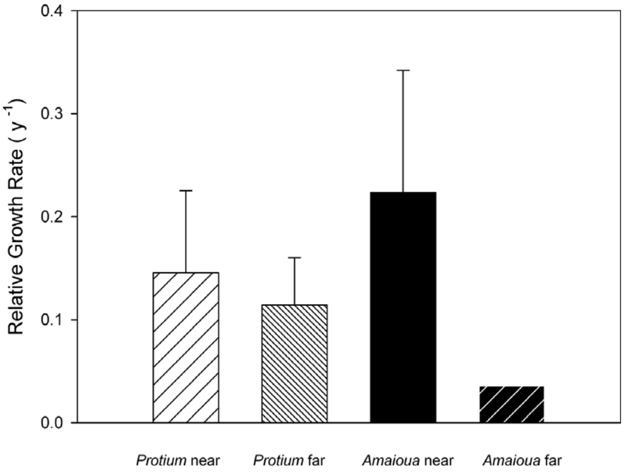

Figure 2 Relative growth rate (RGR) per year based on stem diameter increases in *Protium* sp. and *Amaioua guianensis* trees near and far away from leaf-cutting ant nests over the study period. Error bars signify 95% confidence intervals of the mean.

Sap flow velocity

Over the 7-d observation period, sap flow velocity differences between trees near the nest and trees far from the nest were significant only for *A. guianensis* where near-nest trees showed a mean sap flow velocity of 16.0 ± 2.14 cm h^{-1} compared with trees further away that had a mean sap flow velocity 5.41 ± 3.12 cm h^{-1} ($t = 7.36$; $P < 0.001$; $n = 3$). No significant differences between near-nest trees (16.7 ± 3.98 cm h^{-1}) and trees far from the nest (18.6 ± 11.4 cm h^{-1}; $t = 0.407$; $P \leq 0.691$; $n = 5$) were observed for *Protium* sp.

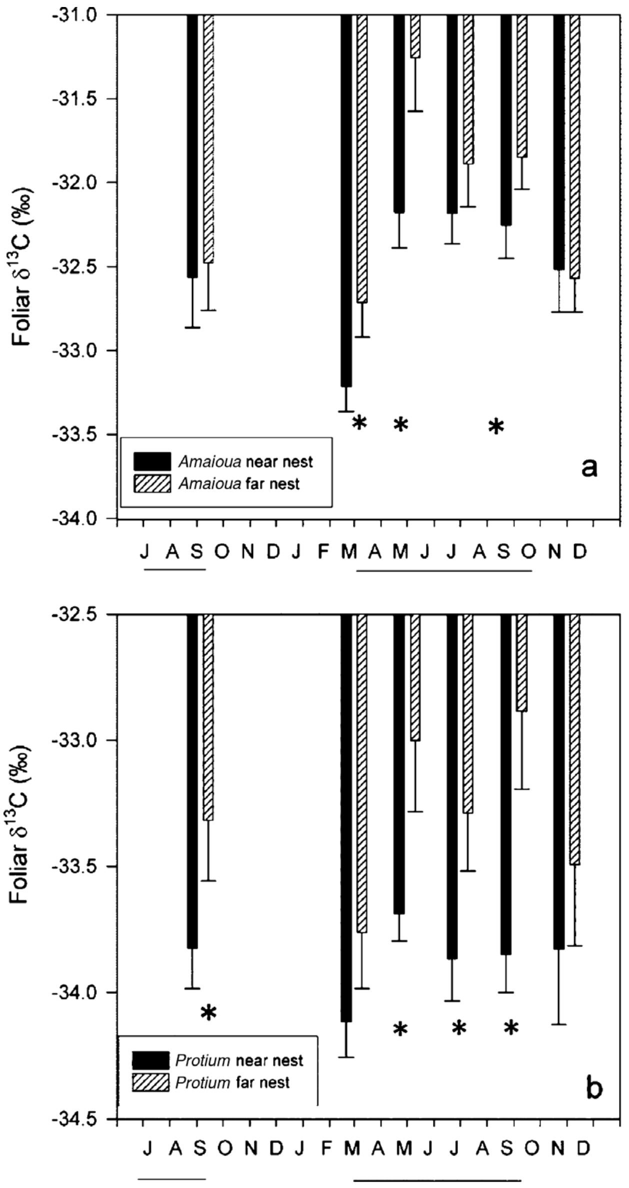

Figure 3 Average foliar $\delta^{13}C$ difference between trees near leaf-cutting ant nests and trees far from the nests for *Amaioua guianensis* (a) and *Protium* sp. (b) sampled in September 2005, March 2006, May 2006, July 2006, September 2006 and November 2006. The approximate dry-season months are underlined on the x-axis. n = 13 in each sample. The $*$ indicates significant difference between trees near and far from the nests for a sampling event at P = 0.05. Error bars signify 1 SE.

Foliar $\delta^{13}C$

Both species showed higher (less negative or more enriched) foliar $\delta^{13}C$ values over the dry season, from March to September (Figure 3). In addition, trees far from nests had, on average, significantly higher foliar $\delta^{13}C$ values than trees near nests on several occasions. For *Amaioua guianensis*, repeated-measures ANOVA indicated significant differences in foliar $\delta^{13}C$ within the months of sampling ($F = 14.1$, df = 5, $P < 0.001$) while the interaction between time (months of sampling) and the distance of the tree from the nest (whether near or far from the nest) was not significant at $P = 0.05$, indicating that both groups of trees (near nests and far from nests) had similar patterns over time. For *Protium* sp., the repeated-measures ANOVA did not find any significant difference in foliar $\delta^{13}C$ between months of sampling, nor was there any significant interaction between time and distance from nest. For every sampling instance, there was no significant difference in foliar $\delta^{13}C$ values for near-nest trees of either species between the three nests with the exception of November 2005 when a significant difference in foliar $\delta^{13}C$ was seen ($F_{2,24} = 4.86$, $P < 0.05$) for *Protium* sp.

Leaf water potential

Amaioua guianensis trees showed less negative predawn leaf water potential values for near-nest trees (−0.66 ± 0.10 MPa) than trees far from the nest (–0.98 ± 0.35 MPa; $t = -2.56$; $P = 0.021$; $n = 9$). Midday leaf water potentials in all cases were more negative than predawn leaf water potentials as expected; however there was no significant difference between trees near and far from the nest (near nest = −1.95 ± 0.56 MPa; far from the nest = –2.22 ± 0.55 MPa; $t = -1.01$; $P = 0.328$; $n = 9$). *Protium* sp. trees exhibited the reverse situation in both predawn (near nest = −1.23 ± 0.62 MPa; far from the nest = –0.81 ± 0.60 MPa; $t = -1.76$; $P = 0.091$; $n = 9$) and midday (near nest = −1.63 ± 0.66 MPa; far from the nest = –1.01 ± 0.48 MPa; $t = 2.90$; $P \leq 0.001$; $n = 9$).

Seedling abundance and species richness

The density of seedlings was significantly lower near nests (mean ± SD = 9.47 ± 7) than further away (17.8 ± 15) ($t = -2.44$, df = 31, $P = 0.01$). Species richness was lower as well (4.76 ± 3) near nests as compared with further away (10.2 ± 4.8; $t = 4.57$; $P \leq 0.001$; $n = 23$). The forest floor had greater canopy cover (89.7% ± 2.5%) than nest sites (84.7% ± 2.1%), ($t = 3.09$; $P = 0.021$; $n = 8$; data transformed into arcsine of the square root).

DISCUSSION

Leaf-cutting ant nests constitute nutrient-rich patches in oligotrophic forest soils and are thus logically surmised to benefit plant growth (Moutinho *et al.* 2003, Sternberg *et al.* 2007). Foliar $\delta^{15}N$ results indicate that trees growing near leaf-cutting ant nests took up nutrients from the nests to a significantly greater extent than trees further away, thereby agreeing with other recent studies (Farji-Brener & Ghermandi 2008, Sternberg *et al.* 2007). While this study has found that on average, trees near nests showed a higher relative growth rate (RGR) than trees further away, the extent of this difference in growth and water relations differed with species, at least for the two most abundant species in the forest studied. Seedling abundance and species richness on the other hand was smaller on the nests as compared with further away on the forest floor.

Plant species respond differently to nutrient concentrations in an oligotrophic system

The absence of any significant difference in RGR in near-nest trees between nests suggests that the three nests chosen for this study were adequate. While near-nest trees from both *A. guianensis* and *Protium* sp. had greater RGR than trees further away, this nest-proximity-related difference in RGR was significant for *A. guianensis* but not for *Protium* sp. This observation is also supported by the water relations results, where *A. guianensis* trees near nests are more hydrated than trees further away, while there was no significant difference for *Protium* sp., with the exception of foliar δ^{13}C results.

It is likely that *A. guianensis* responds to localized increased nutrient availability by growing more roots in those high nutrient patches, as observed for other species elsewhere by Moutinho *et al.* (2003); although field observation of increased root growth requires identification of *A. guianensis* roots in soil cores that fell outside the scope of this study. Sap flow velocities are higher in near-nest *A. guianensis* trees as compared with trees further away indicating greater water uptake in near-nest trees. Predawn and midday leaf water potential values are significantly lower (less negative) in near-nest *A. guianensis* trees as compared with trees further away, indicating lower xylem tension in near-nest trees that results from greater water availability in the soil-plant-atmosphere continuum. This greater water availability in near-nest *A. guianensis* trees also appears to exist over a longer period across seasons, as seen from the lower foliar δ^{13}C in near-nest trees compared with leaves from trees located far from nests (Figure 3). The difference between trees near nests and trees far from nests increases over the dry season and equalizes over the wet season (November 2006) on account of increased water availability. Apart from increased root proliferation, other factors such as the possibility of higher water-holding capacity of the organic-matter-enriched soil and reduced evapotranspiration from bare nest surfaces could contribute to the greater water availability in nest sites, although Meyer *et al.* (2011) observed that soil moisture in nest soils was actually lower than further away in the forest. Thus increased root growth could still be the major reason for the greater degree of hydration, as the limited volume of nest soil may hold insufficient water (even with continual recharge) to account for the higher sap flows in near-nest trees.

Unlike *A. guianensis*, the *Protium* sp. does not reveal a clear and consistent pattern. There is no significant difference in growth, sap flow and leaf water potential between near-nest and far-from-nest trees. This suggests that *Protium* sp. trees do not respond significantly to increased nutrient availability, at least over a time span of a couple of years. However, like *A. guianensis*, *Protium* sp. shows lower foliar δ^{13}C in trees located near nests; this suggests the possibility of factors other than water availability affecting foliar δ^{13}C values, such as the ratio of structural and non-structural carbohydrates that can vary over leaf life span.

If these patterns are explained by the relative abilities of *A. guianensis* and *Protium* sp. to take advantage of increased nutrient availability by expanding their root networks, then this would be an example of species differences in plasticity of response to high nutrient patches in an oligotrophic system. These differences can result from the range of resource availability encountered by different species over their recent evolutionary history. Vegetation in oligotrophic ecosystems are known to possess conservative resource-use strategies (Chapin *et al.* 1986, Valladares *et al.* 2000) while plants that occur in ecosystems with a wide variability of resources can respond quickly to changes in nutrient availability. This study supports the idea that plant communities are overlapping collections of species, each with their own range of water and nutrient requirements and sets of responses.

Leaf-cutting ant nests: subterranean nutrient hotspots but surface bald spots

Interestingly, while most adult trees occurring close to leaf-cutting ant nests showed increased growth in this study, the nests themselves had lower plant species richness and abundance as also noted in Garrettson *et al.* (1998) and Meyer *et al.* (2011). Saplings could face competition for limited water resources in the dry season from well-established adult trees with a high proliferation of roots in the nest waste chambers as shown by Haines (1978), that could decrease the inherently lower soil moisture in nest soil compared with the forest floor possibly due to canopy gaps allowing in more radiant energy (Meyer *et al.* 2011, canopy cover results in this study). Another possibility is that nutrients from waste chambers occur deeper in the soil profile in the nests, inaccessible to seedling roots. Moutinho *et al.* (2003) observed a higher concentration of nutrients in nests at depths >1 m along with high levels of Ca, Mg and K. Nest surfaces are bereft of any leaf litter and are essentially piles of low-nutrient soil, which together with the lack of mycorrhizal associations in the early nest stages can affect seedling growth. Yet another possibility is defoliation by leaf-cutting ants as has been observed in Garrettson *et al.* (1998) and Vasconcelos & Cherrett (1997). Furthermore, as mentioned in Farji-Brener & Medina (2000), the excavation activities by ants inside the nest can also affect the root zone of the saplings, although this again depends upon the ant species – this is true for *Atta cephalotes* while *A. sexdens* or *A. laevigata* do not excavate chambers in the root zone of plants. It is the nest mound surfaces that remain bare and free of any vegetation, thereby constituting bald spots on the forest floor. Thus, while adult trees established near nests can access the high concentrations of nutrients in the subterranean waste chambers resulting in greater growth than trees away from nests, the nest surfaces do not encourage colonization by plants (from low species richness and abundance data) on their surface, possibly to prevent roots from colonizing plants entering nest chambers and otherwise affecting the structural integrity of the nest structures.

CONCLUSION

High nutrient concentrations around leaf-cutting ant nests were generally seen to enhance plant growth; however plant species differ strikingly in their ability to respond to and to utilize these localized nutrient concentrations in an oligotrophic ecosystem. Thus an increase in nutrient availability in an oligotrophic ecosystem does not necessarily translate into higher growth and benefits for all plants native to that ecosystem. While the leaf-cutting ant nests constitute subterranean nutrient concentrations, their surfaces are bare of vegetation.

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