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# Soil fertility and plant growth in soils from pine forests and plantations: Effect of invasive red imported fire ants *Solenopsis invicta* (Buren)

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## Summary

Through nest building and foraging activities, ants alter physical properties and nutritional status of soils through structural modifications and nutrient accumulation. In turn, these alterations may enhance soil quality for plant growth. This study examined the effect of the invasive red imported fire ant, *Solenopsis invicta* Buren, on soil properties and plant growth. In our greenhouse study, ant activity decreased soil pH and increased phosphorus ($P^+$) and potassium ($K^+$) in the soil. We collected soil from within and adjacent to randomly selected nests in two common habitats of Louisiana – longleaf-pine (*Pinus palustris*) forests and longleaf-pine plantations. After physical and chemical properties were measured, *Gardenia japonicus* seedlings were planted in the soil to determine growth rate. In comparison to adjacent soil, ant nest soils from both habitats were lower in moisture content and bulk density and higher in $NH_4^+$. Ant nest soils were also higher in $Ca^{2+}$, $Mg^{2+}$, $K^+$ and $Na^+$ than in adjacent soils in longleaf-pine forests. *G. japonicus* seedlings grown in nest soil from pine forests were an average of three times taller than those grown in adjacent soil, and those from pine plantations were twice as tall as those grown in adjacent soils. These results suggest that invasive fire ants alter the physical and chemical properties of the soil. These soil modifications enhance plant growth since $NH_4^+$, a nutrient that limits growth, has been increased.


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## Introduction

Soil activities of ground-dwelling ants are evident when observing the construction of nest mounds. Ants' nest-building activities transform underlying soil into nutrient-rich patches that may favor seed germination (Levey and Byrne, 1993; Andersen and Morrison, 1998). Some authors have associated modifications to soil physico-chemical properties with mound construction by ants (Nkem et al., 2000; Lenoir et al., 2001; Lafleur et al., 2002), while others have associated these activities with plant distribution patterns (Culver and Beattie, 1983; Dean et al., 1997; Garrettson et al., 1998) and vegetation succession (King, 1977; Farji-Brener and Silva, 1995). Moreover, few authors have tried to link this soil enrichment to plant growth (Horvitz and Schemske, 1986; Dean et al., 1997; Dostál et al., 2005).

Ant activities such as foraging and mound construction result in the redistribution of organic and inorganic material within the soil (Lobry de Bruyn and Conacher, 1990). Due to ant activities, soils from ant nests are often more rich in organic matter and mineral products of decomposition such as $NH_4^+$, $NO_3^-$, P and other base cations than adjacent soils (Wagner et al., 1997; Lenoir et al., 2001; Lafleur et al., 2002; Dostál et al., 2005). Higher available C in nest soils may increase microbial biomass and nutrient cycling rates (Dauber and Wolters, 2000; Lafleur et al., 2002). Moreover, ants may create surface and subsoil conditions that improve aeration, accelerate water infiltration, alter temperature, and modify pH (Wang et al., 1995; Nkem et al., 2000; Lafleur et al., 2002).

Red imported fire ants, *Solenopsis invicta* Buren, are an important component of the soil fauna of most ecosystems in the southern US (Gotelli and Arnett, 2000). In Louisiana, we have found nests of this invasive ant in every ecosystem except for those with 100% closed canopy. In Louisiana, the number of fire ant nests range from 75 mounds per hectare in areas where the canopy is more dense, to over 1200 mounds per hectare in open, disturbed habitats (L.M. Hooper-Bùi and L.D. Foil, unpublished data). They are an important predator of invertebrates, and they may suppress the presence and abundance of other species of ants (Wojcik, 1994). Red imported fire ants are also known to modify pasture soil properties (Herzog et al., 1976; Green et al., 1998) by increasing the protein, carotene, and phosphorus content of plants growing in single pastures (Herzog et al., 1976). However, fire ant importance to nutrient cycling and vegetation growth in forests and plantations remains unknown. Because of this invasive species' extensive presence throughout ecosystems in the southern US, their potential impact on soil fertility could be important.

The objectives of this study were to study soil modifications created by fire ants in controlled conditions, pine forests, and pine plantations, and to study the effect that these modifications have on plant growth. We hypothesized that fire ant activities would increase the nutrient content within the nest soils and favor plant growth.

## Material and methods

### Greenhouse study

#### Greenhouse setup

Approximately 5 cm of medium grain sand was distributed on three greenhouse benches ($0.90 \times 6.00$ m) lined with plastic sheeting. Metal flashing (0.15 m high) was placed against the walls of each bench, and more flashing was used to subdivide each bench into six small arenas ($0.90 \times 1.00$ m each), Aluminum tape connected pieces of flashing to provide a continuous vertical barrier to keep ants from escaping the arenas. Once the flashing was in place, sand was pushed up against the sides of the arenas to prevent ants from excavating near the base of the flashing. Pestick (Phytotronics Inc., St. Louis, MO), applied around the perimeter of the arena 5 cm below the top of the flashing walls, prevented ants from escaping from the arenas. This setup allowed the ants to traverse the surface of the sand, but prevented excavation and nesting as long as the sand was dry. This design is a modification of a method originated by B. Vinson (pers. comm.).

A 3.79-L nursery pot was labeled and filled 2.5 cm from the top with one of three soils and placed in a plant pot saucer on the sand in each arena. The plant saucers were necessary to contain the excavated soil and to keep the sand dry. Three types of soils were used in this experiment; grain-size analysis classified the soils as loamy sand, silty clay, and sandy loam. Each of these soils are either native to or are commonly used in landscaping in Louisiana; ''neutral soil'', i.e. a soil not known to be used or avoided by ants was used. There were four replicates of each soil type with ants (referred to as treatment) and four replicates of each soil type with no ants (to serve as untreated controls). Since the goal of this experiment was to test if the ants were responsible for increases in soil nutrients, no plants were added.

For the treatments, each arena contained a pot with one soil type, and each arena was considered a replicate. One large ant colony was added to each treatment arena; there were no ants in the untreated controls. The untreated controls had to be kept on a separate bench to ensure that no ants invaded the pots during the experiment. However, to save space, the untreated controls were combined into only four arenas. Large weigh boats were used to hold crickets as well as distilled water and 20% sugar water in vials to provision the ants in the arenas.

### Ant collection and care

Red imported fire ants were collected in Baton Rouge, LA near the LSU campus. Mounds were dug up and ants were flooded out of the soil. The ants were then placed in temporary housing. After the ants were released into the arenas, they were fed crickets ad libitum three times per week, and water and sugar water vials were changed and filled as needed. Popsicle sticks and wooden applicators were used as bridges for the ants to access the pots and food containers. To maintain soil moisture, 125 ml or 250 ml of DI water was added to the soil three times per week. The amount of water depended on the soil type; the soil was watered until water exited the drain holes in the pot.

### Soil sampling and analyses

Soil from all pots was sampled prior to adding ants. The sampling continued weekly for 4 weeks and then monthly for 8 months. Sampling was conducted with a small auger powered by a cordless drill. First, excavated soil was removed from the saucer and added to the soil in the pot. This allowed for collecting a "core" representative of the soil throughout the depth of the pot. The soil was placed in Ziploc bags then frozen ($-86\,^{\circ}C$ for 30 min) to kill any ants left in the soil, although most ants ran out of the sample during collection.

Samples were analyzed for pH in a 1:2 soil:water suspension after 30 min of equilibration. Phosphorus availability was determined by placing approximately 2 g dry soil in 40 mL of Bray-2 solution and analyzed using Inductively Coupled Plasma (ICP) spectrometry. Finally, a set of soil samples (approximately 10 g dry weight equivalent) was placed in 100 mL of 1 N $NH_4OAc$ and analyzed for extractable $K^+$, $Na^+$, $Ca^{2+}$ and $Mg^{2+}$ using ICP spectrometry. The analyses of phosphorus and major cations were performed at the Soil Testing and Plant Analysis Lab at LSU.

## Field study and plant growth

### Nest soil sampling

Soil was sampled from two common forest ecosystems in Louisiana – longleaf-pine (*Pinus palustris*) forests (>80 years old) and longleaf-pine plantations (<5 years old). We used location as a replicate and both types of habitat were represented in West-Bay, Boise-Vernon, and Sandy Hollow Wildlife Management Areas, which are geographically separated from one another but have similar characteristics. The forest ecosystems were used because fire ants are thought to have a major impact on the ground-dwelling mammals, vertebrates, birds and herpetofauna, and possibly plant composition.

Soil samples were collected from five randomly selected nests and at four different areas (20, 50, 100, and 300 cm) adjacent to each nest in the two habitats at the three locations (Wildlife Management Areas), for a total of 225 soil samples. Immediately following sampling, soil samples were sieved through a 4-mm mesh, placed in a cooler over ice, and transported to the LSU where they were kept at $4\,^{\circ}C$ prior to analysis.

### Soil analyses

Soil moisture was determined by measuring weight loss after drying in an air-draft oven at $101\,^{\circ}C$ for 24 h. Bulk density was calculated based on dry weight and known core volume. The pH was measured in a 1:2 soil:water suspension after 30 min of equilibration.

The ability of each soil sample to supply mineral N for plant nutrition was determined by direct extraction with 2 N KCl. For each sample, approximately 5 g of dry soil was placed in a 100 mL centrifuge tube, then 50 mL of 2 N KCl was added, and the solution was shaken for 1 h. Then tubes were centrifuged at 5000 rpm for 10 min. For each sample, approximately 15 mL of supernatant was filtered through a fast flow ammonia-free filter into a test tube. Samples were then analyzed for $NH_4^+$ (nitroprusside–salycilate) and $NO_3^-$ (Cd reduction) using a Technicon Auto-Analyser (Pulse Intrumentation, Saskatoon, Canada). Phosphorus, potassium, sodium, calcium, and magnesium availability was determined as described above.

## Plant growth

At each field location, we collected ~4 L of soil from five red imported fire ant mounds and five adjacent locations 3 m radius from the mounds, for a total of 60 samples. Soil samples were placed in

3.79-L pots and planted with *Gardenia japonicus* seedlings provided by Doug Young Nursery in Forest Hill, Louisiana. Gardenias were used because they were readily available and frequently used in greenhouse studies. The 60 pots were then randomly placed on a concrete bench located outdoors. Plants were watered with 1 L of tap water twice per week for 12 weeks. Stem lengths were measured (mm) at the beginning and at the end of the experiment.

## Data analysis

The effect of red imported fire ants on the soil chemistry in the greenhouse was analyzed using PROC MIXED using date as a repeated measure (SAS Institute, 2003). The main effects were soil type and treatment (with or without ants). Several models were tested and low AIC (Akaike Information Criteria, this statistic measures how closely the model fits the data, but it includes a penalty for overly complex models) values were used to pick the best model. Phosphorus, calcium, sodium, potassium, magnesium, and pH were analyzed separately. For the field study, the effect of fire ants on selected soil physico-chemical properties was analyzed using one-way ANOVA tests ($n = 3$). Significant ($P < 0.05$) differences among treatment means were explored using Tukey's HSD tests. The effect of soil type (i.e., nest soil versus adjacent) on plant growth was analyzed using general linear models (GLM). Prior to analysis, data were tested for normality and homogeneity of variances.

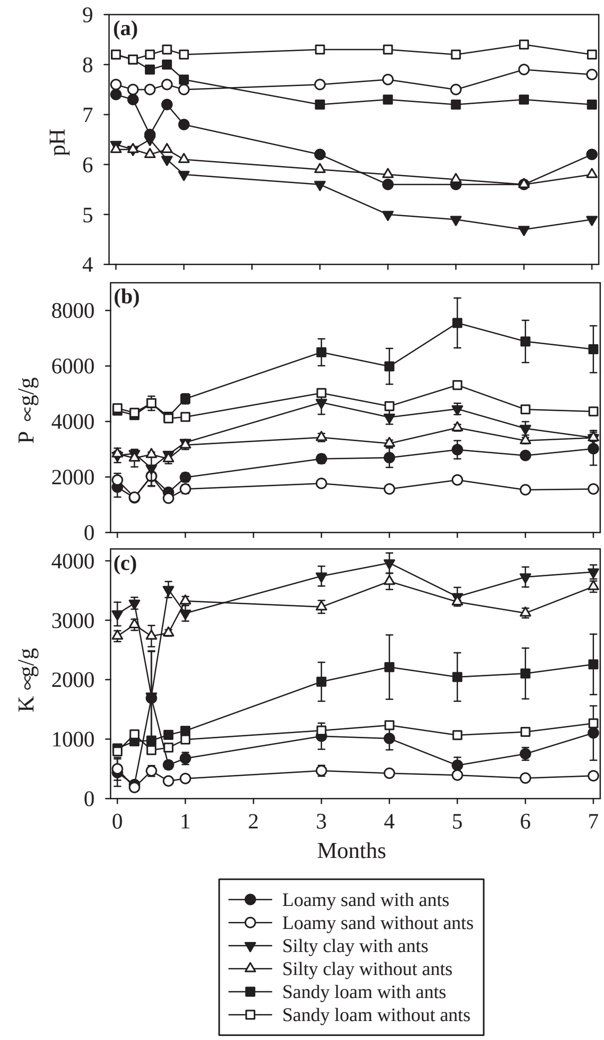


**Figure 1.** Temporal changes of selected phyico-chemical properties of soils with and without ants during an 8-month greenhouse experiment; error bars represent 1 SE of the mean ($n = 4$).

# Results

## Greenhouse study

Ants activity decreased soil pH over the course of the study, while the pH of the soil without ants remained nearly the same (Fig. 1a). The acidity of loamy sand with ants significantly increased with pH decreasing from $7.4 \pm 0.10$ to $6.2 \pm 0.3$ (mean+-SEM; $P < 0.0001$, df = 18, 162, $t = 70.13$), while soil without ants ranged in pH from $7.6 \pm 0.06$ to $7.8 \pm 0.04$. Silty clay with ants also decreased in pH from $6.4 \pm 0.17$ to $4.9 \pm 0.09$ and the pH of soil without ants decreased from $6.3 \pm 0.06$ to $5.8 \pm 0.01$ ($P < 0.0001$, df = 18, 162, $t = 23.4$). Sandy loam soil without ants was pH $8.2 \pm 0.04$ at the initiation of the study, but sandy loam soil with ants showed a significant pH change from $8.2 \pm 0.04$ to $7.3 \pm 0.08$ ($P = 0.0001$, df = 18, 162, $t = 34.9$). The first significant effect of the ants on soil pH was observed 5 months after the study began and was observed thereafter ($P < 0.05$, df = 18, 162, $t = 29.81$).

The presence of ants significantly increased phosphorus (P) in loamy sand and sandy loam but not in silty clay over the 8 months of the study (Fig. 1b). In loamy sand the presence of ants increased P 46% from $1636 \pm 358$ to $3022 \pm 596$ μg/g (mean+SEM, $P < 0.05$, df = 18, 162, $t = 8.6$) while soil without ants had $1568 \pm 54$ and $1888 \pm 246$ μg/g of phosphorus. Presence of ants also significantly increased P 33% in sandy loam from $4396 \pm 82$ to $6608 \pm 846$ μg/g ($P < 0.05$, df = 18, 162, $t = 18.84$). However, in silty clay, concentration of P slightly increased by 18% during the study from $2780 \pm 260$ to $3416 \pm 258$ μg/g with ants and from $2832 \pm 98$ to $3184 \pm 128$ μg/g without ants. The first significant effect of ant presence on amount of P in all soils was observed 3 months after the study ($P<0.05$, df = 18, 162, $t = 13.74$).

The presence of ants in all three soil types did not significantly change $Na^+$, $Ca^{2+}$, or $Mg^{2+}$ during the 8 month duration of the study. The amount of potassium ($K^+$) in loamy sand and silty clay was not affected by the presence of ants. However, in sandy loam, $K^+$ significantly increased 63% in soil with ants (844±34–2257±508 μg/g Fig. 1c) when compared to soil without ants (794±61–1265±16 μg/g; $P<0.05$, df = 18, 162, $t = 40.43$). In sandy loam, significant differences in amount of $K^+$ were observed 3 months after the study ($P<0.05$, df = 18, 162, $t = 9.69$).

## Field study

### Properties of soils

Table 1 summarizes the statistical significance of soil location (i.e. nest versus adjacent) and their soil properties. The activities of ants strongly affected soil moisture content both in longleaf-pine forests ($P = 0.001$) and longleaf-pine plantations ($P<0.001$). For both habitats, the moisture in nest soils was approximately 4%, i.e., 3–8% lower than at any distance from the nest (Fig. 2). Ants also strongly affected soil bulk density in pine forests ($P = 0.004$) and in pine plantations ($P<0.001$), the soil density in ant nests being lower than at any distance from the nest. For both habitats, the bulk density in nest soil was ca. 0.8 g cm$^{-3}$, while at other locations bulk density average approximately 0.95 g cm$^{-3}$. Ants had no effect on soil pH (ca. 4.3 for pine forests and 4.5 for pine plantations).

Extractable $NH_4^+$ was significantly different between soil locations in both pine forests ($P<0.001$) and pine plantations ($P<0.001$) (Table 1). Extractable $NH_4^+$ concentrations were higher in nest soils than in adjacent soils (Fig. 3). Ants had no effect on extractable $NO_3^-$ in any habitats.

Ants had a significant effect on soil extractable P both in pine forest ($P = 0.023$) and in pine plantations ($P = 0.033$, Table 1). Extractable P concentrations were higher in nest soils than adjacent soils (Fig. 4, $P<0.05$). In contrast, soil type had a significant affect on soil extractable $Ca^{2+}$ ($P = 0.034$), extractable $Mg^{2+}$ ($P = 0.001$), extractable $K^+$ ($P = 0.034$), and extractable $Na^+$ ($P = 0.004$) concentrations in pine forests only. Major cation concentrations were statistically higher ($P<0.05$) in nest soils than adjacent soil any distance from the nest in pine forests (Fig. 4). Ants had no affect on major cation concentrations in pine plantations.

### Plant growth

During the 12-week duration of the experiment, a total of 10 seedlings died, 6 planted in nest soils and 4 planted in adjacent soils ($P = 0.492$, df = 1, $F = 0.571$). Excluding individuals that died during the experiment, soil location had a significant effect on *G. japonicus* seedlings grown both in pine forest ($P = 0.043$, df = 1, $F = 8.557$) and pine plantation soils ($P = 0.013$, df = 1, $F = 17.956$). Seedlings grown in ant nest soils had a higher growth rate (pine forests = 23.1% growth, pine plantations = 24.6%) than gardenias grown in soils

**Table 1.** Results of one-way ANOVA tests describing the statistical significance of soil type (i.e. nest soil vs. adjacent soil) on various physical and chemical properties in longleaf-pine forests and longleaf-pine plantations ($n = 3$)

| | Longleaf-pine forest | | Longleaf-pine plantation | |
|---|---|---|---|---|
| Dependent soil variables | *F*-value | Prob. >*F* | *F*-value | Prob. >*F* |
| *Physico-chemical properties* | | | | |
| Moisture content | 10.433 | 0.001 | 13.505 | < 0.001 |
| Bulk density | 7.738 | 0.004 | 23.211 | < 0.001 |
| pH | 0.197 | 0.934 | 0.851 | 0.525 |
| *Indices of nitrogen availability* | | | | |
| $NH_4^+$ | 24.354 | <0.001 | 19.117 | < 0.001 |
| $NO_3^-$ | 0.125 | 0.970 | 0.398 | 0.806 |
| *Extractable nutrients* | | | | |
| Phosphorus | 4.563 | 0.023 | 4.060 | 0.033 |
| Potassium | 3.993 | 0.034 | 2.804 | 0.085 |
| Sodium | 7.790 | 0.004 | 0.196 | 0.935 |
| Calcium | 4.001 | 0.034 | 0.125 | 0.970 |
| Magnesium | 13.292 | 0.001 | 0.418 | 0.792 |

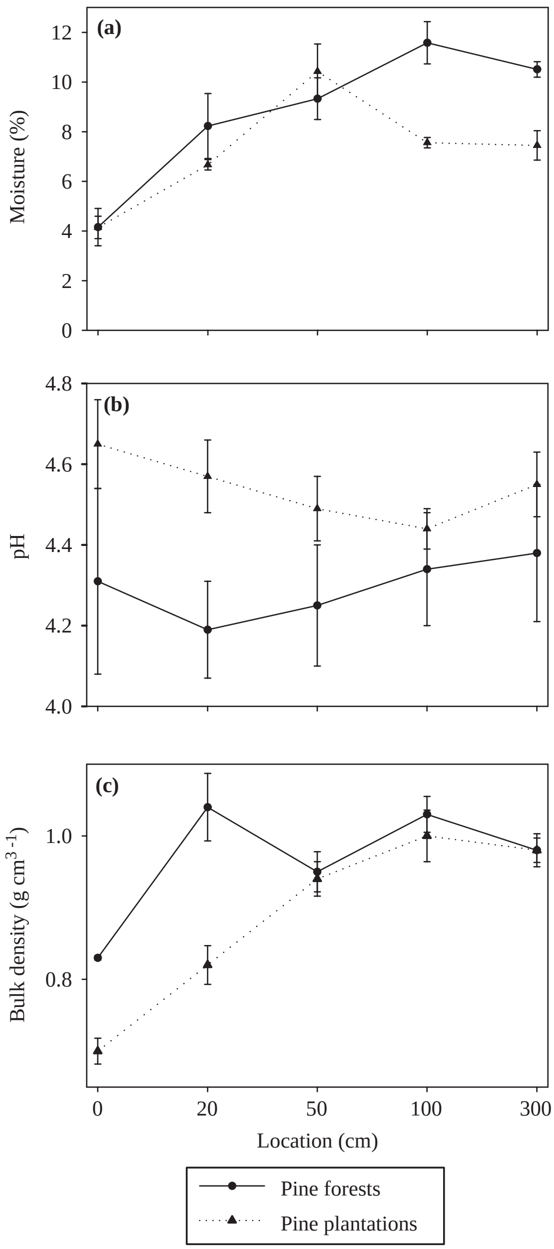


**Figure 2.** Physico-chemical properties of ant nest soils versus adjacent soils from longleaf-pine forests and longleaf-pine plantations located in Louisiana; error bars represent 1 SE of the mean ($n = 3$).

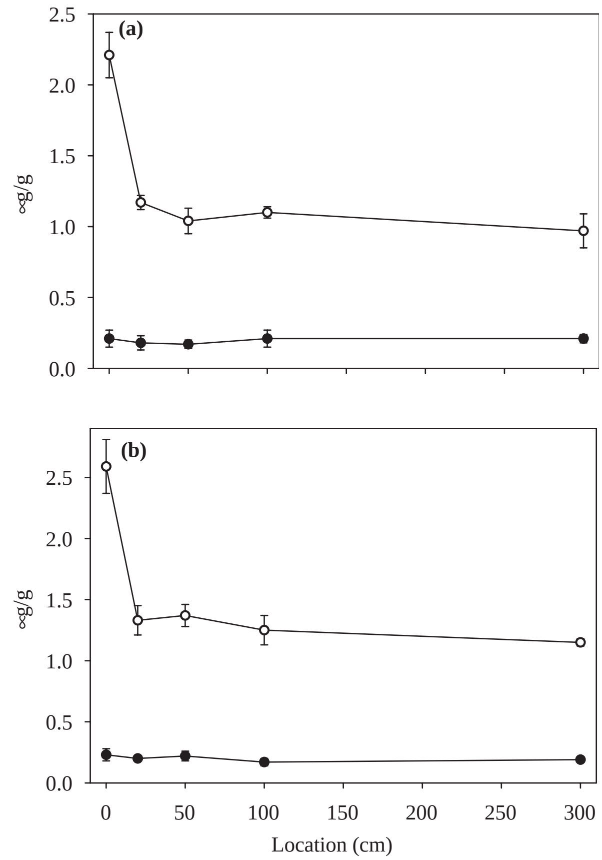


**Figure 3.** Concentration of extractible $NH_4^+$ (○) and $NO_3^-$ (●) in ant nest soils versus adjacent soils from longleaf-pine forests (a) and longleaf-pine plantations (b) located in Louisiana; error bars represent 1 SE of the mean ($n = 3$).

adjacent to ant nests (pine forests = 9.3% growth; pine plantations = 9.3%).

## Discussion

### Linking ant foraging activities to soil fertility

Our controlled greenhouse experiment clearly shows that ants are responsible for changes in soil pH and phosphorus and potassium concentration. Our experiment confirms that ants are able to modify soil chemical properties. We believe those modifications to be the result of ant foraging activities (because ants were allowed to carry prey items to their nest), ant feces, and the decomposition of ants that may have died in the nest during the experiment. With this in mind, we can discuss with more certainty the results we obtained from our field experiments.

The lower moisture content in nest soils compared to adjacent soils may be due to higher water infiltration during rainfall events and higher surface evaporation during periods of low relative humidity. Higher water infiltration would result from increased soil porosity due to ant tunnels. This is corroborated by the very low bulk density measured in nest soils.

In many studies, it has been shown that foraging and daily activities performed by ants may lead to an accumulation of organic matter in nests (e.g. Czerwinski et al., 1971; Eldridge and Myers, 1998).

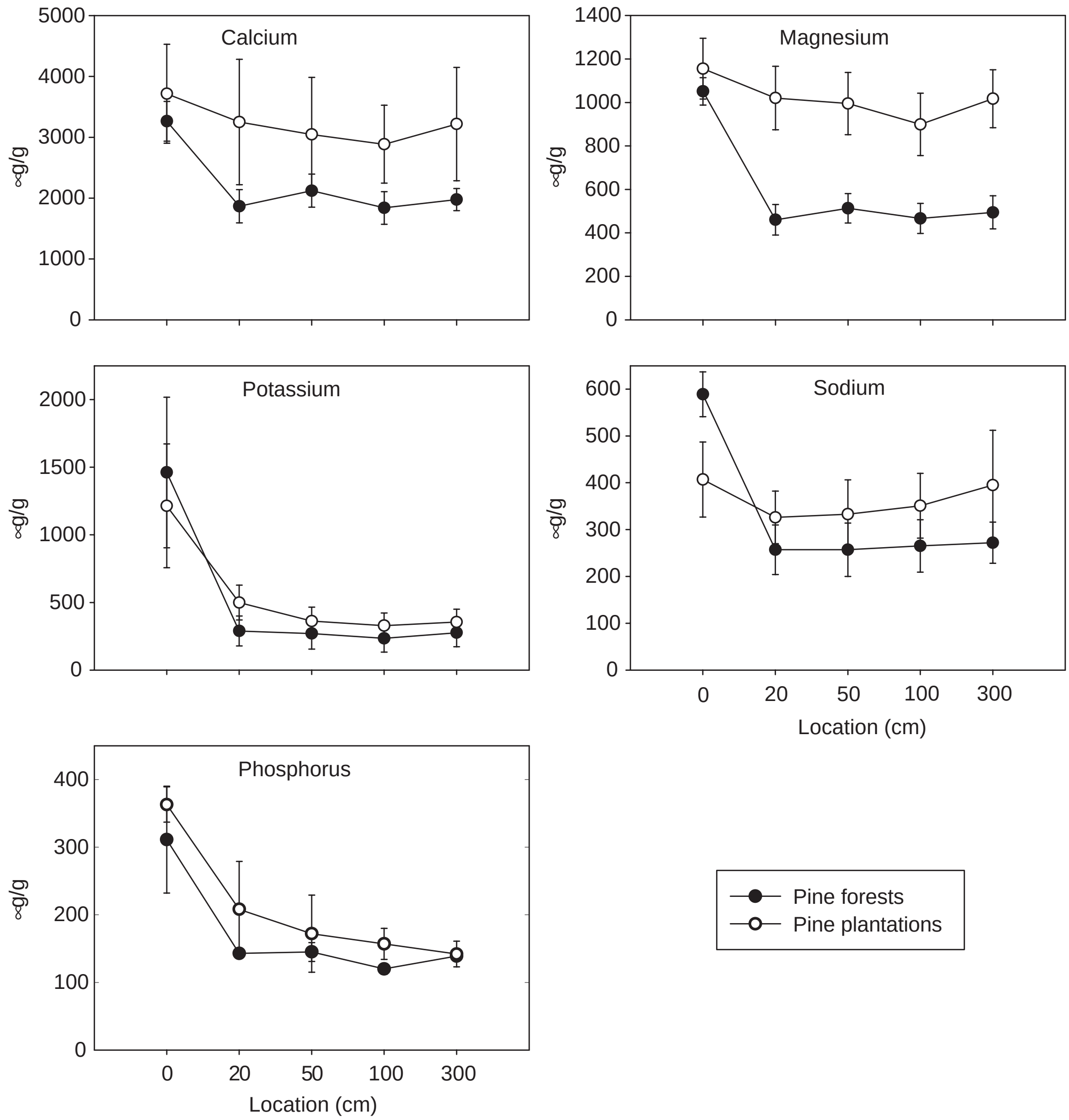


**Figure 4.** Concentrations of Bray-extractable P and $NH_4OAc$-extractable major cations in ant nest soils versus adjacent soils from longleaf-pine forests and longleaf-pine plantations located in Louisiana; error bars represent 1 SE of the mean ($n = 3$).

As for the greenhouse experiment, we believe this to be responsible for the significant differences in physico-chemical properties in nest soils compared to adjacent soils.

The dominant mineral N form was $NH_4^+$ whereas soil $NO_3^-$ remained in low concentrations. This is consistent with many different studies, which showed that conifers occur naturally on soils enriched in $NH_4^+$, and that nitrate in these soils is virtually undetectable (Lavoie et al., 1992; Jobidon et al., 1998; Vitousek et al., 1989). Mineral forms of soil N are often said to be the most limiting nutrients to plant growth in forests. Ant nests were, therefore, of higher N fertility and, by implication, more favorable to plant growth than adjacent soils. Though we did not verify that higher mineral N availability was not simply due to higher total-N pools in nest soils, Lafleur et al. (2002) showed that organic matter in nest soils mineralized proportionately more N and are thus richer in $NH_4^+$ available for plant growth than adjacent soils.

The significantly higher phosphorus and major base cation availability in nest soils sampled in the longleaf-pine forest is similar to what has been found in previous studies on ant nest soils (Nkem et al., 2000; Lenoir et al., 2001; Lafleur et al., 2002). Dostál et al. (2005) demonstrated that activity of *Lasius flavus* increased levels of phosphorus and potassium in nests. Similarly to $NH_4^+$, the higher concentration of phosphorus and base cations can be ascribed to higher mineralization of the organic matter, leading to higher total pools of these nutrients.

### Linking soil fertility to plant growth and to root foraging activities

Our growth experiment clearly showed that plant seedlings grown in ant nest soil grew faster than those planted in adjacent soil. Knowing that plant nutrition is related to concentrations of nutrients in the soil, we can combine the results from the growth experiment with those obtained from the soil fertility experiment and conclude that higher growth rate in nest soil is a result of higher fertility.

In natural ecosystems, the distribution of nutrients in soils is spatially heterogeneous (Hodge et al., 1998). In nutrient-poor soil, plant root systems can proliferate (Drew, 1975), and rates of nutrient uptake can increase (Jackson et al., 1990; Robinson, 1994) when a zone rich in nutrients is encountered. Root proliferation in nutrient rich zones has been widely reported and is considered a response to the heterogeneous nature of the environment (Hutchings and de Kroon, 1994). It has been shown that root length density can be up to four times greater in high nutrient patches than in control soils (van Vuuren et al., 1996) and that $NH_4^+$ availability might be a possible trigger for root proliferation (Robinson, 1996; van Vuuren et al., 1996). The Dostál et al. (2005) study of *L. flavus* associated reduced rhizome biomass with ant activities and found that roots were longer and thinner in association with *Lasius* mounds. Although it may seem intuitively obvious that patch attributes can influence nutrient capture from the patch and, consequently, influence a plant's response to patches, this has seldom been investigated.

Our growth experiment suggests that nest soils have an effect on plant growth. Though cations were found in higher concentration in nest soils from pine forest, only $NH_4^+$ was found in higher concentration in nest soils from both habitats. Thus $NH_4^+$ could be a limiting nutrient for plant growth in pine forests and pine plantations.

In Louisiana's longleaf-pine forests and plantations, fire ant nest soil had soil nutrient concentration significantly higher when compared with adjacent soil. Fire ants have invaded these ecosystems and are so pervasive that they may have a profound impact on soil nutrients and subsequently plant growth. Because plant nutrition and growth are related to concentrations of dissolved nutrients in soil, the boost in soil fertility could have a positive effect on seedling growth and accelerate canopy closure in longleaf-pine plantations and, following disturbance, in longleaf-pine forests. Our growth experiment suggests $NH_4^+$ could be the limiting nutrient for seedling growth in Louisiana's pine forests and pine plantations.

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