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NOTES

# Leaf-cutting Ant Nests and Soil Fertility in a Well-drained Savanna in Western Venezuela[1]

*Key words:* Atta laevigata; *leaf-cutting ants; nutrients; physiognomy; soil; Venezuela.*

TROPICAL SAVANNAS ARE GENERALLY associated with poor soils (Montgomery & Askew 1983), especially those located in northern South America. This dystrophic condition has a major influence on savanna functioning and physiognomy (Sarmiento 1984).

Herbivorous insects also play a major role in the dynamics of savanna ecosystems (Andersen & Londsale 1990). Termite effects on the structure and fertility of soils (Lee & Wood 1971, Salick *et al.* 1983, Coventry *et al.* 1988) and on patterns of vegetation (Spain & McIvor 1988) have been extensively documented. In contrast, the effects of leaf-cutting ants on soil and vegetation in tropical savannas remains mostly unstudied. Documented reviews on savanna ecology (Huntley & Walker 1982; Bourliere 1983; Sarmiento 1984, 1990; Tothill & Mott 1985) fail to mention the role of leaf-cutting ants as modifiers of soil conditions and savanna structure. However, in other tropical ecosystems, leaf-cutter ants have been found to be of extreme importance as soil modifiers (Lugo *et al.* 1973). Species of *Atta* and *Acromyrmex* cut and carry large amounts of plant material to their nests, promoting the accumulation of organic matter and the increase of nutrients in the soil (Haines 1978). Concurrently, the ant nest modifies some physical properties like soil density and porosity facilitating aeration and infiltration (Alvarado *et al.* 1981). This paper documents the changes in soil chemistry of a well-drained savanna, caused by the building of leaf-cutter ant nests.

The study encompassed a 15-ha area of parkland savanna located in Palma Sola Ranch near the city of Barinas (08°28′N, 70°12′W). The hilly landscape is the result of the massive accumulation of rolling stones from the Andes during early Quaternary, with shallow, nutrient poor and well-drained oxisols. Average annual rainfall is 1500 mm concentrated in a seven-month rainy season (May to November). Mean annual temperature is 27°C. These savannas commonly are burned once a year during the dry season (January to April). Physiognomy and floristic composition are representative of the seasonal savannas in the Orinocos Llanos described by Sarmiento (1984, 1990). Woody elements are scattered throughout the grassland or form in small groves (forest islands). Groves include all tree species, those isolated in the grassland as well as most of the species from the gallery forest.

Between November 1990 and April 1991 an area of 2.1 ha was carefully scanned to detect leaf-cutter ant nests. Nests were tagged, measured, and individual ants were collected and identified. For chemical analysis, only well-established adult nests (>60 cm in diameter) were randomly selected. All these belonged to *Atta laevigata* (Fr. Smith) and were located within forest groves. Since not all groves had *Atta* nests, we were also able to compare groves with and without nests to study the consequences of nests on the soils.

Ten soil samples were taken randomly from the upper soil (0–20 cm) from each of the following sites: open grassland, groves lacking ant nests, leaf-cutting ant nests in groves, and the gallery forest. Samples were taken to the laboratory and weighed, dried to constant weight and weighed again to determine relative water content. The following chemical analyses were performed (Jackson 1962): The Walkey & Black chromic acid method to determine organic carbon contents; the micro-Kjeldahl method to determine nitrogen contents: the Olsen's procedure for available phosphorus. Exchangeable metallic cations were determined with 1 N ammonium acetate at pH 7 and cation-exchange capacity was determined by saturating the exchange complex with Na using sodium acetate solution.

A Principal Component Analysis (PCA) was used to ordinate soils according to nutrient content. A one-way ANOVA was applied to compare means from the different types of soils for each chemical parameter.

Thirty groves were found in the 2.1 ha sampling area and their surface ranged from 15 to 400 $m^2$. Only 15 groves had an adult nest. We did not find any adult *A. laevigata* nests in the open grassland nor in the gallery forest.

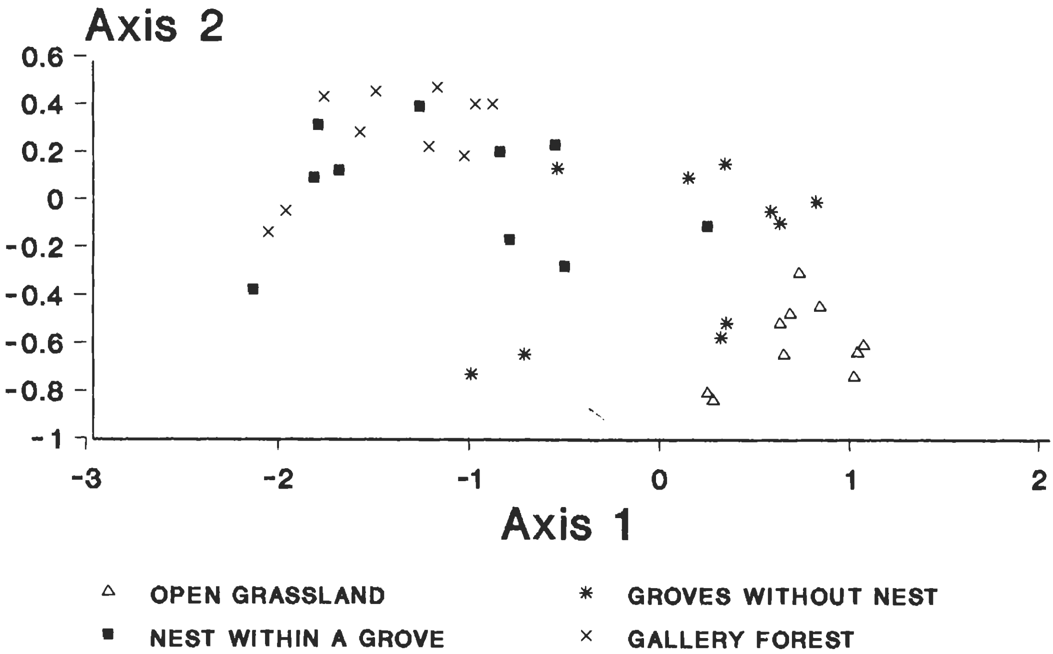


FIGURE 1. Bidimensional ordination for 40 soil samples from four different site conditions using the first two axes (A1 and A2) from a principal component analysis (PCA).

The different soils appear in the ordination space defined by the two first axes (Fig. 1) as a sequence of overlapping groups from gallery forest and nests to open grassland. Correlation analysis for ten different chemical variables and the three first axes (Table 1) showed significant levels between A1 (42.1% variance) and all soil variables with the exception of Na contents. A2 (21.4% variance) and A3 (15.2% variance) were significantly correlated to six soil variables. In 8 out of 10 soil variables compared, there were significant differences between soils from different places (Table 2). A higher content of P and K is clearly differentiating gallery forest soils from the rest. Nitrogen and Mg have higher values in grove's nests and

TABLE 1. *Correlation coefficients (r) between ten soil variables and the three first PCA ordination axes (A). (*) = P < .05, (**) = P < .01. The three axes explain 78.8% of total variance, the variance for each axis is in parentheses.*

| | Axis | | |
|---|---|---|---|
| Variables | A1 (42.1%) | A2 (21.4%) | A3 (15.2%) |
| OC | −0.82** | −0.34* | −0.34* |
| N | −0.94** | 0.04 | −0.05 |
| C/N | −0.41** | −0.64** | 0.52** |
| P | −0.71** | 0.18 | −0.42** |
| K | −0.76** | 0.16 | −0.39** |
| Mg | −0.81** | 0.37* | 0.25 |
| Na | −0.15 | 0.84** | 0.23 |
| Ca | −0.37* | 0.51** | 0.60** |
| CIC | −0.49** | −0.67** | 0.06 |
| Al | −0.59** | −0.05 | −0.57** |

TABLE 2. *Mean and (SD) values for ten soil parameters measured under four different site conditions* (N = *10 samples in each site). Values from the one-way ANOVA comparison for each row are given in the last two columns on the right. Means with the same letter in each row are not significantly different. OG = Open grassland, G = Groves without nests, N = Nests in groves, and GF = Gallery forest. Nitrogen (N) and Organic Content (OC) in (%), Phosphorous (P) in ppm, other cations in mq/100 g.*

| Variables | OG | G | N | GF | *F* | *P* |
|---|---|---|---|---|---|---|
| N | $0.071^{ab}$ | $0.080^{b}$ | $0.103^{c}$ | $0.108^{c}$ | 33.7 | <.001 |
| | (0.007) | (0.011) | (0.013) | (0.008) | | |
| P | $1.50^{a}$ | $2.30^{a}$ | $2.40^{a}$ | $3.80^{b}$ | 16.1 | <.001 |
| | (0.53) | (0.48) | (0.70) | (1.14) | | |
| K | $0.080^{a}$ | $0.088^{a}$ | $0.114^{a}$ | $0.285^{b}$ | 7.2 | <.001 |
| | (0.021) | (0.023) | (0.024) | (0.052) | | |
| Mg | $0.077^{a}$ | $0.101^{a}$ | $0.160^{b}$ | $0.160^{b}$ | 16.2 | <.001 |
| | (0.017) | (0.037) | (0.050) | (0.013) | | |
| Ca | $0.181^{a}$ | $0.229^{ab}$ | $0.350^{c}$ | $0.247^{ab}$ | 8.5 | <.001 |
| | (0.056) | (0.063) | (0.098) | (0.034) | | |
| Al | $1.760^{a}$ | $2.048^{bc}$ | $1.940^{ab}$ | $2.230^{c}$ | 7.7 | <.001 |
| | (0.196) | (0.290) | (0.284) | (0.149) | | |
| Na | $0.065^{a}$ | $0.065^{a}$ | $0.084^{a}$ | $0.079^{a}$ | 0.6 | .674 |
| | (0.008) | (0.030) | (0.007) | (0.023) | | |
| CIC | $5.912^{a}$ | $4.835^{a}$ | $5.375^{a}$ | $5.130^{a}$ | 0.8 | .578 |
| | (1.312) | (1.043) | (0.879) | (0.508) | | |
| OC | $1.153^{a}$ | $1.413^{a}$ | $1.832^{b}$ | $1.430^{c}$ | 41.3 | <.001 |
| | (0.097) | (0.250) | (0.398) | (0.135) | | |
| C/N | $16.49^{a}$ | $17.60^{ab}$ | $18.30^{b}$ | $13.18^{c}$ | 68.7 | <.001 |
| | (0.98) | (1.80) | (2.2) | (0.82) | | |

gallery forest in contrast to lower values in groves without nests and open grassland. Soil from grove's nests was significantly higher in Ca, OC and C/N ratio than all others.

Several studies have shown that ants are responsible for enrichment of the soils in various ecosystems (see Petal 1978, Mandel & Sorenson 1982, Culver & Beattie 1983, Levan & Stone 1983). Accordingly, our results show that *Atta laevigata* nests are richer in nitrogen and magnesium than similar soils in the open grassland and in groves without a nest. They were also the richest in organic carbon and in calcium. The importance of these effects is indeed high if we consider the size of the nests. The nests from ants involved in the studies mentioned above (*Myrmica, Lasius, Pogonomyrmex, Pachyondyla* and *Formica*) are below 1 m in diameter; whereas, *Atta* nests reach more than 6 m in diameter, more than 5 m in depth and may concentrate up to half a ton of accumulated organic matter (see Coutinho 1984). Furthermore, the density of nests found in this savanna is high (7 nests/ha).

The role of *Atta* ants in nutrient conservation by cycling nutrients from the herbaceous layer into deep soil where they are available for trees is important. This is especially so in dystrophic savannas that are burned often, since fires mineralize herbaceous biomass, making nutrients available in the topsoil but also inducing important nutrient loss (Coutinho 1984). The physiognomy of savannas depends on the success of tree establishment, and this in turn is limited by the availability of nutrients (Sarmiento 1984). In this study we present evidence that leaf-cutting ants increase resource patchiness by concentrating nutrients in their nests. *Atta* could be promoting tree growth by improving soil fertility and consequently should have an impact on savanna physiognomy and functioning. This effect has been shown in grasslands from the Central Chaco in Argentina and from Paraguay, where trees colonize preferentially abandoned *Atta* nests, which consequently are having a major role in grassland physiognomy and forest regrowth (Jonkman 1978, Bucher 1982). A similar situation has been reported for termites in Brazilian savannas. The action of building their nests provides the appropriate environment and survival of woody vegetation (Oliveira Filho 1992, Ponce & Da Cunha 1993). This is important since in some savannas of Venezuela termite mounds and leaf-cutter ant mounds are associated (San Jose *et al.* 1989).

As numerous contributions have emphasized the role of variations in the physical environment determining the function and physiognomy of Neotropical savannas, the results discussed here are pointing toward the relevance of biotic factors and animal-soil-plant interactions.

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## RESUMEN

Se investigaron los efectos de los nidos de hormigas cortadoras de hojas sobre las propiedades químicas de los suelos en una sabana parqueada de Venezuela. Los nidos de *Atta laevigata* fueron más ricos en N, Mg, Ca y Materia Orgánica que suelos similares ubicados en el pastizal abierto y en bosquetes sin

nidos. Estos resultados apoyan la hipótesis de que las hormigas del género *Atta* podrían modificar la fisonomía de la sabana, promoviendo el crecimiento de árboles al incrementar la fertilidad del suelo.

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