

SHORT COMMUNICATION

**Leaf-cutter ants' (*Atta laevigata*) aid to the establishment success of *Tapirira velutinifolia* (Anacardiaceae) seedlings in a parkland savanna**

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Together with dispersal, establishment is a fundamental process in the persistence of plant populations and in biological invasions (Harper & White 1974). Because of their interactions with plants, ants play an important role in these processes (Beattie 1985). However, movement of seeds by *Attini* ants remain poorly understood, even though they often influence patterns of establishment and community structure in tropical regions (Kaspari 1993, Roberts & Heithaus 1986).

Leaf-cutting ants (Formicidae, Attini) are very active in parkland savannas in the Orinoco Llanos. They may be playing a role in the invasion of open grasslands by woody elements from the neighbouring deciduous forests (Etter & Botero 1990). Deciduous trees invade the grasslands forming small groves, which look like forest islands in the grass matrix (Sarmiento 1983). The establishment of deciduous trees and the growth of leaf-cutting ant nests can act synergistically, promoting the invasion of the open grassland, whereas fire and cattle seem to be counteracting factors restricting the establishment of deciduous trees (Farji Brener & Silva 1995a). In this paper we present further evidence

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to support the hypothesis of synergistic interactions between leaf-cutting ants and deciduous trees, affecting the physiognomy of parkland savannas. Specifically, we address the role of *Atta laevigata* Fr. Smith ants in the establishment success of *Tapirira velutinifolia* (Cowan) Marcano-Berti seedlings, a common deciduous tree species of savanna groves.

The study was conducted in parkland savanna bordering a gallery forest in Palma Sola Ranch near the city of Barinas, Venezuela (08° 28' N, 70° 12' W). Soils are 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 are commonly burnt once a year during the dry season (January to April). Physiognomy is characterized by two woody components: (a) evergreen, sclerophyllous trees scattered throughout the grassland (*Byrsonima crassifolia* (L.) H.B.K., *Bowdichia virgiloides* H.B.K.) which are absent from the gallery forest, and (b) small groves dominated by mesophyllous, deciduous trees (*Genipa caruto* H.B.K., *Tapirira velutinifolia*, *Godmania macrocarpa* Hemsley) which are common in the gallery forest and rarely found isolated in the grassland.

Seven belt-transects (15 m × 200 m) were set perpendicular to the forest border and sampled from November 1990 to April 1991. In each transect, all groves, *A. laevigata* nests and *T. velutinifolia* trees were recorded and measured. In groves, we measured radial distances in cardinal and intercardinal directions and used the average to estimate the grove area, following Archer *et al.* (1988). *T. velutinifolia* trees were counted and the height and basal diameter were measured. Trees were then classified within three height classes (<50, 50–150, >150 cm). To study the role of *A. laevigata* ants in the establishment of *T. velutinifolia* seedlings, we selected those groves having both species. In each, we observed the ant activity every week between January and March of 1991. Ants carrying *T. velutinifolia* fruits were followed to find out the fate of the fruits and seeds. The density of fruits (and seeds) was measured in each grove in two sites: at the main entrance of the nest and at the base of a randomly selected *T. velutinifolia* tree. Fifty seeds from refuse piles and 50 intact fruits from the soil beneath the trees were randomly selected and carried to the laboratory to evaluate the effects of the fruit removal and predation by ants. The seeds taken from the refuse piles were not much older than those obtained from the fruit (both from the same fruiting season). In the laboratory, each sample was placed in a petri dish on a filter paper and kept moist at room temperature and partial sunlight for two months. They were checked weekly for germination. The results were compared using a chi-squared test, applying the Yates correction. From fruits collected beneath the trees, 75 were randomly selected. Sixty of them were measured, weighed and dried at 70°C to constant weight. The pulp of the other was used to determine nitrogen content using the micro-Kjeldahl method (Jackson 1964).

A total of 30 groves was found in the seven belt-transects. Thirteen groves had both an *A. laevigata* nest and *T. velutinifolia* trees. Nests ranged from 1 to

Table 1. Mean number of fruits or seeds found in 80 cm<sup>2</sup> circular plots within groves. N = 13 groves.

Location	Mean ( $\pm$ SD)	
Base of a <i>T. velutinifolia</i> tree	0.4 ( $\pm$ 0.7)	
Around an <i>A. laevigata</i> nest	8.5 ( $\pm$ 2.8)	(***)

(\*\*\*)  $P < 0.001$ ,  $U = 169$ , Mann-Whitney U-test.

3 m in radius. There were no adult nests or *T. velutinifolia* trees in the open grassland.

Fruits of *T. velutinifolia* are oblong, small and form light, fleshy drupes. The average size ( $\pm$ SD) was 1.21 ( $\pm$ 0.09) cm  $\times$  0.85 ( $\pm$ 0.08) cm and the average fresh weight was 0.91 ( $\pm$ 0.12) g. The pulp was rich in nitrogen (4.1  $\pm$ 1.5%) and had a water content of 43  $\pm$ 4.5%.

We observed the ants actively harvesting the fruits from the soil and carrying them to the nest. The small size of the fruits enables them to be carried by ants to their nests. The high content of nitrogen and water should also be a factor in their selection (Berish 1986, Bowers & Porter 1981). They either ate the pulp and abandoned the seed near the nest entrance or took the fruit into the nest. Seeds from these fruits were found near the nest in the refuse piles. As a consequence of this relocation, the density of fruits and seeds was significantly higher near the nest entrance than beneath the tree crowns (Table 1).

In petri dishes, none of the intact fruits germinated during the two-month period and they ended heavily attacked by fungi. On the contrary, 20% of the seeds from the refuse piles germinated ( $\chi^2 = 11.1$ ,  $P < 0.01$ ). To compare *T. velutinifolia* plants in groves with and without an *A. laevigata* nest we selected groves of similar area among those with *T. velutinifolia* (N = 10). The total number of *T. velutinifolia* trees was 121 in groves with ant nests (N = 5 groves) and 35 in groves without nests (N = 5 groves). As shown in Table 2, tree

Table 2. Density of *Tapirira velutinifolia* (trees m<sup>-2</sup>, mean  $\pm$ SD in each size class) in similarly sized groves† with and without an *A. laevigata* nest. All values differ significantly between the two locations (Mann-Whitney U-test).

Height class (cm)	Groves (N = 10)		
	Without nests N = 5	With nests N = 5	
>150	0.04 $\pm$ 0.02	0.07 $\pm$ 0.02	(*)
150–50	0.05 $\pm$ 0.03	0.16 $\pm$ 0.05	(*)
<50	0.03 $\pm$ 0.02	0.10 $\pm$ 0.05	(**)

† Mean sizes ( $\pm$ SD) of the groves: without nests, 73 ( $\pm$ 29) m<sup>2</sup>; with nests, 94 ( $\pm$ 31) m<sup>2</sup>. ( $U = 16$ ,  $P > 0.10$ , Mann-Whitney U-test.)

(\*) =  $P < 0.05$ , (\*\*) =  $P < 0.01$ .

density was higher in groves with a nest, and this held true for each size class.

Our results suggest that *A. laevigata* ants are acting as 'assistants' for *T. velutinifolia* seeds, and that their activity as fruit (pulp) predators may increase the germination of this tree species. The values of germination presented here are even higher than those reported for *Ficus hondurensis* seeds dispersed by *Atta cephalotes* in a tropical dry forest (Roberts & Heithaus 1986). The increased germination of seeds from predated fruits seems to be the result of cleaning the seed of fruit pulp, thus avoiding fungal infection. Additionally, secretions from the metapleural glands in some ant species are known to have fungicidal properties (Beattie *et al.* 1986). Furthermore, ants concentrate seeds near the nest (nest holes and refuse piles), and this may enhance seedling establishment and survival. Ant nests seem to be safer sites for the growth of *T. velutinifolia* for several reasons. A series of reports show that ants improve soil conditions by building their nests (Culver & Beattie 1983, Dean & Yeaton 1993, Rogers & Lavigne 1974), especially leaf-cutting ants (Haines 1978, Jonkman 1978, Lugo *et al.* 1973). In a parallel paper (Farji Brener & Silva 1995a) we showed that in these savannas, soil from *A. laevigata* nests is richer than soils from the grassland and from the groves without an *A. laevigata* nest. This is specially important under the general dystrophic conditions of savanna soils (Sarmiento 1983). Even in more fertile soils, seedling growth is enhanced in ant nests as shown by Levey & Byrne (1993) in a tropical rainforest community.

The location of ant nests within the grove may also be important. Given that trees are shading out savanna grasses, fire is mostly excluded from the groves. We observed that fire exclusion was especially common in the centre of the grove, where the ant nest is generally located. Fire is a very important mortality factor, especially for deciduous, mesophyllous trees such as *T. velutinifolia*, and this may be why we did not find any *T. velutinifolia* trees in the open grassland. Therefore, by relocating the seeds near their nest, the ants are protecting the future seedlings from fire. This process can be especially important for the *T. velutinifolia* trees that are located in the periphery of the groves.

In summary, our results show that by seed-cleaning activity the ants increase the germination success of *T. velutinifolia* or, at least, produce an accelerating effect on it. Furthermore, by carrying seeds near the nest, the ants appear to increase the probability of a seed to land in a nutrient-rich, fire-safe site that is suitable for germination and seedling growth.

The key issue is whether the increase in growth and survivorship of seedlings on ant nests has any impact at the level of adult plant populations. In this context, the higher mean density of *T. velutinifolia* trees in groves with ant nests, compared with groves without nests (Table 2), suggests that the ants activity increase the probability of growth of *T. velutinifolia* seedlings. It is unlikely that this difference was related to any natural cause other than the influence of ant activity.

On the other hand, it is possible that *A. laevigata* is also a mortality factor for *T. velutinifolia* seedlings; however, further research is required to test this

hypothesis. Although trees can be killed as a result of repeated defoliation by leaf-cutting ants, this is an uncommon phenomenon in natural systems (Cherrett 1983).

In a previous paper (Farji Brener & Silva 1995b) we argue that the growth of both leaf-cutting ant and deciduous tree populations is the result of a synergistic interaction between the two groups of organisms. Ants are not only getting food from the trees but also more mesic conditions for the growth of the nest. Trees are not only growing better in the nest-rich soils but very possibly are producing more fruits and seeds (Hanzawa *et al.* 1988, Rissing 1986). At a community level, these interactions should affect the physiognomy of the savanna, changing tree/grass ratio and increasing the number and size of deciduous groves. However, it is clear that the evaluation of the effects of leaf-cutting ants on the dynamic of parkland savannas will need more long-term study.

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