

Leaf-cutting ants and forest groves in a tropical parkland savanna of Venezuela: facilitated succession?

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ABSTRACT. Some savanna areas in the Orinoco Llanos region in Venezuela are characterized by the abundance of small forest groves, resulting in a parkland landscape. We hypothesized that forest groves are the result of colonization of the open savanna by forest species, facilitated by the activity of leaf-cutting ants. In this paper we present results from a field study conducted on an ecotonal belt between a deciduous gallery forest and an open savanna in the western Llanos of Venezuela. In seven transects, trees, groves and leaf-cutting ant nests were counted, size parameters evaluated and distance from grove to forest measured. Soil chemical analysis and microclimatic measurements were performed in the forest, grassland and groves. Floristic composition of the woodland component of the savanna (scattered trees) was very dissimilar from that of the forest, but the composition of the groves was essentially a mixture of both woodland and forest species. Woodland trees were present in all groves, whereas forest trees were present only in larger groves. The size structures of populations of the two types of trees differed significantly according to the size of the grove; also, woodland tree population structure differed significantly between open savanna and groves. The frequency of groves with *Atta laevigata* nests increased with the size of the grove, and groves with forest trees were positively associated with the presence of nests. *A. laevigata* nests improved the soil of groves, increasing N, Mg, Ca and organic carbon, but other soil properties were not modified. Temperatures at ground level in the dry season were ameliorated in the groves compared with the grassland, and this effect increased with the size of the grove. We concluded that a dynamic process of grove formation is facilitated by the aggregation of a few woodland trees, followed by the successful invasion of forest trees and a leaf-cutting ant nest. The results did not show any clear sequence of arrival of the ants or the forest trees, but it seems clear that these two would act synergistically, improving conditions for each other.

KEY WORDS: *Atta laevigata*, grove dynamics, invasions, leaf-cutter nest, plant succession, woodland savanna.

INTRODUCTION

There is evidence of an increase in woody elements in Neotropical grasslands for the last 300 years (Archer 1989, Archer *et al.* 1988, Bucher 1987, Schofield & Bucher 1986). These changes have been considered to be responses to changes

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in various environmental conditions such as climate (Emanuel *et al.* 1985, Neilson 1987), fire and cattle exclusion (San José & Fariñas 1991) or grazing regimes (Madany & West 1983). However, very little is known about the processes and mechanisms producing these changes in community composition and physiognomy.

Nesting by leaf-cutting ant species has been considered to be the primary cause or at least an accelerator of the invasion of some grasslands by trees in the Gran Chaco region of South America (Jonkman 1976, 1978). Trees are found to grow preferentially on abandoned *Atta* nests (Bucher 1982). A similar process seems to be common in tropical savannas colonized by termites (Glover *et al.* 1964, Oliveira-Filho 1992, Ponce & Da Cunha 1993, Troll 1936).

Leaf-cutting ant nests are considered a major disturbance in tropical and subtropical soils (Alvarado *et al.* 1981, Bucher 1982, Weber 1966). The ants collect leaves from a large area and concentrate them, enriching the soil at specific sites (Haines 1975, 1978). Also, soil physical properties such as drainage and aeration are locally modified by the nests (see Cherrett 1989). These changes induce particular patterns of associated vegetation (Coutinho 1982, Fowler 1977, Fowler & Haines 1983).

Some savanna areas in the Orinoco Llanos region in Venezuela are characterized by a higher frequency of small forest groves, resulting in a parkland landscape (Sarmiento 1983). This is particularly common in the ecotonal areas between deciduous forests and savannas. These groves, previously considered to be relicts of locally declining forests (Vareschi 1960), are now seen as advances of forest trees on the grasslands, occupying sites with a more favourable water balance (Sarmiento & Monasterio 1975). Intense leaf-cutting ant activity has been detected in these forest groves, and it has been suggested that they may be playing a role in the forest invasion of the savanna (Etter & Botaro 1990). Contrary to the tree invasion of abandoned nests shown in the more southern grasslands in South America (Bucher 1982, Jonkman 1978), in these savannas there seems to be a positive association between active nests and forest species.

In this paper we present results from a field study conducted on an ecotonal belt between a deciduous gallery forest and an open savanna. As with the surrounding savannas, this area is burned almost every year at the end of the dry season. Besides forest groves, trees of woodland species grow scattered in the grassland at various densities. These are evergreen, sclerophyllous trees and are considered to be resistant to fires (Sarmiento 1983) in contrast to the deciduous, mesophyllous trees from the forest, which are very sensitive to savanna fires. We hypothesized that forest groves are the result of colonization of the open savanna by forest species, facilitated by the activity of leaf-cutting ants. This advance upon the grassland is apparent in areas where the water table is shallow enough to be reached by deciduous trees, such as those close to river galleries.

THE STUDY AREA

The study was conducted in a parkland savanna close to the city of Barinas (08° 28' N, 70° 12' W) in the western Llanos of Venezuela. The area, within Palma Sola Ranch, has been a study site for savanna research for the last 15 years. The hills are formed by accumulation of massive rolling stones from the early quaternary, fragmented and basculated by Pleistocene Andean tectonics. Soils are shallow oxisols, very well drained and very deficient in nutrients. Detailed information on the ecology of this savanna is found in Sarmiento (1984).

Physiognomy and floristic composition are typical of the Orinoco savannas (Sarmiento 1983). In the almost continuous graminoid layer, the grasses *Trachypogon plumosus* H&B Nees, *Leptocoryphium lanatum* (H.B.K.), *Sporobolus cubensis* Hitchcock, *Elyonurus adustus* (Trin.) Ekman, *Axonopus affinis* Chase, *A. canescens* (Nees & Trin.) Pilger and *Andropogon semiberbis* (Nees) Kunth are abundant. The most common scattered trees are *Byrsonima crassifolia*, *Bowdichia virgilioides* and *Palicourea rigida*.

Although this area is not presently used for any major economic activity such as agriculture or ranching, it is located very close to an expanding city, and therefore has been under human influence for a long time. However, there are, at present, no signs of recent intense impact upon the vegetation.

METHODS

Here we use the term 'woodland trees' to refer to the evergreen, sclerophyllous species considered characteristic of wooded savannas, as dispersed trees in the grassland matrix. We use the term 'forest trees' to refer to the mesophyllous, deciduous species dominant in the canopy of the deciduous forest in the Orinoco Llanos. We defined a 'grove' as any discrete set of three or more trees forming a canopy. Groves are in fact forest-like islands in the graminoid matrix.

Seven transects (15 m × 200 m) were set perpendicular to the forest border, and sampled during the period November 1990 to April 1991. Trees, groves and leaf-cutting ant nests were counted and the following parameters were evaluated: (a) the height, basal diameter and canopy area of each tree both in the open savanna and within each grove were measured; (b) grove diameters were measured in cardinal and intercardinal directions and used to calculate a circularity index and to estimate the grove's area following Archer *et al.* (1988). To calculate the index, one radial distance is randomly selected and divided by the average radial distance. Since groves were very nearly circular, the radial average was used to estimate the area; (c) the shortest distance from grove to forest was also measured; and (d) the age of each nest both in the open savanna and within each grove was estimated as the number of entrances (holes) following Fowler *et al.* (1986). In each nest, soldiers and workers were collected for further identification.

Trees were classified according to three height classes: <50, 50–150 and >150 cm. These classes are relevant to the structure of the graminoid matrix of the savanna. Below 50 cm, the young tree is under the graminoid canopy; 50–150 cm is the layer with the maximum graminoid biomass and directly affected by fire. When the tree grows above 150 cm its probability of reaching reproductive size increases (Silva 1993).

To study the location of trees within groves the relative position of each tree was scored as being either (a) in the centre, (b) close to the centre and (c) in the periphery, of six large groves.

Groves were classified subjectively into six classes according to area: (I) <15 m², (II) 16–25 m², (III) 26–50 m², (IV) 51–70 m², (V) 71–150 m² and (VI) >150 m². Due to the apparent insular nature of groves in the graminoid matrix, their stability was assessed using the approach of island biogeography theory (MacArthur & Wilson 1967). To do this, species composition in the forest was sampled by randomly placing five circular replicates of each of the following radii: 2, 3, 5, 7 and 10 m. Data from the forest and from the groves were analysed following Preston (1962), fitting each set to $S = cA^z$, where species richness (S) is an exponential function of cluster area in square metres (A).

To evaluate soil conditions 10 soil samples were randomly taken at two depths (0–20, 20–40 cm) in the following types of sites: (a) grassland without nest; (b) grassland with nest; (c) grove without nest; (d) grove with nest; and (e) gallery forest. The forest soil was included as a reference. The analysis was intended to show whether the presence of leaf-cutting ant nests significantly modified the soil in the grassland and in the groves. In the sites with nest, the soil was taken not from the refuse pile, but from the surrounding undisturbed soil. Samples were taken to the laboratory and weighed, dried to constant weight and the relative moisture contents then determined. These samples were also analysed for their nutrient content. Organic carbon was determined by the Walkley–Black method (Black 1967), total nitrogen by the micro-Kjeldahl method (Jackson 1962) and total phosphorus by reacting previously digested samples (in HClO₄ and H₂SO₄ at 200°C) with ammonium molybdate and ascorbic acid, then measuring absorbance at 660 nm. Exchangeable cations were extracted with 1 N sodium acetate solution and determined in the extract by atomic spectrophotometry.

Temperature and relative humidity were measured at ground level and at 150 cm above ground during two circadian cycles at the end of the wet season (November 1990) and at the end of the dry season (April 1991) in the following sites: (a) the grassland; (b) a small grove (20 m²); (c) a medium grove (100 m²); (d) a large grove (400 m²); and (e) the forest.

On similar dates, we randomly selected eight nests in which to study the plant material being harvested by ants during a circadian cycle following Cherritt (1968). During a two-minute period every two hours, all material being carried to the nest was removed and taken to the laboratory to be classified, dried and weighed.

Table 1. Some of the commonest tree and shrub species found in open savanna (OS), grove (G) and forest (F) at Barinas, Venezuela. Total area sampled: 21,000 m². X = presence, — = absence.

Species	Family	Location		
		OS	G	F
<i>Byrsonima crassifolia</i> (L.) H.B.K.	Malphiaceae	X	X	—
<i>Byrsonima coccolobaefolia</i> H.B.K.	Malphiaceae	X	X	—
<i>Bowdichia virgilioides</i> H.B.K.	Leguminosae	X	X	—
<i>Palicourea rigida</i> H.B.K.	Rubiaceae	X	X	—
<i>Curatella americana</i> L.	Dilleniaceae	X	X	—
<i>Casearia sylvestris</i> Sw.	Flacourtiaceae	X	X	X
<i>Genipa caruto</i> H.B.K.	Rubiaceae	—	X	X
<i>Tapirira velutinifolia</i> (Cowan) M-Berti	Anacardiaceae	—	X	X
<i>Godmania macrocarpa</i> Hemsley	Bignoniaceae	—	X	X
<i>Cochlospermum vitifolium</i> Spreng.	Cochlospermaceae	—	X	X
<i>Davilla nitida</i> (Vahl) Kubitski	Dilleniaceae	—	X	X
<i>Xylopia aromatica</i> Baill.	Annonaceae	—	X	X
<i>Solanum bicolor</i> Willd.	Solanaceae	—	X	X
<i>Randia aculeata</i> L.	Rubiaceae	—	X	X
<i>Pavonia sessiflora</i> H.B.K.	Malvaceae	—	X	X
<i>Roupala montana</i> Willd.	Proteaceae	—	—	X

RESULTS

The floristic composition of the woodland component of the savanna (scattered trees) was very dissimilar to that of the forest, but the composition of the groves was essentially a mixture of both woodland and forest species. Table 1 shows a list of species from the samples in the gallery forest, the groves and the open grassland. In the case of the groves and the grassland, only a few rare species were not sampled. Species with very low frequency were not included in the list of forest species sampled. Three woodland species were equally frequent in the woody layer of the savanna as well as in the groves (*Bowdichia virgilioides*, *Byrsonima crassifolia* and *Palicourea rigida*). Two forest species were very frequent (*Genipa caruto* and *Tapirira velutinifolia*), but only in larger groves. Authorities for species are in Table 1.

Grove size and species composition

As shown in Figure 1, the number of tree species increased with sample size both in the forest ($r = 0.98$, $P < 0.01$) and in the groves ($r = 0.84$, $P < 0.01$), but floristic richness (S) was higher in the forest. The equation for the forest was $S = 3.66A^{0.39}$ ($R^2 = 0.87$, $N = 5$, $P < 0.02$) and for the groves it was $S = 3.09A^{0.29}$ ($R^2 = 0.77$, $N = 30$, $P < 0.001$), both calculated with sample size in m².

A total of 30 groves were located, five in each of the six size classes. Groves had an almost circular shape, with no consistent orientation, although larger groves were more irregular than the smaller ones. The relative distance from the centre to the edge varied only between 0.94 ± 0.10 and 1.02 ± 0.03 . There was no significant correlation between grove area and distance from the forest

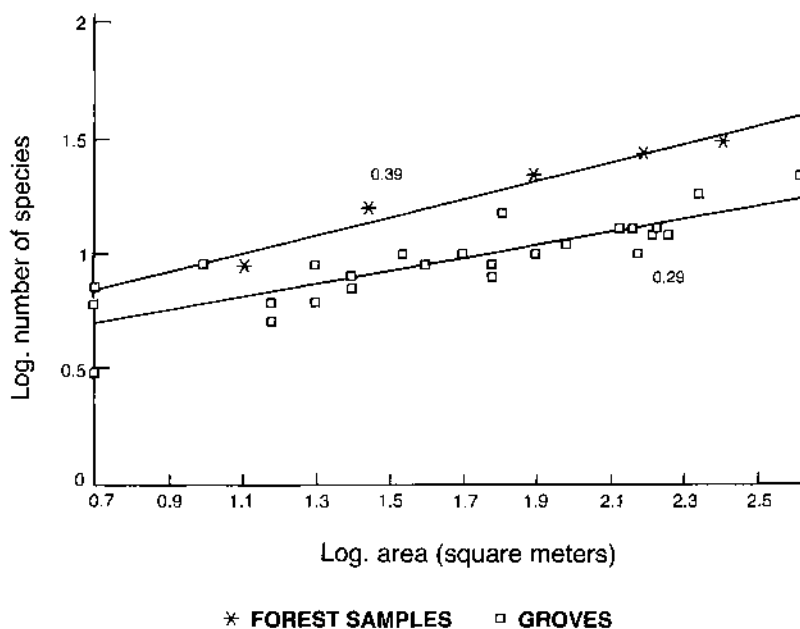


Figure 1. Relationship between the number of woody species and the area studied. Data from the forest samples and from the groves were fitted following Preston (1962). $S = CA^S$, see text.

border ($r = -0.03$, $N = 30$, $P > 0.05$), but the total area occupied by groves decreased significantly with distance from the forest border ($r = -0.80$, $P < 0.01$).

Woodland species were present in most groves of all size classes, especially the three more frequent woodland species, *Byrsonima crassifolia*, *Bowdichia virgilioides* and *Palicourea rigida* (Table 2). Forest trees were essentially absent in groves smaller than 25 m^2 (i.e. the first two size classes). Shrub species, which were absent from the grassland, accompanied the woodland trees in these smaller groves. Two species of forest tree were most frequent in the three larger classes of groves: *Genipa caruto* and *Tapiriva velutinifolia* (Table 2).

Leaf-cutter ants

A total of 24 leaf-cutting ant nests were found, nine of them in the grassland and 15 in groves. All were occupied by *Atta laevigata*. Nests in the grassland were one order of magnitude smaller than those found in the groves (Table 3). As shown in Table 4, the frequency of groves with *A. laevigata* nests increased with the size of the grove ($r = 0.93$, $N = 6$, $P < 0.05$). All groves in the largest class had *A. laevigata* nests. Also, groves with forest trees were more likely to have nests than groves without forest trees. *A. laevigata* nests were found in only 18% of groves without forest trees and in 68% of the groves with forest trees ($\chi^2 = 6.54$, $P < 0.01$). The number of nest entrances was also significantly correlated to grove area ($r = 0.82$, $N = 15$, $P < 0.01$).

Table 2. Percentage of groves of each size class with the presence of each woodland and forest species. Class I: <15 m², II: 16–25 m², III: 26–50 m², IV: 51–70 m², V: 71–150 m², VI: 151–400 m². Total number of groves sampled = 30 (five in each grove size class).

	Grove size class					
	I	II	III	IV	V	VI
Woodland species						
Trees						
<i>Byrsonima crassifolia</i>	100	100	100	100	100	100
<i>Bowdichia virgilioides</i>	100	100	60	80	80	100
<i>Palicourea rigida</i>	80	100	100	100	100	100
<i>Curatella americana</i>	—	20	20	60	20	40
<i>Casseearia</i> sp.	100	100	80	100	100	100
Forest species						
Trees						
<i>Genipa caruto</i>	—	—	60	100	100	100
<i>Tapirira velutinifolia</i>	—	—	80	100	100	80
<i>Godmania macrocarpa</i>	—	—	40	20	20	60
<i>Cochlospermum vitifolium</i>	—	—	—	20	20	40
<i>Davilla nitida</i> (liana)	—	—	40	20	80	100
<i>Xylopia aromatica</i>	—	20	40	20	40	20
Shrubs						
<i>Randia aculeata</i>	—	20	80	80	100	80
<i>Pavonia sessiflora</i>	40	60	40	80	60	100
<i>Solanum bicolor</i>	—	—	60	—	—	60
<i>Miconia albicans</i>	20	40	80	40	40	40
Myrtaceae (spp.)	—	60	—	20	60	80
Circularity coefficient ¹	1.02	0.99	0.94	0.98	0.94	0.98
Mean and (SD)	(0.03)	(0.04)	(0.07)	(0.08)	(0.10)	(0.11)

¹ Grove ratios were measured in cardinal and intercardinal directions and used to calculate the circularity coefficient (see text).

Table 3. Leaf-cutting ant nests (*Atta laevigata*) found in the grassland and in the groves in a parkland savanna of Barinas, Venezuela (total area sampled = 21,000 m²).

<i>A. laevigata</i> nests	Groves	Grassland
Total number	15	9
Number of holes (mean ±SD)	6.2 ±6.1	1.1 ±0.3 (*)
Diameter (cm)	>400	60 ±23
(range)	(60–900)	(30–100)

(*) P < 0.001, U = 118, Mann-Whitney U-test (Sokal & Rohlf 1981).

Foraging activity was intense during both day and night. Leaves from trees (dry and green) made 67% of the harvest in March and 87% in November. Herb leaves were important in March (26%) but not in November (6%).

Soil analysis and microclimate

No significant differences were found between sites in four of the seven nutrients analysed (phosphorus, potassium, sodium and aluminium) as well as in

Table 4. Frequency of *Atta laevigata* nests in relation to grove size (classes as in Table 2).

	Grove size class					
	I	II	III	IV	V	VI
% of groves with nests	20	20	20	60	80	100
Number of holes (mean \pm SD)	3	2	3	3 \pm 1	4 \pm 1	10 \pm 7
Number of nests	1	1	1	3	4	5

cation exchange capacity (CIC), C/N ratio and soil moisture (see Appendix). However, there were significant differences in soil contents of nitrogen, magnesium, calcium and organic carbon between sites (Figure 2). The general trend for these four elements was that soil from groves with nests was significantly richer than soil from groves without nests at both soil depths. Soil from groves with nests was also significantly richer than soil from the grassland with or without nests, except for calcium in the topsoil. The comparison between grassland with nests and without nests was restricted to the topsoil, and showed significant differences in calcium and organic carbon, but with opposite trends. It seems that the presence of a nest in the grassland is not having the same effect as in the groves, and this may be related to the difference in nest size. A complete list of results for 10 soil variables is included in the Appendix.

Daily temperature variation decreased from the grassland to the groves as the size of these increased (Table 5), but the differences between sites were greater at ground level than at 150 cm above ground. In the dry season a maximum of 43°C at ground level was registered in the grassland, whereas the maximum in the large grove was only 27.3°C. Differences decreased in the wet season.

Grove size and tree size

The distribution of the two types of trees according to height class in each of the six grove size classes is shown in Figure 3. The numbers are the sum of four forest species (*Tapirira velutinifolia*, *Genipa caruto*, *Godmania macrocarpa*, *Cochlospermum vitifolium*) and of four woodland species (*Byrsonima crassifolia*, *Bowdichia virgilioides*, *Palicourea rigida*, *Curatella americana*). The first two forest species were much more abundant than the latter two. In the woodland trees, *C. americana* was much less abundant than the other three species. The two smaller classes of groves were totally dominated by woodland trees (Table 2, Figure 3). In the third and fourth classes, the two height distributions were not significantly different. In class V, forest trees in the two lower heights were significantly more numerous than woodland trees ($\chi^2 = 11.4$ and 15.4 , $P < 0.01$) and in class VI, forest trees are also significantly more numerous than woodland trees in the tallest class ($\chi^2 = 4.1$, $P < 0.05$). These differences are reflected in the variation in density of forest and woodland trees of different heights with the

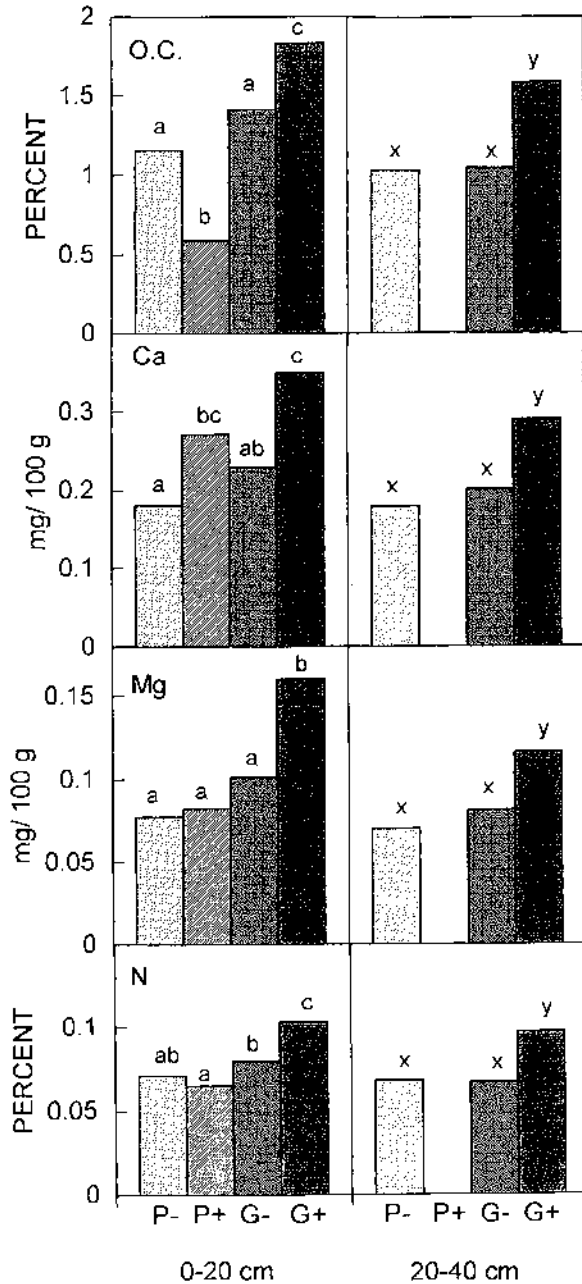


Figure 2. Mean contents of organic carbon (OC), calcium (Ca), magnesium (Mg) and nitrogen (N) in soil samples from open grassland (P) and grove (G) with (+) and without (-) *A. laevigata* nest. Samples were taken at two depths (0-20 and 20-40 cm). In each graph means which are not significantly different have a small letter in common.

Table 5. Temperatures ($^{\circ}\text{C}$) measured at ground level and at 150 cm above ground in two circadian cycles (24 h) at the end of the wet and dry seasons in different sites. Groves, S = small (20 m²), M = medium (100 m²) and L = large (400 m²).

	Grassland	Grove			Forest
		S	M	L	
a. End of the wet season					
Ground level					
Mean	30.2	28.5	27.1	26.7	25.3
Maximum	37.8	32.3	29.6	29.3	27.3
Minimum	24.1	25.4	24.4	24.9	24.1
Amplitude	13.7	6.9	5.2	4.4	3.2
150 cm					
Mean	29.0	28.0	27.6	27.2	27.6
Maximum	34.8	33.1	30.6	32.6	32.8
Minimum	21.6	22.4	21.6	23.1	22.9
Amplitude	13.2	10.7	9.0	9.5	9.9
b. End of the dry season					
Ground level					
Mean	31.7	28.6	26.7	24.5	25.2
Maximum	43.0	35.1	33.1	27.3	26.8
Minimum	24.3	23.9	22.6	21.1	23.1
Amplitude	18.7	11.2	10.5	6.2	3.7
150 cm					
Mean	29.6	28.2	27.6	27.8	27.6
Maximum	36.1	33.3	32.8	32.6	33.3
Minimum	22.1	21.6	22.1	22.1	21.9
Amplitude	14.0	11.7	10.7	10.5	11.4

size of the grove (Figure 4). Small forest trees were significantly more dense than small woodland trees in larger groves, whereas the latter were significantly more dense than the former in smaller groves.

Trees were not randomly distributed within the larger groves (classes V and VI), and the two types of tree differed in their distribution. Forest trees were found more frequently in the centre and the medium belt than in the peripheral belt, whereas for woodland trees the opposite was true (Figure 5, $\chi^2 = 35.7$, $P < 0.01$). However, we observed a central taller tree in about half the groves, and in 80% of the cases this was a woodland tree. Furthermore, the tree with the largest diameter was a woodland tree in two out of three cases.

Woodland trees in open savanna and groves

Height structure of the populations of the three most abundant woodland species differed significantly between the open savanna and the groves (Table 6). However, there is no clear pattern of change from savanna to groves. *B. crassifolia* has a larger proportion of taller trees (>150 cm) and a smaller proportion of small trees (<50 cm) in the groves than in the savanna. In *B. virgilioides* and in *P. rigida* there is a larger proportion of smaller trees (<50 cm) in the groves, but in the latter the fraction of taller trees is much smaller in the savanna than in the groves (Table 6).

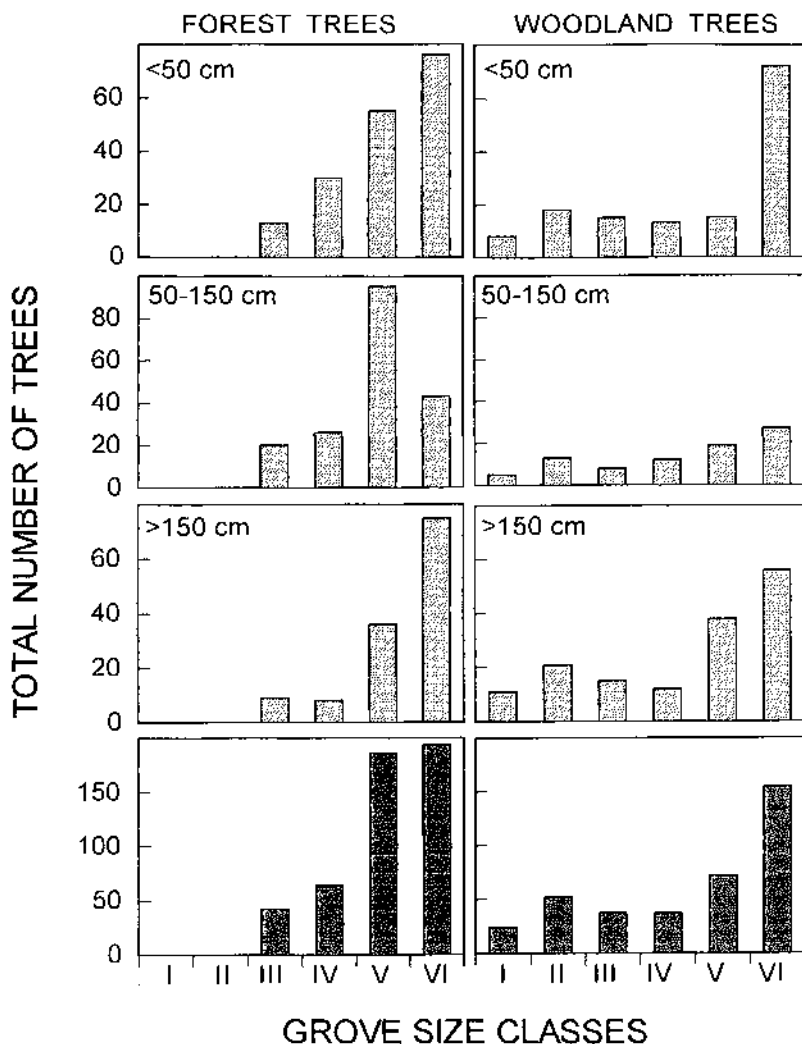


Figure 3. Number of trees in each size class of grove (I: $< 15 \text{ m}^2$, II: $16\text{--}25 \text{ m}^2$, III: $26\text{--}50 \text{ m}^2$, IV: $51\text{--}70 \text{ m}^2$, V: $71\text{--}150 \text{ m}^2$ and VI: $151\text{--}400 \text{ m}^2$), classified into three height classes (cm).

DISCUSSION

The presence in the groves of deciduous species from nearby forest suggests that the forest is a centre of dispersal and that these species are acting as colonizers on the savanna, as shown in areas where fire and grazing are excluded (San José & Fariñas 1983, 1991). Groves seem to be ecological islands, as suggested by the high correlation between species richness and the size of the grove, and the low value of the Y intercept in this correlation (Figure 1). Also, the slope (0.29) of the curve is island-like and suggests a non-equilibrium system (but see Connor & McCoy 1979). However, this value is lower than the slope for the adjusted correlations of richness *vs* area in the forest (slope = 0.39), and

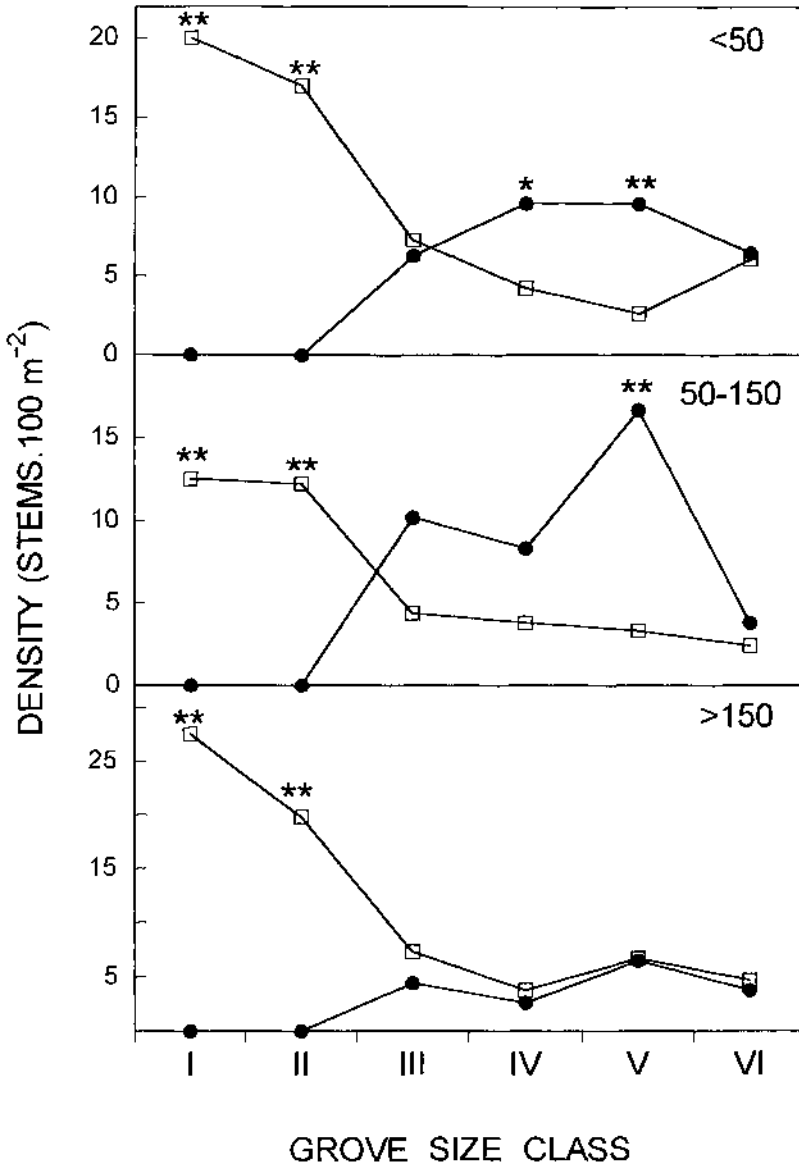


Figure 4. Density of forest trees (filled circles) and woodland trees (empty squares) at three different tree heights (cm) according to grove size (as defined in Figure 3). Asterisks indicate significant differences in pair-wise comparisons in each grove size class (Mann-Whitney U-test, $N = 5$, $* = P < 0.05$, $** = P < 0.01$).

is contrary to that predicted by MacArthur & Wilson's (1967) theory of island biogeography. Given the proximity between groves, it is possible that this is the result of the groves also being centres of dispersal (San José *et al.* 1991). Both the forest and the groves would be actively involved in the colonization process. Furthermore, groves also seem to be playing a role in the colonization of the grassland by woodland trees. At least in two species, *B. crassifolia* and *P.*

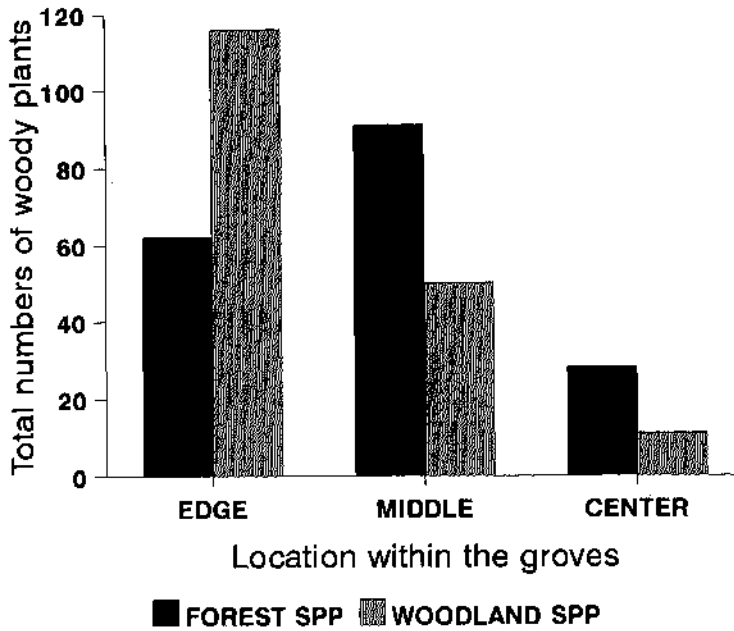


Figure 5. Numbers of forest and woodland trees in different locations within groves (N = 6).

Table 6. Population structure (numbers of trees in each of three height classes) of the three most abundant woodland species in the open savanna and in the groves.

	Height class (cm)	Location		Total
		Savanna	Groves	
a. <i>Byrsonima crassifolia</i>	<50	65	45	110
	50-150	27	28	55
	>150	44	73	117
	Total	136	146	282
$\chi^2 = 12.4, P < 0.01$				
b. <i>Bowdichia virgilioides</i>	<50	45	39	84
	50-150	70	14	84
	>150	38	26	64
	Total	153	79	232
$\chi^2 = 18.8, P < 0.01$				
c. <i>Palicourea rigida</i>	<50	49	56	105
	50-150	70	34	104
	>150	16	47	63
	Total	135	137	272
$\chi^2 = 30.3, P < 0.01$				

rigida, the proportion of trees taller than 150 cm is significantly higher in the groves than in the savanna. Therefore, trees of reproductive age are more likely to be found in the periphery of groves than in the open savanna.

Woodland trees are the only woody component of smaller groves. It is very likely that these small groves would grow, first by the addition of more woodland trees, and later by the invasion of forest species (Table 2). Woodland trees tend to improve site conditions, increasing soil organic matter, creating a more mesic microclimate and decreasing fire frequency by shading out savanna grasses (Belsky *et al.* 1989, Hobbs & Mooney 1986, Kellman 1979). Aggregations of several trees would accelerate these changes, increasing the probability of successful colonization by shrubs and deciduous trees less tolerant to open savanna conditions (San José *et al.* 1991). The different spatial distribution of woodland and forest trees within the grove area, and the fact that in most groves there is a central taller (woodland) tree, gives additional support to the hypothesis that woodland trees are founders of the groves and that as the groves increase in size deciduous trees displace the recruitment of new woodland trees to the periphery. Here, woodland trees enjoy more radiation and since they are resistant to savanna fires this is a minor threat to their survival. Furthermore, they represent a protective fire-break surrounding the groves. Forest trees are more tolerant to shade and less tolerant to water stress and fire than woodland trees. This would explain why recruitment of forest trees is so important in larger groves, and why there is almost none in small groves. Clustering of several groves may produce to a larger grove, and in such instances there would not be a central tree, as we observed in a few cases.

A. laevigata nests increase in size with age (see Fowler *et al.* 1986). The striking difference in nest size between the open savanna and the groves (Table 3) indicates the low survivorship of nests in the open savanna. Both the frequency and the size of nests increase with the area of the grove (Table 4), and this is concurrent with the increasing presence of forest trees (Figure 6). It seems clear that the survival and growth of the nests is favoured under the more mesic conditions of the larger groves (Lewis *et al.* 1974).

The question arises whether the ants promote the changes favouring forest tree invasions, or if the trees favour the establishment of ant nests. A third possibility is that changes introduced by trees favour the ants and, concurrently, changes introduced by ants favour the trees. Bucher (1982) and Jonkman (1978) showed evidence that ant activity was a precursor of tree invasion of grassland. In that case, however, trees invaded large nests which had been already abandoned. In the present study all groves in classes IV and V (51 to 150 m²) had the two more common forest trees (*G. caruto* and *T. velutinifolia*), but not all had *A. laevigata* nests (Table 4). Therefore, it seems plausible that as groves get larger either ants or forest trees arrive, and a synergic interaction may promote each other.

This synergistic hypothesis corresponds to the facilitated successional model (Connell & Slatyer 1977) in a manner similar to the invasion of subtropical

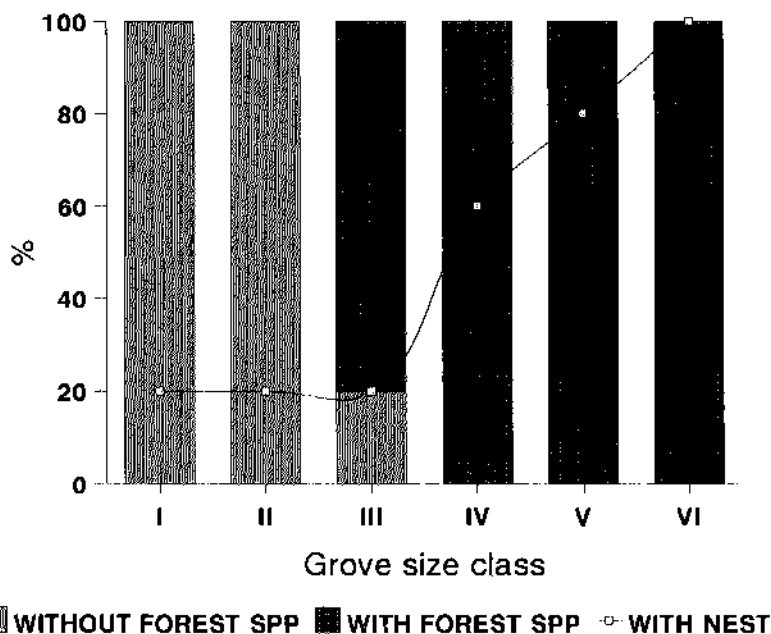


Figure 6. The frequency of *A. laevigata* nests increases with the area of the grove ($r=0.89$, $P<0.05$, $N=6$) and with the increasing presence of forest trees. Curve was hand-fitted.

savannas by *Acacia* trees (Archer *et al.* 1988). We summarize the synergic model presented in Figure 7 as follows. Woodland trees are successful invaders of the savanna grassland, since they are able to cope with water and nutrient stress and with fire. Leaf-cutting ant nests are also growing in the open savanna but with little success (A). The concurrence of a few woodland trees generates a process characterized by changes in the soil and in the fire regime of the site, facilitating the invasion of shrubs and allowing further survival of near-by ant nests or of nests being established within the grove limits (B and C). At this stage some forest tree species get established. The growth of ant nests and forest trees acts synergistically (C). As shown by our results, the ants benefit from direct food availability and better habitat conditions and, as the nest grows, promote changes in soil and nutrient status improving conditions for the survival and growth of forest trees. Groves with nests would grow larger and more quickly than groves without nests, and given the improved soil conditions they should also recover faster from disturbance (D). Thus, the likelihood of a grove reaching a large size without a nest would be very low. As groves reach a larger size, recruitment of woodland trees under the canopy of forest trees does not occur, and a clear zonation is reached with woodland trees in the periphery and forest trees towards the centre. We do not know the life span of ant nests in the groves, but the effects of a large nest presumably last for a long time after the nest is abandoned (Bucher 1982). A similar situation of overall positive effects and synergistic complex interaction have recently reported for woodland

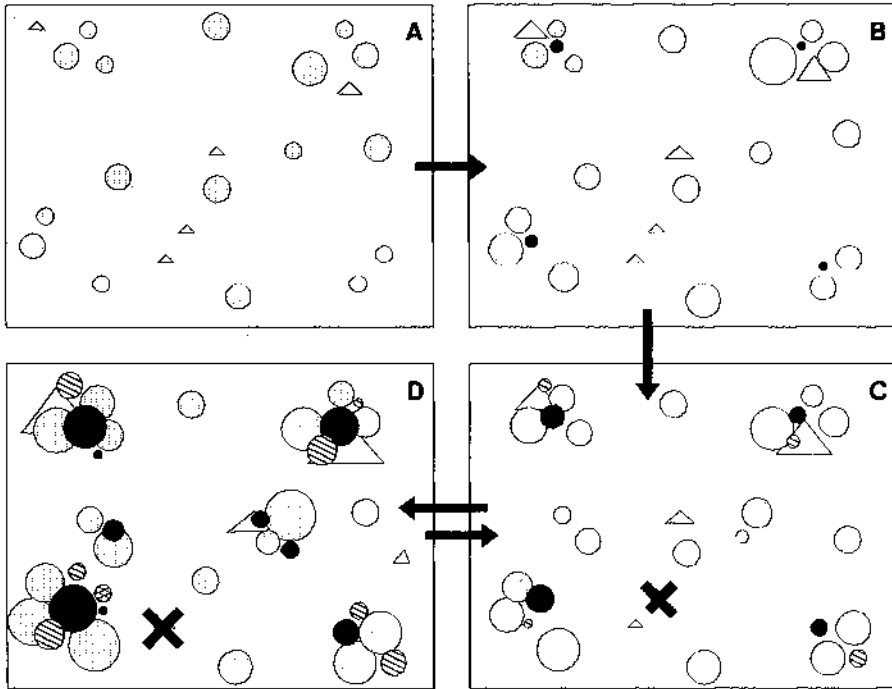


Figure 7. Diagrammatic illustration of the development of groves in a parkland savanna of Barinas, Venezuela. Grove formation is facilitated by the aggregation of a few woodland trees, followed by the successful invasion of forest trees and a leaf-cutting ant nest. Woodland trees, forest trees and leaf-cutting ant nests would act synergistically, improving conditions for each other (see text). (○) woodland trees, (●, ⊗) forest trees, (△) leaf-cutting ant nests.

trees and termites in the seasonally flooded savannas from Mato Grosso, Brazil (Ponce & Da Cunha 1993).

As mentioned above, the large groves are acting as dispersal centres not only of forest trees but also of woodland trees. In this manner, groves and woodlands are interacting synergistically to promote their persistence in these savannas.

In contrast to the case studied by Archer *et al.* (1988), this savanna does not seem to be turning into a shrubland or a forest. Some factors are limiting the invasion of forest trees and the growth of the groves. Fire and cattle are involved, as shown by long-term studies in savannas with exclusion of these two factors (San José & Fariñas 1991). Disturbances, such as those creating gaps in forests, should have enormous consequences in the grove structure and may facilitate reinvasion by savanna grasses bringing back the risk of fire. Cattle and direct human impact may be playing a role in this context. These disturbances would affect groves of all sizes, but would especially decrease the probability of small groves growing to larger sizes. Spatial heterogeneity may also be important. The likelihood of an aggregation of a few woodland trees becoming a large grove would depend on site conditions. Here, such variables as soil, water table depth and other geomorphologically related traits are critical (Medina & Silva 1990, Sarmiento & Monasterio 1975) and should be explored in further studies.

The study of the dynamics of groves and the influential factors would provide further evidence along these lines.

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APPENDIX

Mean values for 10 edaphic variables in different vegetation sites with nest of *A. laevigata* present or absent. Samples from the gallery forest were included only for reference, since the ant is not an inhabitant of this forest. Upper row corresponds to 0–20 cm and lower row to 20–40 cm. In each row, means which are not significantly different have a common superscript ($P < 0.003$).

Vegetation:	Grassland		Groves		Forest
Nest:	Absent	Present	Absent	Present	
Nitrogen	0.071 ^{ab}	0.065 ^a	0.080 ^b	0.103 ^c	0.108 ^c
	0.068 ^a	—	0.067 ^a	0.097 ^b	0.105 ^b
Phosphorus	1.50 ^a	1.70 ^a	2.30 ^a	2.40 ^a	3.80 ^b
	1.40 ^a	—	2.00 ^a	1.90 ^a	3.60 ^b
Potassium	0.080 ^a	0.064 ^a	0.88 ^a	0.114 ^a	0.285 ^b
	0.082 ^a	—	0.083 ^a	0.095 ^a	0.197 ^b
Magnesium	0.077 ^a	0.082 ^a	0.101 ^a	0.160 ^b	0.160 ^b
	0.070 ^a	—	0.081 ^a	0.116 ^b	0.170 ^c
Calcium	0.181 ^a	0.271 ^{bc}	0.229 ^{ab}	0.350 ^c	0.247 ^{ab}
	0.179 ^a	—	0.201 ^a	0.290 ^b	0.248 ^{ab}
Aluminium	1.760 ^a	1.800 ^{ab}	2.048 ^{bc}	1.940 ^{ab}	2.230 ^c
	1.800 ^a	—	1.958 ^{ab}	1.870 ^{ab}	2.140 ^c
Sodium	0.065 ^a	0.085 ^a	0.065 ^a	0.084 ^a	0.079 ^a
	0.040 ^a	—	0.064 ^b	0.082 ^b	0.081 ^b
CIC	5.912 ^a	3.500 ^b	4.835 ^a	5.375 ^a	5.130 ^a
	5.903 ^a	—	4.460 ^b	4.760 ^b	5.255 ^{ab}
OC	1.153 ^a	0.590 ^b	1.413 ^a	1.832 ^c	1.430 ^a
	1.022 ^a	—	1.045 ^a	1.587 ^b	1.315 ^c
C/N	16.49 ^a	9.47 ^b	17.60 ^{ac}	18.30 ^c	13.18 ^d
	15.32 ^a	—	15.88 ^a	16.60 ^a	12.80 ^b
Moisture	10.14 ^{ab}	—	13.10 ^{bc}	13.41 ^c	13.61 ^c
	9.92 ^a	—	11.37 ^{abc}	10.14 ^{ab}	12.25 ^{ab}

Nitrogen, Organic Carbon (OC) and Moisture in percentages; Phosphorus in ppm; other cations in mg (100 g)⁻¹.