

Ant-plant Association in Two *Tococa* Species From a Primary Rain Forest of Colombian Choco (Hymenoptera: Formicidae)

by

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ABSTRACT

Tococa myrmecophytes develop swollen domatia to house ants at the base of their leaves. We measured the amount of herbivory in *Tococa spadaciflora* and *T. guianensis* with and without their associated ants during eight months in a primary rain forest of the central coast of Colombian Choco. We evaluated 87 individual plants in three 900m² plots that were separated by at least 300m. More than 90% of all plants of both species were occupied by *Pheidole* sp., but four more ant species, *Azteca* sp., *Brachymyrmex heeri*, *Crematogaster* sp. and *Wasmannia auropunctata*, also inhabited the plants' domatia. We excluded the ants from half of randomly chosen plants and measured two response variables: herbivory (25% of the leaves/plant) and number of leaves/plant, during three consecutive events separated by four months. *Tococa spadaciflora* was found to be highly susceptible to the absence of its associated ants, as demonstrated by a significant final average herbivory of 91% in the ant-excluded plants vs. 27% in the control plants. *T. guianensis* showed a smaller but also significantly higher percent herbivory (55% vs. 22% respectively). Each plant was occupied by a single ant species, with an average of 74 and 62 ants per plant for *T. spadaciflora* and *T. guianensis* respectively. We discuss the implications of finding two *Tococa* myrmecophilous species living in the same location, and lodging the same mutualist ants but differing in their dependence upon the defensive action of the ants. The ants functionally stratified the plant according to the location of the leaves: the brood chambers and reproductive caste were located in young leaves, while storage material, seeds, garbage and arthropod corpses were located in the lower and old leaves. Live insects, such as Staphylinidae (Sf. Aleocharinae) beetles, coccids, tipulids and small crustaceans were also found inside domatia. We directly observed defensive actions of

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Pheidole ants against several arthropods, including the major defoliator in the region, *Atta cephalotes*.

Key words: ant-plant; *Pheidole*; herbivory, Choco rain-forest, Colombia, *Tococa guianensis*, *Tococa spadaciflora*, Melastomataceae.

INTRODUCTION

Mutualistic relations involve a variety of interactions and benefits among the members of different species, a process which leads to a higher fitness among the partners when associated (Bronstein 1994). True ant-plant associations or myrmecophytes represent a coevolutionary complex where plants undergo modifications such as domatia, hollow twigs and nutritious secretions, in order to attract ants (Hymenoptera: Formicidae) (Buckley 1982; Beattie 1985; Benzing 1991; Koptur 1991); whereas the ants defend the plants against herbivores and pathogens due to their aggressiveness, complex social system, and nutritional requirements (Janzen 1967; Davidson & Epstein 1989; Schupp 1986; Vasconcelos 1993). The abundance of mutualistic associations between plants and ants is particularly noticeable in tropical habitats (Schupp & Feener 1991; Davidson 1997), the density of which is illustrated by reports of 377 myrmecophyte individuals/ha in the Brazilian rain forest (Fonseca & Ganade 1996).

Thirteen Melastomataceae genera are myrmecophytes in the tropical Americas, using either petiolar sacs (i.e. *Tococa* spp., *Maieta* spp.) or hollow stems (*Miconia* spp.) (Jolivet 1996). The domatia are not built or produced by the ants but are rather the result of a plant's preadaptation, in which a specialized tissue grows at the insertion of the blade in the petiole (Bitallion 1982). Some melastome myrmecophytes have shown to have strong mutualistic associations with ant species. For instance, *Maieta guianensis*, which is one of the most abundant Amazonian myrmecophytes (Fonseca & Ganade 1996), showed a significant increase in leaf damage and decrease in fruit productivity when deprived of its associated ant *Pheidole minutula* (Formicidae: Myrmicinae) (Vasconcelos 1993). *P. minutula*, in turn, showed to be one of the most abundant ant-plant associates in the Amazonian Manaus (Fonseca & Ganade 1996). Plants of *Tococa bullifera* were found to be smaller when associated with *Crematogaster laevis* than with *Azteca* sp. in the Amazonian Brazil (Vasconcelos & Davidson 2000) and evidence of competition among *Azteca* spp. vs *Crematogaster* cf. *victima* for occupying *Tococa* sp. plants was detected in Peruvian forests (Davidson *et al.* 1989). Ant-plant interactions in *Tococa* species can be so intertwined to involve simultaneous feeding behaviors in both ways. In Venezuela, radioactive tracers showed that organic wastes from ants are absorbed

by *Tococa guianensis* plants, while the plants in turn actively feed the ants through glandular trichomes containing sugars and lipids that are collected by the ants (Cabrera & Jaffe 1994).

Not only do the ants defend the melastomes against the presence of other Arthropods but also interference from other plants. For instance, the ant *Myrmelachista* that occupies *T. occidentalis*' domatia in the Peruvian Amazon, kills surrounding vegetation by biting and spraying a poison into leaves allowing the vegetative reproduction of pure clonal patches of its mutualistic plant up to 700 m² (Morawetz *et al.* 1992). This same phenomenon, involving the same *Myrmelachista* ant was also reported for *T. guianensis* in Amazonian Ecuador (Renner & Ricklefs 1998). According to Renner and Ricklefs (1998) the *T. occidentalis* studied by Morawetz *et al.* (1992) is a form of the variable *T. guianensis* in Peru.

The Choco rain forest of Colombia was once considered by Gentry (1986) to be the world's richest place in terms of plants, but highly vulnerable to disturbance (Pardo & Cediell 1994). Unfortunately this region has been seldom studied and its unusual biodiversity (Gentry 1996) is threatened by socio-political problems. Eight myrmecophyte melastomes have been reported along the forest Chocoan coast associated with 13 ant species (Aldana *et al.* 1997). The main goal of this research was to determine the effects of herbivorous insects on two *Tococa* plant species in a primary rain forest when deprived from their associated ants. We also pretended to establish the extent of specificity in plant occupancy by ants in *Tococa guianensis* and *T. spadaciflora*, and report field observations about the ant-plant relationships in these two melastomes.

MATERIALS AND METHODS

Description of the plants

Tococa guianensis, also known as *T. chuivensis*, and *T. occidentalis*, occurs from southern Mexico and West Indies (Tobago) all throughout northern South America to Bolivia (Renner & Ricklefs 1998). It is a shrub between 1.5-3.0m high, with myrmecophyte domatia at the superior adaxial part of the petiole, each one with an opening between the main nerves of the blade. The first two meristematic leaves at germination do not have domatia, but in the next pair, only one of both leaves presents domatia. The developed plant has domatia in all its leaves. The domatia's interior is provided with hooked trichoma where ants suspend their larvae (Jolivet 1996). Opposite decussated elliptic-oblong leaves, 10-30 cm length and 12-15 cm width, thin spaced trichomas along the surface. Inflorescence with white flowers, pan-

niculi 9-16 cm long, with few five petal flowers.

T. spadaciflora is a shrub between 0.6-1.5 m high with myrmecophyte domatia in the petioles. The domatia are divided in two open communicated chambers, having a kidney-like shape with lateral prominences. The domatia are initially reddish in color in the meristematic leaves and then change to a darker brownish color. The domatia entrance is through the adaxial part of the leaf's central nerve. The leaves are opposite decussated and lanceolate, ending with an acute apex, smooth border, 45-55 cm length by 8-10 cm width. Both leaves, domatia and stem highly pubescent with rigid trichomes all over the surface. The inflorescence is terminal 1-2, in cluster, also highly pubescent at the base, yellow-greenish flowers, displayed in spadice shape, pink periant, five free petals, fruit in purple berry. Voucher specimens of both plant species were deposited in the herbarium, Biology Department, Universidad del Valle, Cali, Colombia.

Study site

This study was carried out at Cabo Corrientes region, Pacific coast of the Choco Department of Colombia, Municipality of Nuquí, district of Arusí (5°30'N; 77°30'W) (Fig. 1). The life zone corresponds to a very humid tropical forest according to Holdridge's system of classification (Espinal 1967). The place receives an annual average precipitation of 5000mm, distributed in a humid period between August and November and a "dry" (less rainy) period between January and March. The area has a broken topography irrigated by many creeks and is covered by dense primary forest, although some precious timber trees have been selectively extracted (Galeano *et al.* 1993). Soils are moderately evolved, acid, highly saturated and exposed to an intensive leaching of nutrients (Pardo & Cediél 1994).

The field work was done between December 1998 and August 1999. Three 45m x 20m plots were chosen from three regions separated by at least 300m inside the forest, which constitutes a total area of 2700 m² of forest studied. Most individual plants belonging to both *T. guianensis* and *T. spadaciflora* were labeled inside the plots and located through a coordinate system. Three samples of each species were collected, pressed and identified to genus according to Gentry (1996). Plant samples identities were confirmed by comparing with preserved specimens at the Biology Department's Herbarium, Universidad del Valle, Cali, Colombia, where voucher specimens of the two plant species were deposited.

Experiment

The total number of individual plants used for the experiments was

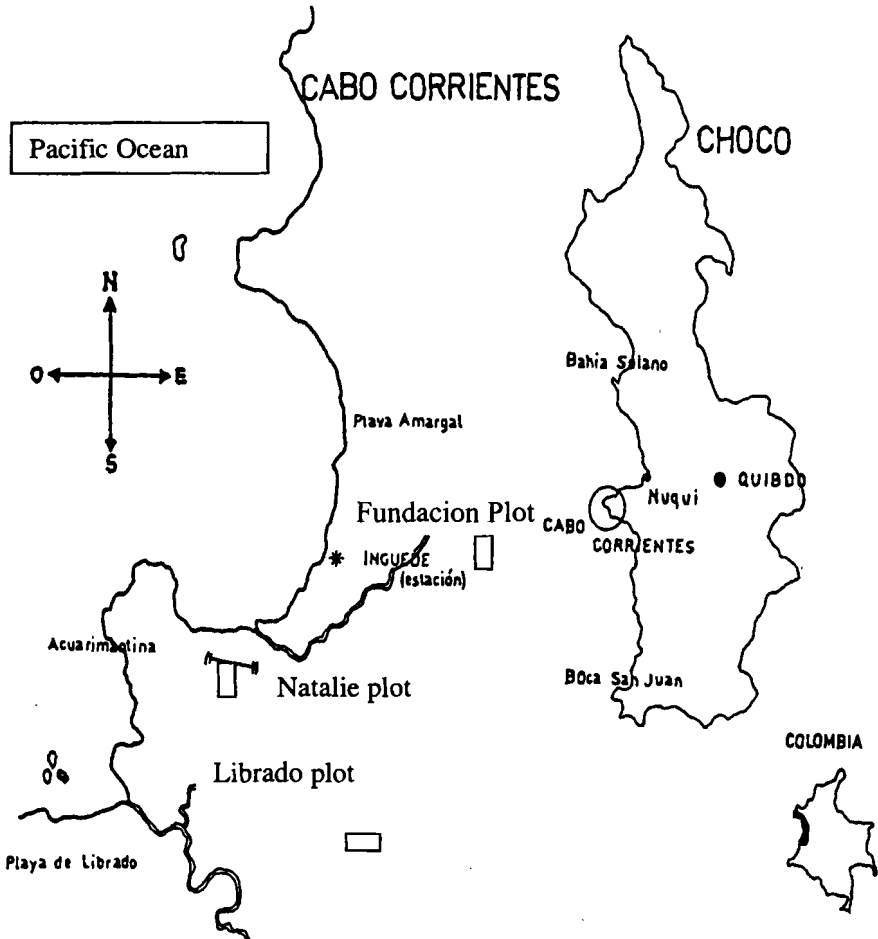


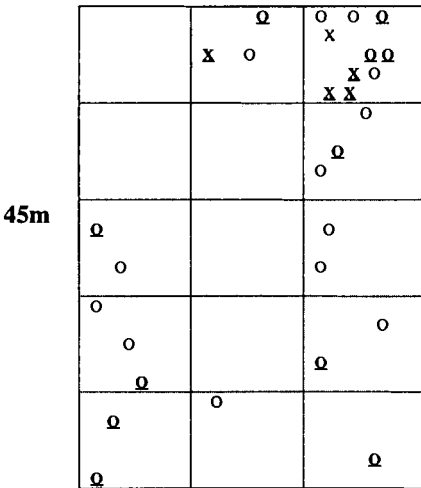
Fig. 1. Location of the study site at three spatial scales: Choco department within Colombia (right lower); study region within Choco department (right upper) and plots within the study site (left)

39 and 48 for *T. guianensis* and *T. spadaciflora* respectively (Fig. 2). Each labeled plant was initially observed for the presence of ants, all of its leaves were counted and flower or fruit presence was registered. Three randomly selected plants from each plot were used to determine the number of ant species in each individual plant and the ant density in each domatia. Each plant was completely inspected for ants by opening all of its domatia. The number of adult ants and any other material inside each domatia were recorded.

In order to obtain direct evidence of ant protection to plants, colonies were removed from half of randomly selected plants of each species by

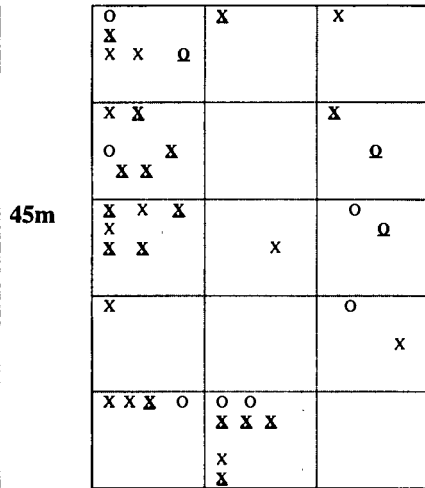
“FUNDACION” Plot

20m



“LIBRADO” PLOT

20m



“NATALIE” Plot

20m

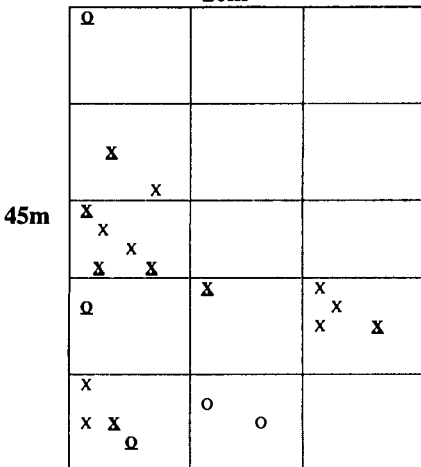


Fig. 2. Distribution of *Tococa guianensis* individual plants (O: treated plants; i.e. without ants, are underlined, n=39) and *T. spadaciflora* (X: treated plants, underlined, n=48) in three plots separated at least 300m in a primary rain forest of the Colombian Choco region.

injecting a light soap solution (approximately 5g per liter) inside all domatia through the entrance hole, using a syringe. A similar method had been implemented to exclude ants from *Maieta guianensis*, but by applying a pesticide instead (i.e. Vasconcelos 1991). Other studies have excluded ant access to the plant by using Tanglefoot (De la Fuente &

Marquis 1999, in *Stryphnodendron microstachyum*). We assume that not using insecticide would help prevent effects of the treatment on potential herbivorous insects approaching the plants. The identity of resident ant species in each of the plants studied was determined by randomly selecting a leaf and dissecting it. Ant presence in other domatia of each plant was rechecked by observing the workers blocking the domatia's entrance after a slight disturbance. All leaves and their domatia were counted three times separated by four months each. Only fully expanded leaves (with domatia) were counted and measured in order to avoid percent of herbivory fluctuations due to the size or age of leaves (Reichle *et al.* 1973), therefore, young leaves (identified by a light green color and smaller size at the tip of the shoot) were excluded from the counts. We measured leaf area on 25% randomly chosen leaves from each plant by tracing directly on graph paper. The area consumed by herbivores was also measured by this direct method; therefore the percent herbivory was obtained through the proportion of these two areas. Herbivory measures were also taken three times separated by four months (same dates as number of leaves/plant).

All samples were transported in ethyl alcohol to the Universidad del Valle in Cali, where ant morphospecies were identified to genus using keys from Mackay & Vinson (1989), Hölldobler & Wilson (1990), Bolton (1994), and those adapted by Baena (1992). For the specific level we used the reference collection from the Entomological Museum of the Universidad del Valle, where voucher specimens of the ants were deposited. Analyses of variance (Zar 1996) using a repeated measurement model were performed using SPSS 9.0 for Windows.

RESULTS

Most individuals (98%) of the 87 plants examined were found lodging ants inside their domatia. In all cases there was just one ant species per plant, which is consistent with results reported by Hölldobler & Wilson (1990) and Cronin (1998). Three ant species, *Pheidole* sp., *Wasmannia auropunctata*, (both Formicidae: Myrmicinae) and *Azteca* sp. (Dolichoderinae) were found in both *Tococa guianensis* and *T. spadaciflora* (Fig. 3). Additionally, each melastome species had one unique ant species as follows: *T. guianensis* exclusively lodged *Crematogaster* sp. (Myrmicinae) while *T. spadaciflora* exclusively contained *Brachymyrmex heeri* (Formicinae).

The plant as a whole was stratified by the ant colony according to functional strata in both *Tococa* species. The upper level, next to the meristematic portion of the plant concentrated the reproductive caste and brood, including winged males and females (when present). Most

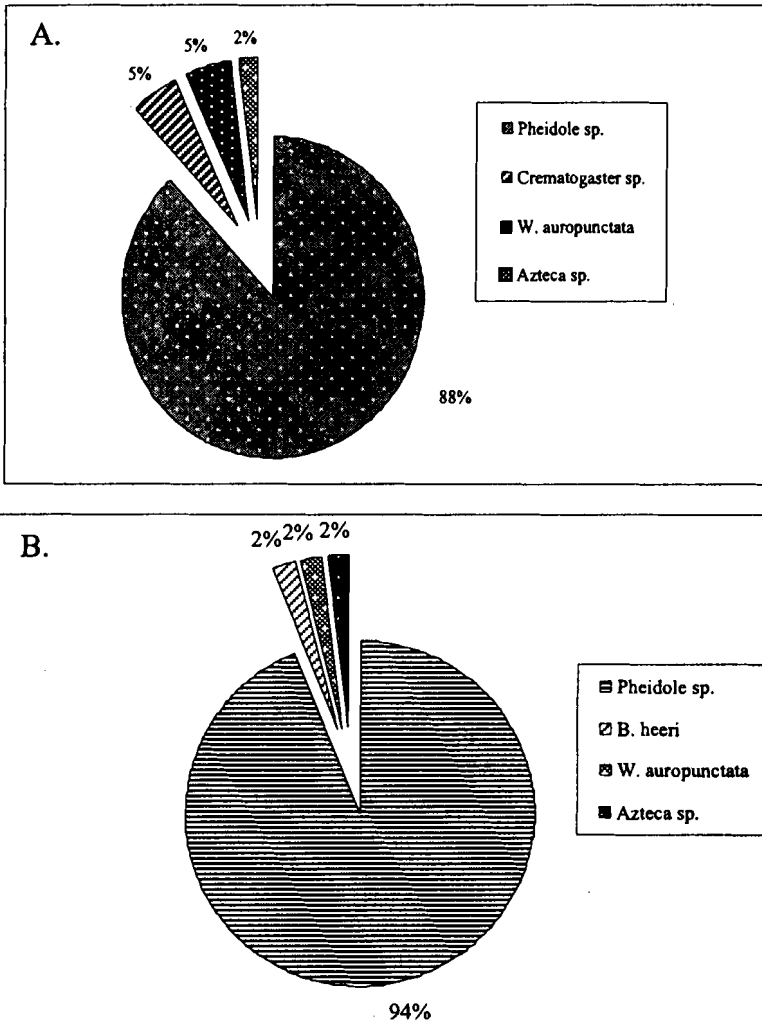


Fig. 3. Proportion of ant species inhabiting domatia *T. guianensis* (A) and *T. spadaciflora* (B) in a primary rain forest of the Colombian Choco, during 1998-1999. Note that *Pheidole* sp. dominated in both species.

adult workers and majors were concentrated in the middle portion of the plant, tending coccids and presumably consuming the rich lipid and sugar heads of the short trichomes inside the domatia. This phenomenon has been demonstrated to occur in *T. guianensis* and *Azteca* sp. (Cabrera & Jaffee 1994). Domatia located at the lowest portion of the plant contained organic material such as soil, refuse piles or food and

Table 1. Variables related with leaves and ants in *Tococa guianensis* and *T. spadaciflora* in a primary rain forest of Colombian Choco, mean \pm the standard error.

Variable	<i>T. guianensis</i> (n=9) mean \pm error	<i>T. spadaciflora</i> (n=9) mean \pm error
Number of leaves per plant	35.5 \pm 4.89	11.1 \pm 1.56
Leaf length (cm)	25	40
Leaf area (cm ²)	571.8	879.6
Number of ants per domatia	62.6 \pm 1.23	74.7 \pm 2.23
Number of ants per plant	2016	855

seeds, some of which were noticed germinating in older leaves. The yellowish oldest leaves contained only solid wastes, including corpses from Ponerinae ants and Myrmicinae ants belonging to *Cephalotes* (i.e. formerly *Zacryptocerus*) and *Attini* tribe ants. We also found live insects inside domatia such as coccids (Homoptera: Coccidae), staphylinid larvae (Coleoptera: Staphylinidae: Aleocharinae), bugs (Heteroptera), tipulid larvae (Diptera: Tipulidae), and small crustaceans. Cushman and Addicott (1991) have also registered dipterans inside domatia in Brazil and Venezuela. It is likely that ants were using coccids to collect honeydew (Jolivet 1996, Blüthgen *et al.* 2000).

While *T. guianensis* displayed smaller leaves, both in length and foliar area (Table 1), it outnumbered *T. spadaciflora* in the average number of leaves per plant. The smaller number of adult worker ants per domatia found in *T. guianensis* was compensated by its average higher number of leaves containing ants, thus resulting in a higher total number of ants per plant in this *Tococa* species (Table 1). The domatia in *T. guianensis* were ~5cm long and divided into two chambers, while domatia in *T. spadaciflora* were larger (~7cm long) and exhibited a wrinkled-kidney shape.

Ant protection against herbivory

The number of leaves in *T. guianensis* was not much affected by the presence of ants (Table 2) although a decreasing but non-significant trend was observed through time within the treatments related to the control (Fig. 4A). In contrast, *T. spadaciflora* treated plants suffered a higher loss of leaves throughout time (Fig. 4B) not replaced at a rate enough to compensate for those leaves lost by herbivores. We assume that leaves were lost by herbivory because the blade of fallen leaves was usually heavily damaged on the forest soil, and many of the still attached leaves were just the remaining petiole. Significant differences between treated plants and their controls were found both after 120 and 240 days (Table 2).

Table 2. Number of leaves per plant in two *Tococa* species when excluded from ants (treatment) and when not excluded from their inhabiting ants (control) through three consecutive periods of time separated by four months. p values labeled * are significant at 0.05 level (\pm the standard error)

Time	<i>Tococa guianensis</i>			<i>Tococa spadaciflora</i>		
	Average No. leaves/plant Without ants	Average No leaves/plant With ants	ANOVA repeated measurements	Average No. leaves/plant Without ants	Average No. leaves/plant With ants	ANOVA repeated measurements
0	32.69 \pm 6.33	37.08 \pm 6.20	p=0.633	11.41 \pm 0.76	14.09 \pm 1.56	p=0.104
120 days	29.00 \pm 5.25	34.26 \pm 4.90	p=0.478	4.14 \pm 0.94	13.90 \pm 2.04	p<0.001*
240 days	24.37 \pm 5.12	34.08 \pm 6.22	p=0.267	2.88 \pm 0.88	10.90 \pm 2.01	p<0.001*

Table 3. Average percentage herbivory per plant in two *Tococa* species when excluded from ants (treatment) and when not excluded from their inhabiting ants (control) through three consecutive periods of time separated by four months. p values labeled * are significant at 0.05 level(\pm the standard error).

Time	<i>Tococa guianensis</i>			<i>Tococa spadaciflora</i>		
	average %herbivory/plant. Without ants	average %herbivory/plant With ants	ANOVA repaeated measurements	average %herbivory/plant Without ants	average %herbivory/plant With ants	ANOVA repaeated measurements
0	2.82 \pm 0.95	5.67 \pm 2.63	p=0.368	5.34 \pm 2.15	7.92 \pm 4.63	p=0.096
120 days	20.97 \pm 7.60	16.33 \pm 6.07	p=0.632	77.93 \pm 6.38	18.78 \pm 6.57	p<0.0001*
240 days	54.59 \pm 10.19	22.41 \pm 6.97	p=0.01*	91.08 \pm 4.58	26.50 \pm 9.27	p<0.0001*

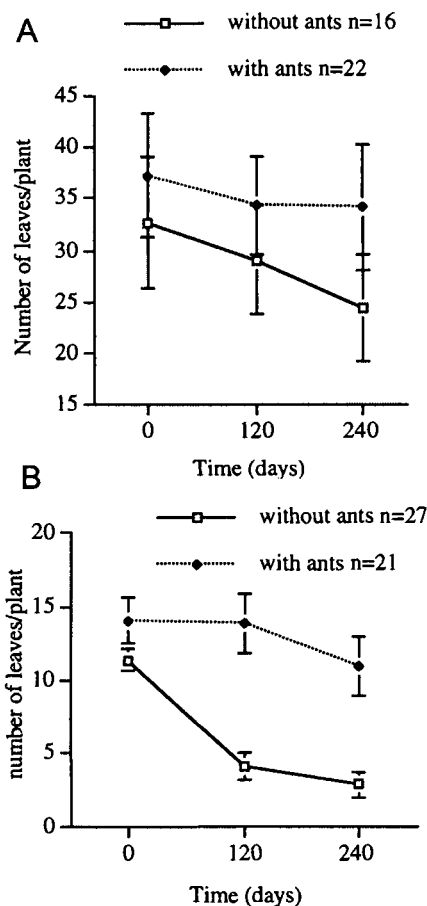


Fig. 4. Number of leaves per plant counted for *Tococa guianensis* (A) and *T. spadaciflora* (B) at time 0, i.e. the time during which ants were removed from the domatia of treated and control plants, and after 4 & 8 consecutive months. Bars represent 1 standard error.

The percentage of herbivory at time "0", i.e. when ants were first removed, was not significantly different for any of the plant species (Table 3, Fig. 5). Nevertheless, after four months *T. spadaciflora* was already highly affected by herbivory (Fig. 5B) contrasting to *T. guianensis*, which was significantly affected by herbivory only after eight months without ants (Fig. 5A). An ANOVA repeated measure model indicated a significant linear trend along time for both *T. guianensis* ($F=36.52$; $df=1,37$; $p<0.001$) and *T. spadaciflora* ($F=119.21$; $df=1,45$; $p<0.0001$). This linear trend was also significantly different for plants with and without ants for both *Tococa* species (ANOVA repeated measures, time x treatment interaction: *T. guianensis* ($p=0.004$) and *T. spadaciflora*: $p<0.0001$). Few cases (ca. 4) of recolonization were observed after eight months in the field, although we quickly removed ants again to continue with the treatment; in all cases the recolonizing species was the same as the plant had before the removal, this includes one case of *Crematogaster* recolonizing *T. guianensis*.

We directly observed defensive actions of *Pheidole* ants against several arthropods including the major defoliator in the region, *Atta cephalotes*. Ants also molested and discouraged other herbivorous insects such as cerambycid beetles, Tettigoniidae and Acrididae as well as non-herbivorous insects such as Coccinellidae (Coleoptera) and *Ectatomma* sp. (Hymenoptera: Formicidae: Ponerinae).

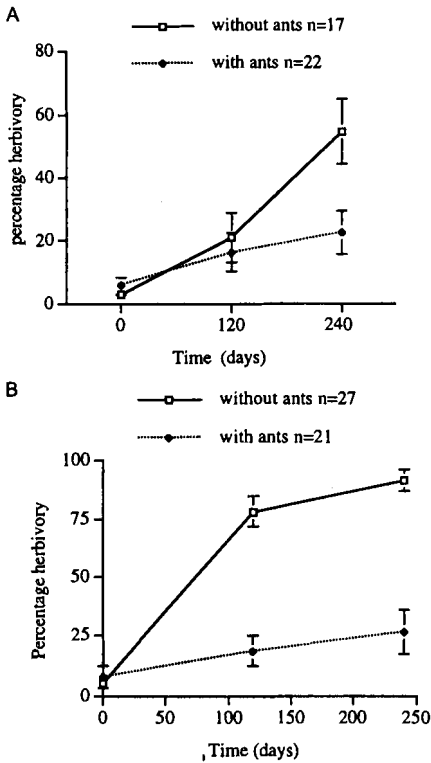


Fig. 5. Percentage of herbivory in *Tococa guianensis* (A) and *T. spadaciflora* (B) after 8 months. Bars represent 1 standard error.

(Vasconcelos 1991). The *Pheidole* species in this study is not *Ph. minutula* and it could be a new species (R, Hamton pers. comm.). Since competition might be playing an important role in determining which species will successfully develop and persist in each of the individual myrmecophyte plants (Davidson *et al.* 1989), our results suggest that *Pheidole* sp. might have this competitive advantage, given that neither *Azteca* sp. nor *Wasmannia auropunctata* dominated the melastomes in this forest. Further, the plant stratification described above by *Pheidole* ants can additionally be showing the degree of specialization of this ant species as a myrmecophyte associate. This pattern is likely to be originated when the first colonization by ants on a young plant is done near the base of the plant, and the colony moves upward as the plant grows (Cabrera & Jaffee 1994). It is worth noting that *Tococa guianensis* has been reported to host ant genera such as *Azteca*, *Allomerus*,

DISCUSSION

Ant species identities

In this study we registered high percentages of *Pheidole* sp. ants in melastome domatia which is consistent with other studies in South America (Fowler 1993, Vasconcelos 1991), but not with the suggestion that *Azteca* species are the most prevalent associated ants in myrmecophytic melastomes on Northern South America (Cabrera & Jaffee 1994). In fact, not only did we find *Pheidole* in 91% of all studied plants, but also this same *Pheidole* species was observed occupying other myrmecophyte species located in the same plots such as *Besleria* sp. (Gesneriaceae) and another unidentified *Tococa* species whose domatia are red colored internally (presumably for attraction, Jolivet 1996). *Pheidole minutula* is considered an obligate plant-ant, which colonizes several myrmecophytic melastomes from *Maieta*, *Clidemia* and *Tococa* genera

Dolichoderus, *Pseudomyrmex*, *Crematogaster*, *Gnamptogenys*, *Solenopsis* and *Myrmelachista* (Renner & Ricklefs 1998), for the *Pheidole* species reported in this study can be added as another partner on this list.

A remarkable finding from our study noted for the first time *Wasmannia auropunctata* living in domatia of both *Tococa spadaciflora* and *T. guianensis* although an unidentified species of *Wasmannia* was reported by Cabrera and Jaffe (1994) in *T. guianensis* domatia. This ant species, which usually nests in leaf litter and decomposing logs and twigs (pers. obs. and in dry forests fragments in Armbrrecht & Ulloa-Chacon 1999) is considered to be a tramp species (Passera 1994), i.e. those pest ants that exhibit particular characteristics as being polygynous, unicolonial, reproduce by budding (Ulloa-Chacon and Cherix 1989) and have been dispersed throughout the world by human activities. *W. auropunctata*, a species that originated from tropical America (Passera 1994), was also found to be one of the main dominants in the ant-mosaic in this same primary rain forest of Colombian Choco (Armbrrecht *et al.* 2001) in a simultaneous study within the same plots reported here. Even though *W. auropunctata* (as a tramp species) has desirable characteristics to defend its host plant (i.e. *Calathea ovandensis*, Horvitz & Schemske 1984) it is not the dominant ant inside any of the myrmecophytes studied. This might indicate that other conditions, such as better competitive ability is favoring the presence of *Pheidole* in the melastomes studied.

Ant protection and reciprocal relations

From our study's results, it is evident that both *Tococa guianensis* and *T. spadaciflora* understory shrubs are engaged in a tight relationship with their symbiotic ants in this Choco primary rainforest of Colombia, as has also been shown by most of the exclusion experiments in ant-plant relations (Bronstein 1998). Despite the risks for establishing such a mutually engaging relationship, the benefit seems to pay off and both partners can take much advantage of it.

On the one hand, plants under the dense canopy are dealing with limited amounts of light for living in one of the most rainy regions of the world, and for being part of the understory vegetation are presumably under intensive competitive conditions from other shrubs. Having a partner that is protecting the costly leaves would allow the plant to invest extra energy in reproduction. We did not test for the fitness outcome in terms of flowers and fruits given the short scale time of the project, but it is likely that less herbivory will eventually lead to a better reproductive net outcome (e.g. Vasconcelos 1991). Consequently the reason of having found the myrmecophyte specialist ant, *Pheidole* sp.

as the most frequent partner of plants in both *Tococa* species (Fig. 2) could be explained partly by this highly beneficial relationship for the plants. On the other hand, the fact that 98% of the plants were actually occupied by ant colonies inside the three plots allows us to consider these two *Tococa* species as important resources and highly beneficial for the housed ants. The benefit of *Tococa* plants for the ants is additionally supported by the presence of (at least) four ant species in each *Tococa* plant species, although three of them in relatively low proportions. We propose two alternative explanations for having other ant species living in *Tococa*'s domatia: either there is an interspecific competition in colonizing new available *Tococa* plants, or empty plants not occupied by *Pheidole* sp. are colonized by other ant species without competition, an explanation that is not so likely given the high percentage of occupancy by ants (98%) in all plants. The low numbers of other ant species occupying *Tococa* plants did not allow us to test differences in the ability of these other ant species to defend the plants against herbivory, so the results in Tables 2 and 3 can be attributed to the defensive action of *Pheidole* sp.

The number of ants and plant strategy for protection

Our study provided evidence of how two similar *Tococa* plants growing under the same conditions and sharing the same mutualist ant species differ in the susceptibility to herbivory when lodged ants are absent. The trade-offs that plants and ants must pay for their mutually beneficial relations to be successful are related to the number of ants that a plant lodges, as discussed by Bronstein (1998). While for the ants might be advantageous to have more internal surface inside the domatia to place their colony, their food and rear homopterans, for the plant is both a risk, and an advantage to have more ants protecting each of its leaves. A risk because the plant is relying its survival on the willingness of the ants to protect it, and an advantage since it is energetically expensive to produce new (big) leaves under the shade conditions of this primary rain forest.

For *T. spadaciflora*, which has more ants per domatia and bigger leaves (than *T. guianensis*), may pay off to have a strong relationship with its mutualist ants. Thus these plants offer larger domatia and provide high interior pubescence to the ants. At the same time, from our results (Tables 2 and 3) it seems that *T. spadaciflora* is quite defenseless without its protective ants. Since some plants increase size dimensions, density of shoots and develop thorns or trichomes as a response to herbivory (Levin 1973; Young 1987; Baur *et al.* 1991), we interpret these increased morphological features of *T. spadaciflora* (relative to *T. guianensis*) as evidence of its susceptibility to herbivory. If this species

is more palatable to herbivorous insects, it might in fact be attracting possible prey (protein sources) for the ants that inhabit it. In fact Bronstein (1998) argues that mutualism is only beneficial when there is a need for "the commodity" they provide, i.e. presence of herbivorous insects, which seems to be the case in our study. The vulnerability of *T. spadaciflora* without ants was clear for both response variables measured (number of leaves and percentage herbivory) which were significantly different. Therefore it becomes apparent that without its mutualist ants, *T. spadaciflora* was not able to replace the leaves lost to herbivores at a rate enough to survive in a time scale of several months or years.

In contrast to *T. spadaciflora*, the strategy adopted by *T. guianensis* appears to be the production of more and smaller leaves. The advantage of having more leaves hosting fewer worker ants per leaf would allow the plant to invest some extra energy in replacing lost leaves from herbivory (assuming that the maintenance of ants implies metabolic costs for the plant, Cabrera & Jaffee 1994). Therefore it seems that *T. guianensis* is not as strongly dependent on *Pheidole* services, which is supported by the lower proportion of the *Pheidole* sp. within *T. guianensis* when compared to *T. spadaciflora* (Fig. 3). In fact, the reduction in the number of leaves per plant was not significantly different in plants with vs. without ants, even after eight months of treatment. Therefore, *T. guianensis* was able to replace the leaves lost to herbivory in a relatively lower time frame (Fig. 4A) when compared to *T. spadaciflora*. Even considering that *T. guianensis* had a significantly higher herbivory percentage after eight months without its housed ants, the difference was of only 32% contrasting the 65% difference detected for *T. spadaciflora* at this same time period.

Synthesizing, our study reports 91% predominance of *Pheidole* sp. inside domatia from two *Tococa* understory myrmecophytes, and provides evidence of high ant protection against herbivory in both myrmecophyte species in a primary forest located in one of the most diverse and humid regions of the world, the Colombian Choco.

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