A TROPHIC MUTUALISM BETWEEN THE MYRMECOPHYTIC MELASTOMATACEAE *TOCOCA GUIANENSIS* Aublet AND AN *AZTECA* ANT SPECIES.

MUTUALISMO TROFICO ENTRE LA MELASTOMATACEA MIRMECOFITICA *TOCOCA GUIANENSIS* Aublet Y UNA ESPECIE DE *AZTECA* (FORMICIDAE)

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ABSTRACT

A survey of southern Venezuela revealed that all seven Melastomataceae species possessing myrmecodomatia were growing on water-saturated sandy soils, and were associated with one or two ant species from a group of 14 collected species. Ninety-six percent of the sampled myrmecophytic melastomes had ant colonies living in their domatia. *Azteca sp, Crematogaster* spp and *Allomerus* spp were the most common ant inhabitants of the domatia; they kept their larvae and associated coccids inside the domatia and deposited wastes such as dead ants and arthropod carcasses in them. We present evidence of a trophic basis for the most common of these ant-plant mutualisms: *Azteca* ants deposit excrement and other organic waste inside 28.9 % of the examined domatia or 90% of the *Tococa guianensis* Aublet plants sampled. Radioactive tracers (tritiated arginine) indicate that these organic wastes are absorbed by the plant, and thus, *T. guianensis is* also an ant-fed plant. In addition, *T. guianensis* produces long and short glandular trichomes containing sugars and lipids, which are collected by the ants, showing that the plant actively feeds ants. These results suggest that the ant-plant associations among melastomes, formerly believed to be based only on ant-defense against herbivores, are more complex and may have evolved in oligotrophic environments containing abundant ants. We suggest that ant abundance may have played a key role in directing evolution to either carnivory or myrmecophytism in some plant groups.

KEY WORDS: ants, mutualism, myrmecophytes, Melastomataceae, ant-fed plants, ant domatia, *Tococa*, *Azteca*.

RESUMEN

En este trabajo, realizado al sur del Orinoco, se encontraron 7 especies de Melastomatáceas con mirmecodomacios, creciendo todas sobre suelos arenosos anegados, asociadas con una o dos especies de hormigas de un total de 14 spp. colectadas. Se encontraron colonias de hormigas habitando los domacios del 96% de las Melastomatáceas estudiadas siendo las especies más comunes *Azteca* sp, *Crematogaster* spp y *Allomerus* spp. Estas hormigas mantienen a sus larvas y a cóccidos asociados dentro de los domacios, donde también depositan desechos constituídos por hormigas y otros artrópodos muertos. Aparentemente, este mutualismo tiene bases tróficas, ya que en el 28,9% de los domacios examinados, o en 90% de las plantas muestreadas de *Tococa guianensis* se encontraron estos depósitos de desechos orgánicos, los cuales son absorbidos y traslocados en la planta como se evidenció mediante marcadores radiactivos. Por ello, *T. guianensis* puede ser considerada una planta alimentada por hormigas. Adicionalmente se encontró que *T. guianensis* produce tricomas glandulares que producen azúcares y/o lípidos, que son colectados por las hormigas. Estos resultados sugieren que las asociaciones hormiga - planta entre melastomas, que inicialmente se consideraban basadas sólo en la defensa contra herbívoros, son más complejas y pueden haber evolucionado en ambientes oligotróficos con abundante mirmecofauna. Sugerimos que la abundancia de hormigas puede haber tenido un papel clave en la orientación de la evolución hacia la carnivoría o hacia el mirmecofitismo en algunos grupos de plantas.

PALABRAS CLAVE: hormigas, mutualismo, mirmecófitas, Melastomataceae, mirmecodomacios, *Tococa*, *Azteca*.

INTRODUCTION

Myrmecophytes are plants that have specialized structures that facilitate the establishment of ant colonies. The mutualism of Melastomataceae is thought to be based on two complementary selective advantages: plants benefit from the protection against insect herbivores and ants benefit from the nesting sites on the plants (Vasconcelos 1991). Nearly 20% of the myrmecophytes known worldwide belong to the family Melastomataceae (melastomes) (Benson 1985, Huxley 1986). These plants produce formicaria or ant domatia consisting of a pair of adjacent leaf pouches, that originate during leaf growth by invagination of the leaf undersurface (Jolivet 1986).

Little is known about the evolution of ant-plant associations in general, and myrmecophytes in particular. Thompson (1981) and Givnish *et al.* (1984) proposed that the availability of water is crucial in orienting evolution toward either carnivory or ant-fed plants. They propose that carnivorous plants evolved in water- and light-saturated habitats on nutrient-poor substrates;whereas ant-fed plants (generally epiphytes) are adapted to dry habitats. Melastomes normally grow in humid areas and are therefore intermediate between the two situations described above. Therefore, in order to test the evolutionary hypothesis proposed by Thompson (1981) and Givnish *et al.* (1984), it is important to investigate possible trophic interactions between plants and ants in this group. In some melastome species, ant-plant mutualism is known to benefit the plant because ants protect the plant against herbivores (Vasconcelos 1991). Here we show that a more complex mutualtrophic relationship between ants and plants exists at least among some Melastomes.

MATERIALS AND METHODS

Field observations

In order to assess the existence of specific ant-plant associations, 105 Melastomataceae plants, mainly *Tococa*, were examined at 14 different sites, between 1° 48' to 5° 35' N and 64° 14' to 67° 40' W,

at altitudes ranging from 80 to 1000 masl, all in Estado Amazonas, Venezuela. Samples of 30 plants and their associated ants were collected by placing previously numbered domatia into plastic bags containing ethyl-acetate to kill the ants, and taken to the laboratory, where each of the domatia was cut open and its contents recorded. Twelve plants of *Tococa guianensis* Aublet from Puerto Ayacucho were collected along with their soil and associated ants, and taken to the laboratory for experiments.

Morphology and Histology

In order to assess the possible nutritional value of plant structures eaten by ants, we did the following anatomical studies Histological analysis of anatomical features on plant sections of *T. guianensis* was based on the technique described by Sass (1958). We made sections using five different plants, cutting in each case domatia, leaves, and petioles.We used FAA as the fixing solution for 24 h, drying the tissues with 50% ethanol (30 min), 70% ethanol (30 min), 95% ethanol (30 min), 95% ethanol + 1-butanol (1:1) (30 min), 1-butanol+ 2-butanol (1:1) (30 min). Inclusion into paraplast was achieved using the following solutions: 2-butanol:paraplast (3:1) (40 min), 2-butanol:paraplast (1:1) (40 min), 2-butanol:paraplast (1:3), leaving the butanol to evaporate for 48 h. Sections were washed with xylol and alcohol, and colored with the following solutions: hemalum, eosin, and carboxylene. Qualitative determination of sugars was achieved by the phenol-sulfuric acid method (Dubois *et al.* 1956). Proteins were visualized using potassium ferrocyanide (Johansen 1940), and lipids revealed using Sudan IV (Jensen 1962).

Collecting of glandular trichomes by ants

Tococa guianensis plants were dug up in the field and planted in the laboratory. Three weeks later each plant was examined in the following way. Five leaves from each of four different plants were chosen at random and then examined under a stereoscope equipped with a millimetric grid. On the main nerve, next to the entrance of the domatia and 1 cm from this entrance, a 1 mm^2 area was

chosen, where the number of trichomes, with and without glandular heads, were counted. Then, *Azteca* ant colonies, collected in plastic bags with *Tococa* leaves, were placed on the plants. The ants immediately occupied the domatia. One month later, five leaves of each of the same four plants were examined again as described before. A control plant was collected and examined in the same way, but ants were not allowed to colonize the plant.

Radioactive labeling

In order to assess nutrient transfer from ant colonies to plants, two different experiments were performed. In one of them, *Azteca* sp workers from colonies living on *Tococa guianensis* plants, were fed during 24 h with honey containing tritiated arginine. In the other experiment, 20 dead ants, previously fed with similarly radioactive honey water, were placed inside two domatia (10 ants in each) of a *T. guianensis* plant without associated ants. Two additional plants growing in the same room, associated with active ant colonies which were fed non-radioactive honey, were used as control. After labeling the ants with radioactive arginine, leaf samples were collected weekly. After three weeks, plants were harvested. Samples of 0.6 g of either leaves, stems, or roots (one sample for each plant part per plant) were homogenized in scintillation solution (0.8 g of PPO and 0.2 g POPOP) and the activity of tritium was measured in a scintillation counter (Cooper 1984).

RESULTS

General observations

In the field, Melastomataceae with ant domatia grew in humid places, in or near swamps, rivers or small lakes, in the forest or in the inundated gallery forests bordered by savanna (Morichales). We never observed myrmecophytes growing in the same habitat of carnivorous plants (*Heliamphora, Drosera, Utricularia, Genlisea* spp), which also occur throughout much of the Venezuelan Amazon).

Tococa guianensis was the most common myrmecophytic melastome in the explored area (see No. of plants in Table 1). We found it in 12 of the 14 sites containing myrmecophytic melastomes, and sampled 61 plants out of a total of 105 plants found. *Tococa* was the most common genus; in addition to *T. guianensis*, we sampled 20 plants of *Tococa coronata* Benth and 12 of *T. macrophysca* Spruce ex Triana. Less than 12 % of the myrmecophytes were from the genera *Myrmidone*, *Clidemia*, and *Maieta* (all Melastomataceae). Of all myrmecophytic melastomes sampled, only 4% (four plants of *T. guianensis*) had no ants living in their domatia (Table 1).

Fourteen ant species were found living in the myrmecophytes (Table 1). Sixty-nine percent of *Tococa guianensis* plants had what we consider to be the same species of *Azteca* associated with them. This ant was the most common species on myrmecophytes; it was found in 52.4% of all plants sampled, followed by a *Crematogaster* species, which was found on 14% of all the plants sampled, and by species of the genera *Pheidole* and *Allomerus*. Ants were found nesting inside the domatia and depositing their waste in some of them.

Plant structures

Close observation of *Tococa guianensis* in the laboratory showed the presence of simple and glandular trichomes in the interior of the domatia and long and short glandular trichomes (Figure 1) on the leaf surface, petioles, stem, and pedicels. These long and short trichomes produce a viscous secretion at their tips (Figure 1C). Colorimetric histological examination of the trichomes showed that the short trichomes terminated in a «head» and contained sugars and lipids, whereas the large trichomes contained only sugars. None contained proteins.

The percentage of «headless» short glandular trichomes on the leaf nerves of the abaxial leaf surface increased significantly when laboratory plants of *T. guianensis* had *Azteca* colonies living on them (Table 2), suggesting that ants eat their tip. We actually saw *Azteca* workers cutting the heads of the trichomes and carrying them to their nests on six occasions.

Table 1. Ant species found on various species of myrmecophytic melastomes in Venezuela. Percentage of each plant species found with a given ant species are reported. Mm: *Myrmidone macrosperma* (Mart.)Mart; Ct: *Clidemia tococoidea* (D.C.)Gleason; Mp: *Maieta poeppigii* Mart. ex Cogn.; Mg: *Maieta guianensis* Aublet; Tm: *Tococa macrophysca* Spruce ex Triana; Tc: *Tococa coronata* Benth; Tg: *Tococa guianensis* Aublet.

Plant species: Nr of plants examined	Ct	Mp	Mg	Mm	Tc	Tg	Tm	all plants
	3	2	6	1	20	61	12	105
Ant species (%):								plants (%):
Allomerus sp 1	0	0	0	0	30	0	0	5.7
Allomerus sp 2	0	0	0	0	0	2	0	1.0
Allomerus sp 3	0	0	0	0	0	5	0	2.9
Allomerus sp 4	0	0	0	0	15	0	0	2.9
Azteca sp	33	50	0	0	30	69	42	52.4
Brachymyrmex sp	0	0	0	0	0	0	8	1.0
Crematogaster sp 1	33	0	0	0	10	13	33	14.3
Crematogaster sp 2	0	0	17	0	5	0	8	2.9
Crematogaster sp 3	0	0	0	0	0	3	0	1.9
Paratrechina sp	0	0	0	0	0	5	0	1.0
Pheidole sp 1	0	50	100	100	0	0	0	7.6
Pheidole sp 2	0	0	0	0	10	0	0	1.9
Solenopsis sp	0	0	0	0	0	8	0	4.8
Wasmannia sp	33	0	0	0	0	3	8	3.8
% of plants with ants	100	100	100	100	100	93	100	96

In some cases the sum of percentages of plants inhabited by a given ant species gives values greater than 100 % due to the fact that more than one ant species were present on the plant. Most ant species have not been given specific names because of the poor taxonomic situation of these groups. For example, Kempf (1972) reports only two *Allomerus* species in his catalog, Brandao (1991) three, whereas we found at least four different species. Davidson *et al.* (1988) reports an additional *Allomerus* species, nonexistent in the taxonomic literature. Consequently, we thought it wiser not to place names to ant species belonging to groups where extensive taxonomic revisions are required. Specimens are deposited at: Museo de Ciencias Naturales - Universidad Simón Bolívar, Venezuela.

Table 2. Percentage of headless short glandular trichomes on laboratory *Tococa guianensis* leaves before and after *Azteca* ants colonized the plant during 1 month. Means are from 20 leaves from 4 different plants (5 leaves from each plant, control represents 5 leaves from 1 plant).

Plant	Mean ± s.d. Nr. of trichomes /cm²	% of headless trichomes
Before ants	53.6 ± 18.2	2.6 ± 3.2
With ants	49.5 ± 20.5	23.8 ± 21.4
U-Mann-Whitney p:	NS	<0.001
Control	43.0 ± 5.1	1.2 ± 2.7
Control 1 month later	48.6 ± 10.5	0.8 ± 1.1
U-Mann-Whitney p:	NS	NS

Colony structure of *Azteca* sp and its diet

The spatial distribution of *Azteca* ant colonies among the various domatia of the host plant is shown in Figure 2 Examination of 142 domatia collected from 30 different *T. guianensis* plants in the field revealed that this distribution followed a distinct pattern (Table 3) Queens, workers, brood, and wastes were preferentially located inside the larger domatia near the base of the plant. In addition, more

workers were found in domatia containing the brood, waste, or scales (Homoptera: Coccidae); scales were found mainly in domatia with wastes (p < 0.05, Pearson correlation for each of the reported correlations). Of the 30 plants examined, 90% had one or more domatia containing «wastes» accumulated at the opposite end from the entrance and occupied about 20% of the inside of the domatia (Figure 2C). Of all 142 domatia examined, 28.9% contained these «wastes». Close examination of the
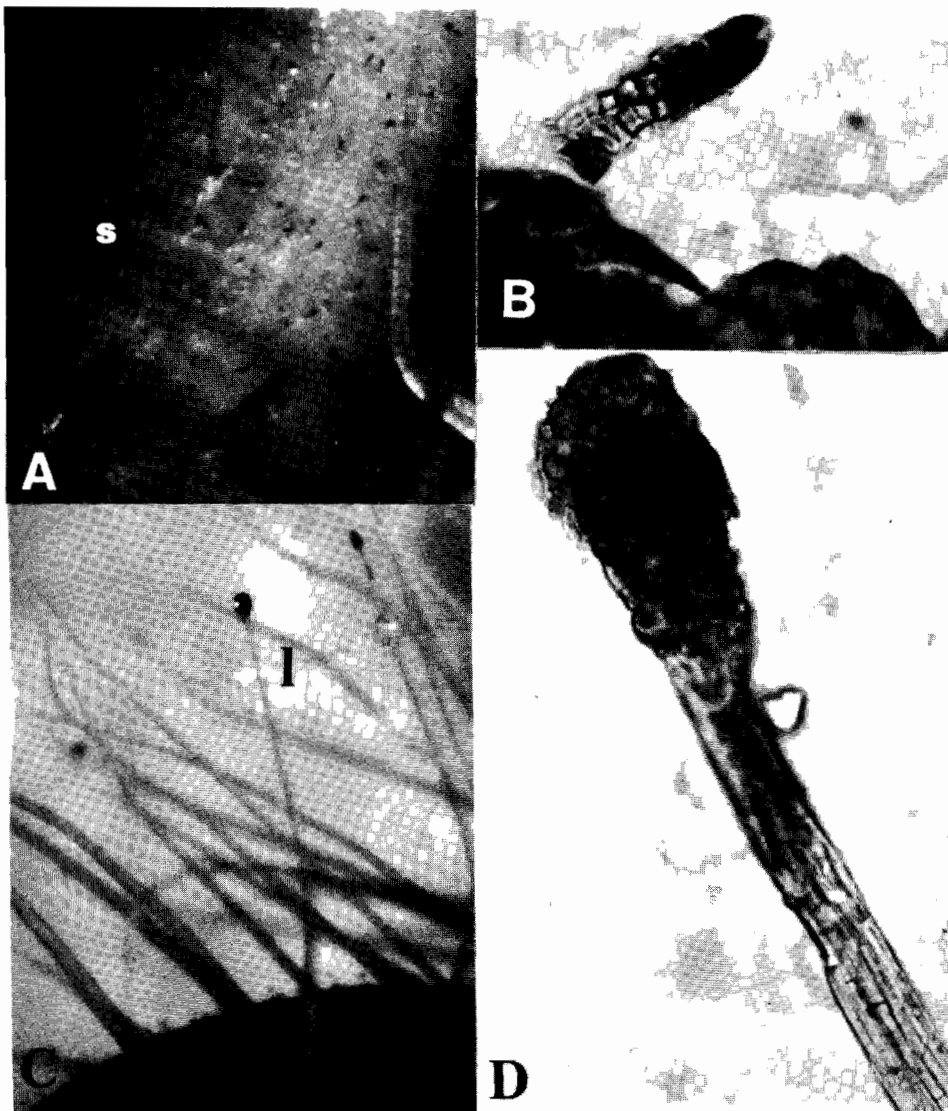

Figure 1: Leaf-structures of *Tococa guianensis*: A: short glandular trichomes (s) on foliar abaxial nerve (31 x), B: histological section of short glandular trichome (400 x), C: long glandular trichomes (l) found on domatia, stem,and leaves (16 x), D: histological section of head of a long glandular trichome (400 x)

«waste» showed that it consisted of dead ants or parts of them, parts of other arthropods, and decomposing organic matter.

Azteca ants in the laboratory proved to be insectivorous. They fed on dead termites, crickets, and sugar solution or honey. They never foraged on seeds, raw meat, bird droppings, dead ants, or flowers.

Nutrient transfer from ants to plant

When ant colonies had been fed radioactive honey water, plants associated with those ants absorbed and accumulated the radioactivity in less than one week. Radioactivity was concentrated mainly in the stem. Nutrient transfer seemed to occur through the domatia, as the plant with dead

radioactive ants placed in its domatia absorbed radioactivity similarly to plants which had live ant colonies inhabiting them (Table 4).

DISCUSSION

Our observations show that practically all myrmecophytic melastomes from our study sites in Estado Amazonas had ants living in their domatia, and that they form associations with a wide range of ant species. The prevalence of *Azteca* sp on these plants seems to be a particular feature of northern South America, as reports from Brazil (Vasconcelos 1991, Fowler 1993) and from   Central America (Tennant 1994) show that other species are prevalent there. One exception to this rule may be *Maieta* spp, which seem to have a more specific mutualistic

Table 3: Pearson correlation coefficients between colony features and size and height of the leaf domatia on *Tococa guianensis*. NS: $p > 0.05$. Size range of domatia: 0.6 to 3.8 cm. Height indicates the leaf sequence from the base of the plant to the top. (n = 142)

	Size	Height	Workers	Pupae	Larvae	Queen	Alates	Scales	Waste	Eggs	Empty
Size	-										
Height	-0.296	-									
Workers	0.448	-0.242	-								
Pupae	0.281	-0.213	0.300	-							
Larvae	0.278	-0.195	0.401	NS	-						
Queens	NS	NS	NS	NS	NS	-					
Alates	0.386	-0.225	0.403	0.607	NS	NS	-				
Scales	0.200	-0.313	0.293	NS	NS	NS	NS	-			
Waste	0.218	-0.350	0.286	NS	NS	NS	NS	0.395	-		
Eggs	NS	NS	0.145	0.498	NS	NS	0.187	NS	NS	-	
Males	NS	-0.174	NS	N.S	NS	NS	NS	NS	NS	NS	
n	-	-	93	18	55	4	35	62	41	6	35
%	-	-	66.5	12.7	38.7	2.8	24.6	43.7	28.9	4.2	24.5

Table 4: Average counts ± s.d. per min per 0.6 g of tissue of *Tococa guianensis* after feeding the mutualistic ants with radioactive honey. Experiment 1: Two plants associated with *Azteca* ant colonies fed radioactive honey. Experiment 2: One plant with dead radioactive ants placed in the domatia. Control: Two plants associated with ants fed non-radioactive honey, growing in the same room.

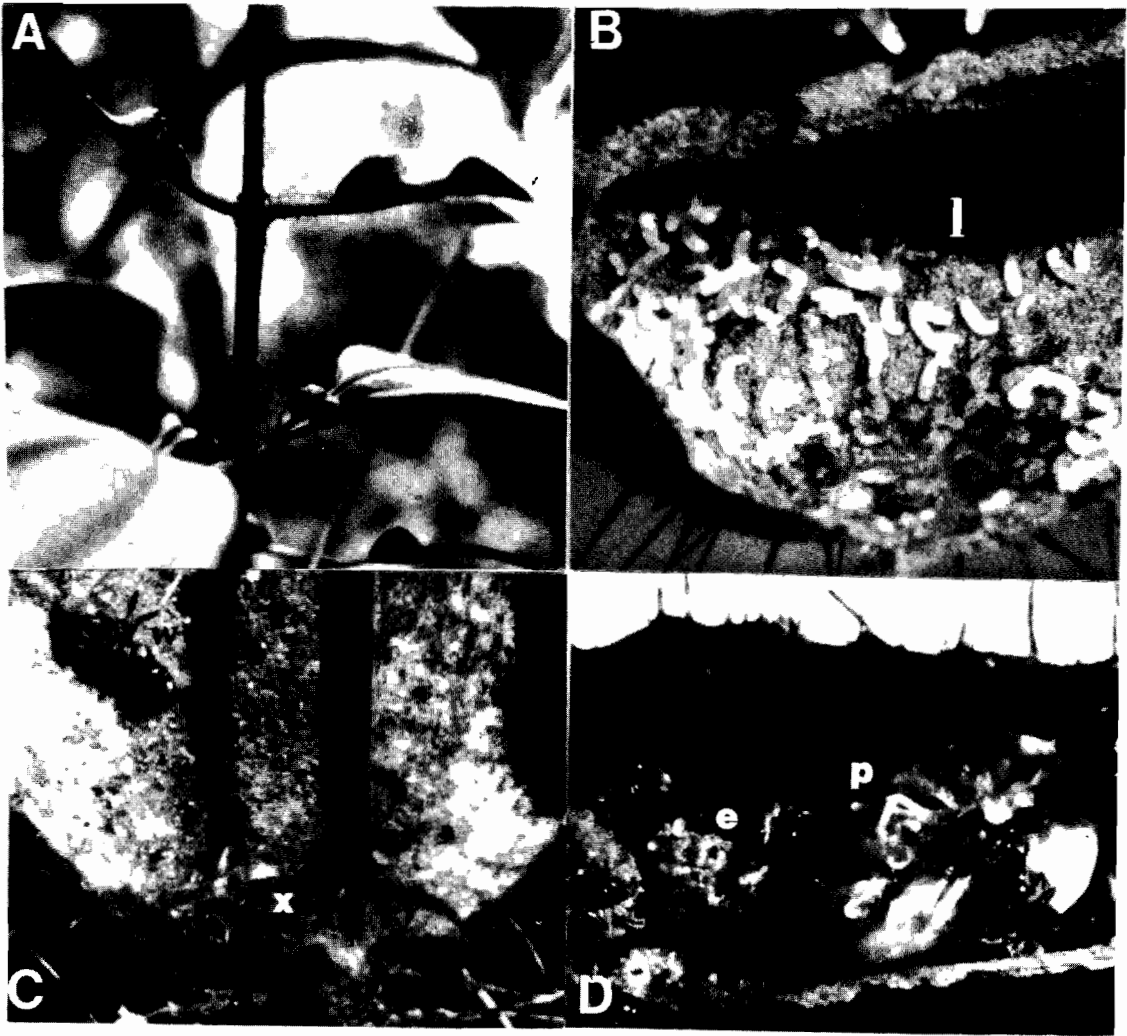| Week	0	1	2	3	
Experiment	control	1	1	1	2
Leaf	8.5±3.4	172±97	68±3	22±23	48
Stem	62±48	-	-	3672±69	19535
Root	17±4	-	-	44±31	16

Figure 2: Domatia of *Tococa guianensis* A: Domatia (d) at the base of leaves (0.25 x), B,C,D: longitudinal preparation of domatia showing ant larvae (l), pupae (p), eggs (e), workers (w), and organic debris (x) (B and C: 10x; D: 6x)

relation with a *Pheidole* species (see also Benson 1985, Davidson *et al.* 1990, Vasconcelos 1991, Fowler 1993).

Allomerus spp seem to be specialized residents of melastome plants as these ants are rarely found outside their host plants (Jaffe, personal observation; see also Davidson *et al.* 1990, Fowler 1993).

We observed a distinct occupation pattern of the domatia by *Azteca* sp ants, where ant colonies first occupied the domatia near the base of the plant, which are larger, and then, as the colonies became larger, the ants colonized the rest of the domatia.

This pattern of occupation of the plant by the ants had, as a consequence, that nearly 30% of the domatia (or 90% of the plants) accumulated important amounts of nitrogen-rich organic debris. This debris represents an important amount of additional nutrient supply for the plant.

The long glandular trichomes found are similar in structure and composition to the extrafloral nectaries mentioned for various myrmecophytic melastomes (although not specifically for *Tococa*) by Couret (1966); whereas the short glandular trichomes resemble the pearl bodies reported for *Tococa*, *Maieta*, and *Myrmidone* by Rouppert

(1926: in O'Dowd 1982). Davidson *et al.* (1989) reported the presence of plant trichomes in myrmecophytes and suggested a function in biasing interspecific competition among ant species: trichome spacing was postulated to restrict the passage of larger ants. Although we cannot comment on this possibility, our results show that these trichomes are consumed by ants.

We showed that *Tococa guianensis* has, in addition to the domatia, glandular trichomes which may help in attracting ants. These structures provide ants with sugars and lipids, and thus represent an energetic cost to the plant. We suggest that these or similar glandular trichomes may be present in other Melastomataceae species as mentioned by Couret (1966). We showed that ants deposit their waste in the domatia allowing nutrients to be transferred to the plant, as shown in detail in the case of *T. guianensis* and *Azteca* sp. The same ant species also inhabits domatia of melastomes of the same and different genera, suggesting that feeding by ants may be a common feature in myrmecophytic melastomes, as nutrient absorption through leaves is a widespread phenomenon among plants (Hutchinson *et al.* 1972, Huxley 1980). The possibility that plants can absorb nutrients released by the debris stored by the ants inside the domatia has been suggested by other authors, for example in some Neotropical species of *Piper* associated with *Pheidole* spp (Risch *et al.* 1977). However, this has only been demostrated experimentally for epiphytes in the genera *Myrmecodia* and *Hydnophytum* (Rubiaceae), which have modified tuberous structures with cavities within which *Iridomyrmex* spp deposits debris. The plants absorb nutrients directly through the walls of the cavities or through roots within the cavities (Janzen 1974, Rickson 1979).

In the case of the association between *Tococa guianenis* and *Azteca* sp, we have no direct evidence that the ants repel herbivores, but we showed that *Azteca* sp workers feed mainly on arthropods, including herbivorous insects, and thus may potentially provide some kind of protection to the plant. All ant species found on the myrmecophytic melastomes examined (Table 1) are from genera known to prey on arthropods (Hölldobler and Wilson 1990, Jaffe 1993). Thus, the presence of colonies

of these ants on a plant may at least reduce the probability of feeding by herbivorous arthropods. Therefore, we might expect that defense against herbivores by ants should be a common feature in myrmecophytic melastomes (Vasconcelos 1991), as has been suggested for other ant-plant associations (Janzen 1969, Jolivet 1986, Davidson *et al.* 1988). Despite these suggestions, only in a few cases has plant protection by ants been demonstrated (Fowler 1993).

The fact that *T. guianensis* is an ant-fed plant may throw new light on the problem of the divergent evolution between carnivorous plants and ant-fed plants. It is presently assumed that ant-fed plants have adapted to nutrient-poor and dry environments, whereas carnivorous plants are more adapted to sunny, humid, but nutrient-poor environments (Thompson 1981, Givnish *et al.* 1984). Another independent adaptive pressure thought to lead to myrmecophytism was ant-mediated allelopathy; that is, ants protect plants from other plants (Janzen 1969).

Givnish *et al.* (1984) postulated that myrmecophytism yields benefits, other than nutrient input, such as defense, mainly in unproductive, shady or dry environments, where leaves are relatively more costly to replace. In contrast, carnivory occurs in humid and sunny areas, where photosynthesis can be enhanced by an increased nutrient input. Thompson (1981) suggested that ant-fed plants did not evolve carnivory because their limited access to water made it costly to produce glandular secretions. Based on this assumption and using a cost/benefit model, Givnish *et al.* (1984) predicted that as myrmecophytic melastomes grow in the shade, where photosynthesis seems to be limited by light rather than by nutrients, plants should not benefit from nutrients derived from ants and that myrmecophytism in this case would be based on plant defense by ants. Our results partially contradict these predictions as we showed that *T. guianensis* invests both in food bodies and extrafloral nectaries and has domatia with specialized mechanisms for the fast absorption of nutrients provided by the ants. This suggests that feeding by ants may be much more common in ant-plant associations than formerly recognized.

In the case of myrmecophytic melastomes, ant-plant associations were shown to be based only on defense against herbivores (Vasconcelos 1991). However, our observations on *T. guianensis* suggest that defense does not necessarily exclude feeding of the plant by ants. Thus, both of these relationships could regulate the evolution of these plants, favoring ant-plant associations.

We want to postulate a new complementary hypothesis explaining the divergent evolution of carnivory and myrmecophytism, which states that the main evolutionary pressure leading either to carnivory or myrmecophily is, in addition to nutrient requirements, the abundance of insects. In areas of southern Venezuela, both myrmecophytic and carnivorous plants are found, but never in the same habitat. Carnivorous plants are restricted to oligotrophic ecosystems at high altitudes in the neotropics (Jaffe *et al.* 1992), whereas myrmecophytes grow in low-altitude sites and forested areas. These characteristics mark an important difference in the amount of ants and other insects present (Jaffe *et al.* 1993): ants are very rare in sites where carnivorous plants grow, whereas they are abundant in sites where myrmecophytes are found.

The evolutionary history of the carnivorous pitcher plants of the genus *Heliamphora* suggest that these plants derived from trapping mainly ants towards trapping a variety of insects (Jaffe *et al.* 1992). Thus, we postulate that in ant-poor environments, which normally are also poor in other insects, and probably have low herbivore pressure, more nutrients may be obtained by capturing and digesting a wider array of insects (the case of evolution in *Heliamphora*) and ants are not needed for protection against herbivores. Alternatively, in ant-dominated ecosystems, the social behavior of ants makes them the plant mutualist «par excellence». Here ants may better serve the plant by providing nutrients and defense against herbivores and other plants, and so myrmecophytism would be favored. This ecological difference could be a key feature, althoughnot the only one, in providing the basis for the evolution to either carnivory or myrmecophytism among the Sarraceniaceae and Melastomataceae and probably among other plant groups.

ACKNOWLEDGEMENTS

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