

Ant Protection against Herbivory in Three Species of *Tococa* (Melastomataceae) Occupying Different Environments¹

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ABSTRACT

The genus *Tococa* is comprised of 47 species of small trees and shrubs distributed from southern Mexico to Bolivia. About 30 of the species have ant domatia that develop at the base of the leaf blade or at the apex of the petiole. Ant exclusion experiments on three different species of *Tococa* occupying different environments were carried out to assess their effect in protecting the plant against herbivores. Additionally, ant behavior was monitored in control plants to study how they might be conferring protection against herbivory. Herbivory was significantly lower on control plants (ants maintained) than on experimental plants (ants removed), demonstrating the role of the ants as defenses against herbivores. Herbivory rates in open and disturbed areas were higher than in the forest understory. Ant exclusion experiments showed that both timid and aggressive ants protect their host plants against potential herbivores by killing or warding off scouts of leaf-cutter ants (*Atta* sp.) and removing the eggs of Lepidoptera and Coleoptera from the surface of the plants.

RESUMEN

El género *Tococa* esta compuesto por 47 especies de arbustos y árboles pequeños distribuidos desde el sur de México hasta Bolivia. Cerca de 30 especies poseen domacios que se desarrollan en la base de la lámina de la hoja o en el ápice del pecíolo. Se llevaron a cabo experimentos de exclusión de hormigas en tres especies de *Tococa* en distintos hábitat con el fin de evaluar su rol potencial de protección contra la herbivoría. Adicionalmente, se observó el comportamiento de las hormigas en las plantas del grupo control con el fin de estudiar su papel como defensa contra los herbívoros. Las diferencias en las tasas de herbivoría entre plantas con y sin hormigas fue siempre significativa, demostrando así el rol de las hormigas como defensa contra los herbívoros. Además, en las zonas abiertas y secundarias, la cantidad de herbivoría fue siempre mayor que en el dosel del bosque. Estos experimentos también demuestran que tanto las hormigas tímidas como las agresivas protegen a las plantas que habitan, ya sea matando o ahuyentando los exploradores de las hormigas cortadoras de hoja (*Atta* sp.) o removiendo los huevos de Lepidoptera y Coleoptera de la superficie de las plantas.

Key words: ant behavior; *Atta*; Azteca; Crematogaster; forest–savanna ecotone; forest understory; gallery forest; gap; myrmecophytism; *Tococa*; Venezuela.

MYRMECOPHYTISM IS THE SYMBIOTIC ASSOCIATION BETWEEN ANTS AND PLANTS in which plants provide the ants with some type of structure that facilitates the establishment of the ant colony on the plant, and ants provide protection against potential herbivores and/or pruning of lianas and epiphytes. Additionally, the plants may provide the ants with food, Beltian bodies as in the case of *Acacia* or Müllerian bodies in *Cecropia*. The structures inhabited by the ants are usually hollow chambers (usually referred to as ant domatia, myrmecodomatia, or simply do-

matia) located in a variety of plant organs, such as roots in *Myrmecodia* (Huxley 1986), stems in *Cecropia* (Janzen 1969) and *Cordia* (Davidson *et al.* 1989), thorns in *Acacia* (Janzen 1966), and leaves in *Hirtella* (Spruce 1908, Prance 1982).

Some of the earlier studies on ant-plants considered the ants to be detrimental rather than beneficial to the plants they occupied (Spruce 1908, Melin 1930). Spruce (1908: 412) summarized this opinion, stating that: "The ants cannot be said to be useful to the plants, any more than fleas are to animals; and the plants have to accommodate to their parasites as best they may." He, however, later changed this opinion (see letters published in the same volume edited by A. R. Wallace; Spruce 1908), and suggested that ants may be beneficial

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to the plants. The beneficial role of ants as anti-herbivore defenses has been clearly demonstrated in ant *Acacia* (Fabaceae; Janzen 1966, 1967) and *Leonardoxa* (Fabaceae; McKey 1984), as well as in other plant genera (Vasconcelos 1991; Fiala *et al.* 1994, 1999; Vasconcelos & Davidson 2000). Experimental or observational data indicate that inhabiting ants have beneficial effects in the more than 23 plant families in which similar associations are known to exist (Beattie 1985, Benson 1985, Jolivet 1996). Ants not only defend their host against potential herbivores but have been reported to provide protection against the growth of vines and epiphytes (Janzen 1967, 1969), and even fungi (Jolivet 1996, Letourneau 1998, de la Fuente & Marquis 1999), to prevent the growth of competing plants in the forest understory (Morawetz *et al.* 1992, Renner & Ricklefs 1998) or to provide CO₂ and N for the host plant (Treseder *et al.* 1995).

Of the more than 420 plant species known to be myrmecophytes, over 50 are in the Melastomataceae, and of those, close to 30 belong to the genus *Tococa* (Benson 1985, Huxley 1986, Michelangeli 2000a). The first report of the possible protective role of ants in *Tococa* was given by Trail (see editorial comments by A. R. Wallace in Spruce 1908), who noted that plants with domatia lacking ants suffered more attacks by herbivores. Since then, few cases of ant-plant associations in the Melastomataceae have been studied.

Recently, Vasconcelos (1991) quantified the protective role of ants inhabiting *Maieta guianensis* (another myrmecophytic Melastomataceae) by removing them and measuring herbivory rates through time. Ants of the genus *Myrmelachista* (Formicinae, Myrmelachistini), which inhabit the domatia of *Tococa occidentalis* in Ecuador and Peru, were found to kill the vegetation surrounding their host plants by biting the main nerves of the competing species' leaves, resulting in monospecific stands of *T. occidentalis* in the forest understory (Morawetz *et al.* 1992, Renner & Ricklefs 1998). Additionally, Svoma and Morawetz (1992) have shown that the trichomes covering the surface of leaves and stems can serve as food bodies for the ants inhabiting *T. occidentalis*; however, no studies have shown whether or not inhabiting ants of *Tococa* provide their host with protection against herbivores.

The behavior of plant-inhabiting ants has been classified as either timid or aggressive (Benson 1985; Davidson *et al.* 1988, 1989; Davidson & McKey 1993). Timid ants are usually smaller, tend to colonize slow-growing shrubs and small trees in the understory, and rarely leave the nest in large

numbers (as in the case of *Leonardoxa*; Gaume *et al.* 1997). Aggressive ants tend to be larger, and they inhabit fast-growing trees in forest gaps of the forest-savanna ecotone, such as *Acacia* or *Cecropia*. When disturbed, large numbers of workers quickly exit the nest (Janzen 1969, Davidson & McKey 1993 and references within).

Different species of *Tococa* occupy a variety of habitats in the Neotropics, and even though some of the species are widely distributed, most of them are restricted geographically or to specific soil or vegetation types (Michelangeli in press). This constraint provided the opportunity to study the role of ant protection in different environments across closely related species and even within different populations of the same widely distributed species.

In this study, to quantify potential differences in herbivory rates of plants with and without ants, I carried out ant-exclusion experiments on three species of *Tococa*. To detect the effect of plant environment, I sampled species and populations growing in different habitats. Additionally, in control plants I conducted observations on the behavior of the inhabiting ants to determine how they protect their host plant and find out if this behavior varied across plant species and environments.

MATERIALS AND METHODS

STUDY SITES.—Fieldwork was carried out at two localities in southern Venezuela: (1) Canaima (6°19'N, 62°49'W; 400 m elev.) on the Carrao River in Canaima National Park, state of Bolívar, Venezuela (visits to Canaima were carried out during June–August 1995 and July 1996); and (2) Yutajé camp (5°36'N, 66°06'W; 140 m) at the base of Cerro Yutajé in the northernmost portion of Amazonas State in Venezuela. Yutajé was visited during June–August 1996. Details about the climate and vegetation are given in Huber (1986) and Ramirez *et al.* (1988) for Canaima and in Berry *et al.* (1995) and Huber (1995a, b) for Yutajé.

PLANT SPECIES STUDIED.—To assess whether or not inhabiting ants provided protection against herbivores and if the degree of protection varied across different habitats, ant-removal experiments were conducted on three species of *Tococa* with distinct habitat preferences: *T. coronata*, *T. guianensis*, and *T. macrosperma*. To evaluate the effect of plant habitat on herbivory in the same plant species, populations of *T. guianensis* were sampled from primary forest understory, small forest gaps (<150 m²), and open areas (savanna-forest ecotone).

TABLE 1. *Population of Tococa studied during the rainy season of 1996, indicating their habitat, genus of inhabiting ants, and ant behavior.*

Species	Locality	Habitat	Ant genus ^a	Number of plants ^b	Behavior ^c
<i>T. coronata</i>	Yutaje	Gallery Forest	<i>Azteca</i> *	20/18	Aggressive
			<i>Pseudomyrmex</i>	0/2	Aggressive
<i>T. guianensis</i>	Canaima	Understory	<i>Crematogaster</i> *	9/9	Timid
			<i>Azteca</i>	1/0	Timid
			<i>Azteca</i>	0/1	Aggressive
<i>T. guianensis</i>	Canaima	Gap	<i>Azteca</i> *	20/20	Aggressive
<i>T. guianensis</i>	Canaima	Forest Edge	<i>Azteca</i> *	20/20	Aggressive
<i>T. guianensis</i>	Yutaje	Gap	<i>Azteca</i> *	20/20	Aggressive
<i>T. macrosperma</i>	Canaima	Understory	<i>Crematogaster</i> *	19/17	Timid
			<i>Allomerus</i>	1/3	Timid

^a Genera followed by an * indicate that at least two different morphospecies seem to be present. Note that three plant populations had more than one inhabiting ant genus present, while in three others, all plants were inhabited by ants of the same genus.

^b Numbers indicate the number of plants inhabited by each genus in control plants/experimental plants.

^c Classification into timid or aggressive, following Beattie 1985, based on field observations and references (see text).

Tococa coronata Benthham is a widespread species in the Amazon, Essequibo, and Orinoco basins, commonly found in flooded and gallery forests. It is usually a tall shrub or small tree up to 6 m tall, and during the rainy season, only 1 or 2 m at the top of the crown is above water. It has domatia immersed in the leaf blade and usually a very sparse pubescence (Michelangeli in press). *Tococa coronata* was sampled in Yutajé (Table 1).

Tococa guianensis Aublet is the most common and widespread species of the genus. It is found from southern Mexico to Bolivia in a variety of habitats, from sea level to 2500 m. The domatia are free from the leaf blade, and although there is some degree of anisophylly, both leaves of any given pair generally have domatia (Michelangeli in press). *Tococa guianensis* was sampled in Canaima and Yutajé (Table 1).

Tococa macrosperma Mart. is a small shrub up to 2 m tall with extreme anisophylly in which usually only one of the leaves of each pair has a domatium. It inhabits the understory of non-flooded forests in the Orinoco and Rio Negro basins (Michelangeli in press). *Tococa macrosperma* has traditionally been placed in its own genus, *Myrmidone*. A recent morphological cladistic analysis (Michelangeli 2000a), however, has suggested that it belongs in *Tococa*, as previously determined by Wurdack (1973). *Tococa macrosperma* was sampled in Canaima (Table 1). Botanical vouchers are deposited at the Venezuelan National Herbarium (VEN) and the Bailey Hortorium, Cornell University (BH).

lution, with the exception of *T. guianensis* growing in the forest understory at Canaima. Although *T. guianensis* occupies a wide range of habitats, it is more abundant in gaps and the forest-savanna ecotone. Only 20 plants could be found for the Canaima understory population.

Prior to ant exclusion, the width and length of the leaves on the three apical nodes on each branch were measured (to later estimate leaf area if necessary; see below). These leaves were later used to estimate herbivory rates. Only the three youngest leaf pairs from each branch were included because some older leaves already showed herbivory. Plants were randomly assigned to two equal-sized groups. One group was marked and left otherwise untouched as the control. In the experimental group, all the domatia (marked young nodes, as well as older ones) were cut open on the adaxial side of the leaf, and the ants were removed by flushing them out with water. Any remaining ants were removed manually using forceps.

At the end of each experiment, the leaves were harvested and dried, and the proportion of leaf area that had been removed was estimated in the lab using a Licor LI-3100 area meter. In some cases, the entire leaf had been removed by the action of the herbivores; the area of the leaf could not be measured directly and instead had to be estimated. This was performed using a formula developed by Vasconcelos (1991) to estimate leaf areas on *M. guianensis*, another myrmecophytic species of Melastomataceae [$A = 0.12 + 0.063(L \times W)$, where L = maximum length and W = maximum width]. A sample of ten leaves with different sizes and ages in each of the three species used in this study

ANT-REMOVAL AND HERBIVORY RATES.—For each experiment, 40 plants were chosen from each popu-

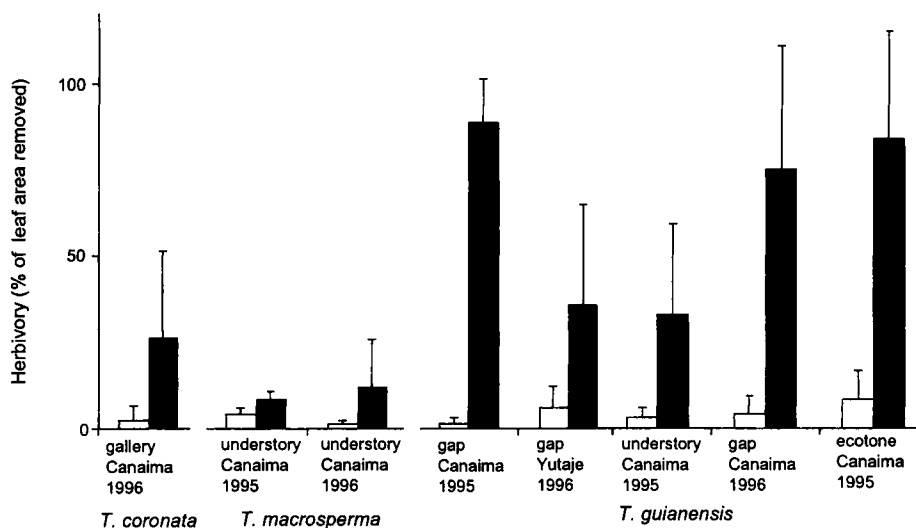


FIGURE 1. Results of the ant-exclusion experiment for eight populations of *Tococa*. Empty bars represent control populations and solid bars represent experimental populations. Results are expressed as percent leaf area removed/28 days \pm 1 SE. Each population is identified by habitat, locality, year of the experiment, and species. Differences between control and experimental groups were always significant (significance of *t*-test in parentheses). *T. coronata*: riverine forest, Yutajé, 1996 ($P < 0.0005$). *T. macrosperma*: forest understory, Canaima, 1995 ($P < 0.0001$); forest understory, Canaima, 1996 ($P < 0.005$). *T. guianensis*: forest gaps, Canaima, 1995 ($P < 0.0001$); forest gaps, Yutajé, 1996, ($P < 0.0005$); forest understory, Canaima, 1996 ($P < 0.005$); forest gaps, Canaima, 1996 ($P < 0.0001$); savanna-forest ecotone, Canaima, 1996 ($P < 0.0001$). For comparisons among populations of *T. guianensis* sampled in Canaima during 1996, see text.

showed a very good fit to his formula. The time of the experiment varied from 26 to 39 days. To compare the results across experiments, all results are prorated to 28 days. For each population studied, a *t*-test (Sokal & Rohlf 1981) was employed to determine if differences in herbivory rates between experimental and control groups were significant.

To determine whether or not the habitat of the plants had any effect on herbivory rates on the three populations of *T. guianensis* investigated during the rainy season of 1996 at Canaima (understory, gap, and savanna-forest ecotone), two one-way ANOVAs (Sokal & Rohlf 1981) with a Bonferroni correction were employed: one to contrast the three control groups (ants remaining) and another for the three experimental groups (ants removed). This approach was chosen over a two-way ANOVA because of the unbalanced design.

OBSERVATIONS ON ANT AND HERBIVORE BEHAVIOR.—Experimental and control plants were visited every two to three days to observe the presence or absence of herbivores. In addition, in control plants, the foraging activities of the inhabiting ants and their interactions with potential herbivores were recorded. On observation days, plants were moni-

tored for five minutes every two hours from dawn to dusk. Twenty-four hour observations in some of the survey populations showed that inhabiting ants conduct most of their activities outside of the domatia from dawn to dusk (Michelangeli 2000b).

Ants from all individual plants included in this study were collected for later identification. Ants were determined by the late W. Brown Jr. (Cornell University) and R. Keller (Cornell University and American Museum of Natural History). Entomological vouchers are deposited at the Entomological Collection of Cornell University and the Museo del Instituto de Zoología Agrícola (MIZA) in Maracay, Venezuela.

RESULTS

ANT EXCLUSION.—Removal of the ant colonies resulted in significantly increased herbivory rates for all plant populations studied, regardless of plant species, habitat, or locality (Fig. 1). When comparing the three populations of *T. guianensis* growing in different habitats at Canaima, herbivory rates in the three control groups were not significantly different (ANOVA, $df = 2, 47$; $P_{\text{Bonf}} > 0.1$; Fig. 1); however, herbivory rates in the three ex-

perimental groups were significantly different (ANOVA, $df = 2, 47$; $P_{\text{Bonf}} < 0.001$; Fig. 1). Pair-wise comparisons indicated that herbivory rates in the gap and savanna ecotone populations were not significantly different ($P > 0.05$), but both of them were significantly different from herbivory rates in the forest understory population ($P < 0.005$). Herbivory rates were lowest in the forest understory group and higher in the gap and savanna-forest ecotone populations.

ANT BEHAVIOR AND HERBIVORES.—All control individuals of *Tococa* monitored during this study were continuously inhabited by ants (see also Vasconcelos & Davidson 2000); however, even within the same population, different plants were inhabited by different species, or even genera, of ants (Table 1).

Based on field observations during this study and descriptions of ant behavior in the literature (Letourneau 1983; Beattie 1985; Fiala *et al.* 1989, 1994; Vasconcelos 1991; Davidson & McKey 1993; Agrawal & Rutter 1998; Gaume & McKey 1999; Irioka *et al.* 2000), all ant colonies were easily and clearly classified as either timid or aggressive. Ants of the genera *Crematogaster*, *Allomerus*, and at least one species of *Azteca* exhibited timid behavior. *Pseudomyrmex* and most species of *Azteca* exhibited aggressive behavior. Timid ants were usually more active near dawn or dusk, and only one or two workers were visible at any time patrolling the surface of the leaves and/or petioles; on some occasions, however, there were none. It took a high level of disturbance for workers to emerge from domatia, and only four to six would emerge at any given time. Aggressive ants were active throughout the day and night, but often more active at dusk and dawn. Groups as large as ten workers (but as few as one, rarely none), could be seen patrolling leaves and branches. Even a minor disturbance resulted in eight or more workers rapidly emerging from the domatia. Similar behavioral patterns have been found in other ant-plant systems (Letourneau 1983, McKey 1984, Jolivet 1996, Gaume *et al.* 1997, Irioka *et al.* 2000). Even though description of ant behavior as either timid or aggressive might be considered subjective and the extremes in a continuum of possible behaviors, the distinction in the field is clear and rarely subject to any doubts. This not only applies to ants inhabiting *Tococa*, but also to those of *Triplaris*, *Tachigali* (P. S. Ward, pers. comm.), and *Hirtella* (pers. obs.).

Aggressive ants inhabited plants in forest gaps, the forest-savanna ecotone, or in shrub lands, whereas timid ants inhabited plants in the forest

understory (Table 1). Aggressive ants were also found on river edges and in flooded or gallery forests. Although aggressive ants were occasionally found in the forest understory, no timid ants were ever found in plants of the open habitats (gaps or savanna). Therefore, populations of *T. guianensis* in different environments were found to host ants with different behaviors (and usually of a different genus), even when these populations were very close to each other (*i.e.*, < 500 m).

The most common herbivores found in the experimental plants were leaf-cutter ants (*Atta* sp.), various species of leaf beetles (Coleoptera: Chrysomelidae), and caterpillars of two different species of Noctuidae (Lepidoptera) and one species of Arctiidae (Lepidoptera). A few unidentified caterpillars and many species of Orthoptera were also found feeding on the leaves of *Tococa* but their frequency and numbers were so low that their effect on the overall herbivory rates was probably negligible. *Atta* ants were the main herbivores in all populations studied with the exception of *T. coronata*. *Tococa coronata* inhabits areas that are flooded at least five months of the year. The experiment was conducted during the rainy season, when only the top 1.0–2.5 m of the crowns on these small trees were above water, thus restricting access to *Atta*; however, one experimental plant was defoliated by *Atta* ants that gained access to it from a neighboring island in the forest via a fallen trunk. Otherwise, individuals of *T. coronata* were attacked mostly by chrysomelid beetles.

Frequent surveillance of the experimental plants revealed that most plants remained unharmed for up to a few weeks after the ant removal, but once “found” by potential herbivores, severe damage occurred in just a few hours. For example, in less than five hours, one *Atta* colony completely defoliated a 2.5 m *T. guianensis* shrub that had remained untouched during the previous 24 days. Some experimental plants therefore had very high herbivory rates, while others remained almost intact. This resulted in high variances for the amount of herbivory within any given species (Fig. 1).

Leaf-cutter ants were never observed defoliating the control plants, and both timid and aggressive ants actively defended their host plants from *Atta* scouts. Most of the damage to control plants was produced by chrysomelid beetles and the caterpillar of a pyralid moth (Pyralidae: Lepidoptera) that made a leaf cylinder prior to feeding. Vasconcelos (1991) found that in *M. guianensis*, the leaf cylinder produced by the pyralid moth *Acrospila gastralis* Guenée was ant-proof, which explains why

pyralid moths are very successful in grazing on ant-inhabited plants.

DISCUSSION

The exclusion experiments presented here clearly demonstrate that the ants protected plants against other herbivores in the three species of *Tococa* studied, regardless of ant species, behavior, or environment. In every population studied, there was a significant increase in herbivory when ants were removed. This effect was greater for plants growing in forest gaps and river edges than in the understory, and even larger for plants growing in open areas. This was most likely due to the distribution and feeding behavior of *Atta* ants, the main herbivore detected during this study, which are more common in disturbed and open areas than in the primary forest (Jaffe & Vilela 1989, Vasconcelos 1999). Even though the majority of the ant species that inhabit the domatia of *Tococa* are considerably smaller than *Atta*, all seemed to effectively protect the plant against the leaf-cutter ants. This was done not by the inhabiting ants fighting entire colonies of *Atta*, but rather by killing or warding off the few scouts that came across the plant. Vasconcelos and Casimiro (1997) have already shown that small *Azteca* ants effectively protect different species of *Cecropia* against the larger *Atta* ants.

There is ample evidence that mechanical damage to plant tissues can reduce future herbivory damage by inducing the production of insect deterrents or toxins (Karban & Myers 1989). Likewise, there is also evidence that mechanical damage can increase future damage by insects because some herbivores are attracted to substances produced by the plant after the damage has been inflicted or because herbivores recognize damaged leaves as palatable (for a complete review of the subject, see Karban & Baldwin 1997). Thus, it would have been beneficial to have another control group in which domatia were damaged but the ants not removed in order to determine if the damage alone could make the plants more susceptible to herbivory. Unfortunately, population sizes of the species studied were not large enough to establish three experimental groups; however, the wide variation in time between treatment (cutting of domatia) and first evidence of increased herbivory suggests that chemical substances and/or visual evidence of damage was neither deterring nor attracting potential herbivores. Ant-exclusion experiments performed in other myrmecophytes have removed the ants using different pesticides that are known to

have no effect on the physiology of the plant (Vasconcelos 1991, Itioka *et al.* 2000). This, however, was not an option in this study because the Canaima populations were within the Canaima National Park, and park regulations do not allow the use of these chemicals.

Most genera of ants found inhabiting *Tococa* during this study have been previously reported either from *Tococa* or from other myrmecophytic Melastomataceae (Beattie 1985; Davidson *et al.* 1989; Vasconcelos 1991, 1993; Davidson & McKey 1993; McKey & Davidson 1993). The exception was one plant occupied by an aggressive species of *Pseudomyrmex* in the *viduus* complex, specialist inhabitants of *Tachigali* (Fabaceae) and *Triplaris* (Polygonaceae; Ward 1999); however, the individual *T. coronata* inhabited by *Pseudomyrmex* was growing next to a *Tachigali* tree containing the same species, and probably the same colony, of ants.

In this study, ants with aggressive behavior were found to generally inhabit plants growing under higher herbivory pressure (*i.e.*, open areas and river edges). Conversely, timid ants typically inhabited plants under lower herbivory pressure (*i.e.*, forest understory). Vasconcelos and Davidson (2000), however, found the reverse pattern for ant populations in Central Amazonia. Itioka *et al.* (2000) working on *Macaranga* showed a relationship between ant aggressiveness and herbivory, while this study shows a three-way correlation with habitat as a third correlated variable. Causal relationships among these three variables are uncertain and in need of further investigation. Habitat could have a direct effect on ant behavior (independently of herbivory) if plants in different environments provide the ants with different food quality (Davidson 1997) or if habitat influences host selection by founding queens with different behaviors (Yu & Davidson 1997). Alternatively, herbivory could have a direct effect on ant behavior (independent of habitat) if the inhabiting ants see herbivores as predators (Davidson & McKey 1993) or if herbivory affects resources such as domatia (Davidson *et al.* 1989, Tennant 1994) and/or food quality (Davidson 1997).

In spite of the amount of herbivory inflicted on experimental plants, follow-up visits to both localities showed that most plants survived the experiment. Even plants that were completely defoliated produced new leaves that were recolonized by ants (*pers. obs.*). High herbivory rates may nevertheless have an important effect on the long-term fitness of the plants, as has been previously shown

for *M. guianensis* (Vasconcelos 1991). Even in the case of *T. macroserma* in which the differences in herbivory between control and experimental plants were the smallest, we cannot rule out the possibility of mutualism without first assessing the effect of low rates of herbivory on plant fitness. There may also be alternative benefits to plants, such as removal of fungal spores, algae, and epiphytes. The fact that in *Tococa* some ants seem to have an active role as anti-herbivore defense (this study), whereas others clean surrounding area of potential plant competitors (Morawetz *et al.* 1992, Renner & Ricklefs 1998), suggests that in the mutualistic association between ants and plants, the ants have evolved different roles in different habitats and/or plant species. Although there are still many open questions about the evolution and natural history of myrmecophytism in *Tococa*, this study not only shows that ants effectively defend their host plant against potential herbivores, but also that the level

of herbivory (and hence of protection conferred by inhabiting ants) differs across environments.

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LITERATURE CITED

- AGRAWAL, A. A., AND M. T. RUTTER. 1998. Dynamic anti-herbivore defense in ant-plants: The role of induced responses. *Oikos* 83: 227–236.
- BEATTIE, A. J. 1985. The evolutionary ecology of ant-plant mutualisms. Cambridge University Press, Cambridge, England.
- BENSON, W. W. 1985. Amazon ant-plants. In G. T. Prance and T. E. Lovejoy (Eds.). *Amazonia*, pp. 239–366. Pergamon Press, Oxford, England.
- BERRY, P. A., O. HUBER, AND B. K. HOLST. 1995. Floristic analysis and phytogeography. In P. A. Berry, B. K. Holst, and K. Yatskievich (Eds.). *Flora of the Venezuelan Guayana*. Volume 1: Introduction, pp. 161–192. Missouri Botanical Garden, St. Louis, Missouri.
- DAVIDSON, D. W. 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. *Biol. J. Linn. Soc.* 61: 153–181.
- , J. T. LONGINO, AND R. R. SNELLING. 1988. Pruning of host plant neighbors by ants: an experimental approach. *Ecology* 69: 801–808.
- , AND D. McKEY. 1993. The evolutionary ecology of symbiotic ant-plant relationships. *J. Hymenopt. Res.* 2: 13–83.
- , R. R. SNELLING, AND J. T. LONGINO. 1989. Competition among ants for myrmecophytes and the significance of plant trichomes. *Biotropica* 21: 64–73.
- DE LA FUENTE, M. A. S., AND R. J. MARQUIS. 1999. The role of ant-tended extrafloral nectaries in the protection and benefit of a Neotropical rainforest tree. *Oecologia* 118: 191–202.
- FIALA, B., H. GRUNSKY, U. MASCHWITZ, AND K. E. LINSSENMAIR. 1994. Diversity of ant-plant interactions: Protective efficacy in *Macaranga* species with different degrees of ant association. *Oecologia* 97: 186–192.
- , A. JAKOB, U. MASCHWITZ, AND K. E. LINSSENMAIR. 1999. Diversity, evolutionary specialization and geographic distribution of a mutualistic ant-plant complex: *Macaranga* and *Crematogaster* in South East Asia. *Biol. J. Linn. Soc.* 66: 305–331.
- , U. MASCHWITZ, T. Y. PONG, AND A. J. HELBIG. 1989. Studies of a South East Asian ant-plant association. Protection of *Macaranga* trees by *Crematogaster borneensis*. *Oecologia* 79: 463–470.
- GAUME, L., AND D. McKEY. 1999. An ant-plant mutualism and its host-specific parasite: Activity rhythms, young leaf patrolling, and effects on herbivores of two specialist plant-ants inhabiting the same myrmecophyte. *Oikos* 84: 130–144.
- , AND M. C. ANSTETT. 1997. Benefits conferred by “timid” ants: Active anti-herbivore protection of the rainforest tree *Leonardoxa africana* by the minute ant *Petalomyrmex phylax*. *Oecologia* 112: 209–216.
- HUBER, O. 1986. Vegetation of the Caroni River basin. *Interciencia* 11: 301–310, 351.
- . 1995a. Geographical and physical features. In P. A. Berry, B. K. Holst, and K. Yatskievich (Eds.). *Flora of the Venezuelan Guayana*. Volume 1: Introduction, pp. 1–62. Missouri Botanical Garden, St. Louis, Missouri.
- . 1995b. Vegetation. In P. A. Berry, B. K. Holst, and K. Yatskievich (Eds.). *Flora of the Venezuelan Guayana*. Volume 1: Introduction, pp. 97–160. Missouri Botanical Garden, St. Louis, Missouri.

- HUXLEY, C. 1986. Evolution of benevolent ant-plant relationships. In B. Juniper and T. R. E. Southwood (Eds.). *Insects and the plant surface*, pp. 257–282. Edward Arnold, London, England.
- ITIOKA, T., M. NOMURA, Y. INUI, T. ITINO, AND T. INOUE. 2000. Difference in intensity of ant defense among three species of *Macaranga* myrmecophytes in a Southeast Asian dipterocarp forest. *Biotropica* 32: 318–326.
- JAFFE, K., AND E. VILELA. 1989. On nest densities of the leaf-cutting ant *Atta cephalotes* in tropical primary forest. *Biotropica* 21: 234–236.
- JANZEN, D. H. 1966. Coevolution of mutualism between ants and acacias in Central America. *Evolution* 20: 249–275.
- . 1967. Interaction of the bull's horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. *Univ. Kans. Sci. Bull.* 47: 315–558.
- . 1969. Allelopathy by myrmecophytes. The ant *Azteca* as an allelopathic agent of *Cecropia*. *Ecology* 50: 147–153.
- JOLIVET, P. 1996. *Ants and plants*. Backhuys Publishers, Leiden, The Netherlands.
- KARBAN, R., AND I. T. BALDWIN. 1997. *Induced responses to herbivory*. University of Chicago Press, Chicago, Illinois.
- , AND J. H. MYERS. 1989. Induced plant responses to herbivory. *Annu. Rev. Ecol. Syst.* 20: 331–348.
- LETOURNEAU, D. K. 1983. Passive-aggression: an alternative hypothesis for the *Piper-Pheidole* association. *Oecologia* 60: 122–126.
- . 1998. Ants, stem-borers, and fungal pathogens: experimental tests of a fitness advantage in *Piper* ant-plants. *Ecology* 79: 593–603.
- McKEY, D. 1984. Interaction of the ant-plant *Leonardoxa africana* (Caesalpiniaceae) with its obligate inhabitants in a rain forest in Cameroon. *Biotropica* 16: 81–99.
- , AND D. W. DAVIDSON. 1993. Ant-plant symbioses in Africa and the Neotropics: History, biogeography and diversity. In P. Goldblatt (Ed.). *Biological relationships between Africa and South America*, pp. 568–606. Yale University Press, New Haven, Connecticut.
- MELIN, D. 1930. Contributions to the study of the theory of selection I. *Zool. Bidrag Uppsala* 13: 87–104.
- MICHELANGELO, F. A. 2000a. A cladistic analysis of the genus *Tococa* (Melastomataceae) based on morphological data. *Syst. Bot.* 25: 211–234.
- . 2000b. Evolution, systematics and ecology of the myrmecophytic genus *Tococa* (Melastomataceae). Ph.D. dissertation. Cornell University, Ithaca, New York.
- . A monograph of *Tococa* Aublet (Melastomataceae). *Flora Neotrop. Monogr.* In press.
- MORAWETZ, W., M. HENZL, AND B. WALLNOFER. 1992. Tree killing by herbicide producing ants for the establishment of pure *Tococa occidentalis* populations in the Peruvian Amazon. *Biodiv. Conserv.* 1: 19–33.
- PRANCE, G. T. 1982. Chrysoballanaceae. In Z. Lucas-de-Febres (Ed.). *Flora de Venezuela*. Vol. IV, pp. 325–487. Instituto Botanico, Caracas, Venezuela.
- RAMIREZ, N., C. GIL, M. LOPEZ, O. HOKCHE, AND Y. BRITO. 1988. Floristic and structural characterization of a shrubland community in the Venezuelan Guayana highland Gran Sabana State of Bolivar. *Acta Cient. Venez.* 39: 457–469.
- RENNER, S. S., AND R. E. RICKLEFS. 1998. Herbicidal activity of domatia-inhabiting ants in patches of *Tococa guianensis* and *Clidemia heterophylla*. *Biotropica* 30: 324–327.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. W. H. Freeman and Company, New York, New York.
- SPRUCE, R. 1908. Notes of a botanist on the Amazon and the Andes during the years 1849–1864. A. R. Wallace Edit. MacMillan, London, England.
- SVOMA, E., AND W. MORAWETZ. 1992. Glandular trichomes, emergences and leaf domatia of the myrmecophyte *Tococa occidentalis* (Melastomataceae). *Bot. Jahr. Syst. Pflanzenges. Pflanzengeogr.* 114: 185–200.
- TENNANT, L. E. 1994. Ecology of a facultative ant-plant “mutualism”. Ph.D. dissertation. Harvard University, Cambridge, Massachusetts.
- TRESEDER, K. K., D. W. DAVIDSON, AND J. R. EHRLINGER. 1995. Absorption of ant-provided carbon dioxide and nitrogen by a tropical epiphyte. *Nature* 375: 137–139.
- VASCONCELOS, H. L. 1991. Mutualism between *Maieta guianensis* Aubl. a myrmecophytic Melastome and one of its ant inhabitants. Ant protection against insect herbivores. *Oecologia* 87: 295–298.
- . 1993. Ant colonization of *Maieta guianensis* seedlings, an Amazon ant-plant. *Oecologia* 95: 439–443.
- . 1999. Levels of leaf herbivory in Amazonian trees from different stages in forest regeneration. *Acta Amazon.* 29: 615–623.
- , AND A. B. CASIMIRO. 1997. Influence of *Azteca alfari* ants on the exploitation of *Cecropia* trees by a leaf-cutting ant. *Biotropica* 29: 84–92.
- , AND D. W. DAVIDSON. 2000. Relationship between plant size and ant associates in two Amazonian ant-plants. *Biotropica* 32: 100–111.
- WARD, P. S. 1999. Systematics, biogeography and host plant associations of the *Pseudomyrmex viduus* group (Hymenoptera: Formicidae) *Triplaris* and *Tachigala*-inhabiting ants. *Zool. J. Linn. Soc.* 126: 451–540.
- WURDACK, J. J. 1973. Melastomataceae. In T. Lasser (Ed.). *Flora de Venezuela*. Vol. VIII, pp. 1–819. Instituto Botanico, Caracas, Venezuela.
- YU, D. W., AND D. W. DAVIDSON. 1997. Experimental studies of species-specificity in *Cecropia*-ant relationships. *Ecol. Monogr.* 67: 273–294.