

Ants Nesting on *Cecropia purpurascens* (Cecropiaceae) in Central Amazonia: Influence of Tree Height, Domatia Volume and Food Bodies

by

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ABSTRACT

Patterns of presence of ant colonies on *Cecropia purpurascens* CC Berg (Cecropiaceae) were investigated in central Amazonia. All individuals of *C. purpurascens* along a 14.3 km transect were searched for ants and their height, internode volume, and number of trichilia were recorded. Of the 50 *C. purpurascens* individuals studied, 32 (64%) were colonized by ants of four species: *Azteca alfari* Emery (Dolichoderinae) (N = 16), *Camponotus balzani* Emery (Formicinae) (N = 14), *C. abdominalis* (Fabricius) (Formicinae) (N = 1) and *Crematogaster brasiliensis* Mayr (Myrmicinae) (N = 1). Probability of *C. purpurascens* being colonized by ants increases with tree height, internode volume, and trichilium number. Of the three variables recorded, tree height was the most important in determining the presence of ants. Trees colonized by the two most common ant species (*A. alfari* and *C. balzani*) did not differ in height, internode volume, or number of trichilia. The patterns observed, the association between the identity of the ants and plant fitness, as well as the usefulness of this particular system for future studies are discussed.

Keywords: Ant-plant interaction, ants, *Azteca alfari*, *Camponotus balzani*, *Cecropia purpurascens*, Central Amazonia, mutualism.

INTRODUCTION

Ants are social insects whose colonies may occupy a large number of nest sites, ranging from terrestrial to arboreal (Hölldobler & Wilson 1990). In the tropics, a large number of ant species nest on vegetation though the use of natural hollows and plant crevices, roots of epiphytes, carton nests or domatia (Davidson 1997, Dejean *et al.* 2001, Hölldobler

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& Wilson 1990, Wilson 1987). Domatia are plant structures that serve no evident purpose other than to shelter ant colonies (*cf.* Beattie 1985). These structures are extremely common in a variety of plant taxa that, besides hosting the ant colony, can also produce food bodies to feed them (Beattie 1985, Janzen 1966 & 1969). The counterpart of this mutualistic system is provided by the ants while foraging on the plant (Janzen 1966, Schupp 1986). Ants protect the leaves against herbivores and kill vine ends that begin to climb on the plant trunks (Janzen 1969, Rocha & Bergallo 1992, Schupp 1986). In addition to protection, ant colonies may provide nutrients to the plant (Sagers *et al.* 2000). These symbiotic ant-plant relationships are likely to be the product of selection based on complex networks of direct and indirect interactions (Davidson & Fisher 1991). Therefore, studies focused on natural history are fundamental to understanding the basic requirements of these relationships, as well as elucidating the phenomena driving evolutionary specializations in ant-plant associations (Davidson *et al.* 1991, Davidson & Fisher 1991).

Cecropia Loefl. species (Cecropiaceae) are conspicuous plants in disturbed landscapes in the neotropics (Brokaw 1998). These plants are commonly associated with ants and, in general, there is a suite of characters that relate *Cecropia* species to ant association, or myrmecophytism (Longino 1989). First, these plants provide domatia as a shelter to the ants. These structures are constituted by hollow stems divided into a series of closed chambers by a septum (Yu & Davidson 1997). Secondly, each internode has a preformed thin spot, the prostoma, where founding queens can enter stems (Yu & Davidson 1997). Thirdly, *Cecropia* species produce two types of food bodies, Müllerian bodies (MB) and Pearl bodies (PB), both harvested by worker ants (Davidson *et al.* 1991). Müllerian bodies are rich in lipids, carbohydrates, proteins and amino acids, and are produced by specialized pads of tissue, known as trichilia, at the bases of leaf petioles (Rickson 1976). Pearl bodies are rich in lipids (O'Dowd 1980) and are produced on the abaxial surface of new leaves.

Myrmecophytic *Cecropia* has long been thought to form associations only with *Azteca* ants (Davidson *et al.* 1991). However, species of other genera, such as *Camponotus*, *Crematogaster*, and *Pachycondyla*, also nest on the domatia (Harada & Benson 1988, Yu & Davidson 1997). Such *Cecropia*-ant associations differ in ways that may affect host-plant fitness, but such relationships are poorly understood (Davidson *et al.* 1991). The distribution patterns of *Cecropia* that are colonized by ants vary with habitat and host species, and are largely explained by events during host colonization by ants (Yu & Davidson 1997). At this

initial stage, different foundresses of *Cecropia* ants may colonize different internodes of the same saplings, although, a single colony usually dominates the entire tree, eventually removing the other colonies (Longino 1989). Mortality from factors other than competition may also affect successful colonization in *Cecropia* plants, since internodes often contain dead queens as evidence of failures in colonization (Longino 1991, Yu & Davidson 1997). These failures occur in sealed internodes, and are therefore not the result of interactions with other colonies (Longino 1991). At some point during sapling growth, colonies begin to survive, producing workers that reopen the prostoma and start gathering Müllerian bodies from trichilia (Longino 1991).

This study is essentially a survey of ant species presence with respect to plant characteristics. Specifically, our aim was to investigate tree characteristics affecting the presence of ants on *Cecropia purpurascens* in central Amazonia, the assemblage of nesting ants and possible differences in the characteristics of trees colonized by distinct species. The following questions were addressed: (i) which ant species are associated with the plant; (ii) whether presence of nesting ants was related to tree height, domatia volume and number of trichilia; and (iii) whether different ant species nested on trees which differed in height, domatia volume and trichilium number?

MATERIAL AND METHODS

Fieldwork was done in the Reserva do km 41 (54°50'W, 02°25'S), a continuous forest belonging to the Projeto de Dinâmica Biológica de Fragmentos Florestais (PDBFF-INPA), situated about 80 km north of Manaus, Amazonas State, north Brazil. The climate of the area is warm, with a rainy season between November and May, and a dry season between June and October. The mean precipitation is 2200 mm per year, and the mean temperature is 26.7°C (Lovejoy & Bierregaard 1990).

Data were collected in August 2000, during the dry season. In a 14.3 km transect, all *Cecropia purpurascens* trees less than 4 m tall were searched for ants by opening the entire stem (trees were at least 3 meters away from each other). When an ant colony was found in the stem, some workers were collected for identification. The height (from ground to the apical meristem), the number of trichilia, and the diameter and height of the last internode (to calculate domatia volume) were recorded for all trees.

The probability of a plant being colonized by ants as a function of its height, trichilium number and domatia volume was analyzed with a logistic regression model (Hosmer & Lemeshow 1989). The tree height,

trichilium number and domatia volume of trees colonized by the two most common ant species were compared by Mann-Whitney U tests.

RESULTS

Of the 50 individuals of *C. purpurascens* found in the transect, 32 (64%) were colonized by ants. Four species were observed nesting on *C. purpurascens* (Table 1). The probability of *C. purpurascens* being occupied by ants increased with the tree height: trees higher than 2.5 m were more likely to be occupied (Fig. 1a, Table 2). The probability of *C. purpurascens* being occupied by ants also increased with the trichilium number (Fig. 1b, Table 2). Ants occupied only plants with more than three trichilia and plants with more than 10 trichilia had the highest probability of being occupied. Finally, the probability of having an ant colony also increased with the domatia volume: *C. purpurascens* trees with an apical domatia volume larger than 15 cm³ were more likely to be occupied (Fig. 1c, Table 2). The larger odds ratio for tree height than for the other two variables (trichilium number and domatia volume) in the logistic regression model indicated that tree height was the most important variable to determine the presence of ants (Table 2).

The two most common ant species used trees with the same morphological characteristics. The median height of trees occupied by *Azteca alfari* (2.14 m, N = 16) was not significantly different from the median height of trees occupied by *Camponotus balzani* (1.96 m, N = 14) (Mann-Whitney U = 126.0; $p > 0.50$, Fig. 2a). The median number of trichilia on trees occupied by *A. alfari* (8.0 trichilia, N = 16) was not

Table 1. Number of *Cecropia purpurascens* trees colonized by each ant species in , central Amazonia, Brazil.

Ant species (subfamily)	Number of trees (% of trees)
<i>Azteca alfari</i> (Dolichoderinae)	16 (50%)
<i>Camponotus balzani</i> (Formicinae)	14 (44%)
<i>Camponotus abdominalis</i> (Formicinae)	1 (3%)
<i>Crematogaster brasiliensis</i> (Myrmicinae)	1 (3%)

Table 2. Values for the logistic regression model for three morphological variables related to the colonization of *Cecropia purpurascens* by ants in central Amazonia, Brazil. $n = 50$ trees. G = log-likelihood ratio chi-square, $n(p/n)$ = number of plants (positive response/negative response). The largest odds ratios is in bold.

Variable	Constant	Parameter	G	$n(p/n)$	P	Odds Ratio
Tree height	-2.723	2.167	22.510	50 (32/18)	<0.001	8.733
Domatia volume	-0.731	0.212	16.459	50 (32/18)	<0.001	1.236
Trichilium number	-3.183	0.538	14.841	50 (32/18)	<0.001	1.712

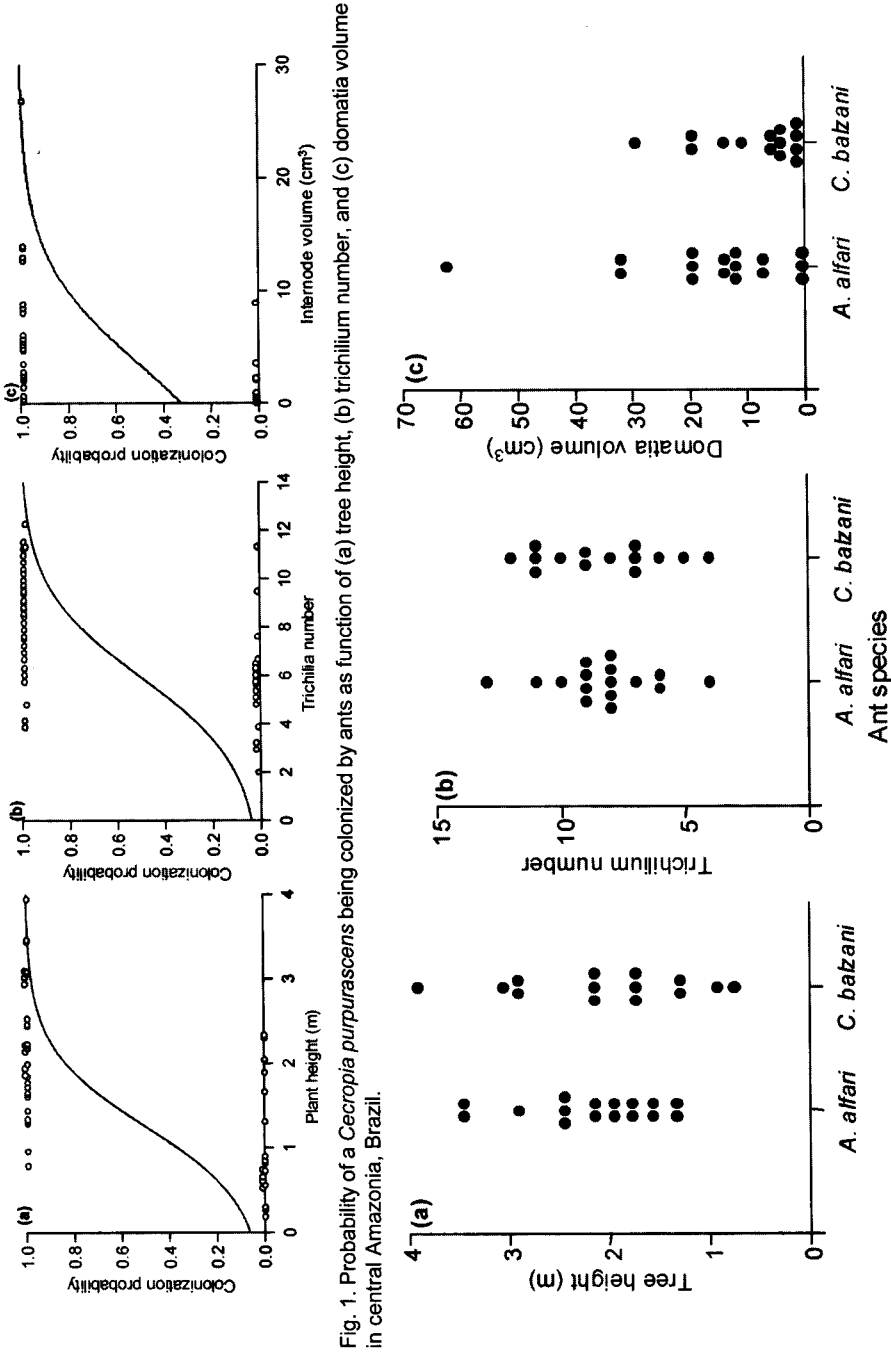


Fig. 1. Probability of a *Cecropia purpurascens* being colonized by ants as function of (a) tree height, (b) trichilium number, and (c) domatia volume in central Amazonia, Brazil.

Fig. 2. Tree height, trichilium number, and domatia volume of *Cecropia purpurascens* colonized by *Azteca alfari* or *Camponotus balzani* in central Amazonia, Brazil.

significantly different from that of trees occupied by *C. balzani* (8.5 trichilia, $N = 14$) (Mann-Whitney $U = 109.5$, $p > 0.90$, Fig. 2b). The median apical domatia volume of trees occupied by *A. alfari* (12.4 cm³, $N = 16$) was not significantly different from the median apical internode volume of trees occupied by *C. balzani* (5.5 cm³, $N = 14$) (Mann-Whitney $U = 150.0$, $p > 0.10$, Fig. 2c).

DISCUSSION

The diversity of ant-plant interactions mediated by domatia and food bodies is lower than in other systems, such as plants that provide only extra-floral nectar to ants (Cogni & Freitas 2002, Koptur 1992, McKey *et al.* 2001). However, even among domatia-mediated associations, interactions involving only one species are rare (Bronstein 1994, Davidson *et al.* 1991). In the present study, four ant species were recorded nesting on *Cecropia purpurascens* domatia. Ants of the genera *Azteca*, *Crematogaster* and *Camponotus* are the frequent *Cecropia* inhabitants at different sites (Longino 1991). In the same area, Fonseca (1995) recorded four ant species nesting on *C. purpurascens* (*Azteca* sp.1, *Azteca* sp.2, *A. alfari*, and *Camponotus* sp.1). These data combined with ours, show that *C. purpurascens* in central Amazonia can be colonized by at least six ant species from three subfamilies. This multiple association in the ant-*Cecropia* system probably arose via repeated *de novo* colonizations or lineage switching over time, rather than through co-cladogenesis of two interacting lineages (Davidson & McKey 1993). The presence of ants from different subfamilies corroborates the idea of repeated colonization of *Cecropia* by unrelated specialized and nonspecialized ant lineages (Davidson & McKey 1993). Additionally, the number of species involved in this multiple association may vary according to the geographic scale analyzed (Thompson 1997 & 1999).

The probability of a plant being occupied by ants was related to tree height, domatia volume, and trichilium number. The occupation of higher trees with larger domatia and numerous trichilia is to be expected, since there is a trade-off between growth and the acquisition of myrmecophytic traits in *Cecropia* plants (Folgarait & Davidson 1994). Thus, the myrmecophytic traits of *C. purpurascens* appear only in later stages of sapling development, when *Cecropia* plants are taller and the critical developmental period for establishment has declined (Davidson & Fisher 1991, Folgarait & Davidson 1994). Before ant colonization, *Cecropia* plants apparently use chemical protection against herbivores (Coley 1986). The existence of mechanisms whereby the ants choose plants at the early stages of colonization is very likely and

should be investigated in further studies since foundresses of plants with appropriate characteristics may have a greater chance of successful colony establishment.

The two most common ant species (*A. alfari* and *C. balzani*) were present in a similar frequency in trees with the same characteristics. This fact and the hostility observed between *Cecropia*-ants (Davidson *et al.* 1991), suggest that intraspecific and interspecific competition for nesting sites may occur among these two ant species. Combat regularly ensued between callow workers of different colonies when plant stems were opened and incipient colonies came into contact. The first species to colonize a tree and to produce a large number of workers remain in the plant, and workers from established colonies also attacked introduced queens (Davidson *et al.* 1991). The coexistence of these two species in this ant-plant system promise future studies focused on competition-colonization and dispersal-fecundity trade-offs across patch heterogeneity (Yu & Wilson 2001, Yu *et al.* 2001).

The identity of the ant species may be very important to the plant, since specialized *Cecropia*-ants differ in ways that may affect host-plant fitness (Davidson *et al.* 1991). For example, colonies of *Azteca* species provide more protection against *Cecropia* herbivores since they have a large number of small, aggressive workers that are active both diurnally and nocturnally (Davidson *et al.* 1991). *Azteca* ants also respond to damage on *Cecropia* leaves by increasing the number of workers after damage, a mechanism that rapidly and effectively repels herbivores (Agrawal 1998). Besides preventing high herbivory rates, *Azteca* ants attack and kill vines impinging on their host *Cecropia* plants (Janzen 1969). In contrast, *C. balzani* workers forage mainly at night, and colonies of this species consist of relatively small numbers of large workers that are extremely timid and seldom venture away from the trichilia to patrol leaves (Davidson *et al.* 1991). Additionally, *C. balzani* does not prune vegetation around its host, and tends coccids within host-plant stems (Davidson *et al.* 1991). The behavioral differences between these ant species, their ability to defend the plant and their influence on plant fitness are also promising topics for future study.

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