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Author(s): Carlos Roberto Fonseca

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Herbivory and the long-lived leaves of an Amazonian ant-tree

CARLOS ROBERTO FONSECA*

Departamento de Zoologia, CP.6109, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil, CEP.13081–970

Summary

1 *Tachigali myrmecophila* (Caesalpinaceae) is an Amazonian myrmecophytic canopy tree. The saplings are shade-tolerant, surviving in a suppressed state for several years in the rainforest understorey, the hollow leaf rachis and petiole being inhabited by the stinging ant *Pseudomyrmex concolor* (Pseudomyrmecinae). An experiment was designed (a) to evaluate the role of insect herbivory in the mutualism between *T. myrmecophila* and *P. concolor* and (b) to test a falsifiable hypothesis proposed by a current trade-off model of chemical and ant defences which predicts that myrmecophytic traits should be limited to plants with leaves of low longevity.

2 Plants from which the ants were experimentally removed had 4.3 times more herbivorous insects than plants with ants. All recorded orders of insects were attacked similarly by the ants. Rates of herbivory were: (a) ten times higher on experimental plants lacking ants, (b) about three times higher on immature than mature leaves, (c) about two and a half times higher in the wet than the dry season. After 18 months, the experimental plants presented an accumulated level of leaf herbivory which was about twice as high as for the plants with ants.

3 Observations on the phenology of control, experimental, and naturally unoccupied plants revealed that the leaf longevity of plants with active ant colonies was unexpectedly high for rainforest (81 months), and about 1.8 and 2.6 times as high as the experimental (45 months) and the naturally unoccupied (31 months) plants, respectively. The high leaf longevity of the myrmecophytic *T. myrmecophila* does not support the current trade-off model of chemical and ant defences. The rate of apical growth was 1.6 times higher for plants with ants than plants from the experimental group. The slow growth rate of *T. myrmecophila*, about 14 cm year⁻¹, is compatible with the resource availability hypothesis.

4 Phenological differences between experimental and naturally unoccupied plants suggest that descriptive-correlative studies would not always give a true picture and that the actual paradigm of ant–plant interactions, derived in part from this approach, should be carefully revised.

5 The results corroborate the hypothesis that the interaction between *Tachigali myrmecophila* and *Pseudomyrmex concolor* is mutualistic, and suggest that attack by phytophagous insects is the prime factor in the evolution of the myrmecophytism.

Keywords: ant-plant, defence, mutualism, myrmecophyte, *Tachigali*

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Introduction

Towards the end of the 19th century, the eminent naturalist Thomas Belt (1874), on observing the

behaviour of some aggressive ants on swollen-thorn acacias during his travels in Central America, formulated the hypothesis of mutualism between ants and myrmecophytes. Since then, associations between ants and myrmecophytes, i.e. myrmecodomatia-bearing plants, have been described for about 250 plant species, from 19 families, and up to 180 ant species, from five subfamilies, in the neotropical region (Wheeler 1942; Benson 1985).

*Present Address: Animal Behaviour Research Group, Department of Zoology, South Parks Road, Oxford OX1 3PS, United Kingdom. Tel. 0865 271214. Fax 0865 310447. E-Mail FONSECA@VAX.OX.AC.UK.

Of the selective forces which have been suggested for the evolution of myrmecophytism in tree species, the impact of herbivory is the most widely accepted (Beattie 1985). In non-myrmecophytes, herbivory almost always decreases the fitness of plants (Bentley, Whittaker & Malloch 1980; Louda 1982; Marquis 1984; but see Maschinski & Whitham 1989), can change the results of competitive interactions (Bentley & Whittaker 1979) and modify the process of plant succession (Brown *et al.* 1987). Leaf herbivory not only decreases the photosynthetically active area, but can also induce leaf abscission (Stiling & Simberloff 1989; but see Williams & Whitham 1986), and facilitate fungal and pathogen infection (Thresh 1981).

Generalizations about the role of herbivory in ant-plant systems are not yet possible because, in addition to the lack of experimental studies, most of the widely studied ant-plants (e.g. *Acacia*, *Cecropia*, *Macaranga*) typically occur in open habitats, while most neotropical ant-plants inhabit primary forest (Benson 1985). Furthermore, all widely studied myrmecophytes produce food-bodies (e.g. Beltian bodies, Müllerian bodies and pearl bodies) but most neotropical myrmecophytes do not directly offer any nutritional benefits to the ants (Benson 1985). Also, in ant-epiphyte systems the supply of nutrients by ants (myrmecotrophy) appears to be an important evolutionary path towards developing myrmecophytic traits (Janzen 1974; Huxley 1978; Rickson 1979), but for terrestrial plants the importance of this route remains uncertain (Risch *et al.* 1977; Letourneau 1983).

Ants are social, territorial and predatory omnivorous insects with a high potential for acting as a biological defence against herbivores. In this sense, myrmecophytism and secondary compounds are alternative defence strategies which reduce the availability of the plant as a food resource to herbivores (Janzen 1967). McKey's (1984) graphic model was the first theoretical framework for understanding the trade-off between chemical and ant defence strategies in myrmecophytes. He argues that ant colonies, due to their high maintenance cost, represent a higher long term cost to plants in relation to quantitative defences (e.g. lignin, *sensu* Feeny 1976). He pointed out that ants are mobiles and they can be relocated to young leaves from old leaves during the process of leaf abscission, thus having a similar behaviour to that of qualitative defences (*sensu* Feeny 1976). The main prediction of McKey's (1984) model is that plant species presenting high leaf longevity should invest in chemical compounds such as tannins and lignins, while ant-defence mechanisms should be restricted to plant species with short-lived leaves.

Tachigali myrmecophila Ducke (Caesalpinaceae) is a myrmecophytic canopy tree of the Amazonian rainforest. Like *Tachigali versicolor* (Foster 1977), it is monocarpic, reproducing only once just before dying (C. R. Fonseca, unpublished data). *Tachigali*

myrmecophila trees are used as nesting and feeding sites by two *Pseudomyrmex* and six *Azteca* sympatric ant species which are involved in a successional process during the ontogenetic development of the host plant in the Central Amazon (Fonseca 1991). The domatia space offered by the host limits the colony size of the stinging ant *Pseudomyrmex concolor* F. Smith (Pseudomyrmecinae), the most common partner of *T. myrmecophila* understorey plants (Fonseca 1991, 1993). This system is suitable for testing the generality of the mutualistic hypothesis because *Tachigali* is a primary forest inhabitant and it does not offer, directly, a food resource to its ants. The main objectives of this study are (1) to test the role of ants as an anti-herbivory defence mechanism in order to assess the hypothesis of mutualism between the partners proposed by Belt (1874), (2) to test the trade-off model on defence hypothesized by McKey (1984), and (3) to compare descriptive-correlative and experimental approaches to elucidation of ant-plant interactions.

Material and methods

STUDY AREA

Field observations were carried out in the continuous 1000-ha reserve *Cabo Frio* of *Terra Firme* forest (*sensu* Pires & Prance 1985) about 100 km north of Manaus, Amazonas, Brazil (2°24'S, 59°52'W). The regional climate is classified as Wet Tropical (Holdridge 1967), the average annual temperature is 26 °C, and the average annual rainfall for 30 years is 2186 mm. In 1989 the study site received 2693 mm of rainfall. The relief is formed by plateaux at an altitude of 80–140 m, with a clay-sandy soil characteristically deep, acid and well drained which can be classified as xanthic ferralsol. The area is near no major river, and the soil is generally poor in nutrients due to prolonged leaching (Sombroek 1966). The vegetation has a variable canopy about 30–40 m in height. Burseraceae, Sapotaceae, Fabaceae and Lecythidaceae are the most frequent tree families (Lovejoy & Bierregaard 1991).

LIFE HISTORY

The hollow rachis of the compound leaves of small understorey *Tachigali myrmecophila* plants are almost always colonized by the highly aggressive *Pseudomyrmex concolor*. The colonization process starts with a solitary fertilized queen of *P. concolor* flying through the understorey looking for unoccupied domatia where a colony could be founded. The queen cuts out a small entrance in an unvascularized area near the mid point of the petiole, removes some of the internal parenchyma and closes the entrance. After about four months, the first workers emerge and begin an incipient patrol activity. Each host plant maintains normally only one mature ant colony. Because the plants

are scattered throughout the forest, one colony is always restricted to a single host. In mature colonies, workers have a 24-hour patrol activity attacking all animals that cause any disturbance to the plant, including insects and mammals.

Pseudomyrmex concolor does not receive any food resource directly from *Tachigali myrmecophila*, nor do the ants feed on the insects captured on the plant surface. Indeed, *P. concolor* is highly specialised to prey on a colony of coccids kept inside the domatia (Wheeler 1921). The coccids *Catenococcus* sp. produce honeydew which is used by the ants as the main energy source. Because *Catenococcus* sp. feeds on the phloem contents of the host, apparently all the nutrient and energy requirements of *P. concolor* comes indirectly from *T. myrmecophila*.

THE EXPERIMENT

In September 1988, fifty young plants (0.5–2.5 m high) of *Tachigali myrmecophila* occupied by colonies of *Pseudomyrmex concolor* were located in the *Cabo Frio* reserve. Environmental criteria were not used in the selection, so the plants experienced a wide range of light conditions. The plants were paired according to the similarity of their number of leaves and leaflets. Individuals from each pair were randomly assigned to the control (C) or experimental (E) group. The groups presented similar mean height (C, 1.52 m; E, 1.63 m), and number of leaves (C, 7.28; E, 7.32) and leaflets (C, 39.96; E, 41.32). The experiment was carried out from August 1988 to January 1990. At the beginning of the experiment, ant colonies of the experimental group were removed by introducing 1 mL of an aqueous solution of a synthetic pyrethroid (Deltamethrin, 25 g/L) into each domatium through the ant-made entrance hole. I was unable to detect any collateral effect caused by the insecticide on the plants. Ten months after the beginning of the experiment, 11 experimental plants had incipient colonies, so the solution was applied again. During the experiment five plants were damaged by external factors, leaving 22 control and 23 experimental plants.

Herbivores were censused every two months from September 1988 to January 1990. The insects were identified to the order level in the field, and whenever possible a voucher specimen was collected for further identification. Number of herbivores in control and experimental groups were compared by a *G*-test with replications, considering the plants as sampling units and the censuses as replicates. The temporal heterogeneity between censuses was assessed through the additive properties of the *G* distribution (Sokal & Rohlf 1981). Based on the mutualistic hypothesis more herbivores were expected on the experimental plants. The herbivores were compared by order, using a *G*-test, to verify whether the taxa were affected in a similar manner.

Rates of herbivory on 10 control and 10 exper-

imental plants were estimated from December 1988 to February 1989, the beginning of the wet season, and from June to August 1989, the beginning of the dry season. Six mature leaflets were chosen randomly on each plant, and when a young leaf was available, all young leaflets (4–8) were used. The rate of herbivory (*H*) was estimated for each leaflet, during 60–62 days, using the total leaflet area (*L*) and the eaten area (*E*) at the initial time (*i*) and final time (*f*), *T* being the number of days between estimates. The rate of herbivory of a leaflet is the mean daily herbivory expressed as percentage of its total area according to the expression:

$$H = [(Ef/Lf - Ei/Li) \times 100]/T.$$

The total leaflet area was estimated by the product of the length (*l*) and the width (*w*), using the regression $L = 4.261 + 0.657lw$ ($r^2 = 0.975$, $P < 0.001$). This regression was calculated from 31 leaflets collected from 10 plants, their area being estimated by a Delta T Area Meter (Delta T Devices, Burwell, Cambridge, United Kingdom) with 1 cm² precision. The eaten area was estimated with the aid of a 5-mm × 5-mm grid, each point being multiplied by 0.25 cm². For expanding leaflets it was assumed that the growth rate was the same for the leaflet and the eaten areas (Reichle *et al.* 1973). Differences in rates of herbivory between groups (control and experimental), seasons (wet and dry) and leaf maturity levels (young and mature) were tested by a three-way factorial ANOVA (2 × 2 × 2), considering the plants as replicates. Rates of herbivory per plant were contrasted after the transformation $\text{Ln}(1 + 1000H)$ to homogenize the variance.

An estimate of damage was made bimonthly for each leaflet of both control and experimental plants. At least 2300 estimates were made bimonthly. Leaflet damage was estimated according to the following classes: (0) intact leaflet, (1) 1–25% of damage, (2) 26–50%, (3) 51–75%, (4) 76–99% and (5) leaflet absent. The cumulative level of herbivory per plant was calculated as the mean of the estimated damage for all leaflets on leaves present since September 1988. The same analysis was performed on leaves which had appeared before the beginning of the experiment (termed bottom leaves) and after this time (top leaves). While bottom leaves were already mature when the ants were removed, top leaves emerged and developed in the absence of patrolling ants. Variation in the level of herbivory of a plant during 18 months of experiment was the variable employed for the comparison between groups. A paired *t*-test, with one tail, was applied to test the null hypothesis that the increase in the herbivory level was the same in both groups. Under the alternative hypothesis the experimental group would demonstrate a greater increase in the level of herbivory.

The apical length of each plant, defined as the distance between the apex at a given time and a

marked leaf, which had the second apical position in September 1988, was measured bimonthly to the nearest 1 cm. The regression coefficient β of the plot between apical length and time (months) was used to compare the apical growth between the control and experimental groups. As the distribution of β was not normal, the values were transformed by $\ln(1 + \beta)$. Before analysis, the apical growth rate was controlled for initial plant height. A *t*-test, with one-tail, was used to test the null hypothesis that both groups had the same apical growth; under the alternative hypothesis the experimental group would produce a lower rate of apical growth.

The number of vines naturally growing in contact with the experimental and control plants of *Tachigali myrmecophila* was also recorded bimonthly.

NATURAL LEAF PHENOLOGY

The natural leaf phenology of *Tachigali myrmecophila* was recorded over 18 months, beginning in August 1988, for 17 naturally unoccupied plants between 0.5 and 2.5 m high. The production and loss of leaves were recorded. Leaf fall and production on these plants was compared with the plants from the control and the experimental groups. The leaf longevity (L) of each plant was estimated according to the following population model (Begon & Mortimer 1986),

$$L = \{[(Nti + p)/f] - 1\}T,$$

Nti being the number of leaves present at the beginning of observation, and p and f , respectively, the number of leaves produced and lost during the time interval T . A one-way ANOVA was used for the comparison among groups. Leaf longevity was compared following a logarithmic transformation.

Results

NUMBER OF HERBIVORES

The incidence of herbivores was 4.3 times higher on plants from which the ants had been experimentally removed ($n = 78$) than on the control plants ($n = 18$, Table 1). This difference is highly significant ($G_8 = 6.82$, $P < 0.01$), despite the high heterogeneity observed between censuses ($G_7 = 32.55$, $P < 0.001$). All eight herbivore censuses showed a higher number of herbivores on plants without ants; in five censuses this tendency was significant (G_1 , $P < 0.05$).

Insects of the order Homoptera ($n = 45$, 47%) were the most frequent herbivores of *Tachigali myrmecophila*, followed by Lepidoptera ($n = 25$, 27%), Coleoptera ($n = 16$, 16%), Orthoptera ($n = 8$, 8%) and Heteroptera ($n = 2$, 2%). All observed insect orders occurred more frequently on plants without ants, except the least frequent order Heteroptera (C, 1; E- 1). These differences are significant for Homoptera (C, 7; E, 38; $G_1 = 22.13$, $P < 0.001$), Lep-

idoptera (C, 5; E, 20; $G_1 = 8.98$, $P < 0.01$) and Coleoptera (C, 3; E, 13; $G_1 = 6.30$, $P < 0.05$). The low heterogeneity between orders ($G_4 = 1.52$, $P > 0.05$) suggests that the ant protection has a similar effect on all orders.

RATES OF HERBIVORY

The mean (\pm SE) daily rate of herbivory on *Tachigali myrmecophila* occupied by *Pseudomyrmex concolor* was 0.014 ± 0.008 ($n = 31$ plants), about 10 times lower than on the plants from which the ants were experimentally removed (0.133 ± 0.061 , $n = 27$ plants), the difference being highly significant ($F_1 = 13.810$, $P = 0.001$, Table 2). Within the plant canopy, young leaves presented an average rate of herbivory of 0.123 ± 0.074 ($n = 18$ plants), 2.7 times higher than the mature leaves (0.046 ± 0.027 , $n = 40$ plants), the difference being highly significant ($F_1 = 8.583$, $P = 0.005$). During the wet season the average rate of herbivory was 0.099 ± 0.055 , $n = 29$ plants), 2.5 times higher than on the dry season (0.040 ± 0.021 , $n = 29$ plants), although this difference was not significant ($F_1 = 0.272$, $P = 0.272$). The rates of herbivory were not independent among treatments. The treatment group interacted significantly with season ($F_1 = 6.429$, $P = 0.014$) but only marginally with leaf maturity ($F_1 = 3.139$, $P = 0.083$). Leaf maturity did not interact with season ($F_1 = 0.119$, $P < 0.731$). There was a significant interaction between the effects of ant removal, leaf maturity and season ($F_1 = 6.839$, $P < 0.012$).

CUMULATIVE LEVEL OF HERBIVORY

The differences in daily herbivory rate described above were reflected in the herbivory level between the control and experimental groups (Fig. 1). The plants without ants showed a greater increase in the mean (\pm SE) level of herbivory (1.59 ± 0.52 , $n = 23$) than the plants with ants (0.82 ± 0.50 , $n = 22$) during the 18 months of the experiment, a difference of about two times (one-tailed $t_{43} = 5.14$, $P < 0.001$). Considering only the leaves that appeared after the beginning of the experiment (top leaves), which spent the immature phase unprotected, the increase in the level of herbivory in plants without ants (2.53 ± 1.10 , $n = 23$) was about twice as high as in plants with ants (1.30 ± 1.00 , $n = 22$), this difference being highly significant (one-tailed $t_{43} = 3.98$, $P < 0.001$). Considering the leaves already present on the plants before the beginning of the experiment, the difference was less pronounced, but still highly significant (one-tailed $t_{43} = 3.08$, $P < 0.005$). The level of herbivory showed an increase of 1.54 ± 0.69 in the plants without ants and 1.02 ± 0.40 in the control group, a difference of about 50%.

Table 1 Numbers of herbivores on plants of *Tachigali myrmecophila* that were naturally occupied by the ants *Pseudomyrmex concolor*, and in plants from which the ants had been experimentally removed

Date	Control (<i>n</i> = 22)	Experimental (<i>n</i> = 23)	Total	d.f	<i>G</i> *	<i>P</i>	
Nov 89	0	7	7	1	5.891	<0.05	
Jan 90	2	7	9	1	2.141	ns	
Mar 90	1	11	12	1	7.487	<0.01	
May 90	5	6	11	1	0.039	ns	
Jul 90	4	12	16	1	3.801	ns	
Sept 90	3	15	18	1	7.558	<0.01	
Nov 90	3	11	14	1	4.210	<0.05	
Jan 91	0	9	9	1	8.246	<0.01	
Total				8	39.374	<0.001	
Sum	18	78	96	Pooled	1	6.823	<0.01
				Heterogeneity	7	32.551	<0.001

* For the G test, since the number of plants in the control and experimental groups is different, the expected frequencies were adjusted in order to avoid bias. One was added to each frequency cell because this test cannot handle null frequencies.

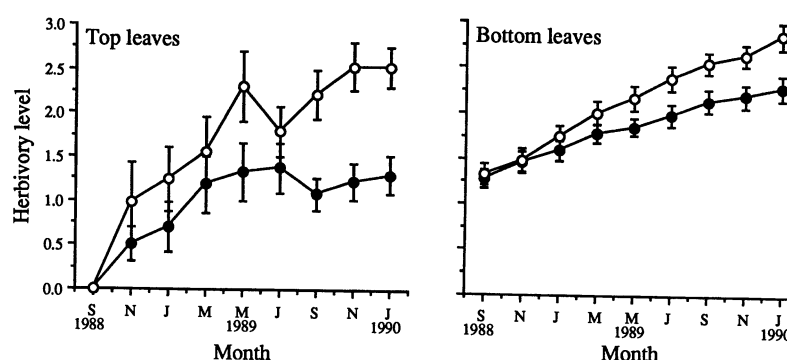


Fig. 1 Dynamics of the leaf herbivory levels on *Tachigali myrmecophila* in plants naturally occupied by the ant *Pseudomyrmex concolor* (n = 22, ●) and in plants from which the ants were experimentally removed (n = 23, ○). (a) Top leaves are those which emerged after the beginning of the experiment, in September 1988, or were present as buds at that time. (b) Bottom leaves are those already present on the plants at the beginning of the experiment. The circles represent the means and the lines enclose ± 1 SE.

Table 2 (a) Rates of herbivory on *Tachigali myrmecophila* (% eaten/day) naturally occupied by the ants *Pseudomyrmex concolor* (control) and on individuals from which the ants had been experimentally removed, for both mature and immature leaflets, during the dry and wet season. The values are the mean \pm SD. The number of estimates are enclosed in parentheses. (b) Three-way factorial ANOVA ($2 \times 2 \times 2$) for rates of herbivory with respect to occupancy status, leaf maturity and season. The rates of herbivory were transformed by $\ln(1 + 1000rh)$

(a)		Group	
Season	Leaf maturity	Control	Experimental
Wet	Mature	0.025 \pm 0.022 (10)	0.114 \pm 0.102 (10)
	Immature	0.006 \pm 0.004 (7)	0.714 \pm 0.547 (2)
Dry	Mature	0.007 \pm 0.005 (10)	0.036 \pm 0.026 (10)
	Immature	0.023 \pm 0.012 (4)	0.129 \pm 0.110 (5)

(b) Source of variation	d.f.	SS	MS	F	P
G	1	33.491	33.491	13.810	0.001
LM	1	20.814	20.814	8.583	0.005
S	1	2.992	2.992	1.234	0.272
G \times LM	1	7.613	7.613	3.139	0.083
G \times S	1	15.591	15.591	6.429	0.014
LM \times S	1	0.290	0.290	0.119	0.731
G \times LM \times S	1	16.586	16.586	6.839	0.012
Error	50	121.259	2.425		

Group (G); Leaf maturity (LM); Season (S).

APICAL GROWTH

All 45 plants of the experiment, except one, showed a significant correlation (P < 0.05) between apical length and time, in months. The mean (± SE) regression coefficient, representing the rate of apical growth, was 1.6 times greater for plants with ants (1.147 ± 1.142 cm month⁻¹) than for plants experimentally without ants (0.731 ± 0.742 cm month⁻¹). The observed difference is significant (one-tailed t₄₃ = 1.759, P < 0.05), showing that the removal of Pseudomyrmex concolor negatively affects the growth of Tachigali myrmecophila. The initial frequency of vines touching the control (none on 22 plants) and experimental plants (one on 23 plants) showed no difference after 18 months of experiment.

NATURAL PHENOLOGY

At the beginning of observation, plants from the control, experimental, and naturally unoccupied groups had the same height (one-way ANOVA, F_{2,59} = 2.10, P > 0.05) and the same number of leaves (F_{2,59} = 2.26, P > 0.05). During the 18 months of observations, the presence of ants did not significantly affect the rate of leaf production (F_{2,59} = 0.121, P > 0.05). However, the number of leaves lost was significantly affected by the presence of Pseudomyrmex concolor (F_{2,59} = 3.93, P = 0.05, Table 3). The number of leaves lost in the occupied group (2.32) was lower than the experimental (3.25) and the unoccupied groups (4.00).

The occupied plants of Tachigali myrmecophila revealed a strikingly high leaf longevity of 81.1 months, about 1.8 times higher than for experimental plants (44.7 months) and 2.6 times higher than naturally unoccupied plants (30.7 months), the groups being quite different (F_{2,56} = 13.74, P < 0.001; Fig. 2). Interestingly, the leaf longevity of plants from the experimental group is about 1.5 times as high as the naturally unoccupied plants, the means being significantly different (GT2-method, MSD_{0.05}[3,56] = 0.469, P < 0.05). The estimate of the leaf longevity is independent of both the initial height and the initial number of leaves (Multiple regression, F_{2,1} = 0.10, P > 0.05, R² = 0.095).

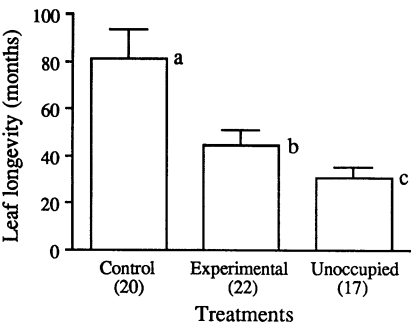


Fig. 2 Leaf longevity of Tachigali myrmecophila plants that were occupied by Pseudomyrmex concolor (Control), of plants from which the ants were experimentally removed, and of naturally unoccupied plants, during the 18 month study. The rectangles represent the mean, and the lines enclose ± 1 SE. The number of plants in each group are in the parenthesis. Heterogeneity among groups was tested by one-way ANOVA, and the comparisons between groups by the GT2-method (Sokal & Rolhf 1981). Means with different letters are significantly different (P < 0.05).

Discussion

Tropical understorey communities consist of juveniles of shade-tolerant shrub and tree species (Hubbell & Foster 1986) and, in most cases, it is these juveniles rather than germinating dormant seeds that replace canopy adults (Schupp et al. 1989). In Venezuela such advanced regeneration accounted for about 95% of all trees > 1 m tall surviving in gaps after 4 years (Uhl et al. 1988). Furthermore, higher mortality rates occur in smaller seedlings than taller ones (Uhl & Murphy 1981; Turner 1990). In this environment, survival and growth are the two main components of fitness; reproduction being manifest only at a much later stage. For Tachigali this is especially true because of its monocarpic life history (Foster 1977).

The benefit of the myrmecophytic defence was evaluated in this study by a comparison between ant-protected plants and experimentally ant-free plants. Tachigali myrmecophila plants without the protection of Pseudomyrmex concolor had 4.3 times more herbivorous insects than ant-protected plants, facing an overall increase of ten times in the rate of herbivory with a cumulative level of herbivory twice as great. Also, the leaf longevity of the experimental group was almost 1.8 times lower than the control group. The

Table 3 Leaf phenology of Tachigali myrmecophila individuals that were occupied by Pseudomyrmex concolor (Control), of individuals from which the ants had been experimentally removed, and of naturally unoccupied individuals, during the 18-month study. The values are the mean ± SE. Heterogeneity among groups was tested by one-way ANOVA, and the comparisons between groups by the GT2-method (Sokal & Rolhf 1981). Means with different letters are significantly different (P < 0.05)

Table with 6 columns: Phenological trait, Control (n = 22), Experimental (n = 23), Unoccupied (n = 17), F, and P. Rows include Initial height (m), Initial number of leaves, Number of leaves produced, and Number of leaves dropped.

growth rate, the best estimate of plant fitness for immature plants, was 1.6 times lower for ant-free plants. All these results suggest that *Pseudomyrmex concolor* is highly beneficial to *Tachigali myrmecophila*. McKey's (1984) model, by comparing the cumulative cost of the chemical and ant defence strategies, assumes implicitly that the benefits of both strategies are equal. I envisage that the kind of defence strategy adopted by the plant should be determined not only by their cost but also by the efficiency of the strategies in relation to the ecological pressures faced. So the benefit of both strategies should enter any trade-off model of defence strategies.

The leaf longevity of more than 6 years for *Tachigali myrmecophila* protected by *Pseudomyrmex concolor* is amazingly high when compared with the levels for Panamanian trees (Coley 1983, 1988). For Barro Colorado Island, Panama, the average leaf life span of species in the shade appears to be 2.5 years, although there are several in which 50% of the leaves survive for more than 5 years (e.g. *Ouratea*, *Rheedia*) and at least *Aspidosperma* (Apocynaceae) can reach about 13 years (P. Coley, personal communication). In forest gaps, in Panama, the leaf longevity of light-demanding tree species varied between 3.9 and 21 months (6.8 months), while the leaf longevity of shade-tolerant species varied between 7.5 and 35 months (21.7 months, Coley 1988). The leaf longevity of unprotected *T. myrmecophila* plants is 45 months, much higher than the leaf longevity recorded for the non-myrmecophytic *Tachigali versicolor* on Panama (23 months, Coley 1988). The leaf longevity of *T. myrmecophila* is also higher than all current records for myrmecophytic species: *Acacia cornigera* (6–9 months, Janzen 1967), *Cecropia* sp. (6 months; McKey 1984), *Ocotea atirrensis* (> 24 months; Bentley 1979) and *Leonardoxa africana* (36 months; McKey 1984). Thus, *Tachigali myrmecophila* should be considered a species with outstandingly long leaf life span (see also Coley & Aide 1990). The existence of ant defence in a species with long-lived leaves is not compatible with the falsifiable prediction of McKey's (1984) model for a trade-off between chemical and ant-defence which predicts that myrmecophytic traits should be limited to plants with low leaf longevity.

Why have so a high leaf longevity? The resource availability hypothesis formulated by Coley *et al.* (1985) predicts that upon resource shortage the plants should invest strongly in defence mechanisms and consequently present a high leaf longevity and a limited growth rate. Small *Tachigali myrmecophila* plants occur in the low light conditions of the understorey of dense tropical forest where carbon is hard to obtain (Richards 1952) and nutrients are also scarce, mainly in leached soils of Central Amazonia (Sombroek 1966). The apical growth rate of *T. myrmecophila* of about 14 cm year⁻¹ is very low when compared with 41 tree species studied in forest gaps on Barro Colorado Island but could be expected according the inverse

relationship between growth rate and leaf longevity predicted by the resource availability hypothesis (Coley *et al.* 1985; Coley 1988). The growth rate of *T. myrmecophila* is higher than that of *Trichilia cipo* (Meliaceae, 5 cm year⁻¹), another slow-growing, shade tolerant species (Coley 1983). The decrease in apical growth, caused by the absence of *Pseudomyrmex concolor*, seriously affects the fitness of those individuals of *Tachigali myrmecophila* which remain for year in the 'sapling bank' of the forest, awaiting the better light and nutrient conditions provided by gaps (Denslow 1980, 1987). Janzen (1966) and Schupp (1986) have shown a greater impact of ant removal on apical growth with *Cecropia* and *Acacia* than was demonstrated with *Tachigali myrmecophila*. However, these genera are characteristically pioneers growing preferentially in open sites with a great input of light. It seems that the *Tachigali myrmecophila* life-history represents an extreme in the reproduction or survival dichotomy.

The survival of *Tachigali myrmecophila* seems to be dependent on a very high investment in defence represented by the cost of the continuous maintenance of an ant colony. *Pseudomyrmex concolor* feeds on the coccids *Catenococcus* sp. which are tended inside the leaf domatia of *T. myrmecophila*. The coccids suck the phloem contents transferring nutrients indirectly from the host plant to the ant colony. The workers never forage outside the host plant and do not eat the insect herbivores attacked (Fonseca 1993). The *P. concolor* colonies are limited by the space provided by the domatia of the host plant and an average of about 460 workers of *P. concolor* occur per square metre of leaf area of the host plant (Fonseca 1993). Taking the mean (\pm SE) wet weight of *P. concolor* workers as 2.41 ± 0.56 mg ($n = 100$, 10 workers from each of 10 colonies), it is estimated that *Tachigali myrmecophila* supports 1.104 g of ants per m² of leaf. Using Nash's (1989) equation which correlates the standard metabolic rate (sVO₂) and the body mass (wet weight, mg) of the ants, it is estimated that each square meter of *Tachigali myrmecophila* leaf is investing a minimum of 0.35 mL O₂ h⁻¹ at 20 °C on ant protection.

Taking the mean (\pm SE) dry weight of *Pseudomyrmex concolor* workers as 0.714 ± 0.16 mg ($n = 100$), it can be estimated that there is a dry weight of 0.33 g of workers per square meter of leaf area. This value is three times lower than the weight of *Pseudomyrmex ferruginea* in *Acacia cornigera* (1.04 g) and one and a half times lower than that of *Petalomyrmex phylax* in *Leonardoxa africana* (0.48 g, McKey 1984). However, both *Acacia* and *Leonardoxa* feed the ants directly with their food bodies. In the *Tachigali* system, *P. concolor* works in part as secondary consumer receiving the energy produced by the photosynthesis of *T. myrmecophila* through the activity of the coccids, suggesting that the total amount allocated to the myrmecophytic strategy may be up to one order of magnitude higher. The 0.33 g

dry weight of ants per m² of leaf can be considered an underestimate of the costs of the ant defence strategy in *Tachigali*. However, detailed ecophysiological data are required before drawing further conclusions.

MYRMECOPHYTISM AND HERBIVORY PRESSURE

The foraging activity of phytophagous insects was affected by the patrolling behaviour of *Pseudomyrmex concolor*. Caterpillars of the moths *Hyalophirus infernalis* and *Chrysoplectrum pervivax* (Hesperiidae) and an unidentified beetle larva present specialized behaviour in order to escape ant predation. Other insects, like Homoptera and Orthoptera, were captured or displaced frequently. Such ability of *Pseudomyrmex* to drive out both generalist and specialist insects was also recorded in *Acacia* (Janzen 1967). The rates of herbivory found on leaves of *Tachigali myrmecophila* are affected by both the pattern of activity of *Pseudomyrmex concolor* and the distinct pressures made by the phytophagous insects. Specialist insects, such as *Hyalophirus infernalis*, have a strong preference for immature leaves, but *Pseudomyrmex concolor* has a higher patrolling activity on upper leaves, thus decreasing the incidence of those insects. Not surprisingly, when the ants were removed the rate of herbivory on immature leaves during the wet season increased by up to two orders of magnitude. The marginally significant interaction between group and leaf maturity suggests that ants are driving the herbivores from the top to the lower positions in the crown of the plant, thereby preferentially protecting those leaves which have a higher life expectancy as well as a higher photosynthetic efficiency (Downhower 1975). The temporal changes in the population dynamics of the *T. myrmecophila*'s herbivores were reflected in the rates of herbivory. Although no significant seasonal effect was detected, the interaction between group and season suggests that when the insect populations are high the herbivores are driven to unoccupied plants. Furthermore, occupancy status, leaf maturity and season interacted significantly suggesting again that the patrolling activity of the ants drives the herbivores to enemy-free environments.

During the maturation process different defence mechanisms are required due to substantial changes in the herbivory pressure (Feeny 1976; Rhodes & Cates 1976; McKey 1979). Herbivory rates are, in general, higher on young than old leaves (Coley 1980). The absence of the ant protection in *Tachigali myrmecophila* was particularly important during the beginning of the maturation process of the leaves, the rates of herbivory in immature leaves were about 2.7 times higher than on mature ones, which agrees with the general pattern. Coley (1980) reported a daily herbivory rate of 0.775% for young leaflets of the non-myrmecophytic *Tachigali versicolor*, during the

rainy season in Panama. This rate for young leaflets is similar to that obtained with experimental *T. myrmecophila* (0.714%) but is much higher than that from plants protected by *P. concolor* (0.006%). The herbivory on mature leaflets of *T. versicolor* (0.005%) is more similar to that of control plants (0.024%) than to that of experimental plants (0.117%) of *T. myrmecophila* in the same season. This suggests that the ants are not only an important defence mechanism for immature leaves but they are also effective for mature leaves.

The removal of ants from the experimental plants did not affect the incidence of vines, this may be due to the low frequency of vines in the understorey of the study site. Nonetheless, I have observed workers of *Pseudomyrmex concolor* actively chewing and biting the tips of vines growing in contact with *Tachigali myrmecophila* plants. This activity frequently damages the apical cells, slowing the growth of the vines. The pruning activity of *P. concolor* was unimportant to the fitness of the young *T. myrmecophila* in the experimental conditions. Nonetheless, this allelopathic effect (*sensu* Janzen 1969) may be important to *T. myrmecophila* in the environment of gaps and in the canopy. In the tropics, the connection between adjacent trees by vines is an important factor of tree mortality (Schupp 1986). I have also observed cleaning activity by *P. concolor*. The workers remove epiphyllae and debris on leaf surfaces; this could well increase photosynthetic rates and the benefit:cost ratio that modifies leaf longevity (Mooney 1972).

EXPERIMENTAL OR CORRELATIVE APPROACHES?

Bailey (1923) asserted in his concluding remarks that 'There is no evidence to indicate that the structural peculiarities of *Tachigali paniculata* are initiated by ants ... or that they originated as adaptations for attracting a defending army of ants. The relations between the host plant ... and the ants are not those of a mutually beneficial symbiosis'. These words were quoted, about two decades later, by another eminent researcher in order to reinforce that opinion (Wheeler 1942). At that time, ecological experiments with falsifiable predictions were not commonplace and, although continuous field observation has been shown to be a successful way to generate scientific hypotheses, the interpretation of the observed data was made under the supremacy of the existing paradigm.

The mutualistic hypothesis (Belt 1874) has been well supported by some experimental (Janzen 1966, 1967; Vasconcelos 1991; Schupp 1986) and descriptive-correlative works (Janzen 1972; McKey 1984; Letourneau 1983; Fiala *et al.* 1989). The descriptive-correlative approach, i.e. the comparison of plants that are occupied by ant colonies with those that are naturally unoccupied, has been used frequently, with

variable degrees of success, to evaluate the effect of myrmecophytism as an antiherbivory strategy. However, observations on the phenology of *Tachigali myrmecophila* revealed that the leaf longevity of naturally unoccupied plants (31 months) was lower than that of the experimental plants (45 months). The comparison between ant-protected plants with these two groups produced a quantitatively different result. This difference suggests that generalizations derived from descriptive-correlative works should be viewed with caution. In general, it is normally assumed that the correlation between occupancy status and herbivory level is the result of the efficiency of the ants against herbivores. However, the absence of the ants can be the effect, not the cause, of the high level of herbivory of the host. In other words, is the performance of naturally unoccupied plants poorer because of the absence of the ants, or are the ants unable to colonize or survive in plants with a low general productivity? This problem may be particularly relevant to systems in which the myrmecophyte offers directly some kind of food to the ant colony (Davidson & Fisher 1991).

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