

## Nesting space limits colony size of the plant-ant *Pseudomyrmex concolor*

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The size and structure of the colony of the stinging plant-ant *Pseudomyrmex concolor* occupying two morphologically distinct *Tachigali* myrmecophytic host species was studied in order to discriminate between factors limiting the ant colony size; specific hypotheses being a) food, b) territory size and c) nesting space. From intraspecific comparisons it is suggested that the ant colony size is primarily controlled by the total domatia space offered by the host plant. The space-limited hypothesis explains why plant-ants demonstrate host-limited foraging territories. I analyse the space-limited hypothesis from the host's point-of-view by using a cost-benefit graphic model. It is suggested that domatia size can be selected in a way that increases the plant's net benefit from the mutualistic relationship.

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Wilson (1971) estimated that at any given time there are about  $10^{15}$  living ants on the earth. This is not astonishing if it is considered that in some temperate localities the ant density can be 140 workers per  $m^2$  (Kajant et al. 1971), and in the tropics the ants can represent up to half the insect biomass (Fittkau and Klinge 1973). In the crowded environment of rainforests practically every square inch of surface is under the domain of at least one ant colony. Interference between ants is not limited to the ground level but the whole three-dimensional structure of the forest is occupied. Actually, many ant genera are arboreal, passing a part or whole of their life in trees (Hölldobler and Wilson 1991). At the extreme are the ants which nest in ant-plants, or myrmecophytes, inside special plant structures called myrmecodomatia (Wheeler 1942, Benson 1985, Beattie 1986, Huxley 1986).

Much of the ecological success of the ants can be explained by their cooperative behaviour within genetically related colonies (Wilson 1971). In general, colonies are founded by queens, and grow by worker production to reach a mature size, when production of new reproductive alates starts (Hölldobler and Wilson

1991). The size of a single mature ant colony varies by many orders of magnitude from a few individuals in the largest ant *Dinoponera* (Ponerinae), to hundreds of thousands in the predatory army ants *Eciton* (Rettenmeyer 1963). Ant colony size in myrmecophytes varies from a few tens of workers of *Pheidole* inhabiting the small shrub *Maieta* (Melastomataceae), to an estimated colony size of 1.8–3.6 million workers in some polygynous *Pseudomyrmex* inhabiting *Acacia* (Janzen 1973). Although the mature colony size is known for many ant species most of its variation remains not understood (Hölldobler and Wilson 1991). Several factors can contribute to determine the mature colony size (Sudd and Franks 1987). It has been suggested that food competition among colonies is an important factor limiting the productivity and fitness of many species (Pontin 1961, 1963, Boomsma et al. 1982). In the tropics, where ant diversity and density is high, the evenly dispersed spacing pattern of ant nests suggests that territorial interference among and within species could be structuring the community (Levings and Traniello 1981, Levings and Franks 1982). Hölldobler and Wilson (1991) list the mature colony size of many ant species pointing out that

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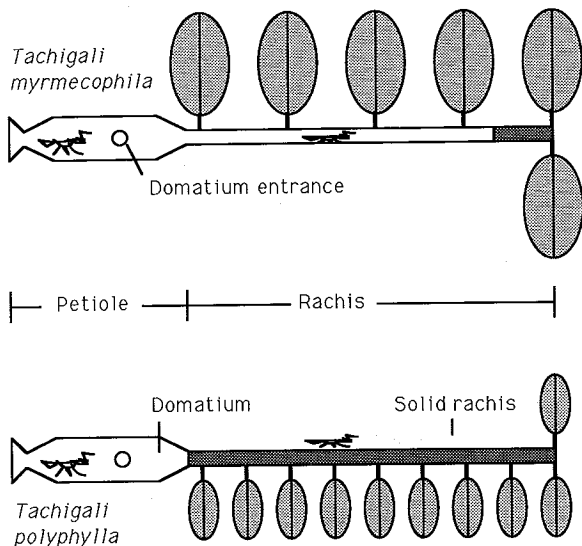


Fig. 1. Schematic representation of the compound leaves of *Tachigali myrmecophila* and *Tachigali polyphylla*. *Pseudomyrmex concolor* nests and tends coccids inside the expanded petiole and rachis of *Tachigali* leaves. Some leaflets on one side of each leaf are not shown.

there is a strong relationship between preferred nest site and mature colony size. Although not explicit, these data suggest that nesting space can limit the colony size of those species with specialized nest requirements.

The life history of the stinging ant *Pseudomyrmex concolor* (F. Smith) is closely integrated with its leguminous tree host, *Tachigali*; its nests are exclusively inside leaf rachis domatia; its territory comprises roughly the whole tree; and most food seems to be provided by its associated coccids *Catenococcus* sp., a *Tachigali* herbivore. In this paper I analyse the colony size and structure of *Pseudomyrmex concolor* in two species of myrmecophytic *Tachigali* with distinct leaf morphology. Using intraspecific comparisons I can discriminate between factors limiting the ant colony size; specific hypotheses being: a) food, b) territory size, and c) nesting space.

## Material and methods

The plants were collected in the Cabo Frio reserve, a continuous 1000 ha reserve of Terra Firme forest (sensu Pires and Prance 1985) about 100 km north of Manaus, Amazonas (2°24'S, 59°52'W). This reserve is linked to the Biological Dynamics of Forest Fragment Project (Instituto Nacional de Pesquisas do Amazonas/Smithsonian Institution), being a control plot of undisturbed rainforest. The vegetation has a variable canopy about 30–40 m and the *Arecaceae* provides a predominant understorey component. The regional climate is classi-

fied as Wet Tropical (Holdridge et al. 1971), the average annual temperature is 26°C, and the average annual rainfall for the last 30 years is 2186 mm. The relief is formed by plateaux at an altitude of 80–140 m with a clay-sandy soil that is characteristically deep, acid and well drained (Sombroek 1966).

## Natural history

In Cabo Frio, *Pseudomyrmex concolor* nests inside the expanded leaf petiole and rachis of small host trees of *Tachigali myrmecophila* Ducke and *Tachigali polyphylla* Poepp. & Endl. which are scattered in the forest (Fig. 1). Workers from adjacent plants show strong agonistic behaviour among each other when submitted to replacement manipulations, and behavioural observations during day and night periods indicate that one ant colony is unable to occupy more than one host tree. Characteristically, each leaf, with a single domatium, contains a variable number of workers and immature ants as well as alates, male and female. One to some queens can be normally found clumped in a single leaf domatium. *Pseudomyrmex concolor* actively patrols the leaves of *Tachigali*, protecting the plants against herbivores (Fonseca 1991). However, the workers do not eat these insects. The only recorded food of *P. concolor* is the honeydew and the bodies of the small coccids *Catenococcus* sp. that they tend inside the domatia. *Pseudomyrmex concolor* occurs mainly in young plants. In most cases, only one ant colony is found occupying a tree, the colony being spread over all the domatia of the tree. However, when the tree grows taller this ant species is replaced by another ant species, thus beginning a successional process that involves at least two *Pseudomyrmex* and six *Azteca* species in this region. Then, during the transition period two ant colonies can coexist in a conflicting situation in a single host plant (Fonseca 1991).

## Colony collection

Young plants of *Tachigali myrmecophila* and *T. polyphylla* occupied by *Pseudomyrmex concolor* were located. All saplings used ranged from 0.5 to 2.5 m in height and were unbranched. For each species, the plants were grouped according to the number of leaves, from 4 to 11. An individual from each group was chosen randomly, thus for each species there are eight individuals with increasing numbers of leaves. As I was unable to find a plant of *Tachigali myrmecophila* with 11 leaves, it was replaced by an individual with 12 leaves. This procedure permitted the selection of a desired variation both in morphological traits of *Tachigali* and in ant colony size and structure.

Between 8 and 10 October 1988, I collected integrally all ant colonies of *Pseudomyrmex concolor* in order to

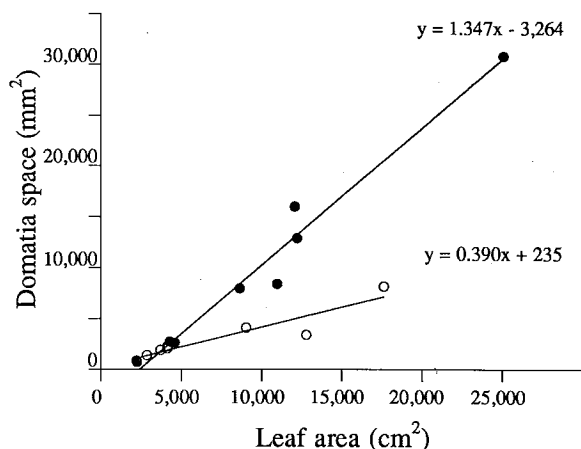


Fig. 2. Relationship between domatia space and leaf area in *Tachigali myrmecophila* (closed circles,  $n = 8$ ) and *Tachigali polyphylla* (open circles,  $n = 8$ ).

describe their colony structure. Adhesive plastic was put over the entrance of every domatium to prevent the workers getting out. Then, an alcoholic solution (70%

G.L.) was introduced into each domatium for preserving the internal material. Most collections were made after rainfall when the workers were inside the domatia to minimize the loss of workers. Workers outside the domatia were counted and added to the total inside.

Each domatium was dissected and the contents examined under a dissecting microscope (10–30 $\times$ ). The number of workers, pupae, larvae, eggs, queens, and alate males and females was recorded, as well as the number of coccids, *Catenococcus* sp.

### Plant morphology

The number of leaves and leaflets on each individual *Tachigali* were counted. Each leaf was tagged, detached, pressed and dried. The leaf area was estimated by a Delta T Area Meter (Delta T Devices, Burwell, Cambridge, U.K.) with 1 cm<sup>2</sup> precision. Each domatium was put in a plastic bag. In the laboratory, the domatia were longitudinally dissected and the length and largest width were measured by a ruler with 0.5 mm precision. As there is no change in the shape of the

Table 1. Information on completely dissected plants of *Tachigali myrmecophila* ( $n = 8$ ) and *Tachigali polyphylla* ( $n = 8$ ) occupied by the ant *Pseudomyrmex concolor*. Each row is an independent plant. Q is the number of queens. F and M are number of alated females and males, respectively.

Plant code	Number of leaves	Number of leaflets	Leaf area (cm <sup>2</sup> )	Domatia space (mm <sup>2</sup> )	Number of coccids	Number of workers	No. of pupae	No. of larvae	No. of eggs	Q	F-M
<i>Tachigali myrmecophila</i>											
1	4	16	2268	699	30	59	23	40	76	2	0-0
2	5	31	4315	2704	143	334	65	110	68	2	0-0
3	6	42	8659	7936	206	466	106	362	323	1	0-0
4	7	38	4609	2631	101	118	24	128	122	2	0-0
5	8	56	12228	12860	454	737	243	1173	496	8	0-0
6	9	62	12087	15999	294	697	143	421	18	5	6-0
7	10	67	10981	8408	163	553	83	432	128	1	24-0
8	12	98	25099	30767	345	1104	199	1216	255	4	65-2
<i>Tachigali polyphylla</i>											
9	4	36	2894	1390	44	86	18	68	37	1	0-0
10	5	36	2258	850	30	28	8	28	55	2	0-0
11	6	55	4151	2215	50	141	43	60	92	6	0-0
12	7	53	3724	1902	76	52	33	18	98	6	0-0
13	8	100	12794	3377	50	83	16	75	110	4	10-3
14	9	77	4155	2020	71	22	15	17	96	7	0-0
15	10	170	17633	8165	365	257	67	625	241	1	2-35
16	11	133	9044	4087	635	324	101	428	236	2	0-0
<i>Tachigali myrmecophila</i>											
X*	7.6	51.3	10030	10250	217	509	104	485	185	3.1	12.1 <sup>†</sup>
S.D.*	2.7	25.3	7183	9825	139	345	80	462	161	2.4	23.7
<i>Tachigali polyphylla</i>											
X*	7.5	82.5	7081	3001	165	124	37	165	121	3.6	6.3 <sup>†</sup>
S.D.*	2.5	48.5	5568	2330	219	111	32	230	77	2.5	13.2

\* Median (X) and standard deviation (S.D.) were calculated by species ( $n = 8$  plants) and are valid only within the scope of the previously described sample procedure. <sup>†</sup> Considering female and male alates together.

Table 2. Correlation among the numbers of different developmental stages of *Pseudomyrmex concolor*. Correlation coefficients (r) and probabilities (P) are respectively below and above the diagonal. Sample size is 16 for all comparisons except those involving alates where n is 5. ns represents  $P > 0.05$ .

	Eggs	Larvae	Pupae	Workers	Queens	Alates
Eggs	1	0.001	ns	ns	ns	0.005
Larvae	0.823	1	0.001	0.001	ns	0.005
Pupae	0.396	0.839	1	0.001	ns	ns
Workers	0.405	0.823	0.978	1	ns	ns
Queens	-0.261	0.006	0.379	0.323	1	ns
Alates	0.949	0.953	0.643	0.653	-0.191	1

domatium in relation to its size, the space inside a domatium was estimated by the product of its length and width.

$F_{[1,6]} = 40.498$ ,  $P < 0.001$ ), this difference being highly significant ( $F_{[1,12]} = 123.35$ ,  $P < 0.001$ ).

## Results

### Plant morphology

*Tachigali myrmecophila* (*Tm*) leaves normally have smaller leaflet number, larger leaflet size and larger domatium space, than leaves of *Tachigali polyphylla* (*Tp*) with comparable leaf length. Although both species have about the same number of leaves and consequently about the same number of domatia (*Tm* = 61, *Tp* = 60, each leaf has a single domatium), *T. myrmecophila* plants have 3.4 times more domatia space per leaf than *T. polyphylla* (*Tm* = 1344 mm<sup>2</sup>, *Tp* = 400 mm<sup>2</sup>). The difference in leaf area is about 1.4 times (*Tm* = 1316 cm<sup>2</sup>, *Tp* = 944 cm<sup>2</sup>). The distinction in morphological traits between the species is displayed in Fig. 2. The slopes of the regression between domatia space and leaf area show that *T. myrmecophila* ( $\beta = 1.347$ ,  $F_{[1,6]} = 197.179$ ,  $P < 0.001$ ) offers 3.5 times more nest space to the ants per unit leaf area than *T. polyphylla* ( $\beta = 0.390$ ,

### Colony foundation, growth and reproduction

Field observation suggests that colonies of *Pseudomyrmex concolor* are founded by only one queen (haplo-metrosis), nevertheless the data presented in Table 1 indicate that later on they become polygynous. Only four from 16 colonies studied (25%) were monogynous. The polygynous colonies had from two to eight dealate queens, normally being clumped into one or a few domatia. In two dissected colonies two domatia had both dealate queens and a high number of eggs, suggesting that in *Pseudomyrmex concolor* more than one queen may be responsible for egg production. Interestingly, the correlation between number of dealate queens and egg production is not significant ( $r = -0.261$ ,  $n = 16$ ,  $P > 0.05$ ), suggesting some process of hierarchical dominance among the queens.

The number of individuals of *Pseudomyrmex concolor* at a given stage of development seems to be a good predictor of the number of individuals in the following stage (Table 2). The number of eggs is highly correlated with the number of larvae ( $r = 0.823$ ,  $n = 16$ ,  $P < 0.001$ ) but not significantly correlated with the number of pupae and workers ( $P > 0.05$ ). The number of larvae is highly correlated with number of pupae ( $r = 0.839$ ,  $n = 16$ ,  $P < 0.001$ ) and workers ( $r = 0.823$ ,  $n = 16$ ,  $P < 0.001$ ). The number of pupae is highly correlated with the number of workers ( $r = 0.978$ ,  $n = 16$ ,  $P < 0.001$ ).

In *Tachigali myrmecophila* the number of eggs is only significantly determined by the number of coccids ( $r^2 = 0.523$ ,  $n = 8$ ,  $P < 0.05$ ). The determination coefficient with both leaf area ( $r^2 = 0.262$ ,  $n = 8$ ,  $P > 0.05$ ) and domatia space ( $r^2 = 0.209$ ,  $n = 8$ ,  $P > 0.05$ ) are not significant. In *T. polyphylla* the number of eggs is well determined by the number of coccids ( $r^2 = 0.812$ ,  $n = 8$ ,  $P < 0.001$ ), leaf area ( $r^2 = 0.610$ ,  $n = 8$ ,  $P < 0.05$ ) and domatia space ( $r^2 = 0.760$ ,  $n = 8$ ,  $P < 0.005$ ). A step-wise regression (Sokal and Rohlf 1981) was applied to the pooled data, as a test to discriminate the most important variable to explain the egg production in

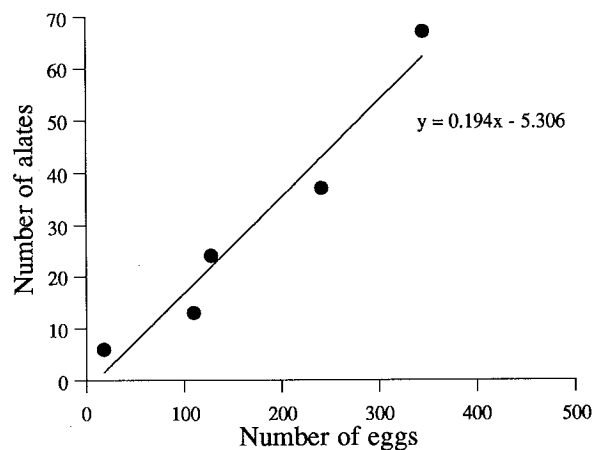


Fig. 3. Relationship between number of alates and number of eggs of reproductively active *Pseudomyrmex concolor* colonies ( $n = 5$ ).

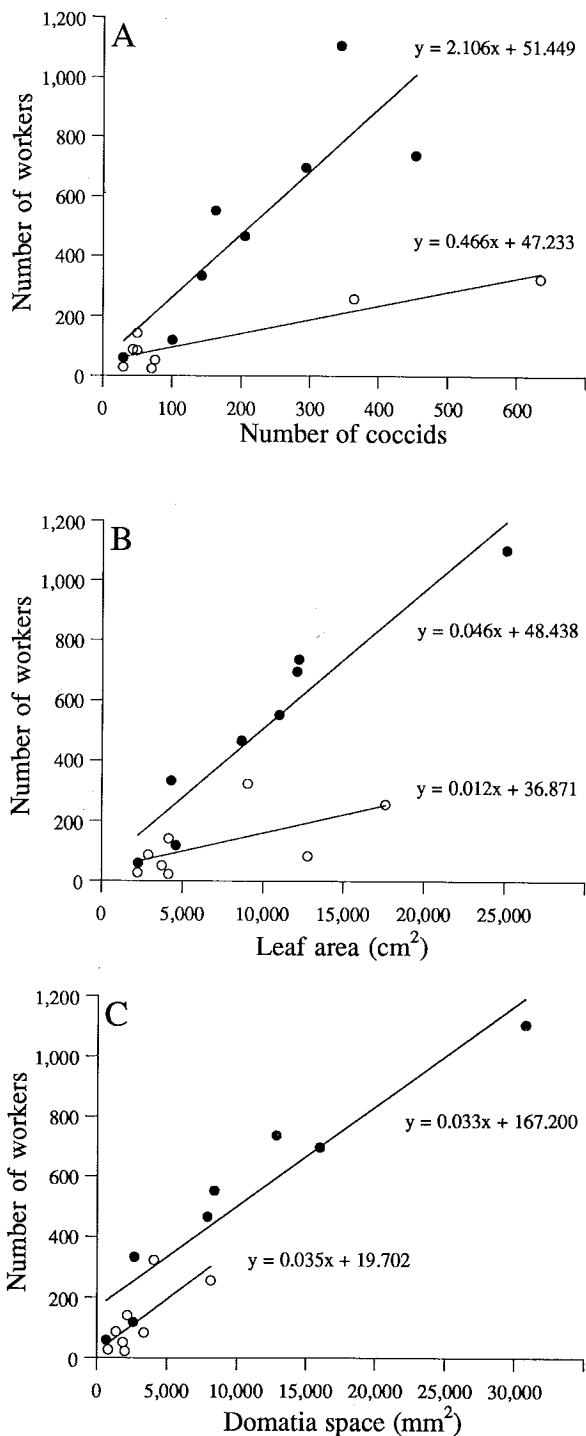


Fig. 4. Relationships between number of workers of *Pseudomyrmex concolor* and A) coccids, B) leaf area and C) domatia space in *Tachigali myrmecophila* (closed circles,  $n = 8$ ) and *Tachigali polyphylla* (open circles,  $n = 8$ ).

*Pseudomyrmex concolor* colonies, using four as F-termer. Only coccids fitted the model ( $\beta = 0.471$ ,  $F_{[1,14]} = 11.306$ ,  $P < 0.01$ ), leaf area ( $F = 0.457$ ) and domatia space ( $F = 0.275$ ) being kept out of the model. This suggests that a simple mechanism associated with the queens' feeding status can control the rate of colony growth of *P. concolor*.

The number of alates in a mature colony of *Pseudomyrmex concolor* is highly correlated with the number of eggs ( $r = 0.949$ ,  $n = 5$ ,  $P < 0.005$ , Fig. 3). The regression line suggests that when the number of eggs accumulated in a colony in a given time is higher than 30, about 20% of the ants produced by the colony will be alates. The number of alates is not correlated with the number of dealate queens ( $r = -0.191$ ,  $n = 5$ ,  $P > 0.05$ ).

The sex ratio of the alates within a colony can be highly skewed to either male or female (Table 1). Although female bias was recorded only in *Tachigali myrmecophila*, and male bias in *T. polyphylla*, this is probably an indirect effect of differences in colony size and maturity. Although few data are available they suggest that larger colonies have a bias for female production while small colonies produce more males than females.

#### Ant colony size

The size of the colonies of *Pseudomyrmex concolor* occupying *Tachigali myrmecophila* is larger than those inhabiting *T. polyphylla* with a comparable number of leaves (Table 1). *T. myrmecophila* colonies have on average 2.6 times more workers per domatium ( $T_m = 66.7$ ,  $T_p = 25.4$ ), 2.9 times more pupae ( $T_m = 13.7$ ,  $T_p = 4.7$ ) and 2.9 more larvae ( $T_m = 63.6$ ,  $T_p = 22.0$ ), than the colonies on *T. polyphylla*. Nevertheless, the average number of eggs per domatium is only 1.5 times bigger in *T. myrmecophila* colonies ( $T_m = 24.3$ ,  $T_p = 16.1$ ). Also, the average number of coccids per domatium is 1.3 times higher in *T. myrmecophila* (28.5) than in *T. polyphylla* (22.0).

#### Limiting factor for ant colony size

The number of workers of *Pseudomyrmex concolor* inhabiting *Tachigali myrmecophila* is highly determined by the domatia space ( $r^2 = 0.901$ ,  $n = 8$ ,  $P < 0.001$ ), leaf area ( $r^2 = 0.914$ ,  $n = 8$ ,  $P < 0.001$ ), and number of coccids ( $r^2 = 0.723$ ,  $n = 8$ ,  $P < 0.005$ ). For *T. polyphylla*, the determination coefficients between number of workers and both domatia space ( $r^2 = 0.536$ ,  $n = 8$ ,  $P < 0.05$ ) and coccids ( $r^2 = 0.851$ ,  $n = 8$ ,  $P < 0.001$ ) are significant, but with leaf area the coefficient is only near the significant level ( $r^2 = 0.384$ ,  $n = 8$ ,  $0.10 \leq P \leq 0.05$ ). The generally high determination coefficients of the

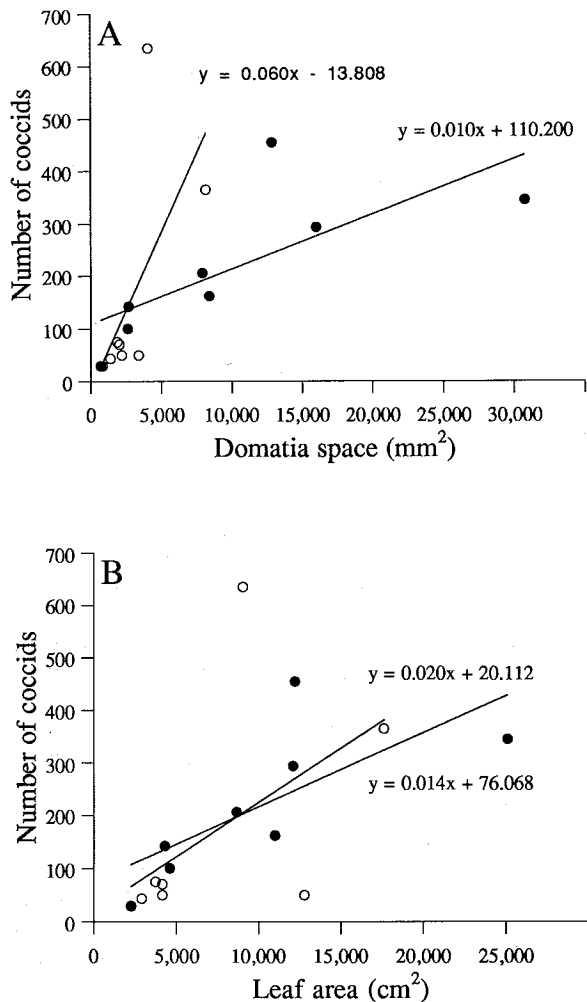


Fig. 5. Relationships between number of coccids and A) domatia space and B) leaf area in *Tachigali myrmecophila* (closed circles,  $n = 8$ ) and *Tachigali polyphylla* (open circles,  $n = 8$ ).

associations described above seem to be the result of the general trend of all variables to increase with the increase in plant size.

The intraspecific comparison between the linear regressions of colony size of *Pseudomyrmex concolor* inhabiting *Tachigali myrmecophila* and *T. polyphylla* sheds light on the factors affecting ant colony size. Although high determination coefficients between workers and coccids were found for colonies occupying both *Tachigali* species, the slope of the regression for *T. myrmecophila* ( $\beta = 2.106$ ,  $F_{[1,6]} = 15.645$ ,  $P < 0.01$ ) is about 4.5 times higher than for *T. polyphylla* ( $\beta = 0.466$ ,  $F_{[1,6]} = 34.147$ ,  $P < 0.001$ ), this difference being highly significant ( $F_{[1,12]} = 33.106$ ,  $P < 0.001$ , Fig. 4A). This means that the same number of coccids predicts different numbers of workers of *P. concolor* according to the host plant species. Thus, a factor other than food must be limiting ant colony size.

The slope of the regression between workers and leaf area for *Tachigali myrmecophila* ( $\beta = 0.046$ ,  $F_{[1,6]} = 63.964$ ,  $P < 0.001$ ) is about 3.7 times higher than for *T. polyphylla* ( $\beta = 0.012$ ,  $F_{[1,6]} = 3.733$ ,  $P > 0.05$ ), this difference being highly significant ( $F_{[1,12]} = 40.753$ ,  $P < 0.001$ , Fig. 4B). Again, there is another factor which constrains the number of workers in *Tachigali*.

There are no significant differences ( $F_{[1,12]} = 0.000$ ,  $P > 0.05$ ) between the slopes of the regressions between number of workers and domatia space in *Tachigali myrmecophila* ( $\beta = 0.033$ ,  $F_{[1,6]} = 54.794$ ,  $P < 0.001$ ) and *T. polyphylla* ( $\beta = 0.035$ ,  $F_{[1,6]} = 6.919$ ,  $P < 0.05$ , Fig. 4C). This means that independently of the host plant species the same colony size is predicted if a given domatia space is available for the colony of *Pseudomyrmex concolor*.

As an additional statistical approach a stepwise regression was used with the pooled data from both *Tachigali* species using workers as the dependent variable, and domatia space, leaf area and coccids as independent variables in the full model. The F-to-enter was 4.0. It is expected that only the variables relevant to explain the number of workers in both species will be significant. Only domatia space fitted the model ( $\beta = 0.038$ ,  $F_{[1,14]} = 100.319$ ,  $P < 0.001$ ), leaf area ( $F = 0.597$ ) and coccids ( $F = 3.111$ ) being kept out of the model. Therefore, both these analyses suggest that in the *Pseudomyrmex/Tachigali* system nesting space is the most important factor controlling ant colony size.

#### Limiting factor for coccids

The same type of intraspecific comparisons as were made above can be performed to ask what factor is controlling the number of coccids occupying each species of *Tachigali*. In *T. myrmecophila* there are good determination coefficients between the number of coccids and both domatia space ( $r^2 = 0.542$ ,  $n = 8$ ,  $P < 0.05$ ) and leaf area ( $r^2 = 0.527$ ,  $n = 8$ ,  $P < 0.05$ ). In *T. polyphylla* the determination coefficients are not so good for either domatia space ( $r^2 = 0.401$ ,  $n = 8$ ,  $0.05 \leq P \leq 0.10$ ) or leaf area ( $r^2 = 0.270$ ,  $n = 8$ ,  $0.20 \leq P \leq 0.10$ ).

The slope of the regression between coccids and domatia space for *Tachigali myrmecophila* ( $\beta = 0.010$ ,  $F_{[1,6]} = 7.091$ ,  $P < 0.05$ ) is about 5.7 times lower than that presented by *T. polyphylla* ( $\beta = 0.060$ ,  $F_{[1,6]} = 4.015$ ,  $0.05 \leq P \leq 0.10$ ), this difference being highly significant ( $F_{[1,12]} = 14.727$ ,  $P < 0.01$ , Fig. 5A). So, there is another factor constraining the number of coccids in *Tachigali*. The relationship between number of coccids and number of workers was analysed previously, the number of coccids per worker being different for the two *Tachigali* species (Fig. 4A).

There is no significant difference ( $F_{[1,12]} = 0.615$ ,  $P > 0.05$ ) between the slopes of the regressions between number of coccids and leaf area between *Tachigali myr-*

*mecophila* ( $\beta = 0.014$ ,  $F_{[1,6]} = 6.673$ ,  $P < 0.05$ ) and *T. polyphylla* ( $\beta = 0.020$ ,  $F_{[1,6]} = 2.220$ ,  $P > 0.05$ , Fig. 5B). The same leaf area predicts the same number of coccids in both *Tachigali* species. Therefore, leaf area seems to control the number of coccids.

A stepwise regression was applied to the pooled data. Only workers fitted the model ( $\beta = 0.346$ ,  $F_{[1,14]} = 8.358$ ,  $P < 0.05$ ), leaf area ( $F = 0.688$ ) and domatia space ( $F = 0.665$ ) being kept out of the model. Thus, by this analysis the predatory activity of *Pseudomyrmex concolor* seems to control the total number of coccids in *Tachigali* domatia.

## Discussion

The upper limit of the colony size of *Pseudomyrmex concolor* is constrained by the space available for nesting activities offered by the leaf domatia of *Tachigali*. However, the three-trophic level interaction between ant, coccid and myrmecophyte seems to be the key factor in the understanding of the ant colony growth and maturation. *P. concolor* feeds upon the coccid colony which feeds on the phloem sap of *Tachigali*. Consequently, the energy and nutrients consumed by the ants are produced by the photosynthetic activity of *Tachigali*. Plants growing in a productive environment (e.g. good light conditions) and experiencing a low level of herbivory are able to maintain a high production of coccids and consequently a high rate of egg and alate production.

If the ants do not patrol the leaves and drive off herbivores, the photosynthetic rate of the plant will decrease and so will the production of coccids. Then, if an ant colony permits the plant to be highly damaged by herbivores, the ant colony would become food limited and the coccid colony overexploited. As a result, the ant colony would not reach the maximum colony size permitted by the host and would probably present a lower fitness, as measured by the number of alates.

*Pseudomyrmex concolor* is a very aggressive ant which bites and stings most of the insect herbivores that it finds on the host plant. However, this patrolling behaviour is not associated with foraging because the potential prey are thrown off the plant. How can such behaviour evolve? The three-trophic level framework proposed above seems to shed light on the evolution of the aggressiveness in ant-plant systems where the plants do not offer directly any food reward for the ants. Ants presenting a higher efficiency of patrolling activity against herbivores, and presumably competitors (Davidson et al. 1989), were provided indirectly with higher food availability and were able to present higher colony growth and reproduction than colonies presenting a timid behaviour.

The phylogeny of the pseudomyrmecine ants confirms the view that they repeatedly have developed

obligate associations with myrmecophytes (Ward 1991). As Janzen (1966) stated, increased aggressiveness seems to be a convergent behavioural trait among *Pseudomyrmex* plant-ants because most free-living species show very timid behaviour. Outstandingly aggressive behaviour can be found in *Pseudomyrmex* from different lineages associated with *Acacia*, *Tachigali* and *Triplaris* (Benson 1985). In cases where the ant feeds directly on the plant products (e.g. Beltian bodies of *Acacia*) there is a direct linkage between the plant photosynthetic rate and the ant colony fitness.

## Host-restricted foraging and space-limited colony size

The ratio between energy intake and the time spent to retrieve the food is an important variable in many central place foraging models (Brown and Orians 1970, Hölldobler and Lumsden 1980). Most of the ants nesting in myrmecophytes strongly maximize this ratio because their nesting and feeding sites are sometimes virtually the same. Host-restricted foraging is a general rule among dominant ants associated with myrmecophytes. In a Peruvian rainforest, six of the numerically dominant ant species occurring in eight myrmecophytes foraged only on the host surface (Davidson et al. 1989). In about 15 myrmecophytes occurring in the Cabo Frio reserve my observations corroborate this ant foraging pattern. Although many ants are generalists in their food habits, plant-ants usually tend coccids inside domatia. These coccids represent a regular food source for the ants, acting as a buffer for colony growth during decreasing food productivity. *Pseudomyrmex concolor* seems to be an extreme case, feeding its colony almost entirely with the coccids *Catenococcus* sp., and these ants are never found off the host plants except during defensive events when they fall down in order to remove either ant competitors, or phytophagous or predatory insects.

If food were the limiting factor on the development of plant-ant colonies, what would explain this limitation in territory area? The nesting space-limited hypothesis presented in this paper can explain these facts satisfactorily. If the colony size is space-limited and the host offers directly or indirectly enough food to its partners, there is no reason to extend the territory beyond the plant boundary. As a corollary, ants that are able to escape the space limitation are not expected to exhibit host-restricted foraging. Davidson et al. (1989) recorded three *Azteca* species that are able to build carton nests outside the host domatia. As expected, the foraging areas of all these species were not restricted to their host. Furthermore, *Crematogaster* cf. *victimia* occupying *Maieta guianensis* and *Clidemia heterophylla* (Melastomataceae) was considered "unusual as a common plant-ant not restricted to its host" (Davidson et al. 1989). In the Cabo Frio reserve, *Maieta guianensis* occurs in ag-

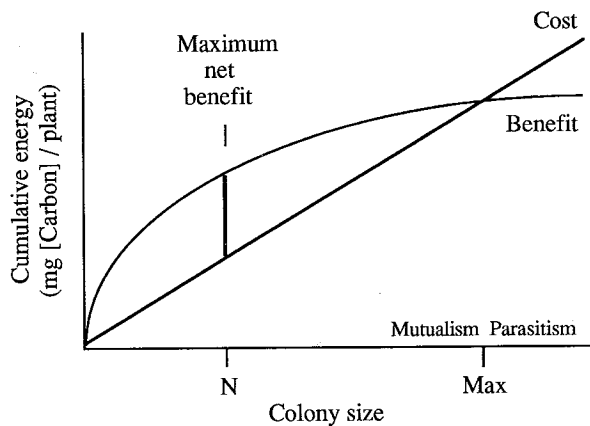


Fig. 6. Graphic model of cost and benefit to a myrmecophyte of maintaining increasing ant colony size. *N* is the colony size that produces the greatest net benefit to the plant. *Max* is the colony size with null net benefit.

gregated patches produced by asexual reproduction and an ant colony can be spread over several stems in the same clone. So, the trails on the forest floor cannot be considered an exception to the host-restricted rule. Interestingly, Davidson et al. (1989) had no direct evidence that *Crematogaster cf. victima* was foraging off the host plant.

*Pseudomyrmex concolor* and *P. nigrescens* are closely related species, both classified within the *P. viduus* group (P. S. Ward, 1991, pers. comm.). Both species inhabit *Tachigali* at my study site, but *P. concolor* occurs only in small trees up to 7 m, while *P. nigrescens* occurs mainly on medium sized trees but also occupies large canopy trees (Fonseca 1991). While colonies of *P. concolor* are relatively small, the colonies of *P. nigrescens* can be one or two orders of magnitude larger. This suggests that phylogenetic constraints are not limiting the colony size of *Pseudomyrmex*. The absence of phylogenetic constraints on mature colony size was suggested at a larger taxonomic scale by Hölldobler and Wilson (1991). Furthermore, Janzen (1973) has estimated that only one colony of the polygynous *Pseudomyrmex venefica* may contain 1.8–3.6 million workers spread over hundreds of acacias. As Janzen (1973) pointed out, “[the ant colony] size is set by how large a stand of acacia can grow in the face of competition with other plants”, suggesting that although this outstanding ant species has broken the boundary of an individual host plant, it could not escape the limit imposed by the overall nesting site.

### The plant's point of view

How does colony size affect the plant performance? Host plants are generally responsible either directly (e.g. by Mullerian and Beltian bodies) or indirectly

(e.g. by coccids) for production of most of the food resource obtained by the ant colony. Assuming that the requirement of energy and nutrients for the production and maintenance of a worker is uniform, it is reasonable to suppose that to support colonies of larger size the plant needs to allocate a directly proportional amount of resources, the cost growing continuously (Fig. 6).

The simple presence of ants has been demonstrated to decrease herbivorous insect activity in several ant-defence mutualisms (Way 1963, Bentley 1977, Beattie 1986). The higher the density of patrolling workers the higher will be the effectiveness of the plant defence. Nevertheless, as more workers are added to the patrolling activity on the leaf surface, the importance of each individual in the search and aggression against the herbivores becomes lower. At some stage their patrolling efficiency approaches a maximum and eventually the benefit to the host plant reaches a limit.

The intersection of the cost and benefit curves represents the maximum ant colony size in which the net benefit is positive and, by definition, mutualistic interaction is possible (Fig. 6). If these arguments are correct, some colony sizes present a negative net benefit to the plants, the ants playing a parasitic role in the relationship. The almost complete absence of patrolling activity by some ant species inhabiting *Acacia*, and the corresponding drop in the benefit curve, leads to their parasitic life style (Janzen 1975). Many ant-plants offer domatia space and other myrmecophytic traits later in their development (Davidson and Fisher 1991). This suggests that ant-plant seedlings are delaying the development of myrmecophytic traits until a size when they are able to maintain the cost of a bigger and efficient ant colony.

According to the model, there is a colony size where the net benefit reaches a maximum and the plant should present the best performance. In myrmecophytes, domatia are produced as modular structures. The number of domatia as well as their size will define the total space available to be occupied by the ants. If ants are space-limited the control of these variables would permit the plant to manipulate the colony size. In myrmecophytic *Tachigali* there is always one domatium per leaf, but the size of the domatia seems to be species specific. In *Tachigali* the ratio of domatia space to leaf area is highly uniform and is probably the result of a simple allometric rule. Nevertheless, this ratio can be visualized as the relationship between investment in myrmecophytic defence and the amount of tissue to be defended. If this is the case, *Tachigali myrmecophila* is investing about three times more in myrmecophytic defence than *T. polyphylla* (Fig. 2). This difference in ant defence allocation could be expected if *T. myrmecophila* leaves suffer either a higher herbivory pressure or a smaller allocation in chemical defences than *T. polyphylla* leaves.



## Consequences of space limitation for the ant community

In the complex environment of the wet tropical rainforest many sites below and above ground are available as ant nesting sites: dead matter, hollow and hollowable live stems and many diverse structures of the plants. Nevertheless, only colonies in appropriate nesting sites will be successful and the ability to find them should be rewarded by natural selection. The evolutionary capability to nest in a completely new micro-habitat has evolved many times in the tropics and in some cases results in a higher fitness associated with this enemy-free environment. I have observed queens of *Pseudomyrmex concolor* being killed by both opportunistic spiders and foraging *Crematogaster* ants. Saplings of the ant-plant *Cecropia* frequently contain numerous incipient *Azteca* ant colonies. During the plant development only one colony survives, the main cause of queen mortality being parasitism (Wheeler 1942, Longino 1991). The brood of the ant *Pachycondyla luteola* seems to be particularly susceptible to hymenopteran parasitoids because of its non claustral behaviour (Davidson and Fisher 1991). The solitary alate queen is primarily concerned with her own survival and finding a nesting site free of competitors, predators and parasites. Nonetheless, the consequences of her choice will appear afterwards with the colony development. A new life-history may be associated with some unexpected drawbacks. For example, plant-ants are relatively safe from food competitors but they are limited by the nest space offered by the myrmecophytes.

The spatial distribution of plant-ant colonies will be highly dependent on the host distribution, and as the plants in the tropics are scattered, the interaction process during the early stages of colonization is more significant than the interaction between mature colonies. The negative interspecific association pattern found among plant-ants occupying many Peruvian myrmecophytes suggests that direct interference among and within ant species is structuring the ant occupation pattern in myrmecophytes (Davidson et al. 1989). Competition for myrmecophytic nesting site is supposed to occur among *Tachigali* ant species. In the Cabo Frio reserve, at least eight ant species are able to colonize *Tachigali*. These species present a vertical pattern of distribution that enables them to coexist. Here, finer subdivisions of the nesting site niche permit the maintenance of a higher diversity of ant species (Fonseca 1991).

Whether space-limited ant colony size is restricted to plant-ants is a question to be examined. One of the biggest colony sizes of neotropical ants is reached by the predatory army ants *Eciton* that nest in a bivouac of workers and soldiers. Some *Azteca* colonies build a carton nest about 3 m high on the trunks of the trees containing an extraordinary colony size. Also the work force of a mature colony of the dominant African

weaver ant *Oecophylla longinoda* that binds leaves into tight nest compartments usually consists of more than 500 000 individuals. It is suggested that in the tropics these species are actually exceptions to a general rule of nesting space-limited ant species.

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