

**Interactions between
Tetrathylacium macrophyllum
(Flacourtiaceae) and its live-stem
inhabiting ants**

in the Parque Nacional Corcovado,
Sección Piedras Blancas, Costa Rica



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ABSTRACT

Tetrathylacium macrophyllum (Flacourtiaceae) is an ecologically little known tropical treelet occurring in South and Central America and growing mainly in primary forest on steep slopes close to small rivers and creeks. In this study 205 trees were investigated in the vicinity of the Biological Station La Gamba in the Corcovado National Park, Section Piedras Blancas, Costa Rica. The branches of *T. macrophyllum* are partially hollow stems with natural openings. The stem cavities are produced by the plant itself by the degeneration of the pith canal. In that process parts of the branch split, leaving a natural entrance hole for the ants. The hollow canal is not continuous, as only 53 % of the pith degenerates. Every new growth unit (on average 5 internodes) adds an additional hollow segment, which reaches a mean length of 13,34 cm. The hollow pith canals serve as domatia for ants. About 85 % of the ants belong to four genera, the two most significant are *Crematogaster* and *Azteca*, while *Pachycondyla* and *Pheidole* are of minor importance. Due to the shady environment in primary forest, the domatia are developed relatively late, when the tree has reached a height between 1 and 4 m. In this stage a succession of ant colonisation takes place, leaving *Crematogaster* and *Azteca* the most successful inhabitants, together occupying 70 % of the investigated trees. Only 15 % of the investigated trees were occupied exclusively by *Pachycondyla* and/or *Pheidole*. These were neither observed to defend their host tree nor to tend coccids. Therefore these species seem to have neither a positive nor a negative effect to their host. In contrast *Crematogaster* and *Azteca* defend their host, reduce herbivory by approximately 50 % and tend coccids. Both *Crematogaster* and *Azteca* produce carton structures to seal the natural entrance holes and to protect their coccids. In case of *Azteca* extensive carton galleries are constructed that connect all occupied domatium chambers. These carton tunnels are situated at the lower side of the branches and contain many tiny holes just big enough for the ants to enter. The low presence of epiphytes on *Azteca*-occupied trees seems to be connected with the presence of the extensive carton galleries. Experiments showed that *Azteca* ants remove material from the plant's surface to construct and repair their carton tunnels. The defense strategies between *Crematogaster* and *Azteca* differ notably. Whereas *Crematogaster* ants simply attack leaf beetles and other herbivores on the plant's surface and remove lianas, *Azteca* shows a more unusual and so far unknown defense strategy. The extensive carton galleries are used to protect their host from other insects, especially leaf-cutter ants (*Atta* sp.). If *Atta* ants enter an *Azteca*-occupied tree, the workers and soldiers place themselves with open mandibles inside the carton tunnel close to the holes. When crossing the carton tunnel, the *Atta* ants almost inevitably step into one of the holes and then are caught by the *Azteca* ants. In an experiment, more than half (64,65 %) of the *Atta* ants placed on a twig with *Azteca*-galleries got trapped by *Azteca* within 30 minutes. The trapped ants are either dropped to the ground or dragged into the nest, serving probably as an additional food source. In that way *T. macrophyllum* is well protected against the risk of leaf-cutter attacks. This protection is restricted to trees in primary forest because *Crematogaster* and *Azteca* ants are completely absent in secondary forest, where *Pheidole* and other ant species are most common. This may be due to different climatic conditions that may inhibit the survival of the coccids, thus leaving *Crematogaster* and *Azteca* without their major food source. In general, the interactions between *T. macrophyllum* and its live-stem inhabiting ants are not highly specialized and the ant inhabitants may also occur on other plant species with similar myrmecophytic traits.

1. INTRODUCTION

Several tropical plants have evolved morphological and biochemical adaptations to attract ants. Ant-attractants can be found in different phylogenetic tribes, as well in the paleotropics as in the neotropics. These facts show that they evolved independently from each other and are convergent structures.

Plant structures that represent morphological adaptations are extrafloral nectaries (EFN) (*Passiflora*, *Acacia* etc.), food bodies (FB) (*Acacia*, *Barteria*, *Cecropia*, *Macaranga*, *Piper*, etc.) and domatia (*Acacia*, *Cecropia*, *Duroia*, *Maieta*, *Piper*, *Schomburgkia*, *Tillandsia*, *Triplaris*, etc.) to feed or shelter the ants (Beattie 1985, Jolivet 1996). Plants possessing either one, two or all of these ant attractants are called myrmecophytes or ant-plants.

These plant structures provide nesting space and can be formed by very different plant organs and tissues, e.g. the leaf (*Duroia*, *Maieta*, *Toccoca*, etc.), the petiolus (*Piper*, *Tachigalia*, etc.), thorns (*Acacia*), hollow roots (*Pachycentria*), pseudobulbs produced by the hypocotyl (*Hydnophytum*, *Myrmecodia*), hollow stems (*Cecropia*) or hollow branches (*Ocotea*, *Pithecellobium*, *Triplaris*, etc.). The ants access the domatia either by chewing a hole (*Acacia*, *Cecropia*, *Leonardoxa*, *Piper*) or through relatively large openings (*Tetrathylacium*) (Beattie 1985, Davidson & McKey 1993, Jolivet 1996).

Ants that house this plant-borne domatia are either specialized on a specific myrmecophytic plant (e.g. *Azteca-Cecropia*, *Pseudomyrmex-Acacia*) or can colonise a variety of plants (e.g. *Azteca*, *Crematogaster*) (Janzen 1983, Davidson & McKey 1993, Jolivet 1996, Bronstein 1998).

In Costa Rica several ant-plants have been studied in detail on the atlantic-slope rain forest and the central and north pacific-slope forest, e.g., *Acacia*, *Cecropia*, *Cordia*, *Ocotea*, *Piper* and *Triplaris* (Risch 1977, Janzen 1983, Letourneau 1983, Longino 1989, Ickes & Ishii 1995, Longino 1996). Less attention has been paid to a plant species associated with ants that was mentioned by Tennant 1989, *Tetrathylacium macrophyllum* (*costaricense*) (Flacourtiaceae).

This ant-plant occurs in Costa Rica only in the south-west pacific wet forest of the Corcovado region (Janzen 1983). According to Tennant 1989 (in Jolivet 1996: p.95) it is colonised mainly by ants of the genera *Azteca* and *Crematogaster*, but also by a variety of other ant species.

Taxonomy & Ecology of *Tetrathylacium macrophyllum*

The genus *Tetrathylacium* belongs to the pan-tropical family Flacourtiaceae. Two species are known: *T. macrophyllum* Poepp. & Endl. (Synonyms: *T. costaricense* Standl., *T. nutans* Sleum., *T. pacificum* Standl., *Edmonstonia pacifica* Seem.) and *T. johanseni* Standl., which both occur on the south pacific part of Costa Rica. In contrast to *T. macrophyllum*, *T. johanseni* has no myrmecophytic traits.

T. macrophyllum is a treelet growing mainly in the forest under storey. It is found preferentially on steep slopes near rivers and creeks in primary forest (Janzen 1983), less common it is found in dryer secondary forest. The average height is 8 meters but it

may reach a maximum height of 15 - 20 meters. The distribution area of *T. macrophyllum* is mainly the Colombian pacific forest of the Choco-Region (Gentry 1997), extending to Ecuador and Peru to the south (Brako & Zarucchi 1993, Jorgensen & Léon-Yamez 1999) and to the Corcovado region of Costa Rica to the north (Janzen 1983). Characteristic of most of this distribution area is the high annual rainfall (> 5000 mm). The altitudinal distribution ranges from 0 up to 1500 m.

No detailed information about the myrmecophytic traits is available. The only known is that the tree provides pre-formed chambers on the branches. This chambers break up at one side, thus allowing entrance to ants without excavation (Longino 1996) (see Fig. 12).

Taxonomy and behaviour of inhabiting *Azteca* sp.

In a recent phylogenetic revision of the ant genus *Azteca* Longino (1996) reported *Azteca* ants colonising *T. macrophyllum*. They belong to the *Azteca nigricans* species complex and are referred to as *Azteca* JTL 001. Workers of live-stem inhabiting ants are rarely observed to forage on the plant's surface. In contrast to the aggressive *Azteca* species colonising *Cecropia*, they appear rather timid. Only in case the domatium chambers are broken up aggressively they start attacking the intruder. Thus, colonies of this species are inconspicuously.

This species constructs an extensive system of galleries that connect the occupied domatium chambers. These galleries are made of black, very crusty carton, containing tiny, circular holes. No explanation for the functional significance of these holes has been suggested so far.

Homoptera (Coccoidea: mealy bugs and scales) are regularly found on the inner side of the domatium chambers and on the branch surface underneath the carton galleries (Longino 1996).

Scope of the study

Though a rough overview of this particular ant-plant system has been given in Jolivet 1996, more detailed research is necessary to gain more understanding of this interaction. In the present study the following questions will be investigated:

- 1) How intense is the association between the plant and its ants?
- 2) Is *T. macrophyllum* indeed a myrmecophytic plant?
- 3) What is the effect to the plants from the interaction?
- 4) What is the effect for the ants from the interaction?
- 5) Does the association differ in dependence on different habitats?

2. MATERIAL AND METHODS

Voucher specimens

Herbarium specimens of *Tetrathylacium macrophyllum* Poepp. & Endl. have been deposited in the herbarium of the Museo Nacional de Costa Rica, San Jose.

Tetrathylacium macrophyllum Poepp. & Endl., Puntarenas, Parque Nacional Corcovado, Sección Piedras Blancas, La Gamba: Bird trail, 8° 41' N, 83° 13' W, 300 m, primary tropical rain forest, February 2000, M. Schmidt, 1;2 (CR)

Specimens of *Azteca* JTL 001 have been deposited in the Museo Nacional de Costa Rica, San Jose.

Study site

The study was conducted in the vicinity of the Corcovado National Park, Seccion Piedras Blancas, Costa Rica, at the Biological Station La Gamba. All trees investigated were growing in the closer vicinity of the research station. La Gamba is located in the Puntarenas province at 8° 41' North and 83° 13' West, approximately 37 km north from the panamanian border and about 5 km to the east of the Golfo Dulce coast.

Situated at 200 m elevation, this part of the nationalpark is covered mainly by primary tropical wet forest. Outside the National park there is also a secondary forest where parts of the study were conducted. This secondary forest has been selectively logged 20 years ago.

The climate depends on pacific influence. The rainy season is from May to November, and the dry season from December to April. The total annual rainfall, that has been recorded for the last three years, is about 5000 mm/year. High rainfall and the relative short distance to the southamerican continent seem to be the most important factors that this forest is closely related to the Choco-forest at the Columbian pacific coast. About 50 % of the trees (< 10cm dbh) in La Gamba, also occur in the Choco-forest (Gentry 1997, Weber et al. 2001).

Data recorded in the trees investigated

Between February and April 2000, 205 individual trees of *Tetrathylacium macrophyllum* were investigated. 185 trees grew in the primary forest in a distance of 10 m from "Bird trail", "Ocelot trail" and the upper part of the Quebrada Chorro. 20 trees grew in secondary forest on the road from La Gamba to Golfito, close to the western end of La Gamba. For each of the 205 trees the following parameters were protocolled:

- 1) Height (in m)
- 2) Diameter in breast height (dbh in cm)
- 3) Crown size (using 5 size classes: 1, very small; 2, small; 3, medium; 4, large; 5, very large)
- 4) Presence and identity of ants (0, no ants; 1, occupied; ant genus)
- 5) Presence of carton tunnels produced by *Azteca* ants (0, without; 1, with)
- 6) Percentage of carton tunnel of the total length of branches (in %)
- 7) Percentage of branches covered by epiphytes (in %)
- 8) Distance to river (in m)
- 9) Percentage of canopy cover (in %)
- 10) Sloping of the ground (in %)
- 11) Type of forest (primary or secondary forest)
- 12) Presence of flowers or fruits (0, without; 1, with)

All experiments were carried out only with *Tetrathylacium* trees of the primary wet forest, except ant occupancy that was compared between primary and secondary forest. No further comparison was made for the rest of the studies.

Experiments regarding

a) Domatia

The branches are partially hollow, thus forming domatia or domatium chambers. The absolute size of the domatia was measured. The volume of the domatium chambers depends mainly on the variation of its length, whereas the diameter of the “hollow pith canal” (HPC) - due to its stable size - has only a small impact on the total size. Therefore the length of the hollow pith canals was used as an parameter of domatium size.

The HPC consists of two different types. The first and larger portion is accessible by ants through natural openings or chewed entrance holes, whereas the second and smaller portion is not accessible. The non-accessible HPCs can mainly be found in the younger parts of the branches and normally connect to the accessible HPC in the continuing growth or the ants chew additional entrance holes.

The relative domatia size (in %) was calculated as:

$$\text{relative domatia size (in \%)} = \frac{\text{total length of domatium chambers per branch} \times 100}{\text{total length of branch}}$$

To document the growth of the domatium chambers the relative domatium size was compared to the mean branch diameter, the diameter in breast height and tree height of 10 individuals. These 10 trees (between 1 m and 10 m height) were either unoccupied by ants or occupied by *Crematogaster*.

A total number of 18 branches from six trees (three branches / tree) higher than 4 m was used to measure the mean total length and the mean relative length of domatium chambers. Comparable branches in the upper part of the trees were selected.

Measurements of branch diameter were made in the middle of the youngest 20 internodes. Using a calliper rule the measurements were made to the closest 0,1 mm. Mean branch diameter was calculated as the mean average of the 20 measurement points.

Trees smaller than 4 meters height were measured using an inch rule, whereas trees taller than 4 meters were visually estimated to the nearest meter.

b) Live-stem inhabiting ants

Collection of live-stem inhabiting ants was done to evaluate ant-diversity of *T. macrophyllum*. To distinguish different ant-occupancy patterns of the tree's domatia, ants were collected from 38 randomly selected trees in primary and 6 in secondary forest. Whereas all investigated trees from secondary forest were higher than 4 meters, trees from primary forest ranged from 1 - 12 m height: 0 - 2 m (n = 9), 2 - 4 m (n = 9), 4 - 12 m (n = 20).

From each tree at least three branches with a minimal length of one meter were cut from the upper part of the tree. Each investigated branch held at least three domatia, and an overall sample included minimum 10 and maximum 20 domatia/tree which were investigated in detail. I regarded the domatia as occupied when I found: ants with their brood, ants with their typical carton constructions, queens or members of the sexual caste. In case of *Azteca* occupation could also be verified visually from the ground. This is due to their extensive clearly visible carton gallery at the lower side of the branches.

To proof the influence of worker size of the ants on occupation patterns, body size of the four main ant inhabitants were measured, using head length and mesosomal length as indicators of body size (Seifert 1996). Difficulties of size differences in polymorphic ant species were avoided as 50 individuals/species were randomly chosen for measurement. In case of monomorphous *Pachycondyla* only 26 individuals were measured. Measurements were conducted with a stereo microscope (Wild Heerbrugg M3) and an ocular micrometer (calibrated with an object micrometer), using an amplification of 40 x.

c) Natural openings and ant-made cavities

Hollow pith canal length with and without access and solid pith canal length of *Azteca* and *Crematogaster*-occupied trees were compared to test their impact on ant excavated domatia size. To proof this effect I created 3 subsets of 6 plants each. One subset had *Azteca*, another *Crematogaster* as its main inhabitants, the third subset was not occupied by ants (all samples from primary forest). From each tree at least 3 branches with a minimal length of 1 m were cut from the upper part of the tree. Each investigated branch held at least 3 domatia, and an overall sample included minimum 10 and maximum 20 domatia/tree which were investigated in detail.

The plants of the first two subsets were chosen as similar as possible, the third subset included mainly younger and therefore smaller trees, because bigger trees were practically all ant-occupied.

d) Leaf damage

Leaf damage was investigated in the same three subsets as in chapter “Natural openings and ant-made cavities” to look for the protective influence of *Azteca* and *Crematogaster*. For the collected leaves from the 3 subsets (leaves: *Azteca*-subset n = 356, *Crematogaster*-subset n = 376, no ants-subset n = 142) the cumulative leaf damage as a percentage of leaf area was estimated to the nearest 5 %. Additionally the mean leaf damage was calculated.

e) Epiphytes

Epiphytic cover of all 185 investigated primary forest trees, as percentage of branches covered by epiphytes, was estimated visually to the nearest 10 %. (Coverage of epiphylls on leaves was not measured due to measurement difficulties.) The epiphytic cover was estimates as the percentage of total branch length that is covered by epiphyts (such as orchids, Bromeliaceae, Araceae, mosses and so on). In that estimation it has the same effect if for example, 25 % of the branches are totally covered by epiphyts and the

other 75 % are free of epiphytes, or if 25 % of all branches are covered. In both cases the estimation would be 25 %.

I compared the results with several other factors for possible correlations. For each factor the correlation coefficient r^2 was calculated.

The following factors were compared:

- 1) Total height
- 2) Diameter in breast height (dbh)
- 3) Canopy size of the investigated trees (estimated visually using five categories; 1 = very small, 2 = small, 3 = medium, 4 = big and 5 = very big)
- 4) Presence of carton nests made by *Azteca*
- 5) Percentage of carton nest of the total branches (estimated visually to the nearest 10 % and later on put into four categories: 0 – 25 %, 25 – 50 %, 50 – 75 % and 75 – 100 %)
- 6) Distance to surface water (estimated visually in meters)
- 7) Percentage of canopy covered from the surrounding trees (estimated visually to the nearest 10 %)
- 8) Sloping of the ground (estimated visually to the nearest 10 %)

f) Removal of adhesive tape

To proof a possible correlation between epiphytic cover and carton nest building ants, a removal experiment was conducted. Because small epiphytes (e.g. mosses) could not be transferred to other branches without strongly destroying the plant tissue of the epiphyte, adhesive tape (TESA[®] textil fiber adhesive tape, 19 mm width) was used for this experiment. Ten *Azteca*- and six *Crematogaster*-occupied trees which were easily accessible were randomly selected and the adhesive tape was mounted around two branches per tree. So the total number of adhesive tapes was $n = 20$ for *Azteca* and $n = 12$ for *Crematogaster*. In case of *Azteca* the carton tunnel was locally destroyed to place the sticky tape on the surface of the tree.

One week after mounting the tapes, the adhesive tapes were checked whether the ants had removed tape material. Four categories were used:

- 1) Nothing removed
- 2) Small parts removed
- 3) Large parts removed
- 4) Totally removed (this means that a corridor was cut through the tape)

g) Defense strategy

To test the protective effect of domatia inhabiting ants, leaf cutter ants (*Atta* sp.) were used as a potential natural threat to the plant. In four experiments workers and soldiers of leaf cutter ants ($n = 116$) from nearby nests were placed on *Azteca*-occupied trees. For half an hour the behaviour of the leaf cutter ants was checked every five minutes and recorded as one of 4 behavioural categories.

In case *Atta* ants left the branch to rest on a leaf, they were put back on the branch again. Preliminary test showed that *Crematogaster* did not interact with *Atta* at all. Therefore the experiment was only conducted with *Azteca*-occupied trees.

Four different behavioural categories of *Atta* could be observed, after setting free *Atta* ants:

- 1) Forage freely (free)
- 2) Drop down (dropped)
- 3) Leave the tree (abandoned tree)
- 4) Get caught by the domatia inhabiting ants (trapped)

h) Foraging territory

This experiment was conducted to test whether ants do leave the tree or whether they are strictly arboreal. First tuna baits were placed on the base of *Azteca*- (n = 14) and *Crematogaster*-occupied (n = 6) trees. The trees from primary forest had been randomly selected before. After one and two hours, it was checked whether the ants got access to the bait or not. Ants descending to approach the tuna bait at the base of the tree were regarded as “arboreal and terrestrial”. In contrast those remaining in the canopy were considered as strictly “arboreal”.

i) Artificial domatia

Artificial domatia were placed in the ants territory to proof two aspects, firstly whether the ants also nest in “dead” cavities and secondly how strong the territorial dominance is. Weak dominance is the fact if other insects could enter and stay in the artificial domatia.

Transparent straws were fixed on *Azteca* (n = 12) and *Crematogaster* (n = 10) trees. The straws were always fixed to ant-occupied regions of the tree. The straws were closed on its ends with adhesive tape and had artificial openings – similar to the natural openings in size and location. During 2 months the straws were investigated weekly for ant occupation or “other insect”-occupation.

3. RESULTS

Domatia

Description. Saplings and small plants of *T. macrophyllum* have thin and solid twigs. At a plant height of about 1 m the outermost internode of the new growth unit swells, and parts of the soft pith become hollow as a result of degeneration of the pith. Later the swollen internode splits and thus forms a natural constitutional opening to the hollow pith canal. Thus a cavity with a natural entrance hole is formed at the youngest internode. The cavities themselves do not correspond to internode sections, but the thicker nodes serve as “starting points” for pith degeneration.

New growth unit. A new growth unit usually consists of an average of 5 internodes (4 to 7) and the natural opening are formed always at the youngest and/or the second youngest internode. The degeneration of the pith mainly occurs at the outermost part of

the shoot, while most of the inner part remains solid without any pith degeneration. Only small sections of degenerated pith material occur at the innermost side of the new growth unit. These domatium chambers do not have an opening to the outside and are therefore considered as hollow pith canal without access (Fig. 1).

The domatium chamber is formed during the growth process of the new growth unit. Once the growth process has finished, the domatium chamber of one particular new growth unit has reached its final size. Each new growth unit adds a new domatium chamber to the tree.

The young leaves of the new growth units are light green in colour, relatively soft and vertically hanging without a typical smell. Older leaves are dark green in colour, relatively hard, standing horizontally and have a typical smell of smoked clothes and/or liver pâté. The young leaves expand to full size before beginning to toughen.

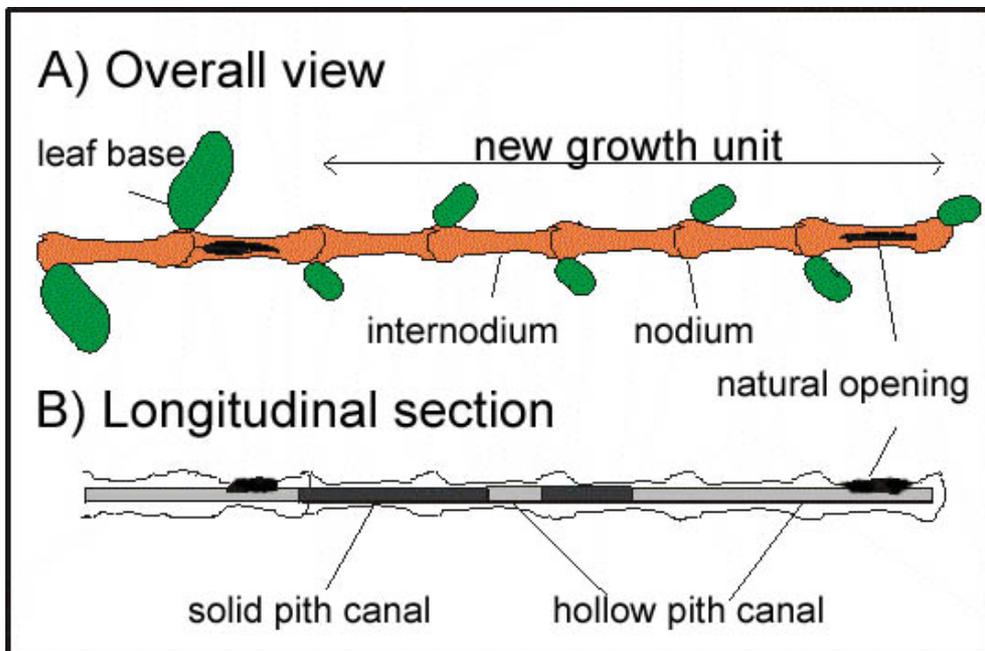


Fig. 1. Schematic view of the branch tip from outside and longitudinal section.

Trunk. The degeneration of pith material, and therefore the formation of domatium chambers, can only be found in (secondary) branches and never in the trunk. After trees have fallen down due to the steep slopes, several branches can take the part of the trunk by providing the vertical axis. As these “new” trunks are morphological branches, they can contain domatium chambers.

Development. The relative portion of hollow pith canal in relation to total branch length depends on the age, and therefore the tree height, the diameter in breast height and the diameter of the branches. There is a correlation between tree height and dbh on a logarithmic scale. A number of 10 trees, with different tree height and dbh, were chosen to investigate the development of the domatium chambers in greater detail (Fig. 2). The selected trees were either unoccupied or occupied by *Crematogaster*, because *Azteca* ants can actively enlarge the domatia size (see results: Natural openings and ant-made cavities).

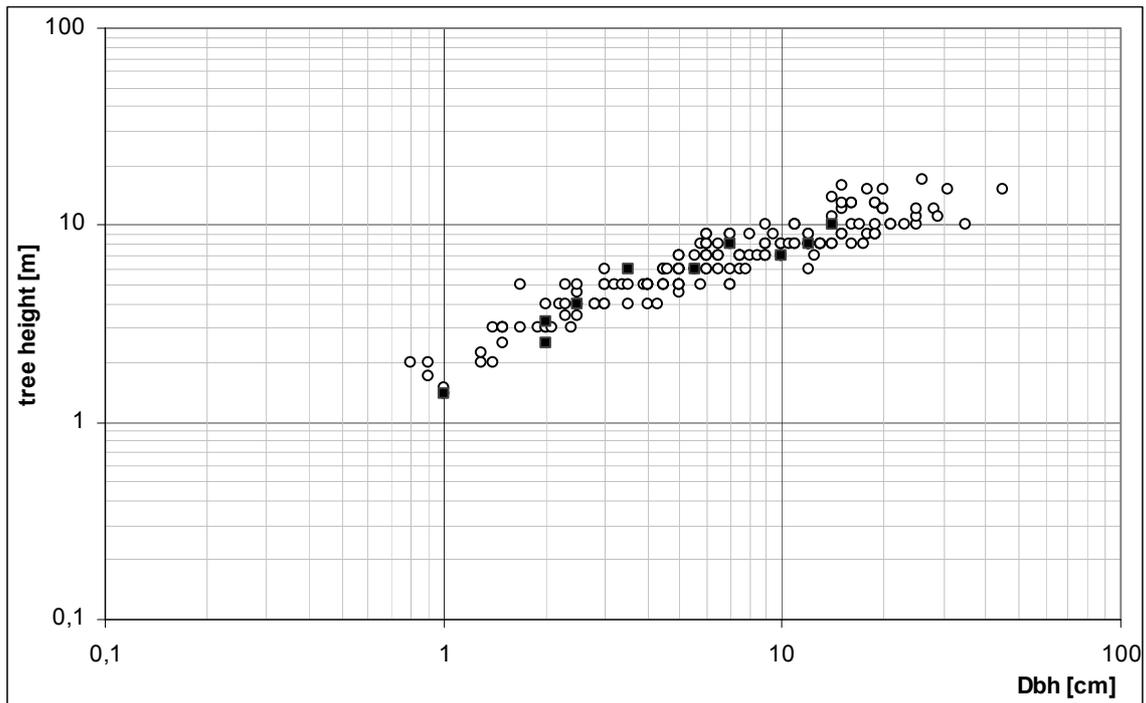


Fig. 2. Relation between tree height and diameter in breast height (dbh) for trees of primary forest. The smallest 6 of the 185 investigated trees did not reach breast height, so only 179 trees are represented in the figure. Each circle (○) and each black square (■) marks an individual. For more detailed investigations 10 trees, represented with black squares, were chosen (see Fig. 3, 4 and 5). The selected trees were either unoccupied or occupied by *Crematogaster*.

Branch diameter increases with diameter in breast height (dbh). At dbhs smaller than approximately 4 cm there is a rapid increase of branch diameter. At larger dbhs there is less increase in branch diameter (Fig. 3).

Relative domatia size also depends on age and therefore dbh. Similar as in case of branch diameter, there is a rapid increase up to a dbh of about 3 - 4 cm. At larger dbh no increase of relative domatia size can be observed (Fig. 4). The mean relative domatium size for these taller individuals is 52,44 % (\pm SD 9,33, n = 7).

The dbh of 3 - 4 cm is reached at a tree height of approximately 4 m height (see Fig. 2). At this size the relative size of domatium length does not become larger. The percentage of hollow and thus solid stems, reaches its final stage. When this maximum size is reached, further increase of nesting space requires further growing of new growth units. Likewise the absolute nesting space increases as long as the host-plant continues to grow.

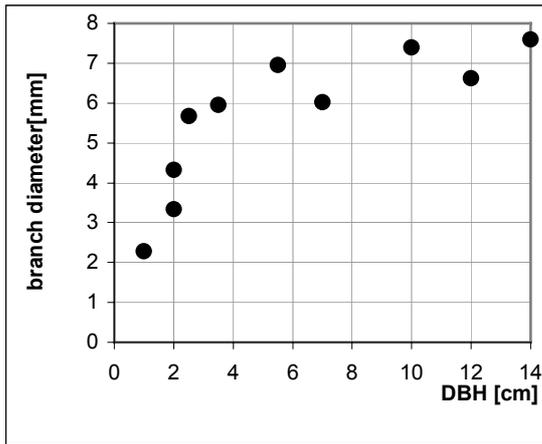


Fig. 3. Mean branch diameter and diameter in breast height (dbh) for 10 selected trees. Three branches were measured per tree.

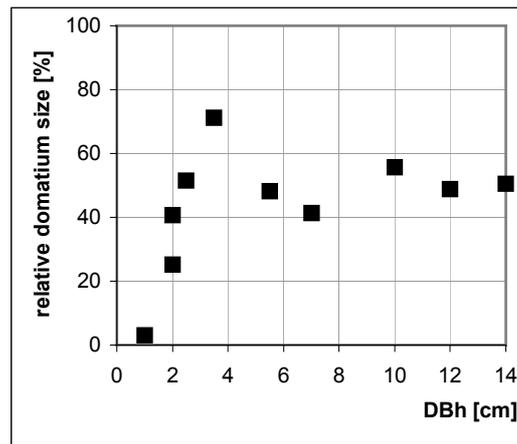


Fig. 4. Relative domatium size and diameter in breast height (dbh). As dbh increases during lifespan, increase of relative domatium size occurs mainly in a first growth periode.

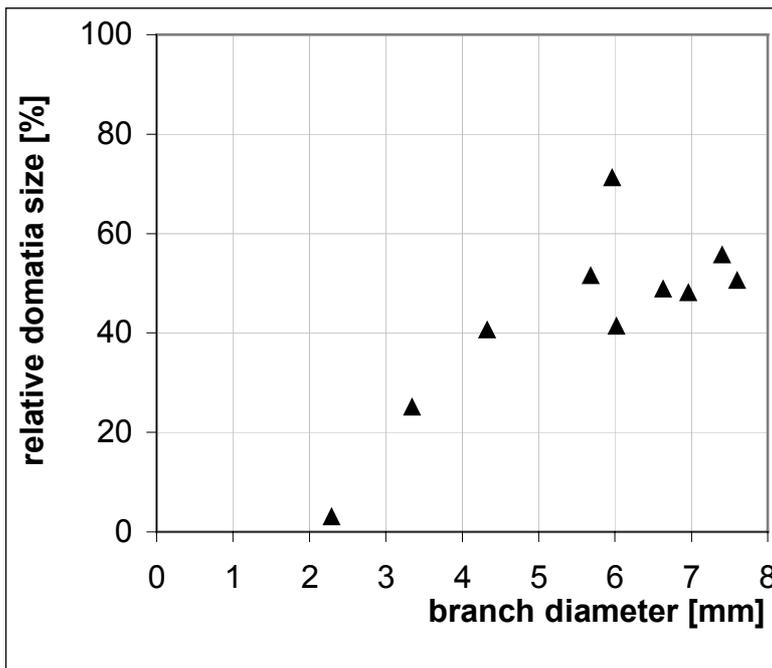


Fig. 5. Relative domatium size and mean branch diameter.

Domatia length. The comparison between relative domatia size and branch diameter (Fig. 5) shows another detail. A fully developed domatium chamber has an diameter between 4 and 5 mm. Trees with a branch diameter smaller or equal to this diameter can not have a fully developed pith canal. Trees with larger branch diameters provide a fully developed pith canal that have a mean relative domatia length of 52,44 % of total branch length.

Relative domatia size of 52,44 % consists mainly of hollow pith canals with natural openings (HPC +) but also of smaller hollow pith canals without openings (HPC -). Detailed values are given in Tab. 1:

Tab. 1. Absolute and relative length of domatium chambers. HPC + : hollow pith canal with natural opening, HPC - : hollow pith canal without natural opening. HPC + is more frequent than HPC -, so it has a greater impact on relative length.

	HPC +	HPC -
Average absolute length (\pm SD) [cm]	13,34 (\pm 7,69)	1,99 (\pm 2,87)
relative length [%]	49,92 %	3,47 %

Live-stem inhabiting ants:

Taxonomy. Ants of four genera were mainly found to inhabit the domatium chambers of *Tetrathylacium macrophyllum*: *Crematogaster* & *Pheidole* (Myrmicinae), *Azteca* (Dolichoderinae) and *Pachycondyla* (Ponerinae).

Colonization pattern. The smallest tree found with ant-occupied domatia was 2,25 m high, whereas the highest ant-unoccupied tree was 4 m high (Tab. 2). The frequency of different ant inhabitants changed notably with tree height (Tab. 3).

More than one ant species or colony can occupy a tree. Ant-occupied trees (> 4 m) were found to house an average number of 1,57 ant species (\pm SD: 0,69; n = 20). *Pachycondyla* as well as *Pheidole* ants were never found to occupy a tree by their own, they always occurred together with other ant species. In contrast *Azteca* and *Crematogaster* ants, due to their bigger nest requirements, are able to inhabit a tree by their own. Further size characteristics of these four species are shown in Tab. 4.

Dominant and subdominant ants. *Crematogaster* and especially *Azteca* are “dominant” ants as they occupy large parts of the trees. *Pheidole* and *Pachycondyla* are “subdominant” ants as they occur only in parts of the trees where *Azteca* and (to a smaller extend) *Crematogaster* are absent. For example on an *Azteca*-occupied tree *Pheidole* ants occupied only *Azteca*-abandoned twigs. On another tree *Pheidole* occupied only parts of the tree that did not match with the *Azteca* territory. Distribution of dominant and subdominant ants is shown in Fig. 6.

Tab. 2. Frequency of ants among inhabitants of smaller and bigger trees in primary forest. Total number of trees: 38

tree height [m]	number of trees	<i>Crematogaster</i>	<i>Azteca</i>	<i>Pheidole</i>	<i>Pachycondyla</i>	other ants	no ants
0,4	1						1
0,8	1						1
0,95	1						1
1	3						1
1,4	1						1
1,5	1						1
1,7	1						1
2	5						1
2	1						1
2,25	1	1					
2,25	1			1			
2,75	1	1			1		
3,25	1	1					
4	1	1					
4	1						1
4	1		1				
4	1			1	1		
5	1		1	1			
5	1					1	
6	1			1	1		
6	1	1		1			
6	1	1	1		1		
6	1				1		
6	1		1				
7	1	1			1		
7	1	1	1				
7	1		1	1		1	
8	1	1					
8	1	1					
8	1	1					
8	1	1			1		
10	1	1					
12	1					1	

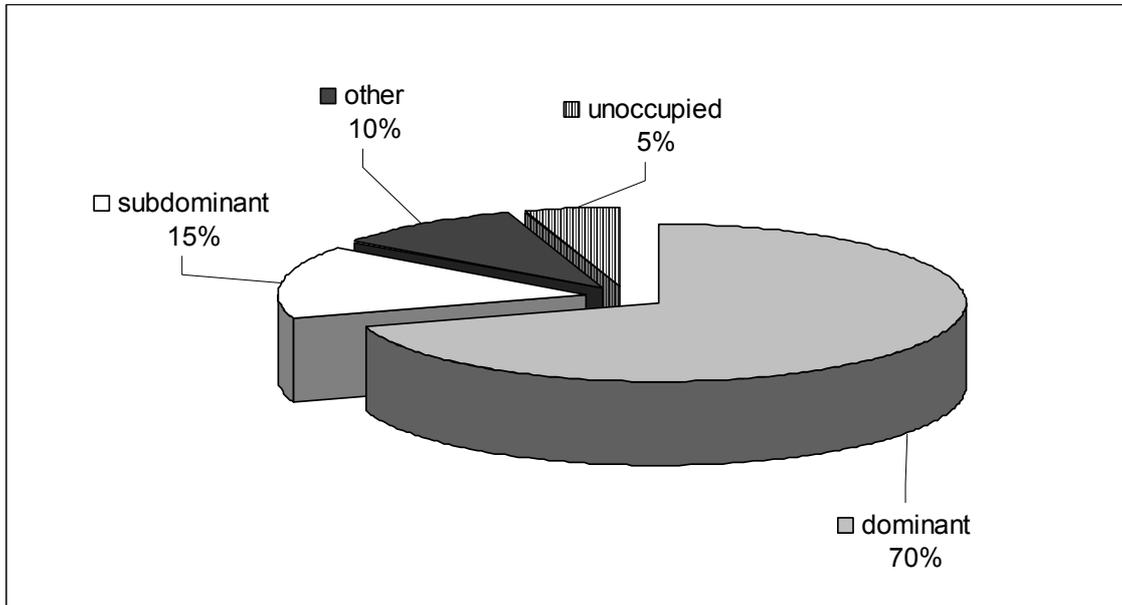


Fig. 6. *Tetrathylacium* trees of primary forest (> 4 m) occupied by either *Crematogaster* or *Azteca* or both, are combined in the category “dominant”, while those occupied exclusively by *Pheidole* and/or *Pachycondyla* are called “subdominant”. In case that subdominant species occurred together with dominant ones they were placed into the „dominant” category. Other ant species than the already mentioned ones are combined in the category “other” (n = 20).

Tab. 3. Percentage of ant-occupation in three different tree size classes. Note, that more than one ant species may colonize the host-plant, so total sum may exceed 100 %.

<i>tree height</i>	<i>Crematogaster</i>	<i>Azteca</i>	<i>Pheidole</i>	<i>Pachycondyla</i>	other ants	no ants
0 - < 2 m (n = 9)	0	0	0	0	0	100
2 - < 4 m (n = 9)	33,3	0	11,1	11,1	0	55,5
≥ 4 m (n = 20)	50,0	30,0	25,0	30,0	15,0	5,0

Tab. 4. Characteristics of main ant inhabitants in primary forest. Head and mesosomal length of workers of the 4 ant genera: * n = 50, ** n = 26.

ant genera	smallest colonised tree (n = 38)	head length [mm] (± SD)	mesosomal length (mm) (± SD)	maximum number of occupied domatia per tree (trees > 4 m, n = 18)	scale insects
<i>Crematogaster</i> *	2,25 m	0,61 (± 0,6)	0,73 (± 0,1)	> 20	yes
<i>Pheidole</i> *	2,25 m	0,44 (± 0,12)	0,48 (± 0,1)	5	no
<i>Pachycondyla</i> **	2,75 m	1,4 (± 0,1)	2,3 (± 0,1)	2	no
<i>Azteca</i> *	4 m	0,68 (± 0,12)	0,7 (± 0,1)	> 20	yes

Worker size and nesting space requirements. Nesting space in the domatium chambers is restricted, so body size of ants might have an influence on colony structure. Subdominant *Pheidole* are the smallest and *Pachycondyla* the largest ants, marking the extreme position in size diagram. The dominant “medium-sized” *Azteca* and *Crematogaster* have nearly the same body size (Fig. 7).

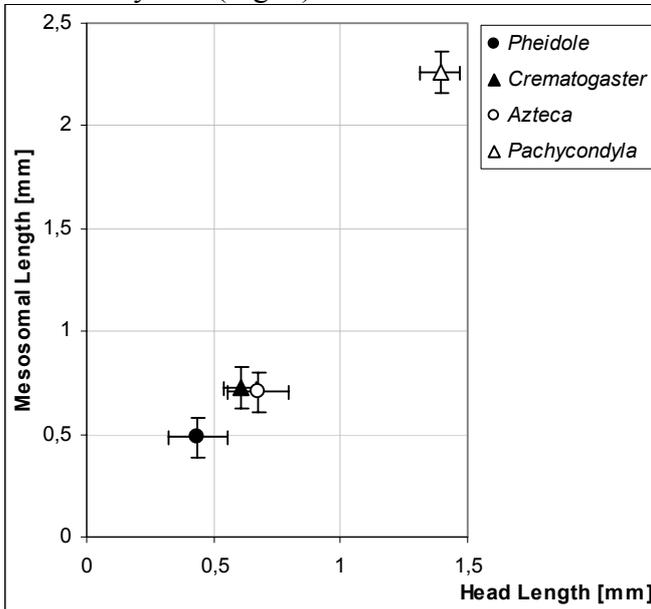


Fig. 7. Mean mesosomal and head length of workers were used to indicate size differences between the 4 main ant genera. Logarithmic scale.

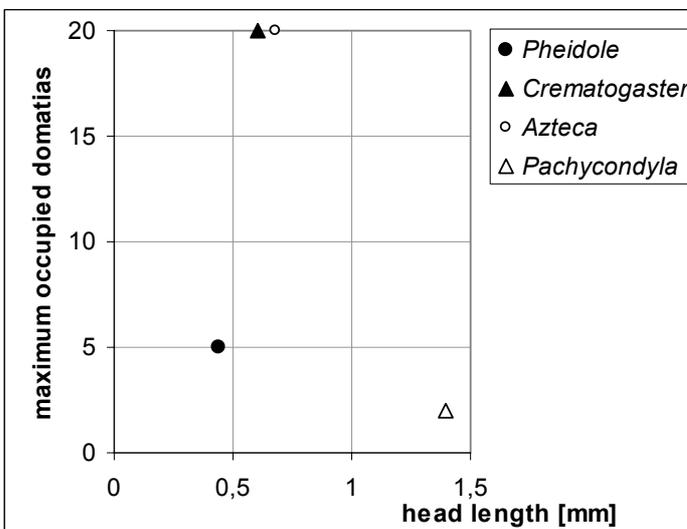


Fig. 8. Number of maximally occupied domatium chambers and worker size (head length) for the our main ant inhabitants. For *Crematogaster* and *Azteca* the amount of occupied domatium chambers can exceed 20, because only 20 domatium chambers have been investigated per tree.

It was found that medium-sized ants occupy far more domatium chambers than large- and small-sized ants (Fig. 8). Nesting space requirements are by far larger in case of medium-sized *Crematogaster* and *Azteca*, than in small sized *Pheidole* and large sized *Pachycondyla*. That is the reason why colonies of the medium-sized ants can occupy great parts of the tree. In contrast, colonies of the large- and small-sized ants occupy only small parts of the tree. Hardly more than a single branch is occupied by *Pheidole* or *Pachycondyla*.

Occupation in primary and secondary forest. To compare the distribution of ants between primary and secondary forest, only mature trees, higher than 4 m, were considered (Fig. 9). This is because (1) only trees of this size were found in secondary forest and (2) only trees higher 4 m are also occupied by *Azteca*. *Crematogaster* and *Azteca*, the most frequent ants in primary forest are completely missing in secondary forest. In contrast *Pheidole* are the major inhabitants in secondary forest with 86 % of the trees occupied. Note that only 6 trees in secondary forest have been investigated, because the main distribution of *T. macrophyllum* is in primary forest.

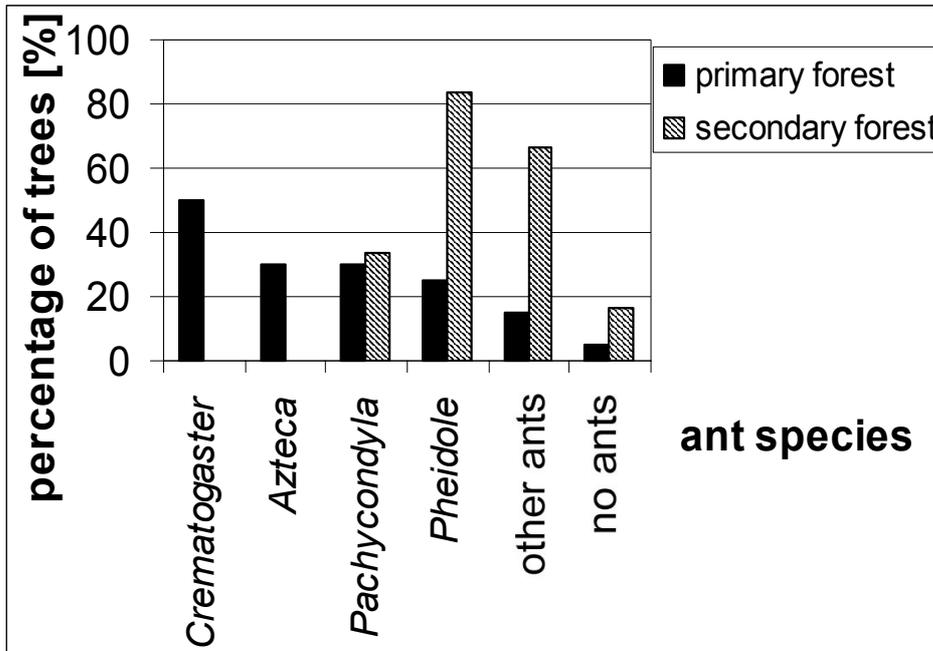


Fig. 9. Percentage of trees (> 4 m) inhabited by specific ants. Note that more than one species (colony) may occupy the same tree, so total sum exceeds 100 %. For primary forest: n = 20, for secondary forest: n = 6. *Crematogaster* and *Azteca* are the only ants that cultivate scale insects. As only parts of the tree were investigated (20 domatia/tree), the given percentages are minimum values!

In smaller trees (< 4 m) in secondary forest several foundresses and incipient colonies of different species were found. For example, a 3,5 m high tree in secondary forest housed 7 different foundresses / incipient colonies of the following genera: *Acanthognathus*, *Dolichoderus*, *Pachycondyla*, *Pheidole*, *Pseudomyrmex*, *Zacryptocerus* and a still unidentified species of Myrmicineae (*Pheidole* ?).

In larger trees of primary forest (≥ 4 m) a maximum of three different ant species/tree was found. Only one species lives in one domatium chamber! But two ant species could be found at the same branch occupying different domatia.

Colonization of *Azteca*. In case of *Azteca* all 156 trees could be taken into account because presence or absence of the conspicuous carton tunnels was easy to detect. The average occupancy of *Azteca*, of trees higher than 4 m (n = 156), is 30,6 %. But there is a notably relation between tree height and occupancy (Fig.11). The oldest and biggest trees that had provided much nesting space for the longest time were more frequently colonized by *Azteca*. Even though the amount of large and old trees with high *Azteca* occupancy is very low. Most of the trees investigated were between 4 and 8 m high (Fig. 10).

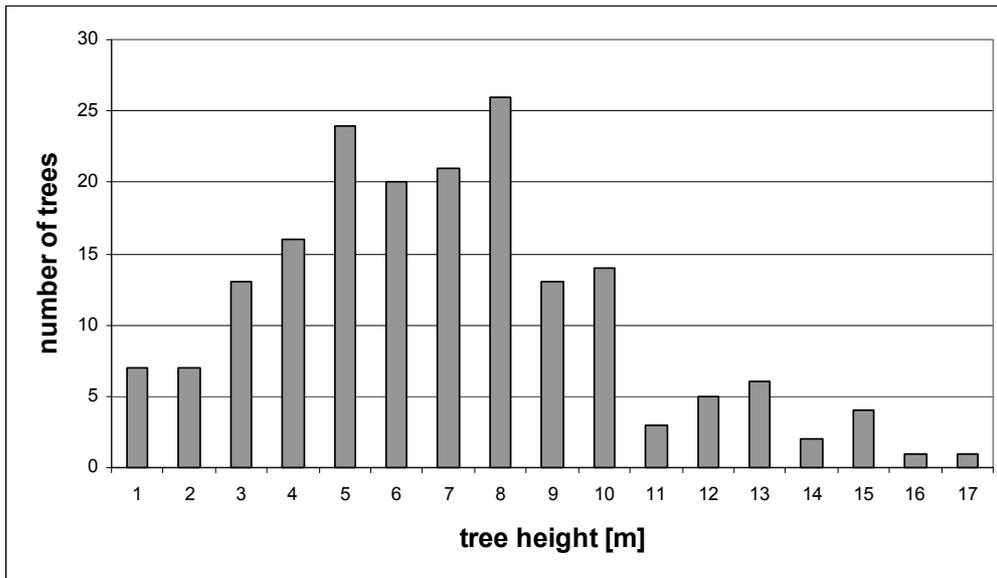


Fig. 10. Tree height in primary forest (n = 185). The number of trees reached its maximum between 4 and 8 m height.

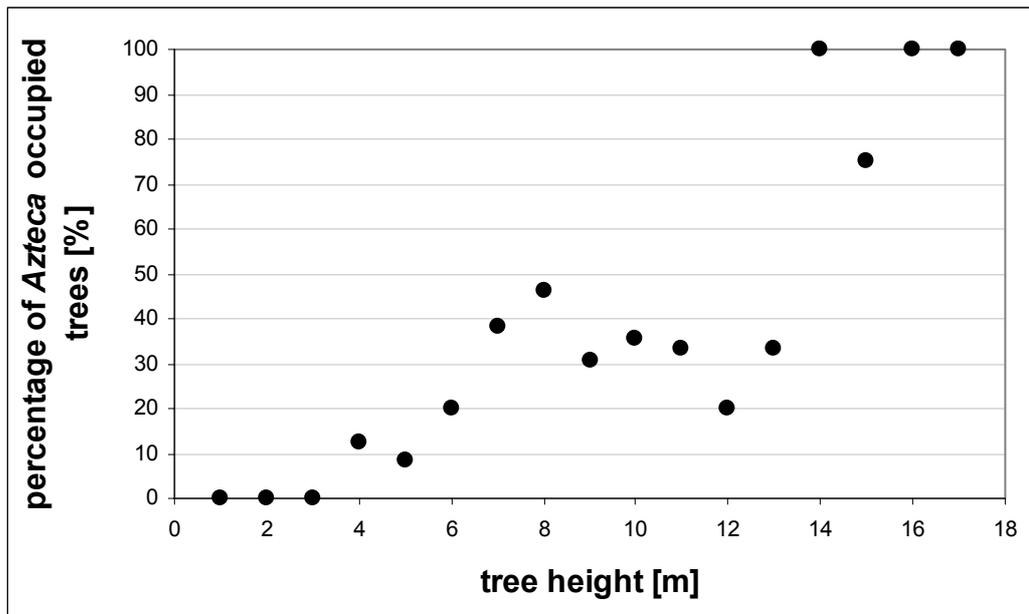


Fig. 11. Relation between tree height and percentage of *Azteca*-occupied trees.

The main ant inhabitants of *T. macrophyllum* build carton structures, but they do so in a different manner:

***Pachycondyla*.** Workers construct an approximately 4 cm long carton tube inside the ultimate part of the domatium chamber. Colonies are very small, hardly comprising more than a dozen individuals. They have not been found to occupy more than two domatium chambers. Nests were found either on relatively small trees but mainly at the edge of a *Crematogaster* territory. If disturbed by humans the ants flee into their nearby domatia or leave the area of disturbance if they are far from their domatia. Workers were observed to forage for food on the entire plant's surface and do not tend coccids. If the domatium was damaged, the whole colony (workers also take larvae) left the domatium chamber in a split second, presumably searching for a different cavity. In no case they were observed to defend the domatia or parts of the ant-plant, even the large workers possess a powerful

sting. The absence of a defense mechanism together with the small “compact” colony size, the ability of quick withdrawing and the absence of coccids are characteristics for a subordinate ant species that is an opportunistic cavity nester.

Pheidole. Ants cover the natural openings by a carton roof only leaving one or two small entrance holes to enter. The colonies were never found to inhabit more than 5 domatium chambers, mainly at the edge of *Crematogaster* or *Azteca* colonies or in relatively young trees. Even in young trees relatively small colonies of 2 to 3 domatium chambers were able to produce lots of winged sexual individuals.

Colonies were also found in dead twigs of *T. macrophyllum* formerly abandoned by the *Azteca* colony that occupied most of the live stems of that tree. They were also often found at the edge of *Azteca* and *Crematogaster* colonies in the vicinity of *Pachycondyla* colonies. That means that for example two domatium chambers were occupied by *Pheidole* and the next one held a *Pachycondyla* colony. *Pheidole* do not tend Coccids but forage for food on the plant’s surface. In the vicinity of *Pachycondyla* colonies these two species were observed to forage partly on the same area without any “dispute”. Neither *Pachycondyla* nor *Pheidole* were observed to defend their foraging territory. If the domatium was broken up artificially, *Pheidole* attacked only weakly the intruder.

The small colony size, early reproduction and the weak colony defense are typical characteristics of an opportunistic ant species.

Crematogaster. Workers cover the natural openings (Fig. 12) but also build bulb-like carton structures on the branch around the base of the leaves (Fig. 13). Inside these structures coccids are tended at the base of the leaf petioli. The coccids measure several millimetres and have a white curly wax surface on their back. This carton structures have small entrance holes allowing only the ants to enter. Apart from tending coccids the ants additionally forage on the plant’s surface. The foraging territory is defended against other ant species. Especially arboreal ants from the surrounding vegetation were observed to be victims of *Crematogaster* attacks, as these foragers entered the *Crematogaster* territory on *T. macrophyllum*. Also potential herbivores such as leaf bugs were observed to be aggressively attacked by half a dozen to a dozen *Crematogaster* ants (Fig. 14). Climbing vegetation was observed to be attacked and pruned by workers (Fig. 15). *Crematogaster* colonies are very large and can extend over the whole tree. The large and well defended colonies as well as the exclusion of the subordinate plant-ants defines this competitive dominant species.

Azteca. These ants build the most extensive carton structures. Inside the domatia they cover the end of the chambers by an about 1cm long carton-like substance (knöllen). This inner carton surface might work as a small dump place as parts of dead ants were sometimes found there. This dump place is characterised by a high amount of microscopic transparent worms, possibly Nematodes. The ants also make carton walls inside the domatium to subdivide the room into smaller chambers. Next the first opening is covered by a carton roof containing a variety of tiny holes, just big enough for these ants to enter. The largest structures are the carton tunnels outside the branch that connect all the openings of the inhabited domatium chambers. The tunnel runs horizontal at the lower part of the branches and vertical to connect different branches (Fig. 16). Due to the big size of the *Azteca* colony their carton tunnels can extend over the whole canopy. In some cases the *Azteca* nest expands into the nearby vegetation, especially when the neighbouring trees have soft branches and pith.



Fig. 12. Natural opening closed with a carton roof by *Crematogaster*. Arrows indicate the entrance holes left free. In this rare case the natural opening is a double slit, normally only a single slit is formed.



Fig. 13. Carton structures at the leaf petiole produced by *Crematogaster* to protect their coccids. In contrast to the intact carton structure in the upper left, the other carton roof was partly removed to see the coccids.



Fig. 14. *Crematogaster* workers attacking a beetle.

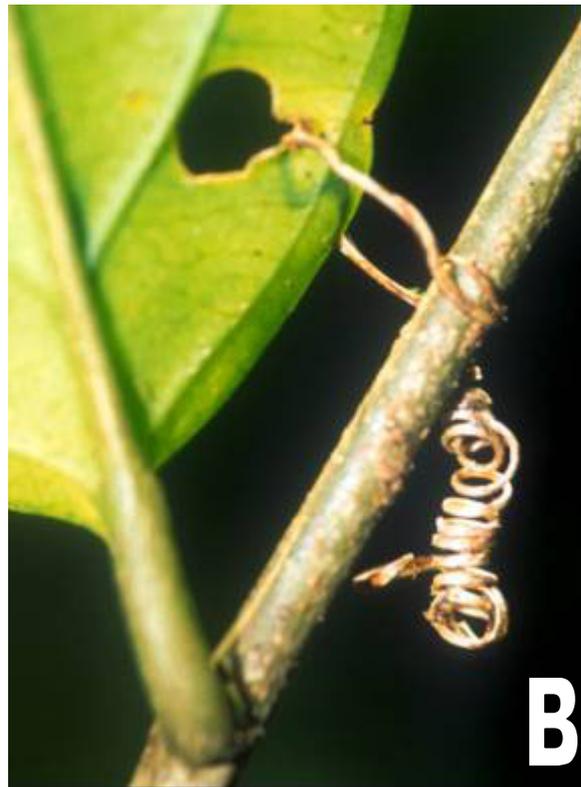
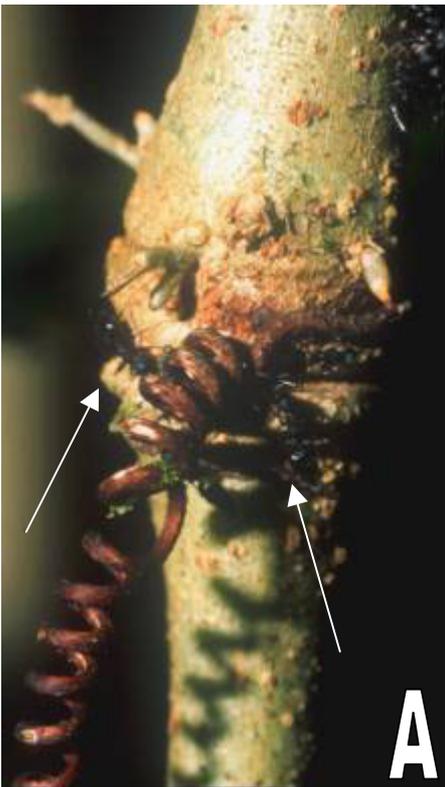


Fig. 15. A) *Crematogaster* workers pruning a climbing epiphyte. B) *T. macrophyllum* with the remains of a pruned climber.

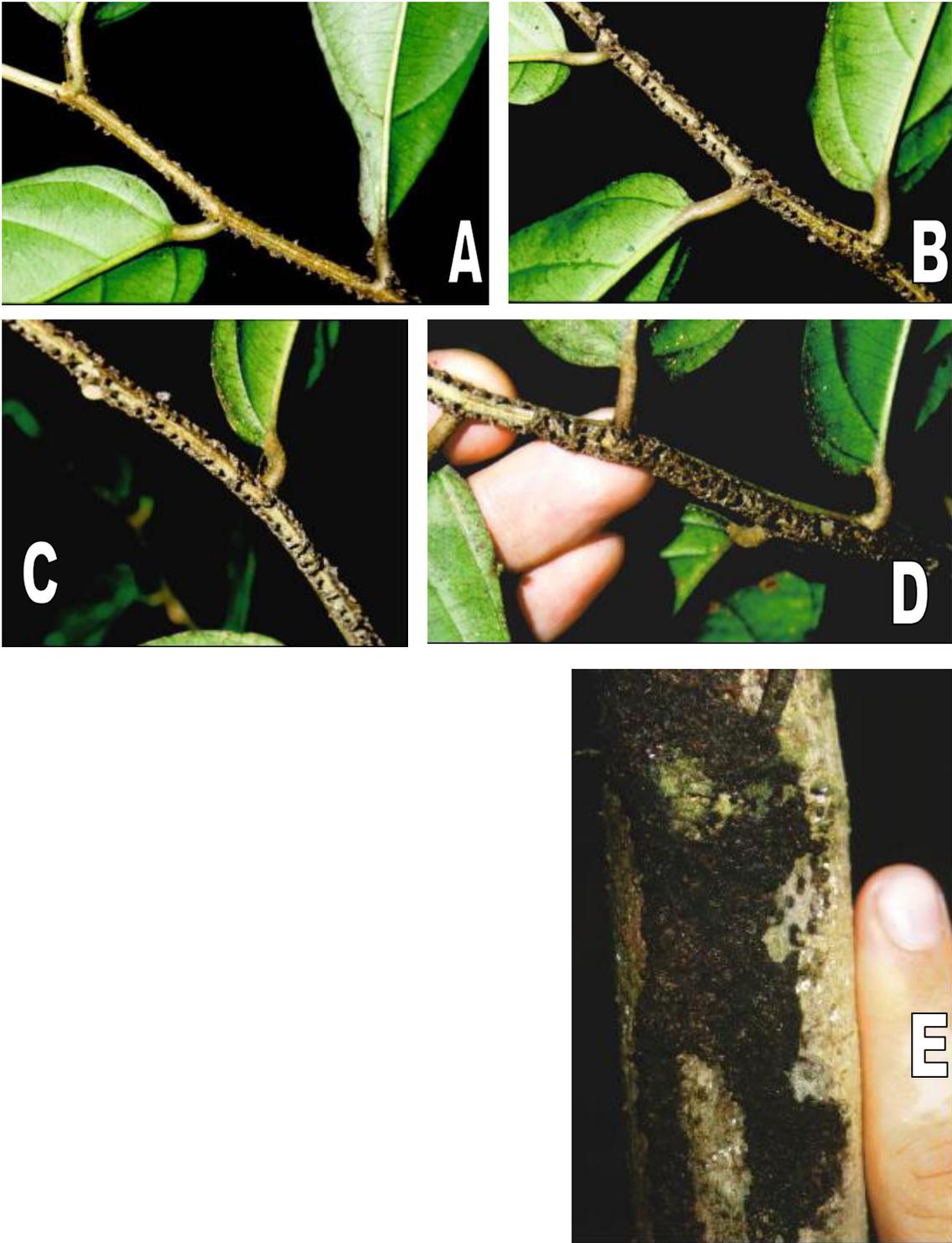


Fig. 16. A - D) Different stages in construction of carton tunnels produced by *Azteca*. Small entrance holes are left in the tunnel by the workers to enter or leave. E) Large nests also occupy older branches where broad carton tunnels are constructed.



Fig. 17. Large redish coccids inside an *Azteca*-occupied domatium chamber.



Fig. 18. Coccid below the *Azteca* build carton tunnel (arrow).

The carton tunnels also contains tiny holes where the ants enter and leave. In case of emergency or if bothered, the ants withdraw from the plant surface into the carton tunnel, placing workers and soldiers with open mandibles inside the tiny holes. Foraging activity was less than in case of *Crematogaster*. Activity outside the carton tunnels, where most of the activity takes place, is reduced to a minimum. If outside the tunnel workers mainly stay on the branch hardly entering the mature leaves. The only leaves frequently entered are the young, soft, vulnerable, partly pendulous leaves of the newest growth unit. In contrast to this timid behaviour the ants aggressively attack an intruder when the domatium is broken up. Pink coccids are tended at the base of the leaf petioli on the branch inside the carton tunnel. There are also coccids tended inside the domatia.

Coccids. Two different coccids were observed. Pink coccids between 1 and 10 mm length were found in *Azteca* and some *Crematogaster* nests. They have three honeydew sites on a frontal-caudal line on their backside, one at the top another at the center and the third at the end of the back. They feed on plant sap by their proboscis which reaches up to 15 mm. In *Azteca* nests a greater number of coccids can be observed than in *Crematogaster* nests. The other coccids were mainly found in *Crematogaster* nests, white in colour with a curly wax surface.

A “fake” coccid was also observed in a *Crematogaster* colony. It was the larvae of a coccinellid beetle that mimicked the regular coccids.

Natural openings and ant-made cavities

Azteca. Established colonies of *Azteca* are found to chew holes into the young and still soft new growth units of the host plant, creating “artificial” entrance holes (Fig. 20). In that way the ants gain access to the interior and partly excavate the soft pith. Some of the hollow pith canals without access (domatium chambers without natural openings) can be connected to hollow pith canals with access (Fig. 23 & 24). Thus the former non-accessible hollow pith canals can be reached by *Azteca* (Fig. 19). One internode normally holds 1 or 2 (rarely up to 5) *Azteca*-made entrance holes with a diameter of about 1 - 2 mm. These holes are also kept free on the older parts of the branch (Fig. 21).

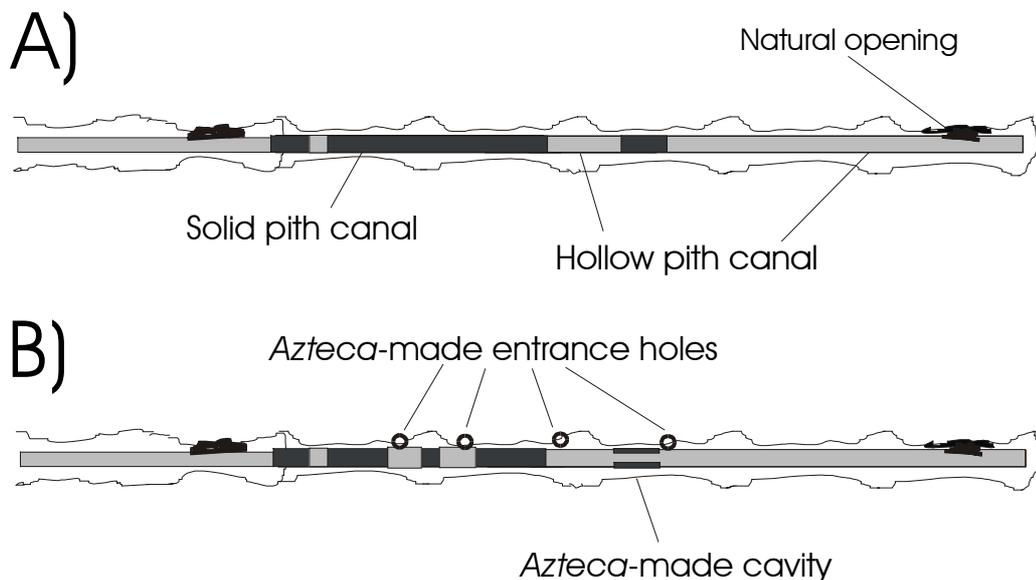


Fig. 19. Longitudinal sections of the new growth unit. A) Natural situation of distribution of solid and hollow pith canal with and without natural openings. B) *Azteca*-occupied branch shows the influence of the excavation process. *Azteca*-made cavities connect HPC without access to HPC with access. Additional entrance holes connect to former solid pith material that had been excavated by *Azteca* ants.

Other ant species. *Crematogaster*, *Pachycondyla* and *Pheidole* only uses the domatium chambers provided by the host-plant. They do neither enlarge the hollow pith canal nor chew holes nor excavate the soft pith. The observations show that only *Azteca* enlarges the domatium chambers (Fig. 22). The hollow pith canal with access and thus the nesting space is larger in case of *Azteca*. More details of the *Azteca* and *Crematogaster* subset is shown in Tab. 5.



Fig. 20. A) Entrance holes cut by *Azteca* workers in the soft tissue of a new terminal shoot. **B)** Note the outermost part of the carton tunnel (arrow) that connects this newly grown domatium chambers to the rest of the nest.

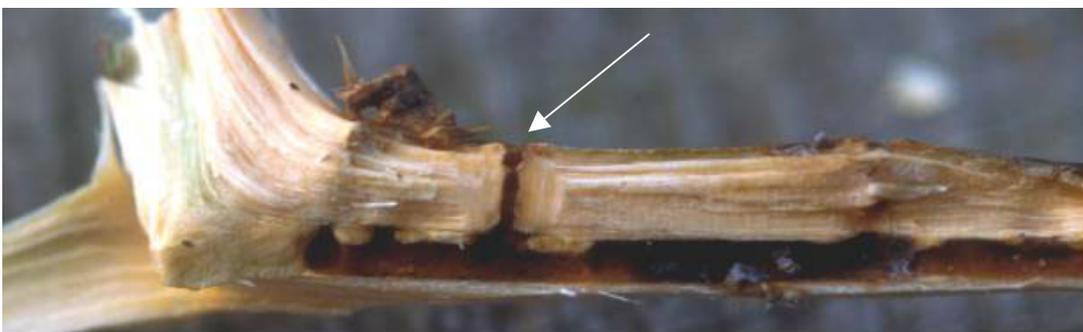


Fig. 21. Entrance hole of an *Azteca*-occupied domatium chamber in an older branch.

Tab. 5. Comparison between *Azteca*- and *Crematogaster*-occupied trees. Each subset consists of 6 trees (3 branches investigated per tree) with similar characteristics. SPC: solid pith canal, HPC - : hollow pith canal without access, HPC + : hollow pith canal with access. Total number of branches per subset: n = 18. Total number of leaves: *Azteca* n = 356, *Crematogaster* n = 376.

Azteca								Crematogaster							
Tree height [m]	branch diameter [cm]	SPC [%]	HPC- [%]	HPC+ [%]	leaf length [cm]	leaf damage [%]		Tree height [m]	branch diameter [cm]	SPC [%]	HPC- [%]	HPC+ [%]	leaf length [cm]	leaf damage [%]	
5,0	5,8	23,0	6,0	71,0	30,7	6,6		4	5,6	48,5	3,5	48	31,9	6,9	
7,0	8,2	40,2	0,9	58,9	33,8	3,1		6	6,9	51,3	10,3	38,4	30,3	5,3	
9,0	6,1	42,4	0,4	57,1	29,5	7,2		6	5,9	28,5	0	71,5	32,9	3,2	
10,0	7,3	32,1	0,8	67,1	36,7	11,6		7	7,8	43,1	1,2	55,6	30,6	3,9	
6,0	8,1	23,7	0,3	76,0	35,1	3,2		8	6,0	58,4	4,3	37	32,1	7,2	
7,0	7,4	26,9	0,5	72,6	27,9	0,9		10	7,6	49,4	1,5	49	34,7	7,7	
average	7,3	7,1	31,4	1,5	67,1	32,3	5,4	average	6,9	6,7	46,5	3,5	49,9	32,1	5,7
±SD	1,9	1,0	8,4	2,2	7,6	3,4	3,9	SD	2,0	0,9	10,1	3,7	12,7	1,6	1,8
±SE	0,8	0,4	3,4	0,9	3,1	0,2	0,2	SE	0,8	0,4	4,1	1,5	5,2	0,1	0,1

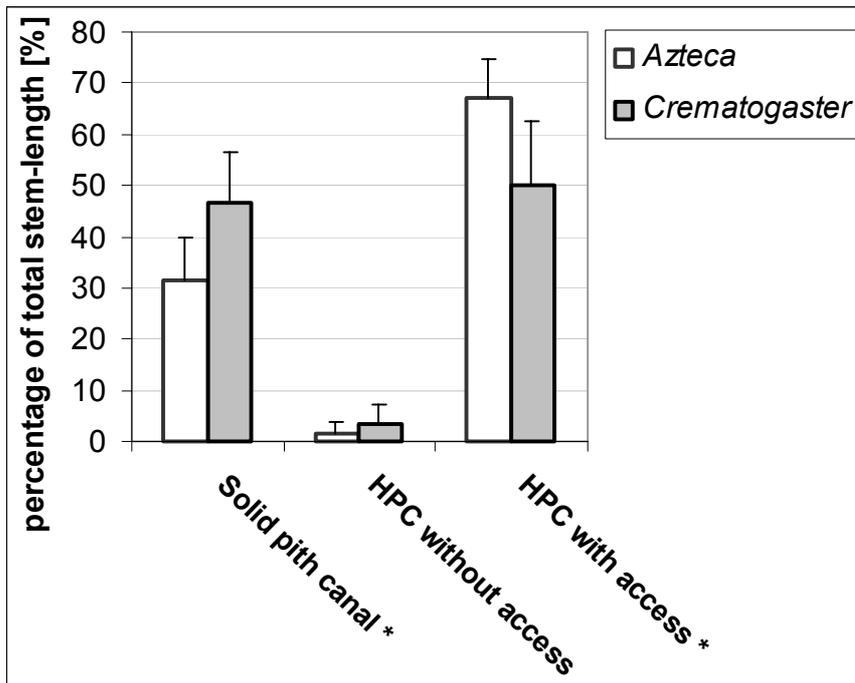


Fig. 22. Effects of excavation activity on the relative portion of solid and hollow pith canal (HPC). Categories marked with asterisks (*) show a significant difference between *Azteca*- and *Crematogaster*-subsets according to a paired T-test: = $p < 0,05$, (number of investigated branches: $n = 18$).

Ant maintenance of entrance holes. The natural openings are always located in the youngest internode of the new growth unit. As a new growth unit represents mostly 5 internodes (rarely 4, 6 or 7) such openings occur regular on the first, sixth, eleventh and so on internode of a branch. The older or longer the branch the more openings exist. The only differences between the openings of the branch are due to their size. The youngest openings are the biggest ones measuring up to 35 mm in length and about 6 mm in width.

As secondary thickening growth takes place the subsequent openings become smaller and more narrow, very often even closed. The sixth and following openings of one branch are mostly completely closed.

It was observed that the ants occupy mainly the younger outer tips of the branches where most of the leaves are located. But established older colonies do also use older domatium chambers where the openings are quite small. If the openings disappear in the growth process ants of the genera *Azteca*, *Crematogaster* and *Pheidole* keep an entrance hole free by chewing out a little canal. *Pachycondyla* ants only use one domatium chamber and were always found in chambers with relative wide openings easy to enter.



Fig. 23. *Crematogaster*-occupied branch of *T. macrophyllum*, cut open. Dark coloured hollow pith canal (HPC) with natural opening and smaller, light green coloured hollow pith canal without natural opening. The natural opening is indicated by an arrow.



Fig. 24. *Azteca*-occupied hollow pith canal. Note that a small canal (arrow) has been cut, so the hollow pith canal (HPC) without natural opening is connected to the occupied HPC with natural opening.

Leaf damage

The percentage of leaf damage depends on the presence of ant inhabitants. In comparison to plants without ant inhabitants, the percentage of damaged leaf area decreases if ants are present. If no ants are present the mean leaf damage area is 10,88 % (\pm SD = 3,24) in comparison to *Azteca*-occupied trees with 5,44 % (\pm SD = 3,85) and *Crematogaster* inhabited trees with 5,71 % (\pm SD = 1,84). In case of *Azteca* the leaf damage is reduced by 50 % and in case of *Crematogaster* by 47,52 % (Fig. 25).

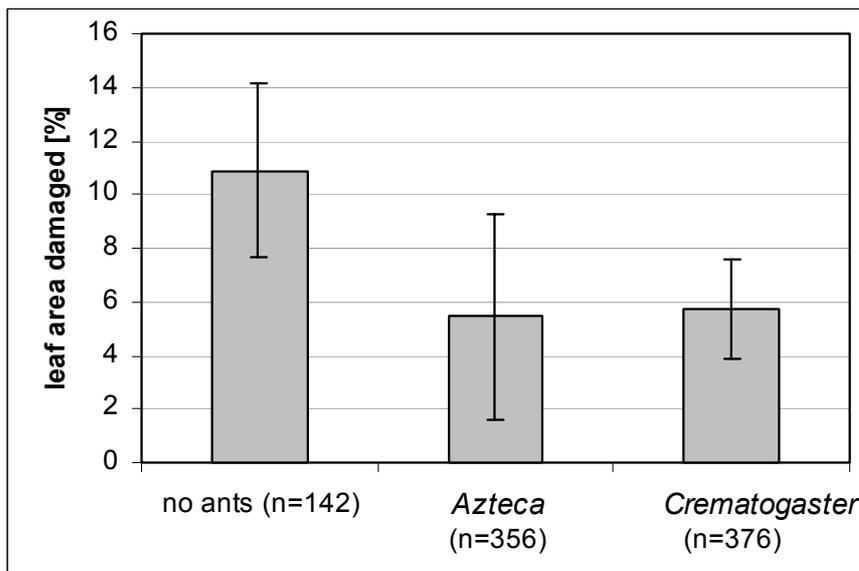


Fig. 25. Mean leaf damage (\pm SD), as a percentage of leaf area damaged in comparison to total leaf area. The number of investigated leaves in brackets. Six trees were randomly selected for each of the three subsets.

Epiphytes

High deviation. Epiphytic cover per investigated tree in primary forest varies highly between the 185 investigated individuals of *T. macrophyllum* (mean epiphytic cover = 37,9 %, \pm SD 22,2). To find possible causes for this large variation, the epiphytic cover was compared with “abiotic”: e.g. height of tree, canopy cover, distance to water, canopy size, sloping of ground, dbh and “biotic” factors: e.g. colonisation of different ant species, extension of nest (see Appendix). The coefficient of determination (r^2) showed that the “abiotic” factors had minor influence on the epiphytic cover (Tab. 6):

***Azteca* influence.** In case of *Azteca*, “biotic” factors show greater influence (Tab. 7). The presence of *Azteca* colonies (only taking the 156 individuals \leq 4 m into account) and the extension of *Azteca* nests had higher influence on epiphytic cover. The highest coefficient of determination was reached comparing the extension of the *Azteca* nest per tree and epiphytic cover of 48 trees that were colonized by *Azteca* ants (Fig. 26).

The relative high negative correlation, between the extension of the *Azteca* nest and the epiphytic cover means that with an increase in nest size there is a decrease in epiphytic cover (Fig. 27).

The more branches of the tree are occupied the less they are covered by epiphytes. The extension of the *Azteca* nest is indicated by the black carton tunnels running on the lower side of the branches and on the upper part of the trunk. In most cases the *Azteca* nest was either not or hardly covered by epiphytes that mainly occurred outside the nest territory. The borders of the nest can be spotted by a sudden change from epiphyte free to epiphyte covered branch parts. In comparison to the surrounding vegetation, *Azteca*-inhabited trees seem rather cleared from epiphytes.

Tab. 6. Comparison between epiphytic cover and different abiotic factors, using the coefficient of determination.

abiotic factor	coefficient of determination	number of trees
height of tree	$r^2 = 0,06$	(n = 185)
canopy cover	$r^2 = -0,03$	(n = 185)
distance to water	$r^2 = -0,11$	(n = 185)
canopy size	$r^2 = 0,05$	(n = 185)
sloping of ground	$r^2 = 0,02$	(n = 185)
dbh	$r^2 = 0,16$	(n = 185)

Tab. 7. Comparison between epiphytic cover and different biotic factors, using the correlation coefficient.

abiotic factor	coefficient of determination	number of trees
presence of <i>Azteca</i> colonies	$r^2 = -0,35$	(n = 156)
extension of <i>Azteca</i> nest	$r^2 = -0,70$	(n = 48)

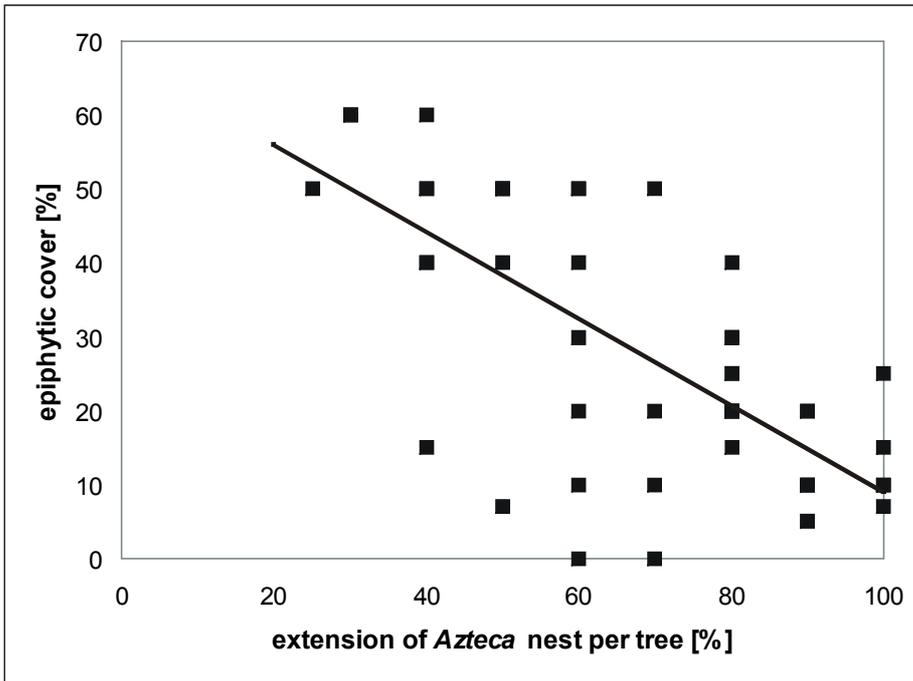


Fig. 26. Regression of epiphytic cover as a function of the extension of *Azteca* nest per tree. Correlation coefficient for this regression is $r^2 = -0,70$.

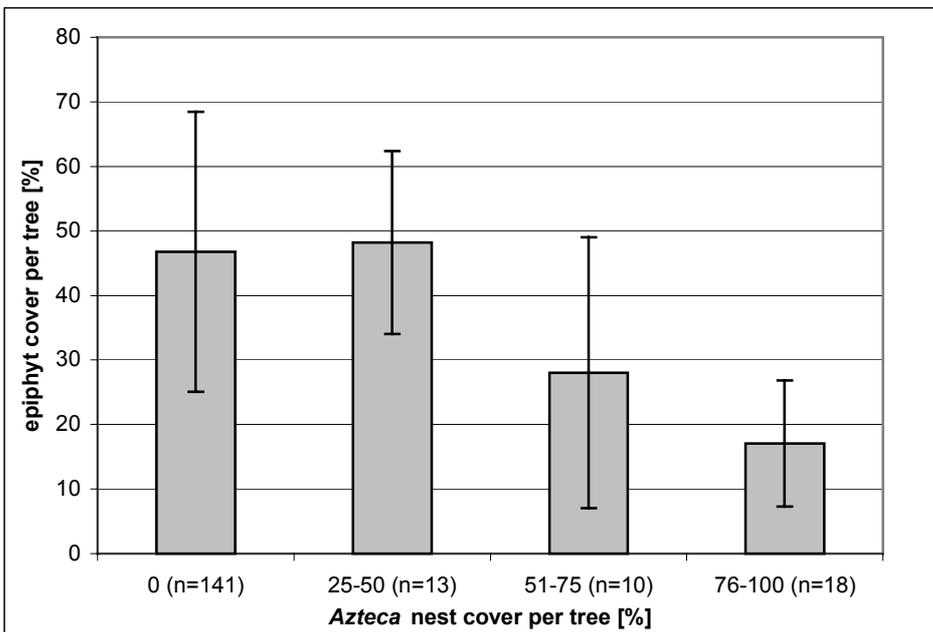


Fig. 27. Epiphyte cover (\pm SD) in relation to *Azteca* nest cover as a percentage of total branch length. The first category with 0 % *Azteca* nest cover means that no ants are present. The smallest *Azteca* nest covered 25 % of the tree.

Removal of adhesive tape

To prove experimentally the ability of *Azteca* ants to remove epiphytes, blue adhesive tapes were placed on the branches of *Crematogaster*- and *Azteca*-occupied trees. The removal behaviour of the ants was observed and classified into 4 categories (see Fig. 28). *Crematogaster* left the tapes mainly untouched with 66,6 % in category 1 (nothing removed) and 33,3 % in category 2 (small parts removed).

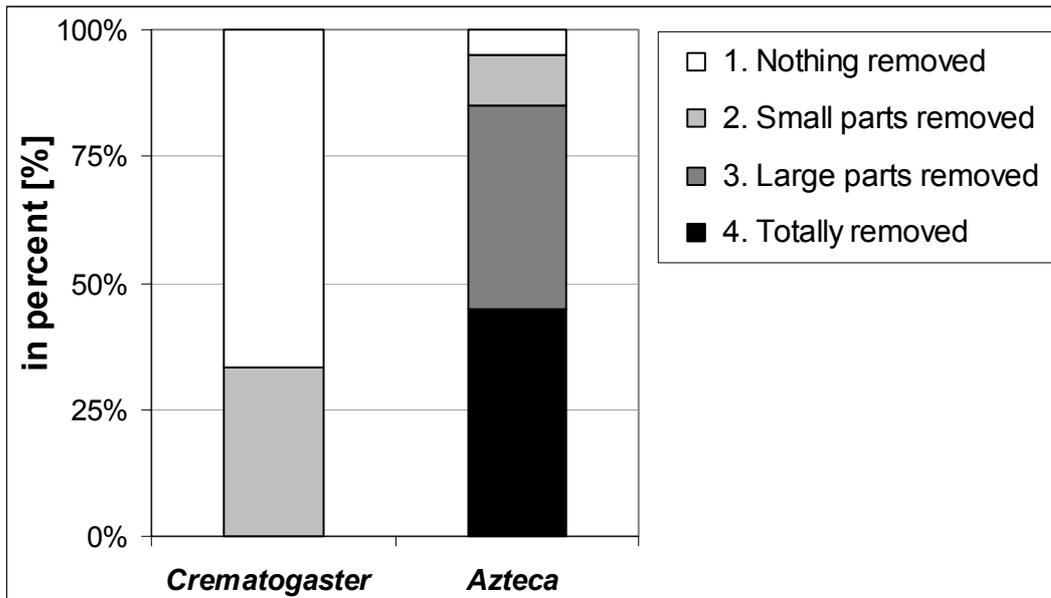


Fig. 28. The different of adhesive tape removal of *Crematogaster* (n = 12) and *Azteca* (n = 20) is represented in 4 behavioural categories. Control of the tapes was conducted one week after they were placed on the branches.

In contrast only a minority of the adhesive tapes was left untouched (category 1: 5 %) or slightly removed (category 2: 10 %) by *Azteca*. Because *Azteca* either removed the tape in large parts (category 3: 40 %) or removed it totally (category 4: 45 %), which means that a corridor was cut through the tape.

Parts of the tape were used to reconstruct the damaged carton tunnel! Around the place the tape was pasted the tape fiber was the main source of construction. But the blue tape fiber also could be found incorporated in the carton tunnel up to 1 m from its original place (Fig. 29).

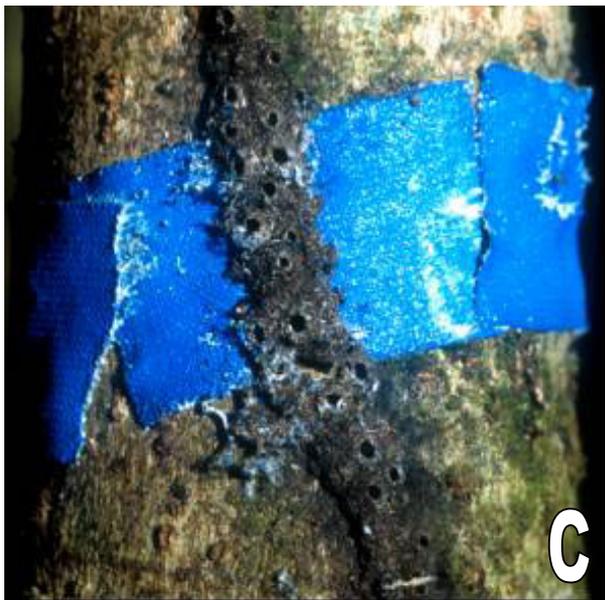
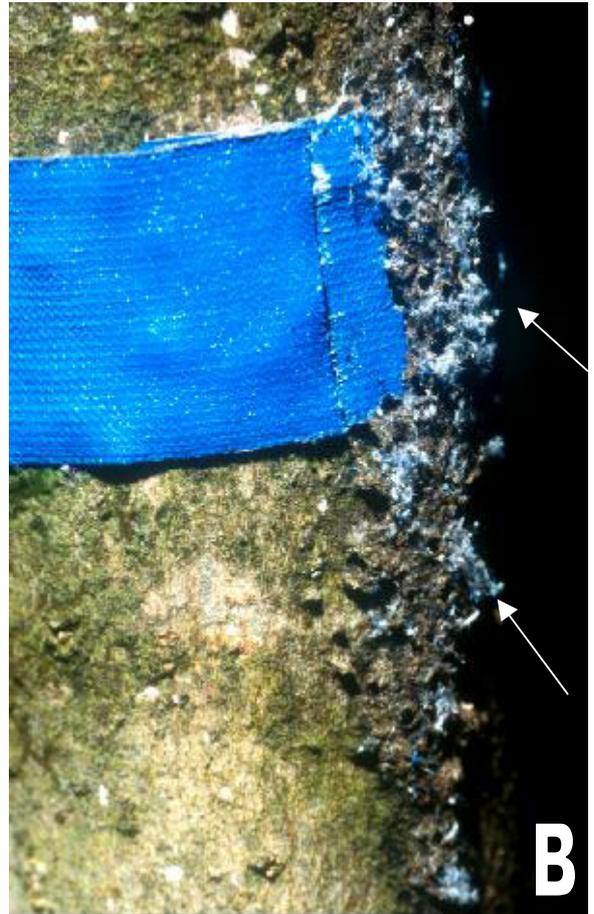
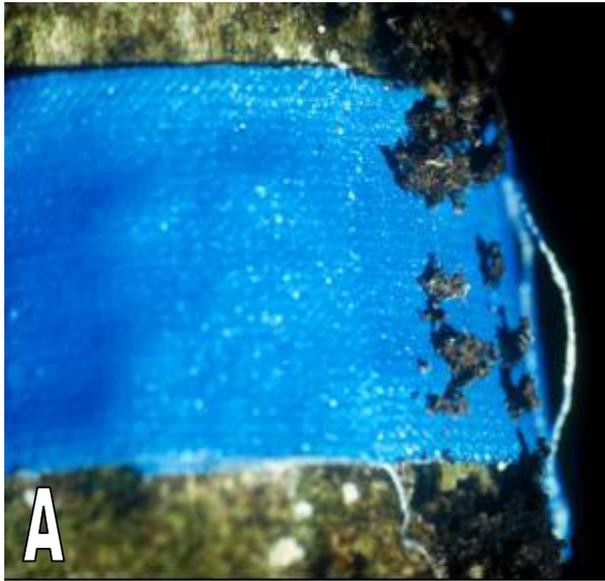


Fig. 29. A blue adhesive tape was placed on the trunk after the *Azteca* made carton tunnel was locally displaced. B) One week later the *Azteca* colony had repaired the damaged carton tunnel. Note the small light blue pieces incorporated in the newly constructed tunnel (arrows). C) Frontal view before and D) after displacing the tunnel a second time. The ants had cut most of the adhesive tape that was used as construction material for the tunnel.

Defense strategy

***Crematogaster*.** Only *Crematogaster* and *Azteca* ants have been observed to attacked intruders and defending their territory. *Crematogaster* ants attacked leaf beetles and other beetles on branches and leaves.

***Azteca*.** These ants occupy all the domatium chambers available within their territory. These ants are rather timid outside their nest and few ants were observed to enter the leaf. Only the young leaves of the new growth unit are frequently visited. Even though these ants seem timid at the first moment they have a particular defense strategy that copes with insect enemies much bigger and stronger than *Azteca*.

In case of emergency *Azteca* withdraw into their carton tunnels and place workers and soldiers to the tiny entry holes (Fig. 30). Intruding insects running on the tree's surface will rarely encounter *Azteca* ants outside their tunnels. But it is inevitable that those insects will pass over the carton tunnels and with high probability step into one of these tiny holes. In that moment the *Azteca* ant in the hole grabs the insects' leg with its mandibles and thus detains the intruder.

The attempt to free itself becomes an even more difficult situation for the victim as it starts to pull out its hold leg and steps into other tiny holes. In that moment the intruder is detained by two, three or more ants which means that it is totally trapped by the ants. From that point on the ants can either liberate the victim as observed in case of a fly (Fig. 31) or pull them into the carton tunnel and cut it up with their mandibles, as observed in case of a beetle (Fig. 32) and other ants. In that way the victim could serve as an additional food source for the *Azteca* colony.

***Azteca* vs. leaf-cutter ants.** Even though most of the *Atta* castes are much bigger than *Azteca*, the number of trapped *Atta* was very high (Fig. 33). It resulted that after half an hour only a minority (2,6 %) of the intruders could move freely on branches of *T. macrophyllum*. The only ants that could free themselves (if detained only by one leg) were of the most biggest caste of *Atta*. Only these individuals of the biggest caste had enough power to free their detained leg. *Atta* ants of the biggest caste had the highest chance free themselves and leave the tree. After 30 minutes 25,9 % of the *Atta* ants did leave the tree. Some few individuals simply dropped from the tree (6,9 %), but the majority was trapped by *Azteca* (64,6 %) (Fig. 34).

The only tree attacked by leaf cutter ants could be found in secondary forest, where *Azteca* colonies are totally missing. This individual tree was about 7 m tall and had lost practically all its leaves.

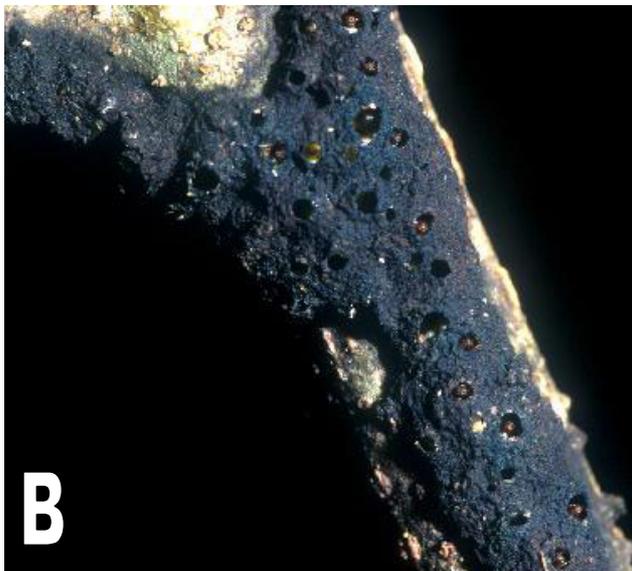


Fig. 30. A+B) Alerted *Azteca* ants inside their carton tunnel. Workers and soldiers wait inside the tiny holes with open mandibles. C-F) View of the ants in greater detail.

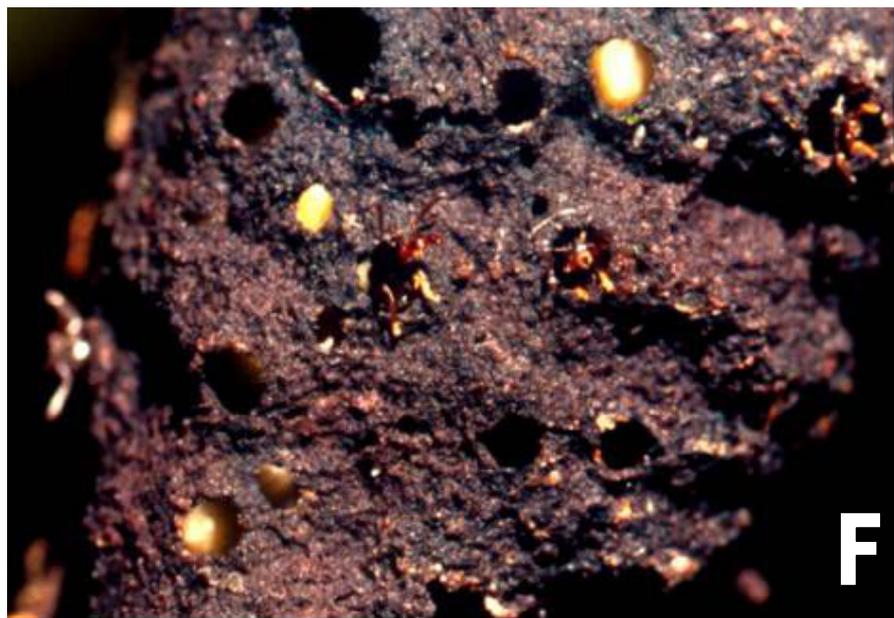
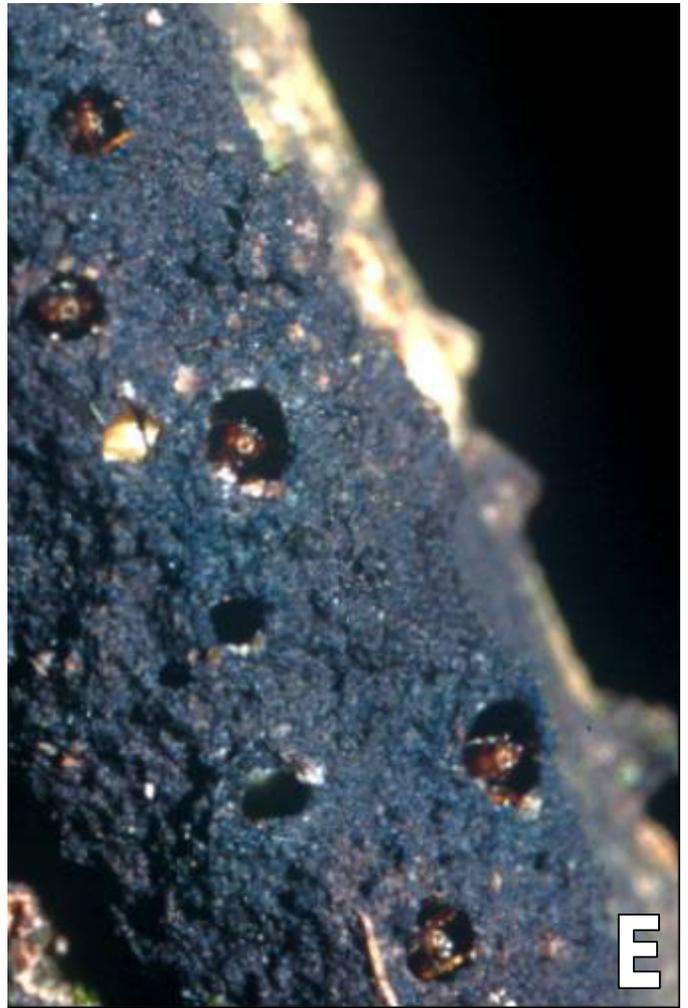
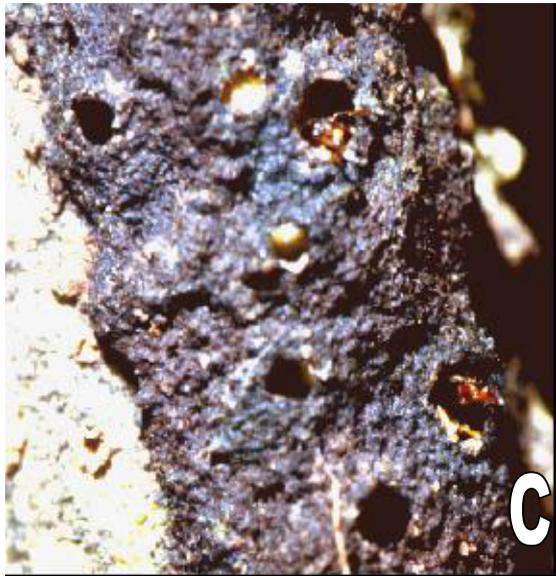




Fig. 31. *Azteca* ants inside their carton tunnel having trapped a diptera.



Fig. 32. *Azteca* ants having trapped an insect and pulled inside the carton tunnel.



Fig. 33. A-C) *Azteca* ants inside their carton tunnels having trapped the legs of larger *Atta* ants. D) The remains of an *Atta* ant after *Azteca* ants having killed the intruder.

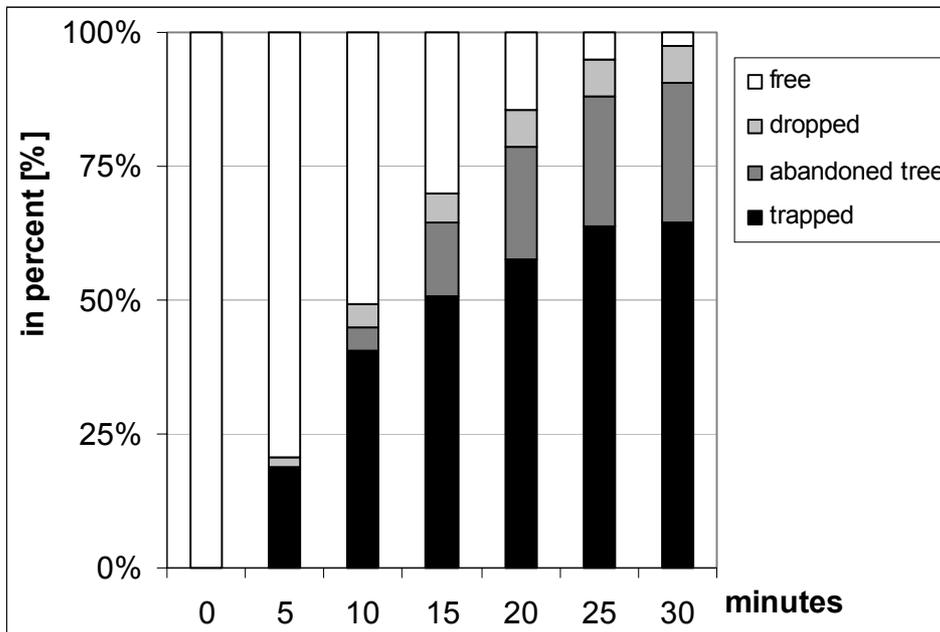


Fig. 34. Fate of *Atta* ants on *Azteca* colonized *T. macrophyllum*. Four test series with a total number of $n = 116$ leaf cutter ants.

Foraging territory

Crematogaster ants were mainly arboreal but one investigated colony left the tree for foraging activity (Tab. 8). This happened in case of a young colony on the smallest tree investigated (3,5 m height). On the other hand *Azteca* ants are strictly arboreal, they never left the canopy to forage on the tuna baits.

Tab. 8. Percentage of colonies leaving the tree for foraging on tuna baits.

Foraging territory	<i>Azteca</i> sp. (n = 14)	<i>Crematogaster</i> sp. (n = 6)
Arboreal	100	83
Arboreal & terrestrial	0	17

Artificial domatia

In the experiment neither *Azteca* nor *Crematogaster* colonised the artificial domatia (AD). Even though a difference between the two ant species was observed. While all of the ADs in *Azteca* territory were empty, at least one AD in *Crematogaster* territory held another insect, a small grasshopper (Tab. 9).

Tab. 9. Percentage of occupied artificial domatia (AD). AD were fixed to colonised trees of *Azteca* sp. and *Crematogaster* sp. The AD were observed for any type of occupancy during two months. The only insect that entered an AD was a little grasshopper.

Artificial Domatia (AD)	<i>Azteca</i> sp. (n = 12)	<i>Crematogaster</i> sp.(n = 10)
unoccupied AD	100	90
Ant-occupied AD	0	0
Occupied by other insects	0	10

Miscellaneous additional observations

- 1) Flowering and fruiting trees were relatively rare and at least 6 m high (Tab. 4). From the trees higher than 6 m (n = 128) only a minority of 9,37 % (n = 12) was observed to have fruits or flowers. Note that the observation was made in the known flowering period (December-April). *Azteca* occupied 4 and *Crematogaster* 8 of the 12 fruiting trees.
- 2) The most obvious enemies to the investigated ants are spiders from the subfamily Salticidae. Several different species were found on ant-occupied trees. Spiders from another subfamily used a highly specific hunting technique to pray on *Azteca* ants. This spider could lure the ants outside their tiny holes and caught them with its spinning fibre. The attacking ants were immobilised with the spinning fibre that stucked the mandibles of the ants to the plants surface. Even though the spider was hardly bigger than *Azteca* ants, using this technique it can face an attack of up to 20 ants, immobilising most of them. In the end the spider prayed 6 - 8 ants that were stucked together and then left the tree with this “food-ball” abseiling to the ground. This hunting technique was observed twice.
- 3) Once I could observe the “Cacique” bird (*Cacicus* sp.) feeding (?) on *Azteca* ants. Similar as the woodpecker (*Phloeoceastes* sp.) this bird searches for insect prey below the bark.
- 4) During the expansion of both *Azteca* and *Crematogaster* colonies on the same tree I observed the only direct encounter of such colonies. The colonies had approximately the same size. This was the only time I could observe *Azteca* ants in a forage column outside the carton tunnels. Without extensive fights *Crematogaster* ants withdrew into the surrounding vegetation, so that *Azteca* could overtake their domatium chambers. During this process I saw *Azteca* ants returning with larva to their nest. Perhaps the larva originated from the fleeing *Crematogaster* colony.

- 5) In the investigated area I found an *Azteca* colony with its typical carton structures on the outer branches of a small *Ocotea nicaraguensis* (Lauraceae) tree. This species belongs to the group of *Ocotea* species that do have hollow stems and is regularly inhabited by plant-ants.
- 6) A completely defoliated and ant-unoccupied 5 m high *T. macrophyllum* was found in secondary forest.
- 7) Due to the steep slope where *T. macrophyllum* mainly grows the number of fallen or heavily inclined trees was 28 out of 156 (≥ 4 m), which is 17,9 % .
- 8) In the herbarium of the “Museo Nacional de Costa Rica” one of the currently 47 herbarium specimen did not originate from Costa Rica. This specimen came from the department Narino, Colombia, where the species - due to the notes on the label - is abundant. The colombian specimen also had domatium chambers and in one I found the dry rest of a catapillar. The leaves had many gall like structures, which did not occur in the costarican specimens.

4. DISCUSSION

The ant’s point of view

Ant attractants. *T. macrophyllum* does not provide food sources such as extrafloral nectaries or food bodies. So far domatia seem to be the only attractants to ants. The presence and size of the domatia depend on the age or rather on the size of the tree. The domatia of *T. macrophyllum* reach their final size at a tree height of about 4 m. Even though some ant colonisation takes place before the plant has reached this size, from the height of 4 m the trees are “mature” regarding their myrmecophytic traits.

Succession. In *Tetrathylacium macrophyllum* a succession of ant inhabitants, with *Pheidole* and *Crematogaster* establishing early and *Pachycondyla* and especially *Azteca* establishing relatively late, can be observed. Succession in plant-ants is also known from different myrmecophytes such as *Cordia nodosa*, *Tococa* and *Clidemia* species (Davidson et. al 1989), *Tachigali myrmecophila* and *Tachigali polyphylla* (Fonseca 1993) or various *Cecropia* species (Davidson & Fisher 1991, Longino 1991).

As the relatively large natural openings of the domatia do not prevent the access of specific ant species, interspecific competition is inevitable. Especially in the colony founding stage the foundresses or incipient colonies are competing for domatium chambers. The sooner the colony establishes and the faster it grows, the more difficult is it to displace it (e.g. McKey 1984). *Pheidole* and *Crematogaster* are observed to be the first to occupy *T. macrophyllum*, so they might have an advantage as they avoid to compete against established *Azteca* colonies which are the most dominant. *Azteca* has better chances to develop on bigger trees which can provide a greater number of free domatium chambers. Once an *Azteca* colony has established

it expands its arboreal territory. During expansion it may force other ant colonies to withdraw, even in case of large *Crematogaster* colonies.

Pheidole. Ants were found either in relatively small trees, or outside the territories of established *Crematogaster* or *Azteca* colonies, or at twigs abandoned by *Azteca*.

The small *Pheidole* ants can produce individuals of the sexual caste by only inhabiting two or three domatium chambers. The small colony size of *Pheidole* is a disadvantage facing the larger and stronger colonies of *Crematogaster* and *Azteca* that can occupy the whole tree. The risky and “on the edge” living space of *Pheidole* together with its early reproduction rate and the small size of the colony defines the opportunistic strategy of this subordinate species (Davidson & McKey 1993). The small *Pheidole* colonies nest equally in live and dead stems of *T. macrophyllum*. This species is specialized on hollow stems or cavities but with high probability a generalist due to its host. These ant species with its small colonies are also expected in other natural cavities of other plant species.

Crematogaster. The large colonies of *Crematogaster* are specialized live stem nester as they are tending coccids inside and outside the domatia. As a typical behaviour of a specialized plant-ant, they limit their nesting and foraging territory in most of the cases to the host tree itself. *Crematogaster* can aggressively attack herbivores on leaves within their territory. Workers, and very likely also the foundresses, have the ability of sealing the natural opening with a carton roof. This behaviour seems to be specialized to hosts with hollow live stems that provide relatively large openings.

Pachycondyla. This species has a notably life history that is in some points similar to *Pheidole*. The only member of Ponerinae inhabiting *T. macrophyllum* is by far the largest ant species while the colony is by far the smallest in terms of individuals. The fact that within a few seconds the whole colony can leave the domatia in case of emergency, shows the extraordinary mobility of this species. Colonies can occur at relatively young trees but mainly at the edge of *Crematogaster* territories. The very small colony size and the high mobility of *Pachycondyla* are typical of an opportunistic cavity nester (Davidson & McKey 1993). The life history resembles that one of *Pachycondyla crenata* (Longino 1999) but exact species identification has still to be done. *Pachycondyla* is a nomadic general cavity nester without any obvious specialisation on *T. macrophyllum*.

Azteca. This ants are specialists on hollow live stems but generalists on host species as these species have not only be found on *T. macrophyllum* and *Ocotea nicaraguensis*, but also on a variety of other mainly hollow live stem bearing host trees, such as *Licania* (Chrysobalanaceae), *Grias* (Lecythidaceae) and an unidentified tree of Moraceae (Longino 1996). The percentage of *Azteca* occupation on these trees, other than *T. macrophyllum*, is unknown. Similar as *Crematogaster*, *Azteca* has the ability to seal the natural openings with carton and tend coccids. In comparison to related *Azteca* species, the pilosity of the queen’s mandibles is very high (Longino 1996). Longino gives a possible explanation for the high pilosity (*Azteca* JTL 001 is part of the *A. nigricans* complex): “The stiff setae on the mandibles of ants in the *A. nigricans* complex appear as though they would impede cutting into plant stems. Perhaps ants in the *A. nigricans* complex, rather than being specialized to excavate entrances in a particular kind of host plant, are instead specialized to find preexisting entrance holes into plant cavities, regardless of plant species. Strongly pilose mandibles may

be an adaptation for efficient and rapid construction of carton nest material, which would be necessary to close large and/or irregular preexisting entrances.” (Longino 1996, p. 149).

Therefore foundresses of *Azteca* are specialized to occupy myrmecophytes such as *T. macrophyllum*. Nevertheless this *Azteca* species has been found as well to occupy hollow branches without regular natural openings on *Ocotea nicaraguensis* (Burger & Werff 1990). Possibly the ability of the queen of cutting into plant material is not totally reduced, but “not as good” as in related species. This gives the queens an advantage of occupying domatia with natural openings, but not totally impeding them from hosts such as *O. nicaraguensis*. Workers are still able to chew additional entrance holes into the young and soft stem and keep them free as secondary growth and lignification takes place.

Nesting space and space use. *Crematogaster* and *Azteca* colonies use the resources of *T. macrophyllum*, such as nesting space and cultivation of coccids, most efficiently. The medium worker body size and the relatively large colony size seem to be properly adapted to an ant-plant of this size. Although the small *Pheidole* ants use the single domatium chambers most efficiently in terms of individuals, larvae and eggs, the small colony size prevents an occupation of the whole ant-plant.

Comparing the nesting space, there is a clear difference between the two “medium-sized” ant species. While *Crematogaster* ants do only nest in plant borne domatia, *Azteca* ants additionally enlarge the nesting space by excavating the soft pith. The enlarged domatia do not serve only for more nesting space but also for additional space to tend more coccids. If we consider domatium size as the “anti-herbivore” investment of the plant, *Azteca* “forces” *T. macrophyllum* to a higher investment!

The defending capacity of their relatively large colony size makes *Crematogaster* and *Azteca* the dominant ants. In contrast the smaller and vulnerable colonies of subordinate (or subdominant) *Pheidole* and *Pachycondyla* are excluded from *Crematogaster* and *Azteca* territories.

Carton structures. A further notable feature of *Crematogaster* and *Azteca* are their carton constructions. Both species protect their coccids by carton structures on the plant’s surface, thus monopolising their food resources (see Davidson & McKey 1993). But only the carton tunnels of *Azteca* connect the inhabited domatia of their polydomous nest. That way the predatory risk of workers travelling between single chambers is reduced. The nest size is actually enlarged by the extensive carton gallery. Even though the tunnels are used for transport and for tending coccids, they can not be regarded as true nesting space as eggs, larva and alates only occur inside the domatia.

Several carton nest-building *Azteca* species are known and some of them are plant ants. Costarican *Azteca constructor* builds a spindle-shaped carton nest inside *Cecropia obtusifolia* (Longino 1991) and three *Azteca* species in Peruvian Amazon have been observed to build carton nests on a variety of plant species in the vicinity of their myrmecophyte hosts (Davidson et al. 1989).

Coccids. The large colony size of *Crematogaster* and *Azteca* and their defending capacities are sustained by the continuous food production of the coccids. The two species breed two different coccid species and although no exact systematic information about the coccids is available, the pink coccids of *Azteca* JTL 001 (*nigricans* complex) have also been reported from other live stem inhabiting *Azteca* species, such as *Azteca longiceps* (Longino 1996).

Unfortunately no information about the origin of the first coccids of the colony could be obtained. So it remains unclear if the coccids originate from an established colony and are simply carried by the founding queen, or if the founding queen would have to find a coccid by random (see Hölldobler & Wilson 1990). If the second option is true, this could be an explanation for the relatively late establishment of *Azteca* colonies.

There is also no information about the chemical composition of the honeydew and the efficiency of food production of the two coccid species. Differences of food production could be the reason why *Azteca* colonies are more dominant than *Crematogaster* colonies. The importance of different homopteran “efficiency” on ant activity has been demonstrated in the *Leonardoxa africana* ant-plant-homopteran mutualism (Gaume et al 1998).

Conclusion. Studies in paleotropical *Macaranga* species (Euphorbiaceae) have shown that the most important attractant to ants are domatia (Fiala & Maschwitz 1992). Total nesting space, rather than territory or food, of two *Tachigali* ant-plants species was suggested the main limiting factor for *Pseudomyrmex concolor* colony size (Fonseca 1993). A similar positive relationship between ant colony size and total number of domatia offered by the host, was shown in 8 different amazonian ant-plant-mutualisms (Fonseca 1999). The “nesting space limitation hypothesis” says, that in well adapted ant species, queen-, worker- and colony size are closely related to domatia size and total nesting space of the host plant (Fonseca 1993).

This hypothesis would favour our *Crematogaster* and *Azteca* colonies as the most adapted species in terms of worker- and colony size locally available. The nesting space limitation hypothesis together with the different efficiency of host colonisation, colony structure, the defense mechanisms and the local availability of the ant species, seem to be the most important factors determining the particular occupation pattern of *T. macrophyllum*.

Finally, from the ant’s point of view, the interaction is a positive effect onto them. The encountered nesting space serves as shelter for ants and their brood and offers the possibility to tend coccids as a food source.

The plant’s point of view

Potential positive effects. Although leaf damage and thus herbivory is not high on unoccupied, *Crematogaster*- and *Azteca*-occupied trees show leaf damage reduction of about 50 %. Similar values are known from myrmecophytic *Macaranga* species (Fiala et al. 1991). Herbivore protection effects great parts of the tree as these colonies are relatively large. It is also known from another *Azteca* species that bigger ant colonies protect their plants better than smaller ones (Duarte Rocha & Bergallo 1992). While *Crematogaster* directly attacks

herbivores on branches and leaves, *Azteca* uses a special defense strategy to impede the access of non-flying herbivores, especially leaf cutter ants, to the leaves.

Impeded access of leaf-cutter ants. Leaf-cutter ants are the most serious herbivores in neotropical forests (Blanton & Ewel 1985). Also ant-plants have to face this risk as has been reported in case of *Cecropia*, because repeated attacks by leaf-cutter ants reduce the growth of this trees and therefore reduce plant fitness (Vasconcelos & Casimiro, 1997).

The defense strategies against leaf-cutter ants are reported as aggressiveness and high recruiting behaviour in case of *Azteca alfari* on *Cecropia* (Vasconcelos & Casimiro, 1997) and *Azteca* sp. on *Citrus* trees (Jutsum et al. 1981).

In contrast *Azteca* JTL 001 does not attack aggressively, but uses its carton tunnels with its tiny holes as a defense wall. That mode *Azteca* ants can fight and disable even more powerful intruders, minimizing its proper risk of losing workers and soldiers. Also the amount of energy per defense event is reduced. Of course it takes energy to construct the tunnel system, but continuous production of honeydew provides a steady and stable amount of energy. By investing into a defense mechanism in “peaceful times” the energy consumption in “war times” can be reduced!

It is the first time ants were observed to use such a special technique to disable other insects. I believe that this is not only a defense strategy but also a low-risk predation strategy, as *Azteca* can use the intruder as an additional food source. A secondary effect to *T. macrophyllum* is a potential protection against leaf-cutter ants and other non-flying herbivores.

Although special data of *T. macrophyllum* leaf attractiveness to leaf cutter ants is missing, the leaves of other costarican *Azteca*-inhabited ant-plants such as *Pithecolobium saman* (new leaves), *Cocoloba caracasana* (new leaves) and especially *Cordia alliodora* have been tested palatable to very palatable for *Atta* ants (Rockwood 1976, Janzen 1983, Rockwood & Hubbell 1987, Powel & Stradling 1991). Young and therefore soft leaves without chemical defense are generally preferred (Howard 1988, Nichols-Orians & Schultz 1989). As chemical defense has been reduced in some myrmecophytes (Davidson & Fisher 1991), the young, soft, light green leaves of *T. macrophyllum*'s new growth units are likely to be a palatable food source for leaf cutting ants.

Thus I suggest that lack of defense mechanism in young leaves (secondary plant chemistry, toughness) could be made good by *Azteca* defense of these myrmecophytes (see also Janzen 1969).

Epiphytes. *Azteca*'s carton structures are at least partly made by epiphytic material. Even though *Azteca*-occupied *T. macrophyllum* appear cleaned by epiphytes, there is no obvious positive or negative effect to the host plant. The only suggestion is that the ant colony impedes the growth of large and heavy epiphytes, that could raise the tree's risk of falling down. Due to the steep slope, where the host tree mainly grows, the risk of falling down is approximately one out of six (17,9 %). It is possible that a high number of heavy epiphytes (such as large Bromeliaceae), especially on the branches, increases the risk of imbalance. The removal of epiphytes could therefore decrease this risk. Nevertheless there is no proof of such a risk minimizing effect.

Potential negative effect and ant colonisation. A potential negative effect the ants cause to the plants is the presence of coccids. As 70 % of the trees are occupied either by *Crematogaster* or *Azteca* or both, the same number deals with (plant sap sucking) coccids. The honeydew producing homopteras take saccharose, aminoacids and ions from the plant's phloem (Dettner & Peters 1999). Quantity of the lost phloem has not been investigated so far. But as long as the tree gets enough light, enough carbonhydrate is produced during the photosynthetic process (Nultsch 1991, Davidson & McKey 1993). The only potential negative effect of the coccids is that they could serve as disease transmitter between individual trees.

Small and young saplings without domatia receive less light on the rainforest floor, lacking enough resources to maintain an ant colony, whether taller trees seem to receive enough light to maintain ant colonies. Therefore the delayed expression of myrmecophytic traits, in this case domatia chambers, until later sapling development is a useful adaptation to shady environments (see Davidson & Fisher 1991).

Azteca ants excavating the soft pith do not injure the plants vital vessels, only the ant-made entrance holes cause a local minor damage to them.

Habitats

Individuals of *T. macrophyllum* occur mainly in primary rainforest on moderately to steep slopes close to creeks or standing water. Some individuals can be found in dry secondary forests far away from creeks or standing water presumably in a sub-optimal situation. For unknown reasons the ant occupation varies significantly between primary and secondary forest. The dominant and most frequent *Crematogaster* and *Azteca* ants – both tending coccids – of the primary forest are completely missing in secondary forest. There subordinate *Pheidole* ants are the main inhabitants of *T. macrophyllum*. Possibly the dryer environment inhibits the proliferation of the coccids that are important to the vitality of the dominant ant species. In absence of competition with dominant ant species the subordinate *Pheidole* develop to the most frequent ant inhabitant of *T. macrophyllum*.

Although in general there are more myrmecophytic species growing in succession or secondary forests than in primary forest (Schupp & Feener 1991), *T. macrophyllum* belongs to the less frequent shade tolerant ant-plants.

Intensity of the ant-plant interaction

Myrmecophyte. Total ant occupation of trees higher than 4 m in primary forest is about 95 %. In 85 % of the trees there is a regular relationship with the same four ant species. Jolivet says: "The true myrmecophytes or plants having regular relationship with the ants are the ones offering lodging (myrmecodomic) or food (myrmecotrophic) or both (myrmecoxenic). I actually ignore the plants with extrafloral nectaries..... Generally the ones which offer food-bodies, also give lodging, the contrary not being true." (Jolivet 1996, p 62). That way *T. macrophyllum* is a true myrmecophyte sensu Jolivet!

Four different ant species. It is not exceptional that a myrmecophytic tree species regularly houses 4 different ant species. Studies in Amazonian forest revealed that the mean number of ant partners of 16 investigated host tree species was 4,1. Nevertheless in most of the cases (12 out of 16) there was one dominant species occupying by far most of the host plants (> 50 %). The study showed that an uneven distribution of plant ants on their myrmecophytic host can regularly be encountered (Fonseca & Ganade 1996). In contrast the distribution of the four plant ants of *T. macrophyllum* is not that uneven. Especially the distribution of the two dominant species, with 50 % and 30 % for *Crematogaster* and *Azteca* respectively, is relatively even.

The sympatric coexistence of two dominant species in the same local area is generally unusual for ant-plant interactions. It is known only from some *Cecropia* species which show a similar occupation pattern involving *Azteca* species (Davidson & Fisher 1991). In that case *Azteca* is believed to be a secondary associate of the myrmecophyte, in other words *Azteca* is taking over a new host plant, superseding the former ant partner of the host species. At least two carton building *Azteca* species are also known for the invading of other myrmecophytic hosts such as *Cordia nodosa* and *Tococa* sp (Davidson & McKey 1993).

In case of *Azteca* JTL 001, of the *Azteca nigriceps* complex, an invading behaviour is also very likely, considering the distribution of its closest systematic relatives, that are known to inhabit costarican lowland atlantic forest (Longino 1996). The distribution of the *Azteca nigriceps* complex, together with sympatric coexistence of two dominant ant species and the fact that established *Azteca* colonies are able to drive away established *Crematogaster* colonies, sustains the hypothesis that also in our case *Azteca* is a secondary associate. The highest radiation of neotropic plant-ant genera occur in *Pseudomyrmex* and *Azteca*, indicating the successful properties of these two species (Davidson & McKey 1993).

Specialisation. Domatia of *T. macrophyllum* have relatively large natural openings offering a great number of ant species to enter. There are no mechanisms or “securities” (hollow branches without openings) that regulate the establishment of selected ant species, as in case of *Macaranga* (Fiala et al. 1991) or *Acacia* (Janzen 1983). The lack of specialization on particular ant species, let locally available general and specialized live-stem nester to be expected to nest in *T. macrophyllum*.

Subordinate *Pheidole* and *Pachycondyla* are not specialized on *T. macrophyllum*, while dominant *Crematogaster* and *Azteca* are specialized on ant-plants of this size with easily accessible domatium chambers. Nevertheless *Azteca* is a host generalist and it is also expected from *Crematogaster* that it occupies hosts with very similar myrmecophytic traits.

The investment of *T. macrophyllum* to its ant partners is less than in highly specialized *Acacia*, *Piper* or *Cecropia* myrmecophytes, as these ant-plants offer not only lodging but also food bodies. Hollow twigs are the most basic form of a myrmecophytic trait (see Beccera et al. 1989) and some authors are even denying the myrmecophytic character of hollow branches (Davidson & McKey 1993). Nevertheless the investment (domatium chambers) of *T. macrophyllum* is enough to establish a regular interaction with its ant partners.

Conclusion. Concluding the data obtained in this study, *Pheidole* and *Pachycondyla* cause neither a positive nor a negative effect to the plant-host. The opportunistic use of nesting space makes these ants comensualistic partners of *T. macrophyllum*.

In contrast, the most common, dominant ant species *Crematogaster* and *Azteca* reduce herbivore activity either by attacking aggressively or using a special defense strategy impeding leaf cutter ants the access to the young leaves. The “anti-herbivore” investment for the host plant is higher in case of *Azteca* (enlarged nesting space, higher number of coccids). Therefore *Crematogaster* is a more efficient partner, at least in shady environments (e.g. in small trees. If the amount of light and water supply are not the limiting factors (e.g., in higher trees) the difference in “anti-herbivore” investment for the two species is reduced. A highly similar occupation pattern is known from *Cecropia* trees, where *Azteca* species predominate on *Cecropia* in open sunny environments. Slower growing *Cecropia* trees in shaded habitats are often occupied by different species including *Crematogaster*, *Pachycondyla* and *Camponotus* (Formicineae) (Davidson & Fisher 1991).

The effect of the epiphyte clearing behaviour of *Azteca* remains unclear, providing a possible additional positive effect to *T. macrophyllum*.

In order of the fact that only 70 % of the trees are occupied by *Crematogaster* and/or *Azteca*, the interaction has to be classified as facultative, as no obligation for coexistence neither for the plant nor the ants can be proven. Nevertheless both, the dominant ant partners and the host plant, are gaining an advantage of the interaction.

So the true character of the interaction between *T. macrophyllum* and *Crematogaster/Azteca*, in the investigated region, is a facultative symbiosis.

The *T. macrophyllum* – *Crematogaster/Azteca* interaction is clearly less intense than the obligate symbiotic interactions of aggressive *Pseudomyrmex ferruginea* - *Acacia allenii* (Janzen 1983), *Azteca* - *Cecropia* (Janzen 1969, Schupp 1986, Vasconcelos & Casimiro 1997), *Crematogaster borneensis* - *Macaranga* (Fiala et al. 1989) or of rather timid *Pheidole bicornis* - *Piper* sp. (Letourneau 1983), *Pheidole minutula* - *Maitea guianensis* (Vasconcelos 1991) or *Petalomyrmex phyla* - *Leonardoxa africana* (Gaume et al. 1997). It is also clear that the relationship is not of a parasitic character as *Pseudomyrmex nigropilosa* - *Acacia* (Janzen 1975) or *Cataulacus* - *Leonardoxa africana* (McKey 1984).

Comparing *T. macrophyllum* to other ant-plants, the paleotropical understory treelet *Leonardoxa africana* seems to be a similar myrmecophyte. The main partner of *L. africana* are “timid” ants, its domatia are swollen internodes and ants tend two different coccid species (McKey 1984, Gaume et al. 1997, Gaume et al. 1998). Nevertheless there are some striking differences: *L. africana* has extrafloral nectaries, the hollow branches do not have natural entrances (McKey 1984), the symbiotic ant partner have a very small body size which is thought to have a positive effect on the protection efficiency against herbivores (Gaume et al. 1997).

In contrast the most similar ant-plants in the neotropic region are *Triplaris melaenodendron* (Polygonaceae), *Cordia alliodora*, *C. nodosa* (Boraginaceae) (Longino 1996) and some Lauraceae such as *Ocotea nicaraguensis*, *O. atirrensis*, *O. dendrodaphne*, (Ishii & Ickes 1995) *O. wedeliana*, *O. paulii*, *Licaria brenesii* and *L. multinervis* (Burger & Werff 1990). All

these trees have in common that they provide live nodes as the only investment to their ant partners. The most important difference to *T. macrophyllum* is that none of these myrmecophytes has natural openings. The ant partners are specialized on hollow live stems but in most of the cases host generalists. In case of *Triplaris* and *Cordia* these ants belong to the dominant genera *Crematogaster*, *Pseudomyrmex* and *Azteca* or the subordinate genera *Zacryptocerus* (Longino 1996).

The ant partners of *T. macrophyllum* belong to this “pool” of plant-ants and the myrmecophytic traits are practically the same as in other ant-plants with hollow live stems. Thus there are enough reasons to add *T. macrophyllum* to this “cluster” of ant-plants with live stems.

Further questions

Further questions arise by considering the geographic distribution of *T. macrophyllum* and its ants. As already discussed in the case of *Conostegia setosa* (Alonso 1998) the local spatial, geographic and temporal distribution of the ant occupants has an important impact on the occupation pattern of the host tree. Myrmecophytes have different or no ant partners along their geographic and altitudinal distribution; e.g., *Leonardoxa africana* (McKey 1984), *Cecropia* (Longino 1989) or *Cordia nodosa* (Longino 1996). It is even possible that the myrmecophytic traits of the host, e.g., the size of the domatia, depends on the geographic location of the ant-plant (McKey 1984, Alonso 1998). Studies about habitat specialization revealed that many plant-ants show greater specificity to habitats than to host species (Davidson & Fisher 1991, Davidson & McKey 1993).

T. macrophyllum occurs from Peru to Costa Rica (Janzen 1983, Brako & Zarucchi 1993, Gentry 1997, Jorgensen & Léon-Yamez 1999) but *Azteca* JTL 001 occurs only in Costa Rica and Panama (Longino 1996). No information about the distribution of the other plant ants of *T. macrophyllum* is known to the author. Due to the very different distribution range of *T. macrophyllum* and *Azteca* JTL 001 and the relative low percentage of occupied individuals, it is unlikely that these two species are the original partners. Further investigations have to focus on the ant partners and their specific relationships with *T. macrophyllum* in the center of its distribution area, namely in the north western rainforests of south America (e.g., in the Colombian Choco-region). The study of *T. macrophyllum* in its core distribution area will be imperative to our understanding of the nature of this myrmecophytic species.

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7. APPENDIX

Abiotic and biotic factors recorded in 185 trees of *T. macrophyllum* in primary forest.

tree n°	tree height	dbh	crown size	<i>Azteca</i> occupied	percentage of <i>Azteca</i> occupation	distance to river	canopy cover	sloping of ground	epiphytic cover	Flowers/ fruits
	m	cm	1 to 5		%	m	%	degree	%	
1	0,4	-	1	0	0	4	90	10	5	0
2	0,8	-	1	0	0	6	100	45	50	0
3	0,95	-	1	0	0	10	100	45	10	0
4	1	-	1	0	0	6	80	0	5	0
5	1	-	1	0	0	12	100	60	55	0
6	1	-	1	0	0	50	90	30	10	0
7	1,4	1	1	0	0	5	50	45	60	0
8	1,5	1	1	0	0	50	40	30	0	0
9	1,7	0,9	1	0	0	10	70	45	80	0
10	2	1,4	1	0	0	4	80	60	10	0
11	2	1,3	1	0	0	6	70	0	40	0
12	2	0,8	1	0	0	4	70	5	50	0
13	2	1,3	1	0	0	6	70	5	70	0
14	2	0,9	1	0	0	8	80	45	10	0
15	2,5	2	2	0	0	15	80	45	50	0
16	2,5	1,5	2	0	0	50	70	20	0	0
17	2,75	1,5	2	0	0	10	70	45	80	0
18	3	2	2	0	0	3	80	60	50	0
19	3	2	2	0	0	6	70	0	30	0
20	3	1,7	2	0	0	6	50	0	10	0
21	3	1,5	2	0	0	10	80	25	20	0
22	3	2,4	2	0	0	8	60	5	50	0
23	3	1,5	2	0	0	10	50	45	30	0
24	3	1,4	2	0	0	8	60	5	15	0
25	3	1,9	2	0	0	20	80	45	40	0
26	3,25	2,1	2	0	0	12	50	45	50	0
27	3,5	2	2	0	0	5	75	20	50	0
28	3,5	2,5	2	0	0	5	60	60	10	0
29	3,5	2,3	2	0	0	5	60	60	5	0
30	4	2,8	3	0	0	2	60	60	60	0
31	4	3	2	0	0	5	50	0	10	0
32	4	2,5	1	0	0	4	50	60	10	0
33	4	4,3	3	0	0	4	50	60	20	0
34	4	2,5	2	0	0	6	50	45	10	0
35	4	2,2	2	0	0	10	80	45	50	0

tree n°	tree height	dbh	canopy size	<i>Azteca</i> occupied	percentage of <i>Azteca</i> occupation	distance to water	canopy cover	ground slope	epiphytic cover	Flowers/fruits
	m	cm	1 to 5		%	m	%	degree	%	
36	4	2,5	2	0	0	7	70	60	10	0
37	4	2,8	2	0	0	10	60	45	80	0
38	4	2,3	2	1	60	1	50	5	30	0
39	4	2,5	2	0	0	8	60	5	40	0
40	4	4	3	1	40	5	50	5	40	0
41	4	3	3	0	0	1	50	60	20	0
42	4	2	1	0	0	7	75	10	50	0
43	4	3,5	2	0	0	8	70	45	60	0
44	4,5	2,5	2	0	0	10	50	45	80	0
45	4,5	5	3	0	0	50	20	30	20	0
46	5	3,4	3	0	0	3	50	45	80	0
47	5	4	3	0	0	3	50	60	30	0
48	5	3	2	0	0	6	80	60	20	0
49	5	4,5	2	0	0	5	50	60	20	0
50	5	5	2	0	0	5	50	60	90	0
51	5	4	3	0	0	7	50	30	40	0
52	5	4,5	3	0	0	8	60	45	50	0
53	5	5	3	0	0	3	40	45	60	0
54	5	4	3	1	40	10	40	60	50	0
55	5	3,9	2	0	0	10	40	45	50	0
56	5	2,3	3	1	80	0,5	40	5	40	0
57	5	2,5	2	0	0	0,5	60	15	10	0
58	5	1,7	3	0	0	1	40	5	20	0
59	5	4	2	0	0	1	40	5	25	0
60	5	5	3	0	0	8	50	10	15	0
61	5	3,5	3	0	0	0,5	50	60	20	0
62	5	7	3	0	0	1	50	60	60	0
63	5	4,5	3	0	0	5	50	45	20	0
64	5	7	3	0	0	20	60	45	60	0
65	5	3,2	3	0	0	15	70	45	20	0
66	5	3,5	2	0	0	7	50	60	20	0
67	5	5,8	3	0	0	50	50	60	25	0
68	5	4	3	0	0	50	50	60	50	0
69	5	3	2	0	0	50	50	45	15	0
70	6	4,6	3	0	0	5	40	30	70	0
71	6	5	2	0	0	8	40	45	50	0
72	6	6	2	0	0	8	50	45	70	1
73	6	5	3	0	0	3	40	60	70	0

tree n°	tree height	dbh	canopy size	<i>Azteca</i> occupied	percentage of <i>Azteca</i> occupation	distance to water	canopy cover	ground slope	epiphytic cover	Flowers/fruits
	m	cm	1 to 5		%	m	%	degree	%	
74	6	5,5	3	1	50	10	60	45	40	0
75	6	4,5	4	1	80	2	40	5	20	0
76	6	5	4	1	50	4	50	45	50	0
77	6	5,5	3	0	0	1	50	60	20	0
78	6	4,5	3	1	60	1	50	60	10	0
79	6	6,5	3	0	0	2,5	60	30	70	0
80	6	12	4	0	0	1,5	30	10	25	0
81	6	6	3	0	0	8	50	45	90	0
82	6	7,5	3	0	0	3	50	45	50	0
83	6	5,5	3	0	0	10	60	30	60	0
84	6	7	3	0	0	20	50	45	70	0
85	6	5	3	0	0	30	60	45	35	0
86	6	7,8	3	0	0	15	60	60	35	0
87	6	5	3	0	0	20	50	45	25	0
88	6	3	2	0	0	8	70	45	15	0
89	6	4,5	2	0	0	50	60	50	30	0
90	7	10	3	0	0	3	50	45	90	0
91	7	5	3	1	90	7	50	60	20	0
92	7	12,5	4	0	0	8	30	45	30	0
93	7	6,5	2	1	60	1	40	5	50	0
94	7	7,5	4	1	50	1	30	15	50	0
95	7	9	3	0	0	8	50	30	60	1
96	7	9	4	1	90	10	50	45	10	0
97	7	10	4	0	0	2	30	60	20	0
98	7	10	4	0	0	2	40	60	30	0
99	7	8,5	4	1	25	15	40	45	50	0
100	7	6	4	0	0	15	40	45	60	0
101	7	7,5	3	0	0	1,5	50	30	70	0
102	7	8	4	0	0	10	50	25	50	0
103	7	6,5	3	0	0	12	60	60	40	0
104	7	10	3	0	0	10	60	60	30	0
105	7	5	2	0	0	15	50	45	30	0
106	7	9	3	0	0	50	40	60	50	0
107	7	7,5	3	0	0	50	40	40	30	1
108	7	6	3	1	70	50	50	45	20	0
109	7	5,5	3	1	80	50	40	30	25	0
110	7	6	3	1	60	50	50	30	20	0
111	8	12	4	0	0	8	50	45	80	0

tree n°	tree height	dbh	canopy size	Azteca occupied	percentage of Azteca occupation	distance to water	canopy cover	ground slope	epiphytic cover	Flowers/fruits
	m	cm	1 to 5		%	m	%	degree	%	
112	8	13	3	1	90	4	40	0	20	0
113	8	12	4	0	0	6	30	45	70	0
114	8	13	4	1	90	6	40	45	30	0
115	8	9	5	1	80	2	40	60	15	0
116	8	11	4	1	30	5	40	45	60	0
117	8	12	4	1	40	5	40	45	60	0
118	8	11	4	0	0	6	40	70	30	0
119	8	10	4	0	0	10	40	45	50	0
120	8	6,5	4	0	0	5	60	45	40	0
121	8	14	5	1	40	10	40	45	40	0
122	8	7	4	0	0	8	40	45	30	0
123	8	10	5	0	0	8	50	45	20	0
124	8	5,8	3	0	0	8	50	30	50	0
125	8	6	3	1	100	15	50	45	10	0
126	8	10,5	4	1	90	10	40	45	10	1
127	8	12	3	0	0	10	30	45	40	0
128	8	9	4	0	0	2	30	60	30	0
129	8	6	3	1	80	2	50	60	20	0
130	8	12	4	1	100	6	40	60	7	0
131	8	13	4	1	50	3	40	60	7	0
132	8	17,5	5	1	70	5	50	30	50	0
133	8	14	4	0	0	10	50	45	50	0
134	8	16	4	0	0	20	25	45	60	0
135	8	13	4	0	0	30	50	45	50	0
136	8	7	3	0	0	50	30	45	30	0
137	9	12	3	0	0	8	50	45	50	0
138	9	19	5	0	0	12	25	45	60	0
139	9	7	4	1	70	10	40	60	10	0
140	9	6	3	1	80	7	40	60	20	0
141	9	19	5	0	0	5	60	60	40	0
142	9	8	4	0	0	10	40	45	40	0
143	9	18	4	0	0	15	40	45	50	0
144	9	15	3	0	0	30	50	30	40	0
145	9	9,4	4	0	0	15	60	45	50	0
146	9	12	4	0	0	50	45	30	0	0
147	9	15	4	0	0	50	50	60	40	0
148	9	7	3	1	100	50	30	50	25	0
149	9	6	3	1	100	50	50	45	15	0

tree n°	tree height	dbh	canopy size	<i>Azteca</i> occupied	percentage of <i>Azteca</i> occupation	distance to water	canopy cover	ground slope	epiphytic cover	Flowers/fruits
	m	cm	1 to 5		%	m	%	degree	%	
150	10	21	5	0	0	4	30	60	15	1
151	10	17	5	0	0	8	30	60	30	1
152	10	23	5	0	0	12	30	60	50	0
153	10	35	5	1	90	3	30	60	5	0
154	10	14	5	1	90	4	30	60	10	0
155	10	11	4	1	60	6	30	60	40	0
156	10	19	4	0	0	6	40	45	80	0
157	10	11	4	0	0	4	30	60	40	0
158	10	11	4	1	40	6	40	45	50	1
159	10	14	4	0	0	10	30	45	40	1
160	10	21	5	0	0	30	40	45	60	0
161	10	25	4	1	30	17	30	45	60	0
162	10	16	4	0	0	30	40	45	60	0
163	10	9	4	0	0	50	30	30	40	0
164	11	29	4	0	0	13	50	20	60	0
165	11	25	5	0	0	20	50	60	45	1
166	11	14	4	1	40	50	50	50	15	1
167	12	28	5	0	0	15	30	45	80	0
168	12	15	4	0	0	10	40	25	70	0
169	12	25	5	0	0	5	40	30	40	0
170	12	20	4	1	80	15	40	45	25	0
171	12	20	2	0	0	30	50	30	80	1
172	13	16	4	1	70	4	30	30	0	0
173	13	19	5	1	90	6	40	45	5	0
174	13	16	5	0	0	15	30	45	50	0
175	13	19	5	0	0	30	25	20	35	0
176	13	15	4	0	0	30	25	20	35	0
177	13	16	4	0	0	30	25	20	35	0
178	14	14	4	1	60	1	30	0	0	0
179	14	15	4	1	80	15	30	45	30	0
180	15	20	4	1	60	15	30	60	50	0
181	15	31	5	1	50	3	30	45	50	0
182	15	45	5	0	0	25	20	45	70	0
183	15	18	5	1	80	15	40	45	20	0
184	16	15	4	1	100	2	40	60	10	0
185	17	26	5	1	30	10	30	15	60	0

8. DEUTSCHE KURZFASSUNG

Interaktionen zwischen *Tetrathylacium macrophyllum* (Flacourtiaceae) und ihren Domatien bewohnenden Ameisen

im Corcovado Nationalpark, Sektion Piedras Blancas, Costa Rica

EINLEITUNG

Eine Reihe von tropischen Pflanzen hat sich im Laufe der Evolution an das Zusammenleben mit Ameisen angepasst. Es bildeten sich morphologische und biochemische Anpassungen heraus um Ameisen anzulocken und längerfristig zu halten. Solche Ameisen-spezifischen Adaptionen finden sich in verschiedenen taxonomischen Gruppen sowohl in der Neo- wie auch der Paleotropis. Das zeigt, dass diese Entwicklungen unabhängig voneinander stattgefunden haben.

Pflanzliche Strukturen zur Anlockung von Ameisen können sein: (1) extraflorale Nektarien (EFN) (z.B. bei *Passiflora*, *Acacia* etc.), (2) Futterkörperchen (FB) (z.B. bei *Acacia*, *Barteria*, *Cecropia*, *Macaranga*, *Piper*, etc.) und (3) Domatien (z.B. bei *Acacia*, *Cecropia*, *Duroia*, *Maitea*, *Piper*, *Schomburgkia*, *Tillandsia*, *Triplaris*, etc.) um die Ameisen zu ernähren oder ihnen Nisträume zur Verfügung zu stellen. Pflanzen, die zumindest eines dieser Merkmale aufweisen, werden als Myrmekophyten oder Ameisenpflanzen bezeichnet.

Domatien können aus unterschiedlichen pflanzlichen Geweben und Organen entstehen, wie z.B. dem Blatt (*Duroia*, *Maitea*, *Tococa*, etc.), dem Petiolus (*Piper*, *Tachigali*, etc.), aus Dornen (*Acacia*), hohlen Wurzeln (*Pachycentria*), vom Hypocotyl erzeugten Knollen (*Hydnophytum*, *Myrmecodia*), hohlen Stämmen (*Cecropia*) oder hohlen Ästen (*Ocotea*, *Pithecellobium*, *Triplaris*, etc.). Die Domatien bewohnenden Ameisen sind entweder sehr wirts-spezifisch (z.B. *Azteca-Cecropia*, *Pseudomyrmex-Acacia*) oder sie besiedeln eine Reihe unterschiedlichster Myrmekophyten (z.B. *Azteca*, *Crematogaster*).

In Costa Rica wurde bereits eine Reihe von Ameisenpflanzen genauer untersucht z.B. *Acacia*, *Cecropia*, *Cordia*, *Ocotea*, *Piper* und *Triplaris*. Der Gegenstand der vorliegenden Diplomarbeit bildet die wenig bekannte Pflanze *Tetrathylacium macrophyllum*, die innerhalb Costa Ricas nur an der südlichen Pazifikküste (Corcovado Region) vorkommt. Von dieser Pflanze war bloß bekannt, dass sie Hohlräume in den Ästen besitzt, welche von Ameisen bewohnt sein können. Der Zugang zu diesen Hohlräumen wird durch natürliche schlitzförmige Öffnungen ermöglicht.

Das Ziel dieser Untersuchung war es, folgende Fragen zu klären:

- 1) Ist *T. macrophyllum* wirklich eine Ameisenpflanze?
- 2) Welche Auswirkungen ergeben sich für die Ameisen?
- 3) Welche Auswirkungen ergeben sich für die Pflanze?
- 4) Wie intensiv ist die Interaktion zwischen Pflanze und Ameisen?
- 5) Gibt es habitatspezifische Unterschiede?

Als Untersuchungsort diente die nähere Umgebung der biologischen Station La Gamba, im Corcovado Nationalpark, Sektion Piedras Blancas, Costa Rica. Dieses Gebiet zeichnet sich durch ein hügeliges Landschaftsprofil mit zumeist tropischen Primärwäldern aus. Der hohe jährliche Niederschlag von ca. 5000 mm sowie die relative geographische Nähe zum südamerikanischen Kontinent erklärt die große Ähnlichkeit der Flora mit dem kolumbianischen Choco-Regenwaldgebiet. Der Untersuchungszeitraum war zwischen Februar und April 2000, also gegen Ende der lokalen Trockenzeit (Dezember bis April).

Die untersuchten Pflanzen wachsen an Steilhängen meist in der Nähe von Oberflächengewässern und erreichen eine durchschnittliche Höhe von 8-15m. Insgesamt wurden 205 Bäume untersucht, wovon 185 aus dem Primärwald und die restlichen 20 aus dem Sekundärwald stammten.

ERGEBNISSE

Domatien. Bei einer Baumhöhe von ca. 1m beginnen die Enden der Äste anzuschwellen und der Markkanal teilweise zu degenerieren, wodurch ein Hohlraum entsteht. Zusätzlich bildet sich im Bereich des jüngsten Internodiums eine schlitzförmige Öffnung, welche diesen Hohlraum zugänglich macht. Ab dieser Baumhöhe kommen mit jedem Wachstumsschub meist 5 (4-7) Internodien hinzu (in weiterer Folge als Zuwachszone bezeichnet). An der Spitze dieser Zuwachszonen bilden sich nun regelmäßig Öffnungen die zu den Hohlräumen führen (siehe Fig. 1). Zwischen einer Baumhöhe von 1 bis 4 m verlängert sich mit jeder neuen Zuwachszone der relative Anteil der neu gebildeten Hohlräume, also der Domatienkammern. Da der Durchmesser des hohlen Markkanals mit 5-6 mm konstant ist, verändert sich bei neugebildeten Zuwachszone nur die Länge der Kammern. Während ein 2 m hoher Baum nur etwa 25 % der neuen Zuwachszone mit Hohlräumen ausgebildet hat, sind Zuwachszone von Bäume ab 4 m Höhe bereits zu 53 % mit Domatienkammern versehen. Ist eine Zuwachszone mit einem bestimmten Hohlraumanteil einmal gebildet, verändert sich seine Gestalt im weiteren Verlauf nicht mehr. Zusätzliche Hohlräume können nur durch weitere Zuwachszonen gebildet werden.

Im Inneren des Äste kann man drei unterschiedliche funktionelle Einheiten unterscheiden (in Klammer der durchschnittliche Anteil an der Gesamtlänge):

- 1) Hohle Markkanäle mit Öffnungen (49,9 %)
- 2) Hohle Markkanäle ohne Öffnungen (3,5 %)
- 3) Nicht degenerierte Markanteile (46,6 %)

In erster Linie ist nur die unter Punkt 1 angeführte funktionelle Einheit für die Ameisen nutzbar.

Domatien bewohnende Ameisen. Die Domatienkammern der Untersuchungspflanze wird hauptsächlich (zu 85 %) von 4 verschiedenen Ameisengattungen besiedelt: *Crematogaster* und *Pheidole* (Myrmicinae), *Azteca* (Dolichoderinae) und *Pachycondyla* (Ponerinae). Während in einer Domatienkammer immer nur eine Ameisenart gefunden wurde, können jedoch auf einem Baum mehrere Arten koexistieren (im Schnitt 1,57 Arten/Baum).

Crematogaster und *Azteca* können große Teile der Bäume besiedeln, während *Pheidole* und *Pachycondyla* nur kleine Teile bzw. nur wenige Domatien besiedeln. *Crematogaster* und/oder *Azteca* wurden auf 70 % der untersuchten Bäume gefunden, während nur 15 % der Bäume ausschließlich mit *Pheidole* und/oder *Pachycondyla* besiedelt waren (siehe Fig. 6).

Sukzession. Der kleinste besiedelte Baum war 2,25 m hoch während der höchste unbesiedelte Baum 4m hoch war. Die Erstbesiedelung von *T. macrophyllum* findet also immer in dieser Entwicklungsstufe statt. Die 4 Ameisenarten besiedeln die Domatien zu unterschiedlichen Zeitpunkten. *Pheidole* und *Crematogaster* wurden ab einer Baumhöhe von 2,25 m, *Pachycondyla* ab 2,75 m und *Azteca* erst ab 4 m in den Domatien gefunden.

Die Besiedlung durch *Azteca* nimmt ab 4 m kontinuierlich mit der Baumhöhe zu. Während beispielsweise nur 12 % der 4 m hohe Bäume von *Azteca* besiedelt waren, lag die Besiedlungsdichte der 10 m hohen Bäume bei 36 % und die der 15 m hohen bei 75 %. Allerdings lag die Besiedlungsdichte bei 12 m hohen Bäumen bei nur 20 % (siehe Fig. 11).

***Pachycondyla*.** Bei den Vertretern der Ponerinae handelt es sich bei weitem um die größten Individuen der 4 Ameisenarten, aber auch um die mit den kleinsten Kolonien. *Pachycondyla* Ameisen mit einer Koloniegröße von maximal einem Dutzend Individuen, besiedeln nur 1 bis 2 Domatienkammern. Sie betreiben foraging auf der Pflanze und ziehen sich bei Gefahr entweder in ihrer Domatienkammern zurück oder verlassen größeren Störungen schlagartig die Domatien. Es werden keine Läuse gehalten und sie attackieren weder Herbivoren noch Fremdkörper auf der Pflanze (z.B. Epiphyten oder Klebebänder). Die Gesamtheit dieser Eigenschaften definiert diese Ameisenart als einen opportunistischen Hohlraum-Nister.

***Pheidole*.** Diese Ameisenart hat zwar die kleinsten Individuen, bildet jedoch viel individuenreichere Kolonien als *Pachycondyla*. Aufgrund der kleinen Körpergröße werden allerdings kaum mehr als 3-5 Domatien besiedelt. Der Eingang zur Domatienkammer wird bis auf ein Eingangsloch mit einer Kartondecke versiegelt. Die relativ rasche Produktion von Geschlechtstieren, die schwache Verteidigung ihres Territoriums, die Abwesenheit von Läusen zusammen mit der kleinen Koloniegröße sind ebenfalls Indizien für eine opportunistische Lebensweise.

***Crematogaster*.** Die Arbeiter dieser Art sind mittlerer Größe und die Kolonien können sich über große Teile des Baumes erstrecken. Kartonstrukturen werden nicht nur zum Versiegeln der Eingangsöffnungen gebaut, sondern auch um kuppel-förmige Strukturen an den Blattbasen zu konstruieren (siehe Fig. 12 und Fig. 13). In diesen Kuppeln sowie im Inneren der Domatien

werden Läuse gehalten, die zur Nahrungsversorgung dienen. *Crematogaster* Arbeiter wurden beobachtet als sie Herbivoren (z.B. Blattkäfer) attackierten oder anliegende Lianen abbissen (siehe Fig. 14 und Fig. 15). Die mächtige Koloniegröße, die Verteidigung des Territoriums vor Herbivoren und Lianen und der Ausschluss subdominanter Ameisen machen *Crematogaster* zu einer kompetitiven dominanten Ameisenart.

***Azteca*.** Die Individuen sind ebenfalls mittlerer Größe und die Kolonien können sich nicht nur über den ganzen Baum, sondern teilweise sogar auf die benachbarte Vegetation ausdehnen. Charakteristisch für diese Art ist das extensive System von Kartongängen, welches an der Unterseite der Äste und entlang des Stammes verläuft und alle besiedelten Domatien verbindet (siehe Fig. 16). Die Gänge erinnern zunächst an Termitengänge, aber mit dem großen Unterschied, dass die Kartontunnel von *Azteca* regelmäßig kleine Öffnungen beinhalten, durch die sie diesen Tunnel verlassen können. Allerdings sind die Ameisen nur selten außerhalb der Gänge zu sehen, mit Ausnahme der jüngsten Blätter die regelmäßig patrouilliert und auch verteidigt werden. Ansonsten sind *Azteca* Ameisen eher unauffällig und scheu. Nur wenn die Domatienkammer beschädigt wird, kommt es zu einer aggressiven Verteidigung des Nistraumes. *Azteca* züchtet Läuse im Inneren der Domatien sowie unterhalb der Kartongänge (siehe Fig. 17 und Fig. 18). Obwohl das Angriffsverhalten ein anderes ist als bei *Crematogaster*, (siehe Kapitel Verteidigungsstrategie) sprechen die restlichen Charakteristika ebenfalls für eine kompetitive dominante Ameisenart.

Künstliche Eingangslöcher. Im Gegensatz zu allen anderen Ameisenarten können *Azteca* Ameisen die Domatienkammern aktiv vergrößern indem sie den noch weichen Markkanal der Zuwachszonen aufbeißen. Dadurch gelingt es ihnen zu der bereits genannten funktionellen Einheit der „hohlen Markkanäle ohne Öffnungen“ vorzudringen, wobei sich der Nistraum sprunghaft vergrößert (siehe Fig. 19 und Fig. 24). Zusätzlich beißen sie neue Eingangslöcher zu den Domatien frei, die im Laufe der Zeit regelmäßig gewartet werden. Dadurch wird auch ein Verschließen durch das sekundäre Dickenwachstum verhindert (siehe Fig. 20 und Fig. 21).

Primär- und Sekundärwald. Während sich die dominanten *Crematogaster* und *Azteca* als die häufigsten Domatienbewohner im Primärwald erwiesen haben (50 % bzw. 33 % aller Bäume respektive), fehlen diese Arten im Sekundärwald völlig. Dort trifft man am häufigsten auf *Pheidole* Ameisen (siehe Fig. 9) sowie eine Reihe im Primärwald fehlender Ameisen wie etwa *Acanthognathus*, *Dolichoderus*, *Pseudomyrmex* oder *Zacryptocerus*.

Herbivorie. Es wurde festgestellt, dass Blätter von *Azteca*- bzw. *Crematogaster*-besiedelten Pflanzen einen geringeren relativen Blattfraß aufweisen als nicht-besiedelte Pflanzen (siehe Fig. 25). Im folgenden sind die 3 Untergruppen samt dem prozentuellen Anteil des Blattfraßes und der Standardabweichung in Klammer angegeben:

- | | |
|-------------------------------------|---------------------|
| 1) Keine Ameisen: | 10,88 % (SD = 3,24) |
| 2) <i>Azteca</i> -besiedelt: | 5,44 % (SD = 3,85) |
| 3) <i>Crematogaster</i> -besiedelt: | 5,71 % (SD = 1,84) |

Es kommt also bei *Azteca* zu einer durchschnittlichen Verringerung der Herbivorie von 50 % und bei *Crematogaster* von 47,52 %. Allerdings ist der Blattfraß selbst bei unbesiedelten Bäumen relativ gering.

Epiphyten. Bereits auf den ersten Blick fällt bei *Azteca*-besiedelten Bäumen die geringe Bedeckung mit Epiphyten auf. Bei näherer Untersuchung zeigte sich eine hohe negative Korrelation ($r^2 = -0,70$) zwischen Epiphytenbewuchs und der Ausdehnung des *Azteca*-Nestes (siehe Fig. 26).

Klebebandexperiment. In diesem Versuch wurde versucht den Zusammenhang zwischen geringem Epiphytenbewuchs und *Azteca*-Besiedelung experimentell nachzuweisen. Zu diesem Zweck wurde blaues Textilklebeband auf Äste mit *Azteca*-Nestern aufgebracht, da sich kleine Epiphyten nicht ohne grobe Beschädigung verpflanzen ließen. Um die Klebebänder besser anzubringen, musste der Kartongang auf einer Länge von etwa 3 cm zerstört werden. Nach etwa einer Woche war nicht nur der beschädigte Kartongang rekonstruiert, sondern auch das darunter liegende Klebeband weggebissen. Die Textilfasern des Klebebandes dienten jedoch als Baumaterial für die beschädigte Stelle, selbst an beschädigten Stellen in bis zu 1 m Entfernung wurden die blauen Fasern als Bausubstanz verwendet (siehe Fig. 29). Dieser Umstand belegt, dass für die Konstruktion des Kartontunnels Material von der Oberfläche verwendet wird. Um die relativ Epiphyten-freien Äste der *Azteca*-Nester zu erklären scheint plausibel, das alles was sich in „greifbarer Nähe“ befindet und daher auch Epiphyten zur Konstruktion der ausgedehnten Kartongänge verwendet werden.

Verteidigungsstrategie. Nur *Crematogaster* und *Azteca* Ameisen wurden bei der Verteidigung ihrer Wirtspflanze beobachtet. Während *Crematogaster* Arbeiter Blattkäfer und andere Käfer auf Ästen und Blättern attackieren, reagieren *Azteca* Ameisen nach einer gänzlich anderen Strategie. Insekten die auf Ästen von *T. macrophyllum* entlang laufen, die von *Azteca* Ameisen bewohnt sind, nehmen ein ungeahntes Risiko auf sich. Die alarmierten *Azteca* Arbeiter und Soldaten postieren sich im Kartontunnel jeweils an einer der vielen kleinen Öffnungen und lauern mit offenen Mandibeln auf den Eindringling (siehe Fig. 30). Wenn nun das fremde Insekt über diesen Karton läuft und in eines der Löcher steigt, schnappt die darunter postierte *Azteca* Ameise das Insektenbein und klammert sich daran fest. Während des Versuchs sich aus dieser Situation zu befreien, steigt das Insekt in das nächste Loch, wo es ein weiteres Mal festgehalten wird (siehe Fig. 31). Spätestens nach 15 - 30 Minuten wird das fremde Insekt entweder fallengelassen oder in den Kartongang gezerrt und in das Innere des Nests gebracht (und dient vermutlich als zusätzliche Proteinquelle).

Blattschneiderameisen. Die Verteidigungsstrategie von *Azteca* scheint besonders im Hinblick auf Blattschneiderameisen (*Atta* sp.) sehr effizient zu sein. In 4 Versuchen mit insgesamt 106 Blattschneiderameisen, die auf *Azteca*-besiedelten Bäumen platziert wurden, konnte bereits nach einer halben Stunde das folgende Ergebnis beobachtet werden. Während nur eine Minderheit von 2,58 % der *Atta*-Ameisen sich noch frei auf den Ästen bewegte, ließen sich 6,89 % vom Baum fallen und 25,86 % hatten den Baum selbstständig verlassen. Die überwiegende Mehrheit von 64,65 % allerdings war in die „*Azteca*-Falle“ gegangen (siehe Fig. 33).

Diese Verteidigungsstrategie bereichert also nicht nur die Nahrung der *Azteca*, sondern bietet der Wirtspflanze einen effektiven Schutz gegen das Risiko einer Blattschneiderameisen-Invasion.

DISKUSSION

Ist *T. macrophyllum* wirklich eine Ameisenpflanze?

Da insgesamt 85 % der Bäume von *T. macrophyllum* regelmäßig mit den selben 4 Ameisenarten assoziiert sind, handelt es sich nach Jolivet um eine echte Ameisenpflanze:

"The true myrmecophytes or plants having regular relationship with the ants are the ones offering lodging (myrmecodomic) or food (myrmecotrophic) or both (myrmecoxenic)."

Welche Auswirkungen ergeben sich für die Ameisen?

Die Ameisen finden in den Domatien optimale Nist- und Brutbedingungen. *Azteca* und einige *Crematogaster*-Ameisen halten Schildläuse (Coccidae), die sich vom Phloemsaft des Baumes ernähren und den Ameisen Nahrung in Form von Honigtau anbieten. Somit liegt der Vorteil der Ameisen im vorgefundenen Wohnraum und bei zwei der vier Arten in der Nahrung durch die Schildläuse. Eine Einschränkung bei der Besiedlung stellt allerdings die interspezifische Konkurrenz zwischen den einzelnen Ameisenarten dar. Hier manifestiert sich eine Unterscheidung in zwei dominante (*Crematogaster* und *Azteca*) sowie zwei subdominante (*Pheidole* und *Pachycondyla*) Arten.

Welche Auswirkungen ergeben sich für die Pflanze?

Bei pflanzlichen Individuen mit den beiden häufigsten Ameisenarten *Azteca* (insgesamt 33 % aller Pflanzen über 4 m) und *Crematogaster* (50 % aller Pflanzen über 4 m), verringert sich der Blattfraß um 50 %. *Azteca* Ameisen reinigen die Äste von epiphytischen Moosen und Keimlingen höherer Pflanzen. Ihre typischen Kartongänge dienen als Verteidigungswall, von dem aus sie die um vieles größeren Blattschneiderameisen in die Flucht schlagen können. *Crematogaster* Ameisen wurden beim Abbeißen von Lianen und Attackieren von blattfressenden Käfern beobachtet.

Wie intensiv ist die Interaktion zwischen Pflanze und Ameisen?

Zusammenfassend kann man sagen, dass beide Partner, *T. macrophyllum* und die bewohnenden Ameisen, einen Vorteil aus der Interaktion zieht. Im Vergleich zu den spezialisierten Assoziationen von *Azteca-Cecropia*, *Pseudomyrmex-Acacia* oder *Pheidole-Piper*, handelt es sich im Fall von *T. macrophyllum* jedoch um eine eher generalistische Beziehung. Durch die natürlichen Öffnungen der Domatien fehlen Barrieren, die eine hohe Spezialisierung der Ameisen notwendig machen würde. Trotzdem sind die Ameisenbewohner auf diese Art der Domatien, nämlich „lebende Asthohlräume“, spezialisiert, wenngleich sie auch auf anderen Myrmekophyten mit ähnlichen Domatien vorkommen können.

Gibt es Habitat-spezifische Unterschiede in der Interaktion?

Standort-spezifische Unterschiede in der Interaktion zeigen sich in der Besiedlung der Bäume. Während im Primärwald *Azteca* und *Crematogaster* dominieren, fehlen diese Ameisenarten völlig im Sekundärwald, wo *Pheidole* dominiert. Möglicherweise sind die klimatischen

Bedingungen im Sekundärwald für die Schildläuse sehr ungünstig, wodurch sich die Ameisenzönose verändert.

Ausblick. Interessant ist die Tatsache, dass sich mehrere Ameisenarten eine ökologische Nische im selben geographischen Gebiet teilen. Eine mögliche Erklärung dafür ist die unterschiedlichen Besiedlungsstrategien der einzelnen Ameisenarten. Offen bleibt die Frage, wie die Ameisenbesiedlung im Hauptverbreitungsgebiet (Choco-Gebiet: Kolumbien bis nach Ecuador) von *Tetrathylacium macrophyllum* aussieht. Weitere Untersuchungen in ihrem Hauptverbreitungsgebiet sind zum besseren Verständnis dieser Ameisenpflanze unumgänglich.

Hinweis: Detaillierte Angaben zu Material und Methode, genaue Resultate und die Referenzliste sind dem englischen Text zu entnehmen.

9. CURRICULUM VITAE

Born November 11th, 1974 in Vienna, Austria

Education:

1981-1985: Elementary School in Vienna

1985-1989: Grammar School "Bundesrealgymnasium Wien III"

1989-1994: Technical High School "Technologisches Gewerbemuseum Wien",
Department for Electronics and Biomedical Engineering

June 16th, 1994: Graduation from Technical High School with "*Excellence*"

Autumn 1994: Exam of biology to get permission for Life Science

Since March 1995:

Biological Sciences, at the University of Vienna, the Alma Mater Rudolphina, Austria,

September 1997 to July 1998:

Biological Science at the "Universidad Autonoma de Madrid", Spain
enabled by an "Erasmus"-scholarship

Since September 1998:

Specialisation in zoology and ecology, with special focus on tropical ecology and related topics.

Since March 1999:

Student at the Institute of Risk Research, University of Vienna, visiting several risk related courses about Energy, Safety, Risk-evaluation and –management

February to May 2000:

Thesis work in a tropical rainforest in Costa Rica: "Interaction between *Tetrathylacium macrophyllum* (Flacourtiaceae) and its live-stem inhabiting ants", enabled by a scholarship for scientific work in foreign countries

Languages:

-German (native)

-Spanish (excellent; several courses, one year residence in Spain, several months in Latin America)

-English (excellent; extensive visits to the U.S.A and Australia)

-Portuguese (fair; summer course in Portugal, additional course in Vienna at the Latin America Institute)