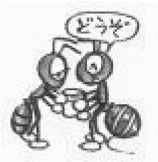
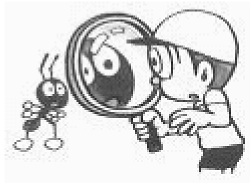
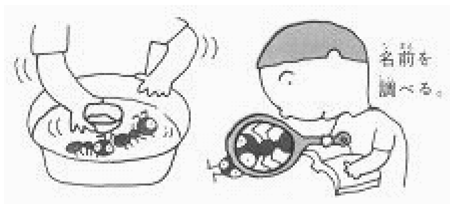


The ecology of ant gardens in the Colombian Amazon.



WAGENINGEN UR

Maaike Bader

The ecology of ant gardens in the Colombian Amazon.

October 1999

Practical period tropical nature management (H300-667)

Maaike Bader (Wageningen University)

Tutors:
Drs. Frans van Dunné (Hugo de Vries Laboratory, University of Amsterdam)
Prof. Dr. Antoine M. Cleef (Hugo de Vries Laboratory, UvA & Vertebrate Ecology & Tropical Nature Management, Wageningen University)
Dr. Pieter Ketner (Vertebrate Ecology & Tropical Nature Management, Wageningen University)

UNIVERSITEIT VAN AMSTERDAM

WAGENINGEN UR

Wageningen University and Research Centre
(Formerly 'Wageningen Agricultural University)'

Contents

Preface

This is a report relating to a month that I spent in the Colombian Amazon region, assisting Veronica with the fieldwork for her thesis. Fieldwork was carried out by Veronica from April to August 1998. I joined her in august and we dissected gardens together. It was only a small contribution to her work, and only to the practical work. The results presented here are a translation of some of the results she presents in her thesis report (Mora 1999). The discussion is adapted to my own ideas.
The present report is not a thesis report, but it includes, in a shorter version, the whole research, because it is interesting.
It was a pleasure to get acquainted with the phenomenon of ant-gardens, and, while going through the literature, with the amazing world of ants in general. Also the experience of working and living in a tropical rainforest has been very interesting.

I thank Veronica, for her patience with my Spanish, for hot chocolate with cheese and for teaching me about ants.
Thanks also to Antoine and Frans and Tropenbos Colombia for organizing my stay.
Thanks to all the lovely people of Araracuara.

My stay in Araracuara, in combination with my thesis research in the Colombian Andes, has been made possible thanks to the financial support of the following organizations: FONA, Wageningen; Wagenings Universiteits Fonds, Wageningen; Alberta Mennega Stichting, Odijk, and Tropenbos Colombia, Bogotá (appendix I).

Maaike Bader.

1 Introduction

Of the many amazing relations that make tropical rainforests, the mutualistic relationship between ants and epiphytes is probably one of the more obvious and better studied. One interesting group of epiphytes are those that house ants in special structures, like leaf-, stem-, root- or rhizome cavities; the so called ant-house epiphytes (Benzing 1991). Another group is that of epiphytes growing in ant-gardens. An ant-garden consists of an arboreal ant-nest with epiphytic plants growing from it, using the nest as a rooting medium. This is the first study on the ant-gardens of the Colombian Amazon.
The study was conducted in a tropical lowland rain forest near Araracuara in southeastern Colombia. In this secondary forest some areas contain many ant-gardens, also at lower layers of the forest, which made those areas very suitable for the study.

The study was carried out within the project 'Establishment, development and diversity of the epiphytic vegetation in regenerating tropical rainforests'. In this project different aspects of the spatial distribution of epiphytes are studied. The ant-garden study investigates the role of ants as a dispersion-vector for epiphytes in a tropical lowland rain forest. The title of the project is: 'Structure and development of ant-gardens in secondary tropical rainforests in Araracuara, Colombia.' [1]

The research has four main components: the colonization by ants, the initial development of the gardens, the spatial relationships between gardens and the structure of the gardens. These four subjects are treated separately in experiments or observations.

---

[1] Estructura y desarollo de jardines de hormigas en bosques tropicales secundarios en Araracuara, Colombia.

2 General background

2.1 Ant-gardens

Plants growing on ant-made substrates are found in neotropical as well as paleotropical rainforests. The first scientific description of this association in South America is that of Ule (1902)(fig. 1), who named them “ameisengärten”: ant-gardens (not to be confused with the fungus gardens that leafcutter-ants (Atta) make). He concluded that the ants actively collected seeds and cultivated them for the roots to strengthen the nest, and that the plants could not survive without the ants, on which they are dependent for seed dispersal, protection from predators and providing of organic matter around the roots (Ule 1906). This conclusion was challenged by Wheeler (1921), who considered the relationship of plants and ants in ant-gardens to be casual and opportunistic, rather than one of strict interdependence. He proposed the antnests are first formed around an established epiphyte and than further colonized by epiphytes growing from seeds that accidentally fall on top of it.

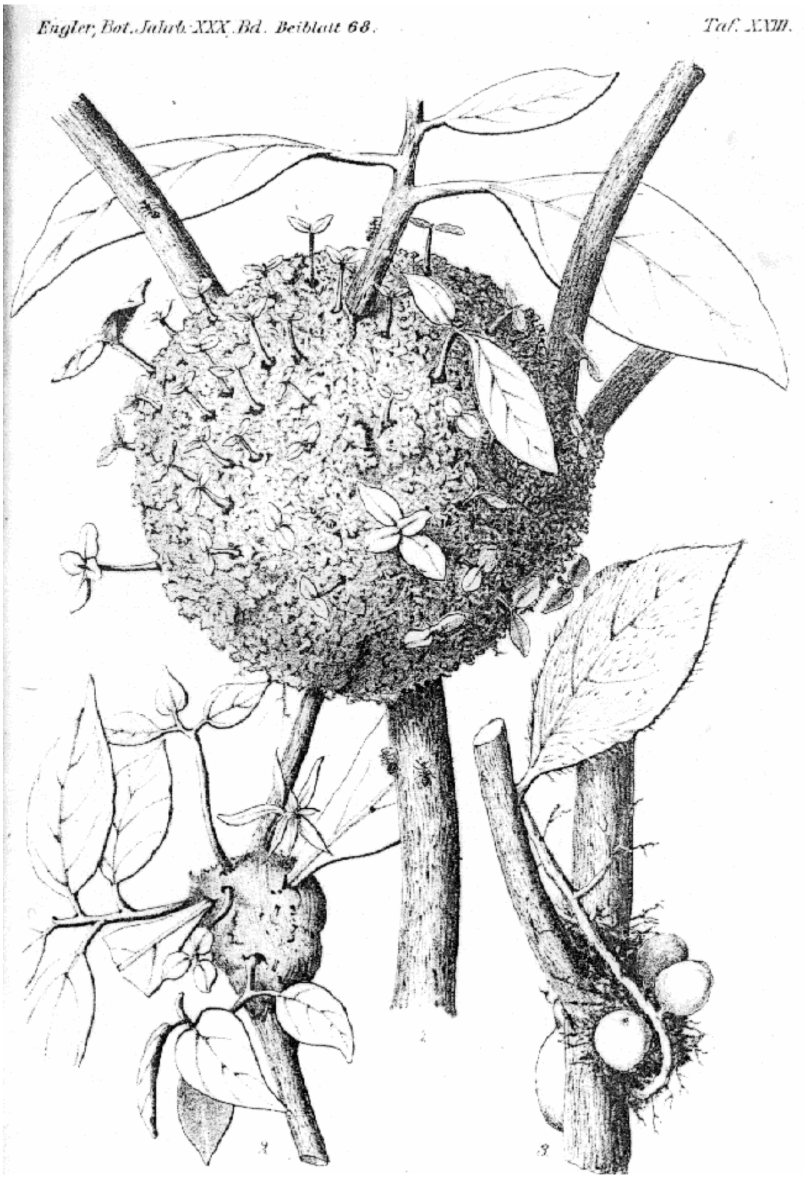


Figure 1 Different stages in the development of an ant-garden, as drawn by Ule (1902). The big garden (top) is very regular and the epiphytes are very small compared to the gardens in this study.

An interesting discovery Wheeler made was that many ant-gardens contain two unrelated species of ants, in different combinations of *Crematogaster*, *Camponotus*, *Azteca* and *Anchoetus*. He suggested that different ant-species sharing nests, a relationship he called ‘parabiosis’, could be ecologically equivalent to one single species with differentiated working classes of different sizes.

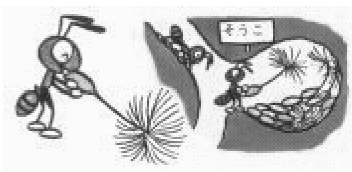
Parabiosis was also reported by Weber (1943), who even found three species of ants living together in ant-gardens; a large *Camponotus*, a smaller *Crematogaster* and a tiny *Solenopsis*-species. Weber agreed with Wheeler that the ant-epiphyte relations in ant-gardens are casual and not highly specialized like Ule said.
Since then many studies have been carried out on ant-garden ecology (e.g. Kleinfeldt 1978, Madison 1979, Davidson 1988, Davidson Seidel and Epstein 1990, Yu 1994). These do indicate a high specialization; a complicated mutualistic relationship between the ants and ant-garden epiphytes.

2.2 Benefits of the ants to the plants.

The fact that many ant-garden epiphytes are hardly ever seen outside ant-gardens indicates that there is a certain dependence of these plants on the ants they live with. There are three important ways in which the ants can benefit the plants: the nest provides the plants with a rich substrate for the roots, the seeds are dispersed by ants and the ants can defend the plant against herbivores.

Many authors have used the name ‘carton’ for the ant-garden substrate. The material is however very different from the carton of many wasp-nests, that consists of chewed wood. The ant-garden material typically is rich in organic matter. It is a mixture of soil, plant material, vertebrate feces and ant secretions (Yu 1994). Adding to the complexity of the material are honeydew and the ants’ potentially microbiocidal secretions (Maschwitz and Hölldobler 1970). ‘Humus’ (Belin-Depoux 1991) might be a better term to use than ‘carton’. Roots are ramified finely through the nest-chamber walls. Nests of *Azteca* ants are more brittle and poorer in organic matter than those of parabiotic species (e.g. *Camponotus femoratus* and *Crematogaster linata parabiotica*). It is found that all but two ant-garden epiphytes are less successful on *Azteca* nests, probably due to this difference in substrate quality (Benzing, 1991). The ant-garden epiphyte *Codonanthe crassifolia* (Gesneraceae) provides stem nectaries at the leaf-nodes. Sometimes ants build ‘carton’ shelters around these food-sources, which are then used by the roots that grow from the nodes (Kleinfeldt 1978).

Various authors have observed seeds being harvested by ant-garden ants and taken to the nest (Ule 1901, Kleinfeldt 1978, Davidson 1988). We have observed this phenomenon ourselves near Araracuara, where we saw ants collecting seeds from an *Anthurium gracilae* growing from their nest. The seeds with attached pulp were cut from the berries they were in and carried up to the nest.



Attractiveness of Ant-garden epiphyte seeds is thought to have two components. Many seeds offer nutritional rewards, like arils or sweet gelatinous coatings. Seeds are often placed in brood-chambers, where the developing ant-larvae probably feed on the gelatinous coatings (Kleinfeldt 1986, Davidson 1988). However, also epiphyte seeds that offer no obvious food substances are collected by ants and even preferred over some seeds with nutritional reward. Also seeds that have passed through the guts of frugivorous bats are still recognized and collected by the ants. These

observations suggest there must be other factors making the seeds attractive. The specificity of this attractiveness is demonstrated by the observation that congeners of ant-garden ants reject seeds of ant-garden epiphytes that the ant-garden ants themselves collect selectively (Davidson and Epstein 1989)
Chemistry of seed attractants has been studied by Seidel (1988 , in Davidson *et al* 1990), who speculated that fungistatic properties of seed-compounds may help control ant nest pathogens. Some circumstantial evidence supports this hypothesis. Unlike similar piles of debris, ant-gardens do not show any signs of saprophytic fungi. Also the chemical structures found are similar to typical fungistats, e.g. volatile essential oils released by resins that some bees line their nests with (Davidson and Epstein 1989). However, mycelia of at least one fungus (*Cladosporium myrmecophilum*) do regularly permeate active nests, but has no obvious impact on animal or plant inhabitants (Benzing 1991).

A third way, in which the ants may be of benefit to the plant, is by protecting them from herbivore-damage. Although not all ant-garden ants are described as aggressive, some (e.g. *Camponotus* sp.) do protect their 'garden' avidly. We experienced this ourselves when collecting nests for further research. The big soldier-class ants would appear as soon as the nests or the plants on it were touched, and start searching the leaves. And bite us if they got the chance for it. Also more docile ants might restrict herbivore damage, by cleaning insect eggs and larvae from plant surfaces (Davidson and Epstein 1989). Kleinfeldt (1978) studied *Crematogaster* nests with *Codonanthe* growing from them. She didn't find the ants lessened herbivore damage in this case (Kleinfeldt 1978).

2.3 <u>*Benefits of the plants to the ants.*</u>

The name "ant-garden" that Ule (1901) gave the discussed ant-epiphyte relationship suggests a purposeful planting of seeds by the ants. Talking about purpose in animal behavior is always difficult, especially for ants, but purposeful or not, the ants profit greatly by their agricultural business.

The most obvious role the plants seem to play in the life of the ants is providing structure to the ant-nest. Plants differ greatly in their root-characteristics, which is reflected in the amount of nest material they can hold and their usefulness for nest-structure. The fat roots of *Anthurium* sp. hold little humus and might even be disadvantageous to the nest structure by excluding other epiphytes and clogging up nest-chambers (Davidson 1988). Other roots, like those of *Codonanthe* and *Peperomia* are much finer and are densely ramified through the nest chamber walls, giving them additional strength and coherence.

Apart from the mechanical function of the roots the plants have another important positive influence on the ant-nests. By the transpiration of their leaves they dry out the nests between rainfalls. Maintaining a dry nest preserves the structural integrity of the nest material. Experiments have shown that defoliated ant-gardens (with the root structure intact but no transpiration activity) sometimes loose 75% of the nest material, whereas control nests lost none (Yu 1994).

The ants also benefit from the plants when these offer food substances, which is often the case. There are the food rewards attached to seeds: fruit pulp, gelatinous seed-coatings or seed arils. These are also collected independently of the seeds themselves (Davidson 1988). Another useful property of the epiphyte seeds may be their fungistatic properties, which could help the ants to control nest pathogens.
Also ant-garden epiphytes often offer extra-floral nectaries or pearl bodies. Ants also tend Homoptera on the cultivated flora, but the foraging areas are much bigger than the garden: areas over an eighth of a hectare have been reported (Yu 1994), or 10 m away from the garden (Davidson 1988).
The feeding habits of the ants might also explain why most ant-gardens are found in areas with a lot of sunlight, like in treefall gaps and along riverbanks. In these areas homoptera resources are richer and plants with extrafloral nectaries tend to occur at higher frequencies here (Davidson 1988).

3 General description of the area

3.1 Position

The study was conducted near the indigenous community of Araracuara in the lowlands of the Colombian Amazon basin. Araracuara is situated in the province of Caquetá on the northern border of the Caquetá River (0°37' S, 72°23' W)(fig. 2).

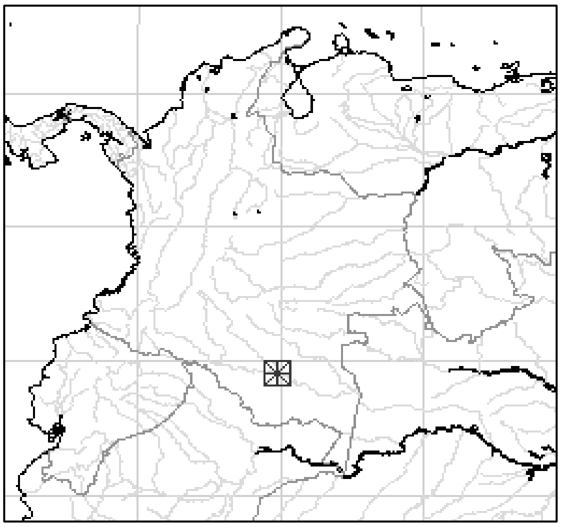


Figure 2 Position of Araracuara in Colombia.

3.2 Climate

The Araracuara region belongs to the humid parts of Amazonia. The mean annual rainfall is 3060 mm (1979-1990) and mean annual temperature is 25.7°C (1980-1989). Köppen-classification would be Afi: tropical, all months >60 mm.

Temperature varies little throughout the year. The diurnal variation is considerable though, with an average monthly maximum around 31°C and minimum around 22°C (night temperature).

Two wetter and two drier periods can be distinguished. December to February and August have less rainfall (still with monthly averages well over 100 mm). Wet periods are April to June and September to November, when the equatorial low-pressure trough passes over the area (Duivenvoorden and Lips 1995).

3.3 Geology and geomorphology

The Caquetá River is one of the main tributaries of the Amazon River. It is of Andean origin and a white-water river (looking orange because of the transported sediments). The other rivers in the area are Amazonian rivers (i.e. of local origin) and clear- or rarely black-water rivers. The Caquetá is an anastomosing river, gently meandering but also containing stable forested islands. The Amazonian rivers are generally meandering (Duivenvoorden and Lips 1995).

The Araracuara region is part of the Middle Caquetá area, which is situated at 150 to 300 m above sea level. It consists of four major geomorphologic units: the alluvial plain and upland terraces of the Caquetá River; the alluvial plains and upland terraces of the Amazonian rivers; a Tertiary sedimentary plain; and a hard rock unit, mainly consisting of Paleozoic sandstone plateaus (Duivenvoorden and Lips 1995)(fig. 3). Our two study areas were situated on the sandstone plateau west of Araracuara. This plateau rises about 130-150 meter above the mean low water level of the Caquetá River, which cuts through the plateau forming a spectacular gorge, and lies about 300 m above sea level. The sandstone belongs to the Paleozoic Araracuara Formation and is finely textured and horizontally bedded. The weathering product of this sandstone is extremely poor in elements other than Si (Duivenvoorden

and Lips 1995). Part of the plateau has a savanna-vegetation. Other parts, like those where the study areas were situated, do grow a high (secondary) forest.

Figure 3 The Caquetá river cutting through the sandstone plateau near Araracuara.

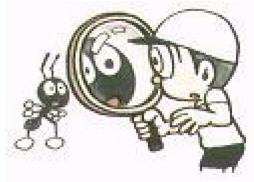
3.4 History and landuse

The history of the Araracuara region is dominated by the presence of the Southern Agricultural Penal Colony from 1938 to 1971. Before that the activities of several rubber companies dramatically decreased the indigenous population in the area. The penal colony brought in many people from other parts of Colombia and had a considerable influence on the region. The socio-economic and direct military influence of the colony extended for approximately 600 km. in the Middle Caquetá region. The agricultural practices meant clearing of extensive areas of rainforest for crops and pasture for cattle grazing. Other activities of the colony were extraction of wood and other forest products, hunting and fishing.
The social and work area of the penal colony was organized into camps, farms and chagras (traditional small-scale agriculture as practiced by the indigenous population), with increasing levels of freedom for the convict-workers. Results of the agricultural practices were rather poor and it seemed the farming and livestock were more important for keeping the inmates occupied than for making the colony self-sufficient.
Especially the grazing of cattle has had a high environmental cost. After the penal colony closed in 1971 the cattle grazing was continued by the various organizations that administered the area through time. Hundreds of hectares of grazing land have been ruined for other forms of plant production by compaction of the soil. At present it barely sustains a type of grass unsuitable for grazing (Losada 1994). Since 1993 the administration is in the hands of Sinchi. They do not consider the introduced cattle a sustainable landuse option and have gotten rid of the remaining herd (140 head) of Araracuara. At present there is only a little cattle left near Puerto Santander. In Araracuara there are only two horses and some goats and no cattle (pers.obs. 1998).

Also logging activities by the penal colony have inflicted a lot of damage on the natural ecosystems in the area (Losada 1994).
Many indigenous people came to the area after the penal colony closed in 1971 and reinstated the traditional agricultural system of shifting cultivation. In this system small patches of forest are cut down and burned and the crops planted in the ashes ('slash and burn'). After about two years these fields, the so-called chagras, are no longer used for low crops and another piece of forest is cut and the process repeated. The 'abandoned' chagras are called rastrojos and often contain fruit trees that are still maintained and harvested for some time. Crops cultivated on the chagras are yucca (many varieties), coca, pineapple, platano, maize, tobacco, peanuts, vegetables and fruit (Verkley and van Nederveen Meerkerk 1998). The local people supplement their diet by hunting and fishing. The fish is also sold to Bogotá.
The Araracuara region is now the home of many families from various indigenous tribes: Huitoto, Muinane, Andoke, and Cocama. For economic or political reasons many have chosen to move from their original home grounds. Araracuara is classified an Indian reserve. (see also appendix II)

4 Methods

4.1 *The colonization experiment.*



This part of the study was carried out in a young (ca. 8 yr) forest near Araracuara. The trees in this patch were 3 to 9 m high and there was little undergrowth.
Within a 15x15-m plot seven small ant-gardens were collected and dissected. Ants were collected from the nests for identification. These were kept in alcohol in photo film boxes. Plants were collected for further use. After having spent a night under water to kill any ants or brood still present, the little plants from the nests were replaced in the same plot, tied to tree trunks. These plants were mapped, as well as the ant-gardens still present and the empty spaces where the dissected nests were collected from.
The little plants and emptied spots on the trees were followed through time. It was marked if and when new colonization by ants took place (Criterion: do ants come out to defend the plant when touched?). Also occurrence of organic matter or seedlings of other species were checked for.

4.2 *Following the development of little gardens.*

Along the dirt road that passed the study areas, various small gardens, in an early stage of development, were identified and labeled. Drawings were made of the plants present in these gardens. Every two weeks the gardens were revisited and it was marked which plants disappeared, which remained and which were new.

4.3 Mapping nests and vegetation.

Two plots of 20x20 m were established, one near Araracuara (across the road from the colonization experiment-plot) and another 4 km westwards, near Monochoa, both on the same sandstone plateau. They were situated in forests that were over 10, and ca. 30 years old respectively, relatively undisturbed, and in both the forest floor was covered with the fern *Selaginella* sp. The plots were subdivided in 5x5-m subplots to facilitate mapping. The altitude of the nests was measured using a measuring stick of 5 m. If the nests were too high a clinometer was used.
The map of the nests in the two plots includes the position of the nests and their plant cover per species. Position was expressed as coordinates within the plot and height from the ground. Presence and abundance of plant species was estimated using binoculars for the higher nests. Plant cover per species was estimated by first estimating total plant cover and then dividing this over the plant species present. Therefor percentages of the different species always added up to 100%.
Where possible, ants were collected from the mapped nests for identification. No ants were collected from high nests, unless the ants could be seen walking down from the nest over the tree trunk or vines hanging from the nest. Climbing up to the nests would have been too time-consuming.

4.4 Describing the structure of the gardens.

Gardens of different size (very small, small, medium, big; minimum of 5 per size class) and plant-composition were collected to be dissected and described. The gardens were collected from inside and around the two 20x20-m ‘mapping plots’. In the field the nests were first measured and drawn and a preliminary collection of ants was made, using pincers to catch them. Then the nests were collected by cutting the supporting branches with garden scissors or a machete. Gloves were very necessary during this procedure because the ants would get rather aggressive. The nest was then placed in a plastic bag and sprinkled with alcohol to kill the ants.

Only a few nests were collected every day and taken to the laboratory to be dissected. Plants were carefully separated from the nest. As the roots were totally integrated in the nest, the nest would get disintegrated at removing the plants. The structure of nest chambers, the characteristics of the roots and the position of ant brood were noted down, as well as any other striking observations.
The plants were counted per species and age-class (seedling/ juvenile/ adult). Then the plants were separated into a ‘root’-part and a ‘aerial’-part. The root and aerial plant parts were dried per garden per species. Separating individual plants was not possible because the roots were all tangled up inside the nest. Also clonal growth habit of some plants made it difficult to distinguish individuals. Roots belonging to different species could be separated based on morphological characteristics. The nest-material (‘carton’ or ‘humus’) was also dried. Drying took place in a concrete stove heated by petroleum-burners.
While dissecting the nests eggs, larvae and more adult ants were collected from the different working casts (soldiers, workers and males).

All ants collected have been identified at the Von Humboldt Institute in Villa de Leyva, Colombia.
Dry weight of the plant parts and nest material was measured at the University of Antioquia in Medellín, Colombia.

5 Results

5.1 *Species*

Epiphytes encountered growing in the ant-gardens are a taxonomically divers collection. Families represented are: Bromeliaceae (*Streptocalix angustifolius* Beer and *Aechmea brevicollis* L.B. Smith), Araceae (*Anthurium gracile* (Rudge.) Scholt and *Philodendron megalophyllum* Scholt), Clusiaceae (*Clusia androphora* Cuatr. and *Markea ulei* (Dammer) Cuatr.), Piperaceae (*Peperomia macrostachya* (Vahl) Dietrich), and Gesneriaceae (*Codonanthe crassifolia* (Foche) Morton).

Two species of ants were present in all nests, including those of the colonization experiment and those of which the development was monitored. The species involved are a *Crematogaster* species of the *limata* group (F. Smith) and *Camponotus femoratus Fabricius*.
Eight other ant-species were found inside the plots, but not in any of the gardens. Five of these species belonged to the Ponerinae-family. The Formicinae, Ecitoninae and Myrmicinae were represented by one species each.

5.2 *The colonization experiment.*

Of the 30 plantlets planted, 16 were colonized by ants, by *Camponotus femoratus* and *Crematogaster* group *limata*. Only 4 plantlets died. All colonized plants were alive, but some uncolonized plants also survived for the length of time of the experiment.

Epiphyte species	**N**	**Alive**	**Colonized**
Anthurium gracile	10	10	8
Aechmea brevicollis	8	7	2
Codonanthe crassifolia	8	5	3
Markea ulei	1	1	1
Streptocalyx angustifolius	3	3	2
Total	30	26	16

Table 1. State of the epiphyte plantlets 4 months after 'planting'.

The plants were colonized with two types of nest material. Nests built around *Anthurium gracile* were composed of course particles, like bits of wood. The other material, found with *Codonanthe crassifolia*, was finer and darker. In the field a positive relation was observed between the amount of nest-material present and the aggressiveness of the ant-response to disturbance.

5.3 *Following the development of little gardens.*

In the Araracuara study-area, there was little development in the vegetation on the small nests that were followed. No new plants appeared.
In Monochoa the nests were more divers and more dynamic. Eight new plantlets appeared. No plantlets died in either area.

5.4 *Mapping nests and vegetation.*

A total of 211 nests were mapped and described, 90 in Araracuara, 58 in the experimental plot and 63 in Monochoa. These were situated in 27 different tree-species.

Only three epiphytes were found growing independent of ants-nests (two of *Anthurium gracilae* and one *Philodendron megalophyllum*). Additionally 27 ant-garden epiphytes, mostly *P. megalophyllum*, were found growing on the forest floor, but these were not rooted strongly in the ground, and often the remains of other epiphytes and ant-garden material were found attached to these plants.

The height distribution of the ant-gardens is similar in both study-areas. In Araracuara 63.4 % of the nests was located between 3 and 6 meters from the ground; in Monochoa 66.7 % was situated in the same range.

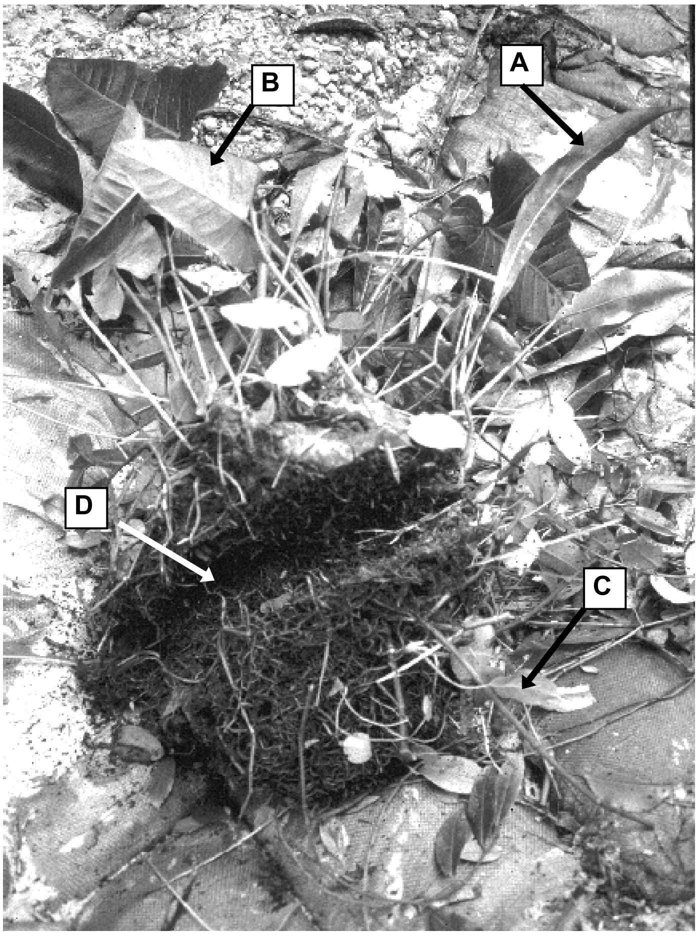


Figure 4 Ant-garden after collecting. This big nest was contained very aggressive ants and was cut of the supporting branch with the machete, hence the cut through the middle (D). Some easily recognized epiphytes are *Anthurium gracile* (A), *Philodendron megalophyllum* (B) and *Peperomia macrostachya* (C).

A positive correlation was found between height and nest size (Spearman rank correlation test, $P<0.05$ in Araracuara, and $P<0.01$ in Monochoa) and between nest size and the number of epiphyte-species encountered on the nest ($p<0.001$in Araracuara, and $p<0.05$ in Monochoa).

In a TWINSPAN analysis two classes of epiphytic nest-vegetation were distinguished. These coincide with the distribution between the two plots.

The first is characterized by a dominance of *Peperomia macrostachya* and was found in the Monochoa plot. The second is characterized by a dominance of *Codonanthe crassifolia* and occurred only in the Araracuara plot. Both have a variable but generally high percentage cover of *Anthurium gracile* and *Philodendron megalophyllum* (fig. 4). No mono-specific nests were found.

5.5 *Describing the structure of the gardens.*

A total number of 32 nests were opened up, 18 from Araracuara and 14 from Monochoa. Eight species of epiphytes were recorded on the nests. Inside all the nests two species of ants were found.

The nests consist of cavities, mostly 1 or 2 cm in diameter, which are separated by 'carton' walls. Epiphyte roots ramified through the entire nest, growing in the walls of the cavities (fig. 5). The breed of the ant *Crematogaster* group *limata* was always situated in cavities at the periphery of the nest, less than 2 cm from the surface. The breed of *Camponotus femoratus* lived in cavities more inside the nest, that were often relatively large, with thick walls. The male ants were often found in separate cavities, cared for by worker ants. It could not be established where the queen and virgin queens were situated within the nest.

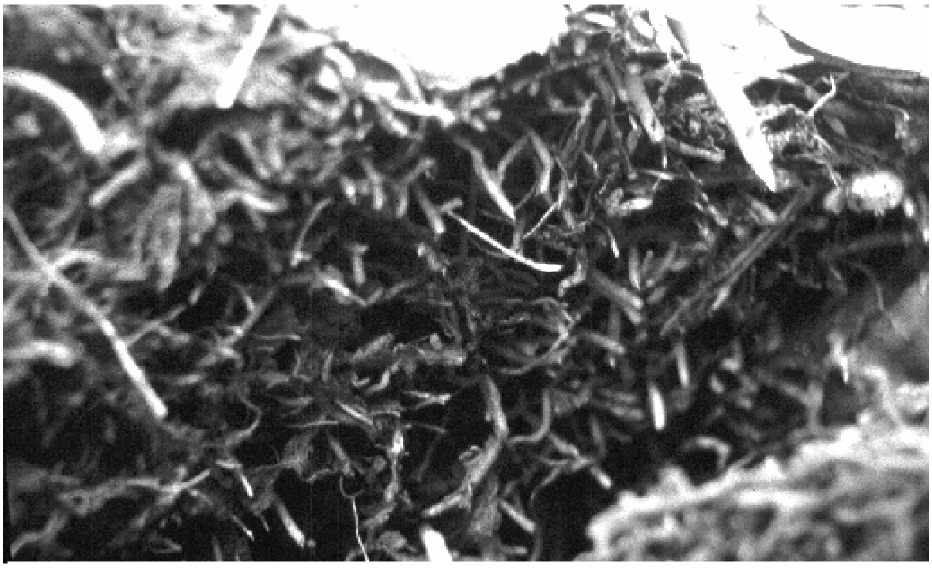


Figure 5 Close up showing the inner structure of the ant garden in figure 4.

The shape of the nests was variable, mostly ranging from a sphere to a cone. The two main factors causing irregular shapes are leaves falling on the nest, which are then incorporated, and the roots of Anthurium gracile, which are rather voluminous.

The material of the nests is of organic origin, and consists of a mix of decomposing humus and whole or shredded leaves from the epiphytes or the host tree. It is generally smooth, especially in the inner part of the nest, and slightly humid (never soaked or compacted).

6 Discussion

6.1 *Colonization & interactions.*

The fact that over half of the plants in the colonization experiment was recolonized within 4 months, while no nests were started independent of epiphytes, could be an indication that epiphytes are the primers of ant gardens. The reverse order; the ants starting a nest and planting the first epiphytes, can not be excluded, however. This scenario seems especially plausible when ant colonies expand and build new nests close to the first, a tendency that has been observed in *Camponotus femoratus* by Davidson (1988).

Even though some of the plants in the colonization experiment survived being without an ant nest for 4 months, no epiphytes were found growing outside ants nests anywhere in the plots. This could indicate that the ant gardens are especially important for the germination and early establishment of the epiphytes, and less for survival after that. However, four months is not enough time to conclude that these plants would survive, and they would probably be unable to develop further on their own. The fact that none of the plants on the nests that were followed through time died, while some of the colonization-experiment plants did, does indicate the beneficial influence of the ants on the plants.

The moment of colonization coincided with an increase in the amount of roots in *Anthurium gracile* and *Codonanthe crassifolia*, but the presence of ant nest material did not noticeably increase the growth rate of the plants, this in contrast to the results of Kleinfeldt (1978), who found that *Codonanthe crassifolia* grew faster in ant-gardens than outside them. The limited timespan and the small number of plants tested in this study may have prevented the detection of subtle (statistical) differences.

6.2 *Mapping nests and vegetation*

The high number of host-species and the variability in their occupation by ant-gardens does not indicate specificity between ant-gardens and the host-trees that carry them. By building their own nests and cultivating some of their own food-plants, ant-garden epiphytes are probably less dependent on the surrounding vegetation than other canopy ants are. However, Davidson (1988) found that some tree-species hosted ant-gardens significantly more often than others. Many of the common ant-garden hosts in Davidsons study have extrafloral nectaries, providing an extra food-source to the ants. Two other 'myrmecophytic' host-species have pearl bodies on their leaves and may also offer some protection for nests against other competing or predatory ants because of their long, dense stem-trichomes. It is likely that also the surrounding vegetation has an influence on the suitability of a tree as an ant-garden host (Davidson 1988). Not only the species composition, but also the structure would be important factors in this. In fact the host-specificity as recorded by Davidson may in part be a reflection of the suitability of different habitats, tree-fall gaps being extra suitable because of the higher light intensities, which benefit the ant-garden epiphytes as well as certain (host-)species. Seeing the plots in the present study were more or less homogenous, the influence of such different habitats was not presented, which may explain why no host-specificity was observed.

The main difference between the nest-vegetations in the two plots consisted of the replacement of *Codonanthe crassifolia* with *Peperomia macrostachya*. These species have a similar growth form, more or less pendulous, with adventitious roots growing from the nodes. Their role in the nests also seems to be similar, bounding it together with their stem, which is anchored to the nest by the roots. Codonanthe roots also delimit nest cavities, while the roots of Peperomia do not, and are more superficial and fragile. This species is, however, rich in nectaries and fruits, which may also explain its attractivity for the ants.

Most gardens were found above 3 m height, which is probably related to the increasing light intensities towards the canopy. In fact, when searching nests for collection for studying their structure, nests had to be collected mostly from outside the plots, in treefall gaps and along the road, because in the plots, in closed forest, not enough nests could be reached from the ground.

6.3 *Describing the structure of the gardens*.

The sharing of nests by two or more species of ants, ‘parabiosis’, has been observed by various authors (Wheeler 1921, Weber 1943, Madison 1979, Davidson 1988). The combination of *Camponotus femoratus* and *Crematogaster* group *limata* has been reported to occupy 94% of all ant-occupied gardens in South-eastern Peru (Davidson 1988), some gardens containing a third species (*Solenopsis* sp.). The difference in size may be part of the explanation for the peaceful co-habitation of these species. The large and aggressive *Camponotus* feeds on higher quality food sources and also takes care of the transport of seeds into the nest, while the smaller *Crematogaste*r is left to exploit the smaller nectaries (Davidson 1988).
The epiphytes found in the nests are mostly the same as those reported for ant-gardens in various other locations in South America (Ule 1902, Wheeler 1921, Weber 1943, Madison 1979, Belin-Depoux 1991), although not all species reported for other parts were present here.
The word ‘carton’ seems rather inappropriate for the material of these nests. While carton suggests a papery substance, like the chewed wood that many wasp-nests are constructed from, the material of ant gardens is more like a humous soil (fig. 4).

7 Literature

Barker, G. and S.L. Sutton 1997. Influence of Areal *Azteca* Nests on the Epiphytic Community of Some Belizean Orange Orchards. Biotropica **29**(2): 237-242.
Belin-Depoux, M. 1991. Écologie et évolution des jardins de fourmis en Guyane Francaise. Rev. Ecol. (Terre Vie) **46**: 1-38.
Benzing, D.H. 1991. Myrmecotrophy: origins, operation, and importance. In: Huxley C.R. and D.F. Cutler (eds.) 1991. Ant-plant interactions. Oxford University Press, New York.
Catling, P.M. 1995. Evidence for Partitioning of Belezean Ant Nest Substrate by a Characteristic Flora. Biotropica **27**(4): 535-537.
Davidson, D.W. 1988. Ecological studies of neotropical ant gardens. Ecology **69**(4): 1138-1152.
Davidson, D.W. and W.W. Epstein 1989. Epiphytic Associations with Ants. In: Lüttge, U. (ed) 1989. Vascular plants as epiphytes, evolution and ecophysiology. Springer-Verlag, Berlin.
Davidson, D.W., J.L. Seidel and W.W. Epstein 1990. Neotropical ant gardens II. Bioassays of seed compounds. Journal of Chemical Ecology **16**(10): 2993-3013.
Dejean, A., I. Olmsted and R.R. Snelling 1995. Tree-Epiphyte-Ant Relationships in the Low Inundated Forest of Sian Ka'an Biosphere Reserve, Quintana Roo, Mexico. Biotropica **27**(1): 57-70.
Duivenvoorden, J.F. and J.M. Lips 1995. A land-ecological study of soils, vegetation, and plant diversity in Colombian Amazonia. Tropenbos series 12, Stichting Tropenbos, Wageningen.
Gentry, A.H. 1993. A field guide to the families and genera of woody plants of Northwest South America (Colombia, Equador, Peru) with supplementary notes on herbaceous taxa. Conservation International, Washington DC.
Hölldobler, B. and E.O. Wilson 1990. The Ants. The Belknap Press of Harvard University Press, Cambridge, Massachusets.
Kleinfeldt, S.E. 1978. Ant-gardens: the interaction of *Codonanthe crassifolia* (Gesneraceae) and *Crematogaster longispina* (Formicidae). Ecology **59**: 449-456.
Losada, M.U. 1994. La Colonia Penal de Araracuara. Socioeconomía y recursos naturales 1938-1971. Estudios en la Amazonia Colombiana VIII, Tropenbos Colombia, Bogotá.
Madison, M. 1979. Additional observations on ant-gardens in Amazonas. Selbyana **5**: 107-115.
Maschwitz and B. Hölldobler 1970. Der Nestkartonbau bei *Lasius Fuliginosus*. Z Vrgl Physiol **66**: 176-189.
Mora Gil, V. I. 1999. Estructura y desarrollo de gardines de hormigas en bosques tropicales secundarios (Araracuara, Caquetá, Colombia). Thesis UdA, Medellín.
Tobin, J.E. 1995. Ecology and diversity of tropical forest canopy ants. In: Lowmand, M.D. and N.M. Nadkarni (eds.) 1995. Forest canopies. Academic Press, Inc., San Diego, California.
Ule, E. 1902. Ameisengärten im Amazonas-gebiet. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie **30**: 45-52.

Ule, E. 1905. Wechselbeziehungen zwischen Ameisen und Pflanzen. Flora **94**: 491-497.
Ule, E. 1906. Ameisenpflanzen. Botanische Jahrbücher Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie **37**: 335-352.
Verkleij J.S.A. and D.M.C. van Nederveen Meerkerk 1998. Changes in land use between 1986 and 1998 in the Araracuara region of the Colombian Amazon. A pilot study to explore the possibilities to apply the geographical information system ILWIS. Thesis LUW, Wageningen.
Weber, N.A. 1943. Parabiosis in neotropical ‘ant-gardens’. Ecology **24**:400-404.
Wheeler, W.M. 1921. A new case of parabiosis and the ‘ant-gardens’ of British Guiana. Ecology **2**:89-103.
Yu, D.W. 1994. The Structural role of Epiphytes in Ant Gardens. Biotropica **26**(2): 22-226.

Appendix I

Tropenbos

The ant-garden study was carried out for Tropenbos Colombia. They financed part of the project and organized the facilities in Araracuara. Tropenbos Colombia is part of the Tropenbos Foundation, which is based in the Netherlands. The Tropenbos Foundation was established in July 1988 in order to continue and expand the international Tropenbos Program, which was set up in 1986 by the Dutch government.

The main objectives of the Foundation are:

- to contribute effectively to the conservation and wise use of tropical rain forests, by generating relevant knowledge, deepening insights and developing and testing methods for forest policy and management;
- to involve local research institutions and to strengthen research capacity in tropical rain forest countries.

The Tropenbos Foundation formulates, coordinates and finances research programs in tropical rainforest countries. The research is often interdisciplinary and involves local organizations. The aim is to provide information that is needed by policy makers and forest users, and to produce results which have significance for application on a local as well as a broader scale. Apart from Colombia, Tropenbos has sites in Guyana, Côte d'Ivoire, Cameroon and Indonesia.

The objective of Tropenbos Colombia is 'to generate strategic knowledge for sound landuse planning and the conservation and wise use of humid forests in the Colombian Amazon region'.
The office is in Bogotá and the research areas are all in Araracuara or in other communities in the Araracuara region. In Araracuara the Tropenbos administration and organization are in the hands of Alejandro Jaramillo. Local people are hired for practical jobs and guiding of researchers. In the community of Peña Roja bridges and platforms have been established in the tree-crowns for canopy research.

To give an idea of the type of research carried out for Tropenbos Colombia, here is a list of project titles from 1997 (Tropenbos annual report 1997)

- Forest dynamics in Amazonian Colombia: The case of three landscapes in the Middle Caquetá.
- Diversity of the flora and vegetation of the West Guayanan hard rock formations in Colombian Amazonia.
- Moisture and nutrient cycling in Colombian humid tropical forest; the Dynamite model.
- Reproductive characteristics (pollination and seed dispersal) of two contrasting Amazonian rain forest communities: a study at canopy level.
- Management model for commercial fishing in the Middle and Lower Caquetá.
- Indigenous model for regional natural resource management in the Middle and Lower Caquetá.

- Non-timber forest plant resource assessment in Northwest Amazonia
- Strategy development for wise utilization of secondary forests.
- Creation of educational material for the Andoke community of the Middle Caquetá.
- Production of the liana Yarú, ecology of the liana Yarú.
- Fungal diversity during regeneration of Amazon forests.

Appendix II

This is a little paragraph about some 'daily life' issues in Araracuara, which is not scientifically significant, but may be interesting to students or others planning to visit Araracuara. Of course there is much more to tell, but that is for the visitors themselves to find out.

Daily life in Araracuara

Living and research accommodation in Araracuara is provided by Sinchi (Instituto Amazonico de Investigaciones Cientificas), a Colombian governmental administrative and research-organization. Across the river lies the settlement Puerto Santander in the province of Amazonia. Services are distributed over the two villages, which are connected by free-lance ferry operators. Araracuara has the hospital and school ('el internado') and Sinchi-facilities. Puerto Santander has two bakeries, the church and the Telecom-office, with the only telephones outside the hospital. Both have a shop (Puerto Santander has several), selling crackers, jam, rice, beans, toilet paper and other necessities. Local transport is on foot or by boat. A passenger flight from Bogotá to Leticia comes in at the Araracuara airstrip once a week. Once a month there is a freight plane. Goods for the shops are brought in by boat from Florencia, a two-day trip (one-way) to the foot of the Andes. Araracuara and nearby villages are the main research area for Tropenbos in Colombia.