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ADDITIONAL OBSERVATIONS ON ANT-GARDENS IN AMAZONAS

*Michael Madison**

In 1901 the botanist Ernst Ule published a paper entitled 'Ameisengärten im Amazonasgebiet' in which he presented observations on structures which he called 'ant-gardens.' These are arboreal nests of several species of ants which invariably have growing from them epiphytic angiosperms. The epiphytic flora, which is restricted to ant-gardens, includes species of *Codonanthe*, *Philodendron*, *Anthurium*, *Aechmea*, *Peperomia*, and *Markea*, among others. Ule proposed that the relationships of the ants and the plants in these ant-gardens is highly specialized, and that the plants could not survive without the ants on which they are dependent for dispersal of their seeds, protection from predators, and provision of organic matter around the roots. The ants presumably benefit in this relationship by having the roots of the plants serve as an architectural framework for their nests.

Twenty years later the entomologist W. W. Wheeler made a study of ant-gardens in Guyana and published a review highly critical of Ule's conclusions, which he regarded as 'a classical example of the uncritical mixture of observation, inference, assertion, and speculation, which abound in the work of observers in the tropics' (Wheeler 1921, p. 100). Wheeler considered the relationship of the ants and plants in ant-gardens to be a casual and opportunitistic one, rather than one of strict interdependence. Wheeler's chief contribution to our knowledge of ant-gardens was his discovery that a majority of the ant-gardens contains two unrelated species of ants, in various combinations of *Crematogaster*, *Camponotus*, *Azteca*, and *Anchoetus.* He called the mutualistic relationship of the cohabiting pairs of ant species 'parabiosis,' and suggested that the association of a large and a small species of ant is ecologically equivalent to a single species which has differentiated workers of various sized classes.

Weber (1943) added further observations on ant-gardens in northern South America. He found a number of ant-gardens in which three species of ants occurred parabiotically: a large *Camponotus*, a smaller *Crematogaster*, and a tiny species of *Solenopsis*. Weber followed the views of Wheeler that the ant-plant interaction in these cases is a casual one in which the ants are warding off plant predators and the plant roots provide an architectural framework for the ant nests.

Despite their local abundance and obvious biological interest, the Amazonian ant-gardens have not yet been the subject of a thorough investigation. The present paper reports additional observations which vindicate several of Ule's original hypotheses, and suggest that the ant-plant relationship in ant-gardens is much subtler than had been suspected.

LOCATION OF STUDY SITES

The observations here reported were made in the course of one of the plant collecting expeditions of the Projeto Flora Amazonas, supported by NSF grant INT77-17714. This expedition originated in Manaus, Brazil, and the party traveled by boat up the Rio Negro to São Gabriel de Cachoeira, making general plant collections at various sites along the way. Observation of ant-gardens was carried on most intensively at the following localities:

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*The Marie Selby Botanical Gardens, 800 S. Palm Ave., Sarasota, FL 33577 U.S.A.

caatinga at the mouth of the Rio Marié, 66° 24′W × 0° 26′S; caatinga at Porto Camanaus, 67° 03′W × 0° 12′S; and Serra Curicuriarí, 66° 53′W × 0° 18′S. In addition studies were made at a phytosociological survey plot at Igarapé Tarumã, near Manaus. Voucher plant collections will be deposited at INPA, SEL, and other institutions.

Ant-gardens were also investigated in the region of Limoncocha, Prov. Napo, Ecuador, 76° 38′W × 0° 23′S, in June 1978, on an expedition of the Marie Selby Botanical Gardens. Voucher specimens for these studies are deposited at SEL, QCA, F, and elsewhere.

OCCURRENCE AND STRUCTURE OF ANT-GARDENS

Ant-gardens are found throughout northern and western Amazonia, and have been reported from Guyana by Wheeler (1921), Suriname and Venezuela by Weber (1943), Brazil and Peru by Ule (1905), Matto Grosso by Mann (1912), and Ecuador and Colombia by Madison (unpublished). While an occasional ant-garden may be found in nearly any forest locality, they are much more abundant in certain vegetation types. Along the Rio Negro in Brazil medium to high caatinga forest on white sand soils had the greatest density of ant-gardens, which are much less common in forest on clay soils, in igapó vegetation, and in campinas. A man-made habitat of increasing frequency in Amazonia, consisting of stands of trees killed by flooding due to road construction, also supported abundant ant-gardens as well as epiphytes not associated with ants.

In the forest at Rio Marié, a caatinga forest on white sand with a canopy at about 20 m, 34 ant-gardens occurred in a 1 × 10 m sample plot. At Igarapé de Tarumã, a plot 15 × 15 m in a stand of trees killed by flooding included 17 ant-gardens.

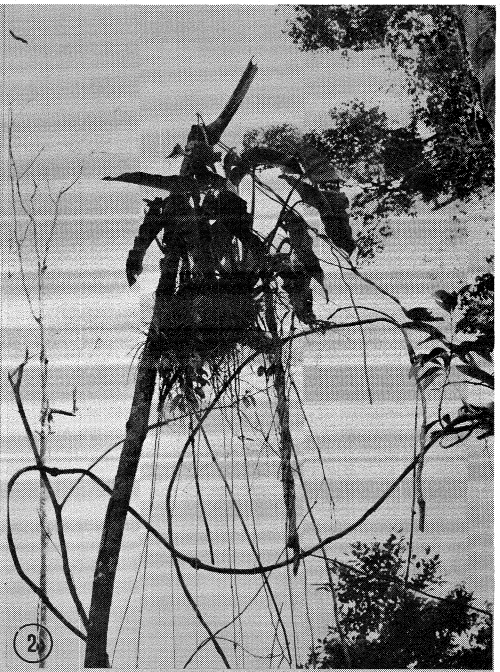
The ant-gardens observed in Amazonas were similar in appearance and structure to those observed in Para and Peru by Ule (1901), and in Guyana, Suriname, and Venezuela by Weber (1943) and Wheeler (1921). They are spherical, or more commonly subspherical to elongate, and 2-30 cm in diameter (Figures 1-5). Mostly they are constructed around narrow twigs or the trunks of saplings. The nests are made of a carton-like material with grains of sand intermixed, permeated with chambers of various sizes, often 5-15 mm tall and slightly wider. The walls of the chambers are thoroughly penetrated by the roots of epiphytes.

In a majority of the ant-gardens the carton is confined to the spherical nest, but in some cases carton-covered galleries extend along the epiphytes or host tree, in places giving rise to secondary chambers. In some cases a series of ant-gardens in several parts of a tree are connected by carton-covered trails, and evidently are portions of a single colony.

All the arboreal ant nests of this general shape and consistency that I observed had epiphytic plants growing from them.

THE EPIPHYTIC FLORA

The epiphytic flora of the ant-gardens in Amazonas is essentially that reported for other South American localities by Ule (1901), Wheeler (1921), and Weber (1943), and included the following species: *Aechmea brevicollis* L.B.Smith, *Aechmea mertensii* Schult.f., *Anthurium gracile* (Rudge)Lindl., *Anthurium scandens* (Aubl.)Engler, *Anthurium solitarium* Schott, *Asplundia* sp., *Codonanthe calcarata* (Miq.)Hanst., *Codonanthe uleana* Fritsch, *Codon-*



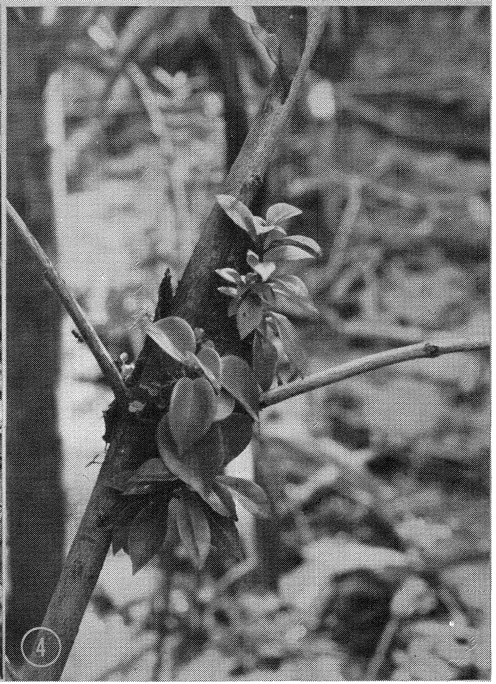


Figure 1. Ant-garden with *Codonanthe calcarata* and *Philodendron myrmecophilum*.
Figure 2. Ant-garden with *Philodendron myrmecophilum*, *Peperomia macrostachya*, and juvenile *Streptocalyx angustifolius*.
Figure 3. Ant-garden with *Codonathopsis uleana* (larger leaves) and *Codonanthe calcarata*.
Figure 4. Ant-garden with young plants and seedlings of *Peperomia macrostachya* and *Codonanthe calcarata*. The plants have not reached reproductive maturity and the seedlings are growing from seeds brought to the nest by the ants.

anthe sp., *Codonanthopsis dissimulata* (H.E.Moore)Wiehler, *Codonanthopsis ulei* Mansf., *Epiphyllum phyllanthus* (L.)Haw., *Ficus myrmecophila* Warb., *Markea formicarum* Damm., *Peperomia macrostachya* (Vahl) A. Dietr., *Peperomia* sp., *Philodendron myrmecophyllum* Engler, *Philodendron traunii* Engler, and *Streptocalyx angustifolius* Mez. The *Codonanthe* and *Codonanthopsis* species frequently occurred alone in ant-gardens, while most of the other species occurred gregariously, seemingly in random combinations. The species of *Codonanthe* and *Codonanthopsis* were by far the most common epiphytes in the ant-gardens; *Anthurium gracile* and *Aechmea mertensii* were next most common, and the other species occurred only sporadically. Often where they did occur they would be found in a dozen or more adjacent ant-gardens.

THE ANTS

Early in the expedition a fire destroyed all our equipment, so I was not able to make collections of the ants. My casual observations support those of Wheeler (1921) and Weber (1943), namely that at least half a dozen species of ants make ant-gardens, and that not infrequently two species will share the same ant-garden. Some of the ants were not the least bit aggressive, and paid little attention when the ant-gardens were disturbed, but others (*Camponotus* sp.) were extremely aggressive and capable of inflicting painful wounds. Even the vibrations caused by the approaching observer stimulated the ants to come swarming out of the nest and to patrol the epiphytes out to their tips. In response to more active attack, such as poking the nest with a machete, they would leap into space and attempt to bite or sting whatever they landed on.

The species of ants found in ant-gardens by Wheeler (1921) and Weber (1943) include the following: *Anochetus emarginatus* (Fabr.), *Azteca traili* (Emery), *Azteca ulei* (Forel), *Azteca* sp., *Camponotus femoratus* (Fab.), *Crematogaster limata* (Smith), *Crematogaster parabiotica* (Forel), *Dolichoderus debilis* (Mann), *Odontomachus affinis* (Guerin), and *Solenopsis parabiotica* (Weber).

DISPERSAL OF THE EPIPHYTES

All the species of epiphytes found in ant-gardens have fleshy fruits less than 1.5 cm in diameter, except the *Peperomia* species. The fruits of the peperomias are achenes 2-5 mm long, and about 1.5 mm thick, considered by Ridley (1930) and vanderPijl (1969) to be dispersed externally on animal vectors. The other species, with fleshy fruits containing various small seeds, are typical of endozoochorous fruits dispersed by birds and mammals.

One of Ule's (1901, 1905, 1906) more controversial hypotheses was that the ants disperse the seeds of the ant-garden epiphytes, and in fact sow the seeds to establish new gardens or to enrich existing ones. Wheeler (1921) was highly critical of this, suggesting instead that the ants may scavenge seeds which have already been dispersed by other zoochores, but this could not be interpreted as deliberate gardening on the part of the ants. However, Wheeler was unable to make any direct observations of seed dispersal.

For those species of any epiphytes which I was able to observe in fruit, the ants disperse the seeds at least some of the time despite the fact that these are typical endozoochorous fruits. In *Codonanthe calcarata*, *Codonanthe* sp., and *Aechmea mertensii* the ants excavate the ripe berries and remove the seeds to their nests (Fig. 6). The seeds of the *Codonanthe* species have a well-developed fleshy aril, and *Aechmea mertensii* has a fleshy funiculus; these are eaten by the ants either at the berry or back at the ant nest. Fruits of *Peperomia macrostachya* have a large sticky oil gland at the base evidently of epidermal origin and apparently serving as an elaiosome, although I did not observe the ants eating it. The peperomia fruits are removed by the ants from the fruiting spike and carried to the ant-nests.

The interest of the ants in these seeds may be partly in the aril or funiculus, which serves as an edible elaiosome. Hans Wiehler has pointed out (personal communication) that the seeds of *Codonanthe* spp. are quite unlike those of any other neotropical gesneriad, and in fact strikingly mimic ant pupae. They are ovoid, white, and 2-3 mm long and about 1 mm in diameter. The seeds of *Anthurium gracile*, one of the other common ant-garden epiphytes, are remarkably convergent in size, shape, and color to those of *Codonanthe* spp., and lack the mucilaginous coat typical of other anthuriums. The seeds of *Aechmea mertensii* and *A. brevicollis*, and the fruits of *Peperomia* spp., share this size and shape, though not color. Although I did not observe ants carrying seeds of *Anthurium gracile*, in one case I found cavities chewed in the berries from which the seeds had been removed, a situation suggestive of primary dispersal by ants excavating the seeds in a manner similar to that observed in *Codonanthe calcarata.*

EXTRAFLORAL NECTARIES

Though extrafloral nectaries have not been reported in the literature for ant-garden epiphytes, several kinds are to be found in the ant-garden species of *Codonanthe*, *Codonanthopsis*, and *Philodendron*. In addition, in *Codonanthe uleana* and *Codonanthopsis ulei* a floral nectary is exploited by the ants. This is a conspicuous gland 1.5-2.5 mm long located at the base of the corolla spur. Early in the development of the flower, before maturation of the corolla is complete, the calyx lobe covering this region reflexes and the ants evidently chew through the corolla spur to expose the nectary, on which they feed. The nectary is quite conspicuous, red or red-orange in *Codonanthopsis ulei* and yellow in *Codonanthe uleana*, whereas the calyx and exterior of the corolla are a pale cream color. The calyx lobe remains reflexed and the nectary continues to function through anthesis and the development of the fruit.

Two other kinds of extrafloral nectaries are found in *Codonanthe*. In *Codonanthe* sp. the nectaries are five small red glands located abaxially at the sinuses between the calyx lobes. Though I did not observe large nectar drops produced by them, they were visited and fed upon by the ants both during and after anthesis until the fruit ripened. The second kind of extrafloral nectary consists of waxy red glands 0.5-1 mm across scattered on the abaxial surfaces of the leaves. In most of the ant-gardens the ants ignored these, but in one garden tenanted by a small amber-colored ant with a striped abdomen the ants were feeding on the leaf nectaries.

Though extrafloral nectaries have not been reported for the family Araceae, they occur in all the ant-garden species of *Philodendron* observed and several other Amazonian species as well. The nectaries are colored spots occurring in a ring around the petiole at its apex, where it joins the blade, and corresponding to the region of the geniculum in other aroids (Fig. 8). These nectaries are copious producers of a sweet aromatic fluid which is


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Figure 5. Ant-garden on a felled tree with *Codonanthe* sp., *Aechmea mertensii*, and *Epiphyllum phyllanthus*.
Figure 6. Ants excavating the seeds from a ripe berry of *Codonanthe calcarata*.
Figure 7. Ant-garden with *Markea* sp., showing the swollen succulent roots which are sometimes eaten by the ants.
Figure 8. Ant feeding on the extrafloral nectary of *Philodendron myrmecophilum*.

eaten by the ants. Ants feeding at these nectaries did not respond to disturbance of the nest as did their comrades, but remained feeding.

AUTOGAMY

A majority of the ant-garden epiphytes, including *Codonanthe calcarata*, *Codonanthe uleana*, *Codonanthe* sp., *Anthurium gracile*, *Anthurium scandens*, *Epiphyllum phyllanthus*, *Peperomia macrostachya*, *Peperomia* sp., *Aechmea mertensii*, and *Aechmea brevicollis*, are autogamous. These species, all of which are in cultivation at SEL, regularly have close to 100% fruit set (5-50% in the gesneriads) in cultivation in the absence of any pollinators. Whether or not the other species of ant-garden epiphytes are autogamous is not known, but even if they are not, the level of autogamy in the Amazonian ant-garden flora is much higher than what one would expect for the tropical flora as a whole.

DISCUSSION

The observations reported here on the occurrence, structure, and flora of Amazonian ant-gardens reiterate those of earlier workers. However, new observations on seed dispersal, extrafloral nectaries, and autogamy suggest that the relationship of ants and plants in ant-gardens is more complex and subtle than had been suspected, and is in need of reassessment.

Wheeler (1921) and Weber (1943) proposed that the ant-gardens represent a casual, mutualistic relationship in which the plants benefit by having a rich soil packed around their roots and possibly by gaining protection from predators, while the ants benefit in having a structural framework for their nests provided by the roots of the epiphytes. Ule held essentially this view, with the added concept that the ants are the sole dispersers of the epiphyte seeds, and hence the epiphytes are entirely dependent on the ants.

The relationship of the ants and plants in ant-gardens is clearly not one of strict dependence, since the ants may establish colonies in hollow trees or elsewhere without any epiphytes, and all the species of epiphytes (except *Codonanthe* spp.) are at least occasionally found growing without associated ants. Nonetheless, in certain areas, such as the white sand caatingas investigated in this study, the overwhelming majority of the ant colonies and epiphytes of the relevant species are associated in ant-gardens. Evidently the association confers considerable adaptive advantages to both the ants and the plants. The plants benefit by 1) protection from predators by pugnacious bodyguards, 2) provision of mineral nutrients from the ant nest materials, 3) external storage of water in the walls of the nest, which by its sponge-like character moderates the severity of fluctuations in the availability of water in the epiphytic habitat, and 4) dispersal of seeds or fruits. The ants presumably benefit from 1) nectar from the extrafloral nectaries, 2) elaiosomes of the epiphyte seeds or fruits, and 3) an architectural framework for their nests provided by the epiphyte roots, particularly important in view of the occasional torrential rains in the region.

Excepting the extrafloral nectaries and modifications of seeds, these features do not represent adaptations unique to ant-gardens. That is, scavenging of seeds and manufacture of arboreal nests of carton and earth by the ants, and production of tough adventitious roots by the epiphytes, occur and have adaptive value independent of the ant-gardens. The ant-garden association is thus at least partly a fortuitous interaction of pre-existing features.

On the other hand, the extrafloral nectaries and specialized seeds and fruits of many of the epiphytes seem best interpreted as adaptations of the plants for association with ants.

The high incidence of autogamy in the ant-garden epiphytes may be favored in part by aggressive behavior of the ants toward pollinators. Although in general ants feeding on extrafloral nectar do not hinder pollinators (Bently 1977), in some *Codonanthe* species in which the flowers are borne on the surface of the nest it seems likely that pollinators would be deterred. An additional factor favoring autogamy in ant-gardens is the low faunal density of the caatinga vegetation. As has been pointed out by Spruce (1908), Janzen (1974a) and others, tropical white sand-black water ecosystems are extremely poor in mineral nutrients and support very low faunal densities. The low density of potential pollinators in the region where ant-gardens are most abundant may in itself favor autogamy. It is also possible that the balance of trophic relationships between the ants and plants may require a more reliable and abundant supply of fruits and elaiosomes than would be expected from outcrossing epiphytic species. That is, the ants are differentially incorporating into their nests those epiphytes which are more likely to produce a steady supply of fruits and elaiosomes, viz., the autogamous species.

In 1974, Janzen published two important reviews on white sand ecosystems: one (1974a) is a general analysis of white sand-black water regions throughout the tropics, and the second (1974b) deals with ant-epiphyte relationships on a white sand heath at Bako, Sarawak. Janzen did not report on ant-epiphytes from the neotropics, but the parallels between the ant-gardens described here and the ant epiphytes at Bako are striking. In both situations we find several species of ant and several species of epiphytes occurring in close association. The epiphytes exhibit myrmecochory (many species), autogamy (*Hydnophytum formcarium*, *Lecanopteris carnosa*, *Myrmecodia* spp., *Phymatodes sinuosa* at Bako), and provide food for the ants (in Asia by the abundant production of pearl bodies by *Pachycentria tuberosa*; these bodies were overlooked by Janzen because in the wild they are quickly removed by the ants, but they are readily evident in ant-free cultivated plants). The ants in turn are provided with domatia. In most of the Asian species of epiphytes the domatia are formed by modified stems and leaves, and in the neotropical species by roots. It is notable that the ants and principal families of ant-epiphytes in Asia (Rubiaceae, Asclepiadaceae, Polypodiaceae) are quite unrelated to those of the neotropics (Gesneriaceae, Bromeliaceae, Araceae). The ant-epiphyte systems are thus of entirely independent origin in the two regions and represent a complex case of convergent evolution.

Janzen (1974a,b) concluded that the principal ecological bases of the ant-epiphyte relationship at Bako were the mineral nutrition of the plants by the ants through scavenging of nutrients from the surrounding area, and the provision of domatia for the ants. If one adds the feeding of the ants by elaiosomes and nectar, the same features characterize the south American ant-gardens as well.

While the present report adds to the anecdotal literature on ant-gardens, what is needed are careful quantitative studies and experiments on their ecology, addressing among others the following questions: What is the contribution of the ant nests to the mineral nutrition of the epiphytes? What is the role of epiphyte nectar and elaiosomes in the diet of the ants?

What is the phenology of fruit and nectar production of associated epiphyte species? To what extent are the ants primary vs. secondary dispersors of epiphyte seeds? Is there a correlation of ant species and epiphyte species? How do the several parabiotic species of ants in an ant-garden partition the resources provided by the epiphytes?

Perhaps most critically in need of study is the foundation and development of new ant-gardens. Wheeler (1921) pointed out that the ant species of ant-gardens in Guyana establish new colonies by single fecundated queens, and not by division of a parent colony. However, the occurrence in a tree of several ant-gardens connected by carton-covered galleries is suggestive that establishment by division of large colonies may also occur. How a colony established by a single queen comes to be associated with its typical epiphyte flora, often of 3-4 unrelated plant species, remains an intriguing mystery.

NOTE ADDED IN PROOF

After this paper was written, a paper appeared by Sally Kleinfeldt (Ecology 59: 449-456, 1978) on ant-gardens in Costa Rica. This paper reported studies of a simplified system with only a single epiphyte species (*Codonanthe crassifolia*), but the observations on extrafloral nectaries and seed dispersal are in agreement with those reported here for Amazonas.

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