

ANT GARDENS OF SURUMONI, VENEZUELA

ARAGUA CEDEÑO*

Instituto de Zoología Tropical, Universidad Central de Venezuela, Apartado 47058,
Caracas 1041-A, Venezuela. E-mail: acedeno@strix.ciens.ucv.ve

TATIANA MÉRIDA

Centro de Microscopía Electrónica, Universidad Central de Venezuela, Apartado 47114,
Caracas 1041-A, Venezuela

JORGE ZEGARRA

Apartado 50012, Caracas 1050-A, Venezuela. E-mail: jzegarra@strix.ciens.ucv.ve

ABSTRACT. Studies of the spatial distribution, floristic composition, insect fauna, and internal characteristics of ant gardens (AGs) were conducted during several visits to the Surumoni research crane site in southern Venezuela in 1997 and 1998. AGs were more abundant in the sunniest sector of the study area. Four families of epiphytes were represented in the AGs, with Araceae being the dominant one. Frequent plant species were *Anthurium gracile*, *A. trinerve*, *Codonanthe calcarata*, *Aechmea tillandsioides*, and *Philodendron deflexum*. Colonies of various ant species were found living in AGs, of which the most prominent were *Crematogaster* cf. *limata parabiatica*, *Camponotus femoratus*, *Anochetus emarginatus*, *Paratrechina* sp., *Gnamptogenys ?tortuolosa*, *Oligomyrmex* sp., *Wasmannia* sp., *Pheidole* sp., and *Solenopsis* sp. Dramatic changes in climate brought about by El Niño affected the microclimate of AGs, altering their suitability as temporal nests for ants. The main components found in the interior of a typical AG are carton, fine roots associated with cyanobacteria, ant brood, workers and queen(s), and a soil-like deposit here termed "substrate." The major interactions in an AG may be as follows: ants bring allochthonous material (plant sap, insects, seeds) to the nest as food for their larvae, build nest carton, and disperse epiphyte seeds and cyanobacteria. Epiphytes grow more efficiently associated with ants. Their external roots lend structural support to the nest, and their fine roots obtain superior nutrients from their detritus and fixed nitrogen from their association with cyanobacteria. Cyanobacteria also may recycle carbon from root exudates and ant detritus.

Key words: Surumoni, rain forest canopy, ant garden, ant, epiphyte, cyanobacteria

INTRODUCTION

Ant garden (AG) is the traditional name for a mutualistic system that develops from an arboreal ant nest around the roots of one or more epiphytes. AGs are abundant in the canopy of Amazonian forests (Ule 1901, Wheeler 1921, Weber 1943, Belin-Depoux et al. 1987, Davidson 1988, Yu 1994). They are found on host plants that often provide ants with food resources or special nesting sites (Davidson & Epstein 1989).

Most AGs are located in the intermediate strata (midcanopy) of forests, and studies of them are generally limited to observation through binoculars unless climbing techniques are used (Weber 1943, Kleinfeldt 1978, Davidson 1988). The special crane installed by the Austrian Academy of Sciences (OEAW) for the study of the rain forest canopy in the Venezuelan Amazon territory now allows direct access to AGs. Their spatial distribution, floristic composition,

and internal characteristics can be studied with a minimum of perturbation.

MATERIALS AND METHODS

The Surumoni rain forest is located in Amazonas State, Venezuela, 65°36'W, 3°08'N, approximately 13 km from the south wall of Cerro Duida (2358 m elevation at summit), with strong orographic influence on the local climate. This climate shows low seasonality. Total annual rainfall was 3443.8 mm in 1996, 2259 mm in 1997 (January–November), and 2841 mm in 1998 (January–September) (rainfall measurements taken from Surumoni crane tower station). A short dry period occurred each year between November and February, and the mean annual temperature was 26°C. The crane study area resembles a 200 m long ellipse. The two foci, separated by 120 m, are oriented in a north-south axis near the Orinoco River, on the western bank of its minor affluent, the Caño Surumoni. The forest ground layer in the study area is seasonally inundated. The predominant vegetation ex-

* Corresponding author.

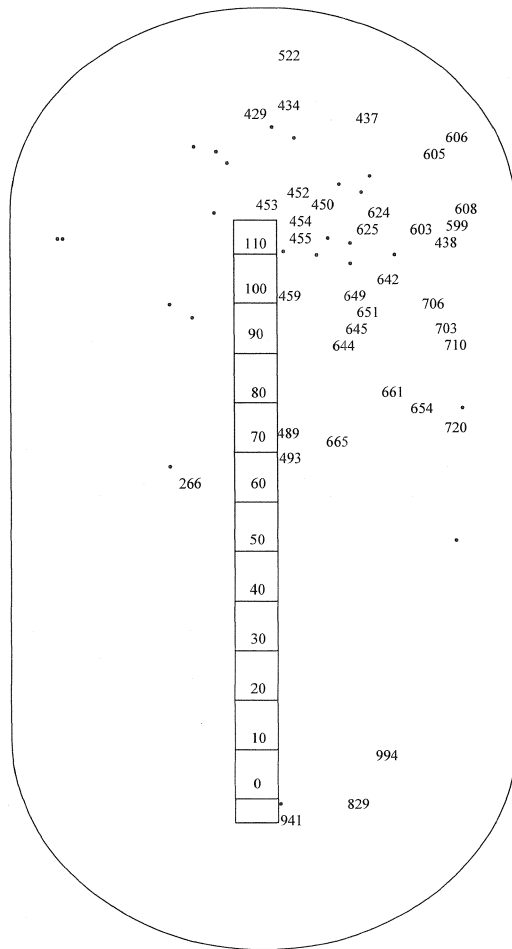


FIGURE 1. Outline of study area showing distribution of ant garden host trees. Numbered trees are indicated with their individual numbers. Black dots indicate unnumbered trees.

hibits an arboreal stratum greater than 20 m high. More than 75% of trees maintain foliage during the dry season; and the forest is located less than 200 m above sea level. Thus, it is classified as a tall, evergreen, lowland, and riverine forest (Dezzeo & Huber 1995). All trees in the crane area with trunk diameter greater than 10 cm (at 1.5 m from the ground) were number-tagged and identified at the time of flowering (W. Morawetz unpubl. data).

The crane at Surumoni is a mobile swing crane running on two 120 m long rails. It is operated by remote control from an observation gondola that hangs from its 40 m long arm. This system allows one to three researchers to closely observe almost every point within an area of 1.46 ha of rain forest.

Climate and Orinoco river flow allowed for three field visits, one at the end of the dry season (March 1997), the second at the end of the rainy season (November 1997), and the third in September 1998. AGs, mainly located in the mid-canopy, were found and censused from the forest floor with the aid of binoculars. Direct access was achieved later with the crane. The following external parameters were recorded: host tree identification number (if any), position in host tree, dimensions (length and width measured only in crane-accessible AGs), and epiphyte and ant species present. Nests were filmed and photographed.

As intensive sampling is not permitted in the crane area, samples from nest interiors for examination of root system and ant brood were obtained using a small metal corer (10 mm internal diam.). Preserved in flasks with 70% ethanol or kept dry in paper towels, the samples were transported to the laboratory for microscopic analysis. Small fractions of the ethanol-fixed root samples were transferred to equal parts 50% glycerin and 70% ethanol. After 10 to 30 minutes, they were transferred to 50% glycerin for 5 minutes. Fine free-hand sections, made with a single-edged razor blade, were mounted on slides in a drop of glycerin solution sprinkled with phenol crystals, as semi-permanent preparations. This process can be reversed without damage to samples. Morphometric and photographic records were made with a Zeiss-MC63 light microscope. Voucher plant and ant specimens have been deposited in the Herbario Nacional de Venezuela (Fundación Jardín Botánico) and the Colección de Insectos del Museo de Biología del Instituto de Zoología Tropical, respectively, both at the Universidad Central de Venezuela in Caracas.

RESULTS

Distribution of AG host trees in the crane area is shown in FIGURE 1. AGs were more abundant in the sunniest, northeastern sector of the crane study area. Light measurements taken from the high canopy for the total crane area were 227.1 w/m^2 (D. Anhuf & J. Szarzynski pers. comm.). Radiation measured in the understory (1.5 m above ground) about noon (11:30–13:30) in January 1998 was 5.15 w/m^2 for the total crane area and 5.80 w/m^2 in the NE sector (J. Hernández unpubl. data).

In all, 137 AGs on 65 host trees were studied at heights varying from 3 to 26 m. Many host trees had a trunk diameter of less than 10 cm; these were mainly juvenile forms and not tagged. The number of AGs on a host tree varied from one to nine.

TABLE 1. Number of ant gardens, out of 137 studied, where epiphytes occurred either alone or with other species.

Family	Species	Number of ant gardens where found (% of total)
Araceae	<i>Anthurium gracile</i>	86 (62.8)
	<i>Anthurium trinerve</i>	27 (19.7)
	<i>Anthurium</i> sp.	1 (0.7)
	<i>Philodendron deflexum</i>	12 (8.8)
Bromeliaceae	<i>Aechmea tillandsioides</i>	23 (16.8)
	<i>Aechmea</i> sp.	1 (0.7)
Cactaceae	<i>Epiphyllum phyllanthus</i>	1 (0.7)
Gesneriaceae	<i>Codonanthe calcarata</i>	25 (18.2)
	<i>Codonanthe crassifolia</i>	1 (0.7)

Epiphytes and Ants in the Gardens

Four families of epiphytes represented in the Surumoni AGs are shown in TABLE 1. The dominant plant is *Anthurium gracile*, alone or with other plants, which occurred in 86 (63%) of all AGs studied. The smallest nests have *A. gracile* as the only epiphyte (FIGURE 2). AG size increases as other plants are incorporated into the nests. Larger AGs usually contain *P. deflexum* or bromeliads (FIGURES 3–5).

In March 1997, samples were collected from the interior of 16 AGs. All had brood of *Crematogaster* cf. *limata parabiatica* (Forel), seven contained only this ant species, and nine were in parabiosis with *Camponotus femoratus* Fabricius. Brood of the latter was never found. In most instances, workers were seen in the vicinity of nests or coming out of them in large numbers, when lightly disturbed.

In November 1997, *Crematogaster* cf. *l. parabiatica* was found outside several AGs studied in March and others not previously studied. The ants were engaged in activities suggesting reconditioning of the nests; none contained brood. Apparently, they were nesting in the soil, as observation of many workers and three queens travelling back and forth between an AG and a soil site would seem to indicate. The nest's exact location in the dense litter and undergrowth could not be found. The only fully occupied AGs found at the end of the November field trip were two large nests of *Anochetus emarginatus* and *Paratrechina* sp., both with brood. They were sharing the AG with the termite *Nasutitermes* sp. The apparent compartmentalization in the two nests was similar: *Anochetus emarginatus* at the top, the small *Paratrechina* sp. in the middle, and the termite at the bottom of the garden.

In September 1998, the authors found new

AGs occupied by workers and sexuals of seven different ant species. Several of these ants are still in the process of being properly identified. Workers and a few sexuals of the large ponerine *Gnamptogenys ?tortuolosa* were found sharing a nest with minute workers of both *Wasmannia* sp. and *?Oligomyrmex* sp. (key by B. Bolton 1994) in one AG and with *Solenopsis* sp. in another. Size differences of workers were found in what may be *Crematogaster* cf. *l. parabiatica* from two separate colonies, but whether they are different species was unresolved at the time of this writing. Workers of *Crematogaster* sp. (not *l. parabiatica*), *Camponotus* sp. (not *C. femoratus*), *Pheidole* sp., and *?Azteca* sp. also were found in other AGs. Only a colony of *Anochetus emarginatus* survived the two-year period in one AG. A small nest with a complex carton structure, but lacking epiphytes, was dissected. FIGURE 5 shows the carton nest, built on a small twig, with the leaves giving support to the carton. Contained inside were numerous larvae, pupae, workers, and 39 queens of *Cr. cf. l. parabiatica*. The carton nest also had a lesser number of larvae, workers, and one queen of a dolichoderine ant (probably of the genus *Dolichoderus* = *Monacis*).

Garden Interiors

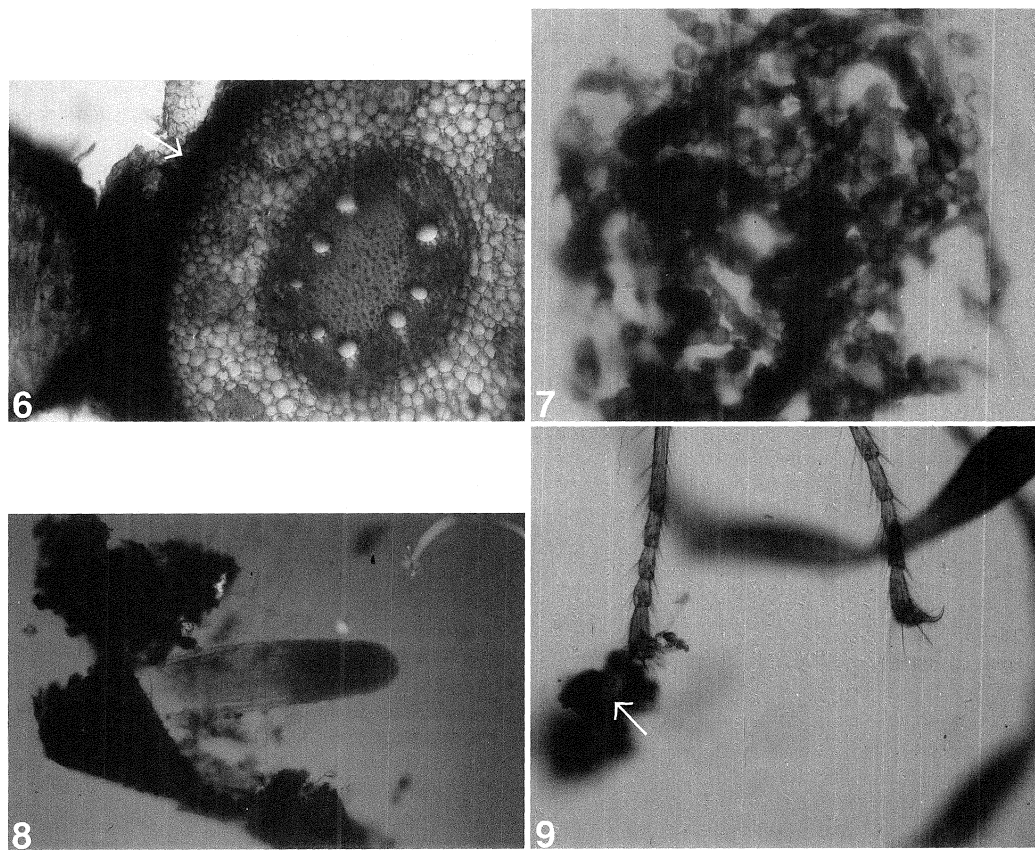
All samples taken from AGs in March 1997 contained the following components: carton, a fine root system, cyanobacteria, different stages of *Crematogaster* cf. *l. parabiatica* (larvae, pupae, workers, but no sexuals), and a complex mixture of organic debris and soil particles that the authors called "substrate."

Carton structure was studied from cross sections revealing a dense root system interlaced with cyanobacterial masses and substrate. Carton built by *Crematogaster* cf. *l. parabiatica*, with occasional leaf inclusions, probably added by *Camponotus femoratus* (Davidson & Epstein 1989), differs from that made by either *Anochetus emarginatus* or *Paratrechina* sp. These species have a more elaborate and complex carton structure (J. Zegarra et al. unpubl. data). *Crematogaster* carton also differs from that found in the large nests of *Gnamptogenys ?tortuolosa*.

Cross section diameters of fine roots of *Anthurium gracile*, *Codonanthe calcarata*, *Philodendron deflexum*, *Epiphyllum phyllanthus*, and *Aechmea tillandsioides* were of two mean sizes: Type I (1.6 mm) and Type II (0.3 mm). Common anatomical features of the two root types are strong suberization of cell walls, particularly in the rhizodermis, and presence of lenticels and cork structures related to water and nutrient absorption. To investigate absorption capacity, the



FIGURES 2-5. Ant gardens. FIGURE 2: Small ant garden showing carton built around the roots of *Anthurium gracile*. FIGURE 3: *Philodendron deflexum* and *A. gracile*. FIGURE 4: *Aechmea tillandsioides* at bottom. FIGURE 5: Carton nest of *Crematogaster* cf. *limata parabiatica* and ?*Dolichoderus* sp.



FIGURES 6-9. Details of epiphyte roots and cyanobacteria. FIGURE 6: Transversal root section of *Philodendron deflexum* showing outer, dark ring of cyanobacteria (100×). FIGURE 7: Detail of cyanobacteria (400×). FIGURE 8: Slightly crushed cyanobacterial packet showing pruned root tip of *Epiphyllum phyllanthus* (100×). FIGURE 9: Cyanobacterial packet on tarsal claw of ant.

authors took measurements to determine the ratio between the outer zone (rhizodermis + cortex), hereafter referred to as A, and the stele zone, called B. A to B ratios were 2:1 and 4:1 for type I and 1:1 for type II. The best ratio is exhibited in *Anthurium gracile* (1:1), indicating that it had the most efficient root for water and nutrient absorption. A dark layer of cyanobacteria is shown around the roots in FIGURE 6, and detail of the cyanobacteria in FIGURE 7. Cyanobacterial masses surrounding the fine roots also were observed as pellets or tiny "packets," which wrapped root tips or single rhizodermal cells, forming round conglomerates. Some of these packets obtained from the nest interior are root "clippings" apparently pruned by ants during nest maintenance. Under the light microscope, rootlet tips are clearly seen cut at regular intervals, surrounded by a network of cyanobacteria (FIGURE 8). Cyanobacterial masses in the tarsal claws of a worker of *Crematogaster* cf. *l.*

parabiotica (FIGURE 9) suggest that they may be dispersed by ants. Preliminary elemental analysis (Electron Probe Microanalysis) shows that cyanobacteria contains 97.7% nitrogen (T. Mérida et al. unpubl. data).

DISCUSSION

The El Niño influence caused a pronounced contrast in precipitation during the 1997-1998 period, time of the authors' field trips to Surumoni. The previous year (1996), with a total rainfall of 3443.8 mm, was the rainiest year in the last 31 years; and the forest floor remained flooded for 5-6 weeks during June and July (J. Szarzynski pers. comm.). In contrast, 1997 was the driest year in the same period, with 2259 mm from January to November. The dry interval persisted through January and February 1998 (50 mm and 78 mm, respectively). These dramatic changes must have affected the microcli-

mate of the AGs and conditioned their suitability as nests for ant colonies. In November 1997, the authors found that most AGs occupied in March 1997 had been abandoned and were dry and highly deteriorated. Seven small nests, seemingly occupied only by *Crematogaster* cf. *l. parabiota*, had no brood. By January 1998, many AGs had fallen (J. Hernández pers. comm.). In September 1998, other ant species were found to be using many of the old surviving AGs as well as new ones. It appears that, at least in Surumoni and presumably mediated by climatic conditions, AGs are temporal nests for a variety of ant species. Ant colonies found in AGs could inhabit soil nests when drought and climatic factors make arboreal nests unsuitable for living; they then could recolonize existing AG nests when the soil water level increased. Other soil-living arthropod species, as well as small vertebrates, climb trees before the forest floor becomes flooded, probably being signaled by edaphic changes (Adis & Latif 1996).

AGs are located in greater abundance in the northern section of the study area (FIGURE 1), but most occur in the NE sector that exhibits more reflected sunlight. Light preferences by plants ultimately determine their occurrence in sunny locations and some authors have reported these preferences (Belin-Depoux et al. 1987, Davidson 1988, Yu 1994, Benzing 1996). Crane-access to AGs was fortuitously favorable in this environment.

AGs develop in two principal ways (Ule 1901, Wheeler 1921): from nest carton or the roots of an established epiphyte. The authors found in Surumoni that most AGs develop after carton is built around the roots of *Anthurium gracile* or other plants. *Anthurium gracile* is the most frequently found plant in the Surumoni AGs. Plant features may account for this dominance: 1) its external roots are green, holdfast, sclerified, and velamentous (Benzing 1996), and it affixes to the host trunk in the manner of clamps, hugging the tree branch (FIGURE 2). This secures the epiphyte against winds and rainstorms, which can be powerful in this region. 2) Inside the AG, the fine root system is massively associated with cyanobacteria that are free, nitrogen-fixing microorganisms (FIGURES 6–8). Symbiotically fixed nitrogen is rapidly utilized by other plant and animal species (Jones & Wilson 1978, Coxson & Nadkarni 1995). 3) The cortex to stele ratio equips the plant with optimal water and nutrient absorption capacity compared to other plants (T. Mérida et al. unpubl. data). The combination of photosynthetic and nitrogen-fixing capacities makes this symbiotic association of *A. gracile* and cyanobacteria a highly productive and efficient biological system

(Fay 1981). These features help make *A. gracile* a ubiquitous pioneering plant of Surumoni AGs.

In the AGs sampled in March, the authors only found brood of *Crematogaster* cf. *l. parabiota*. Since only 16 samples from 32 AGs were cored, the possibility of missing the brood of *Camponotus femoratus* cannot be excluded. In September 1998, the authors dissected a carton nest and found 39 queens of *Cr. cf. l. parabiota* with brood and one queen of *?Dolichoderus* sp. with few larvae. Thus, the authors conclude that “parabiota” species, such as *Ca. femoratus*, incorporate later into the development of the AG. Swain (1980) argued that the relationship, at least in relation to foraging, might be parasitic. Further studies on habitat and resource partitioning of these two ant species are needed. The large number of previously unreported ant species found in AGs in September 1998 again suggests that AGs might function as temporal nesting sites, a hypothesis to test in the future.

Furthermore, if AGs are refuges for ant brood, they are also reservoirs of superior nutrients for epiphytes. The major interactions in Surumoni AGs, in consequence, may be as shown in FIGURE 10. Opportunistic food-gatherers, the ants procure organic supplies (allochthonous material) for their larvae by collecting dead insects or extra-floral nectar, plant and fruit saps, arthropod exudates, food bodies, and seeds (Tobin 1995). Ant workers also disperse plant seeds and probably cyanobacterial cells. Epiphytes derive nutrients from ant organic refuse and nitrogen from cyanobacteria. The nest is strengthened by the plant’s external roots, which are interwoven into the carton. Cyanobacteria thrive on root exudates and may play a role in recycling carbon-rich refuse materials that fertilize the carton (Gibson & Jordan 1982).

Many factors conspire against AG survival in Surumoni, principally strong winds, heavy rains, and long drought periods. If an AG falls because a host tree or branch breaks, ants abandon it; however, opportunistic termites often occupy it temporally (J. Zegarra pers. obs.). Eventually, it is invaded by the roots of neighboring plants that form root mats (Wheeler 1921). In this manner, AGs play a nutrient role in rain forest dynamics. Additionally, Yanomami Amerindians use root mats as agricultural fertilizer in their shifting cultivation systems (T. Mérida pers. comm.).

Additional studies using regularly scheduled surveys of AGs are needed to help understand how the interiors of living nests are maintained, how AG ants migrate, how “parabiota” relationships are initiated, and how climatic conditions are correlated with nest habitability.

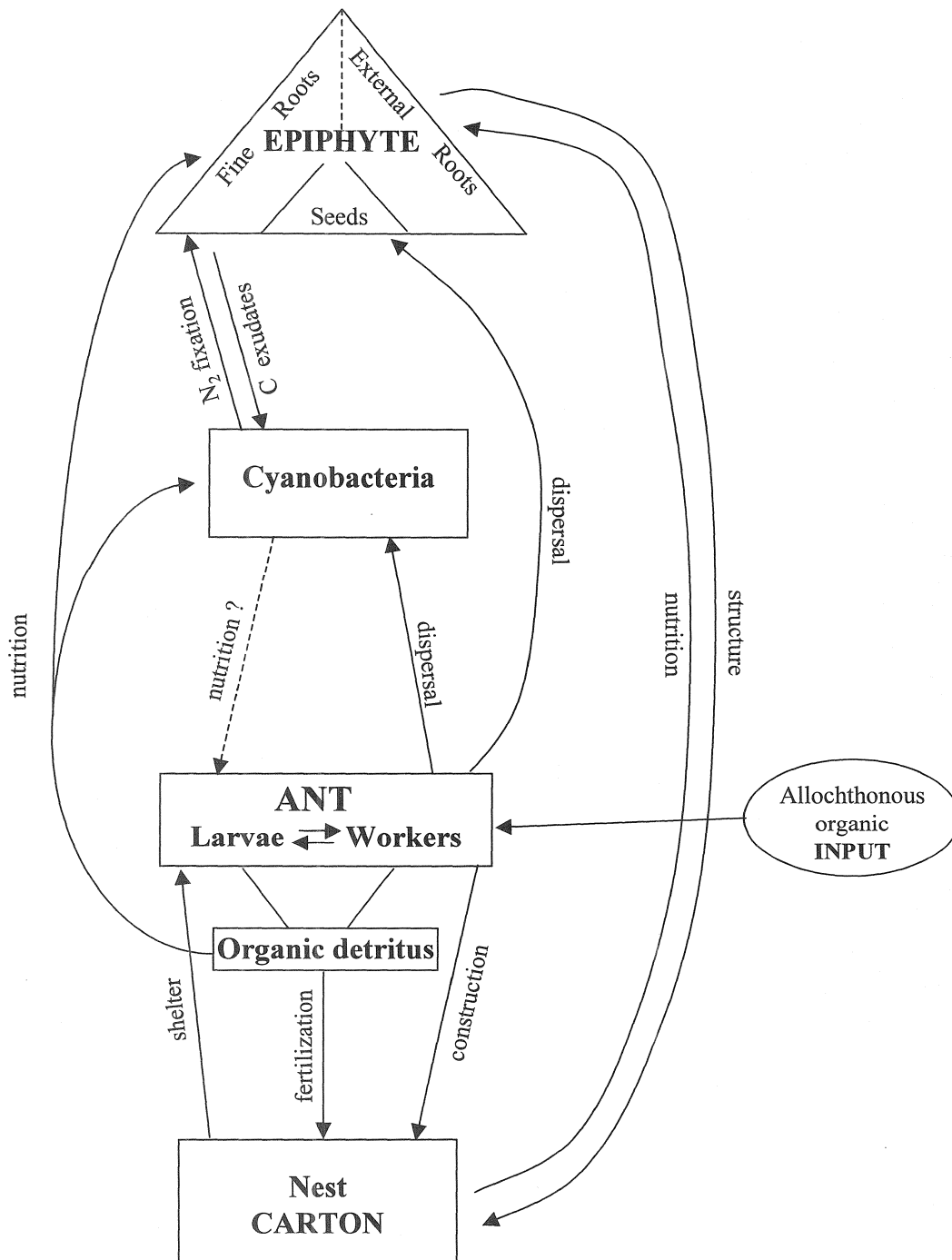


FIGURE 10. Diagram of interactions among major components of an ant garden.

ACKNOWLEDGMENTS

Pluviometric, temperature, and light data are from D. Anhof and Geog. J. Szarzynski (Geographisches Institut der Universität Mannheim) and J. Hernández (Universidad Central de Venezuela). Epiphyte species were identified by S. Engwald, J. Nieder, M. Klawun, and W. Barthlott (Botanisches Institut der Rheinischen Friedrich-Wilhelms Universität Bonn). Jacques Delabie (Centro de Pesquisas do Cacau, CEPLAC, Itabuna, Brazil) identified *Crematogaster* cf. *I. parabiatica* and *Camponotus femoratus*.

We thank OEAW for field and data support; Eder Peña for assistance with databases, analysis, and field support; Gustavo Palacios and Nancy Hernández for helping with most figures and graphics; Ismael Hernández for helpful comments; and especially Harold Heatwole for improving the manuscript. Funds were provided by CONICIT (S1-96000542) and Consejo de Desarrollo Científico y Humanístico of the Universidad Central de Venezuela (03.244.97).

LITERATURE CITED

- Adis, J. and M. Latif. 1996. Amazonian arthropods respond to El Niño. *Biotropica* 28: 403–408.
- Belin-Depoux, M., J.C. Roeland and C. Sarthou. 1987. Biological aspects of the plant-ant relationships in the rain forest: Ant-gardens in French Guiana. Pp. 369 in V. Labeyrie, G. Fabres and D. Lachaise, eds. *Insects-Plants*. Dr. W. Junk Publishers, Dordrecht.
- Benzing, D.H. 1996. Aerial roots and their environments. Pp. 875–894 in Y. Waisel, A. Eshel and U. Kafafi, eds. *Plant Roots: The Hidden Half*. Marcel Dekker, New York.
- Bolton, B. 1994. *Identification Guide to the Ant Genera of the World*. Harvard University Press, Cambridge.
- Coxson, D.S. and N.M. Nadkarni. 1995. Ecological roles of epiphytes in nutrient cycles of forest ecosystems. Pp. 495–543 in M.D. Lowman and N.M. Nadkarni, eds. *Forest Canopies*. Academic Press, San Diego.
- Davidson, D.W. 1988. Ecological studies of neotropical ant gardens. *Ecology* 69: 1138–1152.
- Davidson, D.W. and W.W. Epstein. 1989. Epiphytic association with ants. Pp. 200–233 in U. Lüttge, ed. *Vascular Plants as Epiphytes*. Springer-Verlag, Berlin.
- Dezzeo, N. and O. Huber. 1995. Tipos de bosques sobre el Cerro Duida, Guayana Venezolana. Pp. 149–158 in S.P. Churchill et al., eds. *Biodiversity and Conservation of Neotropical Montane Forests*. The New York Botanical Garden, New York.
- Fay, P. 1981. Photosynthetic micro-organisms. Pp. 1–29 in W.J. Broughton, ed. *Nitrogen Fixation*, Vol. I. Ecology. Oxford Scientific Publications, New York.
- Gibson, A.H. and D.C. Jordan. 1982. Ecophysiology of N₂-Fixing Systems. Pp. 301–314 in O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler, eds. *Physiological Plant Ecology*, Vol. III. Springer, New York.
- Jones, K. and R.E. Wilson. 1978. The fate of nitrogen fixed by a free-living blue-green algae. *Ecol. Bull.* 26: 158–163.
- Kleinfeldt, S.E. 1978. Ant-gardens: The interaction of *Codonanthe crassifolia* (Gesneriaceae) and *Crematogaster longispina* (Formicidae). *Ecology* 59: 449–456.
- Swain, R.B. 1980. Trophic competition among parasitoid ants. *Ins. Soc.* 27: 377–390.
- Tobin, J.E. 1995. Ecology and diversity of tropical forest canopy ants. Pp. 129–147 in M.D. Lowman and N.M. Nadkarni, eds. *Forest Canopies*. Academic Press, San Diego.
- Ule, E. 1901. Ameisengärten im Amazonas-Gebiet. *Engler's Botan. Jahrb.* 30: 45–51.
- 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: 222–226.