

THE VASCULAR EPIPHYTES ON A *VIROLA MICHELII* TREE (MYRISTICACEAE) IN FRENCH GUIANA

Martin Freiberg

Abteilung Spezielle Botanik, Universität Ulm, Albert-Einstein-Allee 11, D-89069 Ulm, Germany

Key words: biodiversity, canopy, French Guiana, Orchidaceae, tropical rain forest, vascular epiphytes, *Virola*.

While the number of vascular epiphyte species worldwide has been estimated rather precisely (Kress 1989), species numbers on a local scale vary tremendously. This is mainly due to the complex influences of environmental factors, extension of study area (Ibisch *et al.* 1996), and differences in sampling methods. Attempts have been made to reduce those methodological problems by introducing guidelines for sampling epiphyte diversity (Hietz & Wolf 1996). Moreover, only a thorough documentation of the conditions at the epiphytic growth site enables us to compare epiphyte ecology and distribution at different sites. The expression of a particular distribution pattern is influenced by geographical location and climate (latitude, height above sea level, seasonality, temperature, wind speed, sunshine, cloudiness, precipitation, etc.) (Sugden & Robins 1979, Ibisch *et al.* 1996), characters of the phorophyte (species, age, height, leaf phenology, crown diameter, bark roughness, bark pH, bark texture, etc.), and locations within the phorophyte (branch inclination, branch diameter, orientation, height above forest floor, distance to periphery, air humidity) (Johansson 1974, Wolf 1993, Freiberg 1996a). Additionally, the individual history of growth sites (diaspore dispersal and establishment, accumulation and decomposition of detritus, nutrient capital of humus, competition, interaction with animals), which includes stochastic components, influences epiphyte distribution patterns in the canopy and consequently affects epiphyte diversity. Despite the large number of factors influencing epiphyte growth, some species are randomly distributed within the canopy. Other species reveal certain patterns of site preferences, e.g. epiphytes growing only on trunks or twigs (Johansson 1974, Catling & Lefkovitch 1989), in spatial subdivisions

of the canopy (Johansson 1974, Kelly 1985, ter Steege & Cornelissen 1989), on branches of certain sizes (Catling *et al.* 1986), or on branches with a certain inclination, lateral position or distance from the crown center (Freiberg 1996a).

In this paper the epiphyte distribution of a completely sampled emergent phorophyte is presented. The patterns of some selected species will be discussed. Data on the phorophyte environment are provided to give a base for future comparison with epiphyte studies in other locations.

STUDY SITE AND METHODS

The investigated *Virola michelii* tree was located close to the Aratai Station in the Reserve Naturelle Des Nouragues, French Guiana, South America (45 m a.s.l., 3°59'24" N, 52°35'27" W). Average precipitation was between 3500 and 4000 mm per year. The average air temperature was 24.9°C, the minimum 20.8°C in December, the maximum 33.1°C in May. On average there was no arid month, but in dry years September and October may become arid (Cockle 1997).

The tree was at a distance of 120 m from the nearby Arataye river, which at this point was about 50 m wide. The tree grew on a slight slope of 20°–40° inclination, so that the base of the trunk was about 10 m above the level of the river. The tree's buttresses were 6 m high. Its diameter at 1.5 m, including the buttresses, was 3.2 m, the diameter above the buttresses was 75 cm. The first major ramifications were at 33 m, the maximum height was 52 m and the average crown diameter at its largest extension 20 m. Major branches emerged at a right angle from the trunk and the outer part of the branches some-

times hung down at an angle of -60° to the horizontal. The bark was not peeling, and whitish red exudates seeped out of injured parts.

The tree was climbed using modified single rope techniques described elsewhere (Perry 1978, Perry & Williams 1981). The whole tree was subdivided into 518 sample plots, each being a section of about 1 m of trunk or branch. All vascular epiphyte species from a sample plot were documented. Most species were determined using the "Guide to the vascular plants of Central French Guiana" (Mori *et al.* 1997), whose nomenclature was used, and with specimen comparison in the Herbarium of French Guiana in Cayenne (CAY). Specimens not flowering during the study period were cultivated and determined later.

RESULTS AND DISCUSSION

In total, 72 holoeiphytes and 2 hemieiphytes in 19 families were recorded on the tree (Fig. 1). This is rather in the upper range of what has been reported from Africa, e.g., 0–22 in West Africa (Johansson 1974), 12–45 in Zaire (Biedinger & Fischer 1996), 10–37 in Rwanda (Biedinger & Fischer 1996), but is about as high as in other studies in the Neotropics, e.g., 8–107 in Mexico (Valdivia 1977), 22–54 in the highlands and 9–43 in the Amazonian lowlands of Ecuador (Freiberg & Freiberg, unpubl. data), or at neighboring sites in French Guiana, e.g., 33–65 in Saül (Freiberg 1996a, Ek 1997) or 15–49 at Saut Pararé (Freiberg, unpubl. data).

Two-thirds of all species were found in less than 5% of the sample plots, and one third was sampled only once or twice (Fig. 1). The abundance distribution curve thus followed the logarithmic function which has been described for epiphytes elsewhere (Ek 1997). More than 50% of all species belong to the family Orchidaceae, followed by Araceae, Bromeliaceae and Polypodiaceae. The four most important families include more than 75% of all species, which is about the same proportion as recorded in other studies (e.g., Gentry & Dodson 1987, Ek 1997).

Maxillaria uncatata (Orchidaceae) was found in nearly 80% of all sample plots and was the most abundant species occurring in all parts of the canopy. A similar distribution for this species has been reported before on two trees near Saül, French Guiana (Freiberg 1996a) and from Guyana (ter Steege & Cornelissen 1989). The next most frequent species were *Maxillaria alba* (in 40% of all sample plots),

Tillandsia anceps (Bromeliaceae, 20%), *Pleurothallis pruinosa* (Orchidaceae, 20%), *Maxillaria conferta* (18%) and *Codonanthe crassifolia* (Gesneriaceae, 17%).

Two hemieiphytes (*Asplundia heteranthera*, Cyclanthaceae; *Philodendron rudgeanum*, Araceae) were found in the basal trunk section of the tree (Fig. 2). While *P. rudgeanum* extended up to the main part of the trunk, the other two species in this section had their highest frequency close to the inner part of the crown just below the first ramification (*Maxillaria rufescens* and *Tillandsia bulbosa*). On this part of the tree, rainwater from the main branches was channelled towards the trunk. It is assumed that bryophytes established successfully at this location because evaporation was reduced by the shade of the upper part of the crown. Those bryophytes then provided a favorable substrate for vascular epiphytes, which otherwise only occurred in the inner part of the crown.

While 57% of all canopy species had their highest abundance in the inner part of the crown, 35% were most frequent in the middle and 8% in the outer part of the crown. This corresponds to the epiphyte distribution found in other canopies (Johansson 1974, ter Steege & Cornelissen 1989, Freiberg 1996a). "Disjunct" distribution, e.g., presence in the inner and outer, but absence in the middle part of the crown, was not recorded. This supports the hypothesis of Johansson (1974) and findings in other studies (ter Steege & Cornelissen 1989) that epiphytes in the canopy are arranged along continuous environmental gradients. Exclusive presence in only one of the three parts was rare; most of the species were found in at least two neighboring crown parts. *Hecistopteris pumila*, *Philodendron melinonii*, *Satyria* sp. and *Ludovia lancifolia* were exclusively present in the inner part of the crown. The fruits of the three angiosperms were zoochorous. Bats defecate the tiny seeds of *L. lancifolia* during flight shortly before they land on the main trunk (Cockle 1997). Therefore this species was not dispersed to other parts of the crown, which explains its restricted distribution. The berries of *P. melinonii* and *Satyria* sp. were ornithochorous and it would be interesting to study whether the behavior of the dispersing birds supplies a similar explanation for the distribution of these plants in the canopy.

The miniature fern *Hecistopteris pumila* was also restricted to the basal part of the crown, where it grew mainly on the sides of the large branches. The highest

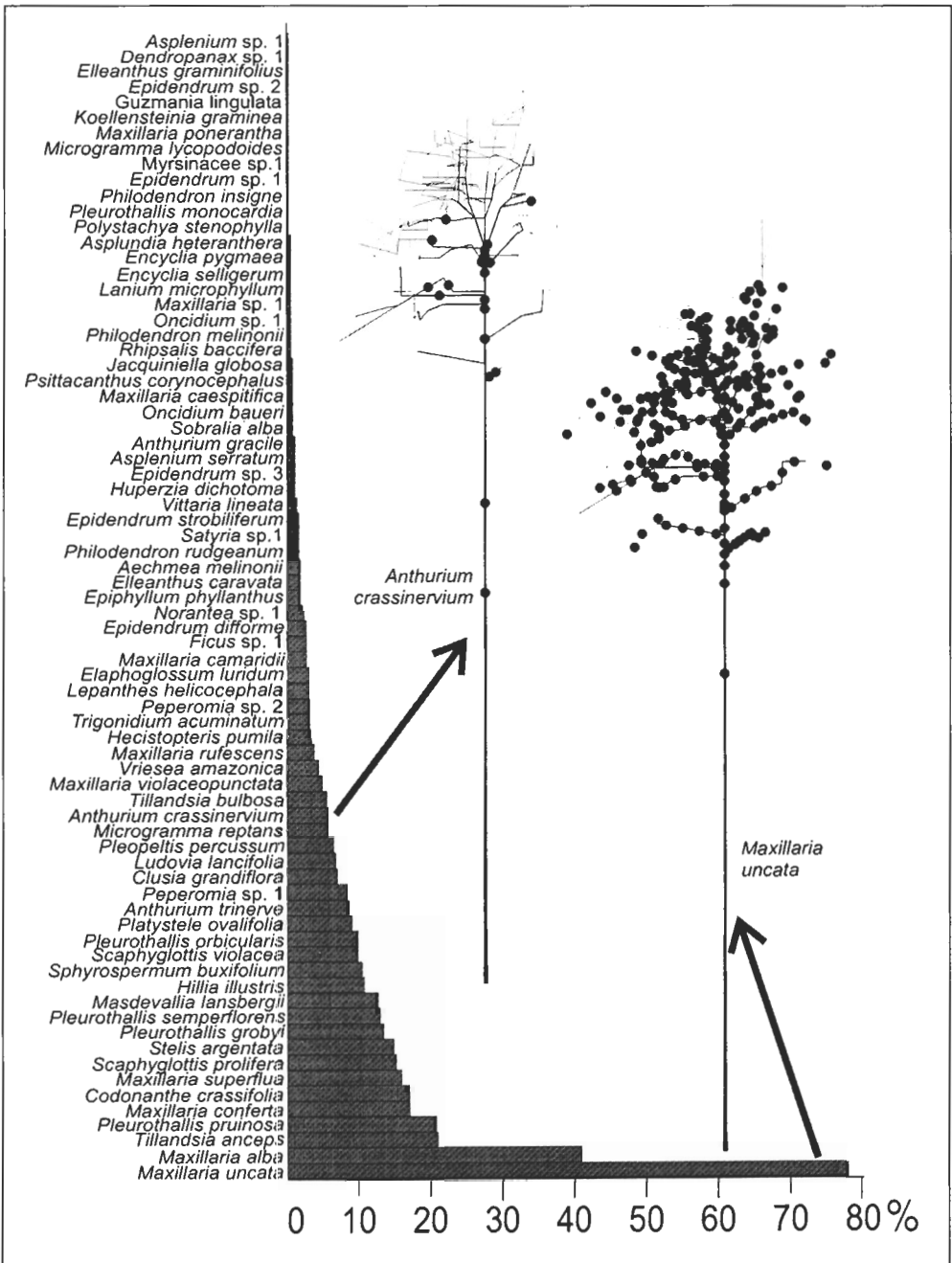


FIG. 1. The percentage of tree section of a total of 518 sections in which epiphyte species occur. The growth sites of *Anthurium crassinervium* and *Maxillaria uncata* in the tree are given as examples. The north-south-silhouette of the tree is shown. Each circle represents the presence of the species in a section. Height, width and diameter are drawn to equal scale; the total height of the tree is 52 m.

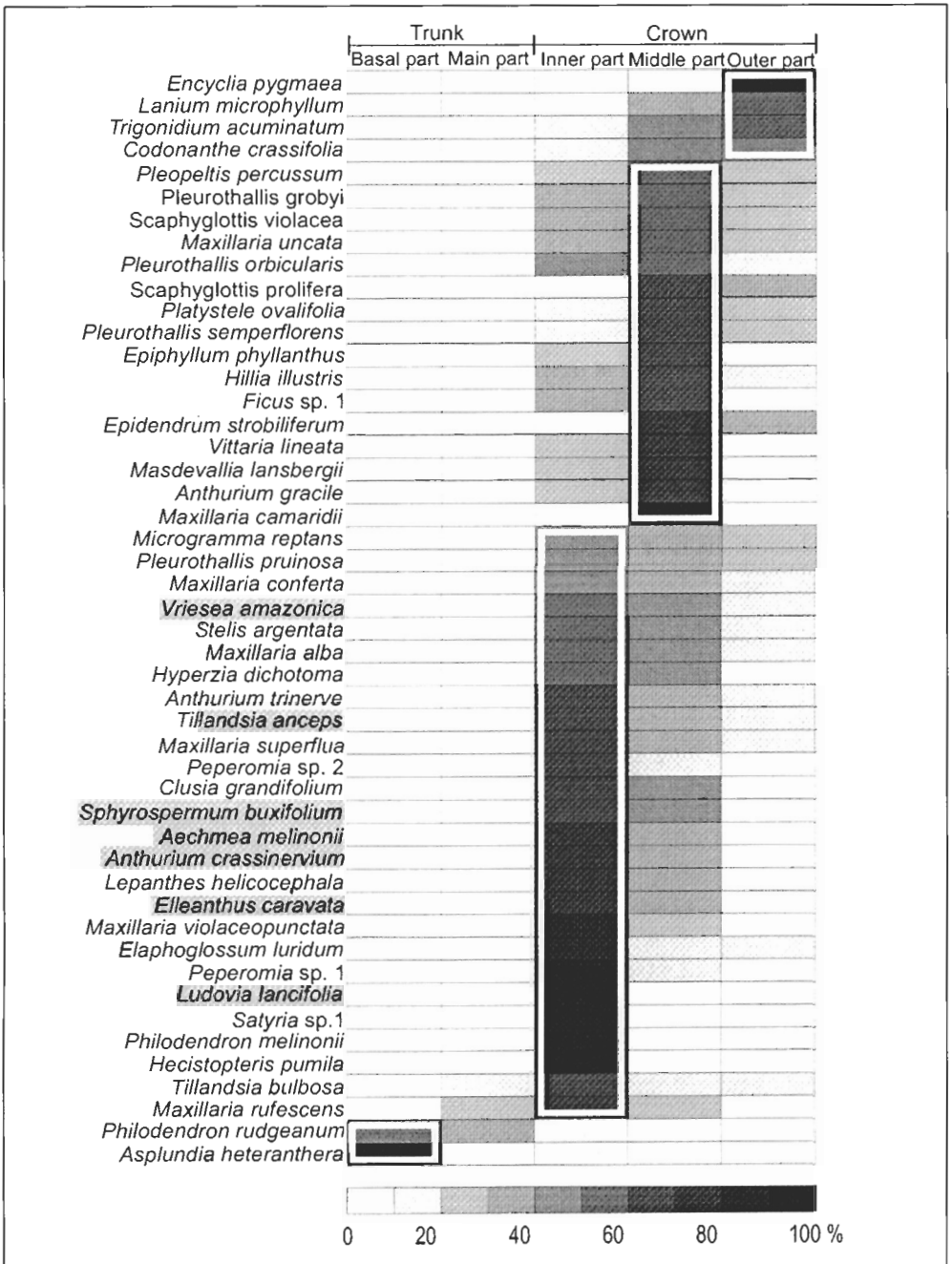


FIG. 2. Abundance of epiphyte species within the tree. The 5 classes of porophyte subdivision are adapted from Johansson (1974). The basal part of the trunk includes the first 3 m of the trunk. The crown is subdivided into three parts of equal branch length. Species are arranged according to their highest frequency (white rectangles). Only species that occur in at least 10 sample plots are listed.

accumulation of humus, bryophytes and epiphytes, as well as the thickest layer of litter, was measured just at these locations (Table 1). Presumably this fern would rather quickly be covered by litter if it grew on top of the branches. The sides of the branches, however, are safe in this respect but still profit from the accumulation of detritus and humus on top of the branches, which stores considerable quantities of water. This water reduces the daily drying out of the ramosphere through evaporation (Freiberg 1997), even on the sides of the branches, so that the poikilohydric *H. pumila* can exist there.

All epiphytes that collect detritus, either with leaf rosettes (*Anthurium crassinervium*, *Aechmea melinonii*, *Tillandsia anceps*, *Vriesea amazonica*), trash baskets (*Elleanthus caravata*, *Ludovia lancifolia*), or by other morphological means (*Sphyrospermum buxifolium*, *Maxillaria alba*), had their highest abundance in the inner part of the crown. It is not clear, however, whether the other species in this part of the phorophyte profited from the more favorable environment created by the detritus-collecting species, and settled after these had established themselves, or whether the non-collectors were remnants of earlier successional stages. Without exception, all species in the middle part of the crown were small epiphytes growing more or less attached to the bark. No shoots reached the aerosphere (Freiberg 1996b). In this crown section even *Ficus* sp. 1 and *Hillia illustris* were young saplings, while in the inner part of the crown they grew as large shrubs. Due to the dryness of the middle part they might not have been able to reach

the generative stage, but only information on a long time-scale would help to verify this hypothesis.

Maxillaria alba and *M. camaridii* are systematically closely related orchids and resemble each other vegetatively and generatively. However, the former species was creeping and its shoots covered large areas of the branch, and the latter was not. Therefore, in contrast to *M. camaridii* the growth form allowed *M. alba* to effectively collect detritus. This creates a microclimatically more stable environment compared to neighboring sites without detritus (Freiberg 1997). The comparatively greater independence from mesoclimatic conditions might be the advantage helping *M. alba* to grow in other parts of the crown. The restriction of *M. camaridii* to the middle part of the crown (Fig. 2) could be due to competition in the inner part and unfavorable conditions in the outer part. An evaluation of the reproductive success of both species would elucidate this hypothesis.

Twenty-two species found in this study also occurred in emergent canopy trees in Säul, 80 km southeast of Aratai (Freiberg 1996a). In Säul, all of these species were equally distributed in the canopy, while, with the exception of *Codonanthe crassifolia*, in Aratai they were more abundant in the inner and middle than in the outer part of the crown. The preference for the inner part of the crown over the outer could be due to less favorable conditions in the latter in Aratai. Climatic differences between Säul and Aratai might explain these differences, but the average rainfall in Säul (2400 mm/year, Mori *et al.* 1997) and in Aratai (3500–4000 mm/year) would suggest more

TABLE 1. Basic growth parameters of the phorophyte. The tree is subdivided according to Johansson (1974).

	Trunk		Crown			Total
	basal 3 m	rest	inner	middle	outer	
Number of registered species	4	18	55	57	34	72
Registered species [%]	5	25	76	79	47	100
Surface [m ²]	10	73	69	63	33	268
Average cover, vascular epiphytes [%]	<0,01	1,1	31,7	11,6	4,1	–
Average cover, bryophytes [%]	0,0	2,1	34,2	24,7	11,1	–
Accumulated humus volume [m ³]	0,0	0,003	0,25	0,06	0,01	0,323
Average thickness of humus layer [mm]	0,0	0,4	6,8	1,4	0,4	–
Average thickness of litter layer [mm]	0	0	4,8	0,8	0,1	–
Average diameter of branches [cm]	110	64	20	10	7	–
Total length of branch sections [m]	3	33	130	216	138	520
Average inclination of branches [°]	90	90	26	25	30	–

favorable conditions in Aratai. The influences of seasonality, humidity, and fog, however, are even more important in explaining epiphyte distribution, but those data are not available. A source of climatic differences between Saül and Aratai could be the actual growing sites of the phorophytes. The trees in Saül grew in a swampy area at the foot of a small hill, while the Aratai tree grew exposed on a slight slope. It is speculated that this exposition leads to less favorable epiphyte growth conditions in Aratai than in Saül, despite the higher annual rainfall. As mentioned above, *Codonanthe crassifolia* revealed a reversed pattern. It grew equally distributed, or was even more abundant, in the inner part of the crown in Saül, while it was more abundant in the periphery of the tree at Aratai. Ants feed on the fleshy funiculus and arillus of the seeds as well as on the extrafloral nectaries of *Codonanthe*, and carry the seeds into ant gardens (Moore 1973). The establishment of *Codonanthe* seedlings in ant gardens is therefore somewhat independent of environmental conditions. It needs to be shown whether ants disperse *Codonanthe* preferentially to "empty spaces" in the canopy, which corresponds to the outer part of the crown in Aratai.

CONCLUSIONS

The distribution of all vascular epiphytes was analyzed on an emergent canopy tree in French Guiana by mapping the occurrence of all species in 518 sample plots on the tree. Some distribution patterns were explained by morphological growth characters, mode of seed dispersal, or features of the canopy substrate. For a thorough understanding of epiphyte ecology, however, much more data from other trees and locations are desirable. Those data should be published together with detailed descriptions of the epiphyte and phorophyte environment (see Introduction). Although these data might not be relevant enough for publication, they would be important to other scientists who would like to use them as comparisons with results obtained at different sites.

ACKNOWLEDGMENTS

I thank Uwe Rascher (University of Darmstadt) for assistance in mapping the epiphytes on the tree, and Phillippe Gaucher of the Association Aratai for permission to work at the Aratai station as well as for friendly support. Dr. E. Freiberg and Dr. R. Lücking made valuable comments on the manuscript. Financial support was given by a DFG grant (FR 1150/3-1).

REFERENCES

- Biedinger, N., & E. Fischer. 1996. Epiphytic vegetation and ecology in Central African forests (Rwanda, Zaire). *Ecotropica* 2: 121–142.
- Catling, P.M., Brownell, V.R., & L.P. Lefkovich. 1986. Epiphytic orchids in a Belizean grapefruit orchard: distribution, colonization, and association. *Lindleyana* 1: 194–202.
- Catling, P.M., & L.P. Lefkovich. 1989. Associations of vascular epiphytes in a Guatemalan cloud forest. *Biotropica* 21: 35–40.
- Cockle, A. 1997. Modalités de dissémination et d'établissement de lianes de sous-bois (Cyclanthaceae et *Philodendron*) en forêt Guyanaise. Doctoral thesis, University of Paris 6, Paris.
- Ek, R.C. 1997. Botanical diversity in the tropical rain forest of Guyana. *Tropenbos-Guyana Series* 4: 1–237.
- Freiberg, M. 1996a. Spatial distribution of vascular epiphytes on three emergent canopy trees in French Guiana. *Biotropica* 28: 345–355.
- Freiberg, M. 1996b. Phenotype expression of epiphytic Gesneriaceae under different microclimatic conditions in Costa Rica. *Ecotropica* 2: 49–57.
- Freiberg, M. 1997. Spatial and temporal pattern of temperature and humidity of a tropical premontane rain forest tree in Costa Rica. *Selbyana* 18: 77–84.
- Gentry, A.H., & C.H. Dodson. 1987. Diversity and biogeography of neotropical vascular epiphytes. *Ann. Missouri Bot. Gard.* 74: 205–233.
- Hietz, P., & J.H.D. Wolf. 1996. Vascular epiphytes. Pp. 60–63 in Gradstein, S.R., Hietz, P., Lücking, R., Lücking, A., Sipman, J.M., Vester, H.F.M., Wolf, J.H.D., & E. Gardette (eds.). How to sample the epiphytic diversity of tropical rain forests. *Ecotropica* 2: 59–72.
- Ibisch, P.L., Boegner, A., Nieder, J., & W. Barthlott. 1996. How diverse are Neotropical epiphytes? An analysis based on the "Catalogue of the flowering plants and gymnosperms of Peru." *Ecotropica* 2: 13–28.
- Johansson, D.R. 1974. Ecology of vascular epiphytes in West African rain forest. *Acta Phytogeogr. Sueci.* 59: 1–136.
- Kelly, D.L. 1985. Epiphytes and climbers of a Jamaican rain forest: vertical distribution, life-forms and life histories. *J. Biogeography* 12: 223–241.
- Kress, W.J. 1989. The systematic distribution of vascular epiphytes. Pp. 234–261 in Lüttge, U. (ed.). *Vascular plants as epiphytes*. Berlin.
- Mori, S.A., Cremers, G., Gracie, C., de Granville, J.-J., Hoff, M., & J. D. Mitchell. 1997. Guide to the vascular plants of Central French Guiana. Part 1. Pteridophytes, Gymnosperms, and Monocotyledones. *Mem. New York Bot. Gard.* 76: 1–422.
- Moore, H.E. 1973. A synopsis of the genus *Codonanthe* (Gesneriaceae). *Baileya* 19: 4–33.
- Perry, D.R. 1978. A method of access into the crowns of emergent and canopy trees. *Biotropica* 10: 155–157.

- Perry, D.R., & J. Williams. 1981. The tropical rain forest canopy: a method providing total access. *Biotropica* 13: 283–285.
- Sugden, A.M., & R.J. Robins. 1979. Aspects of the ecology of vascular epiphytes in Colombian cloud forest, I. The distribution of the epiphytic flora. *Biotropica* 11: 173–188.
- ter Steege, H., & J.H.C. Cornelissen. 1989. Distribution and ecology of vascular epiphytes in lowland rain forest of Guyana. *Biotropica* 21: 331–339.
- Valdivia, P.E. 1977. Estudio botánico y ecológico de la región del Río Uxpanapa, Veracruz. No. 4: Las Epífitas. *Biotica* 2: 55–81.
- Wolf, J.H.D. 1993. Epiphyte communities in montane rain forest in the northern Andes. I. Lower montane communities. *Phytocoenologia* 22: 1–52.

Accepted 05 April 1999.