

## FLORISTIC COMPOSITION OF VASCULAR EPIPHYTES IN A NEOTROPICAL CLOUD FOREST, MONTEVERDE, COSTA RICA

STEPHEN W. INGRAM<sup>1,2</sup> AND KAREN FERRELL-INGRAM<sup>1</sup>

Marie Selby Botanical Gardens, 811 South Palm Ave., Sarasota, Florida 34236 USA

NALINI M. NADKARNI

MS Lab II, The Evergreen State College, Olympia, Washington 98505 USA

**ABSTRACT.** Neotropical montane forests are characterized partially by their great abundance and high diversity of epiphytes. We vouchered a species list of vascular epiphytes from a four-hectare lower montane site in Monteverde, Costa Rica, and compared the floristic composition of epiphytes to other epiphyte-rich communities. We collected at four different seasons using single-rope techniques to access the forest canopy. Collections included 56 pteridophyte species from 10 families, and 200 angiosperms from 27 families. Orchidaceae were approximately four times more speciose (92 species) than Bromeliaceae (22 species), the next most species-rich angiosperm family. Together, Orchidaceae, Pteridophyta, Bromeliaceae, Araceae, Ericaceae, Piperaceae, and Gesneriaceae accounted for 84% of the vascular epiphyte flora. The number of angiosperm families represented by epiphytes in the lower montane study site equals those present in all of Mexico, and exceeds the number for lowland sites in Costa Rica (La Selva) and Ecuador (Centinela and Río Palenque), and a montane site in Ecuador (Cajanuma).

### INTRODUCTION

Neotropical montane forests feature unusually abundant and diverse epiphytes (Grubb *et al.* 1963, Sugden & Robins 1979). In the most diverse tropical forests, epiphytes account for up to 35% of the total vascular plant flora and nearly half of the individual plants (Gentry & Dodson 1987a). Epiphyte biomass can exceed the foliar biomass of terrestrial herbs and shrubs in lower montane forests (Nadkarni 1984). Epiphyte floristic composition and contribution to total forest flora is known for only a very few forests. Documenting the epiphyte flora of epiphyte-rich tropical forests will enhance our knowledge of these communities and is a first step in understanding the biotic and abiotic conditions that affect epiphyte distribution (Gentry & Dodson 1987b).

The terrestrial flora of Monteverde is well-known relative to that of other tropical cloud forests (Haber 1991), but the epiphyte flora is incompletely known because of the difficulty of making epiphyte collections (Ingram & Lowman 1995). Many species, especially orchids in the Subtribe Pleurothallidinae, are very small, vegetatively similar, and easily overlooked. In this study we used several methods to collect epi-

phytes from standing tree canopies within an established study site. The local vascular epiphyte flora compiled here constitutes part of a long-term study of the ecological roles of epiphytes in nutrient cycling (e.g., Nadkarni & Matelson 1992, Vance & Nadkarni 1990). We compare the familial composition of the vascular epiphyte flora with other neotropical sites rich in epiphytes. The epiphytic bryophyte flora from this site is in preparation (S. R. Gradstein, D. Griffin, S. Ingram, K. Ferrell-Ingram & N. Nadkarni unpubl. data).

### STUDY SITE

The Monteverde Cloud Forest Reserve is located along the crest of the Cordillera de Tilarán in north central Costa Rica (10°18'N, 84°48'W). Our 4 ha study site is within primary "leeward cloud forest" (*sensu* Lawton & Dryer 1980), which is transitional between lower montane wet and lower montane rain forest, at 1500–1550 m elevation. The site lies on the Pacific (leeward) slope of the continental divide and receives about 2 500 mm of rain annually. Although Monteverde experiences a dry season from January to May, clouds and blowing mist may occur at any time of year. Trees (>10 cm diameter at breast height (dbh)) in the study site grow at a density of 559 individuals ha<sup>-1</sup> (Nadkarni *et al.* 1995) and stand 18–30 m tall. Epiphyte bryophytes and associated organic matter cloak the inner canopy branches of large trees to depths of up to 20 cm (Ingram & Nadkarni 1993).

<sup>1</sup> Research Associate, Marie Selby Botanical Gardens, 811 South Palm Avenue, Sarasota, FL 34236 USA.

<sup>2</sup> Current address for reprints and correspondence: Rt. 2 Box 352, Bishop, CA 93514.

## METHODS

Vascular epiphytes and hemiepiphytes were collected from lower tree trunks, recently fallen trees and branches, the upper trunks and inner canopies of standing trees, and outer canopy branches of standing trees. Upper trunks and inner canopies of canopy-level trees were climbed using single-rope techniques (Perry 1978, Nadkarni 1988). Whenever possible, data on host branch circumference, height above ground, and tree zone were recorded (APPENDIX 1). Plants that occurred on trunks less than 1 m above ground were ignored to avoid terrestrial plants that occasionally ascend several dm up tree trunks. Epiphytes were categorized according to which of five tree zones they occupied (modified from Johansson (1974)): 1-lower trunk 1–2 m; 2-upper trunk > 2 m; 3-inner third of canopy; 4-middle third of canopy; 5-outer third of canopy. Almost all of the mature host trees were identified to species.

Twenty branches from among eight trees cut and lowered for a related biomass project (July, 1992) were also sampled for epiphytes. Branch lengths were measured, divided into thirds, and one 20 cm long plot that encircled the branch was marked at the center of each branch zone. The number of vascular species was determined within each plot and compared on a surface area (circumference [cm] × 20 cm) basis. Epiphyte species richness was compared among inner, middle, and outer canopy branch segments. Plant collections were made during the dry/misty season (February, 1992), the late dry season (April, 1993), the early wet season (July, 1992), and the late wet season (November, 1992). Voucher specimens are deposited at the Herbario Nacional de Costa Rica (CR) and Marie Selby Botanical Gardens (SEL). Specimens of four species collected within the study site during a previous study (Ingram 1989) reside at the Herbarium of the University of California, Santa Barbara (UCSB). Nomenclature follows R. C. Moran (*Flora Costaricensis*, in prep.) for pteridophytes, Dahlgren *et al.* (1985) for monocotyledons, and Cronquist (1981) for dicotyledons.

## RESULTS

Two-hundred fifty-six vascular epiphyte species from 105 genera representing 27 angiosperm families and ten pteridophyte families occurred at the study site (APPENDIX 1). Pteridophytes accounted for 56 species, monocotyledons for 132 species, and dicotyledons for 68 species. At least 30 of these species constituted new records for Monteverde (Haber 1991). The epiphytes were collected from 31 different tree species belonging

to 15 families, in addition to hemiepiphytic *Blakea*, *Clusia*, *Ficus*, and *Oreopanax* species, the parasite *Psittacanthus sheryi*, a tree fern (*Cyathea* sp.), and many unidentified shrubs, lianas, and understory trees. Approximately 14% of our collections and 11% of the species were collected from the dominant tree of this forest, *Ocotea tonduzii*. One large, recently fallen *Bourreria costaricensis* tree hosted 24 different epiphytes.

The five angiosperm families with the most epiphytes at our study site are the five most species-rich angiosperm families worldwide (Kress 1986). Orchidaceae were approximately four times more abundant than Bromeliaceae, the second most species-rich angiosperm family (FIGURE 1). Orchidaceae, Pteridophyta, Bromeliaceae, Araceae, Ericaceae, Piperaceae, and Gesneriaceae together accounted for 84% of the local epiphyte flora. Twenty-one angiosperm families accounted for the remainder, none containing more than five species; 11 of those families contribute a single species. One family (Cunoniaceae) was represented by an “accidental epiphyte” (*sensu* Benzing 1990). The ten most species-rich genera all belong to the six most epiphyte-rich families (including ferns) from the site (TABLE 1). Four families of epiphytic angiosperms not found at other neotropical sites where epiphyte floras have been documented (TABLE 2) include Alzateaceae, Campanulaceae, Convolvulariaceae (Liliaceae), and Lentibulariaceae. Epiphytes from Monteverde in the Grossulariaceae and Scrophulariaceae are sometimes treated as Saxifragaceae and Bignoniaceae, respectively, in other floras.

Orchids comprised 36% of the vascular epiphyte flora, and 46% of the angiosperm epiphytes at our site. The Subtribe Pleurothallidinae alone accounted for more than half of the orchid species. One species of *Lepanthes* and one of *Pleurothallis* collected during this study were previously undescribed (C. Luer pers. comm.). Four of the ten most species-rich genera belong to Orchidaceae (TABLE 1).

Of the epiphytic angiosperms collected 79% are predominantly or completely herbaceous, and 21% are classified as woody shrubs or trees (APPENDIX 1). At least 12 of the species grow hemiepiphytically, either ascending trunks and losing their terrestrial connection (e.g., *Marcgravia brownii* and some Araceae), or germinating in the canopy and growing roots down to the ground (e.g., *Ilex* and *Clusia* spp.). We include these species as epiphytes because they spend at least part of their life cycle under similar ecological conditions as other epiphytes. All hemiepiphytes were observed and collected from upper trunks or inner canopies (APPENDIX 1), except for two *Clusia* species collected from fallen

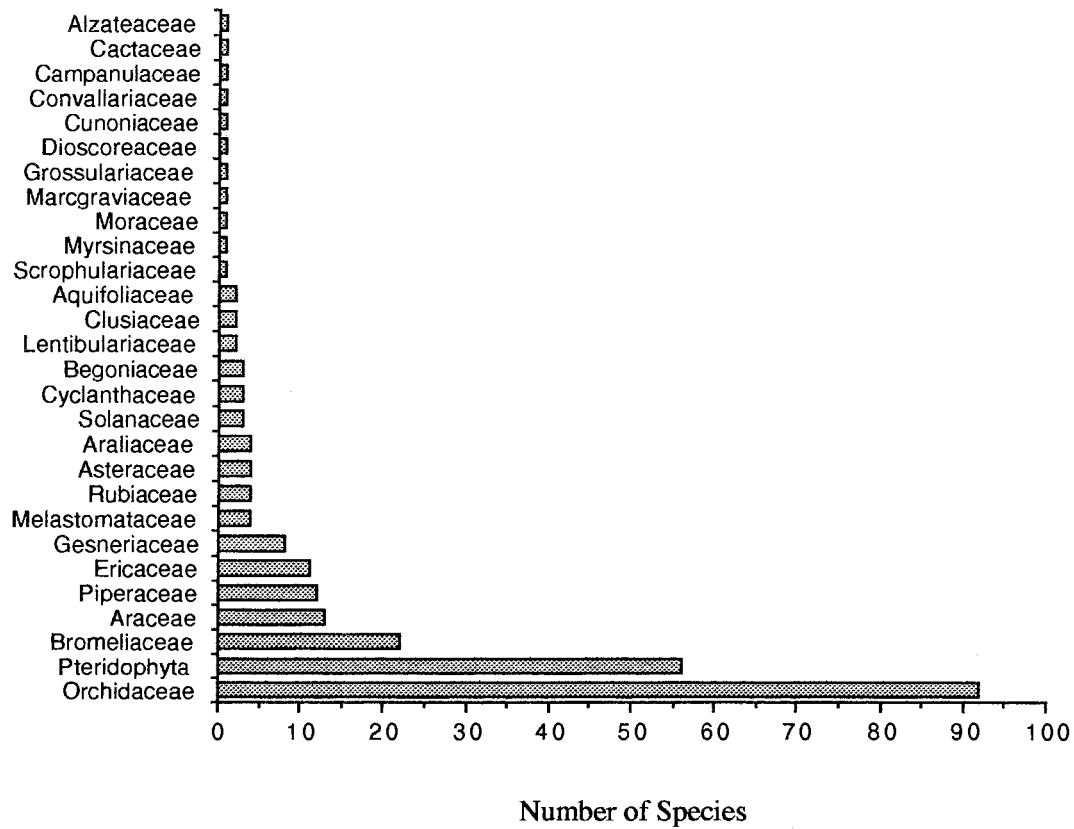


FIGURE 1. Familial composition of vascular epiphytes from 4 ha study site, Monteverde, Costa Rica.

branches that had probably been rooted in the inner or middle canopy of their host trees. Two or three additional species of *Clusia* probably also occur in the study site (W. Haber pers. comm.).

The branches sampled for species richness included 20 inner, 26 middle, and 50 outer canopy

TABLE 1. Number of species and the family of the ten most species-rich genera in the 4 ha study site, Monteverde, Costa Rica.

Family	Genus	Number of species
Orchidaceae	<i>Pleurothallis</i>	20
Lomariopsidaceae	<i>Elaphoglossum</i>	14
Piperaceae	<i>Peperomia</i>	12
Orchidaceae	<i>Epidendrum</i>	11
Orchidaceae	<i>Maxillaria</i>	10
Bromeliaceae	<i>Vriesea</i>	10
Araceae	<i>Anthurium</i>	9
Aspleniaceae	<i>Asplenium</i>	8
Orchidaceae	<i>Lepanthes</i>	7
Bromeliaceae	<i>Guzmania</i>	6

segments of varying lengths. There were no significant differences in species richness per branch area ( $\text{dm}^2$ ) among the inner, middle, and outer canopy zones (TABLE 3). There was a significantly greater species richness on inner canopy branches (Kruskal-Wallis test statistic,  $H=6.696$ ,  $P < 0.05$ ) because of the greater surface area (circumference) of the inner branches. Plots from inner, middle, and outer canopy zones averaged 3.15, 2.58, and 2.06 species/plot, respectively. No correlation between branch circumference and species richness per branch area was evident. This finding is consistent with angiosperm species richness comparisons obtained from the inner canopy of *Ocotea tonduzii* in this forest (Ingram & Nadkarni 1993).

The occurrence of epiphytes in specific tree zones listed in the Appendix indicates where they were collected, and not necessarily where they typically grow. Nevertheless, some observations of epiphyte occurrence are striking. Ferns, with the exception of Grammitidaceae and some *Elaphoglossum* species, usually grew in tree zones 1 and 2. Filmy ferns (Hymenophyllaceae) were

TABLE 2. Site characteristics and relative composition of the largest groups of the epiphyte flora from five neotropical forest sites.

Site	Río Palenque <sup>a</sup>	Centinela <sup>b</sup>	Cajanuma <sup>c</sup>	La Selva <sup>d</sup>	Monteverde <sup>e</sup>
Elevation (m)	150–220	600	2900	30–200	1500
Annual rainfall (mm)	2980	3000	2–4000	4000	2500
Area (ha)	167	ca. 100	0.0175	1500	4
No. of epiphytic angiosperm families	18	19	25*	19	27
No. Vascular Epiphyte Species	238	337	128	368	256
% Orchidaceae	34	39	37	30	36
% Pteridophyta	12	11	26	18	22
% Bromeliaceae	7.5	7	5	8	9
% Araceae	15	15	2	22	5
% Ericaceae	1	3	5.5	<1	4
% Piperaceae	8	6	2	2	5
% Gesneriaceae	5	5	<1	4	3

<sup>a</sup> Dodson & Gentry 1978 and Gentry & Dodson 1987b.

<sup>b</sup> Gentry & Dodson 1987b.

<sup>c</sup> Bøgh 1992.

<sup>d</sup> B. Hammel, pers. comm., in Gentry & Dodson 1987b.

<sup>e</sup> This study.

\* Does not include Loranthaceae.

never observed higher than 6 m on tree trunks. *Epidendrum subnutans* and *Xylobium elongatum*, both common orchids, occurred only on tree trunks below 4.5 m. Most pleurothallid orchids (except *Dracula* cf. *erythrochaete* and several *Pleurothallis* spp.) were collected in tree zones 3, 4 or 5, or from small branches recently fallen from the canopy. A Spearman rank correlation test revealed a significant positive correlation (0.521 with 360 df,  $p \leq 0.001$ ) between epiphyte height and host branch circumference.

### DISCUSSION

The predominance of Orchidaceae, Pteridophyta, Bromeliaceae, and Araceae at the study site is consistent with the ranking of these taxa with respect to their total number of epiphytic species (Kress 1986). The relatively large number

of epiphytic families, and the high species diversity of orchids are noteworthy characteristics of the epiphyte flora of this site.

The number of epiphytic angiosperm families that occur at our study site (27) is the same as that found in all of Mexico (Aguirre-Leon 1992). One reason for the high number of families represented by epiphytic members at Monteverde is the equability of the cloud forest canopy environment for arboreal plants. Accumulations of dead organic matter on branches make up more than half of the dry weight of canopy (non-tree) organic matter (Ingram & Nadkarni 1993), and provide moist, temperate substrate for epiphytes (Bohman *et al.* 1995). *Dioscorea lepida*, for example, which characteristically grows as a vine from a subterranean tuber, was observed growing (and flowering) from a small tuber embedded within the dead organic matter of a recently fallen tree canopy. The typically terrestrial Cunoniaceae was represented by a 60 cm tall *Weinmannia wercklei* juvenile growing in the canopy of *Pouteria reticulata* next to a canopy-level *W. wercklei* tree. The high number of dicotyledonous epiphyte families found in Costa Rica, compared with paleotropical regions, indicates a moderate, moist climate during the past 10–20 million years (Burger 1980).

The high diversity of orchids at the study site is due partly (similar to the high family diversity) to a propitious combination of biogeography and climate (see Raven & Axelrod 1974). Costa Rica probably has a greater density of orchid species than any other neotropical country due, in part,

TABLE 3. Branch dimensions, and epiphyte species richness ( $\text{dm}^{-2}$ ) from within-tree canopy zones, Monteverde, Costa Rica. Kruskal-Wallis test indicated no significant differences ( $H = 1.538$ ,  $P = 0.464$ ) in species richness per unit area among canopy zones.

Canopy zone	Mean branch circum. (cm) (s.d.)	Range (cm)	Mean species richness $\text{dm}^{-2}$ (s.d.)
Inner	28.7 (8.47)	12.3–48.7	0.58 (0.45)
Middle	20.7 (6.39)	10.1–29.6	0.68 (0.44)
Outer	14.3 (4.89)	4.7–28.9	0.82 (0.68)

to its great habitat diversity (R. Dressler pers. comm.).

TABLE 2 compares the floristic composition of vascular epiphytes from our site with those at four other neotropical locations (TABLE 2). Although the sampled areas differ in size, the relative composition of the epiphyte floras at the family level reveal interesting patterns. La Selva, Río Palenque, and Centinela have well-documented floras and large proportions of epiphytes (Hammel 1990, Gentry & Dodson 1987a, 1987b). The four groups richest in epiphyte species (orchids, ferns, aroids, and bromeliads) are the four best represented groups at all sites from Table 2 other than Cajanuma, Ecuador. A greater number of families with epiphytic members occurs at the two higher elevation sites (though 17 of 25 families at Cajanuma are listed as "accidental" epiphytes) (Bøgh 1992). Orchids and pteridophytes comprise approximately 60% of the epiphytes at Cajanuma, and at our study site. Similarly, pleurothallid orchids account for 17% of the epiphytes from Monteverde and 19% from Cajanuma (Bøgh 1992). Araceae contribute more species than the pteridophytes at the three low-elevation sites (TABLE 2). Ericaceae are more species-rich at the two montane sites, and Gesneriaceae are represented by more epiphytic species at the three lower elevation areas.

Bromeliad species comprise a slightly greater percentage of the epiphyte flora at Monteverde than elsewhere, though all sites exhibit a similar proportion of Bromeliaceae. Cajanuma has proportionally more ferns and ericads, groups that generally tend to be more speciose at higher elevations, but fewer Araceae, Gesneriaceae, or Piperaceae than other sites. Conversely, Centinela and La Selva support especially diverse Orchidaceae and Araceae, respectively, and fewer Ericaceae than other sites for which records exist. Aroid diversity may increase substantially with slight decreases in elevation, and is generally greatest in very wet lowland forests (Croat 1992).

La Selva supports a comparatively diverse flora of which 25% is comprised of epiphytes (including parasitic Loranthaceae and Viscaceae) (Hammel 1990). Nineteen angiosperm families and ferns make up the vascular epiphyte flora from La Selva. The greater number of epiphyte families at the Monteverde site (4 ha) than at La Selva (1,500 ha) is probably mainly due to the addition of the temperate floristic element of the Monteverde flora. Epiphytic species of Aquifoliaceae, Asteraceae, and several tropical montane families fail to penetrate lowland elevations in the neotropics.

If the numbers of epiphytic species and families are plotted against annual precipitation, following Gentry and Dodson (1987b), the species

diversity at Monteverde fits expectations, but the number of families is much higher (27 vs. ca. 15) than expected. Plant species richness generally increases with annual precipitation to about 4000 mm (Gentry 1988). Higher than expected epiphyte diversity at Monteverde is probably partly due to the greater amount of effective precipitation than measured with a standard rain gauge. The canopy at our study site intercepts 500-2000 mm of precipitation annually as mist and fog, in addition to 2500 mm of rainfall (Clark 1994).

Epiphyte diversity is generally greatest in wet aseasonal forests on fertile soils at "middle elevations" (Gentry & Dodson 1987b). In the Andes, plant species diversity decreases from 1500 to 3000 m, but little or no decrease in diversity is evident from lowland forests to around 1500 m (Gentry 1988). Our study indicates relatively high epiphyte diversity, especially at the family level, at a mid-elevation site in Costa Rica. Although the percentage of the Monteverde flora that grows epiphytically remains unknown, we expect it will exceed 25%. Whether epiphytes constitute as much as 35% of the flora, as at Centinela Ridge, Ecuador (Gentry & Dodson 1987b) before its deforestation, remains to be seen.

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APPENDIX 1. List of vascular epiphytes from Monteverde study site. All collection numbers cited are those of S. Ingram; voucher specimens listed are deposited at SEL unless otherwise indicated. Tree zones used are modified from Johansson (1974): 1—lower trunk 1–2 m; 2—upper trunk > 2 m; 3—inner third of canopy; 4—middle third of canopy; 5—outer third of canopy. Two values for height above ground or branch circumference represent the range of measurement taken from additional collections. Plant habit given is typical for plants collected, but may vary with location on host tree. “H” preceding growth form designates a hemiepiphyte.

Name/Author	Coll. #	Tree zones	Hgt. above ground (m)	Branch circum. (cm)	Plant habit	Growth form
<b>PTERIDOPHYTES</b>						
<b>Aspleniceae</b>						
<i>Asplenium cirrhatum</i> Rich. ex Willd.	(1314)	1	1	345	erect	fern
<i>A. cuspidatum</i> Lam.	(1333)	2	4.5	13	erect	fern
<i>A. dissectum</i> Sw.	(1293)	2–3	7–15	36, 85	caespitose	fern
<i>A. gomezianum</i> Lellinger	(1357)	1	2	80	caespitose	fern
<i>A. pululahuae</i> Sodirol	(1668)	1–2	1.5, 4	40, 56	caespitose	fern
<i>A. rosenstockianum</i> Brade	(1355)	1	1	18	caespitose	fern
<i>A. rutaceum</i> (Willd.) Mett.	(1342)	1	1	16, 20	erect	fern
<i>A. salicifolium</i> L.	(1736)	2	4	100	caespitose	fern
<b>Blechnaceae</b>						
<i>Blechnum fragile</i> (Liebm.) C. V. Morton & Lellinger	(1358)	1	2	63	scandent	fern
<b>Davalliaceae</b>						
<i>Nephrolepis pendula</i> (Raddi) J. Sm.	(1574)	2	15	100, 250	pendent	fern
<i>Oleandra bradei</i> H. Christ	(1286)	3	10	120	scandent	fern
<b>Grammitidaceae</b>						
<i>Ceradenia jungermannioides</i> (Kotszsch) L. E. Bishop	(1843)	2	12	180	caespitose	fern
<i>Cochlidium rostratum</i> (Hook.) Maxon ex. C. Chr.	(1532)	5	13	4	caespitose	fern
<i>C. serrulatum</i> (Sw.) L. E. Bishop	(1509)	5	12, 13	6, 7	caespitose	fern
<i>Lellingeria limula</i> (H. Christ) A. R. Sm. & R. C. Moran	(1324)	treefall		16	erect	fern
<i>Micropolypodium taenifolium</i> (Jenman) A. R. Sm.	(1478)	3–5	11, 15	15, 33	erect	fern
<i>Terpsichore alfarii</i> (Donn. Sm.) A. R. Sm.	(1757)	1	1, 1.5	30, 65	caespitose	fern
<i>T. taxifolia</i> (L.) A. R. Sm.	(1520)	3–5	3.5, 13	4, 20	caespitose	fern
<b>Hymenophyllaceae</b>						
<i>Hymenophyllum microcarpum</i> Desv.	(1315)	1	1, 2	36, 345	scandent	fern
<i>H. subrigidum</i> H. Christ	(1844)	2	12	180	scandent	fern

## APPENDIX 1. Continued.

Name/Author	Coll. #	Tree zones	Hgt. above ground (m)	Branch circum. (cm)	Plant habit	Growth form
<i>Trichomanes capillaceum</i> L.	(1345)	1-2	1, 3.5	34	scandent	fern
<i>T. diaphanum</i> H.B.K.	(1316)	1	1.5	20	scandent	fern
<i>T. krausii</i> Hook. & Grev.	(1356)	1	1.5	23	scandent	fern
<i>T. ludovicinum</i> Rosenst.	(1755)	2	6	35	scandent	fern
<i>T. radicans</i> Sw.	(1319)	1	1.5	13	scandent	fern
Lomariopsidaceae						
<i>Elaphoglossum ambiguum</i> (Mett. ex H. Christ) Alston	(1544)	1	1.5	34	erect	fern
<i>E. atrobarbatum</i> Mickel	(1322)	branchfall		25	erect	fern
<i>E. auricomum</i> (Klotzsch) T. Moore	(1458)	5	15.3	15	erect	fern
<i>E. auripilum</i> H. Christ	(1857)	3	13	80	pendent	fern
<i>E. erinaceum</i> (Fée) Hook.	(1472)	1	2	185	erect	fern
<i>E. guatemalense</i> (Klotzsch) T. Moore	(1503)	4	12	35	erect	fern
<i>E. lanceiforme</i> Mickel	(1746)	branchfall		12	erect	fern
<i>E. latifolium</i> (Sw.) J. Sm.	(1530)	1, 3	1, 13	29, 59	erect	fern
<i>E. lingua</i> Brack.	(1491)	3	11, 15	37	erect	fern
<i>E. lonchophyllum</i> (Fée) Moore	(1582)	1	1	19	erect	fern
<i>E. pallidum</i> (Baker) C. Chr.	(1557)	2-3	11-12	90, 120	pendent	fern
<i>E. palmense</i> H. Christ	(1825)	5	15.3	8, 31	erect	fern
<i>E. peltatum</i> (Sw.) Urb.	(1455)	1, 5	1, 15.3	10	scandent	fern
<i>E. sherringii</i> (Baker) C. Chr.	(1308)	branchfall		6, 60	erect	fern
<i>Lomariopsis maxonii</i> (Underw.) Holttum	(1849)	1-2	1-5	8, 19	scandent	fern
Lycopodiaceae						
<i>Huperzia dichaeoides</i> (Maxon) Holub	(1700)	3	11	13	pendent	fern
<i>H. filiformis</i> (Sw.) H. Christ	(1271)	fallen epiphyte			pendent	fern
Ophioglossaceae						
<i>Ophioglossum palmatum</i> L.	(1588)	3	16	320	erect	fern
Polypodiaceae						
<i>Campyloneurum angustifolium</i> (Sw.) Fée	(1361)	2, branchfall	9.5	70, 115	erect	fern
<i>C. falcoideum</i> (Kuhn ex Hieron.) M. Meyer ex Lellinger	(1672)	2, branchfall	14	16, 250	scandent	fern
<i>C. sphenodes</i> (Kunze ex Klotzsch) Fée	(1296)	1-2	1, 10	20, 486	scandent	fern
<i>Niphidium crassifolium</i> (L.) Lellinger	(1534)	treefall			erect	fern
<i>Pleopeltis fructuosa</i> (Maxon & Weath. in Weath.) Lellinger	(1811)	1, 5	2, branchfall	3, 43	scandent	fern



Name/Author	Coll. #	Tree zones	Hgt. above ground (m)	Branch circum. (cm)	Plant habit	Growth form
<i>P. macrocarpa</i> (Bory ex Willd.) Kaulf. var. <i>complanata</i> (Weath.) Lellinger	(1518c)	1	2	5	scandent	fern
<i>Polypodium fraxinifolium</i> Jacq.	(1318)	1-4	1.5, 15	24, 60	scandent	fern
<i>P. furfuraceum</i> Schldt. & Cham.	(1671)	branchfall		22	erect	fern
<i>P. myriolepis</i> H. Christ	(1578)	branchfall		51	erect	fern
<i>P. ptilorhizon</i> H. Christ	(1280)	3, 4, treefall	8, 15	10, 60	scandent	fern
Vittariaceae						
<i>Antrophyum chlorosporum</i> Mickel & Beitel	(1791)	1	1	5	caespitose	fern
<i>A. lineatum</i> (Sw.) Kaulf.	(1278)	2	7.3, 9.5	115, 120	pendent	fern
<i>Vittaria lineata</i> (L.) Sm.	(1344)	2	17	80	pendent	fern
ANGIOSPERMS						
Alzateaceae						
<i>Alzatea verticillata</i> Ruiz Lopez & Pavon	(1827)	3	15	80	erect	H treelet
Aquifoliaceae						
<i>Ilex hemiepiphytica</i> Hahn (ined.)	(1713)	2-3	10-17	80, 300	erect	H treelet
<i>I. vulcanicola</i> Standley	(1839)	2	8	200	erect	H treelet
Araliaceae						
<i>Oreopanax capitatus</i> (Jacq.) Decne. & Planchon	(1867)	2	treefall	140	erect	H treelet
<i>Oreopanax oerstedianus</i> Marchal	(1794)	2	7-11	200, treefall	erect	H treelet
<i>Schefflera rodrigueziana</i> Frodin ex M. J. Cannon & Cannon	(1871)	3	13	250	erect	H tree
<i>S. robusta</i> (A. C. Smith) A. C. Smith	(1569)	3	15	65, 90	scandent	treelet
Araceae						
<i>Anthurium davidsoniae</i> Standley	(1731)	1	1-1.3	10, 12	erect	herb
<i>A. friedrichsthali</i> Schott	(1339)	2, 3, 4	10, 12	6, 63	pendent	herb
<i>A. microspadix</i> Schott	(1330)	1	1, 2	10, 61	scandent	herb
<i>A. monteverdense</i> Croat & R. A. Baker	(1551)	2-3	9.9, 15	80, 205	erect	herb
<i>A. obtusilobum</i> Schott	(1332)	1, 2	2, 4	38, 160	erect	herb
<i>A. pittieri</i> Engl.	(1581)	1	2	8	erect	herb
<i>A. protensum</i> Schott	(1714)	2	12	45, 150	erect	herb
<i>A. ramonense</i> Engl. & K. Kr.	(1795)	2	4	50	erect	herb
<i>A. scandens</i> (Aublet) Engl. ssp. <i>pusillum</i> Sheffer	(1470)	2-5	2, 16	5, 400	scandent	herb
<i>Monstera dissecta</i> (Schott) Croat & Grayum	(1826)	2	5	130	scandent	H herb

## APPENDIX 1. Continued.

Name/Author	Coll. #	Tree zones	Hgt. above ground (m)	Branch circum. (cm)	Plant habit	Growth form
<i>Philodendron wilburi</i> Croat & Grayum	(1734)	2	8	200	scandent	herb
<i>Stenospermation sessile</i> Engl.	(1262)	3	12	20, 130	erect	herb
<i>Syngonium glaucopetiolatum</i>	(1553)	2	11.5	150	scandent	herb
<b>Asteraceae</b>						
<i>Neomirandea parasitica</i> (Klatt) R. King & H. Robinson	(1351)	3	12.2	12, 60	erect	herb
<i>Pentacalia candelariae</i> (Benth. ex Oerst.) H. Robinson	(1817)	branchfall		70	pendent	shrub
<i>P. streptothamnus</i> (Greenman) H. Robinson	(1848)	3	4	15	pendent	herb
<i>Sinclairia polyantha</i> (Klatt) Rydb.	(242-4-4/UCSB)	3			scandent	shrub
<b>Begoniaceae</b>						
<i>Begonia glabra</i> Aubl.	(1833)	1	2	15	scandent	herb
<i>B. heydei</i> C.DC.	(1667)	1, 2, 3	1, 12.6	4, 50	erect	herb
<i>B. strigillosa</i> A. Dietr.	(1676)	1, 3	1.5, 10	20, 190	erect	herb
<b>Bromeliaceae</b>						
<i>Catopsis nitida</i> (Hook.) Griseb.	(264/UCSB)	branchfall			erect	herb
<i>Guzmania angustifolia</i> (Baker) Wittm.	(1294)	1-4	1, 17	20, 39	erect	herb
<i>G. compacta</i> Mez	(1533)	1, 2, 3	1.7, 19	7, 30	erect	herb
<i>G. coriostachya</i> (Griseb.) Mez	(1524)	branchfall		60	erect	herb
<i>G. nicaraguensis</i> Mez & C. Baker	(1812)	branchfall		2, 6	erect	herb
<i>G. plicatifolia</i> L. B. Sm.	(1340)	2	15, 16	120, 200	erect	herb
<i>G. stenostachya</i> L. B. Sm.	(1321)	1	1	8	erect	herb
<i>Pitcairnia atrorubens</i> (Beer) Baker	(1679)	1	2.5	ca. 500	erect	herb
<i>P. brittoniana</i> Mez	(1317)	1, 2	2.5, 3	28, 60	scandent	herb
<i>Tillandsia adpressa</i> Andre var. <i>tonduziana</i> (Mez) L. B. sm.	(1754)	treefall		22	clumping	herb
<i>T. excelsa</i> Griseb.	(1855)	3	12	15	erect	herb
<i>T. insignis</i> (Mez) L. B. Sm. & Pittendr.	(1694)	3	15	7, 67	erect	herb
<i>Vriesea comata</i> (Mez & Wercklé) L. B. Sm. & Pittendr.	(s.n.)	no data			erect	herb
<i>V. graminifolia</i> Mez & Wercklé	(1737)	branchfall			erect	herb
<i>V. hygrometrica</i> (André) L. B. Sm. & Pittendr.	(1490)	5	11, 15	8, 16	erect	herb
<i>V. notata</i> L. B. Sm. & Pittendr.	(1305)	branchfall		13	erect	herb
<i>V. pedicellata</i> (Mez & Wercklé) L. B. Smith & Pittendr.	(1325)	1, branchfall	1	24, 70	erect	herb

Name/Author	Coll. #	Tree zones	Hgt. above ground (m)	Branch circum. (cm)	Plant habit	Growth form
<i>V. stenophylla</i> (Mez & Wercklé)						
L. B. Smith & Pittendr.	(1323)	treefall		11	erect	herb
<i>V. tonduziana</i> L. B. Sm.	(1701)	2, treefall	16	2, 150	erect	herb
<i>V. umbrosa</i> L. B. Sm.	(1845)	3	10	40	erect	herb
<i>V. viridiflora</i> (Regal) Wittm. ex Mez	(1539)	3, 5	15	14, 60	erect	herb
<i>V. vittata</i> (Mez & Wercklé)						
L. B. Sm. & Pittendr.	(1830)	3, branchfall	12	15, 90	erect	herb
Cactaceae						
<i>Epiphyllum</i> cf. <i>lepidocarpum</i> (Weber)						
Britton & Rose	(1602)	2, 3	10, 15	20, ca. 600	pendent	herb
Campanulaceae						
<i>Burmeistera microphylla</i> J. D. Smith	(1741)	3, branchfall	14	25, 28	erect	herb
Clusiaceae						
<i>Clusia stenophylla</i> Standley	(1265)	branchfall			erect	H treelet
<i>Clusia</i> sp. A.	(1801)	branchfall		210	erect	H treelet
Convallariaceae						
<i>Maianthemum monteverdense</i> LaFr.	(1526)	2, treefall	15	65, ca. 600	arching	herb
Cunoniaceae						
<i>Weinmannia wercklei</i> Standley	(1854)	3	12	140	erect	shrub
Cyclanthaceae						
<i>Asplundia microphylla</i> (Oersted) Harling	(1820)	2	6.5	230	scandent	herb
<i>A. vagans</i> Harling	(1725)	2	4	35	scandent	herb
<i>Sphaeradenia irazuensis</i> (Cuf.) Harling	(1802)	3, branchfall	9	15, 20	erect	herb
Dioscoreaceae						
<i>Dioscorea lepida</i> C. Morton	(1298)	3, branchfall	10	100	vining	herb
Ericaceae						
<i>Cavendishia bracteata</i> (R. & P. ex J. St.-Hill) Hoer.	(1283)	3	12	80	erect	shrub
<i>C. capitulata</i> J. D. Smith	(1688)	branchfall		63	erect	shrub
<i>C. complectens</i> Hemsley ssp. <i>complectens</i>	(1660)	2	14	15	erect	shrub
<i>C. melastomoides</i> (Klotzsch) Niedenzu						
var. <i>albiflora</i> Luteyn	(1496)	treefall			erect	shrub
<i>Disterigma humboldtii</i> (Klotzsch) Niedenzu	(1452)	2-5	11, 16.5	7, 140	scandent	shrub

## APPENDIX 1. Continued.

Name/Author	Coll. #	Tree zones	Hgt. above ground (m)	Branch circum. (cm)	Plant habit	Growth form
<i>Gaultheria gracilis</i> Small	(1289)	3	12	75	erect	shrub
<i>Psammisia ramiflora</i> Klotzsch	(1724)	3	4	40	erect	shrub
<i>Satyria warszewiczii</i> Klotzsch	(1834)	2	5	35	arching	shrub
<i>Sphyraspermum buxifolium</i> Poeppig. & Endl.	(1492)	4, 5	12.7, 15	9, 30	erect	shrub
<i>S. cordifolium</i> Benth.	(1454)	5	12.5, 15.3	8, 15	erect	shrub
<i>Vaccinium poasanum</i> J. D. Smith	(1837)	4	treefall	150	erect	shrub
Gesneriaceae						
<i>Capanea grandiflora</i> (Kunth) Decne. ex Planchon	(1808)	1	2	20	arching	herb
<i>Columnea anisophylla</i> DC.	(1348)	1	2.5, 2.3	88, 48	erect	shrub
<i>C. consanguinea</i> Hanst.	(1705)	1	1.5	20	arching	herb
<i>C. lepidocaula</i> Hanst.	(1310)	3, treefall	14	40	arching	herb
<i>C. microcalyx</i> Hanst.	(1302)	2, 3	4, 22	305	pendent	herb
<i>C. verecunda</i> C. Morton	(1683)	2	22	19, 300	erect	shrub
<i>Drymonia conchocalyx</i> Hanst.	(1655)	2	2	30	arching	shrub
<i>D. rubra</i> C. Morton	(1304)	2, 3	4, 10	53, 15	arching	shrub
Grossulariaceae						
<i>Phyllonoma</i> cf. <i>tenuidens</i> Pittier	(235/UCSB)	2	treefall		erect	shrub
Lentibulariaceae						
<i>Utricularia jamesoniana</i> Oliver	(1756)	5	treefall	6	erect	herb
<i>U. praetermissa</i> P. Taylor	(1528)	4	12.6	18	erect	herb
Marcgraviaceae						
<i>Marcgravia brownei</i> (Triana & Planchon) Krug & Urban	(1690)	treefall		95	scandent	H shrub
Melastomataceae						
<i>Blakea anomala</i> J. D. Smith	(1733)	2, 3	7, 15	150	erect	shrub
<i>B. tuberculata</i> J. D. Smith	(1684)	2	16	ca. 600	erect	H treelet
<i>Miconia grandidentata</i> Almeda	(1822)	3	14	200	erect	shrub
<i>Topobea brenesii</i> Standley	(1805)	3	13	340	erect	H tree
Moraceae						
<i>Ficus crassiuscula</i> Warburg ex. Standley	(1840)	2	4-7	215	scandent	H shrub
Myrsinaceae						
<i>Cybianthus costaricanus</i> Hemsley	(1531)	3	13	35, 250	erect	shrub

Name/Author	Coll. #	Tree zones	Hgt. above ground (m)	Branch circum. (cm)	Plant habit	Growth form
Orchidaceae						
<i>Acostaea costaricensis</i> Schltr.	(1336)	5	12, 19	1, 6	caespitose	herb
<i>Ada chlorops</i> (Endres & Rchb.f.) N. Williams	(1735)	branchfall		13	erect	herb
<i>Barbosella prorepens</i>	(1677)	3	22	8	caespitose	herb
<i>Brachionidium pusillum</i> Ames & C. Schweinf.	(1556)	branchfall		95	scandent	herb
<i>Campylocentrum longicalcaratum</i> Ames & C. Schweinf.	(1501)	5	12	9	erect	herb
<i>Cochleanthes picta</i> (Rchb.f.) Garay	(1695)	1	1.3, 2	ca. 500	erect	herb
<i>Cryptocentrum calcaratum</i> (Schltr.) Schltr.	(1459)	branchfall		4, 55	erect	herb
<i>Cyclopogon</i> aff. <i>elatus</i> (Sw.) Schldl.	(1740)	branchfall		25	erect	herb
<i>C. prasophyllum</i> (Rchb.f.) Schltr.	(1274)	branchfall		8	erect	herb
<i>Dichaea cryptarrhena</i> Rchb.f. ex Kraenzl.	(1675)	1, 2	1, 10	20, 55	pendent	herb
<i>D. lankesteri</i> Ames	(1846)	1	2.5	75	pendent	herb
<i>D. cf. oxyglossa</i> Schltr.	(1592)	1	2.3	50	pendent	herb
<i>Dracula</i> cf. <i>erythrochaete</i> (Rchb.f.) Luer	(1836)	3	12	85	erect	herb
<i>Elleanthus</i> cf. <i>tonduzii</i> Schltr.	(1798)	branchfall		27	erect	herb
<i>Encyclia pseudopygmaea</i> (Finet) Dressler & Pollard	(1658)	3	22	100, 20	scandent	herb
<i>Epidendrum</i> cf. <i>albertii</i> Schltr.	(1593)	2	3.5	25	erect	herb
<i>E. anoglossum</i> Schltr.	(1476)	5	15, 19	5, 8	erect	herb
<i>E. laucheanum</i> Rolfe ex Bonh.	(1868)	branchfall		14	arching	herb
<i>E. myodes</i> Rchb.f.	(1752)	treefall		45	arching	herb
<i>E. palmense</i> Ames	(1572)	branchfall		15	erect	herb
<i>E. ramonianum</i> Schltr.	(1477)	4, 5	15, 19	12, 17	erect	shrub
<i>E. sancti-ramoni</i> Kraenzl.	(1652)	treefall		78	erect	herb
<i>E. selaginella</i> Schltr.	(1483)	5	15	3	erect	herb
<i>E. subnutans</i> Ames & C. Schweinf.	(1545)	1	1	85	arching	herb
<i>E. summerhayesii</i> Hágsater	(1495)	treefall			erect	herb
<i>Epidendrum</i> sp. A	(1693)	3	7, 13	15, 100	erect	herb
<i>Erythroides killipii</i> Ames	(1335)	treefall		110	erect	herb
<i>Eurystyles</i> cf. <i>auriculata</i> Schltr.	(1276)	branchfall	12	3.5, 75	erect	herb
<i>Lepanthes acostae</i> Schltr.	(1561)	treefall		200	caespitose	herb
<i>L. confusa</i> C. Schweinf.	(1529)	5	12.6		caespitose	herb
<i>L. ferrelliae</i> Luer	(1570)	branchfall		10	caespitose	herb
<i>L. jimenezii</i> Schltr.	(1467)	5 (treefall)		6, 12	caespitose	herb
<i>L. mentosa</i> Luer	(1312)	treefall		15, 120	caespitose	herb

## APPENDIX 1. Continued.

Name/Author	Coll. #	Tree zones	Hgt. above ground (m)	Branch circum. (cm)	Plant habit	Growth form
<i>L. minutilabia</i> Ames	(1792)	branchfall		3	caespitose	herb
<i>L. pygmaea</i> Luer	(1297)	branchfall		4	caespitose	herb
<i>Lockhartia hercodonta</i> Rchb.f. ex Kraenzl.	(1793)	branchfall		8	arching	herb
<i>Lycaste</i> aff. <i>leucantha</i> Klatt	(1595)	1, 2	1.5, 6	280, 160	erect	herb
<i>Masdevallia chontalensis</i> Rchb.f.	(1653)	4	13	45	caespitose	herb
<i>M. molossoides</i> Kraenzl.	(1462)	3, 5	12, 19	2, 15	caespitose	herb
<i>M. nidifica</i> Rchb.f.	(1334)	5	15, 20	5, 10	caespitose	herb
<i>M. schizopetala</i> Kraenzl.	(1543)	5	15	3	caespitose	herb
<i>M. striatella</i> Rchb.f.	(1744)	branchfall		12, 24	caespitose	herb
<i>Maxillaria</i> cf. <i>brunnea</i> Linden & Rchb.f.	(1706)	1, treefall	5	90, 25	erect	herb
<i>M. fulgens</i> (Rchb.f.) L. O. Williams	(1571)	3	15	40	erect	herb
<i>M. inaudita</i> Rchb.f.	(1255)	2, treefall	6	7, 85	erect	herb
<i>M. linearifolia</i> Ames & C. Schweinf.	(1548)	treefall			arching	herb
<i>M. cf. microphyton</i> Schltr.	(1486)	5	15	15	erect	herb
<i>M. minor</i> (Schltr.) L. O. Williams	(1829)	treefall			scandent	herb
<i>M. cf. parvilabia</i> Ames & C. Schweinf.	(1788)	branchfall		15	erect	herb
<i>M. reichenheimiana</i> Rchb.f.	(283/UCSB)	3	16	60	erect	herb
<i>M. sigmoidea</i> (C. Schweinf.) Ames & Correll	(1814)	branchfall		70	erect	herb
<i>M. umbratilis</i> L. O. Williams	(1307)	treefall		48	erect	herb
<i>Myoxanthus sempergemmatum</i> (Luer) Luer	(1515)	3	12.6	30, 36	erect	herb
<i>Oerstedella endresii</i> (Rchb.f.) Hags.	(1279)	treefall		4	erect	herb
<i>O. exasperata</i> (Rchb.f.) Hags.	(1796)	branchfall		12	erect	shrub
<i>Oncidium bracteatum</i> Warsc. & Rchb.f.	(1687)	4	7	6, 12	erect	herb
<i>O. globuliferum</i> Kunth.	(1864)	branchfall		4	vining	herb
<i>O. heteranthum</i> Poeppig & Endl.	(1259)	branchfall		4, 6	erect	herb
<i>Ornithocephalus</i> aff. <i>gladius</i> Hook.	(1815)	branchfall		4	erect	herb
<i>Platystele microtatantha</i> (Schltr.) Garay	(1497)	branchfall		27, 30	caespitose	herb
<i>Pleurothallis cardiothallis</i> Rchb.f.	(1657)	branchfall		12	erect	herb
<i>P. casuialis</i> Ames	(1267)	branchfall		15	caespitose	herb
<i>P. cogniauxiana</i> Schltr.	(1789)	2, treefall	4	10	caespitose	herb
<i>P. costaricensis</i> Rolfe	(1260)	tree-, branchfall		5, 55	caespitose	herb
<i>P. crescentilabia</i> Ames	(1326)	treefall	20	35	erect	herb
<i>P. cuspidata</i> Luer	(1710)	branchfall		5	caespitose	herb
<i>P. eumecocaulon</i> Schltr.	(1273)	5	15	7, 29	caespitose	herb
<i>P. aff. fractiflexa</i> Luer	(1723)	1	1.8	40	caespitose	herb
<i>P. cf. gonioglossa</i> Schltr.	(1598)	treefall		12	caespitose	herb

Name/Author	Coll. #	Tree zones	Hgt. above ground (m)	Branch circum. (cm)	Plant habit	Growth form
<i>P. homalantha</i> Schltr.	(1663)	1	1	35	caespitose	herb
<i>P. immersa</i> Linden & Rchb.f.	(1771)	branchfall		18	caespitose	herb
<i>P. imraei</i> Lindley	(1320)	branchfall		18	caespitose	herb
<i>P. pompalis</i> Ames	(1650)	branchfall			caespitose	herb
<i>P. cf. powellii</i> Schltr.	(1804)	3	10	20	erect	herb
<i>P. rowleei</i> Ames	(1552)	1, 2	1.3, 10.5	16, 200	caespitose	herb
<i>P. ruscifolia</i> (Jacq.) R. Br.	(1488)	2-5	8, 16	6, 200	caespitose	herb
<i>P. segoviensis</i> Rchb.f.	(1468)	treefall		17	caespitose	herb
<i>P. segregatifolia</i> Ames & C. Schweinf.	(1575)	2, 3	11, 22	7, 210	caespitose	herb
<i>P. strumosa</i> Ames	(1851)	treefall		4	caespitose	herb
<i>Pleurothallis</i> sp. nov. (aff. <i>homalantha</i> )	(1252)	branchfall		12	caespitose	herb
<i>Restrepia subserrata</i> Schltr.	(1250)	tree-, branchfall		10, 7	caespitose	herb
<i>Scaphyglottis amparoana</i> (Schltr.) Dressler	(1709)	treefall		90	caespitose	herb
<i>S. cf. lindeniana</i> (A. Rich & Galeotti)						
L. O. Williams	(1816)	treefall		90	arching	herb
<i>Sobralia amabilis</i> (Rchb.f.) L. O. Williams	(1696)	2, treefall	4.5	150	erect	herb
<i>Stelis microchila</i> Schltr.	(1576)	5 (treefall)		6	caespitose	herb
<i>S. pardipes</i> Rchb.f.	(1538)	5	15	17	caespitose	herb
<i>S. parvula</i> Lindley	(1716)	tree-, branchfall		5, 20	caespitose	herb
<i>S. triangulabia</i> Ames	(1479)	5	15, 16	6, 8	caespitose	herb
<i>S. aff. tristyla</i> Lindl.	(1475)	3	15	15	caespitose	herb
<i>Stellilabium monteverdense</i> J. Atw.	(1514)	5	12	2	erect	herb
<i>Trichosalpinx cf. cedralensis</i> (Ames) Luer	(1856)	4	12	16	caespitose	herb
<i>Xylobium elongatum</i> (Lindl.) Hemsley	(1659)	1, 2	2, 4.5	35, 55	erect	herb
Piperaceae						
<i>Peperomia angularis</i> C. DC.	(1567)	treefall		30	erect	herb
<i>P. costaricensis</i> C. DC.	(1680)	2, 3	7-25	ca. 200	scandent	herb
<i>P. dotana</i> Trel.	(1296)	1, 3	1.3, 10	90, 20	erect	herb
<i>P. hylophila</i> C. DC.	(1449)	4, 5	15, 16	20, 4	erect	herb
<i>P. palmana</i> C. DC.	(1288)	1	1, 2	29, 165	erect	herb
<i>P. peltimba</i> C. DC. ex Trel.	(1329)	1	1.2-2	8, 362	scandent	herb
<i>P. pittieri</i> C. DC.	(1338)	treefall		63	erect	herb
<i>P. serpens</i> (Sw.) Loudon	(1702)	1	2	6, 37	scandent	herb
<i>P. cf. reptabunda</i> Trel.	(1453)	branchfall		22	erect	herb
<i>P. rotundifolia</i>	(1760)	branchfall		15	scandent	herb
<i>P. tenella</i> (Sw.) A. Dietr.	(1787)	branchfall		80	erect	herb
<i>P. tenellaeformis</i> Trel.	(1269)	branchfall		11	erect	herb

## APPENDIX 1. Continued.

Name/Author	Coll. #	Tree zones	Hgt. above ground (m)	Branch circum. (cm)	Plant habit	Growth form
<b>Rubiaceae</b>						
<i>Hillea tetrandra</i> Sw.	(1869)	branchfall		50	scandent	shrub
<i>H. triflora</i> (Oersted) C. Taylor	(1254)	treefall		34, 70	erect	shrub
<i>Psychotria maxonii</i> Standley	(1290)	3	15	15	erect	shrub
<i>P. pithecobia</i> Standley	(1256)	3, 4, 5	12.6, 14	7, 250	erect	shrub
<b>Scrophulariaceae</b>						
<i>Schlegelia fuscata</i> A. Gentry	(1850)	2	12	200	scandent	H shrub
<b>Solanaceae</b>						
<i>Lycianthes synanthera</i> (Sendter) Bitter	(1858)	2, 3	13, 14	80, 520	erect	shrub
<i>Markea neurantha</i> Hemsley	(1343)	3	18	140	scandent	shrub
<i>M. venosa</i> Standley	(1251)	branchfall		80	erect	shrub