THE MONTANE VEGETATION AND FLORA OF MARGARITA ISLAND, VENEZUELA

ANDREW M. SUGDEN[1]

The island of Margarita (11°N, 64°W) is physically and politically a part of Venezuela, constituting most of the state of Nueva Esparta, which also includes the two much smaller islands of Coche and Cubagua. The three islands lie on the continental shelf to the north of the peninsula of Araya, and Margarita is separated from the mainland by a channel approximately 25 km wide. Margarita is the most extensive and mountainous of the Venezuelan islands and is the only one to support moist evergreen montane vegetation.

The montane vegetation of Margarita has particular ecological interest because of its exceptionally low altitude and its apparent reliance on frequent and regular nocturnal cloud cover for the maintenance of moist conditions—features that are shared by only two other localities (the Serranía de Macuira, on the Guajira peninsula, Colombia; and Cerro Santa Ana, on the Paraguaná peninsula, Venezuela) on the Caribbean coast of South America (Sugden, 1982a, 1982b, 1983). Some factors that have been suggested as determinants of the peculiar physiognomy of montane rain forests at higher altitudes—for instance, low temperature and low insolation due to diurnal cloud cover (Leigh, 1975; Grubb, 1977)—are apparently unimportant in the Margarita mountains, while others such as wind have greater significance, as will be shown in this article.

The montane forests of Margarita are also of phytogeographic interest due to their insularity and their location between the South American mainland and the arc of the Lesser Antilles. Johnston (1909) collected about 165 species of vascular plants in the mountains, eight of which were apparently endemic. Subsequent collecting has increased the total number of montane species to at least 220, while the number of endemics (due to further collections from elsewhere) has dwindled to four or five dubious ones. It has been shown by Ortega (1982) and Sugden (1983) (for the pteridophyte and woody floras, respectively) that most of the montane species are quite widely distributed in the Neotropics; not surprisingly, the affinities with the mainland are stronger than those with the Lesser Antilles. I have presented evidence to suggest that the montane vegetation of Margarita is of recent origin (probably less than 10,000 years B.P.), and that the flora owes its present character and composition to random events of long-distance dispersal and establishment (Sugden, 1983).

The first account of the montane vegetation of Margarita was written by Johnston (1909). He recorded dense evergreen woods above 300 m, which

[1]Botany School, Downing Street, Cambridge CB2 3EA, England. Present address: Elsevier Publications, 68 Hills Road, Cambridge CB2 1LA, England.

Journal of the Arnold Arboretum **67**: 187–232. April, 1986.

became increasingly stunted and laden with epiphytes at higher altitudes. He described the top of the mountain, covered on the sheltered side with crooked trees, their branches thick with moss and dripping with moisture, and on the windward side by low shrubs and large bromeliads. This vegetation contrasted strongly with that of the lowlands, which—like most of the Caribbean lowlands of South America—supported dry deciduous woodlands and thorn and cactus scrub. This contrast also attracted the attention of Alexander (1958), who (like Johnston) considered that regular cloud cover above 400 m was responsible for the difference. He further suggested that the extremely stunted vegetation close to the highest ridges and summits owed its character to persistent high winds.

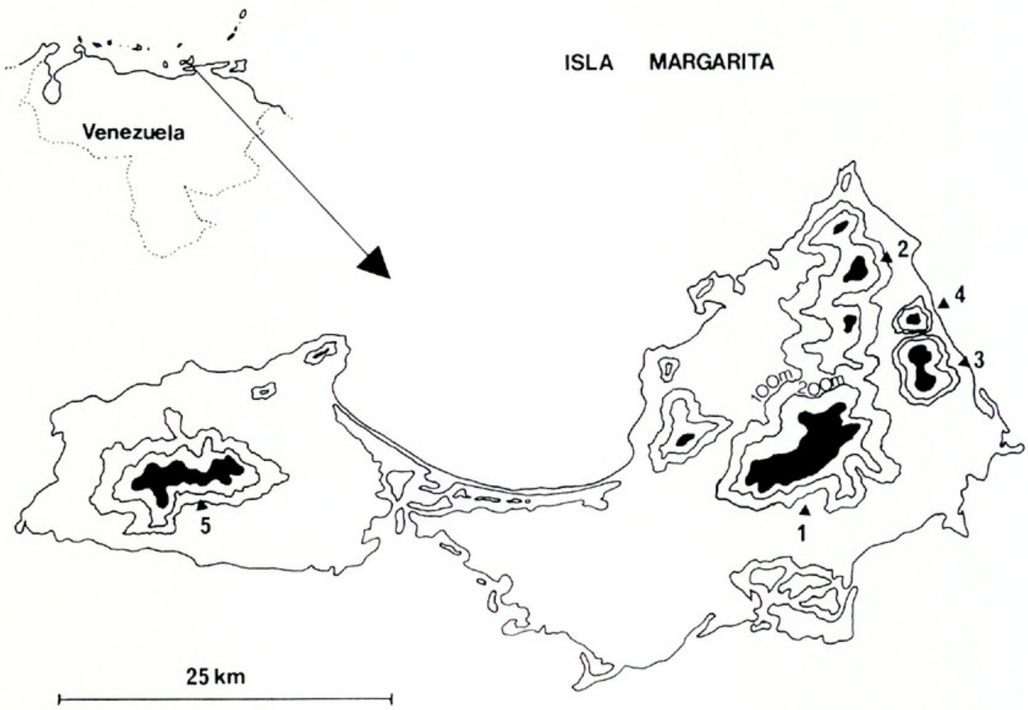
Ortega (1982) divided the upland vegetation into the categories of *selva pluvial intermedia* (intermediate rain forest), *selva nublada* (cloud forest), *bosque enano* (dwarf forest), and *bosque degredado en forma de páramo* (degraded forest in the form of páramo), the last of these occurring on the highest wind-swept slopes of Cerro Copey (930 m), the main massif of the island. I included all these types together under the general term of upper montane rain forest (Sugden, 1983).

All of these descriptions and classifications were included as brief adjuncts to floristic, geographic, and phytogeographic accounts and analyses. The purpose of the present account is to provide a more comprehensive and definitive description of the montane vegetation, which will serve as a basic source of information and also as an introductory framework for other analyses of physiognomy, regeneration, leaf anatomy (Sugden, 1985), and tree architecture in the Margarita mountains. Good descriptions of the dry vegetation on the lower slopes and plains of Margarita have been given by Johnston (1909), Marcuzzi (1950), and Alexander (1958).

GEOGRAPHY AND GEOLOGY

Margarita has the shape of an irregular dumbbell (see MAP 1), with two mountainous extremities connected by a low-lying isthmus, much of which consists of the mangrove swamps of La Restinga. The mountains of the eastern part of the island (Paraguachoa) comprise a central massif rising to 930 m with several smaller outliers to the north and east. The main ridge, the Serranía del Copey, runs in a northeast–southwest arc, with its highest point variously known as Cerro San Juan, Cerro Grande, or Cerro Copey (Jam, 1962); in the present account the last of these names is used. A steep-sided valley separates the northern end of the ridge from Cerro Tragaplata (also known as Cerro Chico), a broad dome 700 m high. On the eastern coast, separated from the main ridge by the plain of La Asunción, stand a pair of outlying mountains, the saddle-shaped Cerro Matasiete (660 m) and the pyramidal Cerro Guayamurí (490 m).

These four mountains, Copey, Tragaplata, Matasiete, and Guayamurí, support all of the undisturbed montane vegetation of eastern Margarita. Geologically, they are very similar to one another; the upper slopes (above ca. 350



MAP 1. Margarita Island, showing principal localities mentioned. Areas above 400 m marked in black. 1 = Cerro Copey, 2 = Cerro Tragaplata, 3 = Cerro Matasiete, 4 = Cerro Guayamurí, 5 = Macanao.

m) consist of peridotite, an ultramafic igneous rock, which in places is serpentinized (Jam & Mendez-Arocha, 1962; Y. Chevalier, pers. comm.).

The mountains of Macanao (the western part of the island) attain a maximum elevation of 780 m and form a single rugged ridge with three principal peaks. The highest of these, Cerro Los Cedros, is a sharp peak supporting a small patch of evergreen forest on the windward side of its summit. The entire range of Macanao consists of metamorphic schists and gneisses (González de Juana & Vignali, 1972).

CLIMATE

At 11°N latitude, Margarita is subject to strong east–northeasterly trade winds for almost the entire year and also lies within the anomalous region known as the South Caribbean Dry Zone (Lahey, 1958), where mean annual precipitation is always less than 1000 mm and often less than 500 mm. The climate of Margarita becomes increasingly wet with higher altitude and with greater proximity to the eastern (windward) coast (Contreras, 1967). In the eastern lowlands there are two short rainy seasons, in December–January and July–August, while in Macanao there is only one, in July–August (see FIGURE 1); mean annual precipitation in the two areas is ca. 550 mm and 300 mm, respectively. The total annual rainfall varies considerably at both ends of the island, ranging from 96 to 1532 mm over 20 years at La Asunción (Alexander, 1958), and from 138 to 720 mm over 12 years at Boca del Pozo (data from information

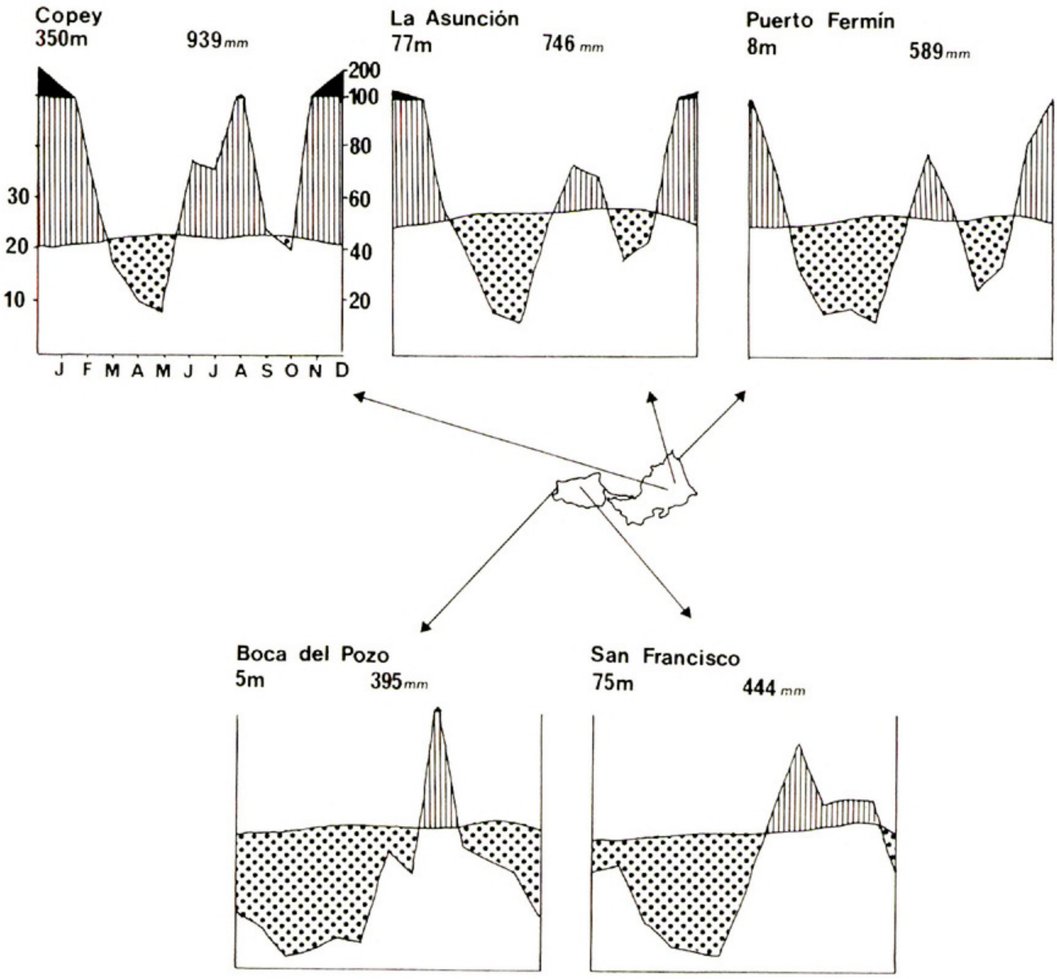


FIGURE 1. Climatic diagrams for Margarita Island (localities as in MAP 1). Left scale, mean monthly temperature (°C); right scale, mean monthly precipitation (mm); altitude and mean annual precipitation also shown. Data covering most years from 1953 to 1981, taken from information kindly supplied by Ministerio del Ambiente y de los Recursos Naturales Renovables (MARNR), Caracas. Diagrams show increase in precipitation with altitude at eastern end of island, increased aridity at western end.

kindly supplied by the Ministerio del Ambiente y de los Recursos Naturales Renovables, Porlamar).

The increase in precipitation with altitude is not known, since there are no climatic stations above 400 m. The highest station, at 350 m on the eastern slopes of Cerro Copey, has recorded a mean annual precipitation of ca. 950 mm, with a range of 222 to ca. 1900 mm since 1951.

Precipitation at higher altitudes is certainly greater, due to cloud droplet interception by the vegetation. On most nights throughout the year, the eastern mountains are capped with orographic clouds, which generally descend late in the afternoon and lift during mid-morning. On 271 days between September, 1982, and September, 1983, I recorded the times of day when clouds descended and lifted on Cerros Copey, Matasiete, Tragaplata, and Guayamurí and made notes on the approximate altitude of the cloud base at dusk on each mountain.

The observations were made from suitable vantage points in the lowlands and during the course of routine fieldwork on Cerro Copey. On only seven occasions were clouds absent from the peaks for more than 48 hours; there were no periods of more than 72 hours without cloud cover. During the same year, there was one interval of ten days when the clouds never lifted from the summits even at midday. The cloud base is generally lower on the windward sides of the mountains. Thus, on Cerros Guayamurí, Matasiete, and Tragaplata, the clouds descend to ca. 350 m on the eastern slopes and to 400–500 m on the western. On Cerro Copey, which is farther inland, the lower limits on the windward and leeward slopes are ca. 450 m and 550 m, respectively.

No systematic records have been made of cloud cover on the mountains of Macanao, but limited observations suggest that it is far less regular (Alexander, 1958); cloud-free periods of up to several weeks may be common. The cloud base appears to be at about 600 m. According to Alexander, the Macanao mountains receive less cloud cover because they are aligned more or less parallel to the prevailing wind; the eastern mountains present a more perpendicular face to the wind, forcing the air to rise rather than to pass on either side. A further cause for reduced cloud cover on Macanao may be a warming of the airstream as it passes over the island from east to west; this could cause a generally higher cloud base in the west.

The extent to which cloud-droplet interception contributes to the total precipitation on the mountains is unknown. Generally the vegetation on the upper slopes of Cerro Copey is dripping with moisture after the clouds have lifted in the morning, although there is relatively little surface moisture even on the understory leaves and branches by late afternoon. The soil surface is never dry to the touch, and on the highest windswept slopes of Cerro Copey it is generally wet and slippery. Streams flow only after rain, which fell heavily on 27 days and lightly or intermittently on an additional 34 during my 271 days of observation. Whatever the total precipitation, however, it is reasonably certain that cloud cover on these mountains increases humidity and offsets the highly seasonal rainfall regime; the probability of periodic drought decreases dramatically with increasing altitude.

A steep temperature gradient, 0.97°C/100 m altitude increase, has been recorded on Cerro Copey by Drs. C. Schubert and E. Medina (pers. comm.) using soil probes at depths of 30–40 cm. The mean annual temperature at the summit, recorded in this way, was approximately 19°C. Monthly and daily maximum and minimum temperatures have not been recorded in the mountains; in a maritime, low-altitude situation of this kind, however, strong variation and extremes of heat and cold would not be expected.

The strength of the wind increases with altitude, and at the summit of Cerro Copey there is an almost perpetual gale. There are no extensive data on wind speed on the mountain, but according to the technicians at the summit telecommunications station, gusts of more than 80 km per hour have been recorded by their anemometer. The direction of the wind varies little during the year. I have observed light southerly or southwesterly winds on infrequent occasions during the July–August rainy seasons. Otherwise, the flow of the trade winds is interrupted only by the passage of hurricanes and tropical storms within 150

FIGURE 2. Cerro Matasiete, showing contrasting dry vegetation (lower slopes) and evergreen vegetation (upper slopes).

km of the island, which has occurred seven and nine times, respectively, during the last century (Alexander & Bertness, 1982).

UPLAND VEGETATION

METHODS

Fieldwork was carried out in August, 1981, January, 1982, and September, 1982–September, 1983. The greater part of the work was carried out on Cerro Copey, which has a road to its summit and therefore has easily accessible vegetation; this vegetation is mostly undisturbed. Occasional ascents were also made on foot to the summits of Matasiete (twice), Guayamurí (once), Tragaplata (once), and the mountains of Macanao (twice).

Herbarium collections and floristic notes were made during the course of regular visits (every two to three weeks) to a dozen sites between 400 m alt. and the summit of Cerro Copey, and particular efforts were made to ensure that fertile specimens were eventually collected from unfamiliar plants initially encountered in the vegetative condition. Collections and notes were also made routinely during the trips up and down the summit road, occasional forays into other parts of Cerro Copey, and the ascents of the other mountains. I have checked and supplemented the floristic information thus obtained by reference to the excellent collections from Isla Margarita in the herbarium of the Sociedad de Ciencias Naturales La Salle, in Caracas, and to Johnston's flora (1909) and some of his duplicates at Kew. A previous list of the woody plants of the eastern mountains of Margarita (Sugden, 1983) requires some revision and updating in light of the recent fieldwork.

The principal criteria for distinguishing vegetation types in the upland zone included height of canopy, diameter of boles, and presence and levels of abundance of various habits, life-forms, major taxa (deciduous trees, bryophytes, vascular epiphytes, woody lianas, palms, understory shrubs, herbs), and (in some cases) individual species. Except for easily quantifiable characters such as bole diameter, these observations were mainly qualitative but nevertheless detailed. Quantitative characterizations of leaf anatomy in the major vegetation types, and of floristics and physiognomy in one of them, are the subjects of separate articles (Sugden, 1985; Sugden, in preparation).

Soils were sampled at ten sites between 400 and 900 m alt. on Cerro Copey. At each site a pit was dug to a depth of ca. 50 cm in order to assess physical characteristics; supplementary information was also obtained from road cuts nearby. Samples for chemical analysis were taken from the top 5 cm and from the upper mineral layer (10–30 cm), the exact depth depending on the site. Analyses were carried out by the Centro de Ecología, IVIC, Caracas (details of standard procedures available on request).

Results

General Remarks

The ecotone between the predominantly deciduous vegetation of the lower slopes and the mostly evergreen upland vegetation is generally well defined (Figure 2) and is particularly obvious during the long dry seasons. More often than not, it is marked by the appearance of large trees of *Clusia rosea* with wide, spreading crowns and also by the appearance of an epiphytic and herbaceous flora that becomes increasingly diverse with higher altitude. Although a few deciduous tree species are present above the ecotone, for convenience I shall use the term "evergreen upland vegetation" to embrace all the physiognomic types found above this level.

The precise level of this ecotone corresponds closely to the level of the cloud base on each mountain. Thus, evergreen upland vegetation begins at ca. 350 m alt. on the windward slopes and ca. 450 m alt. on the leeward slopes of Cerros Guayamurí, Matasiete, and Tragaplata, and at ca. 400 m alt. on the windward side and 500–550 m alt. on the leeward side of Cerro Copey. On all four mountains thin ribbons (often less than 30 m wide) of "gallery forest" extend downward along the deeper gullies with permanent groundwater, occasionally to as low as 100 m above sea level; these are especially well developed on Cerro Copey.

The evergreen upland vegetation can be divided into four quite distinct physiognomic types, which can be further subdivided according to physiognomic and/or floristic criteria into a total of ten subtypes:

1. Transition Forest
   a. with *Clusia rosea*
   b. without *Clusia rosea*
2. Cloud Forest
   a. tall

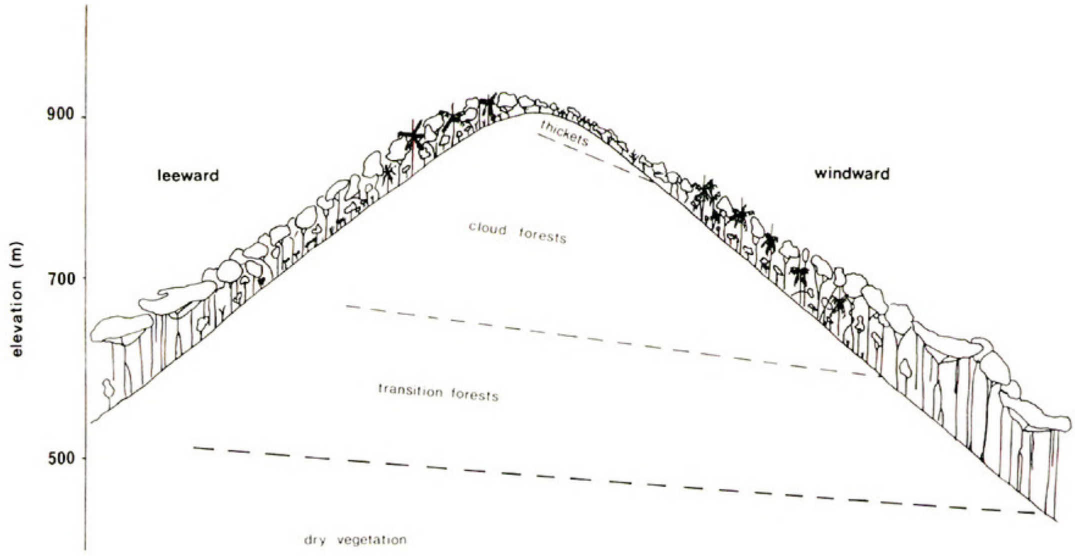


FIGURE 3. Idealized profile of Cerro Copey, showing distribution of vegetation types. (Trees not drawn to scale.)

   b. pole
   c. lower palm
   d. upper palm
3. Wet Thicket
   a. tall woody
   b. short woody
   c. herbaceous
4. Grassland

The descriptions that follow are of the upland vegetation of Cerro Copey, where the distinctions between the various vegetation types and subtypes are best developed; as the highest and most extensive mountain on the island, Cerro Copey has the greatest physiognomic and floristic diversity. Cerros Guayamurí, Matasiete, and Tragaplata, and the mountains of Macanao, are considered briefly in a subsequent section.

The flowering plants of Cerro Copey, and their distributions in the vegetation types, are listed in TABLE 1. My observations of the fern flora are not sufficiently detailed to justify similar treatment. A complete list of the pteridophytes of Margarita, almost all of which occur on Cerro Copey, has been compiled by Ortega (1982), and some of these species will be mentioned in the descriptions that follow. TABLE 2 provides an outline of the principal chemical features of the soils in each of the four major vegetation types. The principal physiognomic differences between these types are summarized in TABLE 3. An idealized profile of the vegetation is shown in FIGURE 3.

Types of Vegetation

1. TRANSITION FOREST. The term "transition forest" is analogous to the *selva de transición* of Steyermark and Huber (1978), used to denote the forests

intermediate between the savannas and cloud forests on the slopes of the Venezuelan Cordillera de la Costa, near Caracas. On Cerro Copey Transition Forest is the first mainly evergreen vegetation type encountered on the ascent. It occupies an altitudinal band of 150–200 m and reaches a maximum elevation of ca. 700 m on the leeward slopes. It is distinguished from the forests at higher altitudes by its relatively low number of vascular epiphytes and bryophytes and its comparatively high frequency of woody lianas and individuals of deciduous tree species. Transition Forest has the widest leaf-size spectrum (for canopy trees) of any of the major vegetation types, from the leptophylls of *Calliandra panlosia* to the mesophylls of *Croton xanthochloros* (Sugden, 1985).

Soils in the Transition Forest are normally up to 80 cm (rarely more than 100 cm) deep. There is a thin layer of dryish litter, covering a humus layer 1–5 cm thick that contains abundant roots. The mineral horizons are clayey, but with a distinct crumb structure, and yellowish brown. These soils have the highest pH (6.25–6.85) of any of the upland ones and also have a very high magnesium content (see TABLE 2).

There are two subtypes of Transition Forest:

a. **With Clusia rosea.** Located on the more sheltered slopes of Cerro Copey, Transition Forest with *Clusia rosea* (FIGURE 4) is the tallest vegetation on Margarita, reaching heights of up to 30 m; in windier places the canopy is considerably lower (15–20 m). The characteristic architecture of *C. rosea* (with spreading plagiotropic branches overlapping to produce an imbricate effect), together with its very dark foliage, enables ready identification from a distance; indeed, *C. rosea* is the only species that is readily distinguishable in aerial photographs of the island. From within the forest, *C. rosea* can be recognized by its masses of thick, usually pale gray, conspicuously lenticellate aerial roots. Other large trees prominent in this vegetation are *Croton xanthochloros, Terminalia amazonia,* and *Ficus nymphaeifolia,* all deciduous and with a leafless period of less than one month. *Ficus nymphaeifolia,* like *C. rosea,* is a "strangling" hemiepiphyte. In this vegetation, as in all the types subsequently described, the canopy is quite closed and uniform, without "emergent" trees.

The lower strata under *Clusia rosea,* which is the sole canopy species in much of the forest, are generally poorly developed. The understory is open and free of obstacles. Herbaceous species are rare, and shrubs are virtually absent. Woody lianas are more frequent, and a *Philodendron* sp. is a common herbaceous climber.

b. **Without Clusia rosea.** This forest subtype is more heterogeneous than the previous one. It occurs over a similar range of altitudes, and its chief features, apart from the rarity of *Clusea rosea,* are a higher diversity of tree species and a somewhat lower (10–15 m) canopy. Many of the common Cloud Forest species (see below) occur here; *Guapira* cf. *fragrans, Daphnopsis americana, Maytenus karstenii, Myrcia* cf. *coriacea,* and *Roupala montana* are especially prominent. Important deciduous species are *Calliandra panlosia, Croton xanthochloros, Tabebuia chrysantha,* and *Terminalia amazonia.* Few tree species are confined to this zone; those that are common here and rare on other parts of the mountain include *Calliandra panlosia* and *Linociera caribaea.*

TABLE 1. **The distribution of flowering-plant species in the montane vegetation types of Cerro Copey.**

		TRANSITION FOREST		CLOUD FOREST				WET THICKET			
		with Clusia rosea	without Clusia rosea	Tall	Pole	Lower palm	Upper palm	Tall woody	Short woody	Herbaceous	GRASS-LAND
WOODY CANOPY PLANTS											
Aquifoliaceae	Ilex guianensis (Aublet) Kuntze	–	–	+	+	+	+	+	+	–	–
Araliaceae	Dendropanax arboreum (L.) Decne. & Planchon	–	–	+	+	+	+	–	–	–	–
	Oreopanax capitatum (Jacq.) Decne. & Planchon	–	–	+	+	+	–	–	–	–	–
Bignoniaceae	Tabebuia cf. chrysantha Nicholson	+	+	+	+	+	+	+	+	–	–
Bombacaceae	Ceiba pentandra (L.) Gaertner	+	+	–	–	–	–	–	–	–	–
Boraginaceae	Cordia cf. hirta I. M. Johnston	–	+	+	+	–	–	–	–	–	–
	Cordia polycephala (Lam.) I. M. Johnston	–	–	–	–	–	–	–	+	–	–
Burseraceae	Protium cf. tenuifolium (Engler) Engler	+	+	+	+	–	–	–	–	–	–
Celastraceae	Maytenus cf. karstenii (Klotzsch) Reissek	+	+	+	+	+	+	+	+	–	–
Chrysobalanaceae	Licania membranacea Sagot ex Loes.	–	–	+	+	+	–	–	–	–	–

Clusiaceae	*Clusia* cf. *flava* Jacq.	-	-	-	-	+	+	++	+	(+)	-
	Clusia cf. *myriandra* (Bentham) Planchon & Trelease	-	-	-	-	-	-	+	+	-	-
	Clusia rosea Jacq.	+	(+)	(+)	(+)	(+)	(+)	-	-	-	-
Combretaceae	*Terminalia amazonia* (Gmelin) Exell	+	+	+	+	+	+	-	-	-	-
Compositae	Sp. indet. (Mutisieae)	-	+	-	-	-	-	+	-	-	-
Erythroxylaceae	*Erythroxylum densum* Rusby	-	-	-	-	-	-	+	+	(+)	-
Euphorbiaceae	*Croton xanthochloros* Croizat	+	+	+	+	(+)	(+)	-	-	-	-
	Margaritaria nobilis L.f.	-	+	+	+	+	+	(+)	-	-	-
Flacourtiaceae	*Casearia* cf. *decandra* Jacq.	?	?	+	-	-	-	-	-	-	-
	Casearia guianensis (Aublet) Urban	+	+	(+)	-	-	-	-	-	-	-
	Casearia zizyphoides H.B.K.	(+)	+	-	-	-	-	-	-	-	-
	Sp. indet.	-	+	+	-	-	-	-	-	-	-
Lauraceae	*Ocotea leucoxylon* (Sw.) Mez	-	-	+	+	+	+	+	+	(+)	-
	Persea caerulea (Ruiz & Pavon) Mez	-	-	+	+	+	(+)	-	-	-	-
Leguminosae	*Calliandra panlosia* J.R. Johnston	+	++	+	+	-	-	-	-	-	-
	Cassia fruticosa Miller	-	(+)	(+)	(+)	(+)	(+)	(+)	+	-	-
	Inga macrantha J.R. Johnston	-	-	+	+	+	+	+	+	-	-
Marcgraviaceae	*Ruyschia tremadena* (Ernst) Lundell	-	-	-	-	-	-	-	+	(+)	-
Melastomataceae	*Blakea monticola* J.R. Johnston	-	-	+	+	+	+	+	+	-	-

TABLE 1 (*continued*).

		TRANSITION FOREST		CLOUD FOREST				WET THICKET			
		with *Clusia rosea*	without *Clusia rosea*	Tall	Pole	Lower palm	Upper palm	Tall woody	Short woody	Herbaceous	GRASSLAND
	Clidemia hirta (L.) D. Don	–	–	–	–	–	–	(+)	+	(+)	–
	Miconia prasina (Sw.) DC.	–	–	+	+	–	–	–	–	–	–
Moraceae	*Ficus nymphaeifolia* Miller	+	+	+	+	–	–	–	–	–	–
	Ficus yoponensis Desv.	–	(+)	–	–	–	–	–	–	–	–
Myrsinaceae	*Rapanea guianensis* Aublet	(+)	+	+	+	+	+	+	+	–	–
Myrtaceae	*Marlieriopsis eggersii* Kiaerskou	–	–	+	+	+	+	+	–	–	–
	Myrcia cf. *coriacea* (Vahl) DC.	+	+	+	+	+	+	+	+	–	–
	Myrciaria sp.	+	+	+	+	–	–	–	–	–	–
Nyctaginaceae	*Guapira* cf. *fragrans* (Dum.-Cours.) Little	+	+	+	+	+	+	+	+	(+)	–
	Pisonia aculeata L.	+	+	–	–	–	–	–	–	–	–
Ochnaceae	*Ouratea guildingii* (Planchon) Urban	+	+	–	–	–	–	–	–	–	–
	Ouratea pyrifolia (Griseb.) Engler	–	–	–	–	–	+	+	–	–	–
Olacaceae	*Schoepfia schreberi* Gmelin	(+)	+	–	–	–	–	–	–	–	–

	Ximenia americana L.	(+)	+	-	-	-	-	-	-	-	-
Oleaceae	*Linociera caribaea* (Jacq.) Knobl.	(+)	+	(+)	(+)	-	-	-	-	-	-
Opiliaceae	*Agonandra brasiliensis* Bentham & Hooker	(+)	+	-	-	-	-	-	-	-	-
Palmae	*Acrocomia sclerocarpa* Martius	-	+	-	-	-	-	-	-	-	-
	Bactris falcata J.R. Johnston	-	-	+	+	-	-	-	-	-	-
	Euterpe karsteniana Engel	-	-	+	+	+	+	-	-	-	-
Polygonaceae	*Coccoloba* cf. *rugosa* Desf.	-	-	+	+	-	-	-	-	-	-
	Coccoloba sp. 1	+	+	-	-	-	-	-	-	-	-
	Coccoloba sp. 2	+	+	-	-	-	-	-	-	-	-
Proteaceae	*Roupala montana* Aublet	+	+	+	+	+	+	+	+	+	(+)
Rubiaceae	*Coutarea hexandra* (Jacq.) K. Schum.	(+)	+	-	-	-	-	-	-	-	-
	Guettarda odorata (Jacq.) Lam.	(+)	+	+	+	-	-	-	-	-	-
	Guettarda scabra (L.) Vent.	+	+	+	+	+	+	+	-	-	-
Rutaceae	*Amyris ignea* Steyerm.	+	+	-	-	-	-	-	-	-	-
	Amyris simplicifolia H. Karsten	?	?	-	-	-	-	-	-	-	-
	Esenbeckia grandiflora Martius	-	-	+	+	+	-	-	-	-	-
	Esenbeckia pilocarpoides Kunth	-	+	-	-	-	-	-	-	-	-
Sapindaceae	*Cupania americana* L.	+	+	(+)	(+)	(+)	(+)	-	-	-	-
Styracaceae	*Styrax glaber* Sw.	-	-	+	+	+	+	-	-	-	-

TABLE 1 (*continued*).

		TRANSITION FOREST		CLOUD FOREST				WET THICKET			
		with *Clusia rosea*	without *Clusia rosea*	Tall	Pole	Lower palm	Upper palm	Tall woody	Short woody	Herbaceous	GRASSLAND
Symplocaceae	*Symplocos martinicensis* Jacq.	–	–	+	+	+	+	+	+	–	–
Thymeleaceae	*Daphnopsis americana* (Miller) J.R. Johnston	(+)	+	+	+	+	+	+	(+)	–	–
Violaceae	*Rinorea lindeniana* (Tul.) Kuntze	+	+	+	+	(+)	–	–	–	–	–
WOODY UNDERSTORY PLANTS											
Begoniaceae	*Begonia glabra* Aublet	–	–	(+)	+	+	–	–	–	–	–
Boraginaceae	*Tournefortia hirsutissima* L.	–	–	+	+	+	+	–	–	–	–
	Tournefortia volubilis L.	–	–	+	+	+	–	–	–	–	–
Ericaceae	Cf. *Orthaea* sp.	–	–	–	–	–	–	–	+	–	–
Erythroxylaceae	*Erythroxylum hondense* H.B.K.	–	–	+	+	+	+	–	–	–	–
Euphorbiaceae	*Acalypha macrostachya* Jacq.	–	–	+	+	–	–	–	–	–	–
	Actinostemon concolor Muell. Arg.	(+)	+	–	–	–	–	–	–	–	–
	Croton margaritensis J.R. Johnston	–	–	–	–	–	+	+	+	–	–

Malpighiaceae	Bunchosia sp.	–	–	+	+	–	–	–	–	–	–
	Hiraea reclinata Jacq.	+	+	–	–	–	–	–	–	–	–
Melastomataceae	Miconia laevigata (L.) DC.	–	–	(+)	(+)	–	–	–	–	–	–
Palmae	Geonoma pinnatifrons Willd.	–	–	+	+	+	–	–	–	–	–
Piperaceae	Piper aequale Vahl	–	–	?	?	–	–	–	–	–	–
	Piper dilatatum L.C. Rich.	–	–	?	?	–	–	–	–	–	–
	Pothomorphe peltata (L.) Miq.	+	+	–	–	–	–	–	–	–	–
Rubiaceae	Chiococca alba (L.) Hitchc.	+	+	–	–	–	–	–	–	–	–
	Gonzalagunia spicata (Lam.) Gómez	–	+	+	+	(+)	–	–	–	–	–
	Psychotria barbiflora A. DC.	–	–	?	?	+	–	–	–	–	–
	Psychotria carthaginensis Jacq.	–	–	+	+	+	–	–	–	–	–
	Psychotria muscosa (Jacq.) Steyerm.	–	–	+	+	++	(+)	–	–	–	–
Solanaceae	Cestrum sp. 1	–	–	+	+	+	–	–	–	–	–
	Cestrum sp. 2	–	–	–	–	–	–	+	–	–	–
	Solanum arboreum Humb. & Bonpl. ex Dunal	–	–	+	–	–	–	–	–	–	–
	Solanum nudum Humb. & Bonpl. ex Dunal	–	–	+	+	+	(+)	–	–	–	–
Violaceae	Rinorea melanodonta Blake	+	+	+	+	+	(+)	–	–	–	–

TABLE 1 (*continued*).

		TRANSITION FOREST		CLOUD FOREST				WET THICKET			
		with *Clusia rosea*	without *Clusia rosea*	Tall	Pole	Lower palm	Upper palm	Tall woody	Short woody	Herbaceous	GRASS-LAND
SUFFRUTESCENT SPECIES											
Acanthaceae	*Justicia secunda* Vahl	–	–	+	+	+	+	–	–	+	+
Campanulaceae	*Centropogon cornutus* (L.) Druce	–	–	–	–	–	–	–	+	+	–
Ochnaceae	*Sauvagesia erecta* L.	–	–	–	–	–	–	–	–	+	+
Oxalidaceae	*Oxalis frutescens* Ruiz & Pavon	–	–	–	–	–	(+)	–	+	+	+
LARGE HERBS											
Bromeliaceae	*Aechmea fendleri* André	+	+	+	+	+	+	–	–	–	–
	Vriesea splendens (Brongn.) Lemée	–	–	+	+	+	+	–	–	–	–
Commelinaceae	?*Commelinopsis persicariifolia* (DC.) Pichon	–	–	?	?	–	–	–	–	–	–
Cyperaceae	*Scleria arundinacea* Kunth	–	–	+	+	+	+	–	–	–	–
	Scleria bracteata Cav.	–	+	+	+	+	+	+	+	+	–
Gramineae	*Andropogon bicornis* L.	–	–	–	–	–	–	–	+	+	+

	Ichnanthus nemoralis (Schrader) Hitchc.	-	-	+	+	+	(+)	-	-	-	-
	Lasiacis anomala Hitchc.	-	-	+	+	+	+	+	-	-	-
	Lasiacis ligulata Hitchc. & Chase	-	-	+	+	+	+	+	-	-	-
	Olyra cordifolia H.B.K.	-	+	+	+	+	-	-	-	-	-
Marantaceae	*Maranta arundinacea* L.	-	-	+	+	+	-	-	-	-	-
Musaceae	*Heliconia caribaea* Lam.	-	-	+	+	+	-	+	-	-	-
	Heliconia psittacorum L.f.	-	-	+	+	-	-	-	-	-	-
Piperaceae	*Peperomia glabella* (Sw.) A. Dietr.	+	+	+	+	+	-	-	-	-	-
Urticaceae	*Pilea involucrata* (Sims) Urban	-	+	-	-	+	-	-	-	-	-
SMALL HERBS											
Cyperaceae	*Eleocharis geniculata* (L.) Roemer & Schultes	-	-	-	-	-	-	-	-	+	+
	Fimbristylis complanata (Retz.) Link	-	-	-	-	-	-	-	-	-	+
	Rhynchospora barbata (Vahl) Kunth	-	-	-	-	-	-	-	-	-	+
	Rhynchospora candida (Nees) Boeckeler	-	-	-	-	-	-	-	-	-	+
	Rhynchospora gracilis Vahl	?	?	?	?	?	?	?	?	?	?
	Rhynchospora nervosa (Vahl) Boeckeler	+	+	+	+	+	+	+	-	-	-
	Rhynchospora rugosa (Vahl) Gale	-	-	-	-	-	-	-	-	-	+

TABLE 1 (*continued*).

		TRANSITION FOREST		CLOUD FOREST				WET THICKET			
		with *Clusia rosea*	without *Clusia rosea*	Tall	Pole	Lower palm	Upper palm	Tall woody	Short woody	Herbaceous	GRASS-LAND
	Scleria lithosperma (L.) Sw.	?	?	+	+	+	+	?	?	?	?
	Sp. indet. 1	–	–	–	–	–	–	–	–	–	+
	Sp. indet. 2	–	–	–	–	–	–	–	–	–	+
	Sp. indet. 3	–	–	–	–	–	+	–	–	–	–
Gentianaceae	*Coutoubea spicata* Aublet	–	–	–	–	–	–	–	–	–	+
	Voyrea aphylla Pers.	–	–	+	+	+	+	–	–	–	–
Gramineae	*Andropogon leucostachys* Kunth	–	–	–	–	–	–	–	–	+	+
	Fimbristylis autumnalis (L.) Roemer & Schultes	?	?	?	?	?	?	?	?	?	?
	Ichnanthus pallens (Sw.) Munro	–	(+)	+	+	+	+	(+)	–	–	–
	Pharus latifolius L.	–	–	+	+	–	–	–	–	–	–
Iridaceae	*Trimezia martinicensis* (Jacq.) Herbert	–	–	–	–	–	–	–	–	–	+
Orchidaceae	*Encyclia pygmaea* (Hooker) Dressler	–	–	–	–	–	–	–	–	–	+

	Erythrodes venezuelana Garay & Dunsterv.	-	-	+	+	+	+	-	-	-	-
	Eulophidium maculatum (Lindley) Pfitzer	+	+	+	-	-	-	-	-	-	-
	Spiranthes adnata (Sw.) Bentham	-	-	+	+	+	+	-	-	-	-
CLIMBERS											
Apocynaceae	Mandevilla subsagittata (Ruiz & Pavon) Woodson	-	-	-	+	+	-	-	-	-	-
Asclepiadaceae	Cynanchum parviflorum Sw.	-	-	-	-	-	-	-	+	+	-
	Ditassa oxyphylla Turcz.	-	-	-	-	-	-	-	+	+	-
	Matelea cf. humboldtiana Spellman & Morillo	-	-	+	-	-	-	-	-	-	-
Bignoniaceae	Macfadyena unguis-cati (L.) A. Gentry	+	+	-	-	-	-	-	-	-	-
	Phryganocydia corymbosa (Vent.) Bur. ex Schumann	+	+	-	-	-	-	-	-	-	-
Compositae	Mikania johnstonii Robinson	-	-	-	-	?	?	-	-	-	-
Dioscoreaceae	Dioscorea polygonoides Humb. & Bonpl. ex Willd.	-	-	+	+	+	+	-	-	-	-
Gentianaceae	Drymonia serrulata (Jacq.) Martius	+	+	-	-	-	-	-	-	-	-
Leguminosae	?Bauhinia sp.	+	+	-	-	-	-	-	-	-	-

TABLE 1 (*continued*).

		TRANSITION FOREST		CLOUD FOREST				WET THICKET			
		with *Clusia rosea*	without *Clusia rosea*	Tall	Pole	Lower palm	Upper palm	Tall woody	Short woody	Herbaceous	GRASS-LAND
	Machaerium robiniifolium Vogel	+	+	–	–	–	–	–	–	–	–
Malpighiaceae	*Heteropterys laurifolia* (L.) Juss.	+	+	+	+	+	+	(+)	–	–	–
	Heteropterys macrostachya Juss.	–	–	+	+	(+)	–	–	–	–	–
Passifloraceae	*Passiflora cyanea* Masters	–	–	–	–	–	(+)	+	+	–	–
	Passiflora laurifolia L.	–	–	+	+	+	–	–	–	–	–
Polygalaceae	*Securidaca* cf. *diversifolia* (L.) Blake	+	+	–	–	–	–	–	–	–	–
	Securidaca cf. *volubilis* L.	–	+	–	–	–	(+)	–	–	–	–
Rubiaceae	*Emmeorhiza umbellata* (Sprengel) Schumann	–	–	–	–	+	+	+	–	–	–
Sapindaceae	*Serjania* sp.	+	+	+	+	–	–	–	–	–	–
Smilacaceae	*Smilax* cf. *solanifolia* A. DC.	–	–	+	+	+	+	–	–	–	–
SCANDENT PLANTS											
Compositae	*Mikania trinitaria* DC.	–	–	–	–	+	–	–	–	–	–

	Wedelia caracasana DC.	-	-	-	-	-	(+)	+	+	-	-
	Wedelia fruticosa DC.	-	-	-	-	-	-	-	+	+	-
	Wulffia baccata (L.f.) Kuntze	+	+	+	+	+	+	+	+	-	-
Solanaceae	*Solanum lancifolium* Jacq.	+	+	+	+	+	+	+	-	-	-
WOODY HEMIEPIPHYTES											
Ericaceae	*Vaccinium latifolium* Bentham & Hooker f.	-	-	-	-	+	+	+	+	-	-
Marcgraviaceae	*Norantea guianensis* Aublet	-	+	+	+	-	-	+	+	-	-
Rubiaceae	*Hillia parasitica* Jacq.	-	-	-	-	-	+	+	+	-	-
EPIPHYTES											
Araceae	*Anthurium* cf. *hookeri* Kunth	+	+	+	+	+	+	-	-	-	-
	Philodendron cf. *aristeguietae* Bunting	-	-	+	-	-	-	-	-	-	-
	Philodendron sp.	+	+	+	+	+	+	+	-	-	-
Bromeliaceae	*Glomeropitcairnia erectiflora* Mez	-	-	-	-	-	(+)	+	++	+	-
	Guzmania lingulata (L.) Mez	-	-	+	+	+	(+)	-	-	-	-
	Guzmania cf. *lychnis* L.B. Smith	-	-	-	-	+	-	-	-	-	-
	Guzmania monostachya (L.) Rusby ex Mez	+	+	-	-	-	-	-	-	-	-
	Tillandsia lescaillei Wright	-	-	-	-	-	+	-	-	-	-
	?*Tillandsia* sp.	-	-	+	-	-	-	-	-	-	-

TABLE 1 (*continued*).

		TRANSITION FOREST		CLOUD FOREST				WET THICKET			
		with *Clusia rosea*	without *Clusia rosea*	Tall	Pole	Lower palm	Upper palm	Tall woody	Short woody	Herbaceous	GRASS-LAND
	Vriesea johnstonii Mez	-	-	?	?	?	?	-	-	-	-
	Vriesea simplex (Vell.) Beer	-	-	?	?	?	-	-	-	-	-
Cactaceae	*Rhipsalis* cf. *baccifera* (J.S. Miller) Stearn	+	-	-	-	-	-	-	-	-	-
Lentibulariaceae	*Utricularia alpina* Jacq.	-	-	-	-	+	+	+	-	-	-
Orchidaceae	*Campylocentrum micranthum* (Lindley) Rolfe	-	-	-	+	-	-	-	-	-	-
	Dichaea graminoides (Sw.) Lindley	-	-	?	?	?	?	-	-	-	-
	Dichaea muricata (Sw.) Lindley	-	-	+	+	+	+	+	-	-	-
	Dichaea picta Reichb. f.	-	-	+	+	+	+	(+)	-	-	-
	Elleanthus arpophyllostachys Reichb.	-	-	+	+	+	+	-	-	-	-
	Epidendrum anceps Jacq.	-	-	-	-	-	-	-	-	?	-
	Epidendrum cochleatum L.	?	?	?	-	-	-	-	-	-	-
	Epidendrum johnstonii Ames	-	-	-	-	-	+	+	-	-	-
	Epidendrum nocturnum Jacq.	-	-	+	+	+	+	+	+	+	+

Epidendrum rigidum Jacq.	-	-	-	-	-	-	-	-	-	?
Epidendrum secundum Jacq.	-	-	-	-	-	-	-	+	+	+
Huntleya lucida (Rolfe) Rolfe	-	-	?	?	-	-	-	-	-	-
Jacquiniella globosa (Jacq.) Schlechter	?	?	?	-	-	-	-	-	-	-
Maxillaria venusta Lindley & Reichb. f.	-	-	-	-	+	+	(+)	-	-	-
Maxillaria virguncula Reichb. f.	-	-	?	?	-	-	-	-	-	-
Platystele johnstonii (Ames) Garay	-	-	-	-	+	+	+	-	-	-
Pleurothallis discoidea Lindley	-	-	+	+	+	+	-	-	-	-
Pleurothallis floribunda (Lindley) Lindley	-	-	?	?	?	?	-	-	-	-
Pleurothallis foliata Griseb.	-	-	?	?	?	?	-	-	-	-
Pleurothallis revoluta (Ruiz & Pavon) Garay	-	-	-	-	-	+	+	-	-	-
Pleurothallis ruscifolia (Jacq.) R. Br.	-	-	+	+	+	+	-	-	-	-
Pleurothallis sclerophylla Lindley	-	-	-	-	-	-	-	-	?	?
Pleurothallis velaticaulis Reichb. f.	-	-	+	+	+	+	-	-	-	-
Pleurothallis sp.	-	-	+	+	+	+	-	-	-	-

Key to symbols: ++ = abundant, + = common, (+) = rare, - = absent, ? = uncertain (refers mainly to authenticated records of species not encountered in the present study).

TABLE 2. **Soil chemistry in the principal vegetation types of Cerro Copey.***

Vegetation type & soil depth (cm)	pH	Carbon (%)	Available P (µg/g)	Total N (mg/g)	Cation exchange capacity	Ca	K	Mg	Na
					(milliequivalents/100g)				
Transition Forest									
0-5	6.85	11.96	4.93	8.47	38.14	22.95	0.026	18.83	1.318
20-30	6.25	2.63	0.73	2.45	13.53	0.97	0.058	16.70	0.912
Cloud Forest									
0-5	4.95 - 5.85	3.17 - 8.79	0.80 - 2.89	2.38 - 4.97	24.67 - 35.71	5.55 - 15.60	0.276 - 0.630	4.53 - 9.10	0.328 - 0.627
15-20	5.45 5.65	1.93 - 2.27	0.43 - 2.40	1.40 - 2.45	11.30 - 21.72	1.44 - 3.99	0.090 - 0.142	1.57 - 3.84	0.175 - 0.254
Wet Thicket									
0-5	4.95 - 5.10	4.08 - 20.29	1.10 - 12.20	2.45 - 13.96	21.30 - 44.76	1.63 - 27.00	0.057 - 0.905	1.94 - 15.20	0.157 - 1.529
10-20	5.45 - 5.70	3.35 - 3.62	0.85 - 2.26	2.38 - 3.50	13.53 - 22.6	3.77	0.101 - 0.297	4.40 - 5.53	0.342 - 0.351
Grassland									
0-5	5.60	1.81	2.53	1.33	10.71	1.34	0.065	1.21	0.122
15-20	5.55	1.00	1.50	0.84	12.76	0.69	0.026	0.69	0.081

* Analysis by Centro de Ecología, IVIC, Caracas.

TABLE 3. **Summary of the physiognomic and floristic characteristics of the vegetation types of Cerro Copey.***

Vegetation type	Canopy height (m)	Maximum DBH (cm)	Deciduous trees	Woody lianas	Vascular epiphytes	Bryophytes	Under-story herbs	Palms	Under-story shrubs	Mean leaf area (cm^2)
Transition Forest										
+ *Clusia rosea*	15 - 30	75	+	++	(+)	-	(+)	-	(+)	29.2
- *C. rosea*	10 - 15	40	+	++	(+)	-	(+)	(+)	(+)	
Cloud Forest										
Tall	15 - 22	75	(+)	+	+	+	++	+	+	23.0
Pole	13 - 16	35	(+)	+	+	+	+	+	+	
Lower palm	10 - 12	30	(+)	(+)	++	++	+	++	++	
Upper palm	6 - 9	25	(+)	-	++	++	+	++	(+)	
Wet Thicket										
Tall	3 -4	15	-	-	+	+	-	-	-	12.3
Short woody	1 - 2	10	-	-	+	+	-	-	-	
Herbaceous	0.5 - 1	n.a.	-	-	-	(+)	-	-	-	
Grassland	<0.5	n.a.	n.a.	n.a.	n.a.	(+)	n.a.	n.a.	n.a.	n.a.

* Symbols as in Table 1.

FIGURE 4. Transition Forest with *Clusia rosea.*

The irradiance in the understory and on the forest floor is greater than under *Clusia rosea,* and the undergrowth is more dense. Although the lower layers consist mainly of saplings of canopy tree species, there are also a few species of subcanopy trees, notably *Myrciaria* sp. and *Esenbeckia pilocarpoides.* Shrubs are rare. Herbaceous cover is sporadic; clumps of the sedge *Rhynchospora nervosa* occur in shaded gullies, and in places there are dense patches of the spiny bromeliad *Aechmea fendleri.*

Epiphytes, as in the other subtype of Transition Forest, are not abundant. They include the large-leaved *Anthurium hookeri,* a dwarf form of *Aechmea fendleri,* and an additional bromeliad, *Guzmania monostachya,* which is often abundant on exposed knolls close to the lower limit of the Transition Forest. Woody and herbaceous climbers are more frequent than under *C. rosea,* although the species composition is similar.

2. Cloud Forest. Cloud Forest is distinguished from Transition Forest by a far greater abundance of vascular epiphytes, bryophytes, and herbaceous ground cover, by the presence of palms, and by the decreased frequency of deciduous trees. The range of leaf sizes is narrower than in Transition Forest; all the trees have either notophylls or microphylls (Sugden, 1985). Cloud Forest occupies an altitudinal band 250–350 m wide that extends to the summits and ridges on the leeward side of the mountain (Figure 3).

The soils vary considerably in depth. On gentle slopes at lower altitudes (600–700 m), the profile may be up to 200 cm deep, while on steeper slopes near the summit the soil depth is usually no more than 40–50 cm and often as little as 20–30 cm. The litter and fermentation layers are more or less continuous but thin (normally less than 2 cm); deeper accumulations of litter and humus are sometimes found between boulders and among emergent roots. There is no distinct zonation in the mineral horizons, except for a gradual change (in the deeper soils) from a dull humic brown to reddish brown with increasing depth. At higher altitudes the mineral horizons become more clayey, and there is an increased concentration of roots in the upper 5 cm of soil, with fine roots often penetrating the litter layer. In the deeper soils, a discontinuous, hard, nodular layer is often encountered at depths of 70–120 cm. Despite the considerable structural variation in the Cloud Forest soils, there is relatively little variation in their chemistry (see Table 2).

There are four subtypes of Cloud Forest:

a. **Tall cloud forest.** This is undoubtedly the most species-rich of all the evergreen upland vegetation types, with a comparatively high diversity of all life-forms. Together with pole cloud forest (see below), it occupies the lower part of the altitudinal band of Cloud Forest; its lower limit is contiguous with Transition Forest, and its upper limit rarely exceeds 700 m even on leeward slopes. The height of the canopy ranges from 15 to 22 m, with trees attaining girths of up to 200 cm. Tall cloud forest is best developed in gullies sheltered from the wind.

Most of the tree species and individuals are evergreen, although the deciduous *Croton xanthochloros* and *Tabebuia chrysantha* (particularly the former) are frequent. The most abundant tree species are *Licania membranacea, Guapira*

FIGURE 5. Understory of tall cloud forest, showing abundant *Adiantum tetraphyllum*.

cf. *fragrans, Marlieriopsis eggersii, Myrcia* cf. *coriacea,* and *Maytenus karstenii.* The trees are generally upright, except on the steeper slopes, where they often lean downhill. Larger individuals of *Terminalia amazonia,* also an abundant species, sometimes have small buttresses. The understory is composed mainly of the saplings of canopy trees, especially *Guapira* cf. *fragrans* and *Myrcia* cf. *coriacea.* Subcanopy trees, including *Esenbeckia grandiflora, Guettarda odorata, Myrciaria* sp., and the palms *Euterpe karsteniana* and *Bactris falcata,* are frequent but not abundant. Prominent shrubs include *Psychotria muscosa, Solanum nudum,* and *Cestrum* sp. Large herbs, especially *Heliconia psittacorum, Maranta arundinacea, Aechmea fendleri,* and *Vriesea splendens,* are common; the most abundant one is *Adiantum tetraphyllum* Humb. & Bonpl. ex Willd. (FIGURE 5), the fronds of which arise singly from a creeping underground rhizome. Small herbs, including several grass and orchid species, are frequent (see TABLE 1).

Vascular epiphytes are mostly herbaceous and are confined mainly to the lower boles and branches, where they are abundant. Orchids (*Pleurothallis* spp., *Epidendrum* spp.), bromeliads (*Guzmania lingulata, Vriesea splendens*), aroids (*Anthurium hookeri, Philodendron* spp.), and ferns are well represented. Epiphytic bryophytes, especially the festoon-forming species such as *Taxilejeunea pterogonia* (Lehm. & Lindenb.) Schiffner, *Macromitrium cirrosum* (Hedwig) Bridel, *Orthostichopsis crinita* (Sulliv.) Broth., and *Phyllogonium fulgens* (Hedwig) Brid., and filmy ferns are patchily distributed; some boles have a substantial (up to 80%) covering, while others are more or less naked. Woody hemiepiphytes are present, although uncommon; *Clusia rosea* and *Ficus nymphaeifolia* occasionally occur, as do some of the hemiepiphytes (*Blakea monticola, Clusia* cf. flava, *Hillia parasitica, Norantea guianensis*) common in the Wet Thicket (see below) at higher altitudes. Epiphylls are evident for the first time in this altitudinal sequence of vegetation types. The older, shaded foliage of saplings and understory palms is often thickly encrusted with lichens and hepatics.

Woody climbers are frequent, represented almost exclusively by *Heteropterys laurifolia* and *H. macrostachya,* the latter easily recognized by the silvery, densely tomentose lower leaf surfaces. Both of these species are common in the understory in their preclimbing, straggling-shrub stage; when adult, their stems reach a maximum diameter of 2–3 cm. The scandent sedge *Scleria bracteata,* climbing by means of its minutely barbed leaf surfaces, frequently festoons the more open parts of the understory.

b. **Pole cloud forest.** This subtype extends over a range of altitudes similar to those of the tall cloud forest, differing from the latter in its lower stature (13–16 m), higher density of trees, and lower maximum bole girth (rarely more than ca. 100 cm) (see FIGURE 6). The term "pole" reflects the absence of trees of large girth. Pole cloud forest generally occurs on gentle slopes exposed to the prevailing winds, and its trees are mostly upright, with dense crowns. The crowns are often separated from their neighbors by clear spaces caused by mutual abrasion in the wind (FIGURE 7). The tree flora is very similar in composition to that of the tall cloud forest, although relative abundances are

FIGURE 6. Interior of pole cloud forest.

somewhat different (Sugden, in preparation); in particular, *Licania membranacea* is less common, and *Guapira* cf. *fragrans* and *Myrcia* cf. *coriacea* more common.

The woody understory is very similar to that of the tall cloud forest, with saplings of *Guapira* cf. *fragrans* and *Myrcia* cf. *coriacea* especially abundant. Shrubs and large herbs have a lower diversity, with the former represented

FIGURE 7. Canopy of pole cloud forest from below, showing mutual abrasion of neighboring crowns.

almost exclusively by *Psychotria muscosa,* and the latter by *Maranta arundinacea, Vriesea splendens,* and *Adiantum tetraphyllum.* There are also fewer species of small herbs.

The epiphytic flora is less luxuriant than that of the tall cloud forest, although there are no marked floristic differences. Again, the majority of the epiphytes are found in the shaded understory layers. Festooning bryophytes are less common, and these and the filmy ferns frequently dry out in spite of regular cloud cover.

Heteropterys laurifolia and *H. macrostachya* are again the most abundant woody climbers, and as in the tall cloud forest the juvenile individuals of both species are important components of the lower understory. Mature individuals with their crowns in the forest canopy rarely have stem diameters exceeding ca. 2 cm.

c. **Lower palm forest.** As its name implies, palm forest can be distinguished from the two previous Cloud Forest subtypes by a greater abundance of the palm *Euterpe karsteniana.* The height of the forest is reduced to 10–12 m, and *E. karsteniana* becomes an important component of the canopy, rather than a subcanopy tree. The individuals of this species usually have a single bole arising from a small (to ca. 30 cm tall) pyramid of stilt roots, among which there are frequently a number of juvenile shoots.

Lower palm forest occurs in a narrow (ca. 700–750 m) band on the windward slopes of Cerro Copey and in a somewhat wider one (ca. 750–850 m) on leeward slopes. Trees in this forest are smaller in both height and girth than in the previous Cloud Forest subtypes; boles are generally vertical, but a few lean by up to 20°.

Floristic differences between lower palm forest and the taller Cloud Forest subtypes are few. In the former, *Croton xanthochloros* and *Bactris falcata* are absent or nearly so. *Guapira* cf. *fragrans, Myrcia* cf. *coriacea, Maytenus karstenii,* and *Ilex guianensis* continue to be important components of the canopy.

The understory is generally denser than in the taller Cloud Forests, chiefly due to the abundance of *Psychotria muscosa*; saplings of canopy trees are common but less abundant. The subcanopy tree *Esenbeckia grandiflora* is commoner here than on any other part of the mountains.

Large and small herbs are less well represented, in both diversity and abundance. *Aechmea fendleri* and *Maranta arundinacea,* in particular, are uncommon, although *Adiantum tetraphyllum* occurs frequently. The understory and substrate are permanently damp, and the exposed boulders, roots, and fallen boles have a covering of mat- and cushion-forming bryophytes, especially *Leucobryum giganteum* C. Mueller and *L. antillarum* Schimper ex Besch.

The vascular epiphytic flora is similar in diversity and abundance to that of the tall cloud forest, except that the woody hemiepiphytes are more frequent. Epiphytic bryophytes, as on the substrate, are better developed than in the previous subtypes. Woody climbers, by contrast, are rare.

d. **Upper palm forest.** The last of the Cloud Forest subtypes, which extends to the summit of Cerro Copey on the leeward side, is distinct from lower palm forest in its lesser stature (6–9 m) and in the inclination of the trees (see FIGURE 8). Most boles are strongly (20–90°) inclined downhill, and they are frequently twisted and gnarled, branching at all levels in the forest profile. As a result of this habit and the generally boulder-strewn terrain, progress through upper palm forest is far more difficult than through the other forest types. Nevertheless, the principal components of the canopy are very similar to those of the lower palm forest, the only notable absentees being *Licania membranacea* and *Esenbeckia grandiflora.* Individuals of *Euterpe karsteniana* have more massive (up to 1 m tall and 70 cm across at the base) stilt-root systems and often have up to six shoots of canopy height as well as numerous juvenile shoots among the roots.

The understory is quite different from that of the lower palm forest. Shrubs are almost absent, and the density of young saplings is low. *Adiantum tetraphyllum* is present, although at a relatively low density, while *Aechmea fendleri* occurs more frequently than on any other part of the mountain, forming extensive spiny groves that contribute to the general impenetrability of the forest. Abundant scandent shoots of *Scleria bracteata,* with minutely serrated leaves and sheaths, supply an additional irritant and impediment to progress through the forest. Small herbs are few, represented chiefly by *Ichnanthus* sp., *Spiranthes adnata,* and *Elaphoglossum* sp. The boulders, lower boles, and exposed roots are covered with thick cushions of *Leucobryum giganteum* and *L. antillarum*; as in the lower palm forest, the understory is perpetually damp except in places where the canopy is thin and broken.

The epiphytic flora is notable for a much greater abundance of woody hemi-

FIGURE 8. Interior of upper palm forest, showing abundant bryophytes and leaning trees.

epiphytes (e.g., *Hillia parasitica, Clusia* cf. *flava*), which often form thick, tangled masses in the upper canopy. The flora of herbaceous epiphytes is similar in composition to that at lower altitudes, except for an increased frequency of the large bromeliad *Glomeropitcairnia erectiflora*. Woody climbers are entirely absent.

3. WET THICKET. Wet, windswept thickets less than 4 m tall dominate the windward slopes of Cerro Copey from ca. 800 m to the summit. They are distinguished from upper palm forest by their lesser stature, the absence of palms, and the reduced diversity and density of herbaceous epiphytes and bryophytes. The woody canopy plants are mostly microphyllous, and their leaves are significantly thicker than those of their counterparts in the Cloud Forest (Sugden, 1985).

The soils of the thickets are quite shallow—usually less than 40 cm deep. The litter layer is discontinuous, and the fermentation layer is barely discernible except where pockets of humus accumulate between boulders and large superficial or raised roots. Normally the top 15–20 cm is a coherent, wet, pale red-brown silty clay containing fragments of rotting leaves. The remainder of the profile, which gradually gives way to rock fragments and finally to bedrock at 30–40 cm depth, is more silty, more readily fragmented, and pale brown. Roots are sparse throughout, in contrast to their distribution in the forest soils, and wormcasts provide evidence of considerable animal activity. Although slightly more acidic (pH 4.95–5.70) than the Cloud Forest soils, the Wet Thicket soils display no chemical properties markedly different from those of the other upland soils (see TABLE 2).

There are three subtypes of Wet Thicket:

a. **Tall thicket.** This vegetation, which has a lower limit contiguous with upper palm forest on the windward slopes, is characterized by a canopy 3–4 m tall, an absence of boles more than ca. 10 cm in diameter, and an abundance of *Clusia* cf. *flava* (see FIGURE 9). Most of the woody species of the Cloud Forest are present in stunted form, but *C.* cf. *flava* is clearly the dominant species, forming extensive pure stands. *Blakea monticola* is also very common. Tall thicket has no discernible understory but is almost impenetrable due to the tendency of *C.* cf. *flava* to retain its dense branches at all levels. A hemiepiphyte, this species often has no discernible bole, and individuals are frequently much broader than tall. There are a small number of saplings, no shrubs, and few herbaceous species apart from *Scleria bracteata*. Herbaceous vascular epiphytes occur infrequently compared to the levels observed in the Cloud Forest; one of the common species in the tall thicket is the endemic orchid *Epidendrum johnstonii*. Bryophytes are much less abundant than in the palm forests, in spite of the permanent wetness of the boles and lower branches; generally, there is only a thin covering of creeping mosses and slimy algae.

Tall thicket occurs on all the slightly less exposed parts of the upper windward slopes of Cerro Copey and is also present in a narrow band a few meters wide along the ridges dividing the windward slopes from the leeward, where it forms the ecotone between the short thickets (see below) and the upper palm forest.

b. **Short woody thicket.** This vegetation differs from tall thicket in its lesser stature (1–2 m), its more even abundance of woody species, and its greater profusion of large herbs. *Clusia* cf. *flava* is still very common, but markedly stunted forms of Cloud Forest canopy tree species are much more frequent than in the tall thicket (see FIGURE 10). The large tank bromeliad *Glomeropitcairnia erectiflora* is a very prominent feature of this vegetation, usually

FIGURE 9. Canopy of tall thicket, showing *Clusia* cf. *flava* (Cf) and *Blakea monticola* (Bm).

FIGURE 10. Canopy of short woody thicket, showing abundant *Clusia* cf. *flava,* and flowering individuals of *Glomeropitcairnia erectiflora* (horizon).

growing epiphytically with its yellowish foliage fully exposed in the canopy. The trunkless tree fern *Cnemidaria grandifolia* (Willd.) Proctor is common here. *Scleria bracteata,* with very reduced internodes, is abundant. As in the tall thicket, most of the smaller forest herbs and epiphytes are absent. Interestingly, a high proportion of all species in the short woody thicket appear to germinate epiphytically, especially in the accumulations of organic matter in the axils of the dead basal leaves of individuals of *Glomeropitcairnia erectiflora.*

Short woody thicket dominates the most-exposed slopes near the principal

FIGURE 11. Grassland at 900 m on Cerro Copey.

ridges and summits of Cerro Copey. Progress through this vegetation is exceptionally difficult. The ground is invisible, there is nothing substantial to grasp hold of, the leaves and stems of *Scleria bracteata* lacerate the skin, and large bromeliads empty tankfuls of water into one's boots. In addition, a gale blows almost perpetually.

c. **Herbaceous thicket.** The last of the three Wet Thicket subtypes consists mainly of herbs 0.5–1 m tall. Floristically, it is not dissimilar to the herbaceous component of the short woody thicket. *Glomeropitcairnia erectiflora* is again abundant, and *Scleria bracteata* often occurs in extensive pure stands. The ferns *Dicranopteris flexuosa* (Schrader) Underw. and *Pteridium aquilinum* L. are frequent. Orchids, particularly *Epidendrum nocturnum* and *E. secundum*, occur as isolated individuals or in small clumps. Woody species are present but not abundant and do not constitute the main structural component of the vegetation. They include scandent or loosely branched shrubs such as *Wedelia caracasana, Centropogon cornutus,* and *Clidemia hirta*; suffrutescent species such as *Oxalis frutescens* and *Sauvagesia erecta*; and occasional individuals of stunted trees, especially *Rapanea guianensis, Myrcia* cf. *coriacea,* and *Roupala montana.*

Herbaceous thicket occupies sites similar in aspect, topography, and altitude to those inhabited by short woody thicket.

4. GRASSLAND. Grassland (FIGURE 11) is by far the most restricted vegetation type of all those described here, occurring in a few patches of several hundred square meters close to the summit of Cerro Copey in moderately sheltered sites. It warrants consideration as a separate vegetation type due to the absence of the large, coarse herbs that dominate the herbaceous thicket, and to the presence of smaller herbaceous species that are rare or absent in other vegetation types. The most abundant species, which was never observed to flower and hence remains undetermined, appears to be a species of *Trachypogon.* Clumps of *Andropogon bicornis* and *A. leucostachys,* and of several small sedges, are frequent. *Scleria bracteata* is absent. There is no evidence to suggest that the Grassland represents sites of earlier disturbances.

Grassland soils are typically drier than any of the Wet Thicket ones, and the mineral horizons are distinctly silty. The litter and fermentation layers are very thin, and the carbon content at the top of the profile is low compared to that of the other soils (see TABLE 2). Small stones are distributed throughout the profile, and the overall depth rarely exceeds 50–60 cm.

Ecotones and Variations

The boundaries between the various vegetation types and subtypes range from abrupt to gradual, and it is always possible to find intermediate types. Abrupt ecotones are generally found between the two subtypes of Transition Forest, between Cloud Forest and Wet Thicket, and between Wet Thicket and Grassland. The ecotones within the Cloud Forest and the Wet Thicket are characteristically more gradual, except where they accompany sharp changes in topography (e.g., on the main ridge of Cerro Copey—see FIGURE 12). Zo-

FIGURE 12. Main ridge of Cerro Copey, looking southeast, showing contrast between windblown vegetation (right) and sheltered vegetation (left).

nation of the vegetational subtypes tends to be more marked on the windward slopes; on leeward slopes, there is more intergradation, the canopy is less dense, and epiphytes are usually less abundant.

There are patches of vegetation that do not correspond well to the scheme outlined above, but these are limited in extent. For example, areas more or less devoid of palms can be found within the lower and upper palm forests, while other floristic and physiognomic criteria remain unchanged. On exposed knolls in the pole cloud forest, canopy height is sometimes reduced to as little as 10 m, but this reduction is not associated with features of the stunted vegetation at higher altitudes. Patches of upper palm forest with an open and broken canopy—and a correspondingly well-lit understory with abundant *Scleria bracteata* and relatively few epiphytes—occur on the leeward sides of some of the principal ridges.

Gaps in the canopy caused by falling trees are a common feature of the taller Cloud Forest subtypes. Gaps are smaller and less frequent in the palm forests and are (obviously) absent from the Wet Thicket. An interesting characteristic of many of the gaps is that the uprooted tree does not die but produces epitrophic shoots from the fallen bole, some or all of which may eventually reach the canopy and also become rooted independently.

Human activity in the evergreen vegetation of Cerro Copey appears to have been limited. Of all the vegetation types described here, only Transition Forest may have been subject to significant disturbance in the past, partly due to selective felling for construction materials and partly due to goats, which have been far more numerous on the island than they are at present. Cerro Copey is now a National Park, and cutting of the vegetation above 100 m is prohibited. Nevertheless, the construction of the summit road in the early 1970's, and the attendant disturbances, has led to the invasion of a considerable number of weedy species, mostly from the lower slopes. These species, listed in the APPENDIX, are presently confined largely to roadsides and the landslides provoked during construction.

Vegetation of Matasiete, Guayamurí, and Tragaplata

On Cerros Matasiete and Tragaplata, which are similar to each other in size, there is a compression and mixing of the vegetation types seen on Cerro Copey. The limit of Transition Forest on these mountains is lower. *Clusia rosea* Transition Forest is especially well developed, and aerial photographs clearly show that it occupies at least 50 percent of the total area above 350 m on both mountains. At the upper limit of the Transition Forest on the leeward slopes (550–600 m), there is a much more marked and sudden increase in wetness than on Cerro Copey, and vascular epiphytes and festooning bryophytes become abundant quite suddenly. This narrow band of Cloud Forest between the Transition Forest and the highest ridges has the physiognomy of lower palm forest, but with a low frequency of palms. On the windward sides of the ridges and summits, there is a wide band of tall woody thicket with abundant *Clusia* cf. *flava,* and on Cerro Tragaplata there is also a small area of short woody thicket close to the summit. Neither peak supports any Grassland.

Cerro Guayamurí supports near its summit a curious mixture of Transition Forest, Cloud Forest, and Wet Thicket, with a physiognomy that can only be described as patchy and apparently disorganized. The area of the upper slopes is so small (less than 20 ha) and the topography so rugged that there is no clear zonation. The summit, although less than 500 m high, is very moist, and epiphytes including festooning bryophytes are abundant. In the apparent absence of *Clusia* cf. *flava,* the Wet Thicket on the windward slopes is a tangled mass of wind-pruned trees, especially *Guapira* cf. *fragrans, Clusia rosea,* and *Calliandra panlosia.*

The upper slopes of these three mountains are not sufficiently well explored for accurate floristic comparisons to be made with Cerro Copey. It is clear, nevertheless, that the overall species richness (especially on Cerro Guayamurí) is less than that on Cerro Copey. In general, species that are common on Cerro Copey (except for the Wet Thicket species) are also present on Matasiete and Tragaplata, although not necessarily on Guayamurí; notable absentees from the latter include palms and many of the epiphytic species. No species has been encountered on any of the smaller mountains that is not known from Cerro Copey.

Upland Vegetation of Macanao

The western mountains of Margarita, on the peninsula of Macanao, support a series of vegetation types that are interestingly different from those of Cerro Copey and its smaller satellites. Although the principal peaks of Macanao—Soledad and Los Cedros—are as high as Matasiete and Tragaplata, and although there is a trend toward increasingly evergreen vegetation with higher altitude, there is no vegetation that approaches that of the eastern mountains in terms of wetness or abundance of epiphytes.

The highest parts of the Macanao mountains are best ascended from the village of San Francisco, which is situated at the mouth of a steep valley on the northern side of the range. To within 100 m of the principal summit (Los Cedros), the steep slopes are clothed in deciduous woodland of varying height and density. *Bursera simaruba* (L.) Sarg. and *Ceiba pentandra* are common trees, reaching heights of up to 15 m. In previous times *Cedrela* sp. was abundant, but it has been mostly removed over the past century for timber. In the gullies and on some of the more sheltered slopes, there are more evergreen trees, especially species of Capparidaceae. Limited areas have been cleared for the cultivation of mango and manioc, but neither crop is very successful due to the very sporadic rains. Columnar cacti are a prominent feature of all the slopes, particularly in the deciduous woodland; old, much-branched individuals of *Ritterocereus* sp. attain heights of up to 12 m. At higher altitudes, a scandent *Hylocereus* sp. occurs frequently, while at lower levels *Opuntia* spp. and a species of *Melocactus* are common in the ground layer. Epiphytes are infrequent on the dry slopes and are mainly represented by small xeromorphic *Tillandsia* spp.

As one approaches the summit of Los Cedros from the leeward side, there is an abrupt floristic change at ca. 550 m. The deciduous species of the lower slopes are replaced by small, mainly evergreen ones approximately 6–10 m tall, including *Clusia* cf. *minor* L., *Erythroxylum undulatum* Plowman, and *Psidium* sp. Some deciduous species, particularly *Coccoloba* sp., are also present and are confined to this upper zone. Large columnar cacti persist. There is a sudden increase in the frequency of epiphytes; xeromorphic species such as *Rhipsalis* sp., *Campylocentrum micranthum, Anthurium scandens* (Aublet) Engler, and *Tillandsia bulbosa* Hooker are common, and many branches are festooned with bearded lichens.

The vegetation of the summit is sparse and patchy, with stunted wind-pruned trees standing individually or in small groups on an otherwise bare expanse of loose stones and compacted gravel (possibly the result of human intervention). Most of the trees, usually no more than 5 m tall, support a dense epiphytic flora consisting of a mixture of mesomorphic and xeromorphic forms. *Guzmania monostachya,* a small tank species, is abundant on the boles and lower branches; the larger tank species *Vriesea platynema* Gaudich., with water-filled leaf axils, forms substantial colonies on the middle branches, while xeromorphic bromeliads (*Vriesea heterandra* (André) L. B. Smith, *Tillandsia bulbosa,* and *T. kegeliana* Mez) occupy the outermost twigs. In addition, there are several small leathery-leaved orchids and climbing epiphytic ferns.

On the windward side of the summit of Los Cedros, which like all other parts of the mountain is very steep (> 30°), there is a patch of evergreen forest extending some 70–80 m down the slope. In floristic terms this can best be described as an impoverished mix of Transition Forest and Cloud Forest. The commoner trees include *Guapira* cf. *fragrans, Cupania americana, Coccoloba* sp., and *Clusia minor.* There are no palms, and *Clusia rosea* is absent. The epiphytic flora is similar to that of the summit, with such notable additions as *Vriesea splendens, Guzmania lingulata, Anthurium hookeri,* and several large ferns that are present in the shaded understory. As on the lower slopes, there is only a sparse ground cover, and the soil surface is often fully exposed. The litter is dry and discontinuous, and there is a barely discernible fermentation layer covering the mineral soil; the latter has a loose, silty consistency and is pale gray-brown. Small stones, boulders, and outcrops of bedrock are frequent.

This patch of evergreen vegetation, no more than two or three hectares in extent, is being rapidly degraded by local commercial plant collectors.

DISCUSSION

In the Neotropics, montane vegetation that is largely dependent on cloud interception and strongly influenced by wind is a relatively unusual phenomenon. It occurs on two other small mountains on the Caribbean coast of South America, which have been considered in previous articles (Sugden, 1982a, 1982b, 1983); these are Cerro Santa Ana (830 m), on the peninsula of Paraguaná, Venezuela, and the Serranía de Macuira (865 m), on the peninsula of Guajira, Colombia. Of the three, the Margarita mountains have the richest vascular flora and exhibit the most marked physiognomic zonation and variety; nevertheless, the range of physiognomic types in the three localities is essentially similar, with relatively tall forest on sheltered slopes contrasting with low, windswept thickets on the more exposed upper slopes.

Varying levels of exposure to strong, cloud-bearing winds have been shown to have important effects, even if rainfall is high, on the distribution of montane vegetation types elsewhere in the Caribbean region. A good example is the Cordillera de Tilarán, Costa Rica (Lawton & Dryer, 1980), where the cloud flux on the windward slopes results in a richer and denser epiphytic flora than is found on the leeward slopes, even though the annual rainfall is higher (> 2000 mm) and the dry season much shorter (four months) than on Margarita. Wind reduces the canopy height of these forests to 2–8 m near the main ridge of the Cordillera (1850 m), while in sheltered gullies on the leeward side it may attain 30–40 m (Lawton & Dryer, 1980). Persistent wind also affects forest stature on smaller (i.e., ca. 1000 m alt. or less) wet mountains in the region, especially in Panama (Myers, 1969), the Lesser Antilles (Beard, 1944, 1955), and Puerto Rico (Howard, 1968; Baynton, 1969).

In a previous article (Sugden, 1982a) I discussed the question of the classification of the montane vegetation of the Serranía de Macuira. Most of the arguments also apply to the Margarita vegetation and need only be summarized here. The classification scheme of Holdridge (1967) was found to be unsatisfactory for the wetter vegetation types since it does not take into account the effects of cloud interception, seasonality, or persistent high wind. The Cloud Forest on Margarita conforms well to the category of Upper Montane rain forest *sensu* Grubb and Tanner (1976) and can be subdivided according to the scheme of Beard (1955) into "Montane Rain Forest" (pole and tall cloud forest), "Montane Thicket" (lower palm forest), and "Elfin Woodland" (upper palm forest). The palm forests described here are not to be confused with the "Palm Brake" of Beard (1944), which is a formation with a very broken and uneven canopy consisting mainly of palms 15–18 m high and having few, rather scattered, dicot trees of very variable size. Beard (1955) subsequently removed this formation from his classification scheme on the grounds that it is a successional stage following severe disturbance, rather than a relatively stable "climax" formation.

The Wet Thicket of Margarita is best regarded as a specialized, wind-pruned facies of Upper Montane forest or Elfin Woodland. Neither the Wet Thicket nor the Grassland should be regarded as páramo or "subpáramo" (as they are frequently described on herbarium labels), which are very different formations determined by low temperatures at high altitudes rather than by wind.

The Transition Forest is clearly too dry to conform to the categories of Upper or Lower Montane rain forest. However, it is not dissimilar to the Tropical Dry Forest of Holdridge (1967), a vegetation type that is normally characterized by a mixture of evergreen and deciduous trees with a canopy 15–25 m high, and occurs in lowland areas with mean annual rainfall of 1000–2000 mm. There are also some parallels with the Semi-Evergreen Seasonal forest of Beard (1944), which has a canopy 20–26 m high, a mixture of evergreen and deciduous trees (mostly unbuttressed), and a relative scarcity of epiphytes.

The possible factors that determine the physiognomy of the various montane vegetation types can be summarized as follows. Cloud cover and flux determine the level of the ecotone between the dry vegetation types and the Transition Forest, and increasing cloud flux at higher altitudes sustains a richer and denser epiphytic flora. High winds cause the extreme reduction in stature observed in the Wet Thicket. A combination of wind and a thin, unstable substrate may lead to the reduced stature of upper palm forest on exposed slopes. On leeward slopes a reduction in soil depth at higher altitudes may limit the growth of the trees. In some instances individual species may have a significant effect on the physiognomy of an entire vegetation type, for instance *Clusia rosea* in Transition Forest. All of these possibilities merit further investigation.

Some of the observed trends, including the virtual absence of understory shrubs from the upper palm forest, and the steady decrease with altitude in the density and diversity of woody lianas, have no ready explanations. The latter trend is commonly observed on larger, wet, tropical mountains (cf. Grubb & Tanner, 1976), but it is surprising to find the same phenomenon over such a narrow range of elevations as on Margarita. Since there are relatively few species of either shrubs or lianas in the Margarita forests, the observed trends may reflect the habitat requirements of individual species rather than those of the life-form as a whole.

The relationship between soils and vegetation on the Margarita mountains would repay further investigation. Soils derived from ultramafic rock are often very infertile and inimical to plant growth (Proctor & Woodell, 1975). However, the limited results presented here (Table 2) suggest that the montane soils are not particularly infertile, and there is little to indicate that differences in soil chemistry are responsible for the physiognomic variety of the vegetation. All the soils have a pH favorable to plant growth and, with the possible exception of the Grassland soils, have no obvious mineral deficiencies. A high ratio of magnesium to calcium, normally typical of ultramafic soils (Proctor & Woodell, 1975), is found only in the Transition Forest soil.

The montane forests of Margarita clearly provide an interesting opportunity for investigating the factors limiting the distribution of vegetation types on wet tropical mountains. Their existence indicates that the peculiar features of montane forest physiognomy can be achieved at relatively high temperatures, on apparently fertile soil, and in the absence of the constraints imposed by regular daytime cloud cover. Given these conditions, and the evident versatility of many of the tree species with regard to habitat, the Margarita forests represent a useful, and in a sense experimental, site for further studies. The present account of the vegetation was in part stimulated by Johnston's (1909, p. 281) earlier observation that "there is an interesting field for study in the distribution of the individual species of plants whether in groups or singly, whether in one place or scattered in many, and whether on one slope and not another." The mountains of Margarita are easily accessible, especially since there is now a road to the summit of Cerro Copey, and the natural vegetation is protected from destruction by Venezuelan law. It would be a pity if another 75 years were to elapse before further effort is made to explore the questions raised herein.

ACKNOWLEDGMENTS

This work was mostly supported by a grant from the Natural Environment Research Council; I am grateful to Corpus Christi College, Cambridge, the Percy Sladen Fund, and the Royal Society/CONICIT (Venezuela) exchange program for further support.

Permission to work in the forests of Cerro Copey was kindly granted by the Instituto Nacional de Parques (INPARQUES), Caracas, and the help of the superintendent of parks in Isla Margarita, Ruben Riera, was invaluable. Generous assistance with the processing of collections was provided by the director and staff of the Herbario Nacional de Venezuela; I am also grateful to Dr. Jesús Hoyos for allowing me to consult the collections and records of the herbarium of the Sociedad de Ciencias Naturales La Salle, Caracas. I am indebted to experts at the Herbario Nacional, and at the Royal Botanic Gardens, Kew, the British Museum (Natural History), the New York Botanical Garden, and the Smithsonian Institution for help with the determination of collected material. Drs. Peter Grubb and Edmund Tanner made useful comments on an earlier draft of this article.

Ernesto Medina and Helen d'Abreu (Centro de Ecología, IVIC, Caracas) helped in many ways throughout the project; Ernesto Medina kindly organized the analysis of soil samples. I am very grateful indeed for the hospitality of Olivia Walker, Marie-Claude Muller, and Domingo Nedelka in Caracas, and of Carmen Zingg de Machado in Margarita, without which this project would have been much more difficult.

LITERATURE CITED

ALEXANDER, C. S. 1958. The geography of Margarita and adjacent islands, Venezuela. Univ. Calif. Publ. Geogr. **12:** 85–182.

——— & J. BERTNESS. 1982. A comparative study of modern and ancient beach morphologies: insights to the paleoclimate of Margarita Island, Venezuela. J. Geol. **90:** 663–678.

BAYNTON, H. W. 1969. The ecology of an elfin forest in Puerto Rico, 2. The microclimate of Pico del Oeste. J. Arnold Arbor. **49:** 419–430.

BEARD, J. S. 1944. Climax vegetation in tropical America. Ecology **25:** 127–158.

———. 1955. The classification of tropical American vegetation types. *Ibid.* **36:** 89–100.

CONTRERAS, A. 1967. Características pluviométricas del Estado Nueva Esparta. Mem. Soc. Ci. Nat. La Salle **27:** 46–75.

GONZÁLEZ DE JUANA, C., & M. VIGNALI. 1972. Rocas metamórficas e igneas en la península de Macanao, Margarita, Venezuela. Mem. VI Conf. Geol. del Caribe, pp. 63–68.

GRUBB, P. J. 1977. Control of forest growth and distribution on wet tropical mountains with special reference to mineral nutrition. Ann. Rev. Ecol. Syst. **8:** 83–107.

——— & E. V. J. TANNER. 1976. The montane forests and soils of Jamaica: a reassessment. J. Arnold Arbor. **57:** 313–368.

HOLDRIDGE, L. R. 1967. Life zone ecology. 124 pp. Tropical Science Center, San José, Costa Rica.

HOWARD, R. A. 1968. The ecology of an elfin forest in Puerto Rico, 1. Introduction to composition studies. J. Arnold Arbor. **49:** 381–418.

JAM, P. 1962. Aspectos geográficos del Estado Nueva Esparta. Mem. Soc. Ci. Nat. La Salle **22:** 34–50.

——— & M. MENDEZ-AROCHA. 1962. Geología de las islas de Margarita, Coche y Cubagua. Mem. Soc. Ci. Nat. La Salle **22:** 51–93.

JOHNSTON, J. R. 1909. Flora of the islands of Margarita and Coche, Venezuela. Contr. Gray Herb. **37:** 1–149.

LAHEY, J. F. 1958. On the origin of the dry climate in northern South America and the southern Caribbean. Dept. Meteorol. Univ. Wisconsin Sci. Rep. **10:** 1–290.

LAWTON, R., & V. DRYER. 1980. The vegetation of the Monteverde cloud forest reserve. Brenesia **18:** 101–116.

LEIGH, E. G. 1975. Structure and climate in tropical rain forest. Ann. Rev. Ecol. Syst. **6:** 67–86.

MARCUZZI, G. 1950. Notas preliminares sobre la fauna y flora de la isla de Margarita. Mem. Soc. Ci. Nat. La Salle **10:** 207–256.

MYERS, C. W. 1969. The ecological geography of cloud forest in Panama. Am. Mus. Novit. **2396:** 1–52.

ORTEGA, F. J. 1982. La fitogeografía de las pteridofitas de la isla de Margarita. Mem. Soc. Ci. Nat. La Salle **42:** 135–150.

PROCTOR, J., & S. R. J. WOODELL. 1975. The ecology of serpentine soils. Adv. Ecol. Res. **9:** 255–366.

STEYERMARK, J. S., & O. HUBER. 1978. Flora del Avila. 971 pp. Sociedad Venezolana de Ciencias Naturales, Caracas.

SUGDEN, A. M. 1982a. The vegetation of the Serranía de Macuira, Guajira, Colombia: a contrast of arid lowlands and an isolated cloud forest. J. Arnold Arbor. **63:** 1–30.

———. 1982b. The ecological, geographic, and taxonomic relationships of an isolated Colombian cloud forest, with some implications for island biogeography. *Ibid.* 31–61.

———. 1983. Determinants of species composition in some isolated Neotropical cloud forests. Pp. 43–56 *in* S. L. SUTTON, T. C. WHITMORE, & A. C. CHADWICK, eds., Tropical rain forest: ecology and management. Special Publication Number 2 of the British Ecological Society. Blackwell, Oxford.

———. 1985. Leaf anatomy in a Venezuelan montane forest. J. Linn. Soc., Bot. **89:** 231–241.

———. (In preparation.) Physiognomy and regeneration in a Venezuelan montane forest.

APPENDIX. **Invasive species of roadsides and landslides.**

TREES AND SHRUBS

Boraginaceae	*Cordia curassavica* (Jacq.) Roemer & Schultes
Euphorbiaceae	*Croton populifolius* Miller

Leguminosae	*Mimosa arenosa* Poiret
Moraceae	*Cecropia peltata* L.
Solanaceae	*Solanum asperum* Vahl
	Solanum sp.
Sterculiaceae	*Melochia tomentosa* L.
Ulmaceae	*Trema micrantha* Blume
Verbenaceae	*Lantana camara* L.
	Lantana canescens H.B.K.

CLIMBERS AND SCRAMBLERS

Apocynaceae	Sp. indet.
Compositae	*Calea solidaginea* H.B.K.
	Vernonia moritziana Schultz Bip.
	Vernonia scorpioides (Lam.) Pers.
Convolvulaceae	*Evolvulus sericeus* Sw.
	Jacquemontia nodiflora (Desr.) G. Don
	Jacquemontia pentantha (Jacq.) G. Don
Euphorbiaceae	*Phyllanthus niruri* L.
Leguminosae	*Canavalia oxyphylla* Standley & Williams
	Chaetocalyx scandens (L.) Urban

HERBS AND SUFFRUTESCENT PLANTS

Amaranthaceae	*Achyranthes indica* (L.) Miller
Boraginaceae	*Heliotropium angiospermum* Murray
Campanulaceae	*Isotoma longiflora* (L.) Presl
Compositae	*Bidens pilosa* L.
	Conocliniopsis prasiifolia (DC.) R. M. King & H. Robinson
	Emilia javanica Fosberg
	Eupatorium ballotaefolium H.B.K.
	Pluchea odorata (L.) Cass.
	Psila trinervis (Lam.) Cabrera
	Sonchus asper (L.) Miller
	Sonchus oleraceus L.
Cyperaceae	*Scleria hirtella* Sw.
Euphorbiaceae	*Chamaesyce dioica* (H.B.K.) Millsp.
Gramineae	*Ichnanthus acuminatus* Sw.
	Panicum latifolium L.
	Paspalum conjugatum P. Bergius
	Paspalum fimbriatum H.B.K.
	Paspalum millegrana Schrader
	Paspalum saccharoides Nees
	Polypogon cf. *semiverticillatus* (Forsskål) Hylander
Leguminosae	*Desmodium axillare* (Sw.) DC.
Lythraceae	*Cuphea denticulata* H.B.K.
Orchidaceae	*Habenaria monorrhiza* (Sw.) Reichb. f.
Rubiaceae	*Borreria laevis* (Lam.) Griseb.
	Diodia apiculata (Willd. ex Roemer & Schultes) Schumann
	Diodia teres Walter
	Spermacoce verticillata L.
Verbenaceae	*Stachytarpheta jamaicensis* (L.) Vahl

Note added in proof. A new flora of Margarita Island has recently been published: Hoyos, J. Flora de la Isla Margarita, Venezuela. 927 pp. Monografía no. 34, Sociedad y Fundación La Salle de Ciencias Naturales, Caracas.