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Climatic factors and tree stature in the elfin cloud forest of Serrania de Macuira, Colombia

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ABSTRACT

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Cloud cover, solar radiant flux density, temperature and relative humidity regimes were studied along the altitudinal gradient of Serrania de Macuira (865 m), Guajira, Colombia. The regional climate at Macuira is characterized by the presence of small cumulus clouds, persistent trade winds from the northeast, and low and highly seasonal rainfall. During the day time, the clouds remain above the highest peaks of the Serrania, decreasing radiation, air temperature, relative humidity and evaporation in relation to the lowlands. At night the clouds come into contact with the forest, supplying water by means of mist and fog interception. Owing to this pattern, the cloud forest trees on top of the mountain experience low air saturation deficits only during the night, early morning and late afternoon. This shows that the low stature of trees in this forest is not the result of an uninterrupted low saturation deficit that would inhibit mineral pumping by means of transpiration.

The soil temperature gradient in Macuira was steeper than that reported for higher and more massive mountains of the tropics. This steeper gradient is the result of high temperatures in the dry lowlands around the mountain. Strong winds seem to be the cause of the reduction in tree stature in the more exposed slopes and ridges, but are not the general explanation for small trees in this forest. Wind speed is much lower in gullies than on ridges and slopes, nevertheless, trees are also small. We think that the climatic factor that has a more pronounced effect on the physiognomy of this forest is cloud water. The effects of high water content of the soil on soil chemistry, would be worth investigating as a general explanation for the small stature of these trees.

INTRODUCTION

Tropical montane rain forests are usually characterized by persistent or frequent fog, low air and soil temperatures, high relative humidity, high soil water content, and low levels of solar radiation. These and other climatic factors, such as wind speed and evaporation, have not often been documented owing to difficult access and lack of an adequate network of weather stations (Wadsworth, 1948; Dale, 1964; Grubb and Whitmore, 1966, 1967; Baynton, 1968;

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Odum et al., 1970). However, some hypothesized explanations of tree structure and physiognomy in cloud forests are based on climatic factors. Odum (1970) suggested that short forests result when the saturation deficit is persistently low and dry air is not available for the mineral pumping in the transpiration stream. Grubb (1977) presented some evidence against this hypothesis, and suggested that the zonation of montane forests could be explained in terms of the availability of certain nutrients; the rate of mineralization of humus could decrease with either lower mean temperature (high altitudes) or increase in soil water content (see also Grubb, 1971). Grubb (1974, 1977) also proposed that the most important consequence of cloud cover in montane habitats is a decrease in radiation load, which prevents sunlight raising leaf temperature toward the optimal level. This reduction in leaf temperature may reduce the rate of photosynthesis to the extent of limiting the supply of metabolites to the roots (Hantrick and Bowling, 1973). Lawton (1982) and Lawton and Dryer (1980), suggested that elfin stature in these forests is an adaptive response to greater winds along exposed ridges.

In this study, daily variations of cloud cover, radiant flux density, relative humidity, evaporation, and air and soil temperatures along the altitudinal gradient of Serrania de Macuira are described. The possible effects of climatic conditions on the physiognomy of elfin cloud forests are discussed.

MATERIALS AND METHODS

Study site

This study was conducted in the elfin cloud forest (Fig. 1) at Serrania de Macuira (~12°N, 71°W), Guajira Peninsula, Colombia (Fig. 2). Serrania de Macuira is located within the south Caribbean Dry Zone (Sugden, 1982) where rainfall is scarce and unevenly distributed. This area is characterized by mean annual rainfall <1000 mm (450 mm around Macuira), rains are concentrated between September and November, and air masses are constantly moving from the ocean towards the continent (Lahey, 1958; Snow, 1976). Serrania de Macuira has three peaks, Palua (865 m), Huarech (853 m) and Jiborne (753 m) which are separated from each other by dissected terrain (Sugden, 1982). Macuira is made of granite nucleus surrounded by gneiss and schists (Macdonald, 1964). The elfin cloud forest of Macuira is located on the upper slopes above 500–550 m on the windward side, and above 600–650 m on the leeward side of the mountain. The cloud forest is surrounded by a dry deciduous forest and thorn woodlands on the slopes and lowlands, respectively. The transition between the dry deciduous forest and the cloud forest is very sharp; 50 m in altitude and 100–150 m on the slope. The physiognomy and floristics of the forests have been described by Rieger (1976), Sugden and Robins (1979) and Sugden (1982). Mist and fog inter-

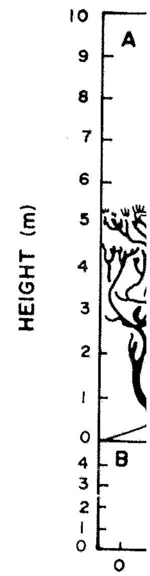

Fig. 1. Physiognomic
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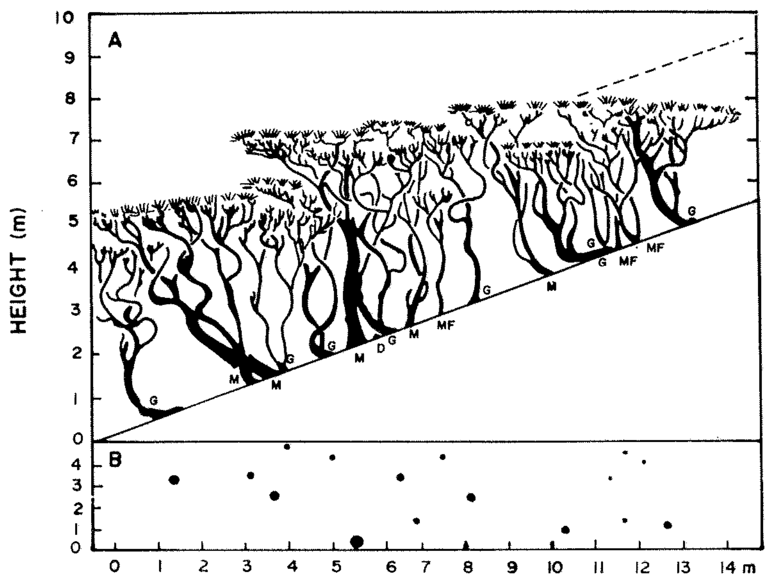

Fig. 1. Physiognomic and floristic profile of an elfin cloud forest. Slope at 700 m on the windward side (NE) of Cerro Huarech, Serrania de Macuira. The letters at the base of the trees correspond to the following species: D = *Dendropanax arboreus*, G = *Guapira fragrans*, M = *Myrcia splendens*, MF = *Myrciantes fragrans*. In the lower panel, the diameter and position of the trees in the 15 m by 5 m plot. The abundant ephiphytes have not been drawn. The drawing is to scale.

ception at Macuira and other cloud forests along the Caribbean coast of South America have been described by Cavelier and Goldstein (1989). Before this study there were no records of climatic conditions on this mountain.

Climatic measurements

The frequency of cloud cover was studied by means of satellite images and field observations. For images (GOES-E black/white) taken every day at 7:00, 12:00 and 19:00 h, from 15 June to 15 July 1984, the presence or absence of a small cumulus cloud (~ 300 km^2), and large clouds covering Macuira and the Guajira Peninsula (synoptic systems) were recorded. There was a clear distinction between the small, local cumulus cloud formed by the Serrania and the very large synoptic clouds. Since we examined images three times a day, we probably recorded most if not all of the synoptic systems that affected the area during the study period. In the field, the time the cloud base was observed on the mountain at 650 m and 750 m was recorded. These observations were made from 700 m on one of the ridges of Cerro Huarech during early morning and late afternoon between 15 June and 28 July 1984.

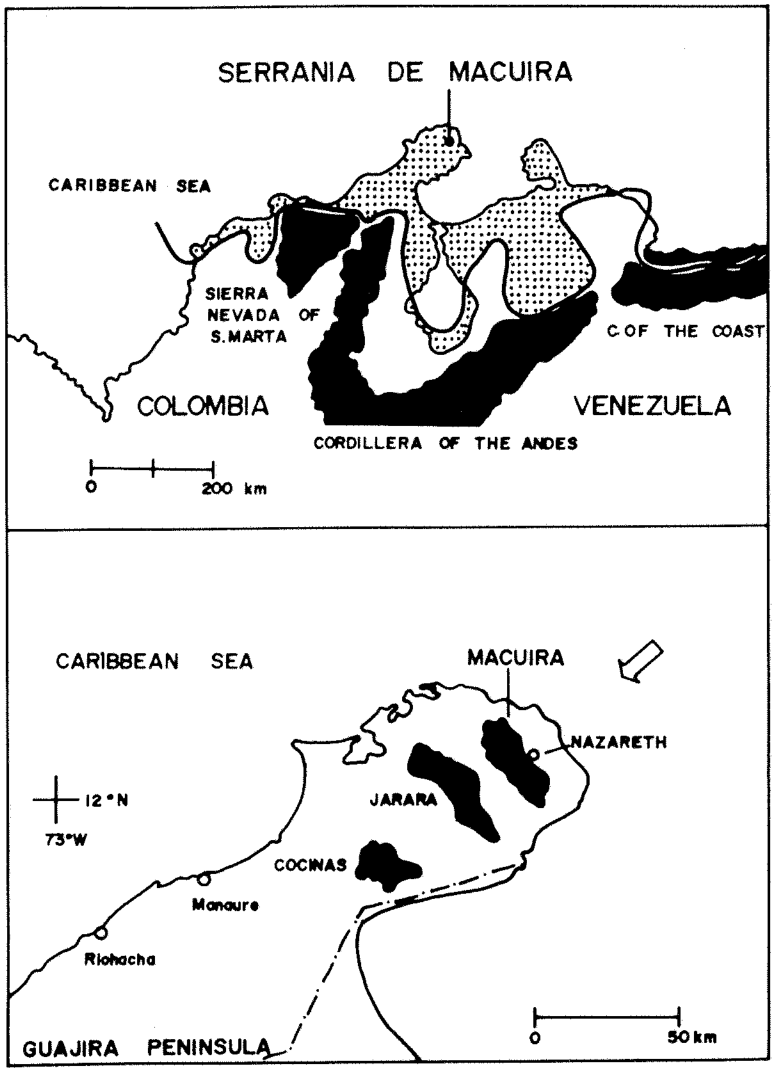

Fig. 2. In the upper panel, map of northern Colombia and Venezuela showing the location of Serrania de Macuira. The solid line is the 1000 mm isohyet, and the stippled area represents the Caribbean dry zone (adapted from Lahey, 1958; Cavelier and Goldstein, 1989). In the lower panel, location of Serrania de Macuira in the Guajira Peninsula. The arrow represents the prevailing wind direction (NE). For both panels, the black areas represent mountains more than 200 m in altitude.

Climatic measurements along the altitudinal gradient of Macuira were made at stations located at 85, 200, 300 and 700 m (Fig. 3). The data were collected manually during the day, between 15 June and 13 July 1984. Radiant flux

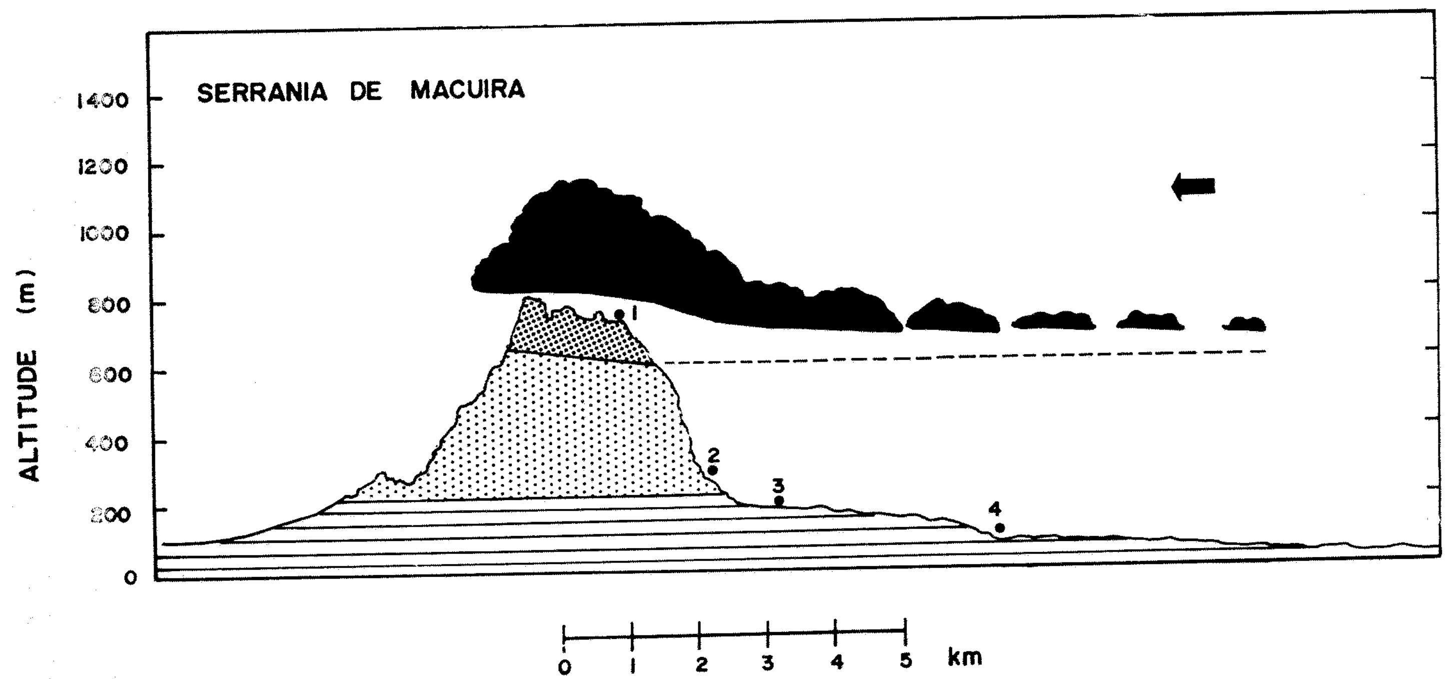

Fig. 3. Location of weather stations (June–July 1984) along the altitudinal gradient of Serrania de Macuira. The stations were located in the elfin cloud forest (1), dry deciduous forest (2) and thorn woodlands (3,4). The cloud base is at the condensation level observed during mid-morning. The dashed lines represent the condensation level at night, and the arrow represents the prevailing wind direction (NE).

density (RFD, W m^{-2}) was measured with pyranometers (LI-COR, LI-200 s), photosynthetically active radiation, (PAR, μmol m^{-2} s^{-1}) was measured with quantum sensors (LI-190), air and soil (surface, −5 cm and −30 cm) temperatures (°C) were measured with copper–constantan thermocouples and a microvoltmeter, relative humidity (%) was measured with Assman psychrometers, evaporation (g m^{-2}) was measured with Piche evaporimeters, and wind speed (m s^{-1}) was measured with a three-cup anemometer. The counters of the pyranometer, anemometer and the column of water in the evaporimeter were recorded every half an hour, while quantum sensors, thermocouples and the psychrometer were read as instantaneous measurements every half an hour. All instruments, except soil thermocouples, were located 1–2 m above the ground. Piche evaporimeters were exposed to direct solar radiation and prevailing wind direction (NE). The mean daily values (15 June–13 July) of soil temperature at −30 cm were used to calculate the soil temperature gradient of the mountain.

Mean monthly values (1971–1980) of sunshine duration, rainfall, pan evaporation, air temperature, wind speed and relative humidity at Nazareth weather station (85 m altitude and 7 km north of Macuira), were calculated from data obtained at HIMAT (Instituto Colombiano de Hidrologia, Meteorologia y Adecuacion de Tierras), Bogota.

RESULTS

Regional climate of the Serrania de Macuira

To provide an understanding of the steep climatic gradient between the elfin cloud forest of Serrania de Macuira (550–865 m), and the surrounding lowlands, a short description of the annual climatology of the region is presented here. Seasonal variations in the lowlands can be used as an indicator of the seasonal variations in the cloud forest, and to evaluate to what extent the observations taken over the month-long study period are representative of conditions in the forest throughout the year.

In the lowlands adjacent to the mountain, there was a decrease in annual sunshine duration from 3000 h in mid-Guajira (around Serrania de Cocinas) to 2600 h over Nazareth in upper Guajira Peninsula, 7 km north of Serrania de Macuira (Fig. 4). A decrease in annual sunshine duration was also noticed around Sierra Nevada de Santa Marta and around Serrania de los Motilones, near Venezuela (Fig. 4). Sunshine duration was distributed bimodally, and with the exception of April–May, the course of evaporation was coupled with that of sunshine duration (Fig. 5). Monthly relative humidity, air temperature and winds remained constant throughout the year. The mean annual rainfall in the lowlands was 450 mm, with a short rainy season from September to the end of the year. Rainfall was higher than pan evaporation during

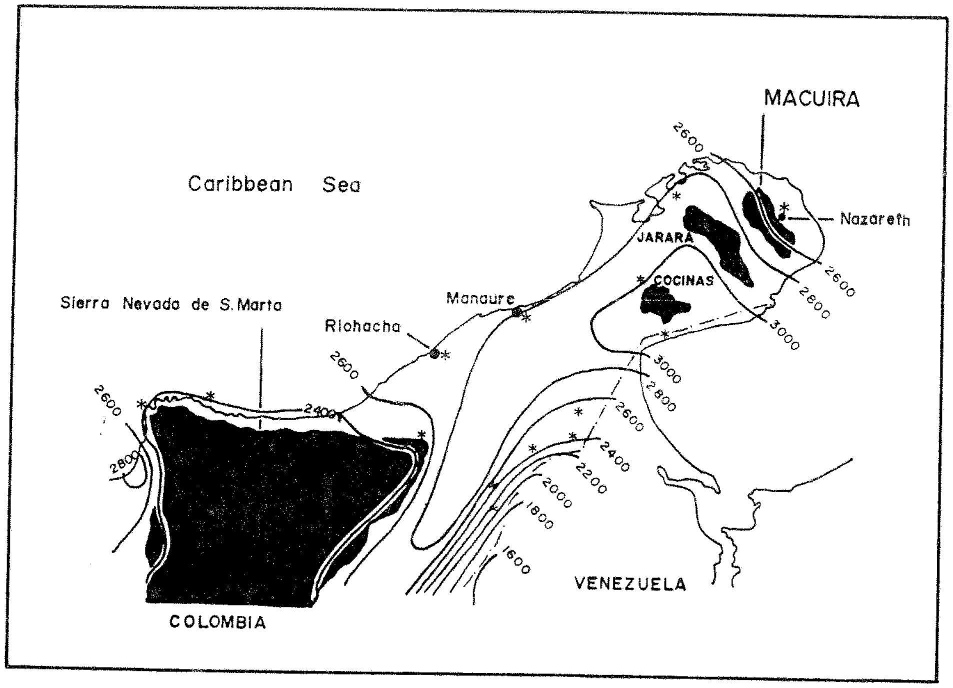

Fig. 4. Annual sunshine (h) over Guajira Peninsula, measured with Campbell-Stokes sunshine recorders (Bernal, 1986). *Represent the meteorological stations in Colombia that contributed to the map.

only 1 month a year. Regardless of the time of the year, days with rainfall were few. In the dry season, rain fell on 1–4 days each month, while in the rainy season, it fell on 4–12 days (Cavelier, 1986).

Climate along the altitudinal gradient

Cloud cover

A small area of clouds appeared over Serrania de Macuira (not related with synoptic systems) on more than 95% of images from 15 June to 15 July 1984 (Table 1). Synoptic systems, covering not only Macuira but also the northern portion of the Guajira Peninsula, were observed on 30% of images at 13:00 h, on 26% at 19:00 h, but only 13% at 07:00 h. These values show that local cloud over Macuira was largely independent of regional cloud.

The small area of cumulus cloud over the elfin cloud forest was formed by free (thermal) and forced (orographic) convection, and by the accumulation of small clouds pushed by the trade winds from the Caribbean sea towards the land. One of the consequences of this movement of discrete clouds from the sea to the Serrania, were light pulses on the canopy. The light pulses were

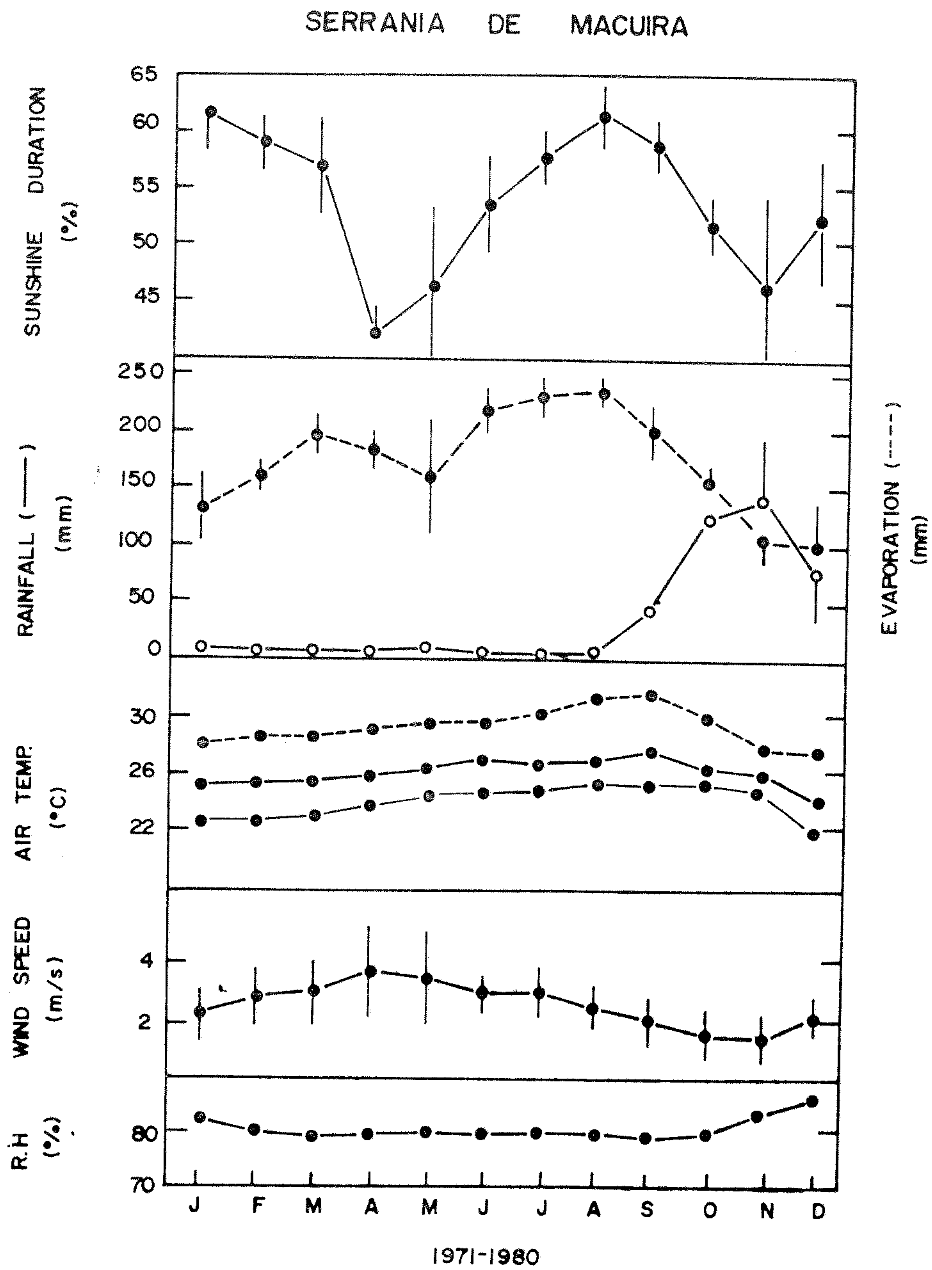

Fig. 5. Mean monthly values (1971–1980) of some climatic variables at Nazareth weather station (85 m in altitude), 7 km north of the top of Serrania de Macuira. The bars represent ±1 S.E.M. If there is no bar, the error is smaller than the circle.

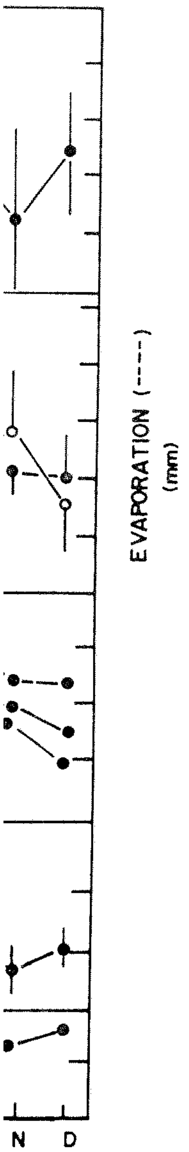

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TABLE 1

Cloud cover on Serrania de Macuira[1]

	07:00 h		15:00 h		19:00 h	
	L	s	L	s	L	s
June						
15	x	p	x	p	x	p
16	–[2]	–	x	x	p	x
17	–	–	x	p	x	p
18	x	p	x	p	x	p
19	x	p	p	p	x	p
20	x	p	–	–	p	p
21	x	p	x	p	x	p
22	–	–	–	–	x	p
23	x	p	x	p	p	p
24	x	p	p	p	x	p
25	x	p	p	p	x	p
26	x	p	x	p	x	p
27	–	–	x	p	x	p
28	p	p	p	p	p	p
29	x	p	x	p	p	p
30	p	p	p	p	x	p
July						
01	x	p	x	p	–	p
02	x	p	p	p	x	p
03	x	p	–	–	–	–
04	–	–	–	–	–	–
05	x	p	x	p	–	–
06	x	p	x	p	–	–
07	x	p	x	p	p	p
08	x	p	p	p	–	p
09	p	p	–	–	x	p
10	x	p	–	–	–	–
11	x	p	x	p	x	p
12	x	p	–	–	x	p
13	–	–	–	–	x	p
14	–	–	x	p	x	p
15	–	–	x	p	–	–
Mean (% images observed)	13	100	30	95	26	95

[1]Presence (p) or absence (x) of large (L=regional) and small (s=local) cumulus clouds.
[2]Satellite images not available (–).

not present during very cloudy or clear days, and were rare during early morning and late afternoon when cloud cover was almost continuous.

The cumulus cloud over the Serrania de Macuira, rose during the day and fell during the night. In this case the displacement of the condensation level was vertical and the driving force of the movement was temperature varia-

TABLE 2

Daily courses of cloud cover at Serrania de Macuira[1]

Date	Cerro Huarech[2]							Cerro Palua		
	750 m			650 m				750 m		
	Fall (pm)	Rise (am)	1 *N* (h)	Fall (pm)	Rise (am)	2 *N* (h)	(1–2)	Fall (pm)	Rise (am)	*N* (h)
June										
15	5:45	7:00	–	8:00	6:00	–	–	5:00	8:00	–
16	3:20	8:30	14.8	5:30	6:00	10.0	4.8	2:40	8:00	15.0
17	6:10	7:00	15.8	7:30	6:30	12.5	3.3	5:30	8:00	17.5
18	5:15	7:00	12.9	7:30	6:00	11.5	1.4	4:20	8:00	14.3
19	5:30	6:30	13.2	7:30	6:00	11.5	1.7	4:30	7:50	15.0
20	5:05	6:00	12.5	9:00	6:00	11.5	1.0	4:30	6:30	14.0
21	6:30	5:00	12.0	6:00	5:00	8.0	4.0	4:30	9:00	16.5
22	5:30	7:15	12.7	9:00	6:20	12.5	0.2	4:30	8:30	16.0
23	4:50	7:30	14.0	9:00	6:30	9.5	4.5	4:00	8:15	15.7
24	5:30	7:30	15.0	7:00	6:30	9.5	5.5	5:00	8:30	16.3
25	5:07	6:45	13.5	7:00	5:30	10.5	3.0	4:30	7:30	14.3
26	6:00	7:30	14.5	7:30	6:30	11.5	3.0	5:00	8:40	16.0
27	5:10	7:00	13.0	7:30	6:00	11.0	2.0	5:00	8:10	15.1
28	5:30	7:15	14.5	7:30	6:45	11.0	3.5	4:30	7:20	14.3
Average	5:30	7:00	13.7	7:30	6:00	10.8	2.9	4:30	7:45	15.4

[1]Time the cloud base fell and rose on Cerro Huarech at 750 m and 650 m, and on Cerro Palua at 750 m.

[2]Number of hours of cloud cover (1,2) and difference between the altitudes (1–2).

tion. At dawn, when air temperature was lower and relative humidity was higher, condensation occurred at about 550 m. During the morning, owing to higher temperatures and lower relative humidity, cloud base rose over the higher peaks of the Serrania without dissipating. By late afternoon, air temperature fell, relative humidity rose again, and the cloud base returned to its lower position (500–550 m) remaining there until next morning. The variation of the condensation level on the mountain is given in Table 2. On Cerro Huarech, cloud base fell to an average of 750 m at 17:30 h and to 650 m at 19:30 h. When the cloud base rose in the morning, it passed 650 m at 06:00 h, and 750 m at 07:00 h. Cloud base was above 650 m for an average of 10.5 h and above 750 m for 13.5 h (Table 2). In summary, clouds cover the elfin cloud forest mainly during the night, early morning and late afternoon. Higher mountain slopes were covered with clouds for longer periods.

Daily courses of some climatic variables

Mean daily (06:00–18:00 h) *RFD* measured between 15 June and 13 July 1989, decreased with altitude. At Nazareth (85 m) the mean solar *RFD* was 'ro Palua

) m

l n)	Rise (am)	N (h)
)	8:00	–
)	8:00	15.0
)	8:00	17.5
)	8:00	14.3
)	7:50	15.0
)	6:30	14.0
)	9:00	16.5
)	8:30	16.0
)	8:15	15.7
)	8:30	16.3
)	7:30	14.3
)	8:40	16.0
)	8:10	15.1
)	7:20	14.3
)	7:45	15.4

on Cerro Palua at

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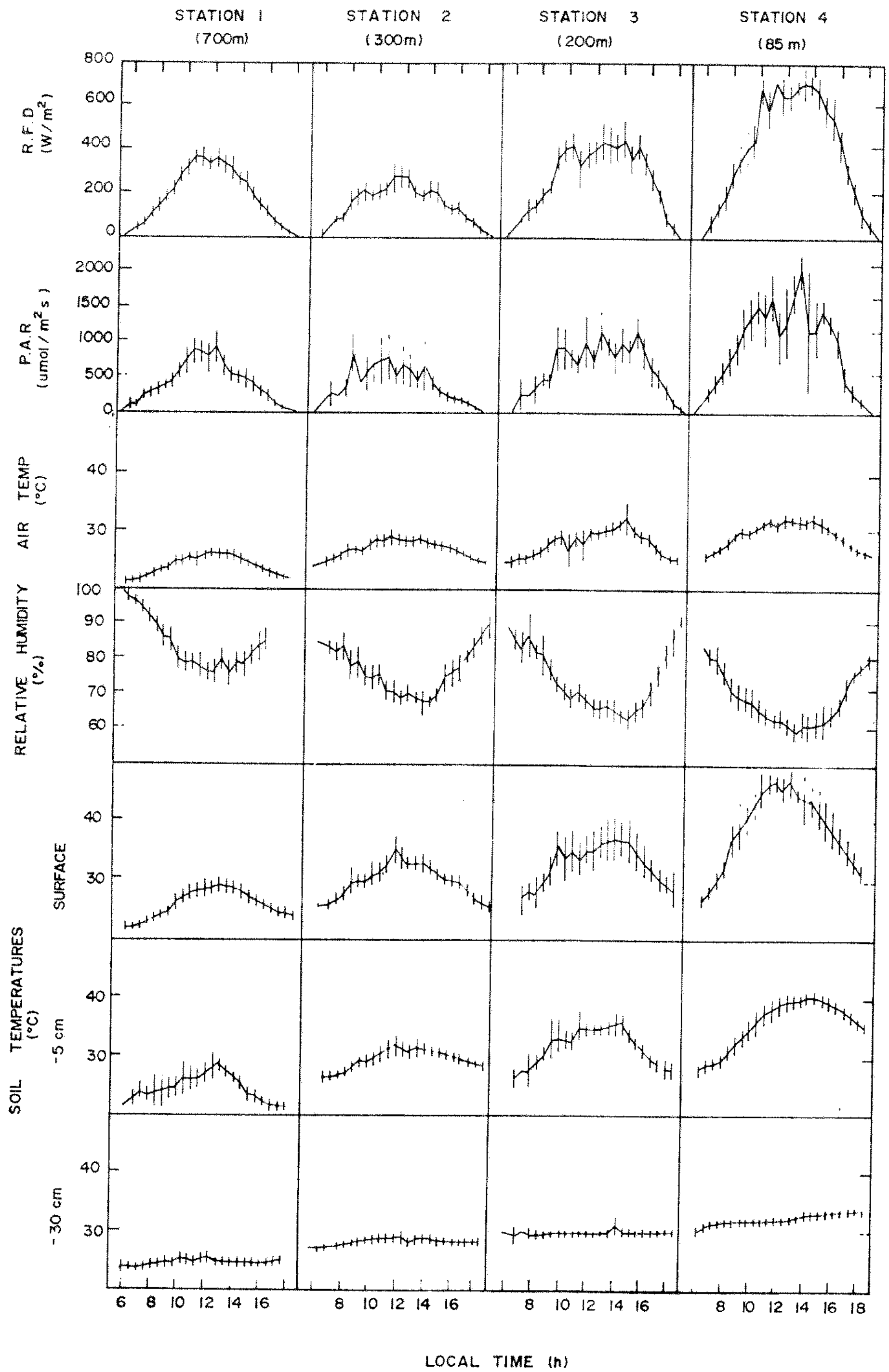

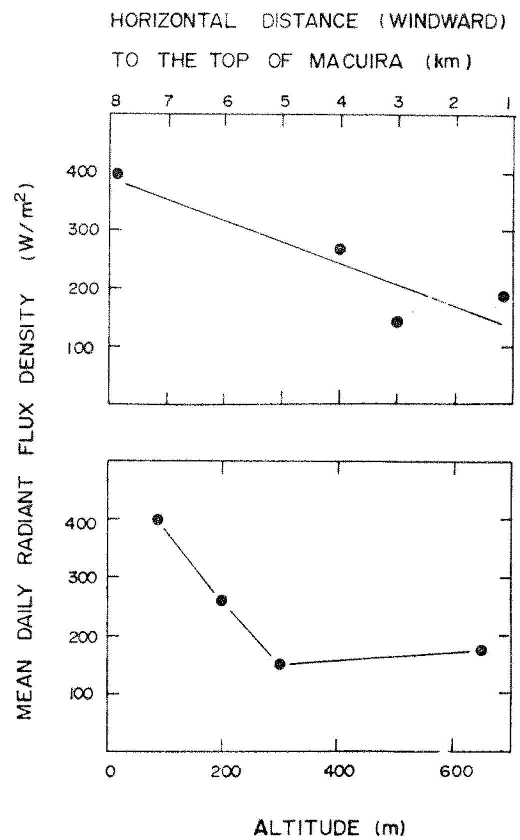

Fig. 7. Relationship between (a) horizontal distance to the top of Serrania de Macuira (km) and mean daily radiant flux density, and (b) relationship between altitude and mean daily radiant flux density.

400 W m^{-2}, and in the cloud forest (650 m) was only 184 W m^{-2}, a decrease of 53% (Fig. 6). If the decrease in *RFD* was calculated using mean daily maxima rather than the daily mean, reduction of *RFD* with altitude was only 39%. This suggests that the decrease in *RFD* was greater during the morning and afternoon hours than at mid-day. This is consistent with the patterns of cloud

Fig. 6. Mean daily courses of radiant flux density (*RFD*), photosynthetically active radiation (*PAR*), air temperature, relative humidity and soil temperatures along the altitudinal gradient of Serrania de Macuira. Station 1 in the elfin cloud forest (700 m), Station 2 in the dry deciduous forest (300 m), Stations 3 and 4 in the thorn woodland (200 m and 85 m, respectively). The vertical lines represent ±1 S.E.M. 15 June–15 July 1984 (mid-dry season). The variability of *PAR* is greater than *RFD* because only spot measurements were made for *PAR* and half an hour total runs for *RFD*.

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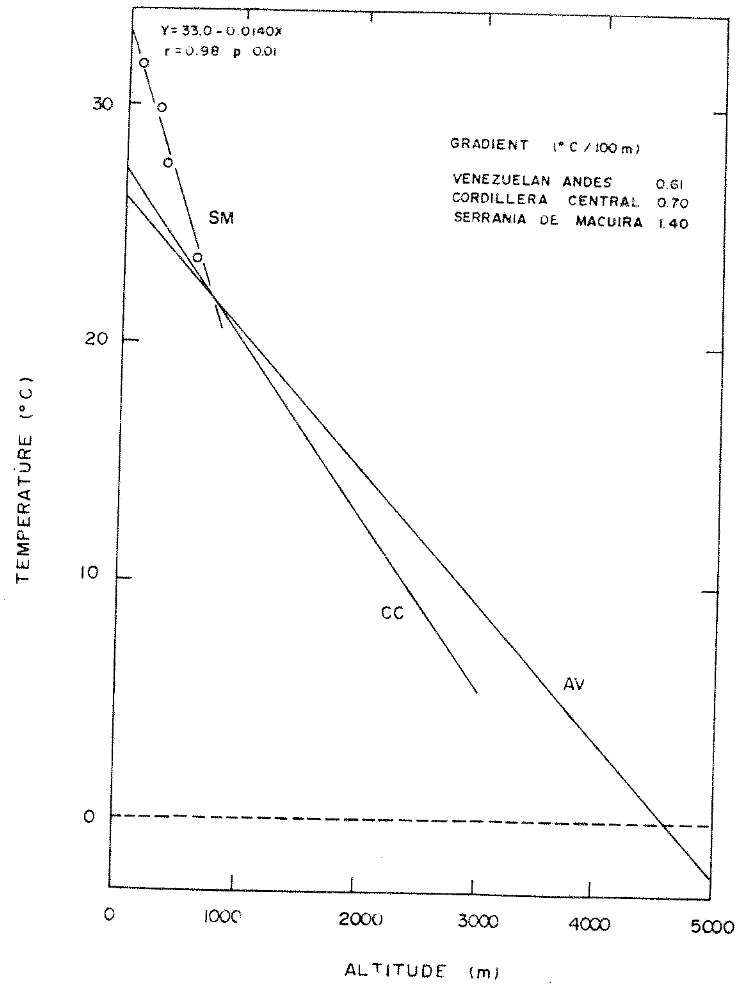

Fig. 8. Soil temperature gradients (−30 cm) in tropical mountains. Serrania de Macuira (SM), Cordillera de la Costa, Dominican Republic (CC) and Venezuela Andes (AV) from Schubert and Medina 1982 (no data points were presented for these mountains).

cover over Macuira at 650 m and 750 m. Although *RFD* decreases with altitude, the horizontal distance to the peak of the mountain (windward side) is a better predictor of the mean daily *RFD* (Fig. 7).

Mean diurnal air temperature decreases from 29.4 °C at 85 m, to 23.8 °C at 700 m (Fig. 6). The mean range between daily maximum and minimum air temperature also decreases from 6.8 °C in the thorn woodlands at 85 m to 5.0 °C in the elfin cloud forest at 700 m. Soil temperature and the amplitude between daily maxima and minima also decreased with altitude (Fig. 6). On

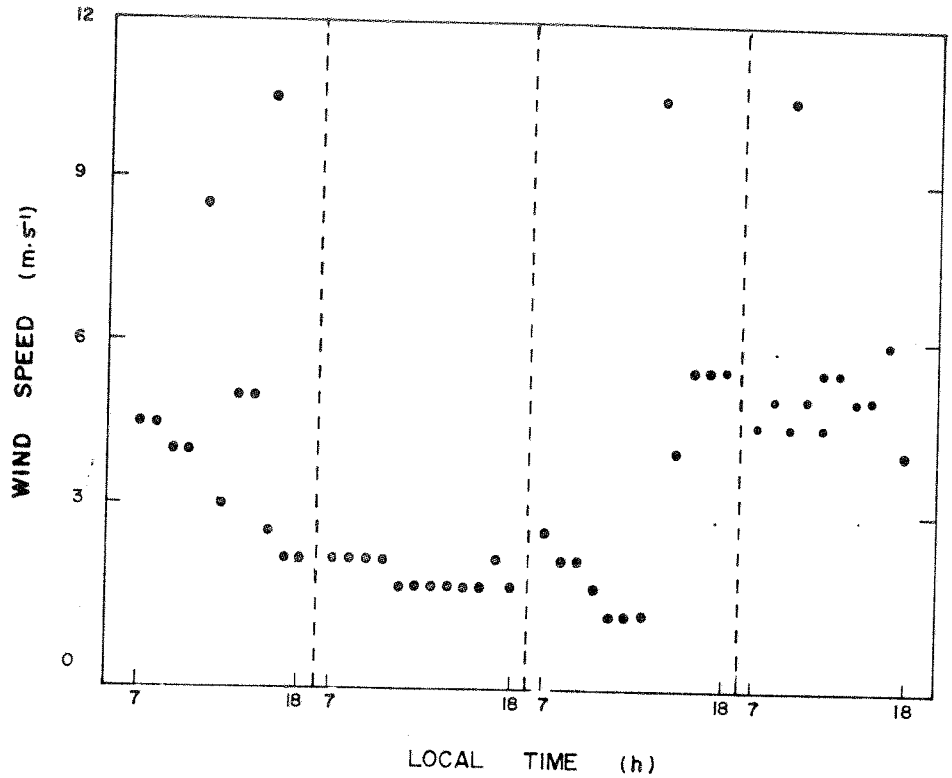

Fig. 9. Daily variations of wind speed on a ridge at 700 m, 18–21 June 1984. The values are hourly total runs.

the mountain slopes, soils were warmer than air only during the day, while in the lowlands, soils were also warmer than air during the night. Thus, at night only the lowlands adjacent to the Serrania can modify the temperature and vapour pressure deficit of the surrounding air and therefore the position of the cloud base. During the day, the whole mountain and surrounding areas, heat the air and determine the position of the condensation level. The soil temperature gradient in Macuira, using the mean diurnal temperature at −30 cm, was 1.4°C per 100 m. The soil temperature at this depth is fairly constant. The difference between mean daily maximum and minimum is 2.9°C in the cloud forest (700 m) and 4.0°C in the lowlands (85 m). This gradient is much steeper than the 0.6–0.7°C per 100 m found in higher and more massive mountains in other tropical locations (Fig. 8).

Mean mid-day relative humidity increased from 60% at 85 m, to 76% at 700 m. At the elfin cloud forest station (700 m), relative humidity over 90% occurred during the first 3.5 h of the day and during the last 2.5 h of the afternoon. This pattern shows that clouds stay longer over the forest during the morning than during late afternoon.

Wind speed was the only climatic variable that did not show a clear altitudinal gradient. Above the canopy of the cloud forest, wind speed was highly variable between hours and between days. Wind speed could change from 1 to 11 $m\ s^{-1}$ from one hour to the next (Fig. 9). Wind speed was significantly higher ($P<0.01$) on ridges than on gullies. On a ridge a 650 m, mean daily wind speed was 3.5 $m\ s^{-1}$ while in a gully at the same elevation, wind speed was only 1.5 $m\ s^{-1}$. On average, wind speed increased from 3.5 $m\ s^{-1}$ during the day to 5.4 $m\ s^{-1}$ during the night. The daily course of evaporation followed the course of total *RFD* and air temperature; evaporation increased during the morning, reached a maximum at mid-day and decreased during the afternoon. Evaporation, measured with Piche evaporimeters and averaged over 12 h, decreased from an average of 1400 $g\ m^{-2}\ h^{-1}$ in the lowlands to 489 $g\ m^{-2}\ h^{-1}$ in the cloud forest; a decrease of 65%. At night, fog interception occurs in the cloud forest, while evaporation continues in the lowlands. In the cloud forest, evaporation decreased with altitude and exposure to the prevailing winds. On ridges, evaporation decreased from 489 $g\ m^{-2}\ h^{-1}$ at 700 m to 337 $g\ m^{-2}\ h^{-1}$ at 750 m. In a gully at 700 m, evaporation was 407 $g\ m^{-2}\ h^{-1}$.

DISCUSSION

Daily variations in cloud cover over Serrania de Macuira, have a double effect on the water regime of the trees in the elfin cloud forest. At night, when the cloud base is low, water is supplied to the forest by means of mist and fog interception (Cavelier and Goldstein, 1989). During the day, the cloud base rises over the peaks without completely dissipating, increasing water demands. The forest remains under these shallow-moist-layer conditions throughout the 8 months of the dry season. As a result, the forest experiences relative humidity of <90% during most of the day, and thus the canopy is rarely wet during the day-time. In contrast, the forests in the Luquillo mountains in Puerto Rico, can experience a shift from shallow-moist-layer to deep-moist-layer conditions (heavy cloudiness, low insolation, more rain and lower temperatures) from one day to another (Odum et al., 1970). Odum (1970) suggested that short forests result when the saturation deficit is low without interruption, and dry air is not available for transpiration, reducing the transport of minerals in the transpiration stream (see also Leigh, 1975). The elfin cloud forest of Macuira is an example of a cloud forest where there is an interrupted regime of saturation, and nevertheless, there are stunted trees. Factors which have been presented as evidence against Odum's hypothesis (Grubb, 1977), are the negligible effect of water flow on the amount of nutrients taken by plants in low concentration solutions, the uptake of phosphorus via mycorrhiza, low microbial breakdown of organic matter and low diffusion rates of nutrients through soils, (which is effective earlier than the uptake and transport of nutrients in the plant), and the direct supply to young leaves via the phloem, (which is not affected by the transpiration stream through the xylem).

A second effect of the cloud cover is a decrease in *RFD*. The attenuation of radiation by clouds is 40% in the elfin cloud forest of Pico del Oeste in Puerto Rico (Baynton, 1968) and 16% in the Blue Mountains in Jamaica (Aylett, 1985). Stunted trees in the cloud forest of Macuira, seem not to be caused simply by a decrease in solar radiation levels. Firstly, *RFD* values similar to those measured in the cloud forest, can be found on the slopes of the mountain close to the upper limit of the deciduous forest where trees, as shown by Sugden (1982), are much taller. Secondly, *PAR* during most of the day is higher than the 500 μmol m^{-2} s^{-1} required to saturate CO_2 uptake under constant light in *Cyrilla racemiflora* and *Clethra occidentalis*, two tree species in a Jamaican cloud forest (Aylett 1985). Canopy structure (leaf area index) and leaf inclination can reduce radiation levels for some leaves and radiation may become a limiting factor for at least part of the canopy.

The unusually steep gradient in soil temperature, 1.4°C per 100 m at −30 cm depth, is the result of large differences in humidity, water content of the soil, and cloud cover between the extremes of the gradient. In particular, soil temperatures in the dry and sunny lowlands around Macuira are higher than those in wetter areas, whereas the temperature at the top of Macuira is not very different from those at similar altitude on large mountains. Until recently, soil temperature gradients in small and large mountains were thought to be the same (Grubb and Whitmore, 1966; Baynton, 1968; Grubb, 1971). Although the soil temperature gradient is steeper in Macuira, it does not explain the short forest because at ~500 m, soil temperatures are similar on Macuira and on larger mountains with taller forests at this altitude. For example on the Sierra Nevada de Santa Marta, Colombia (5775 m) soil temperature at 700 m is about 22.5°C (van der Hammen, 1984) and there are lowland rain forests (selva ecuatorial alta sensu Cleef et al., 1984) with trees 25–30 (35) m tall (Cleef et al., 1984). The soil temperature gradient at the Sierra Nevada de Santa Marta between 1400 and 3400 m is 0.56°C per 100 m, with lower soil than air temperatures between 500 and 1400 m (0.4–1.0°C) and with higher soil than air temperatures between 3400 and 4100 m (1.6–2.6°C) (van der Hammen, 1984).

Strong winds have been noted in the elfin forests of Costa Rica (Lawton and Dryer, 1980), the Lesser Antilles (Beard, 1944, 1955), Puerto Rico (Baynton, 1968; Howard, 1970) and Margarita Island (Sugden, 1986). Lawton (1982) suggested that elfin stature is an adaptive response to greater wind stress along exposed ridges, while Sugden (1986) suggested that a combination of high winds and thin and unstable substrate, may lead to the reduced stature in the upper palm forest on exposed slopes on Isla Margarita. Strong winds seem to be the cause of the extreme reduction in stature in exposed ridges, but there is no experimental evidence to support this hypothesis. Furthermore, strong winds cannot explain the general low tree stature in the Macuira forest. Wind speed in gullies is much lower than on ridges and slopes, nevertheless, trees are still small.

While *RFD, PAR,* relative humidity, and air and soil temperature change gradually along the altitudinal gradient, only the cloud base changes abruptly. The boundary between the cloud forest and the deciduous forest is very sharp, and is very well correlated with the cloud base at night, and the altitude below which there is no fog interception (Cavelier and Goldstein, 1989). This observation suggests that the most direct effect of cloud cover on forest structure and physiognomy is through the interception of cloud water. Cloud water could potentially have a double effect on the physiology of trees: (1) by maintaining a water film on leaves, and thus reducing CO_2 fixation and total carbon gain; or (2) by keeping the soils wet, and among others, reducing mineralization rates (Tisdale and Nelson, 1975) or promoting fast chemical weathering of rock minerals (Russell, 1973). In Macuira, owing to the cloud pattern, leaves are rarely wet during the day, while soils are wetted and dried on a daily basis (Cavelier, 1986; Cavelier and Goldstein, 1989). A high concentration of kaolinite ($>50\%$) in the clay fraction of the soils of Macuira, (Cavelier, 1986), suggests advanced weathering, while little accumulation of organic matter (OM=2.5–3.5%, Cavelier, 1986), and high soil respiration rates (Cavelier and Penuela, 1990) suggest relatively fast mineralization rates. While in Macuira (865 m) relatively high temperatures and alternations of wet and dry periods seem to promote high mineralization rates, experimental evidence in other mountains suggests that nitrogen mineralization at high altitudes is limited by low temperatures and high soil water content. For example, Marrs et al. (1988) found in a series of soils along an altitudinal transect on Volcan Barva (2906 m) in Costa Rica, that nitrogen mineralization rates were increased by between one and three orders of magnitude when both temperature and aeration/moisture content were improved.

In summary, we think that the climatic factor that has the most pronounced effect on the physiognomy of this elfin cloud forest is cloud cover at night. Clouds would supply water by means of fog interception promoting fast weathering of soils. Relatively high temperatures and daily wetting and drying of the soils would promote relatively high mineralization rates. Cloud cover is probably one of the few common factors involved in the zonation of mountain forests where there are differences in species composition, the bed rock and physical and chemical properties of the soil. The effects of cloud cover on other forests should be investigated to provide a better understanding of the controlling factors of the zonation of forests in tropical mountains.

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