Journal of Tropical Ecology (1989) 5:309-322. With 8 figures

Mist and fog interception in elfin cloud forests in Colombia and Venezuela

JAIME CAVELIER* *and* GUILLERMO GOLDSTEIN†

Departmento de Biologia, Facultad de Ciencias, Universidad de los Andes, Merida, Venezuela

ABSTRACT. Fog interception and rainfall were measured during one year in three elfin cloud forests on small mountains along the Caribbean coast of South America and one in the Venezuelan Andes. (1) While rainfall increases from west to east in the small mountains along the coast, fog interception decreases. In 1985, the total annual rainfall and fog interception were 853 mm and 796 mm in the cloud forest of Serrania de Macuira, 1630 mm and 518 mm in Cerro Santa Ana and, 4461 mm and 480 mm in Cerro Copey. In the Andean forest of El Zumbador, the 1985 rainfall was 1983 mm and the annual fog interception was only 72 mm. (2) Fog interception seems to be an important source of water to the elfin cloud forests of the small mountains which are surrounded by dry vegetation types and where the rainfall regime is highly seasonal. (3) Fog interception increases with altitude (in the same mountain), exposure (windward slopes) and leaf inclination. These variations of fog interception could partially explain the observed distribution of epiphytic flora in some of these cloud forests.

KEY WORDS: cloud forest, Colombia, fog interception, leaf angle, mist, mountain forests, Neotropics, tropical mountains, water sources, Venezuela.

INTRODUCTION

On the wetter slopes of the highest tropical mountains, there is a continuous forest cover from sea level to about 4000 m. Within the continuous forest cover it is possible to recognize four major formation types: lowland rain forest (LRF), lower montane rain forest (LMRF), upper montane rain forest (UMRF) and subalpine rain forest (Grubb 1977). These forests types seem to be related to the frequency of cloud cover. While the LRF experiences negligible fog, the LMRF has frequent fog and the UMRF has long persistent cloud cover close to the ground (Grubb & Whitmore 1966). Although the montane forests are associated with cloud cover, only the UMRF is usually called Cloud Forest; it is characterized by the abundance of mosses and liverworts which derive much of their water from the clouds (van Reen 1983). Some cloud forests are characterized by a low canopy less than 8 m high, gnarled and stunted trees which are often stilt-rooted and have thick and tough leaves. Some of these trees also have branches pointing away from the wind (Beard 1944). These particular cloud forests may be regarded as the stunted facies of either LMRF or UMRF (Grubb & Whitmore 1966) and will be referred to here as elfin cloud forests (ECF) following Sugden (1982).

Present addresses: * School of Botany, Downing Street, Cambridge, U.K. † Laboratory of Biomedical and Environmental Sciences, 900 Veteran Avenue, UCLA, Los Angeles, CA 90024, USA.

Although some research has been done on the climate (e.g. Baynton 1968, Grubb & Whitmore 1966, Huber 1986, Odum *et al.* 1970), floristics (e.g. Howard 1970, Lawton & Dryer 1980, Steyermark & Huber 1978, Sugden 1982, Tanner 1977), and physiology of the species in cloud forests (Cavelier 1986, Kapos & Tanner 1985, Medina *et al.* 1981) there is little information on the relative dependence of these forests on their two main water sources; cloud water (fog interception) and rainfall (Baynton 1969, Vogelmann 1973). 'Fog interception' is used here to refer to the small cloud droplets that do not settle on horizontal surfaces and thus are not collected in a rain gauge. These droplets are blown by the wind against the vegetation where they coalesce to form larger drops that run off and fall to the ground (Chanery 1981).

The present research was designed to measure rain and fog interception in three elfin cloud forests on small mountains along the dry Caribbean Coast of South America and in one forest in the Andes of Venezuela. The study was also designed to evaluate the importance of fog as a water source in cloud forests growing in relatively dry areas where rainfall is a highly seasonal and unpredictable water source. Variations of fog interception with altitude, exposure and leaf inclination are also considered.

MATERIALS AND METHODS

Study sites

Rainfall and fog interception were measured during one year in four tropical elfin cloud forests. The 'Caribbean' sites are (a) Serrania de Macuira, Guajira, Colombia (865 m), (b) Cerro Santa Ana, Peninsula de Paraguana, Venezuela (815 m), and Cerro Copey, Margarita Island, Venezuela (987 m). The 'Andean' site was located in El Zumbador Forest (3100 m), Estado Tachira, Venezuela (Figure 1).

The small mountains are entirely located within the South Caribbean Dry

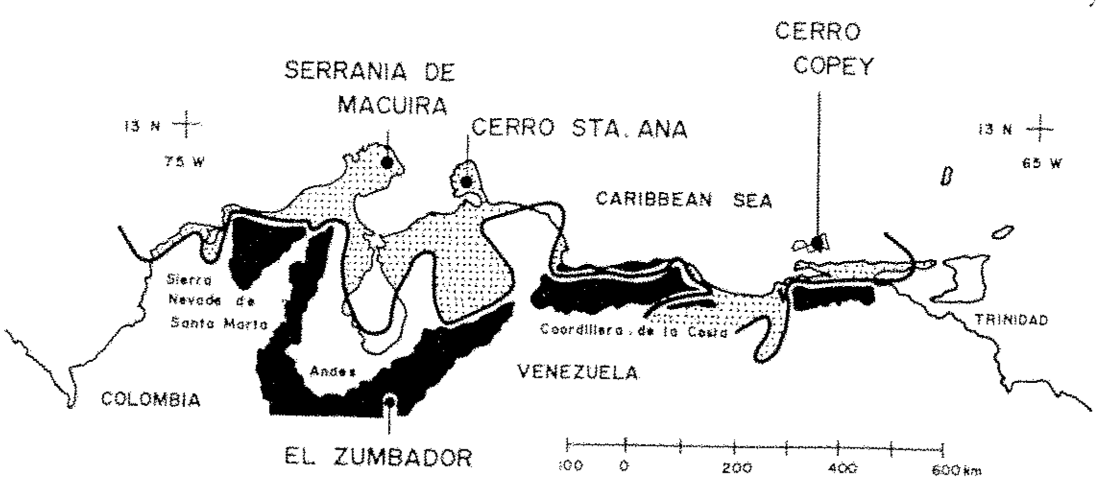

Figure 1. Map of the Caribbean coast of South America and location of the study sites. The dotted areas represent the Dry Zone, where annual rainfall is less than 1000 mm (adapted from Lahey 1958). The black areas represent land over 500 m altitude.

Zone (Sugden 1982) where the average annual rainfall is less than 1000 mm (Lahey 1958, Snow 1976). In this area, rainfall is not only scarce but also unevenly distributed. At Macuira, the average rainfall in the lowlands is 450 mm per year, with a short rainy season from mid September to the end of November (Sugden 1982). At Santa Ana the rainfall regime is very similar to that at Macuira. At Copey, on the other side of the dry area, the average rainfall on the lowlands is 600 mm. Rainfall is distributed bimodally with a main rainy season from November to February and a secondary rainy season from July to September (Andressen 1966). In contrast to the Caribbean cloud forests, the Zumbador forest is in a very wet area. At 2500 m, on the same mountain of El Zumbador, the annual average rainfall is 1125 mm with a very long rainy season from March to November (Monasterio 1980). There is no information available on rainfall on top of any of the mountains studied. The highest station on Cerro Copey is at 350 m. Here, mean annual precipitation (1951–1981) is 950 mm with a range of 222 mm to 1900 mm (Sugden 1986).

Along the Caribbean coast of South America, the atmospheric humidity is too low for cloud formation, except where the air stream is forced up and cooled by the slopes of the small mountains (Sugden 1982). During the day, when the temperature is high and the relative humidity is low in the lowlands, the small cumulus clouds formed on the windward side of the mountains rapidly dissipate on the leeward; the cloud base is well above the mountain peaks and rarely envelops the forest. During late afternoon, when the temperature in the lowlands decreases, the cloud base drops covering the forests above 550 m. In El Zumbador, clouds usually envelop the forest early in the afternoon and dissipate during the night. The mean air temperature (derived from soil temperature at −30 cm depth) in the cloud forest of Macuira at 700 m is 24°C, while in El Zumbador forest it is only 8°C (Cavelier 1986).

To summarize: the ECF of Macuira, Santa Ana and Copey are in a very dry area where rainfall is scarce and unevenly distributed. Clouds are usually present, but envelop the forest mainly during the night. In contrast, the ECF of El Zumbador is in a very wet area where rainfall is abundant and evenly distributed. Clouds seem to cover the forest mainly during the afternoon.

The flora of Macuira has been studied by Rieger (1976) and Sugden (1982); the flora of Santa Ana by Tamayo (1941) and the flora of Copey by Johnston (1909), Ortega (1982) and Sugden (1986). We are not aware of any study on the flora of El Zumbador.

Measurements

Open-ended cylindrical fog catchers were made from plastic window screen of 40 mesh (open spaces) per cm². The cylinders, 8 cm in diameter, protruded 8 cm above a funnel in which the cylinder was placed. This type of fog catcher has been used to collect cloud water in the cloud forests of South Africa (Marloth 1904, 1907), Mexico (Vogelmann 1973) and California (Oberlander 1956). Rainfall was measured with plastic funnels, 8 cm in diameter. The rain gauge without the screen collects only rainfall, while the gauge with the screen collects both rainfall and cloudwater as the wind moves tiny fog droplets into the mesh. Volume differences between rain and fog collectors give a relative amount of fog interception and non-vertical rainfall.

In order to compare the efficiency of the fog catchers with that of the forest as a whole, two 5 m by 5 m pieces of polythene were set out on the forest floor to collect throughfall (fog drip) and two fog catchers and funnels were positioned above the canopy to collect cloud water and rain. To estimate the amount of fog drip per unit area, the collected water volumes were divided by the area of the polythene multiplied by the cosine of the angle of the mountain slope where the collectors were set up. These measurements were made in Macuira from 30 December 1985 to 12 January 1986.

Measurements of fog interception were made in the ECF of Macuira to study the variation in fog interception with changes in altitude and topography. Firstly, to study the variation in fog interception with altitude, fog-catchers and rain gauges were set up at 600 m, 650 m and 750 m on the windward ridge of the mountain. Measurements were made on a daily basis from 25 December 1985 to 13 January 1986. Secondly, to study the variations of fog interception with exposure, collectors were placed on a windward and leeward side of a gully at 650 m and on a windward slope at 700 m. These measurements were made on nine days in July 1984.

Rainfall and fog interception were measured throughout a 12-month period (1984–1985) in the ECF of Serrania de Macuira, Cerro Santa Ana, Cerro Copey and El Zumbador. Because of the remoteness of the sites, measurements were made every fortnight in all forests except Copey, where the information was gathered every five days. The rainfall in El Zumbador during July and August 1985 was estimated from the average rainfall at 2500 m on the same mountain (Monasterio 1980), since the rain gauges were stolen.

In order to study the effect of leaf angle on fog interception, the following experiment was established. Leaves of *Eugenia procera* and *Rapanea guianensis*, were mounted with wire at angles between 0° and 90°. With a spraygun, thin fog was produced and sprayed against the leaves. The intercepted water was collected in small vials located directly below the leaves. The results are given as percentage of the water collected in leaves at 90° (vertical).

RESULTS

Estimation of throughfall volumes

In a 13-day period in the ECF of Serrania de Macuira, the fog-catchers on the forest canopy collected significantly more water than the collectors on the forest floor. At 700 m, fog interception (fog-catchers) was 5909 cm^3 and throughfall was only 16.9 mm; in other words, 350 cm^3 in the fog-catcher corresponds to 1 mm of throughfall. This value must be an underestimate of the total cloud water collected by the forest because trunk flow was not taken into account. Assuming that trunk flow is on average 10% of the rainfall (Clas-

1963), a conversion factor of 318 cm^3 (fog-catcher) to 1 mm (throughfall) will be used here to scale the values obtained in the fog-catchers.

Variation of fog interception with topography

Fog interception increased with altitude and exposure. In a 20-day period, fog interception was 47 mm at 750 m and only 17 mm at 600 m. Using the

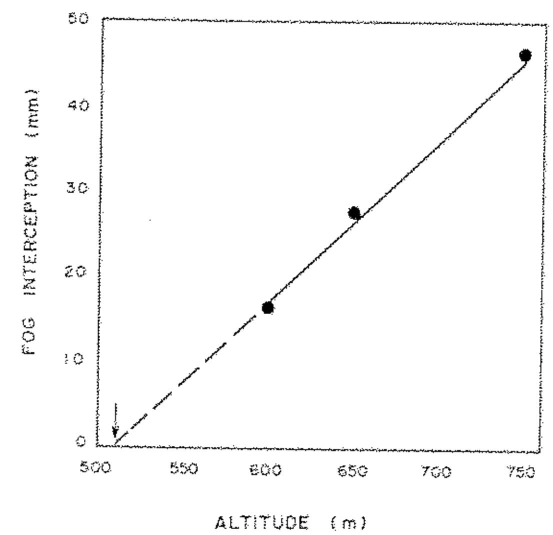

Figure 2. Relationship between altitude and fog interception during a week in the Serrania de Macuira. By extrapolation, fog interception ceases below about 513 m (arrow).

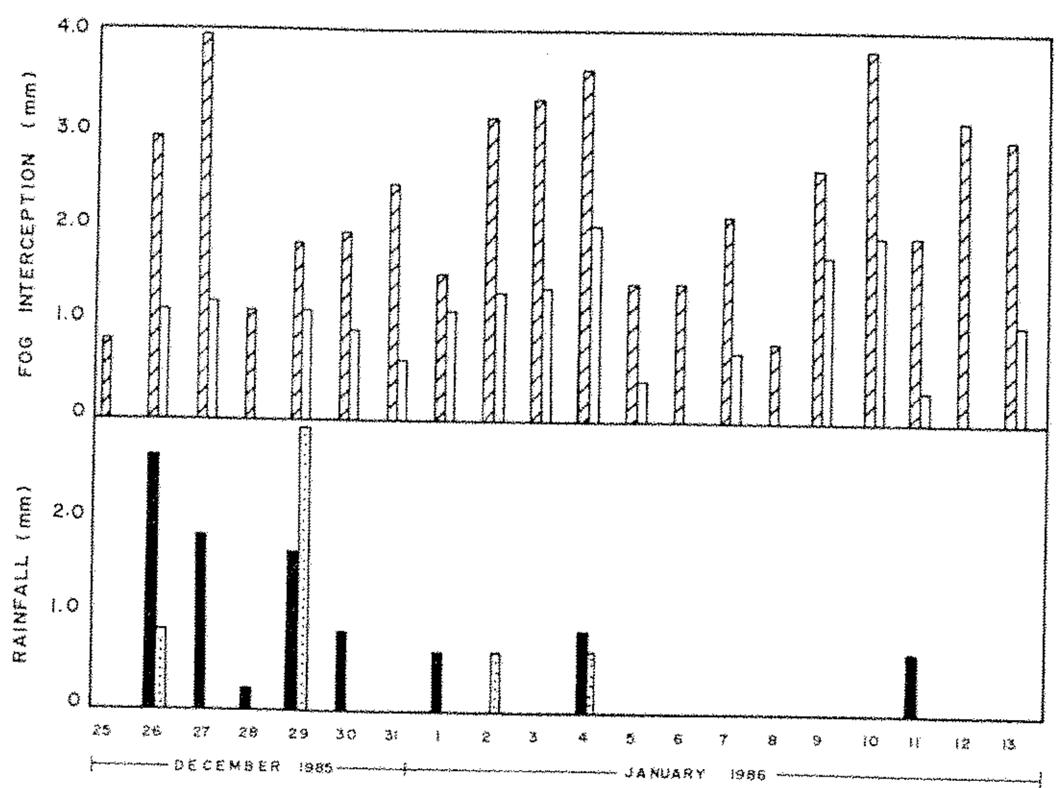

Figure 3. (A) Daily fog interception at 750 m (▨) and at 600 m (□), and (B), daily rainfall at 750 m (■) and at 600 m (⊡) in the elfin cloud forest of Serrania de Macuira.

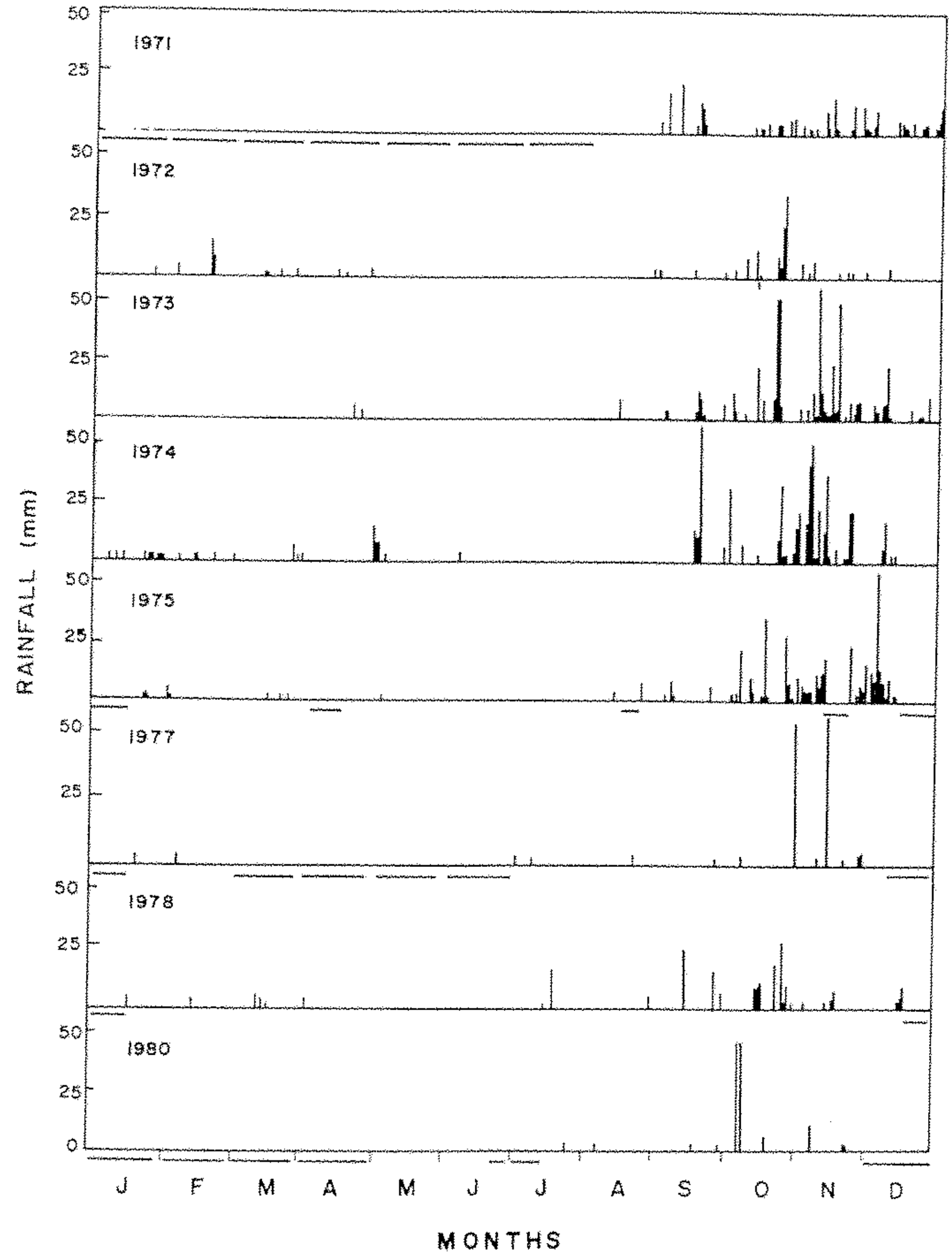

Figure 4. Daily rainfall during eight years in Nazareth (85 m) 5 km north of Serrania de Macuira. Horizontal dashed lines represent periods with no rainfall measurements. Data from HIMAT, Colombia.

relationship between altitude and fog interception one could estimate the elevation at which interception of cloud water ceases (Figure 2). The low limit at 513 m corresponds to the boundary between the dry deciduous forest and the elfin cloud forest placed by Sugden (1982) at 500 m to 550 m.

While fog interception is almost a daily feature of the weather in the cloud forest, rainfall is much rarer. At 600 m it only rained on four out of the 20 days

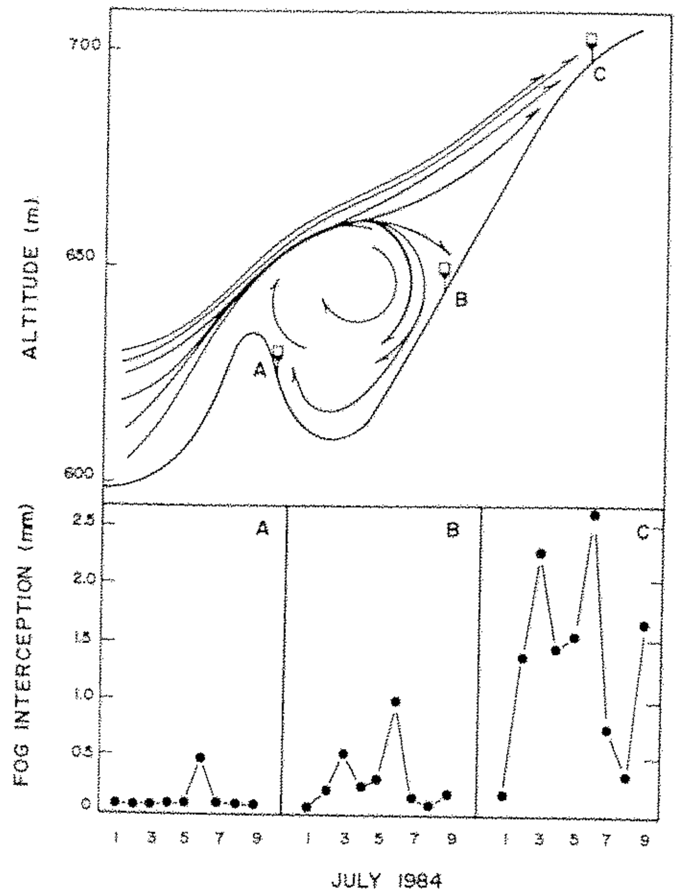

Figure 5. Daily fog interception on a leeward slope (A) and windward slopes (B, C) in the elfin cloud forest of Serranía de Macuira. The arrows in the upper panel, represent the observed cloud flux in the gully where measurements were made.

of measurements and no precipitation was recorded on nine consecutive days. At 750 m the number of days with rainfall increased to eight, and six consecutive days had no rainfall at all (Figure 3). This daily water supply of cloud water by means of fog interception contrasts with the highly seasonal and variable rainfall regime of the surrounding lowlands (Figure 4).

In a nine-day period in July 1984, fog interception was 2.5 times higher on a windward slope than on a leeward slope. This difference could be explained in terms of the observed cloud flux pattern on slopes and gullies in the cloud forest (Figure 5).

Rain and fog interception in the Andes and Caribbean mountains

There is a positive gradient of rainfall from west to east on top of the mountains of the Caribbean dry zone of Colombia and Venezuela. During 1985, total annual rainfall was 853 mm in Macuira, 1630 mm in Santa Ana and 4461 mm in Copey. While the rainfall increases towards the east, the total fog interception decreases in the same direction. The annual fog interception was 796 mm in Macuira, 518 mm in Santa Ana and 480 mm in Copey. In the Zumbador

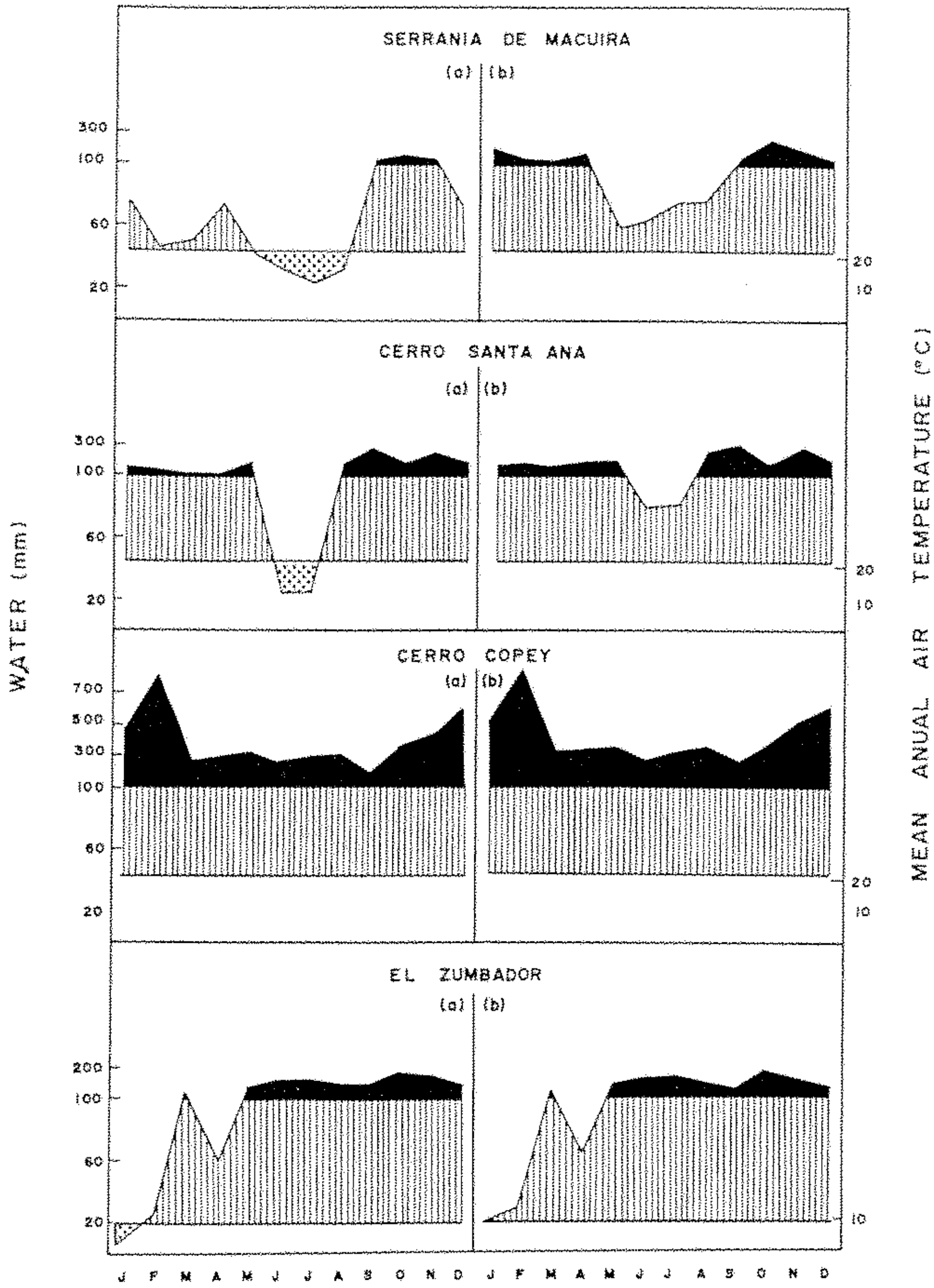

Figure 6. Climate diagrams (following Walter & Leith 1964) of the study sites using only rainfall (a), and rainfall + Fog interception (b).

forest, the annual fog interception was only 72 mm. Here, rainfall was also lower than in some of the Caribbean study sites, but given the lower temperatures in El Zumbador, the 1938 mm of rain were enough to compensate the relatively small evaporative demands.

If the aridity is estimated for the forests using the climate diagrams *sensu* Walter & Leith (1964), where the average monthly air temperature in °C and rainfall in millimetres are in the proportion 1:2, there are five dry months in

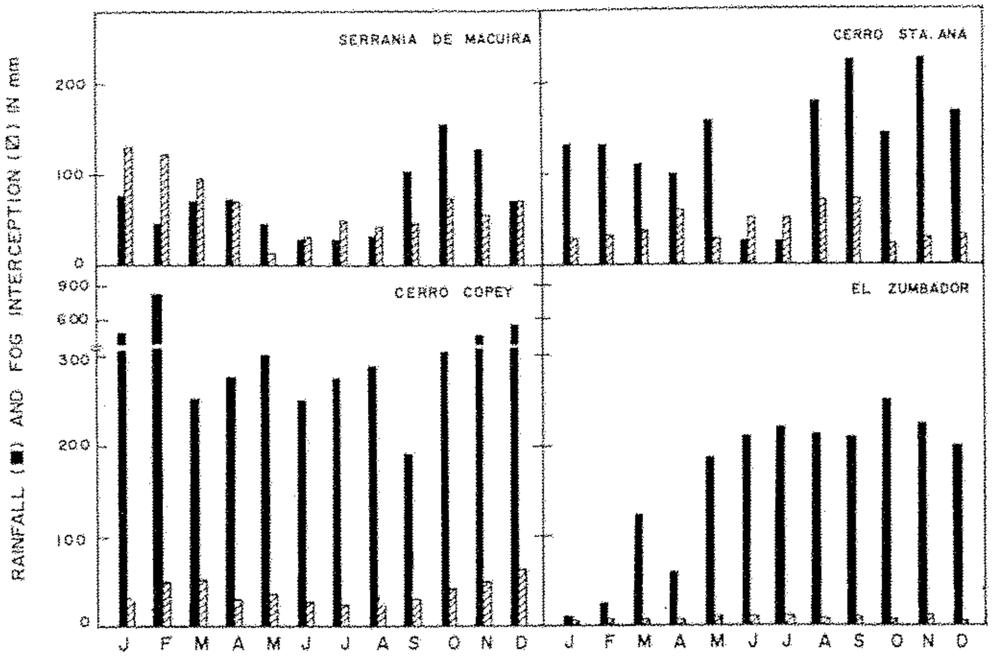

Figure 7. Monthly rainfall (■), and fog interception (▨) during 1984–5 in the four elfin cloud forests studied.

Macuira, two in Santa Ana and one in El Zumbador. However, when fog interception is added to rainfall, there is no dry season in any of the forests (Figure 6). The contribution of fog to the monthly water supply varies a great deal between wet and dry seasons. During the driest month, fog interception represents 63% of the water supply in Macuira, 66% in Santa Ana and only 9% in Copey. During the wettest month, fog accounts for 33% of the water income in Macuira, 12% in Santa Ana and only 6% in Copey. In the Andean forest of El Zumbador, cloud water accounts for 3% of the water supply during the rainiest month and up to 19% during January, the driest month of the year (Figure 7). It is clear that in the tropical cloud forests studied, fog interception is an important source of water for tree growth, particularly in the elfin cloud forests of the small mountains which are surrounded by dry vegetation types.

Leaf angle and fog interception

There is an increase in fog interception with increasing leaf angle (Figure 8). The experimental data fit well the cosine of the leaf angle, suggesting that the amount of water collected is a function of the projected area of leaves at different angles (i.e. leaves with steeper angles have more exposed leaf area for fog interception).

DISCUSSION

Since the beginning of the century, the use of rain gauges with a fog collector attached to them has been a common technique to measure fog interception

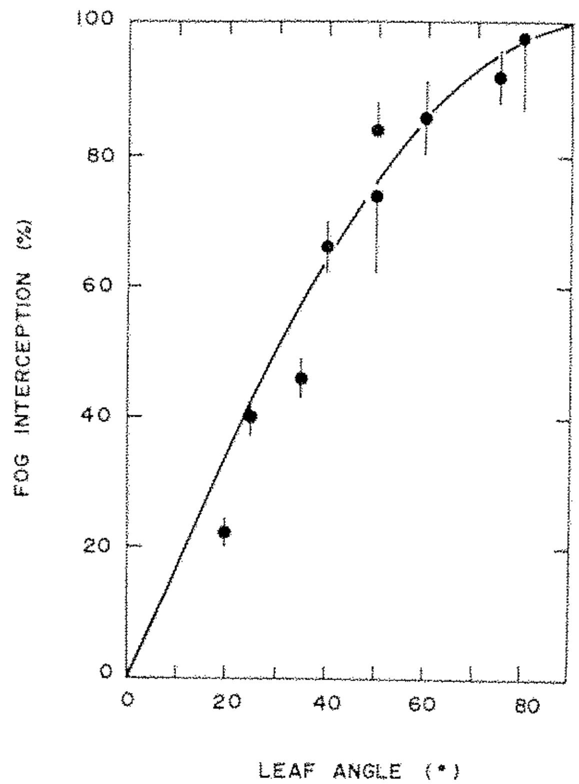

Figure 8. Relationship between leaf angle and fog interception. The points represent the experimental data (± 1 standard error) and the continuous line and cosine function between 0° and 90°.

(Marloth 1904, 1907). In recent years, however, more sophisticated instruments like the Caltech Rotating Arm Collector and filter papers have been introduced to measure the droplet size distribution and potential deposition rates (Chylek 1987, Jacob *et al.* 1984). Nevertheless, the essential problem of relating the results given by sophisticated or primitive cloud collectors to cloud water captured by an actual canopy is still unresolved. More recently some models have been introduced to estimate both gross and net deposition and to examine how they respond to changes in meteorological and canopy structure parameters (Lovett 1981). The ideal solution to the problem would be to measure the rate of water deposition to the forest floor as throughfall and stemflow during the cloud events and relate these volumes to the results given by artificial collectors.

In this study we measured fog interception in four tropical elfin cloud forests by means of fog catchers attached to rain gauges. With the throughfall (fog drip) and fog interception measurements in Macuira, a preliminary attempt has been made to relate cloud water volumes collected by fog catchers to water volumes collected by tree canopies. These volume estimates should be taken as a first quantitative attempt in understanding the potential contribution of fog to the hydrological balance of the ECF, since no stemflow measurements were made and canopy structure varies from forest to forest.

Variation of fog interception with topography

In the ECF of Macuira, fog interception increases with altitude. This difference can be attributed to the increase in wind speed with altitude, the daily period of cloud cover and the increase in the number, and probably the size, of cloud water droplets. The increase of fog interception with altitude and exposure could partially explain the variation of habitat within the cloud forest shown by the distribution of epiphytes; leeward slopes and gullies support fewer species and smaller populations of bromeliads than do sheltered ridges or windward slopes (Sugden 1982, Sugden & Robins 1979).

In Macuira, there is a strong correlation between the altitude at which no interception is expected and the lower limit of the ECF (Figure 2). This association of the lower limit of the clouds with the lower limit of a given forest type has been observed in New Guinea (Brass 1941, 1956), in the Andes (Bates 1948, Grubb & Whitmore 1966) and in Mexico (Vogelmann 1973) among others. It has been suggested that the distribution of tropical montane rain forest types is related to the frequency of fog cover (Grubb & Whimore 1966).

Rain and fog interception in the Caribbean and Andean forests

Sugden (1986) has suggested that cloud cover on the small mountains along the Caribbean coast of South America, increases humidity and offsets the highly seasonal rainfall regime. The results of our study support this hypothesis in the ECF of Macuira and Santa Ana, and to a lesser extent in the cloud forest of Cerro Copey, where the monthly rainfall is relatively high. The 1985 rainfall in this forest could be significantly higher than the annual average. Sugden (1986) observed that the annual rainfall in the surroundings of Cerro Copey is highly variable.

The unpredictable showers, the highly seasonal rainfall regime, and the rainfall variation from year to year around Serrania de Macuira, Cerro Santa Ana and Cerro Copey, contrast with the regularity of cloud cover and water supply by means of fog interception. During several consecutive weeks, fog interception may be the only water source for these evergreen forests. There was no rainfall for up to six consecutive days in Macuira during the 1986 rainy season, while fog interception occurred every day (Figure 3). If fog interception were not the major source of available water for plants, trees and other species in the ECF would be dependent on water supplied by scattered showers. In Macuira, daily evaporative demands range from 1.7 mm to 3.6 mm on a sunny day (Cavelier 1986).

One of the findings of this study was that the importance of fog as a water source increases as rainfall decreases (Figure 7). Little water supply in the form of fog interception has been measured on Pico del Oeste in the mountains of Puerto Rico (Baynton 1969). In this region of abundant rain, fog is of minor importance as a water supply since it accounts for less than 10% of the total water input. In contrast, high fog interception during dry months has been observed in the cloud forest of eastern Mexico (Vogelmann 1973).

Mist and fog interception measurements are scarce and difficult to compare, given the great variability of screens used in the fog-catchers. The most suitable data for comparison are the throughfall measurements after a cloud event. In Macuira, the maximum cloud water deposition was 2.4 mm per night which is in the range of values found in other tropical and temperate forests (Ekern 1964, Oberlander 1956, van der Weff 1978).

Possible physiological implications of cloud water

One of the most striking results of this study is the small volume of water collected by the fog catchers in the Zumbador forest as compared to the Caribbean sites. This could be explained in terms of smaller droplet size distribution and liquid water content in the stratiform clouds which predominate in the high Andes (Andressen 1978, Grubb & Whitmore 1966) as compared to the cumuliform clouds involved in the Caribbean mountains. Fog interception in the ECF of Macuira, Santa Ana, and to a lesser extent in Cerro Copey, occurs mainly during the night and seems to be an important water supply for these forests. In El Zumbador, fog is intercepted by the vegetation mainly during the afternoon and early night, but it deposits little water on the foliage. Leaves are rarely wet during the day in the forest of Macuira and Santa Ana, while the leaves in the species of El Zumbador are usually wet. It is possible that permanently wet leaves would experience lower transpiration and CO_2 fixation, reducing the total carbon gain. This could partially explain the reduction in tree stature in upper montane rain forest in high tropical mountains. On the other hand, the low stature in the cloud forests of the small Caribbean mountains could be the result of high wind speed and low nutrient availability, particularly phosphorus (Cavelier 1986).

The steep angle of the upper leaves in the canopy of tropical trees has been considered as a drought avoidance mechanism (Medina 1983). The leaf inclination would reduce the absorbed radiation per unit leaf area during rare sunny periods in cloud forests, avoiding overheating due to stomatal closure at moderate water deficits (Medina *et al.* 1981). On the other hand, leaf inclination also increases the efficiency of fog interception (Figure 8). If leaf inclination has been selected to increase fog interception, one would expect to find steeper leaf angles in the cloud forest where fog is an important water source. Since the species in the Andean forest of El Zumbador, where fog interception represents only 3.6% of the total water supply, also have very steep leaf angles, this character may be of secondary importance in increasing fog interception, its primary importance being a mechanism to avoid high radiation loads.

ACKNOWLEDGEMENTS

This research was sponsored by CAVELCA and the Postgrado de Ecologia Tropical, Universidad de los Andes, Merida, Venezuela. We thank Manuel Barrios (Serrania de Macuira), Amabiles Mendez (Cerro Santa Ana), Jose Characoto (Cerro Copey) and Elisaul Rangel (Universidad de los Andes, Merida) for collecting the rainfall and fog interception data in the study sites. We also thank C. Mejia, A. Laignelet, A. M. Penuela, M. Posada, A. Verala for helping in the collection of data in the cloud forest of Serrania de Macuira, Julia Castellanos

(HIMAT, Bogota) for providing the rainfall data for Nazareth, Serrania de Macuira, and Dr P. J. Grubb, Dr I. Woodward, Dr E. V. J. Tanner and Dr A. Sugden for valuable comments on an early manuscript of this paper.

LITERATURE CITED

ANDRESSEN, R. L. 1966. Estudio climatologico de las islas de Margarita, Coche y Cubagua. Estado Nueva Esparta. Ministerio de Agricultura y Cria. Caracas. 58 pp.

ANDRESSEN, R. L. 1978. Crecimiento de la gota de agua y contenido de agua líquida en nubes, Universidad de los Andes, Facultad de Ciencias Forestales, Escuela de Geografía, Merida, Venezuela. 60 pp.

BATES, M. 1948. Climate and vegetation in the Villavicencio region of eastern Colombia. *Geographical Review* 38:555–574.

BAYNTON, H. W. 1968. The ecology of an elfin forest in Puerto Rico, 2. The microclimate of Pico del Oeste. *Journal of the Arnold Arboretum* 49:419–430.

BAYNTON, H. W. 1969. The ecology of an elfin forest in Puerto Rico, 3. Hilltop and forest influence on the microclimate of Pico del Oeste. *Journal of the Arnold Arboretum* 50:80–92.

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

BRASS, L. J. 1941. The 1938–9 expedition to the snow mountains, Netherlands New Guinea. *Journal of the Arnold Arboretum* 22:271–295; 297–342.

BRASS, L. J. 1956. Results of the Archbold Expeditions. No. 75. Summary of the Fourth Archbold Expedition to New Guinea (1953). *Bulletin of the American Museum of Natural History* 111:80–152.

CAVELIER, J. 1986. Relaciones hidricas y de nutrientes en bosques enanos nublados. Tesis de Maestria. Universidad de los Andes, ULA, Merida, Venezuela. 273 pp.

CHANERY, W. R. 1981. Sources of water. Pp. 1–47 in Kozlowski, T. T. (ed.). *Water deficits and plant growth.* Vol. VI, Woody plant communities. Academic Press.

CHYLEK, K. P. 1978. Extinction and liquid water content of fogs and clouds. *Journal of Atmospheric Sciences* 35:296–300.

CLEGG, A. G. 1963. Rainfall interception in a tropical forest. *Caribbean Forester* 24:75–79.

EKERN, P. C. 1964. Direct interception of cloud water on Lanaihale, Hawaii. *Proceedings of the Soil Science Society of America* 28:419–421.

GRUBB, P. J. 1977. Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. *Annual Reivew of Ecology and Systematics* 8:83–107.

GRUBB, P. J. & WHITMORE, T. C. 1966. Comparison of montane and lowland rain forests in Ecuador. II. The climate and its effects on the distribution and physiognomy of forests. *Journal of Ecology* 54:303–333.

HOWARD, R. A. 1970. The 'alpine' plants of the Antilles. *Biotropica* 2:24–28.

HUBER, O. 1986. El Clima, Pp. 17–29 in Huber, O. (ed.). *La selva nublada de Rancho Grande, Parque Nacional 'H. Pittier'. El ambiente fisico,ecología vegetal y anatomía vegetal.* Fondo Editorial Acta Cientifica Venezolana, Caracas. 288 pp.

JACOB, D. J., WALDMAN, J. M., MUNGER, J. W. & HOFFMAN, M. 1984. A field investigation of physical and chemical mechanisms affecting pollutant concentrations in fog droplets. *Tellus* 36B: 272–285.

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

KAPOS, V. & TANNER, E. V. J. 1985. Water relations of Jamaican Upper Montane Rain Forest trees. *Ecology* 66:241–250.

LAHEY, J. F. 1958. On the origin of the dry climate in northern South America and the southern Caribbean. *Department of Meteorology, University of Wisconsin Scientific Report* 10:1–290.

LAWTON, R. & DRYER, V. 1980. The vegetation of Monteverde Cloud Forest Reserve. *Brenesia* 18: 101–116.

LOVETT, G. M. 1981. Forest structure and atmospheric interactions: predictive models for subalpine Balsam Fir Forests. Ph.D. Thesis, Dartmouth College, Hanover, New Hampshire, August 1981. 225 pp.

MARLOTH, R. 1904. Results of experiments on Table Mountain for ascertaining the amount of moisture deposited from the south-east clouds. *Transactions of the South African Philosophical Society* 14:403–408.

MARLOTH, R. 1907. Results of further experiments on Table Mountain. *Transactions of the South African Philosophical Society* 16:97–105.

MEDINA, E. 1983. Adaptations of tropical trees to moisture stress. Pp. 225–237 in Golley, F. B. (ed.). *Tropical rain forest ecosystems: structure and function.* Elsevier Scientific Publishing Company.

MEDINA, E., CUEVAS, E. & WEAVER, P. L. 1981. Composicion foliar y transpiracion de especies lenosas de Pico del Este, Sierra de Luquillo, Puerto Rico. *Acta Cientifica Venezolana* 32:159-165.

MONASTERIO, M. 1980. Estudios ecologicos en los Paramos Andinos. Universidad de los Andes, ULA, Merida, Venezuela.

OBERLANDER, G. T. 1956. Summer fog precipitation in San Francisco peninsula. *Ecology* 37:851.

ODUM, H. T., DREWRY, G. & KLINE, J. R. 1970. Climate at El Verde, 1963-1966. Pp. B-347-418 in Odum, H. T. & Pigeon, R. F. (eds). *A tropical rain forest, a study of irradiation and ecology at El Verde, Puerto Rico.* Division of Technical information. U.S. Atomic Energy Commission.

ORTEGA, F. J. 1982. La fitogeografia de las pteridofictas de la isla de Margarita. *Memorias de la Sociedad de Ciencias Naturales La Salle* 42:135-150.

van REEN, G. 1983. Distribution y ecologia de musgos y hepaticas. Pp. 206-209 in van der Hammen, T. *et al.* (eds). *Studies on tropical Andean ecostystems.* Vol. 1 La Cordillera Central Colombiana, Transecto Parque los Nevados (Introduccion y datos preliminares). J. Cramer.

RIEGER, W. 1976. Vegetationskundliche Untersuchengen der Guajira-Halbinsel (Nordost-Kolumbien) *Giessener Geogrische Schriften Heft* 40:1-142.

SNOW, J. W. 1976. The climate of Northern South America. Pp. 245-379 in Schwerdtfeger, W. (ed.). *World survey of climatology.* Vol. 12. Elsevier, Amsterdam.

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

SUGDEN, A. M. 1982. The vegetation of Serrania de Macuira, Guajira, Colombia: A contrast of arid lowlands and an isolated cloud forest. *Journal of the Arnold Arboretum* 63:1-30.

SUGDEN, A. M. 1986. The montane vegetation and flora of Margarita Island, Venezuela. *Journal of the Arnold Arboretum* 67:187-232.

SUGDEN, A. M. & ROBINS, R. L. 1979. Aspects of the ecology of vascular epiphytes in two Columbian cloud forests. I. The distribution of the epiphytic flora. *Biotropica* 11:173-188.

TAMAYO, F. 1941. Exploraciones botanicas en la Peninsula de Paraguana, Estado Falcon. *Boletin de ka Sociedad Venezolana de Ciencias.* 7:1-44.

TANNER, E. V. J. 1977. Four montane rain forests of Jamaica: a quantitative chracterization of the floristics, the soils and the foliar mineral levels, and a discussion of the interrelations. *Journal of Ecology* 65:883-918.

VOGELMANN, H. W. 1973. Fog interception in the cloud forest of eastern Mexico. *Bioscience* 23:96-100.

WALTER, H. & LEITH, H. 1964. *Klimadiagramm-Weltatlas. I. Lieferung 1964,* VEB Gustavav Fisher Verlag, Jena.

WEFF, H. H. van der, 1978. The vegetation of the Galapagos Islands. Ph.D. Rijksuniversiteit te Utrecht, the Netherlands.

Accepted 18 October 1988