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Fog interception in montane forests across the Central Cordillera of Panamá

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ABSTRACT. Fog interception and rainfall were measured at 14 stations across the Central Cordillera in western Panamá. Fog interception and rainfall were measured monthly during 1988–1989 with artificial fog catchers and rain gauges, respectively. Fog interception was highest on ridges and increased with increasing altitude. Fog interception contributed between 2.4 and 60.6% of the total water input, depending on altitude and exposure to the prevailing winds. Absolute amounts of annual fog interception ranged from 142 to 2295 mm. Although low clouds were more frequent in montane forests, clouds close to the ground also occurred in the lowlands. During the study period, there was a gradient of increasing total rainfall from the Caribbean (3355 mm) to the Pacific side (5759 mm) of the Central Cordillera. Nevertheless, rainfall was more seasonal on the leeward side of the mountain range. Seasonal variation in fog intereption was different from rainfall patterns and no correlation was found between monthly (or annual) rainfall and fog interception. The results of this study showed the importance of montane forests for the preservation of water sources, particularly along ridges of the Fortuna drainage basin that provides more than 50% of the electricity of the Republic of Panamá.

KEY WORDS: fog, fog interception, montane forests, Panamá, rainfall, tropical montane cloud forest.

INTRODUCTION

The slopes of wet tropical mountains are covered with different forests types. In the Andes, for instance, four forest formations can be recognized. Lowland rainforest (LRF) occurs from sea level to 1200 m, lower montane rainforest (LMRF) from 1200 to 2500 m, upper montane rainforest (UMRF) from 2500 to 3200 m and subalpine rainforest (SARF), above the UMRF and below the Páramos, open grasslands with giant rosettes (Cuatrecasas 1934, 1958; Grubb 1977). These altitudinal limits vary with the size of the mountain, exposure to the prevailing wind direction and the distance to the sea (Bruijnzeel *et al.* 1993, Flenley 1979, van Steenis 1972) as reported for small mountains and isolated ridges, such as Serranía de Macuira in Colombia (Sugden 1982), Cerro 'El

Cielo' at the Sierra Nevada de Santa Marta on the Caribbean coast of Colombia (Lozano 1984) and the Luquillo Mountains in Puerto Rico (Weaver 1991, Weaver & Murphy 1990). This phenomenon is known as the 'Massenerhebung' effect (Grubb 1971, 1977).

Wet tropical forests have been associated with a different frequency of low clouds. For instance, LRF experiences negligible fog, while LMRF has frequent fog and UMRF long persistent cloud cover close to the ground (Grubb & Whitmore 1966). Nevertheless, actual measurements of fog interception in these forest types are rare (Baynton 1969, Bruijnzeel 1990, Bruijnzeel & Proctor 1993, Bruijnzeel *et al.* 1993, Cavelier & Goldstein 1989, Cavelier *et al.* 1992, Chaney 1981, Kerfoot 1968, Vogelmann 1973, Weaver 1972, Werff 1978) when compared to the extensive rainfall data in even remote tropical montane sites. These studies suggest that fog can supply different amounts of liquid water to Tropical Montane Cloud Forest (TMCF) *sensu* Hamilton *et al.* (1993). On the one hand, fog can be an important water source as in the case of Serranía de Macuira, where fog interception represents 48% of the total water input (796 mm of fog and 853 mm of rain; Cavelier & Goldstein 1989). Fog also represents an important water source in the *Scalesia pedunculata* forests on the Galapagos Islands where fog drip can be has high as 99% of the water input to the understorey (Werff 1978). On the other hand, clouds can increase the humidity and offset the highly seasonal rainfall regime without contributing much with liquid water to the hydrological balance as suggested by Sugden (1986) for Cerro Copey at Isla Margarita, Venezuela. Indeed, fog interception measurements on this mountain showed that fog contributed only 9.7% of the water input (458 mm of fog and 4461 mm of rain; Cavelier & Goldstein 1989). Similar results were reported for the Pico del Oeste in Puerto Rico, where fog interception represented only 7.2% of the water input (325 mm of fog and 4530 mm of rain; Baynton 1969). Even more, in the Andean forest of El Zumbador (Venezuela) annual fog interception is only 3.5% of the total water input (72 mm of fog and 1983 mm of rain; Cavelier & Goldstein 1989). '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. Cloud water droplets are blown by the wind against the vegetation where they coalesce to form large drops that run off and fall to the ground (Chaney 1981). Fog droplets have to be intercepted by the vegetation and they do not precipitate as rainfall drops do, as the use of the terms 'fog precipitation' (Nagel 1956) or 'horizontal precipitation' (Stadtmüller 1987) seem to suggest.

The objective of this study was to measure fog interception and rainfall across the Central Cordillera of Panamá (along a Pacific–Caribbean transect) passing through the Fortuna drainage basin that drains to the Pacific Ocean. The seasonal measurements across the Central Cordillera (1988–1989) were made using fog catchers at different forest types and along altitudinal gradients (500–1270 m) on both windward and leeward sides of the Cordillera.

Sea. Stations 1–4 were on the leeward side of the mountain, with stations 1–10 drained to the Pacific side. The continental divide is at station 11 (Figure 1). The profile of the Cordillera along the transect where the stations were located is such that there were stations (i.e. 6 and 7) receiving the prevailing winds (i.e. on the windward side) and, nevertheless, draining to the Pacific Ocean. The Fortuna drainage basin was between A and B in Figure 1.

Fog interception and rainfall measurements

Fog interception was measured every 30 days between April 1988 and March 1989 with open-ended cylindrical fog catchers (8.4 cm in diameter and 8.0 cm height) made from plastic screen of 40 mesh (open spaces) per cm^2 (i.e. 64% of the area available for air passage). Rainfall was measured with plastic funnels 56.0 cm^2 in area, located at 1.5 m above the ground connected with PVC tubing (1.5 cm of interior diameter) to 5-gallon containers. This long and narrow tubing minimized the loss of water by evaporation. The rain gauge without the

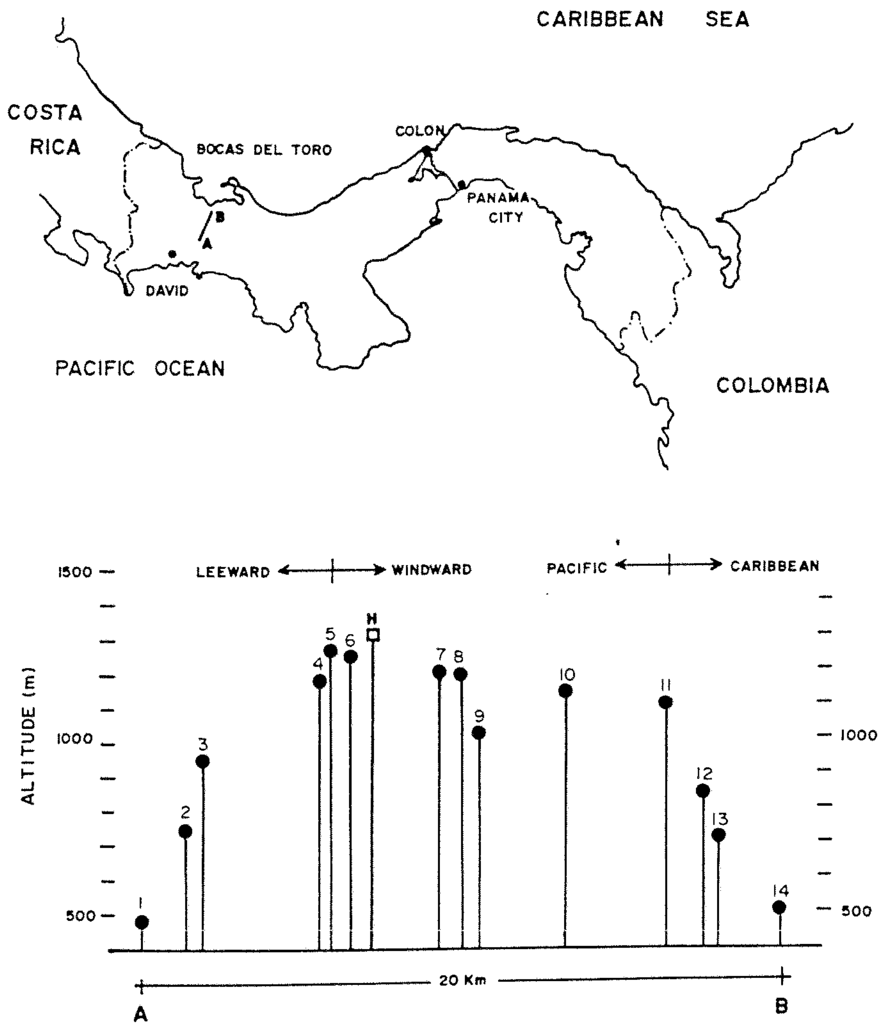

Figure 1. Location of the transect in western Panamá across the Central Cordillera and the altitudes of the 14 stations used to measure rain and fog interception. Solid circles represent fog- and rainfall-stations and the open square the Hornitos weather station.

screen collected only rainfall, while the gauge with the screen collected both rain and cloud water ('non-vertical rain') as wind moved water droplets onto the screen (Nagel 1956). Volume differences between rain and fog catchers (cm^3) gave the relative amounts of fog interception and non-vertical rain. Although these fog catchers are not of 'standard dimension' (i.e. height = 2 × diameter; see Grunow 1952 in Nagel 1956) they have been effectively used to collect cloud water in elfin cloud forests (ECF) of Caribbean mountains and in the Andes of Venezuela (Cavelier & Goldstein 1989) and Colombia (Cavelier *et al.* 1992). In the former studies, a conversion factor of 318 cm^3 to 1 mm was used to scale the water volumes obtained in the fog catcher and the net precipitation measured as throughfall on the forest floor. Because of the structural differences between ECF and the forests of Panamá (i.e. tree stature, number of strata and leaf area index), different calculations were made in the present study to estimate the relative importance of fog. Volume differences between rain and fog catchers (cm^3) were divided by 212 cm^2, equivalent to the entire area of the screen (height = 8 cm × perimeter of the funnel = 26.5 cm). Although fog catchers had 0.36 cm^2 of plastic per square centimetre of screen, the mesh filled with water during cloud events and, thus, the area of interception was the same as the exposed area of the screen. Fog interception for the different stations (expressed in mm) should not be taken as absolute values, but as a relative measure of the contribution of fog to the hydrological balance of different forests. The interpretation of absolute values would require the calibration of the fog catcher's efficiency against the vegetation (i.e. Cavelier & Goldstein 1989).

RESULTS

Annual rainfall and fog interception across the Cordillera

Total rainfall increased from the Caribbean to the Pacific side of the mountain (Figure 2). The maximum rainfall occurred at station 4 (on the Pacific side), the first station on the leeward side of the Cordillera. The minimum rainfall occurred at station 11 (on the Caribbean side), right on the continental divide. Fog interception also varied across the mountain range. The maximum values occurred at stations 11 and 5, both located on ridges: the first, separating the Caribbean from the Pacific drainage basin, and the second, separating the windward- from the leeward-side of the Cordillera. Fog interception contributed from 2.4% (station 1; Pacific side) to 60.6% (station 11; Caribbean side) of the total water input (Figure 2). Fog interception may be an important water source in both lowland and montane forests. For instance, fog interception at station 14 (500 m) was 463.4 mm, while at station 6 (1250 m) it was 447.7 mm.

Seasonal variation in rainfall and fog interception

Total rainfall and seasonality was higher towards the Pacific side of the transect. While rainfall at station 1 was 5759 mm with five dry months (less

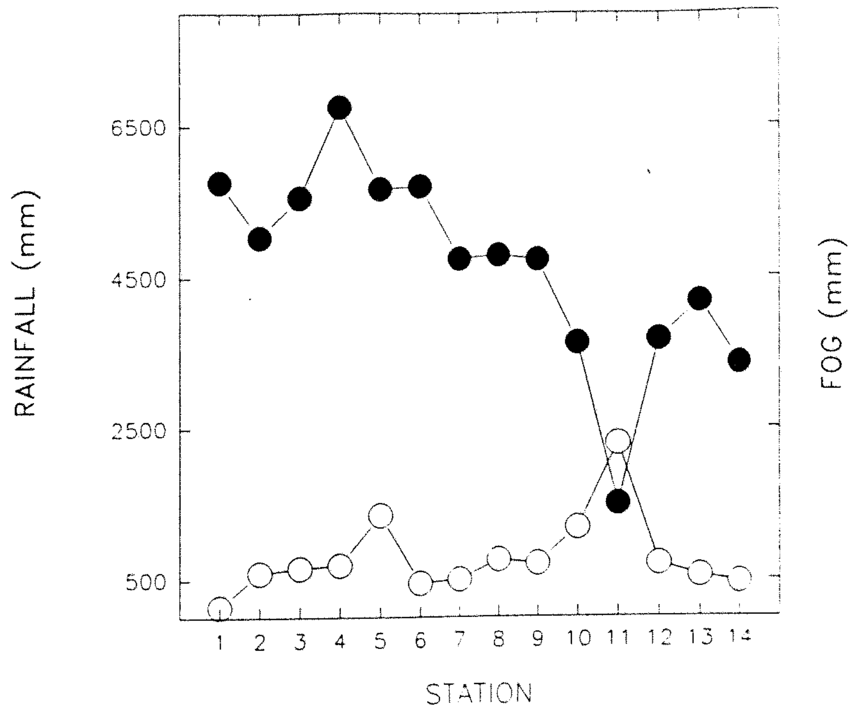

Figure 2. Total annual (April 1988 to March 1989) rainfall (closed circles) and fog interception (open circles) for the 14 stations across the Central Cordillera.

than 100 mm), rainfall at station 13 was 4178 mm with no dry months (Table 1, Figure 3). In the lowlands of the Caribbean side, rainfall was more evenly distributed (station 13, Figure 3). With increasing altitude on the windward side (station 10), the rainy season became concentrated in the period December–February. Conversely, the wettest period shifted to June–October in those stations south of station 10 (i.e. stations 1, 6 and 9; Figure 3).

Seasonal variation in fog interception was different from that of rainfall patterns (Figure 4) and no correlation was found between monthly (or annual) rainfall and fog interception (Figure 5).

Fog interception along altitudinal gradients

Fog interception increased with increasing altitude (Figure 6). The rate of increase was about the same for the windward and leeward side of the Cordillera up to *c*. 850 m. From 850 to *c*. 1200 m the rate of increase was higher for the windward side. Total rainfall did not show the same pattern in this part of the transect (Figure 6).

DISCUSSION

Rainfall patterns

Total annual rainfall and seasonality increased from the Caribbean to the Pacific side of the Cordillera (Figures 2 & 3). This result agrees with long-term records of rainfall measured in the lowlands (Estadística Panameña 1986).

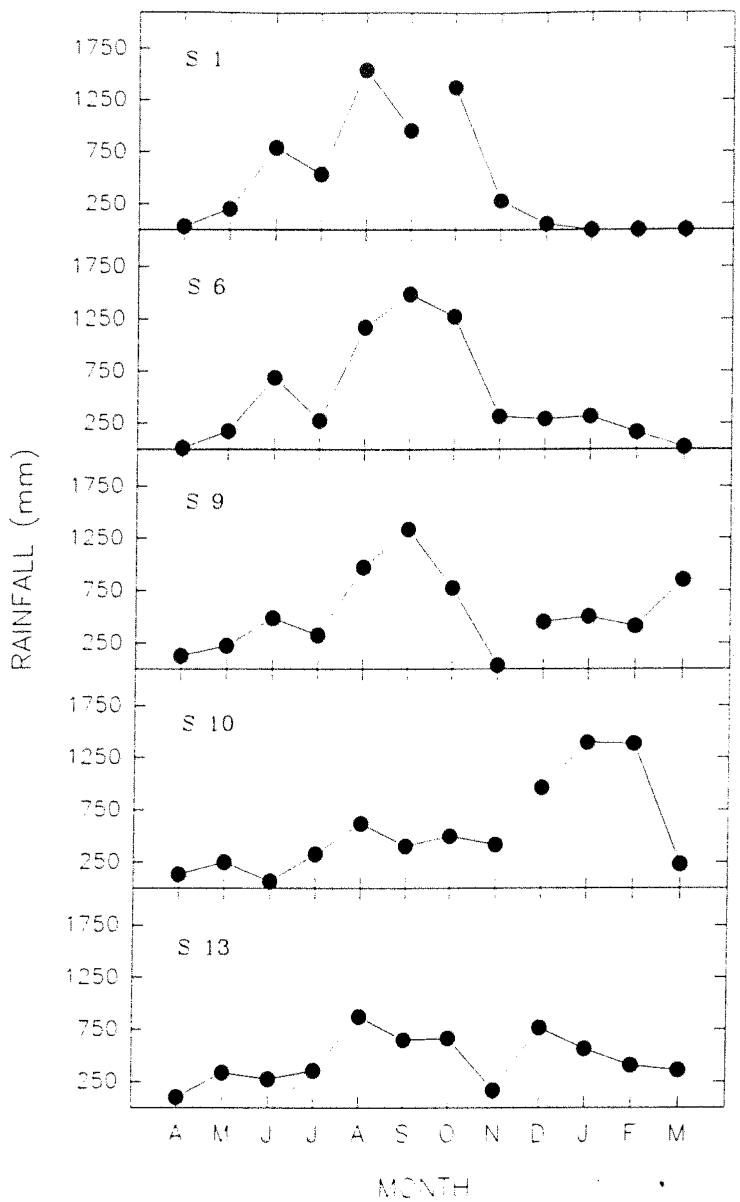

Figure 3. Seasonal variation in rainfall (April 1988 to March 1989) for five selected stations across the Central Cordillera.

Nevertheless, the total rainfall during the study period (April 1988–March 1989) was higher than historical records (1970–1986). For instance, annual rainfall at station 5 (1270 m) was 5669 mm while at the Hornitos weather station (1340 m), mean annual rainfall was 3327 mm with values up to 6609 mm for 1970 (Estadística Panameña 1986). Seasonal rainfall patterns during 1988–1989 were similar to long-term records with lower rainfall during January–April.

In near-by Costa Rica, the analysis of long-term records of rainfall (1930s–1980s) suggests that lowland sites are becoming drier while mid-elevation sites are becoming wetter (Fleming 1986). Fleming (1986) hypothesized that secular changes in annual rainfall are related to the clearing of lowland forests along

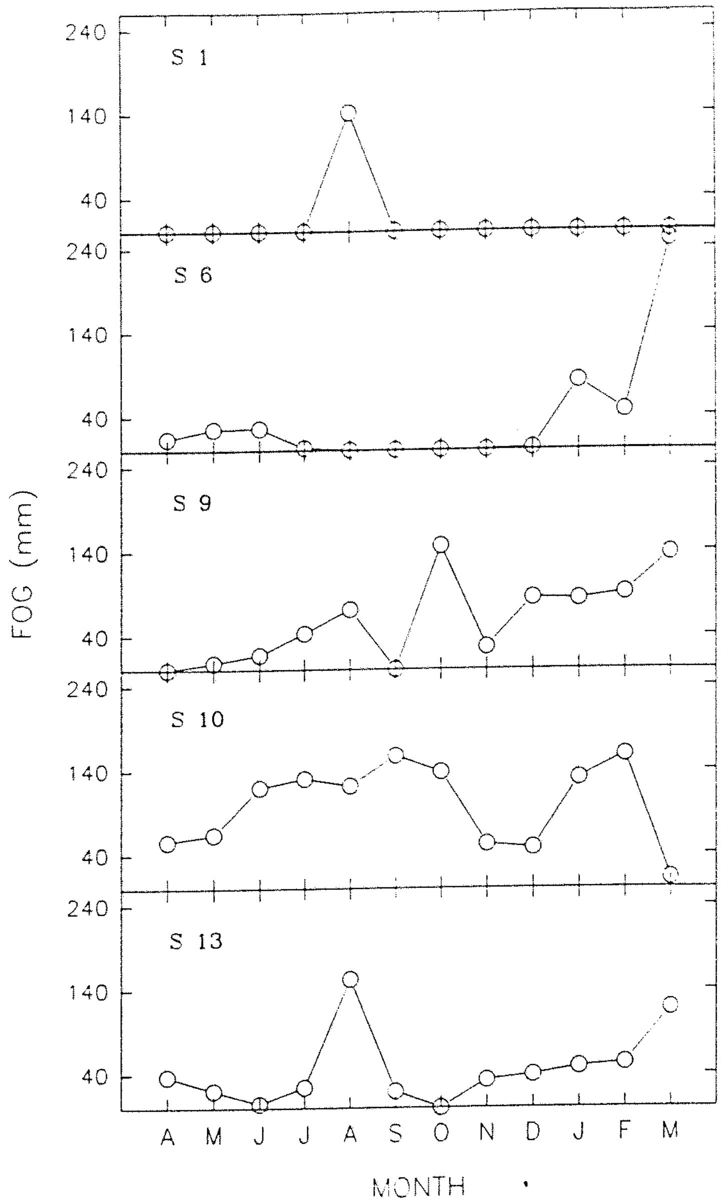

Figure 4. Seasonal variation in fog interception (April 1988 to March 1989) for five selected stations across the Central Cordillera.

the Pacific coast. If this phenomenon is also happening in Panamá, where Pacific lowland forests have also been cleared for cattle ranching, annual rainfall is expected to increase in the mountains. Indeed, long-term records for annual rainfall at Hornitos weather station show that there has been a non-significant increase in annual rainfall (29.6 mm y^{-1}) from 1959 to 1981 (annual rainfall = 29.6 time + 2360.2; $P < 0.1$). If this trend continues, this would favour the water-budget of the Fortuna hydrological project since the reservoir was recently enlarged (in 1993) to provide a higher electricity output. If rainfall is increasing at mid-elevations across the Central Cordillera in Panamá, the preservation of the lower montane rainforests is critical to avoid erosion (i.e. landslides) and to regulate the water flow during the drier months (Bruijnzeel

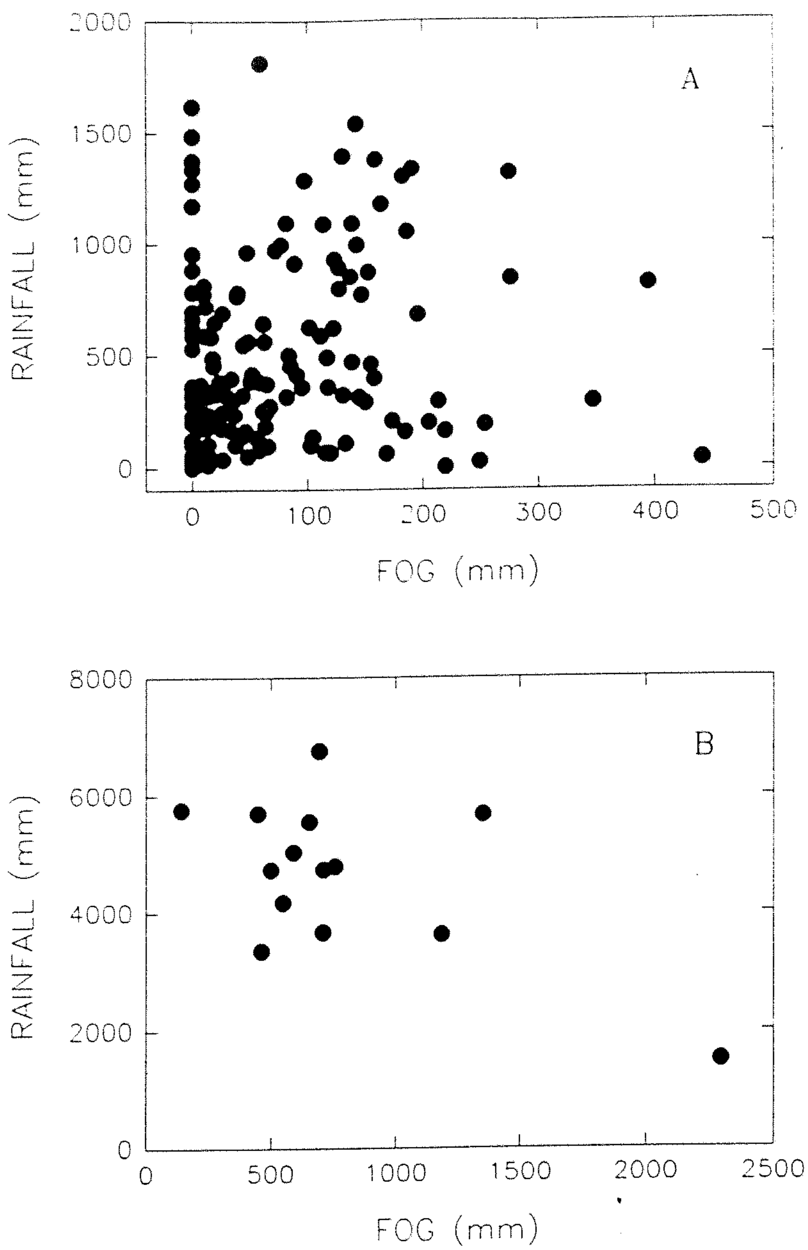

Figure 5. Relationships between (A) monthly fog interception and rainfall, and (b) annual fog interception and rainfall, for the 14 stations across the Central Cordillera.

1990). Furthermore, if fog stripping is indeed an important water source in at least part of the drainage basin (i.e. ridges), deforestation would result in reduction of water yields (Bruijnzeel & Proctor 1993).

Fog interception in different forest types

Although tropical lowland and montane forests are exposed to clouds, there is little information regarding the frequency of cloud cover close to the ground for these forest formations (Grubb 1977, Grubb & Whitmore 1966). Using the fog interception values as a measure of fog persistence, the results of this study suggest that lower montane rainforest at the Central Cordillera of Panamá can

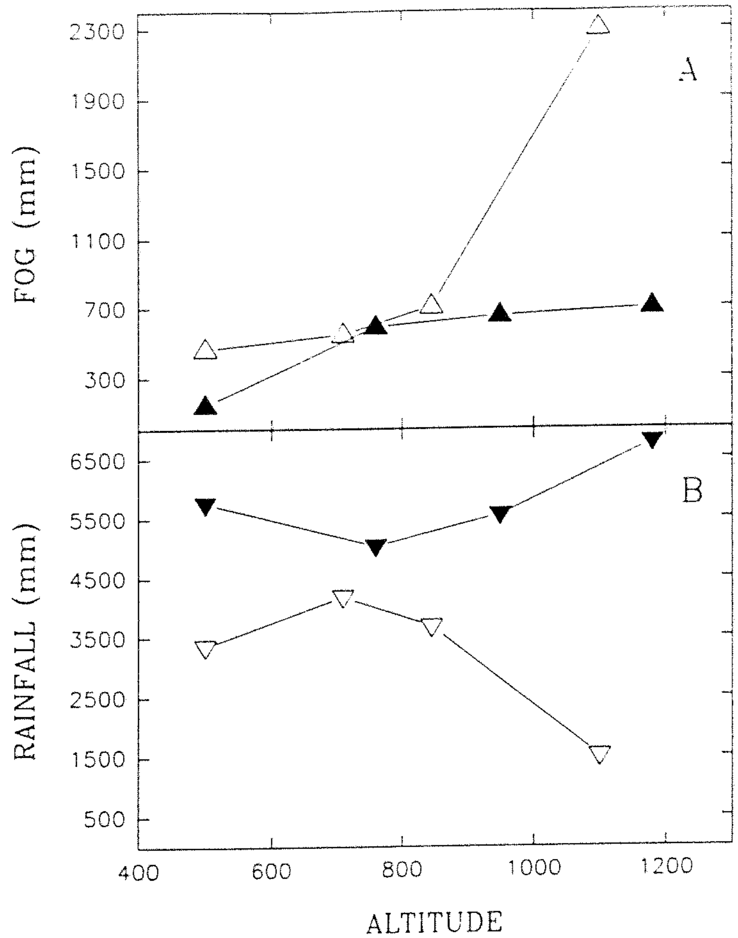

Figure 6. Variation in fog and rainfall interception with altitude in the Central Cordillera. In the upper panel (A), annual fog interception is shown for the windward (open triangles) and leeward slopes (closed triangles). In the lower panel (B), annual rainfall is shown for the windward and leeward slopes.

experience up to 16 times more fog (station 11) than a lowland rainforest (station 1). Nevertheless, certain sheltered areas within the LMRF (stations 9 and 6) can have the same fog frequency as a lowland rainforest (station 12). Variations of fog interception with different exposures within the LMRF were also described for elfin cloud forest in Colombia and Venezuela (Cavelier & Goldstein 1989). In these forests, there was a negative correlation between annual rainfall and fog interception. The ECF with higher rainfall (El Zumbador at 3100 m) also had lower fog interception. Across the Central Cordillera of Panamá, the negative correlation between rain and fog is weak (Figure 5).

Variation of fog interception with exposure to the prevailing winds

Exposure to the prevailing winds is a key factor in determining the frequency of low clouds and values of fog interception. In general, fog interception was more important on ridges than on slopes and valleys (Figure 2). In the case of the Fortuna drainage basin (providing more than 50% of the electricity of the country), the forests on ridges seemed to play a key role in the interception of cloud water in spite of occupying a small area (<10%).

There was an increase in fog interception with increasing altitude, and this is more pronounced on the windward slope (Figure 6). On this side of the mountain, clouds are blown against the vegetation from the bottom (Caribbean lowlands) to the top of the mountain. This movement enhances the saturation of the air, wind speed, the size of the cloud droplets and its water content (Riehl 1979, Strahler 1979). On the contrary, on the leeward side of the mountain, winds blow downward moving clouds partially depleted in liquid water. These downward and drier clouds encounter dry and hot winds moving from the Pacific lowlands, resulting in further reduction in the potential for fog interception. Increases in fog interception with increasing altitude and exposure were also reported for elfin cloud forests along the Caribbean coast of South America (Cavelier & Goldstein 1989). In Panamá, the Bromeliaceae on the windward side of the mountain (receiving more fog) are less xeromorphic than those on the leeward side (*pers. obs.*, 1989). Furthermore, in wetter areas of the Fortuna drainage basin, epiphyllous liverworts were more abundant than lichens that in turn were more abundant in drier forests such as the semideciduous lowland forest of Barro Colorado Island (Coley *et al.* 1993). In ECF, leeward slopes support fewer species and smaller populations of bromeliads than windward slopes (Sugden 1982, Sugden & Robins 1979). In Ecuador, the species of Bromeliaceae that are present on both sides of the Andes occur at lower altitudes on the wetter eastern Andes (Gilmartin 1973). Thus, epiphytic and epiphyllous vegetation can be used as an indirect measure of humidity and rainfall regimes (Wolf 1993).

Although the potential role of tropical montane cloud forest in the hydrological cycle has been discussed on several occasions (Bruijnzeel & Proctor 1993, LaBastille & Pool 1978, Stadtmüller 1987, Veneklaas 1990, Zadroga 1981), actual data on fog interception is scarce. The values of fog interception measured in Panamá and in other sites using artificial fog catchers (Gioda *et al.* 1993), should be scaled to estimate the real contribution of fog to the hydrological cycle of the TMCF. This can be done by measuring canopy drip during rainless perods (Cavelier & Goldstein 1989) or by comparison of amounts of canopy drip with amounts of bulk precipitation (see Bruinjzeel & Proctor 1993 for details). In the meantime, relative values are useful to identify the critical areas where fog is being intercepted at a higher rate and, thus, may play a key role in the water-budgets of high altitude drainage basins.

In Panamá, the Instituto de Recursos Hidráulicos y Energéticos (IRHE) is in charge of the conservation of TMCF at the Fortuna drainage basin that we now know is very important for fog interception (at least on ridges) and for the general stability of the region where most of the electricity for Panamá comes from. Fortuna could be declared a National Park and annexed to La Amistad National Park, a park on the border with Costa Rica. Fortuna and La Amistad

National Park are indeed two of the areas needed for the conservation of TMCF in Central America and the Caribbean (LaBastille & Pool 1978).

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LITERATURE CITED

BAYNTON, H. W. 1989. The ecology of an elfin forest in Puerto Rico, 3. Hilltop and forest influences on the microclimate of Pico del Oeste. *Journal of the Arnold Arboretum* 50:80–92.

BRUIJNZEEL, L. A. 1990. *Hydrology of moist tropical forests and effects of conversion: a state of knowledge review*. UNESCO, International Hydrological Programme, Paris and Free University, Amsterdam.

BRUIZNZEEL, L. A. & PROCTOR, J. 1993. Hydrology and biogeochemistry of tropical montane cloud forests: what do we really know? Pp. 25–46 in Hamilton, L. S., Juvik, J. O. & Scatena, F. N. (eds). *Tropical montane cloud forests*. Proceedings of an international symposium at San Juan, Puerto Rico, 31 May–5 June 1993. East–West Center Program on Environment, UNESCO International Hydrological Programme and International Institute of Tropical Forestry. 264 pp.

BRUIJNZEEL, L. A., WATERLOO, M. J., PROCTOR, J., KUITERS, A. T. & KOTTERINK, B. 1993. Hydrological observations in montane rain forests on Gunung Silam, Sabah, Malaysia, with special reference to the 'Massenerhebung' effect. *Journal of Ecology* 81:145–167.

CAVELIER, J. 1989. Root biomass, production and the effect of fertilization in two tropical rain forests. PhD Dissertation, University of Cambridge, UK. 116 pp.

CAVELIER, J. & GOLDSTEIN, G. 1989. Mist and fog interception in elfin cloud forest in Colombia and Venezuela. *Journal of Tropical Ecology* 5:309–322.

CAVELIER, J., MACHADO, J. L., VALENCIA, D., MONTOYA, J., LAIGNELET, A., HURTADO, A., VARELA, A. & MEJIA, C. 1992. Leaf demography and growth rates of *Espeletia barclayana* Cuatrec. (Compositae), a caulescent rosette in a Colombian Páramo. *Biotropica* 24:52–63.

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

COLEY, P. D., KURSA, T. A. & MACHADO, J. L. 1993. Colonization of tropical rain forest leaves by epiphylls: effects of site and host plant leaf lifetime. *Ecology* 74:619–623.

CUATRECASAS, J. 1934. Observaciones geobotánicas en Colombia. *Trabajos del Museo Nacional de Ciencias Naturales, Serie Botánica* 27:1–144.

CUATRECASAS, J. 1958. Aspectos de la vegetación natural de Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 10:221–264.

ESTADISTICA PANAMEÑA. 1986. Situatión Física, Meteorológica 1986. República de Panamá. Contraloría General de la República, Dirección de Estadística y Censo.

FLEMING, T. H. 1986. Secular changes in Costa Rican rainfall: correlation with elevation. *Journal of Tropical Ecology* 2:87–91.

FLENLEY, J. R. 1979. *The equatorial rain forest: a geological history*. Butterworths, London. 162 pp.

GILMARTIN, A. J. 1973. Transandean distribution of Bromeliaceae in Ecuador. *Ecology* 54:1389–1393.

GIODA, A., ESPEJO, R. & ACOSTA-BALADON, A. 1993. Fog collectors in tropical areas. Pp. 273–278 in Becker, A., Sevruk, B. & Lapin, M. (eds). *Evaporation, water balance and deposition.* Proceedings of Symposium on Precipitation and Evaporation, vol. 3. Bratislava, Slovakia, 20–24 September 1993.

GRUBB, P. J. 1971. Interpretation of the 'Massenerherbung' effect on tropical mountains. *Nature* 229:44–45.

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

GRUBB, P. J., LLOYD, J. R., PENNINGTON, T. D. & WHITMORE, T. C. 1963. A comparison of montane and lowland rain forest in Ecuador, I. The forest structure, physiognomy, and floristics. *Journal of Ecology* 51:567–601.

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

HAMILTON, L. S., JUVIK, J. O. & SCATENA, F. N. 1993. The Puerto Rico tropical cloud forest symposium: introduction and workshop synthesis. Pp. 1–16 in Hamilton, L. S., Juvik, J. O. & Scatena, F. N. (eds). *Tropical montane cloud forests.* Proceedings of an international symposium at San Juan, Puerto Rico, 31 May–5 June 1993. East–West Center Program on Environment, UNESCO International Hydrological Programme and International Institute of Tropical Forestry. 264 pp.

KERFOOT, O. 1968. Mist precipitation on vegetation. *Forestry Abstracts* 29:8–20.

LaBASTILLE, A. & POOL, D. J. 1978. On the need for a system of cloud forests parks in Middle-America and the Caribbean. *Environmental Conservation* 5:183–190.

LOZANO, G. 1984. Comunidades Vegetales del flanco norte del Cerro 'El Cielo', y la flora vascular del Parque Nacional Natural Tayrona (Magdalena, Colombia). Pp. 407–422 in van der Hammen T. & Ruiz, P. M. (eds). *Studies on tropical Andean ecosystems, volume 2. La Sierra Nevada de Santa Marta (Colombia). Transecto Buritaca–La Cumbre.* J. Cramer, Berlin. 603 pp.

MEIJER, W. 1974. Field Guide to Trees of West Malesia. University of Kentucky, Lexington.

NAGEL, J. F. 1956. Fog precipitation on Table Mountain. *Quarterly Journal of the Royal Meteorological Society* 82:452–460.

RIEHL, H. 1979. *Climate and weather in the tropics.* Academic Press, New York. 611 pp.

STADTMÜLLER, T. 1987. *Los Bosques Nublados en el Trópico Húmedo. Una revisión bibliográfica.* Universidad de la Naciones Unidas, Tokio, y Centro Agronómico Tropical de Investigación y Enseñanza, Turrialba, Costa Rica. 85 pp.

STRAHLER, A. N. 1979. *Geografía Física* (Cuarta Edición). Ediciones Omega, S.A., Barcelona. 767 pp.

SUGDEN, A. M. 1982. The vegetation of the Serranía 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 Colombian cloud forests, I. The distribution of epiphytic flora. *Biotropica* 11:173–188.

VAN STEENIS, C. G. G. J. 1972. The effect of montane mass elevation. Pp. 19–20 in van Steenis, C. G. G. J. (ed.). *The mountains of Java.* E. J. Brill, Leiden.

VENEKLAAS, E. 1990. Rainfall interception and aboveground nutrient fluxes in Colombian montane tropical rain forests. PhD Dissertation, University of Utrecht, The Netherlands.

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

WEAVER, P. L. 1972. Cloud moisture interception in the Luquillo Mountains of Puerto Rico. *Caribbean Journal of Science* 12:129–144.

WEAVER, P. L. 1991. Environmental gradients affect forest composition in the Luquillo Mountains of Puerto Rico. *Interciencia* 16:142–151.

WEAVER, P. L. & MURPHY, P. G. 1990. Forest structure and productivity in Puerto Rico's Luquillo Mountains. *Biotropica* 22:69–82.

WERFF, H. H. van der. 1978. The vegetation of the Galápagos Islands. PhD Dissertation, University of Utrecht, The Netherlands.

WOLF, J. H. D. 1993. Ecology of epiphytes and epiphyte communities in montane rain forests, Colombia. PhD Thesis, University of Amsterdam. 238 pp.

ZADROGA, F. 1981. The hydrological importance of a montane cloud forest area of Costa Rica. Pp. 59–73 in Lal, R. & Russell, E. W. (eds). *Tropical agricultural hydrology.* John Wiley & Sons, Ltd. 611 pp.

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