

telescoping effect have received much study (see reviews by Leigh 1975; Grubb 1977, 1989; Bruijnzeel et al. 1993), both phenomena are still not fully explained. The suggestion of Grubb and Whitmore (1966) that the frequency of cloud or fog is the most important factor determining the stature of montane forest is supported by numerous descriptive studies (reviewed by Richards 1952; Lamprecht 1958; Van Steenis 1972; Stadtmüller 1987; Cavellier 1988). The second part of this paper discusses the available evidence of how a cloud cover may cause this effect, and includes recent results for Southeast Asian low-elevation MCF (Bruijnzeel et al. 1993). This then leads to a consideration of the cycling of nutrients in TMCF, and a brief review is made of atmospheric nutrient inputs, soils, and nutrients in litterfall, including the relatively understudied role of epiphytes in the cycling of nutrients in TMCF. Finally, a number of suggestions for further work on the water and nutrient dynamics of TMCF are made, stressing the need for multidisciplinary studies at carefully selected key locations.

Definition and Occurrence of TMCF

Grubb et al. (1963) distinguished the formations lower montane rain forest (LMF) and upper montane rain forest (UMF) that usually occur in sequence above evergreen lowland tropical rain forest. Grubb and Whitmore (1966) suggested LMF had "frequent" and UMF "long, persistent" cloud cover close to the ground, although this statement (like their definitions of LMF and UMF) was not fully quantified. Later, Grubb (1974) suggested that tall LMF might also occur on more-or-less fog-free locations. Montane cloud forests may belong to either LMF or UMF, and here "TMCF" is used for forests (including "elfin cloud forests"—ECF; Stadtmüller 1987) that are frequently covered in clouds or mist. It is recognized that quantitative criteria on what constitutes "frequent" clouds are lacking, but implicit in TMCF is a recognition of the important influence of clouds on a range of ecosystem processes.

Depending on latitude, the lower limit of TMCF on large mountains is generally between 1,500 and 2,500 m, whereas the upper limit is usually from 2,400 to 3,300 m. Local factors may cause cloud formation at much lower altitude (e.g., on small coastal or island mountains), while ECF may occur up to 3,900 m under favorable conditions (Stadtmüller 1987).

Hydrological Aspects

Horizontal Precipitation

While the importance of frequent low cloud to ecosystem functioning in TMCF is widely recognized, its quantification is notoriously difficult (Kerfoot 1968). A variety of terms has been coined to describe the movement of water onto

3. Hydrology and Biogeochemistry of Tropical Montane Cloud Forests: What Do We Really Know?

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Arguably, montane "cloud forests" (MCFs) are among the least understood of humid tropical forest ecosystems as far as their water and nutrient dynamics are concerned (Whitmore 1990). This is in spite of the fact that TMCF is often found in important headwater areas that, although scattered, together occupied about 500,000 km² in the 1970s (Persson 1974). There is a growing recognition of the role of TMCF in supplying water to downstream areas during rainless periods (Zadroga 1981; Hamilton with King 1983; Stadtmüller and Agudelo 1990) and of their high degree of faunal and floristic endemism (La Bastille and Pool 1978; cf. Leo, this volume).

Stadtmüller (1987) produced an important introductory review, highlighting the confusing nomenclature of TMCF and focusing largely on hydro-meteorological studies made in the Neotropics. The present contribution intends to expand Stadtmüller's review with respect to the water dynamics of TMCF.

With increasing altitude on wet tropical mountains, changes in forest structure and physiognomy occur, which have, in the words of Whitmore (1989), "puzzled and irritated" scientists for a long time. The principal changes are a decrease in forest stature and leaf size, and a tendency for the leaves to become thicker and harder (xeromorphic). A related phenomenon is the so-called Massenerhebung, or "telescoping" effect: the occurrence of stunted forests at lower elevations on small outlying mountains compared with those on large mountains (Richards 1952). Although the stunting of montane forests and the

vegetational surfaces via condensation or by direct contact of cloud droplets. In the following, this input of water will be called horizontal precipitation (HP) (Stadtmüller 1987).

The quantity of HP depends partly on vegetational factors and partly on climatic factors. The former include the following: height of the vegetation, canopy size and structure, biomass, arrangement and physical properties of leaves and epiphytes. Climatic factors include moisture content, drop sizes, velocity and direction of the passing air with respect to the orientation of the forested slope or ridge, and the duration of the whole process. Variations between locations will be large. Traditionally, two approaches have been followed in trying to quantify HP (Kerfoot 1968): (1) the use of "fog catchers" and (2) a comparison of amounts of canopy drip measured inside a stand with amounts of rainfall measured in the open. Both methods present problems of measurement and interpretation. Fog catchers, whether of the "gauze cylinder" or "wire harp" type (Nagel 1956; Ekern 1964), suffer from the inherent problem that each forest canopy represents a more-or-less unique situation that cannot be fully simulated. It is possible, however, to obtain an idea of the frequency and the relative importance of moisture contributions by low clouds with these instruments, although amounts of moisture trapped are rather sensitive to the height of the catcher with respect to the canopy or the ground (Ekern 1964; Cavelier and Goldstein 1989). Arguably, the second approach is superior as long as amounts of water intercepted and evaporated from the wetted canopy are taken into account. Without automated meteorological equipment, the procedure of separating daily throughfall totals for fog-free and fog-bound conditions (Kashiyama 1956; Harr 1982; Stadtmüller and Agudelo 1990) is the best method. However, since evaporation rates from a wet canopy may well differ for the two situations, the results will remain approximate (see also the next section).

More recently, a promising alternative approach has been developed by investigators studying rates of "occult" deposition of pollutants (Dollard and Unsworth 1983; Gallagher et al. 1988). This "gradient technique" combines continuous observations of the wind profile (and thus turbulence) above the intercepting surface with measurements of cloud water content (using either such advanced equipment as Knollenberg forward-scattering spectrometer probes or simple wire harps).

The amounts of HP reported from TMCF as determined with fog catchers are summarized in Table 1 whereas measurements of throughfall and rainfall are summarized in Table 2. In both cases, results are variable. For instance, annual totals of HP estimated with fog catchers range from 70 mm for an elfin cloud forest at 3,100 m in Venezuela (Cavelier and Goldstein 1989) up to 940 mm in LMF at 1,300 m in eastern Mexico (Vogelmann 1973). There is no positive correlation between annual totals of HP and ordinary rainfall, but relative values of HP tend to be lower at sites with high rainfall totals and during rainy seasons (Table 1). Cavelier and Goldstein (1989) compared amounts of HP between various low coastal mountains in northern Venezuela

Table 1. Amounts of horizontal precipitation (HP) in tropical montane cloud forest areas as determined by means of fog catchers (d, dry season only; w, wet season only)

Location	Altitude (m)	Vegetation type	HP (mm/d)	HP (% of rain)	Remarks
Colombia, Serranía de Magüta ¹	865	ECF	2.2	63/63d	Magel-type gauge, sampled every 14 d for 12 months
Costa Rica, Cerro Buenavista ²	3500	Paramo	2.1	18	Two aluminum screens (3250 cm ²); 13 months; absolute value for dry days
Costa Rica, Balalaica ³	1300	LMF	4.0	33	Three wire harps at 6 m; weekly samples for 6 months/9 weeks
Hawaii, Mauna Loa ⁴	1580	Various	2.1	30	Louvered screen; frequent readings over 1-2 years; windward slopes
Malaysia, Gunung Siliang ⁵	884	LMF	0.4	9	Magel-type gauge, 6 weeks in dry season
Mexico, Sierra Madre ⁶	1330	MCF	1.6w	15w	Magel-type gauge, sampled weekly for 53 weeks, long dry season (40 weeks)
	1360	Idem	0.8w	85d	
	1900	Idem	0.6w	60d	
	1900	Idem	0.4d	14w	
	1050	ECF	0.9	7	Louvered screen plus tipping bucket, 258 days of observations
Venezuela ¹	815	ECF	1.4	32/66d	See Colombian site
Cerro Sa Ana	987	ECF	1.3	11/9d	
Cerro Copey	3100	ECF	0.2	4/19	

¹Cavelier and Goldstein (1989); ²Dohrenwend (1979); ³Caceres (1981); ⁴Juvik and Ekern (1978); ⁵Bruijnzeel et al. (1993); ⁶Vogelmann (1973); Baynton (1969)

and a high-altitude inland location. While rainfall along the coast increased sharply from west to east, corresponding amounts of HP decreased, albeit less dramatically. Conversely, the inland site received very little HP (Table 1), which was interpreted by Cavelier and Goldstein (1989) in terms of differences in cloud water content (stratus in the Andes vs. cumuliform at the coast), and more persistent fog and higher wind speeds near the coast.

Relative amounts of throughfall recorded in TMCF are also variable (Table 2), ranging from about 70–80 percent of incident rainfall in tall LMF on inland mountains in Tanzania, Papua New Guinea, and Venezuela experiencing relatively light or virtually no cloud incidence (Lundgren and Lundgren 1979; Edwards 1982; Steinhardt 1979) to 130–180 percent in forests on exposed slopes and ridges near the coast (Weaver 1972; Stadtmüller and Agudelo 1990). The difference of 1,160 mm/year⁻¹ between throughfall and rainfall determined (without correcting for evaporation of about 300 mm/year⁻¹ intercepted rainfall) for an MCF on an exposed ridge in eastern Honduras by Stadtmüller and Agudelo (1990) is the highest HP reported to date (cf. Weaver 1972).

Ideally, amounts of water reaching the forest floor as stemflow should also be taken into account. Stemflow in LMF is generally low (e.g., Lundgren and Lundgren 1979; Steinhardt 1979; Caceres 1981), but larger proportions (5–10 percent of rainfall) have been observed in ECF, particularly those that are wind-exposed (Weaver 1972). The high tree density of these forests may be responsible for this (Baynton 1969). Interestingly, stemflow figures for lowland health forest, which also has a high tree density (Whitmore 1990), were higher than those in adjacent ordinary lowland rain forests (Jordan 1978). Bruijnzeel (1989c) hypothesized that the many-stemmed nature of both elfin and health forests might enhance nutrient availability through the funneling of larger volumes of water along the stems (see also the following).

Evaporation

Reference Evaporation Rates

Next to rainfall and HP, the rate of open-water evaporation (E_o) (Penman 1956) is a convenient measure of overall climatic conditions. Evaporation is expected to decrease with elevation as radiation, temperatures, and vapor pressure deficits are all reduced (Braak 1922; Troll 1956; Briscoe 1966). There have been suggestions that the most stunted types of MCF are found in areas with very low atmospheric evaporative demand, even to the extent that rates of water and nutrient uptake are claimed to become suppressed (Odum 1970; Weaver, Byer, and Bruck 1973; Leigh 1975; Ash 1987). However, average values of E_o at sites carrying stunted MCF at low-to-intermediate elevations (e.g., Serrania de Macuira, Venezuela; El Yunque and Pico del Oeste, Puerto Rico; Blue Mountains, Jamaica; Gunung Silam, Malaysia) ranged between 2.0 and 3.75 mm/day⁻¹ (Waterloo 1989). Although these values are lower than those recorded for tropical lowlands (typically around 5 mm/day⁻¹), one should remember that most of the daily evaporation totals in the TMCF belt will be

attained during fog-free periods, usually in the mornings. Values that have been adjusted for this resemble more closely climatic conditions lower down the slopes (Grubb and Whitmore 1966; Langley 1985). As will be shown, water and nutrient uptake in some TMCF do seem suppressed, but not because of a lack of radiant energy or high aerial humidity.

Total Evapotranspiration

Total evaporation of moisture from a vegetated surface consists of three components: (1) evaporation of precipitation intercepted by the vegetation, E_i ; (2) transpiration, E_t ; and (3) evaporation from the ground layer, E_s . Since E_s has been shown to be very small in lowland rain forests (Jordan and Heuveldop 1981; Van der Plas 1992), it can be ignored for most montane forests. E_t and E_i then represent evaporation from wet and dry canopies, respectively.

The magnitude of E_i is determined by a number of climatic and "passive" vegetation factors, whereas E_t is regulated by plant stomatal control in response to changing conditions. Climatic factors include duration and intensity of precipitation (E_i only), wind speed, available energy, and vapor pressure deficit. "Passive" vegetational factors include height, roughness, size, arrangement, and total biomass of the canopy (Rutter 1975).

Before examining the values of E_t and E_i , the evidence on total evapotranspiration (ET) in TMCF is reviewed (Table 3). All but one study (San Eusebio, Venezuela) used the catchment water-balance technique to evaluate forest ET (Ward and Robinson 1989). A number of studies were made on volcanic terrain and must be treated with caution since they may have been influenced by subterranean water transfers (Gonggrijp 1941; Rijsdijk and Bruijnzeel 1990).

Those forests receiving much HP in Table 3 have ET values of 300–400 mm/year⁻¹, whereas those for LMF with only minor incidence of low cloud (e.g., the Colombian forest at 1150 m and the Indonesian forest) are about 1,200 mm/year⁻¹. These estimates for ET need to be adjusted for moisture inputs from HP. As indicated earlier, all estimates of HP are approximate, but reasonable estimates were available in a number of cases, either for the study site itself (e.g., the Philippine forest) or for a similar type of forest in the region (the Colombian forest at 2100 m, Vis 1986; the Costa Rican forest, Caceres 1981). The adjusted values ranged from 570 to 695 mm/year⁻¹ (Table 3), thus remaining well below the average of 1,225 mm/year⁻¹ derived for tropical montane forests that are little affected by low cloud (Bruijnzeel 1990).

The information given in Table 3 could usefully be expanded by a systematic examination of streamflow and rainfall records collected routinely by government departments in countries where TMCF is found in the headwater areas of major river basins (cf. Aitken, Ribevy, and Brown 1972; Calvo 1986; Lugo 1986).

Evaporation of Intercepted Precipitation

Estimates of E_i are normally made by subtracting amounts of throughfall and stemflow from incident rainfall. As explained earlier, the unknown additional

Table 2. Measurements of throughfall (TF), stemflow (SF), and derived estimates of rainfall interception (E_i) in tropical montane forests (values expressed as percent of incident rainfall)

Location	Altitude (m)	MAP (mm)	TF (%)	SF (%)	E (%)	Remarks
Colombia ¹	1000	1600	78	—	—	6 roving gauges; 5 months
	1700	3150	76	—	—	idem; 15 months
	1950	2200	85	—	—	idem
	3000	1700	89	—	—	idem
Colombia ²	2550	2115	87.5	—	12.5	20 fixed gauges; 12 months; weekly collections
	3370	1455	81	0.1	18.5	
Costa Rica ³	1300	2510	101	0.4	?	20 fixed square metal collectors, sampled weekly for 6 months; cf. Table 1
Honduras ⁴	1795	1500	94	—	6	4 fixed troughs; concave, convex, and ridge sites, resp.; daily observations for 12 months
			129	—	?	
			179	—	?	
Indonesia ⁵	1750	3300	80	—	19	4 fixed square metal collectors; weekly samples; 12 months
Jamaica ⁶	1020	3000	81	—	19	randomly located troughs; weekly (?) samples; 1 year

Jamaica ⁷	1550	LMF/UMF	2600+	92+	—	<8	10-14 fixed gauges; 12 months; 2-week intervals
Mauritius ⁸	550	LMF	3175	70/76	—	24/30	3 fixed gauges; 12 months; daily readings; values for 3 c.q. 2 gauges, resp.
New Guinea ⁹	2500	LMF	3800	67	<1	32	8 fixed gauges in 4 plots each; 8 months; 2-week intervals
Philippines ¹⁰	2200	LMF/MCF	3900	86	12?	2	4(?) troughs in 4 plots; 60 months; daily readings; value for SF suspect; TF varied per exposure and includes 9% fog drip
Puerto Rico ¹¹	450	LMF	2540	72	8	20	6 fixed troughs; 12 months; daily readings; low intensity
Puerto Rico ¹²	1000	ECF	5400	115	5	-20	60 fixed collectors in each of 3 plots; windward, ridge and leeward; 8 months; daily readings
Pico del Este	1015		4800	125	10	-35	
	930		6000	96	3	1	
Tanzania ¹³	1500	LMF	1230	78	<1	21	8 fixed gauges; 30 months; daily readings
Venezuela ¹⁴	2300	LMF/MCF	1575	79.5	1	19.5	30 fixed gauges; 12 months; 1-2 readings per week

MAP = mean annual precipitation
¹Vis (1986); ²Venklaas and Van Ek (1990); ³Caceres (1981); ⁴Stadtmüller and Verrion (1985); ⁵Clements and Colon (1975); ⁶Weaver (1972); ⁷Tanner (1980a); ⁸Vaughan and Wiehe (1947); ⁹Edwards (1982); ¹⁰Mamanteo and Verrion (1985); ¹¹Clements and Colon (1975); ¹²Weaver (1972); ¹³Lundgren and Lundgren (1979); ¹⁴Steinhardt (1979)

input of moisture from the persistent low cloud precludes the use of this technique in TCMF. It seems there are no reliable estimates of amounts of intercepted and subsequently evaporated precipitation in "true" TCMF, only for LMF with relatively little cloud incidence (Table 2). Values under the latter conditions are about 25 percent of incident rainfall (range 15–35 percent, Table 2). It is difficult to extrapolate these values to foggier conditions because much will depend on the timing and duration of the fog (e.g., at night or during the day) as well as on possible contributions by advected energy (warmer air from lower elevations or the ocean).

An experimental design is needed that takes into account both temporal and spatial variations in throughfall and stemflow (Baynton 1969; Lloyd and Marques 1988; Veneklaas and Van Ek 1990) in combination with observations on occurrence and intensity of fog or rainfall; duration of canopy wetness; climatic factors needed to evaluate evaporation rates from a wetted canopy (Monteith 1965); and the time lag between the start of the fog and the start of canopy drip in relation to moisture status of epiphytic cover. Arguably, the data collected by Baynton (1969) and Weaver (1972) for ECF in Puerto Rico may be considered the most complete.

One of the outstanding features of MCF is an abundance of vascular and nonvascular epiphytes; the study of intercepted precipitation is complicated by this. The TCMF zone is a favorable environment for epiphytes because of the abundance of atmospheric moisture (Walter 1979). In tall-facies TCMF, the highest densities of epiphytes are found in the canopy, whereas in more stunted forests they also cover the bases of trunks and even rocks (Stadtmüller 1987). Wolf (1993), in a study of 20 epiphyte communities between 1,000 and 4,130 m in the Central Cordillera of Colombia, found a marked change in both species composition and biomass at about 2,400 m (Figure 1). These changes occurred at the transition from LMF to UMF and were accompanied by a dramatic rise in average daytime relative humidity levels, confirming the original contention of Grubb and Whitmore (1966).

Ecophysiological research confirms the importance of moisture availability to bryophytic growth. Hosokawa, Odani, and Tagawa (1964) demonstrated a positive relationship between photosynthetic rate and relative humidity at equal light conditions. Since bryophyte photosynthetic activity is relatively insensitive to low temperatures (Dilks and Proctor 1975), decreasing temperatures do not counteract the positive effects of high humidity at higher elevations where they are often luxuriant (Figure 1b). It is here that one would expect the strongest effects on rainfall and fog interception.

Values for epiphytic biomass in selected montane forests are given in Table 7 (see section on nutrients) and show substantial variation. Hofstede, Wolf, and Benzing (1993) interpreted these differences in terms of canopy structure, tree density and morphology, and disturbance of accumulated "aerial humus" by occasional cyclones (e.g., in Jamaica and Costa Rica) or torrential rains (lower elevations). Nonvascular epiphytes in particular have been shown to be capable of absorbing large volumes of rain and fog (up to 4–5 times

Table 3. Annual evapotranspiration (ET) and transpiration (E_t) vs. rainfall and elevation for selected montane forests

Location	Altitude (m)	Rainfall (mm/yr ¹)	ET (mm)	E _t (mm)	Remarks
Colombia ¹	1150	1985	1265	830	LMF; E _t 22% ² LMF/MCF; E _t 12% ² LMF/MCF; E _t 10% ⁴ LMF; E _t 20%
Costa Rica ³	2400	2695	365	(270)	LMF/MCF; E _t 10% ⁴ LMF; E _t 20%
Indonesia ⁵	1750	3305	1170	510	LMF; E _t 20%
Malaysia ⁶	870	2500	(695)	(310)	LMF/MCF; E _t 15%; ET via site water balance; 6 weeks of observations
Philippines ⁷	2350	3380	390	(250)	LMF/MCF; E _t 13% ⁸ LMR/MCF?; E _t 20%; ET via energy balance
Venezuela ⁹	2300	1575	980	675	ECF; cut shoot method, LAI ¹² 2 m ² m ⁻²
Puerto Rico ^{10,11}	1000	4700	—	75	

Adapted from Brujinzeel (1990).
¹Values for ET not corrected for contributions by horizontal precipitation
²E_t derived as net ET - E, unless stated otherwise
³Herrmann (1971); ⁴Vis (1986); ⁵Calvo (1986); ⁶Caceres (1981); ⁷Conggrip (1941); ⁸Brujinzeel et al. (1993); ⁹De los Santos (1981); ¹⁰Marmateo and Veracion (1985), taking stemflow at 1%; ¹¹Stehardt (1979); ¹²Weaver, Byer, and Bruck (1973); ¹³Gates (1969); ¹⁴Weaver et al. (1986)

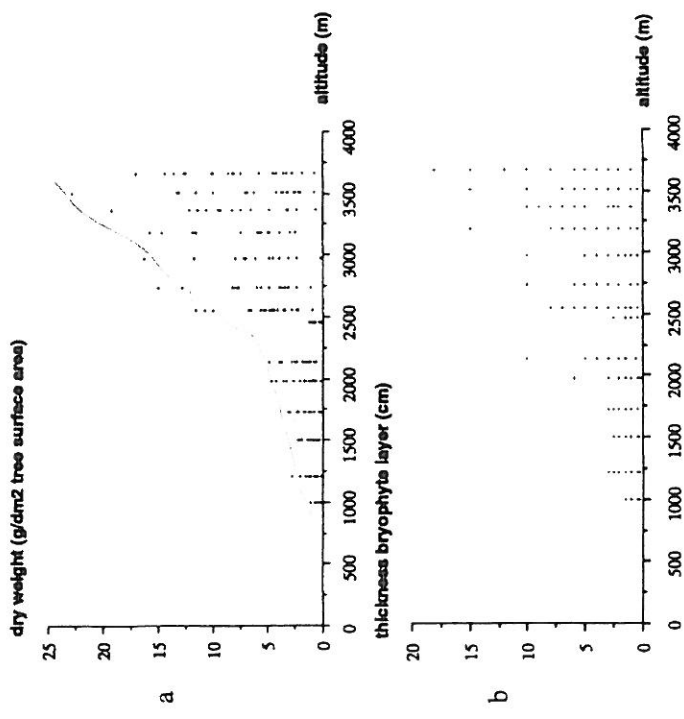


Figure 1. Biomass (a) and thickness (b) of the living epiphytic bryophyte layers as function of elevation in the Central Cordillera, Colombia (after Wolf 1993).

their dry weight; Pócs 1980; Nadkarni 1984), with subsequent losses via evaporation and drainage being rather slow (Veneklaas and Van Ek 1990; Veneklaas et al. 1990). Consequently, the magnitude of the so-called canopy saturation value of a forest (Rutter 1975) is expected to increase with increasing epiphyte loading. Preliminary estimates of the canopy saturation values for two montane forests in Tanzania with strongly contrasting epiphytic biomass (Table 7) were about 1.5 mm and 5.0 mm, respectively (Pócs 1980). Similarly, Veneklaas and Van Ek (1990) derived values of 2–5 mm for two MCFs in the Central Cordillera of Colombia, with the highest value in the mossier forest. By contrast, values for lowland rain forest are usually in the order of 0.8–1.0 mm (Calder, Wright, and Murdiyoso 1986; Lloyd et al. 1988; Huijjes, Wierda, and Veen 1990). Adjusting models of rainfall interception that have proven their value in tropical lowland forests (Brujinzeel and Wiersum 1987; Lloyd et al. 1988; Huijjes, Wierda, and Veen 1990) for TCMCF is an important challenge (cf. Veneklaas and Van Ek 1990).

Transpiration

Reliable quantitative information on rates of E_t in TCMCF is scarce. By subtracting amounts of E_t from total ET for five LMFs with relatively little cloud

incidence, Brujinzeel (1990) obtained values of 510–830 mm/year⁻¹ and found no clear relationship with elevation. Estimates derived in this way must be regarded as relatively crude, however, owing to the possibility of accumulated errors in the estimates of both throughfall (and hence E_t ; Lloyd and Marques 1988) and ET (water-budget technique; Ward and Robinson 1989). While micro-meteorological techniques have yielded the best estimates for E_t of lowland rain forests (Shuttleworth 1988), these are less useful under the topographic and climatic gradients encountered in the TCMCF, particularly in its stunted facies (cf. Baynton 1968, 1969; Monteith 1976).

The available evidence, representing a mixture of the above-mentioned indirect water-budgeting technique and plant physiological approaches, is presented in Table 3 along with the estimates of total ET discussed previously. Average values of E_t in MCF were about 300 mm/year⁻¹ in most cases ($n = 4$) but seem to drop dramatically for ECF ($n = 1$). As indicated already, these estimates should be treated with caution, including the value quoted for ECF, which was based on rates of water absorption by cut shoots (Weaver, Byer, and Bruck 1973) and on leaf energy budget calculations involving a number of assumptions (Gates 1969).

The low rates of water uptake in stunted MCF have been the subject of much speculation (Gates 1969; Odum 1970; Weaver, Byer, and Bruck 1973; Grubb 1974, 1977; Ash 1987; Whitmore 1989; Brujinzeel et al. 1993). Suggested explanations included toxic or anaerobic conditions in the soil, nutrient deficiency caused by reduced mineralization or extreme leaching, and adverse climatic conditions, notably reduced radiation and high atmospheric humidity (Brujinzeel et al. 1993). It could be argued that in heavily fogged locations, transpiration is temporarily halted under conditions of a fully wetted canopy (Rutter 1975). Yet, there is evidence that rates of water uptake by these forests are also low in bright sunshine (Brujinzeel et al. 1993). As already indicated for rates of open-water evaporation (E_o), the bulk of daily transpiration will be effected during such sunny spells, which typically total 3–6 h/day⁻¹ at locations with tall LMF, dropping to about 3 h/day⁻¹ at sites carrying more stunted forests (Grubb 1977). Brujinzeel et al. (1993), working on Gunung Silam (a low coastal mountain in Sabah, Malaysia), expressed average values of E_t (determined by the site water-balance method) as a ratio of corresponding values of E_o for two LMFs of contrasting stature. They observed a much lower value (0.24) for the more stunted forest at 870 m (which was subjected to frequent low cloud) than for tall LMF situated just below the cloud cap at 680 m (0.51). The former value is markedly lower than those usually found for tall montane forests (0.5–0.7; Brujinzeel 1988, 1989c). This suggests that the reduction in E_t/E_o is not caused by the difference in climatic conditions experienced by the two forests, at least not in a direct manner, because this effect is already taken into account in the estimation of E_o (Brujinzeel et al. 1993). This raises the question as to why the trees in TCMCF behave so differently from their counterparts just below the cloud cap.

Enhanced stomatal resistance in response to increases in atmospheric va-

por pressure deficits has been reported for a number of tropical and warm temperate MCFs (Jane and Green 1985; Körner, Allison, and Hilscher 1983; Cavellier 1988). Interestingly, when both stomatal resistance and concurrent values of leaf water potential or rates of transpiration were determined, it was found that the increases in stomatal resistance were not accompanied by a reduction in leaf water potential (Green and Jane 1983). In addition, the increases in resistance were insufficient to prevent an increase in rates of transpiration during times of increased evaporative demand (Körner, Allison, and Hilscher 1983). In other cases, e.g., in the stunted UMF in Jamaica studied by Kapos and Tanner (1985), stomatal response to changing atmospheric conditions was less pronounced. All this suggests that the stomatal control observed for TMCF is not primarily aimed at preventing water stress. Neither does it reflect a different suite of evaporative conditions, as already demonstrated.

The physiological responses described above are typical of plants exposed to soil waterlogging, which leads to poorly developed root systems unable to respond fully to temporarily high atmospheric evaporative demands (Brouwer 1960; Bradford and Yang 1981) such as occur at higher elevations in the tropics during conditions of clear sky (Schmidt 1950; McVean 1974; Caldwell, Robberecht, and Billings 1980). In all studies of plant behavior in TMCF, the soils were wet for most of the time. Further evidence of persistently wet conditions in the soils of most TMCFs will be presented in the next section.

Some support for the view that transpiration in TMCF is suppressed may also be obtained from leaf anatomical observations. Leaves of UMF and ECF are distinctly more "xeromorphic" in appearance than leaves of lowland rain forest and LMF, the leaves becoming smaller, thicker, and harder with increasing elevation (Howard 1969; Grubb 1977; Buckley, Corlett, and Grubb 1980; Tanner and Kapos 1982; Körner, Allison, and Hilscher 1983; Cavellier 1988; Brujnzeel et al. 1993). Yet, these "pachyphylls" (Grubb 1974) do not exhibit greater tolerance to desiccation (Buckley, Corlett, and Grubb 1980). In addition, they exhibit smaller numbers of stomata per unit leaf surface (Grubb 1977; Körner, Allison, and Hilscher 1983), which would be expected in view of the overall decrease in average atmospheric humidity deficits in UMF and ECF. Therefore, it would seem as though the xeromorphic appearance of the leaves in these forests reflects an inability of the trees to transpire at the potential rate, but not because of soil water deficiency (see also the next section). The resulting suboptimal cooling of the leaves may have led to the development of the xeromorphic characteristics, including the frequently observed trend toward vertical inclination of leaf surfaces that may reduce damage by overheating (cf. Medina, Sobrado, and Herrera 1978; Cavellier 1988; Brujnzeel et al. 1993).

There is a need for more observations of transpiration in TMCF. Such studies could make use of a combination of measuring techniques like the heat-pulse velocity method (Durham and Hatton 1989; Olbrich 1991) and the deuterium tracing method (Calder 1992). In a study assessing the usefulness of the two techniques in estimating water uptake by eucalypts, Dye, Olbrich, and Calder

(1992) considered the two methods largely complementary. The heat-pulse velocity technique can provide detailed flow information over time scales of minutes, but estimates are sensitive to the size of wounds caused by the probes. It is particularly suitable for measurement of high flow rates. The deuterium method, on the other hand, gives estimates of the flow rate over periods of, typically, 2-4 days and is more suited and sensitive for measurement of low flow rates. Dye, Olbrich, and Calder (1992) suggested that the deuterium tracing method would be most useful for comparing a relatively longer-term mean transpiration rate against modeled cumulative transpiration based on instantaneous measurements obtained with other methods. In this way, any cumulative systematic error might be detected.

Heat-pulse velocity equipment was used in a recent short-term reconnaissance study comparing climatic and soil hydrological conditions in two forests of contrasting stature on Gunung Rakata (Krakatau), Indonesia. Two sets of probes were placed in a *Neonauclea* tree at 110 m (about 30-m-high lowland forest) and 700 m (about 15-m-high "mossy" forest) each. Both trees had a diameter at breast height of about 20 cm. Half-hourly observations of sapflow rates were made over a period of 3 weeks in conjunction with observations of soil water tensions and the climate above the canopy. As shown in Figure 2, sapflow rates on a sunny day during the dry season of 1992 were distinctly lower at 700 m than those at 110 m, despite very similar totals of incoming radiation. There was no soil water stress at either location. In addition, sapflow in the upper plot started later in the morning than at 110 m, presumably as a result of the canopy at 700 m having been wetted by nocturnal fog or low cloud. As the dry season progressed, the tree at 110 m gradually transpired less water, whereas that at 700 m exhibited a more or

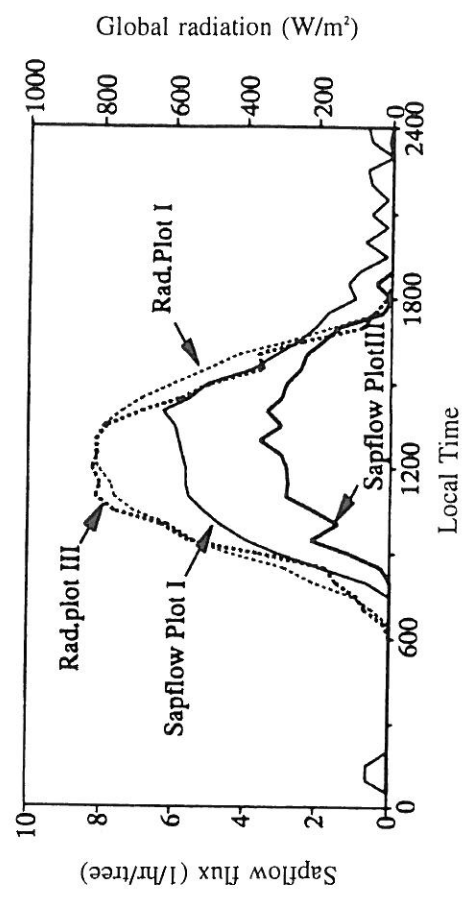


Figure 2. Daily course of short-wave radiation and sapflow in a *Neonauclea* tree at 110 m (plot I) and at 700 m (plot III) for a sunny day during the dry season on Rakata (Krakatau).

less constant pattern (L. A. Bruijnzeel and R. Hafkenscheid, unpublished). The reason for this different behavior is still unclear, but excessive soil moisture levels do not seem to play a major role on Rakata. While fluctuations in soil water tension were much larger at 110 m, the soil at 700 m could not be called very wet. Indeed, in view of its high permeability, it remains to be seen whether the soil at 700 m would ever become waterlogged. Observations of soil water tensions and sapflow during the rainy season are needed to resolve this question. Concentrations of soil nutrients were comparable in both forests (L. A. Bruijnzeel, unpublished).

Soil Water Regime

Although trees in UMF have been reported to die following severe droughts (Lowry, Lee, and Stone 1973; Werner 1988), all observations of soil water dynamics and leaf water potentials in MCF suggested that the trees would never experience severe soil-water deficits (Lyford 1969; Herrmann 1971; Hetsch and Hoheisel 1976; Dohrenwend 1979; Green and Jane 1983; Kapos and Tanner 1985; Jane and Green 1985; Cavelier 1989; Bruijnzeel et al. 1993). It could be argued that most studies never lasted more than 1 year and were too short to assess the effects of rare droughts. However, there is indirect evidence suggesting that the MCF on Gunung Silam, Malaysia, never experiences severe moisture deficit. As shown in Figure 3, amounts of leaf litter on the forest floor in July 1983 and July 1984 (Proctor et al. 1989) showed considerable differences between the 2 years for four forests situated below the usual level of cloud condensation (700 m asl), whereas only minor differ-

ences were found for forests at 790 m and 870 m. Prior to sampling in July 1983, the area had suffered one of the worst droughts in its history (Leighton and Wirawan 1986), which apparently caused extra shedding of litter in forests below but not within the cloud cap. New leaves that formed later in 1983 were probably still on the trees in July 1984, and hence the litter standing crop in the forests below the cloud cap were then lower. While visual evidence in 1984 (e.g., dried ball bryophytes at 790 m and higher) led Proctor et al. (1988) to believe that occasional drought could not be ruled out as a factor in explaining the stunted character of the forest within the cloud cap on Gunung Silam, the evidence presented in Figure 3 suggests otherwise.

The persistently wet conditions prevailing in TCMF compared with the more variable moisture regime of LMF with less cloud are illustrated in Figure 4. In the example from Colombia, where rainfall totals indicate the presence of 4 dry (<60 mm) months, soil water tensions in MCF rarely exceeded a pF value of 1.8, and then only in the uppermost part of the soil profile (Figure 4a). LMF at 1,150 m was largely fog-free and experienced pF values exceeding 2.5 throughout the profile for several months (Figure 4b). However, the tension classes used by Herrmann (1971) do not allow a distinction between various degrees of wetness below pF 1.8. Short-term observations of soil water tension made in LMF of contrasting exposure to fog incidence on Gunung Silam are therefore added for comparison (Figure 4c). The results fully confirm the previous tendencies of persistent wetness in the MCF and a sharp response to a lack of rainfall (e.g., between days 25 and 35) in the forest below the cloud cap.

The above contentions are further confirmed by morphological differences between the soils associated with the two forest types. Transect studies (e.g., Whitmore and Burnham 1969; Fölster and Fassbender 1978; Sevink 1984; Van Reuler 1987; Bruijnzeel et al. 1993) all noted major changes when passing into the zone of frequent low cloud, the most notable of these being increased organic matter content, darker colors, and increased abundance of hydromorphic characteristics. Relative abundance and size of mottles are well-known indicators of the frequency of waterlogged conditions, whereas their absence in an otherwise grey or greyish brown matrix is a sure sign of persistent waterlogging (Wadsworth and Bonnet 1951; Lyford 1969; Hetsch and Hoheisel 1976; Van Reuler 1987). Other indications of such conditions include a high frequency of aerial roots (Gill 1969; Cavelier 1988). On the other hand, no evidence of gleying was found in the stunted mossy forest on Rakata, although accumulation of organic matter was higher than below the cloud cap (Newsome 1986).

Streamflow

If annual streamflow totals are expressed as a ratio of incident rainfall, values for TCMF are among the highest reported for any tropical forest (Bruijnzeel 1990). This reflects the combined influence of extra moisture inputs via HP

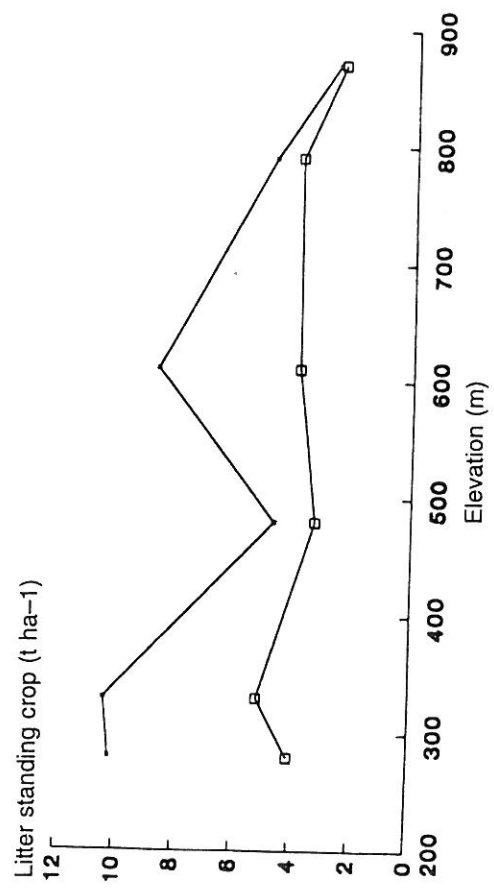


Figure 3. Quantity of leaf litter on the forest floor in six plots at a range of altitudes on Gunung Silam, Sabah, Malaysia, in July 1983 (●) and July 1984 (□) (after Bruijnzeel et al. 1993).

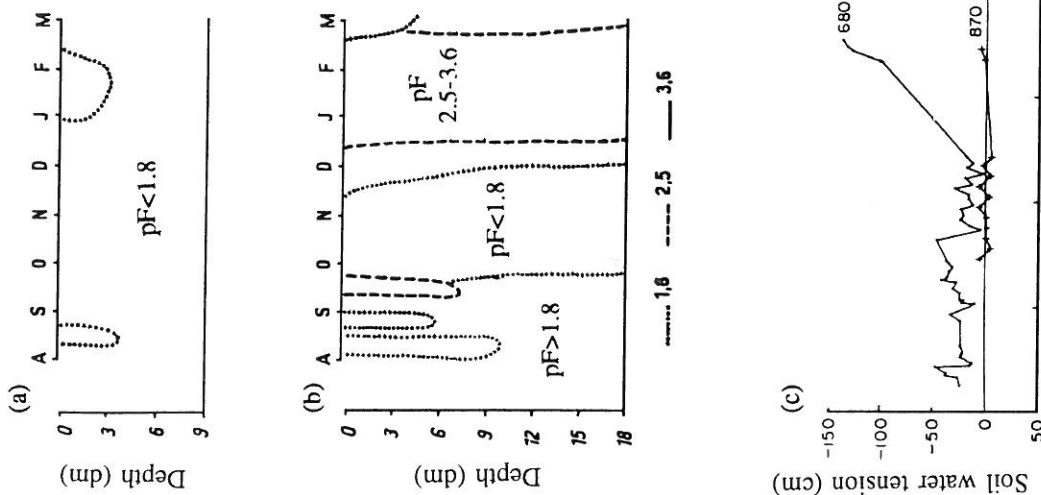


Figure 4. Variations in soil water tension with time in various montane forests: (a) cloud forest at 2,100 m, Colombia; (b) fog-free forest at 1,150 m, Colombia; (c) cloud forest and fog-free forest at 870 m and 680 m, respectively, on Gunung Silam, Sabah, Malaysia (after Herrmann 1971a, b and Bruijnzeel et al. 1993c).

and the low values for ET discussed earlier. As stressed by many (La Bastille and Pool 1978; Zadroga 1981; Hamilton with King 1983; Lugo 1986; Stadtmüller 1987), these high runoff ratios constitute one of the main reasons for the conservation of TMCF. While the importance of TMCF in headwater areas supplying water to densely populated downstream valleys is undisputed,

it remains to be seen whether total water yield will decrease after clearing of TMCF. The hydrological consequences of forest clearance are likely to differ between locations, depending on the relative magnitudes of HP and ET associated with the original and the new vegetation cover. In addition, the degree to which topsoil infiltration capacity can be maintained after forest conversion constitutes a most important factor when assessing the likely impact on seasonal water yield.

It is possible that the change in total water yield following a conversion of TMCF to agricultural use will be minor. Total water use of crops or grass (ET) in the montane tropics roughly equals amounts of water transpired by forest total (Et) (Bruijnzeel 1990), whereas the data on HP and E_i in Tables 1 and 2 suggest that both vary between 5 and 20 percent of incident rainfall for most locations. If contributions of HP under forested conditions were very high (and E_i relatively low—e.g., Stadtmüller and Agudelo 1990), there would be a good possibility of a decrease in total streamflow after conversion. But in cases where contributions of HP are modest, one can be almost certain that forest clearing will cause soils to become wetter and water yield to increase (Steinhardt 1979; Blackie 1979). A different picture may be obtained for the change in seasonal water yield, particularly if infiltration capacities degrade after forest clearing (Bruijnzeel 1989a; cf. Vis 1986). Experimental evidence is lacking, however, and filling this gap in our knowledge is perhaps the most important challenge facing hydrologists working in TMCF areas. In the meantime, there may be scope in a comparison of long-term records of streamflow (and rainfall) collected routinely by government departments with documented changes in land use (cf. Fleming 1986; Lugo 1986).

Biogeochemical Aspects

A variety of reasons has been offered to explain the stunting of montane forests. These include (1) periodic water shortage (despite frequent cloud cover), especially in shallow and stony soils (Van Steenis 1972; Proctor et al. 1988); (2) saturated soils and impeded root respiration (Wadsworth and Bonnet 1951; Hetsch and Hoheisel 1976); (3) reduced leaf temperatures associated with low radiation inputs (Grubb 1977); (4) limited nutrient uptake due to (a) climatically controlled reduction in transpiration rates (Odum 1970; Weaver, Byer, and Bruck 1973), (b) extreme soil acidity or low fertility or both (Van Steenis 1972; Grubb and Tanner 1976), often coupled with (c) reduced decomposition and mineralization rates (Edwards and Grubb 1977; Marrs et al. 1988; Heaney and Proctor 1989); and (5) exposure to strong winds (Jaffe 1980; Lawton 1982; Sugden 1986). Whitmore (1989) believes that there is no single uniform set of causes of forest zonation and its compression on small, wet tropical mountains. Bruijnzeel et al. (1993) examined the various hypotheses in the light of their own data for Gunung Silam (884 m) in Sabah, Malaysia, and those for other locations. As shown earlier in this paper, reasons (1) and

(4a) can be dismissed, whereas wind does rarely play a significant role at equatorial latitudes (unlike the belt affected by the trade winds). Also, reason (3) was shown not to apply on Gunung Silam (Bruijnzeel et al. 1993). On the other hand, we have seen that the soils of most (but not all) TMCFs are continuously wet to very wet, and in the following we shall examine reasons (4b) and (4c).

Soils

Chemical analytical data for several TMCF soils are shown in Table 4. It can be seen that there is a wide range of soil types and that no generalizations about the soil chemistry are free of exceptions. $\text{pH}_{\text{H}_2\text{O}}$ ranges from 3.0 to 7.0. Total organic carbon and total nitrogen are often high and increase with altitude, but there are a number of instances in TMCF where the soil has lower than 5 percent organic carbon and less than 0.3 percent total nitrogen. Total phosphorus has rarely been measured, but values for extractable phosphorus range from 1.1 to 78 $\mu\text{g/g}^{-1}$ dry soil and are usually relatively high with no clear trend to decrease with altitude. Exchangeable bases and percentage base saturation are usually low, but not invariably so. Few measurements have been made of rates of nitrogen mineralization and nitrification. Marrs et al. (1988) showed that both had a clear decline with altitude on Volcán Barva, Costa Rica. However, rates in various Jamaican UMFs measured by Tanner (1977a) at 1,550 m were relatively high, except for a negative nitrogen mineralization rate in his "Wet Slope" forest. In Hawai'i, Vitousek, Matson, and Turner (1988) showed a range of negative rates of nitrogen mineralization, but these were less negative with increasing altitude. They observed no nitrates in any of the soils they analyzed. On Krakatau, rates of nitrification in lowland rain forest and mossy LMF at 700 m were almost equal, although numbers of mineralizing bacteria were lower in the mossy forest (L. A. Bruijnzeel and R. Zoomer, unpublished).

Our conclusion is that there is no overriding soil chemical factor that uniquely characterizes TMCF, although micronutrient supply remains little investigated. The possibility of aluminum toxicity is raised by the high concentrations of this element in the leaves of Venezuelan MCF (mean 1640 $\mu\text{g/g}^{-1}$ dry matter aluminum; Grimm and Fassbender 1981) and in those of a Sri Lankan MCF (mean 1040 $\mu\text{g/g}^{-1}$; Werner and Balasubramaniam 1988). However, Gautam-Basak and Proctor (1983) found much lower foliar aluminum in leaves of a stunted MCF (mean 230 $\mu\text{g/g}^{-1}$) compared with those of a larger stature MCF (mean 860 $\mu\text{g/g}^{-1}$) on Gunung Mulu, Sarawak. Similarly, leaves of stunted *Vaccinium* trees on Gunung Gedeh, Java, had similar concentrations of aluminum (but much higher concentrations of polyphenols) as tall *Vaccinium* trees at a lower elevation (L. A. Bruijnzeel and W. H. O. Ernst, unpublished). Often the soils of TMCF are of too high or low pH for aluminum to have an effect on plant growth. Iron and manganese toxicities associated

with waterlogging may occur but waterlogging is by no means a universal feature of TMCF (Bruijnzeel et al. 1993). Further observations are desirable.

Litterfall and Limiting Nutrients

A summary of litterfall measurements that have been made in TMCF is given in Table 5. These measurements show that the quantities of litterfall are relatively low compared with those for lowland forests (cf. values in Proctor 1984). Nutrient concentrations in the litterfall are variable, but a distinct trend to lower nitrogen (but not phosphorus) concentrations can be observed in those cases where measurements have been made at two or more altitudes on the same mountain (Figure 5). However, when comparisons are made between element concentrations in fresh leaves and litterfall (Table 6), they indicate proportionally more retranslocation of phosphorus than nitrogen back into the branches before leaf abscission.

These observations on litterfall nutrients seem generally in agreement with the idea supported by fertilization experiments (Tanner et al. 1990; Tanner, Kapos, and Franco 1992) that nitrogen or phosphorus, or both, may limit the growth of some tree species in cloud forests. On the other hand, Bruijnzeel et al. (1993) showed that the net uptake (i.e., that associated with biomass increment) of nutrients in a stunted MCF on Gunung Silam was only a small fraction of the corresponding amounts of nutrients (including nitrogen and phosphorus) arriving at the forest floor in rainfall and throughfall, whereas corresponding losses in drainage water were small. An excess supply of nutrients over net uptake was also demonstrated for stunted UMF in Jamaica by Bruijnzeel (1989b), using data on rainfall chemistry and rates of net nutrient uptake from Tanner (1977b) and Tanner (1985), respectively. Similarly, high atmospheric nutrient inputs (Trinidad Pizarro 1985) and very low tree growth rates (Weaver et al. 1986) suggest an even higher excess of nutrients over net uptake for ECF in the Luquillo Mountains, Puerto Rico. Conversely, rates of net uptake in a tall-statured montane forest in Venezuela were similar to or higher than corresponding amounts of nutrients in rainfall (Steinhardt 1979).

Bruijnzeel et al. (1993) have stressed the possibility that foliar phenolic compounds may play a role in MCF stunting on Gunung Silam and elsewhere. Generally speaking, nitrogen stress and water deficit are among the most important factors affecting the concentration of phenolic metabolites in plant tissue (Horner, Gosz, and Cates 1988), but neither of these were thought to be decisive in the case of Gunung Silam (Bruijnzeel et al. 1993). Nevertheless, concentrations of polyphenols in fresh leaf litter were much higher in the stunted forest on Gunung Silam than in tall-statured forest just below the cloud cap. This contrast in concentrations was not observed for mature litter, and the polyphenols thus can be expected to enter the soil during rain. Here they may have a toxic effect on roots and interfere with various metabolic processes. Polyphenols have been shown to affect photosynthetic rates (Einhellig et al. 1970; Patterson 1981; Kuiters and Sarink 1987), cell division

Table 4. The soil types and their chemical features under a range of tropical montane cloud forests

Place	Altitude	Soil Type	Horizon & Depth (cm)	pH(log units)	C (%)	N (%)	P ^{total} (ppm)	P ^{extra} ($\mu\text{g/g}^{-1}$)	K Na Ca Mg				BS (%)	Authors	
									(m eq/100g ⁻¹)	(m eq/100g ⁻¹)	(m eq/100g ⁻¹)	(m eq/100g ⁻¹)			
Colombia, Cordillera Central	3550	—	—	4.7	—	—	—	—	0.3	0.1	1.2	0.8	—	Veneklaas (1990)	
Colombia, Macutá	600	—	A ₁ -20*	—	1.76	0.26	2.0	—	0.3	0.9	2.0	2.4	13.3	Cavelier (1988)	
Costa Rica, Volcán Barva	1500	Humitropept	A _h -0-22	3.2	12.0	—	—	12.9	0.38	0.38	1.72	0.94	100.7	Grievé, Proctor, and Cousins (1990)	
2000	Topofibrist	O _g -0-15	3.9	16.2	—	—	4.7	0.34	0.31	0.56	0.51	88.3	1.9		
2600	Vitrandept	O _h -0-10	3.3	17.2	—	—	55.7	1.30	0.31	17.0	9.8	113	25.1		
1000	Typic Humitropept	A _h -0-11	4.5	14.8	0.4	600	4.9	0.02	0	0.05	0.05	1.6	6.0	Payton (1993)	
1470	Humic Humaquept	O ₁ -0-20	3.6	39.0	2.1	—	65.5	0.01	0	0.02	0.01	1.4	5.0		
2100	Humic Kanhapludult	E _h -0-12	3.2	37.0	2.5	—	77.9	0.11	0.04	0.22	0.00	—	—	Payton (1993)	
2400	Lithic Topofolist	H/A _h -0-12	3.5	11.0	0.7	—	29.3	0.02	0.05	0.27	0.005	3.8	8.9		
2820	Lithic Rendoll	A _h -0-15	7.0	12.0	1.3	1800	—	0.02	0.02	6.92	0.20	—	—		
Colombia, 2500	—	—	—	4.0	—	—	—	—	0.3	0.1	1.2	0.8	—		
Colombia, 3550	—	—	—	4.7	—	—	—	—	0.3	0.2	1.3	1.3	—		
Malaysia, Sarawak, Kinabalu	2500	—	2-10	3.9	34.6	1.96	—	37	1.17	0.23	0.51	8.17	78.7	13	Kitayama (1992)
2600	—	—	2-10	3.9	38.0	0.98	—	4	1.17	0.42	4.08	7.21	79.6	16	
2800	—	—	3-20	4.6	7.7	0.45	—	13	0.26	0.10	0.40	0.27	9.8	10	
3000	—	—	1-5	5.4	15.5	0.83	—	9	0.63	0.20	1.83	2.42	33.4	64	
3200	—	—	5-10	3.9	11.6	0.91	—	28	0.68	0.18	1.07	1.09	34.3	9	
3400	—	—	2-30	4.7	8.8	0.56	—	11	0.40	0.21	3.41	0.47	22.1	20	
Malaysia, Sabah, Gunung Silam	790	—	0-15	5.6	8.5	—	—	1.1	0.17	0.08	0.9	5.4	105	6.1	Proctor et al. (1988)
870	—	—	0-15	4.0	22.9	0.40	—	16.8	0.53	0.41	1.2	5.6	105	7.4	Watloo (1989)
Indonesia, Kalimantan, Bukit Raya	1750	Aquept	0-18	—	25.7	—	—	—	—	—	—	—	13.5	2	Van Reuler (1987)
2150	Aquept	0-33	4.3	13.3	—	—	—	—	—	—	—	12.4	2		
Malaysia, Sarawak, Mull Ridge	1550	—	0-8	3.7	29.2	1.7	—	—	1.38	0.51	6.05	6.1	120	12	Tanner (1977a)
1550	—	—	0-10	4.0	3.9	0.35	—	—	0.80	0.18	6.18	3.9	29	38	
1550	—	—	0-10	4.4	9.0	0.52	—	—	0.32	0.08	1.57	0.44	37	7	
Malaysia, Sarawak, 'Gap'	1550	—	0-10	4.4	9.0	0.52	—	—	0.32	0.08	1.57	0.44	37	7	
Malaysia, Sarawak, Mull Ridge	1310	Organic	O _h -0-15	3.9	13.1	0.77	280	37	0.48	0.10	0.11	0.30	45.4	2.2	Tie et al. (1979)
Gunung Mulu	1930	Organic	O _g -0-15	3.4	42.5	1.81	360	78	0.56	2.82	0.05	0.72	73.8	5.6	
2090	Organic	O _g -0-45	3.0	43.2	1.40	—	68	0.05	0.29	0.12	0.68	52.8	1.1		
2370	Organic	O _h -0-30	3.2	39.9	1.14	—	38	0.26	0.20	0.68	0.90	81.4	1.7		
Malaysia, Sarawak, Kinabalu	2350	—	2-10	3.9	34.6	1.96	—	37	1.17	0.23	0.51	8.17	78.7	13	Kitayama (1992)
2600	—	—	2-10	3.9	38.0	0.98	—	4	1.17	0.42	4.08	7.21	79.6	16	
2800	—	—	3-20	4.6	7.7	0.45	—	13	0.26	0.10	0.40	0.27	9.8	10	
3000	—	—	1-5	5.4	15.5	0.83	—	9	0.63	0.20	1.83	2.42	33.4	64	
3200	—	—	5-10	3.9	11.6	0.91	—	28	0.68	0.18	1.07	1.09	34.3	9	
3400	—	—	2-30	4.7	8.8	0.56	—	11	0.40	0.21	3.41	0.47	22.1	20	
Malaysia, Sabah, Gunung Silam	790	—	0-15	5.6	8.5	—	—	1.1	0.17	0.08	0.9	5.4	105	6.1	Proctor et al. (1988)
870	—	—	0-15	4.0	22.9	0.40	—	16.8	0.53	0.41	1.2	5.6	105	7.4	Watloo (1989)

continued

in fine roots (Vaughan and Ord 1990), ion uptake (Glass 1973, 1974; Kobza and Einhellig 1987; Kuiters and Sarink 1987), and stomatal aperture (Einhellig and Kuan 1971). Some or all of these interferences may be at work in stunted TCMFs (low nutrient uptake, low E_p). Further work is needed to test the validity of the "toxin resistance" hypothesis.

It is uncertain what causes the high concentrations of polyphenols in the leaves of stunted TCMFs. Brujinzeel et al. (1993) found a weak inverse relationship between concentrations of total nitrogen and total phenolics, but the relationship differed between sites, suggesting that other factors may also play a role. Interestingly, leaf phenolic compounds such as flavonoids were also produced in larger quantities by plants subjected to increasing doses of UV-B radiation. The flavonoids are thought to play a role as internal "filters" that absorb and reduce the UV flux reaching certain plant tissues. Plant response to enhanced UV-B radiation included stunting and changes in leaf anatomy (Teramura 1983; Caldwell, Teramura, and Tevini 1989) that resemble those found in many TCMFs, i.e., small, thick, and hard leaves (cf. the section on transpiration). At first sight, increased intensities of UV-B may not be able to explain the occurrence of stunted MCF with xeromorphic leaves at low elevations, because intensities of UV-B only become sufficiently higher at elevations of 2,500–3,000 m (Caldwell, Robberecht, and Billings 1980). However, the finding that plants usually exposed to low levels of visible light and growing under well-watered conditions (both conditions that are common to TCMF) tended to be more sensitive to enhanced UV-B radiation than plants from environments with (more constant) high levels of visible light (Teramura 1983; Sullivan, Teramura, and Ziska 1992; Ziska, Teramura, and Sullivan 1992) may be pertinent. After all, the one factor that TCMFs have in common regardless of elevation is a soil that is persistently wet or very wet. The connections between soil water regime, root development, water and nutrient uptake, and radiation regime, particularly that of UV-B, in TCMF merit further attention (cf. Flenley 1992, and this volume).

Epiphytes and Their Effect on Nutrient Cycling

Epiphytes are usually conspicuous in MCF and contribute a substantial mass of living and dead organic matter (including humus) to the tree canopy. Epiphyte mass is difficult to quantify, but some estimates are included in Table 7. The epiphyte mass is only a small proportion of that of the total biomass for MCF, but when compared with the foliar biomass, it can assume substantial proportions. There is no evidence that epiphytes obtain mineral nutrients directly from the host trees, but they can be regarded as nutritional "pirates" (Benzing and Seeman 1978) in that they can intercept nutrients in aerosols, litterfall, rainfall, throughfall, and animal droppings. In the absence of epiphytes, these nutrients would become more quickly available to the trees. Epiphytes can, in the words of Nadkarni (1984), become "major participants in the impoundment and movements of mineral elements in a forest ecosystem." Some

Table 4. continued

Place	Altitude	Soil Type	Horizon & Depth (cm)	pH(log units)	C (%)	N (%)	P ^{total} (ppm)	P ^{extra} (μg/g ¹)	BS (%)				Authors	
									K	Na	Ca	Mg		
USA, Hawai'i	1675	—	—	—	—	—	—	—	0.74	—	5.75	1.1	—	Vitousek, Matson, and Turner (1988)
Venezuela, Parque Nacional "Henri Pittier"	1170	Typic Dystropept	0-11	4.9	3.8	—	—	—	1.67	—	21.0	2.6	—	Zinck (1986)
Venezuela, Santa Ana	600	A, 0-12*	—	—	—	—	—	—	0.6	1.7	4.1	2.4	19.6	45
Copey	600	A, 0-12*	—	—	—	—	—	—	0.2	0.3	1.6	2.5	17.1	27
Zumbador	3100	A, 0-25*	—	—	—	—	—	—	0.1	0.2	1.4	1.6	14.3	23
Venezuela, Andes	2300	—	—	—	—	—	—	—	0.4	0.2	0.1	0.2	84.0	1.1
Occidentales	—	—	—	—	—	—	—	—	0.43	0.1	1.3	0.59	17.5	14
* Two samples analyzed in each case and reported separately in the present table. — = no data available.														

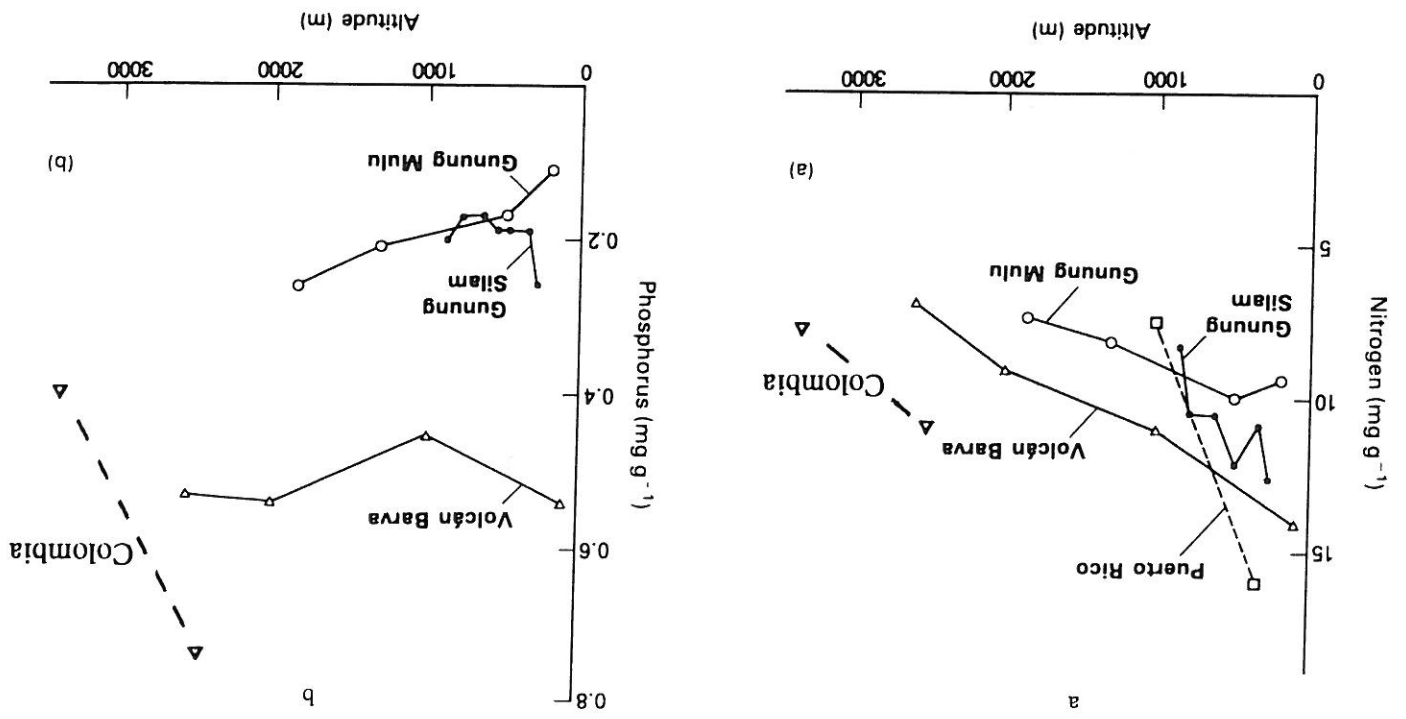
Table 5. Concentrations (as % oven-dry weight) of nitrogen, phosphorus, potassium, sodium, calcium, and magnesium in (a) leaf litterfall, (b) total small litterfall, and (c) epiphytic litterfall from cloud (or high montane >2500 m) forests

Location	Altitude (m)	Litterfall	Mass	N	P	K	Na	Ca	Mg	Authors	
Colombia, Cordillera Central	2500	a	4.6	1.11	0.074	0.89				Venklaas (1990)	
	3350	a	2.8	0.78	0.040	0.35					
		b	7.0	1.16	0.086	0.84					
Costa Rica, Monteverde	1500	a	4.8	1.47	0.08	0.12				Nadkarni and Matelson (1992a, b)	
		b	7.0	1.32	0.09	0.17					
	c	0.5	1.50	0.10	0.02						
Costa Rica, Volcan Barva	2000	a	4.8	0.90	0.054	0.22	0.03	1.1	0.19	Heaney and Proctor (1989)	
		b	5.8	0.79	0.046	0.21	0.03	1.05	0.17		
	a	4.6	0.68	0.053	0.30	0.02	1.04	0.23		Venkataraman and Chinnamani (1978)	
b	5.3	0.64	0.049	0.28	0.02	0.98	0.21				
India, Western Ghats	2600	a	4.6	0.68	0.053	0.30	0.02	1.04	0.23		
		b	5.8	0.79	0.046	0.21	0.03	1.05	0.17		
	b	2.1	1.1	0.062	0.52	—	1.60	0.24			
Jamaica, Mor Ridge	1550	a	4.9	0.60	0.018	0.23	0.13	0.58	0.33	Tanner (1977b, 1980a)	
		b	6.6	0.59	0.020	0.22	0.11	0.51	0.29		
		a	6.6	0.59	0.020	0.22	0.11	0.51	0.29		
		a	5.3	0.84	0.025	0.59	0.087	0.91	0.32		
		b	5.5	0.90	0.027	0.71	0.085	0.90	0.31		
		b	4.4	0.66	0.039	0.41	0.099	1.01	0.42		
	Malaysia, Sabah, Gunung Silam	790	a	3.66	1.05	0.017	0.10	0.1	0.68	0.33	Proctor et al. (1988)
			b	5.53	1.08	0.019	0.09	0.08	0.68	0.29	
		a	3.32	0.83	0.020	0.09	0.09	0.58	0.30		
		b	4.80	0.86	0.023	0.10	0.08	0.57	0.26		
		a	5.7	0.81	0.021	0.37	0.0051	0.19	0.18	Proctor, Anderson, and Vallack (1983)	
		b	11	0.78	0.023	0.28	0.0051	0.19	0.15		
Malaysia, Sarawak, Gunung Mulu National Park	1310	a	2.3	0.74	0.026	0.18	0.010	0.19	0.20		
		b	3.6	0.79	0.030	0.16	0.011	0.16	0.17		
	a	2.45	0.77	0.024	0.14	—	0.53	0.24	Weaver et al. (1986)		
Puerto Rico, Luquillo Mountains	1000	a	3.4	1.2	0.062	0.57	0.0041	0.73	0.26	Fassbender and Grimm (1981)	
		b	7.0	0.99	0.057	0.47	0.0039	0.62	0.21		
	a	3.4	1.2	0.062	0.57	0.0041	0.73	0.26			
Venezuela, Andes Occidentales	2300	a	3.4	1.2	0.062	0.57	0.0041	0.73	0.26	Fassbender and Grimm (1981)	
		b	7.0	0.99	0.057	0.47	0.0039	0.62	0.21		
		a	2.45	0.77	0.024	0.14	—	0.53	0.24	Weaver et al. (1986)	
		b	3.6	0.79	0.030	0.16	0.011	0.16	0.17		
		a	2.3	0.74	0.026	0.18	0.010	0.19	0.20		
		b	11	0.78	0.023	0.28	0.0051	0.19	0.15	Proctor, Anderson, and Vallack (1983)	
	1550	a	4.9	0.60	0.018	0.23	0.13	0.58	0.33	Tanner (1977b, 1980a)	
		b	6.6	0.59	0.020	0.22	0.11	0.51	0.29		
		a	6.6	0.59	0.020	0.22	0.11	0.51	0.29		
		a	5.3	0.84	0.025	0.59	0.087	0.91	0.32		
		b	5.5	0.90	0.027	0.71	0.085	0.90	0.31		
		b	4.4	0.66	0.039	0.41	0.099	1.01	0.42		

Location	Altitude (m)	Element Concentrations		Retranslocation		Authors
		N(%)	P(%)	N(%)	P(%)	
Colombia, Cordillera Central	2550	a	1.8	0.13	14	Veneklaas (1990)
	3370	b	1.1	0.07	15	
		a	1.5	0.09	16	
		b	0.9	0.03	28	
	1500	a	1.97	0.14	14	Nadkarni and Mateison (1992a)
		b	1.47	0.08	18	
Costa Rica, Monteverde	1550	a	1.05	0.05	21	Tanner (1977a, b)
		b	0.60	0.018	33	
'Mor Ridge'		a	1.61	0.07	23	64
		b	0.84	0.025	34	
'Wet Slope'		a	1.27	0.08	16	64
		b	0.66	0.039	17	
'Gap'		a	1.76	0.10	18	51
		b	0.93	0.038	25	
Malaysia, Sabah, Gunung Silam	790	a	1.7	0.05	32	Proctor et al. (1989)
		b	1.1	0.02	62	
	870	a	1.3	0.05	29	57
		b	0.8	0.02	42	
Venezuela, Andes Occidentales	2300	a	1.74	0.08	22	Fassbender and Grimm (1981)
		b	1.20	0.06	20	

Table 6. Element concentration, nitrogen/phosphorus quotients, and nitrogen and phosphorus retranslocation of (a) live foliage and (b) leaf litter in tropical montane forests. Retranslocation is calculated as (element concentration in mature leaves - element concentration in litterfall) ÷ (element concentration in mature leaves)

Figure 5. Changes in (a) nitrogen concentrations and (b) phosphorus concentrations in leaf or nonwoody litterfall in studies made at a range of altitudes on one mountain (after Heaney and Proctor 1989; data for Colombia from Veneklaas 1990).



epiphytes can also fix nitrogen or harbor nitrogen-fixing symbionts, although the fluxes involved are still speculative. For epiphylls (those epiphytes that are restricted to the surfaces of leaves), Bentley and Carpenter (1984) calculated from N^{15} studies that they could contribute up to 25 percent of host leaf nitrogen in a rainforest understory. Bentley (1987) described the conditions that might influence the epiphyll nitrogen fixation, but concluded that "the contribution of new nitrogen by epiphylls to an ecosystem is probably fairly small."

Estimates of the nutrient pool contained in epiphytes are given in Table 7. Nadkarni (1984) estimated that for a range of montane forests, the "mineral capital contained in epiphytes is up to 45% of that which is held in the foliage." More recently, Hofstede, Wolf, and Benzing (1993) have shown that the proportions were much higher in the Colombian cloud forest. Here the epiphytes held 7.4 times more nitrogen, 6.5 times more phosphorus, 3.5 times more potassium, and 2.8 times more calcium than the leaves. The epiphyte nutrients can be transferred to other ecosystem pools by crown wash, herbivory litterfall of the epiphytes themselves, and in some cases, by host-tree canopy-root systems (Nadkarni 1981). The canopy-root systems are not a universal feature of TMCF, however. A high microbial activity in epiphyte-derived canopy organic matter of a Costa Rican cloud forest has been found by Vance and Nadkarni (1990). They made a preliminary estimate that 0.7 kg/ha¹ of nitrogen were immobilized in microbial tissue and considered that "because of their high biomass and activity, microorganisms in the canopy could be important in regulating nitrogen availability in this forest." This conclusion seems justified, at least as far as nitrogen availability to epiphytes is concerned.

The question of epiphyte litterfall has been dealt with by Nadkarni and Matelson (1992b). The authors found that a specially designed sampling system was necessary to give a reasonably good estimate of the highly clumped epiphyte litterfall. They found the quantities of nutrients contained in this litterfall to be about 1–8 percent of corresponding amounts in foliar litterfall and pointed out that epiphyte litterfall shows substantial differences in decomposition rates from the litterfall of terrestrially rooted plants.

Research Perspective

One must conclude that epiphytes can be an important component in the nutrient cycling of TCF but that much remains to be discovered about them.

Although TMCF structure is very characteristic, there does not seem to be any environmental factor (except for the frequency of low cloud) shared by all TMCFs. Therefore, research focusing on a single factor is unlikely to provide generally valid answers. Attention to TMCF ecology has greatly increased in the last two decades, but surprisingly little information is available on the key processes determining productivity, viz. carbon economy and the influ-

Table 7. The mass (kg/ha¹) of live and dead (including organic matter and humus) epiphytes and their contents (kg/ha¹) of mineral nutrients in tropical montane cloud forest

Location	Altitude (m)	Mass	N	P	K	Na	Ca	Mg	Authors
Colombia	3700	44000	443	35	103	—	108	—	Hofstede, Wolf, and Benzing (1993)
Colombia	3370	12000	—	—	—	—	—	—	Vencklaas (1990)
Costa Rica, Monteverde	1700	4730	105	3	23	7	12	4	Nadkarni (1984)
Jamaica, 'Morr Ridge'	1550	2800	25	2	22	—	18	9	Tanner (1980b, 1985)
Jamaica, 'Mull Ridge'	1550	500	—	—	—	—	—	—	—
Puerto Rico, Pico del Este	1000	7360	—	—	—	—	—	—	Weaver (1972)
Tanzania, Uluwuru Mountain	2120	14000	—	—	—	—	—	—	Pöcs (1980)
Mossy elfin forest	2120	14000	—	—	—	—	—	—	—
Submontane rainforest	1415	2130	—	—	—	—	—	—	—

ence of climatic and soil conditions thereupon. Also, while forest structure and productivity are functionally related, different factors may underlie low stature and low productivity. An approach that explicitly separates effects on forest structure and functioning is required if causal relationships are to be identified. The study of the forest carbon balance may offer a convenient framework to assess effects on specific abiotic and biotic factors on productivity, and for reinterpreting results of research undertaken in the past. High priority should be given to the estimation of canopy photosynthesis and the way it is influenced by radiation climate, and to the quantification of respiratory losses, especially those associated with nutrient uptake.

The linkages between soil water regime, root development and morphology, and (rapid) fluctuations in radiation (including UV-B) and fog incidence, and water and nutrient uptake in TMCF merit further attention. The frequency of occurrence of excess soil water has been little studied in TMCF, either alone or in relation to root morphological adaptations (e.g., aerial roots, occurrence of root lenticels, etc.) and oxygen deficiency. The postulated connection between levels of phenolics in leaves and UV-B irradiation requires field observations and experimentation. Finally, the role of cloud water chemistry (notably its acidity and sulphate concentrations) requires further study, particularly in view of the importance that is usually attached to the role played by acidic cloud water (in combination with various photochemical oxidants) in the widespread decline in forest productivity in the temperate zone (Schier and Jensen 1992). Information on cloud water chemistry in TMCF is now beginning to be collected (e.g., Weathers et al. 1988; Bruijnzeel et al. 1993), but its impact on tree physiological behavior has remained unstudied so far.

These aspects could probably be dealt with best in a network of multidisciplinary studies conducted at a limited number of sites for which there is sufficient floristic and climatic background information. Such key sites need to be carefully chosen because the study of the role of atmospheric and edaphic factors in TMCF is often hindered by the change in community floristics that usually accompanies the transition from tall forest below the clouds to smaller statured forest within the clouds (Brown 1919; Van Steenis 1972; Proctor et al. 1988). Fortunately, there are a few locations carrying cloud forest where this floristic transformation is incomplete, such as on Rakata Island, Indonesia (Whittaker, Bush, and Richards 1989); Margarita Island, Venezuela (Sugden 1986); and Maui Island, Hawaii (Kitayama and Mueller-Dombois 1993). Similarly, certain species are known to occur in both cloud forest and lower elevation forest type, with corresponding changes in tree stature (e.g., *Microphtolis garciniaefolia* in Puerto Rico; W.L. Silver, personal communication). Arguably, the study of the physiological behavior of such species in combination with observations of climatic and edaphic conditions along the elevational gradient might be particularly instructive (Whitmore 1989). In addition, similar studies in adjacent forests of contrasting stature but subjected to the same overall climatic conditions, such as the UMRFs in Jamaica described by Tanner (1977), could be equally enlightening. Finally,

the fact that there are structural and ecological similarities between UMRF and Heath forests (Richards 1952; Whitmore 1989) could also be used as a starting point for comparative studies.

Summary

Tropical montane cloud forest (TMCF) covered about 500,000 km² in the early seventies but is disappearing rapidly in parts of Latin America and South-east Asia to make way for other land uses. Despite their importance for the continued supply of water to densely populated lowlands, the hydrological functioning of TMCF has been studied far less than that of lowland rain forest. The first part of this paper reviews TMCF hydrology.

The most notable changes in forest physiognomy with increasing elevation are a decrease in stature and a tendency for the leaves to become more xeromorphic. Both the stunting of montane forests and the related Massenerhebung effect have remained unexplained. The second part of the paper reviews the evidence.

An important feature of TMCF is the stripping by the vegetation of moisture from passing low cloud (horizontal precipitation—HP). (Its quantification at the ecosystem level presents major difficulties, exacerbated by the presence of epiphytes.) Additions of moisture via HP may reach hundreds of millimeters per year. Typical values range between 5 and 20 percent of ordinary rainfall but may exceed the latter under more seasonal conditions.

The few studies of evapotranspiration in TMCF indicate annual totals of 300–400 mm, i.e., well below corresponding values for fog-free montane forests (1,100–1,300 mm/year⁻¹). Correcting for “occult” contributions of precipitation, evapotranspiration varies between 570 and 770 mm/year⁻¹. More data are needed. Evidence is accumulating that transpiration rates in TMCF are also low (0.7–1.4 mm/day⁻¹), even during periods of bright sunshine.

Converting TMCF to pasture may influence total water yield and seasonal distribution of flow negatively, because of the loss of moisture inputs via HP, although experimental evidence is mostly lacking on the associated threshold value for HP. Deterioration of infiltration characteristics after clearing could cause further degradation of the flow regime. Research to this end should be given high priority.

A variety of reasons has been proposed to explain the stunting of TMCF. While it is acknowledged that wind may be a factor in nonequatorial latitudes, none of the current hypotheses is capable of explaining the occurrence of stunted forest at low altitudes in all cases published to date. Nutrient budgeting computations (and fertilization experiments) have shown that stunted TMCF takes up only a small fraction of the nutrients arriving at the forest floor via water-bound pathways. The excess supply over net uptake contradicts to the widely established idea that nitrogen is a key limiting element in TMCF.

Living foliage and fresh leaf litter in a number of stunted TMCFs contained high concentrations of polyphenols. Upon washing into the soil, the polyphenols may interfere with photosynthesis, cell division in fine roots, transpiration, and ion uptake. High levels of phenolic compounds in leaves may play a role as internal "filters," absorbing and reducing the flux of ultraviolet-B (UV-B), radiation reaching certain plant tissues. The interrelationships between soil water regime (notably excess water), root development, uptake of water and nutrients, radiation regime (including UV-B), and photosynthesis require more study.

Apart from their often high degree of endemism and other ethical reasons, the demonstrated low productivity and water use of TMCF are strong arguments for preserving these forests.

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