

CLIMATIC CONDITIONS AND TROPICAL MONTANE FOREST PRODUCTIVITY: THE FOG HAS NOT LIFTED YET

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Abstract. Tropical montane cloud forests (TMCF) differ from lowland moist forests in structure (low stature, small and tough leaves, low diversity) and functioning (low productivity, low nutrient-cycling rates). To explain these differences, a variety of hypotheses have been proposed, most of which are related directly or indirectly to climate, but none of these provides a satisfactory explanation for all typical TMCF traits. The single climatic factor shared by all TMCF, the frequent occurrence of low cloud, has multiple effects, but not all are well understood. In this paper we describe and analyze the climatic and soil-moisture conditions prevailing in TMCF as reported in the literature. TMCF evapotranspiration is limited by both climatic conditions and canopy conductance. TMCF productivity is low, but our understanding of these forest's carbon balance is incomplete. Leaf photosynthetic capacity is not particularly low, but canopy photosynthesis probably is, due to persistent cloudiness (low radiation) and a low leaf-area index (LAI). We suggest that the low LAI of TMCF is controlled by light climate and by leaf structure and longevity. TMCF productivity is probably further limited by a substantial investment of carbon in the growth and functioning of a relatively large root system, which is itself a consequence of unfavorable soil conditions.

Key words: carbon balance; cloud forest; evapotranspiration; leaf-area index; leaf chemistry; leaf structure; montane rain forest, lower cf. upper; soil moisture; tropical montane cloud forest.

INTRODUCTION

With increasing altitude on wet tropical mountains, changes in forest structure occur (Whitmore 1989). The principal changes are a decrease in forest stature, and a tendency for the leaves to become smaller, thicker, and harder ("xeromorphic"). The altitudinal zonation is compressed on small outlying mountains compared with large mountains (Richards 1952). Although the stunting of tropical montane forests has been studied for >80 yr (cf. Grubb 1977), it has remained poorly explained. However, the original contention of Brown (1919) that the frequency of fog is the most important factor determining the stature of montane forest, is supported by numerous descriptive studies (reviewed by Richards [1952], Van Steenis [1972], and Stadtmüller [1987]). Subdivisions of montane forest types based on physiognomy have also been related to the presence of fog: Grubb and Whitmore (1966) suggested that taller-statured lower montane rain forest had "frequent," and shorter-statured upper montane rain forest "long per-

sistent" cloud cover close to the ground. Both forest types are often also referred to as (tropical montane) "cloud forests" (TMCF), which are usually defined as forests that are "frequently covered in clouds or mist" (Stadtmüller 1987:19). Quantitative criteria on what constitutes "frequent" or "long persistent" cloud are lacking, but implicit in the term "TMCF" is a recognition of the important influence of cloud on forest structure and functioning.

TMCF have been found to have lower productivity (estimated as litterfall or diameter increment), lower concentrations of nitrogen and/or phosphorus in leaves, and lower nutrient-cycling rates in comparison to lowland tropical rain forest. A variety of hypotheses have been proposed to explain the structural and functional characteristics of TMCF. These include: (1) periodic water shortage (in spite of the frequent cloud cover), especially in the case of shallow and stony soils; (2) saturated soils and impeded root respiration; (3) reduced leaf temperatures and photosynthesis associated with low radiation inputs and low air temperatures; (4) limited nutrient uptake due to (a) climatically controlled reduction in transpiration rates, (b) extreme soil acidity or low fertility or both, often coupled with (c) reduced decomposition and mineralization rates; (5) exposure to strong winds; and (6) presence of high

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concentrations of phenolic compounds in soil moisture interfering with metabolic processes.

Nutrient aspects of TMCF will be discussed in the companion paper by Tanner et al. (1998). The present paper (1) summarizes and evaluates data on tropical montane environmental conditions and their effect on TMCF structure and function, and (2) offers some suggestions for further research.

GENERAL HYDRO-METEOROLOGICAL CONSIDERATIONS

Depending on latitude, the lower limit of tropical montane cloud forests (TMCF) on large mountains is generally between 1500 and 2500 m while the upper limit is usually from 2400 to 3300 m. Local factors may cause cloud formation at much lower altitude (down to 400 m on small coastal or island mountains), while upper montane rain forest (UMRF) may occur up to 3900 m under favorable conditions (Stadtmüller 1987). Given the wide altitudinal range in which TMCF occur, mean temperature and annual rainfall vary considerably among locations. However, all TMCF experience sustained high atmospheric-humidity levels.

Besides precipitation, the rate of open-water evaporation E_o (Penman 1956) is a convenient measure to characterize overall climate conditions at a location. Evaporation generally decreases with elevation as radiation, temperatures, and vapor-pressure deficits are all reduced (Brown 1919 and many others). However, in subtropical trade-wind regions evaporation increases again when mountains reach up into the dry air above the trade-wind inversion (Juvik and Nullet 1994). There have been suggestions that the most stunted types of TMCF 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 (Weaver et al. 1973, Ash 1987). However, average values of E_o at sites carrying stunted TMCF at low to intermediate (<1000 m) elevations (e.g., Serranía de Macuira, Venezuela; El Yunque and Pico del Oeste, Puerto Rico; Gunung Silam, Malaysia; Rakata Island, Indonesia) ranged between 2 and 4 mm/d (Waterloo 1989, Hafkenschied 1994), values that are high enough to enable the uptake of nutrients (cf. Grubb 1977).

The actual presence of fog, the only meteorological factor that distinguishes TMCF locations from other montane rain-forest locations, has various effects on ecosystems. Fog constitutes an extra hydrological input ("horizontal" or "occult" precipitation) which may amount to several hundred millimeters of water per year, depending on cloud characteristics, wind speed, and vegetation structure (Bruijnzeel and Proctor 1995). Fog also represents a distinct chemical input, even if it does not lead to a measurable increase in net precipitation (Unsworth and Crossley 1987). Cloud droplets generally have higher acidity and nutrient concen-

trations than rain (Asbury et al. 1994) and this may affect leaf physiology and nutrient relations (Schier and Jensen 1992). Persistent leaf wetness itself has been shown to induce chronic reduction of photosynthesis in some plants (Ishibashi and Terashima 1995). Finally, the presence of fog may reduce irradiance to 10–50% of that under sunny conditions (Monteith and Unsworth 1990). While persistently strong winds do influence forest stature in some locations (notably in the trade-wind belt; Sugden 1986), wind rarely plays a significant role at equatorial latitudes (Proctor et al. 1988, Hafkenschied 1994) and is not considered further.

PERIODIC WATER DEFICIENCY VS. WATERLOGGING

Although trees in upper montane rain forests growing on very shallow soils have been reported to die following severe droughts (Lowry et al. 1973, Werner 1988), all observations of soil water dynamics and leaf water potentials in tropical montane cloud forests (TMCF) suggest that the trees rarely, if at all, experience severe soil water deficits (Lyford 1969, Herrmann 1971, Hetsch and Hoheisel 1976, Dohrenwend 1979, Kapos and Tanner 1985, Bruijnzeel et al. 1993). Bruijnzeel et al. (1993) demonstrated that one of the worst droughts in the area's history caused significant extra shedding of leaves below but not within the cloud belt at Gunung Silam, Malaysia. Similarly, soil moisture levels in ridge-top TMCF in Puerto Rico remained unaffected by the severe drought that hit the island in 1993–1994 (F. N. Scatena, *personal communication*).

Many studies of soils in TMCF have reported persistently (near-)saturated conditions, which stand in sharp contrast to the more variable moisture regimes of the lower montane rain forests found below the average base of the cloud cap. This is confirmed by morphological differences between soils; transect studies generally note major changes when passing into the zone of frequent low cloud, the most striking of these being increased organic matter content, darker colors, and increased abundance of hydromorphic characteristics (Hetsch and Hoheisel 1976, Van Reuler 1987). Other indications of such conditions include a high frequency of aerial roots (Brown 1919, Gill 1969). On the other hand, gleying or waterlogging has not been observed consistently in TMCF (Kapos and Tanner 1985, Hafkenschied 1994).

EVAPOTRANSPIRATION

Total evapotranspiration (ET) consists of evaporation of intercepted precipitation (E_i) and transpiration (E_t). Rainfall interception, E_i in TMCF (tropical montane cloud forest) is roughly 200–400 mm/yr, whereas E_t has been estimated at 250–300 mm/yr, well below values found in lowland forest (Bruijnzeel 1990, Bruijnzeel and Proctor 1995). The processes of transpiration and photosynthesis are strongly coupled—both depend on diffusion through stomates—so it is of

interest to examine why rates of E_t are low in TMCF. As described above, TMCF sites have somewhat lower values for open-pan evaporation (E_o) than forests not affected by low cloud, but there is evidence that transpiration (E_t) is even more reduced. Bruijnzeel et al. (1993) expressed average values of daily E_t (determined by the site water-balance method) as a ratio to corresponding values of E_o for two lower montane rain forests (LMRF) of contrasting stature in East Malaysia; they observed a much lower value (0.24) for the more stunted forest (subjected to frequent low cloud) than for tall forest situated just below the cloud cap (0.51). Additional evidence of low E_t rates in TMCF was found by Hafkenscheid (1994) on the island of Rakata (Krakatau), Indonesia, where heat-pulse equipment was used to monitor sapflow in *Neonauclea calycina* trees of similar diameter at breast height at 110 m (in 30–35 m tall lowland forest) and at 710 m (in 7–15 m tall “mossy forest”). Half-hourly observations of sap flow rates were made over a period of 3 wk during the dry season of 1992 in conjunction with measurements of soil water tension and the climate above the canopy. On sunny days sap flow rates in the TMCF were reduced by ~70% (on average) compared to values observed at 110 m, despite very similar totals of incoming radiation and only modest reductions in E_o at 710 m (<15% on average). There was no soil water stress or excess at either location, and soil nutrient concentrations were comparable.

The evidence presented above suggests that canopy conductances of TMCF are lower than in lowland forests or LMRF without frequent low cloud, even during sunny weather. Canopy conductance is mainly a function of leaf-area index (LAI) and leaf diffusive conductance for water vapor (in turn largely determined by stomatal conductance, g_s). LAIs of TMCF are clearly lower than those of lowland forests, ranging from ~6 in LMRF with little low cloud (Grubb 1977) down to ~2 in dwarf cloud forests (Weaver et al. 1986). Measured data for g_s cover a wide range. Maximum values may be as high as 0.2–0.3 mol·m⁻²·s⁻¹ (Aylett 1985, Jane and Green 1985, Vitousek et al. 1990, Meinzer et al. 1992), but much lower values have been found as well (Medina et al. 1981, Kapos and Tanner 1985). Stomatal densities and sizes (Cintron 1970, Grubb 1977) are not lower in TMCF compared to lowland forests. It seems therefore that g_s in TMCF is not inherently low but stomatal behavior is such that conductance is often reduced.

CARBON BALANCE

Tropical montane cloud forest (TMCF) is generally believed to be less productive than lowland rain forests, an assertion that is mainly based on the occurrence of smaller amounts of litterfall (recently summarized in Bruijnzeel and Proctor [1995]) and smaller rates of trunk diameter increment (Brown 1919, Weaver et al.

1986, Tanner et al. 1990). However, in the absence of reports on belowground productivity in TMCF, it is perhaps more correct to state that these forests exhibit a low aboveground net primary productivity. There have been no studies aimed at quantifying the overall carbon balance of TMCF. However, such studies are essential if further insight is to be obtained into the interrelationships of forest structure and productivity. Carbon fixed by photosynthesis is not only used for growth but also for maintenance and ion uptake (Lambert et al. 1983). At present, very limited data are available on the magnitude of any of these processes at the ecosystem level in TMCF.

The limited evidence on photosynthetic rates in TMCF suggests that the capacity of the photosynthetic apparatus of leaves in TMCFs is not systematically lower than that in lowland forests. As indicated earlier, reported values for (g_s) in stomatal conductance TMCF are variable, but maximum values are not particularly low and the latter are known to correlate with maximum photosynthetic rates (Körner et al. 1979). Maximum rates of net photosynthesis of about 7–11 $\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ have been reported for *Metrosideros polymorpha* in Hawai'i (Vitousek et al. 1990, Meinzer et al. 1992), and rates of 5–7 $\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ have been reported for three Jamaican upper montane rain-forest species (Aylett 1985). Both are within the range for non-pioneer lowland species.

To understand the relation between photosynthesis and forest productivity, gas-exchange data must be related to the distribution of leaf area and to light climate. Cloudiness and fog may significantly reduce the amounts of solar radiation reaching TMCF during a considerable part of the day. Long-term records of irradiation in TMCF are scarce, but the few studies that are available all point to reductions of 15–50% compared to lowland sites (Baynton 1969, Müller 1982, Aylett 1985, Cavelier and Mejia 1990, Turton 1990, Bruijnzeel et al. 1993). This contrast in radiation load will be smaller when the comparison is made against elevations carrying tall forest just below the base of the cloud cap (Cavelier and Mejia 1990, Bruijnzeel et al. 1993). Nevertheless, the observation that LAIs (leaf-area indexes) of TMCFs are low (Grubb 1977, Weaver et al. 1986) may indicate that further expansion of leaf area would only lead to leaves that function below their light-compensation point. The interaction between solar radiation, LAI, and photo-canopies is illustrated in Fig. 1, which shows the simulated carbon gains of a forest canopy with specified photosynthetic characteristics for the two hypothetical extreme cases of permanently sunny or overcast conditions. During cloudy conditions, carbon gain at the top of the canopy is lower and the rate of decrease with depth in the canopy (cumulative LAI) is faster (Fig. 1a). The integrated carbon gain of the total canopy increases with canopy LAI up to the point where additional leaves

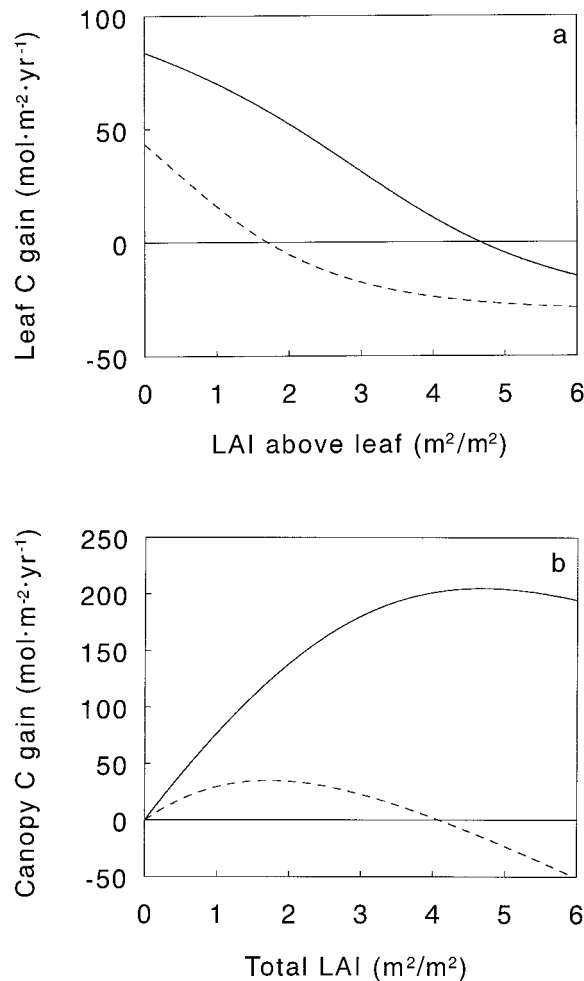


FIG. 1. Simulated carbon gain of a tropical montane forest canopy in permanently sunny (—) and permanently overcast (---) weather. (a) Annual carbon gain as a function of cumulative leaf-area index from the top of the canopy, calculated as the annual sum of net photosynthesis minus nighttime respiration. Assumptions: (1) day length 12 h, daily course of photosynthetic photon flux density (PPFD) given by a squared sine curve (cf. Hirose and Werger 1987) with midday PPFD of 2000 (sunny) or 400 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (overcast); (2) spherical leaf-angle distribution, exponential decrease of PPFD with cumulative leaf-area index (LAI), with extinction coefficients of 0.55 (sunny) or 0.72 (overcast) (cf. Goudriaan 1977); (3) relationship between gross leaf photosynthesis and PPFD of all leaves given by a non-rectangular hyperbolic function (Johnson and Thornley 1984) with maximum photosynthetic rate of 10 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, quantum yield of 0.05 mol/mol, and convexity parameter of 0.75; (4) constant day and night leaf respiration rate of 1 $\mu\text{mol}\cdot\text{m}^{-1}\cdot\text{s}^{-1}$. (b) Total canopy carbon gain as a function of leaf-area index. Assumptions as in (a).

respire more than they assimilate (Fig. 1b). Although the model is simple and the estimates of parameter values are based on limited information, there are a number of structural features of TMCF that seem to support the idea that low irradiance is a key controlling

factor. The general absence of an understory of woody plants in TMCF suggests that only some specialized shade-adapted life-forms (often ferns and bryophytes) tolerate this light climate (Van Steenis 1972). Clearly, the relationships between (macro-) light climate, LAI and canopy photosynthesis in TMCF require further study.

Photosynthetic products are used for the formation and maintenance of leaves, stems (trunk, branches, twigs), reproductive parts, and roots plus symbionts. Compared to lowland rain forests, TMCF exhibit similar leaf biomass (LAI is lower because leaf mass per area is higher), smaller biomass of trunks and branches, but similar or higher root biomass (Grubb 1977, Medina and Klinge 1983, Cavelier 1989). Although the actual costs for the growth and maintenance of the different plant parts in TMCF are difficult to estimate, it seems likely that the costs for roots are relatively high. Presumed low availability of nutrients or the presence of toxic substances associated with waterlogged soils (Crawford 1971) could cause enhanced costs for root production and functioning (Van der Werf et al. 1992). Specific construction costs of biomass of plants at high altitudes could possibly be higher than those at low altitudes due to higher lipid and lignin contents (Larcher 1983, Poorter 1994; cf. the next section). In conclusion, it seems likely that the low aboveground biomass production in TMCF is related both to low photosynthetic carbon gain and to high maintenance and construction costs.

FOLIAR STRUCTURE AND PHENOLIC CONCENTRATIONS

The small, thick, and hard leaves of tropical montane cloud forests (TMCFs) are often classified as "xeromorphic," although they are not particularly well-suited to tolerate water stress (Buckley et al. 1980, Kapos and Tanner 1985). Alternatively, leaf xeromorphy has been interpreted as a response to limited availability of nutrients (Loveless 1961, 1962, Medina et al. 1990). Plants that produce such "pachyphylls" (Grubb 1977) invest more carbon per unit leaf area. As discussed above, carbon gain per unit leaf area of these "expensive" leaves is no higher than that for "normal" leaves. Why don't trees in TMCF invest C in greater leaf area, or allocate it to other organs? The radiation environment could select for low LAI (Fig. 1), while the presence of thick, strong leaves could point to selection for leaf longevity, in order to compensate for the generally low carbon gains per unit time (Williams et al. 1989, Poorter 1994). Average leaf life-span has been estimated at 14–18 mo for montane forest trees and at 12–14 mo for lowland forest trees (Grubb 1977); additional direct information would be most useful. The construction of one square meter of leaf area with a leaf mass per area of 0.15 kg/m² and a specific construction cost of 1.6 g glucose/g dry matter requires 8 mol of carbon,

a considerable investment under unfavorable photosynthetic conditions (cf. Fig. 1b). The costs may be reduced on an annual basis if leaf life-span is extended; longer life-spans may also serve to make more efficient use of already invested nutrients by increasing the mean residence time of a nutrient in the plant (Aerts and Van der Peijl 1993; cf. the relatively high proportions of nitrogen and phosphorus retranslocated from the leaves in TMCF before abscission; Veneklaas 1991, Bruijnzeel and Proctor 1995).

The toughness and chemistry of TMCF leaves may also protect them against such hazards as mechanical damage (wind, hail), herbivory, pests and diseases, epiphylls, acid mist or high radiation loads (Levitt 1980). Clearly, great toughness and thick cell walls are of rather general value, especially to exposed, long-lived leaves. Additionally, high concentrations of flavonoids (a phenolic compound) have been reported in TMCF leaves. Bruijnzeel et al. (1993) reported concentrations of polyphenols in fresh leaf litter in stunted TMCF in Malaysia (and elsewhere) to be much higher than in tall-statured forests below the cloud cap. This contrast in concentrations was not observed for older litter, and thus the polyphenols can be expected to enter the soil during rain. Here they may have a toxic effect on roots and interfere with metabolic processes such as photosynthesis rates, cell division in fine roots, stomatal aperture and ion uptake (Kuiters 1990, Kuiters and Mulder 1993). Some or all of these interferences may be at work in stunted TCMF. Further work is needed to test the validity of this "toxin-resistance" hypothesis as well as to evaluate the cause of enhanced phenolic concentrations. Generally speaking, nitrogen stress and water deficit are among the most important factors affecting the concentration of phenolic metabolites in plant tissue (Horner et al. 1988). However, neither of these were decisive in the case described by Bruijnzeel et al. (1993), although there was a weak inverse relationship with total nitrogen concentration. Recently, Northup et al. (1995) presented evidence of an inverse relationship between foliar concentrations of phenols (particularly condensed tannins) and soil pH. They advanced various mechanisms through which enhanced concentrations of phenols could be helpful in minimizing losses of nitrogen and mitigating the adverse effects of soil infertility in general, and of aluminum toxicity in particular. In a more general model on the role of secondary metabolites in ecosystems, Baas (1989) assumed a role for these substances in regulating both detrimental and beneficial relationships between plants and their abiotic (climate, soil) and biotic (heterotrophic organisms, herbivores, competitors) environment, thus influencing the carbon and nutrient economy of the ecosystem.

RESEARCH PERSPECTIVES

Although the structure of TMCF (tropical montane cloud forest) is characteristic, there is no single envi-

ronmental factor (except for the frequency of low cloud, which has multiple effects) 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, particularly overall carbon economy and the influence of climate 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 may be required if causal relationships are to be identified. The study of the forest carbon balance offers a convenient framework to assess effects of 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 among soil water regime, soil acidity and aluminum toxicity, root development and morphology, and (rapid) fluctuations in radiation and fog incidence, all merit further attention in relation to water and nutrient uptake in TMCF. The postulated connection between foliar concentrations of phenols and pH (Northup et al. 1995) and possibly toxic levels of aluminum in the soil requires field observations and experimentation. The role of cloud water chemistry (notably its acidity and sulfate concentrations) needs further study, particularly in view of the importance 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 (Bruijnzeel et al. 1993, Asbury et al. 1994) but its impact on tree physiology has remained unstudied so far. Finally, the striking structural and ecological similarities between upper montane rain forests (UMRF) and heath forests (Richards 1952, Whitmore 1989) could provide a useful starting point for comparative studies. Heath forests usually occur on exceedingly acid soils and their leaves are known to be rich in polyphenols and low in nitrogen (Proctor et al. 1983a,b, Medina et al. 1990).

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