Land Use and Water Resources Research

Hydrology of tropical montane cloud forests: A Reassessment[1]

L.A. Bruijnzeel

Co-ordinator, Tropical Environmental Hydrology Programme (TRENDY), Faculty of Earth Sciences, Vrije Universiteit, Amsterdam, The Netherlands. Tel. +31 20 444 7294, Fax +31 20 646 2457; e-mail: ***brul@geo.vu.nl;*** web site: **http://www.geo.vu.nl/users/trendy**

Abstract

Extending an earlier review of the literature (Bruijnzeel and Proctor, 1995), this paper incorporates the results obtained by post-1993 hydrological and hydrometeorological studies in tropical montane cloud forests (TMCF) situated mostly in Latin America and the Caribbean. Based on the presently available information on the hydrological functioning of TMCF, the most pressing gaps in our understanding are highlighted and suggestions offered as to where and how these could be addressed.

Introduction

Although the importance of fog deposition on vegetated surfaces as an extra source of moisture has been acknowledged for a long time (see Kerfoot, 1968) for a review of early literature), the paper by F. Zadroga (1981) on the hydrological significance of tropical montane cloud forests (TMCF) in northern Costa Rica probably marks the start of the enhanced interest in these remarkable forests in the last two decades. Arguably, this increased interest is in no small measure due to the unstinting efforts of one man, Professor Lawrence S. Hamilton, who recognized the far-reaching implications of Zadroga's preliminary work and who kept stressing the hydrological and ecological importance of TMCF on numerous occasions. Hamilton's efforts culminated in the organization of the First International Symposium on Tropical Montane Cloud Forests, held in San Juan, Puerto Rico, from 31 May until 5 June 1993 (the proceedings of which were published as Hamilton *et al*., 1995), and the launching of *'A Campaign for Cloud Forests'* by the International Union for the Conservation of Nature (IUCN) in 1995 (Hamilton, 1995a). The hydrological and biogeo-chemical evidence on TMCF were reviewed in detail at the Puerto Rico Symposium by Bruijnzeel and Proctor (1995). These authors stressed, *inter alia*, how little is actually known about the hydrological functioning of different types of montane forest exposed to varying degrees of cloud impaction; the role of epiphytes with respect to cloud water interception and retention; cloud forest carbon dynamics and the factors limiting their growth; and, above all, the uncertainty surrounding the water use of different types of TMCF and the effect of TMCF conversion to pasture or temperate vegetable cropping on down-stream water yield. Bruijnzeel and Proctor (1995) also called for the establishment of a pan-tropical network linking carefully selected data-rich TMCF research sites where these important questions could be addressed in an integrated manner.

The nomenclature of montane forests, including TMCF, is confusing. Stadtmüller (1987) has listed at least 35 different names that have been used to typify cloud forest. Therefore, before reviewing the results of hydrological research in TMCF (with emphasis on post-1993 work, i.e. published or initiated after the Puerto Rico Symposium), a simple classification of TMCF types is proposed that allows hydrological distinctions to be made between the differ-ent forest types. In addition, background information is provided on the chief controls governing TMCF occurrence. Finally, the paper identifies the chief remaining research questions

[1] Paper dedicated to Professor Lawrence S. Hamilton for his continued inspiration and enthusiasm for the case of tropical montane cloud forest conservation.

and offers suggestions as to where and how these questions might be addressed.

Tropical montane cloud forests: definitions and occurrence

With increasing elevation on wet tropical mountains, distinct changes in forest appearance and structure occur. At first, these changes are gradual. The tall and often buttressed trees of the multi-storied lowland rain forest (main canopy height 25–45 m, with emergents up to 60 m), gradually give way to *lower montane forest*. With a mean canopy height of up to 35 m in the lower part of the montane zone and emergent trees as high as 45 m, lower montane forest can still be quite impressive. Yet, with two rather than three main canopy layers, the structure of lower montane forest is simpler than that of lowland forest. Also, the large buttresses and climbers that were so abundant in the lowland forest have all but disappeared and on the branches and stems epiphytes (orchids, ferns, bromeliads) become more numerous with increasing elevation (Whitmore, 1998).

The change from lowland to lower montane forest seems largely controlled by temperature as it is normally observed at the elevation where the average minimum temperature drops below 18^{o}C. At this threshold many lowland tree species are displaced by a floristically different assemblage of montane species (Kitayama, 1992). On large equatorial inland mountains this transition usually occurs at an altitude of 1200–1500 m but it may occur at much lower elevations on small outlying island mountains and away from the equator (see also below). As the elevation increases, the trees not only become gradually smaller but also more 'mossy' (changing from *ca.* 10% to 25-50% moss cover on the stems). There is usually a very clear change from relatively tall (15–35 m) lower montane forest to distinctly shorter-statured (2–20 m) and much more mossy (70–80% bryophytic cover) *upper montane forest* (Frahm and Gradstein, 1991). Although this time the two forest types are not separated by a distinct thermal threshold, there can be little doubt that the transition from lower to upper montane forest coincides with the level where cloud condensation becomes most persistent (Grubb and Whitmore, 1966). On large mountains in equatorial regions away from the ocean this typically occurs at elevations of 2000–3000 m but incipient and intermittent cloud formation is often observed already from *ca.* 1200 m upwards, i.e. roughly at the bottom end of the lower montane zone.

On small oceanic island mountains, however, the change from lower to upper montane-looking forest may occur at much lower altitudes (down to less than 500 m above sea level) (Van Steenis, 1972). Mosses also start to cover rocks and fallen trunks on the soil surface in the upper montane forest zone. With increasing elevation and exposure to wind-driven fog, the tree stems become increasingly crooked and gnarled, and bamboos often replace palms as dominant undergrowth species (Kappelle, 1995). The eerie impression of this tangled mass wet with fog and glistening in the morning sun has given rise to names like 'elfin' forest or 'fairy' forest to the more dwarfed forms of these upper montane forests (Stadtmüller, 1987).

A third major change in vegetation composition and structure typically occurs at the elevation where the average maximum temperature falls below 10^{o}C. Here the upper montane forest gives way to still smaller-statured (1.5–9 m) and more species-poor *subalpine forest* (or scrub) (Kitayama, 1992). This forest type is characterized not only by its low stature and gnarled appearance but also by even tinier leaves, and a comparative absence of epiphytes.

Mosses usually remain abundant, however, confirming that cloud incidence is still a paramount feature (Frahm and Gradstein, 1991). On large equatorial mountains the transition to subalpine forest is generally observed at elevations between 2800 and 3200 m. As such, this type of forest is encountered only on the highest mountains, mostly in Latin America and Papua New Guinea, where it may extend to *ca.* 3900 m (Whitmore, 1998).

It follows from the preceding descriptions that most lower montane, and all upper montane and subalpine forests, are subject to various degrees of cloud incidence. As indicated earlier, definitions, names and classification of the respective vegetation complexes are myriad, as well as overlapping and, at times, contradictory (Stadtmüller, 1987). Bruijnzeel and Hamilton (2000) proposed to distinguish the following forest types that become increasingly mossy with elevation:

(i) lower montane forest (tall forest little affected by low cloud but rich in epiphytes);
(ii) lower montane cloud forest;
(iii) upper montane cloud forest; and
(iv) subalpine cloud forest.

In doing so, the widely adopted broad definition of cloud forests as 'forests that are frequently covered in cloud or mist' (Stadtmüller, 1987; Hamilton *et al.*, 1995) is included whilst at the same time recognizing the important influence of temperature and humidity on montane forest zonation. However, a more or less 'a-zonal' cloud forest type should be added: (v) low-elevation dwarf (or 'elfin') cloud forest (see below).

The large variation in elevation at which one forest formation may replace another is caused by several factors. For example, the transition from lower to upper montane forest is mainly governed by the level of persistent cloud condensation (Grubb and Whitmore, 1966). Cloud formation, in turn, is determined by the moisture content and temperature of the atmosphere. Naturally, the more humid the air, the sooner it will condense upon being cooled during uplift. With increasing distance to the ocean the air tends to be drier. As such, it will take longer to cool to its condensation point and the associated cloud base will be higher. Likewise, for a given moisture content, the condensation point is reached more rapidly for cool air than for warm air. Thus, at greater distance from the equator, the average temp-erature, and thus the altitude at which condensation occurs, will be lower (Nullet and Juvik, 1994). Superimposed on these global atmospheric moisture and temperature gradients are the more local effects of sea surface temperatures and currents, the size of a mountain and its orientation and exposure to the prevailing winds, as well as local topographic factors (Stadtmüller, 1987). It goes almost without saying that sea surface temperatures influence the temperature of the air overhead and thus the 'starting point' for cooling. Also, where warm, humid ocean air is blown over a comparatively cold sea surface, a low-lying layer of persistent coastal fog tends to develop. Well-known examples are the fog-ridden west coast of California where tall coniferous forests thrive in an otherwise sub-humid climate (Dawson, 1998), and the coastal hills of Chile and Perú, where, under conditions approaching zero rainfall, forest groves are able to survive solely on water stripped from the fog by the trees themselves (Aravena *et al.*, 1989).

The occurrence of low-statured mossy, upper montane-looking forest at low elevations on small, isolated coastal mountains has puzzled scientists for a long time. This phenomenon is commonly referred to as the 'mass elevation' or 'telescoping' effect (Van Steenis, 1972; Whitmore, 1998). The sheer mass of large mountains exposed to intense radiation during cloudless periods is believed to raise the temperature of the overlying air, thus en-abling plants to extend their altitudinal range. Whilst this may be true for the largest mountain ranges it is not a probable explanation for mountains of intermediate size on which the effect is also observed. Instead, the contraction of vegetation zones on many small coastal mountains must be ascribed to the high humidity of the oceanic air promoting cloud formation at (very) low elevations rather than to a steeper temperature lapse rate with elevation associated with small mountains.

Further support for this comes from the observ-ation that the effect is most pronounced in areas with high rainfall and thus high atmospheric humidity (Van Steenis, 1972; Bruijnzeel *et al*., 1993). Whilst the cloud base on small islands is often observed at an elevation of 600 to 800 m, dwarf cloud forests reach their lowermost occurrence on coastal slopes exposed to both high rainfall and persistent wind-driven cloud. Examples from the equatorial zone include Mount Payung near the western tip of Java and Mount Finkol on Kosrae island (Micronesia) where dwarf forest is found as low as 400–500 m (Hommel, 1987; Merlin and Juvik, 1995). An even more extreme case comes from the island of Gau in the Fiji archipelago where the combination of high precipitation and strong winds has led to the occurrence of a wind-pruned dwarf cloud forest at an altitude of only 300–600 m above sea level (Watling and Gillison, 1995).

The previous examples illustrate the importance of site exposure. Generally, the lower limits of mossy forest of any kind (upper montane, subalpine, or dwarf cloud forest at low elevation) on drier and more protected leeward slopes lie well above those on windward slopes. In extreme cases, such as in the Colombian Andes, the difference in elevation may be as much as 600 m (Stadtmüller, 1987). Also, leeward forests tend to be better developed than their more exposed windward counterparts. In the Monteverde Cloud Forest Preserve, northern Costa Rica, the trees of 'leeward cloud forest' are 25–30 m tall *vs*. 15 –20 m in nearby floristically similar 'windward cloud forest'. Moreover, towards the exposed crests of the windward slopes the height of the vegetation decreases further to –10 m along an altitudinal gradient of only 30–50 m (Lawton and Dryer, 1980).

Although the stunted appearance of low-elevation dwarf cloud forest resembles that of the transition from high-elevation upper montane to subalpine cloud forests at first sight, the two differ in several important respects. At low elevations, the leaves are much larger and the floristic composition is very different (Grubb, 1974). Also, the degree of moss cover on the ground (but not the vegetation) is generally much less pronounced at lower altitudes (Frahm and Gradstein, 1991). Lastly, the temperatures and thus overall evaporative demand to which the forests are exposed, are much higher at lower elevations (Nullet and Juvik, 1994). The soils of upper montane and dwarf cloud forests (regardless of elevation) are typically very wet and, in extreme cases, persistently close to saturation. As a result, decomposition of organic matter is slow and topsoils become peaty and acid (Bruijn-zeel and Proctor, 1995). Recent work in the Blue Mountains of Jamaica suggests that the most stunted upper montane cloud forests suffer from toxic levels of aluminium in their soils which, in turn, affect nutrient uptake by the trees and a host of other forest ecological processes (see Hafkenscheid, 2000 for details). At the other end of the scale, the very tall (up to 50 m) montane oak forests found at high elevations (up to 3000 m) on the large inland mountain massifs of Latin America (Kappelle, 1995) and Papua New Guinea (Hyndman and Menzies, 1990) more than likely reflect a fortunate combination of slightly warmer and drier air (due to the 'mass elevation' effect, distance to the sea and topo-graphic protection) and the presence of well-drained soils in which the toxic conditions described by Hafkenscheid (2000) for the wettest localities do not easily develop.

Thus far, the focus has been on the climatic gradients and other factors governing the elevation of the cloud *base*. Another climatological phenomenon, which influences the vertical temperature profile of the air and the *top level* of cloud formation, is the so-called 'trade wind inversion'. As part of a large-scale atmospheric circulation pattern (the Hadley cell), heated air rises to great elevation in the equatorial zone, flowing poleward and eastward at upper atmospheric levels and descending in a broad belt in the outer tropics and subtropics from where it returns to the equator. This subsidence reaches its maximum expression at the oceanic subtropical high pressure centres and along the eastern margins of the oceanic basins. As the air descends and warms up again, it forms a temperature inversion that separates the moist layer of surface air (that is being cooled while rising) from the drier descending air above. The inversion forms a tilted three-dimensional surface, generally rising towards the equator and from East to West across the oceans. Over the Pacific ocean, the inversion is found at only a few hundred metres above sea level off the coast of southern California, rising to about 2000 m near Hawai'i and dissipating in the equatorial western Pacific (Nullet and Juvik, 1994). As such, the low elevations at which the inversion occurs on mountains situated away from the equator may well be another reason as to why the vegetation zonation tends to become compressed on smaller mountains (Stadtmüller, 1987). The consequences of the trade wind inversion for the occurrence of the upper boundary of montane cloud forest are profound. For instance, at 1900–2000 m on the extremely wet windward slopes on islands in the Hawai'ian archipelago, the montane cloud forest suddenly gives way to dry subalpine scrub because the clouds (which generally deliver more than 6000 mm of rain per year below the inversion layer) are prevented from moving upward by the presence of the temperature inversion (Kitayama and Müller-Dombois, 1992). One of the best-known examples of the trade wind inversion and its effect on vegetation zonation comes from the Canary Islands. Situated between 27 and 29 degrees North, a daily 'sea of cloud' develops between 750 m and 1500 m which sustains evergreen Canarian laurel forests in an otherwise rather arid environment (Ohsawa *et al*., 1999).

As a result of the various climatic and topographic gradients described in the previous paragraphs, concentrations of montane cloud forests in the tropical and subtropical parts of the world occur approximately as shown on the generalized map below. Further details on TMCF distribution can be found in Hamilton *et al.* (1995) whereas a draft directory of TMCF sites has been published by Aldrich *et al*. (1997).

HYDROLOGICAL PROCESSES IN TROPICAL MONTANE CLOUD FORESTS

Rainfall and cloud interception

One of the most important aspects in which cloud forests differ from montane forests that are not affected much by fog and low cloud concerns the deposition of cloud water onto the vegetation. Whilst the hydrological and ecological importance of this extra input of moisture is widely recognized, its quantification is notoriously difficult (Kerfoot, 1968) (2). Two approaches are usually followed: (i) the use of 'fog' gauges, of which there are many types; and (ii) a comparison of amounts of canopy drip as measured inside the forest with amounts of rainfall measured in the open. Both methods are fraught with difficulties of measurement and interpretation of the results. Therefore, before presenting recent research results obtained with either method, the chief limitations of the two approaches are discussed below.

Fog gauges. The inherent problem of fog gauges is that no gauge, whether of the 'wire mesh cylinder' (Grünow) type (Russell, 1984) (28), the 'wire harp' type (Goodman, 1977) (29), the 'louvered-screen' type (Juvik and Ekern, 1978) (30), or the more recently proposed poly-propylene 'standard' fog collector of Schemenauer and Cereceda (1994) (31), can mimic the complexities of a live forest canopy. Also, each forest represents a more or less unique situation that defies standardization. Therefore, fog gauges can only be used as comparative instruments (e.g. for site characterization) and, provided they are protected against direct rainfall and equipped with a recording mechanism, for the evaluation of the timing and frequ-ency of occurrence of fog. Where concurrent information on wind speed is available as well, the liquid water content of the fog may also be evaluated (Padilla et al., 1996) (32). However, the catch of a fog gauge is highly dependent on its position with respect to the ground and nearby obstacles. It has been recommended, therefore, to install gauges at a 'standard' height of 2 m (Schemenauer and Cereceda, 1994) (31) or 3 m (Juvik and Ekern, 1978) (30). Often, however, studies using fog gauges in the tropics have not specified gauge height or position, rendering interpretation of the results more difficult (Bruijnzeel and Proctor, 1995) (1).

A major problem of interpretation associated with wire mesh cylindrical or large screen collectors concerns the distinction between cloud water and wind-driven rain. Hafkenscheid (2000) (23) obtained a large discrepancy in apparent fog interception totals (365 vs. 670 mm/year) using Grünow-type gauges above two montane forest canopies in Jamaica spaced only 150 m apart (see also the discussion of recent results below). Adding a protective cover may eliminate some but not all wind-driven rain in particularly exposed situations (Juvik and Nullet, 1995a) (33). For such conditions Daube et al. (1987) (34) proposed the use of a wire harp collector enclosed in an opaque rain-proof fibreglass box in which air flow is restricted by two baffles. The front baffle causes the passing air to accelerate and project heavy rain drops against the rear baffle where they are drained away. The lighter fog particles continue on and impact against the collecting harp. This type of fog collector has been used successfully above a fog-ridden lower montane forest in southern Queensland, Australia by Hutley et al. (1997).

There has been considerable debate as to what is the most suitable type of fog gauge under the windy and rainy conditions that prevail on many tropical mountains (Juvik and Nullet, 1995a; Schemenauer and Cereceda, 1995). Metal louvered screen collectors have been shown to drain their catch (both rain and cloud water) more efficiently than wire mesh screens (Juvik and Ekern, 1978), whereas cylindrical designs are considered superior to two-

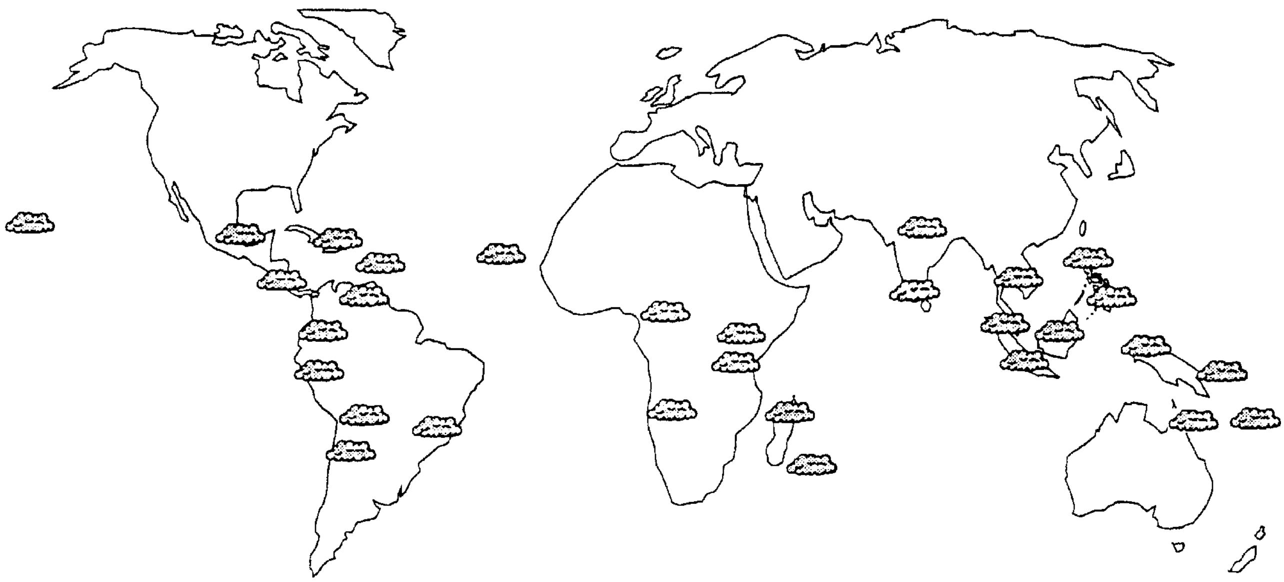


Figure 1 Generalized occurrence of tropical montane cloud forests (adapted from Hamilton *et al.*, 1995).

dimensional screens in terms of presenting the same silhouette and catchment surface configuration regardless of wind direction (Juvik and Nullet, 1995a). On the other hand, the catching surface of cylindrical gauges is generally much smaller than that of a large screen such as that proposed by Schemenauer an Cereceda (1994). The latter may thus generate measurable deposition rates when fog liquid water contents are low or winds are light (Schemenauer and Cereceda, 1995). There is a need to test the relative performance of the various gauge types under typical cloud forest conditions. One such experiment, which is to involve all of the gauge types listed above, will be initiated later this year on an exposed ridge carrying low-elevation dwarf cloud forest in the Luquillo Mountains, eastern Puerto Rico (18ºN, i.e. in the maritime trade wind belt; Vugts and Bruijnzeel, 1999). Similar tests are needed under equatorial and more inland conditions where wind speeds are generally lighter and fog liquid water contents are likely to differ from those at coastal locations.

Measurement of net precipitation. Subtracting amounts of throughfall plus stemflow (net rainfall) as measured below the forest canopy from gross rainfall measured above the forest or in a nearby clearing gives the amount of precipitation intercepted by the canopy and evaporated back to the atmosphere during and shortly after the event. This process is usually referred to as rainfall interception (*Ei*) or wet canopy evaporation and implies a *net loss of water* to the forest. Where fog or cloud only is present, a similar process of cloud interception may be defined. However, because neither the actual amounts of cloud impaction nor those evaporated from the wetted vegetation are easily quantifiable, a more practical approach is to measure net precipitation and equate the amount to *net* cloud impaction. As such, the term 'cloud interception' implies a *net gain of water* to the ecosystem. In the more complex case of rainfall plus cloud incidence it is again most practical to follow the same approach and quantify the net overall effect of the various processes by simply measuring net precip-itation. For a proper quantification of net precipitation amounts large numbers of gauges are needed to account for the high spatial variability of rain forest canopies. In addition, it is advisable to apply a 'roving' gauge technique that includes so-called 'drip' points (where rain or fog drip becomes concentrated because of peculiarities in the configuration of the trees) in a representative manner. Although amounts of throughfall sampled in this way in lowland rain forest have been shown to be significantly higher than when a fixed gauge network is used (Lloyd and Marques, 1988), the roving gauge technique has been little used so far in TMCF (Bruijnzeel and Proctor, 1995) and published results may therefore represent underestimates (cf. Hafkenscheid *et al*., 2000).

The classic approach to evaluate contributions by cloud water to forests has been to compare amounts of net and gross precipitation for events with and without fog (Kashiyama, 1956; Harr, 1982). However, given the high spatial variability in net precipitation already referred to, this method only works well if cloud water contributions are substantial or if the confidence intervals for net precipitation estimates are narrow. For example, both Hafken-scheid (2000) and Schellekens *et al*. (1998) reported that regression equations linking gross and net precipitation in TMCF in Jamaica and Puerto Rico, respectively, did not differ significantly for events with and without fog, thus rendering the approach meaningless from the statistical point of view in these particular cases.

Alternative approaches. In view of the above-mentioned difficulties with the more traditional approaches various alternative methods have been advanced but these too have met with variable success. Exploiting the fact that concentrations of sodium and chloride in cloud water are generally much higher than in rainfall (Asbury *et al.*, 1994; Clark *et al.*, 1998), Hafkenscheid *et al.* (1998) attempted to evaluate the contribution of cloud water to net precipitation in two upper montane cloud forests in Jamaica of varying exposure using a *sodium mass balance approach*. Whilst a reasonable estimate was obtained for the most exposed forest, an unexpectedly high cloud water input was derived for the less exposed forest, suggesting that application of the chemical mass balance approach may be less than straightforward in complex mountainous terrain. A similar approach makes use of the difference in isotopic composition of rain and fog water (fog being enriched in the heavier isotopes ^{2}H and ^{18}O relative to rainfall in the same region; Ingraham and Matthews, 1988; 1990). Dawson (1998) applied this *isotope mass balance technique* successfully to establish the contribution of fog water to a redwood forest in California. Contrasts in isotopic composition of rain and fog in eastern Puerto Rico, however, were within the analytical error range (L.A. Bruijnzeel and F.N. Scatena, unpublished data).

A more experimental process-based approach has been followed recently by M. Mulligan and A. Jarvis (*pers. comm*, February 2000) who *monitored the changes in weight of a known mass of living mossy epiphytes* suspended below the canopy of a TMCF in Colombia. Their alternative 'cloud trap' was protected against rainfall and extended over the first 5 m above the forest floor in near-stagnant air. No fog drip was recorded from this device, suggesting that most of the intercepted cloud water was evaporated again. A different result might have been obtained if the interceptor had been allowed to be wetted by throughfall or if it had been placed at a more exposed location. Finally, considerable progress has been made during the last decade in the estimation of cloud water deposition in complex terrain using *physically-based models* (Joslin *et al*., 1990; Müller, 1991; Müller *et al.*, 1991; Walmsley *et al.*, 1996, 1999). Such models include assumptions about the shape and spacing of the trees, their fog water collection efficiency, the frequency of fog, and the vertical rate of change of the liquid water content within ground-based clouds. Topographical data are used as a forcing function in wind flow models to derive a spatially explicit representation of the wind field. Although the application of such advanced models has given promising results for the estimation of cloud water deposition onto montane coniferous forest in Canada (Walmsley *et al.*, 1996), virtually none of the required input data is presently available for TMCF environments. Clearly, the application of physically-based models to remote tropical mount-ains remains a major challenge for some years to come. Therefore, a 'hybrid' approach in which (some) physical modelling is combined with empirically-derived estimates of fog characteristics, such as those employed successfully to evaluate fog water contributions to catchment water budgets in the Maritime Provinces of Canada by Yin and Arp (1994), may constitute a suitable alternative that is worth exploring in a tropical montane context.

Results of post-1993 rainfall and cloud interception studies in TMCF. Measurements made with various types of fog gauges in areas with TMCF as reviewed by Bruijnzeel and Proctor (1995) suggested typical cloud water deposition rates of 1–2 mm/day (range 0.2–4.0 mm day^{-1}), with a tendency towards lower values during the dry season and with increasing distance to the ocean. Several studies employing fog gauges or measuring net precipitation in TMCF environments have been published since 1993, the results of which are summarized in Tables 1 (cloud interception data) and 2 (overall interception data).

The new results for cloud water deposition largely fall within the previously established range. A minimum of 0.27 mm day^{-1} has been reported for the montane zone on Hawai'i above the temperature inversion (Juvik and Nullet, 1995b) whereas a maximum of 6.3 mm day^{-1} (or 2300 mm year^{-1}!) has been claimed for an exposed site at 1100 m on the Pacific-Caribbean water divide as part of a transect study in western Panama (Cavelier *et al.*, 1996) .

However, there are strong indications that the latter figure is unrealistically high. First, it is based on measurements with uncovered Grünow-type fog gauges, the poor performance of which has been discussed already. Secondly, the rainfall at this windy site is reported as only 1495 mm year^{-1} whereas annual totals at similar elevations on either side of the main divide were consistently above 3600 mm (Cavelier *et a*l., 1996), suggesting severe underestimation of the rainfall and thus overestimation of the fog input at this site. Finally, Cavelier *et al.* (1997) obtained a very low throughfall fraction (63% or *ca.* 2200 mm year^{-1}) for lower montane forest at a similar elevation (1200 m) in the same area (cf. Table 2). Adding the 2300 mm of allegedly intercepted cloud water to the 3500 mm of rain received annually by this forest would suggest a total precipitation input of *ca.* 5800 mm year^{-1}, of which *ca.* 3600 mm (5800 minus 2200 mm of throughfall) would then be required to have been lost through evaporation

Table 1 Post-1993 studies of cloud water interception (*CW*) in tropical montane environments. Figures represent annual averages unless indicated otherwise

Location	Elevation (m)	Forest Type	MAP (mm)	*CW* (mm/d)	(%)+	Remarks
Australia[1]	1000	LMCF	1350	0.94	35	*CW* equal to 'excess' *TF*
Costa Rica[2]	1500	LMCF	2520	2.43	28	Artificial foliage collector 1410 cm^2 at 17 m height
Costa Rica[3]	1500	LMCF	3300	0.53	6	*CW* equal to 'excess' *TF*#
		fragment LMCF		1.25	14	
		secondary LMCF		0.70	8	
Guatemala[4]	2400	UMCF	2500	0.72	13	Idem
	2750	UMCF		1.65d	281d	Dry season (Jan-March)
Guatemala[5]	2550	UMCF	2500	0.64	8	Idem
				1.30d	3d	Dry season (Nov-March)
Hawai'i[6]	2600	SA(C)F	<500	0.61·	38	Louvered fog gauge (3m)
Honduras[4]	900-1400	LMCF	4200	0.3d	6d	*CW* equal to 'excess' *TF*; Dry season (Jan-May)
	1500	LMCF	2500	0.37d	12d	Dry season (Jan-March)
Jamaica[7]	1850	UMCF	2850	1.84	22	Grunow fog gauge above forest canopy
	1825			1.0	12	
	1850			0.53	6	Covered gauge in clearing
	1810			0.53	6	Net precipitation method*
	1825			0.15	2	Idem*
Panama[8]	1100	LMF	>3600¨	6.30¨	154	Grunow fog gauges
	1250	LMF	5700	1.23	8	
Puerto Rico[9]	1015	ECF	4500	1.33	7	Net precipitation method*
Venezuela[10]	2300	LMCF	3000	0.29	7	'Standard' collector (5m); 7 months (rather dry)

[1]Hutley *et al.* (1997); [2]Clark *et al.* (1998); [3]Fallas (1996); [4]Brown *et al.* (1996); [5]Holder (1998) ; [6]Juvik and Nullet (1995b); [7]Hafkenscheid (2000); [8]Cavelier *et al.* (1996); [9]Schellekens *et al.* (1998) (41); [10]Ataroff (1998); MAP = mean annual precipitation; LM(C)F = lower montane (cloud) forest; UMCF = upper montane cloud forest; SA(C)F = (dry) subalpine (cloud) forest; ECF = low-elevation dwarf cloud forest; *TF* = throughfall; +expressed as percentage of associated rainfall; #adding the 320 mm/year of rainfall intercepted by a nearby LMF that is only seasonally affected by cloud (Fallas, 1996), would raise these values to: 1.40, 2.13 and 1.58 mm/day, and 15%, 23% and 17%, respectively; ·expressed as mm/event (0.27 mm/calendar day); *minimum value due to exclusion of fog deposition during and shortly after rainfall (cf. Hafkenscheid *et al.* 2000); ¨see text for explanation.

from the wet canopy ('rainfall interception'). As will be shown below, reported *total* evaporative losses (i.e. both wet and dry canopy evaporation) from lower montane rain forests do not exceed 1380 mm year^{-1}. Nevertheless, although the claim of excessively large cloud water inputs in western Panama by Cavelier *et al*. (1996) must thus be ascribed to instrumental error and misinterpretation of the data, similarly large (but short-term) additions of cloud water (up to 5 mm day^{-1}) have been observed occasionally on rainless days at the highest elevations in the Sierra de las Minas, Guatemala (Brown *et al*., 1996; Holder, 1998) (Figure 2c).

Typical ranges of net precipitation determined for the respective types of montane forests as reviewed by Bruijnzeel and Proctor (1995) were:

(i) 67–81% (average 75%; *n* = 9) for lower montane forest not affected much by cloud;
(ii) 80 – 101% (average 88%; *n* =4) for lower montane cloud forest; and
(iii) 81 – 179% (average 112%; *n* = 10) for upper montane and low-elevation dwarf cloud forests[1] .

The cited averages for the respective forest types do not change very much after incorp-orating the results of post-1993 studies (Table 2). The extent of the change, however, depends on the forest type to which each 'new' study is assigned and this presents difficulties in several cases. For example, throughfall fractions obtained for 'leeward' lower montane cloud forests in Costa Rica and, especially, Venezuela are so low (65% and 54%, respectively; Table 2) that these forests effectively behave like LMRF not affected by cloud. This is partly a result of the protected location of the two sites but possibly also reflects their high epiphyte

[1] It should be noted that the examples from Honduras and the Philippines listed as LMF/MCF in Table 2 of Bruijnzeel and Proctor (1) have been classified as upper montane cloud forests in the presently adopted system.

Table 2 Post-1993 studies of throughfall (*TF*), stemflow (*SF*) and *apparent* rainfall interception (*Ei*) fractions in tropical montane environments

Location	*Elevation (m)*	*Forest Type*	*TF*	*SF (% of P)*	*Ei*	*Remarks*
Australia[1]	1000	LMCF	90	2	8	25 fixed troughs; 10-21 day sampling interval
Costa Rica[2]	1500	LMCF	65	-	35	20 fixed standard gauges; 1-3 day sampling interval
Costa Rica[3]	1500	LM(C)F	90/131d*	-	10	10 fixed troughs; daily
		LMCF	06/175d	-	-6	
	remnant	LMCF	114/174d	-	-14	4 fixed troughs, daily
	secondary	LMCF	108/135d	-	-8	
Guatemala[4]	2200	LM(C)F	81	<1	18	3-6 fixed gauges with
	2400	L/UMCF	113	1-2	-15	large (52 cm dia) funnels;
	2750	UMCF	281d	2	-183	4-7 day intervals
Guatemala[5]	2550	UMCF	108	-	-8	58 fixed gauges, weekly;
			100w	-	(0)	Rainy season (April-Oct)
				153d	-	-53 Dry season (Nov-March)
Hawai'i[6]	2600	SA(C)F	75	-	25	2 fixed recording troughs;
Honduras[4]	900-1400	LMCF	95	-	5	3-6 fixed large diameter
	idem		106d#	-	-6	gauges; 4-7 day intervals
	1500	LMCF	111d+	-	-11	
Jamaica[7]	1810	UMCF	73	12	14	1 recording trough + 12
	1825	UMCF	60·	18	22	roving gauges (3-4 days)
Panama[8]	1200	LMRF	63	<1	37	50 fixed troughs; daily
Puerto Rico[9]	1015	ECF	89	(5)¨	6	3 recording gutters + 10 roving gauges (1-3 days)
Venezuela[10]	2300	LMCF	55	<<1	45	6 fixed trough gauges; weekly sampling

[8]Cavelier et al. (1997) (59); other studies as listed in Table 1.
LM(C)F = lower montane (cloud) forest; UMCF = upper montane cloud forest; SA(C)F = (dry) subalpine forest; LMRF = lower montane rain forest not affected significantly by cloud; ECF = low-elevation dwarf cloud forest; *Ei = P – (TF + SF)*, apparent interception, including ungauged contributions by cloud water; *dry season: December-April; #idem, January-May; +idem, January-March; ·underestimate due to insufficient number of gauges (see Hafkenscheid et al., this volume for details); ¨based on data from Weaver (1972) (105).

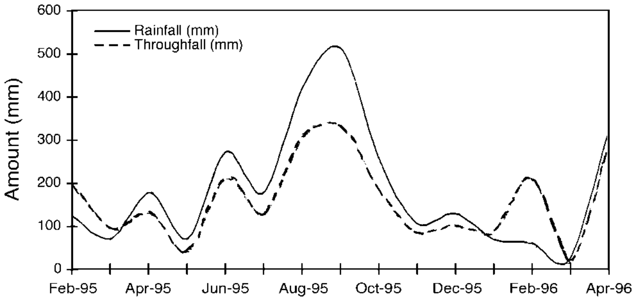


Figure 2a Seasonal rainfall and throughfall patterns at 2200 m elevation in the lower montane cloud forest zone, Sierra de las Minas, Guatemala (adapted from Brown *et al.*, 1996).

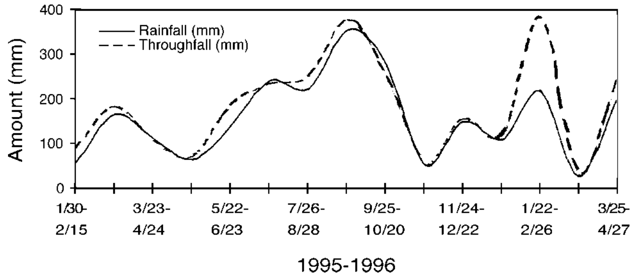


Figure 2b: Seasonal rainfall and throughfall patterns at 2400 m elevation in the transition zone from lower to upper montane cloud forest , Sierra de las Minas, Guatemala (adapted from Brown *et al.*, 1996)

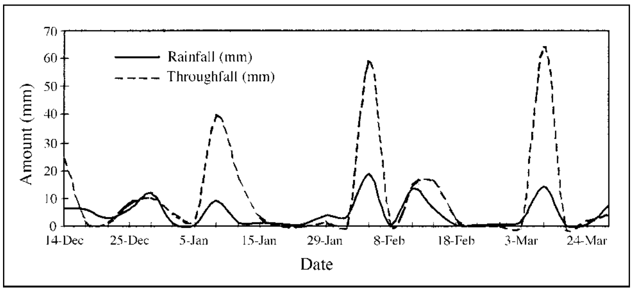


Figure 2c Rainfall and throughfall patterns during the dry season at 2750 m elevation in the upper montane cloud forest zone, Sierra de las Minas, Guatemala (adapted from Brown *et al.*, 1996)

loading (Clark *et al.*, 1998; Ataroff, 1998; cf. Cavelier *et al.*, 1997). Epiphytes, especially 'tank' bromeliads and moss 'balls', are known to have very high water storage capacities and to release their water slowly (Pócs, 1980; Nadkarni, 1984; Veneklaas *et al.*, 1990; Richardson *et al.*, 2000; Mulligan and Jarvis, 2000). The remaining new studies in (undisturbed) lower montane cloud forests listed in Table 2 ($n = 4$; i.e. leaving the two transitional Guatemalan forests at 2200 and 2400 m aside as they rather resemble LMRF and UMCF, respectively) produced results that are in agreement with previously established values for this type of forest. Adding these new results to the existing dataset for LMCF raised the average net precipitation fraction from 88% to 92% ($n = 8$). Incorporating the 'anomalous' results for Monteverde (study no. 2) and Venezuela (study no. 10) as well would not only lower the 'old' average value from 88% to 85% but particularly extend the bottom end of the reported range (from 80% to 55%). Alternatively, assigning these two studies plus the Guatemalan forest at 2200 m (study no. 4) to the class of LMRF not affected much by low cloud would bring the associated average value down from 75% to 72%.

Adding the new results obtained for upper montane and elfin cloud forests (Guatemala, Jamaica, Puerto Rico) also lowers the associated average value of net precipitation slightly (from 112% to 109%). However, this is entirely due to the inclusion of the very low figure obtained for a forest at 1810 m in Jamaica (study no. 7 in Table 2; the results for a nearby forest at 1825 m were excluded because they were considered underestimates). The very high stemflow fractions obtained for the two Jamaican forests are noteworthy and ascribed to the presence of multiple-stemmed and crooked trees (Hafkenscheid *et al.*, this volume).

Given the rapid conversion of TMCF to other land uses (mostly pasture; Bruijnzeel and Hamilton, 2000), the finding of enhanced net precipitation in small primary and secondary forest fragments compared to nearby tall undisturbed forest in Costa Rica (Fallas, this volume; study no. 3 in Table 2) is of great interest. More work is urgently needed to confirm these preliminary (because based on very few, fixed gauges) results.

Summarizing, the extended dataset suggests a steady increase in average net precipitation fractions from lower montane forest, through lower montane cloud forest to upper montane and low-elevation dwarf cloud forests (Table 2). However, more work is needed to elucidate the precise role of epiphytes in the interception process, both for rainfall and cloud water, as evidenced by the very low throughfall fractions obtained for some cloud forests despite considerable inputs of cloud water (e.g. nos. 2 and 10 in Tables 1 and 2). Future work could profitably combine several of the approaches outlined in the previous sections, notably the use of isotopes, electronic field monitoring of epiphytic water content, and modelling.

Most of the data collated in Tables 1 and 2 pertain to annual averages. However, in many areas (e.g. Central America) cloud interception is a highly seasonal process which assumes its greatest importance during the dry season. As such, a cloud forest with an overall net precip-itation figure well below 100% may still experience a much higher value during particular times of the year. A case in point is the Sierra de las Minas, Guatemala, where in the lower montane cloud forest zone at 2200 m average throughfall is 81% (study no. 4 in Table 2). At the height of the rainy season (August, September) relative throughfall drops to about 65% but during the dry season (January – March) it exceeds incident rainfall (Figure 2a). At 2400 m (transition zone to upper montane cloud forest), cloud interception is important year-round but again reaches its peak during the dry season (Figure 2b; cf. the seasonal contrast observed by study no. 5 in the same area; Tables 1 and 2). Cloud interception is still more pronounced at 2750 m (upper montane cloud forest zone). In the period January–March 1996, throughfall exceeded rainfall by 147 mm (181%; study no. 4 in Table 2), with the excess reaching maximum values of as much as 40–50 mm over 3–4 day periods (Figure 2c). Such findings contradict the suggestion by

Vogelmann (1973) that fog incidence in eastern Mexico decreased with elevation in the cloud belt and during the dry season compared to the rainy season. However, Vogelmann's contention was based on measurements made with cylindrical wire-mesh fog gauges, the limitations of which have been stressed already. It is more than likely therefore that these early measurements largely reflect effects of wind-driven rain, notably during the rainy season (cf. Cavelier *et al.*, 1996). More importantly, the findings from Guatemala underline the importance of TMCF for sustained dry season flows (cf. Zadroga, 1981). We will come back to this important point in the section on TMCF and water yield.

There is a need for additional studies like that of Brown *et al.* (1996) to document the changes in net precipitation with elevation, slope aspect and season in different regions.

Transpiration and total water use

In their review of pre-1993 work on TMCF water use (both total evapotranspiration, *ET* and transpiration, *Et*), Bruijnzeel and Proctor (1995) had to draw mostly on catchment and site water balance studies. In addition, in the absence of direct estimates of *Et*, only approximate values — obtained by subtracting apparent interception totals *Ei* from *ET* — could be presented. Apart from the general limitations of the water budget technique for the evaluation of *ET* (see Bruijnzeel (1990) for a detailed discussion in a tropical context) there is the added complication in the case of TMCF that unmeasured inputs by cloud interception lead to correspondingly lower values of *ET*. As such, the estimates of *ET* for cloud-affected forests cited below represent *apparent* values only.

The pre-1993 dataset on *ET* for tropical montane forests (Bruijnzeel, 1990; Bruijnzeel and Proctor, 1995) can be summarized as follows:

(i) equatorial lower montane forest with negligible fog incidence: 1155–1380 mm year^{-1} (average 1265 mm year^{-1}; $n = 7$);
(ii) lower montane cloud forest with moderate fog incidence: 980 mm/year ($n = 1$); upper montane cloud forest with high fog incidence: 310–390 mm year^{-1}; $n = 3$). Corresponding 'guess-timates' for *Et* are: (i) 510–830 mm year^{-1}; (ii) 675 mm year^{-1}; and
(iii) 250–285 mm year^{-1}, respectively (see Bruijnzeel and Proctor (1995) for details).

Whilst information on total water use (*ET*) of cloud forests of any type is scarce, therefore, the data for upper montane cloud forest are at least consistent. Conversely, there is considerable uncertainty about the water use of lower montane cloud forest. The only estimate available (the cited 980 mm year^{-1}) concerns a tall forest at 2300 m elevation in Venezuela which is based on energy budget calculations that included numerous assumptions (Steinhardt, 1979). Bruijnzeel *et al*. (1993) derived an *ET* of 695 mm year^{-1} for a 'stunted lower montane forest' at 870 m on a coastal mountain in East Malaysia which in reality may rather represent a transition to (low-elevation) upper montane cloud forest on the basis of its mossiness and low stature. However, the latter estimate was based on short-term site water budget measurements conducted during a particularly dry period. Assuming cloud incidence, and thus the duration of canopy wetting and halted transpiration (Rutter, 1967) during this period were all less than normal, the extrapolated annual figure for *Et* may well be too high (Bruijnzeel *et al*., 1993).

Despite the need for additional information on TMCF water use signalled by Bruijnzeel and Proctor (1995), comparatively little new evidence has become available since 1993. The results of four recent studies in three different types of cloud forest are summarized in Table 3. Inspection of Table 3 shows that all new estimates are considerably higher than the ones derived previously for the respective forest types. At 1260 mm year^{-1}, *ET* of a tall lower montane forest subject to 'frequent, low intensity rainfall associated with low cloud' in Queensland, Australia is very close to the average value of *ET* for lower montane forests *not* affected by fog and low cloud cited earlier (1265 mm year^{-1}). Similarly, *Et* for this forest (845 mm year^{-1}) approximates the maximum values inferred by Bruijnzeel (1990) for non-cloud forests. However, the investigators stressed that their evaporation estimates should be seen as maximum values because the observations concerned a small forest plot dominated by a single emergent tree. If a larger plot had been monitored, which included different species, openings in the canopy or individuals with less exposed crowns, the result might well have been lower (Hutley *et al.*, 1997). Likewise, at 1050 and 890 mm year^{-1}, the estimates of *ET* for two upper montane cloud forests of contrasting stature in the Blue Mountains of Jamaica (Hafkenscheid et al., this volume) are much closer to the single value reported earlier for tall *lower* montane cloud forest (980 mm year^{-1}; Steinhardt, 1979) than for upper montane cloud forests proper (310–390 mm year^{-1}). Although the *Et* values derived for the Jamaican forests may represent overestimates because of the shortcomings of the micro-meteorological technique used by this particular study, they were confirmed by soil water depletion patterns (see Hafkenscheid *et al.* (this volume) for details). Also, the taller of the two forests was relatively sheltered from fog incidence and this may have caused the forest to behave more like lower montane cloud forest. However, this would not explain the similarly high value inferred for the adjacent, more exposed ridgetop forest. Further work is needed. Finally, two very contrasting estimates (1145 *vs.* 435 mm year^{-1}) have been reported for the *ET* of low-elevation dwarf cloud forest in Puerto Rico (Garcia-Martino *et al*., 1996; Holwerda, 1997; Schellekens *et al*., 1998). The highest of these estimates must be considered suspect for two reasons. First, it is based on the subtraction of an average runoff figure from an average rainfall figure (though corrected for cloud water input), both of which were estimated from regressions linking rainfall/runoff to elevation (Garcia-Martino *et al*., 1996)). Secondly, it is much higher than the value established by Holwerda (1997) for the reference open-water evaporation total for the dwarf forest zone (670 mm year^{-1}). It is probable, therefore, that this overestimation of *ET* reflects catchment leakage problems (cf. Bruijnzeel, 1990), or unjustified extrapolation of the regression equations. On the other hand, the lower of the two estimates is also problematic (again overestimated) for the same reasons as indicated for the Jamaican study (cf. Hafkenscheid *et al*., this volume).

Despite these recent additions to the literature on TMCF water use, it must be concluded that our knowledge remains fragmentary and at times contradictory. Further work is

Table 3 Post-1993 water budget studies in tropical montane cloud forest environments

Location	Elevation m)	Forest type	*MAP*	*ET* (mm/year)	*Et*
Australia[1a]	1000	LM(C)F	1350	1260	845
Jamaica[2b]	1810 1825	UMCF[+] UMCF[*]	2850	1050 890[#]	620 510
Puerto Rico[3c]	1000	ECF	4450	1145	-
Puerto Rico[4,5d]	1015	ECF	4450	435	170

[1]Hutley et al. (1997) (35); [2]Hafkenscheid et al., this volume; [3]Garcia-Martino et al. (1996) (69); [4]Holwerda (1997) (70); [5]Schellekens et al. (1998) (41); MAP = mean annual precipitation; LMCF = lower montane cloud forest; UMCF = upper montane cloud forest; ECF = low-elevation dwarf cloud forest;
[a]*Et* evaluated from soil water budget (net precipitation vs. change in soil water storage); *ET* = *Ei* + *Et*;
[b]*Et* evaluated from micro-meteorological measurements above nearby secondary forest; scaling up to forest plots according to relative values of leaf area index; values must be considered approximate; *ET* = *Et* + *Ei;*
[c]*ET* evaluated as difference between average rainfall (with 10% cloud water added) and runoff, both of which in turn estimated from regression equations against elevation;
[d]*Et* via micro-meteorological technique and probably overestimated; *ET* = *Et* + *Ei*, with *Ei* = 6%;
[+]relatively tall-statured forest;
[*]stunted ridge top forest;
[#]value lowered by 300 mm by the present writer to account for underestimation of throughfall and corresponding overestimation of *Ei* (see Hafkenscheid et al. (this volume) for details);

urgently needed (see also the next section). In theory, future studies could make use of a variety of plant physiological techniques (cf. Dawson, 1998; Smith and Allen, 1996; Wulschleger *et al.*, 1998). A recent study that employed sapflow gauges to study transpiration in montane cloud forest in Hawai'í is that reported by Santiago *et al.* (2000). Their measurements demonstrated a clear dependence of (maximum) instantaneous transpiration rates on tree leaf surface areas which, in turn, were governed by site drainage conditions. Stand LAI (leaf area index), and therefore *Et*, was much lower on waterlogged, level sites compared to better drained, sloping sites (Figure 3). However, transpiration rates were often too low for monitoring by the sapflow method. Similar problems were encountered in Jamaican cloud forest by Hafkenscheid *et al.* (this volume). It would seem, therefore, that there may be scope for alternative approaches, such as the use of stable isotopes (Dawson, 1998).

Tropical montane cloud forests and water yield

Due to the combination of added moisture inputs from cloud water interception (Tables 1 and 2) and relatively low water use (Table 3), water yields for a given amount of rainfall from cloud forested headwater areas tend to be higher than streamflow volumes emanating from montane forests not affected by fog and low cloud. Similarly, flows from cloud forest areas tend to be more stable during extended periods of low rainfall. Therefore, fears have been expressed that the conversion of TMCF to other land uses could result in significant declines in overall and dry season flows (Zadroga, 1981; Brown *et al.*, 1996).

The original extent of TMCF worldwide was given as about 50 million ha (Persson, 1974). Although this estimate was probably somewhat higher than reality (Hamilton, 1995b) and no accurate information is available as to how much might now remain, there can be little doubt that cloud forests are disappearing rapidly. In Central America and the Caribbean, LaBastille and Pool (1978) considered as early as the 1970s that cloud forests were declining faster than any other forest type. Similarly, it has been estimated that some 90% of the cloud forests of the northern Andes of Colombia has been lost, mostly to pastures and agricultural fields (Doumenge *et al.*, 1995). On a pan-tropical scale, data compiled by FAO for the period 1981–1990 indicate that annual forest loss in tropical highlands and mountains was 1.1%, which is higher than for any other tropical forest biome, including the much more publicized decline of lowland rain forests (Singh, 1994). The causes of cloud forest disappearance and degradation are myriad but worldwide, the greatest loss comes from its conversion to grazing land, especially in seasonally dry climates. Other,

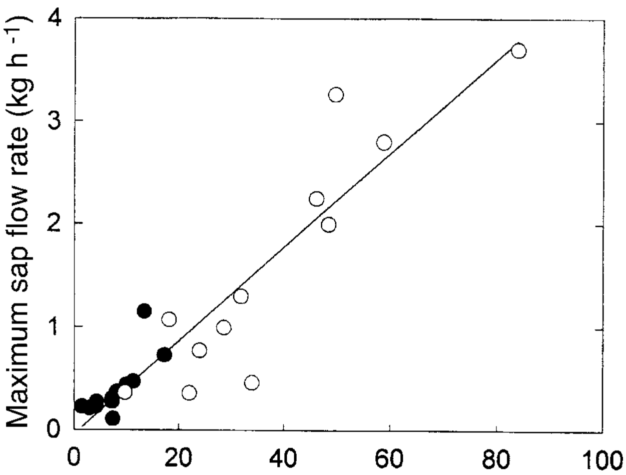


Figure 3 Relationship between maximum sapflow rate and total leaf area from level, waterlogged sites (closed circles) and from sloped, better drained sites (open circles) in TMCF in Hawai'i (after Santiago *et al.*, 2000) (reproduced with permission).

regionally important causes include: conversion to temperate vegetable cropping and harvesting of wood for charcoal production. Timber harvesting, mining, unsustainable harvesting levels of non-wood products (e.g. orchids and bromeliads), recreation and eco-tourism, introduction of alien species, and the establishment of an ever increasing number of telecommunication installations on cloud forested mountain tops (Doumenge *et al.*, 1995; Hamilton, 1995b; Bruijnzeel and Hamilton, 2000). Finally, as discussed more fully below, there is increasing evidence that TMCFs are also threatened by global warming.

Where tropical forests of any kind are replaced by annual cropping or grazing there are bound to be profound changes in the area's hydrology (Bruijnzeel, 1990). The beneficial effects on soil aggregate stability and water intake capacity afforded by the high organic matter content and abundant faunal activity of forest soils may linger for a year or two after clearing. However, exposure of the soil surface to the elements generally leads to a rapid decline thereafter, particularly if fire was used during the clearing operation (Lal, 1987). An additional aspect in densely populated agricultural steeplands is that considerable areas may become permanently occupied by compacted surfaces, such as houses, yards, trails and roads (Ziegler and Giambelluca, 1997). In areas with heavy grazing pressure, soil infiltration capacities suffer further from compaction by trampling cattle (Gilmour *et al.*, 1987). As a result, conversion of forest to annual cropping or grazing is almost inevitably followed by increases in amounts of surface runoff (Bruijnzeel, 1990).

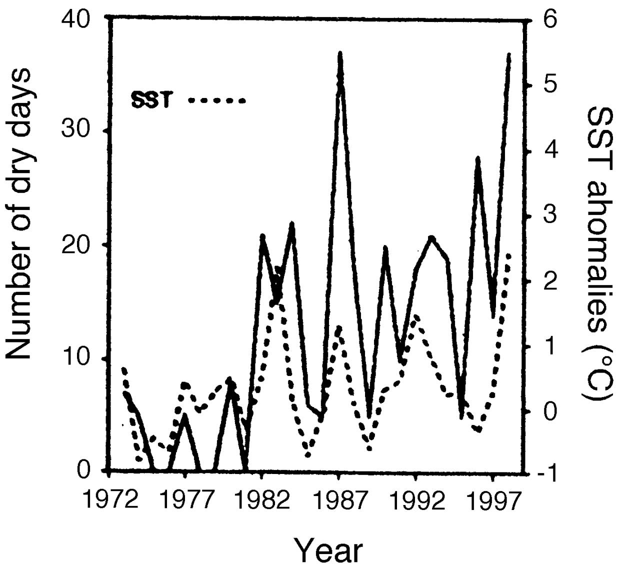
A second consequence of forest clearing relates to the associated changes in net rainfall: no longer are there trees to intercept rainfall or fog. Neither, of course, are levels of forest water use (transpiration) maintained. Whilst annual crops and grass also intercept rainfall and cloud water, and take up water from the soil, the associated amounts are (much) smaller than for forest due to the generally larger total leaf surface area and deeper root systems of forests compared to crops or grass (Calder, 1998). Thus, the clearing of montane forest that does not experience appreciable inputs of cloud water (i.e. LMRF) will result in an increase in the total volume of streamflow, typically by 100–400 mm year^{-1} (depending on rainfall; Bruijnzeel, 1990). In theory, the extra amount of moisture available in the soil due to the reduction in *Ei* and *Et* after converting (non-cloud) forest should permit an increase in baseflow levels — *given good soil management*. In practice, however, the degeneration of the soil's infiltration capacity after forest removal is often such that this potential gain in soil water is more than offset by the increase in overland flow and peak runoff during the wet season, with diminished streamflow during the dry season as the result (Bruijnzeel, 1989, 2000a).

The risk of reduced dry season flows following forest clearance becomes even more serious in the case of clearing TMCF. The extra inputs of water to the forest ecosystem afforded by cloud interception can be substantial, particularly in cloud forests at exposed locations (Tables 1 and 2). Also, such extra additions assume particular importance during periods of low rainfall (cf. Figure 2c). Whilst the cloud stripping ability of any trees that have been left standing remains more or less intact and could even be enhanced due to greater exposure to passing fog as long as only small patches of forest are cut (cf. study no. 3 in Table 2), it would surely disappear altogether in the case of a wholesale conversion to vegetable cropping or grazing (Zadroga, 1981). The eventual effect on streamflow will depend on the relative proportions of the catchment that were occupied by the respective types of cloud forest. For example, exposed ridgetop forests may intercept large amounts of cloud water but their spatial extent is limited (Brown *et al.*, 1996).

In recent years, diminished dry season flows have been reported for various parts of the tropics that experienced a considerable reduction in montane forest cover, including Costa Rica (Monteverde area; Pounds 8., 1999), Honduras (Cusuco National Park) and Guatemala (Sierra de las Minas) (Brown *et al.*, 1996), and (possibly) Flores, eastern Indonesia (Patthanayak and Kramer, 2000). However, it is not clear to what extent these reductions in flow are primarily the result of the loss of the fog stripping capacity of the former forest, or of diminished rainfall, reduced infiltration and water retention capacities of the soil due to erosion after forest clearance, or, in some cases, increased take offs for irrigation. For instance, the two catchment pairs in Honduras and Guatemala for which Brown *et al.* (1996) derived a 50% reduction in dry season flow after conversion to vegetable cropping, were rather different in size and elevational range, and therefore in their exposure to fog and rainfall. A more convincing, albeit non-tropical, case was provided by Ingwersen (1985) who observed a (modest) decline in summer flows after a 25% patch clearcut operation in the same catchment in the Pacific Northwest region of the U.S. for which Harr (1982) had inferred an annual contribution by fog of c. 880 mm. The effect disappeared after 5–6 years. Because forest cutting in the Pacific Northwest is normally associated with strong increases in water yield (Harr, 1983), this anomalous result was ascribed to an initial loss of fog stripping upon timber harvesting, followed by a gradual recovery during regrowth. Interestingly, the effect was less pronounced in an adjacent (but more sheltered) catchment and it could not be excluded that some of the condensation not realized in the more exposed catchment was 'passed on' to the other catchment (Ingwersen, 1985; cf. Fallas, 1996). Identifying the precise cause(s) of the observed decreases in dry season flows and finding ways of restoring them, should be given very high research priority in the years to come.

On a related note, there is increasing evidence that TMCFs are also threatened by regional and global warming of the atmosphere. The latter tends to raise the average level of the cloud condensation level (Scatena 1998; Still *et al.*, 1999; Nair *et al.*, 2000). Apart from any adverse hydrological consequences (such as diminished opportunities for cloud water inter-ception), a lifting of the cloud base is bound to produce important ecological changes as well. The organisms living in TMCFs are finely attuned to the rather extreme climatic and soil conditions prevailing in these already stressed ecosystems (Benzing, 1998; Pounds *et al*., 1999; Hafkenscheid, 2000). One of the best documented cases in this respect is provided by the Monteverde Cloud Forest Preserve in Northern Costa Rica (Pounds *et al*., 1999). Here, a decrease in fog frequency since the mid 1970s has been inferred using the number of days with no measurable precipitation as an index of fog frequency. The most extreme decreases within an overall downward trend occurred in 1983, 1987, 1994 and 1998, which appeared to be correlated with higher sea surface temperatures (Figure 4a). Anoline lizard populations in the area have declined in association with this pattern, with major population crashes in 1987, 1994 and 1998. Currently, 20 out of 50 species of frogs and toads, including the spectacular and locally endemic golden toad, have disappeared. At the same time, species from drier, lower elevations are invading and becoming residents (Pounds *et al.*, 1999).

The evidence presented in Figure 4 does suggest a worrying relationship between global warming and drying of the air on the one hand, and reduced streamflows on the other in the case of northern Costa Rica (cf. Fleming, 1986). It could be argued that these data pertain to an area that is rather protected from the moisture-bearing trade winds coming from the Caribbean and that one should therefore be careful to generalize such findings to 'all' cloud forest situations. For example, simulation studies of the effects of global warming on rainfall patterns predict a distinct rise in some cloud forest areas, such as the Pacific slopes of the Andes in South-west Colombia (Mulligan, 2000). Nevertheless, recent model studies by Nair *et al.* (2000) suggest that widespread deforestation in the Atlantic lowlands of northern Costa Rica does indeed raise the average cloud base during the dry season, and much more so than small changes in sea surface temperatures would (cf. Still *et al.*, 1999). Further evidence of the importance of land cover in the lowlands on the height of the cloud base comes from Puerto Rico. Here, the average cloud condensation level was lifted temporarily by several hundred metres after Hurricane Hugo had effectively defoliated the forests on the lower slopes of the Luquillo Mountains in September 1989. The resulting drop in forest water use caused a significant rise in the temperature of the overlying air and thus in the average position of the cloud base. Interestingly, the effect disappeared in a few months after the leaves had grown back again (Scatena and Larsen, 1991; see also photographs in Bruijnzeel and Hamilton, 2000). In the same area, Scatena (1998) interpreted the presence of isolated stands of large and very old (>600 years) Colorado trees (*Cyrilla racemiflora*) at elevations well below the current cloud base that experience relatively low rainfall (<3000 mm year^{-1}) as evidence of a gradual upward shift in vegetation zonation over the past several centuries. *Cyrilla* is currently a dominant tree in areas above the cloud base (>600 m) and is most common where mean annual rainfall exceeds 4000 mm. Similarly, Brown *et al.* (1996) reported the occurrence of pockets of mossy cloud forest below the current average cloud base in Honduras. There is a need for more systematic research linking such empirical evidence to records of current and sub-recent climatic change (cf. Scatena, 1998).



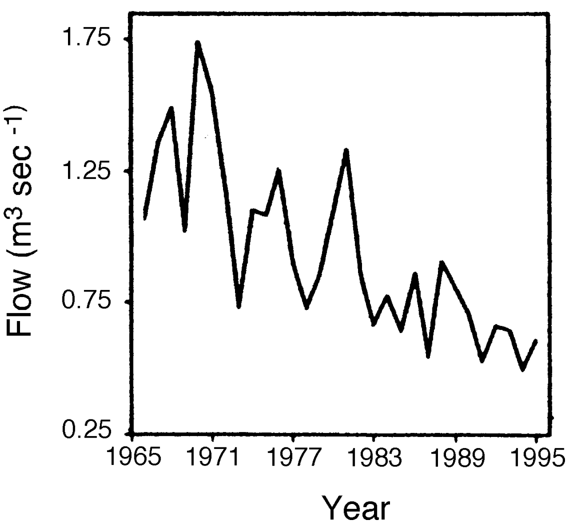


Figure 4 Trends for (a) sea surface temperature anomalies and number of rainless days, and (b) minimum streamflows in northern Costa Rica since the 1970s (adapted from Pounds *et al.*, 1999)

On single mountains, a lifting of the average cloud condensation level will result in the gradual shrinking of the cloud-affected zone (Figure 5a). On multiple-peaked mountains, however, the effect may be not only that, but one of increased habitat fragmentation as well (Figure 5b), adding a further difficulty to the chances of survival of the remaining species (Sperling, 2000). Much more research is needed to confirm and extend the results obtained so far at Monteverde (Pounds *et al.*, 1999) and, to a lesser extent, Puerto Rico (Scatena, 1998). Apart from amphibians (Pounds *et al.*, 1999), the epiphyte communities living in the more exposed parts of TMCF canopies might prove to be equally suited to detecting changes in climatic conditions, rainfall and cloud water chemistry, and possibly enhanced ozone and UV-B levels as well (Lugo and Scatena, 1992; Benzing, 1998; cf. Gordon *et al.*, 1994).

Putting cloud forests on the hydrological research agenda

Having reviewed the post-1993 evidence on the hydrological functioning of TMCF, what are the primary remaining gaps in knowledge? Arguably, the most urgent research questions in relation to the perceived 'added' hydrological value of TMCF over other montane forests are:

- Does conversion of TMCF to vegetable cropping or pasture indeed lead to reductions in dry season flows, or even total water yield? And if so, is this mainly because of the loss of the cloud interception function, or does the reduction in dry season flow rather reflect a deterioration in infiltration opportunities after deforestation?

- Do changes in (dry season) flow after forest clearance differ for the respective types of montane forest (i.e. LMRF, LMCF, and UMCF) and thus local climatology (e.g. distance to the ocean, exposure)?

- To what extent does global warming or the clearing of forests *below* the cloud belt affect the regional hydrological function of TMCF through a raising of the average level of cloud condensation? What are the associated changes in fog stripping opportunities, forest water use and, ultimately, streamflow?

Furthermore, most hydrological studies in TMCF have concentrated on quantifying net precipitation (crown drip).

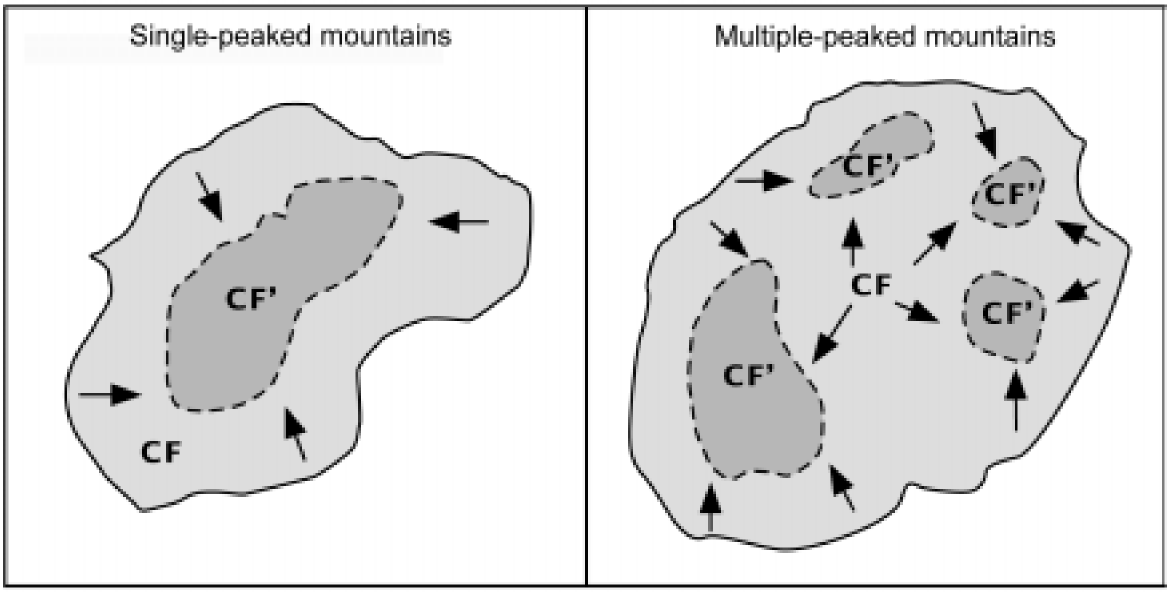


Figure 5 Possible changes in spatial cloud forest distribution in response to a rise in the cloud condensation level on (a) a single peak and (b) a mountain with several peaks (after Sperling (2000), reproduced with permission).

Whilst these have indicated important differences between contrasting forest types and topographic situations, published results differ widely in their reliability and comparisons between sites and forests are, therefore, rather difficult to make (Bruijnzeel and Proctor, 1995) (cf. Tables 1 and 2). *There is a real need for more systematic observations of cloud water interception and net precipitation along elevational gradients according to an internationally accepted (standard) measuring protocol.* This would require the adoption of a robust standard cloud water collection device that may be used for comparative purposes (site characterization; cf. Schemenauer and Cereceda, 1994, 1995; Juvik and Nullet, 1995a; Daube *et al.*, 1987). Net precipitation measurements should involve the use of a sufficient number of roving throughfall gauges to allow for an adequate representation of 'drip points' (cf. Lloyd and Marques, 1988; Hafkenscheid *et al.*, this volume). In addition, the potential contrast in concentrations of stable isotopes in rain and cloud water to evaluate cloud water contributions to overall net precipitation totals (cf. Dawson, 1998) deserves further exploration in a TMCF context. The same holds for the further development and testing of physically-based cloud water deposition models on tropical mountains (cf. Joslin *et al.*, 1990; Mueller, 1991; Yin and Arp, 1994; Walmsley *et al*., 1996).

Finally, before a sound understanding can be obtained of the influence of TMCF on streamflow amounts, reliable information is urgently needed on the water uptake rates (transpiration) of these forests. Such information is lacking almost entirely at present (Table 3; Bruijnzeel and Proctor, 1995). There are no published studies that have combined hydrological process work (rainfall and cloud interception, water uptake) and streamflow dynamics in any TMCF environment, although such work was recently initiated in South-western Colombia (M. Mulligan, *pers. comm.*).

Having defined the chief hydrological research needs in TMCF in the previous sections, where could these be best addressed? Arguably, the most cost-effective approach would be to identify sites with ongoing work (hydrological and/or ecological) and plan additional observations and experiments as required as part of a network that covers the range of environmental conditions encountered in the pan-tropical cloud forest belt (cf. Figure 1). A preliminary inventory of current climatological and hydrological research efforts in TMCF (Bruijnzeel, 2000b) established:

(i) A notable lack of work in African TMCF; and

(ii): An almost total absence of studies linking streamflow dynamics with hydrological process work or land use change.

On the basis of previously executed or ongoing work, representativity of site geology and climate, and logistical considerations, the sites listed in Table 4 may be considered to be the most promising for inclusion in such a pan-tropical TMCF research network (see Bruijnzeel (2000b) and key references in Table 4 for details).

To answer the questions raised earlier with respect to the effect on water yield of converting TMCF to other land uses would ideally require setting up a paired catchment experiment in which flows from a forested control catchment are compared against flows from a cleared catchment *after initial intercalibration of the two areas in the undisturbed state* (Hewlett and Fortson, 1983). 'Direct' comparisons of streamflow emanating from forested and cleared catchments may easily give biased results due to potential differences in ungauged, sub-terranean water transfers into or out of the catchments, especially in the kind of volcanic terrain prevailing at almost all of the sites listed in Table 4 (cf. Bruijnzeel, 1990; Brown *et al.*, 1986). However, because most of the remaining forest in these areas is officially protected, the paired catchment approach is almost certainly not a feasible approach. The other option would be to compare streamflows from catchments with contrasting land uses whilst accounting for differences in deep leakage

Table 4: Selected key research sites in tropical montane cloud forests.

Site	*Elevation*	*MAP range (m)*	*Forest types (mm/yr)*	*Key references*
'Maritime' tropics:				
Mt Kinabalu, Sabah Malaysia	600-3400	2600-4100	LRF – SACF	Kitayama, K. (1992) Frahm, J.P. (1990a) Frahm, J.P. (1990b)
Hawai'i islands		500-3200	<7000	LMRF-SACF Kitayama, K. & Müller-Dombois, D. (1992) Juvik, J.O. & Ekern, P.C. (1978) Juvik, J.O. & Nullet, D. (1995b) Santiago, L.S. *et a*l. (2000) Nullet, D. & Juvik, J.O. (1997)
Luquillo Mnts, Puerto Rico	600-1050	<4500	LMCF-ECF	Vugts, H.F. & Bruijnzeel, L.A. (1999) Schellekens, J. *et al.* (1998) Richardson, B.A. *et al.* (2000) Garcia-Martino, A.R. *et al.* (1996) Holwerda, F. (1997) Scatena, F.N. (1998) Baynton, H.W. (1968) Baynton, H.W. (1969) Weaver, P.L. (1972)
Blue Mnts, Jamaica	1500-2265	2600-4000	LMRF-UMCF	Hafkenscheid, R.L.L.J. (2000) Tanner, E.V.J. (1977) Kapos, V. & Tanner, E.V.J. (1985)
'Continental' tropics:				
Cauca, Southwest Colombia	1375-2895	>5000	LMCF-UMCF	Mulligan, M. & Jarvis, A. (2000) Mulligan, M. (2000) *
Merida, Venezuela	2200-3000	<2950	LMCF-UMCF	Ataroff, M. (1998)
Monteverde, Costa Rica	1200-1850	2500	LMCF	Zadroga, F. (1981) Lawton, R. & Dryer, V. (1980) Clark, K.L. *et al.* (1998) Fallas, J. (1996) Nadkarni, N.M. (1984) Pounds, J.A. *et al.* (1999) Still, C.J. *et al.* (1999) Nair, U.S. *et al.* (2000)
Talamanca, Costa Rica	2000-3300	<6300	LMCF-UMCF	Kappelle, M. (1995) Calvo, J.C. (1986)
Sierra de las Minas, Guatemala	1400-2700	2500	LMRF-UMCF	Brown, M.B. *et al.* (1996) Holder, C.D. (1998)

*see also http://www.kcl.ac.uk/herb

and within-basin processes (interception of rainfall and cloud, transpiration, soil water depletion, deep drainage). Some of the more suitable sites for such an experiment include Mt Kinabalu, Malaysia and Sierra de las Minas, Guatemala (forest clearance for vegetable cropping); and Monteverde, Costa Rica and the Cauca area, Colombia (conversion to pasture). The effects of timber harvesting (oaks and *Podocarpus*) and forest clearing for orchards or grassland under somewhat drier climatic conditions may be studied in the Talamanca area, Costa Rica (Kappelle, 1995) or in the Merida area, Venezuela (cf. Ataroff, this volume).

In view of the ongoing monitoring of amphibian and bird populations (Pounds *et al.*, 1999), bryophyte communities (cf. Nadkarni, 1984), and climate change modelling efforts (Still *et al.*, 1999; Nair *et al.*, 2000) at the Monteverde cloud forest preserve, this site must rank as the prime location for continued long-term observations of ecological changes due to climate change. However, for an evaluation of the associated hydrological impacts, additional process studies will be needed as well. Ideally, these should include observations in the various cloud forest types distinguished in the area by Lawton and Dryer (1980). In addition, pasture areas with differently sized forest remnants may be included (cf. Fallas, this volume). After quantification of the hydrological fluxes associated with the respective land cover types has been achieved, the information may be fed into a spatially distributed model as part of an upscaling exercise[1] . Predictions of changes in streamflow for various TMCF clearing scenarios may then be validated against existing streamflow records for catchments with known land use history (cf. Watson *et al*., 1999).

At several of the sites listed in Table 4 (e.g. Malaysia, Hawai'i, Puerto Rico), observations of climatic variables along the elevational gradient have been made whereas in others (e.g. Guatemala, Puerto Rico) preliminary estimates of net precipitation vs. elevation are available as well. It would be of great interest to both regional water resource planning and TMCF conservation efforts to also initiate gradient studies of forest water and energy budgets (including transpiration) at key sites (cf. Vugts and Bruijnzeel, 1999). We seem to have reached a crucial point where additional hydrological information is required if true progress in the promotion of the water values of TMCF — and therefore their chances of being afforded adequate protection — is to be made (Bruijnzeel, 2000b). This, together with the rapid disappearance of TMCF in many areas (Doumenge *et al*., 1995) is why it is 'decision time' for cloud forests.

It is encouraging to note, therefore, that in 1999 IUCN, WWF International, the World Conservation Monitoring Centre (Cambridge, U.K.) and UNESCO-IHP joined hands to form the '*Tropical Montane Cloud Forest Initiative*'. The objectives of the Initiative include: 'the building and strengthening of networks of TMCF conservation and research organisations around the globe' and 'to increase recognition and resources for cloud forest conservation around the world, emphasizing their role in maintaining water catchments and biodiversity' (for further details, see http://www.wcmc.org.uk/forest/cloudforest/english/homepage.htm).

The Steering Committee of the Initiative brings together representatives from the founding organizations, scientists actively working in TMCF, and NGO representatives from Asia, Latin America and Africa. In June 2000, a 40-page document entitled: '*Decision time for cloud forests'* (Bruijnzeel and Hamilton, 2000) was published by the Initiative to help raise awareness among a non-scientific audience[2] .

A concerted effort is needed now to put tropical montane cloud forests firmly on the agendas of tropical hydrologists, conservationists, resource managers, donor agencies and policy makers. The chances of achieving this have never been better than today but time is running out!

1 Preliminary discussions to this end were initiated between the Tropical Science Center, Costa Rica, the Vrije Universiteit, Amsterdam, The University of Alabama, Huntsville, and various European partners in spring 2000.

[2] Freely available as long as stocks last from the Humid Tropics Programme, UNESCO-IHP, Paris, or from the author.

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