Tropical montane cloud forest: environmental drivers of vegetation structure and ecosystem function

Running title: Cloud-forest environment

Timothy J. Fahey and Ruth E. Sherman

Department of Natural Resources, Cornell University

Edmund V.J. Tanner

Department of Plant Sciences, University of Cambridge

Proofs should be sent to: Timothy J. Fahey (tjf5@cornell.edu)

ABSTRACT

Tropical montane cloud forests (TMCF) are characterized by short trees, often twisted with multiple stems, with many stems per ground area, a large stem diameter to height ratio, and small, often thick leaves. These forests exhibit high root to shoot ratio, with a moderate leaf area index, low above-ground production, low leaf nutrient concentrations and often with luxuriant epiphytic growth. These traits of TMCF are caused by climatic conditions not geological substrate, and are particularly associated with frequent or persistent fog and low cloud. There are several reasons why fog might result in these features. Firstly the fog and clouds reduce the amount of light received per unit area of ground and as closed-canopy forests absorb most of the light that reaches them the reduction in the total amount of light reduces growth. Secondly, the rate of photosynthesis per leaf area declines in comparison with that in the lowlands, which leads to less carbon fixation. Nitrogen supply limits growth in several of the few TMCFs where it has been investigated experimentally. High root:shoot biomass and production ratios are common in TMCF, and soils are often wet which may contribute to N limitation. Further study is needed to clarify the causes of several key features of TMCF ecosystems including high tree diameter:height ratio.

INTRODUCTION

Distinctive forest vegetation on tropical mountains that are frequently or persistently immersed in ground-level clouds often is described as tropical montane cloud forest (TMCF). These forests often exhibit a variety of ecological features that distinguish them from tropical forests that are more rarely exposed to ground-level clouds, especially a stunted and gnarled canopy with high cover of epiphytes (especially bryophytes and filmy ferns, Hietz 2010). The overriding role of cloud immersion in shaping this vegetation's physiognomy is emphasized by its recurrence across sites for which other environmental factors (e.g. temperature, precipitation, altitude, wind, slope, soils) exhibit wide variation; and in tropical regions with different biogeographic affinities. The mechanisms contributing to distinctive TMCF physiognomy and ecology have received long and detailed study, beginning with Shreve (1914) and Brown (1919), and including a recent synthesis volume detailing current advances (Bruijnzeel *et al.* 2010). The objectives of this paper are to provide a concise overview of ecological interactions that characterize these distinctive forests and to suggest directions for future study. We define TMCF primarily on the basis of frequent cloud immersion, distinguishing these tropical montane forests from other tropical forests in drier and warmer environments.

A variety of schemes for classifying tropical montane forest vegetation zones has been devised, and the designation of TMCF generally coincides with tropical montane rain forest (Grubb 1971) or upper montane rain forest and subalpine forest; this includes forests affected by frequent and/or persistent ground-level cloud (Grubb 1977). Greater cloud immersion typically accompanies decreased temperatures with increasing altitude (Bruijnzeel & Hamilton 2000). We emphasize at the outset that the designation of a discrete TMCF type can be misleading because most commonly the

composition and structure of tropical montane vegetation exhibits more or less continuous variation across complex environmental gradients (Lieberman *et al.* 1996). Moreover, precise delineation of the distribution of TMCF is problematic because direct observations of ground-level clouds are not available on an extensive basis. Mulligan (2010) demonstrated that limits of TMCF-classified vegetation coincide best with forested landscapes where greater than 70% of the time satellite-visible clouds and/or ground-level condensing conditions (modelled) occur. Also, strictly speaking tropical cloud forests are not restricted to mountains (Gradstein *et al*. 2010), but they are most commonly observed between about 1000 m and 2500 m asl; they are found in sites with a range of temperatures. Jarvis & Mulligan (2010) demonstrated that the climate of TMCFs is significantly different from other tropical montane forests, especially in terms of lower T_{max} and T_{mean}, mostly because they occur at higher altitude. TMCFs tend to be much closer to coasts, as the oceans provide a continuous source of atmospheric moisture to supply cloud formation. Also, cloud forests tend to occur more frequently on topographically exposed landscapes, ridges or peaks, than other montane forests. The geological settings of TMCFs are not distinctive and their soils exhibit a wide range of properties. A particularly distinctive feature of TMCF distribution is the so-called Massenerhebung (or mass-elevation) effect: the elevation of TMCF is much lower on smaller than on larger mountain massifs (Grubb 1971); the smaller mountains tend to be closer to the sea. The tropical Massenerhebung effect reflects greater cloud immersion on smaller mountains resulting from lower temperatures and a steeper adiabatic lapse rate owing to proximity to the sea; hence, this effect further emphasizes the key role played by climate and cloud immersion in defining TMCF distribution.

A suite of biotic features characterizes TMCF in contrast to other tropical forests (Table 1). These features vary among TMCFs as a result of differences in environments and floras; for example, not all TMCFs are stunted, and stunting and twisting are not confined to wet TMCF. Also, most research relating environment and vegetation in TMCF has been conducted in the neotropics and a few other locations (e.g. Hawaii), and wider study is needed to better characterize global relationships. Nevertheless, we would argue that certain ecological features comprise a useful, unifying set that defines and aids in analyzing the TMCF phenomenon. The low height, or stunting, of the canopy is common in most TMCF. Although decreased forest canopy height accompanies declining temperature at high elevation in most of Earth's mountains, stunting in the TMCF can be extreme (Weaver *et al.* 1986). Moreover, the TMCF stems are often gnarled and twisted or leaning, and multi-stemmed trees are common (Bellingham & Sparrow 2009). The leaf area index (LAI) in most TMCFs is lower than for lowland forests (Moser *et al.* 2007, Unger *et al.* 2012). The ratio of stem diameter to tree height increases with altitude on most tropical mountains (Girardin *et al.* 2014a), and stem density is usually higher in TMCF than in lower montane forests. Canopy openings are often more frequent in TMCF (Asner *et al.* 2014) which together with the humid climate and low LAI favours high abundance of tree ferns (Lieberman *et al.* 1996), and other ferns (Salazar *et al*. 2013). Leaves of many TMCF species are classified as microphylls (Sugden 1985, Tanner & Kapos 1982), and leaf thickness is often high. A final canopy feature that is particularly distinctive in most TMCF is the high abundance of epiphytes, especially liverworts, mosses and filmy ferns (Hietz 2010); at the extreme all stem surfaces can be clothed in a thick layer of epiphytes, and epiphyte-derived canopy soil (decaying organic matter) accumulates (Bohlman *et al.* 1995, Golley *et al.* 1971).

Although soils of TMCF exhibit a wide range of physical and chemical properties, certain below-ground features appear to be common (Roman *et al.* 2010). Root biomass and the root:shoot ratio of TMCF are higher than in most other closed-canopy forests, and some evidence suggests distinctively high below-ground production (Girardin *et al.* 2010, Moser *et al.* 2011). Most TMCF soils exhibit high soil organic matter content and many have a deep organic horizon developed over the mineral soil; this organic horizon may be peat (due to waterlogging) or mor humus (due to acidity and phenolics) or intermediate (Roman *et al.* 2010). Perhaps most importantly TMCF soils are often wet because of the combination of high precipitation and low evaporative demand (cool and humid), and as a result of persistent saturation many TMCF soils are low in oxygen, exhibiting reducing conditions (Silver *et al.* 1999). Together with slow nutrient recycling through dead organic matter, these reducing conditions can contribute to chronic nutrient limitation of plant production, especially N limitation (Tanner *et al.* 1998).

HYPOTHETICAL FRAMEWORK

The environmental and biotic factors that characterize the ecological interactions in TMCF are summarized in a conceptual diagram (Figure 1). Because the distinctive features of TMCF (Table 1) are expressed over a wide range of environments and to differing degrees among TMCFs, the contribution of various driving factors undoubtedly differs among TMCFs; indeed, this variation provides insights for understanding the causes of the TMCF phenomenon.

Following on early work of Shreve (1914), Brown (1919) and many others, we hypothesize that the primary factor shaping the TMCF is the climatic driver: the combination of relatively low temperatures, high humidity and cloud immersion. This

primary driver either directly influences, interacts with, or is augmented by a suite of secondary factors to limit the above-ground productivity of TMCF and contribute to their distinctive structure. Here we provide a brief summary of a hypothetical causal framework for the ecosystem features of TMCF followed by a detailed overview of current evidence. We again emphasize that TMCF actually exhibits a broad range of ecosystem features.

The key role played by cloud immersion in shaping the TMCF ecosystem seems clear, but the mechanisms by which cloud immersion leads to the distinctive physiognomy and functions of TMCF are not entirely obvious. Light availability undoubtedly limits net photosynthesis in TMCFs (Figure 1) compared with forests in less cloudy climates. For example, TMCF at 1550 m asl in Jamaica received 19% less shortwave radiation than a site in the drier lowlands near sea level (Aylett 1985). The low air temperature in high-elevation TMCF limits C assimilation (Wittich *et al.* 2012) and net primary productivity (Figure 1) in much the same way as noted for temperate alpine tree-line environments (Tranquillini 1979). Moreover, in the cloudy conditions of TMCF leaf temperatures are typically lower than for sunlit leaves, further constraining photosynthesis.

Nutrient limitation of above-ground production is suggested by the high root:shoot production ratio observed in TMCF (Moser *et al.* 2011), and current evidence points to low nitrogen availability as the most common cause of nutrient limitation in TMCFs (Cleveland *et al.* 2011, Fisher *et al.* 2013), though there is good evidence that both P and N are limiting in some TMCF (Homeier *et al.* 2012). Chronic N limitation of above-ground productivity (Figure 1) results from some combination of low input, high

losses and delayed recycling owing to suppressed microbial activity in the usually cool and wet TMCF environment.

High annual precipitation in TMCF, including the contribution of wind-driven rain or cloud drip, assures that most TMCFs are not much affected by soil drought. Quite the contrary, high rainfall and low evaporative demand associated with cool, humid atmospheric conditions result in soils that, in many sites, are often at or near saturation (Figure 1). The mechanisms whereby saturated soils contribute to TMCF dynamicsare complex. First, the direct effect of low oxygen on root function probably plays a varying role, depending upon plant species and the frequency and extent of anaerobic conditions in soil. In some situations root penetration of soil may be restricted leading to shallow rooting and low resistance to uprooting during windstorms (Soethe *et al.* 2006). Also, nutrient uptake by roots may be further curtailed by low-oxygen conditions. Together these influences contribute further to chronic N limitation and low canopy C assimilation. Moreover, a higher proportion of assimilated C is allocated below ground to acquire soil nutrients and maintain wind-firmness, feeding back to lower above-ground net primary productivity (ANPP, Figure 1).

Another striking feature of TMCF ecosystems is the frequently high accumulation of epiphytes, especially bryophytes, made possible by the high atmospheric moisture (Figure 1). The effect of high epiphyte loads on the other features of TMCF ecosystems has received limited attention. It is possible that the high mass loading of water-saturated bryophytes might lead to structural stability problems in some TMCFs, thereby contributing to observed canopy stunting, high tree diameter: height ratios and greater allocation to root systems. The role of wind in shaping TMCFs (Figure 1) has been suggested (Lawton 1982) and high winds can induce some of the canopy traits of

cloud-forest trees (Cordero 1999), but TMCF stunting is also expressed in low-wind environments (Martin *et al.* 2007). The high frequency of canopy openings in some TMCFs has been ascribed to low ANPP and slow closure of forest openings, thereby favouring high density of understorey stems (Asner *et al.* 2014).

A final consideration in the structure and function of TMCF is the contribution of phylogenetic vs phenotypic factors. Stunting of TMCF trees is seen in species that grow much taller at lower altitudes; for example, in Jamaica one of the most common species in the most stunted (mor ridge) forest, *Clethra occidentalis*, also grows to nearly 30 m tall in lowland wet limestone forest. Other species common in the most stunted TMCF in Jamaica are found only as epiphytes at lower altitude (e.g. *Clusia havetioides*) or absent at lower altitudes (e.g. *Lyonia jamaicensis*). Conversely, some TMCF, which show extreme stunting, are dominated by species which are rare or absent at lower altitudes, for example the trees dominating the elfin forest on Pico del Este in Puerto Rico (Howard 1968). Thus, TMCF structure can result from inflexible species characteristics but also from flexible responses to the extreme environment in plastic species.

MECHANISMS AND EVIDENCE

Cloudiness and effects of cloud immersion

Persistent cloudiness and cloud immersion reduce insolation relative to clear sky in TMCFs (19% in Jamaican TMCF, Aylett 1985, Hafkenscheid 2000; 40% in Puerto Rican TMCF, Baynton 1968; 62% in Bolivia, Schawe *et al.* 2010), but surprisingly little research has been conducted to quantify the effects of reduced photosynthetic photon flux density (PPFD) on photosynthetic C gain in TMCF vegetation. In a subtropical montane cloud forest, eddy flux measurements demonstrated that whole-canopy CO_2

uptake was reduced by 21% under foggy conditions that reduced insolation by 64% in comparison to non-foggy conditions (Mildenberger *et al*. 2009; Figure 1). Moreover, the light climate in TMCF is one of very low PPFD in fog potentially followed by very high PPFD in bright sunlight; the switch between high and low light in TMCF could be deleterious. However, evidence to date does not suggest that TMCF species exhibit highly distinctive photosynthetic physiology in comparison with lowland trees. For example, an investigation of the photosynthetic characteristics of leaves from TMCF at 3025 m asl in the Peruvian Andes concluded that, the maximum carboxylation capacity and the maximum rate of electron transport were not different from values for lowland rain forest leaves (on a leaf area basis, when calculated for a standard temperature of 25°C), but dark respiration was higher (van de Weg *et al.* 2012). Moreover, van de Weg *et al.* (2009) observed that leaf optical properties of cloud-forest species were similar to those of rain-forest trees, with typical ranges of plasticity in leaf mass per area with depth in the canopy. In a pantropical survey, Wittich *et al.* (2012) concluded that light-saturated photosynthesis may decline slightly with increasing altitude in tropical mountains, but the explanation of this observation was not clear and possibly is related to inorganic nutrition and low temperature; they suggested that low N and P availability might limit compensatory responses of enzyme activity that could otherwise balance effects of low temperature. In sum, the combination of low total PPFD and low temperatures appears to constrain net C gain in TMCF (Figure 1), but further research is needed to clarify the exact mechanisms. An additional influence of cloud immersion on photosynthesis may result from leaf wetness: water films on the abaxial leaf surface could constrain diffusion of CO_2 into the leaf mesophyll and limit photosynthesis (Letts & Mulligan 2005). However, data on leaf wetness in cloud-forest trees is needed to confirm the importance of this mechanism.

Cloud immersion strongly affects the ecosystem water balance both by reducing evapotranspiration and through the enhanced precipitation inputs associated with wind-driven fog collected on canopy surfaces. Both potential and actual evapotranspiration rates are considerably lower in TMCF than for adjacent lower montane forests (McJannet *et al.* 2010, Santiago *et al.* 2000, Schawe *et al.* 2010), but the magnitude of this difference varies with climatic features both among (Mulligan 2010) and within (Lawton *et al.* 2010) montane regions. Recent advances in the measurement of fog interception have clarified the role of cloud immersion in augmenting precipitation in TMCF. Holwerda *et al.* (2010) concluded that cloud-water interception exceeded 1 mm d^{-1} in a Puerto Rican elfin forest, and Häger & Dohrenbusch (2011) estimated as high as 3560 mm y^{-1} of horizontal precipitation in north-western Costa Rica. Giambelluca *et al.* (2010) estimated over 1000 mm y^{-1} in a wet cloud forest in Hawaii; however, they concluded that most of the intercepted water was re-evaporated rather than reaching the ground as cloud drip. The combined effect of reduced evapotranspiration and enhanced precipitation associated with cloud immersion might increase the frequency and duration of soil saturation in TMCFs (Schawe *et al.* 2010; Figure 1).

A final direct effect of cloud immersion contributing to the TMCF ecosystem is associated with the composition and abundance of epiphytic plants. The diversity and biomass of both vascular and non-vascular epiphytes is high in most TMCFs, and cloud immersion undoubtedly contributes to this pattern (Figure 1). The most distinctive feature of the epiphyte vegetation in many TMCFs is the high abundance of non-vascular species and filmy ferns (*Hymenophyllum* spp.) that often cover nearly all stem surfaces (Hietz 2010, Horwath 2011). The epiphytic bryophytes of TMCF are predominantly

leafy liverworts (Jungermanniales) in contrast to lowland rain forest where true mosses can be equally common (Horwarth 2011). Among ferns, the genera *Hymenophyllum* and *Elaphoglossum* and the family Grammitidaceae are characteristic of TMCF (Hietz 2010, Kessler *et al.* 2001, Krömer *et al.* 2005). High atmospheric moisture particularly favours these taxa, and absorption of cloud water probably contributes to their water supply (Shreve 1911, Tobón *et al.* 2010). The possible role of cloud-water in supplying growth-limiting mineral nutrients to epiphytic vegetation, or favouring epiphytic N_2-fixing taxa also is notable (Hietz *et al.* 2002). Conversely, epiphyte vegetation including epiphylls could restrict tree photosynthesis by growing over leaves and reducing light availability (Grubb 1977). To our knowledge, no measurements of this effect have been made for TMCF.

Nutrient limitation

The role of mineral nutrient limitation in contributing to TMCF ecosystem dynamics has been an enduring theme of TMCF studies. An early idea that reduced convective transport associated with low transpirational water flux limits nutrient acquisition (Odum 1970) has been largely discounted (Bruijnzeel & Veneklaas 1998, Grubb 1977), but relatively low foliar nutrient concentrations (on a mass basis) clearly pointed to the likelihood of nutrient limitation (Grubb 1977). Tanner *et al.* (1998) summarized experimental evidence for nutrient limitation of TMCF productivity and noted that most, but not all, studies indicated nutrient limitation. Moreover, they concluded that N was usually the principal limiting nutrient (Figure 1), a conclusion that has been borne out in more recent fertilization studies (Cleveland *et al.* 2011, Fisher *et al.* 2013). These results agree with some observations of decreasing foliar N:P ratios with increasing altitude in tropical mountains (Soethe *et al.* 2008, van de Weg *et al.* 2009).

Photosynthetic parameters of TMCF trees also support N rather than P limitation of C assimilation (van de Weg *et al.* 2012). However, colimitation by N and P may occur in some TMCF (Homeier *et al.* 2012), depending upon local soil properties (Wittich *et al.* 2012). Moreover, recent measurements of nitrate leaching from a TMCF in Costa Rica (Brookshire *et al.* 2012) call into question the universal role of soil N availability in limiting TMCF productivity. A resolution to this apparent paradox - that tree growth is limited by N in soils from which water with low concentrations of nitrate is draining - may simply be a question of relative amounts, as nitrate is very soluble and it may be impossible for tree mycorrhizas to take it all up. Early studies in Puerto Rico reported nitrate in stream water (McDowell & Asbury 1994) in an area where fertilization of forest recovering from a hurricane resulted in about a doubling of leaf-litter production (Zimmerman *et al.* 1995).

Evidence about the mechanisms contributing to apparent N limitation of TMCF productivity is not entirely conclusive; any or all of low N inputs, delayed recycling or high N losses could contribute to chronic N limitation. Benner *et al.* (2010) concluded that the generally low nutrient status of TMCF compared with other tropical forests probably is not associated with chronically low nutrient inputs but rather with differences in the rates of nutrient cycling or losses. However, low temperatures have been linked to limitation of N_2 fixation in Earth's terrestrial biomes (Houlton *et al.* 2008), and although they are common in lowland tropical forests, symbiotic N_2-fixing tree taxa are uncommon in TMCF. Nitrogen fixation by lichens (Forman 1975) and other canopy epiphytes clearly occurs as indicated both by direct measurements (Benner *et al.* 2007) and by isotopic evidence (Hietz *et al.* 2002). Free-living N_2 fixation also occurs in forest floor and canopy soils, but the quantities remain highly uncertain and more

research is needed (Matson *et al.* 2015). Intriguingly, Benner & Vitousek (2007) observed that the abundance of N_2-fixing canopy epiphytes was stimulated by soil P fertilization in a Hawaiian TMCF, suggesting a possible interaction between P and N supply. The high accumulation of soil organic matter in TMCF is indicative of delayed recycling of nutrients and could contribute to chronic N_2 limitation of NPP (Tanner *et al.* 1998, Unger *et al.* 2012). Declining temperature appears to be the principal rate-limiting factor for declining litter decay with increasing altitude in tropical mountains (Salinas *et al.* 2011, Schuur 2001), but a possible role of excess water and low O_2 is described below; this factor also could contribute to increased losses of N (Figure 1).

Mycorrhizal associations undoubtedly play a key role in mediating nutrient relations in TMCF, but they have received limited attention to date. Although arbuscular mycorrhizas are associated with most TMCF tree genera (Brundrett 2009), many species of Ericaceae, with their distinctive ericoid mycorrhizal associations, are common as TMCF epiphytes (Rains *et al.* 2003) and at environmental extremes in tropical mountains (Gentry *et al.* 1995). Moreover, in some tropical regions, tree species supporting ectomycorrhizal associates from the families Fagaceae and Pinaceae are common in TMCF. These mycorrhizal associations exhibit some systematic differences in nutrient acquisition mechanisms (Marschner & Dell 1994); studies of their efficacy across TMCF ectones where taxa with the different associations are present or absent might be particularly informative for understanding nutrient relations of TMCF.

Nutrient limitation could contribute to TMCF ecosystem dynamics either directly by constraining photosynthetic activity or indirectly by diverting C from above-ground growth to below-ground resource acquisition (Figure 1). Fisher *et al.* (2013) concluded

that N fertilization of TMCF promoted higher stem growth not by increasing C assimilation but through effects on below-ground allocation. Some studies have demonstrated that root:shoot ratios increase with altitude on tropical mountains (Kitayama & Aiba 2002, Leuschner *et al.* 2007), and Girardin *et al.* (2013) provided evidence for a step increase in the cloud immersion zone. Moreover, some evidence suggests that below-ground production is especially high in TMCF (Girardin *et al.* 2010, Moser *et al.* 2011), although measurement of below-ground production is notoriously difficult and uncertain. Taken together, these observations suggest that the low stature and low ANPP of TMCF results in part from relatively high below-ground C allocation associated with chronic N (and sometimes P) limitation (Figure 1).

Excess soil water and reducing conditions

Although not all TMCFs exhibit frequent and persistent soil saturation (Roman *et al.* 2010), this is clearly a common feature in many TMCFs (Schawe *et al.* 2010). Chronically high water content of soils leads to the depletion of oxygen. Indeed, field studies indicate that anaerobic conditions increase along some tropical montane elevation gradients (Silver *et al.* 1999). Low soil oxygen has been suggested as a factor limiting the LAI of some TMCF (Santiago *et al.* 2010). However, it seems likely that the tolerance of low soil oxygen varies considerably among TMCF species so that the contribution of reducing conditions will vary with the phylogenetic history of the extant floras. Rapp *et al*. (2012) attributed the low ANPP of TMCF in part to such species effects. Notably, some tall, highly productive forests are found in low oxygen floodplain soils and swamps (Grubb 1977) including TMCF (e.g. at Monteverde, Costa Rica; R. Lawton, pers. comm.)

Under anaerobic conditions organic matter decomposition is slow and incomplete, contributing to the high accumulation of soil organic matter in TMCF. Schuur (2001) demonstrated that lower tissue quality of leaf litter in wetter sites also can contribute to reduced decay rates, high SOM accumulation and delayed nutrient recycling. Such a mechanism appears not to be universally important in TMCF, however, as Silver *et al.* (2010) indicated, net N mineralization rates are not consistently different between TMCF and low-elevation tropical forest in Puerto Rico. Moreover, TMCF in their study exhibited higher gross N mineralization rates than low-elevation soils and no effect of anaerobic conditions was observed. Clearly, further study of the interactions between soil N dynamics and soil saturation in TMCF is warranted.

Other mechanisms associated with excess soil water could contribute to nutrient limitation in TMCF. For example, anaerobic conditions can limit root growth and physiological activity in many species. Indeed, aerial and canopy roots are a common feature of wet TMCF (Gill 1969, Nadkarni 1981, Santiago *et al*. 2000). Low-oxygen conditions also may favour losses of N by denitrification, and high losses of soil nutrients may accompany the greater hydrologic outputs in wetter tropical soils. Although losses of mineral N forms should be constrained on N-limited sites (but see Brookshire *et al.* 2012), leaching of organic N may be favoured by the accumulation of recalcitrant organic matter under cool or anaerobic conditions (Perakis & Hedin 2002). Also, by restricting the depth distribution of tree roots, anaerobic conditions may either restrict access to available nutrients or promote their losses. It is also possible that shallow rooting in some TMCF reflects ease of access to soil water and superficial nutrient supply; however, as noted previously, shallow rooting also may reduce the

wind-firmness of trees and increase the frequency of disturbance with possible long-term effects on nutrient losses.

Topographic effects

Variation of topography in tropical montane landscapes clearly plays a role in regulating TMCF structure, and provides further indications about the contributing mechanisms. Most TMCFs occur under highly variable topography including steeper slopes (Asner *et al.* 2014) and more landslides (Larsen & Torres-Sanchez 1998, Shreve 1914) than lower montane landscapes. Tanner (1977) demonstrated that systematic variation in forest structure of TMCF was related to landscape position and subsequent studies have confirmed this relationship (Wardle *et al.* 2015). For example, several studies report that canopy height in TMCF is lower on steep slopes (Roman *et al.* 2010), an observation that would also question the universal role of poor soil drainage in shaping TMCF ecosystems. This pattern might be explained in part by disturbance history associated with landslides or more generally by soil stability and tree rooting (Soethe *et al.* 2006). Werner & Homeier (2014) proposed a nutrient feedback mechanism to explain striking contrasts in forest structure and composition between slope positions in tropical montane landscapes: downslope nutrient transport could result in spatial contrasts in soil nutrient availability, reinforced by differences in organic recycling owing to litter quality responses to soil fertility. However, in some situations TMCF stunting is most strongly expressed in saddles where soils are enriched and moisture may accumulate (Wilcke *et al.* 2010). Girardin *et al.* (2014b) associated the strong expression of the TMCF structural features with local topography that favoured cloud convergence and formation. At Monteverde, Costa Rica, maximum TMCF stunting also has been associated with topographic effects on wind exposure and cloud formation (Lawton

1982, Lawton *et al.* 2010). Conversely, Schwarzkopf *et al.* (2011) noted that extreme differences in TMCF structure were unrelated to topographic variables in an Andean landscape.

Forest structure in TMCF

Stunting of trees and low canopy height are commonly observed in TMCF (Grubb 1977). Because trees in closed-canopy forest compete intensely for the light resource, height growth is important to individual tree success. Thus, unless there are other advantages of being stunted, trees would be expected to attain the maximum height that resource limitations permit; however, greater relative competition for soil resources than light in TMCF might contribute to lower investment in height growth. In any case, all the environmental factors that constrain plant production (low insolation, cold temperatures, nutrient limitation) undoubtedly contribute to tree stunting in TMCF (Figure 1). Less clear is the explanation for increases in the ratio of tree diameter to height with increasing elevation on tropical mountains (Grubb 1977, Lieberman *et al.* 1996). The consistency of this relationship is indicated by a summary for 11 altitudinal transects in different regions of the world (Figure 2).

The factors influencing D:H relationships in trees have been analyzed and debated, and include mechanical constraints (King *et al.* 2009, McMahon 1973); drought and hydraulic constraints (Niklas & Spatz 2004, Sperry *et al.* 2008); influences of neighbouring trees on both access to light and exposure to wind (King 1996); and phylogenetic constraints. Because canopy height is low in TMCF the advantage of monopodial growth to limit light competition is reduced and multi-stemmed architecture can have selective value (Givnish 1984). Such architecture is common in many TMCFs (Figure 1; Bellingham & Sparrow 2009, Culmsee *et al.* 2010).

In addition, trees would be expected to maintain a safety factor against mechanical buckling to reduce risks associated with storm winds (de Gouvenain & Silander 2003) although for multi-stemmed individuals a sprouting trunk can compensate for failure of stems. King *et al.* (2009) suggested trees in locations protected from wind in lowland tropical forest approached the theoretical buckling height, whereas most TMCF forests exhibit very low values (Table 2). Feldpausch *et al.* (2011) summarized the factors related to D:H variation across a large data set for the world's tropical forests. Among the climatic influences was an effect of temperature, but this effect was confined only to the influence of altitude, reflecting the relationships in Figure 2. Recently, Asner *et al.* (2014) observed that TMCF trees maintained crown shapes in which a greater proportion of the foliage was held low in the canopy than for trees at lower altitudes which might contribute to mechanical stability.

Perhaps the single most likely cause of the increasing D:H ratio with altitude is increasing windspeeds (Woodward 1993). As noted above Lawton (1982) attributed high D:H ratio in a cloud-forest tree species to wind exposure, and King *et al.* (2009) observed a higher mechanical safety factor for lowland rain-forest trees on exposed ridges than protected coves. The possible role of soil properties influencing tree stability has also been suggested (Soethe *et al.* 2006) as shallow rooting in thin or waterlogged soils could necessitate wide root crowns for trees to remain wind-firm.

Another possible factor influencing the low canopy height and high D:H ratio of TMCF is the extra canopy loading associated with high epiphyte and canopy soil biomass in the cloud immersion zone (Köhler *et al.* 2007). Although the dry biomass of canopy epiphytes is typically only a small fraction of the tree canopy mass, epiphytic bryophytes can hold several times their dry mass in water when they are immersed in

clouds (Köhler *et al.* 2007), and canopy soil adds still more to the canopy load (Bohlman *et al.* 1995). The water-saturated mass of canopy epiphytes in several cloud forests ranges from 13 to 45 Mg ha^{-1}, values which are substantial relative to leaf and branch biomass. For example, the biomass of wet epiphytes and canopy soil in the Monteverde cloud forest in Costa Rica (33.1 Mg ha^{-1}; Nadkarni 1984) is about half of leaf and branch biomass (60 Mg ha^{-1}; Nadkarni *et al.* 2004), and comparable proportions are likely in other cases (Horwath 2011). The theoretical critical height ($H_{critical}$) at which buckling would occur can be calculated on the basis of tree architecture and wood properties (Niklas 1994), and notably, the ratio of actual canopy height to buckling height (H_{actual}:$H_{critical}$; the static mechanical safety factor) is particularly low for some epiphyte-laden forests (0.25-0.31; Table 2); much higher values are noted for lower montane forest (e.g. 0.7 at 750 m asl in Costa Rica; Lieberman *et al.* 1996). However, some stunted cloud forests have much smaller epiphyte loads; the H_{actual}:$H_{critical}$ ratio of the stunted mor forest in Jamaica is 0.30, yet the epiphyte mass is only 2.1 Mg ha^{-1}. Thus, although the possible role of mechanical constraints associated with epiphyte loading in stunted TMCF deserves further study, the evidence at present is not conclusive.

The role of phylogenetic factors affecting canopy height and forest structure also deserves attention. In some notable cases particular species – e.g. from Pinaceae, Fagaceae, *Eucalyptus* spp. -- attain much greater heights within the cloud zone than the species that form the main canopy. In the Dominican Republic, the native *Pinus occidentalis* grows along the entire elevation gradient, attains heights much greater than the TMCF trees and is also somewhat stunted in the main cloud immersion zone (Martin *et al*. 2007). Plastic species such as this could lend themselves to experimental investigations of the relative importance of the potential causal factors. For example,

temperature and light can be varied independently in field experiments with potted plants, though it will be more difficult to manipulate direct contact of leaves with fog or canopy epiphyte loading.

Feedbacks and non-linearity in TMCF

Early concepts and observations in tropical montane forest ecology suggested the existence of spatial discontinuities in the composition and structure of vegetation along the altitudinal gradient (Holdridge 1967). Such a pattern might arise either as a result of discontinuity in one or more key macro-environmental drivers (e.g. geologic substrates, topography or climatic variables) or because of strong feedbacks between vegetation (or other biota) and micro-environmental factors. Although some detailed studies have discounted the existence of discontinuous variation in forest composition across the altitudinal gradient in tropical mountains (Lieberman *et al.* 1996), some cases of sharp discontinuities involving the vegetation feedback switch have been documented. For example, Martin *et al.* (2007) demonstrated that a sharp ecotone between species-rich TMCF and monodominant pine forest is maintained by vegetation effects on natural fire disturbance, together with the influence of frequent cloud immersion especially during the dry season (Martin & Fahey 2014).

Distinctive TMCF structure, particularly in its most extreme form, also may depend upon feedback mechanisms in which vegetation traits and soil properties reinforce the limitation on the productivity and stature of the forest (Werner & Homeier 2014). Recent syntheses conclude that nutrient limitation of TMCF productivity results not from lower amounts of limiting soil nutrients but by the inability of trees to access these nutrients (Benner *et al.* 2010, Roman *et al.* 2010). Some evidence supports a positive feedback mechanism whereby litter of lower chemical quality is produced in

TMCF, suppressing efficient recycling of nutrients by microbial decomposition (Schuur *et al.* 2001, Werner & Homeier 2014). The role of soil saturation on such a feedback also seems plausible: inhibition of root function by anaerobic soil could reduce water uptake (Weaver *et al.* 1973) reinforcing soil saturation and contributing to low litter quality (Schuur 2001).

An additional vegetation-soil feedback that contributes to TMCF structure and function is the apparently high proportional allocation of C to root systems (Girardin *et al.* 2010, Kitayama & Aiba 2002, Moser *et al.* 2011), leaving less C to support above-ground growth and LAI. Again, a feedback involving soil saturation seems plausible. For example, the higher below-ground allocation could limit LAI, and thereby promote soil saturation by reducing AET. Also, observations of Leuschner *et al.* (2007) emphasize the much higher coarse-root biomass in high-elevation TMCF with frequently saturated soils; high allocation to coarse roots could contribute to overcoming structural stability problems in saturated soils (Coutts 1983, Soethe *et al.* 2006).

In conclusion, recent research has contributed to an improved understanding of tropical montane cloud forest structure and function and its dependence on unique climatic conditions in the altitudinal zone where fog is persistent (Figure 1). However, additional research is needed to clarify several features of TMCF ecosystem dynamics: (1) The role of phylogeny vs. phenotype in shaping the characteristic traits of TMCF vegetation; (2) Photosynthetic physiology of TMCF foliage in fog-shrouded environments; (3) Below-ground carbon allocation and fine-root production and turnover in TMCF; (4) Factors leading to N vs. P limitation of TMCF productivity, including the role of mycorrhizal associations; (5) The role of saturated soils and low soil oxygen in TMCF ecosystems; (6) Causes of contrasting patterns of variation in TMCF

structure in relation to topographic position among different locations; (7) Drivers of high diameter:height ratio of TMCF; (8) The role of high epiphyte abundance in regulating TMCF ecosystem dynamics.

Recognizing the great variation of vegetation structure and dynamics among TMCF locations, comparative research approaches across TMCF sites should help to provide new insights into the causal factors driving the behaviour of these remarkable forests.

LITERATURE CITED

AIBA, S. & KITAYAMA, K. 1999. Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecol*ogy 140:139–157.

ASNER, G. P., ANDERSON, C. B., MARTIN, R. E., KNAPP, D. E., TUPAYACHI, R., SINCA, F. & MALHI, Y. 2014. Landscape-scale changes in forest structure and functional traits along an Andes-to-Amazon elevation gradient. *Biogeosciences* 11*:*843-856.

AYLETT, G. P. 1985. Irradiance interception, leaf conductance and photosynthesis in Jamaican upper montane rain forest trees. *Photosynthetica* 19:323–337.

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

BELLINGHAM, P. J. & SPARROW, A. D. 2009. Multi-stemmed trees in montane rain forests: their frequency and demography in relation to elevation, soil nutrients and disturbance. *Journal of Ecology* 97:472–483.

BENNER, J. W. & VITOUSEK, P. M. 2007. Development of a diverse epiphyte community in response to phosphorus fertilization. *Ecology Letters* 10:628-636.

BENNER, J. W., CONROY, S., LUNCH, C. K., TOYODA, N. & VITOUSEK, P. M. 2007. Phosphorus fertilization increases the abundance and nitrogenase activity of the cyanolichen *Pseudocyphellaria crocata* in Hawaiian montane forests. *Biotropica* 39:400-405.

BENNER, J., VITOUSEK, P. M. & OSTERTAG, R. 2010. Nutrient cycling and nutrient limitation in tropical montane cloud forests. Pp. 90–100 in Bruijnzeel, L. A., Scatena, F. N & Hamilton, L. S. (eds.). *Tropical montane cloud forests: science for conservation and management.* Cambridge University Press, New York.

BOHLMAN, S. A., MATELSON, T. J. & NADKARNI, N M. 1995. Moisture and temperature patterns of canopy humus and forest floor soil of a montane cloud forest, Costa Rica. *Biotropica* 27:13-19.

BROOKSHIRE, E. N. J., HEDIN, L. O., NEWBOLD, J. D., SIGMAN, D. M. & JACKSON, J. K. 2012. Sustained losses of bioavailable nitrogen from montane tropical forests. *Nature Geoscience* 5:123-126.

BROWN, W. H. 1919. *Vegetation of Philippine mountains, the relation between environment and physical types at different altitudes.* Bureau of Printing, Manila. 434 pp**.**

BRUIJNZEEL, L. A. & HAMILTON, L.S. 2000. *Decision time for cloud forests*. International Hydrological Programme. IHP Humid Tropics Programme series, no. 13. Paris, UNESCO.

BRUIJNZEEL, L. A. & VENEKLAAS, E. 1998. Climatic conditions and tropical montane forest productivity: the fog has not lifted yet. *Ecology* 79:3-9.

BRUIJNZEEL, L. A., SCATENA, F. N. & HAMILTON, L. S. 2010. *Tropical montane cloud forests: science for conservation and management*. Cambridge University Press, Cambridge. 740 pp.

BRUNDRETT, M. C. 2009. Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. *Plant and Soil* 320:37-77.

CLEVELAND, C. C., TOWNSEND, A. R., TAYLOR, P., ALVAREZ-CLARE, S., BUSTAMANTE, M., CHUYONG, G., DOBROWSKI, S. Z., GRIERSON, P., HARMS, K. E., HOULTON, B. Z., MARKLEIN, A., PARTON, W., PORDER, S., REED, S. C., SIERRA, C. A., SILVER, W. L., TANNER, E. V. J. & WIEDER, W. R. 2011. Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis. *Ecology Letters* 14:939-947.

CORDERO, R. A. 1999. Ecophysiology of *Cecropia schreberiana* saplings in two wind regimes in an elfin cloud forest: growth, gas exchange, architecture and stem biomechanics. *Tree Physiology* 19:153-163.

COUTTS, M. P. 1983. Root architecture and tree stability. *Plant and Soil* 71:171–188.

CULMSEE, H., LEUSCHNER, C., MOSER, G. & PITOPANG, R. 2010. Forest aboveground biomass along an elevational transect in Sulawesi, Indonesia, and the role of Fagaceae in tropical montane rain forests. *Journal of Biogeography* 37:960–974.

FELDPAUSCH, T. R., BANIN, L., PHILLIPS, O. L., BAKER, T. R., LEWIS, S. L., QUESADA, C. A., AFFUM-BAFFOE, K., ARETS, E. J. M. M., BERRY, N. J., BIRD, M., BRONDIZIO, E. S., DE CAMARGO, P., CHAVE, J., DJAGBLETEY, G., DOMINGUES, T. F., DRESCHER, M., FEARNSIDE, P. M., FRANÇA, M. B., FYLLAS, N. M., LOPEZ-GONZALEZ, G., HLADIK, A., HIGUCHI, N., HUNTER, M. O., IIDA, Y., SALIM, K. A., KASSIM, A. R., KELLER, M. KEMP, J., KING, D. A., LOVETT, J. C., MARIMON, B. S., MARIMON-JUNIOR, B. H., LENZA, E., MARSHALL, A. R., METCALFE, D. J., MITCHARD, E. T. A., MORAN, E. F., NELSON, B. W., NILUS, R., NOGUEIRA, E. M., PALACE, M., PATIÑO, S., PEH, K. S.-H., RAVENTOS, M. T., REITSMA, J. M., SAIZ, G., SCHRODT, F., SONKÉ, B., TAEDOUMG, H. E., TAN, S., WHITE, L., WÖLL, H. & LLOYD, J. 2011. Height-diameter allometry of tropical forest trees. *Biogeosciences* 8:1081-1106.

FISHER, J. B., MALHI, Y., TORRES, I. C., METCALFE, D. B., VAN DE WEG, M. J., MEIR, P., SILVA-ESPEJO, J. E. & HUASCO, W. H. . 2013. Nutrient limitation in rainforests and cloud forests along a 3,000-m elevation gradient in the Peruvian Andes. *Oecologia* 172:889-902.

FORMAN, R. T. T. 1975. Canopy lichens with blue-green algae: a nitrogen source in a Colombian rainforest. *Ecology* 56:1176–1184.

GENTRY, A. H., CHURCHILL, S. P., BALSLEV, H., FORERO, E., & LUTEYN, J. L. 1995. Patterns of diversity and floristic composition in Neotropical montane forests. Pp. 103-126 in Churchill, S. P., Balslev, H., Forero, E. & Luteyn, J. L. (eds.). *Biodiversity and conservation of Neotropical montane forests. Proceedings of the Neotropical Montane Forest Biodiversity and Conservation symposium, The New York Botanical Garden, 21-26 June 1993*. New York Botanical Garden, New York.

GIAMBELLUCA, T. W., DELAY, J. K., NULLET, M. A., SCHOLL, M. A. & GINGERICH, S. B. 2010. Interpreting canopy water balance and fog screen observations: separating cloud water from wind - blown rainfall at two contrasting forest sites in Hawaiʻi. Pp. 342-351 in Bruijnzeel, L. A., Scatena, F. N. & Hamilton, L. S. (eds.). *Tropical montane cloud forests: science for conservation and management*. Cambridge University Press, New York.

GILL, A. M. 1969. The ecology of an elfin forest in Puerto Rico, 6. Aerial roots. *Journal of the Arnold Arboretum* 50:197-209.

GIRARDIN, C. A., MALHI, Y., ARAGÃO, L. E. O. C., MAMANI, M., HUASCO, W. H., DURAND, L., FEELEY, K. J., RAPP, J., SILVA-ESPEJO, J. E., SILMAN, M. R., SALINAS, N. & WHITTAKER, R. J. 2010. Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology* 16*:*3176-3192.

GIRARDIN, C. A. J., ARAGÃO, L. E. O. C., MALHI, Y., HUARACA HUASCO, W., METCALFE, D. B., DURAND, L., MAMANI, M., SILVA-ESPEJO, J. E. & WHITTAKER, R. J. 2013. Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests. *Global Biogeochemical Cycles* 27:252-264.

GIRARDIN, C. A. J., FARFAN-RIOS, W., GARCIA, K., FEELEY, K. J., JØRGENSEN, P.M., MURAKAMI, A. A., PÉREZ, L. C., SEIDEL, R., PANIAGUA, N., FUENTES CLAROS, A. F., MALDONADO, C., SILMAN, M., SALINAS, N. REYNEL, C., NEILL, D. A., SERRANO, M., CABALLERO, C. J., La TORRE-CUADROS, M., MACIA, M. J., KILLEEN, T. J. & MALHI, Y. 2014a. Spatial patterns of above-ground structure, biomass and composition in a network of six Andean elevation transects. *Plant Ecology & Diversity* 7:161-171.

GIRARDIN, C. A. J., SILVA ESPEJOB, J. E., DOUGHTY, C. E., HUASCO, W. H., METCALFE, D..B., DURAND-BACA, L., MARTHEWS, T. R., ARAGAO, L. E. O. C., FARFÃN-RIOS, W.,

GARCIA-CABRERA, K., HALLADAY, K., FISHER, J. B., GALIANO-CABRERA, D. F., HUARACA-QUISPE, L. P., ALZAMORA-TAYPE, I., EGUILUZ-MORA, L., SALINAS-REVILLA, N., SILMAN, M. R., MEIR, P. & MALHI, Y. 2014b. Productivity and carbon allocation in a tropical montane cloud forest in the Peruvian Andes. *Plant Ecology & Diversity* 7:107-123.

GIVNISH T. J. 1984. Leaf and canopy adaptations in tropical forests. Pp. 51–84 in Medina, E., Mooney, H. A. & Vazquez-Yanes, C. (eds.). *Physiological ecology of plants of the Wet Tropics*. Dr Junk Publisher, The Hague.

GOLLEY, F., McGINNIS, J. & CLEMENTS, R. 1971. La biomasa y la estructura de algunos bosque de Darien, Panama. *Turrialba* 21:189-196.

GRADSTEIN, S. R., OBREGON, A., GEHRIG, C. & BENDIX, J. 2010. Tropical lowland cloud forest: a neglected forest type. Pp. 130-133 in Bruijnzeel, L. A., Scatena, F. N. & Hamilton, L. S. (eds.). *Tropical montane cloud forests: science for conservation and management.* Cambridge University Press, New York.

DE GOUVENAIN, R. C. & SILANDER, J. A. 2003. Do tropical storm regimes influence the structure of tropical lowland rain forests? *Biotropica* 35:166-180.

GRIEVE, T. G. A., PROCTOR, J. & COUSINS, S. A. 1990. Soil variation with altitude on Volcán Barva, Costa Rica. *Catena* 17:525-534.

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

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

HAFKENSCHEID, R. L. L. J. 2000. *Hydrology and biogeochemistry of tropical montane rain forests of contrasting stature in the Blue Mountains, Jamaica.* Doctoral dissertation, Vrije Universiteit Amsterdam. 302 pp.

HÄGER, A. & DOHRENBUSCH, A. 2011. Hydrometeorology and structure of tropical montane cloud forests under contrasting biophysical conditions in north-western Costa Rica. *Hydrological Processes* 25:392–401.

HIETZ, P. 2010. Ecology and ecophysiology of epiphytes in tropical montane cloud forests. Pp. 67-76 in Bruijnzeel, L. A., Scatena, F. N. & Hamilton, L. S. (eds.). *Tropical montane cloud forests: science for conservation and management.* Cambridge University Press, New York.

HIETZ, P., WANEK, W., WANIA, R. & NADKARNI, N. M. 2002. Nitrogen-15 natural abundance in a montane cloud forest canopy as an indicator of nitrogen cycling and epiphyte nutrition. *Oecologia* 131:350-355.

HOLDRIDGE, L. R. 1967. *Life zone ecology.* Tropical Science Center, San Jose. 206 pp.

HOLWERDA, F., BRUIJNZEEL, L. A., OORD, A. L. & SCATENA, F. N. 2010. Fog interception in a Puerto Rico elfin cloud forest: a wet-canopy water budget approach. Pp. 282-292 in Bruijnzeel, L. A., Scatena, F. N. & Hamilton, L. S. (eds.). *Tropical montane cloud forests*: s*cience for conservation and management*. Cambridge University Press, New York.

HOMEIER, J., HERTEL, D., CAMENZIND, T., CUMBICUS, N. L., MARAUN, M., MARTINSON, G. O., POMA, L. N., RILIG, M. C., SANDMANN, D., SCHEU, S., VELDKAMP, E., WILCKE, W., WULLAERT, H. & LEUSCHNER, C. 2012. Tropical Andean forests are highly susceptible to nutrient inputs - rapid effects of experimental N and P addition to an Ecuadorian montane forest. *Plos One* 7:e347128.

HORWATH, A. B. 2011. *Epiphytic bryophytes as cloud forest indicators: stable isotopes, biomass and diversity along an altitudinal gradient in Peru.* PhD Thesis, University of Cambridge.

HOULTON, B. Z., WANG, Y. P., VITOUSEK, P. M. & FIELD, C. B. 2008. A unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature* 454:327-330.

HOWARD, R. A. 1968. Ecology of an elfin forest in Puerto Rico. 1. Introduction and composition studies. *Journal of the Arnold Arboretum* 49:381-418.

JARVIS, A. & MULLIGAN, M. 2010. The climate of cloud forests. Pp. 39-56 in Bruijnzeel, L. A., Scatena, F. N. & Hamilton, L. S. (eds.). *Tropical montane cloud forests: science for conservation and management.* Cambridge University Press, New York.

KESSLER, M., PARRIS, B. S. & KESSLER, E. 2001. A comparison of the tropical montane pteridophyte floras of Mount Kinabalu, Borneo, and Parque Nacional Carrasco, Bolivia. *Journal of Biogeography* 28:611–622.

KING, D. A. 1996. Allometry and life history of tropical trees. *Journal of Tropical Ecology* 12:25-44.

KING, D. A., DAVIES, S. J., TAN, S. & NOOR, N. S. M. 2009. Trees approach gravitational limits to height in tall lowland forests of Malaysia. *Functional Ecology* 23:284-291.

KITAYAMA, K. 1992. An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio* 102:149–171

KITAYAMA, K. & AIBA, S.-I. 2002. Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *Journal of Ecology* 90:37–51.

KÖHLER, L., TOBÓN, C., FRUMAU, K. F. A. & BRUIJNZEEL, L. A. 2007. Biomass and water storage dynamics of epiphytes in old-growth and secondary montane cloud forest stands in Costa Rica. *Plant Ecology* 193:171-184.

KRÖMER, T., KESSLER, M., GRADSTEIN, S. R. & ACEBEY, A. 2005. Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. *Journal of Biogeography* 32:1799–1809.

LARSEN, M. C., & TORRES-SÁNCHEZ, A. J. 1998. The frequency and distribution of recent landslides in three montane tropical regions of Puerto Rico. *Geomorphology* 24:309-331.

LAWTON, R. O. 1982. Wind stress and elfin stature in a montane rain forest tree: an adaptive explanation. *American Journal of Botany* 69:1224-1230.

LAWTON, R. O., NAIR, U. S., RAY, D., REGMI, A., POUNDS, J. A. & WELCH, R. M. 2010. Quantitative measures of immersion in cloud and the biogeography of cloud forests. Pp. 217-227 in Bruijnzeel, L. A., Scatena, F. N. & Hamilton, L. S. (eds.). *Tropical montane cloud forests: science for conservation and management.* Cambridge University Press, New York.

LETTS, M. G. & MULLIGAN, M. 2005. The impact of light quality and leaf wetness on photosynthesis in north-west Andean tropical montane cloud forest. *Journal of Tropical Ecology* 21:549-557.

LEUSCHNER, C., MOSER, G., BERTSCH, C., RODERSTEIN, M., & HERTEL, D. 2007. Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador. *Basic and Applied Ecology* 8:219-230.

LIEBERMAN, D., LIEBERMAN, M., PERALTA, R. & HARTSHORN, G. S. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology* 84:137-152.

MARSCHNER, H. & DELL, B. 1994. Nutrient uptake in mycorrhizal symbiosis. *Plant and Soil* 159: 89-102.

MARTIN, P. H. & FAHEY, T. J. 2014. Mesoclimate patterns shape the striking vegetation mosaic in the Cordillera Central, Dominican Republic. *Arctic, Antarctic and Alpine Research* 46:755-765.

MARTIN, P. H., SHERMAN, R. E. & FAHEY, T. J. 2007. Tropical montane forest ecotones: climate gradients, natural disturbance, and vegetation zonation in the Cordillera Central, Dominican Republic. *Journal of Biogeography* 34:1792–1806.

MATSON, A. L., CORRE, M. D., BURNEO, J. I. & VELDKAMP, E. 2015. Free-living nitrogen fixation responds to elevated nutrient inputs in tropical montane forest floor and canopy soils of southern Ecuador. *Biogeochemistry* 122:281-294.

McDOWELL, W. H. & ASBURY, C. E. 1994. Export of carbon, nitrogen, and major ions from three tropical montane watersheds. *Limnology and Oceanography* 39:111-125.

McJANNET, D. L., WALLACE, J. S. & REDDELL, P. 2010. Comparative water budgets of a lower and an upper montane cloud forest in the Wet Tropics of northern Australia. Pp. 479-490 in Bruijnzeel, L. A., Scatena, F. N. & Hamilton, L. S. (eds.). *Tropical montane cloud forests*: *science for conservation and management.* Cambridge University Press, New York.

McMAHON, P. 1973. Size and shape in biology: elastic criteria impose limits on biological proportions, and consequently on metabolic rates. *Science* 179:1201-1204.

MILDENBERGER, K., BEIDERWIEDEN, E., HSIA, Y.-J. & KLEMM, O. 2009. CO_2 and water vapor fluxes above a subtropical mountain cloud forest—the effect of light conditions and fog . *Agricultural and Forest Meteorology* 149:1730-1736.

MOSER, G., HERTEL, D. & LEUSCHNER, C. 2007. Altitudinal change in LAI and stand leaf biomass in tropical montane forests: a transect study in Ecuador and a pan-tropical meta- analysis. *Ecosystems* 10:924-935.

MOSER, G., LEUSCHNER, C., HERTEL, D., GRAEFE, S., SOETHE, N. & IOST, S. 2011. Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): the role of the belowground compartment. *Global Change Biology* 17:2211-2226.

MULLIGAN, M. 2010. Modeling the tropics-wide extent and distribution of cloud forest and cloud forest loss, with implications for conservation priority. Pp. 14-38 in Bruijnzeel, L. A., Scatena, F. N. & Hamilton, L. S. (eds.). *Tropical montane cloud forests: science for conservation and management.* Cambridge University Press, New York.

NADKARNI, N. M. 1981. Canopy roots: convergent evolution in rainforest nutrient cycles. *Science* 214:1023-2024.

NADKARNI, N. M. 1984. Epiphytic biomass and nutrient capital of a neotropical elfin forest. *Biotropica* 16:249-256.

NADKARNI, N. M., SCHAEFER, D. A., MATELSON, T. J. & SOLANO, R. 2004. Biomass and nutrient pools of canopy and terrestrial components in primary and secondary montane cloud forest, Costa Rica. *Forest Ecology and Management* 198:223–236.

NIKLAS, K. J. 1994. Interspecific allometries of critical buckling height and actual plant height. *American Journal of Botany* 81:1275-1279.

NIKLAS, K. J. & SPATZ, H. C. 2004. Growth and hydraulic (not mechanical) constraints govern the scaling of tree height and mass. *Proceedings of the National Academy of Sciences USA* 101:15661-15663.

ODUM, H. T. 1970. Rain forest structure and mineral-cycling homeostasis. Pp. H3-H52 in Odum, H. T. & Pigeon, R. F. (eds.). *A tropical rainforest.* Division of Technical Information, U.S. Atomic Energy Commission, Oakridge.

PERAKIS, S. S. & HEDIN, L. O. 2002. Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds. *Nature* 415:416-419.

PROCTOR, J., LEE, Y. F., LANGLEY, A. M., MUNRO, W. R. & NELSON, T. 1988. Ecological studies on Gunung Silam, a small ultrabasic mountain in Sabah, Malaysia. I. Environment, forest structure and floristics. *Journal of Ecology* 76:320–340.

RAICH, J. W., RUSSELL, A. E. & VITOUSEK, P. M. 1997. Primary productivity and ecosystem development along an elevational gradient on Mauna Loa, Hawai'i. *Ecology* 78:707–721.

RAINS, K. C., NADKARNI, N. M. & BLEDSOE, C. S. 2003. Epiphytic and terrestrial mycorrhizas in a lower montane Costa Rican cloud forest. *Mycorrhiza* 13:257-264.

RAPP, J. M., SILMAN, M. R., CLARK, J. S., GIRARDIN, D. G., GALIANO, D. & TITO, R. 2012. Intra-and interspecific tree growth across a long altitudinal gradient in the Peruvian Andes. *Ecology* 93:2061-2072.

ROMAN, L., SCATENA, F. N. & BRUIJNZEEL, L. A. 2010. Global and local variations in tropical montane cloud forest soils. Pp. 77-89 in Bruijnzeel L. A., Scatena F. N. & Hamilton, L. S. (eds.). *Tropical montane cloud forests: science for conservation and management.* Cambridge University Press, Cambridge.

SALAZAR, L., HOMEIER, J., KESSLER, M., ABRAHAMCZYK, S., LEHNERT, M., KRÖMER, T. & KLUGE, J. 2013. Diversity patterns of ferns along elevational gradients in Andean tropical forests. *Plant Ecology & Diversity* 8:13-24.

SALINAS, N., MALHI, Y., MEIR, P., SILMAN, M., ROMAN CUESTA, R., HUAMAN, J., SALINAS, D., HUAMAN, V., GIBAJA, A., MAMANI, M. & FARFAN, F. 2011. The sensitivity of tropical leaf litter decomposition to temperature: results from a large-scale leaf translocation experiment along an elevation gradient in Peruvian forests. *New Phytologist* 189:967–977.

SANTIAGO, L. S., GOLDSTEIN, G., MEINZER, F. C., FOWNES, J. & MUELLER-DOMBOIS, D. 2000. Transpiration and forest structure in relation to soil waterlogging in a Hawaiian montane cloud forest. *Tree Physiology* 20:673-681.

SANTIAGO, L. S., JONES, T. J. & GOLDSTEIN, G. 2010. Physiological variation in Hawaiian *Metrosideros polymorpha* across a range of habitats: from dry forests to cloud forests. Pp. 456-464 in Bruijnzeel, L. A., Scatena, F. N. & Hamilton, L. S. (eds.). *Tropical montane cloud forests: science for conservation and management*. Cambridge University Press, Cambridge.

SCHAWE, M., GEROLD, G., BACH, K. & GRADSTEIN, S. R. 2010. Hydrometeorological patterns in relation to montane forest types along an elevational gradient in the Yungas of Bolivia. Pp. 199-207 in Bruijnzeel, L. A., Scatena, F. N. & Hamilton, L. S. (eds.). *Tropical montane cloud forests: science for conservation and management.* Cambridge University Press, Cambridge.

SCHUUR, E. A. G. 2001. The effect of water on decomposition dynamics in mesic to wet Hawaiian montane forests. *Ecosystems* 4:259-273.

SCHUUR, E. A. G., CHADWICK, O. A. & MATSON, P. A. 2001. Carbon cycling and soil carbon storage in mesic to wet Hawaiian montane forests. *Ecology* 82:3182-3196.

SCHWARZKOPF, T., RIHA, S. J., FAHEY, T. J., & DEGLORIA, S. 2011. Are cloud forest tree structure and environment related in the Venezuelan Andes? *Austral Ecology* 36:280-289.

SHERMAN, R. E., MARTIN, P. M. & FAHEY, T. J. 2005. Vegetation-environment relationships in forest ecosystems of the Cordillera Central, Dominican Republic. *Journal of the Torrey Botanical Society* 132:293-310.

SHREVE, F. 1911. Studies on Jamaican Hymenophyllaceae. *Botanical Gazette* 51:184-209.

SHREVE, F. 1914. *A montane rain-forest: a contribution to the physiological plant geography of Jamaica*. Carnegie Institution of Washington, Washington, D.C. 176 pp.

SILVER, W., LUGO, A. E. & KELLER, M. 1999. Soil oxygen availability and biogeochemistry along rainfall and topographical gradients in upland wet tropical forest soils. *Biogeochemistry* 44:301–328.

SILVER, W. L., THOMPSON, A. W., HERMAN, D. J. & FIRESTONE, M. K. 2010. Is there evidence for limitations to nitrogen mineralization in upper montane tropical forests? Pp. 418-427 in Bruijnzeel, L. A., Scatena, F. N. & Hamilton, L. S. (eds.). *Tropical montane cloud forests: science for conservation and management.* Cambridge University Press, New York.

SOETHE, N., LEHMANN, J. & ENGELS, C. 2006. Root morphology and anchorage of six native tree species from a tropical montane forest and an elfin forest in Ecuador. *Plant and Soil* 279:173-185.

SOETHE, N., LEHMANN, J., & ENGELS, C. 2008. Nutrient availability at different altitudes in a tropical montane forest in Ecuador. *Journal of Tropical Ecology* 24:397-406.

SPERRY, J. S., MEINZER, F. C. & McCULLOH, K. A. 2008. Safety and efficiency conflicts in hydraulic architecture: scaling from tissues to trees. *Plant, Cell & Environment* 31:632-645.

SUGDEN, A. M. 1985. Leaf anatomy in a Venezuelan montane forest. *Botanical Journal of the Linnean Society* 90:231-241.

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

TANNER, E. V. J. & KAPOS, V. 1982. Leaf structure of Jamaican upper montane rain-forest trees. *Biotropica* 14:16-24.

TANNER, E. V. J., VITOUSEK, P. M. & CUEVAS, E. 1998. Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology* 79:10-22.

TOBÓN, C., BRUIJNZEEL, L. A. FRUMAU, K. F. A. & CALVO-ALVARADO, J. C. 2010. Changes in soil physical properties after conversion of tropical montane cloud forest to pasture in northern Costa Rica. Pp. 502–515 in Bruijnzeel, L. A., Scatena, F. N. & Hamilton, L. S. (eds.). *Tropical montane cloud forests: science for conservation and management.* Cambridge University Press, New York.

TRANQUILLINI, W. 1979. *Physiological ecology of the alpine timberline.* Ecological Studies Vol. 31. Springer Verlag, Berlin. 137 pp.

UNGER, M., HOMEIER, J. & LEUSCHNER, C. 2012. Effects of soil chemistry on tropical forest biomass and productivity at different elevations in the equatorial Andes. *Oecologia* 170:263-274.

VAN DE WEG, M. J., MEIR, P., GRACE, J. & ATKIN, O. K. 2009. Altitudinal variation in leaf mass per unit area, leaf tissue density and foliar nitrogen and phosphorus content along an Amazon-Andes gradient in Peru. *Plant Ecology & Diversity* 2:243-254.

VAN DE WEG, M. J., MEIR, P., GRACE, J. & RAMOS, G. D. 2012. Photosynthetic parameters, dark respiration and leaf traits in the canopy of a Peruvian tropical montane cloud forest. *Oecologia* 168:23-34.

WARDLE, D. A., BELLINGHAM, P. J., KARDOL, P., GIESLER, R. & TANNER, E. V. J. 2015. Coordination of aboveground and belowground responses to local-scale soil fertility differences between two contrasting Jamaican rain forest types. *Oikos* 124:285-297.

WEAVER, P. L., BYER, M. D. & BRUCK, D. L. 1973 Transpiration rates in the Luquillo Mountains of Puerto Rico. *Biotropica* 5:123–133.

WEAVER, P.L., MEDINA, E., POOL, D., DUGGER, K., GONZALEZ-LIBOY, J. & CUEVAS, E. 1986. Ecological observations in the dwarf forest of the Luquillo Mountains of Puerto Rico. *Biotropica* 18:79–85.

WERNER, F. A. & HOMEIER, J. 2015. Is tropical montane forest heterogeneity promoted by a resource-driven feedback cycle? Evidence from nutrient relations, herbivory and litter decomposition along a topographical gradient. *Functional Ecology* 29:430-440.

WILCKE, W., BOY, J., GOLLER, R., FLEISCHBEIN, K., VALAREZO, C. & ZECH, W. 2010. Effect of topography on soil fertility and water flow in an Ecuadorian lower montane forest. Pp. 402-409 in Bruijnzeel, L. A., Scatena, F. N. & Hamilton, L. S. (eds.). *Tropical*

montane cloud forests: science for conservation and management. Cambridge University Press, New York.

WITTICH, B., HORNA, V., HOMEIER, J. & LEUSCHNER, C. 2012. Altitudinal change in the photosynthetic capacity of tropical trees: a case study from Ecuador and a pantropical literature analysis. *Ecosystems* 15:958–973

WOODWARD, F. I. 1993. The lowland-to-upland transition--modelling plant responses to environmental change. *Ecological Applications* 3:404-408.

ZIMMERMAN, J. K., PULLIAM, W. M., LODGE, D. J., QUIÑONES-ORFILA, V., FETCHER, N., GUZMÁN-GRAJALES, S., PARROTTA, J. A., ASBURY, C. E., WALKER, L. R. & WAIDE, R. B. 1995. Nitrogen immobilization by decomposing woody debris and the recovery of tropical wet forest from hurricane damage. *Oikos* 72:314-322.

TABLE 1. Key characteristics of tropical montane cloud forests.

Ecological feature	Reference
Low canopy height and twisted stems	Weaver *et al.* 1986
Multi-stemmed and leaning trees	Bellingham & Sparrow 2009
Low leaf area index	Moser *et al.* 2007
High ratio of diameter:height	See Figure 2
High stem density	Weaver *et al.* 1986
Many canopy gaps	Asner *et al.* 2014
High tree fern abundance	Lieberman *et al.* 1996
Small, thick leaves	Tanner & Kapos 1982
High epiphyte abundance, bryophytes	Hietz 2010
Deep surface organic horizon	Grieve *et al.* 1990
Persistently wet soil	Silver *et al.* 1999
High root:shoot ratio	Leuschner *et al.* 2007
Nitrogen limitation of ANPP	Tanner *et al.* 1998

TABLE 2. Canopy height, estimated water-saturated biomass of canopy epiphytes and ratio of actual canopy height (H$_{act}$) to buckling height (H$_{crit}$) for six tropical montane forests. Epiphyte biomass from Köhler *et al.* (2007), except for Peru (from Horwath 2011). H$_{crit}$ = C x $\left(\frac{E}{Y}\right)^{1/3}$ × D$^{2/3}$ where, C = constant (0.79 for columnar tapering); E is elastic modulus, Y is stem wood density; and D is stem diameter; $\left(\frac{E}{Y}\right)$ = 117.6 m for angiosperms (Niklas 1994; and pers. comm.).

Location	Altitude (m asl)	Canopy height (m)	Epiphyte mass (Mg ha^{-1})	H$_{act}$:H$_{crit}$
Colombia	3000+	12	12-44	0.23
Puerto Rico	1000	3-5	4.3-7.3	0.12
Costa Rica	1480	20	16.2-33.1	0.31
Peru	2500	7	45	0.25
Jamaica	1550	10	2.1	0.30
Costa Rica	1700	13	4.7	0.14

1/

FIGURE 1. Hypothesized causal diagram for the effects of environmental factors (in red) shaping cloud forest ecosystem properties (blue) and cloud forest structure (green). Features in bold have been observed in all studies to date whereas other features occur only in some cases.
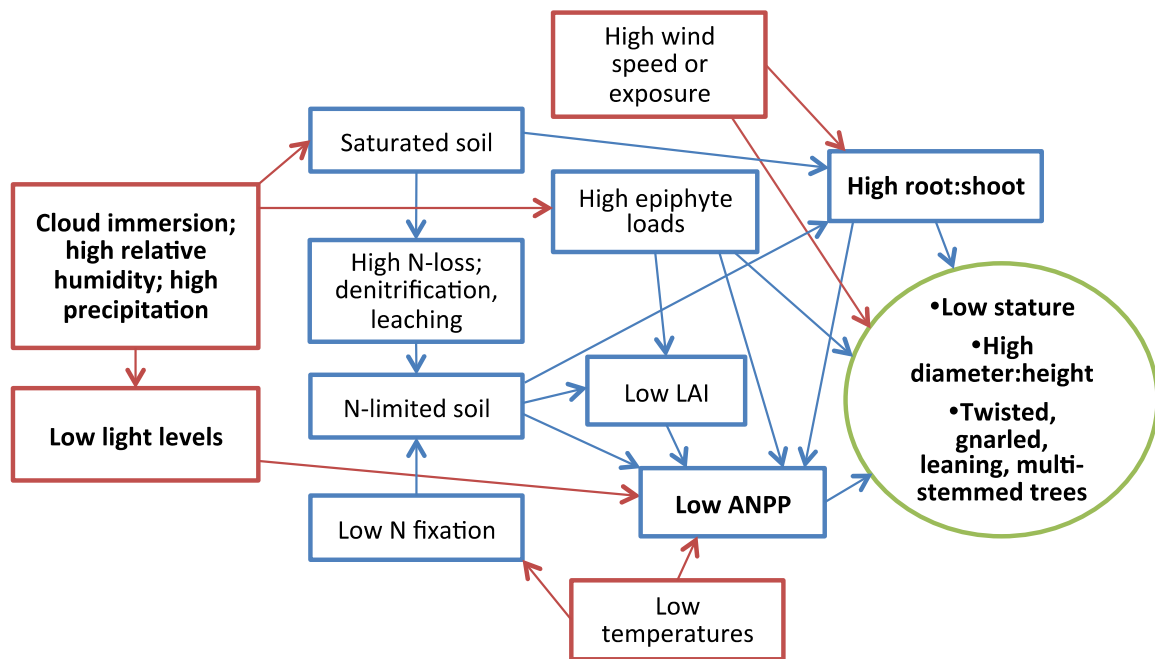
FIGURE 2. Tree diameter to canopy height ratio (cm m^{-1}) for forests along eleven altitudinal transects on tropical mountains. Mean diameter for trees >10 cm dbh except for Ecuador (>5 cm dbh). References as follows: Ecuador (Leuschner *et al.* 2007); Ecuador-2 (Homeier *et al.* 2012); Borneo (Kitayama 1992); Borneo-1 (Aiba & Kitayama 1999 non-ultrabasic soils); Borneo-2 (Aiba & Kitayama 1999 ultrabasic soils); Malaysia (Proctor *et al.* 1988); Costa Rica (Liebermann *et al.* 1996); Hawaii (Raich *et al.* 1997); Dominican Republic (DR, Sherman *et al.* 2005); Peru (Andes Biodiversity and Ecosystem Research Group [ABERG] 2014. Long-term plot inventory data. Unpublished data at http://www.andesconservation.org/).