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# Plant carbon and water fluxes in tropical montane cloud forests

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**Abstract:** Tropical montane cloud forests (TMCFs) are dynamic ecosystems defined by frequent, but intermittent, contact with fog. The resultant microclimate can vary considerably over short spatial and temporal scales, affecting the ecophysiology of TMCF plants. We synthesized research to date on TMCF carbon and water fluxes at the scale of the leaf, plant and ecosystem and then contextualized this synthesis with tropical lowland forest ecosystems. Mean light-saturated photosynthesis was lower than that of lowland forests, probably due to the effects of persistent reduced radiation leading to shade acclimation. Scaled to the ecosystem, measures of annual net primary productivity were also lower. Mean rates of transpiration, from the scale of the leaf to the ecosystem, were also lower than in lowland sites, likely due to lower atmospheric water demand, although there was considerable overlap in range. Lastly, although carbon use efficiency appears relatively invariant, limited evidence indicates that water use efficiency generally increases with altitude, perhaps due to increased cloudiness exerting a stronger effect on vapour pressure deficit than photosynthesis. The results reveal clear differences in carbon and water balance between TMCFs and their lowland counterparts and suggest many outstanding questions for understanding TMCF ecophysiology now and in the future.

**Key Words:** carbon cycling, ecohydrology, ecophysiology, fog-affected forests, foliar water uptake, photosynthesis, primary productivity, sap flow, transpiration, water-use efficiency

## INTRODUCTION

Tropical montane cloud forests (TMCFs) are ecosystems that often experience frequent and direct contact between low-lying clouds and vegetation (i.e. fog; Bruijnzeel *et al.* 2011). This frequent fog alters microclimate by reducing photosynthetically active radiation (PAR) and vapour pressure deficits (VPD) while increasing the frequency and duration of leaf wetting (Bruijnzeel *et al.* 2011, Grubb 1977, Oliveira *et al.* 2014). In addition, due to altitude and typical orographic rainfall patterns, TMCFs often experience mild temperatures and high precipitation. This unique microclimate influences plant carbon (photosynthesis) and water (transpiration) exchange at the scale of the leaf and whole plant (Figure 1). When these processes are scaled to the ecosystem, the effects of microclimate can be detected in both carbon and water cycling. TMCFs are generally considered to have lower rates of leaf-level gas exchange, thus leading to lower ecosystem rates of primary productivity and transpiration as compared with their lowland counterparts (Bruijnzeel &

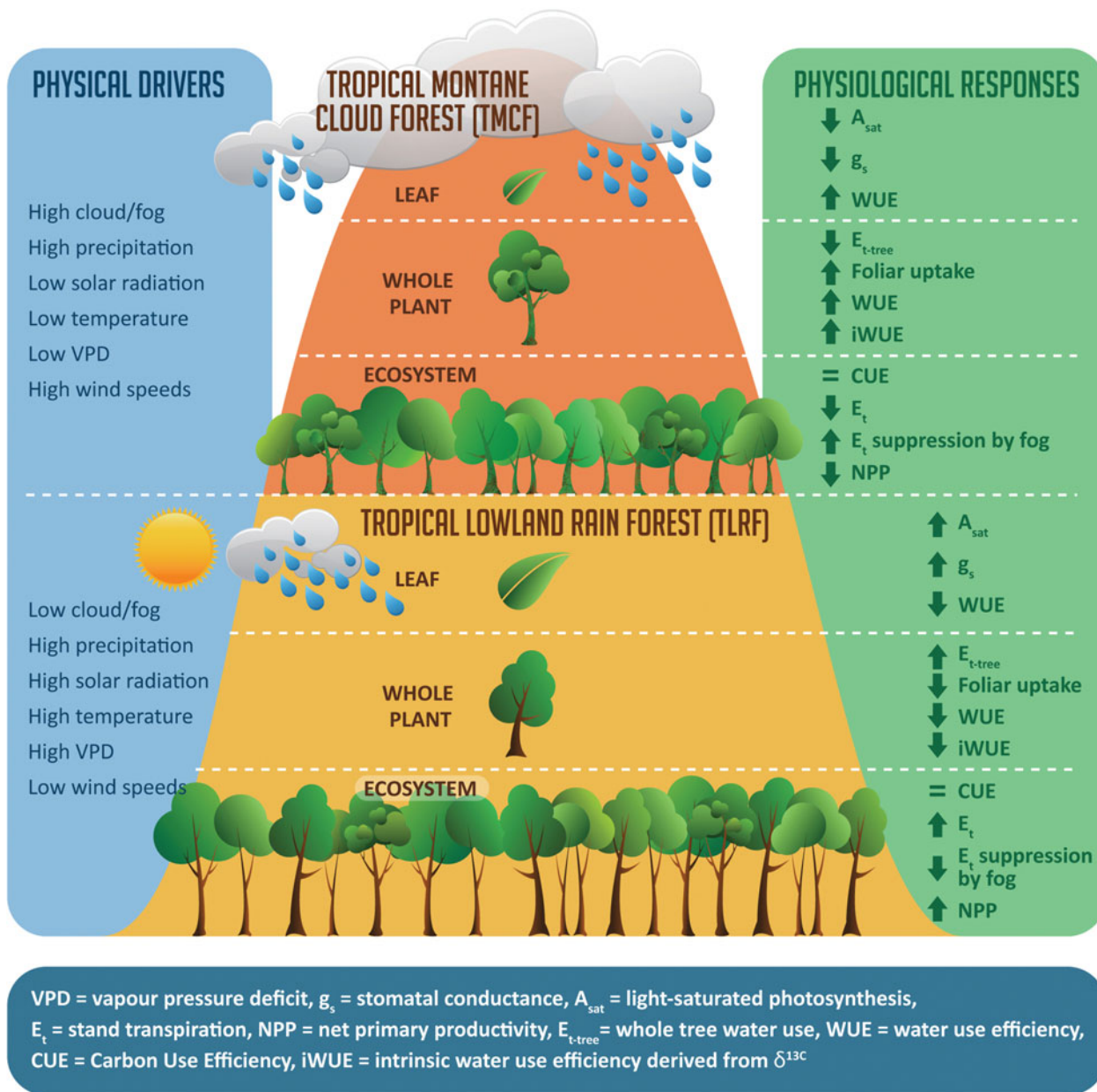
Veneklaas 1998). While TMCFs remain understudied by physiological ecologists in comparison with lowland rain forests, research efforts in the last 20 y have intensified and now allow for a more comprehensive consideration.

To date, there has been no systematic evaluation of research on plant water and carbon relations of TMCFs, nor has the ecophysiology of TMCFs been compared and contrasted with that of tropical lowland ecosystems. We surveyed the TMCF literature for empirical measurements of carbon and water fluxes, as well as carbon- and water-use efficiency, at the scales of the leaf, plant and ecosystem. In doing so, we specifically sought to (1) build a quantitative foundation for understanding the plant ecophysiology of TMCFs in comparison with that of lowland tropical rain forests in the context of their differing microclimates, and (2) identify outstanding research questions that can serve as the basis for future research.

## Approach

Tropical montane cloud forests have been identified as occurring worldwide; however, there is currently no

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**Figure 1.** A generalized comparison of the environmental drivers and their corresponding impacts on carbon and water fluxes in tropical montane cloud forest (TMCF) and lowland tropical rain forest (LRF). Drivers and response variables are depicted at the leaf, whole plant, and ecosystem scales.

standardized biophysical definition. In this review, we include research papers that the authors identified as having been conducted in TMCF and that had relevant information on plant carbon and water relations, as well as those that make note of the role of clouds in mediating a tropical montane forest's microclimate. Overall, we identified relevant data from 28 sites in Australia, Borneo, Colombia, Ecuador, Mexico, Peru, Puerto Rico, Taiwan, Hawai'i (USA) and Venezuela. The sites span an altitudinal range from 865 to 3060 m asl with a mean annual temperature of  $14^\circ\text{C} \pm 0.53^\circ\text{C}$  and

mean annual precipitation of  $3343 \pm 282$  mm. Given the limited number of studies focused on ecophysiology, those identified herein appear to be a fair representation of TMCF. Jarvis & Mulligan (2011), in a synthesis of TMCF biophysical conditions based on a United Nations World Conservation Monitoring Centre database, found an altitudinal range from 22 to 5005 m asl with a mean annual temperature of  $17.7^\circ\text{C}$  and mean annual precipitation of 2027 mm. Wherever possible given data on a sufficient number of sites, we carried out statistical comparisons of carbon and water flux traits between

**Table 1.** Mean light saturated photosynthesis and dark respiration observed in tropical montane cloud forests.

Mean light-saturated photosynthesis ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Dark respiration ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Altitude (m asl)	Precip. ( $\text{mm y}^{-1}$ )	Temp. ( $^{\circ}\text{C}$ )	Location	No. of species	Study
$5.5 \pm 1.7$ (SD)	-	1700	2714	18.9	Borneo	8	Hikosaka <i>et al.</i> (2002)
$9.1 \pm 2.4$ (SD)	-	1445-1480	3600	11–18	Colombia	4	Letts & Mulligan (2005)
$8.3 \pm 1.5$ (SD)	-	2160	7000	11–18	Colombia	4	Letts & Mulligan (2005)
$6.3 \pm 1.0$ (SD)	-	2400	1700-2700	13.6	Venezuela	5	Rada <i>et al.</i> (2009)
$7.0 \pm 0.3$ (SE)	-	3025	1706	11.1	Peru	5	van de Weg (2012)
$7.2 \pm 0.1$ (SE)	$0.66 \pm 0.07$ (SE)	3000	4500	9	Ecuador	10	Wittich <i>et al.</i> (2012)
$8.0 \pm 0.5$ (SE)	$0.43 \pm 0.05$ (SE)	1500	5302	18.8	Peru	15–25 trees	Huaraca-Huasco <i>et al.</i> (2014)
$6.4 \pm 0.4$ (SE)	$0.69 \pm 0.07$ (SE)	1750	5302	17.4	Peru	15–25 trees	Huaraca-Huasco <i>et al.</i> (2014)
-	$0.68 \pm 0.05$ (SE)	2825	1560	13.1	Peru	15–25 trees	Girardin <i>et al.</i> (2014)
-	$0.57 \pm 0.05$ (SE)	3025	1560	11.8	Peru	15–25 trees	Girardin <i>et al.</i> (2014)

tropical lowland rain forests and TMCF; however, we did not conduct an exhaustive survey of lowland forest traits.

### Carbon relations

The low productivity and biomass of TMCF in comparison to the lowland forests is a longstanding observation and has been the subject of considerable research (Bruijnzeel & Veneklaas 1998, Grubb 1971, 1977; Whitmore 1998). Although many hypotheses have been proposed regarding direct or indirect effects of climate on plant and ecosystem function, we still lack a comprehensive and mechanistic understanding of what limits the productivity of TMCFs. Leaf carbon assimilation (i.e. photosynthesis) and respiration are the physiological foundation for productivity and biomass accumulation and can thus provide insight into TMCF processes and patterns, particularly when contextualized with lowland ecosystems. Here, we summarize the available literature on photosynthesis and respiration at the scales of the leaf, plant and ecosystem.

*Leaf: photosynthesis and respiration.* Mean light-saturated leaf photosynthetic rates ( $A_{\text{sat}}$ ) measured in TMCF canopy trees and understorey shrubs range from 5.5–9.1  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , with a mean of 7.2  $\mu\text{mol m}^{-2} \text{s}^{-1}$  across the available studies (Table 1,  $n = 8$  sites in six studies). Lüttge (2007) reported a range of light-saturated photosynthesis rates across tropical forests from 13.0 to 19.0  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , while Wittich *et al.* (2012) recently reported a range from 3.7–20.3  $\mu\text{mol m}^{-2} \text{s}^{-1}$  with a mean of 10.0  $\mu\text{mol m}^{-2} \text{s}^{-1}$  specifically from tropical lowland forests. The rates synthesized by Wittich *et al.* (2012) are significantly higher than those observed for TMCF

trees ( $t = 2.8$ ,  $df = 10.2$ ,  $P < 0.02$ ). Within the TMCF dataset herein, which spans from 1445 to 3025 m asl, there is no evidence for a significant change in  $A_{\text{sat}}$  as a function of altitude (least squares regression;  $P > 0.05$ ). Wittich *et al.* (2012) found a weak, but significant decrease of 1.3  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in photosynthesis for every 1000 m change in altitude. Although altitude serves as a proxy for changes in temperature, there are a number of other factors that may confound a strong univariate relationship with photosynthesis.

The current evidence does not necessarily imply that TMCF species (or even montane species in general) fundamentally differ in  $A_{\text{sat}}$ , but more likely indicates a response to limiting environmental conditions (Körner 1999). TMCFs differ in temperature, the partial pressure of  $\text{CO}_2$  in air, soil nutrient availability, and photosynthetically active radiation (PAR) and here we explore the effects of these factors on photosynthesis. Although, as noted above, temperature decreases with increasing altitude, peak rates of photosynthesis occur over a wide range of temperatures (Lloyd & Farquhar 2008). The partial pressure of  $\text{CO}_2$  also decreases predictably ( $\sim 11\%$  per 1000 m altitude, although the mixing ratio of gases remains the same), reducing the amount of carbon available for assimilation (Gale 1972). However, this is compensated for by a concomitant decrease in the partial pressure of  $\text{O}_2$  and thus photorespiration, as well as an increase in  $\text{CO}_2$  diffusion. Limited available evidence from a tree species occurring along what is often considered a cloud-affected altitudinal gradient in Hawai'i suggests that increases in carboxylation capacity, in concert with changes in leaf nutrients and structure, may offset decreases in the partial pressure of  $\text{CO}_2$  and lead to similar rates of photosynthesis along the gradient (Cordell *et al.* 1998, 1999). Decreases in soil nutrient availability with increasing altitude



may lead to decreases in foliar nutrient concentrations, particularly nitrogen and phosphorus (Benner & Vitousek 2011), which are both critical for the photosynthetic machinery. However, evidence for the effects of nutrient limitation on photosynthesis along altitudinal gradients is generally mixed and needs to be carefully considered in the context of area- vs. mass-based measurements (Cordell *et al.* 1999, van de Weg *et al.* 2009, Wittich *et al.* 2012).

Among all the environmental conditions considered, 15–50% reductions in PAR associated with cloud immersion in TMCF are likely to exert the strongest effects on photosynthesis, leading to the development of shade-acclimated leaves (Bruijnzeel & Veneklaas 1998, Bruijnzeel *et al.* 2010). This may be further compounded by light levels below that of saturation, as well as further reductions in photosynthesis occurring when those clouds also result in leaf wetting (Letts *et al.* 2010). Leaves on lowland trees provided with supplemental light over the course of a year demonstrated an increase in  $A_{sat}$  as compared with controls (Graham *et al.* 2003), indicating acclimation to higher light conditions. There is a clear need for similar studies of both photosynthetic acclimation to light and ambient rates of photosynthesis in TMCFs, particularly in relation to cloud immersion and its effects on light quantity and quality.

The magnitude of leaf dark respiration in TMCFs is of equal interest to that of photosynthesis because of its critical contribution to ecosystem carbon balance. Two studies on canopy trees at four sites in Peruvian TMCFs found respiration, measured at 25°C, to range from 0.43 to 0.69  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , with a mean of 0.59  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (Girardin *et al.* 2014, Huaraca Huasco *et al.* 2014). Such values are not qualitatively different from respiration measured nearby at two lowland sites, where respiration ranged from 0.49 to 0.67  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (Malhi *et al.* 2014), although a comprehensive study of lowland tropical rain-forest canopy trees and lianas in Panama reported a range of 0.72 to 1.79 with a mean of 1.11  $\mu\text{mol m}^{-2} \text{s}^{-1}$  when measured at 25°C (Slot *et al.* 2013). Standardized measurements of dark respiration among TMCFs are of great interest, particularly with respect to establishing the extent to which thermal acclimation will occur in response to warming temperatures (Vanderwel *et al.* 2015).

*Plant and ecosystem: growth rates and primary productivity.* Translating rates of leaf photosynthesis and respiration to the whole plant remains a challenge in all ecosystems. Photosynthetic assimilates can be used immediately for growth or metabolic maintenance, or stored for later use. Understanding plant carbon fluxes is further complicated by the possibility of translocation and allocation to various parts of the plant both above- and below-ground. Thus, while repeat stem diameter measurements are a

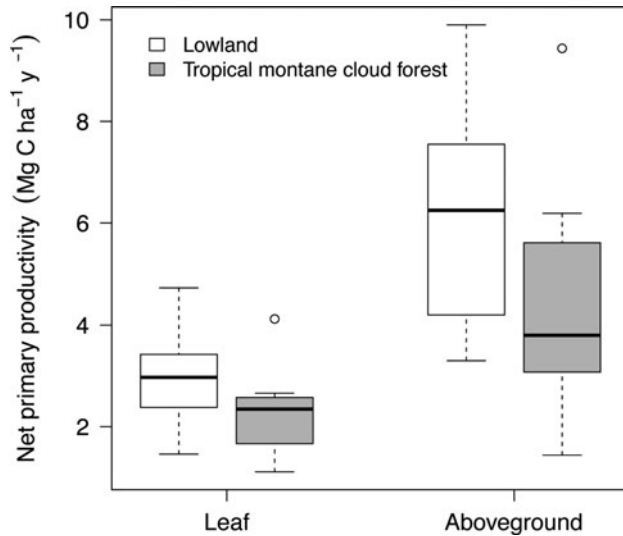
common method for studying whole-plant growth rates (e.g. diameter increment; Herwitz & Young 1994, Holder 2008, Homeier *et al.* 2010, Weaver *et al.* 1986), this approach must be treated with caution and is more appropriately incorporated into whole-ecosystem-level estimates of net primary productivity (i.e. forest growth; Clark *et al.* 2001a).

At the ecosystem scale, complete carbon budgets from field-based studies of TMCFs are just beginning to emerge (Girardin *et al.* 2014, Huaraca Huasco *et al.* 2014). Comprehensive and standardized approaches that facilitate insight into the components of above- and below-ground productivity are critical for building a process-based understanding of the linkages among leaf, plant and ecosystem-scale carbon relations. At present, the most commonly available estimates in TMCF are for one or more aspects of above-ground net primary productivity (NPP), particularly leaf litterfall ( $\text{NPP}_{\text{leaf}}$ ). Mean annual  $\text{NPP}_{\text{leaf}}$  range from 1.11–4.12  $\text{Mg C ha}^{-1} \text{y}^{-1}$ , with a mean of 2.23  $\text{Mg C ha}^{-1} \text{y}^{-1}$  and correlate strongly with  $\text{NPP}_{\text{above-ground}}$  ( $r = 0.82$ , Table 2,  $n = 12$  sites in nine studies). Mean annual rates of  $\text{NPP}_{\text{above-ground}}$ , generated from estimates of woody stem and canopy production, range widely from 1.6–9.44  $\text{Mg C ha}^{-1} \text{y}^{-1}$ , with a mean of 4.30  $\text{Mg C ha}^{-1} \text{y}^{-1}$ . An additional tropical montane cloud forest site in the Dominican Republic, using repeated estimates of above-ground biomass from allometric equations, has found negative rates of  $\text{NPP}_{\text{above-ground}}$  ( $-0.16 \text{ Mg C ha}^{-1} \text{y}^{-1}$ ), an observation attributed to frequent wind and landslide disturbance (Sherman *et al.* 2012). Notably, the sites with the lowest (Hawai'i observed in Cordell *et al.* 1998, Raich *et al.* 1997) and highest  $\text{NPP}_{\text{above-ground}}$  (Peru observed in Huaraca Huasco *et al.* 2014) are also the sites with the lowest and highest light-saturated photosynthetic rates.

Both metrics of TMCF productivity have a mean  $\sim 25\%$  lower than that of lowland rain forests. A synthesis of  $\text{NPP}_{\text{leaf}}$  from across old-growth lowland tropical rain forests in South America reports a range of 1.46–4.74  $\text{Mg C ha}^{-1} \text{y}^{-1}$  with a mean of 3.03  $\text{Mg C ha}^{-1} \text{y}^{-1}$  (Chave *et al.* 2010); this is significantly higher than TMCF (t-test;  $t = 3.2$ ,  $df = 14.6$ ,  $P < 0.01$ , Figure 2). This observation holds when scaled to  $\text{NPP}_{\text{above-ground}}$ . A synthesis in lowland tropical forests (excluding sites  $> 1000 \text{ m asl}$ ) reported a range of 3.3–9.9  $\text{Mg C ha}^{-1} \text{y}^{-1}$  with a mean of 6.22  $\text{Mg C ha}^{-1} \text{y}^{-1}$  (Clark *et al.* 2001b), which is also significantly higher than TMCF (t-test;  $t = 2.5$ ,  $df = 20.5$ ,  $P = 0.02$ ). While above-ground TMCF productivity appears to be distinctly lower than that of the lowlands, insights into below-ground processes remain more difficult to disentangle. Several studies have noted the possibility of a compensatory increase in  $\text{NPP}_{\text{root}}$  with increasing altitude (Leuschner *et al.* 2007), although research to date has demonstrated mixed results (Girardin *et al.* 2013, Moser *et al.* 2011).

**Table 2.** Mean gross primary productivity (GPP), total above- and below-ground net primary productivity (Total NPP), carbon use efficiency (CUE), aboveground net primary productivity (NPP<sub>aboveground</sub>) and leaf net primary productivity (NPP<sub>leaf</sub>) observed in tropical montane cloud forests. Note that for consistency, all measurements were converted megagrams of carbon assuming that carbon is 50% of the weight of biomass.

GPP (Mg C ha <sup>-1</sup> y <sup>-1</sup> )	Total NPP (Mg C ha <sup>-1</sup> y <sup>-1</sup> )	CUE	NPP <sub>aboveground</sub> (Mg C ha <sup>-1</sup> y <sup>-1</sup> )	NPP <sub>leaf</sub> (Mg C ha <sup>-1</sup> y <sup>-1</sup> )	Altitude (m asl)	Precip. (mm y <sup>-1</sup> )	Temp. (°C)	Location	Study
-	-	-	3.13	2.22	1615	2600	20.5*	Jamaica	Tanner (1980)
-	-	-	3.02	2.47	1615	2600	19.5*	Jamaica	Tanner (1980)
-	-	-	3.45	2	1570	2600	18.5*	Jamaica	Tanner (1980)
-	-	-	4.49	2.49	1590	2600	19.0*	Jamaica	Tanner (1980)
-	-	-	1.60 ± 0.25 (SE)	1.15 ± 0.24 (SE)	1660	2570	13.1	Hawaii	Raich <i>et al.</i> (1997)
-	-	-	3.9	2.66	2700	2085	13.7	Borneo	Kitayama & Aiba (2002)
16.7	5.4	0.32	3.7	1.11	1050	4200	18.8	Puerto Rico	Weaver & Murphy (1990), Wang <i>et al.</i> (2003)
9.0	4.1	0.45	1.44	1.37	3060	4500	9.4	Ecuador	Moser <i>et al.</i> (2011), Leuschner <i>et al.</i> (2013)
21.8 ± 0.90 (SE)	7.05 ± 0.39 (SE)	0.32	5.34 ± 0.33 (SE)	1.96 ± 0.28 (SE)	2825	1560	13.1	Peru	Girardin <i>et al.</i> (2014)
25.9 ± 1.08 (SE)	8.04 ± 0.47 (SE)	0.31	5.88 ± 0.31 (SE)	2.52 ± 0.18 (SE)	3025	1560	11.8	Peru	Girardin <i>et al.</i> (2014)
38.6 ± 1.96 (SE)	11.94 ± 0.47 (SE)	0.31	9.44 ± 0.68 (SE)	4.12 ± 0.18 (SE)	1500	5302	18.8	Peru	Huaraca Huasco <i>et al.</i> (2014)
32.3 ± 1.60 (SE)	7.92 ± 0.38 (SE)	0.24	6.19 ± 1.92 (SE)	2.63 ± 0.17 (SE)	1750	5302	17.4	Peru	Huaraca Huasco <i>et al.</i> (2014)



**Figure 2.** A comparison of lowland tropical rain forest and tropical montane cloud forest (TMCF) leaf and aboveground net primary productivity generated by comparing lowland syntheses from Clark *et al.* (2001b) and Chave *et al.* (2010) with data compiled herein on TMCF.

The decreased above-ground net primary productivity observed in TMCF relative to lowland rain forests may be attributed to other factors besides solely a reduction in photosynthesis driven by light (or other factors discussed above) and thus a limited source of carbon. An alternative possibility is that productivity is also limited by the lack of carbon consumption and maintenance activity (e.g. sink dynamics). For instance, it has been proposed that limits on cell division by temperature, water and nutrients occur prior to limits on photosynthesis (Fatichi *et al.* 2014). On temperate mountains, there is evidence that temperature serves as the limiting factor for growth and that there may exist an excess of stored carbon (non-structural carbohydrates) available for use by plants (Körner 2003). However, studies of non-structural carbohydrate storage are only beginning to emerge for tropical lowland forests (Würth *et al.* 2005). Ultimately, a combination of observational and experimental approaches is likely necessary to help resolve the carbon source-sink dynamics that link leaf and plant level growth with patterns observed at the scale of the ecosystem.

### Water relations

High precipitation and frequent cloud and fog cover inevitably influence water balance and storage in TMCFs. In general, at the leaf and plant level, TMCFs transpire less than lowland tropical rain forests (Bruijnzeel *et al.* 2011, Figure 1). While this pattern may adequately characterize annual patterns of transpiration, intra-annual patterns of

water use in TMCFs may be more difficult to characterize due to the highly variable micrometeorological conditions that many TMCFs experience. Factors influencing evaporative demand, including wind speed, relative humidity, temperature and radiation can all vary over short time scales in the TMCF and these fluctuations will in turn affect water fluxes (Giambelluca *et al.* 2009). Thus, despite lower stand-level averages, the maximum reported rates of water use in TMCFs are comparable with lowland forests (Feild & Holbrook 2000, Santiago *et al.* 2000, Zotz 1998).

*Leaf: stomatal conductance.* Mean rates of stomatal conductance ( $g_s$ ) for canopy trees across TMCFs range from 60–561  $\text{mmol m}^{-2} \text{s}^{-1}$ , with a mean of 239  $\text{mmol m}^{-2} \text{s}^{-1}$  (Table 3,  $n = 8$  sites in seven studies). Two of these studies quantified  $g_s$  under saturating light conditions and report somewhat higher values (Cordero 1999, Letts *et al.* 2010), while the other studies reported daytime averages. Average  $g_s$  across these TMCF sites is 40% lower than the average  $g_s$  reported from a lowland rain forest in Panama ( $370 \pm 14 \text{ mmol m}^{-2} \text{s}^{-1}$ , Meinzer *et al.* 1993, 1997). Midday decreases in stomatal conductance ( $g_s$ ) on clear days have been observed in three TMCFs, indicating that despite generally wet conditions, either soil water supply or atmospheric demand limits transpiration (Cavelier 1990, Gotsch *et al.* 2014a, Rada *et al.* 2009). For instance,  $g_s$  dropped from approximately 400  $\text{mmol m}^{-2} \text{s}^{-1}$  in the early morning to 100  $\text{mmol m}^{-2} \text{s}^{-1}$  by midday in a Columbian TMCF (Cavelier 1990). Midday depression was also observed in Maui, following 1 d without rain, although the overall rates were lower; early morning to midday  $g_s$  varied from 100  $\text{mmol m}^{-2} \text{s}^{-1}$  to just 40  $\text{mmol m}^{-2} \text{s}^{-1}$  (Gotsch *et al.* 2014a). During the midday depression, vapour pressure deficit (VPD) exceeded 1.0 kPa. Correlations between VPD and transpiration have been found across a number of ecosystems, highlighting the important role of evaporative demand on plant-water relations (Bucci *et al.* 2004, Dawson *et al.* 2007, Eller *et al.* 2015, Gotsch *et al.* 2014a, b; Motzer *et al.* 2005). Despite frequent precipitation, plant available soil water also varies greatly in TMCF ecosystems and is likely to play an important role in transpiration (Eller *et al.* 2015, Jarvis & Mulligan 2011).

*Plant: individual water-use.* The few studies that have quantified whole plant water use in the TMCFs demonstrate a great deal of variability among sites although comparisons among sites are difficult since different sized trees were studied (Appendix 1). One of the few studies to quantify volumetric sap flow in dominant TMCF trees estimated an average daily transpiration rate of 24.7  $\text{L d}^{-1}$  over a relatively wet 10-d period in Maui, Hawai'i (Gotsch *et al.* 2014a). Clouds were often

**Table 3.** Stomatal conductance observed in canopy trees in tropical montane cloud forests.

Stomatal conductance (mmol m <sup>-2</sup> s <sup>-1</sup> )	Altitude (m asl)	Precipitation (mm y <sup>-1</sup> )	Temp. (°C)	Location	Study
100–425*	865	-	-	Colombia	Cavelier (1990)
401 ± 40 (SE)	1051	4210	-	Puerto Rico	Cordero (1999)
sunny/level: 233 ± 17 (SE)	1200	5000	14.5	Maui	Santiago <i>et al.</i> (2000)
sunny/sloped: 219 ± 32 (SE)					
cloudy/level: 177 ± 24 (SE)					
cloudy/sloped: 187 ± 25 (SE)					
561 ± 255 (SE)	1445–1480	3600	11–18	Colombia	Letts & Mulligan (2005)
459 ± 45 (SE)	2160	7000	11–18	Colombia	Letts & Mulligan (2005)
161 ± 84 (SD)	1950–1975	2067	15.5	Equator	Motzer <i>et al.</i> (2005)
wet season: 71 ± 9 (SE);	2400	1700–2700	13.6	Venezuela	Rada <i>et al.</i> (2009)
dry season: 60 ± 7 (SE)					
105 ± 9 (SE)	2109–2231	3500–5000	10.5	Maui	Gotsch <i>et al.</i> (2014b)

\*No mean reported.

passing through the study site and cloudy periods were interspersed with short periods with clear skies. During this 10-d period, transpiration ranged from 5.5 to 63 L d<sup>-1</sup>. In an elfin forest in Costa Rica, transpiration rates of less than 2 L d<sup>-1</sup> were reported (Feild & Holbrook 2000). This high-altitude site is characterized by more frequent fog and precipitation than lower altitude TMCFs (Bruijnzeel & Hamilton 2000). The suppression of transpiration due to fog and resultant low leaf to air VPDs and leaf wetting has been documented in a number of studies and is probably the cause for such low average daily transpiration in elfin cloud forest (Alvarado-Barrientos *et al.* 2014, Goldsmith *et al.* 2013, Gotsch *et al.* 2014b).

A great deal of variation has also been documented in lowland tropical rain forests; however, rates of daily water use tend to be higher than in TMCFs. During a dry season period in lowland Panama, sap flow ranged from 46.6 to 379 L d<sup>-1</sup> in 18–35-m trees (Goldstein *et al.* 1998). This can be explained by the combined changes in microclimate, including greater VPD and reduced leaf-wetting events. Very few studies have calculated whole-plant transpiration in TMCFs; greater research efforts are necessary to understand seasonal, within-site and among-site variation in whole-plant transpiration.

The presence of fog and resultant leaf wetting can also facilitate the direct absorption of water into leaves, providing an additional source of moisture availability (i.e. foliar water uptake or FWU, see review by Oliveira *et al.* 2014). In a TMCF in Mexico, canopy wetness due to fog and drizzle in the dry season facilitated FWU that resulted in the recovery of 4–16% of the dry-season-transpired water (Gotsch *et al.* 2014b). Cloud water interception (CWI) at this site (i.e. stand-level throughfall and stemflow) is approximately 6–8% of the total dry-season rainfall (Holwerda *et al.* 2010, Muñoz-Villers *et al.* 2012). In TMCFs with more frequent fog occurrence, the

importance of FWU in plant water balance will likely be greater. A recent study on epiphytes in the TMCF of Costa Rica, where the CWI is approximately 30% of rainfall (Hager & Dohrenbush 2011), found that FWU in canopy epiphytes resulted in the recovery of 37% to almost 100% of the equivalent water transpired during a month in the misty/windy transition season (Gotsch *et al.* 2015). While FWU can offset transpiration losses in the TMCF, the microclimate can vary greatly diurnally, leading to periods with high VPD (Holwerda *et al.* 2010). High evaporative demand, especially at night, can lead to water loss via partially open stomates, which will greatly affect whole-plant water use (Dawson *et al.* 2007). In Veracruz, Mexico, nighttime transpiration contributed 14–24% of the dry-season branch-level water loss (Gotsch *et al.* 2014b). Foliar uptake and nighttime transpiration are two processes that are likely important components of the TMCF water cycle; additional research is needed to understand the role that these processes play in plant water status and ecosystem water balance.

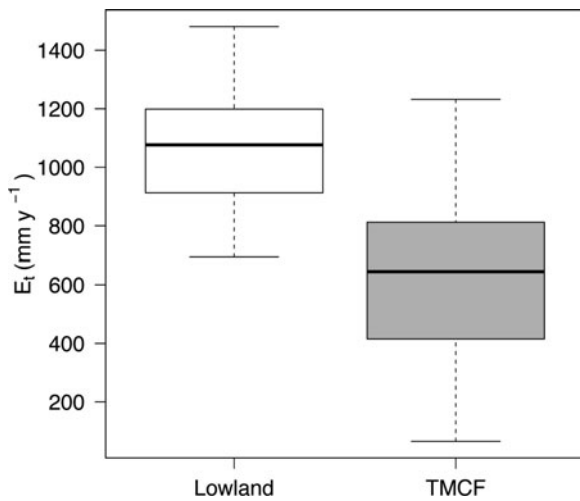
*Ecosystem: stand transpiration.* The high variation in leaf and plant water-use is also evident at the stand level. Estimates of stand-level transpiration ( $E_t$ ) range from c. 65 mm y<sup>-1</sup> to 1232 mm y<sup>-1</sup> in Hawaiian montane cloud forests alone (Giambelluca *et al.* 2009, Santiago *et al.* 2000). Mean  $E_t$  among 10 sites was 630 mm y<sup>-1</sup> (Table 4). The estimate of TMCF  $E_t$  is on the high end of the data reviewed by Bruijnzeel *et al.* (2011), who reported a range of  $E_t$  from 385 mm y<sup>-1</sup> to 646 mm y<sup>-1</sup>. They include data from 15 studies that they define as TMCF and report a negative relationship between altitude and  $E_t$ , which was attributed to changes in temperature, radiation and cloudiness. The highest  $E_t$  occurred in so-called 'lower montane cloud forest' and the lowest rates occur in high-altitude 'elfin forest' (Bruijnzeel *et al.* 2011). In some



**Table 4.** Stand-level transpiration observed in tropical montane cloud forests.

$E_t$ (stand-level tree transpiration)	Altitude (m asl)	Precipitation ( $\text{mm y}^{-1}$ )	Temp. ( $^{\circ}\text{C}$ )	Location	Study
$558 \text{ mm y}^{-1}$	2350	3125	9-14	Venezuela	Ataroff & Rada (2000)
$0.05\text{--}1.17 \text{ mm d}^{-1} *$	1200	5000	14.5	Maui	Santiago <i>et al.</i> (2000)
$812 \text{ mm y}^{-1}$	1265–1420	1837	19.7	Thailand	Tanaka <i>et al.</i> (2003, 2011)
$353 \text{ mm y}^{-1}$	1560	8100	-	Australia	McJannet <i>et al.</i> (2007)
$1232 \text{ mm y}^{-1}$	1219	2500	-	Hawaii (USA)	Giambelluca <i>et al.</i> (2009)
$415 \text{ mm y}^{-1}$	1450	6000	-	Costa Rica	Referenced in Bruijnzeel <i>et al.</i> (2011)
$919 \text{ mm y}^{-1}$	2030	2140	-	Ecuador	Referenced in Bruijnzeel <i>et al.</i> (2011)
$674 \text{ mm y}^{-1}$	900	4450	-	Puerto Rico	Referenced in Bruijnzeel <i>et al.</i> (2011)
$645 \pm 50 \text{ mm y}^{-1}$	2180	2000-3000	14.3	Mexico	Alvarado-Barrientos <i>et al.</i> (2014)

\*Range of daily estimates made on level- and sloped-sites.



**Figure 3.** A comparison of lowland tropical rain forest and tropical montane cloud forest (TMCF) annual stand-level transpiration generated by comparing lowland syntheses from McJannet *et al.* (2007) with data compiled herein on TMCF.

of the studies included, particularly at lower altitudes, the authors do not explicitly identify the site as a TMCF, and as a result we do not include them herein. McJannet *et al.* (2007) synthesized  $E_t$  values from lowland tropical forests and including their own data,  $E_t$  ranged from  $693.5\text{--}1131 \text{ mm y}^{-1}$  with an average of  $957 \text{ mm y}^{-1}$ . Given this, TMCF  $E_t$  is significantly lower than lowland tropical rain forests ( $t = 3.1$ ,  $df = 14.3$ ,  $P = 0.007$ ; Figure 3).

Stand-level studies in TMCFs do provide insight into the environmental drivers of the observed variation. Over a 5-d period in Maui, Hawai'i, transpiration varied by almost an order of magnitude within sites (Santiago *et al.* 2000). In sloped sites, transpiration varied from  $0.17$  to  $1.17 \text{ mm d}^{-1}$ ; transpiration also varied greatly in level sites, although rates were lower ( $0.05\text{--}0.31 \text{ mm d}^{-1}$ ). During this experiment, radiation varied considerably due

to passing cloud cover, which resulted in large variation in VPD. On average, sites in slope areas experienced three to four times more stand-level transpiration than in level, waterlogged areas, a difference attributed to a reduction in leaf area in the level sites (Table 4, Santiago *et al.* 2000). Daily rates of  $E_t$  vary greatly in different TMCF locations.  $E_t$  in an Australian TMCF was  $1.1 \text{ mm d}^{-1}$ , while a Mexican TMCF was  $1.7 \text{ mm d}^{-1}$ , translating to a considerable annual difference ( $353 \text{ mm}$  and  $645 \text{ mm}$ , respectively: Alvarado-Barrientos *et al.* 2014, McJannet *et al.* 2007). Differences in annual precipitation between these two sites ( $8100 \text{ mm}$  for Australia and  $2000\text{--}3000 \text{ mm}$  for Mexico) are substantial and may correlate with additional differences in microclimate including canopy wetness and cloud inundation, which would lead to greater suppression in  $E_t$  at the Australian site. The aforementioned studies all estimated  $E_t$  using sap-flow methods, which apply heat to the plant stem and trace its diffusion to estimate flow rates. Using another methodology, eddy covariance, researchers in a TMCF in Ecuador estimated annual  $E_t$  to be  $471 \text{ mm}$ , which is greater than that found in TMCFs at higher altitudes in Puerto Rico and Costa Rica (Bruijnzeel *et al.* 2011, Holwerda 2005), but similar to  $E_t$  calculated with sap flow in Australia and Mexico (Alvarado-Barrientos *et al.* 2014, McJannet *et al.* 2007).

Ultimately, while large-scale differences in  $E_t$  may correlate with altitude, a great deal of variability in  $E_t$  likely occurs within a given site. Extreme variation in topography, slope and aspect is characteristic of TMCFs. Variation in these physical features of the environment will in turn affect canopy microclimate and soil properties. As a result, even within a very narrow range of altitude, stand-level transpiration can vary widely. Such variation, from the level of the leaf to that of the stand within sites, has largely been unexplored (but see Berry *et al.* 2016, Santiago *et al.* 2000).

**Table 5.** Mean leaf-level water use efficiency observed in tropical montane cloud forests.

Mean WUE ( $\mu\text{mol CO}_2$ per $\text{mmol H}_2\text{O}$ $\text{m}^{-2} \text{s}^{-1}$ )	Altitude (m asl)	Precipitation ( $\text{mm y}^{-1}$ )	Temp. ( $^{\circ}\text{C}$ )	Location	No. of species	Study	Notes
$2.7 \pm 0.2$ (SE)	1051	4210		Puerto Rico	1	Cordero (1999)	Potted saplings
$3.5 \pm 0.5$ (SE)	1445-1480	3600	11-18	Colombia	4	Letts & Mulligan (2005)	
$5.2 \pm 0.5$ (SE)	2160	7000	11-18	Colombia	4	Letts & Mulligan (2005)	
$3.6 \pm 0.6$ (SE)	2400	1700-2700	13.6	Venezuela	5	Rada <i>et al.</i> (2009)	Wet season
$2.4 \pm 0.2$ (SE)	2400	1700-2700	13.6	Venezuela	5	Rada <i>et al.</i> (2009)	Dry season

### Carbon-water relations

The measures of plant carbon and water use considered above are inextricably coupled through gas exchange processes occurring at the leaf surface, whereby  $\text{CO}_2$  uptake for photosynthesis and simultaneous water loss via transpiration under changing environmental conditions are balanced. This coupling can be considered through measurements of the efficiency of gas exchange processes, in terms of both water use efficiency (WUE;  $\text{CO}_2$  assimilation per unit water loss) and carbon use efficiency (CUE; growth per unit  $\text{CO}_2$  assimilation). WUE can be expressed at the leaf, whole-plant and ecosystem scales, whereas CUE is generally considered at the ecosystem scale. The determination of these metrics requires information on both carbon and water relations, ideally recorded simultaneously at the same temporal and spatial scales, but the number of studies that have explicitly calculated WUE and CUE is relatively few compared with those that have considered only carbon or only water fluxes (e.g. those reviewed above). Below, we review the available information on WUE and CUE reported for TMCFs to date.

**Leaf: WUE.** The few studies that have measured WUE in TMCFs range from 2.7–5.2  $\mu\text{mol mmol}^{-1}$ , with a mean of 3.5  $\mu\text{mol mmol}^{-1}$  (Table 5,  $n = 5$  sites in four studies). Letts & Mulligan (2005) assessed light-saturated WUE for plants growing in less-cloudy lower montane TMCF and cloudier upper montane TMCF, and found significantly higher WUE in canopy trees and understorey shrubs (5.2 and 5.1  $\mu\text{mol mmol}^{-1}$ , respectively) at the cloudier site compared with canopy trees and understorey shrubs (3.5 and 4.1  $\mu\text{mol mmol}^{-1}$ ) at the less cloudy site. This was attributed to lower vapour pressure deficit driven by leaf temperature in the cloudy site, rather than a strong change in  $c_i/c_a$ . Studies from lowland tropical rain forests also generally report lower plant WUE values compared with TMCF species, ranging from 1.4–4.0  $\mu\text{mol mmol}^{-1}$  (Cernusak *et al.* 2007, Cunningham 2005, Vargas & Cordero 2013).

Given the high degree of variability in the TMCF microclimate, WUE can also be expected to vary within a given site over short temporal and spatial scales. Unfortunately, studies that have explicitly examined WUE variability in relation to topographical, seasonal, or daily variability in microclimate conditions in TMCFs are especially scarce. Cordero (1999) collected gas-exchange measurements on potted saplings of *Cecropia schreberiana* exposed to two contrasting natural wind regimes in elfin cloud forest in the Luquillo Experimental Forest in Puerto Rico. WUE was approximately 2.8  $\mu\text{mol mmol}^{-1}$ , with no significant difference observed between wind-exposed and wind-protected plants. Similarly, Sobrado (2003), working with  $\delta^{13}\text{C}$ , found no differences in WUE between the wet and dry seasons. However, based on studies from other regions, it is likely that factors such as exposure to wind (Nagano *et al.* 2013), fog occurrence and associated changes in VPD, solar radiation, nutrient availability (Negret *et al.* 2013, Santiago & Dawson 2014, Vasey *et al.* 2012), and soil moisture availability related to edaphic or topographic features (Craven *et al.* 2013, Rada *et al.* 2009), will influence plant water-carbon trade-offs and, ultimately, WUE. More detailed studies aimed at capturing within-site variability are needed across a range of different TMCFs to better elucidate these relationships between microclimate conditions and WUE.

While variation in altitude and the associated microclimate conditions may explain large-scale patterns of WUE in TMCFs, substantial within-site variation may also occur due to differences among species in their physiological strategies and growth patterns (Table 5). Studies that have examined WUE across plant species that are common to different successional stages (i.e. early versus late successional sites) in TMCFs have generally reported lower WUE in early compared with late-successional species (Rada *et al.* 2009, Sobrado 2003). This trend is consistent with findings for tropical lowland rain forests (Bonal *et al.* 2007, Nogueira *et al.* 2004, Vargas & Cordero 2013). Sobrado (2003) compared  $\delta^{13}\text{C}$  for pioneer and mature forest species occurring in a lower montane tropical forest in Venezuela. Results showed more negative  $\delta^{13}\text{C}$  for the mature forest species

( $-29.02 \pm 0.28\%$ ) than the pioneer species ( $-25.64 \pm 0.42\%$  VPDB), suggesting more conservative water use by mature species. Wittich *et al.* (2012) also suggests that the range in WUE among species analysed within each altitude (e.g. 1000, 2000 and 3000 m a.s.l.) is greater than the range between the three zones, consistent with earlier observations about the high degree of within-ecosystem variability in water and carbon fluxes. Rada *et al.* (2009) assessed WUE in four tree species and a climber with canopies in the upper strata of a cloud forest in the Venezuelan Andes during the wet and dry seasons. They reported a relatively large range of WUE between 1.79 and 5.58  $\mu\text{mol mmol}^{-1}$ , and explained these differences based on species differences in physiological strategies to balance deficits with carbon gain. The two species with higher WUEs were considered to depend on strict (conservative) stomatal control, while other species exhibited relatively high water use under drier conditions in support of more opportunistic growth strategies. How such variability translates into patterns of WUE is of particular interest because of the potential for insights regarding how plants regulate gas-exchange processes in response to changing environmental conditions.

*Ecosystem: WUE and CUE.* To our knowledge, there are currently no ecosystem WUE estimates available for TMCFs. Ecosystem-level estimates of WUE require more complex approaches which are often prohibitive in TMCF regions, either due to the complex terrain (precluding the deployment of eddy covariance flux towers due to lack of sufficient fetch) or due to the tremendously high species diversity (posing challenges to sap flux-based measurements due to the extensive instrumentation requirements). A global review by Fernández-Martínez *et al.* (2014) on resource-use efficiencies among different biomes derived from GPP and actual evapotranspiration data, suggested a global convergence in mean resource-use efficiencies. Among these estimates, WUE did not differ statistically among forest types due to high variability.

The few studies that have assessed CUE for TMCFs, located in six different regions, indicate a remarkable degree of similarity across diverse sites, with values ranging between 0.24 to 0.45, with a mean of 0.33 (Table 5). Interestingly, this range in CUE for TMCFs is similar to that reported across a series of 10 lowland rain-forest plots (range from 0.32–0.46 with a mean of 0.39; Malhi *et al.* 2015), as well as in a global synthesis of tropical broadleaved forests (range from 0.33–0.48 with a mean of 0.38; Fernández-Martínez *et al.* 2014). This may suggest a convergence of CUE across different tropical ecosystems. Nevertheless, determining whether these trends in WUE and CUE hold for a greater range of TMCF sites awaits future research on this topic.

## DISCUSSION

Our synthesis of TMCF plant carbon and water fluxes identified a number of trends (Figure 1). With respect to plant carbon relations, research to date suggests that average light-saturated photosynthesis is lower in TMCFs than in lowland rain forests. This pattern is likely due to differences in microclimatic factors in tropical mountains suppressing photosynthesis rather than a lower intrinsic biochemical capacity of TMCF plants (van de Weg *et al.* 2012). Lower net leaf photosynthesis may in turn translate into lower overall net primary productivity in TMCFs relative to lowland rain forests. With respect to plant water relations, average rates of transpiration at the level of the leaf, plant and stand are also generally lower than in lowland rain-forest sites. However, the range of leaf-level conductance in TMCFs overlapped with rates in lowland rain-forest sites, while whole-plant and ecosystem-level estimates were consistently lower in TMCF. WUE tends to increase with altitude due to the TMCF generally having lower evaporative demand than lowland rain forests. Given these observations, we now identify key outstanding questions in tropical montane cloud forest plant carbon and water relations:

1. *Are TMCF plants light-limited?* Research to date demonstrates that mean light-saturated photosynthesis is approximately 25–30% lower in TMCF than in tropical lowland forests. However, the effects of clouds and cloud immersion on photosynthesis and in turn, growth and primary productivity, remain largely unresolved (Alton 2008). While clouds reduce PAR, they also increase the ratio of diffuse to direct radiation such that more consistent light penetrates the canopy (Gu *et al.* 2002). As a result, an increase in ecosystem carbon exchange has been observed on cloudy relative to clear days in several temperate ecosystems (Gu *et al.* 2002, Hollinger *et al.* 1994, Urban *et al.* 2012, but see Alton 2008). Moreover, these changes are driven by clear changes in photosynthetic efficiency, including a lower photosynthetic light compensation point (Hollinger *et al.* 1994, Law *et al.* 2002, Urban *et al.* 2007) and a higher apparent quantum yield (Dengel & Grace 2010, Gu *et al.* 2003, Still *et al.* 2009). These changes thus facilitate an increase in photosynthesis per unit incident light on cloudy days up until saturating light levels. However, while the net effect of a 10–50% reduction in TMCF PAR is more likely to control photosynthetic rates than changes in photosynthetic light use efficiency, studies that systematically compare photosynthetic rates as a function of varying cloud intensity in montane cloud forests are rare (Letts & Mulligan 2005, Reinhardt & Smith 2008). An experimental approach in a lowland rain forest has previously demonstrated that leaves of a canopy

tree species were acclimated to lower light and that supplemental light increased net photosynthesis, as well as plant water use (Graham *et al.* 2003). Manipulative experiments at the scale of the leaf and observations of CO<sub>2</sub> fluxes at the scale of the ecosystem, complemented by simple but complete information on net annual PAR, would serve as compelling approaches to resolving the extent to which TMCF plants are light-limited.

2. *What are the relative roles of plant water supply and demand in regulating TMCF water balance and how important is fog for ecosystem function?* Despite abundant research establishing relationships between evaporative demand and rates of transpiration (Alvarado-Barrientos *et al.* 2014, Goldsmith *et al.* 2013, Gotsch *et al.* 2014b), we still lack a clear understanding of the relative roles of soil and ground water availability, as well as fog water availability and evaporative demand, in controlling rates of transpiration (but see Berry *et al.* 2016, Darby *et al.* 2016, Eller *et al.* 2015). For instance, in a number of TMCFs, fog has been shown to reduce transpiration, lead to additional water inputs to the soil, and directly improve plant water status via foliar water uptake (Alvarado-Barrientos *et al.* 2014, Burgess & Dawson 2004, Dawson 1998, Eller *et al.* 2015, Goldsmith *et al.* 2013, Gotsch *et al.* 2014a, b; Gotsch *et al.* 2015). However, the extent to which foliar water uptake influences ecosystem-level water balance and the degree to which a loss of foliar water uptake due to changes in climate would influence plant and ecosystem-level carbon and water fluxes is unknown. If projected changes in atmospheric conditions lead to increased evaporative demand, transpiration may increase and less of this lost water will be recovered via foliar water uptake. Such changes will inevitably affect plant and stand-level water loss in the TMCF, although the magnitude of these changes could be mediated by concomitant changes in species' WUE and CUE. Understanding the relative importance of these drivers under current conditions will help us understand how projected changes in climate may exacerbate or diminish the role of atmospheric and soil-based drivers for plant and ecosystem water use. A combination of observational and experimental approaches will be needed across a number of TMCF ecosystems to tease apart the importance of these environmental drivers.

3. *How will changes in plant carbon or water relations associated with increasing CO<sub>2</sub> translate to WUE?* A central focus in climate change research over the past several decades has been to determine the potential for plants to acclimate to increases in atmospheric CO<sub>2</sub> concentration via changes in their photosynthetic and stomatal regulation of carbon and water fluxes. Much of this interest lies in the

possibility that stimulation of photosynthetic rates at higher atmospheric CO<sub>2</sub> concentrations could lead to both higher WUE and hence ecosystem productivity, thereby providing a feedback mechanism for increasing the terrestrial CO<sub>2</sub> sink, as well as improving plant resilience to water stress (Franks *et al.* 2013).

The combination of dendrochronology with  $\delta^{13}\text{C}$  analysis provides a particularly powerful approach to assessing historical relationships between atmospheric CO<sub>2</sub> concentration and intrinsic water use efficiency (iWUE) over long timescales and could provide great insight into responses of TMCF species to recent changes in climate. In general, studies conducted in tropical rain forests suggest large increases in iWUE in response to increasing atmospheric CO<sub>2</sub> (Cernusak *et al.* 2013, van der Sleen *et al.* 2015). However, these trends will also be influenced by changes in VPD (which are less well known), such that if leaf temperature increases due to decreasing  $g_s$ , VPD may increase and thereby dampen (but likely not eliminate) the increase in WUE (Cernusak *et al.* 2013). For example, in the study by Bonal *et al.* (2011), herbarium samples of two common tropical rain-forest species in the Guiana Shield were analysed over a 200-year time period for  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ . Based on model results, they reported an increase in iWUE over recent decades by 23.1–26.6%. These results agree with findings from other forests globally (Peñuelas & Azcón-Bieto 1992, Saurer *et al.* 2014). However, emerging evidence suggests that these increases in iWUE in response to rising atmospheric CO<sub>2</sub> concentrations may not be accompanied by increases in CO<sub>2</sub> assimilation and growth, with a 'saturation effect' on productivity likely due to countervailing effects of other limiting resources, such as moisture or nutrients (Gómez-Guerrero *et al.* 2013, Levesque *et al.* 2014, Peñuelas *et al.* 2011, van der Sleen *et al.* 2015). The study by Gómez-Guerrero *et al.* (2013), which assessed stem increment growth and  $\delta^{13}\text{C}$  in high-altitude cloud-affected forests in central Mexico, is most similar to TMCF and found that CO<sub>2</sub>-induced increases in iWUE were not sufficient to counteract impacts of warming-induced drought stress on growth. More research is needed to disentangle the interactive effects of climate change-induced increases in temperature, moisture stress and nutrient limitation on iWUE and CO<sub>2</sub> assimilation to better understand the potential consequences for long-term productivity and resilience of TMCFs to climate extremes.

*TMCF water and carbon relations in a changing climate.* Changes in TMCF cloud immersion are projected as a function of changing land and sea surface temperatures associated with anthropogenic change (Karmalkar *et al.* 2008, 2011; Lawton *et al.* 2001, Pounds *et al.* 1999, 2006; Still *et al.* 1999). Direct observations of changes in tropical montane cloud immersion are currently limited (but



see Richardson *et al.* 2003 for a temperate analogue). However, changes in temperature and precipitation for tropical mountains, which are clearly linked, are more readily available. Tropical mountains are projected to be particularly vulnerable to changes in temperature and precipitation, with current climate regimes possibly disappearing by 2100 (Williams *et al.* 2007). Significant increases in temperature are projected to be further enhanced at high altitudes, while precipitation is projected to be more variable in general, with net increases or decreases possible depending on the location (Karmalkar *et al.* 2008, 2011; Urrutia & Vuille 2009). As with many places in the tropics, long-term observations of these trends in TMCF are limited. However, consistent with modelling projections (Karmalkar *et al.* 2011), Pounds *et al.* (1999, 2006) has observed increases in the number of days without rain as a function of increasing temperatures in Costa Rican TMCF. Taken together, such climatic changes indicate clear increases in temperature that will have associated effects on VPD, likely decreases in cloud immersion further changing VPD and also affecting light availability, and associated, but poorly understood changes in precipitation.

The extent of these changes, and their impacts on tropical montane cloud-forest carbon and plant water relations, remains to be seen. However, the questions posed above can help guide the next generation of research. Studying the extent to which TMCF plants are light-limited will provide the basis for understanding how changes in clouds will affect leaf-level photosynthesis and ecosystem productivity. Studying the relative roles of plant water supply and demand in regulating TMCF water balance will provide the basis for understanding how changes in both precipitation and clouds will change leaf, plant and ecosystem water balance, while a specific focus on fog can elucidate whether it plays a critical role in alleviating water deficits through foliar water uptake. And finally, studying water use efficiency places climate change in context with concomitant increases in CO<sub>2</sub> and its observed effects on plant function. Will the tropical montane cloud forests of the future function similarly, will they function more like tropical lowland rain forests, or will they not be able to withstand the rapid projected changes? Increased research efforts are needed to understand the degree to which anthropogenic climate change will affect the resilience of these unique ecosystems.

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**Appendix 1.** Sap flow observed in tropical montane cloud forests.

Sap flow ( $\text{cm h}^{-1}$ )	Volumetric sap flow ( $\text{L d}^{-1}$ )	Elevation (m asl)	Precipitation ( $\text{mm y}^{-1}$ )	Temp. ( $^{\circ}\text{C}$ )	Location	Study
-	0.7–2.0	1500	3000	17.2	Costa Rica	Feild & Holbrook (2000)
3.3–5.0		1950–1975	2067	15.5	Ecuador	Motzer <i>et al.</i> (2005)
Montane: 0.7–1.4 $\pm$ 0.3 (SD), Premontane: 0.5–1.5 $\pm$ 0.2 (SD)*		1409–1563	2983–3994	-	Costa Rica	Goldsmith <i>et al.</i> (2013)
1.5 $\pm$ 0.5 (SE)	Forest line: 24.7 $\pm$ 5.9 (SE), Cloud forest: 10.7 $\pm$ 3.7 (SE)	2109–2231	3500–5000	10.5	Maui (USA)	Gotsch <i>et al.</i> (2014a)
	Branch-level: 1.8 $\pm$ 0.4 (SE)	2100	2000–3000	14.3	Mexico	Gotsch <i>et al.</i> (2014b)
3.3–5.0		1950–1975	2067	15.5	Ecuador	Motzer <i>et al.</i> (2005)
	~18.75	1560	8100	-	Australia	McJannet <i>et al.</i> (2007)

\*Understorey branches.