LETTER

The incidence and implications of clouds for cloud forest plant water relations

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Abstract

Although clouds are the most recognisable and defining feature of tropical montane cloud forests, little research has focussed on how clouds affect plant functioning. We used satellite and ground-based observations to study cloud and leaf wetting patterns in contrasting tropical montane and pre-montane cloud forests. We then studied the consequences of leaf wetting for the direct uptake of water accumulated on leaf surfaces into the leaves themselves. During the dry season, the montane forest experienced higher precipitation, cloud cover and leaf wetting events of longer duration than the pre-montane forest. Leaf wetting events resulted in foliar water uptake in all species studied. The capacity for foliar water uptake differed significantly between the montane and pre-montane forest plant communities, as well as among species within a forest. Our results indicate that foliar water uptake is common in these forest plants and improves plant water status during the dry season.

INTRODUCTION

Tropical montane cloud forests (TMCF) are among the planet's most rare and endangered ecosystems (Bruijnzeel *et al.* 2010; Ponce-Reyes *et al.* 2012). Although there is no universally agreed upon definition of the frequency, duration or extent to which a tropical forest must be immersed in clouds to be defined as a TMCF, it is generally agreed upon that these forests experience a high frequency of immersion in clouds extending to the ground (i.e. fog; Bruijnzeel *et al.* 2011; Scholl *et al.* 2011). The locations that meet such criteria are exceptional; TMCF occupies just 1.4% of the world's tropical forest area (Scatena *et al.* 2010). Unfortunately, TMCF is extremely vulnerable to a host of anthropogenic pressures (Bruijnzeel *et al.* 2010). In particular, evidence suggests that rising land and sea surface temperatures will affect cloud patterns (Pounds *et al.* 1999; Still *et al.* 1999; Lawton *et al.* 2001; Karmalkar *et al.* 2008), with associated implications for maintaining ecosystem diversity, functioning and services (Martínez *et al.* 2009). As such, there is a critical need for an improved understanding of clouds and their effects on cloud forest plant functioning.

As summarised below, clouds can play a unique and varied role in cloud forest plant ecology, primarily affecting plant functioning by 1) altering leaf energy balance and suppressing plant transpiration, 2) adding water to the soil through drip from the canopy and 3) the uptake of water accumulated on leaf surfaces directly into leaves.

Clouds alter microclimate by changing energy balance and thus reducing vapour pressure deficit (VPD) and photosynthetically active radiation. In turn, this decreases plant water demand. The suppression of leaf-level transpiration has been observed in a number of cloud-affected ecosystems, including TMCF (Burgess & Dawson 2004; Reinhardt & Smith 2008; Gotsch, S.G., Asbjornsen, H., Holwerda, F., Goldsmith, G.R. & Dawson T.E, unpublished data).

Cloud water droplets moving horizontally through cloud-affected ecosystems can be intercepted by and accumulate on plant surfaces, often resulting in leaf wetting. When the plant canopy storage capacity is exceeded, soil water availability can be increased through the resultant drip (Gomez-Peralta *et al.* 2008). Although measuring this 'occult' (hidden), horizontal precipitation is difficult, additional inputs into TMCFs have already been observed to increase water availability well beyond that of vertical precipitation alone (Giambelluca & Gerold 2011). Such inputs can be particularly valuable during the dry season experienced by many TMCFs, when measurable precipitation decreases, but clouds may persist (Vogelmann 1973; Holder 2004).

Finally, the uptake of intercepted water on leaf surfaces into leaves, a phenomenon referred to as foliar water uptake (foliar uptake), has previously been demonstrated in plants from a range of other dew and cloud-affected ecosystems (Stone 1957; Boucher *et al.* 1995; Munné-Bosch *et al.* 1999; Martin & von Willert 2000; Gouvra & Grammatikopoulos 2003; Limm *et al.* 2009), as well as where rainfall is intercepted by plant canopies, but does not always increase soil water availability (Breshears *et al.* 2008). Although leaf wetting events are often considered to negatively affect plant performance (Brewer & Smith 1997), there are now many examples where improvements in plant water status can result from foliar uptake and lead to improved photosynthetic performance and even growth (Boucher *et al.* 1995; Simonin *et al.* 2009). The effect of foliar uptake on plant performance can be especially important in seasonally dry ecosystems where, in the absence of rainfall reaching the soil, water from dew or cloud immersion accumulating on leaves may be the most readily available water source (Dawson 1998). Despite this, the prevalence and significance of foliar uptake in TMCF remains unknown and there have been no comparisons between cloud forests that vary in both their abiotic (e.g. cloud cover and resultant leaf wetting events) and biotic (e.g. plant species composition) characteristics.

We studied cloud cover and leaf wetting patterns, and their relationship with foliar uptake, at neighbouring tropical montane and

pre-montane cloud forests. We expected that differences in seasonal climate patterns and species composition between the two forests would allow us to compare and contrast the effects of varying cloud cover and leaf wetness on plant functioning (Haber *et al.* 2000). Our objectives were to 1) describe and compare cloud cover patterns and leaf wetness for each forest, 2) determine the prevalence of foliar uptake among plant species in each forest and 3) compare the capacity for foliar uptake among study species and between the two forest communities. Although we demonstrate that foliar uptake is widespread and coupled to leaf wetting events commonly occurring due to clouds, we also demonstrate that forests and the individual species within them do not necessarily benefit equally from this unique phenomenon.

METHODS

Study site description

Field study was conducted from 2009 to 2011 along the Pacific slope of the Cordillera de Tilarán mountains near Monteverde, Costa Rica. We studied a relatively aseasonal, old growth lower montane wet forest (*montane*; 10°17.959' N, 84°47.460' W, 1563 m) and a highly seasonal, old growth pre-montane wet forest (*pre-montane*; 10°17.918' N, 84°48.563' W; 1409 m). Forest descriptions are provided by Haber *et al.* (2000). Synoptic climate is summarised by Clark *et al.* (2000).

Cloud cover using remote sensing

To characterise cloud cover patterns, we surveyed daily remote sensing products available between 2002 and 2012 as provided by the Moderate Resolution Imaging Spectroradiometer aboard NASA's *TERRA* and *AQUA* satellites. We employed a Level 2 cloud mask product (MOD35), which uses a series of threshold algorithms to identify cloud cover for each pixel (1 km^2) in a field of view, thus providing a standardised means by which to compare spatial and temporal patterns (Ackerman *et al.* 1998; Platnick *et al.* 2003). Due to satellite orbits and the field site latitude, four daily cloud mask products are available in the following time windows: 09 : 25–11 : 05, 12 : 20–13 : 55, 21 : 15–22 : 50, and 00 : 25–02 : 10.

Cloud mask products were accessed from NASA's EOSDIS website, geo-referenced with a Level 1 geo-location product (MOD03) and checked for QA/QC (EOSDIS 2009). The MOD35 product algorithm categorises pixels as confident clear (confidence > 0.99 of clear skies), probably clear (0.99 ≥ confidence > 0.95), probably cloudy (0.95 ≥ confidence > 0.66) and confident cloudy (confidence ≤ 0.66). Due to its typical use for identifying cloud-free scenes, the cloud mask product is clear-sky conservative; it is more likely to falsely identify scenes with clouds than scenes without clouds. Therefore, we focussed on querying the pixels covering each study forest (c. 2 km apart) to determine whether each time point was designated as confident cloudy or not.

Environmental characterisation and monitoring

To characterise rainfall patterns, bulk precipitation was measured in 2011 by the Monteverde Institute near the pre-montane forest via manual rain gauge and by the Tropical Science Center near the montane forest via tipping bucket rain gauge. To characterise microclimate, leaf wetness, temperature and relative humidity were monitored at each forest. Leaf wetness was monitored between 5 February and 10 April using three leaf wetness sensors painted matte white and attached at a slight incline to understory branches facing different aspects (Model 237, Campbell Scientific; Logan, Utah, USA). Leaf wetness was determined to occur only when all three sensors were below the manufacturer-specified measurement threshold. Temperature and relative humidity were monitored between 1 March and 31 March using an HMP35C probe (Vaisala Instruments; Helsinki, Finland) and used to calculate VPD. All measurements were recorded once a minute for 5 min at 15 min intervals, so as to derive an average value, using CR10X data loggers (Campbell Scientific; Logan, Utah, USA). Volumetric soil water content was measured weekly between 1 March and 31 March in 10 random locations using the 'Hydrosense' model handheld sensor with 20 cm probes (Campbell Scientific; Logan, Utah, USA). The relationship between mean monthly proportion of cloudiness observations and bulk precipitation at each forest in 2011 was evaluated using linear regression. To determine whether cloud cover observations can serve as a proxy for leaf wetness, the relationship between leaf wetness and cloud cover observations was evaluated using a logistic regression where leaf wetness was a binary response (1 = wet, but see below) and cloudiness (1 = cloudy), time of day (06 : 01–18 : 00 or 18 : 01–06 : 00; 1 = night) and their respective interaction were binary predictors. As observations of leaf wetness and cloud cover may be slightly decoupled, models were constructed using single observations of leaf wetness before, at and after the single cloud observation, as well as multiple observations of leaf wetness in time windows (0.5, 1, 2, and 3 h) centred around the single cloud observation. Where there is a time window, the response is the proportion of observations registering leaf wetness relative to the total number of observations. Each model at each site used between 187 and 190 cloud observations. Differences in leaf wetness, VPD and soil water content between forests were evaluated via t-tests. The relationship between the daily number of hours registering leaf wetness and the mean daily VPD was evaluated using ANCOVA, where VPD was a response and leaf wetness and forest were predictors. These and all other statistics were conducted using R 2.14.12 (R Development Core Team 2012).

Sap flow

To characterise foliar uptake *in situ*, we measured sap flow on small branches of woody plants using the heat ratio method, which is particularly effective for measuring low flow rates and reverse flow (Burgess *et al.* 2001). We used the sensor assembly of Clearwater *et al.* (2009), where small sensors are affixed externally to the surface of a small branch. Implementation of this method followed Roddy & Dawson (2012). Briefly, every 15 min, starting temperatures were recorded downstream (proximal to terminal leaves) and upstream (distal), a 4 s heat pulse was applied, and new average temperatures were recorded for 40 s following a 60 s waiting period. Heat pulse velocity (V_h) was calculated as:

$$V_h = \frac{k}{x}\ln\left(\frac{\delta T_1}{\delta T_2}\right) \quad cms^{-1} \tag{1}$$

where k is thermal diffusivity (cm^{2}s^{-1}; see below), x is distance from the heat pulse to the temperature sensors (cm) and δT_1 and

δT_2 are the downstream and upstream temperature changes (°C). We determined k by measuring the time to reach maximum temperature rise following a heat pulse applied daily at 05 : 00, when no sap flow is occurring. We calculated k as:

$$k = \frac{x^2}{4t_m} \quad cm^2 s^{-1} \tag{2}$$

where t_m is time to maximum temperature (s) and x is as above. Given the small variation in time to maximum temperature rise among species (53 ± 6 s SD), we applied this average to all calculations. Our calculation of k (2.83×10^{-3} cm^{2}s^{-1}) was in strong agreement with previous empirical determinations (Burgess *et al.* 2001). A reference velocity ($v_h = 0$) was determined for each sensor at times when sap flow is assumed to be zero by averaging values between 24 : 00 and 05 : 00 at high humidity (> 95%) and no leaf wetness (Rosado *et al.* 2012). This was the only method of determining zero flow we could successfully and repeatedly apply; attempts to stop flow by severing the stems above and below the sensor caused movements of the thermocouples that led to massive errors in determining zero flow. As such, this method could not be used on our small stems.

We measured sap flow for 3 days in March 2011 on 2 small branches of each individual plant of 6 common woody plant species occurring in the understory at each forest. We focussed on the understory to facilitate sampling logistics and used transect-based, plant abundance data to guide our species' choice (Appendix S1; R.O. Lawton & W.A. Haber, *unpublished data*). Mean stem diameter at the pre-montane forest was 3.5 ± 0.7 mm (SD) and 4.2 ± 0.5 mm at the montane forest. At 12 : 00 on the second day of sap flow measurements, we continuously sprayed water on the leaves of one of the two branches from each individual for 3 h. During this time, water potential (Ψ_L) was measured on wetted leaves of each plant at the conclusion of the experiment, as well as on control leaves before and at the conclusion of the experiment ($n = 3$ leaves at each time point). Wetted leaf surfaces were dried just prior to the measurement. Ψ_L was measured with a pressure chamber (Soilmoisture Equipment Corporation; Santa Barbara, California, USA). We were unable to measure Ψ_L for *Sorocea trophoides* and *Tabernaemontana longipes* due to latex.

While monitoring sap flow, rainfall was measured via tipping bucket rain gauge (Onset Corporation, Bourne, Massachusetts, USA). For experimentally wetted leaves of each species, the mean heat pulse velocity over the entire experiment was compared relative to zero using a one-tailed, single sample t-test. Mean Ψ_L measured on wetted leaves at the conclusion of the experiment was compared with mean Ψ_L measured on control leaves via t-test. Finally, the relationship between mean heat pulse velocity over the course of the experiments and the difference in Ψ_L control and wetted leaves at the conclusion of the experiments, as well as between mean heat pulse velocity in the first hour of the experiments and the initial Ψ_L of control leaves was evaluated across both forests by linear regression.

Foliar uptake capacity

To characterise differences in foliar uptake between the two forests, we measured what we define as the 'capacity for foliar uptake' in the 12 most common woody plant species occurring in the understory from each forest (Appendix S1). For each species, we measured 3 leaves each from 3 individuals. To measure uptake capacity, branchlets were collected in late afternoon, re-cut under water and rehydrated overnight. Following rehydration, a single leaf was

excised from the branchlet and measured for Ψ_L. Pressure in the chamber was then slowly increased to -1.0 MPa and maintained for 1 min to induce water deficit. We chose -1.0 MPa based on typical dry season *in situ* leaf water deficits (Goldsmith, *unpublished data*). Leaves were then submerged in water for 1 h, similar to Limm *et al.* (2009). Petioles were sealed with parafilm and left above water to prevent water entry. Following submersion, leaves were dried and immediately measured for Ψ_L. Capacity for foliar uptake was measured as improvement in Ψ_L following submersion following adjustment for initial Ψ_L. Differences between the two forests, as well as differences among species within a forest were evaluated using a nested ANOVA, where forest was treated as a fixed factor with species and individual treated as nested, random factors.

RESULTS

Synoptic climate

During 2011, the cloud mask determination was made between 255 and 263 times each for the four daily products (e.g. images) at each forest, resulting in $\geq$ 17 products month^{-1} for analysis (average across all sites and times was 21.4 products month^{-1}). Cloud mask determinations are not always possible due to incomplete spatial coverage. Both forests demonstrated intra-annual patterns in cloud cover consistent with regional seasonality (Fig. 1). During the wet season (May–October), the proportion of daytime (0.89 ± 0.09 SD) and night-time (0.76 ± 0.15 SD) observations of cloudiness month^{-1} at the montane forest was virtually identical to daytime (0.89 ± 0.09 SD) and night-time (0.77 ± 0.09 SD) observations at the pre-montane forest. However, differences developed over the course of the misty season (November–January). During the dry season (February–April), the proportion of daytime (0.52 ± 0.11 SD) and night-time (0.31 ± 0.25 SD) observations of cloudiness month^{-1} was higher at the montane forest than the daytime (0.36 ± 0.16 SD) and night-time (0.21 ± 0.16 SD) observations at the pre-montane forest. The intra-annual pattern of cloud cover observed in 2011 is consistent with monthly observations made from 2002 to 2012 (Fig. S1).

Over the course of 2011, the montane forest received 3494 mm of bulk precipitation, with 6.0% (208 mm) of the total recorded during the dry season. The pre-montane forest received 2983 mm, with 3.1% (92 mm) of the total recorded during the dry season. Additionally, the monthly bulk precipitation totals at the montane forest exceeded those at the pre-montane forest in 11 of the 12 months. There was a significant linear relationship between the average monthly proportion of cloudiness observations and bulk precipitation at both the montane ($r^2 = 0.32$, $P < 0.001$, $f = 486x$, intercept = 0) and pre-montane forest ($r^2 = 0.52$, $P < 0.001$, $f = 459x$, intercept = 0).

Coefficient estimates (odds ratios) indicate that cloud observations and time of day are significant predictors of leaf wetness at both forests (Fig. S2). The relationships did not vary strongly with differing time windows; however, the confidence intervals became narrower as the time window increased, likely due to an increasing number of wetness observations. The inclusion of the interaction term had a strong effect on coefficient estimates at the pre-montane forest, changing their sign, but not at the montane forest. This may indicate that at the pre-montane forest, there is little unexplained variation after the interaction term has been taken into account. The models with no interaction term provide additional insight: at the montane forest, both cloudiness and time of day are significant predictors of leaf wetness,
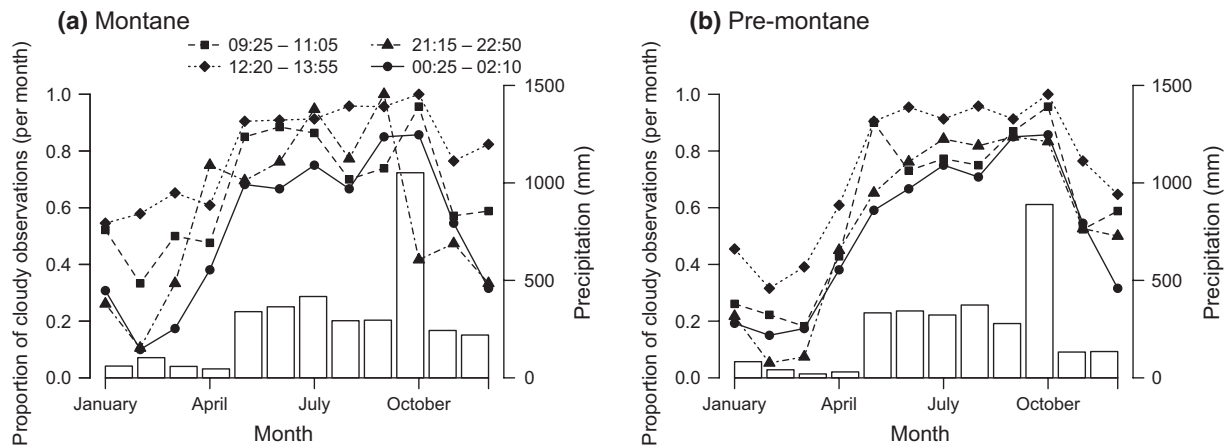
Figure 1 Monthly patterns of cloud observations (lines with symbols) and precipitation (bars) determined for tropical (a) montane and (b) pre-montane cloud forests near Monteverde, Costa Rica for 2011.
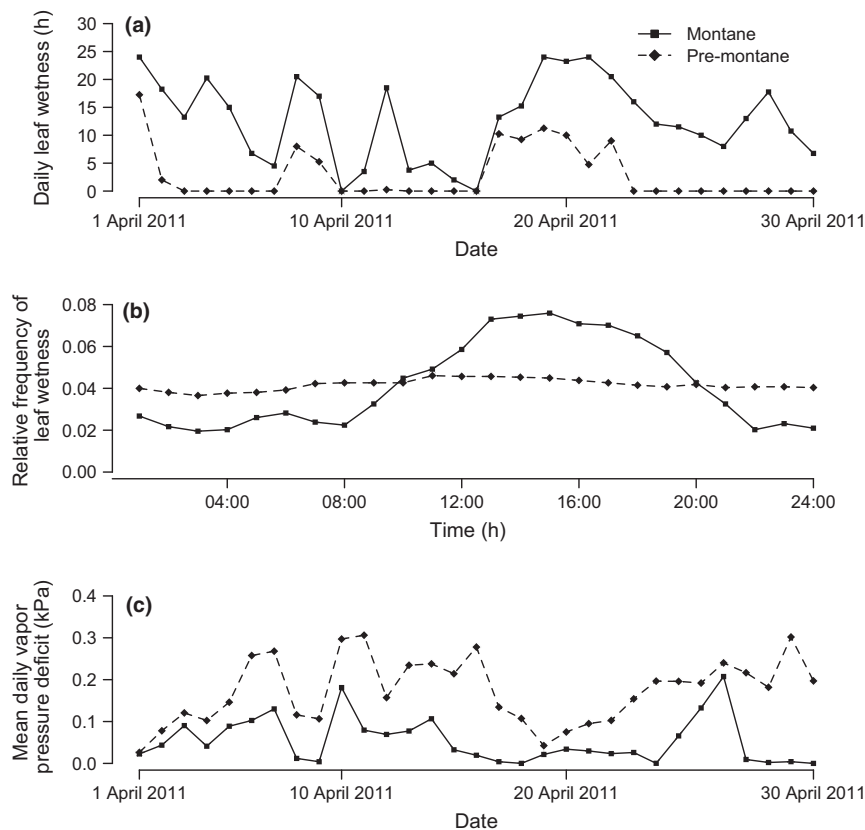

Figure 2 Microclimatic measures determined in the understory of tropical montane and pre-montane cloud forests near Monteverde, Costa Rica between 1 March and 31 March 2011. Measures include (a) the number of hours day^{-1} registering leaf wetness, (b) the relative frequency of leaf wetting events hour^{-1} and (c) the mean daily vapour pressure deficit.

with time of day a stronger predictor. The pattern is similar at the pre-montane forest, but the odds ratios are much lower. The weaker relationship at the pre-montane forest, as well as the significant interaction, is apparent when comparing additional details for models fit to both forests at a time window of 0.5 h (Table S1). The AUC, a measure of accuracy treating the logistic model as a binary classifier where 0.5 would indicate random guess and 1.0 would indicate perfection, is higher at the montane than the pre-montane forest (Agresti 2002). The

AIC, a measure of goodness of fit for comparison of models within a forest where lower numbers indicate better fit, is lower for the pre-montane forest model that incorporates the interaction (Agresti 2002).

Environmental monitoring

During March 2011, the mean number of hours day^{-1} registering understory leaf wetness at the montane forest (12.8 ± 1.3) was sig-
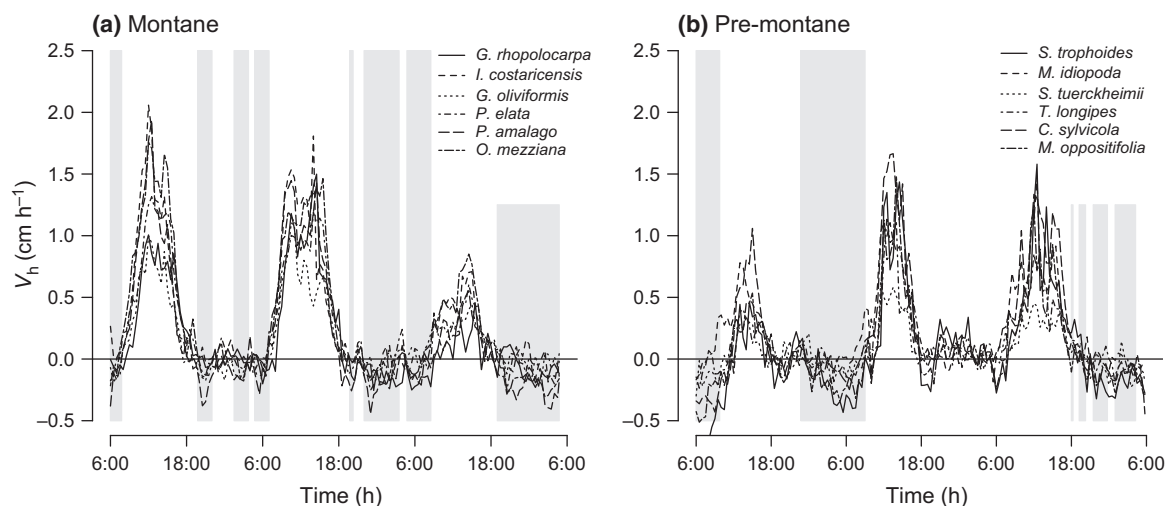
Figure 3 Sap flow (V_h) monitored *in situ* on a single individual of 6 different species in the understory of tropical (a) montane and (b) pre-montane cloud forests near Monteverde, Costa Rica. Light grey bars represent leaf wetting events.

nificantly higher than at the pre-montane forest (2.8 ± 0.8) (Fig. 2a; t = 6.37, d.f. = 50.98, P < 0.0001). There was a daily pattern to leaf wetness at the montane forest, with a higher frequency of daytime wet observations (10 : 00–20 : 00), whereas the pre-montane forest demonstrated an even distribution of wet observations (Fig. 2b). The pre-montane forest had fewer (15 total) and shorter (6.0 ± 1.6 h) leaf wetting events compared with the montane forest, which had more (44 total) and longer (9.0 ± 2.1 h) events. Mean daily VPD was significantly lower in the montane (0.05 ± 0.01 kPa) than the pre-montane (0.17 ± 0.01 kPa) forest (Fig. 2c; t = −6.96, d.f. = 53.57, P < 0.0001). There was a negative relationship between the mean daily VPD and the daily number of hours registering leaf wetness, even when considering the significant effect of forest ($F_{2,59}$ = 46.19, P < 0.001, r^2 = 0.60). The volumetric soil water content was significantly higher at the montane (48 ± 7%) compared with the pre-montane (23 ± 7%) forest (t = −2.64, d.f. = 6.00, P < 0.04).
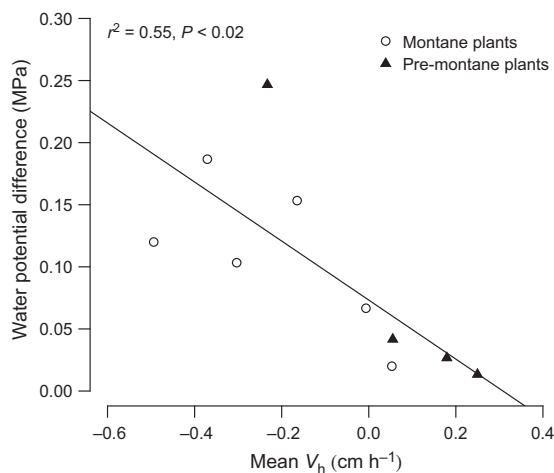

Figure 4 The difference in leaf water potential between control and experimentally wetted leaves as a function of the mean heat pulse velocity (V_h) as measured in 3 h experiments in tropical montane and pre-montane cloud forests near Monteverde, Costa Rica.

Sap flow

While monitoring sap flow, both forests experienced night-time leaf wetness events that persisted for several hours (Fig. 3). The pre-montane forest received measurable rainfall only once during this time, with 0.8 mm recorded between 06 : 00 and 08 : 00 on the first morning of monitoring. This corresponds with the first leaf wetting event and the most negative heat pulse velocities recorded. There was no additional measurable rainfall at either forest, such that all leaf wetting events were likely caused by cloud interception or very light rainfall.

Negative velocities (reverse flow) were observed in all species at each forest and were tightly coupled to leaf wetting events (Fig. 3). These observations were confirmed by the experimental wetting of one of the two branches monitored on each species, which again resulted in negative velocities in all species (Table S2). While negative velocities were often recorded soon after experimental wetting commenced, they did not always persist over the entire 3 h treatment, such that mean heat pulse velocities in experimentally wetted branches were significantly less than zero in only 4 of 12 cases (P < 0.05; Table S2). Mean Ψ_L measured on experimentally wetted branches following the treatment was significantly less negative than mean Ψ_L measured on nearby control branches in 4 of the 6 montane species and 1 of the 4 pre-montane species (*n* = 3, P < 0.05). The species that did not demonstrate high negative velocities in response to experimental wetting: *Meliosma idiopoda, Chione sylvicola, Matayba oppositifolia, Guarea rhopolocarpa* and *Guatteria oliviformis* were the same ones that did not demonstrate differences in Ψ_L between before and after experimental wetting. Across all species at both forests, Ψ_L improved as a function of increasing reverse sap flow rates resulting from experimental leaf wetting (Fig. 4; *f* = −0.237x + 0.073, *n* = 10, *f* = 9.89, P < 0.02, r^2 = 0.55). However, there was no significant relationship between initial Ψ_L and mean heat pulse velocity in the first hour of the experiment (*n* = 10, *f* = 1.49, P = 0.26).

Foliar uptake capacity

The mean capacity for foliar uptake was significantly higher ($F_{1,183}$ = 70.43, P < 0.0001) in the montane (0.67 ± 0.02 MPa) compared with the pre-montane (0.55 ± 0.12 MPa) forest and there
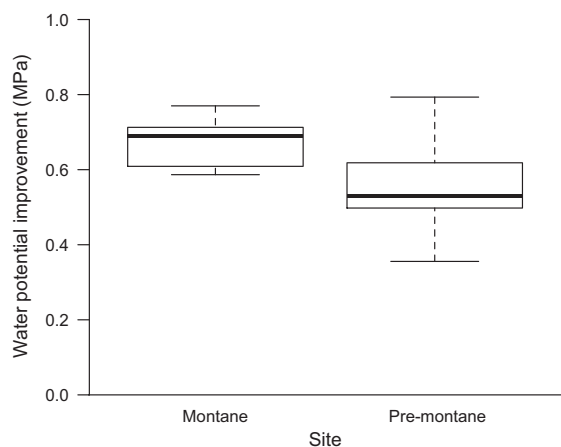
Figure 5 Improvement in mean leaf water potential measured in 12 common understory species in tropical montane and pre-montane cloud forests near Monteverde, Costa Rica following 1 h of experimental wetting.

were significant differences among plant species within a forest (Fig. 5; $F_{22,183}$ = 6.72, P < 0.0001).

DISCUSSION

We characterised the contrasting patterns of cloud cover at pre-montane and montane tropical cloud forests, as well as the associated relationship with leaf wetness. Leaf wetting events were tightly coupled to foliar uptake by all of the common species in the two forests. However, there were significant differences in the capacity for foliar uptake among species and between the two forest communities.

Characterising clouds and leaf wetness

We used a standardised remote sensing method to provide a quantitative approach to describing cloud cover. Cloud cover at each forest demonstrated consistent and long-term, monthly patterns related to that of precipitation, with a decrease occurring over the course of the misty (November–January) and dry (February–April) seasons, as well during the summer veranillo (little summer) that typically occurs in August. Consistent with the progression of daytime cumulus cloud cover over Costa Rica, both forests experienced more daytime cloudy observations than night-time cloudy observations during the dry season (Nair *et al.* 2003).

Although the forests are only c. 2 km apart (c. 1 pixel), there were strong differences in dry season cloud cover and leaf wetness. The pre-montane forest is further leeward (west) and at a lower elevation and therefore subject to a greater rain shadow and likely to less cloud immersion. The pre-montane forest experienced a lower average number of hours of leaf wetness per day, as well as a shorter average duration of each individual leaf wetness event compared with the montane forest. The pre-montane forest also demonstrated a weaker relationship between leaf wetness and cloud observations, likely due to reduced cloud immersion that results from the lower elevation. The remote sensing products analysed herein do not give any indication about cloud immersion (Nair *et al.* 2008; Welch *et al.* 2008). Nevertheless, our results indicate that cloud observations derived from remote sensing are valuable in that they are significant predictors of leaf wetness at both the montane

(c. 3.4–6.1x more likely to experience wetness given clouds) and pre-montane (c. 1.4–2.2x more likely) forests. During the dry season, the montane forest more frequently experiences the conditions that can result in foliar uptake.

The observed patterns of cloudiness, leaf wetness and VPD have a number of implications for leaf, plant, community and ecosystem water balance, particularly during the dry season when vertical precipitation inputs are reduced. Most notably, our observations indicate that the high cloud cover frequency is likely to suppress leaf-level transpiration and result in leaf wetting events that can result in foliar uptake.

Prevalence of foliar uptake

We monitored sap flow to survey the prevalence of foliar uptake resulting from the leaf wetness' patterns described above. Although this is the most direct and only real-time technique currently available to measure foliar water uptake, its application has been limited to date (Burgess & Dawson 2004). Reverse sap flow was observed in response to leaf wetting in all the species we surveyed in both forests. Moreover, the capacity to improve Ψ_L through foliar uptake was observed in all 24 species that were experimentally assessed, indicating that foliar uptake is ubiquitous in both the tropical pre-montane and montane cloud forest plant communities. These results, the first from a TMCF, add to a growing list of species identified as capable of foliar uptake. Research since 1950 has identified at least 70 species as being capable of foliar uptake, representing > 85% of all those studied (Appendix S2). Foliar uptake is likely to be a widespread phenomenon, and seemingly occurs independent of phylogeny, morphology or growth habit (Dawson 1998; Limm & Dawson 2010); however, additional information on its physiological significance is needed.

Significance of foliar uptake

We used both sap flow and water potential measurements to study the significance of foliar uptake among plant species and between forests. Foliar uptake improved plant water status in the laboratory and the field, with greater rates of reverse sap flow resulting in greater water deficit reductions. Although foliar uptake consistently improves leaf water status, there were significant differences in the magnitude of improvement among species. Moreover, the montane plant community demonstrated a significantly higher capacity for foliar uptake compared with the pre-montane plant community. In contrast, previous research has focussed on characterising foliar uptake either within plant species communities (Gouvra & Grammatikopoulos 2003; Limm *et al.* 2009), or across a single species' range (Limm & Dawson 2010). Our results indicate that not all species or forests are likely to benefit equally from the leaf wetting events that could reduce leaf water deficit through foliar uptake. Where foliar uptake occurs in other ecosystems, the reduction in leaf water deficit can result in improved carbon gain (Simonin *et al.* 2009), growth (Boucher *et al.* 1995) and survival (Stone 1957). Thus, foliar uptake is likely to be particularly important during the dry season, when there is reduced soil water availability (Goldsmith, G.R., Simonin, K.A., Vincent, J.B., Young, E.A., & Dawson, T.E., unpublished data). As such, foliar uptake would more likely benefit the drier, pre-montane forest. However, leaf wetting events in the pre-montane forest are less frequent and the plant community is unable capitalise on them physiologically to the same extent as the montane forest plant community.

Mechanisms and pathways for foliar uptake

It has been hypothesised that foliar uptake should occur given a gradient towards more negative Ψ_L (e.g. from the saturated leaf surface to the unsaturated matrix inside the leaf) (Rundel 1982). However, no relationship between initial Ψ_L and reverse sap flow rates was detected. Previous research has also indicated that Ψ_L does not appear to correspond with the magnitude of foliar uptake (Burgess & Dawson 2004; Limm & Dawson 2010; but see Breshears *et al.* 2008). Detecting this water potential gradient is likely limited primarily by the lack of appropriate techniques.

The observed differences in capacity for foliar uptake among plant species and between forests may be a function of differences in the leaf traits that facilitate uptake. Previous research has identified the cuticle (Yates & Hutley 1995; Limm & Dawson 2010), trichomes (Franke 1967) and hydathodes (Martin & von Willert 2000) as possible pathways for water entry into the leaf. Although it is an obvious additional pathway, evidence suggests that films of water are unable to enter stomatal pores (Schönherr & Bukovac 1972). In the absence of specialised traits (e.g. trichomes and hydathodes), diffusion of water through the cuticle is the most likely pathway. Cuticular permeability is a function of chemical composition and micro-architecture (Jetter *et al.* 2000), traits that are in turn modified by age and environmental degradation (Shepherd & Wynne Griffiths 2006). If the cuticle were the pathway, this could provide a potential explanation for observed differences. For instance, if the more seasonal, drier environment at the pre-montane forest favored plants with more desiccation-resistant cuticles, this would also result in a decrease in foliar uptake capacity.

Regardless of the mechanisms and pathways by which water enters the leaf, our results indicate strong differences in plant capacity to use leaf wetting events to improve plant water relations. Such findings should be considered in the context of global climate change.

Climate change projections

Tropical mountains are projected to experience high rates of climate change in the future (Williams *et al.* 2007; Karmalkar *et al.* 2008, 2011). Mean dry season surface air temperature along the Pacific slope of Costa Rica, where Monteverde is located, is projected by regional climate models to increase 3.8 °C, leading to a non-analogue climate before 2100 (Karmalkar *et al.* 2011). Moreover, these changes are projected to be associated with a strong increase in dry season temperature variability. Similarly, dry season precipitation is projected to decrease by 14%, with an accompanying decrease in variability (Karmalkar *et al.* 2011). Finally, evidence suggests that changes in surface temperatures are associated with an increasing number of consecutive dry season days (Pounds *et al.* 1999, 2006), as well as an increase in cloud base height (Still *et al.* 1999; Lawton *et al.* 2001; Nair *et al.* 2003). If these projections come to bear, cloud forest plants may experience increased water demand simultaneous to a decrease in precipitation, cloud immersion and leaf wetting events leading to foliar uptake.

CONCLUSIONS

Although clouds are the most recognisable and defining feature of TMCF, there is still a critical need for information regarding how clouds affect plant functioning. We demonstrated that cloud cover and associated leaf wetting events vary seasonally, as well as over very small distances. We then focussed on foliar uptake, one means by which clouds could affect plant functioning. Foliar uptake was demonstrated to be tightly coupled to leaf wetting events associated with cloud cover, leading to improved water relations. However, there were both species and forest differences in foliar uptake. Thus, if climate change affects cloud cover and associated leaf wetting events, not all plant species or communities will respond equally.

AUTHOR CONTRIBUTIONS

GG and TD initiated and designed the study. GG collected all field data. NM and GG accessed and analysed the remote sensing data. GG performed all other analyses. GG wrote the initial draft of the manuscript that was added to and edited by TD and NM. All authors contributed significantly to the current version.

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