

Comparison of tree transpiration under wet and dry canopy conditions in a Costa Rican premontane tropical forest

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Abstract:

Spatial and temporal variation in wet canopy conditions following precipitation events can influence processes such as transpiration and photosynthesis, which can be further enhanced as upper canopy leaves dry more rapidly than the understory following each event. As part of a larger study aimed at improving land surface modelling of evapotranspiration processes in wet tropical forests, we compared transpiration among trees with exposed and shaded crowns under both wet and dry canopy conditions in central Costa Rica, which has an average 4200 mm annual rainfall. Transpiration was estimated for 5 months using 43 sap flux sensors in eight dominant, ten midstory and eight suppressed trees in a mature forest stand surrounding a 40-m tower equipped with micrometeorological sensors. Dominant trees were 13% of the plot's trees and contributed around 76% to total transpiration at this site, whereas midstory and suppressed trees contributed 18 and 5%, respectively. After accounting for vapour pressure deficit and solar radiation, leaf wetness was a significant driver of sap flux, reducing it by as much as 28%. Under dry conditions, sap flux rates (J_s) of dominant trees were similar to midstory trees and were almost double that of suppressed trees. On wet days, all trees had similarly low J_s . As expected, semi-dry conditions (dry upper canopy) led to higher J_s in dominant trees than midstory, which had wetter leaves, but semi-dry conditions only reduced total stand transpiration slightly and did not change the relative proportion of transpiration from dominant and midstory. Therefore, models that better capture forest stand wet–dry canopy dynamics and individual tree water use strategies are needed to improve accuracy of predictions of water recycling over tropical forests. Copyright © 2016 John Wiley & Sons, Ltd.

KEY WORDS ecohydrology; sap flux; tropics; rainforest; micrometeorology; leaf wetness

Received 14 January 2016; Accepted 12 July 2016

INTRODUCTION

Evapotranspiration (ET) is the combination of physical abiotic water evaporation (transport of water into the atmosphere from surfaces) and biotic leaf transpiration (exchange of water vapour that occurs between plants and the atmosphere) driven by an external source of energy (Katul *et al.*, 2012). This process is one of the most important components of the global water budget because it is directly related to precipitation and land cover. ET from terrestrial surfaces is responsible for around 60% of the atmosphere's water moisture (Shiklomanov, 1998). Within that percentage, 10% comes from vegetation (Hanson, 1991), of which 30% of incoming precipitation is from temperate forests (Ohte and Tokuchi, 2011) and 50% is from tropical forests (Shuttleworth, 1988).

Tropical forest systems are also well-known carbon sinks, having among the largest gross primary productivity in the world (Clark *et al.*, 2003; Malhi and Phillips, 2005). However, tropical forests would not be as productive without an efficient precipitation recycling regime that could maintain a steady source of water, which directly affects growth and precipitation rates regionally and even globally (Baker *et al.*, 2003). Therefore, tropical forest ET comprises a large and important component of the global water cycle, much of which (around 70% in rainforests) is lost through transpiration (Schlesinger and Jasechko, 2014).

Independent of total rainfall, the frequency of rain events influences vegetation growth and plant species composition in tropical forests (Baker *et al.*, 2003). Tropical forest species range from those that require a large amount of water to supply their fast growth and high transpiration losses to those that require a smaller amount of water to sustain their slower growth (Horna *et al.*, 2011). These differences in growth rates and water use result in the wide variation in tree diameter and height

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within the closed canopy structure, as is predominant in mature tropical forests. When precipitation falls on such a canopy, it creates a number of unique microclimates with wetness varying by height and tree characteristics. Vertical canopy leaf distribution directly affects subcanopy humidity and subsequently affects ET rates and photosynthesis within these different layers. However, in wet tropical rainforests, it is unlikely that the entire canopy will be completely dry, with some portions remaining wet for a significant fraction of daylight hours (Dietrich *et al.*, 1982).

Wet canopy conditions may also affect plant growth and functional characteristics. Photosynthesis may be inhibited when the leaf surface is partially or completely covered with water droplets (Fogg, 1947; Smith and McClean, 1989; Brewer and Smith, 1997; Hanba *et al.*, 2004; Letts *et al.*, 2010; Alvarado-Barrientos *et al.*, 2014). Another factor to consider is the possible adaptive strategies some species might possess, such as leaf traits, i.e. trichomes and repellency (Levin, 1973; Brewer and Smith, 1994), and leaf angle (Fogg, 1947) that may influence ET. Such complex relationships between plant traits and atmospheric or biotic drivers present difficulties in the study of ET, such as evaporative cooling (Katul *et al.*, 2012).

Beyond the leaf scale, spatial arrangements of leaves within complex forest stands require the characterization of tree size and canopy position for precise transpiration rate estimation (Andrade *et al.*, 1998; Motzer *et al.*, 2005). Several studies have documented how large, dominant trees are responsible for a disproportionate amount of water being released back to the atmosphere (Nadezhkina *et al.*, 2002; Horna *et al.*, 2011). Additionally, transpiration rates can vary drastically when considering stand position, species composition, canopy architecture (branch number and angling, and leaf area) and ecological succession (Granier *et al.*, 1996; Andrade *et al.*, 1998; Nadezhkina *et al.*, 2002; Horna *et al.*, 2011; Kunert *et al.*, 2015b). Differences between canopy strata levels and closeness to forest gaps can alter the microclimate surrounding these trees that can affect not only transpiration but also canopy photosynthesis (Campbell and Norman, 1998). The effects of tree size and canopy exposure (in terms of energy availability) on tropical stand transpiration have been accounted for in the literature. Some studies showed that tall dominant trees transpired four to ten times more than understory/suppressed trees due to vapour pressure deficit and/or exposure to radiation (Granier *et al.*, 1996; Horna *et al.*, 2011), but the effects of leaf wetness on these tropical trees' water use has been little studied (O'Brien *et al.*, 2004). In these frequently wet forests, dominant trees are likely to dry out more rapidly than suppressed understory trees, which could further enhance differences in gas exchange between canopy layers.

The objectives of this study were to analyse the variation of plant water uptake during different wetness conditions for three tree canopy exposure categories (dominant, midstory and suppressed) in a tropical montane forest environment under frequent rain events. We relied on sap flux and micrometeorological measurements to determine if sap flux rates in three tree size groups (dominant, midstory and suppressed) were impacted by different wetness conditions (dry, 'semi-dry' and wet). Then, we compared the relative contribution of each group to stand transpiration under those wetness conditions. These results are important for quantifying the contribution of a constantly moist canopy to the plant-atmosphere water balance and consequently improving global scale land surface models for more accurate climate predictions.

MATERIALS AND METHODS

Site description

The study site is located at the Texas A&M University Soltis Center for Research and Education near San Isidro de Peñas Blancas in the Alajuela Province, Costa Rica (10°23'13"N–84°37'33"W). The site is approximately 600 m above sea level and shares a border with the Children's Eternal Rainforest, near the Monteverde-Arenal Mountain Cloud Forest Reserve.

The study area has an average annual temperature of approximately 24 °C, average relative humidity of 85% and average annual rainfall of approximately 4200 mm. The rainy season extends from May to December (470 mm month⁻¹), with a relatively 'dry' season from January to April (195 mm month⁻¹) (Teale *et al.*, 2014). Based on the Holdridge classification system, the vegetation is a transitional tropical premontane moist forest (Holdridge, 1967). Trees at the study site range from 25 to 45 m in height, reaching upper canopy at around 25 m with dense foliage, multiple interlacing crowns, but with frequent canopy gaps. The most common species was *Carapa guianensis* Aubl., and the largest trees (diameter at breast height >100 cm) were mostly *Mortoniendron anisophyllum* (Standl.) Standl. & Steyerl (Table I).

The site hosts a 42-m tower equipped with micrometeorological instrumentation. Around the tower, a 2200-m² plot was designated, containing 151 heterogeneous tree individuals ranging from 6 to >200 cm in diameter and 6 to 40 m in height. The steep terrain is volcanic in origin and has an average slope of 45°.

All trees in the plot were categorized by field observations (canopy structure and height) as dominant, midstory or suppressed based on tree height and canopy exposure. Dominant trees were the tallest and received 80

Table I. Individual description of trees measured using sap flux probes.

Category	Diameter at breast height (cm)	Height (m)	Basal area (m ²)	Sapwood area (m ²)	%	Average max J_s (kg m ⁻² h ⁻¹)
Dominant	45.2	27	0.160	0.100	62%	61.6 ± 16.9
Dominant	200	32	3.142	1.230	39%	41.7 ± 13.2
Dominant	19.7	27	0.030	0.029	94%	30.2 ± 12.9
Dominant	80	30	0.503	0.253	50%	36.6 ± 15.7
Dominant	62.8	29	0.310	0.192	62%	44.5 ± 16.7
Dominant	46.2	28	0.168	0.102	61%	33.2 ± 18.0
Dominant	220	38	3.801	1.478	39%	56 ± 15.1
Dominant	150	30	1.767	— ^a	—	47 ± 18.2
Midstory	11.6	13	0.011	0.010	93%	41.7 ± 13.2
Midstory	21.2	13	0.035	0.030	86%	48.4 ± 15.1
Midstory	42.6	22	0.143	0.069	48%	57.2 ± 23.7
Midstory	40.1	25	0.126	0.113	90%	70.2 ± 25.7
Midstory	15.6	16	0.019	0.012	65%	35.3 ± 18.5
Midstory	17.3	16	0.024	0.016	69%	26.1 ± 12.4
Midstory	18.5	15	0.027	0.024	90%	32.5 ± 14.4
Midstory	32	26	0.080	0.066	82%	28.3 ± 14.3
Midstory	40	30 ^b	0.126	0.068	54%	57.8 ± 31.7
Midstory	30.5	27 ^b	0.073	0.053	73%	51.6 ± 24.7
Suppressed	7.7	6	0.005	0.005	100%	25.7 ± 9.9
Suppressed	12.7	6	0.013	0.011	86%	33.7 ± 16.4
Suppressed	10	11	0.008	0.006	82%	42.1 ± 19.4
Suppressed	17	10	0.023	0.019	83%	32.7 ± 11.6
Suppressed	8.3	9	0.005	0.004	78%	21.9 ± 11.5
Suppressed	6.9	10	0.004	0.003	82%	29.6 ± 11.3
Suppressed	12	10	0.011	0.010	90%	28.3 ± 9.8
Suppressed	11.1	11	0.010	0.009	90%	17.0 ± 8.6

^a Unable to retrieve xylem core samples.

^b Labelled midstory because they are located under a larger, 40-m tall tree.

to 100% canopy exposure to solar radiation. Subsequently, midstory trees had closer to 50% canopy exposure, and suppressed had 30% or less exposure. We selected eight dominant trees, ten midstory trees and eight suppressed trees for this study.

Sap flux and sapwood area measurements

Sap flux density (J_s) was measured continuously using 43 thermal dissipation sensors (Granier, 1987) constructed by using the method described in (Phillips *et al.*, 1996) and installed in 26 trees during a 5-month period ranging from 7 July 2014 to 30 November 2014. This method consists of a reference and heated probe inserted in the outer 20 mm of the active xylem.

The number of sensors installed per tree differed by size. Trees less than 20 cm in diameter received one sensor (14 individuals); between 21 and 80 cm, two sensors (8 individuals) and above 80 cm, three sensors (3 individuals) or four sensors (1 individual). The first sensor was placed perpendicular to the slope, roughly facing the north, with the others (if any) spaced evenly around the tree. The sensors were installed at a height of 1.5-m height, or as low as possible above tall buttresses, up to

7 m. Data were collected every 30 s and later averaged over 10-min intervals and stored on a datalogger (CR1000, Campbell Scientific Inc., Logan, UT). Temperature differences between the reference and heated probe were converted into J_s (kg m⁻² s⁻¹) based on Granier (1987) empirical calibration equation [Equation 1]:

$$J_s = 0.119 \left(\frac{\Delta T_M - \Delta T}{\Delta T} \right)^{1.231} = 0.119 K^{1.231} \quad (1)$$

where ΔT_M is the maximum temperature difference when sap flux is assumed to be 0, and ΔT is the actual temperature difference. Herein, J_s is expressed as hourly (kg m⁻² h⁻¹) and daily (kg m⁻² day⁻¹) totals, where daily total sap flux density was the sum of all J_s in a 24-h period. Night-time data fluctuations were small but more erratic on wet, rainy days likely because of weak lower limit of temperature detection (Burgess *et al.*, 2001) or temporarily elevated night-time vapour pressure deficit (Rosado *et al.*, 2012). However, we confirmed that vapour pressure deficit reached 0 every day considered as wet.

Active sapwood area was determined for all trees with sap flux sensors using safranin-fucsin dye injections on

fresh tree cores (Vertessy *et al.*, 1995; McDowell *et al.*, 2002; Gebauer *et al.*, 2008). Sapwood area ranged from 0.003 to 1.47 m², equivalent to ~80% of active xylem for an average cross section. An exponential model was developed to predict sapwood area for the rest of the plot trees from basal area ($A_s = 0.4713 \times A^{0.8493}$; $r^2 = 0.992$, where A_s is sapwood area and A is basal area, both in m²) (Figure 1). All trees had a sapwood radius greater than the sensor depth (>20 mm) (Clearwater *et al.*, 1999). Sapwood area was used to estimate stand transpiration following the methodology used by Moore *et al.*, 2004 with separate size categories for dominant trees ($n=20$ sensors on eight trees), midstory trees ($n=15$ sensors on ten trees) and suppressed trees ($n=8$ sensors on eight trees) but also including 125 additional trees in the plot without sap flux sensors assigned to each size category. The average daily total of sap flux density (J_s) for dominant, midstory and suppressed trees was multiplied by the ratio of total sapwood area to total plot area for each size category and summed to estimate stand transpiration (Moore *et al.*, 2004; Horna *et al.*, 2011).

While others have shown that J_s can vary with depth in the sapwood (James *et al.*, 2002; Poyatos *et al.*, 2007; Zhang *et al.*, 2015), we did not measure J_s at depths beyond 20 mm in our trees because an independent analysis of radial profiles in a subset of nearby trees did not show consistent declines in J_s trends with depth. In this case, we believe that any potential errors in scaling J_s to stand transpiration were minor (~15%, e.g. Miller *et al.*, 2013), as our estimates were within the range observed by others in similar forests (Bruijnzeel and Veneklaas, 1998). To corroborate this assumption, we applied the

transpiration correction for angiosperms developed by Pataki *et al.* (2011) and compared our current database to the resulting corrected database. However, this correction was found to cause gross biases in the tree size comparison and was not applied.

Micrometeorological measurements

Leaf wetness was estimated using dielectric leaf wetness sensors (LWSSs, Decagon Devices, Pullman, WA) installed at five heights above the ground surface (5, 11, 22, 33 and 38 m). The sensor located at 38 m was more embedded inside the forest canopy, and the sensor installed at 33 m was more exposed due to a gap in the canopy. Data were collected every 30 s and averaged at 5-min intervals. Leaf wetness is output in mV; values around 100 mV indicate dry conditions, from 145 and 190 mV indicate partially wet leaves and >200 mV indicate fully wet leaves. Therefore, we developed a leaf wetness index for daylight hours (6 AM to 6 PM) as the sum of all 5-min values expressed on a scale from 0 to 100%. Days when mean index values fell below 15% wet were considered to be dry, between 10 and 50% was considered semi-dry and above 50% as 'wet'. Semi-dry days were further filtered to include only the days that had a dry upper canopy (sensors at 33 and 38 m average less than 10%) and wet understory (sensors at 5 m above 50%); these days had atmospheric conditions (higher δe and radiation) that dried the overstory canopy but not the understory. In total, 37 days of each category were considered in the data analysis.

Photosynthetic active radiation (PAR) (LI-190SA, LI-COR, Lincoln, NE) was measured at the same heights

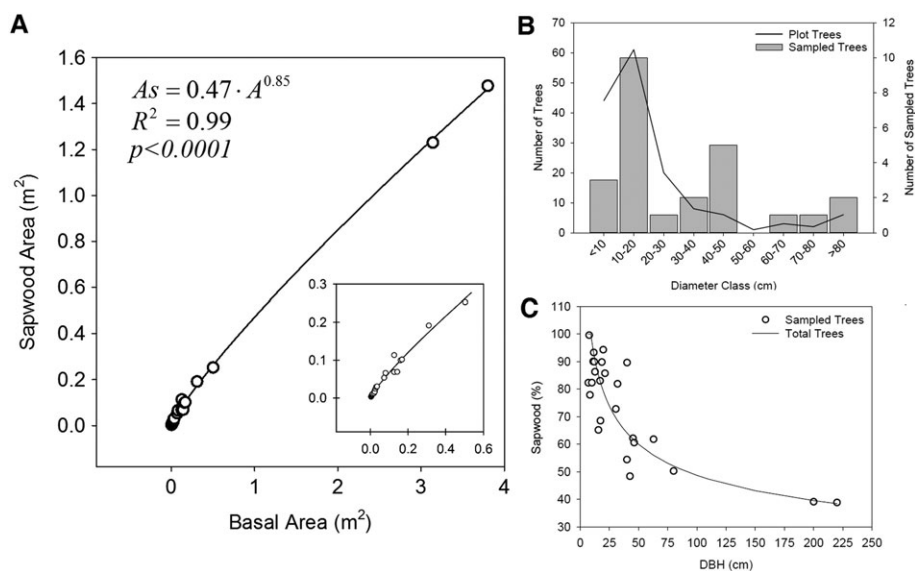


Figure 1. (A) Allometric relationship between sapwood area (A_s) and basal area (A). Inset graph highlights clustered data points, which correspond to tree individuals with basal area $< 1 \text{ m}^2$. (B) Diametric distribution classes for total plot ($n=151$) and total sampled trees ($n=26$). (C) Sapwood area percentage as a function of diameter at breast height (DBH) for all sampled trees

as the LWSs (except at 5 m) and an additional height (27 m). Daily average and maximum PAR measured during daylight hours was averaged through the days selected for each wetness conditions to show the amount of radiation the canopy was receiving, specifically the average maximum low and high for each day of the study period within each category. PAR sensors located at 11 m were designated to represent suppressed trees, sensors between 11 and 27 m as midstory and between 27 and 38 m as dominant. Occurrence and duration of rain events were measured in a nearby clearing using a tipping bucket rain gage (TE525WS, Texas Electronics, Dallas, Texas). Air temperature was measured using temperature probes (model 107, Campbell Scientific, Logan, UT) placed at the same levels as LWSs and was also used to estimate vapour pressure deficit (δe) along with atmospheric and ambient pressure and water vapour concentration (Campbell and Norman, 1998) from a gas profile system (AP200, Campbell Scientific, Logan, UT) [Equations 2, 3 and 4].

$$\delta e = e(T_a) - e_s \quad (2)$$

In which, $e(T_a)$ is the saturation vapour content of air at temperature (T_a) (kPa), and e_s is the actual vapour pressure (kPa) where

$$e(T_a) = 0.614 \cdot e^{\left(\frac{17.5 \cdot T_a}{240.9 + T_a}\right)} \quad (3)$$

$$e_s = \frac{W \cdot P}{1000} \quad (4)$$

In which, W is the water vapour concentration (mmol mol^{-1}) measured by the AP200 and P is atmospheric pressure (kPa).

Statistical analyses

Analysis of variance (ANOVA) was used to test for differences (p values, $\alpha=0.05$ and 0.001) between tree size categories and wetness conditions, followed by the Tukey honest significant difference (HSD) multicomparison *post hoc* test. Generalized least squares (simple and multiple regressions) models were also fitted. Additional analyses included stepwise multiple linear regression and Pearson correlation to evaluate relationship between sap flux rates and micrometeorological variables (leaf wetness index, δe , PAR and air temperature) under different wetness conditions. The response variable was daily total sap flux (J_s), and the independent variables were leaf wetness index, δe and PAR. Regression models were evaluated based on goodness of fit determined from the highest significant R^2 values and entailed sequential (forwards) addition of independent variables in the order PAR, δe , leaf wetness

index plus interaction terms using a manual procedure. Relationships within canopy strata were also assessed. Final multiple regression models were selected using a sequential F -test procedure (Ott and Longnecker, 2010). In this test, for each variable not already included in the model, an F -statistic ($\alpha=0.05$) was calculated, and the final model was selected from all possible models. Statistical analyses were performed with R version 2.6.2 software (R Core Team, 2013).

RESULTS

Micrometeorological drivers

A total of 2573 mm rainfall fell over the 5-month study period. The month of July was the wettest, with a total of 900 mm of rain, and August was the driest with 341 mm. August had 42% more water uptake than July, which resulted in higher daily J_s rates overall and for all tree size categories. PAR was likewise highest during August. Diurnal average PAR was $108 \pm 36 \mu\text{mol m}^{-2} \text{s}^{-1}$ over all days in the month of August, and the peak hour of the day that month averaged $445 \pm 226 \mu\text{mol m}^{-2} \text{s}^{-1}$ at a height of 33 m. Air temperature measured at 33 m averaged 22°C and varied by less than 1°C between months and vertically within the canopy (Figure 2). Tower heights of 38 and 33 m correspond with the dominant zone, 27 and 22 m correspond with the midstory zone, and 11 m

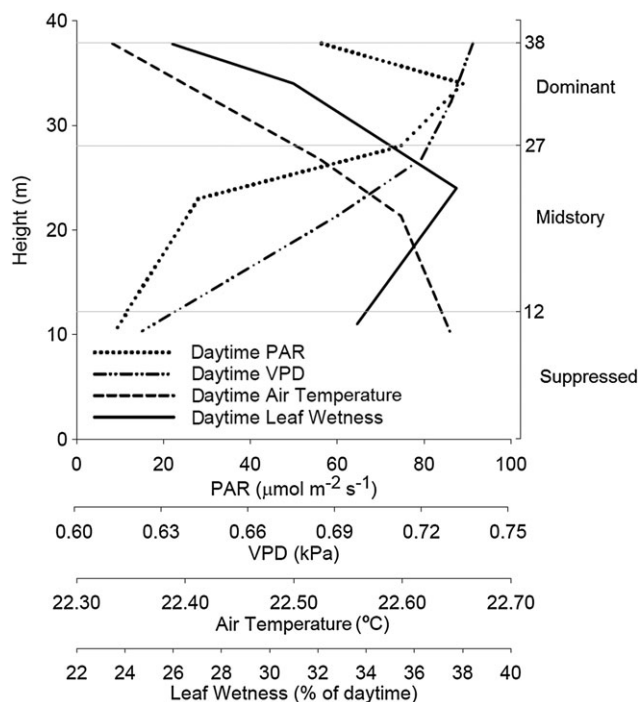


Figure 2. Height profiles of average daytime air temperature ($^\circ\text{C}$), leaf wetness (% of daytime), VPD (kPa) and PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$) for the study period. Canopy height classifications are noted

correspond with the suppressed zone. PAR differed by an order of magnitude between canopy heights and peaked at 33 m because the sensor at 38 m was partially obscured by a tree branch (Figure 2), but it also greatly differed throughout the day due to intermittent cloud coverage. Cloud free days were rarely observed throughout the study period (around 3 days), but during those conditions, PAR would reach as much as $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ for short periods of time.

Mean daily temperatures were warmest at 6 m, at the level of suppressed tree canopies, but only differed by 1°C throughout the canopy. Leaf wetness followed the same profile pattern as air temperature (Figure 2) but contrasted

greatly between levels. Between the most exposed (at 33 m) and the least exposed (at 5 m) sensors, leaf wetness ranged from 25 to 80%, respectively. This implies that because there is not much air temperature variation throughout levels and decreasing gradients of PAR and leaf wetness, less energy is available to dry the leaves of lower level trees.

On dry and semi-dry days, J_s was negatively correlated with leaf wetness ($r = -0.42$), which was also associated with low PAR and δe (Figure 3). PAR was 38 and 73% lower on semi-dry and wet days, respectively, when compared with dry days. Across the three wetness conditions, J_s increased at a similar rate as PAR increased

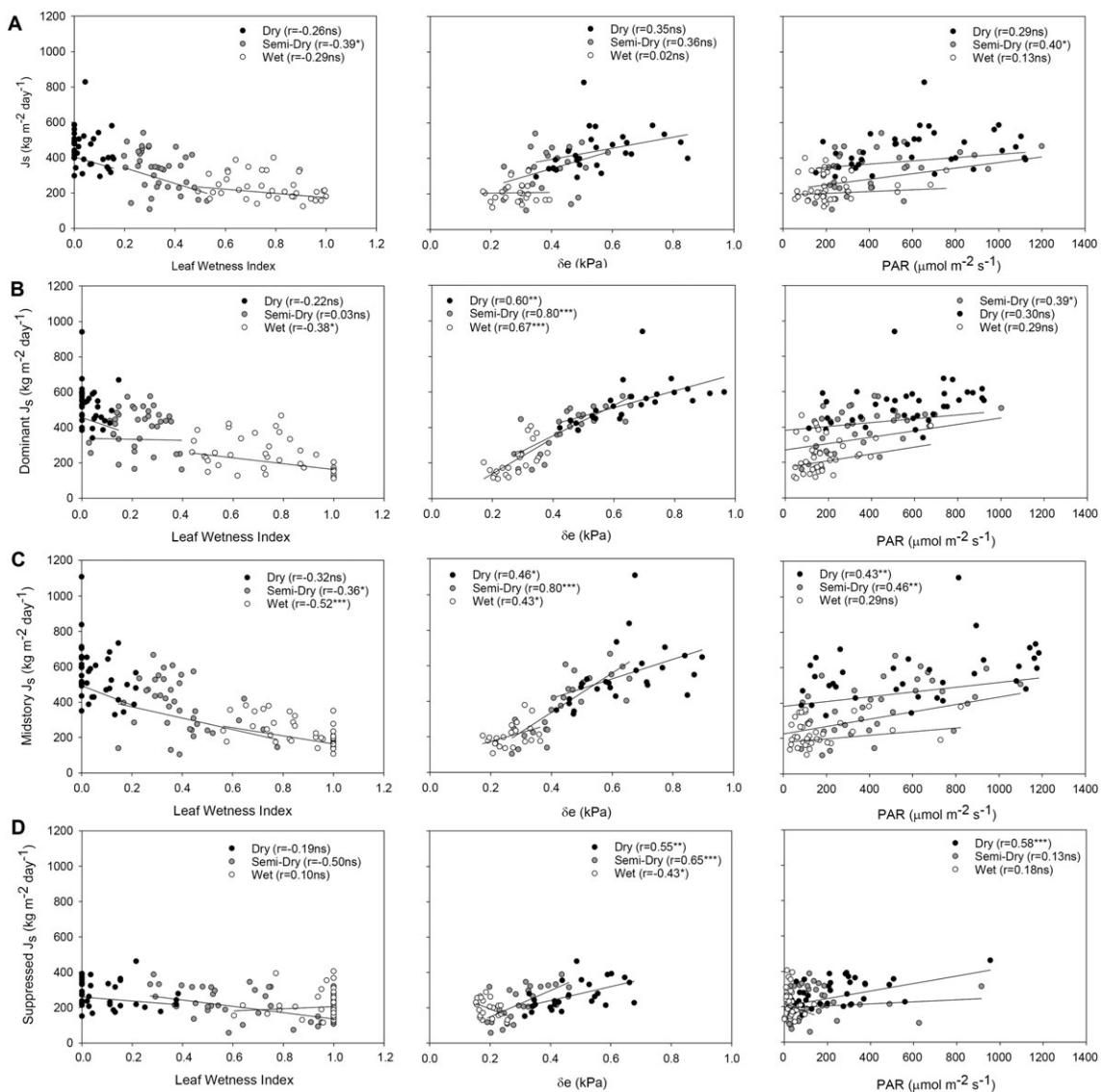


Figure 3. Total daily sap flux related to micrometeorological variables (daily leaf wetness index at 33 m of height, daily average vapour pressure deficit (δe , kPa) and daily maximum photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$), respectively from left to right) under different wetness conditions and canopy levels, as indicated by Pearson correlation coefficient ($\alpha = 0.05$) and regression lines. (A) Average canopy conditions. (B) Dominant canopy conditions. (C) Midstory canopy conditions. (D) Suppressed canopy conditions. Notes: significance levels labelled with *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, and ns = nonsignificant ($p > 0.05$)

($r^2=0.31$); however, J_s was consistently lower for the same level of PAR if leaves were wet (43% less; $r=0.13$) or semi-dry (30% less; $r=0.40$). Lower δe and higher leaf wetness both contributed to this. δe was an important covariate with wetness condition ($r^2=0.45$). We found that the effects of δe and PAR on J_s were dependent on leaf wetness condition. An additional 6% of variation in J_s was explained by leaf wetness after accounting for the effects of δe and PAR ($p < 0.05$). When leaf wetness was 50%, J_s decreased by 10% under average δe and PAR conditions, and when leaves were completely wet (100%), J_s decreased by as much as 28%. Due to large range in PAR conditions observed throughout the day, PAR had little to no influence on sap flux rates when leaves were wet ($r=0.13^{ns}$) or dry ($r=0.29^{ns}$), and some influence during semi-dry days ($r=0.40$, $p < 0.05$). The previous correlations were further broken down by canopy level (Figure 3B–D), which similarly indicated differences with wetness condition, especially in dominant and midstory trees.

Sap flux rates by category and wetness conditions

In general, J_s was highest in canopy trees and lowest in suppressed trees, but the relative differences between groups were not consistent as wetness condition changed (Figure 4). Peak J_s of canopy and midstory trees were similar on dry days (47.6 ± 11.4 and $48.6 \pm 1.5 \text{ kg m}^{-2} \text{ h}^{-1}$, respectively), but on semi-dry days, midstory trees had slightly lower J_s rates than overstory trees. Between dry and semi-dry conditions, J_s daily total was reduced enough to be considered as different for both size categories ($p < 0.001$). As

expected, whether wet or not, suppressed trees had lower J_s than overstory or midstory trees and were much more variable.

On dry days, suppressed tree J_s was practically half that of dominant and midstory trees ($p < 0.001$) and peaked later in the day, 12:30 PM as opposed to 12:00 PM for the other groups, with maximum daily values of 56.8 ± 13.6 , 58.7 ± 1.8 and $28.9 \pm 13.9 \text{ kg m}^{-2} \text{ h}^{-1}$ for dominant, midstory and suppressed, respectively (Figure 4). Average total daily values for J_s on dry days was 498 ± 98 , 493 ± 127 and $290 \pm 75 \text{ kg m}^{-2} \text{ day}^{-1}$ in the three groups, respectively (Figure 5). PAR at dominant and midstory level peaked around 10 AM, while suppressed trees peaked at 11 AM; δe peaked at 1:30 PM for dominant and midstory levels, later than maximum J_s , and at noon for suppressed, with similar intensities between midstory and dominant.

When compared with dry days, J_s on semi-dry days proportionally decreased by only 24, 27 and 18% in canopy, midstory and suppressed trees, with the later reducing less because suppressed trees had low rates even on dry days (Figure 5). On semi-dry days, dominant trees had a slight advantage over midstory trees of 6% (or $18 \text{ kg m}^{-2} \text{ day}^{-1}$), with 14% greater peak of J_s ; however, tree-to-tree variability was too high for the difference to be significant (ns). Suppressed trees again peaked later in the day (1:00 PM), while dominant and midstory peaked both at 12:20 PM. Suppressed trees' daily maximum J_s was 59% lower than dominant trees and 53% lower than midstory trees ($p < 0.001$). Because suppressed trees remain wet more frequently across all wetness conditions, their J_s differed the least. On semi-dry days, with less intensity, PAR peaked at

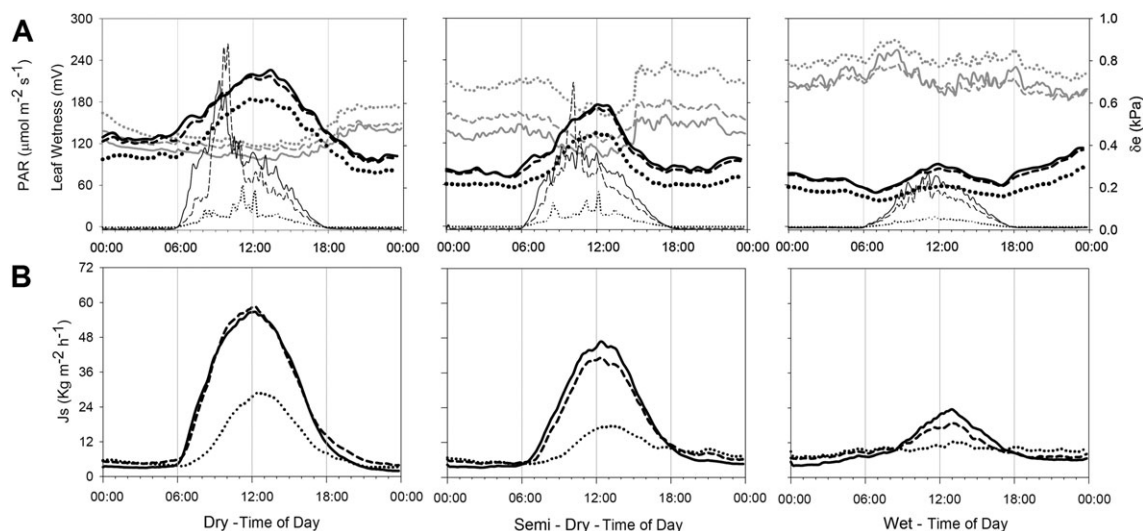


Figure 4. Diurnal average sap flux curves ($\text{kg m}^{-2} \text{ h}^{-1}$) for each tree category (dominant, midstory and suppressed) at each wetness condition (from left to right: dry, semi-dry and wet, respectively) and respective diurnal micrometeorological condition. (A) Micrometeorological variables: vapour pressure deficit (δe , kPa)—thick black lines, leaf wetness (mV)—thick gray lines, photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{ s}^{-1}$)—thin black lines. (B) Dominant: solid line, midstory: dashed line and suppressed: dotted line (same patterns for panel A)

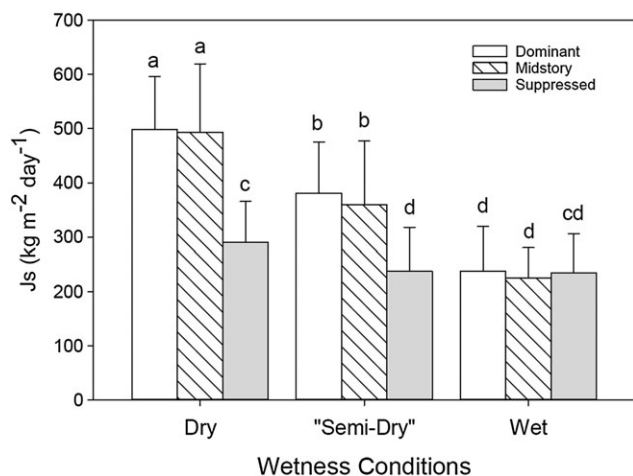


Figure 5. Comparison of total sap flux per day ($\text{kg m}^{-2} \text{day}^{-1}$) for each wetness conditions (dry, semi-dry and wet) and for each tree category (dominant, midstory and suppressed). Tukey HSD denoted with letters, and standard error bars indicate categories with significance differences, as indicated by ANOVA ($p < 0.05$)

the same time for dominant and midstory as dry days but was at noon for suppressed, while δe peaked at noon for all three levels, slightly before maximum J_s . On these days, leaf wetness was lower at the top of the canopy and increased at the understory level, but with a distinct drop around midday. PAR and δe were not the only factors influencing these trends. Maximum daily PAR for dominant trees averaged 2% and 44% less than for midstory trees on dry and semi-dry days, respectively, due to the gap in the middle section of the canopy. Likewise, δe for dominant trees averaged 3 and 2% higher than for midstory trees on dry and semi-dry days, respectively.

On wet days, all the size categories had reduced J_s (Figure 5), signified by uniform wetness through the entire canopy and uniformly low δe throughout the day, with lower values at the understory level. We observed a 45% reduction in daily total J_s on wet days, when compared with dry days. PAR was reduced to values below $70 \mu\text{mol m}^{-2} \text{s}^{-1}$. Peak J_s occurred at 1:00 PM for all the categories, while peak δe was before maximum J_s at noon for dominant and midstory and 12:30 PM for suppressed (Figure 4). These values did not differ from each other ($p < 0.001$), even though dominant trees presented the highest J_s values. Although all of the size categories had significant decrease in sap flux rates and had a delayed peak, suppressed trees differed the least between wetness conditions, with only 2% difference (ns) in daily total J_s between wet and semi-dry conditions. Dominant tree uptake was greater by 38 and 52% on wet days when compared with semi-dry and dry days, respectively. Midstory trees reduced J_s by 38 and 55%, respectively.

Transpiration rates by category and wetness conditions

Daily stand transpiration rates for the entire period of study averaged $1.38 \pm 0.53 \text{ mm day}^{-1}$ and average transpiration of $41.4 \text{ mm month}^{-1}$ (497 mm year^{-1}). Dominant trees, independent of wetness conditions, accounted for around 76% of total stand transpiration from only 13% of the plot's trees, which represent 76% of the stand's active sapwood area. Midstory trees contributed approximately 19% of stand transpiration from 38% of the plot's trees and 18% of active sapwood, and suppressed accounted for only 5%, from 48% of trees with 6% of sapwood area (Figure 6A and B).

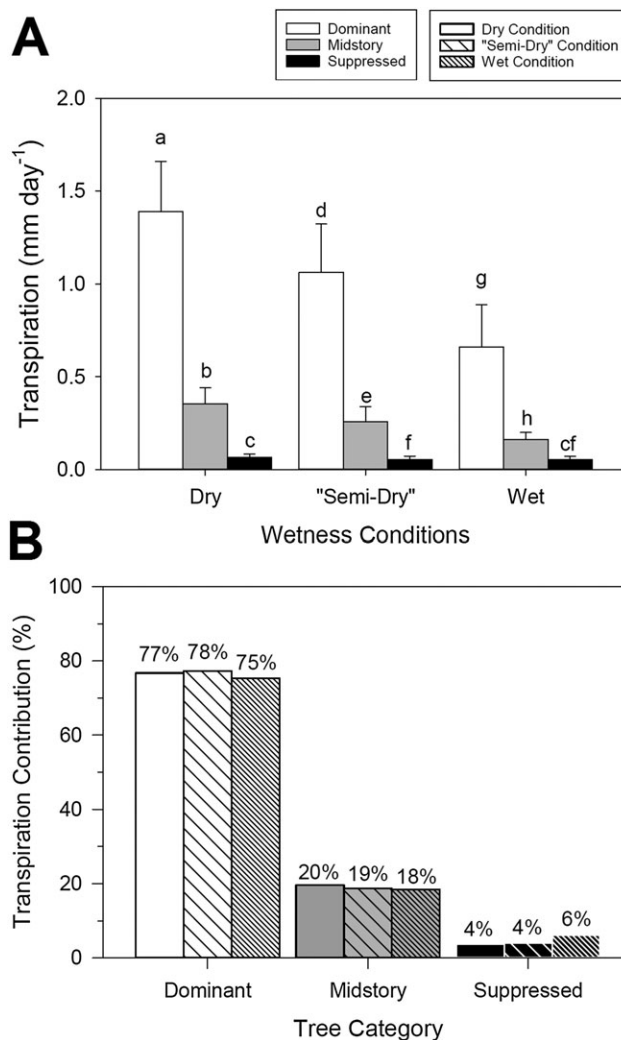


Figure 6. Stand transpiration partitioned per period and percentage transpired from each tree category. (A) Comparison of total transpiration per day (mm day^{-1}) for each wetness conditions (dry, semi-dry and wet) and for each tree category (dominant, midstory and suppressed). Tukey HSD letters with standard error bars indicate categories with significance differences, as indicated by ANOVA ($p < 0.05$). (B) Stand transpiration contribution (%) from each tree category under different wetness conditions

Wet conditions were associated with a 52% decrease of daily total transpiration, when compared with dry days. Semi-dry conditions reduced stand transpiration of dominant trees by 24% ($p < 0.001$) compared with a 52% reduction with wet conditions ($p < 0.001$). Midstory trees responded similarly by reducing stand transpiration by 27% ($p < 0.001$) when semi-dry and 54% when wet ($p < 0.001$). However, suppressed tree transpiration only differed between dry and semi-dry conditions ($p < 0.05$) but overall differed very little ($p < 0.05$) between all wetness conditions, resulting in an average rate of 0.05 mm day^{-1} for all conditions.

DISCUSSION

At our frequently wet tropical rainforest site, while PAR and δe were major drivers of transpiration variation between wet and dry days, the added effect of leaf wetness appeared to further reduce transpiration. Further, the effect of leaf wetness on J_s differed between exposed trees in the upper canopy and less-exposed trees in the understory. This implies that δe and/or PAR were coupled with other environmental variables, like leaf wetness, to significantly influence water uptake. O'Brien *et al.* (2004), when studying environmental variables that influence tree transpiration in another Costa Rican site, found strong negative correlations with sap flux rate and leaf wetness (-0.62) or relative humidity (-0.96), while, δe (0.96), irradiance (0.84), air temperature (0.90) and wind speed (0.72) were all strongly positively correlated. However, they did not control for the interacting effects between these drivers. Moreover, we assessed whether leaf wetness condition affects the relative contribution of dominant, midstory and suppressed trees under varying conditions typical of tropical forests. Surprisingly, while the proportion of J_s was affected by wetness condition, the relative proportion of each group to total stand T remained constant (Figures 5 and 6).

Although wet leaf conditions significantly reduced dominant and midstory water uptake, semi-dry conditions did not reduce J_s as much as we expected. This illustrates that transpiration does not respond proportionally to canopy wetness. Models with simple linear reductions in transpiration with leaf wetness on days with less intense rainfall events, in which upper canopies dry faster, would drastically underestimate ET and tree growth. Maintaining dry conditions in the upper canopy is significant for precipitation recycling in the tropics. Because these forests remain wet for prolonged periods after precipitation events, effects were long-lasting. At their Indonesian rainforest site, Horna *et al.* (2011) found that sap flux rates were lower for as long as 16–22 h after a rainfall event when air humidity was higher than usual and when

leaf wetness affected 44–55% of the canopy. They concluded that transpiration estimations were lower than expected for all the tree height categories due to these wetness conditions.

Suppressed trees assimilated less water, as expected, because they receive much lower levels of PAR, which results in slower rates of leaf drying (Kume *et al.*, 2006) and less energy to photosynthesize. Brewer and Smith (1997) highlight how forest growth is driven by microclimate variation that can result in very patchy wetness conditions, especially within canopy strata, because the most shaded level is less affected by radiation and wind turbulence than upper levels. Therefore, trees classified as suppressed would probably grow faster if they were less wet or dried more rapidly, e.g. near natural forest clearings (Kunert *et al.*, 2015b).

From our results, we can infer that water droplets on leaf surfaces are an important physical factor limiting water uptake after accounting for the primary drivers δe and PAR. Another is the establishment of epiphytic organisms on foliage that act like trichomes, which are hair-like leaf appendages that extend across the epidermis' surface (Levin, 1973), by creating a barrier between the leaf surface and water droplets (Dietz *et al.*, 2007). Considering the microclimate in which suppressed trees are growing (constant high humidity and low solar radiation), they are highly susceptible to harbouring these organisms, as observed in the leaves of our study site. A layer of water over the leaves can potentially inhibit photosynthesis, as has been reported previously (Fogg, 1947; Smith and McClean, 1989; Brewer and Smith, 1997; Hanba *et al.*, 2004; Letts *et al.*, 2010; Alvarado-Barrientos *et al.*, 2014). On the other hand, tropical species may actually be adapted to optimize function under low PAR intensities ($< 1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$) and saturated δe ($< 0.7 \text{ kPa}$) given frequent wet and foggy conditions (Gotsch *et al.*, 2014) or by optimizing physiological processes during short dry periods. Additional adaptations to wet environments have been reported, such as rapid leaf drying (O'Brien *et al.*, 2004) or the ability to maintain photosynthesis when wet (Smith and McClean, 1989). This effect may be driven by sensitivities to leaf temperatures. According to Katul *et al.* (2012), there is a cooling effect minutes after rainfall whereby the humidity and leaf temperatures become ideal for optimum tree physiological functioning. Therefore, on semi-dry days, trees in transitional tropical premontane moist forests may actually become more efficient water users right after rain, dew or/and fog events during the dry-down phase. Because we did not see evidence of midday stomatal suppression with semi-dry conditions, our trees showed a more pronounced decreasing hierarchical pattern (dominant, midstory and then suppressed) than during dry days (Figure 5).

The response to leaf wetness may also vary due to species leaf anatomy. Tree species that occur in locations in which dewfall, rainfall and fog are extremely frequent have strategies to repel water on their leaves. Smith and McClean (1989) show that habitat and microclimate are also factors to be considered as environments under dense fogs and dewfall frequently host specialized species with leaf features that reduce the effect of long duration of leaf wetness. These adaptations are evidence that these trees have developed strategies to be as productive as possible under such normally suppressing conditions. Studies show that trees from wet montane forested environments can develop features like foliar water uptake, and leaf repellency and/or the presence of trichomes that can reduce the area exposed to water beads to prevent photosynthesis and water uptake suppression (Smith and McClean, 1989; Brewer and Smith, 1994; Ishibashi and Terashima, 1995; Brewer and Smith, 1997; Holder, 2007; Gotsch *et al.*, 2014). Although leaf anatomy was not analysed for this study, the trees in our site show evidence that they are specialized to endure prolonged wetness characteristic to this region, like possessing ovate and lanceolate shapes that can facilitate water drainage during a rain event.

The amount of transpiration estimated in this study, although low, is consistent to other findings in the literature for other vegetation types, especially in tropical montane cloud forests that are known to have transpiration around 250–300 mm year⁻¹ (Bruijnzeel and Veneklaas, 1998). Our daily rates also were similar to previously reported values in tropical forests (Bruijnzeel *et al.*, 2011; Horna *et al.*, 2011; Alvarado-Barrientos *et al.*, 2014; Kunert *et al.*, 2015b). The Pataki *et al.* (2011) correction, which was developed for a range of temperate angiosperms, was investigated and deemed inappropriate for this study. Applying the correction across all trees and dates severely dampened the extreme rates that occurred on drier and wetter days (Figure 7). This decision was further corroborated by an independent analysis (Miller *et al.*, 2013). However, future work is needed to develop robust estimates of radial profiles in tropical forests, given the unique microclimate conditions and high diversity in these ecosystems. As others have indicated, tropical species show major sapwood area inconsistencies due to different sizes, species, individual traits (e.g. age and susceptibility to cavitation and/or tyloses) and microclimate (e.g. seasonal and diurnal vapour pressure deficit variations) as observed in our site (Jimenez *et al.*, 2000; Meinzer *et al.*, 2001; James *et al.*, 2003; Ford *et al.*, 2004a; Ford *et al.*, 2004b).

Not only were rates of transpiration impacted by wetness but also the relative proportion of exposed trees in the stand disproportionately influenced stand transpiration. Dominant trees comprised the greatest total

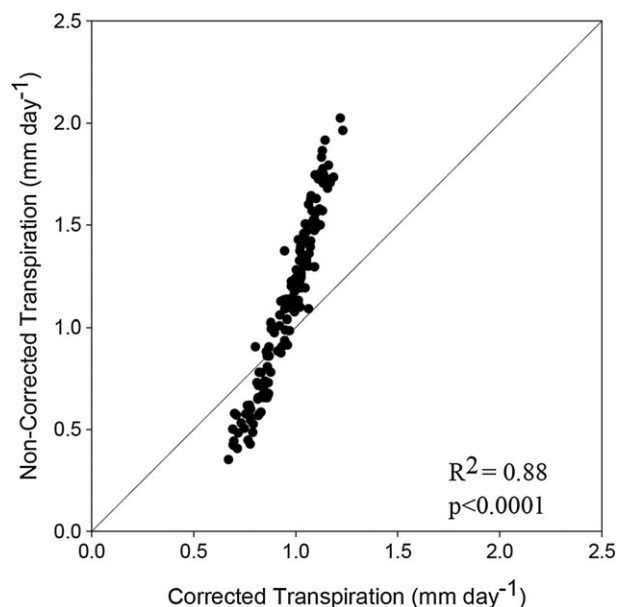


Figure 7. Cross-validation between corrected (proposed by Pataki *et al.* 2011) and non-corrected (following Granier *et al.* (1987) calibration) transpiration values

sapwood in the stand and largest water use per unit sapwood than the midstory on semi-dry days. The strong relationship between sapwood and basal area or diameter at breast height has been widely studied (Wullscheleger *et al.*, 1998; West *et al.*, 1999; Meinzer *et al.*, 2001; Lundblad and Lindroth, 2002; Nadezhdina *et al.*, 2002; Meinzer *et al.*, 2005). In our study, total sapwood area had a strong influence on the relative contribution of each size category to total stand transpiration.

Total sapwood area varied among groups, which strongly impacted stand transpiration estimates. Even though dominant trees amounted to only 13% of the plot's trees, they contributed an estimated 76% to stand transpiration. Sapwood area of dominant trees averaged approximately 56% of the cross-sectional area, while the average for the stand was 87%. However, it is important to note that this percentage is over cross sections that can reach ~3 m² per tree compared with only ~0.004 m² for a typical suppressed tree. This underscores the importance of using a representative sampling method based on the size distribution appropriate for the forest type (Andrade *et al.*, 2005; Kunert *et al.*, 2015a).

CONCLUSIONS

Our findings confirm the distinctive influence of leaf surface wetness on plant water uptake, even for trees adapted for very wet environments. It is reasonable to assume that these trees are adapted to take advantage of the short-term leaf dryness that occurs between frequent

rain events, in order to perform adequately photosynthesis. Tree size also has a crucial role in plant and atmosphere interactions in rainforests, as a minority of large trees are responsible for most of the transpiration. Not only does canopy exposure (not necessarily tree height) directly affect transpiration rates but also the ratio of sapwood area to basal area is also a key factor to consider when quantifying how much water is used by an individual tropical tree versus a stand of tropical trees. This suggests that harvesting of large dominant trees could cause a large hydrological disequilibrium to an ecosystem.

Future studies should address how neglecting leaf wetness and its apportionment within the canopy can affect the accuracy of climate modelling, particularly in regions in which precipitation recycling is high. Global circulation models need to more accurately predict latent and sensible heat (Akkermans *et al.*, 2002), interception, ET (Amthor *et al.*, 2001; Hobbins *et al.*, 2001; Akkermans *et al.*, 2002; Davies-Barnard *et al.*, 2014; Lin *et al.*, 2015), precipitation amount (Lloyd *et al.*, 1988; Martins *et al.*, 2015) and duration (Lorenz *et al.*, 2014), and even forest greenness and coverage estimations (Bonan and Levis, 2006), all of which are affected by canopy wetness. This study suggests that improvements in ET parametrizations may be needed for more accurate atmosphere–land models, particularly for predictions under varying climate scenarios where rainfall frequency is altered.

ACKNOWLEDGEMENTS

This research was supported by the Office of Science (BER) US Department of Energy (DE-FOA-0000749). Thanks are given to Amelia Min-Venditti, Ryan Andrews and Courtney Merket for field support. Also, special thanks are given to the TAMU Soltis Center staff, particularly Eugenio Gonzales and Johan Rodriguez, for their logistics and infrastructure support.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest regarding the publication of this paper.

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