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Upscaling transpiration in diverse forests: Insights from a tropical premontane site

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Abstract

Upscaling water use of individual trees to stands using sap flux techniques is a common method for partitioning site water balance, but few such studies have occurred in the tropics. Increasing interests in the role of tropical forests in global cycles have spurred upscaling studies in natural tropical forests, which present challenges from greater tree species and functional diversity, and potential factors that would reduce transpiration, such as frequent cloud cover and wet canopy conditions. In a premontane wet tropical forest in central Costa Rica, sap flow was measured in 15 trees stratified into 5 size classes based on tree diameters. None of the trees belonged to the same species, genus, or even family. We also accounted for potential radial variation in sap flux density. Data were scaled to estimate transpiration within a small 2.2-ha watershed using stand surveys of sapwood area. Stand transpiration averaged only 1.4 ± 0.7 mm day^{-1} within this forested watershed due to persistent low radiation, evaporative demand, and frequent wet canopy conditions. Our systematic approach used tree size attributes to scale water use to the stand, given difficulties to quantify species differences in such a diverse ecosystem. Contrary to previous evidence on temperate trees, the large trees sampled did not exhibit flow reductions in deeper sapwood, which warrants further study. These results highlight some unique aspects of measuring transpiration in wet tropical forests that are important to consider for future studies in diverse stands.

KEYWORDS

Costa Rica, radial profile, sap flow, sap flux, transitional rainforest

1 | INTRODUCTION

Evapotranspiration from tropical forests is a major source of water vapour to the atmosphere on the global scale (Fisher et al., 2009) approaching 1,400 mm per year (Zhang, Kimball, Nemani, & Running, 2010). For example, one third of precipitation that falls over the Amazon basin is supplied by recycled evapotranspiration, which is further facilitated by the deep-rooted trees (e.g., Trenberth, 1999). Despite its critical role in global climate, causes of variation in tropical forest transpiration have not been closely studied. Ecohydrological processes in humid environments are fundamentally different from those in dryland regions, in that they are controlled not by acute or chronic limitations in water availability (Porporato, D'Odorico, Laio, Ridolfi, & Rodriguez-Iturbe, 2002) but by limitations in energy availability (Loescher, Gholz, Jacobs, & Oberbauer, 2005).

In these environments, plant- and canopy-centric processes, such as canopy interception, stemflow, and leaf water uptake, as well as the spatial heterogeneity in these processes, may have a profound influence on land–atmosphere fluxes (Loescher, Powers, & Oberbauer, 2002). Through these mechanisms, vegetation alters the water balance in such systems in an entirely different manner than in dryland regions (Bonan, 2008; Calder, 1998) and likely differs with land cover (Pypker, Bond, Link, Marks, & Unsworth, 2005). Considering the issues with altered precipitation regimes facing tropical regions around the globe (Foster, 2001; Schuur, 2003), an improved understanding of the spatiotemporal variability in transpiration in diverse tropical forests is critically needed to predict forest responses and feedbacks to changing precipitation and species composition under future climate and land use scenarios (Fisher et al., 2009).

Tropical montane forests (TMFs) are one of the least understood and investigated ecosystems in the world, particularly in regard to hydrologic cycling (Motzer, Munz, Kuppers, Schmitt, & Anhuf, 2005), despite an increased interest within the last two decades to investigate the processes governing montane forests (Bruijnzeel, Mulligan, & Scatena, 2011; Gotsch, Asbjornsen, & Goldsmith, 2016; Oliveira, Eller, Bittencourt, & Mulligan, 2014). The ratio of transpiration to streamflow rates is known to be lower in TMFs than in lowland rainforests (Motzer et al., 2005), perhaps because the canopies in montane areas are prone to remaining wet for longer portions of time due to cooler temperatures and increased cloud cover (Dietz, Leuschner, Holscher, & Kreilein, 2007).

The influence that leaf wetness exerts on transpiration in TMF canopies is largely unknown (Eller, Burgess, & Oliveira, 2015; Horna, Schuldt, Brix, & Leuschner, 2011; O'Brien, Oberbauer, & Clark, 2004). However, in a recent study, leaf wetness was shown to reduce transpiration by an additional 28%, after accounting for the effects of incident solar radiation (R_s) and vapour pressure deficit (VPD; Aparecido, Miller, Cahill, & Moore, 2016). Energy in the form of solar radiation is a limiting variable, and evapotranspiration is closely coupled with it in lowland tropical forests across a wide range of tree species (Meinzer, 2003; Meinzer, James, Goldstein, & Woodruff, 2003). However, our ability to accurately predict evapotranspiration in forests with frequent wet canopy conditions may require additional inputs. Thus, the frequency and intensity of rainfall could impose an important (Ishibashi & Terashima, 1995; Kume et al., 2011) yet poorly understood control on evapotranspiration beyond those considered by the standard models that rely only on R_s and VPD (Jones, 1992). It is possible that vertical variation in leaf wetness alters the proportioning of transpiration in the canopy. Despite clear patterns of reduced wetness duration at the top of the canopy, Aparecido et al. (2016) did not find large differences in the transpiration response to leaf wetness between trees in the overstory and less exposed midstory (i.e., both proportionally decreased), which suggests plants may have developed adaptations to the frequently wet environment. By contrast, understory trees had a constant rate of water use independently of the canopy wetness condition. Nevertheless, the relative importance of canopy exposure, species adaptations to wet environments, and changes in aerodynamic properties with age and stand management has not been explored extensively in these forests.

All tropical forests are broadly characterized by their complex structure arising from high species diversity and relative stability of annual and interannual climate cycles. For tropical rainforest trees, researchers (e.g., Wright et al., 2005) have hypothesized that species-specific differences in physiology, morphology, and architecture, as well as environmental influences, including site microclimate and topography, contribute to variation in functional traits that determines species occurrence and coexistence. Although it is well known that climate gradients in montane environments amplify the spatial variability in species composition along ecotonal boundaries, the effect of species-specific differences on transpiration is less clearly understood. The few studies that address this in Neotropical forests have suggested that variation in transpiration is controlled less by species-specific differences than by physical tree attributes, including tree height and hydraulic architecture (Andrade et al., 1998; Kunert

et al., 2017; Meinzer, Goldstein, & Andrade, 2001). Given many upscaling studies in temperate forests apportion transpiration within stands using species-specific sap flux estimates (Ewers et al., 2002; Granier & Lostau, 1994; Moore, Bond, Jones, Phillips, & Meinzer, 2004; Oren, Philips, Ewers, Pataki, & Megonigal, 1999), such approaches may be inappropriate in diverse tropical forests.

We investigated transpiration at the tree-to-stand scale in a tropical premontane forest in Costa Rica. The objectives of this study were to determine (a) how transpiration responds to primary drivers, specifically solar radiation and atmospheric VPD, and whether those responses differ with tree characteristics; and (b) how rainfall and canopy wetness affects temporal patterns in transpiration. This work also will be directly compared with the results presented by Aparecido et al. (2016) in a nearby location ~250 m south-east, who estimated 497-mm annual transpiration in a study of 17 species from which only three species overlap with this study.

The following assumptions underlie this study: (a) Tropical montane tree species can be reasonably classified into functional groups according to size in order to predict transpiration. As such, failure to represent a wide range of tree sizes in sap flux studies is likely to bias estimates of stand transpiration. (b) All species are similar in their water use, after accounting for differences related to canopy position and tree size.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted at the Texas A&M University Soltis Center for Research and Education near San Isidro de Peñas Blancas, Costa Rica (10°23.0′N, 84°37.0′W). The Soltis Center is composed of 250 ha of mixed secondary and primary forest, ranging from 450 to 650 masl and adjacent to the Children's Eternal Rainforest preserve. The vegetation is a transitional tropical premontane moist forest situated at higher elevations than surrounding lowland forests, but below that of cloud affected forests of the Monteverde highlands (Holdridge, 1967). Trees range from 25 to 35 m in height, reaching upper canopy at around 25 m with dense foliage, multiple interlacing crowns, but with frequent canopy gaps. The geology consists of volcanic mudflows and landslides, with underlying saprolitic tuff. The soil is andisolic with clay to clay-loam texture and originates from Caribbean volcanic ash.

Weather variables have been continuously monitored at the Soltis Center since June 2010 using a combination of manual rain gauges and an on-site meteorological tower. Annual rainfall is approximately 5,000 mm, with a rainy season from May to December and a relatively "dry" season from January to April when monthly rainfall totals are ~60% less than in rainy season. Air temperature shows little seasonal variation, with monthly averages ranging from 21 to 24 °C, a low of 15 °C, and a high reaching 32 °C (Figure 1). Solar radiation (R_s, W m^{-2}) is highest during the dry season. A small, 2.2-ha watershed, known locally as "Howler Hollows," has been the subject of previous investigations (e.g., Buckwalter, Tourtellotte, Brumbelow, Cahill, & Miller, 2012; DuMont et al., 2013; Houser et al., 2013; Teale et al.,
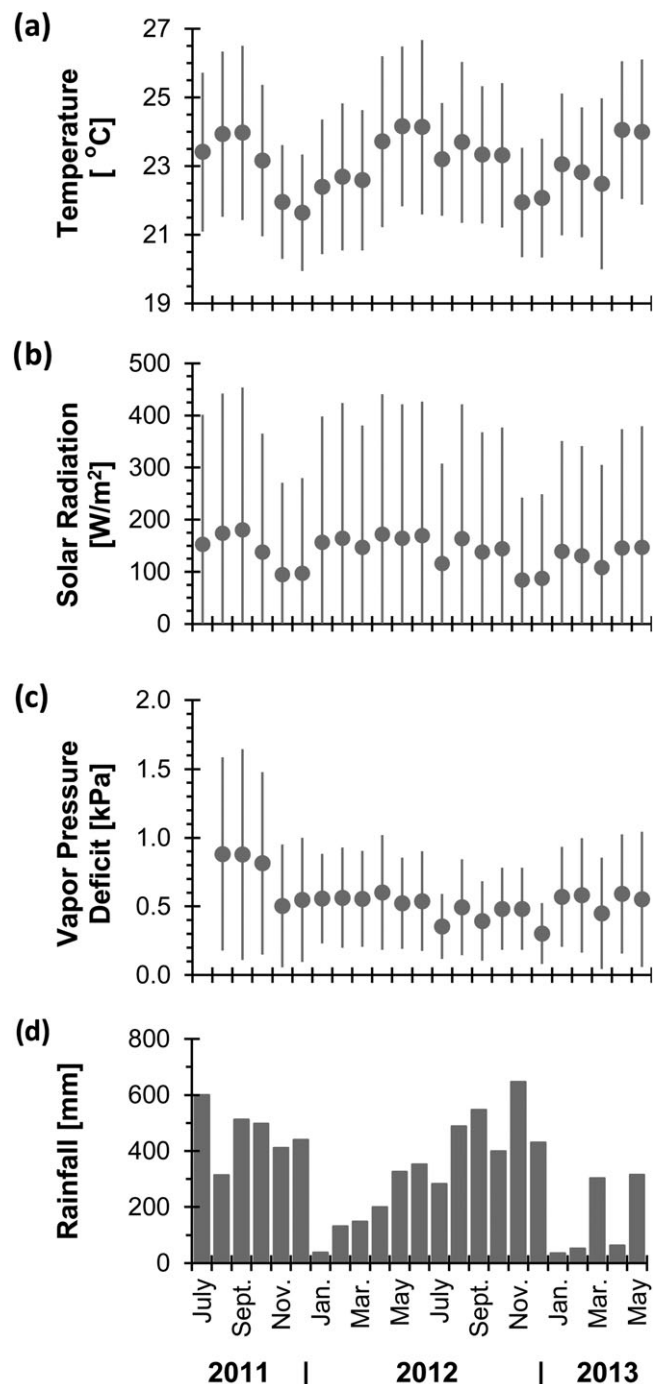
FIGURE 1 Monthly mean values with standard deviations for (a) air temperature, (b) solar radiation, (c) vapour pressure deficit, and (d) total rainfall for a 2-year period that encompasses the sap flux measurement period from January 16 to November 14, 2012

2014; Washington-Allen et al., 2012) and defines the spatial extent of this study site.

2.2 | Stand characterization

Four 30-m diameter plots were randomly delineated within the watershed. Diameters (diameter at breast height) of all 92 trees within the plots were measured (Figure 2a). To determine active-xylem sapwood depth, we visually inspected 5-mm cores with the aid of safranin dye as described in Aparecido et al. (2016). Xylem
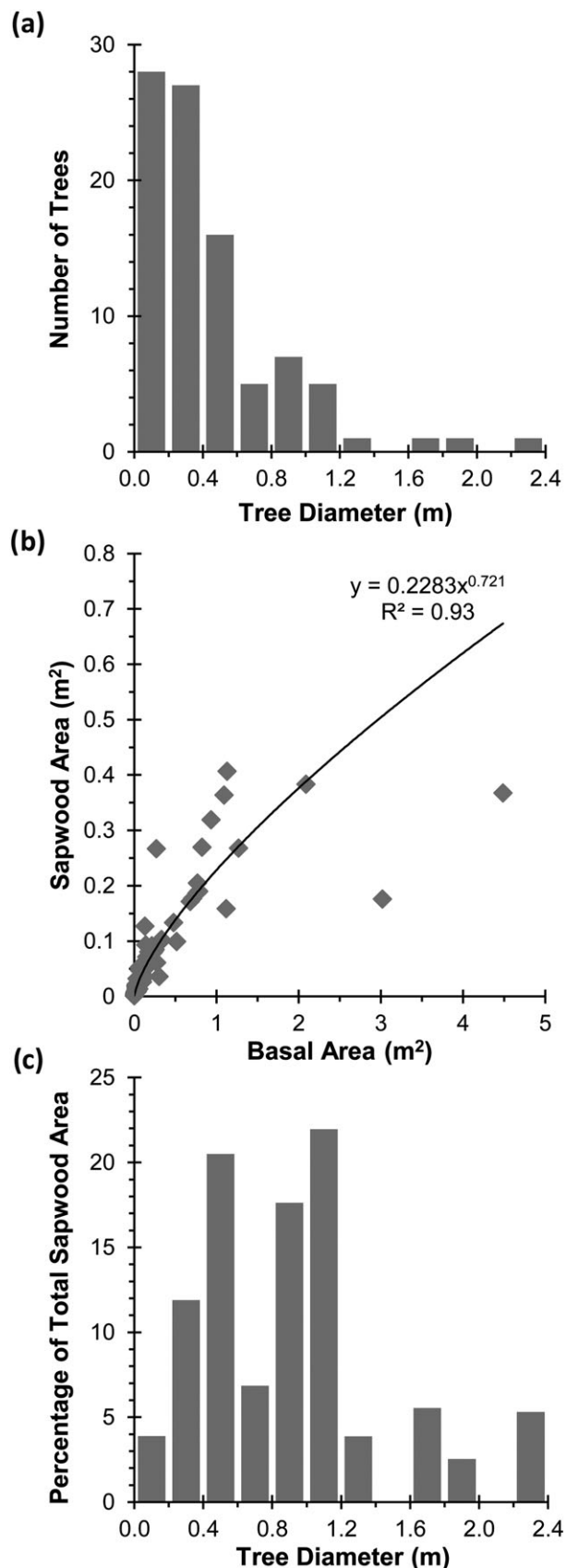

FIGURE 2 Stand inventory for our measurement site, including (a) the number of trees in each diameter class, (b) the relationship between basal area and sapwood area (for trees equipped with sap flow sensors and an additional 26 trees spanning the full range in diameters), and (c) the proportion of sapwood area in each diameter class (using the relationship in panel a to predict unmeasured trees)

depth was assessed on each tree equipped with sap flow sensors and an additional 26 trees spanning the full range in diameters. From these measurements, a basal area to sapwood area relationship was developed to estimate sapwood area of the unmeasured trees (Figure 2b) and a histogram of the percentage of total sapwood area by tree diameter (Figure 2c).

One of the four plots was selected for the placement of sap flow sensors based on proximity to a nearby clearing where solar panels were located. The other plots were not accessible for sap flux measurements. Typically, sap flux studies measure only the dominant tree species, four species at most, and replicate by species at a given site to determine each species' contribution to stand transpiration (Moore et al., 2004; Wullschleger, Hanson, & Todd, 2001). However, our ability to compare variation within species was limited due to the high diversity within the plot, as few species had more than one tree represented. Instead, following our assumption that tree size was a controlling factor for sap flux rates, we randomly selected three trees within each of five diameter ranges to receive sensors (Table 1). Having five size categories helped evenly distribute tree selection across the full range of tree diameters in the plot (i.e., distribution, rather than replication, was the systematic approach utilized). Each of the 15 trees was a unique species originating from 15 unique families (Table 2).

2.3 | Transpiration measurement and upscaling

Transpiration rates were determined for the 15 trees using heat dissipation sap flow sensors (Granier, 1985) that were laboratory made using the methods described in Phillips, Nagchaudhuri, Oren, and Katul (1997). Each tree had two sensors installed on opposite sides, perpendicular to the slope, at ~1.4-m measuring sap velocity in the outer 20 mm of xylem. Measurements were taken every 30 s and averaged within trees every 10 min from January 16 to November 14, 2012 (total of 10 months). Sap flux density (J_s, kg m^{-2} s^{-1}) was calculated based on the following equation:

$$J_s = 0.119 \cdot K^{1.231}, \tag{1}$$

where K is a dimensionless constant determined by the following equation:

$$K = (\Delta T_M - \Delta T)/\Delta T. \tag{2}$$

ΔT_M is the maximum temperature difference when sap flux is assumed to be zero, and ΔT is the actual temperature difference between the two probes, calculated from the mV output. Due to the high frequency of $VPD = 0$ at our site, zero flows were determined on a daily basis.

TABLE 1 Size classes for upscaling from sap flux density to watershed-level transpiration based on diameter at breast height (*DBH*)

Size class	Diameter range (cm)	Total sapwood area (m^2)		
		Instrumented plot	All plots	Watershed level
Class 1	*DBH* ≤ 7.5	0.019	0.021	0.164
Class 2	7.5 < *DBH* ≤ 17	0.076	0.144	1.12
Class 3	17 < *DBH* ≤ 21	0.123	0.227	1.77
Class 4	21 < *DBH* ≤ 33	0.222	0.504	3.92
Class 5	33 < *DBH* ≤ 240	0.768	6.02	46.8

TABLE 2 Size and species of trees instrumented with sap flow sensors, ordered by diameter

Size class	Height (m)	Diameter (cm)	Sapwood depth (cm)	Family	Genus	Species
1	6.1	4.2		Pyllanthaceae	*Phyllanthus*	*skutchii* Standl.
1	9.8	6.3		Asteraceae	*Koanophyllon*	*hylonomum* (B.L. Rob.) R. M. King & H. Rob.
1	11.1	7.4		Lacistemataceae	*Lozania*	*pittieri* (S.F. Blake) L.B. Sm.
2	8.4	10.6		Anacardiaceae	*Mosquitoxylum*	*jaimacense* (Krug & Urb.)
2	11.1	15.8		Euphorbiaceae	*Pousandra*	*trianae* (Müll. Arg.) Baill.
2	16.3	16.5		Melastomataceae	*Miconia*	*serrulata* (DC.) Naud.
3	10.1	16.9[a]	7.3	Malvaceae	*Heliocarpus*	*appendiculatus* Turcz.
3	15.8	19.2[a]	5.0	Myrtaceae	*Virola*	*koschnyi* Warb.
3	13.7	20.6		Eleocarpaceae	cf. *Sloanea*	Sp.
4	14.7	27.8[a]	9.0	Annonaceae	*Annona*	*macrocarpa* (Wercklé.)
4	10.4	27.8[a]	8.5	Fabaceae	*Inga*	Sp.
4	16.4	32.8		Calophyllaceae	*Calophyllum*	*brasiliense* (Cambess)
5	15.3	42.0[a]	9.0	Moraceae	*Brosimum*	Sp.
5	15.3	43.8		Rubiaceae	*Chomelia*	*venulosa* (W.C. Burger & C.M. Taylor)
5	35.4	119.9[a]	12.0	Meliaceae	*Carapa*	*guianensis* (Aublet)

Note. Size classes were based on diameter.

[a]Indicates tree individuals that underwent radial profile measurements.

Previous papers have called attention to the need to determine the radial sapwood profile of the velocities in order to upscale from sap velocity to the total volumetric sap flow of a tree (Caylor & Dragoni, 2009; Dragoni, Caylor, & Schmid, 2009). To determine if this correction was necessary in this study, depth profile measurements of sap flux density (Figure 3) were obtained in six of the larger trees using compensation heat pulse profile probes inserted to a depth of 60 mm with measurements every 10 mm (Green, Clothier, & Jardine, 2003) over a period of several days. However, the profiles deviated significantly from the previously published model for angiosperms in temperate areas (Ford, Hubbard, Kloeppel, & Vose, 2007; Pataki, McCarthy, Litvak, & Pincetl, 2011). These previous models were based on a Gaussian curve, given as

$$J_i/J_o = a \cdot \exp\left[-0.5\left(\frac{x-b}{c}\right)^2\right], \tag{3}$$

where J_i/J_o is the relative flux, x is the relative sapwood depth, and a, b, and c are fitted parameters. We tested three potential models against our data (Figure 3): a Gaussian curve using the parameters reported by Pataki et al. (2011) (a = 1.033, b = 0.0996, c = 0.4263), a Gaussian curve with best-fit parameters (a = 1.034, b = 0, c = 1.440), and a linear regression model (m = −0.24, y_0 = 1.77). The Nash–Sutcliffe efficiency (NSE) coefficient was calculated for each to compare its predictive power against a null (no slope) model. The Gaussian model with Pataki parameters had an NSE = −5.2, indicating that the mean of the data was a far better predictor than the model itself. The best-fit Gaussian curve (NSE = 0.19, p < .01) and the linear model (NSE = 0.22, p < .001) gave better predictions. Additionally, size-related differences in profile patterns were not detected, nor were patterns consistent between trees.

Given the profiles measured and their high degree of variation, we chose to assume a constant sap flux density throughout the sapwood area. Total transpiration per tree (Q) was found using the equation:

$$Q_i = \overline{J_{s,i}} A_i \rho_s, \tag{4}$$

where Q_i is an individual tree i's total volumetric sap flow rate (m³ s⁻¹), $\overline{J_{s,i}}$ is mean sap flux density (Equation 1), A_i is the tree's total sapwood

area (Table 1, m²), and ρ_s is the density of its sap, equal to that of water, 1.0 g cm⁻³. Total tree water use was reported in units of L day⁻¹.

Similarly, to estimate stand transpiration at the watershed scale, the following equation was used:

$$Q_T = \sum_{k=1}^{5} \overline{J_{s,k}} A_k \rho_s, \tag{5}$$

where Q_T is the volumetric flow of water from all trees in the watershed (m³ s⁻¹), $\overline{J_{s,k}}$ is the mean sap flux density from the three instrumented trees in size class k, and A_k is the total sapwood area for all trees in size class k (Table 2). To find the mean estimated transpiration rate over the watershed, T (mm), Q_T is divided by the total watershed area, A_w, equal to 22,000 m² for this study:

$$T = Q_T/A_w. \tag{6}$$

2.4 | Climate measurements

Climatic variables were measured on a nearby 10-m micrometeorological tower located in a small clearing instrumented with a pyranometer (LI-200, LI-COR, Lincoln, Nebr.), tipping bucket rain gauge (TE525WS, Campbell Scientific Inc., Logan, UT), and temperature and relative humidity sensor (HMP45C, Campbell Scientific) from which VPD was calculated. Leaf wetness was estimated using two leaf wetness sensors (LWS) at 1.5 m above the ground surface (Decagon Devices, Pullman, Wash.): one at a nearby location below the canopy and the other in a nearby open area. All measurements were compiled at 5-min intervals. LWS data were only available for limited periods in the wet season of 2011 and 2012. The use of dielectric sensors as a proxy for actual leaf wetness is limited by several factors, including leaf surface traits to retain or repel water (Armstrong, Barthakur, & Norris, 1993; Sentelhas, Monteiro, & Gillespie, 2004) and the high level of spatial variation in wetness condition and duration throughout a complex canopy (Giesler, Horst, & Yuen, 1996; Magarey, Seem, Weiss, Gillespoe, & Huber, 2005). Therefore, we constrain our use of LWS data to generalized relationships between sap flux and leaf wetness.

2.5 | Data analyses

Linear and nonlinear model fits were applied to determine the degree of relationship between daily total transpiration (dependent variable) and daily average climatic variables (VPD, R_s) during daylight hours (independent variables). Best model fit was determined by the coefficient of variation (r^2), Pearson correlation (r), and p values (α < 0.01). The analysis was done in the R software package (version 2.13.1; R Core Team, 2013). The general linear model function [lm()] was used to fit a linear model to climatic variables in log-transformed and nontransformed forms, and the nonlinear model function [nls] was used to fit an exponential power model. Regression models were also used to test for relationships between average sap flux density per tree and total tree water use with tree diameter, as indicated by r^2 and α < 0.05.
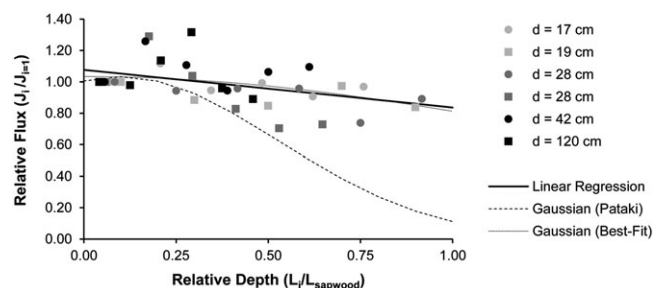

FIGURE 3 Radial sap flux measurements. Relative flux was calculated by normalizing the value at a given depth, J_i, to the value in the outer 1 cm, $J_{i=1}$. Relative depth was calculated by normalizing the depth of each measurement, L_i, to the total sapwood depth, $L_{sapwood}$, measured via core sampling (Table 1). Symbol colours range from light to dark grey according to tree diameter (d), see also Table 2

3 | RESULTS

3.1 | Environmental controls on sap flux

Day 178 represents a typical, but rare, rain-free day (Figure 4 "Dry Day"). From Aparecido et al. (2016), only 27% of days that year had wet leaves less than 10% of the daylight hours. On dry days, such as Day 178, sap flux rates tracked solar radiation (R_s), with VPD having a secondary influence. Day 181 represents a day with significant leaf wetness that influenced J_s after the rain ended (Figure 4 "Wet Day"). After sunrise on the wet day, radiative and evaporative demands increased dramatically, whereas J_s remained near zero until leaves were sufficiently dry. On wet mornings, such as Day 181, J_s lagged behind R_s for about 2 hr, until the leaves dried out below 80% leaf wetness. Such a lag could also be associated with stem water storage; however, lags were longer on wet mornings than dry mornings. This suggests a threshold for leaf wetness of approximately 80% above which transpiration does not occur. Although J_s ceases during periods of saturated leaf wetness (LW > 80%), evaporation of intercepted rainfall continues, given VPD > 0 kPa at the wet leaf surface.

Over long time periods containing a mix of wet and dry days, J_s among trees in size Class 5 was more closely related to R_s than VPD (r^2 = 0.52 and 0.32, respectively, p < .01, Figure 5a,b). Sap flux rates were highly variable at higher levels of VPD (above 1 kPa), but tended to approach a maximum at high levels of VPD (Figure 5a), which was much lower in trees of Classes 1–4 than Class 5. Similarly, J_s was more variable at higher levels of R_s, particularly in Class 5 trees, but did not

indicate any suppression of J_s at high R_s (Figure 5b). During the wet season, J_s peaked in the early afternoon with all classes having similar patterns throughout the day (Figure 6a). Size Classes 4 and 1 had the highest J_s rates, whereas Classes 2, 3, and 5 were the lowest (Figure 6a). Most of these trends continued into the dry season, but maximum J_s was higher and occurred earlier, around midday (Figure 6b). When sap flux densities were grouped by time of day (morning vs. afternoon), distinct differences in these relationships were noted, indicating the presence of hysteretic behaviour (Figure 7), indicating that the response to VPD and R_s was time dependent. In general, when given the same VPD, sap flux rates were higher in the mornings than the afternoons (Figure 7c,e). However, on dry days only, this trend reversed for late afternoon and early evening values. These patterns were similar among all size classes, but Class 5 had consistently higher sap flux than Classes 1–4 on wet mornings, whereas, on dry days, differences in diurnal trends between size classes were less notable (Figure 7c,e). Although the average diurnal trends in R_s were similar on wet and dry days (Figure 7b), substantial differences were noted in the areas of their hysteresis loops for both size groupings (Figure 7d,f), indicating greater contrasts between morning and afternoon responses. On wet days, sap flux density had similar morning and afternoon behaviours; similar light levels had only small differences. However, on dry days, rates were much higher in the afternoons than in the mornings, given the same level of light.

Individual tree estimates of mean J_s were not related to tree diameter (Figure 8a, p > .05), but tree diameter was a good predictor of total tree water use (r^2 = 0.89, Figure 8b). The large *Carapa* tree,
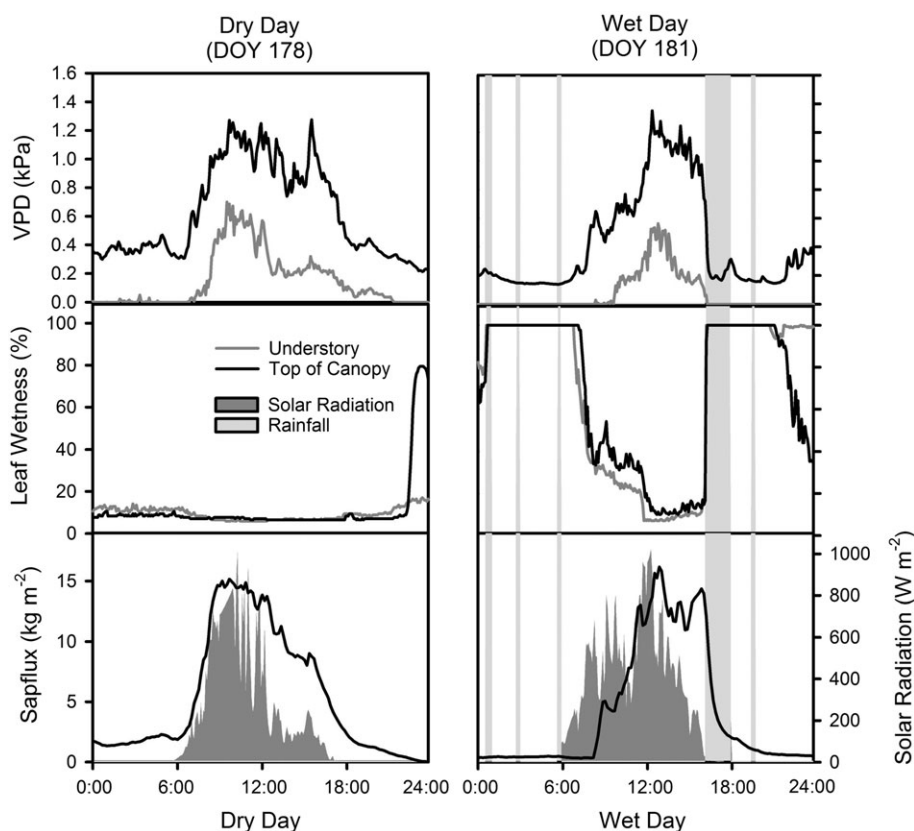

FIGURE 4 Patterns of sap flux, solar radiation, and rainfall, along with understory and top of canopy leaf wetness and vapour pressure deficit (VPD) for two select days in June 2011, a dry day (DOY 178) and a wet day (DOY 181)
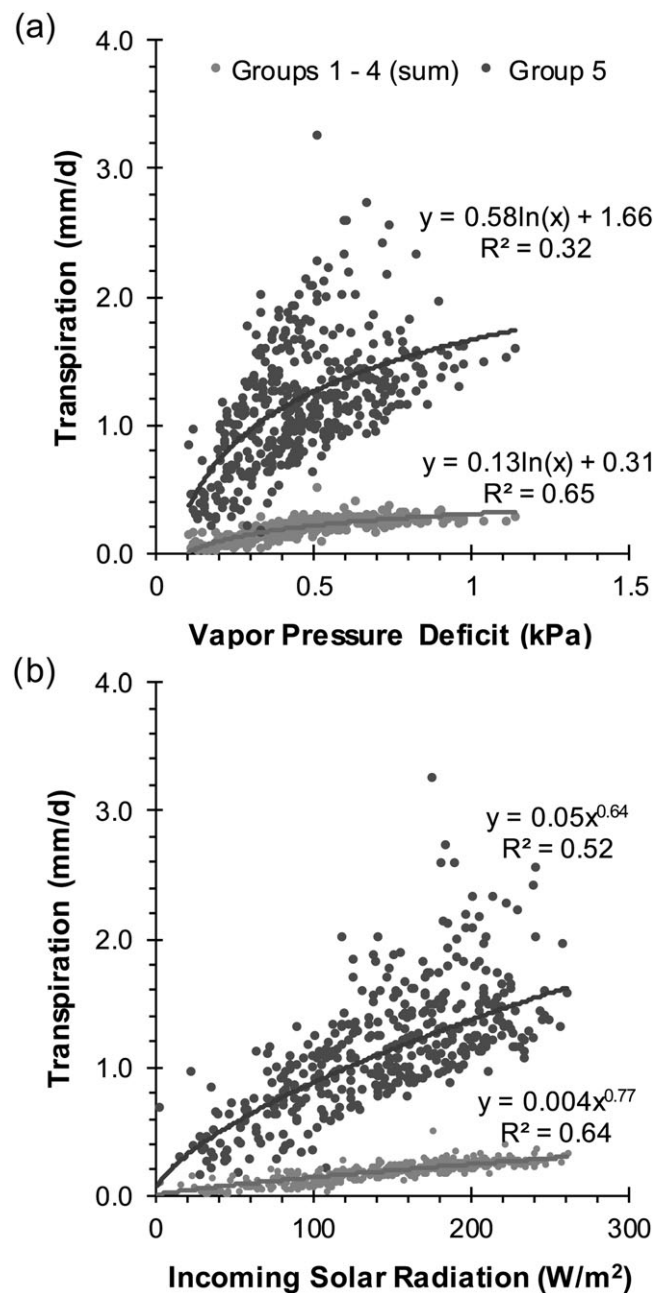
FIGURE 5 Daily stand transpiration (mm/day) in relation to average vapour pressure deficit (a) and incoming solar radiation (b) partitioned into Classes 1–4 (dark grey) and Class 5 (light grey)

being nearly 3× larger than the next largest tree, exerted high leverage on the regression fit.

3.2 | Stand-level transpiration

Over a 10-month period in 2012, stand transpiration approached a maximum rate of 3.0 mm day^{-1} but was often much lower (Figure 9), averaging 1.4 ± 0.7 mm day^{-1}. A disproportionate fraction of total stand transpiration came from the largest diameter trees, Class 5, which contributed more than 80% to the stand total. This was attributed to a greater total sapwood area in Class 5, rather than higher sap flux density (Figure 9; Table 1).

4 | DISCUSSION

4.1 | Insights in upscaling transpiration in tropical forests

Our study addresses a critical theme in the field of ecohydrology that seeks to better understand the contrasts between water-limited and energy-limited systems and to apply those principles across scales (Asbjornsen et al., 2011). Furthermore, it contributes to the growing body of work to optimize sap flux scaling methods from trees to stands (Čermák, Kučera, & Nadezhdina, 2004; Kostner, 2001; Oren, Philips, Katul, Ewers, & Pataki, 1998) to watersheds (Ford et al., 2007; Moore et al., 2004) by extending these concepts to diverse tropical forests. In our study, stand transpiration amounted to only 1.4 ± 0.7 mm day^{-1} due to persistent low radiation, evaporative demand, and frequent wet canopy conditions. These results matched transpiration estimates of Aparecido et al. (2016) nearby site, which were 1.4 ± 0.5 mm day^{-1} over a 12-month period in 2014.

Given the challenges of quantifying species differences in such a diverse ecosystem, our findings suggest that tree size can serve as an appropriate scaler for water use in tropical forests where estimates of species-level mean values are impractical. This arises where species replicates are spaced very far apart or where transpiration is widely distributed among individuals of many species, each contributing only a small fraction to site water balance. Our stand consisted of more than 15 unique families, with only minor overlap between the genus and species at the study site only 250 m away (Aparecido et al., 2016). Those in common between the two sites were *Inga* sp. (n = 1), *Brosimum* sp. (n = 1), and *Carapa guianensis* (n = 3), which were categorized as Class 5, Class 3, and Classes 5, 3, and 2, respectively. It was apparent that any inherent trait unique to a particular genus or species was extremely difficult to distinguish from other size and edaphic factors; for instance, even those within the same diameter class had differing canopy exposure.

For instance, on average, sap flux density of *Inga* sp. (521 kg m^{-2} day^{-1}, 40-cm diam.), reported by Aparecido et al. (2016), was only one third the rates observed in the *Inga* sp. in this study (1,552 kg m^{-2} day^{-1}, 28-cm diam.) despite its larger size. To the contrary, sap flux density of *Brosimum* sp. (308 kg m^{-2} day^{-1}, 19-cm diam.), also reported by Aparecido et al. (2016), was 50% greater than the rates observed in the *Brosimum* sp. in this study (197 kg m^{-2} day^{-1}, 42-cm diam.). Interestingly, the *C. guianensis* individual in this study with such a large diameter (120 cm) had very similar rates of sap flux as a 43-cm-diameter individual reported by Aparecido et al. (2016), 628 and 647 kg m^{-2} day^{-1}, respectively. The other two *C. guianensis* individuals from Aparecido et al. (2016) had lower rates of 209 and 134 kg m^{-2} day^{-1} and diameters of 17 and 8 cm, respectively. This provides only limited support for our assumption that tree size may be a better way to partition transpiration within a stand than species, because size appeared to affect differences among *Inga* and *Carapa* individuals, but not *Brosimum*. Such a mismatch is reasonable, given that crown exposure is a likely factor influencing rates of J_s within species, whereas total tree water use is more a function of cross-sectional conducting xylem. We used basal diameter rather than crown size or exposure to classify trees for this
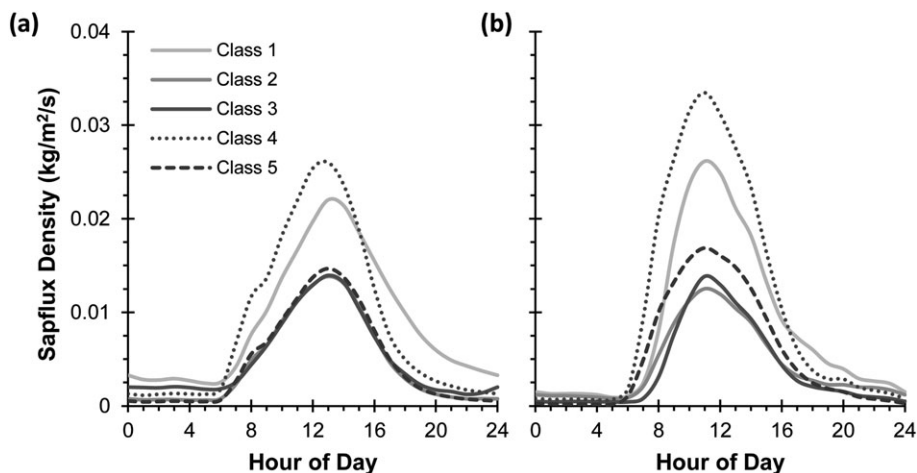
FIGURE 6 Mean 10-min sap flux density by tree size class (see Tables 1 and 2) for (a) February (wet season) and (b) March (dry season) of 2013

study. It is clear from Table 2 that height and diameter were weakly correlated. Height was an equally poor predictor of J_s as diameter was (Figure 8, height results not shown, see Table 2). Yet tree diameter explained nearly 90% of the variation in total tree water use (Figure 8), largely as a function of sapwood area, although the large *Carapa* tree had a lower sapwood area for its size than the smaller trees (Figure 2b). One species, *Inga* sp., had much higher than predicted water use for its size, whereas another species, *Brosimum* sp., had much lower than predicted water use for its size. Although we were unable to resolve any species-related trends, our systematic approach to sample across tree diameters resulted in a robust stand transpiration estimate. Nevertheless, a study with higher replication within species is required to elucidate the relative contribution to stand transpiration among co-occurring species.

Our study site consisted of a smaller size cohort of secondary regrowth trees than the stand studied by Aparecido et al. (2016), and our small trees contributed more to the total sapwood area of the stand. This suggests that the relative proportion of water use by size category cannot be generalized across sites. Being able to make generalities about water use patterns is particularly important in highly diverse stands where species-level estimates are not feasible. We recommend our systematic sampling approach to characterize water use for a representative array of tree sizes, rather than a representative array of tree species, in sites with high diversity.

A comparison between the large exposed trees in size Class 5 and the other smaller trees in Classes 1–4 indicated some interesting temporal patterns on a subdaily basis that differ between wet and dry conditions (Figure 7). In water-limited environments, greater magnitudes of hysteresis (area within the loop) for *VPD* have been associated with overnight rehydration (higher morning J_s) and stomatal limitation (lower afternoon J_s)—especially in the drier months, associated with lower soil water potential (Zhang, Manzoni, Katul, Porporato, & Yang, 2014; Zheng, Wang, Zhu, Li, & Yu, 2014). However, no previous study has implicated leaf wetness as a driver of hysteretic trends (Zhang et al., 2014), which may be influenced by plant adaptations to wet leaf conditions in the humid tropics (Aparecido, Miller, Cahill, & Moore, 2017). We observed a larger magnitude of hysteresis for R_s on dry days compared to wet days than previously reported (Zheng et al., 2014). On "dry" mornings, the lagged sap flux response to R_s (Figure 7d) is

likely due to wet leaves from overnight rain or dew. Consequently, it is reasonable to expect a much higher proportion of site water balance allocated from evaporation to transpiration once the canopy dried. This effect diminishes on wet days, as wetness often persists into the afternoon because of periodic rain showers. Observed differences between size classes further substantiate this, because Classes 1–4 hysteresis patterns contrasted more between wet and dry days than the more exposed (presumably faster drying) trees in Class 5. The upper canopy of tall forests such as this is aerodynamically rough and more coupled to the atmosphere than the lower canopy layers where air is less mixed (Jones, 1992). Quantitative assessments of leaf wetness variation and its effects throughout the canopy are needed, because our leaf wetness data could not be used to make direct comparisons of wetness condition between size classes.

When extrapolating the average daily transpiration of 1.4 mm day^{-1} over the 10-month measurement period to a full year, annual transpiration is approximately 511 mm year^{-1}, which is consistent with other findings in literature for similar vegetation types, especially in tropical montane cloud forests that are known to have transpiration around 250–645 mm year^{-1} (Bruijnzeel & Veneklaas, 1998). Estimates from tropical montane cloud forests were between 355 and 645 mm year^{-1}, depending on elevation, with lower values at highest elevations (Bruijnzeel et al., 2011; McJannet, Fitch, Disher, & Wallace, 2007). Within lowland tropical forests, Horna et al. (2011) reported daily transpiration rates from 0.09 to 1.05 mm day^{-1} and an annual total of only 253 mm for a mature tropical Indonesian stand; Kunert, Aparecido, Higuchi, Santos, and Trumbore (2015) found annual total stand transpiration of 845 mm year^{-1}, and ranging from 0.29 to 4.74 mm day^{-1} in a mature Amazonian forest stand; and in a pine plantation in Mexico, Alvarado-Barrientos, Holwerda, Asbjornsen, Dawson, and Bruijnzeel (2014) found that transpiration was greater during sunny conditions with 2.6 ± 0.2 mm day^{-1}, and lowest during fog events with 0.3 ± 0.1 mm day^{-1}, with an annual total of ~650 mm.

Others have scaled transpiration to the stand using similar methods as ours (Bucci et al., 2008; Granier, Huc, & Barigah, 1996; Horna et al., 2011), for example, by using a range of tree diameters (Horna et al., 2011) or a range of crown dominance (Aparecido et al., 2016; Kunert et al., 2017). More commonly, though, measurements
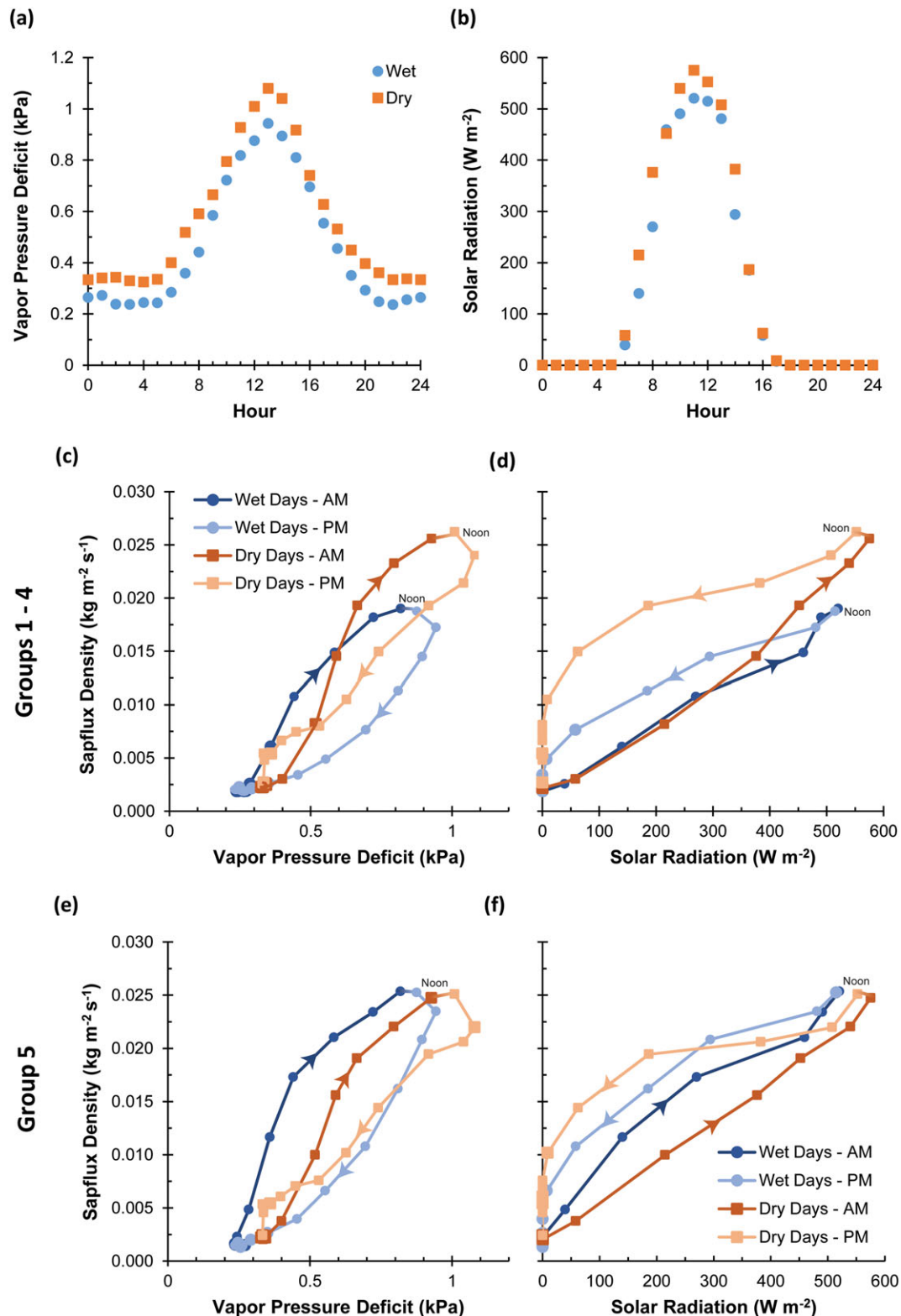
FIGURE 7 Diurnal patterns in vapour pressure deficit (a) and solar radiation (b) along with plots demonstrating hysteresis in the relationship between hourly average sap flux density and hourly averages of these variables, shown for Classes 1–4 (c,d) and for Class 5 (e,f). Peak sap flow rates occur near midday (labelled noon)

extend only to individual trees (Kunert et al., 2015; Meinzer, James, & Goldstein, 2004; O'Brien et al., 2004). However, we caution against subsampling biases that tend to overestimate stand transpiration if, for example, instrumented trees are predominantly in the larger class sizes (i.e., overstory). Aparecido et al. (2016) clearly identified

disproportionately lower transpiration in understory trees. Considering that leaves dry out more slowly in the lower canopy, tropical understory trees may use proportionately less water than temperate understory trees, relative to the overstory. Horna et al. (2011) also pointed out the importance of accurate representation of understory
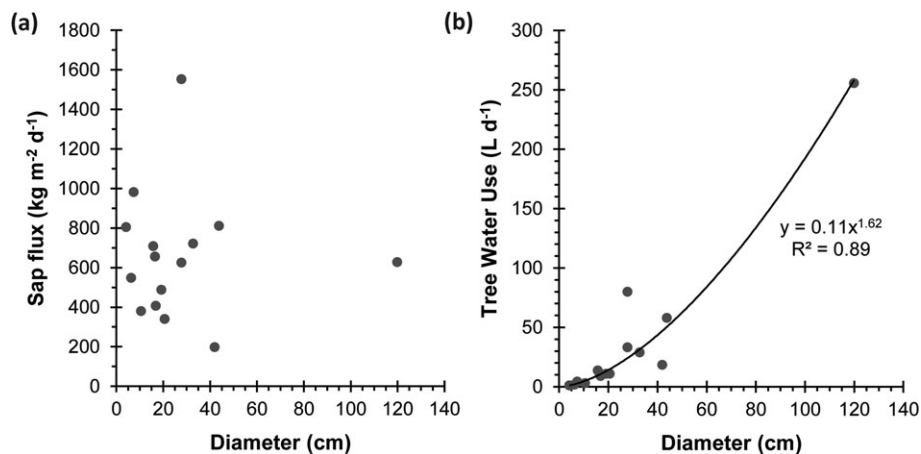
FIGURE 8 Sap flux density (a) and total tree water use (b) as a function of tree diameter. Following Holwerda, Alvarado-Barrientos, and Gonzalez-Martinez (2016), tree water use increased as a power function of diameter ($y = ax^b$)
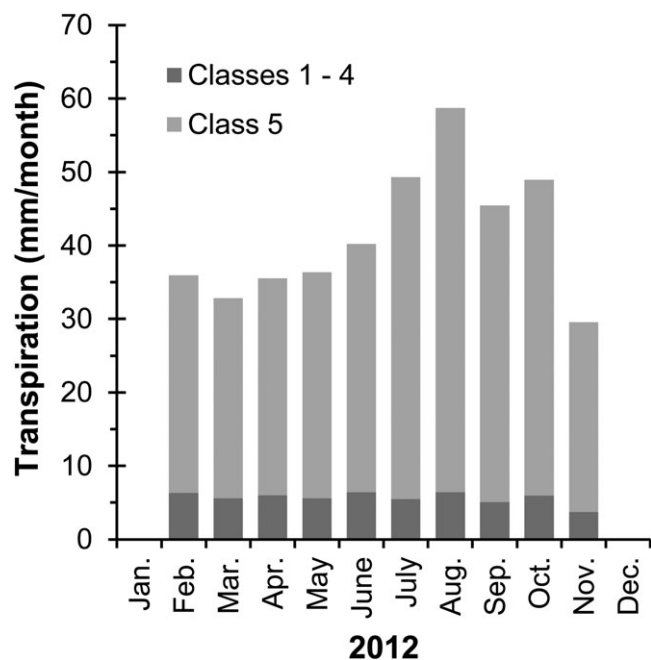

FIGURE 9 Contribution of five tree size classes to monthly total stand transpiration for the period of January 16 to November 14, 2012. Totals shown separately for Classes 1–4 combined (dark grey) and for Class 5 (light grey)

trees and accounted for it in Indonesian forests. More accurate estimates of transpiration are needed to better partition biological responses to changing water resources across the globe (Jasechko et al., 2013).

Although R_s and VPD were strong drivers of transpiration responses, we also found evidence that leaf wetness suppressed transpiration until a significant threshold of dryness was surpassed. This is important given how frequently leaves were wet in this system, and also suggests that transpiration may be suppressed by leaf wetness in other humid regions (Alvarado-Barrientos et al., 2014; Berry, Gotsch, Holwerda, Munoz-Villers, & Asbjornsen, 2016; Chu et al., 2014; Gotsch et al., 2014; Reinhardt & Smith, 2008; Ritter,

Regalado, & Aschan, 2008). We observed that transpiration during the two driest months with full records (February and March) was about 26% lower than the two wettest months (July and September, see Figure 9). However, observations in the Amazon rainforest indicated that plants responded more strongly to soil moisture fluctuations (Malhi et al., 2002). Empirical evidence of stomatal behaviour under short-term high VPD or short-term declines in soil moisture is inconsistent for lowland tropical forests (Roberts, Gash, Tani, & Bruijnzeel, 2005) and even rarer for montane tropical rainforests. Ultimately, the interplay between atmospheric demand, leaf wetness, and soil water limitation determines whether transpiration increases or decreases, depending on the relative strength of these opposing responses.

We found only modest decreases in transpiration during drier months (Figure 6), when transpiration is expected to account for a greater portion of the water budget. Compared with the extensive studies of transpiration responses to water deficits in temperate regions, considerably less is known about the onset of drought-related reductions in transpiration in the wet tropics, with potential implications for water resources management and early detection of drought stress. Likewise, our largest trees show no evidence of suppressed water use when dry. Our study showed that, by far, the largest trees make up the greatest contribution of total sapwood in this stand. This is important for several reasons. First, large trees in temperate regions tend to have lower proportions of sapwood area to total basal area than those in tropical regions, which suggests large old-growth tropical trees are growing more actively than their temperate counterparts; see Moore et al. (2004) for a case where temperate old-growth trees are relatively lower water users. Second, large tropical tree canopies are more exposed and thus dry out more rapidly than the understory. Third, selective harvest of a few large trees can be expected to disproportionately reduce stand sapwood area, at least temporarily, which could alter site water balance (Breda, Granier, & Aussenac, 1995). By contrast, see Moore and Owens (2012), Ilstedt et al. (2016), and Lane and Mackay (2001) for cases where thinning forests only temporarily altered water balance, if at all.

5 | CONCLUSIONS

This study characterized variable responses to environmental drivers of transpiration, which were more pronounced in larger trees. Wet leaf conditions apparently affected transpiration of smaller sized trees the most, because the lower canopy leaves remained wet for longer durations (Aparecido et al., 2016). On the basis of these findings, we recommend an approach to scaling transpiration that neither overestimates water use of small understory trees nor underestimates water use of dominant exposed trees. Hence, in tropical premontane forests, a more accurate estimation of stand transpiration should reasonably account for tree size variability and canopy exposure over a range of climatic conditions, including wet leaves. Applying these insights for upscaling sap flow measurements to tropical stands and watersheds is necessary to improve global and regional climate modelling, forest management practices, and policy-making strategies for a more sustainable environment.

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