RESEARCH ARTICLE

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Dry-season decline in tree sapflux is correlated with leaf turgor loss point in a tropical rainforest

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Abstract

1. Water availability is a key determinant of forest ecosystem function and tree species distributions. While droughts are increasing in frequency in many ecosystems, including in the tropics, plant responses to water supply vary with species and drought intensity and are therefore difficult to model. Based on physiological first principles, we hypothesized that trees with a lower turgor loss point (π_{tlp}), that is, a more negative leaf water potential at wilting, would maintain water transport for longer into a dry season.

2. We measured sapflux density of 22 mature trees of 10 species during a dry season in an Amazonian rainforest, quantified sapflux decline as soil water content decreased and tested its relationship to tree π_{tlp}, size and leaf predawn and midday water potentials measured after the onset of the dry season.

3. The measured trees varied strongly in the response of water use to the seasonal drought, with sapflux at the end of the dry season ranging from 37 to 117% (on average 83 ± 5 %) of that at the beginning of the dry season. The decline of water transport as soil dried was correlated with tree π_{tlp} (Spearman's $\rho \geq 0.63$), but not with tree size or predawn and midday water potentials. Thus, trees with more drought-tolerant leaves better maintained water transport during the seasonal drought.

4. Our study provides an explicit correlation between a trait, measurable at the leaf level, and whole-plant performance under drying conditions. Physiological traits such as π_{tlp} can be used to assess and model higher scale processes in response to drying conditions.

KEYWORDS
drought tolerance, hydraulic conductance, sap flow, sapflux density, tropical trees, turgor loss point, water potential, wilting point

1 | INTRODUCTION

Variation in water availability is a key driver of forest ecosystem function (Granier et al., 2007) and tree species distributions (Esquivel-Muelbert et al., 2017). However, our knowledge of tree responses to changes in water supply and the diversity of these responses across species is still incomplete. This hampers our ability to make informed predictions, especially given the forecasted increase in rainfall variability and drought frequency under climate change (Duffy, Brando, Asner, & Field, 2015). This challenge is amplified in tropical forests, which shelter globally important stores of biodiversity (Jenkins, Pimm, & Joppa, 2013) and carbon (Saatchi et al., 2011), play a critical role in rainfall recycling through evapotranspiration (Eltahir & Bras, 1994) and appear to be vulnerable to drought (Choat et al., 2012). Although Amazonia is a carbon sink, carbon uptake by the vegetation has been affected by drought episodes that reduced tree growth and increased tree mortality (Brienen et al., 2015). These effects were stronger on tall trees and on some groups of species (Phillips et al., 2010), but models still fail to account for the magnitude and variability of these effects (Powell et al., 2013).

Plant responses to decreasing water availability result from a complex interplay of mechanisms operating across scales within the plant (Fatichi, Pappas, & Ivanov, 2016). As the soil dries, stomatal closure reduces sapflux and water loss from transpiration, preventing excessive negative pressure in the water column and impairment of the vascular system, but at the cost of reduced carbon assimilation (Jones & Sutherland, 1991). This cost-benefit scheme motivated a classification of plants as isohydric or anisohydric (Tardieu & Simonneau, 1998), a dichotomic categorization that has recently been criticized on conceptual grounds (Martínez-Vilalta & Garcia-Forner, 2017). In addition, this categorization has mainly been applied to ecosystems composed of few codominant species with contrasting strategies (e.g., piñon–juniper woodland; McDowell et al., 2008), but diverse communities shelter a continuum of responses to drying conditions (Klein, 2014) involving variation in mechanisms in addition to stomatal closure such as xylem resistance to cavitation, deep rooting, deciduousness or stem capacitance (Pivovaroff et al., 2016). The high taxonomic and functional diversity and the typical absence of species dominance in tropical forest communities call for a trait-based approach (Paine, Deasey, & Duthie, 2018). However, the quest for relevant and reliably measurable functional traits that quantify plant performance under drying conditions still remains a major challenge of trait-based plant functional ecology (Sack et al., 2016; Shipley et al., 2016).

It has been hypothesized that the leaf water potential at turgor loss point (henceforth denoted π_{tlp}, in MPa), also known as the wilting point, may be a good candidate (Bartlett, Scoffoni, & Sack, 2012; Hochberg, Rockwell, Holbrook, & Cochard, 2018). The π_{tlp} is the negative water potential at which the leaf wilts. The π_{tlp} also corresponds to the soil water potential below which the plant cannot take up sufficient water to recover overnight from wilting after a day of transpiration. The π_{tlp} has direct mechanistic significance, as one of the first plant responses under water stress is a reduction in turgor-driven cell expansion and division, and thus growth (Fatichi et al., 2016). Leaf

dehydration, reflected in turgor decrease, also largely contributes to stomatal closure (Brodribb, Holbrook, Edwards, & Gutiérrez, 2003; Rodriguez-Dominguez et al., 2016). Thus, π_{tlp} is correlated with diverse metrics of the stringency of stomatal control of leaf water potential (Martin-StPaul, Delzon, & Cochard, 2017; Meinzer et al., 2016).

Here, we test the hypothesis that π_{tlp} is informative of whole-tree hydraulic performance under seasonal drought. We monitored the sapflux density, an integrated measurement of whole-plant water use and transpiration (Bretfeld, Ewers, & Hall, 2018; Granier, Biron, Bréda, Pontailler, & Saugier, 1996), of 22 co-occurring mature trees of 10 species during a particularly harsh dry season in an Amazonian rainforest. On the same trees, we measured π_{tlp}, as well as leaf predawn and midday water potentials after the onset of the dry season (Ψ_{pd} and Ψ_{md}, in MPa), as proxies of water availability in the root zone and daily maximum hydric stress, respectively. We hypothesized that (a) trees with a more negative π_{tlp} would better sustain sapflux density through the dry season; (b) trees with less negative Ψ_{pd} have a better access to soil water and thus also better sustain sapflux density; and (c) larger trees are more sensitive to soil drought because of stronger hydraulic constraints and evaporative demand and thus would show a stronger decline in sapflux density.

2 | MATERIALS AND METHODS

2.1 | Study sites and sampling

Field measurements were conducted at the Nouragues Ecological Research Station in French Guiana. It is located 120 km south of Cayenne within an undisturbed forest (4°05′N, 52°40′W; Bongers, Charles-Dominique, Forget, & Thery, 2001). The site receives ca. 3,000 mm/year rainfall, with significant seasonal and interannual variation due to the movement of the Inter-Tropical Convergence Zone. A long dry season typically lasts from the end of August to the end of November with 2–3 months with precipitation <100 mm/month. Data were collected in three 1-ha permanent forest plots located on a small plateau with clay–sand soil (named Petit Plateau) and where all trees ≥ 10 cm diameter at breast height (dbh, in mm) were mapped, measured and identified. Twenty-two mature canopy trees of 10 species known to present contrasting leaf drought tolerance (Maréchaux et al., 2015) were sampled during the dry season of 2015 (Table 1).

2.2 | Environmental data

Micrometeorology was measured at the site every half-hour during the whole year using a micrometeorological station located in an open area. The station included instruments for the measurement of incoming irradiance (Hukseflux SR11, Delft, the Netherlands), temperature and relative humidity (Vaisala HMP155A, Vantaa, Finland), wind speed and direction (Young, Wind monitor 05,103, Traverse City, MI, USA) and rainfall (Campbell Scientific SBS500, Shepshed, Leicestershire, UK). Irradiance, temperature, relative humidity and wind speed all together influence transpiration rate (Bladon, Silins, Landhäusser, & Lieffers,

2006; Granier, Huc, & Barigah, 1996), and daily potential evapotranspiration (PET, in mm) was computed from these variables using the Penman–Monteith equation (Allen, Pereira, Raes, & Smith, 1998).

Soil water content was measured using a time-domain reflectometry probe (CS616, Campbell Scientific, Shepshed, Leicestershire, UK). Due to field constraints, these measurements were conducted close to the surface layer, at 20 cm soil depth, similarly to many previous studies of forest sites (e.g., Novick et al., 2016), where most of the root biomass occurs in the topsoil layer (Fisher et al., 2007; Humbel, 1978). Given that sampled trees were located within a small neighbourhood (imposed by cable lengths <30 m between sensors and data loggers, see below) on a flat plateau with homogeneous and well-drained soil (Bongers et al., 2001), we assumed soil water measurements were a good indicator of soil water availability (but see Jackson, Cavelier, Goldstein, Meinzer, & Holbrook, 1995; Meinzer et al., 1999). Soil water content data were averaged daily, and missing data were gap-filled based on look-up tables established on recorded values (Figure 1, $N = 54/365$ data points). They were then normalized to 1 at field capacity, estimated when excess water from abundant rain events has drained away, and zero at soil residual water content, computed from the site soil composition (Bongers et al., 2001; Marthews et al., 2014). This normalization defines the relative soil water content (RSWC; Meir et al., 2015).

2.3 | Sapflux density

For each tree, sapflux density was continuously measured from Julian Day 256 to Day 310 (except a few data gaps due to battery failure). Measurements were obtained with Granier-type sensors (UP GmbH Headquarters, Ibbenbüren, Germany). These sensors consisted of two probes (20-mm long × 2 mm in diameter) that were inserted radially into the outer xylem. Preliminary tests showed that xylem thickness of all selected trees was greater than 2 cm, and probes were thus in contact with active xylem only. The upper probe was heated, and the lower one (reference) was not. The two holes for the probes were drilled 15 cm apart into the trunk, *c.* 1.5 m above the ground. Sapflux density was inferred from the measured difference in temperature between the heated and the reference probe (Granier, 1987). The probes were covered with a large aluminium-coated sheet of plastic bubble wrap to minimize bias caused by the sun heating the trunk or by water throughfall. Heat flux density was logged every 30 s (CR1000 Datalogger, Campbell Scientific, Shepshed, Leicestershire, UK) and averaged every 30 min. The Granier method yields hourly sapflux density (f_s, in kg dm^{-2} hr^{-1}), which may be summed to define the daily sapflux density (D_s, in kg dm^{-2} day^{-1}). We used D_s to investigate seasonal variation in trunk water transport. We hence avoided potential time-lags among environmental variables, transpiration and sapflux measurements near the base of the trunk due to internal trunk water storage (Goldstein et al., 1998). This method does not account for sapflux in the inner sapwood, which represents a small fraction of the total daily sapflux (Jiménez, Nadezhdina, Čermák, & Morales, 2000; Lu, Müller, & Chacko, 2000). We did not attempt to correct for this potential bias, as our analyses do not aim to quantify absolute tree water use but only D_s variation throughout the season.

2.4 | Leaf water potentials

Leaf water potentials at predawn (Ψ_{pd}, in MPa), midday (Ψ_{md}, in MPa) and turgor loss point (π_{tlp}, in MPa) were measured on each tree at the beginning of the dry season (between calendar days 251 and 257; Figure 1). Top canopy branches were collected by climbing the trees using the single-rope technique (Anderson, Koomjian, French, Altenhoff, & Luce, 2015). Ψ_{pd} and Ψ_{md} were measured on one to three leaves per tree with a Scholander-type pressure chamber (model 1,000, PMS Instruments, Corvallis, OR, USA, Sack et al., 2010) right after sampling and within 5 min of leaf excision, between 5:30 am and 7:00 am and between 11:30 am and 1:00 pm, respectively. In the analyses, Ψ_{pd} was used as an estimate of maximum leaf water potential at the beginning of the dry season. The Ψ_{pd} is often interpreted as an estimate of water availability in the root zone at measurement time on the basis that plant and soil water potentials equilibrate overnight (Stahl, Herault, et al., 2013), although some uncertainty can arise due to disequilibria (Bucci et al., 2004; Donovan, Richards, & Linton, 2003).

π_{tlp} was measured using a rapid method of determination based on a well-established correlation of π_{tlp} with the leaf osmotic potential at full hydration (Bartlett, Scoffoni, Ardy, et al., 2012) which is measurable with an osmometer (Vapro 5,520, Wescor, Logan, UT). This method was further validated on tropical tree species at our site (Maréchaux, Bartlett, Gaucher, Sack, & Chave, 2016). A detailed protocol of the method is provided elsewhere (Bartlett, Scoffoni, Ardy, et al., 2012). π_{tlp} values for individuals of the genus *Qualea* (Vochysiaceae; species *Qualea rosea* Aubl. and *Qualea c.f. tricolor*) were not used, as their dense network of leaf secondary veins can bias the method (Maréchaux et al., 2016); this venation type occurs for fewer than 2% of tree species in Guianese forests (Engel, Brousseau, & Baraloto, 2016).

2.5 | Data analysis

For each tree, we tested the sensitivity of daily sapflux density (D_s) to changes in potential evapotranspiration and soil water supply. We first fitted a multiple regression model with daily sapflux density (D_s) as the dependent variable and daily potential evapotranspiration (PET) and relative soil water content (RSWC) as independent variables:

$$D_S = \beta_0 + \beta_E \times PET + \beta_S \times RSWC + \varepsilon \qquad (1)$$

where β_0 is the intercept, β_E and β_S are the regression coefficients for PET and RSWC, respectively, and ε is the error term assuming a normal distribution. While PET and soil moisture are typically correlated at seasonal and monthly time-scales, they were decoupled at daily time-scales (Pearson's $r = 0.03$; $p = 0.84$; see also Grossiord et al., 2018; Novick et al., 2016). Testing a model including an interaction term between PET and RSWC showed this term was not significant for any of the trees, and therefore, this term was not included in (1). We used PET rather than vapour pressure deficit (e.g., Grossiord et al., 2018; Novick et al., 2016; Oren et al., 1999), as PET is a better proxy of the above-ground environmental influence on transpiration. In

TABLE 1 Characteristics of the 22 sampled trees and quantification of the sensitivity of their whole-plant water use to soil water supply and potential evapotranspiration during the dry season

Species	Tree code	Leaf fall	dbh (mm)	π_{tlp} (MPa)	Ψ_{pd} (MPa)	Ψ_{md} (MPa)	$D_{s,begin}$ (kg dm^{-2} day^{-1})	$D_{s,end}$ (kg dm^{-2} day^{-1})	R^2	R_S	β_S (kg dm^{-2} day^{-1})	Φ_S	R_E	β_E
Dicorynia guianensis	DG1	N	460	-1.53	–	-2.7	14.2	8.8	**0.80**	0.72 [0.52, 0.87]	28.27 [20.76, 33.95]	0.62	0.11 [0.04, 0.24]	0.66 [0.43, 0.95]
D. guianensis	DG2	N	622	-1.62	-0.30	-1.85	13.6	7.6	**0.74**	0.71 [0.51, 0.84]	33.87 [24.63, 41.94]	0.55	0.05 [0.01, 0.14]	0.51 [0.21, 0.91]
D. guianensis	DG3	N	661	-1.60	-0.35	-1.7	11.8	9.3	**0.59**	0.32 [0.11, 0.56]	11.01 [5.22, 15.37]	0.79	0.30 [0.10, 0.56]	0.62 [0.39, 0.84]
D. guianensis	DG4	Y	598	-1.70	-0.05	-1.55	–	10.7	–	–	–	–	–	–
D. guianensis	DG5	Y	761	-1.60	-0.25	-1.5	11.4	7.9	–	–	–	0.69	–	–
Vouacapoua americana	VA1	Y	662	-2.19	-0.2	-0.8	11.7	11.8	–	–	–	1.00	–	–
Qualea rosea	QR1	N	232	–	-0.15	-1.6	8.5	9.9	**0.53**	0.10 [0.00, 0.26]	-5.49 [-8.61, -1.75]	1.17	0.47 [0.22, 0.74]	0.63 [0.38, 0.82]
Q. rosea	QR2	N	636	–	-0.3	-1.7	11.1	4.2	**0.85**	0.84 [0.69, 0.94]	33.64 [25.65, 39.93]	0.37	0.03 [0.00, 0.09]	0.36 [0.11, 0.62]
Q. rosea	QR3	N	515	–	-0.45	-1.1	3.4	3.9	**0.55**	0.06 [0.00, 0.22]	-1.34 [-2.39, 0.02]	1.14	0.45 [0.21, 0.71]	0.21 [0.14, 0.28]
Qualea c.f. tricolor	QT1	N	715	-1.66	-0.15	-0.8	6.4	5.1	**0.70**	0.32 [0.15, 0.51]	5.67 [3.84, 7.40]	0.80	0.31 [0.16, 0.54]	0.30 [0.20, 0.39]
Q. c.f. tricolor	QT2	N	907	-1.81	-0.4	-1.95	8.5	8.5	0.07	0.00 [0.00, 0.00]	0.23 [-4.59, 4.74]	1.00	0.07 [0.00, 0.25]	0.19 [-0.04, 0.36]
Licania alba	LA1	N	417	-1.92	-0.2	-1.75	6.9	6.4	**0.54**	0.08 [0.01, 0.22]	2.78 [0.79, 4.81]	0.93	0.49 [0.29, 0.72]	0.40 [0.28, 0.51]
L. alba	LA2	N	326	-2.00	-0.25	-2.0	4.4	4.1	**0.42**	0.05 [0.00, 0.19]	1.78 [-0.12, 3.84]	0.95	0.39 [0.15, 0.60]	0.29 [0.18, 0.38]
L. alba	LA3	N	390	-1.91	-0.15	-1.95	9.7	8.0	**0.53**	0.15 [0.05, 0.33]	8.08 [3.72, 13.01]	0.82	0.33 [0.13, 0.58]	0.63 [0.37, 0.81]
Licania rodriguesii	LR1	N	530	-2.01	-0.2	-1.75	10.3	9.8	**0.24**	0.04 [0.00, 0.24]	2.61 [-0.48, 6.58]	0.95	0.22 [0.04, 0.43]	0.35 [0.13, 0.50]
Lecythis poiteaui	LP1	N	414	-2.93	-0.45	-2.9	10.5	10.6	**0.43**	0.00 [0.00, 0.00]	-0.07 [-3.54, 3.76]	1.01	0.43 [0.16, 0.70]	0.52 [0.30, 0.69]
L. poiteaui	LP2	Y	657	-2.54	-0.65	-3.2	3.1	1.2	**0.74**	–	–	0.39	–	–
Eschweilera coriacea	EC1	N	337	-1.61	-0.2	-1.5	6.3	5.9	**0.46**	0.08 [0.00, 0.22]	3.06 [0.53, 5.47]	0.93	0.34 [0.10, 0.59]	0.34 [0.19, 0.46]
E. coriacea	EC2	N	283	-1.59	-0.25	-1.55	7.1	5.7	**0.61**	0.31 [0.13, 0.51]	6.96 [3.91, 9.53]	0.80	0.24 [0.06, 0.48]	0.33 [0.15, 0.44]
E. coriacea	EC3	N	353	-1.80	-0.25	-1.8	5.3	4.6	**0.57**	0.22 [0.06, 0.41]	3.40 [1.63, 4.76]	0.87	0.30 [0.07, 0.58]	0.21 [0.10, 0.29]
Goupia glabra	GG1	N	351	-2.06	-0.2	-0.65	4.1	3.4	**0.41**	0.22 [0.05, 0.43]	3.36 [1.25, 5.08]	0.82	0.16 [0.03, 0.33]	0.15 [0.06, 0.21]
Sextonia rubra	SR1	N	859	-1.61	-0.4	-1.1	2.9	2.6	0.11	0.09 [0.00, 0.31]	1.85 [0.01, 3.61]	0.91	0.02 [0.00, 0.14]	0.06 [-0.03, 0.13]

Note. Leaf fall: indicates if the tree shed most of its leaves during the sampling period (binary trait Y/N); dbh: diameter at breast height (in mm); π_{tlp}: leaf water potential at turgor loss point (in MPa); Ψ_{pd} and Ψ_{md}: predawn and midday leaf water potential (in MPa) measured at the beginning of the dry season; R^2: coefficient of determination of the multiple regression with D_s as dependent variable and PET and RSWC as independent variables (1); values in bold indicate significant regressions ($p < 0.05$); $D_{s,begin}$ and $D_{s,end}$: daily sapflux density (in kg dm^{-2} day^{-1}) averaged across the first 10 days and the last 10 days of the sampling period (respectively, calendar days 256 to 265 and 301 to 310). The sensitivity of tree water transport to decreasing soil water content was quantified using three metrics for each tree: R_S, proportion of variance explained by RSWC in (1); β_S: coefficient of RSWC in (1); and Φ_S: ratio between $D_{s,end}$ and $D_{s,begin}$. The sensitivity of tree water transport to atmospheric demand was quantified using two metrics for each tree: R_E, proportion of variance explained by PET in (1); β_E: coefficient of PET in (1). Values in brackets are 95% confidence intervals calculated via bootstrapping. For trees that shed most of their leaves during the period, not all metrics could have been computed. π_{tlp} values are not reported for *Qualea* species because the method of determination is not robust for this genus (Maréchaux et al., 2016).

addition to humidity, PET accounts for the role of radiation and wind, which are known to have strong effects in tropical rainforests that are often light-limited (Wagner et al., 2016) and somewhat decoupled from the atmosphere (De Kauwe, Medlyn, Knauer, & Williams, 2017).

Equation (1) allowed us to partition the variance in tree sapflux density due to potential evapotranspiration and soil water supply (Bretfeld et al., 2018). We implemented variance partitioning using a commonality analysis (Ray-Mukherjee et al., 2014). This analysis quantifies the variance in D_s that is independently accounted for by PET (R_E) or by RSWC (R_S). Hence, R_E and R_S represent the relative strengths of atmospheric drivers (potential evapotranspiration, PET) and soil water supply (relative soil water content, RSWC) in controlling tree water transport, and β_E and β_S represent the absolute magnitudes of their effects, respectively, and independently of each other. Ninety-five per cent confidence intervals for β_E, β_S, R_E and R_S were calculated via bootstrapping (1,000 runs; *boot* package, Canty & Ripley, 2015; Davison & Hinkley, 1995).

For each tree, we also computed the average D_s across the first 10 days of measurements (days 256 to 265, $D_{s,begin}$) and the last 10 days (days 301 to 310, $D_{s,end}$). We defined Φ_S as the ratio between $D_{s,end}$ and $D_{s,begin}$ for each tree. Given the decreasing trend in RSWC during our sampling period (Figure 1), a lower Φ_S, as well as a higher R_S and a higher β_S, quantifies a higher sensitivity of water transport as soil water content decreases. Likewise, a higher R_E and a higher β_E quantify a stronger control and higher sensitivity of tree water transport to the atmospheric demand. We used Pearson's correlation to test the consistency among the three metrics of sensitivity to soil water supply (Φ_S, R_S and β_S) on the one hand and between the two metrics of sensitivity to atmospheric demand (R_E, β_E) on the other hand.

We also tested whether R_S, β_S and Φ_S, as well as R_E, β_E, covaried with dbh, π_{tlp}, and Ψ_{pd} and Ψ_{md} at the beginning of the dry season across trees using nonparametric Spearman's tests given the clear nonlinearity of some relationships. When these tests were significant, we also fitted linear or nonlinear regressions on log-transformed values. To do so, π_{tlp} was multiplied by −1, and β_S was incremented by 1, in order to produce positive values.

All analyses were made at the individual tree level, at which performance and traits were measured, recognizing that both intra- and interspecific trait variation shape communities through variation in individual performance (Bolnick et al., 2011). All statistical analyses were conducted using the R software (R Core Team, 2013) and were preceded by normality and homoscedasticity tests when required (*car* package; Fox & Weisberg, 2011).

3 | RESULTS

3.1 | Contrasting sapflux densities among trees during the dry season

During the duration of sapflux data collection (55 days), total cumulative rainfall reached 50.5 mm (Figure 1a), arising from 16 days of rain, each with less than 10 mm. Soil water content showed a clear decrease during this period, relative to the soil saturation and water

percolation typical of the rest of the year (Figure 1b). Soil water depletion was further evidenced by the decrease in sapflux density for some trees (see Supporting Information Figure S1).

The sampled trees showed contrasting daily sapflux densities, with a range of 2.9 to 14.2 kg dm^{-2} day^{-1} at the beginning ($D_{s,begin}$) and of 1.2 to 11.8 kg dm^{-2} day^{-1} at the end ($D_{s,end}$; Table 1, Figure 2; both coefficients of variation across trees equal 43%). Φ_S, the sapflux density at the end of the session divided by that at the beginning, varied between 0.37 and 1.17, with an average of 0.83 across trees (Table 1, Figures 2 and 3).

Four of the 22 sampled trees shed most of their leaves once during the sampling period, that is, two *Dicorynia guianensis* Amshoff (Fabaceae) trees, one *Lecythis poiteaui* O.Berg (Lecythidaceae) and one *Vouacapoua americana* Aubl. (Fabaceae) (Table 1). These trees' sapflux density declined quickly towards zero and then rose again when new leaves flushed (Figure 3). All other trees maintained most or a significant fraction of their leaf area during the study period, and the four individuals that shed their leaves were removed from subsequent analyses. Notably, in our sample, some trees of the same species shed their leaves while others did not. Deciduousness was unrelated to π_{tlp} values in our dataset (Table 1).

During the sampling period, the variation in tree daily sapflux density (D_s) was well described by the model with PET and RSWC for most but not all trees ($p < 0.05$ for 16 of 18 trees), with model coefficient of determination ranging from 0.07 to 0.85 across sampled trees (Table 1). The variance in D_s explained by PET alone (R_E) varied from 2% to 49% across trees (on average 26 ± 4 *SE*), while that explained by RSWC alone (R_S) varied from 0% to 84% (on average 24 ± 6 *SE*). The magnitude of the effect of PET on D_s (β_E) varied from 0.06 to 0.66 kg dm^{-2} day^{-1} mm^{-1} across trees (on average 0.38 ± 0.04 *SE*), while that of RSWC (β_S) varied from −5.5 to 33.9 kg dm^{-2} day^{-1} (on average 7.8 ± 2.8 *SE*). The few negative β_S values, or their corresponding R_S, were not significantly different from 0 (i.e., their confidence interval included 0).

3.2 | Determinants of sapflux sensitivity to drying conditions

The π_{tlp} ranged from −1.53 to −2.93 MPa across trees, Ψ_{pd} ranged from −0.15 to −0.45 MPa, and Ψ_{md} ranged from −0.65 to −2.9 MPa. Pairwise correlations between π_{tlp}, dbh, Ψ_{pd} and Ψ_{md} were not significant (Spearman's tests, all $p > 0.43$). The three metrics of sensitivity of sapflux to soil water content (RSWC), R_S, β_S and Φ_S, were tightly intercorrelated (all $p < 10^{-6}$, $|r| > 0.95$), but the two metrics of sapflux sensitivity to potential evapotranspiration (PET), R_E and β_E, were not ($p = 0.31$). R_E was negatively correlated with R_S and β_S and positively to Φ_S (all $p \leq 0.01$, $r = −0.57$, $−0.61$ and 0.66 for $R_E \sim R_S$, $R_E \sim \beta_S$ and $R_E \sim \Phi_S$, respectively), but β_E was not related to any of the three metrics of sapflux sensitivity to soil water supply (all $p \geq 0.16$).

R_S, β_S and Φ_S were all correlated with tree π_{tlp} (Figure 4 and summary statistics therein). By contrast, R_E and β_E were statistically independent of π_{tlp} (both $p > 0.22$). These results were qualitatively unchanged after removing the individual with the most negative π_{tlp} (LP1 in Table 1), which belongs to one of the most drought-tolerant species at our site
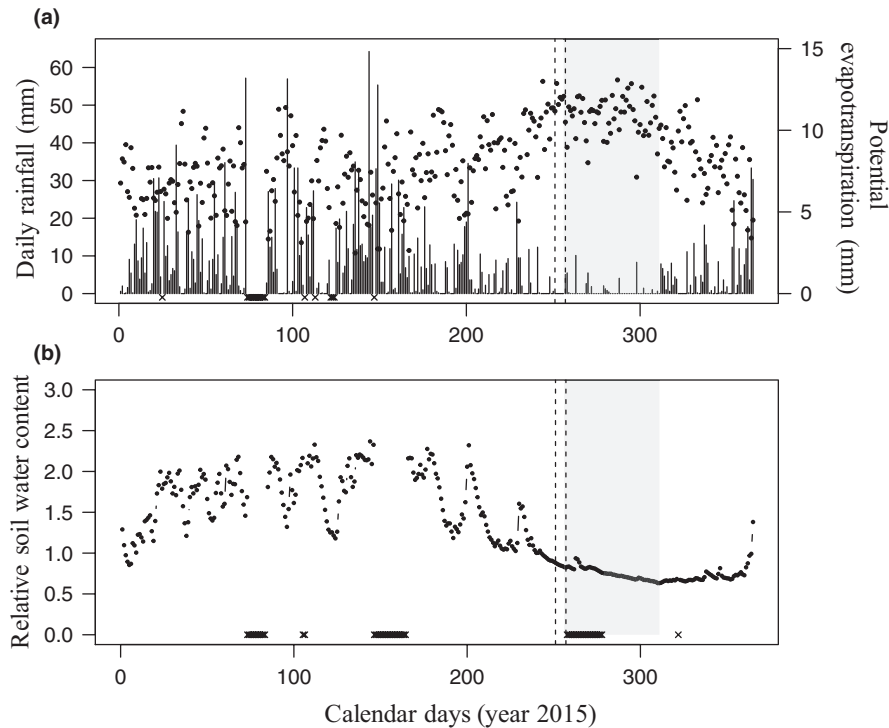
FIGURE 1 Variation in (a) daily rainfall (in mm, bars, left axis) and potential evapotranspiration (in mm, points, right axis) and (b) daily averaged relative soil water content for 2015. Dotted black lines: period during which leaf water potentials were measured; shaded grey band: period during which sapflux density was continuously measured and half-hourly logged. Daily averaged soil water content was computed from a time-domain reflectometry probe set at 20 cm depth and normalized to one at field capacity, estimated when excess water from abundant rain events has drained away, and zero at soil residual water content, computed from the site soil composition. Black crosses: gap-filled values during the sampling period

(Maréchaux et al., 2015). R_S, β_S and Φ_S were not correlated with tree Ψ_{pd} or Ψ_{md} or dbh (all $p > 0.29$). R_E was not related to Ψ_{pd} or Ψ_{md} ($p > 0.30$), but was negatively correlated with tree dbh (Figure 5a). β_E was not related to Ψ_{pd} or dbh, but was negatively related to Ψ_{md} (Figure 5b).

4 | DISCUSSION

As expected, trees studied at our site exhibited a large range of hydraulic responses under decreasing soil water content (RSWC). At another

site in French Guiana, Stahl, Burban, et al. (2013) found that gas exchange and transpiration decreased strongly with RSWC for some but not all trees, in agreement with the present findings. Across the studied trees, π_{tlp} correlated with the sensitivity of sapflux to RSWC, but not to atmospheric demand, which did not decline consistently during the dry season as RSWC did. Thus, trees with more drought-tolerant leaves, as indicated by a more negative π_{tlp}, better sustained plant water transport as the soil dried throughout the dry season.

Our study hence demonstrates the potential for a leaf-level trait to be used to quantify changes in whole-plant water
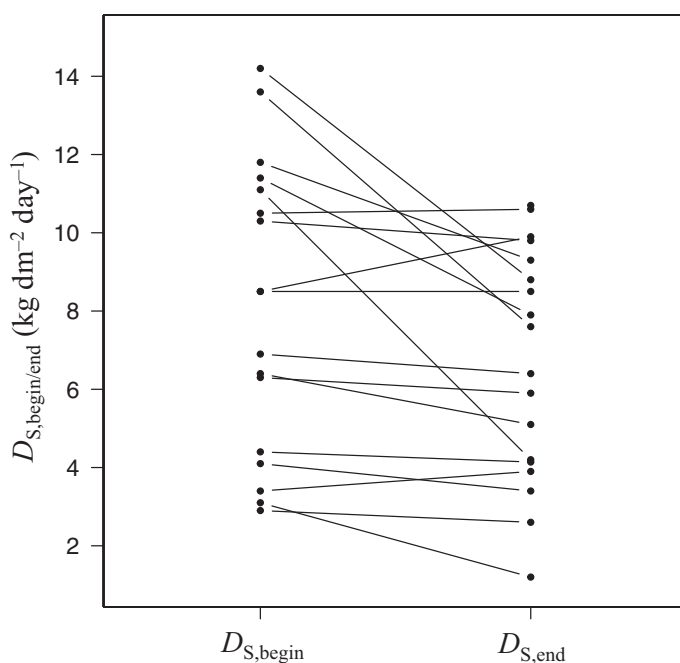

FIGURE 2 Average D_s across the first 10 days of measurements (days 256 to 265, $D_{s,begin}$) and the last 10 days (days 301 to 310, $D_{s,end}$) for the 22 sampled individuals. Lines show the change from $D_{s,begin}$ to $D_{s,end}$ for each 0 tree
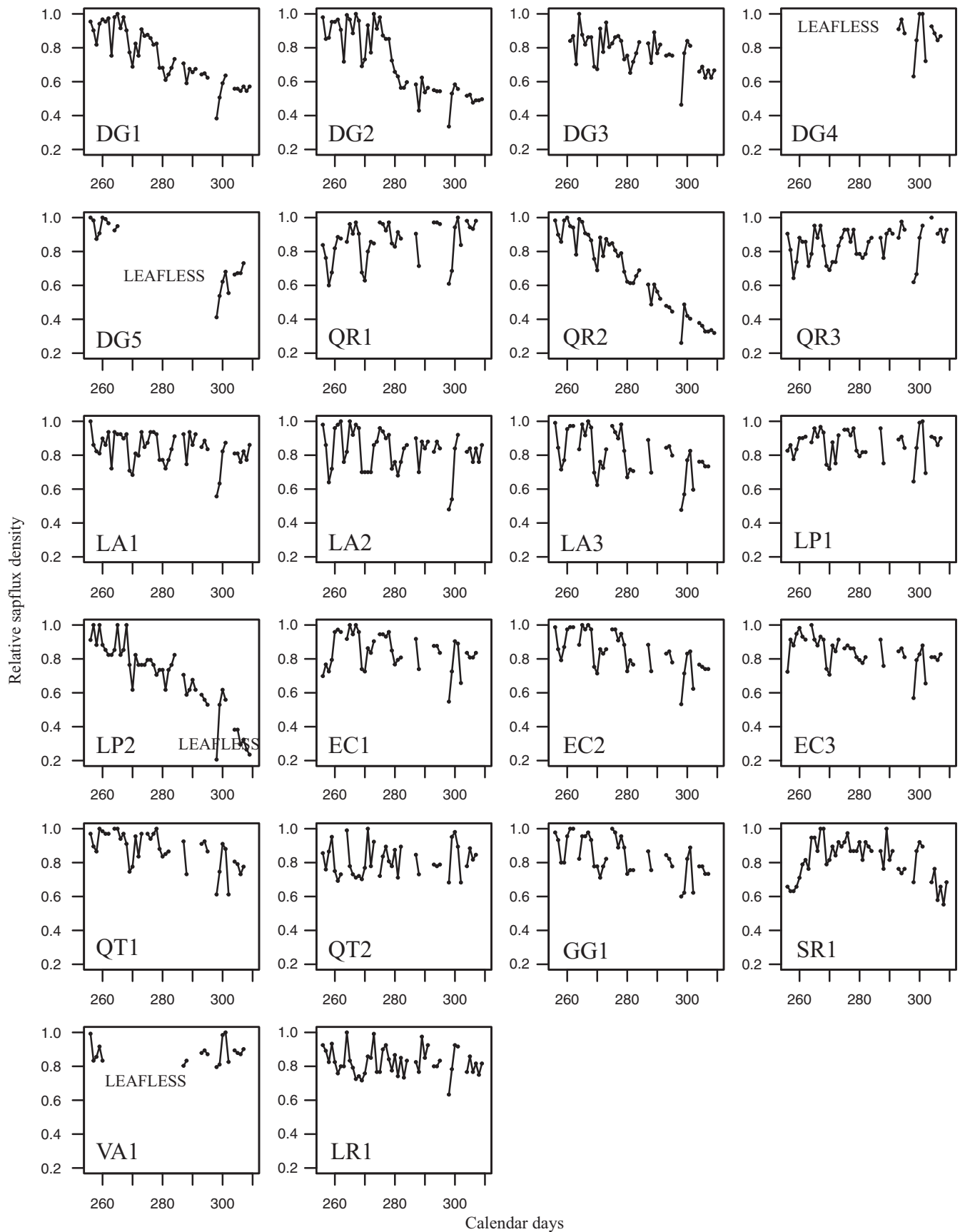
FIGURE 3 Variation in relative daily sapflux density for the 22 sampled individuals. For each tree, daily sapflux density (D_s, in kg dm^{-2} day^{-1}) is given relative to its maximum during the sampling period. See Table 1 for tree codes
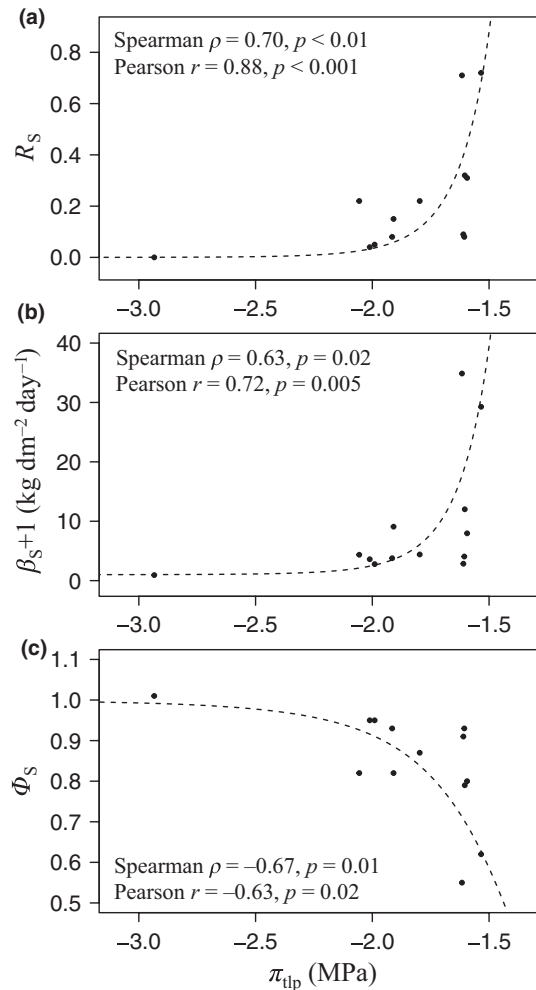
(a) Spearman $\rho = 0.70$, $p < 0.01$
Pearson $r = 0.88$, $p < 0.001$

(b) Spearman $\rho = 0.63$, $p = 0.02$
Pearson $r = 0.72$, $p = 0.005$

(c) Spearman $\rho = -0.67$, $p = 0.01$
Pearson $r = -0.63$, $p = 0.02$

FIGURE 4 Correlation between the sensitivity of tree sapflux density to decreasing soil water content as quantified by three alternatives metrics [(a): R_S, (b): β_S and (c): Φ_S] and tree leaf water potential at turgor loss point (π_{tlp}, in MPa). R_S and β_S were quantified for each tree as the proportion of variance explained by RSWC and the coefficient of RSWC in the multiple regression with D_s as dependent variable and PET and RSWC as independent variables. Φ_S was defined for each tree as the ratio between the daily sapflux density averaged across the last 10 days of the sampling period ($D_{s,end}$) and the one averaged across the first 10 days of the sampling period ($D_{s,begin}$). A higher R_S, a higher β_S and a lower Φ_S quantify a higher sensitivity of water transport as soil water content decreases. Dashed lines correspond to the nonlinear curves fitted on log-transformed data. Note that to do so, π_{tlp} was multiplied by −1, and β_S was incremented by 1, in order to produce positive values. These results were qualitatively unchanged after removing the individual with the most negative π_{tlp} (LP1 in Table 1; Spearman's tests: respectively, $p = 0.03$ and $\rho = 0.62$; $p = 0.08$ and $\rho = 0.53$; $p = 0.05$ and $\rho = -0.58$)

transport under soil drying conditions. Such linkages between rapidly measured traits and whole-plant performance are a fundamental requirement of trait-based plant functional ecology that has remained challenging (Shipley et al., 2016), particularly so for water use and drought tolerance traits, given the multiple mechanisms underlying these processes (Sack et al., 2016).

We therefore suggest that the measurement of π_{tlp} is informative of the responses of plant water use, and hence potentially growth and whole-plant performance, during dry seasons (Mart, Veneklaas, & Bramley, 2016). Some of the trees shed their leaves, in species already known to be semi-deciduous (Loubry, 1994). However, at our study site, deciduousness was not directly related to leaf drought tolerance as indicated by π_{tlp}, in contrast with drier tropical forests (Sobrado, 1986; Xu, Medvigy, Powers, Becknell, & Guan, 2016), suggesting these adaptive strategies may respond to different constraints in rainforests as found elsewhere (Wright & van Schaik, 1994; Wu et al., 2016). This also suggests a particular relevance for π_{tlp} in largely evergreen systems in which leaves tend to be retained during the dry season.

Our results extend to the whole plant scale the previously recognized linkage between π_{tlp} and stomatal closure (Bartlett, Klein, Jansen, Choat, & Sack, 2016; Brodribb et al., 2003; Martin-StPaul et al., 2017). In addition, recent studies have reported that π_{tlp} was correlated with lethal water potentials and could therefore be useful to predict the vulnerability of trees to major drought events (Bartlett et al., 2016; Powell et al., 2017). π_{tlp} has also been found to inform species distributions relative to water supply within and across biomes (Baltzer, Davies, Bunyavejchewin, & Noor, 2008; Bartlett, Scoffoni, & Sack, 2012) and community assemblages (Bartlett et al., 2015), both of which have proven challenging to model in the tropics. Overall, this recent research substantiates the proposal that π_{tlp} may be used to quickly quantify the integrated whole-plant response to drying conditions, as previously demonstrated for saplings in glasshouse conditions based on leaf-level measurements (Meinzer et al., 2017, 2016), and here evidenced on mature trees in field conditions through sapflux measurements. Our study suggests the possibility of a causative relationship between leaf drought tolerance and sapflux density responses to soil drying. This hypothesis requires further testing through more in-depth measurements of soil water content and leaf water potentials on a larger number of trees, which remained here limited due to field constraints at our remote site. A recent global sapflux database initiative (Poyatos et al., 2016) constitutes a great opportunity to further test this idea on a larger range of plant drought tolerance, sites and drought intensity.

In contrast to π_{tlp}, leaf predawn water potential Ψ_{pd}, a putative proxy for root water availability, did not correlate with sapflux sensitivity to RSWC. One explanation may be that our sampling of Ψ_{pd} after the onset of the dry season was limited to a period when water stress was not very strong, and water availability was likely homogeneous across the range of root depths. The range of Ψ_{pd} across trees was actually similar or even greater than the range typically observed during dry seasons in tropical forest sites with similar rainfall (e.g., Bretfeld et al., 2018; Santiago et al., 2018). However, it remained relatively small and probably not sufficient to reveal the contrasting abilities of root systems to allow prolonged access to soil water during stronger droughts, as found elsewhere (Jackson et al., 1995; Meinzer et al., 1999; Stahl, Burban, et al., 2013; Stahl,
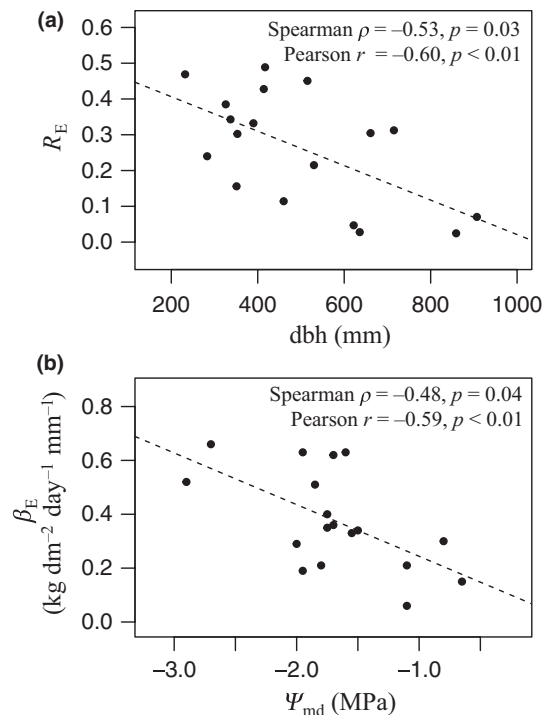
FIGURE 5 Correlation between the sensitivity of tree sapflux density to changes in atmospheric demand as quantified by two alternatives metrics [(a): R_E, (b): β_E] and tree diameter at breast height (dbh, in mm) and leaf water potential at midday (Ψ_{md}, in MPa), respectively. R_E and β_E were quantified for each tree as the proportion of variance explained by PET and the coefficient of PET in the multiple regression with D_s as dependent variable and PET and RSWC as independent variables. A higher R_E and a higher β_E quantify a higher sensitivity of water transport to changes in atmospheric demand. Dashed lines correspond to the fitted linear curves

Herault, et al., 2013). Another explanation may be that Ψ_{pd} values did not capture the actual differences in water availability in the root zone across trees due to predawn disequilibria, for example caused by night-time transpiration or slow equilibration of tissues (Bucci et al., 2004; Donovan et al., 2003), although high night-time air humidity typically prevents such disequilibria in tropical forests (Stahl, Herault, et al., 2013).

Large trees have been reported to be more vulnerable to intense droughts (Bennett, McDowell, Allen, & Anderson-Teixeira, 2015; Phillips et al., 2010), which may result from stronger evaporative demand and higher xylem vulnerability to cavitation (Rowland et al., 2015). However, tree size, as inferred from the diameter at breast height (dbh), was not correlated with π_{tlp} or with Ψ_{pd} or Ψ_{md} after the onset of the dry season at our site. This finding is in agreement with previous reports at our site or nearby (Maréchaux et al., 2016; Stahl, Herault, et al., 2013). In our study, large trees did not show greater sensitivity of sap flow to the decrease in soil water supply, and their sap flow was less tightly controlled by day-to-day variation in atmospheric demand during a regular dry season, as compared with smaller trees. This may be due to higher capacitance in large trees that may buffer water transport fluctuations over short time-scales

during a seasonal drought (Scholz, Phillips, Bucci, Meinzer, & Goldstein, 2011), although such a buffering mechanism may not be sufficient to mitigate the harsher hydraulic constraints on taller trees under more severe droughts (Meakem et al., 2017). Contrary to tree size, more negative midday leaf water potential (Ψ_{md}) was a direct measure of stronger leaf water stress after the onset of the dry season and was associated with a greater effect of above-ground environment on water flux during the dry season.

Our finding that the leaf-level hydraulic trait, π_{tlp}, influences whole-plant functioning is in line with a body of evidence of hydraulic coordination among the different plant organs (Meinzer et al., 2008; Nolf et al., 2015). Measurement of π_{tlp} is much easier than other drought tolerance traits in tropical forests. By comparison, the xylem water potential at 50% loss of xylem conductivity (P_{50}, in MPa), which quantifies xylem vulnerability to cavitation, has been particularly challenging to measure on tropical tree species, as the sapwood of tropical trees often has long vessels that induce measurement artefacts (Cochard et al., 2013). Beyond stomatal closure, resistance to cavitation is thought to be a key feature for survival to intense droughts (Anderegg et al., 2016; Martin-StPaul et al., 2017), but these methodological issues have tainted measurements over the past decades, and a global compilation of P_{50} values worldwide did not contain a single Amazonian tree species (Choat et al., 2012). Two global meta-analyses reported a weak correlation between π_{tlp} and P_{50}, with π_{tlp} being less negative than P_{50} (Bartlett et al., 2016; Martin-StPaul et al., 2017), in agreement with our findings of π_{tlp} being informative of seasonal sapflux decrease. Better documenting P_{50} variability for tropical rainforest species using robust methods of measurements, as well as its coordination with root and leaf drought tolerance, is an important challenge considering the climatic threats to rainforests.

Our finding that a leaf-level trait predicts the response of plant water transport under decreasing soil water availability opens useful avenues for vegetation modelling approaches. Soil water availability is an important climatic driver of tree growth variability, even in rainforest ecosystems (Wagner, Rossi, Stahl, Bonal, & Hérault, 2012), but species responses have been poorly predicted by commonly measured traits (Wagner et al., 2014). This suggests that further trait-based exploration of the determinants of tree growth variability should include physiological traits such as π_{tlp} (Paine et al., 2018). As growth is turgor-mediated (Muller et al., 2011), this new perspective could help shift models from carbon source-driven to sink-driven plant modelling approaches (Fatichi, Leuzinger, & Körner, 2014).

Dynamic vegetation models often simulate the effects of soil water shortage on plant functioning by lowering leaf gas exchange rates using a multiplicative soil-dependent water stress factor (e.g., Clark et al., 2011). This approach has yielded unrealistic vegetation responses to drought (Powell et al., 2013). Among other things, it overlooks the fact that plant responses depend on plant drought tolerance (Verhoef & Egea, 2014), which varies widely across and within plant functional types. Our measures of sensitivity of plant water transport to increasing soil drought integrate plant responses across organs, similar to the model

water stress factor. One important potential application of our findings is the use of π_{tlp} to parameterize water stress functions within models, thus integrating the diversity of plant responses to drought according to well-defined concepts of plant hydraulics (Christoffersen et al., 2016; Drake et al., 2017; Hochberg et al., 2018; Xu et al., 2016).

AUTHORS' CONTRIBUTIONS

I.M., D.B., and J.C. planned and designed the research; I.M., D.B., M.K.B., B.B., S.C., E.A.C., J.-Y.G., E.M., A.M. and J.C. collected the data; E.M., and M.D. contributed to data compilation; I.M. analysed the data with support from D.B.; I.M. wrote the manuscript with contributions from D.B., M.K.B., S.C., E.A.C., L.S., C.S. and J.C.; and all authors gave final approval for publication.

DATA ACCESSIBILITY

The trait dataset used in this study is provided in Table 1. Sapflux and climate dataset deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.jm1jf49 (Maréchaux et al., 2018). Sapflux data will also be available as part of the SAPFLUXNET database after the embargo period (Poyatos et al., 2016).

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