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Soil moisture thresholds explain a shift from light-limited to water-limited sap velocity in the Central Amazon during the 2015-16 El Niño drought

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Abstract

Transpiration is often considered to be light- but not water-limited in humid tropical rainforests due to abundant soil water, even during the dry seasons. The record-breaking 2015-16 El Niño drought provided a unique opportunity to examine whether transpiration is constrained by water under severe lack of rainfall. We measured sap velocity, soil water content, and meteorological variables in an old-growth upland forest in the Central Amazon throughout the 2015-16 drought. We found a rapid decline in sap velocity (-38% ± 21%, mean ± SD.) and in its temporal variability (-88%) during the drought compared to the wet season. Such changes were accompanied by a marked decline in soil moisture and an increase in temperature and vapor pressure deficit. Sap velocity was largely limited by net radiation during the wet season; however, it shifted to be primarily limited by soil moisture during the drought. The threshold in which sap velocity became dominated by soil moisture was at 0.33 m^3/m^3 (around -150 kPa in soil matric potential), below which sap velocity dropped steeply. Our study provides evidence for a soil water threshold on transpiration in a moist tropical forest, suggesting a shift from light limitation to water limitation under future climate characterized by increased temperature and an increased frequency, intensity, duration and extent of extreme drought events.

Keywords: Drought, tropical forests, water cycle, soil moisture, evapotranspiration

1. Introduction

Transpiration in tropical forests plays a critical role in regulating the global water cycle and climate (Chambers and Artaxo, 2017). Changes in forest transpiration have critical implications for biosphere-atmosphere interactions at the local, regional, and global scales, influencing water and carbon budgets as well as surface temperature (Fisher et al., 2008; Wright et al., 2017; Grossiord et al., 2020; Li et al., 2016). The Sixth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) showed robust projected increases in drought duration and frequency with less rainfall and drying soil in the tropics (Arias, Paola, et al. 2021; Vogel et al., 2020). A warmer and drier climate has already led to a series of impacts on tropical forest ecosystems (Nepstad et al., 2002; McDowell et al., 2018). Transpiration underlies the physiological responses of plants to drought, with warmer and drier conditions leading to constraints on water uptake and subsequent downstream limitations on carbon uptake (Liu et al., 2020). Understanding the physiological and ecological processes of tropical forests in response to a more extreme environment is crucial to improve model predictions of the structure and function of moist tropical forests under climate change (Ahlström et al., 2017; Gatti et al., 2014).

Transpiration is often limited by light availability in moist tropical forests (Roberts et al., 1993; Shuttleworth, 1988; Von Randow et al., 2004; Meir et al., 2015; Nepstad et al., 2007; da Costa et al., 2010) with moderation by drought (Grossiord et al. 2019). Deep soil water may remain relatively abundant during dry seasons through rainfall recharge and via water redistribution (e.g., by hydraulic lift; Lee et al., 2005; Oliveira et al., 2005). Thus soil moisture storage in the rooting zone can be sufficient to maintain transpiration during the dry season (Juárez et al., 2007; Wu et al., 2017; Yang et al., 2018). Soils have significant water storage capacity, and thus soil moisture responses to drought can take several weeks to months after the dry periods —a phenomenon called soil moisture memory (Da Rocha et al., 2009; Shuttleworth, 1988). Tropical evergreen forests can progressively exploit water in the deeper layers of the soil during the dry season when the shallow soil dries (Nepstad et al., 1994). Therefore, transpiration in moist tropical forests is considered relatively insensitive to dry periods relative to the global average.

As the climate becomes warmer and drier, it is more likely that a threshold could be reached after which soil moisture, instead of light availability, becomes a primary regulator of transpiration. In

2015–16, an unprecedented warm-phase El Niño drought occurred across the Amazon, providing an opportunity to examine the physiological process of trees under future climate (Jiménez-Muñoz et al., 2016). During this drought, record-breaking air temperature and extreme soil moisture deficits occurred, accompanied by increased canopy turnover rate (Leitold et al., 2018), a decline in sap velocity (Fontes et al., 2018; Gimenez et al., 2019), and increased influence of vapor pressure deficit (VPD; the atmospheric evaporative demand; Grossiord et al. 2020). The 2015-16 drought was the warmest and driest drought since 1990 (Jiménez-Muñoz et al., 2016), providing a rare opportunity to investigate how warmer droughts predicted to occur in the future could impact transpiration in moist tropical forests.

In this study, we capitalized on the extreme 2015-16 drought through dry- and wet-season measurements of transpiration and associated drivers in an old-growth upland forest in the central Amazon to test for water limitations and identify if thresholds occurred. Our hypothesis is that sap velocity during this event shifted from light-limitation to soil moisture limitations under the particularly severe conditions experienced .

2. Methods

2.1 Study site

The study was conducted at the K34 tower (2.609 S, 60.209 W, 130 m) within the ZF-2 research station in the Central Amazon, approximately 90 km north of the city of Manaus, Brazil. This site has intermediate levels of rainfall within the Amazon biome and is typically light-limited (Fontes et al., 2018). The K34 tower is 50-meter tall, located at the Reserva Biológica do Cuieiras, is inside of extensive areas of undisturbed tropical forest (Araújo et al., 2002). The topography of the region is characterized by a sequence of plateaus, slopes, and valleys (Ohta et al., 1998), with the K34 tower located in a plateau area. The climate is characterized as tropical rainforest (*Af*, according to Köppen climate classification) with the mean annual temperature 26.68 ºC, annual rainfall of 2252 mm, and a moderate drier period between July and September (Araújo et al., 2002). The vegetation is characterized by dense, old-growth, evergreen broadleaf upland forest with a high diversity of tree species (Lima et al., 2007). Trees are on average 30 m in height (Luizão et al., 2004). The most abundant botanical families in the ZF-2 research station include *Lecythidaceae, Sapotaceae, Fabaceae, Chrysobalanaceae, Burseraceae, Annonaceae,*

Moraceae, and *Euphorbiaceae* (Vieira et al., 2004). The soil on the study site is dominated by kaolinite, quartz, iron oxides and hydroxides, and Al, with high clay content but lacking P, Ca, Mg, and K (Broedel et al., 2017; Luizão et al., 2004; Teixeira et al., 2014). In the top 30 cm of the soil, clay contents constitute 65–75% and reach 80–90% into the 2 ~ 4 m soil layer (Negrón-Juárez et al., 2020).

2.2 Sap velocity measurements and processes

We used heat pulse sap velocity sensors (SFM1, ICT international, Australia) to measure the sap velocity of four representative individuals at the K34 tower from February, 2015 to December 31, 2017 (Table S1). These individuals are selected from the most abundant families and based on the proximity of the crowns to the footprint of the K34 tower. Sensors were installed near breast height on each tree following the protocols described in (Christianson et al., 2017). The sensors measure sap velocity (cm h^{-1}) at 0.75 cm depth in the stem based on the heat ratio method (Burgess et al., 2001; Steppe et al., 2010). The distance between needles is 5 mm, a factory default setting recommended by the manufacturer (Burgess and Downey, 2014). The needle was configured to emit a 20 Joule pulse of thermal energy every 15 min. The sap velocity Tool version 1.4.1 (Phyto-IT) was used to calculate sap velocity for each tree using raw data measured by sensors and biophysical characteristics (e.g., diameter and bark thickness). We conducted a systematic removal of sap velocity observations associated with measurement failures and sensor removals in the field. We assume that zero-flow conditions occur predawn and calibrate all observations based on true zero flow conditions.

To quantify the dynamics of sap velocity and its variability, we first aggregated the raw sap velocity data at every 15-minute timestep to a daily 90% quantile. The reason we used daily 90% quantiles for aggregation is to robustly represent the extreme conditions during a day while removing the influence of outliers or large fluctuations caused by short-term weather effects. Then we calculated weekly sap velocity variability (i.e., the standard deviation of daily sap velocity in each week) and normalized weekly sap velocity variability (i.e., sap velocity variability divided by mean sap velocity in each week) from daily sap velocity. Normalized weekly sap velocity variability (unit: percentage) describes the magnitude of sap velocity

fluctuation compared to the absolute value of sap velocity, and thus represents a critical indicator of sap velocity in response to environmental changes.

2.3 Environmental variables measurements

Environmental variables including air temperature, relative humidity, VPD, net radiation, and soil moisture were measured at the K34 tower. Air temperature and relative humidity were measured using thermohygrometers (HC2S3, Campbell Scientific, Logan, UT, USA) at 50 m (above the canopy) at the K34 tower data collection every minute and recorded as 30-minute averages. VPD at 30-minute averages was calculated using air temperature and relative humidity following the Clausius–Clapeyron equation. Net radiation (W/m^2) was calculated from longwave in, longwave out, shortwave in, and shortwave out solar radiation, which were collected with 5-min averages at 50 m using an NR-LITE sensor (Kipp & Zonen, Delft, Netherlands). This dataset was provided by the Large-Scale Biosphere-Atmosphere Program (LBA) project (Araújo et al., 2002).

Volumetric soil water content (SWC) was measured every 30 min at five soil depths: 5cm, 10cm, 20cm, 40cm, and 100 cm from January 2015 to July 2017. These measurements were performed with a Water Content Reflectometer (CS655 Campbell Scientific, Logan, UT, USA) located approximately 12 m from the K34 tower within the vegetation. Mean SWC of the top four layers (i.e., 5cm, 10cm, 20cm, and 30cm) was used to examine environmental controls on sap velocity.

We also used daily precipitation and daily maximum temperature from 1990 to 2017 at the Embrapa meteorological station at Adolfo Ducke Forest Reserve, located North of Manaus and about 50 Km South of the K34 tower (available in the Embrapa InfoClima portal: https://www.cnpaf.embrapa.br/infoclima/). These long time series daily data were then aggregated to monthly sum precipitation and monthly mean maximum temperature and used to compare climate conditions in 2015 to the long-term average.

2.4 Soil water retention curve

We used the following model that describes the soil water-release curve of van Genuchten (1980):

$$\theta = \theta r + \frac{\theta s - \theta r}{\left[1 + (\alpha |\psi|)^n\right]^m} \quad (1)$$

where θ is the volumetric soil water content (m^3/m^3), θ_s and θ_r are the saturated and residual water content (m^3/m^3), respectively, ψ is the absolute value of the matric potential (kPa). α (kPa^{-1}), n and m are parameters. m is taken to be 1-1/n. Parameters of the van Genuchten equation were derived specifically for Manaus soil in Tomasella et al. (1996). We used the calibrated parameters θ_s, θ_r , α and n for 0.3m depth soil from Table 2 in Tomasella et al. (1996), and converted the soil moisture threshold to soil matric potential threshold.

2.5 Statistical analysis

We first quantified the changes in the precipitation, VPD, air temperature, net radiation, SWC, and sap velocity before, during, and after the El Niño drought from 2015 to 2016. To do this, we aggregated precipitation from hourly to daily sum, and aggregated 30-minute observations to 90% quantile daily observations for the rest of the variables for six two-week periods, i.e., wet seasons (March 1st to March 14th) in 2015 and 2016, early dry seasons (June 28th to July 12nd) in 2015 and 2016, late dry season (August 19th to September 1st, 2015), and drought (September 22nd to October 5th, 2015). Sap velocity and climate variables during these two-week periods represent the typical conditions for these periods. We also calculated the weekly sap velocity variability and the normalized weekly sap velocity variability to investigate sap velocity dynamics.

To examine the environmental controls on sap velocity, we used partial correlation analysis and multiple linear regression analysis to analyze the relationships between net radiation, SWC, and sap velocity for each individual tree during the six periods. Because net radiation and SWC are often correlated, the partial correlation analysis measures the degree of association between sap velocity and each variable with the confounding effects of other control variables excluded statistically at the same time (Beer et al., 2010). We also tested the interaction effect between SWC and net radiation on sap velocity for each of the six periods, respectively, in the multiple linear regression model. We only presented the model results with the interaction term when it was significant ($P < 0.05$). Data used in the multiple linear regression analysis and partial correlation analysis are daily 90% quantiles calculated from half-hour data.

To identify the timing when sap velocity shifted from light-limited to soil moisture-limited and the critical thresholds of soil moisture, we further conducted two moving-window partial correlation analyses between net radiation, SWC, and sap velocity for each tree individual. First, we conducted a partial correlation analysis for every 15-day period from August 1st, 2015 to September 1st, 2016 with a 3-day moving step. Then we zoomed into the period from August 17th, 2015 to November 1st, 2015, and used a 10-day window period with a 1-day moving step, focusing on identifying the accurate timing of water stress. Based on the partial correlation coefficients between soil moisture and sap velocity (*Rswc*), we identified the date when soil water stress started to occur as the first window period when *Rswc* of the following three consecutive window periods are significant ($P < 0.05$). The statistical significance was determined by a two-tailed Student's t-test.

3. Results

3.1 Rapid transpiration collapse during the drought

The 2015-16 El Niño drought was characterized by extreme climatic conditions, including low rainfall and dry soil, and high radiation, temperature, and VPD (Figs.1-2). Continuous low precipitation caused a substantial decrease in soil moisture, which happened simultaneously with a 38% ± 21% (mean ± SD.) drop in sap velocity across all tree individuals, compared to the 2015 wet season (Figs. 1 and 3a). Precipitation showed a 96.8% decline from 115.91 mm during the wet season (March 1st to March 14th, 2015) to 3.71 mm during the drought period (September 22nd to October 5th, 2015) and 90.4% decrease compared to the same period in the non-drought year 2016 (38.8 mm) (Figs. 2a and S1a). Shallow (i.e., 5 cm beneath the surface) soil moisture dropped markedly in response to the drought, from 0.40 m^3/m^3 in the 2015 early dry season to 0.22 m^3/m^3 during the drought (i.e., a 45% decrease, Fig. S2). Deep soil moisture (100 cm beneath the soil surface) was comparatively constant year-round, but still dropped 0.024 m^3/m^3 (6%) to 0.38 m^3/m^3 during the drought (Fig. S2). Compared to the same period in 2016, soil moisture at 5cm and 100 cm decreased from 0.34 m^3/m^3 (by 35%) and 0.41 m^3/m^3 (by 7%), respectively (Fig. S2). On an average, soil moisture of the top 30 cm decreased 31.6% from the 2015 early dry season (0.38 m^3/m^3) to the drought (0.26 m^3/m^3), and showed gradual recovery to 0.37 m^3/m^3 in 2016 (Fig. 2b). At the same time, net radiation reached its maximum, i.e., 724 W/

m^2, during the drought (Fig. S1). The transition from drought to the 2016 wet season was accompanied by a marked reduction in net radiation from 650 W/m^2 to 534 W/m^2 on average (Fig. 2c). VPD, air temperature, and canopy temperature showed similar changes, with gradual increases from wet to late dry seasons, reaching their maximum during the drought (33.8 hPa, 34.8 ℃ and 35.9 ℃, respectively), and dropped back to normal by the 2016 wet season (Fig. 2d-f). The rapid rise during the drought accounted for 215% and 6.8 ℃ increase in VPD and air temperature, respectively, compared to 2015 wet season (Fig. 2d-f). In early October, with increasing rainfall events, soil moisture started to increase, and sap velocity showed recovery as well (Fig. 1). Compared to long-term climate conditions, precipitation in September reached the minimum in 2015 (26.1 mm), while the mean precipitation in September was 93.7 mm during 1990-2016 (Fig. 2g). More extremely, the maximum temperature in September reached its maximum (36.7 ℃) in 2015, or 2.9°C above the 1990-2016 average (33.8 ℃, Fig. 2h).

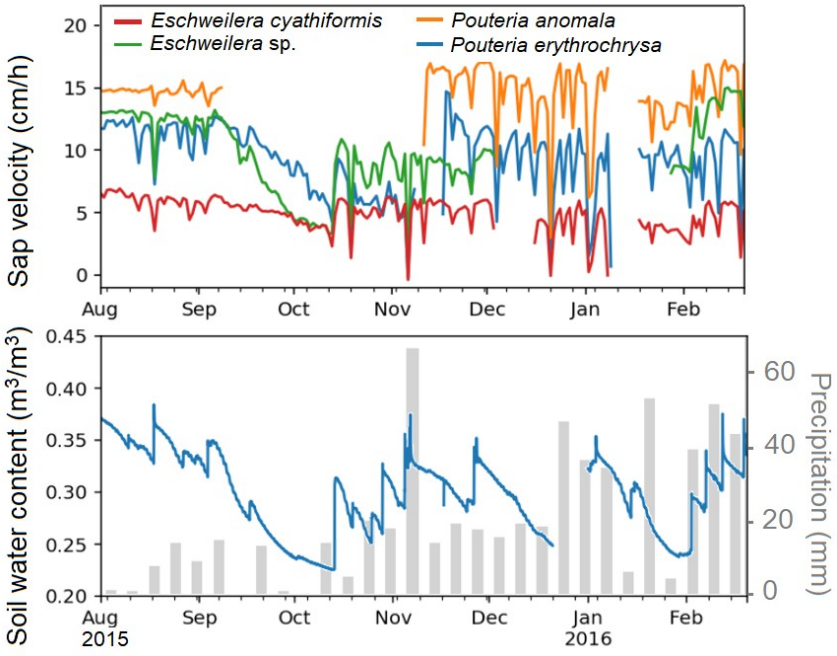

Fig. 1 Dramatic drop in soil water content accompanied by a substantial decrease in sap velocity during the 2015 El Niño drought. No data was collected for *Pouteria anomala* during September - November 2015. Weekly sum precipitation is shown as the gray bar.

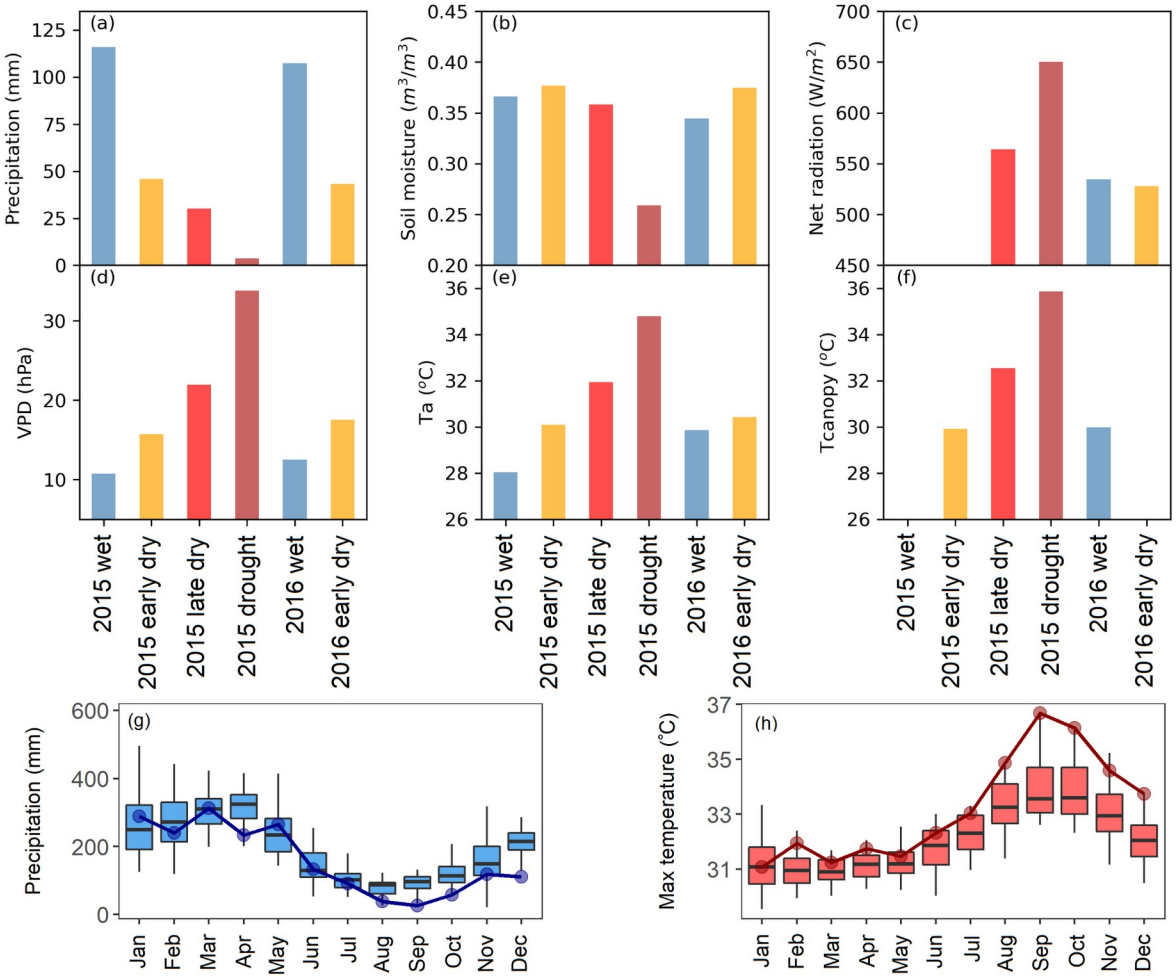

Fig. 2 Extreme changes in environmental variables during the 2015 El Niño drought. (a)-(f): Changes in environmental variables including during the wet season, early dry season, late dry season, and drought. No data was collected for net radiation during 2015 wet and early dry seasons, and for canopy temperature during 2015 wet season and 2016 early dry season. (g)-(h): Monthly precipitation (g) and maximum temperature (h) in 2015 (shown as line and points) compared with long-term mean during 1990-2016. The central line, lower and upper hinges in the box plots represent the median, 25th and 75th percentiles, respectively, of the precipitation or maximum temperature during 1990-2016.

Sap velocity of *Eschweilera cyathiformis*, *Eschweilera* sp., and *Pouteria erythrochrysa* declined rapidly by 41% (from 9.3 cm/h to 5.5 cm/h), 57% (from 14.9 cm/h to 6.4 cm/h), and 15% (from 12.1 cm/h to 10.3 cm/h), respectively (No data was collected for *Pouteria anomala* during the

drought, Fig. 3a). Sap velocity recovered after a rainfall event in October, 2015 and kept the same magnitude during most of 2016-2017 as before drought (Fig. S3). The normalized sap velocity variability (i.e., the ratio of standard deviation of sap velocity and mean sap velocity) was the highest during wet seasons (49% ± 5%, mean ± SD.), gradually decreased during early and late dry season, reached its minimum during the drought (7.6% ± 1.5%, mean ± SD.), and recovered before the wet season in 2016 (Figs. 3b and S3c-d). For example, sap velocity variability of *Eschweilera cyathiformis*, *Eschweilera* sp., and *Pouteria erythrochrysa* decreased by 85.2% (from 54% to 8%), 79.5% (from 44% to 9%), and 87.8% (from 49% to 6%), respectively, from wet season to drought in 2015 (Fig. 3b).

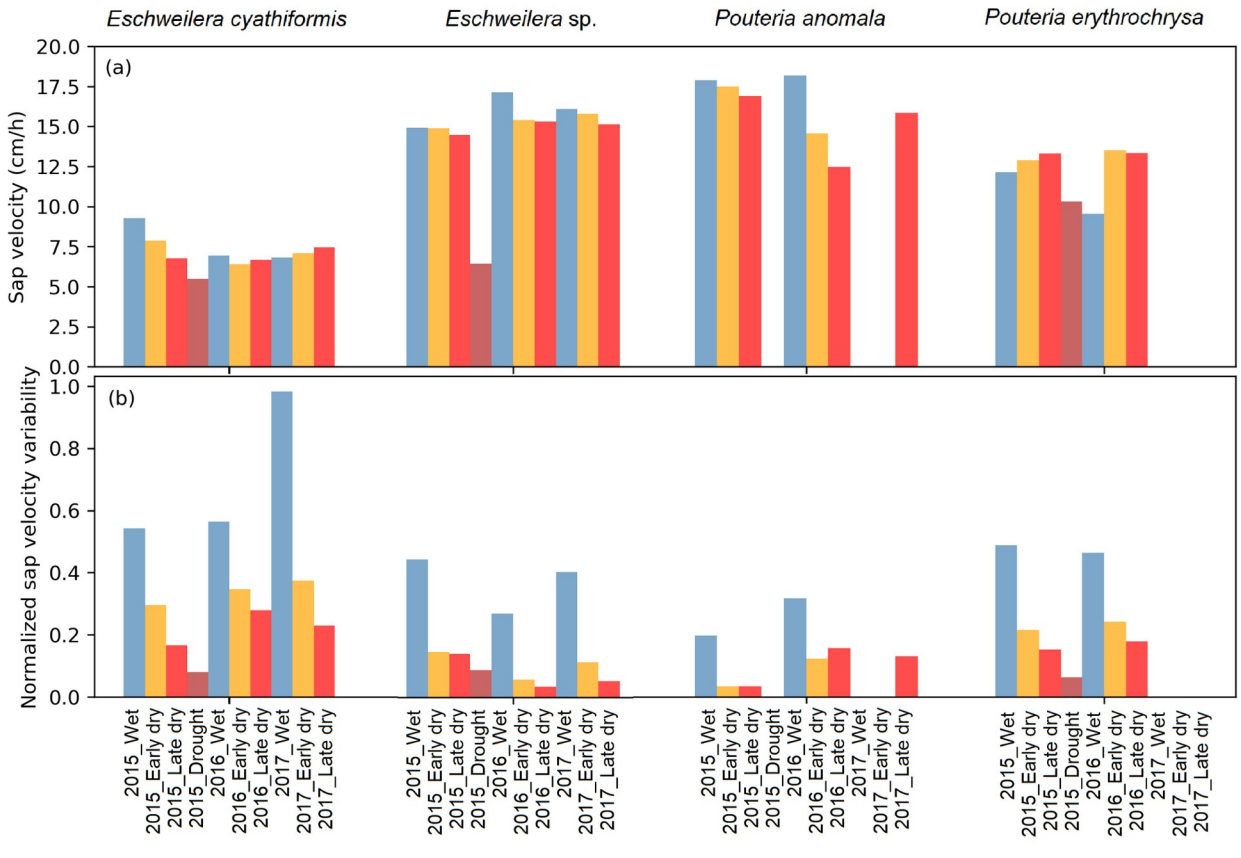

Fig. 3 Sap velocity (a) and normalized sap velocity variability (b) during wet season, early dry season, late dry season, and drought from 2015 to 2017. No data was collected for *Pouteria anomala* during the drought in 2015, and wet and early dry season in 2017.

3.2 Water and light limitations on sap velocity

We found a strong positive correlation between sap velocity and net radiation during the entire study period, and a strong positive correlation between sap velocity and soil moisture only under low soil moisture (Fig. 4). Sap velocity declined with the decrease in soil moisture when soil moisture was below 0.3 m^3/m^3 (Fig. 4a), which occurred during the most severe drought period (Fig. S2). The variability of sap velocity in each soil moisture bin was small under low soil moisture (0.7 – 1.7 cm/h), but became large when soil moisture was above 0.3 m^3/m^3 (2.0 – 3.3 cm/h, Fig. 4a). The relationship between net radiation and sap velocity is generally consistent across tree individuals, although with some minor variations (Fig. 4b). The response of sap velocity to the increase in net radiation is linear for *Eschweilera cyathiformis*, but nonlinear for *Pouteria anomala* and *Pouteria erythrochrysa,* reaching a plateau when net radiation approaches 500 W/m^2. These results indicate a strong soil moisture control under dry conditions.

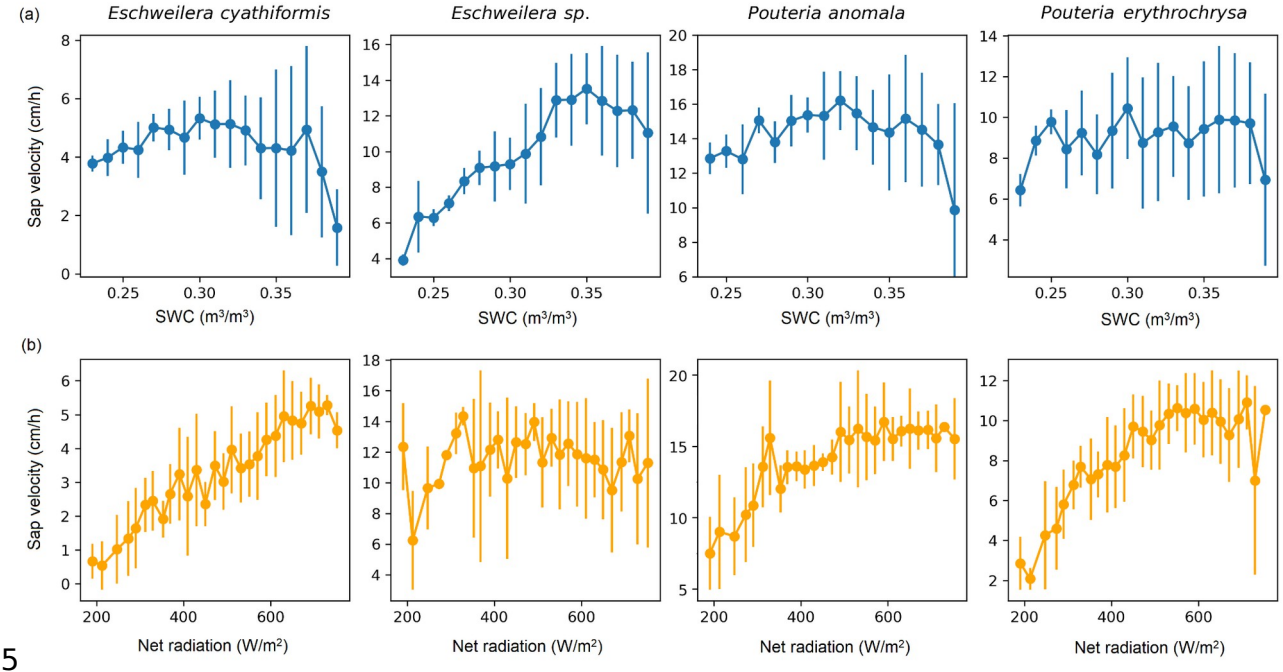

Fig.4 Relationships between sap velocity and soil moisture (a) or net radiation (b). Data used here are daily 90% quantile calculated from half-hour data. Data are binned at every 0.1 m^3/m^3 of soil moisture (a) and every 20 W/m^2 of net radiation (b). The dots and error bars for each bin show the mean and standard deviation for sap velocity, respectively.

We further found a clear shift from light to water limitation for all tree individuals using partial correlation analyses (Fig. 5). Sap velocity was largely limited by net radiation during wet and dry

seasons, but in contrast, only limited by soil moisture during the drought. The partial correlation coefficients between sap velocity and soil moisture (*Rswc*) showed gradual increases from late dry season to drought, and reached maximum values during the drought, i.e., 0.81, 0.98, and 0.88 for *Eschweilera cyathiformis*, *Eschweilera* sp., and *Pouteria erythrochrysa,* respectively (Fig. 5, $P < 0.05$). However, during the 2016 wet and early dry seasons, we found a dominant net radiation control on sap velocity. The partial correlation coefficients between sap velocity and net radiation (R_{NETRAD}) were higher than 0.87 for all tree individuals (Fig. 5, $P < 0.05$). It's worth noting the negative correlation between sap velocity and soil moisture during wet season (Fig. 5 and at low radiation level in Fig. S4) is actually a light effect, i.e., decreased radiation in rainy days reduces sap velocity, which happens simultaneously when soil becomes moister. This finding directly supports our hypothesis that sap velocity was light-limited during the wet season and normal dry season but shifted to be soil moisture-limited during the drought. We also found predominant interaction effects between soil moisture and net radiation during wet and early dry seasons in 2016, but not during the late dry season and the drought in 2015, using the multiple linear regression models (Table S2, $P < 0.05$). This indicates that, with the increase in net radiation, sap velocity significantly increased under wet soil conditions but decreased under dry soil conditions (Fig. S4).

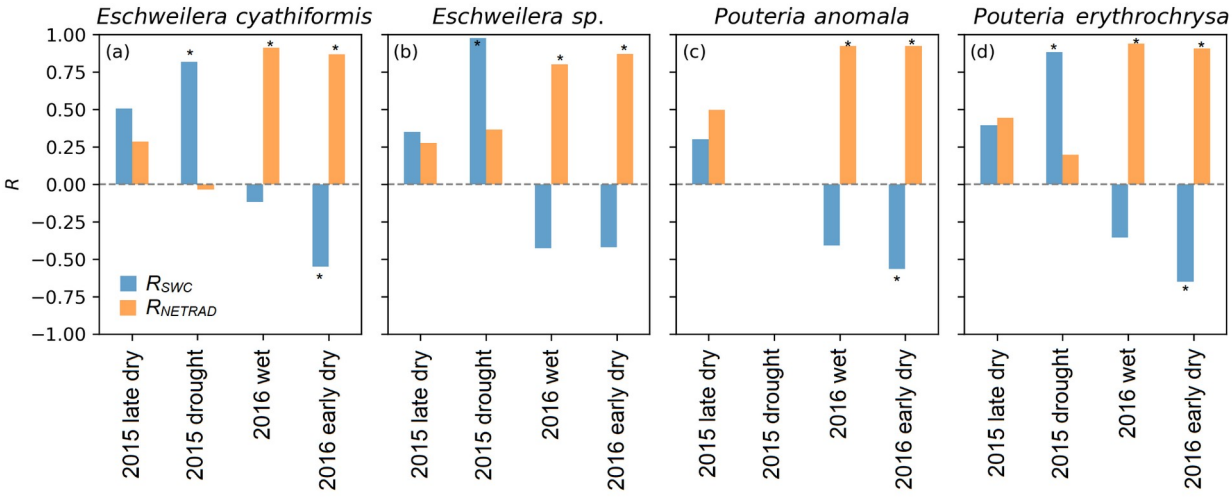

Fig. 5 Partial correlation coefficients (*R*) between sap velocity and soil moisture or radiation during wet season, early dry season, late dry season, and drought. $P < 0.05$ (*). No sap velocity data were collected for *Pouteria anomala* during the 2015 drought.

3.3 Soil moisture threshold on sap velocity

Water stress started to occur on sap velocity across all individuals (i.e., sap velocity was significantly positively correlated with soil moisture, $Rswc > 0$ and $P < 0.05$) in early September 2015, continued through the rest of September and first half of October, then became intermittent and disappeared after several rainfall events (Figs.6 and S5). There was a profound light limitation in August before the drought, and from October, 2015 to the whole of 2016, but not in September, 2015 (Figs. 6 and S5). The period with strong water limitation was also the period when soil moisture started to decrease (Fig. S2). There were several rainfall events in the middle of the drought, during which soil moisture rapidly increased to some extent and the water limitation disappeared for a short time (e.g., September 15th, 2015, Fig. 6). Based on the timing of water stress, we identified the soil moisture threshold as 0.33 m^3/m^3 (mean of the top four layers, Table 1). The corresponding soil matric potential threshold was -144 kPa on average across individuals (Table 1 and Fig. S6), consistent with those found by Tomasella and Hodnett (1996). Sap velocity of *Eschweilera* sp. was limited by soil moisture 2 days later than *Eschweilera cyathiformis* and *Pouteria erythrochrysa* (i.e., Sep. 3 -Sep. 12), when soil moisture and matric potential were 0.327 m^3/m^3 and -185 kPa, respectively (Table 1).

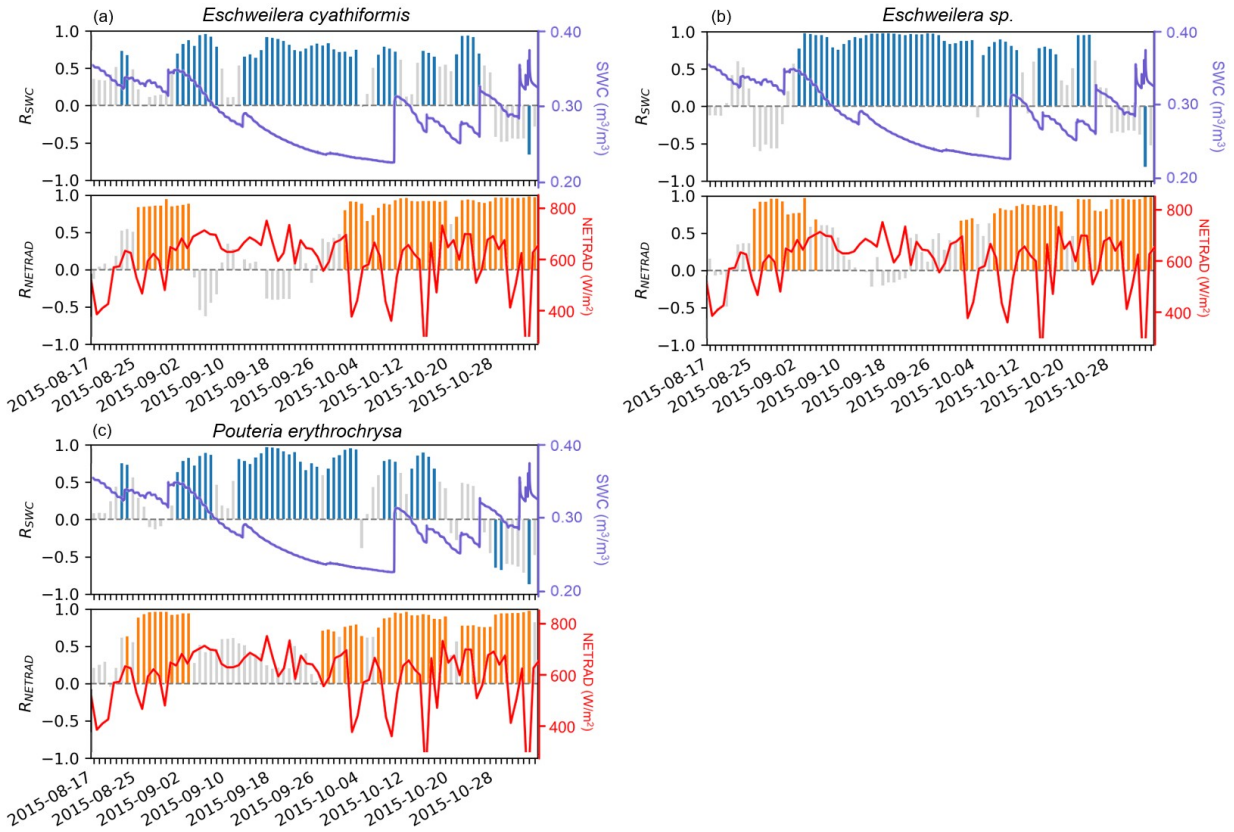

Fig. 6 Moving window of partial correlation coefficient (*R*) between sap velocity, soil moisture, and net radiation. The moving step and window length are 1 day and 10 days, respectively. The blue and orange bars represent the significant partial correlation coefficient between sap velocity and soil moisture (*Rswc*) and between sap velocity and net radiation (R_{NETRAD}), respectively ($P < 0.05$). The gray bars represent non-significant coefficients ($P > 0.05$).

Table 1 Identified periods and thresholds of soil moisture on sap velocity. The water limitation period is the first window period when *Rswc* of the following three continuous window periods are significant $P < 0.05$ from Fig.6. Mean soil water content of the top four layers (i.e., 5cm, 10cm, 20cm, and 30cm) and the corresponding soil matric potential (calculated based on equation (1), Fig. S6) are shown for each tree.

Species	Water stress period	Soil water content (m^3/m^3)	Soil matric potential (-kPa)
Eschweilera cyathiformis	Sep. 1 -Sep. 10	0.332	123
Eschweilera sp.	Sep. 3 -Sep. 12	0.327	185

Pouteria erythrochrysa	Sep. 1 -Sep. 10	0.332	123
Mean		0.330	144

4. Discussion

This study showed a shift from light-limited to water-limited transpiration of humid rainforests and a soil moisture threshold that determines when the shift occurs even in regions where water is often abundant. Previous studies have suggested that tropical evergreen forests in the Central Amazon are not limited by water (Nepstad et al., 1994; Yang et al., 2018). However, during the 2015-16 El Niño drought, photosynthesis decreased due to stomatal closure (Santos et al., 2018), and sap velocity declined because of widespread embolism in the xylem (Fontes et al., 2018). When soil becomes very dry and plant roots cannot absorb enough water to satisfy transpiration from its leaves, the xylem water tension could raise above a threshold, causing rupture of the water column and vessels to become embolized (Oliveira et al., 2021). Embolism reduces the water transport capacity, further increasing xylem water tension and generating more embolism, causing the leaf to lose turgor, the stomata to close, and consequently the decrease in transpiration (Garcia et al., 2021). Taller trees exhibited lower embolism resistance and greater stomatal sensitivity, suggesting a conservative hydraulic strategy of trees to endure drought, with trade-offs between investing in xylem to reduce hydraulic vulnerability and actively regulating stomatal responses to protect against low water potentials (Garcia et al., 2021).

Considering the broad environmental variation across Amazonia, our finding may not apply to other regions in the Amazon. Steep gradients of soil fertility and precipitation across the Amazon basin give rise to considerable variation in floristics, forest structure, and functional traits. Diverse topography (e.g., plateaus, slopes and valleys) at a local scale also causes variation in actual water available to forests, shaping the plant response to drought (Harper et al., 2010; Hutyra et al., 2007). For example, during the same 2015-16 El Niño drought, no water stress was found in the lowland eastern Amazon (Brum et al., 2018). The presence of deeper roots systems (Nepstad et al., 1994) combined with hydraulic redistribution (Oliveira et al., 2005) in the Eastern Amazon are possible mechanisms that may contribute to a higher tolerance of these tropical forests to drought (Esteban et al., 2021). In addition, unlike the high clay content soils in the Central Amazon, Eastern Amazon has high sand content soils (Negrón-Juárez et al.,

2020). Plants in the Eastern Amazon have direct access to groundwater, while plants in the Central Amazon plateaus are more dependent on rainfall and thus experience higher water deficits (Cosme et al., 2017; Fan et al., 2017; Fontes et al., 2020). As a result, plateau species tended to have hydraulic safety traits while valley species tended to have hydraulic efficiency traits, and the latter are relatively unaffected during droughts (Barros et al., 2019; Cosme et al., 2017; Tomasella et al. 2008). In addition, a previous study of Broedel et al. (2017) in the same Manaus site as the current study found no evidence of water stress during the less intense drought of 2005. It is likely that the water stress found in this study is restricted to the most intense droughts and El Niño droughts.

The soil moisture threshold observed in this study has critical implications for tropical ecosystems under future climate change. Humid rainforests in the Central Amazon is generally limited by light but not by water , and they may not depend on drought-resistance hydraulic strategies during the drought, due to typically having sufficient water to satisfy growth and survival requirements (Juárez et al., 2007; Yang et al., 2018). However, extreme climate conditions with declines in precipitation and increases in temperatures are projected in the future in the Amazon, likely reducing plant available water and placing tropical rainforests at risk (Fung et al., 2005). If important ecological thresholds are passed, the resulting changes in ecosystem service and function could be rapid and potentially substantial (Meir et al., 2015), such as high mortality (Meir et al., 2015). The specific threshold of soil moisture in other Amazon regions need to be identified for a comprehensive understanding of soil water stress under extreme climate conditions (Longo et al., 2018). Such soil moisture thresholds also provide a crucial benchmark to test and improve model simulations of future land-atmosphere feedbacks under climate change, which are currently inadequate due to moisture deficit insensitivity (Galbraith et al., 2010; Powell et al., 2013). It is possible that the physiological effects of elevated CO2 may ameliorate these water stresses in the future (Swann et al., 2016), however at scales greater than the leaf it is not clear whether these effects are sufficient to allow plants to sustain functioning when soils are dry, and further, whether feedbacks to precipitation in response to CO2-driven physiological changes may actually make the Amazon even more vulnerable to drought (Kooperman et al., 2018). These thus represent further uncertainties in projecting Amazon responses to future drought.

Collecting field data on soil moisture profiles and sap velocity across species at spatially diverse sites is an essential step to identify soil moisture thresholds in other tropical regions to advance mechanistic understanding and to improve predictive land surface models of ecosystem function. However, realistic and sufficient sampling to obtain plot-level estimates in diverse plant communities is very challenging (Baraloto et al., 2010). The measurements of sap velocity in this study provide the only data available that cover the entire drought period, thus allow us to reveal the shift from light to water limitation. However, it's worth noting that these valuable and high-quality field data have very limited sample size due to logistical constraints. The findings hold true for the studied individual tree species sampled in this study, but other species or other sizes of trees in the studied rainforest might respond differently during the same magnitude of drought. Further field measurements that are based on more complete sampling strategies, such as sufficient sampling intensity, full representation of each species, and key functional traits, are needed to fully understand the variation across regions and species. In addition, this study consists of the first step to understand water constrain on humid rainforest, and further investigation with more species, more sizes, and soil evaporation is needed to calculate stand evapotranspiration and estimate the effect of drought on water relations at a stand-level.

5. Conclusion

This study provides robust evidence on water stress in the humid rainforest in Central Amazon by showing an integration of multiple lines of observations including soil (soil moisture), plants (sap velocity), and atmosphere (precipitation, net radiation, VPD, and temperature) revealing plant physiological response during the progression of a severe drought. Sap velocity was largely limited by net radiation during wet and dry seasons, as is expected for the Central Amazon, but shifted to be limited only by soil moisture during the drought. The soil moisture threshold in the Central Amazon was identified, implying that even tropical rainforests in water abundant regions can be rapidly pushed out of the hydraulic safety zone and limited by soil water deficits during extreme droughts. The ability of tropical forests in the Amazon to survive in the future largely depends on their acclimation and adaptation to drier conditions.

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Data availability statement

The data that support the findings of this study are openly available at https://ngt-data.lbl.gov/dois/NGT0100/. All data that support the findings of this study are included within the article (and any supplementary files).

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