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 and normal dry seasons; 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 m³ 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.

1. Introduction

Transpiration in tropical forests plays a critical role in regulating the global water cycle and climate (Chambers and Artaxo, Doughty et al., 2015). 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., Li et al., Wright et al., Grossiord et al., 2020). The Sixth Assessment Report of the Intergovernmental Panel on Climate Change showed robust projected increases in drought duration and frequency with less rainfall and drying soil in the tropics (Vogel et al., Arias et al., 2021). A warmer and drier climate has already led to a series of impacts on tropical forest ecosystems (Nepstad et al., 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 (Gatti et al 2014, Ahlström et al 2017).

Transpiration is often limited by light availability in moist tropical forests (Shuttleworth 1988, Roberts et al 1993, Von Randow et al 2004, Nepstad et al 2007, da Costa et al 2010, Meir et al 2015) 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 (Shuttleworth 1988, Da Rocha et al 2009). 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 (Vourlitis et al 2002). 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 warmers 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 eddy-covariance 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 50 meter tall K34 tower is located at the Reserva Biológica do Cuieiras, in an extensive areas of undisturbed tropical forest (Araujó 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 °C, annual rainfall of 2252 mm, and a moderate drier period between July and September (Araujó 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 (Luizão et al 2004, Teixeira et al 2014, Broedel et al 2017). 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 31 December 2017 (table S1 (available online at stacks.iop.org/ERL/17/064023/mmmedia)). These individuals were 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 heat pulse sap velocity sensor includes a heater and two temperature-sensing probes (one upper and one lower of the heater) to 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). Each probe has two thermistors, on the inner and outer part of the sapwood, respectively. The distance between each probe to the heater 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). Instead of using the value of sap flow (calculated from sap velocity and amount of sapwood), we chose to use the value of raw sap velocity, because we mainly focused on the temporal changes of sap velocity before, during, and after the droughts, not on the comparison of actual values between different tree species. 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 min 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 (HC253, Campbell Scientific, Logan, UT, USA) at 50 m (above the canopy) at the K34 tower every minute and recorded as 30 min averages. VPD at 30 min 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: 5 cm, 10 cm, 20 cm, 40 cm, 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. 5 cm, 10 cm, 20 cm, and 30 cm) 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: www.cnpanl.br/infoclima/). These long times 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):

\[
\theta = \theta_r + \frac{\theta_s - \theta_r}{[1 + (\alpha |\psi|)^{n}]}^{m}
\]

where \(\theta\) is the volumetric SWC (m\(^3\) m\(^{-3}\)), \(\theta_s\) and \(\theta_r\) are the saturated and residual water content (m\(^3\) m\(^{-3}\)), respectively, \(\psi\) is the absolute value of the matric potential (kPa), \(\alpha\) (kPa\(^{-1}\)) and \(n\) 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 \(\theta_s\), \(\theta_r\), \(\alpha\) and \(n\) for 0.3 m 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 min observations to 90% quantile daily observations for the rest of the variables for six two-week periods, i.e. wet seasons (1 March to 14 March) in 2015 and 2016, early dry seasons (28 June to 12 July) in 2015 and 2016, late dry season (19 August to 1 September 2015), and drought (22 September to 5 October 2015). To directly compare sap velocity and environmental conditions in the same period in 2015 versus 2016, we use LateDry1_2016 and LateDry2_2016 to represent the same period as the late dry season and drought in 2015, respectively, in figures 2 and 5. 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 1 August 2015 to 1 September 2016, with a 3 day moving step. Then we zoomed into the period from 17 August 2015 to 1 November 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 \((R_{swc})\), we identified the date when soil water stress started to occur as the first window period when \(R_{swc}\) 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 (figures 1 and 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 (figures 1 and 3(a)). Precipitation showed a 90.4% decrease in 2015 drought (3.71 mm) compared to the same period in 2016 (38.8 mm, shown as LateDry2_2016 in figure 2(a)). Soil moisture in the top 30 cm decreased 31.6% from the 2015 early dry season \(0.38 \text{ m}^3\text{ m}^{-3}\) to the drought \(0.26 \text{ m}^3\text{ m}^{-3}\), and showed gradual recovery to \(0.37 \text{ m}^3\text{ m}^{-3}\) in the 2016 dry season (figure 2(b)). Shallow (i.e. 5 cm beneath the surface) soil moisture dropped the most in response to the drought, from \(0.40 \text{ m}^3\text{ m}^{-3}\) in the 2015 early dry season to \(0.22 \text{ m}^3\text{ m}^{-3}\) during the drought (i.e. a 45% decrease, figure S2).
Figure 2. Extreme changes in environmental variables during the 2015 El Niño drought. (a)–(f) Changes in environmental variables including precipitation, soil moisture, net radiation, VPD, air temperature, and canopy temperature during 2015 and 2016. LateDry1_2016 is the same period as LateDry_2015 while LateDry2_2016 is the same period as Drought_2015 (see details in section 2). No data was collected for net radiation during 2015 wet and early dry seasons, and for canopy temperature during 2015 wet season and dry seasons in 2016. (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.

and recovered to 0.34 m³ m⁻³ in 2016 during the same period as the 2015 drought. Deep soil moisture (100 cm beneath the soil surface) was comparatively constant year-round, but still dropped from 0.024 m³ m⁻³ (6%) to 0.38 m³ m⁻³ during the drought (figure S2). Net radiation reached its maximum, i.e. 724 W m⁻², during the drought, which is 26% higher than the same period in 2016 (574 W m⁻², figure 2(c)). 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 °C and 35.9 °C, respectively), and dropping back to normal by the 2016 (figures 2(d)–(f)). In early October, with increasing rainfall events, soil moisture started to increase, and sap velocity showed recovery as well (figure 1). Compared to long-term climate conditions, precipitation in September reached the minimum in 2015 (26.1 mm), compared to the mean precipitation in September of 93.7 mm during 1990–2016 (figure 2(g)). More extremely, the maximum temperature in September reached its maximum (36.7 °C) in 2015, or 2.9 °C above the 1990–2016 average (33.8 °C, figure 2(h)).

Sap velocity of *Eschweilera cyathiformis*, *Eschweilera* sp., and *Pouteria erythrochrysa* declined rapidly by 41% (from 9.3 cm h⁻¹ to 5.5 cm h⁻¹), 57% (from 14.9 cm h⁻¹ to 6.4 cm h⁻¹), and 15% (from 12.1 cm h⁻¹ to 10.3 cm h⁻¹), respectively (no data was collected for *Pouteria anomala* during the drought, figure 3(a)). Sap velocity recovered after a rainfall event in October 2015 and kept similar magnitude during most time of 2016–2017 as before drought (figure 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 (figures 3(b) and S3(c)–(d)). For example, sap velocity variability of *Eschweilera cyathiformis*,
Figure 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.

*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 (figure 3(b)).

### 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 (figure 4). Sap velocity declined with the decrease in soil moisture when soil moisture was below 0.3 m$^3$ m$^{-3}$ (figure 4(a)), which occurred during the most severe drought period (figure S2). The variability of sap velocity in each soil moisture bin was small under low soil moisture (0.7–1.7 cm h$^{-1}$), but became large when soil moisture was above 0.3 m$^3$ m$^{-3}$ (2.0–3.3 cm h$^{-1}$, figure 4(a)). The relationship between net radiation and sap velocity is generally consistent across tree individuals, although with some minor variations (figure 4(b)). 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.

We further found a clear shift from light to water limitation during the drought for all tree individuals using partial correlation analyses (figure 5). Sap velocity was largely limited by net radiation during wet and normal dry seasons in 2016, but in contrast, only limited by soil moisture during the 2015 drought (figure 5, $P < 0.05$). It is worth noting the negative correlation between sap velocity and soil moisture during the wet season (figure 5 and at low radiation level in figure 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 (figure S4).

### 3.3. Soil moisture threshold on sap velocity

We found strong water limitation on sap velocity only during the 2015 drought, not during 2016 normal dry season or wet seasons (figures 6 and S5). Specifically, water stress started to occur on sap velocity across all individuals (i.e. sap velocity was significantly positively correlated with soil moisture, $R_{swc} > 0$ and $P < 0.05$) in early September 2015,
Figure 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.

Figure 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. During 2015 and 2016. LateDry1_2016 is the same period as LateDry_2015 while LateDry2_2016 is the same period as Drought_2015 (see details in section 2).

continued through the rest of September and first half of October, then became intermittent and disappeared after several rainfall events (figures 6 and S5). There was a consistent and profound light limitation throughout most period in 2015 and 2016, including 2016 normal dry season, but not during 2015 drought (figure S5). The period with strong water limitation was also the period when soil moisture started to decrease (figure 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. 15 September 2015, figure 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 figure S6), consistent with those found by Tomasella and Hodnett (1996). Sap velocity of Eschweilera sp. was limited by soil moisture 2 d later than Eschweilera cyathiformis and Pouteria erythrochrysa (i.e. 3 September–12 September), when soil moisture and matric potential were 0.327 m$^3$ m$^{-3}$ and $-185$ kPa, respectively (table 1).

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, Meinzer et al 2004). 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). Isohydric and anisohydric species exhibited contrasting responses to droughts; the sap flux of iso- hydric species experienced dramatic declines during drought, while the sap flux of anisohydric species showed relatively smaller variations (Yi et al 2017). This suggests that anisohydric species may benefit from actively regulating stomatal responses to mitigate the risk of hydraulic failure associated with maintaining high transpiration rates during droughts (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 (Hutyra et al 2007, Harper et al 2010). 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, Da Rocha et al 2004). In addition, unlike the high clay content soils in the Central Amazon, the 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). 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 are 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, Malhi et al 2002). 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, such as high mortality (Meir et al 2015). The specific thresholds 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, Bencze et al 2014). 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 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 allowing us to reveal the shift from light to water limitation. However, it is worth noting that these valuable and high-quality field data have a 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 the first step to understand water constrain in the 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 of Central Amazon by showing 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.

Data availability statement

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