

Transpiration of *Swartzia tomentifera* in response to microclimatic variability in the central Amazon: the net effect of vapor pressure deficit

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SILVICULTURE

ABSTRACT

Background: The distribution of precipitation in the Amazon region is changing in last decades, but it is uncertain if transpiration will decrease in response to changes in rainfall distribution. In this study we aimed to assess the effect of climatic variability on whole-tree transpiration (inferred from sap flow measurements). We collected climate data (precipitation, photosynthetically active radiation –PAR, relative humidity, vapor pressure deficit –VPD, and temperature) and measured sap flow rates (SFR) in trees of *Swartzia tomentifera*. The SFR was measured in the dry season and wet season using the heat ratio method.

Results: Sap velocity was positively correlated with PAR and temperature, with partial correlation (r_{part}) of 0.33 to 0.57 ($p < 0.001$) during daytime, while at night r_{part} varied from 0.15 to 0.21 ($p < 0.001$). When the effects of PAR and temperature were controlled (i.e. after removing the effect of PAR and temperature on sap velocity and VPD), the net effect of VPD on sap velocity became slightly negative (r_{part} of -0.08 to -0.14, $p < 0.01$) during daytime. Maximum sap velocities were lower during the dry season (5.9 cm h^{-1}) than in the wet season (9.8 cm h^{-1} , $p < 0.001$).

Conclusion: This study shows that tree transpiration can decrease in the dry season in the central Amazon, associated with an increase in temperature, PAR and vapor pressure deficit. A novelty of this study is to demonstrate that after adjusting for the effect of temperature and PAR, the effect of vapor pressure deficit on sap velocity can become negative.

Keywords: Sap flow rate, Sap velocity, Partial correlation, Transpiration

HIGHLIGHTS

Transpiration decreases in the dry season with increase in vapor pressure deficit (VPD).
Transpirational net VPD effect was found removing temperature and irradiance contribution.
Removing influences of temperature and irradiance reduces transpirational net VPD effect.
During daytime, an increase in net VPD greatly restrained transpiration.

ANTEZANA-VERA, S. A.; MARENCO, R. A. Transpiration of *Swartzia tomentifera* in response to microclimatic variability in the central Amazon: the net effect of vapor pressure deficit. CERNE, v. 27, e-102999, doi: 10.1590/01047760202127012999

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Received: 08/09/2021

Accepted: 10/11/2021



INTRODUCTION

Transpiration is a complex process with a wide range of internal and external factors involved (Yoo et al., 2009), and whose driving force is the leaf to air vapor pressure difference ($\Delta e = e_i - e_a$, being e_i and e_a the vapor pressure inside the leaf and in the air, respectively). At the leaf level, transpiration can be approximated as the product of leaf conductance to water vapor and water vapor mole fraction difference between the leaf intercellular spaces and the air (Farquhar and Sharkey, 1982). While, at the tree level, whole-canopy transpiration can be estimated as the product of sap flow rate and sapwood area (Burgess et al., 2001). Because transpiration is as function of leaf conductance (stomatal plus cuticular conductance) and vapor pressure deficit (VPD), factors that affect stomatal functioning play a key role in controlling transpiration (Farquhar and Sharkey, 1982), particularly when the boundary layer conductance is much higher than stomatal conductance. Even when most of the water vapor is lost through stomatal transpiration, a significant amount of water evaporates from the cuticle when stomata are closed, especially from young expanding leaves (Kane et al., 2020). Stomata are quite responsive to variations in many environmental factors, including –but not only– soil water content (SWC), VPD, irradiance, light quality, CO_2 concentration, and temperature, as well as endogenous factors such as leaf age, hydraulic properties along the xylem path, and abscisic acid content in the leaf tissue (Marengo et al., 2014; Miner et al., 2017; Grossiord et al., 2020).

On a daily basis, stomatal conductance increases in the morning to reach a maximum value before midday, and afterwards it decreases as VPD continues to rise (Marengo et al., 2014), and often there is a lag between canopy transpiration and the sap flow measured at the base of the stem (Schulze et al., 1985). At the tree scale, canopy conductance seems to be more responsive to variations in VPD than in soil water availability, as it can decrease with increasing VPD (Barros et al., 2019). Therefore, transpiration may increase during the dry season provided soil water is not limiting. In fact, at an experimental site in the central Amazon (K34, $2^{\circ}36' 33''$ S, $60^{\circ}12' 33''$ W), evapotranspiration or the latent heat flux (a proxy of evapotranspiration) can increase from 6 to 14% in the dry season (Juárez et al., 2007; Hasler and Avissar, 2007), when soil water uptake can be improved (Broedel et al., 2017). In this regard, however, there is a threshold or tipping point at which a further increase in dry season length (further increase in VPD and decline in SWC) can lead to a decrease in transpiration (Nobre et al., 2016; Grossiord et al., 2020).

Variation in evapotranspiration can be the result of changes in several factors including temperature, VPD, irradiance, and surface conductance (Costa et al., 2010). An increase in transpiration does not mean higher photosynthetic rates, as transpiration often increases with increasing VPD, despite the negative effect of increasing VPD on stomatal conductance (McDowell and Allen, 2015; Grossiord et al., 2020), and also because cuticular transpiration can occur when stomata are closed (Kane et al., 2020).

Over the Amazon region, interannual climatic variability has led to droughts in some parts of the Amazon,

as those observed in 2005, 2010 and 2015–2016 (Marengo et al., 2018) and whose effects on water relationship and carbon assimilation have been widely investigated (Jiménez-Muñoz et al., 2016; Broedel et al., 2017; Yang et al., 2018; Marengo and Antezana-Vera, 2021). However, it is still unclear, if a decline in monthly precipitation leads to a decline of the transpiration in the central Amazon, particularly in driest years. Understanding how tree transpiration responds to variations in precipitation, irradiance and temperature will help to forecast the potential effect of droughts in this part of the Amazon, as factors that affect transpiration also affect carbon assimilation (Marengo et al., 2014). This is important especially taking into account that as a result of global warming longer droughts are forecasted for some parts of the Amazon (Boisier et al., 2015; Jiménez-Muñoz et al., 2016; Marengo et al., 2018). Thus, in this study we aimed to assess the effect of microclimatic variability on whole-tree transpiration. Vapor pressure deficit increases in the dry season in the central Amazon; thus, we hypothesize that an increase in VPD leads to an increase in whole-tree transpiration in the dry season when irradiance, temperature and VPD are higher.

MATERIALS AND METHODS

Study area and plant material

The study was conducted at a terra-firme forest site of the ZF2-Experimental Station of the National Institute for Research in the Amazon (INPA), located 60 km north of Manaus ($02^{\circ}36' 21''$ S; $60^{\circ} 08'11''$ W). The central Amazon is characterized by a humid climate with a mild dry season from June to October (Figure 1). Within this period, July, August and September are the driest months (≤ 100 mm month⁻¹, rainfall data for Manaus over the 1930–2010 period, INMET, 2021), while June and October (~ 110 mm month⁻¹) can be considered transition months. Thus, for maximum contrasting between rainfall seasons, June and October were included in the wet season in this study. The average annual temperature is 26 °C and precipitation often ranges between 2,448 and 2,564 mm yr⁻¹ at the study site (Dias and Marengo, 2016; Marengo and Antezana-Vera, 2021). The soil (yellow latosol) is poor in nutrients with pH of 4.0–4.2 and clay texture (73.5% clay, 15.0% silt and 11.2% sand –on a plateau area, Magalhães et al., 2014). In this

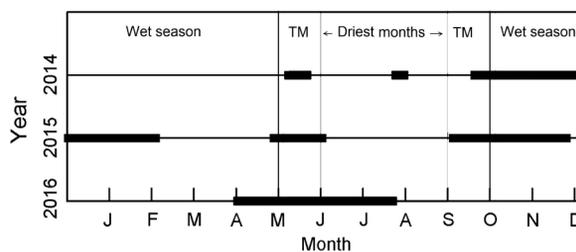


Fig. 1 Schematic representation of the data collection period (black horizontal bar) for the year of 2014–2016. Note that the dry period in this study is represented by the months of July and August, as no data were collected in September. June and October are considered transition months (TM), but included in the wet season for data analysis.

study we collected sap flow data from four trees of *Swartzia tomentifera* (Fabaceae), with a mean diameter of 26.6 cm and 24.8 m tall (i.e. trees of the mid-upper canopy).

The genus *Swartzia* (~180 neotropical species, Torke and Mansano, 2009) is important not only for timber production, but also because non-timber products can be obtained from trees of this genus (Sanz-Biset and Canigueral, 2011). The trees of *S. tomentifera* are of medium stature (up to about 30 m tall), but stem growth is rather slow, 0.96 mm yr⁻¹ (Dias and Marengo, 2021).

Whole-tree transpiration and wood properties

Whole-tree transpiration (WTT) was estimated from sap flow rate (SFR) and the sapwood area of the trees. Altogether, SFR data were collected for 380 days, which included the dry season (61 days) and the wet season (319 days) of 2014–2016. Because of technical problems, we were unable to collect flux data in September, and so the driest period was only represented by July and August, as described in Figure 1. To determine SFR we used the heat ratio method (Burgess et al., 2001), and a sap flow meter (SFM1, ICT International Pty Ltd, Armidale, NSW, Australia). The heat ratio method uses heat pulse velocity data, and from them sap velocity and SFR are computed. The SFM1 comprises an internal battery, a data logger and three 35-mm stainless steel needles. Two of them have thermistors located at 7.5 mm and 22.5 mm from the tip of the needle, while the third needle houses the heater, a high resistance filament –18.0 Ohm (Burgess and Downey, 2014). On each tree the SFR was determined at breast height (~1.3 m from the ground), by inserting radially the probes into the stem of the tree at exactly 5 mm above (upstream probe) and 5 mm below (downstream probe) from the heater needle. The SFM1 was set up to collect data at 30-min intervals (instantaneous sap flow), when a heat energy pulse (20 J, 2.5 s duration; i.e. 8.0 W per pulse, Burgess and Downey, 2014) was applied to the filament heater. To recharge the SFM1 internal battery, an external 12 V-60 Ah battery was used. From heat pulse data, sap velocity was computed using the Sap Flow Tool software (v.1.3, ICT, Armidale, Australia), and then the sap flow rate per tree was obtained as the product of sap velocity (cm h⁻¹) and the cross-sectional area of active sapwood area (A_s , in cm²) of the tree (Burgess et al., 2001). Daily sap flow rate per tree (D_p , in cm³ day⁻¹) was obtained by summing up the sap flow across the whole sapwood area (in cm³ h⁻¹) over a 24-h period.

Even when special care was taken to avoid misalignment, slightly positive or negative SFR values were occasionally recorded at midnight. Thus, the raw data from each probe installation were corrected to have a zero mean value at midnight. This correction was accomplished by adding a constant to the data set to make zero the mean midnight value. The sapwood depth (SWD) was obtained by regressing the maximum sap velocity on thermistor depth, as illustrated in Figure 2. It can be seen in this figure that the SWD corresponded to the intercept of the regression line on the x -axis (hereafter we refer to this approach as the extrapolation method). Then the SWA was calculated as the difference between the total cross section area and the heartwood area. This method was validated using the equation developed by Kunert et al. (2017) –hereafter referred to as Kunert's equation– for Amazonian trees [i.e., $y = 0.8227x^{1.7805}$, where x (cm) is tree diameter, and y the SWA (cm²)].

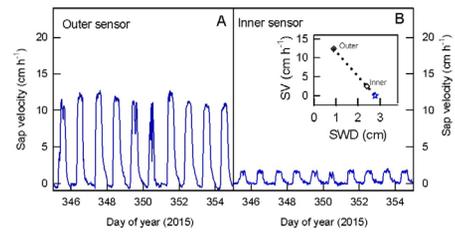


Fig. 2 Illustration of the method used to determine the sapwood depth (SWD). Firstly, the mean maximum sap velocity (SV) recorded by the outer (A) and inner (B) sensor is found (diamonds in the inset of panel B). Then, SWD is obtained as the intercept of regression line (dotted line in the inset) on the x -axis at $SV = 0$ (blue star). The outer and inner sensors were at 0.90 cm and 2.40 cm into the sapwood. The panels show the data collected in Tree number 26 between December 11 and December 20 of 2015. Note that for each probe installation a SWD value was computed, and then a mean values was obtained for a tree.

To determine sapwood fresh volume, dry mass, and fresh mass, a sapwood core sample was extracted from each tree with a 5.15-mm internal diameter increment borer (Haglöf, Langsele, Sweden). The dry mass of the sapwood sample was obtained after oven drying at 80°C to constant mass, and then wood density (dry mass to fresh mass volume) and sapwood water content on a dry mass basis (mass of water to dry matter ratio) were determined.

Microclimatic data

Air temperature (T), relative humidity (RH), and photosynthetically active radiation (PAR) data were collected at a 40 m-tall observation tower (at ~3 km from the experimental site, 02° 35'21" S; 60° 06'53" W). Microclimatic data were recorded at 15-30 min intervals with specific sensors (Humitter 50y, Vaisala, Ov, Finland; LI-190SA, Li-Cor, Lincoln, NE, USA) connected to a data logger (LI-1400, Li-Cor). The logger was set up to record PAR data from 05:30 to 18:30, while temperature and RH were continuously recorded over the 24-h-period. The instantaneous PAR values were integrated over time to obtain a daily value (in mol m⁻² day⁻¹). Vapor pressure deficit (VPD) was calculated from RH and temperature data, as (Buck, 1981): $VPD = e_0 - e_0 \times RH$, where e_0 is the saturation vapor pressure; e_0 (kPa) = $0.61365 \exp[17.5027/(240.97 + T)]$. Daily precipitation data were collected with a tipping bucket gauge connected to a data logger (ECR-100, Em5b, Decagon Devices Pullman USA). To have additional rainfall data (to be used in case of technical problem with the electronic sensor), a conventional rain gauge was installed in the same observation tower to collect further precipitation data. At about two-week intervals and at random locations within the experimental site, we also collected undisturbed soil samples (100 to 200 mm depth) and determined soil water content (after drying the soil samples at 105°C) and then a mean value (SWC in %, v/v) was obtained.

Data analysis

The diurnal relationship between sap velocity (SV) and PAR, temperature and VPD was plotted to observe the general trend. Because the climatic variables are mutually

correlated, we computed the partial correlation (r_{part}) between sap velocity and the climatic variables to assess the individual effect of a given microclimatic variable on sap velocity when the others are controlled. The partial correlation (r_{part}) between two variables (Y and X) can be computed as the correlation between their residuals (R_Y and R_X), and the mathematical procedure can be accomplished in three steps: Firstly, Y is regressed on all X 's except X_j , then the residual R_Y is obtained as: $R_Y = Y - \hat{Y}$, where Y and \hat{Y} represent the observed and fitted value, respectively. In the second step, X_j is regressed on all other X 's and the residual R_j found. In the last step the simple correlation between R_Y and R_j is computed, as follows (Steel et al., 1997).

In this equation, X and Y represent R_j and R_Y , respectively, and \bar{X} and \bar{Y} the means values. For instance, to obtain the r_{part} between sap velocity (SV) and VPD, the variability accounted for the effect of temperature and PAR on sap velocity was removed, and the residual variability ($SV_{residual}$) found. Likewise, by removing the effect of temperature and PAR on VPD, the residual variability ($VPD_{residual}$) was obtained.

$$r = \frac{\Sigma(X-\bar{X})(Y-\bar{Y})}{\sqrt{\Sigma[(X-\bar{X})^2 \Sigma(Y-\bar{Y})^2]}} \quad [1]$$

The influence of time (morning–afternoon) on the sap velocity to VPD (and PAR or temperature) relationship was also examined. Microclimatic and sap velocity data collected between 18:30 and 05:30 were used to obtain nighttime partial correlation, while those recorded between 06:00 and 18:00 were used to obtain partial correlation for daytime data, and except when otherwise stated, the sap velocity (cm h^{-1}) used in statistical analysis corresponded to the mean value of sap velocity recorded by inner and outer sensor, at 30-min intervals.

We also compared the mean daily maximum sap velocity and mean daily SFR between the wet season (October–June) and dry season (July and August, September was not evaluated). In this comparison sap velocity and SFR data were log-transformed prior to statistical analysis (to reduce the effects of outliers) and to have a similar data set size for each season ($n = 61$), we randomly drew a sample from data collected in the wet season. Statistical analyses were carried out using Statistica 7.0 (Stat Soft Inc, Tulsa, OK, US).

RESULTS

Means of temperature (T_{mean}), RH_{mean}, VPD_{mean} and PAR were 26.3°C, 78.3%, 7.59 hPa, and 25.7 mol m⁻² day⁻¹ (Table 1). In comparison with the wet season, mean relative humidity decreased (18%), whereas VPD_{mean} increased (81%) in the dry season. The PAR, temperature, and SWC, on the other hand, showed no significant differences between seasons ($p > 0.05$, Table 1).

Diurnal sap flow velocity

On a daily basis, when the intercorrelation between variables was disregarded, sap velocity increased with increasing PAR, temperature and VPD as illustrated in Figure 3. In a typical sunny day, there is often a time lag between

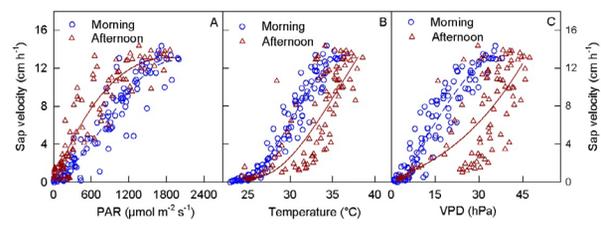


Fig. 3 Illustration of the relationship between sap velocity and PAR (A), temperature (B), and VPD (C), for data collected in the morning (circle, 06:00–12:00) and in the afternoon (triangle, 12:01–18:00). Data were collected in Tree number 6 between 07 and 14 October, 2015. Abbreviations as described in Table 1. The dashed line (morning data) and solid line (afternoon data) indicate the trends.

the increase in stem sap flow and the increase in PAR and temperature measured above the forest canopy (see for example the small increase in sap velocity at temperature below 26°C, Figure 3B). Nevertheless, because of day-to-day variability in microclimatic conditions, over time and across trees a simple correlation can be used to describe the relationship between sap velocity and microclimatic parameters (illustrated in Figure 4). In comparison with the tendencies shown in Figure 3C, when the intercorrelation between the microclimatic variables was removed, the relationship between sap velocity and VPD changed. The consequence of removing the microclimatic intercorrelation was particularly remarkable for the effect of VPD on sap velocity during daytime. It can be seen in Table 2, that an increase in VPD had a slightly negative effect on sap velocity during daytime, with a r_{part} coefficient of -0.08 to -0.14 (mean of -0.11, $p < 0.01$). At night, both temperature and VPD were positively correlated with sap velocity, being temperature more closely associated with sap velocity during the wet season than in the dry season ($r_{part} = 0.21$, $p < 0.001$, Table 2), while VPD had higher correlation with sap velocity in the dry season ($r_{part} = 0.26$, $p < 0.001$, Table 2).

The effect of a microclimatic variable on sap velocity is often evaluated by observing their simple relationship.

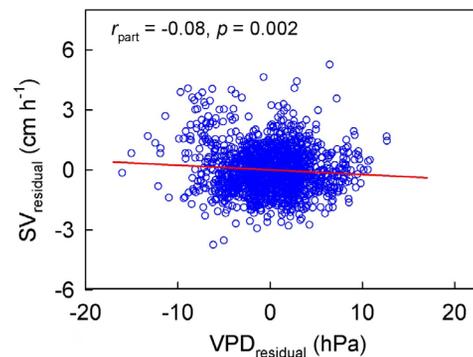


Fig. 4 Illustration of the partial correlation between the residual of vapor pressure deficit ($VPD_{residual}$) and sap velocity ($SV_{residual}$). The partial correlation was computed after removing the effect of temperature and PAR on sap velocity ($SV_{residual}$), while the residual VPD ($VPD_{residual}$) was computed after removing the effect of temperature and PAR on VPD.

Tab. 1 Monthly mean (\pm standard error, SE) of daily photosynthetically active radiation (PAR), maximum (max), mean and minimum (min) temperature (T_{max} , T_{mean} , T_{min}), vapor pressure deficit (VPD_{max}, VPD_{mean}, VPD_{min}), relative humidity (RH_{max}, RH_{mean}, RH_{min}), precipitation, and soil water content (SWC), for the months described in Figure 1. Note that in Figure 1 the dry season only includes the months of July and August. The p value (t-test, dry season vs wet season) is also given; significant p values are in bold face.

Variable	Mean (\pm SE)	Dry season (\pm SE)	Wet season (\pm SE)	p value.
PAR (mol m ⁻² day ⁻¹)	25.69 \pm 0.80	26.34 \pm 1.980	25.55 \pm 0.96	0.763
Rainfall (mm month ⁻¹)	196.4 \pm 31.3	95.10 \pm 1.10	218.94 \pm 35.79	0.008
T_{mean} (°C)	26.29 \pm 0.27	26.90 \pm 0.32	26.15 \pm 0.33	0.182
T_{min} (°C)	23.23 \pm 0.19	22.65 \pm 0.28	23.36 \pm 0.21	0.157
T_{max} (°C)	30.56 \pm 0.44	31.12 \pm 0.28	30.43 \pm 0.56	0.302
RH _{mean} (%)	78.32 \pm 2.32	66.12 \pm 1.17	81.04 \pm 1.97	< 0.001
RH _{min} (%)	55.54 \pm 2.58	42.27 \pm 0.26	58.49 \pm 2.27	< 0.001
RH _{max} (%)	91.74 \pm 1.86	81.66 \pm 2.57	93.98 \pm 1.47	0.067
VPD _{mean} (hPa)	7.59 \pm 0.89	12.01 \pm 0.69	6.60 \pm 0.81	0.005
VPD _{min} (hPa)	2.35 \pm 0.52	5.02 \pm 0.66	1.75 \pm 0.44	0.052
VPD _{max} (hPa)	19.96 \pm 1.54	26.25 \pm 0.33	18.55 \pm 1.61	0.001
SWC (% v/v)	43.81 \pm 1.26	41.53 \pm 0.09	44.31 \pm 1.57	0.115

Following this approach, it can be seen that the relationship between sap velocity and PAR, temperature and VPD varied depending on time of day. For instance, when sap velocity was plotted as a function of PAR it tended to be higher in the afternoon than in the morning (Figure 3A), whereas the relationship between sap velocity, temperature and VPD showed an opposite trend (Figure 3B,C), being this effect

Tab. 2 Partial correlation (rpart) between sap velocity (SV) and PAR, temperature and VPD found in the wet and dry season, and during daytime and nighttime within a season. The p values are given in parenthesis. Over time, data were recorded at 30- min intervals. Units and acronyms are described in Table 1 and Figure 2.

Variable	Climatic factor	Wet season (rpart)	Dry season (rpart)
		Daytime	Daytime
SV versus	PAR	0.35 (< 0.001)	0.46 (< 0.001)
	T (°C)	0.33 (< 0.001)	0.57 (< 0.001)
	VPD	-0.14 (< 0.001)	-0.08 (0.002)
		Nighttime	Nighttime
	T (°C)	0.21 (< 0.001)	0.15 (< 0.001)
	VPD	0.12 (< 0.001)	0.26 (< 0.001)

1: Temperature and VPD were highly correlated both during daytime ($r = 0.88$ –dry season and $r = 0.90$ in the wet season) and at night ($r = 0.53$ –dry season and $r = 0.73$ in the wet season).

higher for VPD than for PAR – this phenomenon has often been termed hysteresis. The relationships between these variables became more evident when the diurnal variation of sap velocity, PAR, VPD and temperature were plotted on a daily basis, as illustrated in Figure 5. With respect to the effect of sapwood depth (SWD) on sap velocity, it was found that the inner sensor recorded lower sap velocity values than the outer sensor (Figure 2). In fact, the inner sensor accounted for only about 40% of the maximum sap velocity recorded by the outer sensor, i.e. 5.34 versus 13.79 cm h⁻¹, for a mean (inner-outer) value of 9.56 cm h⁻¹ (Table 3).

Across trees the mean daily sap flow rate (SFR) was 22.15 L day⁻¹ while the mean SFR (daily sap flow divided by sap wood area) over a 24-h period was 2.64 g(sap) cm⁻² h⁻¹ (Table 3). On average, the nighttime SFR accounted for 9.3%

of the total daily sap flow or 10.3% of the daily SFR (Table 3). While, the mean maximum sap velocity was higher in the wet season (9.8 \pm 0.57 cm h⁻¹, mean \pm standard error) than in dry season (5.90 \pm 0.11 cm h⁻¹, $p < 0.001$, Figure 6A). Likewise, the mean SFR was also higher in the wet season (24.5 \pm 2.1 L day⁻¹) than in the dry season (13.9 \pm 0.75 L day⁻¹, Figure 6B). The sap wood area estimated using the Kunert's equation (Kunert et al., 2017) yielded similar values as those obtained with the extrapolation method. A mean of 300 cm² (Kunert's equation, Table 3) against 302 cm² (per tree) obtained using the new approach (Antezana-Vera and Marengo, 2021). Also, the SFR

Tab. 3 Tree characteristics and mean sap flow parameters. Daytime and nighttime SFR, and the mean values of maximum SV recorded by the inner and outer sensor are shown. For comparison in the last lines show the sap wood area (SWA) and the SFR computed using Kunert's equation (Kunert et al., 2017). Acronyms: SV: sap velocity, SFR: sap flow rate.

Parameters	Mean ¹ (\pm SD)
Tree characteristics	
Tree height (m)	24.8 \pm 1.6
Stem diameter (cm)	26.6 \pm 8.9
Crown diameter (m)	8.1 \pm 2.1
Wood density (g cm ⁻³)	0.82 \pm 0.01
Sap wood depth (cm)	4.49 \pm 2.04
Sap wood area, SWA (cm ²)	302 \pm 175
Sap flow parameters	
Maximum inner SV (cm h ⁻¹)	5.34 \pm 5.06
Maximum outer SV (cm h ⁻¹)	13.79 \pm 5.75
Mean maximum inner-outer SV (cm h ⁻¹)	9.56 \pm 4.98
Total daily SFR (L day ⁻¹)	22.15 \pm 15.05
Daytime SFR (L day ⁻¹)	20.08 \pm 13.14
Nighttime SFR (L day ⁻¹)	2.07 \pm 1.43
Mean daily SFR (g cm ⁻² h ⁻¹)	2.64 \pm 1.31
Nighttime to total SFR (100 \times 2.07/22.15)	9.3%
Nighttime to daytime SFR (100 \times 2.07/20.08)	10.3%
Kunert's equation SWA (cm ²)	300 \pm 167
Kunert's equation (total SFR L day ⁻¹)	20.90 \pm 12.4

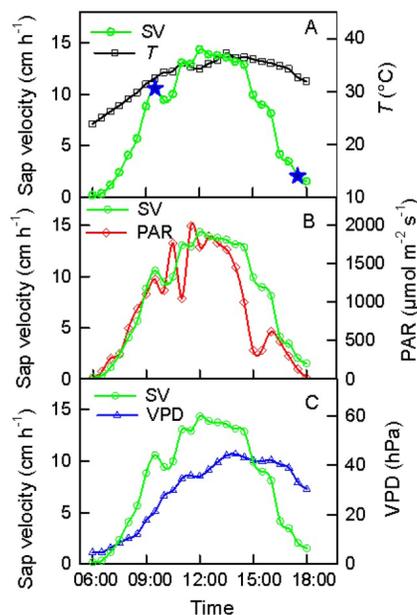


Fig. 5 Diurnal variation of sap velocity and temperature (A), PAR (B), and VPD (C). Data were collected on October 8, 2015, in tree number 6. Abbreviations as described in Table 1. Note that at a temperature of 32.5°C, sap velocity was higher in the morning (10.6 cm h⁻¹) than in the afternoon (2.0 cm h⁻¹), indicated by the blue stars in panel A.

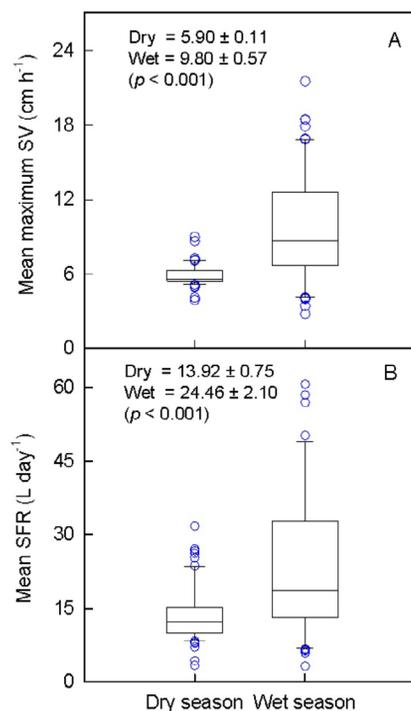


Fig. 6 Box plot of the mean maximum sap velocity (SV) on a daily basis (A) and mean daily sap flow rate, SFR (B) recorded in the wet season (October to June) and during the dry season (July and August). It is also shown the mean value (\pm standard error, $p < 0.001$). For the wet season, a sample of 61 days was drawn at random, to have the same size data set in both seasons. The SV and SFR data were log-transformed prior to data analysis.

values were also similar (20.9 L day⁻¹ –Kunert’s equation versus 22.15 L day⁻¹ our data, Table 3).

DISCUSSION

It was found that sap velocity increased with a rise in PAR and temperature, and that when the intercorrelation between the microclimatic variables was removed, the effect of VPD on sap velocity was greatly reduced, particularly during daytime. Whereas, contrary to expectation tree transpiration was lower in the dry season than in the wet season, which did not support our working hypothesis. The SWC did not differ between the dry and wet season ($p = 0.11$). Therefore, variations in transpiration rates cannot be explained by changes in SWC between seasons.

Barros et al. (2019) reported that a decline in SWC from 51% (maximum SWC) to 42% had no significant effect ($p = 0.10$) on canopy conductance in the central Amazon. Instead, they observed that canopy conductance greatly declined with increasing VPD (unless otherwise stated, we refer to the total effect of VPD simple as VPD; i.e., the effect of VPD without removing the contribution of temperature and PAR). Indeed, canopy conductance seems to be highly responsive to changes in atmospheric conditions. In the central Amazon, variation in surface conductance (a proxy of canopy conductance) has been associated with variation in VPD from 0.018 m s⁻¹ (~ 0.72 mol m⁻² s⁻¹ –in a dense forest, at a VPD of 7.1 hPa) in the dry season to 0.022 m s⁻¹ (~ 0.89 mol m⁻² s⁻¹, VPD of 4.9 hPa) in the wet season (Costa et al., 2010). Moreover, on a daily basis, it has also been reported that in the central Amazon, stomatal conductance (and hence photosynthesis) varies diurnally, with a decline in stomatal conductance when VPD increases above 15 hPa (Marengo et al., 2014). Likewise, at the ecosystem level, photosynthesis can also decline as VPD progressively increased from 3.5 hPa to 32 hPa (Lee et al., 2013). Thus, taking into account that SWC remained rather constant over the year and that VPD_{mean} and VPD_{max} greatly increased in the dry season (40–80%), it can be concluded that the variation in transpiration between rainfall seasons was essentially associated with changes in VPD. This can explain the lower maximum sap velocity and SFR recorded in the dry season (Figure 6). This result conflicts with our hypothesis, as we expected higher transpiration rates in the dry season, which is not supported by data. The most common finding is an increase in evapotranspiration in the dry season in the central Amazon (Hasler and Avissar 2007; Nobre et al., 2016). Hasler and Avissar (2007) reported (at the K34 site in the central Amazon –close to our experimental site) that evapotranspiration was 14% higher in the dry season than in the wet season. Antezana-Vera and Marengo (2021) also reported that total transpiration (estimated from SFR data) of *Minquartia guianensis* tends to increase in the dry season, which suggests that *Swartzia tomentifera* is more sensitive to variations in climatic factors than *Minquartia guianensis*.

The effect of VPD on stomatal conductance is rather complex and consequently the relationship is not straightforward. Although low VPD values enhance stomatal opening (Mendes and Marengo, 2017), in most species high VPD leads to stomatal closing (McDowell and

Allen, 2015; Grossiord et al., 2020). Thus, a small increase in VPD during the dry season can lead to an increase in stomatal conductance, as it seems to be the case in northern Amazonia, when an increase in VPD seems to enhance the ecosystem photosynthesis (Green et al., 2020); whereas, high VPD values appear to have the opposite effect (Lee et al., 2013).

Barros et al. (2019) reported that in comparison with a typical dry season, during the prolonged dry season of 2015, the minimum leaf water potential decreased in the central Amazon (i.e. it becomes more negative). They also found that in response to variations in leaf water content, hydraulic conductivity of trees decreased more rapidly in the central Amazon (K34 site) than in trees adapted to longer dry seasons. A decrease in canopy conductance (Costa et al., 2010) combined with a decrease in hydraulic conductivity (Barros et al., 2019) may explain the decline in the maximum sap velocity and SFR observed in this study during in the dry season (Figure 6).

In this study, maximum sap velocity was lower in the dry season, but it does not mean that the whole ecosystem loses less water by transpiration in the dry season, particularly taking into account the prominent role of emergent trees on ecosystem transpiration (Kunert et al., 2017). *Swartzia* trees are of medium stature, and their abundance (at least in the experimental area) is relatively low (1.5% of trees, above 10 cm diameter). The lower total transpiration of *Swartzia* observed during the dry season suggests that this species is sensitive to variations in environmental conditions. In fact, the years of 2015 and 2016 cannot be considered typical years, as in this period the dry season was longer than expected for the central Amazon, and it was associated with a decline in photosynthesis, over the Amazon region (Yang et al., 2018).

Although most of water is lost through stomatal transpiration, when stomata are closed cuticular transpiration may have a large impact on the water balance of a plant (Schuster et al., 2017). It has been shown that sap velocity and thereby sap flow rate declined in the dry season, which can be explained by a decline in canopy conductance in the dry season (Costa et al., 2010). Another factor that can contribute to a decline in transpiration is leaf shedding, which seems to increase in the dry season (field observation during data collection).

We found a positive correlation between sap velocity and PAR and between sap velocity and temperature. The direct effect of temperature can occur via its effect on stomatal functioning (Kostaki et al., 2020) and also by influencing cuticular transpiration (Burghardt and Riederer, 2008). A rise in temperature enhances guard cell metabolism and thereby stomatal transpiration (Kostaki et al., 2020), and it also improves transpiration by reducing water viscosity. The individual effect of temperature on stomatal opening is rather difficult to be observed, because temperature and VPD are highly correlated (correlation of about 0.90 during, see footnote in Table 2). The effect of light on stomatal opening is a well-known phenomenon, and in this regard our results agree with those reported by Motzer et al. (2005), who found that higher SFR occurred

at midday when irradiance is higher. Horna et al. (2011) and Zhao et al. (2017) also reported a positive correlation between SFR and diurnal irradiance.

We found that there is an effect of time of day on the relationship between microclimatic variables and sap velocity (Figure 3). This hysteric effect is not uncommon (Brum et al., 2018), and it can be explained by observing how fast, sap velocity, PAR, temperature and VPD declined from midday to sunset. It can be seen in Figure 5 that in comparison with PAR, temperature and VPD declined more slowly after midday. Therefore, for a given temperature (or VPD) value, sap velocity was higher in the morning than in the afternoon (for illustration, see the blue stars in Figure 5A). On the contrary, a given light intensity leads to a higher sap velocity value in the afternoon than in the morning. This result concurs with those reported by Schulze et al. (1985), who observed a time lag between the rise in PAR and the increase in basal stem sap flow.

Nighttime transpiration is a phenomenon that seems to occur in many species from contrasting ecosystem (Dawson et al., 2007). In this study it accounted for about 10% of daytime sap flow, which is within the range of values (1 to 25%) found in other Amazonian species (Dawson et al., 2007; Antezana-Vera and Marengo, 2021). It is known that nocturnal sap flow contributes to both nighttime canopy transpiration and water recharge of tree tissue. Goldstein et al. (1998) estimated that stem water reserves can contribute with 9-15% of tropical tree transpiration. However, there is still scarcity of data on the proportion of nocturnal sap flow lost during nighttime transpiration in Amazonian trees. In comparison with the wet season, the higher partial correlation between nighttime sap velocity and VPD in the dry season (Table 2) suggests that canopy transpiration is an important component of sap flow during the dry season, when VPD often increases (Costa et al., 2010). We have shown that, contrary to expectation, maximum sap velocity and SFR declined during the dry season (Figure 6). This can be explained based on the effect of atmospheric dryness on canopy transpiration. Plenty of evidence suggests that, even when stomatal conductance declines under high VPD (Marengo et al., 2014; McDowell and Allen, 2015; Grossiord et al., 2020), in most species transpiration increases with atmospheric dryness until a given VPD threshold is reached. Then, a cascade of events, including hydraulic failure led to a decline in transpiration and under prolonged drought to increased plant mortality (Grossiord et al., 2020).

CONCLUSION

We hypothesized that the whole-tree transpiration of *S. tomentifera* increases in the dry season, but our findings conflict with this premise, as the maximum sap velocity and mean daily SFR decreased in the dry season. A contribution of this study is to show that, contrary to expectation, tree transpiration can decline during the dry season. The decline in maximum sap velocity occurred with a simultaneous increase in temperature, irradiance and VPD during the dry period. It has been documented that a decline in canopy conductance often occurs during the dry season. Therefore, a drop in maximum sap velocity

and SFR in the dry season can be a response to several factors including a decline in canopy conductance and hydraulic conductivity. A novelty of this study is to show that after controlling for the effect of PAR and temperature, the effect of VPD on sap velocity can be greatly reduced, and ultimately VPD and sap velocity can be negatively correlated during daytime. As far as we know this effect of VPD on sap velocity has not been previously shown. These results widen our understanding of the ecophysiology of Amazonian trees and cast light on the potential outcomes of the ongoing climate change, especially those related to rainfall distribution over the Amazon region.

ACKNOWLEDGEMENTS

To the Ministério da Ciência, Tecnologia e Inovações (MCTI-INPA); Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for scholarship to SAAV and fellowship to RAM (grant 303907/2018-5); Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, code 001), and Fundação de Amparo à Pesquisa do Amazonas (FAPEAM). We thank the anonymous reviewers for their important comments and suggestions.

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Funding: RAM

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