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ORIGINAL ARTICLE

Wood and bark water content and monthly stem growth in Amazonian tree species

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ABSTRACT

The knowledge of how trees respond to microclimate variability is important in the face of climate changes. The objectives of this study were to examine the variation in wood water content (WWC) and bark water content (BWC) in Amazonian trees, as well as to assess the effect of microclimatic variability on monthly diameter growth rates (DGR). We extracted a core sample from each of 120 trees (28 species) and determined WWC and BWC on a fresh matter basis. DGR was measured monthly during the 12 months of 2007. The effect of microclimatic variability on DGR was analyzed by redundancy analysis. Average BWC and WWC were 53.4% and 34.7%, respectively, with a large variation in stem water content among species (BWC = 36.2–67.1%; WWC = 26.4–50.8%). There was no significant relationship between stem diameter and WWC or BWC, nor between DGR and wood density ($p > 0.05$). However, wood density was negatively correlated with WWC ($r_s = -0.69$, $p < 0.001$). The high BWC emphasizes the importance of the bark tissue in Amazonian trees. Contrary to expectations, variability of monthly irradiance, rainfall and temperature had no effect on DGR ($p > 0.20$). The unresponsiveness of DGR to microclimatic variability, even in an above-average rainy year such as 2007, indicates that other parts of the tree may have greater priority than the stem for carbon allocation during the dry season.

KEYWORDS: air temperature; rainfall; redundancy analysis; stem diameter; wood density

Conteúdo de água de madeira e casca e crescimento mensal do tronco em espécies arbóreas amazônicas

RESUMO

O conhecimento sobre a resposta das árvores à variação microclimática é importante em face das mudanças climáticas. Os objetivos deste estudo foram examinar a variação do conteúdo de água da madeira (WWC) e do conteúdo de água da casca (BWC) em árvores amazônicas, bem como avaliar o efeito da variabilidade microclimática sobre as taxas de crescimento diamétrico (DGR). Extraímos uma amostra do tronco de 120 árvores (28 espécies) e determinamos WWC e BWC na base da matéria fresca. As medições de DGR foram realizadas mensalmente durante os 12 meses de 2007. O efeito da variabilidade microclimática sobre o crescimento das árvores foi avaliado por meio de análise de redundância. Os valores médios de BWC e WWC foram 53,4% e 34,7%, respectivamente, com uma grande variação no conteúdo de água dos tecidos entre as espécies (BWC = 36,2–67,1%; WWC = 26,4–50,8%). Não houve relação significativa entre o diâmetro do tronco e WWC ou BWC, nem entre DGR e densidade da madeira ($p > 0{,}05$). Entretanto, a densidade da madeira foi negativamente correlacionada com WWC ($r_s = -0{,}69$, $p < 0{,}001$). O alto valor de BWC enfatiza a importância dos tecidos da casca em árvores da Amazônia. Contrariando as expectativas, a variabilidade mensal da irradiância, precipitação e temperatura não afetou DGR ($p > 0{,}20$). A ausência de resposta da DGR à variabilidade microclimática, mesmo em um ano chuvoso acima da média como 2007, indica que outras partes da árvore podem ter maior prioridade do que o tronco para alocação de carbono durante a época seca.

PALAVRAS-CHAVE: análise de redundância; densidade da madeira; diâmetro do tronco; precipitação; temperatura do ar

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INTRODUCTION

The stem water content of trees is an important parameter in tree physiology, as it provides insights into the water relations along the soil-plant-atmosphere continuum (Zweifel *et al.* 2001; Ziemińska *et al.* 2020). Variations in stem water content may affect stem diameter (Stahl *et al.* 2010), which makes it difficult to accurately estimate tree growth. Water content within tree stems varies among species (Kenzo *et al.* 2017; Longuetaud *et al.* 2017), climatic seasons, and between wood and bark (Zweifel *et al.* 2001; Luo *et al.* 2020; Rosell *et al.* 2021). Increased precipitation can cause a rise in stem water content (Dias and Marenco 2016), which may lead to an increase in diameter either by sapwood or bark swelling (Stahl *et al.* 2010), while on the other hand, a decrease in stem water content may lead to stem shrinking and even to negative diameter measurements (Pastur *et al.* 2007). The amount of water stored in the stem can affect tree functioning in several ways. It can buffer fluctuations in water tension in xylem conduits, which decreases the risk of hydraulic failure (Chapotin *et al.* 2006). Stem water can also mitigate the impact of drought and enable leaf formation during the dry season (Borchert 1994; Chapotin *et al.* 2006). However, studies addressing the relationship between tree size and stem water content are scarce. Dias and Marenco (2006) and Kenzo *et al.* (2017) found no correlation between tree diameter and wood water content, but the variation of stem water content with tree size in a year of above-average rainfall had not yet been measured.

Many other factors contribute to tree growth, including site quality (e.g., soil fertility and topography), ontogeny (tree size), and environmental conditions (Bowman *et al.* 2013). Climatic variables such as irradiance, precipitation and air temperature can affect both photosynthesis and tree growth in tropical rainforests (Clark *et al.* 2003; Méndez 2018; Yang *et al.* 2018; Marenco and Antezana-Vera 2021). Air temperature is an important factor in the climate-forest interaction (Kitayama *et al.* 2021) and irradiance plays an essential role in plant functioning, as photosynthesis is highly responsive to changes in light intensity (Marenco *et al.* 2014). However, it is still under debate if in the rainiest part of the Amazon (north and central Amazon) tree growth responds to monthly variation in irradiance and precipitation – and hence to other environmental factors associated with changes in light conditions. Throughout the eastern and central Amazon, the Enhanced Vegetation Index (a surrogate of potential photosynthetic capacity) increased by 25% with increasing sunlight during the dry season (Huete *et al.* 2006), and in the central Amazon, tree growth increased during dry periods (Laurance *et al.* 2009). Likewise, Green *et al.* (2020) reported that, in the rainiest part of the Amazon, photosynthesis increases in the dry season, when solar radiation, temperature, and vapor pressure deficit (a direct function of temperature) are higher (Costa *et al.* 2010; Antezana-Vera and Marenco 2021). On the other hand, ecosystem photosynthesis over the entire Amazon can decline during prolonged droughts (Yang *et al.* 2018), and stem growth can decline during rather prolonged dry seasons (Antezana-Vera and Marenco 2021). Altogether, these results suggest that tree growth can increase in years when water availability is not a limiting factor for photosynthesis.

In this study, we aimed to evaluate the variation in wood and bark water content in Amazonian tree species in an above-average rainy year, as well as to assess the effect of microclimatic variability on stem growth in a *terra-firme* forest in the central Amazon. Considering that photosynthesis can increase during the mild dry season of the central Amazon (Green *et al.* 2020), we hypothesized (a) that stem growth (an estimator of tree growth) increases with a decrease in monthly precipitation in a rainy year, as decreased precipitation is associated with an increase in photosynthetically active radiation and air temperature, and (b) that stem water content is not correlated with stem size, as wood water content tends to remain constant irrespective of tree size when soil water is available to trees (Dias and Marenco 2016; Kenzo *et al.* 2017).

MATERIAL AND METHODS

Study area and microclimatic variables

This study was carried out at the Estação Experimental de Silvicultura Tropical (ZF2 reserve) (02°36'21"S, 60°08'11"W), a forest reserve of the Instituto Nacional de Pesquisas da Amazônia (INPA) located in the state of Amazonas, Brazil, in the central Amazon region. The climate in the region is tropical humid, with mean annual rainfall of 2,420 mm and a mild dry season from June through October, and, within this period, July, August and September are the driest months (< 100 mm per month, INMET 2021). The mean annual temperature is about 26 °C (Dias and Marenco 2016; Antezana-Vera and Marenco 2021). The vegetation is classified as dense *terra-firme* rainforest, and the soil is an Oxisol with low fertility, clay texture, and pH of 4.2 to 4.5 (Magalhães *et al.* 2014).

Precipitation, air temperature and photosynthetically active radiation (PAR) were recorded daily in 2007 above the forest canopy, at the top of a 40-m tall observatory tower located near the study site (02°35'21"S, 60°06'53"W). A light sensor (LI-190SA, Li-Cor, Lincoln, NE, USA) connected to a datalogger (LI-1400, Li-Cor) was used to record PAR at 15-minute intervals (Dias and Marenco 2016), while air temperature (*T*) was collected (at 15-minute intervals) using a TR52 temperature sensor (Thermo recorded TR-52; T&D Co, Nagano, Japan). Mean monthly PAR (mol m^{-2} day^{-1}) was obtained by integrating the instantaneous PAR values over the whole daylight period, i.e., 05:30–18:30. A standard rain gauge located at the same observation tower was used for collecting rainfall data.

Diameter growth rate and wood and bark water content

The study area in the *terra-firme* forest was located on a plateau. Tree species were selected along trails existing in the area based on the availability of at least two trees of the same species and stem diameter at breast height (DBH, 1.3 m from the ground) of at least 10 cm. Overall, we selected 120 mid-upper canopy trees from 28 species, 19 genera and 15 families, which were about 25 cm in diameter and 24 m tall (Table 1; Supplementary Material, Table S1). The increase in stem circumference, or girth increment (at breast height) was measured at monthly intervals, from January to December 2007 (12 measurements per tree) using dendrometer tapes and digital calipers. The tapes had been installed on the trees at least two years before data collection. DBH was obtained by computing the relationship between circumference and diameter: circumference = $\pi \times$ diameter, where $\pi \sim 3.1416$. The diameter growth rate (DGR, hereafter referred to as stem growth), an estimator of tree growth, was calculated as: $(DBH_e - DBH_b)/t$, where DBH_e and DBH_b represent the DBH at the end and beginning of the measurement period, respectively, and t, the time elapsed between two consecutive measurements.

To determine wood water content (WWC), bark water content (BWC) and wood density (WD), a core sample was extracted from each tree (3 to 5 cm in length and 5.15 mm in diameter) with an increment borer (Haglof, Sweden) at about 1.4 m from the ground. The sampling was carried out in April 2007, one of the rainiest months of the year, with the aim to obtain the highest possible water content in the samples.

After extraction, each fresh core sample (comprised of bark and wood) was placed into a small capped test tube. The tubes were tightly sealed to avoid loss of moisture and stored in a thermally insulated box with ice for transport to the laboratory, where the bark and wood portions of each sample were separated and weighed on an analytical balance (0.1 mg precision) for determination of bark and wood fresh

Table 1. Species used in the study. Acronyms: *n* = number of individuals per species; DGR = diameter growth rate; DBH = diameter at breast height; WWC = wood water content (on a fresh matter basis); BWC = bark water content (on a fresh matter basis); WD = wood density. Values are the mean ± standard deviation. WWC and BWC expressed on a dry matter basis are shownin the SupplementaryMaterial, Table S1.

Family	Species	n	DGR (mm month^{-1})	DBH[1] (cm)	WWC (%)	BWC (%)	WD (g cm^{-3})
Apocynaceae	*Geissospermum argenteum* Woodson	2	0.05 ± 0.04	24.27 ± 9.74	29.62 ± 3.93	47.94 ± 9.40	0.84 ± 0.03
Burseraceae	*Protium apiculatum* Swart	8	0.11 ± 0.14	18.28 ± 8.48	31.78 ± 3.02	49.63 ± 3.64	0.63 ± 0.03
	Protium hebetatum Daly	3	0.08 ± 0.02	15.25 ± 1.79	35.98 ± 0.71	51.35 ± 28.39	0.58 ± 0.02
Chrysobalanaceae	*Licania canescens* Benoist	3	0.26 ± 0.21	36.89 ± 2.76	26.38 ± 1.57	37.71 ± 1.41	0.88 ± 0.07
	Licania micrantha Miq.	5	0.16 ± 0.13	24.52 ± 10.18	29.47 ± 3.23	36.19 ± 3.15	0.87 ± 0.02
Euphorbiaceae	*Micrandropsis scleroxylon* (W.A.Rodrigues) W.A.Rodrigues	3	0.08 ± 0.05	37.28 ± 6.07	31.56 ± 2.53	41.38 ± 3.79	0.89 ± 0.02
Fabaceae	*Swartzia tomentifera* (Ducke) Ducke	4	0.08 ± 0.04	26.41 ± 12.82	27.72 ± 2.70	45.71 ± 1.68	0.82 ± 0.04
	Tachigali venusta Dwyer	4	0.41 ± 0.32	26.84 ± 11.94	35.95 ± 5.44	53.74 ± 23.52	0.55 ± 0.06
	Inga laurina (Sw.) Willd.	4	0.33 ± 0.39	28.45 ± 11.19	32.74 ± 0.44	66.56 ± 8.73	0.79 ± 0.05
Lacistemataceae	*Lacistema aggregatum* (P.J.Bergius) Rusby	3	0.16 ± 0.11	20.10 ± 1.38	42.81 ± 3.88	63.91 ± 11.34	0.60 ± 0.06
Lauraceae	*Mezilaurus ita-uba* (Meisn.) Taub. ex Mez	5	0.03 ±0.03	18.27 ± 4.31	34.04 ± 3.26	50.96 ± 9.75	0.75 ± 0.05
Lecythidaceae	*Eschweilera bracteosa* (Poepp. ex O.Berg) Miers	12	0.08 ± 0.07	20.65 ± 4.67	32.99 ± 3.13	60.92 ± 20.07	0.83 ± 0.05
	Eschweilera collina Eyma	7	0.12 ± 0.15	22.61 ± 7.46	34.36 ± 2.49	48.25 ± 4.45	0.77 ± 0.06
	Eschweilera grandiflora (Aubl.) Sandwith	3	0.07 ± 0.07	32.38 ± 16.73	36.86 ± 2.26	55.43 ± 6.51	0.83 ± 0.02
	Eschweilera pedicellata (Rich.) S.A. Mori	5	0.05 ± 0.03	23.83 ± 15.64	33.12 ± 1.78	54.31 ± 2.06	0.78 ± 0.04
	Eschweilera sp.	4	0.03 ± 0.06	20.38 ± 6.65	32.79 ± 2.70	65.86 ± 14.16	0.82 ± 0.05
	Gustavia agusta L.	3	0.03 ± 0.05	17.42 ± 3.69	35.98 ± 1.20	53.96 ± 1.10	0.73 ± 0.07
Malpighiaceae	*Byrsonima duckeana* W.R.Anderson	4	0.16 ± 0.11	39.62 ± 9.79	40.24 ± 2.59	51.36 ± 4.84	0.61 ± 0.07
Malvaceae	*Scleronema micranthum* (Ducke) Ducke	4	0.24 ± 0.24	43.94 ± 11.06	41.38 ± 6.69	51.05 ± 5.25	0.65 ± 0.06
	Theobroma sylvestre Aubl. ex Mart. in Buchner	5	0.05 ± 0.05	13.49 ± 2.01	35.91 ± 4.32	64.93 ± 14.61	0.71 ± 0.04
Olacaceae	*Minquartia guianensis* Aubl.	3	0.03 ± 0.05	32.39 ± 18.68	32.80 ± 1.62	61.70 ± 5.50	0.81 ± 0.05
Sapotaceae	*Micropholis guyanensis* (A.DC.) Pierre	4	0.11 ±0.11	31.14 ± 12.86	32.86 ± 6.73	48.25 ± 6.82	0.71 ± 0.03
	Pouteria cladantha Sandwith	3	0.05 ± 0.30	16.09 ± 4.68	31.63 ± 13.33	46.52 ± 9.67	0.73 ± 0.21
	Pouteria guianensis Aubl.	3	0.30 ± 0.10	42.87 ± 26.96	31.16 ± 5.28	67.10 ± 20.64	0.66 ± 0.09
	Pouteria macrophylla (Lam.) Eyma	4	0.23 ± 0.15	31.38 ± 15.44	31.11 ± 8.67	60.84 ± 3.08	0.91 ± 0.08
	Pouteria sp.	3	0.04 ± 0.06	19.32 ± 4.95	34.37 ± 5.12	55.76 ± 9.19	0.78 ± 0.08
Urticaceae	*Pourouma tomentosa* subsp. *apiculada* (Spruce ex Benoist) C.C.Berg & Heusden	4	0.21 ± 0.24	30.22 ± 8.06	50.84 ± 11.99	57.61 ± 3.80	0.43 ± 0.03
Vochysiaceae	*Erisma bicolor* Ducke	3	0.05 ± 0.02	17.34 ± 2.19	44.17 ± 0.86	50.31 ± 5.20	0.57 ± 0.02
	Mean across species	**4.3**	**0.13 ± 0.12**	**26.13 ± 9.01**	**34.70 ± 3.98**	**53.43 ± 8.63**	**0.73 ± 0.05**

mass. The volume of the fresh wood and bark was calculated from the length and diameter of the samples (measured with digital calipers with 0.01 mm precision).

The dry mass of the wood and bark samples was determined by oven-drying at 102 °C until constant mass (about 72 h), and weighing on an analytical balance (precision of 0.1 mg). WWC and BWC were calculated as the water content to fresh mass ratio (i.e., fresh mass minus dry mass, divided by fresh mass, Osunkoya *et al*. 2007). WWC and BWC were expressed on a fresh matter basis, except when otherwise stated, to enable comparison with other studies. WWC and BWC on a dry matter basis (WWC_D and BWC_D) were calculated as the fresh mass minus dry mass, divided by dry mass). WD was determined as the ratio of dry mass to fresh mass volume (Suzuki 1999).

Data analysis

To assess the difference in growth rates among species, we used Kruskal-Wallis one way analysis of variance on ranks, as the data did not fulfill the normality assumption (Shapiro-Wilk test, $p < 0.05$) for parametric analysis. The Spearman correlation (r_s) was used to determine the association between DBH and WWC and BWC, between WD and mean monthly DGR, and between WD and WWC. The effect of the microclimatic variables [PAR, rainfall, mean temperature (T_{mean}), minimum temperature (T_{min}), and maximum temperature (T_{max})] on monthly DGR was analyzed with redundancy analysis (RDA), which combines multiple regression analysis (MRA) and principal component analysis (PCA). MRA allows the modeling of the effect of explanatory variables on a response variable, while PCA allows the computation of orthogonal vectors, which can be used to reduce data dimensionality. Before performing the redundancy analysis, DGR data were centered (observed value minus the mean), and microclimatic data were standardized (observed value minus the mean, divided by the standard deviation). Standardization of data is required to analyze data expressed in different physical units. In MRA, the addition of explanatory variables to the model inflates the R^2 value (explained variance divided by total variance), thus we used the R^2 adjusted, R^2_{adj} (Borcard *et al*. 2018) to assess the predictive power of the RDA model:

$$R^2_{adj} = 1 - \frac{n-1}{n-m-1}(1 - R^2)$$

where *n* represents the number of months and *m* the number of explanatory variables in the model.

The analyses were performed using R v.3.5.1 (R Core Team, 2018). The RDA was computed using the Vegan 2.5-7 package (Oksanen *et al*. 2020). The adopted significance level was $p \leq 0.05$.

RESULTS

In 2007, the annual rainfall measured at the study area was 2,638 mm. February, October, and September were the driest months, with precipitation of 100−110 mm month^{-1}. Mean monthly PAR was 25.4 mol m^{-2} day^{-1}, and mean monthly T_{mean}, T_{min} and T_{max} were 25.4 °C, 22.4 °C, and 31.9 °C, respectively.

Wood and bark water content

Mean WWC across species was 34.7%, ranging from to 26.4% in *Licania canescens* to 50.8% in *Pourouma tomentosa* subsp. *apiculada*, while mean BWC was 53.4%, ranging from 36.2% in *Licania micrantha* to 67.1% in *Pouteria guianensis* (Table 1). WWC_D varied from 41.3 to 76.5% and BWC_D from 76.9 to 321.6% (Supplementary Material, Table S1).

Both WWC and BWC varied significantly among species (H = 61.8, $p < 0.001$ for WWC; H = 57.0, $p < 0.001$ for BWC) and BWC was higher than WWC in all species (Table 1). There was no significant correlation between WD and DGR, nor between DBH and WWC ($p > 0.20$, Figure 1a,b) or BWC ($r_s = 0.002$, Figure 1d). WD was negatively correlated with WWC ($r_s = -0.69$, $p < 0.001$; Figure 1c). The correlation between WWC and BWC was also nonsignificant ($r_s = 0.29$, $p = 0.14$).

Across species, mean annual DGR was 1.56 mm (0.13 mm month^{-1}), with significant differences among species (H = 41.1, $p = 0.02$). Mean DGR ranged from 0.03 mm month^{-1} (*Eschweilera* sp., *Mezilaurus ita-uba, Gustavia augusta*, and *Minquartia guianensis*) to 0.41 mm month^{-1} in *Tachigali venusta* (Table 1).

Effect of microclimate on tree growth

The RDA showed that the constrained variance (i.e., the proportion of variance explained by microclimatic variability) accounted for 43.8% of the total variance in DGR, thus the residual variance (unconstrained variance) represented 56.2% of total variability (Supplementary Material, Table S2). The R^2 value (0.438), however, was inflated as it does not take into account the number of explanatory variables in the model. When it was adjusted, it became apparent that very little of the total variance was associated with the explanatory variables ($R^2_{ajd} \sim 0.00$), so that none of the five microclimatic variables evaluated had a significant effect on DGR ($p > 0.20$; Supplementary Material, Table S3), including monthly precipitation (Figure 2).

DISCUSSION

The significant variation in WWC and BWC across species and the lack of correlation with DBH in our study is consistent with the results reported by Dias and Marenco (2016) for the same study area and by Rosell *et al.* (2014) for tropical and temperate vegetation types. Our mean values of stem water content (34.7% for WWC and 53.4% for BWC) are within

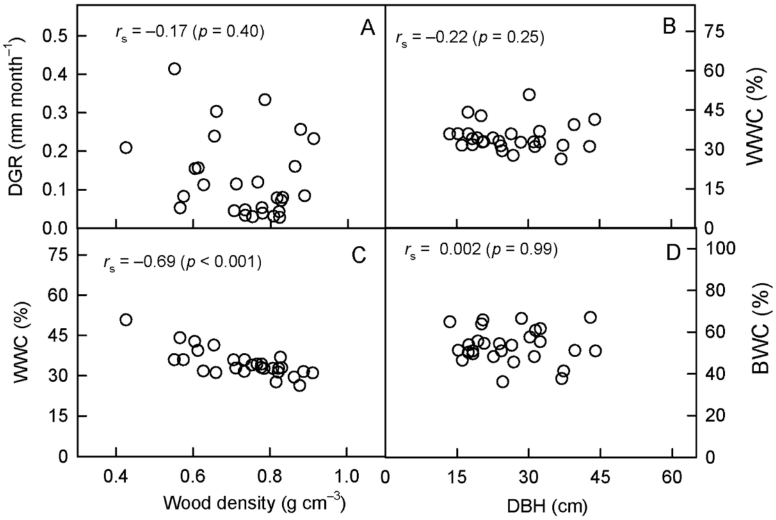

Figure 1. Relationship between: A – wood density (WD) and diameter growth rate (DGR); B – diameter at breast height (DBH) and wood water content (WWC); C – WD and WWC; and D – DBH and bark water content (BWC). WWC and BWC are expressed on a fresh matter basis. Each point represents the mean of two to 12 trees per species (see Table 1).

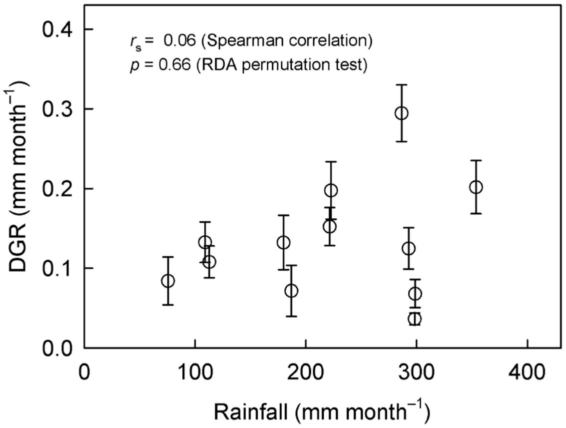

Figure 2. Monthly diameter growth rate (DGR) as a function of monthly rainfall during 2007. Each circle represents the mean monthly DGR across 28 species, while the bar indicates the standard error. The Spearman correlation (r_s) and the *p* value – obtained through a RDA permutation test (Supplementary Material, Table S3) are also shown.

the range reported by Dias and Marenco (2016) during the rainy season (25.5 − 51.4% for WWC and 31.9 − 66.4% for BWC). The observed values for WWC_D (41.3 – 76.5%) and BWC_D (76.9 – 321.6%) are within the range reported by Rosell *et al*. (2014) for over 90 species from different biomes (25 – 780% for sapwood and 39 – 515% for bark). As expected, we found no correlation between mean DBH and either WWC or BWC, a tendency that was also reported by Dias and Marenco (2016) and Kenzo *et al.* (2017).

Phylogenetic factors affect the water content within tree tissues (Hietz *et al*. 2017), which likely contributed to the wide variation in WWC and BWC observed among the 28 species, which agrees with the results reported by Rosell *et al.* (2014) and Dias and Marenco (2016). Our values for BWC were higher than those of WWC across species because wood tends to contain less water than the bark, as the xylem conduits do not alter their dimensions, while the parenchymal tissue in the bark can expand (De Schepper *et al.* 2012). Moreover, the bark has almost twice the amount of soluble sugars (osmotically active compounds) than the sapwood, which can greatly affect the bark water content (Rosell *et al*. 2021). Although a positive correlation between the water content of living bark and wood has been reported across several vegetation types (Rosell *et al.* 2014), we found no significant correlation between WWC and BWC, possibly because our study included only rainforest trees.

The negative correlation between wood density and wood water content in our study agrees with Kenzo *et al.* (2017), who found a similar relationship in a tropical dry forest in Indochina. This result is generally expected, as denser woods have thicker xylem-cell walls, which reduces water storage capacity (McCulloh *et al.* 2011). Contrary to our expectation of a negative relationship between precipitation and girth growth, stem growth did not increase in the dry season. It has been reported that in the wettest parts of the Amazon rainforest (north and central Amazon), photosynthesis or tree growth tends to increase in the dry season (Huete *et al.* 2006; Laurance *et al.* 2009; Green *et al.* 2020), as precipitation events during the rainy season can reduce photosynthesis due to cloud cover. Earlier studies carried out at the same ZF2 reserve also failed to detect a significant correlation between precipitation and stem growth (Silva *et al.* 2003; Dias and Marenco 2016). Decreased stem growth or reduced ecosystem photosynthesis can be found in years when the dry season is more prolonged

(Méndez 2018; Yang *et al*. 2018; Antezana-Vera and Marenco 2021), so the effect of the environmental conditions on tree growth depends on the climatic conditions during the growing period, in particular the frequency and intensity of precipitation, which can change substantially over time (Ciemer *et al.* 2019).

The effect of variability in temperature and irradiance on tree growth in tropical rainforests is still under debate. In a tropical rainforest at La Selva, Costa Rica, Clark *et al*. (2003) reported a negative correlation between stem growth and mean and minimum temperature over a period of 16 years, while, at the same time, no effect of maximum temperature and irradiance variability on the diameter increment of trees was found. In the central Amazon, variation in mean and minimum temperature did not affect stem growth over the 2013-2017 period, while stem growth decreased with increasing irradiance and maximum temperature across a large number of species (Marenco and Antezana-Vera 2021), which highlights the need for further research on this topic.

Production of new leaves (leaf flushing) tends to increase in the dry season (Marenco *et al*. 2019; Janssen *et al*. 2021), therefore the absence of an effect of temperature, irradiance and precipitation on DGR does not necessarily mean that canopy photosynthesis did not increase in the dry season, as assimilated carbon may have been diverted to leaf production. Wood production has relatively lower priority in comparison with production of new leaves, buds, and fine roots (Pretzsch 2009). Although many factors that affect tree growth remain to be investigated, we provided evidence that in an above-average rainy year there is no effect of precipitation, irradiance and air temperature on stem growth, even considering that photosynthesis can increase in the dry season.

CONCLUSIONS

We assessed the variation in wood water content and bark water content of trees on a *terra-firme* forest plateau in the central Amazon and evaluated the effect of monthly precipitation, irradiance, and air temperature on stem growth in a year of above-average rainfall. We found a high bark water content, which highlights the importance of the bark as an active tissue in Amazonian trees, although wood and bark water content did not correlate with stem diameter at breast height among species. In a year with rainfall intensity above the historical mean, monthly stem growth was unresponsive to variation in rainfall, temperature and irradiance, suggesting that, when water availability is not a limiting factor, a higher proportion of assimilated carbon may be diverted to higher priority organs in the dry season.

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REFERENCES

Antezana-Vera, S.A.; Marenco, R.A. 2021. Intra-annual tree growth responds to micrometeorological variability in the central Amazon. *iForest-Biogeosciences and Forestry*, 14: 242–249.

Borcard, D.; Gillet, F.; Legendre, P. 2018. Canonical Ordination. In: Borcard, D.; Gillet, F.; Legendre, P. (Ed.). *Numerical ecology with R*. 2nd ed. Springer, Cham, p. 203-298.

Borchert, R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology*, 75: 1437–1449.

Bowman, D.M.J.S.; Brienen, R.J.W.; Gloor, E.; Phillips, O.L.; Prior, L.D. 2013. Detecting trends in tree growth: not so simple. *Trends in Plant Science*, 18: 11–17.

Chapotin, S.M.; Razanameharizaka, J.H.; Holbrook, N.M. 2006. Water relations of baobab trees (*Adansonia* spp. L.) during the rainy season: does stem water buffer daily water deficits? *Plant, Cell & Environment*, 29:1021–1032.

Ciemer, C.; Boers, N.; Hirota, M.; Kurths, J.; Mueller-Hansen, F.; Oliveira, R.S.; Winkelmann, R. 2019. Higher resilience to climatic disturbances in tropical vegetation exposed to more variable rainfall. *Nature Geoscience*, 12: 174–179.

Clark, D.A.; Piper, S.C.; Keeling, C.D.; Clark, D.B. 2003. Tropical rain forest tree growth and atmospheric carbon dynamic linked to interannual temperature variation during 1984-2000. *Proceedings of the National Academy of Sciences*, 100: 5852–5857.

Costa, M.H.; Biajoli, M.C.; Sanches, L.; Malhado, A.C.M.; Hutyra, L.R.; Da Rocha, H.R.; Aguiar, R.G.; De Araujo, A.C. 2010. Atmospheric *versus* vegetation controls of Amazonian tropical rain forest evapotranspiration: are the wet and seasonally dry rain forests any different? *Journal of Geophysical Research*, 115: G04021.

De Schepper, V.; Van Dusschoten, D.; Copini, P.; Jahnke, S.; Steppe, K. 2012. MRI links stem water content to stem diameter variations in transpiring trees. *Journal of Experimental Botany*, 63: 2645–2653.

Dias, D.P.; Marenco, R.A. 2016. Tree growth, wood and bark water content of 28 Amazonian tree species in response to variations in rainfall and wood density. *iForest-Biogeosciences and Forestry*, 9: 445–451.

Green, J.K.; Berry, J.; Ciais, P.; Zhang, Y.; Gentine, P. 2020. Amazon rainforest photosynthesis increases in response to atmospheric dryness. *Science Advances*, 6: eabb7232.

Hietz, P.; Rosner, S.; Hietz-Seifert, U.; Wright, S.J. 2017. Wood traits related to size and life history of trees in a Panamanian rainforest. *New Phytologist*, 213: 170–180.

Huete, A.R.; Didan, K.; Shimabukuro, Y.E.; Ratana, P.; Saleska, S.R.; Hutyra, L.R.; *et al.* 2006. Amazon rainforests green-up with sunlight in dry season. *Geophysical Research Letters*, 33: L06405.

INMET (2021). Gráficos climatológicos. https://clima.inmet.gov.br/GraficosClimatologicos/AM/82331. Accessed on 15 May 2021.

Janssen, T.; van der Velde, Y.; Hofhansl, F.; Luyssaert, S.; Naudts, K.; Driessen, B.; *et al*. 2021. Drought effects on leaf fall, leaf flushing and stem growth in the Amazon forest: reconciling remote sensing data and field observations. *Biogeosciences*, 18: 4445-4472.

Kenzo, T.; Sano, M.; Yoneda, R.; Chann, S. 2017. Comparison of wood density and water content between dry evergreen and dry deciduous forest trees in central Cambodia. *Japan Agricultural Research Quarterly*, 51: 363-374.

Kitayama, K.; Ushio, M.; Aiba, S.-I. 2021. Temperature is a dominant driver of distinct annual seasonality of leaf litter production of equatorial tropical rain forests. *Journal of Ecology*, 109: 727-736.

Laurance, S.G.; Laurance, W.F.; Nascimento, H.E.; Andrade, A.; Fearnside, P.M.; Rebello, E.R.; Condit, R. 2009. Long-term variation in Amazon forest dynamics. *Journal of Vegetation Science*, 20: 323-333.

Longuetaud, F.; Mothe, F.; Santenoise, P.; Diop, N.; Dlouha, J.; Fournier, M.; Deleuze, C. 2017. Patterns of within-stem variations in wood specific gravity and water content for five temperate tree species. *Annals of Forest Science*, 74: 1-19.

Luo, Z.; Deng, Z.; Singha, K.; Zhang, X.; Liu, N.; Zhou, Y.; He, X.; Guan, H. 2020. Temporal and spatial variation in water content within living tree stems determined by electrical resistivity tomography. *Agricultural and Forest Meteorology*, 291: 108058.

Magalhães, N.D.S.; Marenco, R.A.; Camargo, M.A.B. 2014. Do soil fertilization and forest canopy foliage affect the growth and photosynthesis of Amazonian saplings? *Scientia Agricola*, 71: 58–65.

Marenco, R.A.; Antezana-Vera, S.A. 2021. Principal component regression analysis demonstrates the collinearity-free effect of sub estimated climatic variables on tree growth in the central Amazon. *Revista de Biología Tropical*, 69: 482-493.

Marenco, R.A.; Antezana-Vera, S.A.; Gouvêa, P.R.; Camargo, M.A.; Oliveira, M.F.; Santos, J.K. 2014. Fisiologia de espécies florestais da Amazônia: fotossíntese, respiração e relações hídricas. *Revista Ceres*, 61: 786-799.

Marenco, R.A.; Sousa, F.D.F.; Oliveira, M.F.D. 2019. Leaf phenology, growth and photosynthesis in *Pseudobombax munguba* (Malvaceae). *Revista Ceres*, 66: 1-10.

McCulloh, K.A.; Meizer, F.C.; Sperry, J.S.; Lachenbruch, B.; Voelker, S.L.; Woodruff, D.R.; Domec, J.-C. 2011. Comparative hydraulic architecture of tropical tree species representing a range of successional stages and wood density. *Oecologia*, 167: 27-37.

Méndez, C.R. 2018. *Influência do El Nino 2015- 2016 no incremento diamétrico das árvores da Amazônia Central*. Dissertação de Mestrado, Instituto Nacional de Pesquisas da Amazônia/Fundação Universidade do Amazonas, Manaus, Amazonas. 71p. (https://bdtd.inpa.gov.br/handle/tede/2550). Accessed on 10 Aug 2021.

Nogueira, E.M.; Nelson, B.W.; Fearnside, P.M.; França, M.B.; Oliveira, A.C.A. 2008. Tree height in Brazil's 'arc of deforestation': Shorter trees in south and southwest Amazonia imply lower biomass. *Forest Ecology and Management*, 255: 2963-2972.

Oksanen, J.; Blanchet, F.G.; Kindt, R.; Legendre, P.; Minchin, P.R.; O'hara, R.B.; *et al*. 2020. Package 'vegan'. (https://cran.r-project.org/web/packages/vegan/index.html). Accessed on 15 May 2021.

Osunkoya, O.O.; Sheng, T.K.; Mahmud, N.-A.; Damit, N. 2007. Variation in wood density, wood water content, stem growth and mortality among twenty-seven tree species in a tropical rainforest on Borneo Island. *Austral Ecology*, 32: 191-201.

Pastur, G.M.; Lencinas, M.V.; Cellini, J.M.; Mundo, I. 2007. Diameter growth: can live trees decrease? Forestry: An International Journal of Forest Research, 80: 83–88.

Pretzsch, H. 2009. Diagnosis of growth disturbances. In: Pretzsch, H. (Ed.). *Forest Dynamics, Growth and Yield: From Measurement to Model*. Springer-Verlag, Berlin, p.553–591.

R Core Team, 2018. R: A language and environment for statistical computing. (https://www.R-project.org/). Accessed on 15 May 2021.

Rosell, J.A.; Gleason, S.; Méndez-Alonzo, R.; Chang, Y.; Westoby, M. 2014. Bark functional ecology: evidence for tradeoffs, functional coordination, and environment producing bark diversity. *New Phytologist*, 201: 486-497.

Rosell, J.A.; Piper, F.I.; Jiménez-Vera, C.; Vergílio, P.C.; Marcati, C.R.; Castorena, M.; Olson, M.E. 2021. Inner bark as a crucial tissue for non-structural carbohydrate storage across three tropical woody plant communities. *Plant, Cell & Environment*, 44: 156-170.

Silva, R.P.; Nakamura, S.; Azevedo, C.P.; Chambers, J.; Rocha, R.D.; Pinto, A.C.; Santos, J.; Higuchi, N. 2003. Use of metallic dendrometers for individual diameter growth patterns of trees at Cuieiras river basin. *Acta Amazonica*, 33: 67-84.

Stahl, C.; Burban, B.; Bompy, F.; Jolin, Z.B.; Sermage, J.; Bonal, D. 2010. Seasonal variation in atmospheric relative humidity contributes to explaining seasonal variation in trunk circumference of tropical rain-forest trees in French Guiana. *Journal of Tropical Ecology*, 26: 393-405.

Suzuki, E. 1999. Diversity in specific gravity and water content of wood among Bornean tropical rainforest trees. *Ecological Research*, 14: 211-224.

Yang, J.; Tian, H.; Pan, S.; Chen, G.; Zhang, B.; Dangal, S. 2018. Amazon drought and forest response: largely reduced forest photosynthesis but slightly increased canopy greenness during the extreme drought of 2015/2016. *Global Change Biology*, 24: 1919-1934.

Ziemińska, K.; Rosa, E.; Gleason, S.; Holbrook, N.M. 2020. Wood day capacitance is related to water content, wood density, and anatomy across 30 temperate tree species. *Plant, Cell & Environment*, 43: 3048-3067.

Zweifel, R.; Item, H.; Häsler, R. 2001. Link between diurnal stem radius changes and tree water relations. Tree Physiology, 21: 869-877.

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SUPPLEMENTARY MATERIAL (only available in the electronic version)

Dias & Marenco. Wood and bark water content and monthly stem growth in Amazonian tree species

Table S1. Wood water content (WWC_D) and bark water content (BWC_D) expressed on a dry matter basis for 28 tree species in a terra-firme forest in the central Amazon. The range of the diameter at breast height (DBH) and tree height of the sampled individuals of each species are also shown. Tree height was computed after Nogueira *et al*. (2008).

Species	WWC_D (%)	BWC_D (%)	DBH (cm)	Height (m)
Byrsonia duckena	54.2 ± 0.09	96.4 ± 0.20	25.9 – 48.6	26.2 – 32.6
Erisma bicolor	52.5 ± 0.20	96.7 ± 0.42	15.3 – 19.5	19.7 – 23.0
Eschweilera bracteosa	56.9 ± 0.32	179.2 ± 1.26	13.7 – 27.0	19.2 – 26.0
Eschweilera collina	50.4 ± 0.08	96.6 ± 0.16	12.1 – 29.8	18.2 – 28.1
Eschweilera grandiflora	68.8 ± 0.18	102.1 ± 0.39	19.7 – 49.5	23.0 – 32.8
Eschweilera pedicellata	44.8 ± 0.03	110.9 ± 0.34	13.1 – 50.0	17.3 – 32.7
Eschweilera sp.	42.1 ± 0.09	192.7 ± 14.69	14.4 – 27.6	18.2 – 25.7
Geissospermum agregateum	41.3 ± 0.08	89.0 ± 0.39	13.6 – 37.2	18.4 – 29.0
Gustavia agusta	70.2 ± 0.31	153.2 ± 0.39	13.6 – 21.1	17.7 – 23.1
Inga laurina	63.8 ± 0.21	294.6 ± 1.82	18.4 – 34.0	22.7 – 31.1
Lacistema aggregatum	47.6 ± 0.20	81.3 ± 0.49	15.7 – 19.9	22.3 – 23.3
Licania canescens	51.1 ± 0.14	107.3 ± 0.54	31.3 – 38.7	27.9 – 29.6
Licania micrantha	50.3 ± 0.05	321.6 ± 2.62	14.9 – 38.3	20.6 – 30.4
Mezilaurus ita–uba	76.5 ± 0.40	195.5 ± 1.75	10.9 – 21.8	14.8 – 23.5
Micrandropsis scleroxylon	45.7 ± 0.05	102.6 ± 0.18	30.1 – 41.0	26.7 – 30.3
Micropholis guyanensis	51.4 ± 0.20	90.2 ± 0.26	19.6 – 43.7	22.9 – 31.7
Minquartia guianensis	51.9 ± 0.08	157.1 ± 0.29	16.8 – 52.1	20.4 – 33.2
Pourouma tomentosa	49.8 ± 0.08	97.1 ± 0.32	17.7 – 36.2	22.2 – 29.9
Pouteria cladantha	50.7 ± 0. 04	135.2 ± 0.47	11.9 – 20.4	15.5 – 23.0
Pouteria guianensis	56.9 ± 0.29	115.7 ± 0.15	22.5 – 66.2	23.7 – 37.8
Pouteria macrophylla	63.0 ± 0.20	184.1 ± 1.11	15.3 – 47.7	25.5 – 33.1
Pouteria sp.	46.2 ± 0.04	76.9 ± 0.10	14.2 – 23.0	18.2 – 24.4
Protium apiculatum	52.7 ± 0.14	90.7 ± 0.28	10.5 – 31.1	15.5 – 27.7
Protium hebetatum	56.2 ± 0.02	198.6 ± 2.45	12.0 – 15.5	17.1 – 20.0
Scleronema micranthum	55.8 ± 0.22	88.7 ± 0.27	28.1 – 52.4	26.1 – 33.7
Swartzia tomenifera	53.3 ± 0.18	83.8 ± 0.19	11.4 – 36.6	15.8 – 29.2
Tachigali venusta	51.9 ± 0.07	117.8 ± 1.80	10.6 – 30.6	16.3 – 29.3
Theobroma sylvestre	49.7 ± 0.10	187.6 ± 2.65	11.7 – 15.8	15.7 – 20.4

Table S2. Proportion of constrained variance of the effect of microclimatic variables on monthly diametric growth of 28 tree species in the central Amazon as explained by RDA–axes. The *p*, R^2 and R^2_{adj} values and the unconstrained (residual) variance are also shown.

RDA–axis	Variance	Proportion of variance	*p* value
RDA1	0.11765	0.594492	0.384
RDA2	0.03675	0.185700	0.990
RDA3	0.01945	0.098282	1.000
RDA4	0.01868	0.094391	0.990
RDA5	0.00540	0.027287	0.999
Constrained	0.1979	0.4379	
Unconstrained (residual)	0.2541	0.5621	
Total variance	0.4520	1.00	
$R^2 = 0.4378$ (0.1979/0.452)			
$R^2_{adj} = -0.03$ (~0.00)			

Table S3. Effect of microclimatic variables on monthly diametric growth of 28 central Amazonian tree species assessed by redundancy analysis and p values determined by the ordistep function of the Vegan package of the R program. Because none of the variables had a significant effect on tree growth, only the full model is shown. T_{min} = minimum temperature; T_{max} = maximum temperature; T_{mean} = mean temperature; PAR = photosynthetically active radiation; DF = degrees of freedom; F = ratio between explained and residual variance; *p* value = probability value.

Variable	DF	F	*p* value
Rainfall	1	0.6959	0.660
T_{min}	1	0.7042	0.630
T_{max}	1	0.8658	0.540
T_{mean}	1	0.9344	0.395
PAR	1	1.4909	0.205