



Artigos

Variation in bark water content in three Amazonian species in response to rainfall seasonality

Variação do conteúdo de água da casca em três espécies amazônicas em resposta à sazonalidade da precipitação

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ABSTRACT

Stem water content is an important component of daily water balance, as water reserves in tree tissues can provide water to leaves when transpiration is intense, but how it varies over rainfall seasons is still unknown. The purpose of this study was to determine the variation of wood and bark water content and stem growth in response to microclimatic variability in three Amazonian species. Trees of *Protium apiculatum*, *Lecythis prancei*, and *Rinorea paniculata* (DBH \geq 10 cm) were selected in a central Amazon forest. Wood water content (WWC) and bark water content (BWC) data were obtained in the dry and rainy season. Stem growth was measured at monthly intervals using dendrometric tapes during 24 months. Rainfall, air temperature and irradiance data were also recorded, and the effect of microclimatic variability on stem growth evaluated. WWC did not vary between seasons ($p = 0.28$), but BWC increased in the wet season ($p = 0.07$), particularly in *R. paniculata*. Although stem growth varied intra-annually ($p < 0.01$), none of the climatic variables investigated had a significant effect on stem growth ($p = 0.97$). This work shows that in a typical rainfall year, climatic variability is not large enough to cause significant variation in stem growth, even when rainfall seasonality may cause variation in bark water content.

Keywords: Stem water content; Tree growth; Bark thickness; Redundancy analysis (RDA)

RESUMO

O conteúdo de água do tronco é um componente importante do balanço hídrico diário, pois as reservas nos tecidos das árvores podem fornecer água às folhas quando a transpiração é intensa, mas como esta varia ao longo das estações de chuvas ainda é desconhecido. O objetivo deste estudo foi determinar a variação do conteúdo de água da madeira e da casca e o crescimento do tronco em resposta às variáveis microclimáticas em três espécies arbóreas amazônicas. Árvores de *Protium apiculatum*, *Lecythis prancei* e *Rinorea paniculata* (DAP \geq 10 cm) foram selecionadas em uma floresta da Amazônia central. Dados de conteúdo de água da madeira (WWC) e da casca (BWC) foram obtidos na estação seca e chuvosa. O crescimento do tronco foi medido em intervalos mensais usando fitas dendrométricas durante 24 meses. Os dados de precipitação, temperatura do ar e irradiância também foram registrados, e o efeito da variabilidade microclimática sobre o crescimento do tronco avaliado. O WWC não variou entre as estações ($p = 0,28$), mas o BWC aumentou na estação chuvosa ($p = 0,07$), principalmente em *R. paniculata*. Embora o crescimento das árvores tenha variado intra-anualmente ($p < 0,01$), nenhuma das variáveis microclimáticas investigadas o afetaram significativamente ($p = 0,97$). Este trabalho mostra que em um ano de chuva típica, a variabilidade climática não é grande o suficiente para causar variação significativa no crescimento do tronco das árvores, mesmo quando a sazonalidade das chuvas pode causar variação no conteúdo de água da casca.

Palavras-chave: Conteúdo de água no tronco; Crescimento de árvores; Espessura da casca; Análise de redundância (RDA)

1 INTRODUCTION

The capacitance of tree tissues is a parameter that describes the amount of stored water potentially available to buffer fluctuations of water potential in a tree (LONGUETAUD *et al.*, 2017), and it has been reported that internal water reserves can account for 9-15% of tropical tree transpiration –up to 54 kg per day in a 1.02-m diameter tree (GOLDSTEIN *et al.*, 1998), but that contribution can be even larger in Amazonian trees (YAN *et al.*, 2020). On a daily basis, stored water in tree tissues balances the difference between water efflux from the canopy (transpiration) and water influx from the roots (sap flow), which may lead to diurnal variations in stem diameter (DE SCHEPPER *et al.*, 2012; ANTEZANA-VERA; MARENCO, 2021a).

In the central Amazon the driest period (< 100 mm month⁻¹) lasts only a few months, from July to September (INMET, 2021; ANTEZANA-VERA; MARENCO, 2021b), when roots can extract water from the deepest layers of the soil (BROEDEL *et al.*, 2017).

While the roots determine the amount of water taken up by a tree, the bark and sapwood have a key role in determining its capacitance. Thus, the knowledge of the variability of wood and bark water content in tree species is essential for the understanding of the mechanisms involved in water storage in tree tissues (ZIEMIŃSKA *et al.*, 2020).

Regarding the effects of microclimatic variability on tree growth, Grogan and Schulze (2012) and Marengo and Antezana-Vera (2021) found a positive relationship between growth and rainfall intensity, whereas Elias *et al.* (2020) reported that tree growth can increase in the warmest years, in response to an increase in temperature. Likewise, Dong *et al.* (2012) reported a positive correlation between incoming solar radiation and tree growth. It seems that the effect of climatic variability on tree growth in the central Amazon depends on the length of the dry season, as during prolonged droughts (such as that of 2015-2016) climatic parameters that increase in the dry season (e.g. irradiance, vapor pressure deficit) seem to have a negative effect on tree growth and ecosystem photosynthesis (YANG *et al.*, 2018, ANTEZANA-VERA; MARENCO, 2021b). Other factors also affect tree growth, including site quality (e.g., soil fertility and topography), ontogeny – tree size (BOWMAN *et al.*, 2013) and competition (VATRAZ *et al.*, 2018). Hence, understanding how tree growth of Amazonian species responds to seasonal variations is valuable information for modeling tree growth in response to climate changes.

We hypothesize that wood water content (WWC) and bark water content (BWC) would vary reflecting variation in rainfall seasonality, and expected WWC and BWC would increase in the wet season. We also expected that stem growth would increase with increasing irradiance and temperature, and hence that it would decrease with a rise in rainfall intensity. Thus, the objectives of this study were to determine the variation of wood and bark water content in the dry and wet season of the year and assess the effect of microclimate variability on stem growth rate in three Amazonian species.

2 MATERIALS AND METHODS

2.1 Study area and plant material

The study was conducted at the Tropical Forest Experimental Station (ZF2, at a plot centered at 02°36'21" S and 60°08'11" W) of the National Institute for Research in the Amazon, State of Amazonas, Brazil. This experimental area has a tropical humid climate, with an annual rainfall of 2,420 mm and a mild dry season from June through October, being July–September the driest months (< 100 mm month⁻¹; INMET, 2021). Mean annual temperature is about 26°C (Dias; Marengo, 2016; Antezana-Vera; Marengo, 2021b). The vegetation is classified as dense *terra-firme* forest, and the soil is an Oxisol with low fertility, clay texture, and pH (in water) of 3.9-4.0 (Magalhães *et al.*, 2014).

Microclimate data (rainfall, air temperature - T_{air} and photosynthetically active radiation - PAR) were daily recorded in 2006 and 2007, using a weather station Li-1401 (Li-Cor, Lincoln, NE, USA) above the forest canopy, at the top of a 40-m tall observatory tower (02°35'21"S and 60°06'53"W). A standard rain gauge was used for collecting rainfall data. Light (Li-190SA, Li-Cor Inc., Lincoln, Nebraska, USA) and temperature (Humitter® 50Y, Vaisala Oy, Finland) sensors were connected to a datalogger (LI-1400, Li-Cor). Temperature (T_{air}) data were collected at 30-minute intervals and PAR data at intervals of 15 minutes. From these data, daily values of mean minimum (T_{min}), mean (T_{mean}) and mean maximum temperature (T_{max}), and PAR were obtained. Daily PAR was calculated by integrating the instantaneous PAR values over the whole day period (mol m⁻² day⁻¹), then a mean monthly value was obtained.

Three tropical tree species growing on a terra-firme plateau in central Amazonia were sampled in this study: *Protium apiculatum* Swart (Burseraceae), *Lecythis prancei* S.A.Mori (Lecythidaceae), and *Rinorea paniculata* (Mart.) Kuntze (Violaceae). They had a mean diameter (DBH) of 19.4 cm (Table 1) and mean height of 21.6 m, being tree height estimated after Souza and Marengo (2022). These species were selected based on the availability of at least five trees (DBH ≥ 10 cm) per species in the study area.

Table 1 – Species, mean fresh bark thickness (\pm standard error, SE) and stem growth (T_G , mm month⁻¹)

Species	Fresh bark thickness (mm \pm SE)	TG \pm SE (mm month ⁻¹)	WD (g cm ⁻³)	Height (m)	DBH (cm)
Protium apiculatum	3.55 \pm 0.24 a	0.103 \pm 0.03	0.72 \pm 0.02b	18.84 \pm 1.35	14.23 \pm 1.67
Lecythis prancei	2.61 \pm 0.29 ab	0.087 \pm 0.02	0.80 \pm 0.02a	25.79 \pm 2.57	27.96 \pm 6.16
Rinorea paniculata	2.43 \pm 0.12 b	0.092 \pm 0.02	0.68 \pm 0.01b	20.21 \pm 1.42	16.09 \pm 2.09
Mean	2.86 \pm 0.18	0.094 \pm 0.01	0.73 \pm 0.19	21.61 \pm 1.28	19.43 \pm 2.63
<i>p</i> value	< 0.01	0.93	< 0.01		

Correlations:
 T_G versus WWC: $r = 0.07$, $p = 0.77$
 T_G versus BWC: $r = 0.29$, $p = 0.22$

Source: Authors (2021)

In where: There are also shown, wood density (WD), tree height e diameter at breast height (DBH), and the simple correlation between T_G and wood water content (WWC) and bark water content (BWC); $n = 5$ trees per species.

2.2 Stem water content, wood density and stem growth

Wood and bark samples were collected during March-May (rainy season) and July-September (dry season) of 2006 and 2007, from the same trees used for measuring stem growth. The samples (3 to 5 cm in length) were extracted from the stem at about 1.40 m from the ground, with a 5.15-mm internal diameter increment borer (Haglof, Sweden). After extraction, the fresh core sample (wood and bark) was placed into a small capped test tube and stored in a thermally insulated box with ice and transported to the laboratory, where the wood volume and fresh and dry mass (bark and wood) were determined. The volume of the fresh wood sample was determined from its length (measured with digital calipers, accuracy of 0.01 mm) and the increment borer inside diameter. The dry mass (wood and bark) was obtained after drying the sample in a forced-air oven at 102 °C until constant mass (about 72 h). The relative water content of wood (WWC) and bark (BWC) was calculated as the water content (fresh mass minus dry mass) to fresh mass ratio (OSUNKOYA *et al.*, 2007). While fresh bark thickness was measured using digital calipers. Wood density (WD) was determined as the ratio of dry mass to fresh mass volume (SUZUKI, 1999).

Tree diameter at breast height (DBH) of the studied species was measured at monthly intervals (24 measurements per tree) using dendrometer tapes installed in 2005 (i.e. before the beginning of data collection). The increment in tree girth was measured using digital calipers, with 0.01 mm accuracy. Monthly stem growth in diameter (hereafter referred to as stem growth, TG) was calculated as: $(DBHe - DBHb)/t$, where DBHe and DBHb represent the diameter of a tree at the end (e) and the beginning (b) of the measurement interval, and t the time (one month).

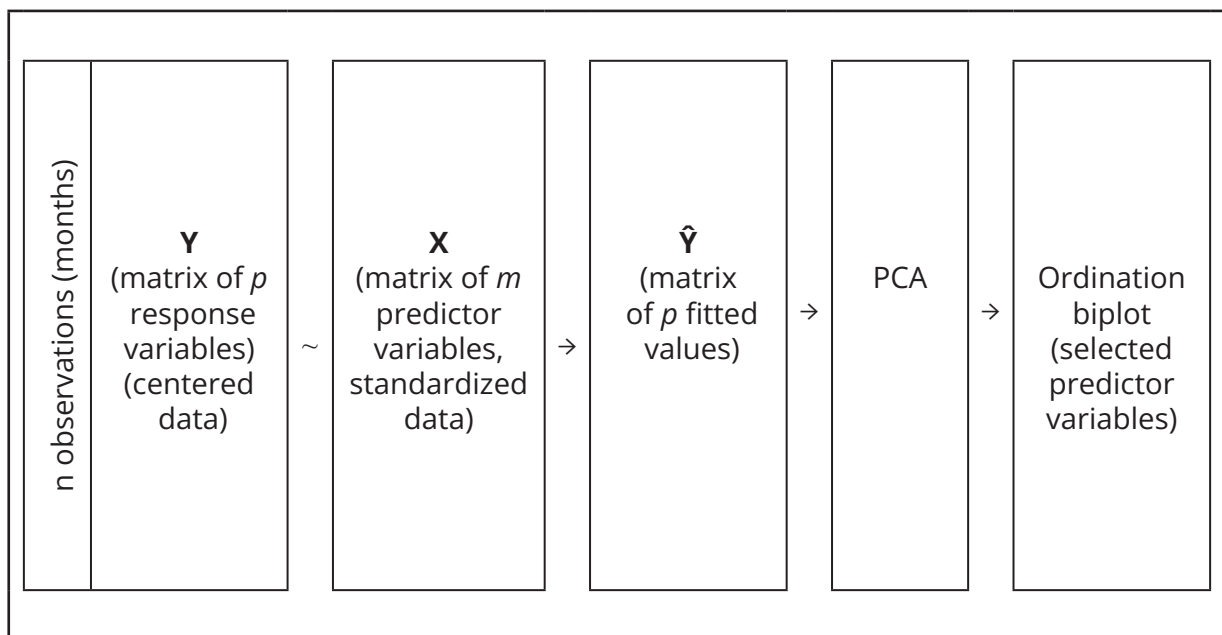
2.3 Data analysis

We conducted a repeated-measures analysis of variance to assess the effect of species and time (months) on T_G , as well as to evaluate the effect of rainfall seasonality on bark water content and wood water content. We followed this approach because the measurements were carried out in the same tree, and when required (to stabilize variance) data were log-transformed prior to data analysis. Whereas the effect of the climatic parameters (rainfall, T_{min} , T_{mean} , T_{max} and PAR) on mean monthly stem growth (T_G) was evaluated using redundancy analysis (RDA). The RDA is a constrained ordination procedure that models linear relationships among predictor variables and response variables. By combining ordination (principal component analysis – PCA) and multiple linear regression (MLR) climatic data (predictors) and T_G of species (response variables) over time (months) can be analyzed simultaneously, as illustrated in Figure 1.

In RDA analysis (Figure 1), the first step is to perform MLR analyses of the response variables as a function of predictor variables (Y~X), and the full model tested. If it is significant, the fitted values (\hat{Y}_i) are subjected to PCA. Then, significant predictor variables are selected (e.g. backward or forward selection). In the forward approach, the significance of *F*-values is tested (by permutations), and the most significant

predictor selected (if its p -value reaches a pre-defined value). The process continues until no additional significant predictor can enter the model (Borcard *et al.* 2018). Finally, a RDA bi(tri)plot can be constructed. Thus, following the RDA protocol, stem growth data were centered (observed value minus the mean) and climatic data were standardized (observed value minus the mean divided by the standard deviation) prior to RDA analysis, which was performed using the Vegan package and R v.4.2.0. We also computed the Pearson (simple) correlation between the mean TG over species (TG-mean) and SWC and BWC, as well as between TG-mean and PAR, rainfall and Tmean. In this study we adopted a significant level of $p = 0.10$.

Figure 1 – Schematic representations of redundancy analysis (RDA)



Source: Authors (2021)

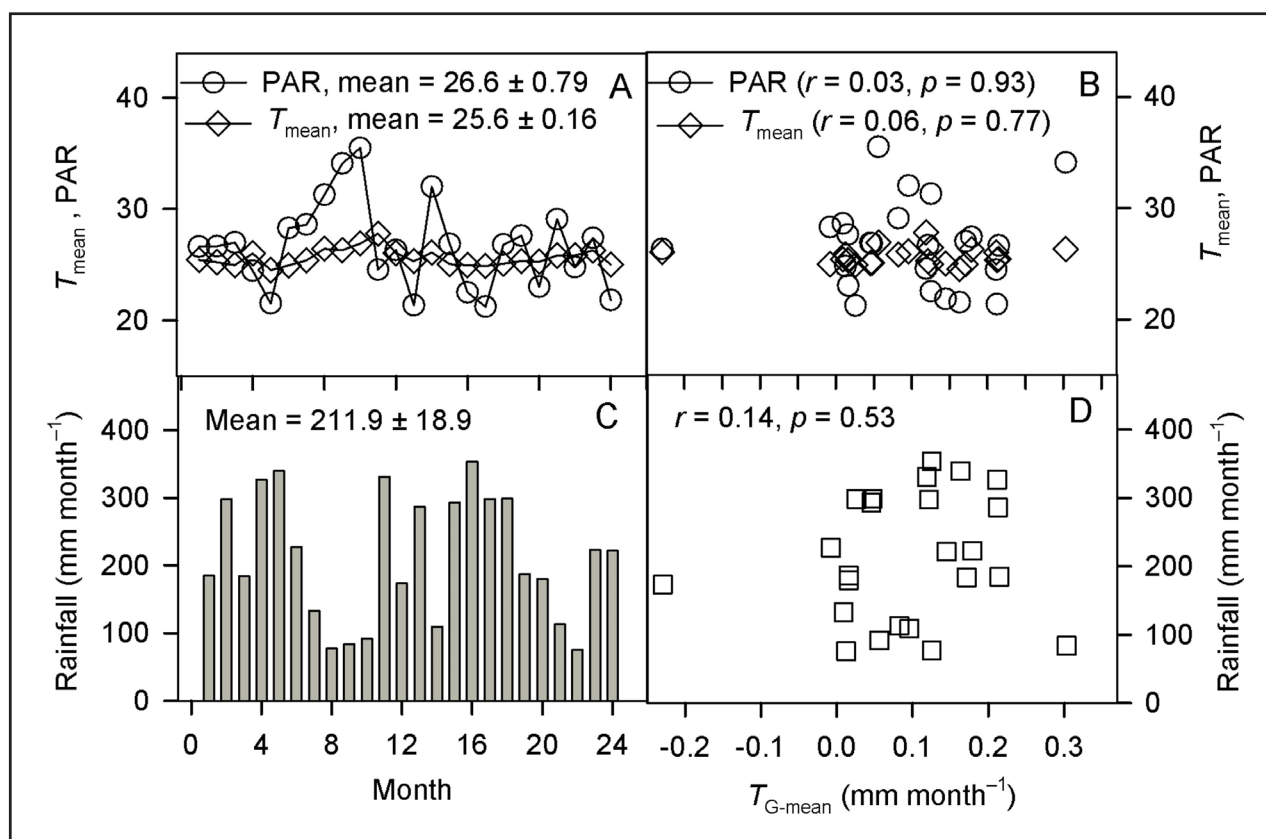
In where: Y represents tree growth; X represents the climatic variables.

3 RESULTS

During the 2006-2007 study period mean monthly temperature and PAR were 25.6°C and 26.6 mol m⁻² day⁻¹, respectively, while mean monthly rainfall was 211.9 mm (Figure 2) or 2,543 mm yr⁻¹.

There was no difference between species in WWC ($p = 0.31$) and likewise, the effect of rainfall seasonality on WWC was not significant ($p = 0.28$, Figure 3A). On the other hand, BWC varied between species ($p = 0.02$), as well as between the wet and dry season of the year ($p = 0.07$), whereas the interaction between season and species was not significant ($p = 0.54$; Figure 3B) indicating that the effect of rainfall seasonality on BWC was similar over species. On average, WD was 0.73 g cm^{-3} , with difference between species (Table 1).

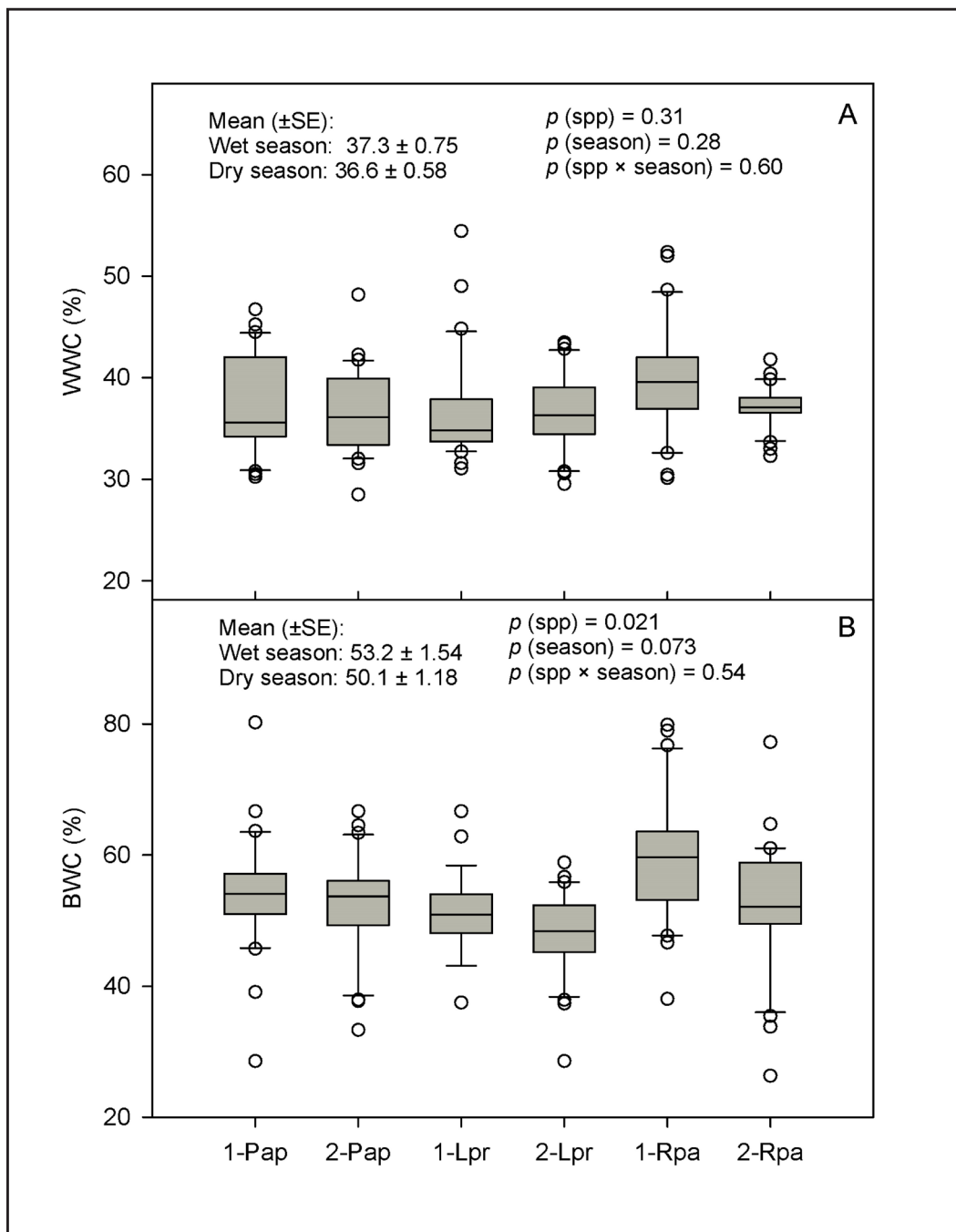
Figure 2 – Climatic data recorded over the experimental period and the correlation between climatic variability and tree growth



Source: Authors (2021)

In where: A: Mean air temperature (T_{mean} , in $^{\circ}\text{C}$, diamond) and photosynthetically active radiation (PAR in $\text{mol m}^{-2} \text{ day}^{-1}$, circle); B: the relationship between mean stem growth over species ($T_{\text{G-mean}}$) and T_{mean} and PAR; C: monthly rainfall (months of 2006 and 2007 indicated by numerals, being January of 2006: month 1, and December of 2007: month 24); D: the relationship between $T_{\text{G-mean}}$ and rainfall. Mean values (\pm SE) of climatic variables and p values of simple correlations (r) are also shown.

Figure 3 – Wood water content (WWC) and bark water content (BWC) of studied species



Source: Authors (2021)

A: Wood water content and B: bark water content during three months of the rainy season (March, April and May) and three months of the dry season (July, August and September) in the studied species (sp). Each box represents the mean of 30 observations (five trees, tree samples per tree and two years, 2006 and 2007). The boundaries of the box indicate the 25th and 75th percentile, while the solid line within the box shows the median, while the outliers are indicated by circles; Acronyms: 1: rainy season; 2: dry season; Pap: *Protium apiculatum*; Lpr: *Lecythis prancei*; Rpa: *Rinorea paniculate*.

The lowest BWC values were observed in *L. prancei*, and the highest in *R. paniculata* during the rainy season, while intermediate BWC values were observed in *P. apiculatum* (Figure 3B). Over species, BWC was 6.2% higher in the wet season than in the dry season. During the dry season, the highest reduction in BWC was observed in *R. paniculata* (14%, 59.4 versus 52.1%, Table 2), and the least in *L. prancei* (3%), an intermediate reduction in BWC was observed in *P. apiculatum*. There was no correlation between stem growth and WWC ($r = 0.07$, $p = 0.77$); neither between stem growth and BWC ($r = 0.29$, $p = 0.22$, Table 1). We also found that fresh bark thickness varied among species; *P. apiculatum* had the thickest bark (3.55 mm), while *R. paniculata* and *L. prancei* had similar bark thickness, about 2.5 mm (Table 1).

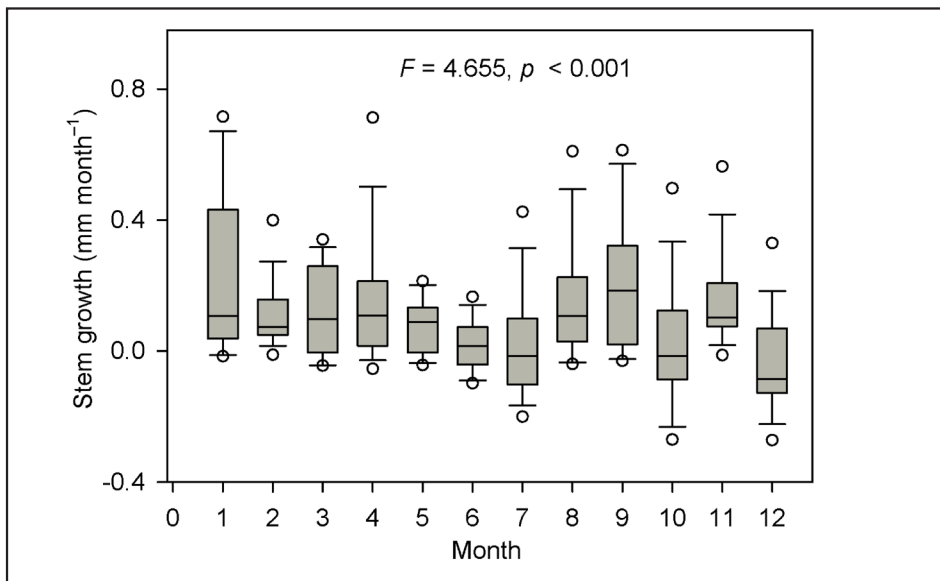
Table 2 – Bark water content (BWC, %) and wood water content (WWC, %) of species within season (mean \pm SE, $n = 5$ trees per species)

Species	Wet season		Dry season	
	WWC (%)	BWC (%)	WWC (%)	BWC (%)
<i>P. apiculatum</i>	37.10 \pm 1.24	53.82 \pm 2.48	36.65 \pm 1.09	51.19 \pm 2.40
<i>L. prancei</i>	36.34 \pm 1.23	49.43 \pm 2.26	36.21 \pm 0.99	47.97 \pm 1.53
<i>R. paniculata</i>	39.71 \pm 1.17	59.35 \pm 1.80	37.14 \pm 0.35	52.07 \pm 1.25
Mean	37.32 \pm 0.75	53.17 \pm 1.54	36.57 \pm 0.58	50.08 \pm 1.18

Source: Authors (2021)

Over the study period mean growth rate was 1.13 mm yr⁻¹ (0.094 mm month⁻¹), with no significant difference between species ($p = 0.93$, Table 1). However, across species, the monthly growth rate varied significantly (Figure 4, $p < 0.01$).

Figure 4 – Monthly stem growth over species during the study period (2006 and 2007)



Source: Authors (2021)

In where: Each box represents the mean of 15 trees in the indicated month. Month 1 corresponds to January and month 12 to December. Data were log-transformed prior to analysis of variance.

Even when the monthly growth rate varied over time, the redundancy analysis showed that all the climatic variables combined had no significant effect on stem growth ($p = 0.977$, Table 3). For illustration, the relationship between the mean stem growth across species ($T_{G\text{-mean}}$) and rainfall, PAR and T_{mean} is shown in Figure 2B, D.

Table 3 – Proportion of variance explained by constrained (RDA) and unconstrained ordination (residual)

Partitioning of variance	DF	Variance	Variance (%)
Constrained	5	0.075775	7.578%
Unconstrained (residual)	18	0.924225	92.420
Total ($n - 1$)	23	1.000	100

$F = 0.295$

$p = 0.977$

$R^2 = 0.076$, adjusted $R^2 = 0.00$

Source: Authors (2021)

In where: DF: degree of freedom; RDA model: T_G of species \sim rainfall, PAR, T_{min} , T_{mean} and T_{max} along 24 months.

4 DISCUSSION

We found no effect of rainfall seasonality on WWC, while BWC varied within season ($p = 0.07$). Mean BWC within species varied from 48% to 59%, which is within the range of values reported by Rossell *et al.* (2014, i.e. 17–76%, median of 41.5%) and Dias and Marengo (2016). Over species and environmental conditions, difference in BWC and WWC can occur due to seasonal variations and phylogenetic factors, which may affect wood traits, including the stem water content of trees (SUZUKI, 1999; HIETZ *et al.*, 2017).

In this study the bark presented higher water content than the wood tissue (lower WWC). This can be explain by taking into account, that xylem conduits do not alter their dimensions, which is in contrast to living tissues that can expand (DE SCHEPPER *et al.*, 2012). Therefore, living components of bark can expand in response to hydration, not only due to variation is soil water content, but even in response to variation in atmospheric humidity (STAHL *et al.*, 2010). In central Amazonia, Dias and Marengo (2016) concluded that the mild dry season is not long enough to deplete soil water beyond the reach of the root system, which allows the trees to grow at quite constant rates over the year. The high soil water availability (inferred from rainfall data, Figure 2C) and the capability of trees for extracting water from deepest soil layers during the dry period (BROEDEL *et al.*, 2017) can explain the relative low variability in WWC between rainfall season, irrespective of stem growth rates.

Variations in stem diameter may be associated with diurnal or seasonal changes in stem water content, and at least in part in response to variation in bark water content (STAHL *et al.*, 2010; DE SCHEPPER *et al.*, 2012). Also, seasonal variations in relative humidity may contribute to variations in stem diameter of rainforest trees (STAHL *et al.*, 2010), as such changes can influence bark water content. Thus, many factors may contribute to tree growth, including site quality where a tree settle and develop, or even tree size (BOWMAN *et al.*, 2013).

We found a mean stem growth rates of 1.13 mm yr⁻¹, which is not unexpected for the central the Amazon, where trees often show a relatively slow growth rate (SILVA *et al.*, 2003; DIAS; MARENCO, 2016; ANTEZANA-VERA; MARENCO, 2021b). Climatic variability did not influence stem growth (Table 3), which indicates that intra-annual changes in rainfall, temperature or irradiance intensity were not too large as to affect stem growth in diameter. Hence, the lack of an effect of the evaluated microclimatic variables on stem growth shows that other factors associated with seasonality (e.g. leaf production) may affect stem growth. Besides climatic factors, tree competition can also affect tree growth (VATRAZ *et al.*, 2018), which ultimately leads to the spatial arrangement of trees in the forest stand (PICARD, 2019).

In the dry season, air temperature and PAR intensity tend to increase (Marengo; Antezana-Vera, 2021). We had hypothesized that stem growth would increase in the dry season, but it did not, which negated our expectation, but on the other hand, BWC increased during the wet season, as we had expected and thus, in this respect the results supported our hypothesis. Although air temperature is evidently an important factor for tree functioning, there is no consensus if intra-annual variations in temperature affect tree growth in tropical rainforests. Clark *et al.* (2003) and Dong *et al.* (2012) reported a negative correlation between minimum (night-time) temperature and tree growth. Likewise, Camargo and Marengo (2022) observed a negative effect of an increase in mean temperature on stem growth, but in contrast, Elias *et al.* (2020) reported that tree growth increased in warmest years in secondary forests of Eastern Amazon.

A nonsignificant correlation between stem growth and stem water content (particularly BWC) indicates that factors that lead to variations in stem water content do not cause the same effect on stem growth. Perhaps because the variations in stem water content, often associated with stem swelling and shrinking of tropical trees (STAHL *et al.*, 2010; DE SCHEPPER *et al.* 2012), are too dynamic which makes the trends of the T_G -WWC relationship difficult to be detected. The bark thickness of our trees was

only a few millimeters thick (lower than the mean of Amazonian trees, 6–7 mm; Pausas, 2015), which suggests that the swelling and shrinking amplitude associated with BWC was small. Indeed, Rossel *et al.* (2014) reported that higher water contents are often associated with thicker barks. As already mentioned, the bark of the study species was rather thin. This is relevant, not only for its effect on BWC, but also because with global warming the rainfall pattern of the Amazon is changing (MARENGO *et al.*, 2018). Drier areas are more susceptible to fires, and under fire episodes trees with thinner barks are more vulnerable to fire temperatures (PAUSAS *et al.*, 2015).

5 CONCLUSION

Bark water content was affected by the rainfall seasonality, but wood water content did not. Nevertheless, variations in bark water content were not large enough to affect stem growth, as the correlation between stem growth and bark water content was insignificant. Contrary to what is often observed in drier years, stem growth did not respond to microclimatic variability, indicating that in a typical rainy year, other factors may cause variations in stem growth. A contribution of this study is to show that variation in stem water content does not seem to have an effect on tree growth in a typical rainy year, which improves our understanding of the effect of climatic variability on Amazonian trees.

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