

ORIGINAL ARTICLE

Radial growth of seven multipurpose-use Amazonian tree species in response to intra-annual variations in rainfall, temperature and atmospheric dryness

Crescimento radial de sete espécies de árvores Amazônicas de uso múltiplo em resposta às variações intra-anuais na pluviosidade, temperatura e déficit de pressão de vapor

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ABSTRACT

The intra-annual increase in irradiance and temperature is associated with a short dry season in the central Amazon. Notwithstanding, the accurate effect of intra-annual microclimatic variability on tree growth of multipurpose-use species is still under investigation. The aim of this study was to evaluate how stem growth in diameter (radial growth) responds to monthly variations in microclimatic factors in the central Amazon. During four years (2018-2021) we recorded climatic data and measured stem growth of 29 trees from seven species. In order to evaluate the effect of microclimatic variability on radial growth we applied principal component regression. On average the species had a stem growth in diameter of $1.50 \pm 0.74 \text{ mm yr}^{-1}$. The radial growth of most species increased with an increase in monthly rainfall intensity and soil moisture, while the effect of mean temperature and vapor pressure deficit varied among species. In *Brosimum parinarioides*, *Licania micrantha*, and *Pouteria guianensis* stem growth decreased with a rise in mean temperature, while the increase in mean vapor pressure deficit slowed down the radial growth in *Brosimum parinarioides*, *Licania micrantha*, *Micropholis guyanensis*, *Pouteria guianensis* and *Theobroma sylvestre*. Minimum and maximum temperatures had a neutral effect on stem growth across species. This study shows that the evaluated multipurpose-use trees are not acclimated to intra-annual climatic variability, as in addition to reducing growth during the dry season, they also responded to monthly changes in mean temperature and vapor pressure deficit, which is relevant in the face of the ongoing climate change.

Keywords: *Protium*; *Eschweilera*; Soil water content; Vapor pressure deficit; Reference evapotranspiration.

RESUMO

O aumento intra-anual da irradiância e temperatura está associado a uma curta estação de seca na região central da Amazônia. No entanto, o efeito preciso da variabilidade microclimática intra-anual sobre o crescimento de árvores de espécies de uso múltiplo continua sob investigação. O objetivo deste estudo foi avaliar como o crescimento do tronco em diâmetro (crescimento radial) responde às variações mensais nos fatores microclimáticos na região central da Amazônia. Durante quatro anos (2018-2021), registramos dados climáticos e medimos o crescimento radial de 29 árvores (sete espécies) em intervalos mensais; e para avaliar o efeito da variabilidade microclimática no crescimento radial, aplicamos a regressão de componentes principais. Em relação às espécies, o crescimento do tronco em diâmetro foi de $1,50 \pm 0,74 \text{ mm por ano}$. O crescimento radial da maioria das espécies foi maior com o aumento da intensidade mensal das chuvas e da umidade do solo, enquanto o efeito da temperatura média e do déficit de pressão de vapor médio variou entre as espécies. Em *Brosimum parinarioides*, *Licania micrantha* e *Pouteria guianensis*, o crescimento do tronco diminuiu com o aumento da temperatura média, enquanto o aumento do déficit de pressão de vapor médio retardou o crescimento radial em *Brosimum parinarioides*, *Licania micrantha*, *Micropholis guyanensis*, *Pouteria guianensis* e *Theobroma sylvestre*. As temperaturas mínimas e máximas tiveram um efeito neutro no crescimento do tronco entre as espécies. Este estudo mostra que as árvores de uso múltiplo avaliadas não estão aclimatadas à variabilidade climática intra-anual, pois além de reduzirem o crescimento durante a estação seca, também responderam às mudanças mensais na temperatura média e ao déficit de pressão de vapor, o que é relevante diante das mudanças climáticas em curso.

Palavras-chave: *Protium*; *Eschweilera*; Conteúdo de água do solo; Deficit de pressão de vapor; Evapotranspiração de referência.



1. INTRODUCTION

Tree growth is the result of a myriad of biochemical reactions and processes of which photosynthesis – a light and water dependent process – is the main driver. Several factors have been associated with tree growth and total photosynthesis in the Amazon region including precipitation (Gatti et al., 2014; Yang et al., 2018; Camargo & Marengo, 2022), irradiance, temperature, and air humidity (Mendes et al., 2013; Zhao et al., 2017; Elias et al., 2020; Antezana-Vera & Marengo, 2021). Studies that aim to assess the effect of the dry season on tree growth in the Amazon have led to contradictory conclusions. For instance, at the ZF2 Reserve (in the central Amazon – 60 km north of Manaus), Silva et al. (2003) and Dias & Marengo (2021) reported a neutral effect of precipitation on stem growth, whereas Antezana-Vera & Marengo (2021) and Camargo & Marengo (2023) observed that stem growth increased in response to an increase in rainfall intensity. Therefore, it is still unclear to which extent each of the individual climatic factors contributes to tree growth, even when a considerable amount of research has been conducted to evaluate the influence of environmental factors on tree growth of tropical rainforest (e.g. Granato-Souza et al., 2019; Giraldo et al., 2023). This happens because there is a complex interaction among the climatic variables, which are frequently correlated, not to mention that during ontogeny a tree can acclimate to changes in environmental conditions. For instance, in comparison with understory saplings, the increase in light-saturated photosynthesis in canopy leaves is associated with an increase in stomatal density and leaf nitrogen (Marengo et al., 2017).

Acclimation is a process that describes the ability of a tree to adjust to new conditions through phenotypic plasticity – the range of phenotypes that a single genotype can express depending on environmental conditions. Some examples of plant acclimation are photosynthetic responses to elevated CO₂ concentration, high temperature, changes in light conditions, or growth under limited water supply (Way & Yamori, 2014; Lambers & Oliveira, 2019; Silveira & Marengo, 2023). In conditions of high temperatures and vapor pressure deficit (VPD), trees close their stomata to avoid water loss, which can result in decreased photosynthesis and plant growth (Marengo et al., 2014; Sanginés de Cárcer et al., 2018). Furthermore, trees can improve water uptake from deeper layers of soil under drought (Broedel et al., 2017).

There is a high intercorrelation between climatic factors which makes it difficult to determine the contribution of each climatic variable on the growth rates of trees (Clark et al., 2003; Antezana-Vera & Marengo, 2021). This is problematic as multicollinearity can affect the accuracy of results aimed to predict the effect of climatic variability on tree growth. In this regard, Principal Component Regression can be used to deal with the collinearity problem, whereby a new set of uncorrelated variables (orthogonal components) are computed from the original data set by principal component analysis (Montgomery et al., 2012). Evaluating the effect of individual climatic variables on tree growth in the Amazon area is relevant to improve our understanding of underlying changes in tree growth caused by climate change.

In this study we focused on multipurpose-use tree species, because non-timber forest products contribute to sustainable development of the Amazon region. The species selected in this study may, at least potentially, have several non-timber uses. Trees of the Sapotaceae family and the *Theobroma* genus can produce edible fruits, while organic compounds extracted from *Brosimum*, *Eschweilera* and *Protium* have a pharmacological potential (Rüdiger et al., 2007; Oliveira et al., 2012; Palheta et al., 2015). This study aimed to assess the effect of monthly variation of rainfall, temperature, irradiance, soil water, and vapor pressure on stem growth of seven multipurpose-use tree species at a *terra firme* rainforest site in the central Amazon.

2. MATERIAL AND METHODS

2.1. Study area

The study was carried out at the Tropical Forest Experiment Station (ZF2 Reserve), located approximately 60 km north of Manaus, on a plateau centered at 02° 36' 21" S, 60° 08' 11" W, 110–120 m above sea level. The study was conducted in an area of approximately 10 hectares. The Plateau vegetation is a dense primary *terra-firme* forest and the soil is classified as oxisol with low fertility, clay texture, and pH 4.0 (Magalhães et al., 2014). Mean temperature is about 26 °C and relative humidity 78%, while annual precipitation often ranges from 2,450 to 2,970 mm (Dias & Marengo, 2016; Marengo et al., 2024). There is a mild dry season, which extends from June to October, with June–September being the driest months (< 100–110 mm month⁻¹). In this area, tree diversity and the number of trees per hectare is very high (Prance et al., 1976; Rankin-de-Mérona et al., 1992). Leaf shedding tends to concentrate in the dry season, while the production of new leaves often increases at the end of the dry season (Janssen et al., 2021; Marengo et al., 2024). By using dendrometer measurements to determine annual stem growth and radiocarbon dating to estimate the age of woody material it has been found that in the central Amazon the trees grow at similar rates over time (Vieira et al., 2005). This makes it possible to estimate the age of trees, using the ratio between stem diameter at breast height (DBH, in cm) and the annual stem growth at breast height:

$$\text{Tree age (years)} = \frac{10 \times \text{DBH}}{\left(\text{Stem growth} \left(\frac{\text{mm}}{\text{yr}} \right) \right)} \quad (1)$$

In Equation 1, the numeral 10 is used to convert centimeters to millimeters.

2.2. Microclimatic variables

2.2.1. Data collection

From January 2018 to December 2021, air temperature (T), photosynthetically active radiation (PAR), relative humidity (RH), and rainfall were recorded above the forest canopy, at the top of a 40-m-tall observation tower, at ~3 km from the experimental site (02°35'21" S, 60°06'53"W). The reference evapotranspiration (ET_o , in mm day⁻¹) was computed as a function of temperature (°C) and extraterrestrial solar radiation (R_s , in mm day⁻¹), as described by Hargreaves & Samani (1985):

$$ET_o = 0.0023 \times R_s (T_{mean} + 17.8)(T_{max} - T_{min})^{0.5} \quad (2)$$

Vapor pressure deficit (VPD, an estimator of atmospheric dryness) was calculated as previously described (Souza & Marengo, 2022): $e_o - (e_o \times RH)$, where e_o (in hPa) is the saturation vapor pressure (Buck, 1981). We also measured soil water content (SWC) at 2-week intervals. For measuring SWC and the climatic data we followed the experimental procedures described by Souza & Marengo (2022).

2.3. Radial stem growth

For this research, 29 trees of seven species were selected. The trees had a mean height of 22.8 m and DBH of 21.8 cm, while the mean wood density was 0.71 g cm⁻³ and the mean tree age 216 years (Table 1).

Table 1. Characteristic of studied species. Data were collected during four years (2018–2021). Abbreviations. SG: stem growth, DBH: diameter at breast height, H: height, WD: wood density, and n : number of tree/species. The values are the mean (\pm standard deviation). For SG, means followed by different lowercase letters differ at $p = 0.05$ (Tukey's test). The age of trees was estimated as shown in Equation 1.

Family	Species	n	SG	DBH	Height	WD	Tree age (years)	Uses or products
			(mm yr ⁻¹)	(cm)	(m)	(g cm ⁻³)		
Moraceae	<i>Brosimum parinarioides</i> Ducke	3	1.66 \pm 1.31 ^{ab}	34.5 \pm 15.2	28.5 \pm 5.6	0.68 \pm 0.09	207	Latex with pharmacological potential ¹
Lecythidaceae	<i>Eschweilera pedicellata</i> (Rich.) S.A.Mori	5	1.01 \pm 0.90 ^{ab}	16.2 \pm 4.4	20.5 \pm 2.8	0.73 \pm 0.04	160	Bioinsecticide, fungicide ^{2,8}
Chrysobalanaceae	<i>Licania micrantha</i> Miq.	4	2.57 \pm 0.80 ^a	23.7 \pm 9.8	24.3 \pm 4.0	0.72 \pm 0.04	92	Edible fruits ⁷
Sapotaceae	<i>Micropholis guyanensis</i> (A.DC.) Pierre	4	1.83 \pm 1.69 ^{ab}	29.1 \pm 12.3	26.3 \pm 5.0	0.73 \pm 0.01	159	Edible fruits ⁴
Sapotaceae	<i>Pouteria guianensis</i> Aubl.	4	1.46 \pm 0.87 ^{ab}	34.9 \pm 23.1	27.6 \pm 6.5	0.87 \pm 0.04	239	Edible fruits ⁵
Burseraceae	<i>Protium apiculatum</i> Swart	4	1.78 \pm 1.18 ^{ab}	20.6 \pm 9.1	22.4 \pm 5.1	0.70 \pm 0.02	116	Oleoresins ⁶
Malvaceae	<i>Theobroma sylvestri</i> Aubl. ex Mart.	5	0.20 \pm 0.21 ^b	10.8 \pm 2.6	15.9 \pm 2.6	0.66 \pm 0.03	540	Edible fruits ⁷
Mean or total	–	29	1.50 \pm 0.74	21.8 \pm 13.6	22.8 \pm 13.7	0.71 \pm 0.09	216	

¹Palheta et al. (2015); ²Oliveira et al. (2012); ⁴Boom (1989); ⁵Alencar (1994); ⁶Silva et al. (2009); ⁷Teixeira et al. (2019). ⁸Rodrigues et al. (2014).

Furthermore, in this experimental site the trees are not regularly distributed (i.e., quite often trees of the same species are not easily found within walking distance). For this reason, we were only able to select three to five trees per species (Table 1). We also focused on species with potential uses, other than timber (i.e., multipurpose tree species). In these trees we measured the monthly increase in girth at breast height for 48 months (January 2018 to December 2021), and computed the increase in diameter as suggested by Dias & Marengo (2021). The stem growth in diameter was measured using stainless steel dendrometer bands, which were installed at least two years prior to data collection.

2.4. Statistical analyses

To assess differences among species and the effect of time (years and months) on stem growth in diameter (radial growth) we used Repeated measures ANOVA, as the same trees were monitored during 48 months. When required, prior to subjecting the data to analysis of variance, they were log-transformed to reduce the effect of outliers and to comply with ANOVA assumptions. Also, to amend departure from sphericity the Greenhouse–Geisser correction was applied. The effect of microclimatic variability (PAR, rainfall, temperature, VPD and ET_o) on stem growth was evaluated using Principal Component Regression (PCR). Before conducting the regression analysis, we applied a first-order autocorrelation (Monserud & Marshall, 2001) to remove the ontogeny effect on stem growth trend over time (SG):

$$SG_i = \phi_0 + \phi_1 SG_{(i-1)} + \epsilon_i \quad (3)$$

where SG_i is the stem growth at month i ; $SG_{(i-1)}$ the growth rate in the previous month, ϕ_0 and ϕ_1 the regression coefficients, while ϵ_i represents the error term.

The detrended SG (SG_{dtr}) was calculated using the equation: $SG_{dtr} = SG_{obs} - SG_{exp}$, where SG_{obs} is the observed SG, and SG_{exp} is the expected SG computed from Equation 3. The microclimatic data (rainfall, PAR, temperature, SWC and ET_o) were standardized (observed value minus the mean divided by standard deviation) and stem growth data (SG_{dtr}) centered (observed value minus the mean). The PCR is performed in several steps, and briefly described by [Equations 4–8](#) (Montgomery et al., 2012):

$$Y = Xb + \epsilon \quad (4)$$

$$Y = Z\alpha + \epsilon \quad (5)$$

$$Z = XT \quad (6)$$

$$\alpha = T'b \quad (7)$$

$$bpc = T(\hat{\alpha}_{pc}) \quad (8)$$

Equations 4 and 5 describe the standard multiple linear regression (MLR, Equation 4) and the PCR model (Equation 5), respectively. Y denotes a vector of observations (stem growth), X a matrix of regressors (the climatic data), b and α are vectors of coefficients, and ϵ the random errors. The Z matrix (Equation 6) contains the columns (z_i) of a new set of orthogonal components; while T is a matrix whose columns represent eigenvectors. The values of $\hat{\alpha}$ (estimator of α , Equation 8) are obtained after regressing Y on z_i . The pc subscript (Equation 8) indicates that only a reduced k number of z_i components has been retained in the model (i.e., PCR reduced model). We used the adjusted R^2 (R^2_{adj}) criterion to define the number of principal components to retain in the reduced model (Jolliffe, 2002). In this analysis, we adopted a p value of $\alpha = 0.05$ to define statistical significance. The analysis of variance was performed using Statistica 7.0 (Stat Soft Inc), while the PCR analysis was performed using PLS (Liland et al., 2021) and R v.4.2.0 (R Core Team, 2022).

3. RESULTS

3.1. Stem growth of species

We found differences in annual SG among species ($p = 0.045$), from 0.20 mm yr⁻¹ in *T. sylvestri* to 2.57 mm yr⁻¹ in *L. micrantha* (Table 1). Likewise, the effect of time (months) was significant ($p < 0.001$), as well as the interaction species \times month ($p = 0.002$, Table 1A, Appendix). On average, the annual mean (\pm SD) SG across species was 1.50 \pm 0.74 mm. With the exception of *T. sylvestri*, which grew more slowly (0.20 mm yr⁻¹) and *L. micrantha* that grew rather faster (2.57 mm yr⁻¹), most of the species grew at similar rates (1.0 to 1.8 mm yr⁻¹, Table 1).

3.2. Responsiveness to microclimatic variability

Due to the decrease in R^2_{adj} value after adding a fifth PC to the model as illustrated for *T. sylvestri*, only the first four principal components

Table 2. Summary of PCR analysis. Beta coefficients (B), p values (p) and the adjusted R^2 (R^2_{adj}) are given for each of the climatic variables examined. Values of p in bold face are significant at $p \leq 0.05$. Abbreviations: PAR: photosynthetically active radiation, T : temperature, T_{max} : mean maximum T , T_{min} : mean minimum T , T_{mean} : mean T , VPD: vapor pressure deficit, VPD_{max} : mean maximum VPD, VPD_{min} : mean minimum VPD, VPD_{mean} : VPD mean, SWC: soil water content, ET_0 : reference evapotranspiration.

Variable	R^2_{adj}	Parameter	PAR	Rainfall	T_{mean}	T_{min}	T_{max}	VPD_{mean}	VPD_{min}	VPD_{max}	SWC	ET_0
Brosimum	0.094	B	-0.005687	0.008673	-0.008316	-0.000698	-0.006807	-0.008097	-0.003963	-0.006088	0.008993	-0.005264
		p	0.072	0.013	0.040	0.855	0.078	0.033	0.252	0.075	0.012	0.149
Eschweilera	0.089	B	0.010061	0.022405	0.007706	0.004399	0.005398	0.000311	-0.001459	0.003343	0.018764	0.009693
		p	0.204	0.006	0.178	0.211	0.199	0.959	0.810	0.461	0.007	0.081
Licania	0.105	B	-0.006108	0.006198	-0.008203	-0.003659	-0.002889	-0.007762	-0.005523	-0.002628	0.006886	-0.001531
		p	0.015	0.023	0.011	0.228	0.336	0.010	0.046	0.323	0.014	0.590
Micropholis	0.149	B	0.018241	0.021216	0.010064	0.003388	0.007078	-0.012074	-0.014476	-0.001762	0.014884	0.013495
		p	0.021	0.007	0.073	0.321	0.086	0.043	0.018	0.689	0.025	0.014
Pouteria	0.067	B	-0.004189	0.005391	-0.005892	-0.001446	-0.003598	-0.005665	-0.003325	-0.003233	0.005737	-0.002558
		p	0.058	0.025	0.037	0.589	0.179	0.032	0.170	0.172	0.021	0.312
Protium	0.154	B	0.012232	0.028788	0.00824	0.00779	0.001942	-0.00181	-0.0017	-0.00054	0.024026	-0.00256
		p	0.182	0.002	0.212	0.059	0.687	0.794	0.809	0.918	0.003	0.312
Theobroma	0.188	B	0.006299	0.007292	0.002229	0.002244	-0.00075	-0.00711	-0.00636	-0.00432	0.004852	0.001647
		p	0.064	0.031	0.355	0.134	0.672	0.007	0.017	0.028	0.090	0.478
Mean	0.243	B	0.004052	0.014297	0.000864	0.001831	5.92E-05	-0.00514	-0.00439	-0.00178	0.012178	0.003132
		p	0.341	0.001	0.777	0.334	0.979	0.118	0.186	0.468	0.001	0.291

were used in the PCR model (Table 2A). Following this criterion, R^2_{adj} values vary from 0.19 in *T. sylvestre* to 0.07 in *P. guianensis* (Table 2).

In almost all of the evaluated species, the stem growth increased with the rise in monthly rainfall and SWC (Table 2). The exception was *T. sylvestre*, in which the positive effect of SWC on radial growth did not reach the significance level ($p = 0.09$, Table 2). Regarding the effect of the other microclimatic variables on stem growth, the species responded differently. *Licania micrantha* and *M. guyanensis* were the most responsive species to microclimatic factors, as besides rainfall and SWC, they also responded to PAR and mean VPD (Table 2). Likewise, *B. parinarioides* and *P. guianensis*, in addition to responding to rainfall and SWC, they were also affected by variations in VPD, with a decrease in radial growth with increasing VPD_{mean} . The increase in VPD_{mean} , VPD_{min} and VPD_{max} led to a decrease in stem growth in *T. sylvestre* (Table 2). On the other hand, *M. guyanensis* was the sole species that responded to reference evapotranspiration ($p = 0.014$, Table 2). Thus, in general, five out of the seven species were negatively affected by a rise in mean VPD. Likewise, the stem growth decreased in three of seven species with the increase in mean temperature (Table 2). For instance, the radial growth of *E. pedicellata* increased with the rise in rainfall and soil water content (Figures 1A and 1B). As illustration, it is also shown in Figure 1, both the effect of mean temperature on the stem growth of *L. micrantha* and that of the VPD_{mean} on the stem growth of *T. sylvestre* (Figure 1E). Concerning the microclimatic conditions during the experimental period, the mean values were: 25.3 mol $m^{-2} day^{-1}$, for PAR, 215.6 mm $month^{-1}$ (rainfall), 25.6 (T_{mean}), 6.92 hPa (VPD_{mean}), and 46.6 (v/v) for SWC (please see the legend in Figure 1).

4. DISCUSSION

We found that in the majority of the species stem growth positively responded to an increase in rainfall intensity and SWC. Furthermore, it is important to note that *T. sylvestre* positively responded to rainfall but not to SWC. Five species were responsive to an increase in VPD_{mean} , while three species were negatively affected by a rise in T_{mean} . The positive effect of increased SWC on tree growth shows that changes in expansive growth are related to changes in leaf water

potential, probably because the driver of cell growth is the increase in turgor (Bradford & Hsiao, 1982; Kozlowski & Pallardy, 1996). The enhancement of stem growth with an increase in monthly rainfall intensity indicates that even during a relative mild dry season—as expected in the central Amazon during a typical year—Amazonian trees respond to variations in soil moisture even when the uptake of water by roots can be improved during drought (Broedel et al., 2017). A positive response to rainfall associated with a neutral effect of SWC on stem growth (e.g. *T. sylvestre*) suggests that the positive effect of rainfall on radial growth is not only associated with an increase in soil moisture, but also with a rise in atmospheric humidity, as there are plenty of evidences demonstrating that stomata tend to close with increasing VPD (Dai et al., 1992; McDowell & Allen, 2015).

The negative effect of T_{mean} in three of the seven species evaluated is rather unexpected, as tree growth can respond positively to increasing temperature in the Amazon region (Laurance et al., 2009; Elias et al., 2020). This result indicates that the decline in SG was not directly related to a decrease in the photochemical performance of leaves, as the optimum temperature for photosynthesis in tropical rainforests is about 29 °C (Liu, 2020). A possibility is that in these species (*Brosimum parinarioides*, *Licania micrantha*, and *Pouteria guianensis*) there is not a tight control of transpiration, and hence microclimatic factors associated with an increase in temperature (e.g. increase in irradiance and decrease in relative humidity) altogether contributed to an increase of transpiration, which may indirectly affect carbon assimilation and stem growth. On the other hand, a rigorous control of transpiration may have led to a neutral effect of temperature on *Eschweilera pedicellata*, *Micropholis guyanensis*, *Protium apiculatum*, and *Theobroma sylvestre* (Table 2), as well as in other species (Antezana-Vera & Marengo, 2021).

The negative effect of VPD on radial growth in five of the seven species shows the importance of atmospheric dryness on biomass gain via photosynthesis. As the effect of VPD was separated from the effect of rainfall and soil moisture (by extracting orthogonal components of climatic parameters), the negative effect of increasing mean VPD (also VPD_{max} in *T. sylvestre*) on radial growth can be ascribed to the negative effect of increasing VPD on stomatal conductance

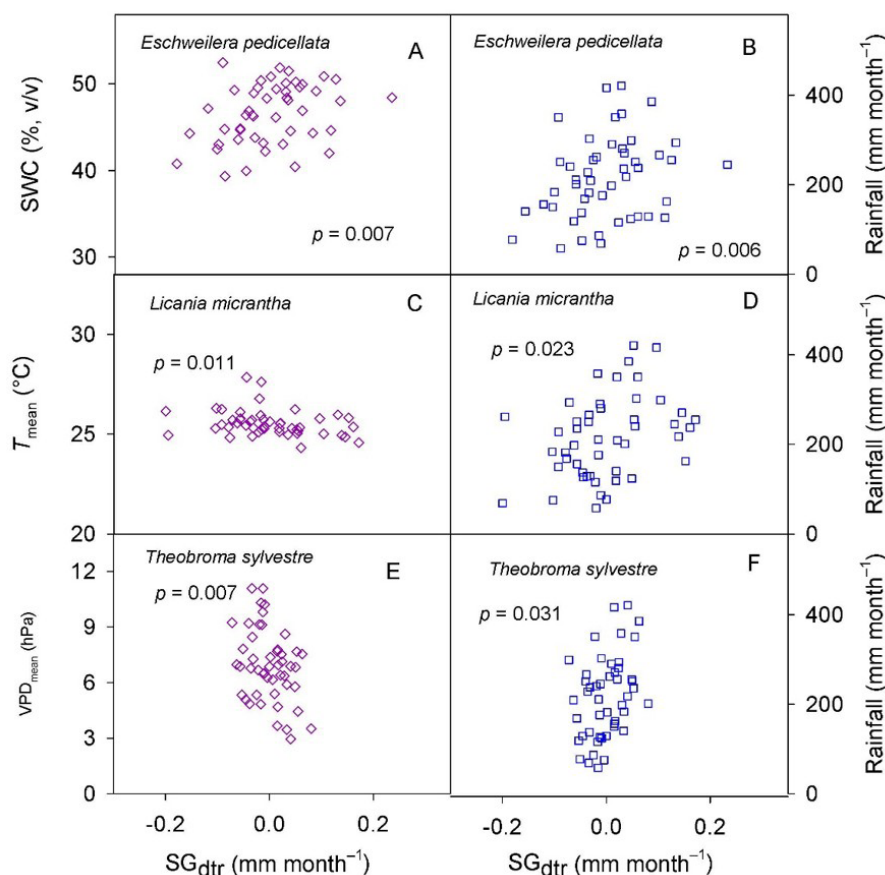


Figure 1. Illustration of the responsiveness of detrended stem growth (SG_{dtr}) of some species to microclimatic factors. Note that the SG_{dtr} data are centered (observed value minus the mean). Abbreviations: T : temperature, T_{mean} : mean T , VPD: vapor pressure deficit, VPD_{mean} : VPD mean, SWC: soil water content. Monthly means of microclimatic parameter (\pm standard error, SE): 25.3 ± 0.81 mol m^{-2} day $^{-1}$ (photosynthetically active radiation), 215.6 ± 13.3 mm month $^{-1}$, (rainfall), 25.6 ± 0.10 °C (T_{mean}), 6.92 ± 0.28 hPa (VPD_{mean}), and $46.6 \pm 0.50\%$ (v/v) for SWC.

(Dai et al., 1992; McDowell & Allen, 2015). In this respect, Yang et al. (2018) reported a decrease in gross photosynthesis in the dry season when temperature and VPD often increase (Souza & Marengo, 2022). Furthermore, it is worth noting that in three species (*L. micrantha*, *M. guyanensis*, and *T. sylvestri*) a rise in minimum vapor pressure also had a negative effect of stem growth (Table 2). This indicates an effect of nocturnal atmospheric conditions on tree growth, as the lowest values of VPD_{min} almost always occurs at night when relative humidity is high (Instituto Nacional de Meteorologia, 2023). This result shows that the stem growth rate of a tree is affected not only by environmental conditions that limit photosynthesis (via the effect of microclimatic conditions on stomatal conductance), but also by nocturnal conditions that tend to increase transpiration and thereby to lower leaf water potential (Camargo & Marengo, 2023). This is relevant because the rainfall pattern in the Amazon region is changing, with decreased rainfall in Northeastern Brazil and part of the Amazon region (Cai et al., 2020). Hence, as the length of the drought period increases, it also increases atmospheric dryness (Lee et al., 2013; Yang et al., 2018). For instance, during the drought of 2015 the decrease in sun-induced fluorescence (a proxy of total photosynthesis) over the whole Amazon region was associated with an increase in vapor pressure deficit (Yang et al., 2018).

The ET_0 had a positive effect on stem growth of *M. guyanensis*. This can be explained by taking into account that ET_0 can be represented as a function of solar radiation and temperature –Equation 2 (Hargreaves & Samani, 1985). The positive effect of temperature on radial growth did not reach the level of significance ($p = 0.07$ for T_{mean}), but that of

PAR significantly improved stem growth ($p = 0.021$), which may have contributed for the improved radial growth with increased ET_0 . The effect temperature on tree growth can occur via its direct effect on photosynthesis, and also by affecting water transport in the xylem, because the viscosity of water decreases with increasing temperature (Kaufmann, 1975). We found that the effect of irradiance was inconsistent, as in *M. guyanensis* (26.3-m tall trees) it had a positive effect, whereas in *L. micrantha* (24.3-m tall trees) the effect of PAR on stem growth was negative. The size of trees does not seem to explain the responsiveness of species to PAR, as the trees of *B. parinarioides* were even taller than those of *M. guyanensis*, and in this species the effect of PAR was neutral. In this respect, further studies are needed to elucidate the effect of irradiance in the studied species. Even when some Amazonian trees can enhance water uptake during the dry season (Broedel et al., 2017) this improvement does not seem to be enough to overcome the scarcity of rainfall during the mild dry season in the study area. Altogether these results suggest that the evaluated multipurpose-use trees are not acclimated to intra-annual climatic variability. Besides decreasing stem growth during the dry season, they also responded to monthly changes in mean temperature and vapor pressure deficit, as mentioned above.

5. CONCLUSION

In this study we report that most of the species responded similarly to variations in rainfall and in soil moisture. The response

to variations in the other microclimatic factors varied among species. Besides responding to rainfall and soil water content, five of the seven species (the exception were *P. apiculatum* and *E. pedicellata*) also responded to variations in atmospheric dryness (measured by the changes in vapor pressure deficit). A contribution of this study is to show that in addition to rainfall, environmental factors related to atmospheric dryness (vapor pressure deficit), which increase in the dry season can influence the stem growth of trees. Also, the results show that the evaluated multipurpose-use trees are not acclimated to intra-annual changes in climatic variables variability, which is important in the current context of climate change.

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AUTHOR CONTRIBUTIONS

MMS: data curation, formal analysis, investigation, writing, review; LALP: investigation, data curation; RAM: funding acquisition, supervision, collaborated with data analysis, and wrote the article with contributions of the others.

APPENDIX

Table 1A. Summary of the Repeated Measures ANOVA of the microclimatic climatic effect on stem growth. Data were log-transformed [$\log_{10}(x+1)$] prior to analysis of variance. Also shown is the adjusted p value (p_{adj}) after Greenhouse-Geisser correction due to departure from sphericity

Source of variation	DF	MS	F	p	p_{adj}
Species	6	0.120208	2.62185	0.045	-
Error	22	0.045849			-
Year	3	0.012900	2.67539	0.054	0.062
Year×Species	18	0.008451	1.75261	0.053	0.061
Error	66	0.004822			-
Month	11	0.031012	20.97113	< 0.001	< 0.001
Month×Species	66	0.003463	2.34152	< 0.001	0.002
Error	242	0.001479			
Year×Month	33	0.005647	3.37051	< 0.001	0.002
Year×Month×Species	198	0.002745	1.63839	< 0.001	0.015
Error	726	0.001675			

Table 2A. Illustration of PCR computation to assess the effect of climatic variables on SG_{dtr} of *Theobroma*. In this example, only the first four principal components ($Z_1 - Z_4$) were selected, as the R^2_{adj} decreased after adding the fifth component. Abbreviations: **PCR**: Principal component regression, DF: degree of freedom, R^2 : coefficient of determination (with increasing Z), R^2_{adj} : adjusted R^2 , SG_{dtr} : mean detrended stem growth across species, α : regression coefficient, $SE(\alpha)$: standard error of α . Microclimatic data were standardized and tree growth data centered prior to statistical analysis.

Source of variation	Sums of Squares	DF	Mean Squares	F value	p value
Regression	0.015866	4	0.003966	3.72	0.011
Residual	0.045865	43	0.001067		
Total	0.061730				
Principal components	α	$SE(\alpha)$	p value	R^2	R^2_{adj}
z1	-0.004179	0.002441	0.094051	0.05066	0.0300
z2	0.006155	0.002639	0.024423	0.1447	0.1067
z3	-0.005199	0.004220	0.224598	0.1709	0.1144
z4	0.012526	0.005611	0.030841	0.2570	0.1879
z5	0.001171	0.006677	0.861633	0.2576	0.1692