

## ORIGINAL ARTICLE

# Stem growth of multipurpose tree species: net effect of micrometeorological variability assessed by principal component regression

Alan Pena de SOUZA<sup>1</sup>, Ricardo Antonio MARENCO<sup>2\*</sup> <sup>1</sup> Instituto Nacional de Pesquisas da Amazônia - INPA, Programa de Pós-graduação em Agricultura do Tópico Úmido, Av. André Araújo 2936, 69067-375 Manaus, AM, Brazil<sup>2</sup> Instituto Nacional de Pesquisas da Amazônia - INPA, Coordenação de Dinâmica Ambiental, Av. André Araújo 2936, 69067-375 Manaus, AM, Brazil\* Corresponding author: [rmarenco@inpa.gov.br](mailto:rmarenco@inpa.gov.br);  <https://orcid.org/0000-0002-3119-1052>**ABSTRACT**

In a typical year in the central Amazon, there is a mild dry season, but its effect on stem growth of multipurpose forest tree species is not yet well known. This study aimed to determine the individual effect of microclimatic parameters on stem growth after removing the influence of intercorrelation among microclimatic variables. Monthly stem diameter increment was measured in six species (46 trees) from January 2018 to December 2020. Microclimatic variables recorded were irradiance, air temperature, rainfall, and vapor pressure deficit. Principal component regression was used to assess the effect of micrometeorological variability on stem growth. On average, stem growth increased with an increase in rainfall and soil water content, but decreased with rise in maximum temperature and maximum vapor pressure deficit. These findings indicate that, when removing the effect of intercorrelation between microclimatic parameters, vapor pressure deficit may, in fact, affect stem growth. We demonstrate that the reduction in stem growth during the dry season can also be related to an increase in maximum temperature and maximum vapor pressure deficit, and not only to a decline in soil water content.

**KEYWORDS:** Amazon rainforest, growth, ecophysiology, soil water availability

## Crescimento do tronco de espécies de árvores de uso múltiplo: efeito líquido da variabilidade micrometeorológica avaliada por regressão de componentes principais

**RESUMO**

Em um ano típico na Amazônia central, há uma estação seca amena, mas seu efeito sobre o crescimento do tronco de espécies de uso múltiplo ainda é pouco conhecido. Este estudo teve como objetivo determinar o efeito individual de variáveis microclimáticas sobre crescimento do tronco após remover a influência da intercorrelação entre os fatores climáticos. O incremento mensal do diâmetro do tronco foi medido em seis espécies (46 árvores) de janeiro de 2018 a dezembro de 2020. As variáveis microclimáticas medidas foram irradiância, temperatura do ar, precipitação pluvial e déficit de pressão de vapor. Utilizou-se regressão de componentes principais para avaliar o efeito da variabilidade micrometeorológica sobre crescimento do tronco. Em média, o crescimento do tronco aumentou com o aumento da precipitação e do conteúdo de água do solo, mas diminuiu com o aumento da temperatura máxima e do déficit máximo de pressão de vapor. Estes resultados indicam que, removendo o efeito da intercorrelação entre os parâmetros climáticos, o déficit de pressão de vapor pode, de fato, ter um efeito sobre o crescimento do tronco. Demonstrou-se que a redução no crescimento do caule durante a estação seca também pode estar relacionada ao aumento da temperatura máxima e do déficit máximo de pressão de vapor, e não apenas ao declínio do teor de água no solo.

**PALAVRAS-CHAVE:** floresta amazônica, crescimento arbóreo, ecofisiologia, disponibilidade de água no solo**CITE AS:** Souza, A.P.; Marenco, R.A. 2022. Stem growth of multipurpose tree species: net effect of micrometeorological variability assessed by principal component regression. *Acta Amazonica* 52: 277-284.

## INTRODUCTION

Tree growth is a complex process with a wide range of internal and external factors involved, and it ultimately reflects a balance between carbon gain by photosynthesis and carbon loss through respiration (Bowman *et al.* 2013). On a given tree, it can be inferred from the increase of biomass through time, which has been estimated by measuring the increment of stem diameter at regular intervals (Dias and Marengo 2016, 2021; Antezana-Vera and Marengo 2021).

Microclimatic factors such as irradiance, precipitation and air temperature affect both photosynthesis and tree growth (e.g., Méndez 2018; Yang *et al.* 2018; Marengo and Antezana-Vera 2021). Rainfall and soil water content seem to affect tree growth in the Amazon region (Méndez 2018; Antezana-Vera and Marengo 2021), but it is still unclear whether trees grow faster in the rainy season than in the dry season. Although tree growth or ecosystem photosynthesis seem to decrease in the dry season in most studies (e.g., Méndez 2018; Yang *et al.* 2018; Antezana-Vera and Marengo 2021), others have reported no effect (Silva *et al.*, 2003; Dias and Marengo 2016, 2021) or even an increase in ecosystem photosynthesis in the central Amazon (Green *et al.* 2020). However, because climatic factors are intercorrelated, it is difficult to evaluate the individual effect of a given microclimatic variable on tree growth (Marengo and Antezana-Vera 2021).

Understanding how tree growth responds to variations in precipitation, irradiance and temperature is especially important as longer droughts are expected in regions of the Amazon (Boisier *et al.* 2015; Jiménez-Muñoz *et al.* 2016). Also, there is an increase in irradiance and maximum temperature during the dry period in the central Amazon that also affects tree growth (Marengo and Antezana-Vera 2021). Therefore, the aim of this study was to determine the orthogonal (uncorrelated) effect of microclimatic factors on stem growth in the central Amazon.

## MATERIAL AND METHODS

### Study site

The study was conducted at the ZF2 -Experimental Station, a protected forest area belonging to Instituto Nacional de Pesquisas da Amazônia - INPA, in the central Amazon, Brazil. The vegetation is a dense *terra-firme* forest and the soil is an oxisol with low fertility, clay texture, and acidic pH (3.9–4.0 in water, Magalhães *et al.* 2014). The region is characterized by a humid climate with a mild dry season from June to October, with only a few months (June–September) with a monthly precipitation lower than 100–110 mm month<sup>-1</sup> (INMET 2021, data for the nearby city of Manaus). June and October can be considered transition months between the dry and rainy periods. The annual temperature is about 26 °C and the mean annual precipitation 2,420 mm. In this

part of the central Amazon, tree density and species diversity are high. For instance, Rankin De-Merona *et al.* (1992) reported a tree density (>10 cm DBH) of 636 trees per hectare with a mean stem length of about 12 m, while Prance *et al.* (1976) recorded 179 species of trees in one hectare ( $\geq$  15 cm DBH). Production of new leaves tends to concentrate in the dry season, but over the year variation in leaf area index is rather low, 4.7–5.0 (Mendes and Marengo 2010). Other characteristics of the study site are described by Antezana-Vera and Marengo (2021).

### Microclimatic variables

From January 2018 to December 2020, 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 (02°35'21"S, 60°06'53"W), at about 3 km from the experimental site. PAR was measured using a quantum sensor (Li-190SA, Li-Cor, NE, USA), and air temperature and RH with a temperature-humidity sensor (Humitter 50y, Oy Vaisala, Finland) connected to a data logger (Li-1400, Li-Cor, Lincoln, NE). Data were collected at 15 min (PAR) and 30 min intervals (T and RH). Daily rainfall was recorded using a rain gauge (Em5b, Decagon, WA, USA). Air temperature (T in °C) and RH (%) data were used to calculate vapor pressure deficit (D, hPa) using the equation:  $D \text{ (hPa)} = e_s - e_a$ , where  $e_s$  (in hPa) is the saturation vapor pressure Buck (1981). We also measured soil water content, SWC (%), at about two-week intervals, by collecting undisturbed fresh soil samples at 10–20 cm depth, which were oven-dried at 105 °C to constant mass. The fresh soil samples ( $n = 12$  per sampling date) were collected near the trees used in the study, and a few decimeters apart from each other. The volumetric SWC (expressed as a percent, on a volume basis) was computed as volume of water per unit volume of the soil sample (Embrapa 2011), being the volume of water obtained gravimetrically as wet soil (fresh sample) minus dry soil mass (oven dried soil sample), assuming 1 g cm<sup>-3</sup>.

### Stem growth in diameter

The trees for this study were located on a *terra-firme* plateau (centered at 02°36'21"S; 60°08'11"W, hereafter referred to as the experimental area), along trails existing in the study area (altogether a few hectometers long). Because it is a natural forest, the distribution of trees in the experimental area does not follow a regular pattern. Instead individual trees of a given species were often a few decimeters apart from each other. Thus, the trees were selected based on the availability of at least four trees of the same species, each of them with a stem diameter at breast height (DBH) (1.3 m from the ground) of at least 10 cm. We also focused on species which could be of multipurpose uses. Using this criterion, 46 mid-upper canopy trees (mean stem diameter of 24.5 cm and 23.9 m

tall) from six species were selected (Table 1). The increase in stem circumference at breast height of these trees was measured once a month from January 2018 to December 2020 using dendrometer tapes and digital calipers. From these measurements, the monthly increase in diameter was computed, as described by Dias and Marengo (2021). We also measured wood density (WD) (dry mass to fresh wood volume, Dias and Marengo 2016), width of the canopy crown (mean diameter of the ground projected crown), climbed the tree and measured its height (with a tape) and determined the diameter-height relationship.

### Statistical analysis

We used principal component regression (PCR) to assess the effects of microclimatic factors on stem growth. We performed this analysis for each of the studied species, as well on the mean stem growth across species. To remove the effect of ontogeny on stem growth, a first-order autoregression was applied using Equation 1 (Monserud and Marshall 2001).

$$G_{Si} = \phi_0 + \phi_1 G_{S(i-1)} + \epsilon_i \quad [1]$$

where  $G_{Si}$  is the stem growth in month  $i$ ;  $G_{S(i-1)}$  is the growth rate in the previous month, and  $\phi$  the regression coefficient, while  $\epsilon_i$  denote the error term.

The detrended stem growth ( $G_{S-dtr}$ ) was obtained as the residual of  $G_{Si}$  (i.e.  $G_{S-dtr} = G_{Si} - \hat{G}_S$ , where  $\hat{G}_S$  is the predicted value). In the next step, the climatic data (rainfall, PAR, temperature, vapor pressure deficit, and SWC) were standardized (observed value minus the mean divided by the standard deviation) prior to PCR analysis (Montgomery *et al.* 2012). The PCR removes the effect of collinearity by

extracting orthogonal vectors (components) from the matrix of explanatory variables (microclimatic variables). Therefore, in PCR it is required to perform principal component analysis (PCA) on the explanatory variables (in this step we added the mean stem growth as a supplementary variable to have a first insight of the relationship between the microclimatic data and mean stem growth). Then, multiple linear regression (MLR) was applied to regress the response variable on the principal components (PC) to obtain the PC alpha coefficients, which were used to compute the beta coefficients of the standardized explanatory variables (Montgomery *et al.* 2012). Thus, the PCR model can be described as:  $G_{S-dtr} \sim PC_1, PC_2 \dots PC_n$ , where the subscripts 1 to  $n$  denote the number of PC included in the model. Because there were nine microclimatic variables, nine orthogonal components were extracted, of which PC associated with small eigenvalues ( $\lambda < 1$ ) were disregarded (Kaiser criterion). Hence, only PC that retained most of the variance of microclimatic variables were used in the final PCR model. A step by step of the whole PCR process is described by Antezana-Vera and Marengo (2021).

Stem growth rates during the driest months (July, August and September) were compared ( $t$ -test) with those of the rainy season. In this comparison, the transition months October and June were included in the rainy season. To have the same dataset size for the rainy (October–June) and dry season (July–September), a random sample was drawn from the rainy season data, and the difference between seasons evaluated by  $t$ -test. To reduce the effect of outliers, in this analysis data were log-transformed. The analyses were performed using R v.4.0.5 (R Core Team, 2021), with PCR computed using the

**Table 1.** Characteristics of species used in the study. Acronyms: DBH = diameter at breast height; WD = wood density;  $G_s$  = stem growth in diameter (raw data);  $n$  = number of trees per species. Some non-timber uses of the species are also shown. Values are shown as the mean  $\pm$  standard deviation.

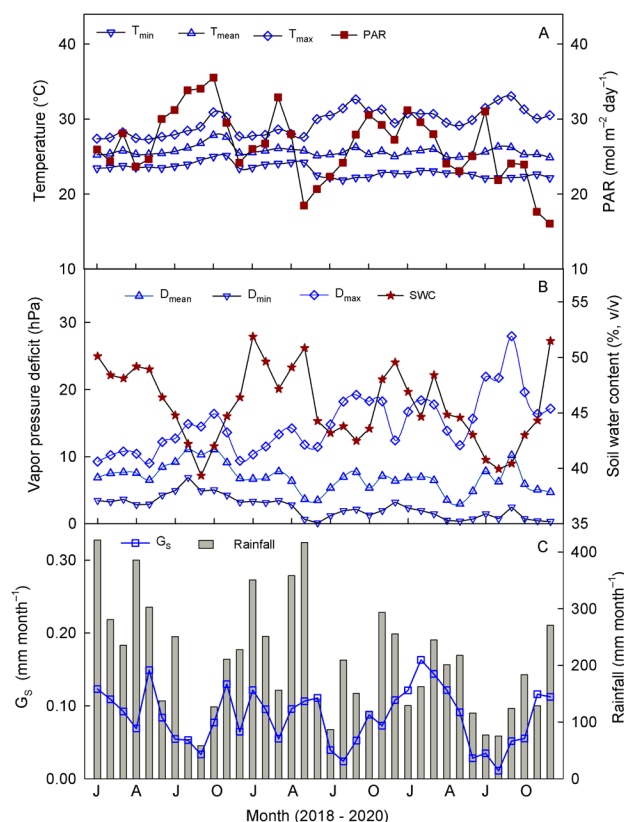
Family/Species	n	DBH (cm)	Height (m)	$G_s$ (mm month <sup>-1</sup> )	$G_s$ (mm yr <sup>-1</sup> )	WD (g cm <sup>-3</sup> )	Crown diameter (m)	Non-timber uses or properties
<b>Apocynaceae</b>								
<i>Geissospermum argenteum</i> Woodson	12	42.70 $\pm$ 19.6	29.0 $\pm$ 8.2	0.077 $\pm$ 0.04	0.919 $\pm$ 0.51	0.793 $\pm$ 0.05	8.18 $\pm$ 1.71	Pharmacological <sup>1</sup>
<b>Fabaceae</b>								
<i>Inga laurina</i> (Sw.) Willd.	5	18.94 $\pm$ 6.6	22.8 $\pm$ 3.6	0.080 $\pm$ 0.09	0.962 $\pm$ 1.10	0.691 $\pm$ 0.03	5.37 $\pm$ 1.10	Trypsin inhibitor <sup>2</sup>
<b>Olacaceae</b>								
<i>Minqartia guianensis</i> Aubl.	10	24.69 $\pm$ 15.8	23.2 $\pm$ 6.0	0.097 $\pm$ 0.06	1.169 $\pm$ 0.76	0.799 $\pm$ 0.03	7.14 $\pm$ 2.46	Medicinal <sup>3</sup>
<b>Bursaceae</b>								
<i>Protium decandrum</i> (Aubl.) Marchand	6	17.95 $\pm$ 2.9	21.6 $\pm$ 1.8	0.088 $\pm$ 0.05	1.057 $\pm$ 0.63	0.648 $\pm$ 0.03	6.10 $\pm$ 0.95	Pharmacological <sup>4</sup>
<i>Protium hebetatum</i> D.C. Daly	9	14.14 $\pm$ 3.6	18.3 $\pm$ 3.2	0.062 $\pm$ 0.04	0.742 $\pm$ 0.44	0.563 $\pm$ 0.05	5.35 $\pm$ 0.95	Pharmacological <sup>4</sup>
<b>Sapotaceae</b>								
<i>Pouteria macrophylla</i> (Lam.) Eyma	4	28.29 $\pm$ 14.9	28.3 $\pm$ 5.5	0.129 $\pm$ 0.08	1.550 $\pm$ 0.98	0.807 $\pm$ 0.10	6.14 $\pm$ 1.90	Produce edible fruits, antioxidant capacity <sup>5</sup>
<b>Mean or total</b>	46	24.45 $\pm$ 10.3	23.87 $\pm$ 4.1	0.089 $\pm$ 0.02	1.07 $\pm$ 0.29	0.717 $\pm$ 0.10	6.38 $\pm$ 1.10	

1: Morais (2012), 2: Macedo *et al.* 2011, 3: Gachet *et al.* (2010), 4: Rüdiger *et al.* (2007), 5: Gordon *et al.* (2011).

PLS Package (Mevik *et al.* 2021). In all analyses, a  $p$  value of  $\alpha = 0.05$  was used to define statistical significance.

## RESULTS

The mean values of the microclimatic variables were  $26.52 \text{ mol m}^{-2} \text{ day}^{-1}$  for PAR,  $206.2 \text{ mm month}^{-1}$  ( $2474 \text{ mm yr}^{-1}$ ) for rainfall,  $25.7^\circ\text{C}$  for mean temperature,  $6.86 \text{ hPa}$  for  $D_{\text{mean}}$ , and  $45.73\%$  (v/v) for SWC. Mean stem growth across species was  $0.089 \text{ mm month}^{-1}$  ( $1.07 \text{ mm yr}^{-1}$ , Table 1; Figure 1) with no significant difference among species (data not shown). Wood density was  $0.717 \text{ g cm}^{-3}$ , crown diameter  $6.38 \text{ m}$ , and the allometric diameter-height relationship was: Height (m) =  $-11.387 + 11.504 \ln(\text{DBH})$ ,  $R^2 = 0.92$ ,  $n = 46$ , being DBH in centimeter). Within a year there were significant differences in monthly stem growth rates, as the trees grew more slowly in the dry season than in the rainy season ( $0.10$  vs  $0.04 \text{ mm month}^{-1}$ ,  $p < 0.001$ , Figure 2).



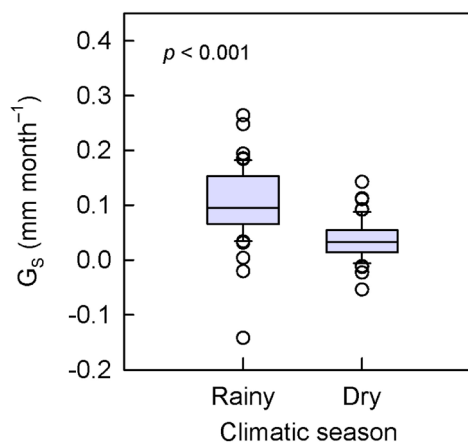
**Figure 1.** Monthly variation of microclimatic variables and mean growth in stem diameter across 46 trees of six species from January 2018 to December 2020 in a *terra-firme* forest in the central Brazilian Amazon. A – mean ( $T_{\text{mean}}$ ), minimum ( $T_{\text{min}}$ ) and maximum ( $T_{\text{max}}$ ) monthly temperature, and monthly mean of daily photosynthetically active radiation (PAR); B – soil water content (SWC), and mean ( $D_{\text{mean}}$ ), minimum ( $D_{\text{min}}$ ) and maximum ( $D_{\text{max}}$ ) monthly vapor pressure deficit; C – monthly rainfall and monthly mean growth in stem diameter ( $G_s$ , raw data). Months indicated by the first letter on the X-axis, starting from January. This figure is in color in the electronic version.

## Stem growth and microclimatic variables inferred from PCA

The PCA extracted almost 80% of total variance of microclimatic data in the first two components, with the vectors associated with SWC and rainfall located in the same quadrant and rather close to the mean stem growth vector, indicating a positive correlation between the mean stem growth and SWC and rainfall (Figure 3). The vectors associated with minimum temperature and minimum vapor pressure deficit are almost at a right angle with that of mean stem growth, suggesting a low correlation between them. The location of other microclimatic variables on the factor plane, such as mean temperature and maximum vapor pressure deficit, suggest a negative correlation with the mean stem growth, as they are located in opposite quadrants.

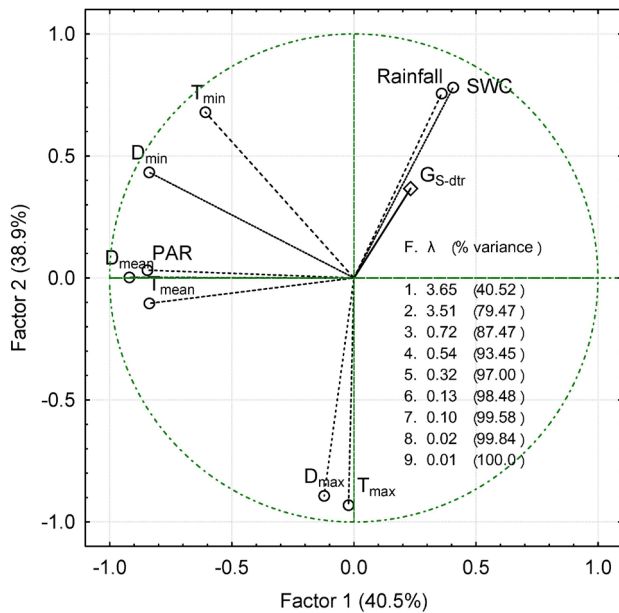
## Orthogonal effect of microclimatic variables on stem growth

The use of PCR allowed us to remove the intercorrelation between the microclimatic variables. As only component 1 and component 2 were associated with eigenvalues equal or greater than one ( $\lambda_1 = 3.65$ , and  $\lambda_2 = 3.51$ , respectively, inset in Figure 3), only these two components, which together accounted for 79.4% of total variance in microclimatic variables, were used in the analysis. On average, stem growth was responsive to variation in rainfall, maximum temperature, maximum vapor pressure deficit and soil water content (Table 2). That is, across species, stem growth responded to variability in four of the nine micrometeorological factors



**Figure 2.** Mean monthly growth in stem diameter ( $G_s$ , raw data) across 46 trees of six species in the rainy season (October to June) (mean  $\pm$  standard error:  $0.104 \pm 0.009 \text{ mm month}^{-1}$ ) and dry season (July to September) ( $0.037 \pm 0.005 \text{ mm month}^{-1}$ ) for the period of January 2018 to December 2020 in a *terra-firme* forest in the central Brazilian Amazon. The line indicates the median, the box the 25th and 75th percentile, and the whiskers the 5th and 95th percentile. Circles indicate outliers. The  $p$  value is for the difference between seasons ( $t$  test). The data were log-transformed prior to statistical analysis. This figure is in color in the electronic version.





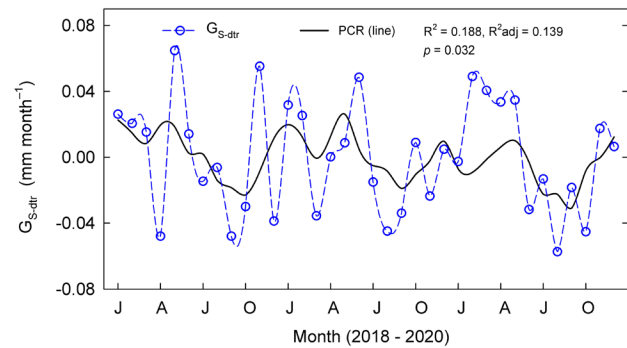
**Figure 3.** Principal component analysis of microclimatic variables measured from January 2018 to December 2020 in a *terra-firme* forest in the central Brazilian Amazon. The detrended stem growth ( $G_{S-dtr}$ ) across species is shown as a supplementary variable. The inset shows the eigenvalues ( $\lambda$ ) and the cumulative variance (%) associated with each factor (F). The first two factors account for 79.4% of variance in the data. Acronyms: mean ( $T_{mean}$ ), minimum ( $T_{min}$ ) and maximum ( $T_{max}$ ) monthly temperature, monthly mean of daily photosynthetically active radiation (PAR), soil water content (SWC), and mean ( $D_{mean}$ ), minimum ( $D_{min}$ ) and maximum ( $D_{max}$ ) monthly vapor pressure deficit. This figure is in color in the electronic version.

considered and the PCR explained almost 19% of the total variance in stem growth ( $R^2 = 0.188$ ,  $R^2_{adj} = 0.139$ ,  $p = 0.032$ , Figure 4). Moreover, four of the six studied species responded to microclimatic variability, of which *Inga laurina* and *Minquartia guianensis* were the most responsive, as they responded to variation in four and six microclimatic variables, respectively (Table 2). *Minquartia guianensis* was negatively affected by increase in PAR, mean temperature, and mean and maximum vapor, but it was positively affected by increase in rainfall and soil water content (Table 2). *Protium hebetatum* and *Geissospermum argenteum* responded to intra-annual changes in two microclimatic factors (Table 2), while *Protium decandrum* and *Pouteria macrophylla* were unresponsive to variations in microclimatic factors. On average, based on the standardized climatic variables, the mean monthly stem growth ( $G_{S-str}$ ) over species was best represented by (Equation 2, coefficients are those shown in Table 2):

$$\text{Mean } G_{S-str} \text{ (mm month}^{-1}\text{)} = -0.00169 \text{ PAR} + 0.00341 \text{ Rainfall} - 0.00215 T_{mean} + 0.00108 T_{min} - 0.00330 T_{max} - 0.00195 D_{mean} - 0.00027 D_{min} - 0.00338 D_{max} + 0.00359 \text{ SWC} \quad [2]$$

## DISCUSSION

In this study we found an  $R^2$  value of 0.19, which cannot be considered low because many factors can affect tree growth



**Figure 4.** Detrended stem growth ( $G_{S-dtr}$ , circles-dashed line) across species and principal component regression (PCR) line (solid line) fitted to data of 46 trees of six species from the central Brazilian Amazon as a function of time (months from January 2018 to December 2020). The  $R^2$  and  $p$  values displayed are those of the PCR. This figure is in color in the electronic version.

(Bowman *et al.* 2013), for instance, Marengo and Antezana-Vera (2021) reported an  $R^2$  value of 0.12 over more than 40 tree species. Because climatic parameters can vary with rainfall seasonality, microclimatic parameters that often increase during the dry season, such as temperature and vapor pressure deficit, tended to negatively affect stem growth, but, on average, only maximum temperature and maximum vapor pressure deficit had significant effects. Mean temperature and PAR also increased in the dry season, but their effect on stem growth was only significant in *M. guianensis*, indicating that this species is rather sensitive to variation in microclimatic factors.

The average stem growth was slower in the dry season, which reflects the sensitivity of evaluated trees to climatic seasonality. The drop in water availability during the dry season often leads to a decline in ecosystem photosynthesis (Lee *et al.* 2013; Yang *et al.* 2018). Although the mean stem growth over species was significantly affected by rainfall and SWC, the magnitude of the effect on individual species differed. For instance, it was more pronounced (based on the regression coefficient size) in *Minquartia guianensis* and *Inga laurina* than in *Protium hebetatum*. Yet, intra-annual variation in climatic factors had a neutral effect on *Protium decandrum* and *Pouteria macrophylla*. Thus, altogether, this shows that microclimatic variability can affect the individual species differently.

Our results clearly showed that an increase in vapor pressure deficit (particularly in maximum vapor pressure deficit) may have a significant effect on stem growth. Vapor pressure deficit is a function of temperature, but the effect of vapor pressure deficit on stem growth was not statistically associated with the effect of temperature or PAR, as the influence of these variables was removed by PCR. Likewise, the results showed that maximum temperature by itself had an effect on stem growth which cannot be ascribed to the effect of vapor pressure deficit.

**Table 2.** Regression coefficient (Beta), standard error (SE of beta) and *p* values obtained from principal component regression to evaluate the effect of climatic variables on detrended tree growth ( $G_{s-dtr}$ ) of six tree species in a *terra-firme* forest in the central Brazilian Amazon. Significant *p* values are in bold. Two principal components (1 and 2) of the PCR were used in the analysis. Abbreviations: mean ( $T_{mean}$ ), minimum ( $T_{min}$ ) and maximum ( $T_{max}$ ) monthly temperature, monthly mean of daily photosynthetically active radiation (PAR), soil water content (SWC), and mean ( $D_{mean}$ ), minimum ( $D_{min}$ ) and maximum ( $D_{max}$ ) monthly vapor pressure deficit.

Parameter	PAR	Rainfall	$T_{mean}$	$T_{min}$	$T_{max}$	$D_{mean}$	$D_{min}$	$D_{max}$	SWC
<i>Protium hebetatum</i>									
Beta	-0.00153	0.00321	-0.00197	0.00108	-0.00314	-0.00177	-0.00019	-0.00320	0.00338
SE	0.00142	0.00145	0.00142	0.00157	0.00163	0.00154	0.00160	0.00157	0.00153
<i>p</i>	0.291	<b>0.036</b>	0.176	0.497	0.065	0.261	0.907	0.052	<b>0.035</b>
<i>Protium decandrum</i>									
Beta	-0.00335	0.00500	-0.00395	0.00064	-0.00442	-0.00379	-0.00146	-0.00466	0.00531
SE	0.00291	0.00297	0.00290	0.00320	0.00333	0.00316	0.00327	0.00322	0.00312
<i>p</i>	0.259	0.103	0.184	0.843	0.195	0.240	0.659	0.159	0.100
<i>Pouteria macrophylla</i>									
Beta	-0.00320	0.00510	-0.00383	0.00089	-0.00461	-0.00363	-0.00122	-0.00482	0.00540
SE	0.00269	0.00275	0.00269	0.00296	0.00308	0.00292	0.00302	0.00298	0.00288
<i>p</i>	0.245	0.075	0.165	0.767	0.146	0.224	0.689	0.117	0.072
<i>Minquartia guianensis</i>									
Beta	-0.00319	0.00390	-0.00361	-0.00012	-0.00317	-0.00357	-0.00183	-0.00343	0.00417
SE	0.00155	0.00158	0.00154	0.00170	0.00177	0.00168	0.00174	0.00171	0.00166
<i>p</i>	<b>0.049</b>	<b>0.020</b>	<b>0.027</b>	0.944	0.085	<b>0.043</b>	0.301	<b>0.055</b>	<b>0.018</b>
<i>Inga laurina</i>									
Beta	-0.00224	0.00657	-0.00322	0.00317	-0.00686	-0.00268	0.00070	-0.00687	0.00689
SE	0.00248	0.00253	0.00247	0.00273	0.00284	0.00269	0.00279	0.00274	0.00266
<i>p</i>	0.373	<b>0.015</b>	0.205	0.255	<b>0.023</b>	0.329	0.803	<b>0.019</b>	<b>0.015</b>
<i>Geissospermum argenteum</i>									
Beta	0.00131	0.00281	0.00071	0.00382	-0.00405	0.00129	0.00306	-0.00374	0.00285
SE	0.00160	0.00164	0.00160	0.00176	0.00183	0.00174	0.00180	0.00177	0.00172
<i>p</i>	0.419	0.097	0.662	<b>0.039</b>	<b>0.036</b>	0.466	0.101	0.044	0.108
Mean $G_{s-dtr}$ over species									
Beta	-0.00169	0.00341	-0.00215	0.00108	-0.00330	-0.00195	-0.00027	-0.00338	0.00359
SE	0.00122	0.00124	0.00121	0.00134	0.00139	0.00132	0.00137	0.00135	0.00130
<i>p</i>	0.177	<b>0.011</b>	0.088	0.427	<b>0.025</b>	0.152	0.844	<b>0.018</b>	<b>0.010</b>

Several studies have been conducted to evaluate the effect of the dry season on tree growth in the central Amazon, and the results have been inconclusive, indicating a dependence on dry season length. For example, Silva *et al.* (2003) and Dias and Marengo (2016, 2021) did not find a decline in stem growth in the dry season, whereas Méndez (2018) and Antezana-Vera and Marengo (2021) reported that stem growth tends to be slower in the dry period than in the rainy period. In this study, we found that the decrease in stem growth was essentially associated with an increase in  $T_{max}$  and  $D_{max}$ , and with a drop in rainfall intensity and SWC, as only *Minquartia guianensis* was responsive to changes in PAR.

The negative effect of PAR on stem growth of *M. guianensis*, which occurred concomitantly with an increase in vapor pressure deficit and a decline in soil water content, indicated that this species is sensitive to variation of these

microclimatic factors, whereas stem growth of *P. decandrum* and *P. macrophylla* was neutral to microclimatic variability. Further studies are needed to elucidate the mechanism associated with sensitivity of Amazonian forest tree species to microclimatic variability.

The differential response of species to microclimatic variability can be related to improved water uptake during the dry period, as well as to enhanced stomatal sensitivity to variations in vapor pressure deficit. At the ecosystem level, deep root water uptake can be increased during drought (Markewitz *et al.* 2010; Broedel *et al.* 2017), which can help to withstand the effect of water stress in mild dry seasons. We have shown that a decline in  $D_{max}$  (also  $D_{mean}$  in *M. guianensis*) was associated with an increase in stem growth, and that vapor pressure deficit tended to increase in the dry season. Photosynthesis is a function of stomatal conductance,

and a decline in stomatal conductance is the most common response to high vapor pressure deficit (Marengo *et al.* 2014, McDowell and Allen 2015). Therefore, it seems possible that a decline in stem growth during the dry season was also caused by an increase in vapor pressure deficit. Sun induced fluorescence (a proxy of photosynthesis) declines in the dry season, in parallel with an increase in vapor pressure deficit (Lee *et al.* 2013; Yang *et al.* 2018).

Maximum temperature had a significant and negative effect on mean stem growth across species. The optimum temperature for photosynthesis is about 29 °C in tropical rainforest (Liu 2020), with a drop in photosynthesis at supra-optimal temperatures (Slot and Winter 2016), which may explain the drop in stem growth with increasing maximum temperatures. Moreover, an increase in temperature affects respiration and photorespiration rates and, in some species, isoprene emission (Sharkey and Yeh 2001; Slot and Winter 2016), and thereby, high carbon loss via respiration can affect biomass allocation to stems.

As we have mentioned earlier, one of the difficulties in assessing the individual effect of climatic variability on tree growth is the collinearity among the climatic parameters. By using PCR to remove the effect of collinearity, we showed that mean stem growth was responsive not only to variation in precipitation, maximum temperature, and PAR (in one species), but also to variation in vapor pressure deficit ( $D_{\text{mean}}$  and  $D_{\text{max}}$ ). This finding is relevant because global temperatures are steadily increasing due to climate change, leading to changes in the distribution pattern of precipitation in the Amazon basin, with longer dry seasons in eastern and southern Amazonia and higher rainfall intensity in the northern Amazon (Marengo *et al.* 2018), and increase in vapor pressure deficit in some parts of the Amazon region (Barkhordarian *et al.* 2019). An increase in vapor pressure deficit may lead to an increase in transpiration, and, ultimately, to a decline in photosynthesis and tree growth. Thus, if the dry season becomes more prolonged in parts of the Amazon region, trees more sensitive to microclimatic variability may be greatly influenced by global warming.

## CONCLUSIONS

We investigated the effect of microclimatic variability on stem growth in multipurpose tree species in a *terra-firme* forest in the central Brazilian Amazon, and used PCR to remove the effect of intercorrelation between microclimatic factors. Across six species, stem growth in diameter increased with a rise in monthly rainfall intensity and soil water content, but the trees grew more slowly with a rise in maximum temperature and maximum vapor pressure. Thus, it seems that the reduction in stem growth observed during the dry season is associated not only with a decline in soil water availability, but also with supra-optimal temperatures and increased vapor pressure

deficit. High temperatures and high vapor pressure can enhance transpiration, which may negatively affect stomatal conductance, and ultimately reduce photosynthesis and stem growth. Our study contributes to enhance the understanding of the vapor pressure deficit effect on stem growth of Amazonian trees.

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