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Original article

Stem growth of Amazonian species is driven by intra-annual variability in rainfall, vapor pressure and evapotranspiration

Miguel Angelo Branco Camargo[1] and **Ricardo Antonio Marenco**[2*]

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ABSTRACT

Intra-annual distribution of precipitation in central Amazonia often leads to a short mild dry season and an increase in irradiance, temperature, and vapor pressure deficit; however, the accurate effect of intra-annual microclimatic variability on stem growth is still under investigation. The objective of this study was to determine how stem growth responds to monthly variations in microclimatic factors in the central Amazon. During five years (2008-2012) we measured diameter stem growth of 109 trees (26 species) and used principal component regression to evaluate the effect of microclimatic variability on stem growth in diameter. We found that the mean stem growth in diameter across species increased in response to an increase in rainfall and reference evapotranspiration, but it decreased with a rise in mean and minimum vapor pressure deficit. A contribution of this study is to show that even when irradiance and temperature had no significant effect on stem growth, small changes in vapor pressure deficit significantly affect stem growth. If the dry season becomes longer, as predicted by models, trees currently more sensitive to microclimatic variability associated with droughts would be the most affected by climate changes.

Keywords: Amazonia, stem growth, tropical rainforest, random forests, microclimatic variability.

Introduction

The Amazon rainforest is of paramount importance for the global carbon cycle because of the large amount of carbon stored in the forest biomass –a total of about 86 Pg of carbon over the Amazon basin, including dead and belowground biomass (Saatchi *et al*. 2007). Tree growth (defined as biomass gain) is a major component of net primary production, and hence it has been used to infer forest productivity. Tree growth is the result of a myriad of biochemical reactions and processes of which photosynthesis, a light-and water dependent process, is of special importance (Kozlowski & Pallardy 1997).

Several factors have been associated with variations in stem growth, photosynthesis, and vegetation greenness in the Amazon region including precipitation, solar radiation, and temperature (Zhao *et al*. 2017; Yang *et al*. 2018; Elias *et al*. 2020). Studies that aim to assess the effect of the dry season on stem growth in the Amazon have led to

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1 Instituto Nacional de Pesquisas da Amazônia, Programa de Pós-Graduação em Botânica, 69067-375, Manaus, AM, Brazil
2 Instituto Nacional de Pesquisas da Amazônia, Coordenação de Uso da Terra e Mudança Climática, 69067-375, Manaus, AM, Brazil

* Corresponding author: rmarenco@inpa.gov.br

contradictory conclusions. For instance, Silva *et al*. (2003) and Dias *et al*. (2022) found no effect of precipitation on stem growth in the central Amazon, while Yang *et al*. (2018) found that photosynthesis, over the entire Amazon region, can decline in the dry season. Likewise, Méndez (2018) and Souza & Marenco (2022) reported a decline in stem growth during the dry season in a *terra-firme* rainforest of the central Amazon.

Besides precipitation, other microclimatic variables such as temperature (Ryan 2010; Slot & Winter 2016; Zhao *et al*. 2017; Méndez 2018), vapor pressure deficit and relative humidity can also affect stem growth of tropical trees (Méndez 2018; Antezana-Vera & Marenco 2021). It is known that climatic variables are often correlated (e.g. Clark *et al*. 2003; Antezana-Vera & Marenco 2021; Souza & Marenco 2022), which makes it rather difficult to assess the individual effects of microclimatic factors on tree growth.

In this context, Principal Component Regression has proved to be a valuable tool for dealing with the collinearity problem, whereby a new set of independent variables can be extracted from the original data by principal component analysis (Montgomery *et al*. 2012). Principal component regression has been used for a long time to assess the climate-tree growth relationship (e.g. Fritts *et al*. 1971; Marquardt *et al*. 2019; Antezana-Vera & Marenco 2021), and although much research has been carried out to assess the effect of environmental conditions on tree growth of tropical rainforests, there is still no consensus about the relative importance of individual microclimatic variables on stem growth. Understanding the effect of microclimatic variability on stem growth of Amazonian trees is particularly important because of the large influence of the Amazon forest on the global carbon balance and regional climate.

Thus, the main objective of this study was to determine the effect of intra-annual variation in precipitation, temperature, and irradiance on stem growth at a *terra-firme* rainforest site in the central Amazon. We hypothesized that stem growth would vary reflecting the availability of water and changes in irradiance and temperature, and expected that the trees would grow faster following an increase in irradiance and temperature. Because in the central Amazon the dry season is often mild and the roots can extract water from deeper layers of the soil (Broedel *et al*. 2017), we did not predict an effect of intra-annual precipitation variability on stem growth.

Materials and methods

Study site

The research was conducted at the Tropical Silviculture Experiment Station (ZF2 Reserve), located about 60 km north of Manaus. The study area is a *terra-firme* forest on a plateau (centered at 02° 36´ 21" S, 60° 08' 11" W, 110–120 m above sea level). In this region tree density can reach up to 637 trees per hectare (Rankin-De-Merona *et al*. 1992), and species diversity is high −up to 179 species ha^{-1} (Prance *et al*. 1976). However, it is not uncommon that trees of the same species are hundreds of meters apart. Thus, for this study, tree species were selected based on the availability of at least three trees of the same species, each of them with stem diameter (at 1.3 m above the ground −diameter at breast height, DBH) of at least 10 cm. In the experimental site, the annual rainfall is about 2,540 mm with a mild dry season from June through October (Antezana-Vera & Marenco 2021; Dias et al. 2022), being July–September the driest months (INMET 2021 – climate data for the nearby city of Manaus). During 2013–2017, reference evapotranspiration (ET$_o$) was 120.8 mm month^{-1}, mean temperature 26.5 °C, and mean relative humidity (RH) 78.9% (Antezana-Vera & Marenco 2021). In this area, the predominant soil type is a clayed Oxisol (Yellow Latosol in the Brazilian classification) with low fertility, and pH (in water) of 4.0-4.3 at 0-20 cm depth (Chauvel 1982; Magalhães *et al*., 2014).

Physical environment, plant material and stem growth

During the period of January 2008 to December 2012, air temperature (T), photosynthetically active radiation (PAR), RH, and rainfall data were daily recorded above the forest canopy, at the top of a 40-m-tall observation tower (02°35´21"S, 60°06´53"W). Temperature and RH were measured with specific sensors (Humitter 50y, Oy Vaisala, Finland) and PAR with a quantum sensor (Li-190SA, Li-Cor, NE, USA) connected to a data logger (Li-1400, Li-Cor, Lincoln, NE). Data were logged at 15 min (PAR) or 30 min intervals (T and RH). PAR data were integrated over time to obtain daily PAR values (mol m^{-2} day^{-1}). Rainfall data were recorded using a rain gauge (Em5b, Decagon, WA, USA). We used RH (%) and temperature (T °C) to calculate vapor pressure deficit (D) as: D (hPa) = $e_s - (e_s \times \text{RH})$, where e_s is the saturated vapor pressure in hectopascal (Buck 1981). The daily reference evapotranspiration (ET$_o$, mm day^{-1}) was computed as (Hargreaves & Samani 1985):

$$ET_o = 0.0023R_a(T_{mean} + 17.8)(T_{max} - T_{min})^{0.5} \qquad (1)$$

where R$_a$ represents the extraterrestrial radiation (expressed in mm day^{-1}), and T_{mean}, T_{min} and T_{max} (in °C) the mean, minimum and maximum temperature, respectively. Then, from daily data, the monthly ET$_o$ was obtained.

In this study we collected data from 109 trees of 26 evergreen species (located on the above- mentioned plateau), which are described in the Supplementary Material (Tab. S1-A). In these trees we measured the breast-height stem growth in diameter (S_G) at monthly intervals during 60 months (January 2008 – December 2012), as previously described (Dias *et al*. 2022). The S_G was measured using stainless steel dendrometer bands, which were installed at least two years before the beginning of data collection.

Statistical analyses

The effect of microclimatic variability (PAR, rainfall, temperature, vapor pressure deficit, and ET_o) on the mean diameter stem growth across species ($S_{G\text{-mean}}$) was evaluated using Principal Component Regression (PCR). Prior to conducting PCR, the $S_{G\text{-mean}}$ data were centered (observed value minus the mean) and the microclimatic variables standardized (observed value minus the mean divided by standard deviation), and then microclimatic data subjected to principal component analysis (PCA) to extract orthogonal factors. The PCR is performed in several steps (Montgomery *et al.* 2012), and briefly summarized as follows (equations 2-9):

$$\mathbf{Y} = \mathbf{X}\mathrm{b} + \epsilon \tag{2}$$

$$\mathbf{Y} = \mathbf{Z}\alpha + \epsilon \tag{3}$$

$$\mathbf{Z} = \mathbf{XT} \tag{4}$$

$$\alpha = \mathbf{T}'\mathrm{b} \tag{5}$$

$$b_{pc} = \mathbf{T}(\hat{\alpha}_{pc}) \tag{6}$$

$$\mathrm{var}(b_{pc}) = \mathrm{var}\,(\mathbf{T}\hat{\alpha}_{pc}) \tag{7}$$

$$\mathrm{SE}\left(b_{j,pc}\right) = \sqrt{\mathrm{var}\left(b_{j,pc}\right)} \tag{8}$$

$$t = \frac{b_{j,pc}}{SE\left(b_{j,pc}\right)} \tag{9}$$

These equations describe the standard multiple linear regression (MLR, Eq. 2) and the PCR model (Eq. 3), and following the classic notation, $\mathbf{Y}$ denotes a vector of observations (dependent variable), $\mathbf{X}$ a matrix of regressors, $\mathbf{b}$ and α vectors of coefficients, and ϵ the random errors. In equation 4, the columns of $\mathbf{Z}$ represent a new set of orthogonal components $-\mathbf{z}_i$ (hereafter termed principal components), while $\mathbf{T}$ is a matrix whose columns represent eigenvectors. The computation of α (coefficients of the PCR model) is described in equation 5, and that of $\mathbf{b}_{pc}$ in equation 6. The values of $\hat{\alpha}$ (estimator of α) are obtained after regressing $\mathbf{Y}$ on the principal components ($\mathbf{z}_i$). In equation 6, the "pc" subscript indicates that only a reduced k number of $\mathbf{z}_i$ components has been retained in the model (i.e. PCR reduced model). The variance (var) of $\mathbf{b}_{pc}$, its standard error (SE) and the t values are computed as described in Eq. 7–9. To determine the number of principal components to be used in the PCR reduced model, we used the adjusted coefficient of determination (R^2_{ajd}), after Jolliffe (2002). While the significance of $\mathbf{b}_{pc}$ was tested on individual coefficients using t-test, and $n - k - 1$ degree of freedom (DF), where n is number of observations (i.e. 60 months in this study) and k the number of principal components in the reduced model (the DF in the PCR analysis of variance). In addition, we also described the relationship between $S_{G\text{-mean}}$ and rainfall, temperature and vapor pressure deficit to illustrate the trend of microclimatic variables. For further information, we used the Random Forest machine learning technique to rank the microclimatic variables (predictors) according to their importance in predicting stem growth ($S_{G\text{-mean}}$). The analyses were performed using R v.4.0.5 (R Core Team, 2021). The PCR was performed using PLS (Liland *et al.* 2021), while the randomForest package was used for computing random forest algorithm (Liaw & Wiener 2002). In all analyses, we used $p \leq 0.05$ to define statistical significance.

Results

Microclimatic variability and its relationship with stem growth: a heuristic approach

We found no correlation between the stem growth of species (S_G) and wood density ($p = 0.44$, Tab. 1), and although the largest trees tended to grow faster, the correlation between stem diameter (DBH) and S_G was not significant ($p = 0.06$, Tab. 1). Thus, data were pooled to assess the effect of microclimatic variability on stem growth over species ($S_{G\text{-mean}}$).

Table 1. The relative importance of climatic variables computed by random forests (RIRF). It is also shown the mean stem growth over species ($S_{G\text{-mean}}$) during the study period, as well as the correlation between stem growth of species (S_G) and wood density (WD) and between S_G and stem diameter of trees at breast height. Abbreviations: PAR: photosynthetically active radiation, T: temperature, T_{max}: mean maximum T, T_{min}: mean minimum T, T_{mean}: mean T, D: vapor pressure deficit, D_{max}: mean maximum D, D_{min}: mean minimum D, D_{mean}: D mean, and ET_o: reference evapotranspiration.

Climatic variable	RIRF (%)
Rainfall (mm month^{-1})	100.0
D_{max} (hPa)	21.9
ET_o (mm month^{-1})	20.9
T_{mean} (°C)	19.5
D_{mean} (hPa)	15.0
T_{max} (°C)	11.8
T_{min} (°C)	10.7
D_{min} (hPa)	8.0
PAR (mol m^{-2} day^{-1})	0.0
Stem growth and Pearson correlation (r):	
$S_{G\text{-mean}}$ (± SE) = 1.31 ± 0.17 mm yr^{-1}	
Stem diameter *vs* S_G : $r = 0.377$, $p = 0.06$	
WD *vs* S_G: $r = -0.158$, $p = 0.44$	

The PCR showed that the maximum R^2_{adj} value (0.1458) was found when the fifth principal component was added to the model (Tab. 2). Hence, the first five components (z_1–z_5) were used for PCR analysis. Furthermore, it is shown in Tab. 2 that although the fifth component (z_5) was associated with a rather low-magnitude eigenvalue ($\lambda_5 = 0.40$, Fig. 1) it had a significant effect on stem growth

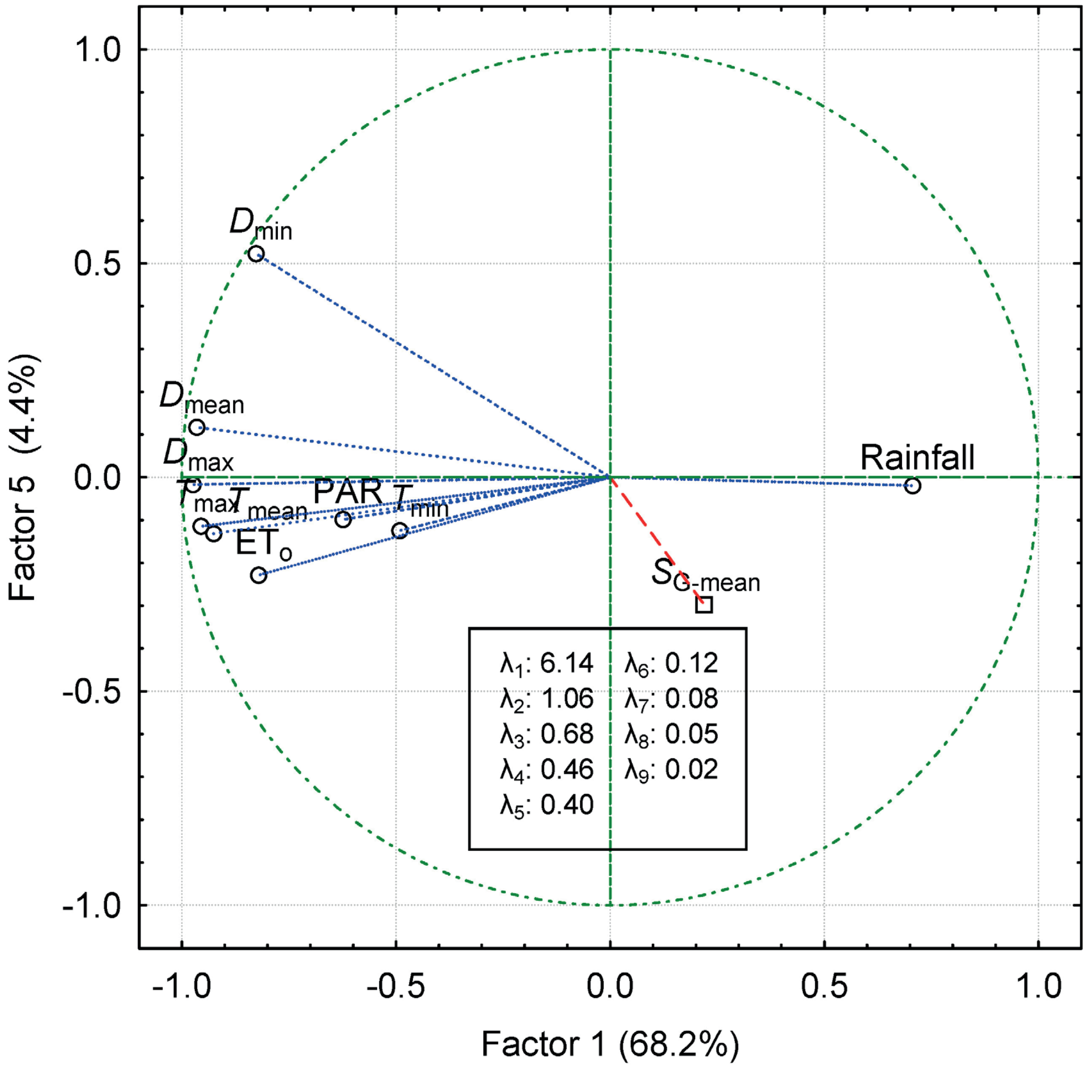

Figure 1. Principal component analysis of microclimatic variables, with the mean stem growth in diameter ($S_{G\text{-mean}}$) as a supplementary variable. The eigenvalues (λ_i) of orthogonal factors are shown in the inset. Note that the first five factors account for 97.1% of total variance (100×8.74/9.0). Abbreviations as described in Tab. 1.

Table 2. Principal component regression of the relationship between $S_{G\text{-mean}}$ and the principal components $z_1 - z_5$. Abbreviations: DF: degree of freedom, R^2: coefficient of determination (with increasing z_i) , R^2_{adj}: adjusted R^2, $S_{G\text{-mean}}$: mean tree growth across species, α: regression coefficient, SE(α): standard error of α. Also, the R^2_{ajd} for Z_6 is also shown. 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	0.042210	5	0.008442	3.013844	0.018003
Residual	0.151258	54	0.002801		
Total	0.193468				
Principal component	α	**SE(α)**	***p* value**	**R^2**	**R^2_{adj}**
z_1	0.0051	0.0028	0.0752	0.0481	0.0317
z_2	0.0058	0.0067	0.3925	0.0590	0.0260
z_3	0.0131	0.0084	0.1245	0.0946	0.0461
z_4	−0.0158	0.0102	0.1265	0.1298	0.0665
z_5	−0.0271	0.0110	0.0172	0.2182	0.1458
z_6 (not used in PCR)	−0.0145	0.0202	0.4751	0.2257	0.1381

($p = 0.0172$), whose p value was even larger than that associated with the first component $-z_1$ ($p = 0.0752$). As the first and the fifth components were more closely associated with stem growth (inferred from p values), only Factor 1 and Factor 5 are shown in Fig. 1. It is worth noting, that the first five factors extracted by PCA from microclimatic data combined accounted for 97.1 % of the total variance [i.e. 100×(6.14 + ... 0.40)/9.0] in microclimatic data (Fig. 1). That is, by discarding very small eigenvalues ($\lambda < 0.4$) only a small fraction (3%) of the total microclimatic variance was disregarded.

It is displayed in Fig. 1 that $S_{\text{G-mean}}$ (indicated by the square symbol) shares the same quadrant with rainfall. Therefore, it can be expected that precipitation positively affects stem growth. Because both $S_{\text{G-mean}}$ and ET_o (in Fig. 1) are negatively correlated with Factor 5, ET_o may be positively correlated with stem growth. The Fig. 1 also shows that D_{min} and $S_{\text{G-mean}}$ (square symbol) are in opposite quadrants indicating that they are negatively correlated. Although the other microclimatic variables (temperature, PAR and D_{mean} and D_{max}) are closely related to Factor 1, it is difficult to infer (from Fig. 1) how these variables can affect stem growth, as the p value of z_1 did not reach a significant level ($p = 0.0752$). In the next section, by using PCR we examine the growth-microclimatic relationship in more detail.

Effect of microclimatic variability on stem growth based on PCR

During the study period mean temperature (T_{mean}) was 25.6 °C, D_{mean} 5.15 hPa and monthly rainfall 242.1 mm month^{-1} (2,905 mm yr^{-1}, Fig. 2, 3). The PCR analysis showed that $S_{\text{G-mean}}$ responded positively to both rainfall and ET_o (Fig. 2A, Tab. 3), whereas D_{min} and D_{mean} had a negative effect on the mean stem growth (Fig. 3, Tab. 3). Temperature, on the other hand, had a neutral effect on $S_{\text{G-mean}}$ (Fig. 2B, Tab. 3). Thus, using the coefficients shown in Tab. 3, the centered $S_{\text{G-mean}}$ as a function of the standardized microclimatic variables can be represented as follows (equation 10):

$$S_{\text{G-mean}}\,(\text{mm month}^{-1}) = 0.000874\text{PAR} + 0.020837\text{Rainfall} + 0.006953T_{\text{min}} + 0.003356T_{\text{mean}} + 0.005285T_{\text{max}} - 0.01976D_{\text{min}} - 0.005033D_{\text{mean}} - 0.002294D_{\text{max}} + 0.016414ET_o \quad (10)$$

Comparison of PCR with the Random Forest model

The PCR model showed that the coefficient associated with rainfall has the largest beta (0.020837). In this respect, the prediction based on Random Forest concurs with the outcome of the PCR model, as Random Forest showed that rainfall was the most important variable (Tab. 1). On the other hand, the Random Forest model predicted that D_{max}, ET_o and T_{mean} performed similarly (importance

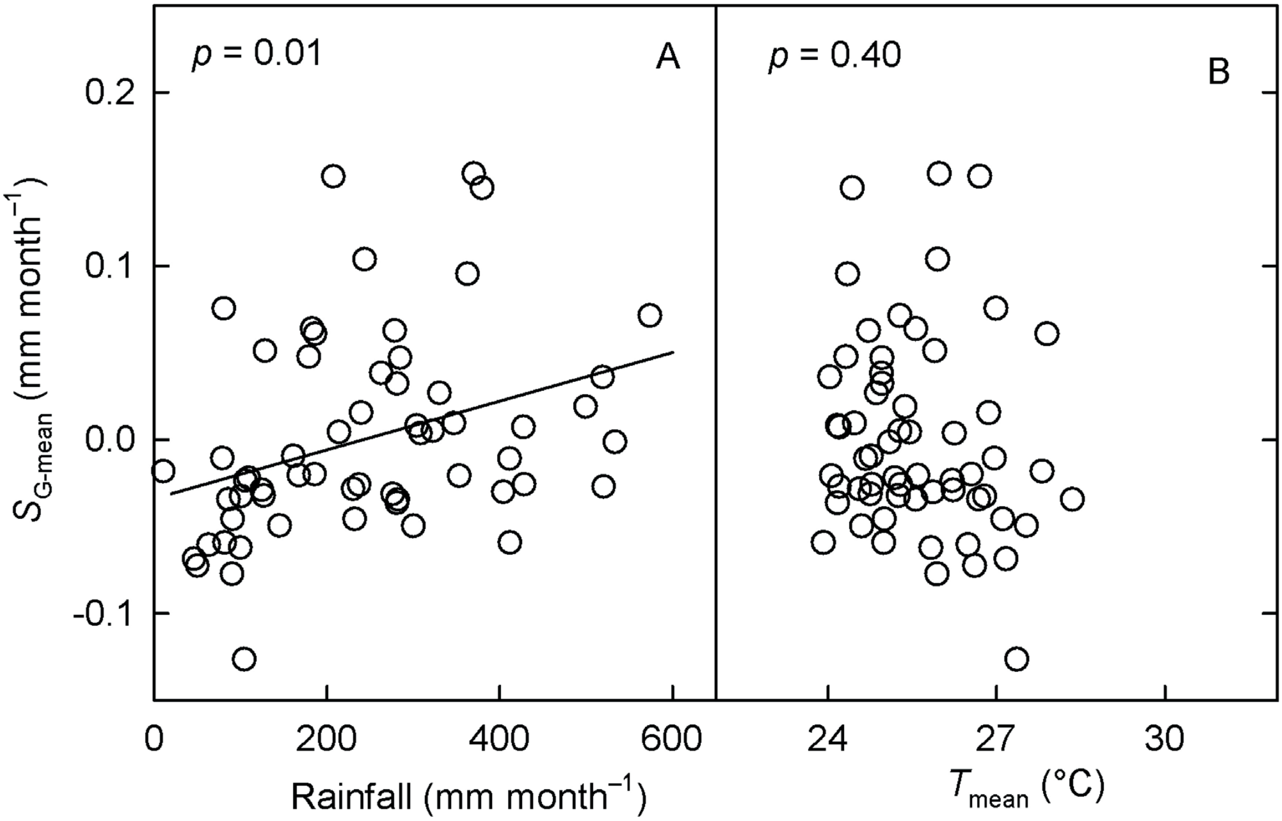

Figure 2. Mean stem growth in diameter ($S_{\text{G-mean}}$) as a function of rainfall (A) and mean temperature (T_{mean}, B). In panel A, the solid line shows the trend. Each symbol represents the mean stem growth across species (26 species) for a given month. Data were collected from January 2008 to December 2012. The means (± SE) of rainfall and T_{mean} were 242.1 ± 18.3 mm month^{-1} and 25.6 ± 0.14 °C, respectively.

of 20-22%); whereas the PCR showed that D_{max} and T_{mean} had no significant effect on stem growth, which is an important aspect to consider when the performance of these models is compared. With respect to the effect of PAR on stem growth, both models converged, as PAR was ranked as non-important by Random Forest, and likewise the PCR model showed that PAR has no significant effect on stem growth.

Discussion

In this study we found that the minimum and mean vapor pressure deficit had a constraining effect on $S_{G\text{-mean}}$, while stem growth increased with increasing ET_o and rainfall. The reduced stem growth with a rise in D_{min} indicates an effect of nocturnal atmospheric conditions on tree growth, as the lowest values of D_{min} often occur at night when

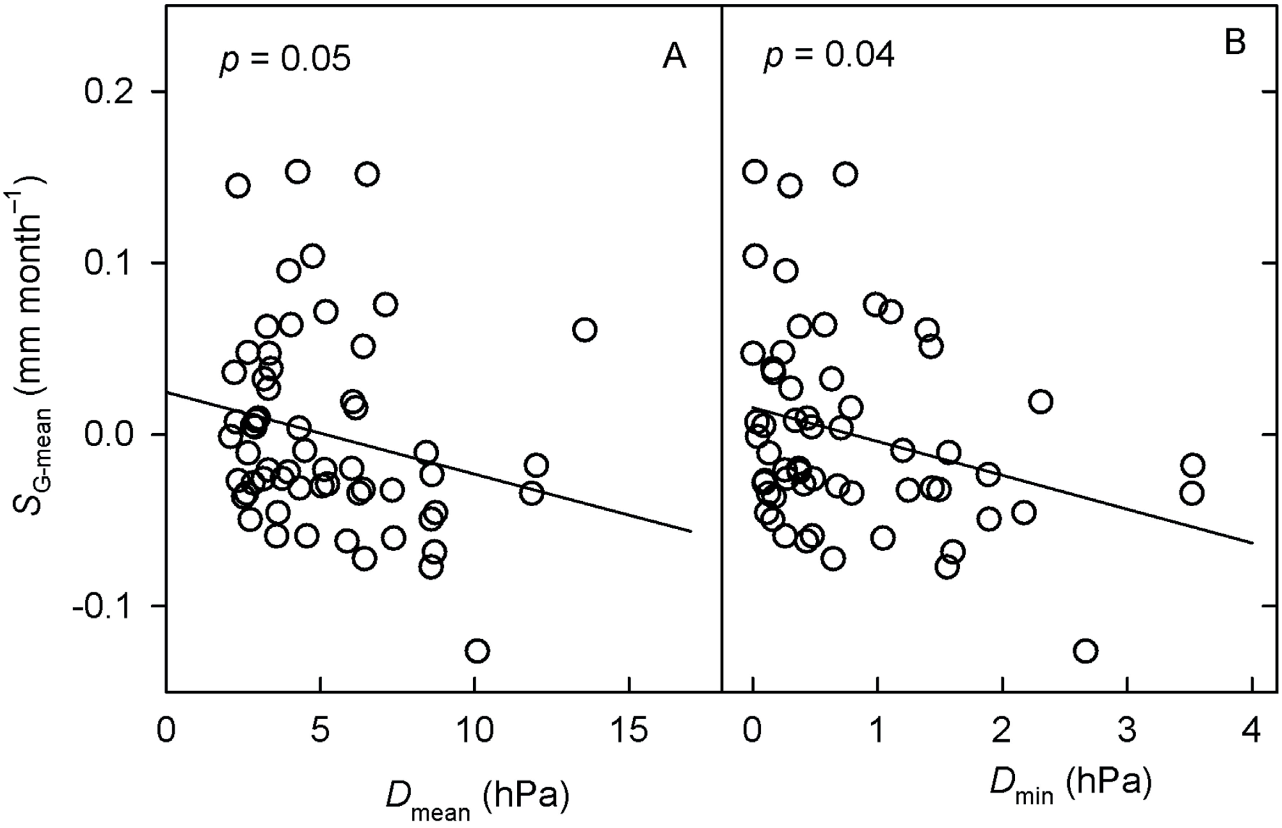

Figure 3. Mean stem growth in diameter ($S_{G\text{-mean}}$) as a function of vapor pressure deficit (D), mean D (D_{mean}, A) and minimum D (D_{min}, B). Further information as described in Fig. 2. The means (± SE) of D_{mean} and D_{min} were 5.15 ± 0.34 and 0.79 ± 0.11 hPa, respectively; whereas mean D_{max} was 16.5 ± 0.70 hPa (data not shown).

Table 3. Regression coefficients (Beta), standard error of coefficients (SE of Beta) and *p*-values obtained by Principal Component Regression (PCR) of the effect of microclimatic variability on mean stem growth ($S_{G\text{-mean}}$) over species. Values in bold font are significant at $p \leq 0.05$. Abbreviations as described in Tab. 1.

Parameter	Beta	SE (Beta)	*p*-value
PAR	0.000874	0.008014	0.91
Rainfall	0.020837	0.008180	**0.01**
T_{min}	0.006953	0.006827	0.31
T_{mean}	0.003356	0.003978	0.40
T_{max}	0.005285	0.002808	0.07
D_{min}	−0.019760	0.009373	**0.04**
D_{mean}	−0.005033	0.002534	**0.05**
D_{max}	−0.002294	0.001354	0.10
ET_o	0.016414	0.006873	**0.02**

relative humidity is high (INMET 2021). This is important, as it shows that stem growth can be affected not only by environmental factors that limit photosynthesis, but also by nocturnal conditions that tend to increase transpiration and thereby to lower leaf water potential. Indeed, it is widely accepted that changes in expansive growth are related to changes in leaf water potential (Bradford & Hsiao 1982; Kozlowski & Pallardy 1997).

The negative effect of D_{mean} can be explained by considering the effect of vapor pressure deficit on stomatal conductance, as the most common response to a rise in vapor pressure deficit is a decrease in stomatal conductance and hence in carbon uptake by photosynthesis (McDowell & Allen 2015; Vinod *et al*. 2023). In fact, Yang *et al*. (2018) reported a decrease in ecosystem photosynthesis in the dry season (over the forests of the Amazon basin) when temperature and vapor pressure deficit often increase (Antezana-Vera & Marenco 2021). The constraining influence of an increase in vapor pressure deficit on stem growth is relevant in the face of global climate change, especially taking into account that in the Amazon region temperature has increased (around 0.16 °C per decade) and the rainfall pattern altered (e.g. decreased rainfall in the eastern and southern Amazon, Marengo *et al*. 2018), which combined may lead to changes in vapor pressure. In this regard, it is known that the dry season is associated with an increase in irradiance, temperature and vapor pressure deficit (Méndez 2018; Antezana-Vera & Marenco 2021; INMET 2021), which may lead to a decline in photosynthesis and tree growth (Yang *et al*. 2018; Antezana-Vera & Marenco 2021).

The positive effect of rainfall variability on stem growth suggests that even during a relative mild dry season, Amazonian trees tend to respond to variation in water availability, even when it has been found that in the central Amazon root water uptake can occur even below 4.8 m depth, during severe dry periods (Broedel *et al*. 2017), which eventually can help to withstand the effect of water stress in mild dry seasons. Even when the enhancing effect of $T_{\max}$ on $S_{\text{G-mean}}$ did not reach a significant level effect ($p = 0.07$), $S_{\text{G-mean}}$ increased with increasing ET_o ($p = 0.02$, Tab. 3). At first glance, it seems unexpected to record a positive effect of ET_o and at the same time a neutral effect of temperature ($T_{\min}$, T_{mean} and $T_{\max}$) on stem growth (Tab. 3). This can be explained by taking into account that ET_o is a function of solar radiation and temperature, including $T_{\max}$ (Eq. 1), and $T_{\max}$ as mentioned above tended to have a positive on stem growth (Tab. 3). The direct effect of temperature on biomass gain can occur through its effect on photosynthesis, via the direct effect of temperature on enzyme activity, electron transport chain, and stomatal conductance (Lloyd & Farquhar 2008; Marenco *et al.* 2014; Vinod *et al.* 2023). In addition, root-zone temperature regulates photosynthesis via its influence on water absorption and stomatal conductance, because temperature affects water viscosity and root permeability to water (Kaufmann 1975; Delucia 1986). The neutral effect of $T_{\min}$ on $S_{\text{G-mean}}$ suggests that variations in night temperatures did not alter significantly metabolic processes, such as root, leaf and stem respiration. This is important, as respiration provides energy and carbon intermediates for growth and maintenance of tissues (Kozlowski & Pallardy 1997). The absence of an effect of temperature on stem growth does not support our working hypothesis, as we had expected that trees would grow faster under warmer conditions, as reported by Elias *et al*. (2020). The optimum temperature for photosynthesis in tropical rainforests is about 29 °C (Liu 2020). Thus, the lack of an effect of temperature on $S_{\text{G-mean}}$ indicates that changes in temperatures over the year were not high enough to alter stem growth. The importance of irradiance on tree growth is indisputable via its effect on photosynthesis. Notwithstanding, we found no effect of PAR variability on stem growth, which indicates absence of adverse photochemical effects associated with the increase in irradiance which often occurs during the dry season (Antezana-Vera & Marenco 2021). In fact, leaf photochemistry tends to remain constant in plants subjected to moderate water stress as shown by Rascher *et al*. (2004).

We have shown that PCR proved to be a useful approach to separate the individual contribution of microclimatic variability on stem growth. Even though Random Forest was effective to identify rainfall as one of the most important variables influencing stem growth and PAR as the least, by using this technique it is rather difficult to assess the individual contribution of microclimatic variables due to the effect of collinearity. Indeed, Random Forest is a powerful algorithm for prediction, but when the primary objective is explanation, principal component regression seems to perform better than Random Forest.

Conclusions

In this study we show that the mean diameter stem growth decreased in response to an increase in mean and minimum vapor pressure deficit, while rainfall and the reference evapotranspiration had a positive effect on $S_{\text{G-mean}}$. Irradiance and temperature, on the other hand, had no significant effect on the mean stem growth. These results do not support our working hypothesis, as we had expected that stem growth would increase with an increase in temperature and irradiance, and that a slight decrease in precipitation during the dry season would not affect stem growth. A contribution of this study is to show that even when temperature and irradiance intra-annual variability did not significantly affect stem growth, besides precipitation, environmental factors related to atmospheric dryness can influence stem growth. These results are important in the context of the current climate changes and enhance our understanding on the drivers of Amazonian trees' radial growth.

Supplementary material

The following online material is available for this article: Table S1 – A. Family and species used in the study. There are also shown stem growth in diameter (SG mm month^{-1} ± standard error), number of tree per species (*n*), mean diameter at breast height (DBH, in cm), height (H, in m), and wood density (WD, in g cm−3). Tree height (H) was computed using the equation of Souza & Marenco (2022), being H (m) = −11.387 + 11.504ln(DBH).

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References

Antezana-Vera SA, Marenco RA. 2021. Intra-annual tree growth responds to micrometeorological variability in the central Amazon. iForest - Biogeosciences and Forestry 14: 242-249. doi: 10.3832/ifor3532-014

Bradford KJ, Hsiao TC. 1982. Physiological responses to moderate water stress. In: Lange OL, Nobel PS, Osmond CB, Ziegler H. (eds). Physiological Plant Ecology II - Water Relation and Carbon Assimilation. Heidelberg, Springer-Verlag. p. 263-324. doi: 10.1007/978-3-642-68150-9_10

Broedel E, Tomasella J, Cândido LA, Von Randow C. 2017. Deep soil water dynamics in an undisturbed primary forest in central Amazonia: Differences between normal years and the 2005 drought. Hydrological Processes 31: 1749-1759. doi: 10.1002/hyp.11143

Buck AL. 1981. New equations for computing vapor-pressure and enhancement factor. Journal of Applied Meteorology 20: 1527-1532. doi: 10.1175/1520-0450(1981)020<1527:NEFCVP>2.0.CO;2

Chauvel A. 1982. Os latossolos amarelos, álicos, argilosos dentro dos ecossistemas das bacias experimentais do INPA e da região vizinha. Acta Amazonica 12: 47-60. doi: 10.1590/1809-43921982123S047

Clark DA, Piper SC, Keeling CD, Clark DB. 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984-2000. Proceedings of the National Academy of Sciences U S A 100: 5852-5857. doi: 10.1073/pnas.0935903100

Delucia EH. 1986. Effect of low root temperature on net photosynthesis, stomatal conductance and carbohydrate concentration in Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) seedlings. Tree Physiology 2: 143-154. doi: 10.1093/treephys/2.1-2-3.143

Dias DP, Antezana-Vera SA, Marenco RA. 2022. Variation in bark water content in three Amazonian species in response to rainfall seasonality. Ciência Florestal 32: 2057-2073. doi: 10.5902/1980509866232

Elias F, Ferreira J, Lennox GD *et al*. 2020. Assessing the growth and climate sensitivity of secondary forests in highly deforested Amazonian landscapes. Ecology 101: e02954. doi: 10.1002/ecy.2954

Fritts HC, Blasing TJ, Hayden BP, Kutzbach JE. 1971. Multivariate techniques for specifying tree-growth and climate relationships and for reconstructing anomalies in paleoclimate. Journal of Applied Meteorology 10: 845-864, doi: 10.1175/1520-0450(1971)010<0845:MTFSTG>2.0.CO;2

INMET – Instituto Nacional de Meteorologia. 2021. Gráficos climatológicos [Weather charts]. http://clima.inmet.gov.br/graficosclimatologicos/am/82331. 27 May 2021.

Hargreaves GH, Samani ZA. 1985. Reference crop evapotranspiration from temperature. Applied Engineering in Agriculture 1: 96-99. doi: 10.13031/2013.26773

Jolliffe IT. 2002. Principal components in regression analysis. In: Jolliffe IT. Principal component analysis. 2nd edn. New York, Springer. p. 167-198,

Kaufmann MR. 1975. Leaf water stress in Engelmann spruce: Influence of the root and shoot environments. Plant Physiology 56: 841-844. doi: 10.1104/pp.56.6.841

Kozlowski TT, Pallardy SG. 1997. Physiology of woody plants. 2nd. edn. London, Academic Press.

Liaw A, Wiener M. 2002. Classification and Regression by randomForest. R News 2: 18-22. https://cran.r-project.org/doc/rnews/rnews_2002-3.pdf

Liland KH, Mevik B-H, Wehrens R. 2021. PLS: Partial Least Squares and Principal Component Regression. R package. version 2.8-0. https://cran.r-project.org/package=pls

Liu Y. 2020. Optimum temperature for photosynthesis: From leaf-to ecosystem-scale. Science Bulletin 65: 601-604. doi: 10.1016/j.scib.2020.01.006

Lloyd J, Farquhar GD. 2008. Effects of rising temperatures and $[CO_2]$ on the physiology of tropical forest trees. Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences 363: 1811-1817. doi: 10.1098/rstb.2007.0032

Magalhães NS, Marenco RA, Camargo MAB. 2014. Do soil fertilization and forest canopy foliage affect the growth and photosynthesis of Amazonian saplings? Scientia Agricola 71: 58-65. doi: 10.1590/S0103-90162014000100008

Marenco RA, Nascimento HC, Magalhães ND. 2014. Stomatal conductance in Amazonian tree saplings in response to variations in the physical environment. Photosynthetica 52: 493-500. doi: 10.1007/s11099-014-0056-3

Marengo JA, Souza CM, Thonicke K *et al*. 2018. Changes in climate and land use over the Amazon region: current and future variability and trends. Frontiers in Earth Science 6: 228. doi: 10.3389/feart.2018.00228

Marquardt PE, Miranda BR, Jennings S, Thurston G, Telewski FW. 2019. Variable climate response differentiates the growth of Sky Island ponderosa pines. Trees 33: 317-332. doi: 10.1007/s00468-018-1778-9

Mcdowell NG, Allen CD. 2015. Darcy's law predicts widespread forest mortality under climate warming. Nature Climate Change 5: 669-672. doi: 10.1038/nclimate2641

Méndez CR. 2018. Influência do El Nino 2015- 2016 no incremento diamétrico das árvores da Amazônia Central. Msc. Thesis, Instituto Nacional de Pesquisas da Amazônia, Brazil.

Montgomery DC, Peck EA, Vining GG. 2012. Principal component regression. In: Montgomery DC, Peck EA, Vining GG (eds.). Introduction to Linear Regression Analysis. 5th edn. Hoboken, Wiley. p. 313-319.

Prance GT, Rodrigues WA, Silva MF. 1976. Inventário florestal de um hectare de mata de terra firme km 30 de Estrada Manaus-Itacoatiara. Acta Amazonica 6: 9-35. doi: 10.1590/1809-43921976061009

Rankin-De-Merona JM, Prance GT, Hutchings RW, Silva MF, Rodrigues WA, Uehling ME. 1992. Preliminary results of a large-scale tree inventory of upland rain forest in the Central Amazon. Acta Amazonica 22: 493-534. doi: 10.1590/1809-43921992224534

R Core Team. 2021. R: A language and environment for statistical computing. https://www.R-project.org/. 15 May 2021.

Rascher U, Bobich EG, Lin GH *et al*. 2004. Functional diversity of photosynthesis during drought in a model tropical rainforest–the contributions of leaf area, photosynthetic electron transport and stomatal conductance to reduction in net ecosystem carbon exchange. Plant Cell Environment 27: 1239-1256. doi: 10.1111/j.1365-3040.2004.01231.x

Ryan MG. 2010. Temperature and tree growth. Tree Physiology 30: 667-668. doi: 10.1093/treephys/tpq033

Saatchi SS, Houghton RA, Alvalá ARCS, Soares JV, Yu Y. 2007. Distribution of aboveground live biomass in the Amazon basin. Global Change Biology 13: 816-837. doi: 10.1111/j.1365-2486.2007.01323.x

Silva RP, Nakamura S, Azevedo CP *et al*. 2003. Use of metallic dendrometers for individual diameter growth patterns of trees at Cuieiras river basin. Acta Amazonica 33: 67-84. doi: 10.1590/1809-4392200331084

Slot M, Winter K. 2016. The effects of rising temperature on the ecophysiology of tropical forest trees. In: Goldstein G, Santiago LS (eds.). Tropical Tree Physiology. Cham, Springer. p. 385-412.

Souza AP, Marenco RA. 2022. Stem growth of multipurpose tree species: Net effect of micrometeorological variability assessed by principal component regression. Acta Amazonica 52: 277-284. doi: 10.1590/1809-4392202103390

Vinod N, Slot M, McGregor IR *et al*. 2023. Thermal sensitivity across forest vertical profiles: patterns, mechanisms, and ecological implications. New Phytologist 237: 22-47. doi: 10.1111/nph.18539

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. doi: 10.1111/gcb.14056

Zhao W, Zhao X, Zhou T *et al*. 2017. Climatic factors driving vegetation declines in the 2005 and 2010 Amazon droughts. PloS One 12: e0175379. doi: 10.1371/journal.pone.0175379