# ORTHOGONAL EFFECTS OF MICROMETEOROLOGICAL VARIABLES ON TWO AMAZONIAN SPECIES OF CONTRASTING GROWTH RATES

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Submitted February 2021; accepted September 2021

Intra-annual micrometeorological variability leads to a mild dry season in the central Amazon, but how rainfall seasonality affects tree growth is still unclear. This study aimed to determine the collinearity-free (orthogonal) effect of microclimatic variability on stem growth of *Eschweilera bracteosa* (slow-growing species) and *Tachigali venusta* (fast-growing species). Stem growth in diameter was measured from January 2008 to December 2012, at monthly intervals. Irradiance, air temperature, rainfall and vapour pressure deficit data were also recorded. Principal component regression was used to assess the effect of micrometeorological variability on stem growth. In the fast-growing species, stem growth increased with increasing precipitation, but it decreased with increases in mean and maximum temperature and vapour pressure deficit. The slow-growing species was only responsive to variations in mean temperature and mean and maximum vapour pressure deficit. Irradiance variability has no effect on stem growth, and showed that fast and slow-growing species could respond differently to microclimatic variability. Therefore, if the dry season becomes longer and dryer, trees more sensitive to micrometeorological variability can be the most affected by climate changes.

Keywords: Amazon rainforest, *Eschweilera bracteosa*, principal component regression, *Tachigali venusta*, stem growth

## INTRODUCTION

The Amazon rainforest is of paramount global importance because of its outstanding biodiversity, and also due to the large amount of carbon stored in the forest biomass, i.e. about 86 Pg of carbon (Saatchi et al. 2007). Tree growth is the result of a myriad of biochemical reactions closely related to the photosynthetic capacity of trees, and thereby metabolic processes that affect photosynthesis can also affect tree growth. Thus, tree growth can be affected by intrinsic (e.g. age and the genetic make-up of the individual) and extrinsic factors, such as microclimatic variability, soil fertility and disturbances associated with logging activity, tree competition, herbivory and disease incidence.

Regarding the effect of microclimatic variability on the performance of a tree, it is accepted that ecosystem photosynthesis and tree growth can be responsive to variations in rainfall and irradiance intensity, temperature and vapour pressure deficit. Although much research has been carried out to assess the effect of climatic factors on tree growth in tropical rainforests (Clark et al. 2003, Antezana-Vera & Marenco 2021, Dias & Marenco 2021) there is still no consensus about the relative importance of individual effects of microclimatic variability on tree growth. In fact, it is difficult to assess the orthogonal (free of collinearity) or individual effect of a given climatic variable on tree growth because climatic variables are often correlated (Clark et al. 2003, Antezana-Vera & Marenco 2021). Therefore, the effects of intra-annual variation of climatic parameters such as irradiance, temperature, precipitation and vapour pressure deficit on tree growth are still under investigation in the Amazon region. Rainfall seems to be the major factor that affects tree growth in tropical rainforests. Whether or not trees grow faster in the wet season than in the dry season in the central Amazon is still under debate. Although in most studies either tree growth or ecosystem photosynthesis seems to decrease in the dry season (Lee et al. 2013, Yang et al. 2018, Antezana-Vera & Marenco 2021), stem

tree growth appears to be rather unresponsive to variation in precipitation in areas or years when precipitation is intense (Clark et al. 2003, Silva et al. 2003). Moreover, a negative effect of increased rainfall intensity and a positive effect of vapour pressure deficit have been reported for the wettest parts of the Amazon (Green et al. 2020).

Depending on the strategy plants adopt to cope with shading, they can be classified as either shade-tolerant (usually slow growing) or light-demanding species (Charrier 2021). In comparison with shade-tolerant species, leaves of light-demanding species often have higher photosynthetic and respiration rates (Calzavara et al. 2019). Therefore, slow-growing and fast-growing species can respond distinctly to changes in irradiance (Marenco & Vieira 2005, Aasamaa & Sõber 2011), water-use efficiency (Maruyama et al. 1997), and optimal temperature for photosynthesis (Slot et al. 2016). They also differ in drought tolerance (Ouédraogo et al. 2013) and hydraulic properties, as fast-growing species seem to be less resistant to cavitation (Eller et al. 2018). However, whether fastgrowing Amazonian trees are more responsive to variations in climatic factors than slow-growing trees is still being investigated. The aim of this study was to determine the collinearity-free effect (orthogonal effect) of micrometeorological variability on stem growth of two Amazonian species with contrasting growth characteristics.

*Eschweilera bracteosa* is a slow-growing species (stem growth of 0.96 mm year<sup>1</sup>) which has high wood density (0.83 g cm<sup>-3</sup>), while *Tachigali venusta* is fast-growing (4.92 mm year<sup>1</sup>) and of low wood density (0.55 g cm<sup>-3</sup>, Dias & Marenco 2021). Both species can be found in *terra-firme* forests. We hypothesised that *T. venusta* would grow faster than *E. bracteosa* with increasing irradiance and temperature, as it seems that fast-growing species can reach higher photosynthetic rates than slow-growing species (Calzavara et al. 2019).

# MATERIALS AND METHODS

The study was conducted at the Tropical Forest Experiment Station (ZF2 Reserve), located at a *terra-firme* rainforest plateau in central Amazonia about 60 km north of Manaus (02° 36' S, 60° 08' W, 110–120 m above sea level). In this region tree density (> 10 cm diameter at breast height–DBH) and species diversity are high, about 170 species ha<sup>-1</sup>

(Prance et al. 1976). The annual precipitation is 2420 mm, with a mild dry season which extends from June through October, July-September being the driest months ( $\leq 100 \text{ mm month}^{-1}$ ). Mean temperature is about 26 °C, with mean minimum and mean maximum of 23.3 and 31.1 °C respectively. Vapour pressure deficit (D) ranges from 2.7 to 21.4 hPa (mean 8.5 hPa), photosynthetically active while radiation (PAR) varies from 17.0 to 39.7 mol m<sup>-2</sup> day<sup>1</sup> (Antezana-Vera & Marenco 2021). The soil is a yellow latosol of clay texture, with pH of about 4.0 and low fertility (Magalhães et al. 2014).

During the years of 2008–2012, air temperature (T), PAR, rainfall and relative humidity (RH) data were recorded daily above the forest canopy, at the top of a 40-m-tall observation tower about 3 km from the experimental site. PAR was measured using a quantum sensor, while temperature and RH, with a temperature-humidity sensor connected to a data logger, as previously described by Marenco and Antezana-Vera (2021). Data were logged at 15 (PAR) or 30 min intervals (temperature and RH). PAR data were integrated over time to obtain daily PAR values. Rainfall data were recorded using a rain gauge. We also computed vapour pressure deficit (D) and reference evapotranspiration (ETo). Vapour pressure deficit was obtained as  $V\!P_{\text{sat}}$  –  $R\!H \times V\!P_{\text{sat}}$  , where  $VP_{sat}$  is the saturation vapour pressure;  $VP_{sat}$  (kPa)  $= 0.61365 \exp[17.502T/(240.97 + T)], T (^{\circ}C)$ being the air temperature (Buck 1981). The D<sub>max</sub> was obtained from RH<sub>min</sub> and mean maximum temperature  $(T_{max})$  data, and  $D_{min}$  from  $RH_{max}$ and mean minimum temperature  $(T_{min})$ . The D<sub>mean</sub> was obtained from mean relative humidity  $(RH_{mean})$  and mean temperature  $(T_{mean})$  data. Mean monthly ETo was computed as: ETo =  $0.0023 \times R_a (T_{mean} + 17.8) (T_{max} - T_{min})^{0.5}$ , where  $R_a$  is the extraterrestrial radiation (Hargreaves & Samani 1985).

In this study we measured tree growth in diameter ( $T_G$ ) in *E. bracteosa* and *T. venusta*. Trees of *E. bracteosa* (n = 12) were 21.1 ± 2.5 m tall and had mean DBH of 18.4 ± 4.0 cm, while those of *T. venusta* (n = 5) were 26.1 ± 7.0 m in height and 32.6 ±16.7 cm in DBH. The stem growth in diameter at breast height was measured at monthly intervals for 60 months (2008–2012), using stainless steel dendrometer bands, which were installed at least two years before the beginning of the experiment.

#### Statistical analyses

To assess the effects of microclimatic variability (rainfall, PAR, temperature and vapour pressure deficit) on stem growth, we used principal component regression (PCR). The first step in PCR was to extract, by principal component analysis (PCA), a set of orthogonal components associated with previously standardised explanatory variables. Microclimatic variables were standardised as the observed value minus the mean divided by standard deviation. The extraction of orthogonal components was essential to remove the collinearity among microclimatic variables. Time-related trend in tree growth can affect PCR results, therefore, before PCR, the effect of ontogeny on stem growth was removed using first-order autoregression (Monserud & Marshall 2001), as shown in equation 1.

$$T_{Gi} = \phi_o + \phi_1 T_{G(i-1)} + \epsilon_i \tag{1}$$

where  $T_{Gi}$  = growth rate in month i,  $T_{G(i-1)}$  = growth rate in the previous month, and  $\phi$  = regression coefficients. The detrended stem tree growth ( $T_{GC}$ ) was obtained as the residual of  $T_{Gi}$ , after computing the predicted value ( $\hat{T}_G$ ), i.e.  $T_{GC}$  =  $T_{Gi} - \hat{T}_G$ .

The PCR model can be written using the equations 2 and 3 as described by Montgomery et al. (2012):

$$Y = Xb + \epsilon \tag{2}$$

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

$$Z = XT$$
(4)

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

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

$$\operatorname{var}(\mathbf{b}_{\mathrm{pc}}) = \operatorname{var}(\mathrm{T}\hat{\alpha}_{\mathrm{pc}})$$
 (7)

$$SE(b_{j, pc}) = \sqrt{var(b_{j, pc})}$$
(8)

$$t = \frac{\mathbf{b}_{j, pc}}{\mathbf{SE}(\mathbf{b}_{j, pc})}$$
(9)

Equation 2 represents the standard multiple linear regression (MLR) model, while equation 3 describes the PCR model, where Y is the vector of observations (dependent variable), X is the matrix of the corresponding regressors, b and  $\alpha$  are vectors of coefficients, and  $\epsilon$  the vector of random errors. In equation 4, the columns of Z represent a new set of orthogonal scores (z-scores or principal components), while T is a matrix whose columns represent eigenvectors (extracted from X using PCA). The computation of  $\alpha$  (vector of coefficients in the PCR model) is described in equation 5 and that of  $b_{pc}$  for standardised regressors, in equation 6. The values of  $\hat{\alpha}$  (estimator of  $\alpha$ ) were obtained after regressing Y on the principal components (z-scores). In equation 6, the "pc" subscript indicates that only a reduced k number of principal components has been retained in the model (hereafter referred to as the reduced model). The variance (var) of  $b_{pc}$  and its standard error (SE) were obtained as described in equations 7 and 8, while the t value was calculated as described in equation 9. In the reduced model, only principal components (z-scores) associated with eigenvalues greater than one were retained (Kaiser criterion). The significance of b<sub>pc</sub> was tested on individual coefficients using *t*-test, and n - k - 1 degree of freedom; where n is number of observations and k the number of principal components in the reduced model. The analyses were performed using R v.4.0.5 (2021) and PCR computed using the Partial Least Squares Package (2021).

#### **RESULTS AND DISCUSSION**

The stem growth in diameter was 0.114 mm month<sup>-1</sup> for *E. bracteosa* and 0.815 mm month<sup>-1</sup> for T. venusta (Table 1). Means of the microclimatic variables were 25.6 °C for mean temperature, 25.7 mol m<sup>-2</sup> day<sup>-1</sup> for PAR, and 242.1 mm month<sup>-1</sup> for rainfall (Table 1). With the exception of minimum temperature which showed no correlation with rainfall and ETo, all the climatic variables were intercorrelated ( $p \le 0.05$ , Figure 1). Moreover, in this figure it can be seen that both E. bracteosa and T. venusta had positive relationship with monthly rainfall, while the correlation with ETo, mean and maximum temperatures and vapour pressure deficit was negative. Also, it is important to note in Figure 1 that although in almost in the same direction, the vector associated with E. bracteosa (Eb triangle) was shorter than that associated with T. venusta (Tv triangle), which suggests that T. venusta is more responsive to microclimatic variability than E. bracteosa. In the next section, the relationship between the microclimatic variables and stem growth is examined in more detail.

Trees amounth	Maara (+ SD)
Iree growth	Mean $(\pm SD)$
E. bracteosa (mm month-1)	$0.114 \pm 0.07$
T. venusta (mm month-1)	$0.815\pm0.52$
Climatic variable	
PAR (mol $m^{-2}$ day <sup>-1</sup> )	$25.73\pm3.97$
T <sub>min</sub> (°C)	$22.3\pm0.77$
T <sub>mean</sub> (°C)	$25.6\pm1.12$
T <sub>max</sub> (°C)	$30.47 \pm 1.53$
Rainfall (mm month-1)	$242.13 \pm 141.6$
D <sub>max</sub> (hPa)	$16.45\pm5.42$
D <sub>mean</sub> (hPa)	$5.15\pm2.67$
D <sub>min</sub> (hPa)	$0.800\pm0.82$
ETo (mm month <sup>-1</sup> )	$127.45 \pm 15.0$

**Table 1**Tree growth  $(T_G)$  in diameter of *Eschweilera bracteosa* (n = 12) and *Tachigali venusta* (n = 5) and means<br/>of microclimatic variables during the study period (2008–2012)

Mean annual rainfall was 2905 mm; ETo = reference evapotranspiration, PAR = photosynthetically active radiation, T = temperature,  $T_{max}$  = mean maximum T,  $T_{min}$  = mean minimum T,  $T_{mean}$  = mean T, D = vapour pressure deficit,  $D_{max}$  = mean maximum D,  $D_{min}$  = mean minimum D,  $D_{mean}$  = D mean, SD = standard deviation and  $T_G$  = increase in in stem diameter measured at monthly intervals



Figure 1 Principal component analysis of climatic variables (circles); in the factor plane the detrended tree growth of *Tachigali venusta* (Tv) and *Eschweilera bracteosa* (Eb) are shown as supplementary variables (triangles), while the eigenvalue corresponding to each factor is shown in the inset; abbreviations are shown in Table 1

We found that the first two factors explained almost 80% of the microclimatic variability and were associated with eigenvalues greater than one (inset in Figure 1). Hence, only the effect of these two factors on stem growth was evaluated by PCR. It was found that stem growth of E. bracteosa was rather unresponsive to variations in climatic factors ( $R^2 = 0.072$ , p = 0.119, Figure 2), as only variations in mean temperature and mean and maximum vapour pressure deficits had effects on stem growth (Table 2). On the other hand, we found that microclimatic variability had significant effect on T. venusta (p < 0.001,  $R^2 =$ 0.317, Table 2, Figure 2). In fact, stem growth of T. venusta was responsive to variation in almost all microclimatic variables, with the exception of PAR (p = 0.82) and minimum temperature (p = 0.49, Table 2). In both species, the effect of microclimatic variability on stem growth was not detected when data were analysed using standard multiple linear regression (Table 3).

The negative effect of  $T_{mean}$  and  $T_{max}$  and the absence of an effect of irradiance and  $T_{min}$  on stem

growth (Table 2) did not support our working hypothesis, as none of the two species responded positively to an increase in temperature or irradiance. However, the absence of a significant effect of PAR on stem growth does not mean that growth is not affected by light, as photosynthesis, the basis of plant growth, is highly responsive to changes in light intensity (Marenco et al. 2001). The positive effect of rainfall on T. venusta concurs with results reported by Marenco and Antezana-Vera (2021) across a large number of Amazonian tree species. On the other hand, the unresponsiveness of the slow-growing E. bracteosa to rainfall variability is consistent with the results of Ouédraogo et al. (2013), who concluded that slow-growing species are less sensitive to water stress. The annual precipitation during the experimental period was about 20% higher than the historical mean, which can also contribute to reduce the effect of rainfall variability on stem growth of E. bracteosa.

In this study, we provide evidence that an increase in  $D_{mean}$  or  $D_{max}$  can lead to a decline in



**Figure 2** Detrended tree growth ( $T_{GC}$ ) and regression line as a function of time in (a) *E. bracteosa* ( $R^2 = 0.072$ , p = 0.119) and (b) *T. venusta* ( $R^2 = 0.317$ , p < 0.001); in both panels, the thick solid blue line corresponds to the regression line (PCR fitted to data  $T_{GC-PCR}$ ), while the diamond represents the detrended tree growth; PCR = principal component regression

Variable	E. bracteosa				T. venusta		
	Beta (B)	SE (ß)	р	Beta (B)	SE (ß)	р	
PAR	-0.001486	0.003482	0.671	-0.003281	0.014474	0.821	
Rainfall	0.002948	0.003667	0.425	0.040463	0.015243	0.010	
$\mathrm{T}_{\mathrm{min}}$	-0.000340	0.007449	0.964	0.021555	0.030959	0.489	
$T_{\text{mean}}$	-0.003107	0.001482	0.040	-0.031032	0.006159	< 0.001	
$T_{\text{max}}$	-0.003313	0.001736	0.061	-0.035160	0.007214	< 0.001	
$\mathbf{D}_{\min}$	-0.002569	0.001630	0.120	-0.021780	0.006773	0.002	
$\mathbf{D}_{\mathrm{mean}}$	-0.003217	0.001531	0.040	-0.031746	0.006363	< 0.001	
$\mathbf{D}_{\max}$	-0.003307	0.001608	0.044	-0.033778	0.006683	< 0.001	
ETo	-0.003243	0.003284	0.327	-0.041740	0.013648	0.003	
DF	$R^2$ (MSE)	F	p value	$R^2$ (MSE)	F	p value	
(2, 57)	0.072 (0.005562)	2.21	0.1192	0.317 (0.096082)	12.80	< 0.001	

Table 2Regression coefficients (beta), standard error (SE of ß) and p values of standardised climatic variables<br/>obtained by PCR in *Eschweilera bracteosa* and *Tachigali venusta* 

Mean SE (both species) = 0.00741; summary of regression parameters is given in the last line; MSE = mean square error, DF = degree of freedom (i.e. two factors (k) and the residual: n-1-k),  $R^2$  = determination coefficient, PCR = principal component regression; other abbreviations as described in Table 1

Table 3	Regression coefficients (beta), standard error (SE of B) and p values of standardised	climatic
	variables obtained by standard multiple linear regression of detrended tree growth in E.	bracteosa
	and T. venusta	

Variable	E. bracteosa			T. venusta		
	Beta	SE	р	Beta	SE	р
PAR	0.000109	0.016954	0.995	0.063062	0.070901	0.378
Rainfall	0.022716	0.017380	0.197	0.079666	0.072681	0.278
$\mathbf{T}_{\min}$	-0.003692	0.018116	0.839	-0.043066	0.075760	0.572
$T_{\text{mean}}$	0.004089	0.030173	0.893	0.110640	0.126183	0.385
$T_{\text{max}}$	-0.016484	0.044137	0.71	-0.006206	0.184579	0.973
$\mathbf{D}_{\min}$	-0.030152	0.019577	0.13	0.048281	0.178037	0.787
$\mathbf{D}_{\mathrm{mean}}$	0.028975	0.042573	0.499	0.012831	0.081870	0.876
$\mathbf{D}_{\max}$	0.001973	0.052155	0.97	-0.275617	0.218108	0.212
ЕТо	0.005445	0.025156	0.83	-0.055257	0.105201	0.602
DF	$R^2$ (MSE)	F	p value	$R^2$ (MSE)	F	p value
(9, 50)	0.143	0.92	0.51	0.355	3.05	0.0054
	(0.005856)			(0.102420)		

Mean SE (both species) = 0.07664; summary of regression parameters is given in the last line; in comparison with Table 2 several coefficients have opposite signs, such as PAR,  $T_{mean}$ ,  $D_{mean}$ , and ETo for *E. bracteosa*, and  $T_{min}$ ,  $D_{min}$ ,  $D_{mean}$  for *T. venusta*; abbreviations as described in Tables 1 and 2

stem growth of *E. bracteosa* and *T. venusta*. Based on the relative magnitude of the regression coefficient (Table 2), it can be concluded that the effect of  $D_{mean}$  and  $D_{max}$  was about 10 times higher in *T. venusta* than in *E. bracteosa*. This indicates that *T. venusta* is highly responsive to changes in atmospheric dryness. Leaves of shade-tolerant species tend to have lower stomatal conductance (Valladares & Niinemets 2008), which helps to explain the relative unresponsiveness of *E. bracteosa* to changes in vapour pressure. Also, in comparison with *E. bracteosa*, *T. venusta* trees were about 20% taller (21.1 vs 26.1 m tall), which may also contribute to the larger responsiveness of *T. venusta* to variability in vapour pressure deficit, as stomatal conductance and boundary layer conductance can increase towards the upper forest canopy. For instance, it has been reported that in the central Amazon maximum stomatal conductance can increase with tree height, from 0.14 mol m<sup>-2</sup> s<sup>-1</sup> in 20-m-tall trees to 0.28 mol m<sup>-2</sup> s<sup>-1</sup> in 27–33-m-tall trees; with boundary layer conductance declining from 1.4 mol m<sup>-2</sup> s<sup>-1</sup> at the top of the canopy to about 0.2 mol m<sup>-2</sup> s<sup>-1</sup> at the forest floor (Roberts et al. 1990).

Overall, the negative effect of mean and maximum vapour pressure deficit on stem growth is consistent with the findings by Lee et al. (2013) who reported that in the Amazon region, ecosystem photosynthesis declined as vapour pressure deficit progressively increased from 3.5 (wet season) to 32 hPa in the dry season. In fact, the most common response is a decline in stomatal conductance with an increase in vapour pressure deficit (Dai et al. 1992, McDowell & Allen 2015).

There is still no consensus regarding the effect of temperature on tree growth of tropical trees. Trees of *T. venusta* are taller than those of *E. bracteosa*, and this may have contributed to their distinctive response to temperature variability, as during daytime air temperature consistently decrease from the upper canopy towards the forest floor (Kruijt et al. 2000). The effect of mean temperature in *T. venusta* and *E. bracteosa* is in agreement with the results of Way and Oren (2010) who observed that tree growth of tropical species can be negatively affected by progressive warming during the growing period.

In tropical rainforests, the optimum temperature for photosynthesis is about 29 °C (Liu 2020), with photosynthetic rates decreasing at supraoptimal temperatures. This can explain the decline in stem growth with rising maximum temperatures in the taller *T. venusta*. Besides the effect of temperature on photosynthesis, a rise in temperature alters transpiration via the effect of temperature on water viscosity (Darcy's Law). It was also found that ETo had negative impact on stem growth of *T. venusta* (Table 2). In comparison with *E. bracteosa*, the higher beta coefficients for temperature observed in *T. venusta* could explain the differential effect of ETo on these two species, as ETo is a function of temperature.

We found that the number of microclimatic variables that affected stem growth differed

between species. There was also difference in the proportion of variance associated with microclimatic variability, 31% (in *T. venusta*) against only 7% of total variance associated with stem growth in *E. bracteosa* (Table 2). PCR regression coefficients were smaller in *E. bracteosa* than in *T. venusta*. Although both species responded similarly to variations in mean and maximum vapour pressure deficit, *T. venusta* and *E. bracteosa* responded differently to variations in ETo and rainfall (Table 2), which indicated that *T. venusta* responded faster to changes in microclimatic conditions.

The species-specific effect of rainfall is in agreement with the results of Ouédraogo et al. (2013), who reported that shade-tolerant, slowgrowing species are less sensitive to drought. It remains to be elucidated if E. bracteosa is less sensitive to rainfall variability than T. venusta because it extracts water more efficiently from the soil, or because it regulates stomatal transpiration more effectively. It has been found that stomatal sensitivity to a decrease in leaf water potential and air humidity is higher in slowgrowing than in fast-growing species (Aasamaa & Sõber 2011). On the other hand, differences in tree size can contribute to the differential effect of maximum temperature and reference Altogether, evapotranspiration. our results showed that T. venusta was more responsive to microclimatic variability than E. bracteosa, which ultimately led to improved growth rates under favourable conditions. Marenco and Vieira (2005) found that in comparison with the slowgrowing Minquartia guianensis, the fast-growing Goupia glabra responded to an increase in irradiance by increasing its photosynthetic rates per unit mass and by decreasing the specific leaf area. Fast-growing species also have higher light compensation point and higher light saturation point than the slow-growing species (Calzavara et al. 2019).

In comparison with the standard error of beta (regression coefficient) obtained by MLR, the mean standard error computed by PCR was smaller (0.0766 against 0.0074 respectively, see footnotes in Tables 2 and 3). Thus, although the MLR model explained 14.3% of variance in *E. bracteosa* and 35.5% of variance in *T. venusta*, none of the regression coefficients had an effect on stem growth. On the other hand, when the collinearity effect was removed, even smallmagnitude PCR coefficients, such as those related with mean temperature and mean vapour pressure (*E. bracteosa*) showed a significant effect on stem growth (Table 2). It is important to note, that some MLR coefficients had opposite sign (e.g. mean vapour pressure deficit, Table 3). This misleading effect of collinearity can lead to misinterpretation of results (Montgomery et al. 2012).

Our results are relevant due to the global importance of the Amazon forest and because of the effects of the ongoing climate changes, which have increased temperature (about 0.16 °C per decade) and altered rainfall distribution, ranging from lower rainfall intensity (longer dry seasons) in eastern and southern Amazonia to higher rainfall intensity in the northern Amazon (Marengo et al. 2018). The dry season is associated with increased irradiance, temperature and vapour pressure deficit (Lee et al. 2013, Antezana-Vera & Marenco 2021), which ultimately can lead to a decline in photosynthesis (Lee et al. 2013, Yang et al. 2018). Drought induced by altered rainfall pattern can affect tree growth not only by reducing soil water availability, but also by modifying atmospheric conditions, as it has been shown that an increase in vapour pressure deficit can negatively affect stem growth (Table 2).

# CONCLUSION

In this study, we show that species of contrasting growth rates respond differently to microclimatic variability. The slow-growing species was responsive to variability in three out of nine climatic parameters evaluated, whereas the fastgrowing species was responsive to variation in seven of the nine climatic parameters examined. The amount of total variance on stem growth explained by climatic variables differed between species, 31% (*T. venusta*) against only 7% in *E.* bracteosa. This indicates that E. bracteosa is less responsive to microclimatic variability than T. venusta. When data were analysed using MLR, none of the microclimatic variables had any effect on stem growth, which highlights the effect of collinearity on the quality of results. A progressive increase in mean and maximum vapour pressure deficit had a negative effect on stem growth in both species. Our results contribute to enhance our current knowledge of the ecophysiology of Amazonian trees and throw light on the potential effects of the severe droughts forecasted by climate models for parts of the Amazon region.

## **ACKNOWLEDEGMENTS**

We thank the Ministry of Science, Technology and Innovation—National Institute for Research in the Amazon (MCTI-INPA) and the National Council for Scientific and Technological Development for scholarship and fellowship to the first and second authors respectively (303913/2021-5). We also thank the Foundation for Research Support of the State of Amazonas and the Coordination for the Improvement of Higher Education Personnel (CAPES code 0001).

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