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Latent competition and the individual effect of microclimatic variables on stem tree growth in the Central Amazon

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FOREST ECOLOGY

ABSTRACT

Background: Tropical forest dynamics are directly conditioned by microclimatic variations and resource competition, which modulate the development patterns of tree species. Despite their importance, there remains a significant scientific gap regarding the combined influence of these factors in high-density tropical forests where individual interactions may be masked. This study evaluates the individual effect of microclimatic variables and competitive status on the tree growth in diameter (TGD) of *terra-firme* species in Central Amazonia. The central hypothesis is that both microclimatic fluctuations and interspecific competition significantly and directly affect tree diameter increments.

Results: Growth of 33 trees from seven species was monitored over 48 months. To isolate the climatic impact from temporal trends, we used Principal Component Regression (PCR) and Principal Component Analysis (PCA). The average TGD was 0,15 mm month^{-1}, with precipitation and soil water content (SWC) as the primary positive drivers for most species. Conversely, vapor pressure deficit (VPD) correlated negatively with growth rates. Regarding biotic factors, Moore's index (Moore, et al. 1973) and four other tested indices showed no significant correlation with diameter. This high-density environment (338 stems/ha) suggests a condition where individual competitive effects are difficult to distinguish.

Conclusion: Tree growth in Central Amazonia is highly sensitive to water availability. The negative TGD-VPD relationship suggests that atmospheric dryness is a limiting factor, potentially associated with adjustments in stomatal conductance. The findings support the hypothesis of "latent competition," where high density masks the impact of specific competitors due to shared resource limitation. These results reinforce the vulnerability of tropical species to projected climate change.

Keywords: Vapor pressure deficit; soil water content; distance-dependent competition; dendrometer monitoring; terra-firme forest.

HIGHLIGHTS

Mean monthly radial growth was 0.15 mm.
Rainfall and soil moisture drove growth; VPDmin/mean limited it.
VPDmax and temperature (min/max) did not affect diameter growth.
High stand density (338 trees/ha) suggests homogeneous competition.

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INTRODUCTION

Tropical forests are ecosystems that play a crucial role in regulating the global climate, the carbon cycle, conserving biodiversity and providing ecosystem services essential for human well-being (Mackey et al., 2020). By acting as critical carbon sinks, these ecosystems play vital roles in mitigating climate change (Koh et al., 2021). However, tropical forests are experiencing increasing anthropogenic pressures, such as deforestation, forest degradation and climate change, which puts their integrity and functionality at risk (Li et al., 2022). Given this scenario of vulnerability, it becomes necessary to elucidate the mechanisms that govern the increase in tree species, with microclimatic variability and competitive interactions being determining factors, still insufficiently resolved, for predicting forest resilience and developing effective conservation strategies (Azuero-Pedraza et al., 2024).

Tree growth, usually measured by diameter growth, is a complex process influenced by a number of interconnected factors, one of which is the direct control exerted by the competitive status between trees and by climatic conditions such as temperature, precipitation, and humidity (Carmo et al., 2022; Schons et al., 2021).. Thermal fluctuations and variations in vapor pressure deficit (VPD) can impose severe physiological constraints by limiting stomatal conductance and affecting the hydraulic integrity of trees. This thermal sensitivity, coupled with the evaporative demand of the atmosphere, makes water availability a critical determinant of productivity in tropical ecosystems (Carvalho et al., 2020). However, considerable uncertainty persists regarding how these microclimatic variables operate together to influence radial increment in high-density forests, where environmental heterogeneity and biotic interactions can modulate individual responses to climate.

In addition to abiotic controls, competition for limiting resources represents a central determinant of forest structure and individual development. These biotic interactions modulate ecosystem dynamics through adjustments in vital rates and structural adaptations, classically quantified in forest ecology through competition indices (Lichstein et al., 2024). Among existing approaches, distance-dependent models stand out for incorporating the spatial configuration and size hierarchy of the immediate neighborhood (Contreras et al., 2011). This analytical tool allows capturing the heterogeneity of local interactions, providing a robust basis for evaluating how the interference of neighboring trees conditions diameter increment patterns in high-density environments, where competition for space and resources is more intense (Tsunoda et al., 2025; West 2024).

Tropical forests, characterized by high basal area due to humidity, high species diversity and dynamic environmental conditions, present intense competition between trees. This competition not only influences species composition but also reduces the forest's ability to sequester carbon, negatively affecting the basal area growth of trees (Joetzjer et al., 2022; Rozendaal et al., 2020). Studies conducted by Schons et al. (2021) show that there are divergences regarding the effects of forest competition. Although competition, inferred by the reduction in radial growth rates, occurs frequently in Amazonian trees, some species appear to be insensitive to the effects of competition due to the influence of other environmental factors (Cunha and Finger, 2013). This structural complexity of natural forests indicates that the efficiency of prediction models varies significantly according to forest structure and successional stage. However, a fundamental uncertainty persists: in high-density environments, such as those in Central Amazonia, are competition indices able to adequately capture fluctuations in individual diameter growth? The omnipresence of competition under these conditions can saturate the system to such an extent that traditional spatial models fail to isolate the interference of immediate neighbors from the overall competitive pressure of the stand. In these cases, competition indices that consider the distance between trees are more efficient for analyzing dynamic diameter growth, since a single competition index may not capture all the dynamics of competition (Orso et al., 2020). The correlation between the values of competition indices and a specific growth characteristic of the target tree, such as diameter, height, or cross-sectional area, is frequently used to evaluate the performance of the indices (Schons et al., 2021).

Climate predictions show that dry seasons in parts of tropical forests, such as the Amazon, will intensify, causing long-term impacts on the ecosystem (Baker et al., 2021). Despite climate projections indicating changes in productivity patterns, there is a critical gap in understanding the synergistic effects between microclimatic variability and competition at the individual tree level in dense upland forests. The central hypothesis of this study is that diameter increment is primarily controlled by microclimatic water constraints, which override the influence of individual competition in saturated stands. To test this proposal, this work aimed to: (i) quantify the influence of microclimatic variables on monthly diameter increment; and (ii) evaluate the sensitivity of different distance-dependent competition indices in predicting individual growth under these environmental conditions.

MATERIAL AND METHODS

Study area

This work was carried out in the Tropical Silviculture Experimental Station – ZF2 Reserve (centered at 02°36′21″ S, 60°08′11″ W) of the National Institute for Amazonian Research (INPA) and located 60 km north of Manaus, Amazonas State, Brazil (point along BR-174) (Figure 1). The study area is located on a plateau of primary tropical rainforest on firm ground, with no history of human intervention. The experimental site is situated at an elevation of approximately 125 m above sea level, exhibiting typical characteristics of Central Amazonia, with high biodiversity of woody and herbaceous species. The soil is classified as Yellow Latosol, with a clayey texture and low natural fertility. According to the Köppen classification, the local climate is type Af (tropical rainy), characterized by high temperatures and abundant and well-distributed annual rainfall, without a defined dry season Alvares et al. (2013). This location is particularly protected for the proposed research, as its condition as a preserved primary forest allows for the isolation of physiological responses to the microclimate and natural competitive interactions, without the statistical noise resulting from external disturbances or forest fragmentation.

Data

To compose the experimental design, individuals located in the canopy and sub-canopy were selected, adopting local abundance as a sampling criterion (minimum of three individuals per species). This strategy was defined to ensure that intraspecific variability was captured, while maintaining the representativeness of the most frequent taxa in the area. Thirty-three trees belonging to seven species were selected (Table 1), a sample size that, although focused, is compensated by the high temporal resolution (48 months of continuous monitoring via dendrometers), allowing robust statistical analyses of repeated measures.

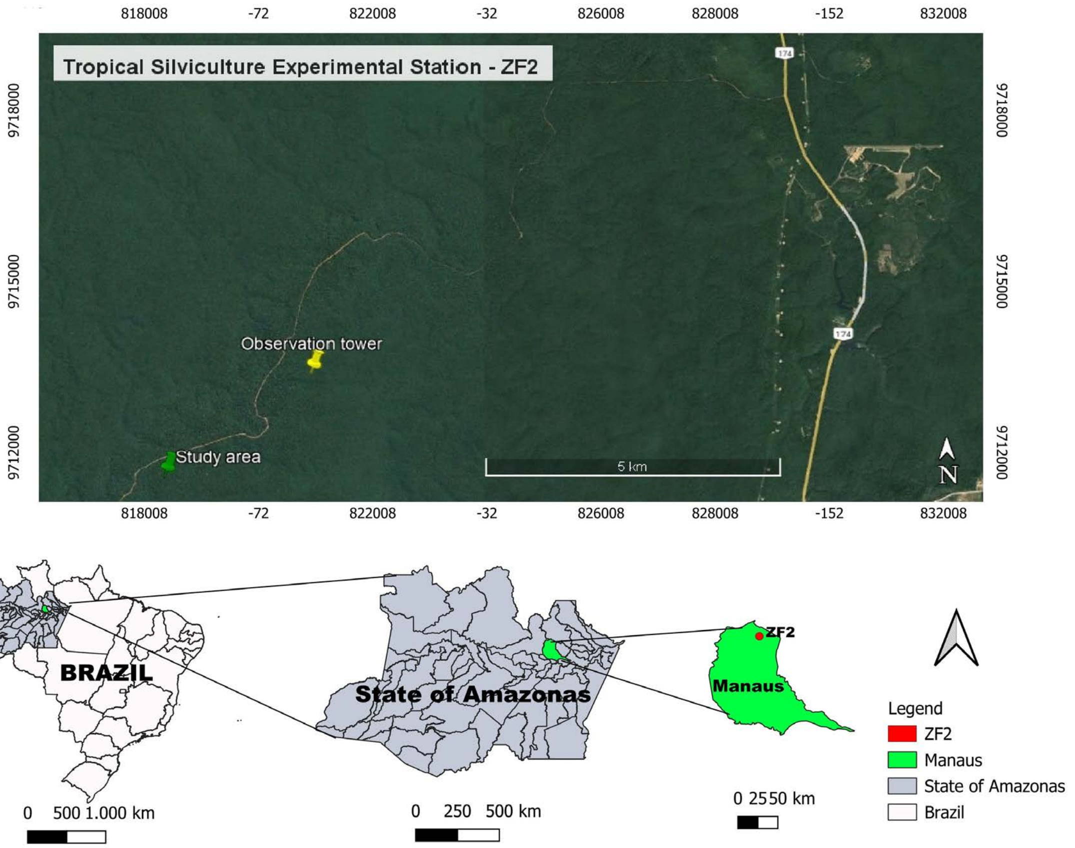

Figure 1: Location map of the study area (ZF2), located north of the city of Manaus, in the state of Amazonas, Brazil. Datum: SIRGAS2000, Dados: IBGE (2023).

Table 1: Species and numbers of individuals per species; mean ± standard deviation of height; crown diameter; diameter at breast height (DBH) and tree growth in diameter (TGD) for the period 2018 – 2021.

Species	n	Height (m)	Crown diameter (m)	DBH (cm)	TGD (mm month^{-1})	TGD (mm year^{-1})
Eschweilera bracteosa	13	22.3 ± 2.89	8.51 ± 1.31	20.29 ± 5.06	0.10 ± 0.08	1.18 ± 0.32
Eschweilera coriacea	4	23.5 ± 3.95	9.81 ± 0.64	25.62 ± 9.00	0.11 ± 0.14	1.26 ± 0.59
Eschweilera grandiflora	3	27.0 ± 5.08	9.13 ± 1.91	32.35 ± 17.16	0.14 ± 0.13	1.69 ± 0.52
Goupia glabra	3	20.1 ± 4.63	7.83 ± 0.77	18.98 ± 5.45	0.29 ± 0.24	3.50 ± 1.04
Gustavia augusta	3	21.1 ± 2.83	5.67 ± 1.15	17.16 ± 4.10	0.05 ± 0.12	0.60 ± 0.50
Pourouma tomentosa	3	25.7 ± 1.89	5.98 ± 1.58	25.76 ± 3.97	0.20 ± 0.13	2.42 ± 0.17
Pouteria reticulata	4	24.0 ± 9.04	9.68 ± 1.25	29.56 ± 20.93	0.16 ± 0.16	1.89 ± 0.71
Total (n) or mean	33	23.39 ± 4.33	8.09 ± 1.23	24.24 ± 9.36	0.15 ± 0.14	1.80 ± 0.27

The ecological context of the sampling corresponds to a dense and hyperdiverse stand, with records of 179 tree species per hectare (individuals with DBH ≥ 15 cm; Prance et al., 1976), and a population density that corresponds to 636 ± 42 trees per hectare (trunks ≥ 10 cm DBH; Rankin-de-Mérona et al., 1992). The trees that make up the dominant structure of the forest have an estimated mean age of 380 years, indicating an ecosystem in a climax stage of succession. The biometric characterization of the selected species, including mean diameter and height, is detailed in Table 1, serving as a basis for calculating competition indices and parameterizing radial growth models.

Ten microclimatic variables were selected to capture environmental variability above the canopy and at ground level. The dataset for these variables was chosen because they represent the main components of the energy balance and water availability in the terra firme ecosystem in the Amazon. Climate data were obtained using specific sensors (LI-1400, Li-Cor, Lincoln, NE, USA and Li-190SA, Li-Cor, NE, USA) and a rain gauge (Em5b, Decagon, WA, USA) installed at the top of a 40-m observation tower (02°35´21”S, 60°06´53”W) (Figure 1), which recorded atmospheric conditions above the forest canopy in the study area. The microclimatic variables considered included temperature, radiation, water availability and atmospheric dryness. Air temperature (T) and relative humidity (RH) data were automatically recorded every 15 minutes, 24 hours a day. Irradiance (photosynthetically active radiation - PAR) was measured during the day, with data collected every 5 minutes and mean every 15 minutes. Precipitation was collected daily. Reference evapotranspiration (ET) was calculated based on local irradiance and temperature data. Daily vapor pressure deficit (VPD) and monthly soil moisture (0-20 cm depth) were also recorded. For statistical analyses, the raw 15-minute data were aggregated into monthly mean (or monthly totals, in the case of precipitation), ensuring temporal compatibility with the diameter growth measurements of the trees.

Tree diameter growth

The monthly increment in diameter represents the tree's individual growth rate in diameter (TGD). To evaluate the pattern of monthly growth in stem diameter (mm/month) of the study trees, data were obtained from measurements taken from metallic dendrometer bands installed on each selected tree at least three years before collecting data for this experiment. These bands were fitted to each individual at chest height (DBH, 1.30 m from the ground), consisting of a stainless-steel band equipped with an expansion spring that follows the radial growth of the trunk with high-precision (10 μm) digital callipers (Mitutoyo Sul Americana, São Paulo, Brazil). Measurements were taken monthly, measuring the variation in distance between two fixed points marked on the dendrometric band. The monthly stem diameter increment was calculated, as: (DBHe – DBHb)/t, where DBHe represent diameter at the end of the monthly interval at the end and DBHb represent diameter at the beginning of the monthly interval (mm); and t, the elapsed time between consecutive measurements.

To evaluate the individual effect of microclimatic variables on stem growth, stem girth was measured on the selected trees (Table 1) over a period of 48 months (Jan 2018 to Dec 2021).

Competition between trees

The models predict competition based on distance-dependent indices, which use spatial information from neighboring trees to express the hierarchical position of an individual and the impact of competitive interactions on its growth. The main model published was Moore's competition index, widely recognized in the literature for its high efficacy in the development of tropical species. This index is calculated using the formula: $\sum_{j=1}^{n} \frac{di^2}{di^2 + dj^2} * Lij$.

Where: n = number of competing trees; j = competing tree (cm); di = diameter at breast height (DBH) of the target tree (cm); dj = diameter at breast height (DBH) of the competing tree (cm); Lij = distance between the target tree and the competitor tree (m). This competition index takes into account the proximity and size of competitors in relation to the target trees. According to the literature, Moore's distance-dependent competition index is among a set of indices that most correlate with growth for tropical trees and is widely used to explain variation in tree growth (Contreras et al., 2011). Competing trees were defined as trees located up to 10 meters from the target trees, with a diameter at 1.5 meters from the ground equal to or greater than 15 cm. We measured the diameter and the distance between the trees. The first condition established a horizontal distance limit, in which only trees located within this radius of up to 10 meters from the trunk of the target tree were included in the neighborhood analysis. This radius delimits the average interaction zone between the canopies of the study trees, and possibly where competition for aerial (light) and root (water and nutrients) resources is considered most significant for the individual growth of these study trees. The second boundary condition consisted of a minimum size criterion, defining that only individuals with a diameter equal to or greater than 15 cm (measured at 1.5 meters from the ground) would be counted as competitors. These restrictions are fundamental for the application of distance-dependent competition indices, as they standardize the calculation to focus on established trees that effectively compete for growth space with the study's target trees. The target trees are the trees selected for this study, on which the competition index was calculated. For each competitor, the diameter (cm), the height (m) of the trunk, the distance between the boles (at breast height) in relation to the target tree (m) and the crown diameter (m) were measured. The heights were obtained by a climber who climbed the trees and with a measuring tape measured the height of the trunk. The distances of the target trees in the study in relation to the boles of the neighbors were measured with the aid of a tape measure. The crown diameter was obtained from angular measurements of crown radius (east, west, north, south), determined by the distance from the trunk of the tree under study and the projection of its crown. The mean crown diameter, in meters, was determined by multiplying the value of the mean crown radius (cr) in meters by two (2.cr).

The competition analysis was carried out taking into account the average growth per tree (TGD) and the total number of trees evaluated (due to the low sample N per species). We also counted the number of trees at each circle around the target tree and estimated the mean tree population over circles. To ensure the statistical robustness of the model, especially given the possibility of non-significant results, the analytical assumptions were rigorously evaluated. A multicollinearity test was performed between the neighborhood variables, and spatial scale dependence was verified to ensure that the inclusion radius was representative of the growth dynamics. This methodological refinement allowed us to confirm that any null correlations reflected the ecological reality of the stand, such as the state of latent competition, and not instrumental limitations or sampling bias. As additional data, we also tested four other different broad distance-dependent indices used to explain tree growth variation to infer competition, incluind index of Hegyi (1974): $\sum_{j=1}^{n} \frac{dj}{di *Lij}$; Martin and Ek (1984): $\sum_{j=1}^{n} \frac{dj}{di} * \frac{1}{\left(Lij+1\right)}$; Pukkala and Kolström (1987): $\sum_{j=1}^{n} \frac{hj}{hi *Lij}$ and Rouvinen and Kuuluvainen (1997): $\sum_{j=1}^{n} \left(\frac{dj}{di}\right)^{2} * \frac{1}{Lij}$, where: hj = height of the competitor tree (m) and hi = target tree height (m).

Data analysis

Diametric structure, periodic increment and evaluation of the indexes and the competition

Tree growth in diameter (TGD) rates was analysed using an analysis of variance (ANOVA) for repeated measures over time. To assess the differences between species and monthly growth rates, as well as their interaction with climatic variables, data were compared using a repeated measures analysis of variance (ANOVA) on trees monitored over 48 months. Significant differences were accepted at $p < 0.05$. Growth data were log-transformed to reduce the influence of outliers in the ANOVA. Departures from sphericity were addressed using the Greenhouse-Geisser correction as conducted by Levasseur et al. (2026). Data were analyzed using repeated measures ANOVA in Statistica 7.0 (StatSoft, Inc.). Within this experimental framework, the random component consisted of the individuals (trees), a necessary approach to control temporal autocorrelation and the non-independence of observations, since the same 33 specimens were monitored successively over 48 months. The fixed factors of the model comprised the species, months, and years of observation. To isolate the impact of environmental variables and mitigate the effect of chronological or ontogenetic trends, the data were subjected to Principal Component Regression (PCR), in which the temporal effect was analytically removed. The temporal effect was removed by extracting the residuals from the time-dependent growth regression, thus isolating the variability associated exclusively with climate fluctuations. This procedure allowed the calculation of growth strictly associated with climatic variability (G), operationalized as the difference between the observed growth (Go) and the expected growth (Ge) derived from the regression (Souza and Marenco 2022).

The selection and validation of the models were based on criteria of statistical significance and predictive power. A critical level of $p < 0.05$ was established for the acceptance of experimental differences and influences of microclimatic variables in all statistical tests. For the structuring of the climate models, Principal Component Analysis (PCA) was applied to the explanatory variables, aiming to reduce collinearity and select the principal components with greater biometric relevance. Regarding the competition models, the selection criterion was based on Pearson's correlation coefficient (r), used to evaluate the responsiveness of the indices in relation to the observed radial increment rate. This approach is widely documented in the literature for identifying indicators of competition in individual trees and is effective in detecting whether neighborhood structure has explanatory power over growth before applying more complex multivariate models (Daniels et al., 1986).

RESULTS

Relationship between the increment in diameter and the microclimatic parameters

This study examined tree growth over a four-year period in an environment with an average temperature of 25.5 °C (ranging from 22.98 °C to 29.93 °C), with a wet season rainfall of 264.77 mm/month and a dry season rainfall of 146.84 mm/month (Figure 2A and C). Other environmental factors included high humidity (79.05%), abundant soil water content (39-52%), and moderate solar radiation. Tree growth, measured by diameter increase, averaged 0.15 mm per month. The monthly increment in tree diameter growth (TGD) was slowest during the dry season and peaked between the end of the dry season and the beginning of the rainy season, indicating a strong correlation between precipitation and tree growth.

There was no significant difference among species regarding the monthly TGD values ($p = 0.067$, Supplementary Table 1), indicating that, on average, all species exhibited the same behavior over time (48 months). Growth behavior differed across the four years of study ($p = 0.008$). However, when comparing growth among months, a significant effect of seasonality on TGD was found ($p < 0.001$). The interaction between species and months was significant, indicating that in one or more months, radial tree growth differed in at least one of the species. This result indicates that, despite all species following the same seasonal trend of cambial expansion and contraction (diameter synchrony), the magnitude and timing of this response vary punctually among taxa in specific months, particularly during the transition periods between the dry and rainy seasons. However, the predominance of the seasonal climate signal is so robust that these momentary interspecific variations were not sufficient to differentiate the average cumulative performance of the species over the 48 months of monitoring.

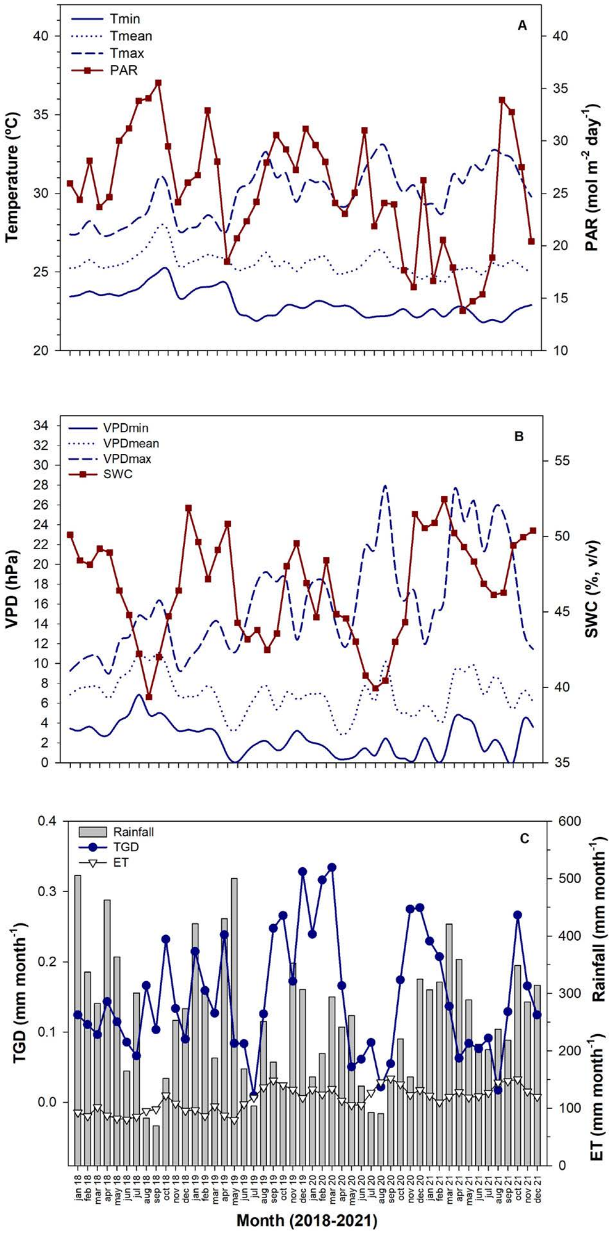

Figure 2: Monthly variation of microclimatic variables and mean diameter growth. A – monthly mean (T_{mean}) temperature and monthly mean of daily photosynthetically active radiation (PAR); B – minimum (VPD_{min}), mean (VPD_{mean}) and maximum (VPD_{max}) of the monthly deficit of vapor pressure and soil water content (SWC), and C – monthly precipitation and monthly tree growth in diameter (TGD, raw data).

In the exploratory analysis via PCA, the individual association between microclimatic variables and mean tree growth over the seven tree species (in the PCA added as a supplementary variable; TGD in red in Figure 3) showed that TGD was positively correlated with rainfall and soil moisture, and inversely proportional to DPV (min and average). The average temperature and PAR were also proportional to the increase in TGD. The variables Rainfall and SWC were negatively correlated with other microclimate variables, in particular with T_{max}, VPD (mean and maximum) and ET.

Inferential analysis via PCR (Table 2) confirmed and quantified these statistical associations. Among the seven species studied, four (*Eschweilera bracteosa*, *Goupia glabra*, *Gustavia augusta* and *Pouteria reticulata*) had TGD significantly influenced by rainfall and SWC ($p<0.05$). The other species also tended to show a positive relationship between rainfall and soil moisture, except for *Pourouma tomentosa*, which had a negative relationship (negative beta coefficient), in other words, the TGD of *P. tomentosa* was inversely proportional to the effect of rainfall and soil moisture. The microclimatic variables with negative correlation with TGD were VPD_{min} (for *Eschweilera coriacea* and *Eschweilera grandiflora*), VPD_{mean} (for *Eschweilera grandiflora* and *Gustavia augusta*), VPDmax (for *Goupia glabra*), T_{mean} (*Gustavia augusta*), Tmax (*Goupia glabra*) and ET (*Goupia glabra*).

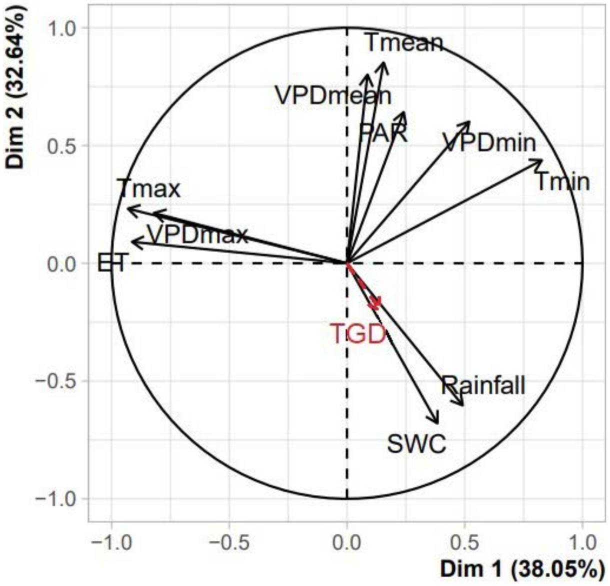

Figure 3: Principal component analysis (PCA) representing the individual association between the microclimatic variables (black arrow) and the mean growth (TGD) of the 7 species (red dotted arrow, added as supplementary variable). Where, VPD_{min}, VPD_{mean}, VPD_{max} denote minimum, mean and maximum vapor pressure deficit respectively; T_{min}, T_{mean}, T_{max} denote minimum, mean and maximum temperatures respectively; SWC indicates soil water content; PAR is photosynthetically active radiation and ET represents reference evapotranspiration.

Table 2: Effects of climatic variables on the monthly increment in diameter of the trees (TGD without the temporal trend) of each species and general mean of the species analyzed using PCR.

Climate Variable		***Eschweilera bracteosa***	***Eschweilera coriacea***	***Eschweilera grandiflora***	***Goupia glabra***	***Gustavia augusta***	***Pourouma tomentosa***	***Pouteria reticulata***	**Overall mean**
PAR	Beta	0.015	0.025	0.028	-0.007	-0.005	0.007	0.036	0.017
	p	**0.043**	0.055	**0.013**	0.144	0.051	0.066	**0.021**	**0.009**
T_{min}	Beta	0.004	0.004	0.001	0.002	-0.002	0.003	0.019	0.005
	p	0.204	0.450	0.799	0.648	0.409	0.422	**0.007**	0.057
T_{mean}	Beta	0.009	0.014	0.014	-0.011	-0.007	0.010	0.027	0.010
	p	0.081	0.134	0.086	0.070	**0.037**	0.050	**0.014**	**0.031**
T_{max}	Beta	0.005	0.009	0.009	-0.014	-0.003	0.004	0.008	0.004
	p	0.166	0.188	0.101	**0.021**	0.327	0.379	0.300	0.244
Rainfall	Beta	0.018	0.022	0.009	0.015	0.006	-0.008	0.046	0.018
	p	**0.015**	0.090	0.375	**0.006**	**0.046**	0.065	**0.003**	**0.006**
SWC	Beta	0.013	0.013	0.000	0.015	0.007	-0.008	0.034	0.012
	p	**0.041**	0.218	0.935	**0.008**	**0.034**	0.050	**0.009**	**0.026**
VPD_{min}	Beta	-0.009	-0.020	-0.030	-0.003	-0.005	0.006	-0.003	-0.011
	p	0.117	**0.048**	**0.001**	0.526	0.124	0.144	0.770	**0.031**
VPD_{mean}	Beta	-0.007	-0.017	-0.026	-0.011	-0.007	0.009	-0.000	-0.010
	p	0.209	0.093	**0.003**	0.054	**0.034**	**0.047**	0.971	**0.050**
VPD_{max}	Beta	-0.000	-0.003	-0.007	-0.012	-0.003	0.003	-0.000	-0.003
	p	0.832	0.625	0.226	**0.020**	0.317	0.368	0.947	0.319
ET	Beta	0.010	0.017	0.017	-0.011	-0.002	0.002	0.018	0.009
	p	**0.044**	0.063	**0.029**	**0.043**	0.532	0.585	0.085	**0.037**

Where: Beta = Beta regression coefficient; p = critical sampling value - obtained from principal component regression to assess the effect of climatic variables on tree growth. Experimental differences were accepted when p<0.05 (significant p-values are in bold). Abbreviations: VPDmin, VPDmean, VPDmax = minimum, mean and maximum vapor pressure deficit, respectively; Tmin, Tmean, Tmax = minimum, mean and maximum temperatures, respectively; SWC = soil water content; PAR = photosynthetically active radiation and ET = reference evapotranspiration.

In terms of the general mean TGD (analysis of the seven species combined), only the VPD (minimum and medium) showed a significantly negative correlation with growth ($p<0.05$). The PAR ($p=0.009$), T_{mean} ($p=0.031$), Rainfall ($p=0.006$), SWC ($p=0.026$) and ET ($p=0.037$), in turn, were positively related to TGD, with rainfall and PAR presenting the highest correlation coefficients. The variables that had no significant influence on the TGD were minimum temperature (T_{min}), maximum temperature (T_{max}) and maximum vapor pressure deficit (VPD_{max}). By using the PCR framework, the reported coefficients reflect the individual contribution of each variable to the TGD after removing collinearity between the original data of the variables, ensuring that the described effects are not inflated by redundancy between correlated effects. Among the ten microclimatic predictors evaluated via PCR, precipitation and soil water content were related to the most robust positive associations with the diameter deficit. Conversely, vapor pressure deficit (minimum and average) was identified as the main environmental factor inversely correlated with radial increment, exerting a restrictive influence on diameter growth.

Tree growth was directly influenced by rainfall and ET. Higher rainfall generally led to increased radial growth, with growth rates exceeding 0.19 mm/month when rainfall surpassed 261.10 mm. Conversely, growth rates fell below 0.08 mm/month when rainfall was less than 141.95 mm (Figure 2C). Tree growth showed a negative relationship with vapor pressure deficit (VPD) (Figure 2B and C). Higher VPD values during the dry season (peaking in September, average of 8.89 hPa) corresponded with reduced tree growth. Conversely, lower VPD values in the wet season were associated with increased growth. Interestingly, the lowest VPD occurred in May, at the end of the rainy season.

Competition Index

Moore's competition index did not significantly correlate with the increase in diameter (r = 0.149; p = 0.405). The low correlation suggests that tree competition in this site was similar among the all evaluated trees. We also calculated competition between trees by applying four other distance-dependent indices to infer competition, including index of Hegyi (1974), Martin and Ek (1984), Pukkala and Kolström (1987) and Rouvinen and Kuuluvainen (1997), but in all of them the effect of tree competition on tree growth was not significant (Table 2 supplementary material).With regards to the populations of trees, over the 33 circles, with a 10 m radius and target tree (≥ 15 cm DBH) in the center, we counted an average (± SD) of 338 ± 47 trees/ha. These results indicate that, under the spatial scale and boundary conditions evaluated, the variation in the immediate neighborhood structure does not explain the observed variability in the individual diameter increment.

DISCUSSION

Relationship between the increase in tree diameter and microclimate parameters

The study reveals varying rates of tree diameter growth over four years in the trees examined. Based on the obtained results, the hypothesis that microclimatic variables, such as precipitation and soil water content, positively influenced trunk diameter increment was corroborated. Among the variables that negatively influenced growth, vapor pressure deficit stood out. Furthermore, the effect of climatic seasonality of the wet and dry seasons on the dynamics of tree increment over the months was observed, since slower growth was noted in most of the studied species during the period of lower water availability, as illustrated in Figure 2 and corroborated by statistical analysis (p < 0.005, Table 2).

Throughout the present study, the lowest tree growth rate was found in 2018, with an average of 0.12 mm month^{-1}, precisely the year with the highest average temperature and the months with the lowest monthly precipitation rates (58.00 mm/month), mainly between July and September. The decrease in water availability during the dry season can reduce the efficiency of the rubisco enzyme, thereby affecting photosynthetic efficiency and reducing carbon fixation, which ultimately compromises tree diameter growth.(Yang et al., 2018; Scafaro et al., 2023). Less carbon gain result in less energy and resources for building woody tissue. However, in the absence of precise data on leaf gas exchange, this reduction in photosynthesis should be interpreted as a voluntary physiological feedback mechanism, and not as a predetermined outcome. In this study, rainfall strongly influences forest dynamics, with a positive correlation (p=0.006) observed between tree diameter growth and precipitation This growth was marked by seasonality, with a higher TGD (>0.19 mm/month) in the rainy season (>261.10 mm/month) and lower TGD (<0.08 mm/month) in the dry season (<141.95 mm/month), with growth returning in October after the start of the rainy season, when the rains begin to become more intense. Water availability modulates radial increment by optimizing carbon assimilation and xylem transport of solutes essential for cambial expansion Stirbet et al., 2020). Conversely, water deficit compromises the flow and partitioning of photoassimilates, restricting the supply of energy and nutrients necessary for wood tissue productivity. The effect of rainfall on tree growth is remarkable important, because it has been shown that the length of dry are increasing in parts of the Amazon region (Espinoza et al., 2022).

In this study, soil water content (SWC) correlated with rainfall variations, with dry months experiencing lower precipitation than evapotranspiration (ET), leading to reduced soil moisture and probably to increased xylem sap tension. This can trigger stomatal closure and decreased TGD (Matsunaga et al., 2021).

Photosynthetically active radiation (PAR) and reference evapotranspiration (ET) significantly influenced species growth (p=0.009; p=0.037, respectively) and positively correlated with TGD. Since evapotranspiration can be represented as a function of temperature and solar radiation, the positive effect observed in *E. bracteosa*, *E. grandiflora*, *G. glabra*, and the overall mean is justified. This occurs because, in some species, Tmean and PAR also exerted a significant positive effect on stem increment. Interestingly, the effect of PAR on trees of similar size was neutral, which weakens the premise that tree height is a primary determining factor in the radial growth dynamics of these species. Consequently, the sub-canopy species in this study likely were not adversely affected by increased radiation, contrasting with prior studies where PAR negatively impacted tree growth or had negligible effects (Antezana-Vera and Marenco, 2021; Bauman et al., 2022).

Among the evaluated microclimatic variables, mean VPD stood out for exerting the most significant negative effect on TGD. This limiting impact on stem increment occurs primarily during the dry season, trees with limited stem growth showed increased VPD, indicating stomatal closure to prevent hydraulic failure, which would consequently potentially reduce net carbon assimilation (Cárcer et al. 2018). Conversely, wet seasons exhibited lower VPD and higher TGD. Over time, TGD inversely related to VPD, but temperature positively correlated with TGD (p=0.031), indicating no negative impact on local vegetation. However, the tropical forest's photosynthetic capacity can be vulnerable to climate changes (e.g. increased temperature and reduced water availability), which can affect tree growth. Predictions suggest that increasing temperatures will decrease carbon uptake in the Amazon due to biochemical and stomatal-related changes, hampering vegetation growth (Machado-Silva et al., 2021). In the current context of climate change, evidence of tree species' sensitivity to water availability serves as an alert to the risk of increased mortality and reduced growth, as the trend is toward a higher frequency of climatic anomalies that negatively influence forest carbon accumulation.

Analysis of competition between trees

In general, the distance-dependent index evaluated proved to be non-significant growth predictor for the studied species. This work showed a low correlation between the evaluated distance competition index and the TGD, which does not corroborate the hypothesis presented that posited a significant relationship between distance-dependent competition and tree growth.

The growth rate of an individual tree is determined by the density of the population according to the growing space available to the tree, with the space of each tree being limited by competing trees, leading to direct competition both for aerial space (at the canopy level) and through the soil (roots) (Hiley, 1959), through the availability of essential factors such as water, light and nutrients, and site quality. In a previous work, Prance et al. (1976) found that the number of trees (≥ 15 cm in diameter) in a single hectare is high (350 trees /ha and 179 species/ha). This high spatial distribution per hectare indicates that all studied trees may be under similar effects of competition when considering the distance between the stems. That is, the high population of trees in our study area (338/ha) can lead to similar competition among trees, which makes it difficult to detect competition between trees (latent completion). This crowded population of trees may explain the low correlation between the competition index and stem growth. It is recognized, however, that the analytical framework based on linear correlations and classical indices may have limitations in capturing complex non-linear interactions. Thus, the lack of statistical significance should be interpreted as evidence that, at the scale evaluated, climate is the dominant driver, while the neighborhood effect remains a uniformly distributed environmental constant among the target trees.

According to Scolforo (2005), although the height-DBH ratio is a preponderant indicator for characterizing tree stability, using indexes that use only DBH and height as variables may not be good descriptors of competitive dynamics when the stand has a high density of primary trees. This is because even when comparing trees with greater differences in diameter, many areas are considered mature stands, where height has already reached its maximum point and under the influence of latent competition. However, the greatest annual increases in height are still observed when individuals are in the young phase. This demonstrates the disadvantage of using indexes characterized only by height, such as Pukkala and Kolström (1987), for example, since tree attributes such as height are required, which are expensive and/or laborious to acquire accurately.

When there are more trees per hectare, the average ground space available for the growth of an individual tree in a stand is smaller. In contrast, with an increase in the DBH of the trees, the average crown size also increases and, consequently, the air space required for growth increases (Lu, 2024). The inclusion of crown area data (diameter, size, and width) directly in the distance-dependent indices can improve the performance of competition prediction. This is because two competing trees may have the same DBH and be at the same distance from a target tree, but they may have different crown areas, which in turn exert different influences on the target tree (Liu et al., 2025).

When the number of trees per hectare is high, as in this area (Rankin-de-Mérona et al., 1992), less space is available for a tree to grow. According to Martin-Blangy et al. (2023), in overstocked stands, such as in the study area, where interactions between crowns are exceptionally intense, the degree of competition depends on the characteristics of the crowns. The weak correlation between the evaluated index and stem growth suggests that light may be an important limiting factor for the proposed trees (i.e., target trees, DBH ≥ 15 cm). We reach to this conclusion because in this study PAR had one of smallest p values related to TGD ($p = 0.009$, Table 2). The level of competition of the trees can be directly associated with the differences in shade tolerance that each one presents (Rahman et al., 2021). Morphological characteristics of the crown and the sociological position of the trees, although not integrated into the quantitative models of this manuscript, represent promising directions for future research. Such attributes may act as biological filters that modulate the individual perception of competition.

CONCLUSION

This study sought to investigate the influence of microclimatic variables and individual competition on diameter growth in a dense forest in Central Amazon. The results support the central hypothesis that climatic drivers exert primary control over radial increment, overriding the influence of environmental competition in saturated stands. PCR analysis includes soil water content as the main positive predictors of diameter growth, while vapor pressure deficit (minimum and average) showed a significant negative association, occasionally acting as a limiting factor for growth. It is proposed that the high stochastic density of the stand results in competitive pressure, here cautiously interpreted as latent competition, which makes target trees more responsive to microclimatic fluctuations than to immediate neighborhood effects. These results indicate that the resilience of the upland ecosystem is intrinsically linked to the stability of the water regime and the regulation of atmospheric aridity, suggesting that traditional silvicultural interventions, such as thinning, may have limited effectiveness in stimulating diameter increase in climax areas, indicating that management should prioritize the conservation of the forest structure that buffers microclimatic stresses. Furthermore, the reliance on linear models and classical indices may not capture nuances of non-linear interactions. Future research should integrate mixed-effects models and peculiarities of leaf ecophysiology to validate the resilience of these species in the face of increasing climate anomalies and explore how canopy architecture modulates individual perception of environmental stresses.

AUTHORSHIP CONTRIBUTION

Project Idea: RAM
Funding: RAM
Database: LALP; MMS; RAM
Processing: LALP; MMS; RAM
Analysis: LALP; MMS; RAM
Writing: LALP;
Review: LALP; MMS; RAM

DATA AVAILABILITY

The datasets analyzed during the current study are available from the corresponding author upon reasonable request.

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