

Seasonal variation in gas exchange and chlorophyll index of *Palicourea racemosa* in an open ombrophilous forest

Variación estacional en el intercambio de gases y el índice de clorofila de *Palicourea racemosa* en un bosque ombrófilo abierto

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SUMMARY

Seasonal variation affects understory and canopy tree plants in different ways. *Palicourea racemosa* is an understory shrub from the Rubiaceae family and is subject to seasonal oscillations of the environment, which can affect plant ecophysiological responses. This species is widely distributed in humid forests from southern Mexico to southeastern Brazil and has broad economic and ecological importance for the regions of occurrence, being used for food, ornamental and traditional medicine purposes. It is of fundamental importance to know ecophysiological responses of this species throughout dry and rainy periods, to understand the dynamics of understory plants in tropical forests. This research aimed at evaluating the effects of seasonality on ecophysiological aspects of *P. racemosa* at the Mata do Pau-Ferro State Park, municipality of Areia, Paraíba, Brazil. Over ten months, upper canopy structure indices were measured in ten individuals, climatic data were collected and their effects on gas exchange and chlorophyll indices in plants were evaluated. Results showed that the environmental variables correlated with the ecophysiological ones, with a strong association of soil moisture, rainfall and leaf area index of the upper canopy on ecophysiological aspects in *P. racemosa* plants, indicating that water availability and irradiance affect gas exchanges and photosynthetic pigment content. Except for intrinsic water use efficiency and instantaneous carboxylation efficiency, all ecophysiological variables showed significant differences over the months, showing the influence of seasonality on the ecophysiological responses of *P. racemosa*.

Key words: photosynthesis rate, physiological responses, Rubiaceae, understory vegetation, water availability.

RESUMEN

La variación estacional afecta a las plantas de árboles del sotobosque y del dosel de diferentes maneras. *Palicourea racemosa* es un arbusto de sotobosque de la familia Rubiaceae y está sujeto a oscilaciones estacionales del medio ambiente, que pueden afectar las respuestas ecofisiológicas de las plantas. Esta especie se encuentra ampliamente distribuida en bosques húmedos desde el sur de México hasta el sureste de Brasil y tiene una gran importancia económica y ecológica para las regiones de ocurrencia, siendo utilizada con fines alimentarios, ornamentales y de medicina tradicional. Es de fundamental importancia conocer las respuestas ecofisiológicas de esta especie a lo largo de los períodos secos y lluviosos, a fin de buscar comprender la dinámica de las plantas del sotobosque en los bosques tropicales. La investigación tuvo como objetivo evaluar los efectos de la estacionalidad en aspectos ecofisiológicos de *P. racemosa* en el Parque Estatal Mata do Pau-Ferro, municipio de Areia, Paraíba, Brasil. Durante diez meses, se midieron índices de estructura del dosel superiores a diez individuos, se recopilaron datos climáticos y se evaluaron sus efectos sobre el intercambio de gases y los índices de clorofila en las plantas. Las variables ambientales se correlacionaron con las ecofisiológicas, con una fuerte asociación de la humedad del suelo, las precipitaciones y el índice de área foliar del dosel superior en los aspectos ecofisiológicos de *P. racemosa*, resultados que indican que la disponibilidad de agua y la irradiancia afectan los intercambios de gases y el contenido de pigmentos fotosintéticos en las plantas. Excepto, por la eficiencia intrínseca del uso del agua y la eficiencia de la carboxilación instantánea, todas las variables ecofisiológicas tuvieron diferencias significativas a lo largo de los meses, debido a la influencia de la estacionalidad en las respuestas ecofisiológicas de *P. racemosa*.

Palabras clave: tasa de fotosíntesis, respuestas fisiológicas, Rubiaceae, vegetación del sotobosque, disponibilidad de agua.

INTRODUCTION

Tropical forests are terrestrial ecosystems that have broad productivity and abundant species diversity, being fundamental in the formation of ecological niches (Pausas and Bond 2020). Among the different physiognomies found in this ecosystem, seasonal forests stand out for presenting ecological and physiological adaptations to each climatic season (Derroire *et al.* 2016). During the dry season, 30 to 50 % of individuals in the forest canopy are deciduous and shed leaves as an adaptation mechanism to water deficit (Vijith and Dodge-Wan 2020).

Climatic seasons directly influence growth, development, propagation and physiology of canopy forest species, as well as affect the understory vegetation, which is composed by shrubs, sub-shrubs, terrestrial herbs and young trees from the forest canopy (Denslow *et al.* 2019). Understory species are affected by different factors, which can be altered according to seasonal variations in environmental conditions that consequently modify the ecological and ecophysiological activities of plants (Lambers and Oliveira 2019). Among the abiotic factors that most influence understory plants are water availability, light intensity and temperature (Giuggiola *et al.* 2018, Elias *et al.* 2019).

Water availability is one of the main environmental factors regulating plant growth, development and photosynthetic capacity. In the photosynthetic process, water deficit induces stomatal closure and limits CO₂ concentration in the mesophyll, which thus hinders CO₂ fixation and transport of photoassimilates throughout the plant (Baraket *et al.* 2020).

Another important environmental factor regulating physiological processes in understory species is light. Irradiance either intensifies the photosynthetic apparatus activity or reduces it due to photoinhibition caused by excess light (Sun *et al.* 2020). Moreover, irradiance variation inside the understory changes the forest microclimate, as air and soil temperatures. Such variation depends on factors relating to canopy structure, such as the opening of natural clearings and leaf shedding during the dry season (Mansur 2017).

Light availability in the understory in forest ecosystems can be measured using variables related to forest canopy, such as leaf area index (LAI), visible sky fraction (VSF) and photosynthetically active radiation (PAR). Different techniques have been used to analyze the canopy structure and light transmission, such as using hemispheric photographs and LAI meters by solar radiation attenuation (Jenicek *et al.* 2018).

Among the understory species, *Palicourea racemosa* (Aubl.) G.Nicholson (Rubiaceae) is a neotropical plant, 4 m in height widely distributed in humid forests from southern Mexico to southeastern Brazil (Zappi *et al.* 2017). This species has high economic and ecological importance for the regions of occurrence, being used for food and ornamental purposes and, in phytochemical-based tra-

ditional medicine, for the treatment of neurodegenerative diseases (Calixto *et al.* 2016).

We hypothesized that: (1) The ecophysiological aspects of the understory species, *P. racemosa*, are influenced by seasonal variation; (2) The plants present strategies to acclimate to the dry period, such as reducing transpiratory rate and stomatal conductance, tolerating water scarcity in the soil and high irradiance; (3) The species has phenotypic plasticity to respond to seasonal variation in light availability and soil water content, with changes in ecophysiological aspects. Thus, this research evaluated the effects of seasonal variation on ecophysiological aspects in *P. racemosa*.

METHODS

Experimental area. The study was carried out at Parque Estadual Mata do Pau-Ferro (6°58'12" S, 35°42'15" W), an approximately 600 ha area located 5 km west from Areia City, state of Paraíba, Northeast Region, Brazil (figure 1). The climate of the region is classified as Aw (Peel *et al.* 2007), which is hot and humid tropical with autumn-winter rains, with annual rainfall ranging from 800-1,600 mm, and average annual temperature of 22 °C. Topography is from undulating to strong undulating.

Data collection. For environmental and ecophysiological data collection, ten adult individuals with average 2.10 m in height and 16 cm in diameter at breast height were randomly selected, and their geographic locations were georeferenced (figure 1). Evaluations were performed from January to September 2018. Climatic data [rainfall and temperature (average, maximum and minimum)] during this period are shown in the ombrothermic diagram (figure 2). Precipitation and temperature data were collected monthly by the Meteorological Station of Center for Agricultural Sciences, Federal University of Paraíba, Campus II (Areia Station - A310, code OMM 81877), about 3.5 linear kilometers from the study area.

To perform an edaphic characterization, four soil samples (0-20 cm depth) were collected under the canopy of each *P. racemosa* plant. After, these samples were combined to form a composite sample from which a sample was taken for soil chemical and granulometric evaluation (table 1).

Gas exchange. To assess the plant gas exchange, the net assimilation rate of CO₂ (A , $\mu\text{mol m}^{-2} \text{s}^{-1}$), stomatal conductance (g_s , $\text{mol m}^{-2} \text{s}^{-1}$), transpiration rate (E , $\text{mmol m}^{-2} \text{s}^{-1}$) and intercellular CO₂ concentration (C_i , $\mu\text{mol mol}^{-1}$) were measured using a portable Infrared Gas Analyzer (IRGA) (model LI-6400XT LI-COR, Inc., Lincoln, NE, USA). Afterwards, transpiration efficiency [instantaneous water use efficiency, $WUE = A/E$, ($\mu\text{mol m}^{-2} \text{s}^{-1}$) ($\text{mmol m}^{-2} \text{s}^{-1}$)⁻¹], intrinsic water use efficiency [$iWUE = A/g_s$, ($\mu\text{mol m}^{-2} \text{s}^{-1}$) ($\text{mol m}^{-2} \text{s}^{-1}$)⁻¹] and instantaneous carboxylation efficiency

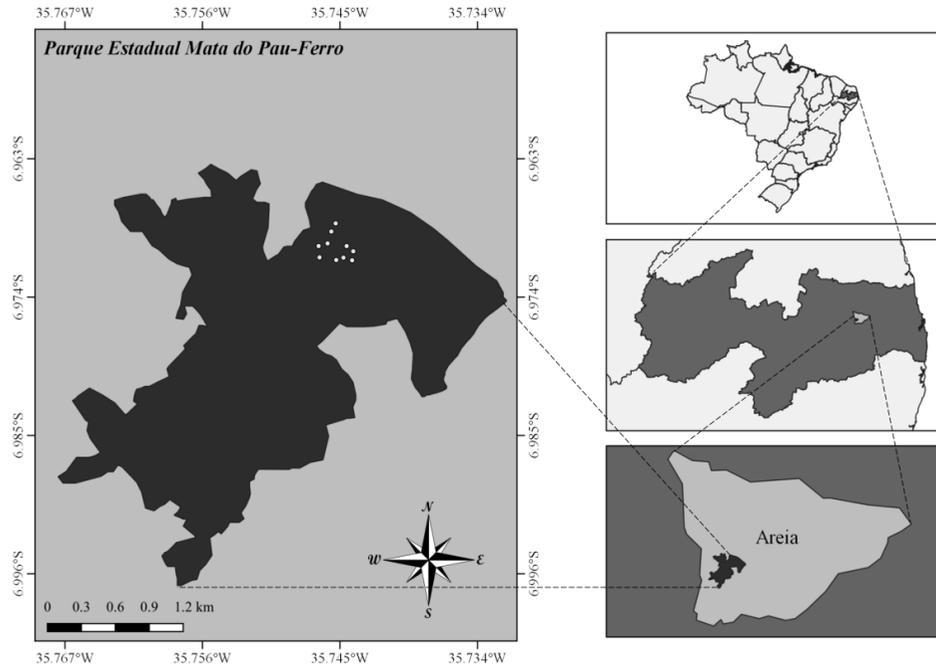


Figure 1. Geographic location of *P. racemosa* individuals at Parque Estadual Mata do Pau-Ferro, Areia, Paraíba, Brazil.
 Ubicación geográfica de individuos de *P. racemosa* en el Parque Estadual Mata do Pau-Ferro, Areia, Paraíba, Brasil.

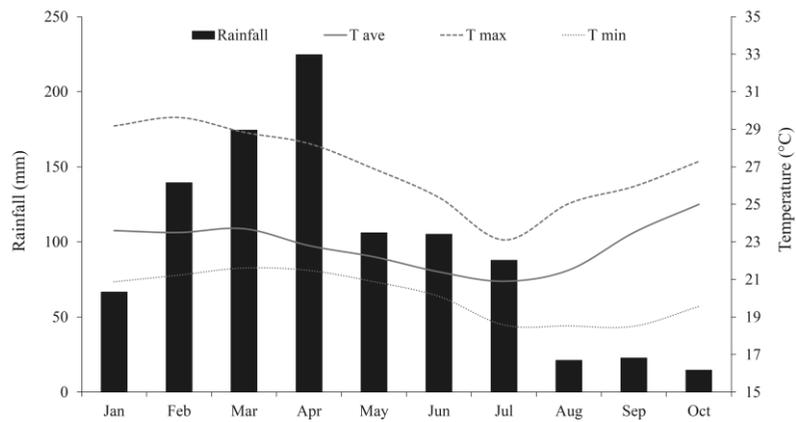


Figure 2. Rainfall, average temperature (T ave), maximum temperature (T max) and minimum temperature (T min) recorded at the meteorological station from Center of Agrarian Sciences, Federal University of Paraíba (Campus II, Estação Areia - A310, code: OMM 81877) during the months of 2018 in which the collections were carried out (Source: Instituto Nacional de Meteorologia - INMET).

Lluvia y temperatura registradas en la estación meteorológica del Centro de Ciencias Agrarias, Universidad Federal de Paraíba (Campus II, Estação Areia - A310, código: OMM 81877) durante los meses de 2018 en los que se realizaron las recolecciones (Fuente: Instituto Nacional de Meteorología - INMET).

Table 1. Chemical and granulometric attributes in 0-20 cm soil at Parque Estadual Mata do Pau-Ferro, Areia, PB.

Atributos químicos y granulométricos de los 20 cm superiores del suelo en el Parque Estadual Mata do Pau-Ferro, Areia, PB.

pH	P	K ⁺	Na ⁺	H ⁺ +Al ³⁺	Al ³⁺	Ca ²⁺	Mg ²⁺	SB	CEC	SOM	Sand	Silt	Clay
H ₂ O	mg dm ⁻³			cmol dm ⁻³					g kg ⁻¹		g kg ⁻¹		
5.21	6.76	104.89	0.08	9.74	0.75	0.50	3.55	8.44	18.18	58.55	650	163	187

[ICE = A/Ci, ($\mu\text{mol m}^{-2} \text{s}^{-1}$) ($\mu\text{mol mol}^{-1}$)⁻¹] were calculated. The measurement protocol with IRGA was: 6 cm² leaf chamber attached with a natural light sensor, 50-60 % air humidity, 300 $\mu\text{mol s}^{-1}$ airflow and 400 $\mu\text{mol CO}_2 \text{mol}^{-1}$ mixer (model 6400-01). Analyses were performed on healthy fully-expanded leaves at the middle third of each individual, from 11:00 am to 12:00 pm and on a cloudy day.

Chlorophyll indices. Chlorophyll (Chl) content (as Falker Chlorophyll Index – FCI) was measured using a portable chlorophyll meter (ClorfiLOG®, model CFL 1030), in which chlorophyll a (Chl a), chlorophyll b (Chl b) and total chlorophyll (Chl a+b) were recorded. Subsequently, the ratio between the chlorophyll a and b indices was calculated (Chl a/Chl b). Four readings were performed on leaves at the middle third of each plant to calculate average.

Canopy structure indices. Leaf area index (LAI), visible sky fraction (VSF) and photosynthetically active radiation (PAR) were measured using hemispherical photographs taken using a forest canopy analyzer (Digital Plant Canopy Imager, CI-110, CID). Measurements were performed above the *P. racemosa* individuals in the forest understory. To achieve better contrast between leaves and sky, analyses were performed under diffused light conditions.

Soil moisture and temperature. Soil moisture (SM) was determined using the gravimetric method proposed by Klein (2008) and calculated as:

$$\text{SM (\%)} = [(WW - DW) / DW] \times 100,$$

where WW is the weight of wet sample (g) and DW is the weight of dry sample (g).

Correspondingly, soil temperature was measured on the surface (ST_{0cm}) and at 20 cm depth (ST_{20cm}) using a portable digital infrared thermometer (Raytek, MT6 model). Soil moisture and temperature were measured at the same time that ecophysiological variables were assessed once a week.

Statistical analyses. Data were submitted to a multivariate analysis using Canonical Correlation Analysis (CCA) and Principal Component Analysis (PCA) to verify associations between the environmental (LAI, VSF, PAR, SM, ST_{0cm}, ST_{20cm}, Rain and Temp) and ecophysiological (A, Ci, E, gs, WUE, iWUE, ICE, Chl a, Chl b and Chl a+b) variables. Besides, Wilks' lambda test (an approximation of F distribution) was used to analyze the significance of canonical roots. Moreover, the analysis of variance was used to test differences in ecophysiological variables over the months, followed by the Tukey test to group means ($P \leq 0.05$). Statistical analyzes were performed in SAS® 9.3.5 software.

RESULTS

Influence of environmental factors on the *P. racemosa* ecophysiology. According to CCA, there were correlations between environmental and ecophysiological variables. However, only the first and second canonical dimension were significant, with R² equal to 0.979 and 0.784, respectively (table 2).

Likewise, for the first canonical dimension, the most important variables were rainfall, soil moisture and leaf area index (0.87, 0.79 and 0.69, respectively), which positively correlated with intercellular CO₂ concentration (0.85), transpiration rate (0.80), chlorophyll a (0.75), total chlorophyll (0.74), chlorophyll b (0.72), stomatal conductance (0.70), net photosynthesis (0.67), instantaneous carboxylation efficiency (0.65), water use efficiency (0.63) and intrinsic water use efficiency (0.59) (table 3).

According to the principal component analysis (PCA), it was noted that axes 1 and 2 corresponded respectively to 32.89 % and 17.06 % of the total inertia, explaining 49.95 % of data variability (figure 3). Moreover, stomatal conductance (gs), transpiration rate (E) and total chlorophyll (Chl a) strongly correlated with rainfall, while chlorophyll a (Chl a), chlorophyll b (Chl b) and intercellular CO₂ concentration (Ci) strongly correlated with soil moisture (SM). On the other hand, leaf area index (LAI) correlated with instantaneous carboxylation efficiency (ICE), net

Table 2. Wilks' lambda multivariate test (an approximation of F distribution).

Prueba multivariante lambda de Wilks (una aproximación de la distribución F).

Canonical dimension	R ²	F	DF ₁	DF ₂	P-value
1	0.979	7.35	80	528.6	< 0.0001
2	0.784	2.40	63	473.5	< 0.0001
3	0.500	1.15	48	417.3	0.238
4	0.435	0.82	35	359.9	0.754
5	0.248	0.41	24	301.2	0.994

R²: canonical correlation; F: approximate F value; DF₁: treatment degrees of freedom; DF₂: error degrees of freedom.

Table 3. Canonical correlations and canonical dimension between environmental and ecophysiological variables.

Correlaciones canónicas y par canónico entre variables ambientales y ecofisiológicas.

Variables	Canonical dimension
Environmental	
Leaf area index (LAI)	0.69
Visible sky fraction (VSF)	-0.19
Photosynthetically active radiation (PAR)	-0.06
Soil moisture (SM)	0.79
Soil temperature at 0 cm (ST _{0cm})	-0.09
Soil temperature at 20 cm (ST _{20cm})	-0.45
Rainfall (Rain)	0.87
Average temperature (T ave)	-0.24
Maximum temperature (T max)	-0.12
Minimum temperature (T min)	-0.16
Ecophysiological	
Net assimilation rate of CO ₂ (A)	0.67
Stomatal conductance (gs)	0.70
Transpiration (E)	0.80
Internal CO ₂ concentration (Ci)	0.85
Instantaneous water use efficiency (WUE)	0.63
Intrinsic water use efficiency (iWUE)	0.59
Instantaneous carboxylation efficiency (ICE)	0.65
Chlorophyll <i>a</i> (Chl <i>a</i>)	0.75
Chlorophyll <i>b</i> (Chl <i>b</i>)	0.72
Total chlorophyll (Chl <i>a+b</i>)	0.74
Chl <i>a</i> /Chl <i>b</i> ratio	0.28
R ²	0.98
Significance	**

**Significant at 1 % probability by the Chi-Square test; R²: canonical correlation.

photosynthesis (A), water use efficiency (WUE) and intrinsic water use efficiency (iWUE) (figure 3).

For axis 1 (first principal component), the eigenvectors of LAI, instant carboxylation efficiency (ICE), water use efficiency (WUE) and intrinsic water use efficiency (iWUE) are grouped right side, presenting positive values. In contrast, the eigenvectors of PAR, ST_{0cm}, VSF, Tave, Tmax, Tmin and ST_{20cm} are arranged left side, showing negative values. This distribution of eigenvectors

demonstrates, therefore, that the environmental variables are distinct from the ecophysiological ones (figure 3).

Analysis of ecophysiological aspects over the months. Significant differences were observed for the ecophysiological variables over the months ($P \leq 0.05$), except for iWUE ($P = 0.0672$) and ICE ($P = 0.0939$) (figures 4, 5 and 6).

In the gas exchange analysis, net photosynthesis (A) ranged from 0.516 (October) to 2.380 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (April) (figure 4A). Likewise, stomatal conductance (gs) was lower in months with water deficit and highest irradiance, ranging from 0.019 (September) to 0.082 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (April) (figure 4B). Transpiration rate (E) varied similarly to stomatal conductance (gs), ranging from 0.676 (September) to 1.690 $\text{mmol m}^{-2} \text{s}^{-1}$ (April) (figure 4C). Intercellular CO₂ concentration (Ci) reduced in months with lower LAI and water availability, with rates fluctuating from 241.24 to 407.51 $\mu\text{mol mol}^{-1}$ (figure 4D).

Water use efficiency (WUE) changed significantly over the months, reducing 66 % from June to October [2.420 to 0.819 ($\mu\text{mol m}^{-2} \text{s}^{-1}$) ($\text{mmol m}^{-2} \text{s}^{-1}$)⁻¹] (figure 5A). Differently, intrinsic water use efficiency (iWUE) and instantaneous carboxylation efficiency (ICE) did not vary along months (figures 5B and 5C).

Chl *a*, Chl *b* and Chl *a+b* were higher in the season of low irradiance and high water availability, with the highest values found in March (43.53, 25.70 and 69.44 FCI, respectively) (figures 6A, 6B and 6C), while the Chl *a*/Chl *b* ratio did not oscillated, remaining constant over the months (figure 6D).

DISCUSSION

CCA and PCA analyses showed that the ecophysiological and environmental variables were significantly correlated, indicating that the ecophysiology of *P. racemosa* plants was influenced by environmental (abiotic) factors. Therefore, the species has variability in gas exchange and chlorophyll contents and those variabilities were correlated with changes in environmental traits. In other words, *P. racemosa* has the capacity to change its phenotype in response to environment; *i.e.* it has phenotypic plasticity in the traits evaluated. Thus, according to CCA (Hair Junior *et al.* 2009), rainfall, soil moisture and leaf area index are considered the most important environmental factors that increased gs, E, Chl *a*, Chl *b*, Chl *a+b*, Ci, A, ICE, WUE and iWUE in *P. racemosa*. On the other hand, PAR and VSF, two variables related with canopy coverage, correlated negatively with ecophysiological traits though showed to be weaker than rainfall. Therefore, seasonal variation in gas exchange and photosynthetic pigments of understory plants may be caused by edaphic factors and forest canopy opening, such as soil water availability and leaf area index that modify the shade to the understory species (Giuggiola *et al.* 2018), although in this case, soil water content seems to be more important than light.

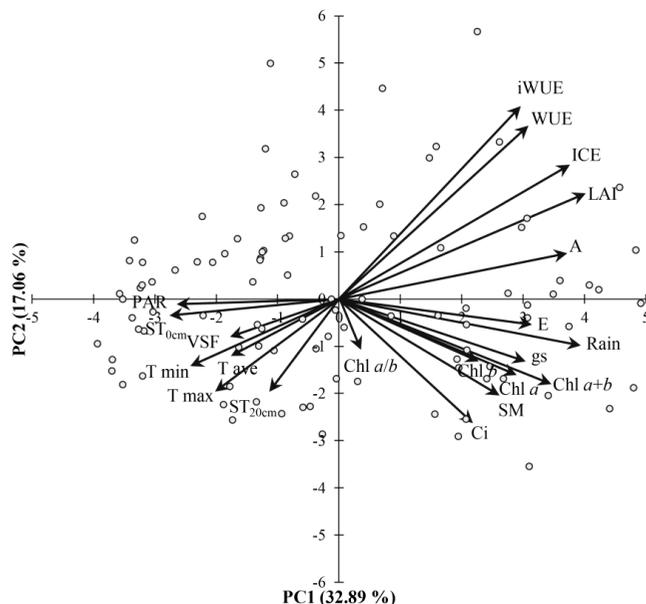


Figure 3. Principal Component Analysis (PC1 and PC2) for environmental and ecophysiological variables in *P. racemosa* individuals. Abbreviations are presented in table 3.

Análisis de componentes principales (PC1 y PC2) para variables ambientales y ecofisiológicas en individuos de *P. racemosa*. Las abreviaturas se presentan en el cuadro 3.

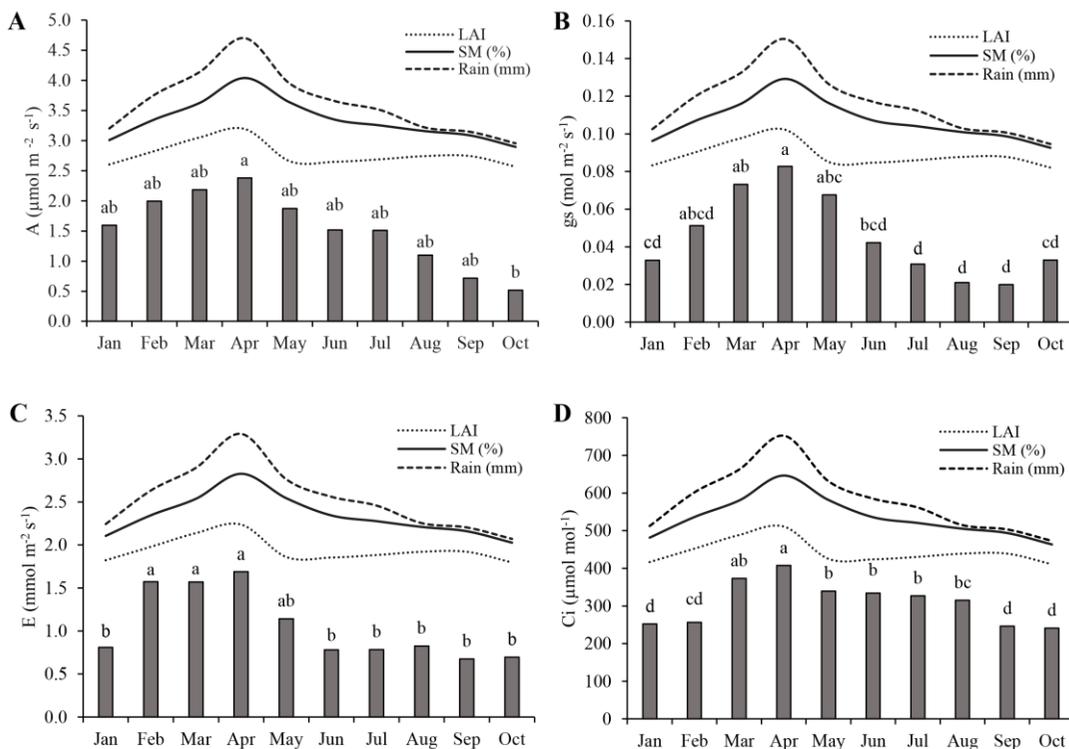


Figure 4. Means of (A) net photosynthesis, (B) stomatal conductance, (C) transpiration rate and (D) intercellular CO₂ concentration in *P. racemosa* plants compared by the Tukey test, along with rainfall (Rain), soil moisture (SM) and leaf area index (LAI), over the months at Parque Estadual Mata do Pau-Ferro, Areia, PB.

Medias de (A) fotosíntesis neta, (B) conductancia estomática, (C) tasa de transpiración y (D) concentración de CO₂ intercelular en plantas de *P. racemosa* en comparación con la prueba de Tukey, junto con lluvia (lluvia), humedad del suelo (SM) e índice de área foliar (LAI), a lo largo de los meses en el Parque Estadual Mata do Pau-Ferro, Areia, PB.

Therefore, soil water deficit and high irradiance during the dry season may have been the main factors that negatively interfered with physiological processes of *P. racemosa* plants (Maréchaux *et al.* 2019). Thus, under these conditions, the plants reduced stomatal conductance, CO₂ assimilation and intercellular CO₂ concentration (Chen *et al.* 2019). Hence, A is lower when light availability in the understory is higher, because as leaf shedding occurs during the dry season, *P. racemosa* plants cannot take advantage of the increase in light as stomata are partially closed. LAI is determinant in the irradiance interception by understory plants. Therefore, a canopy reduction, by anthropic actions or leaf shedding in dry seasons, increases the irradiance levels into the understory, thereby reducing the photosynthetic rate due to the excess of light (Lin *et al.* 2018) as plants are water stressed.

Water deficit and excessive irradiance reduce stomatal conductance (gs) as a result of stomatal closure, which consequently reduces carbon fixation. In other species a reduction in leaf area, besides accelerating leaf senescence, and abscission were observed in water stressed plants (Toigo *et al.* 2020). The mechanism of stomatal opening and closing depends upon the turgescence of guard cells,

evidencing that the opening is favored by adequate water availability in soil. On the other hand, reducing transpiration during the dry season is a plant defense mechanism to prevent excessive water loss. In addition to this mechanism, stomatal closure and leaf area reduction are adaptive mechanisms of plants, making plants tolerant to water stress (Griebel *et al.* 2019). It is evident that *P. racemosa* has no strategies to avoid water stress, like a deep root system, high hydraulic capacitance or a thick boundary layer, and it partially closes the stomata to avoid leaf dehydration, with the consequent reduction in carbon assimilation.

In the case studied, LAI reduction and the consequent increase in light available for *P. racemosa* plants occur together with soil water deficit, hence it is difficult to discriminate the effect of each factor. However, it is clear that gs changed more markedly along the months than A, thus stomatal limitations seem to be very important in the reduction of A. Moreover, the strategy of this species as SM reduces is to close the stomata and reduce transpiration during the dry season (figure 4). This idea is reinforced by the reduced intercellular CO₂ concentration (Ci) in plants in the dry season, which clearly indicates that the stomatal limitation negatively affects the resistance of mesophyll to

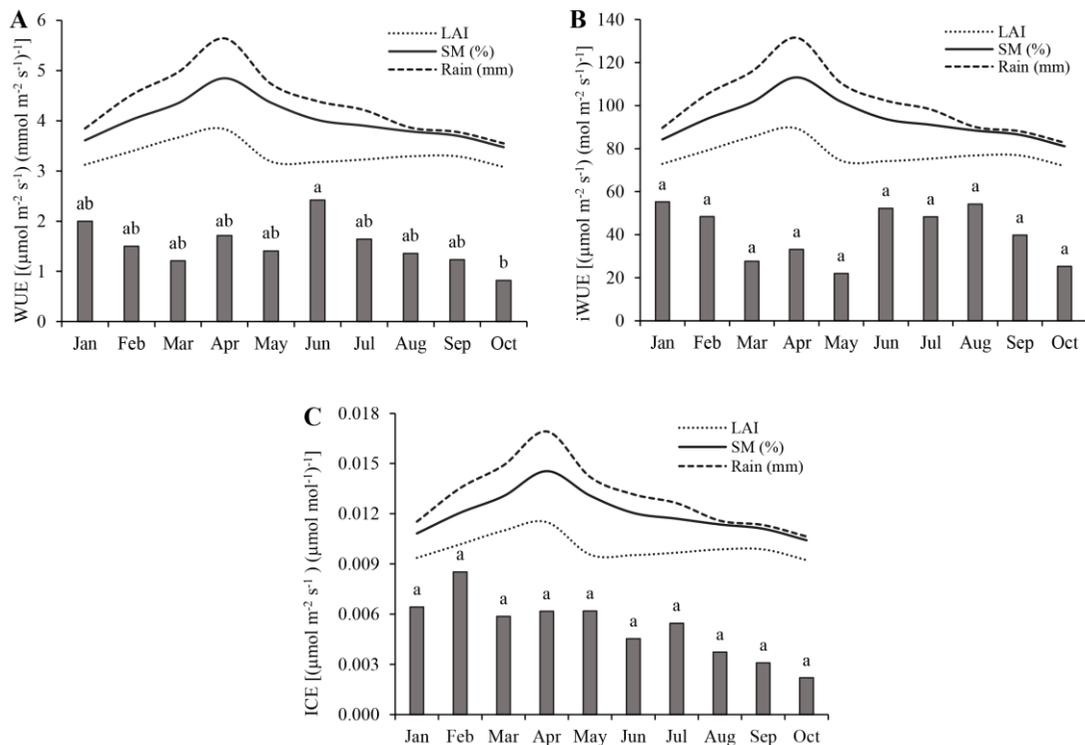


Figure 5. Monthly means of (A) water use efficiency, (B) intrinsic water use efficiency and (C) instantaneous carboxylation efficiency in *P. racemosa* plants compared by the Tukey test, along with rainfall (Rain), soil moisture (SM) and leaf area index (LAI) at Parque Estadual Mata do Pau-Ferro, Areia, PB.

Medias mensuales de (A) eficiencia en el uso del agua, (B) eficiencia intrínseca del uso del agua y (C) eficiencia de carboxilación instantánea en plantas de *P. racemosa* comparadas con la prueba de Tukey, junto con la lluvia (Lluvia), la humedad del suelo (SM) e índice de área foliar (LAI) en el Parque Estadual Mata do Pau-Ferro, Areia, PB.

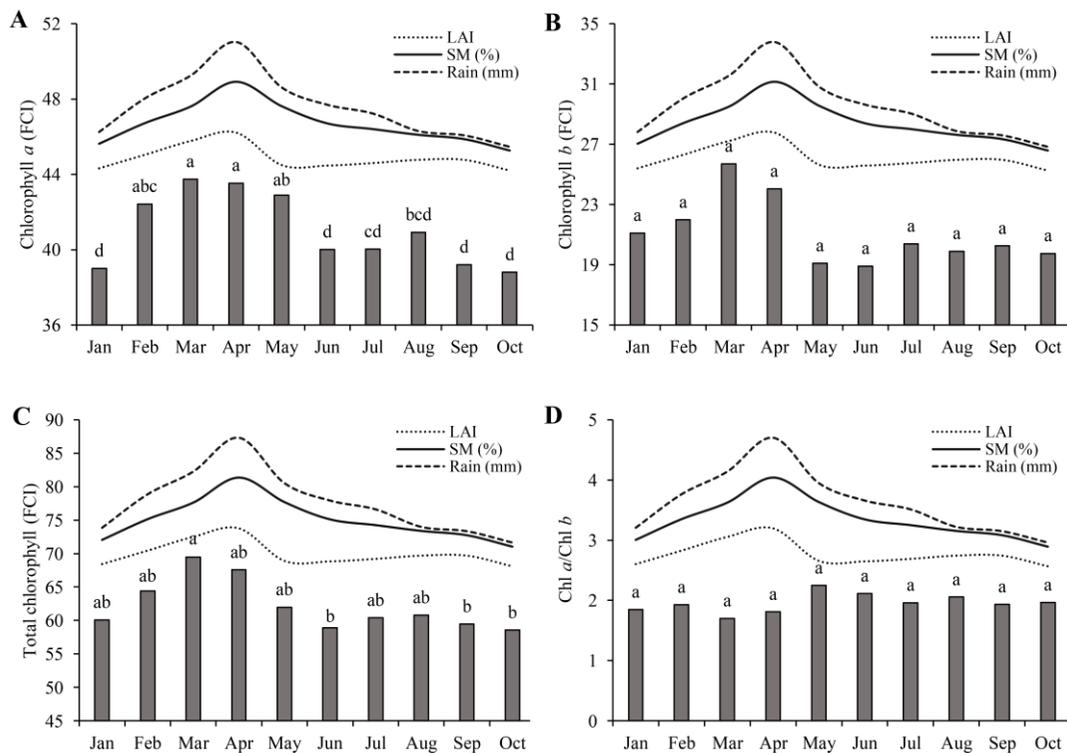


Figure 6. Monthly means of (A) chlorophyll *a*, (B) chlorophyll *b*, (C) total chlorophyll and Chl *a*/Chl *b* ratio (D) in *P. racemosa* plants compared by the Tukey test, along with rainfall (Rain), soil moisture (SM) and leaf area index (LAI) at Parque Estadual Mata do Pau-Ferro, Areia, PB.

Medias mensuales de (A) clorofila *a*, (B) clorofila *b* (C) clorofila total en plantas de *P. racemosa* comparadas con la prueba de Tukey, junto con la precipitación (Lluvia), la humedad del suelo (SM) y el índice de área foliar (LAI) en el Parque Estadual Mata do Pau-Ferro, Areia, PB.

CO₂ diffusion into the substomatal chamber, therefore restricting photosynthesis (Dalastra *et al.* 2014). In this sense, factors such as low water availability, high irradiance and reduced C_i can be limiting for the photosynthetic process, mainly by restricting gas conduction in leaves (Lambers and Oliveira 2019).

Water use efficiency (WUE) in *P. racemosa* plants was similar along the season. The only difference was between June, which had the highest WUE, and October, which had the lowest WUE. However, June was neither the wetter nor the drier period, though that month was the beginning of the dry season: at that moment g_s reduced proportionally more than A (Guo *et al.* 2019). Conversely, intrinsic water use efficiency (iWUE) and instantaneous carboxylation efficiency (ICE) did not vary over the months. Although these physiological variables may be enhanced as a response of high A, C_i and g_s (Ruzicka Júnior *et al.* 2017); it was not observed in the present study. It is important to remark that although light availability to *P. racemosa* was high in the dry season, that light could not be used to increase A and, consequently WUE. Thus, the species is not limited by low light availability during the wet season, although it is under a dense shade. Hence, even during the wet season plants couple stomatal opening to CO₂

demands and no unnecessary water is transpired, as was observed in some nutrient-poor environments (Matimati *et al.* 2014).

Changes in chlorophyll content (Chl *a* and Chl *a+b*) over the months may have occurred as a consequence of these pigments being sensitive to excessive irradiance and water deficit in the dry season, or shade acclimation during the wet season. As Chl *a*/Chl *b* ratio remained steady, it is evident that the species is not limited by light during the wet months, when the shade is dense. When incident light increased and SM decreased, chlorophyll concentration reduced because these environmental conditions induce pigment degradation, thus not only reducing the photosynthetic capacity of the plant (Ribeiro *et al.* 2018), but also protecting plants from photoinhibition and photodamage. As Chl *a*/Chl *b* ratio is similar in every month, chlorophyll degradation occurred both in antenna and centers of reaction, consistently with the reduction of A. It is important to highlight that the species has the capacity to increase chlorophyll concentration during the months of higher water availability and lower incident radiation, and to quickly decrease it when stressful environmental conditions start, possibly to avoid stress by the excess of light.

CONCLUSIONS

Palicourea racemosa shows changes in gas exchange in response to dry and rainy periods. The rainfall and soil moisture are the environmental variables that most affect photosynthesis and water exchange of *P. racemosa*. The increase of incident light during the dry season induces reduction in chlorophylls concentration. Individuals from *P. racemosa* reduced carbon and water exchange in the dry season. The main stress apparently is soil water deficit, while plants adjust chlorophyll content to the level of shade of each season. Consequently, the maximum leaf photosynthetic rate is achieved under the shade during the wet season.

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