

Environmental factors variation in physiological aspects of *Erythroxylum pauferrense*

Variación de factores ambientales en los aspectos fisiológicos de *Erythroxylum pauferrense*

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SUMMARY

Ecophysiological studies are highly important to seek understanding of the plant-environment relationship. The objective of this work was to evaluate the influence of environmental factors on physiological aspects in young plants of *Erythroxylum pauferrense* throughout the day. A completely randomized design with 10 treatments and 4 replicates was used. Treatments were at different evaluation times throughout the day (8:00 h-17:00 h) with a 60-minute interval between them. The physiological variables evaluated were: photosynthesis rate, internal CO₂ concentration, transpiration, stomatal conductance, vapor pressure deficit, instantaneous water use efficiency, intrinsic water use efficiency, instantaneous carboxylation efficiency and leaf temperature. Internal and external temperature, relative humidity of the internal and external air of the greenhouse and photosynthetically active radiation were measured as climatic variables. The climatic variables presented correlations with the physiological parameters, with a strong association between photosynthetically active radiation and internal and external temperature of the greenhouse with the rate of photosynthesis, vapor pressure deficit, leaf temperature, transpiration, intrinsic efficiency of the use of water, stomatal conductance and instant water use efficiency. The influence of climatic factors on the physiological aspects in plants of *E. pauferrense* can be observed. The most suitable period of the day for conducting the physiological evaluations in species is between 11:00 h and 13:00 h.

Key words: gas exchange, guarda-orvalho, irradiance, photosynthesis.

RESUMEN

Los estudios ecofisiológicos son de gran importancia para buscar la comprensión de la relación planta-ambiente. El objetivo de este trabajo fue evaluar la influencia de los factores ambientales en los aspectos fisiológicos en plantas jóvenes de *Erythroxylum pauferrense* a lo largo del día. Se utilizó un diseño completamente al azar con 10 tratamientos y cuatro repeticiones. Los tratamientos fueron diferentes tiempos de evaluación a lo largo del día (8:00 h-17:00 h) con un intervalo de 60 minutos entre ellos. Las variables fisiológicas evaluadas fueron: tasa de fotosíntesis, concentración interna de CO₂, transpiración, conductancia estomática, déficit de presión de vapor, eficiencia de uso de agua instantánea, eficiencia de uso de agua intrínseca, eficiencia de carboxilación instantánea y temperatura foliar. Para las variables climáticas se midió: temperatura interna y externa, humedad relativa del aire interno y externo del invernadero y la radiación fotosintéticamente activa. Las variables climáticas presentaron correlaciones con los parámetros fisiológicos, con una mayor asociación entre la radiación fotosintéticamente activa y la temperatura interna y externa del invernadero con la tasa de fotosíntesis, déficit de presión de vapor, temperatura de la hoja, transpiración, eficiencia intrínseca del uso del agua, conductancia estomática y eficiencia de uso instantáneo del agua. Se puede observar la influencia de los factores climáticos en los aspectos fisiológicos en plantas de *E. pauferrense*. El período del día más adecuado para realizar las evaluaciones fisiológicas en especies es entre las 11:00 h y las 13:00 h.

Palabras clave: intercambios de gas, protector de rocío, irradiancia, fotosíntesis.

INTRODUCTION

Popularly known as guarda-orvalho, *Erythroxylum pauferrense* Plowman is a species of understory, belonging to the family Erythroxylaceae, presenting a size of 1.5 to 4 m

in height. It is found in the northeastern region of Brazil with a geographic distribution exclusively in the state of Paraíba, from where the specimen-type is derived, in the city of Areia (city), at an altitude varying between 500 and 660 m. Its occurrence is more frequent in forested environments in the

interior of these regions, known as Wetland Altitude (Loiola and Costa-Lima 2015). This species is of fundamental ecological importance for the regions, where the fruits serve to feed the local fauna, acting directly on the dispersion and propagation of seeds, in disturbed and threatened environments such as Wetland Altitude (Ribeiro *et al.* 2019).

Given the importance of the species, studies are needed to evaluate the effect of abiotic factors that influence the behavior and physiology of forest species. Among the main abiotic factors that affect the photosynthetic activity of plants are temperature, relative humidity and solar radiation (Taiz *et al.* 2017). These factors can be altered according to the different conditions of the environment, and for this reason can significantly modify the ecophysiological responses of the plants (Silva *et al.* 2010).

From the physiological point of view, plants respond rapidly to variations in solar radiation throughout the day. The luminous intensity mainly influences the process of opening and closing the stomata, controlling the absorption of CO₂ in the leaves, acting directly on the development and productivity of the plant (Kaiser and Paoletti 2014).

The effects of air temperature on the physiological aspects of plants can be classified as direct and indirect (Way and Oren 2010). The direct effect occurs in the processes of photosynthesis, providing changes in the activity of Rubisco and regeneration of the enzyme 1,5-ribulose-bisphosphate (RuBP) in the Calvin cycle (Kerbaux 2012, Duca 2015). The indirect effect is associated with the functioning of the stomata, which may lead to a reduction of water loss through transpiration.

In this context, gas exchange evaluations are highly important to assess the adaptation and stability of plants under certain environmental conditions, since this information will provide subsidies for other investigations that seek to understand the physiological behavior of *E. pauferrense* regarding climatic variation. The tested hypothesis is that the ecophysiological aspects of *E. pauferrense* change according to climatic variations at different times of the day, with a reduction in photosynthetic efficiency in the period of low temperature and less irradiance (photosynthetically active radiation).

Therefore, the objective of the present study was to evaluate the influence of environmental factors on physiological aspects of *E. pauferrense* plants throughout the day, and to indicate the best time for physiological evaluations.

METHODS

The experiment was conducted in a greenhouse, belonging to the Department of Plant Science and Environmental Sciences, Federal University of Paraíba (Campus II), located in Areia city, in the microregion of wetland and mesoregion of wild regions in Paraíba, state of Paraíba, Brazil (6°57'59" S and 35°42'57" W). The region presents variable altitude, between 400 and 600 m, with average temperature of 22 °C and precipitation around 1,400 mm (Ribeiro *et al.* 2018). The climate is tropical, classified according to Peel, Finlayson and McMahon (2007) as Aw', and it is warm and humid with autumn-winter rains.

The seeds of *E. pauferrense* were collected from mother plants in the Mata do Pau-Ferro State Park, Areia (city), state of Paraíba, Northeast Brazil (6°58'12" S and 35°42'15" W). For the production of the seedlings, the pulp was removed from the fruits and the seeds were exposed to running water for a period of 5 minutes. Subsequently, the seeds were disinfested with 2% sodium hypochlorite solution for five minutes before planting.

Planting was carried out in plastic containers with a capacity of 5 dm³, using a substrate composed of vegetal soil and vermiculite in the proportion of 3:1. Samples of the substrate were collected for the analysis of soil chemical attributes found in table 1.

Three seeds per pot were used and the plants thinned after reaching 10 cm in height, selecting the uniform individuals. During the conduction of the experiment, the plants were irrigated daily and the water regime of the pots was maintained with pot capacity in 80 %, according to Souza *et al.* (2000).

A completely randomized design was used, with 10 treatments and five replicates. Each replicate was composed of three plants, totaling 15 seedlings. The treatments were constituted by different schedules of evaluation throughout the day (between 8:00 h and 17:00 h) with intervals of 60 minutes between them.

The physiological variables evaluated were the rate of photosynthesis (A) (μmol m⁻² s⁻¹), internal CO₂ concentration (Ci) (μmol mol⁻¹), transpiration (E) (mmol of H₂O m⁻² s⁻¹), stomatal conductance (gs) (mol m⁻² s⁻¹), vapor pressure deficit (VPD) (kPa), instantaneous water use efficiency (EUA: A/E) [(μmol m⁻² s⁻¹) / (mmol of H₂O m⁻² s⁻¹)], intrinsic water use efficiency (EiUA: A/g_s) [(μmol m⁻² s⁻¹) /

Table 1. Chemical characteristics of the substrate used in the experiment.

Características químicas del sustrato utilizado en el experimento.

pH in H ₂ O	P	K	Na	H+Al	Al	Ca	Mg	BS	CEC	O.M.
	mg dm ⁻³		cmol _c dm ⁻³							
5.5	4.7	110.4	0.19	4.27	0.65	2.73	0.59	4.47	5.48	29.86

BS: base sum; CEC: cation exchange capacity; O.M: organic matter.

(mol m⁻² s⁻¹), instantaneous carboxylation efficiency (EiC: A/Ci) [(μmol m⁻² s⁻¹) / (μmol mol⁻¹)] and leaf temperature (Tleaf) (°C). The evaluations were done on healthy, undifferentiated and fully expanded leaves located in the middle third of the plants, using a portable infrared gas analyzer (IRGA) (Licor, model Li-6400XT). The protocol for IRGA measurements was: 6 cm² leaf chamber with coupled natural light sensor, air humidity between 50-60 %, air flow of 300 μmol s⁻¹ and 400 μmol mol⁻¹ of atmospheric CO₂.

Regarding climatic variables, internal and external temperature (Tin and Tex) (°C), and the relative humidity of the internal and external air (RHin and RHex) (%) of the greenhouse were evaluated using an integrated thermo-hygrometer digital sensor (Hygrotherm). For the determination of the photosynthetically active radiation (PAR) (μmol m⁻² s⁻¹), a quantum sensor coupled to IRGA (Li-6400XT) was used.

Measurements were performed 255 days after emergence, under full daylight conditions (zero cloudiness), thus allowing the real effect of the climatic parameters of the environment on the physiological aspects of the plants.

Data were submitted to a canonical correlation analysis (CCA) and principal components analysis (PCA), to observe the associations between climatic (PAR, Tin, Tex, RHin and RHex) and physiological (A, gs, E, Ci, VPD, WUE, iWUE, ICE and Tleaf) variables. The significance of the canonical roots together was analyzed from Wilks' Lambda multivariate test of significance (approximation of the F distribution). These statistical analyses were carried out using SAS[®] 9.3.5 software (Cody 2015).

RESULTS

Regarding the Wilks's Lambda significance test, it was found that the physiological variables evaluated showed correlations with the environmental variables through the CCA, in which the first and second canonical pair were highly significant, presenting R² of 0.98 and 0.96, respectively (table 2).

In relation to the first canonical pair (R² = 0.98), it is observed that the most important climatic variables were

photosynthetically active radiation and internal and external temperature of the greenhouse (cc of 0.82, 0.72 and 0.70, respectively), presenting positive correlations with the rate of photosynthesis (cc = 0.89), vapor pressure deficit (cc = 0.85), leaf temperature (cc = 0.78), transpiration (cc = 0.76), intrinsic water use efficiency (cc = 0.71), stomatal conductance (cc = 0.69) and instantaneous water use efficiency (cc = 0.55) (table 3).

According to the analysis of principal components (PCA), it is observed that the dimensions of the two compo-

Table 3. Canonic correlations and canonical pair between climate and physiological variables.

Correlaciones canónicas y pares canónicos entre el clima y las variables fisiológicas.

Variables	Canonical pair
Climate	
Photosynthetically active radiation (PAR)	0.82
Internal temperature (Tin)	0.72
External temperature (Tex)	0.70
Relative humidity - internal (RHin)	- 0.46
Relative humidity - external (RHex)	- 0.48
Physiological	
Rate of photosynthesis (A)	0.89
Stomatal conductance (gs)	0.69
Transpiration (E)	0.76
Internal CO ₂ concentration (Ci)	-0.53
Vapor pressure deficit (VPD)	0.85
Instantaneous water use efficiency (WUE)	0.55
Intrinsic water use efficiency (iWUE)	0.71
Instantaneous carboxylation efficiency (ICE)	0.45
Leaf temperature (Tleaf)	0.78
R ²	0.98

Table 2. Wilks's Lambda multivariate test (F distribution approximation).

Prueba multivariada Lambda de Wilks (aproximación de distribución F).

Canonical function	R ²	Fa	GL1	GL2	P-value
1	0.98	15.602	45	208.8	< 0.0001
2	0.96	7.624	32	174.9	< 0.0001
3	0.55	1.627	21	138.3	0.051
4	0.45	1.175	12	98.0	0.312
5	0.18	0.347	5	50.0	0.882

Fa: approximate F value; GL₁: degrees of freedom regarding treatments; GL₂: degrees of freedom regarding error.

nents (axes), with 60.23 in the first and 23.25 in the second, concentrated 83.48 % of the total variability of data (figure 1). Thus, it was possible to register strong correlations among rate of photosynthesis, stomatal conductance, transpiration, intrinsic water use efficiency, instantaneous water use efficiency and instantaneous carboxylation efficiency with photosynthetically active radiation and between vapor pressure deficit and leaf temperature with the internal and external temperature of the environment (figure 1). Along the first axis (PC1), the values of the eigenvectors of the physiological variables, except for C_i , are distributed in the most extreme portion to the right (with positive values), while RH_{in} and RH_{ex} are arranged in the left portion (with negative values), thus evidencing the separation of these variables and the others evaluated (figure 1).

Regarding the recorded climatic variations, it was observed that the photosynthetically active radiation (PAR) presented an expressive increase throughout the day, reaching values ranging from 32.75 to 1570.72, in the period between 11 h and 17 h. It was verified that the maximum internal and external temperature (T_{in} and T_{ex}) had the highest values between 13 h and 15 h, reaching values of 39.7, 39.9 and 38.7 °C inside the greenhouse and 37.7, 38.9 and 36.7 °C in the external environment (figure 2).

The relative humidity of the air inside and outside the greenhouse showed decrease during the day. The highest values were recorded at 8 h (66 % in both locations) and the lowest values at 13 h (28 and 31 %, respectively) (figure 2).

Rate of photosynthesis (A) showed a rapid increase along with photosynthetically active radiation (PAR) in the

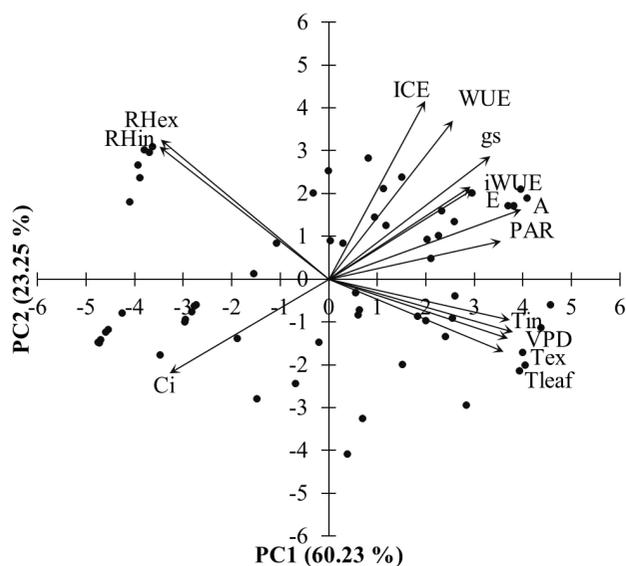


Figure 1. Principal Component Analysis (PC1 and PC2) among the climatic and physiological variables in plants of *E. paufferense*.

Análisis de componentes principales (PC1 y PC2) entre las variables climáticas y fisiológicas en plantas de *E. paufferense*.

first hours of the day, reaching the maximum values at 11 h and 12 h (5.23 and 5.19 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively), and declining at 13 h (4.46 $\mu\text{mol m}^{-2} \text{s}^{-1}$), with the lowest values that were recorded at 17 h (0.73 $\mu\text{mol m}^{-2} \text{s}^{-1}$), when PAR and temperature were also with very low values (figure 3A). The values of stomatal conductance (gs) showed a behavior similar to that of the photosynthesis rate, increasing gradually during the day, with a considerable decline at 13 h, with values varying between 0.0662 and 0.0223 $\text{mol m}^{-2} \text{s}^{-1}$, recorded at 11 h and 17 h, respectively (figure 3B).

The values of transpiration (E) presented the same tendency as rate of photosynthesis and stomatal conductance, with values varying between 3.2854 $\text{mmol m}^{-2} \text{s}^{-1}$ (12 h) and 0.7958 $\text{mmol m}^{-2} \text{s}^{-1}$ (17 h) (figure 3C).

The internal CO_2 concentration (C_i) showed an inverse trend in relation to the other variables, with the highest recorded values of late afternoon at 17 h (figure 3D). C_i values ranged from 221.36 $\mu\text{mol mol}^{-1}$ (12 h) to 320.71 $\mu\text{mol mol}^{-1}$ (17 h) (figure 3D).

The instantaneous efficiency of water use (WUE) showed considerable reduction during the day. The reduction between the highest and lowest value found was of 59%, with higher values between 8 h and 10 h with 2.37 and 2.13 [$(\mu\text{mol m}^{-2} \text{s}^{-1}) (\text{mmol m}^{-2} \text{s}^{-1})^{-1}$], and the lowest values observed at 17 h with 0.97 [$(\mu\text{mol m}^{-2} \text{s}^{-1}) (\text{mmol m}^{-2} \text{s}^{-1})^{-1}$] (figure 4A).

The intrinsic efficiency of water use (iWUE) recorded maximum values at 12 h and 13 h, with 85.39 and 82.82 [$(\mu\text{mol m}^{-2} \text{s}^{-1}) (\text{mol m}^{-2} \text{s}^{-1})^{-1}$]. The lowest values were observed at 17 h, with 34.97 [$(\mu\text{mol m}^{-2} \text{s}^{-1}) (\text{mol m}^{-2} \text{s}^{-1})^{-1}$] (figure 4B).

The instantaneous efficiency of carboxylation (ICE) showed increasing behavior throughout the day, with the highest values recorded at 11h and 12h, with 0.0192 and 0.0238 [$(\mu\text{mol m}^{-2} \text{s}^{-1}) (\mu\text{mol mol}^{-1})^{-1}$]. The lowest values were observed in the period of lowest irradiance at 17 h, with 0.0022 [$(\mu\text{mol m}^{-2} \text{s}^{-1}) (\mu\text{mol mol}^{-1})^{-1}$] (figure 4C).

The vapor pressure deficit (VPD) showed the same trend as T_{leaf} , with maximum values recorded at 12 h and 13 h, reaching 2.00 and 2.19 kPa (figure 4D). Leaf temperature (°C) increased gradually during the day, presenting values that varied from 27.70 to 40.07 °C, registered in the period between 7 h and 13 h (figure 4E). The lowest values of T_{leaf} and VPD were found in periods with low light and temperature availability (7 h and 17 h) (figure 4D and 4E).

DISCUSSION

The results obtained through the canonical correlation analysis (CCA) is indicative of the influence of climatic factors on the physiological characteristics of *E. paufferense* along the day. According to Hair *et al.* (2009), the higher the canonical coefficient (cc), the more important is the variable in the group (climatic and physiological). By means of the positive correlations between the different groups of variables, the influence of PAR and temperature

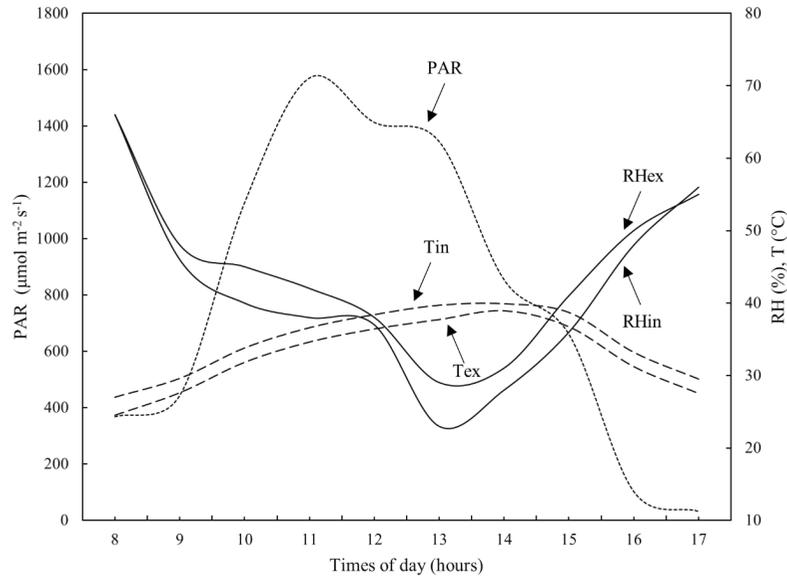


Figure 2. Photosynthetically active radiation (PAR), internal (T_{in}) and external (T_{ex}) temperature, and internal (RHin) and external (RHex) relative humidity in greenhouse during the conduction of the experiment.

Radiación fotosintéticamente activa (PAR), temperatura interna (T_{in}) y externa (T_{ex}), y humedad relativa interna (RHin) y externa (RHex) en invernadero durante la conducción del experimento.

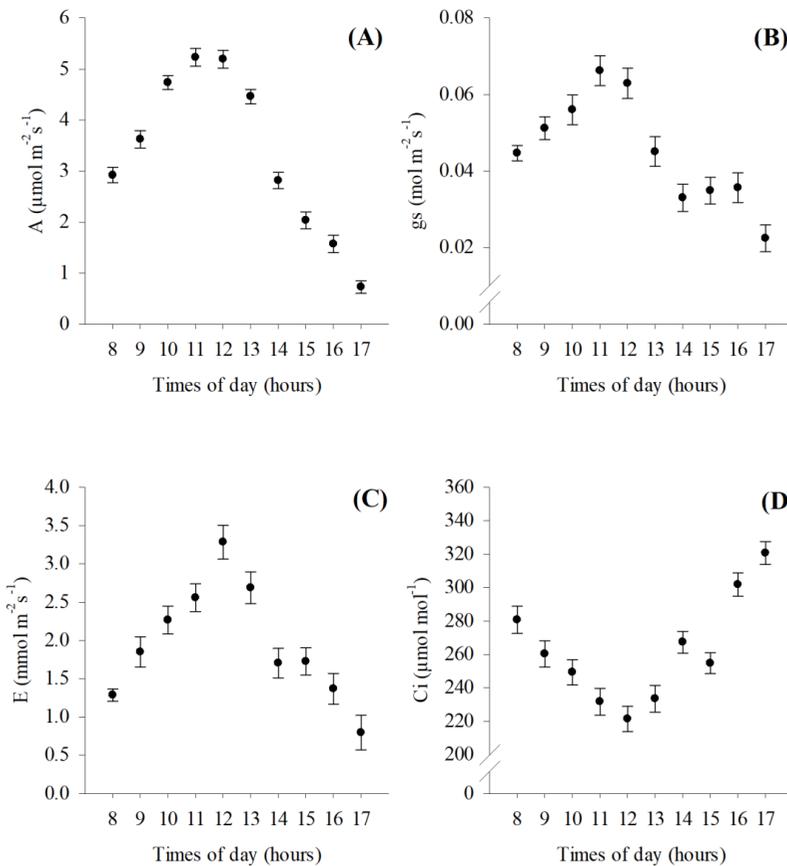


Figure 3. Mean values of rate of photosynthesis (A) (A), stomatal conductance (gs) (B), transpiration (E) (C) and internal CO_2 concentration (D) in plants of *E. paufferense* as a function of time of the day.

Valores medios de la tasa de fotosíntesis (A) (A), conductancia estomática (gs) (B), transpiración (E) (C) y concentración interna de CO_2 (D) en plantas de *E. paufferense* en función de hora del día.

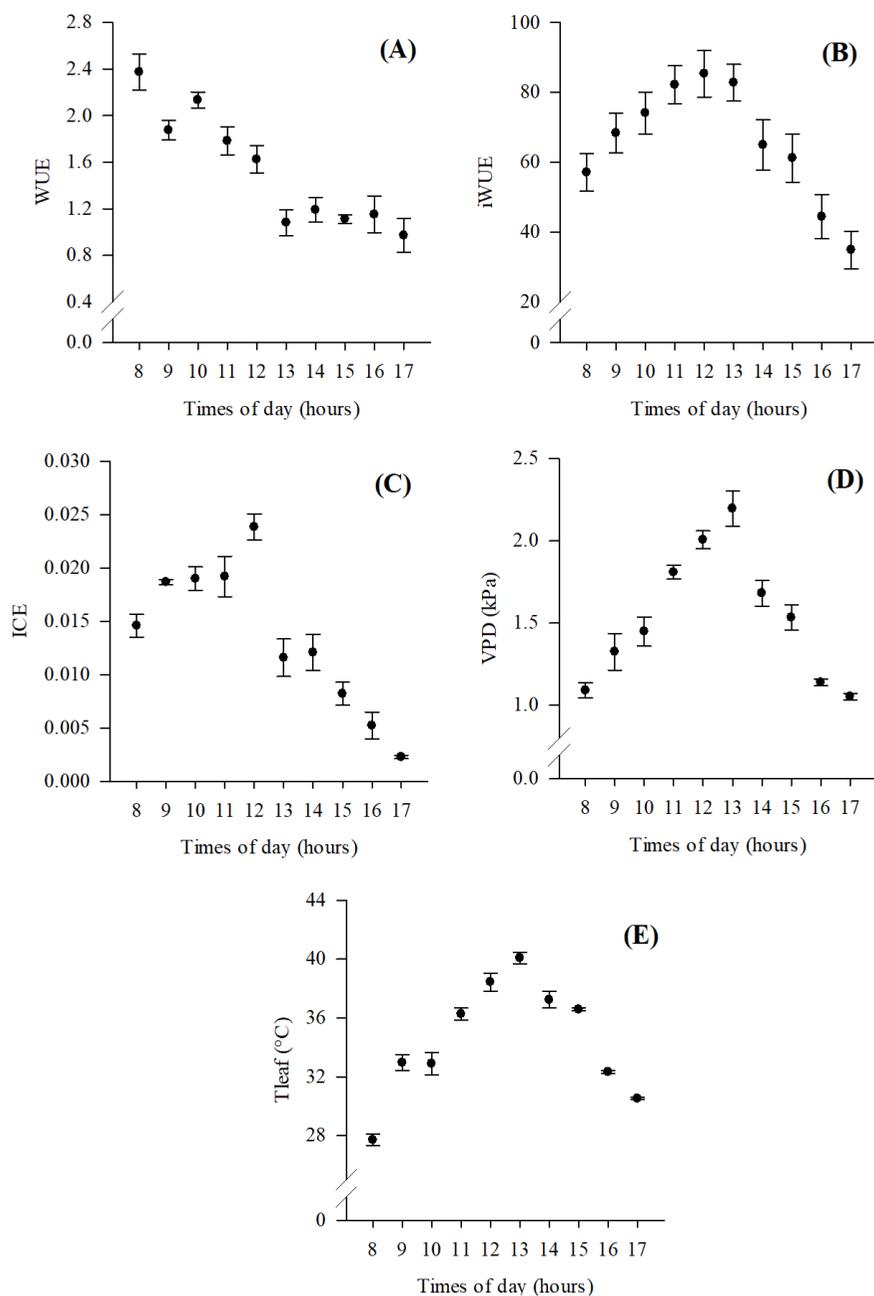


Figure 4. Mean values of instantaneous water use efficiency (WUE) (A), intrinsic water use efficiency (iWUE) (B), instantaneous carboxylation efficiency (ICE) (C), vapor pressure deficit (VDP) (D) and leaf temperature (Tleaf) (E) in plants of *E. paufferense* as a function of time of the day.

Valores medios de eficiencia de uso de agua instantánea (WUE) (A), eficiencia de uso de agua intrínseca (iWUE) (B), eficiencia de carboxilación instantánea (ICE) (C), déficit de presión de vapor (VDP) (d) y temperatura de la hoja (Tleaf) (e) en plantas de *E. paufferense* en función de la hora del día.

(Tin and Tex) on physiological aspects in young plants of *E. paufferense* is evidenced throughout the day (Kerbaui 2012, Taiz *et al.* 2017).

Jadoski *et al.* (2005) in their study found similar values in young *Capsicum annuum* L. plants during the day, with maximum PAR (photosynthetically active radiation) values recorded between 11:30h and 13:30h and maximum

temperatures between 13:30 h and 15:30 h. This decrease observed in the relative humidity of the air is due to the high values recorded in the photosynthetically active radiation and the air temperature, throughout the day (Dalmao *et al.* 2006).

The highest values of A and g were recorded at similar times in the hottest period of the day (> PAR; > Tin

and Tex), confirming the direct relationship between these variables (Dias and Marengo 2007). Such climatic conditions, possibly, provided superior CO₂ entry in the leaves, directly influencing the physiological processes in the photosynthetic apparatus of the plants (Baroli *et al.* 2008). The low values of these variables at 08 h and 17 h are related to the stomatal closure, due to the fact that plants are not under ideal conditions of irradiation and temperature, thus reducing the efficiency in the CO₂ fixation process (Kerbauy 2012).

The closure of stomata at the end of the afternoon may happen due to the strategy of the plants to maintain the turgescence of the leaves during the respiratory period (Marengo and Lopes 2007, Taiz *et al.* 2017). In *Aleurites fordii* plants, Caron *et al.* (2017) observed similar behavior in the transpiration curves, in which the transpiratory rate decreased with the stomatal closure.

Regarding Ci, Dalastra *et al.* (2014) found different results from those of the present study, in which plants submitted to favorable conditions present high concentrations of CO₂ and higher photosynthetic rate, and as concentration decreased, photosynthesis became limited.

WUE is associated with water saving by the plants, that was measured from the relationship between the rate of photosynthesis and transpiration, in which the measured values relate the amount of carbon gained by the plant, per unit of water lost (Jaimez *et al.* 2005). According to Shimazaki *et al.* (2007) the assimilation of CO₂ from the environment causes the loss of water, and the reduction of this loss reduces the entry of CO₂ into the plants. Therefore, the gradual reduction of WUE throughout the day may be associated with observed increases in the rate of photosynthesis and transpiration in young plants of *E. pauferrense*.

The increase in iWUE throughout the day is a reflection of the increases in the rate of photosynthesis and stomatal conductance, indicating that high A values associated with the increase of gs provide an increase in the intrinsic efficiency of water use (Wieser *et al.* 2018).

ICE is a variable that allows analyzing nonstomatic factors that interfere with the photosynthesis rate of plants (Ferraz *et al.* 2012). For Machado, Schmidt, Medina and Ribeiro (2005), ICE has little relation with the internal concentration of CO₂ and with the rate of photosynthesis. Considering the behavior of ICE throughout the day in the present work (figure 4C), it is possible to observe that in addition to stomatal factors, such as WUE and iWUE, nonstomatic factors were affected by the climatic parameters of the environment, due to irradiance and temperature, causing the absence of ATP (anaerobic glycolysis) and NADPH (Nicotinamide adenine dinucleotide) derived from the electron transport chain of photosystem II (PSII) (Silva *et al.* 2015). According to this author, to have the photosynthetic process, ICE depends on the amount of light, temperature, CO₂ availability in the leaf mesophyll and the enzymatic activity.

The increase of Tleaf and VPD in the hottest period of the day (12 h and 13 h) (> PAR; > Tin and Tex) may be associated with a larger stomatal opening, promoting a higher flow of gas exchange in the leaves (Souza *et al.* 2016). The association between these variables can be observed in figures 4D and 4E; a fact that happens because the PVD depends on both the temperature and humidity of the air as well as the leaf temperature (Marengo and Lopes 2005, Taiz *et al.* 2017).

Regarding the influence of climatic factors on physiological parameters of *E. pauferrense* from the CCA and PCA, it was verified that photosynthetically active radiation (PAR) and temperature (Tin and Tex) had stronger influence on the rate of photosynthesis, vapor pressure deficit, transpiration, leaf temperature, intrinsic water use efficiency, stomatal conductance and efficiency instant carboxylation.

Erythroxylum pauferrense presented oscillations in the physiological aspects evaluated as a function of time of day and climatic conditions of the environment.

Low temperatures and less irradiance provided lower physiological development of *E. pauferrense* plants during the day.

The most suitable period of the day to carry out the physiological evaluations in young plants of *E. pauferrense* is between 11 h and 13 h.

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