



## Seasonal variation in gas exchange by plants of *Erythroxylum simonis* Plowman

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### ABSTRACT

*Erythroxylum simonis* is an understory species found in Northeast Brazil. Due to its shaded habitat, *E. simonis* is subjected to seasonal oscillations of the environment, to which it must respond ecophysiologicaly. The objective of this study was to evaluate the effects of seasonality on the ecophysiology of *E. simonis* in a fragment of Seasonal Semideciduous Forest. Leaf area index, visible sky fraction and photosynthetically active radiation were measured for 10 individuals during the dry and rainy seasons. Soil moisture, temperature and monthly precipitation were measured, as well as photosynthetic rate, stomatal conductance, internal CO<sub>2</sub> concentration, transpiration, instantaneous water use efficiency, instantaneous carboxylation efficiency and chlorophyll content. Ecophysiological variables were correlated with environmental variables, with a greater association of rainfall and soil moisture with stomatal conductance, transpiration and photosynthetic rate, indicating that water availability has an effect on the ecophysiology of *E. simonis*. With the exception of instantaneous carboxylation efficiency, gas exchange exhibited significant differences among the months studied, with the highest values being for months with greater water availability, thus showing that the ecophysiology of the species responds to seasonal changes throughout the year.

**Keywords:** ecophysiological responses, photosynthetic rate, seasonal changes, Seasonal Semideciduous Forest, understory

## Introduction

Tropical forests are ecosystems of great importance and are known for their tremendous biodiversity, which is one of the factors that contribute to the great diversity of ecological niches therein (Gardner *et al.* 2010). Tropical forests account for half of the carbon fixed by plants, exerting a significant influence on global carbon balance and reducing the effects of carbon sequestration in the atmosphere (Pan *et al.* 2011). Among the diverse types of tropical forest are seasonal forests, which are characterized by two seasons: a dry season and a rainy season. In this

type of vegetation, leaf abscission is frequently associated with the dry season (Pennington *et al.* 2006), which may be directly related to the low rainfall rates during this period, resulting in greater water stress for the species (Braz *et al.* 2000; Silvério & Lenza 2010; Rebelatto *et al.* 2013). The effect of season on growth and development of forest species mainly impacts vegetation located in the understory, where young individuals of canopy tree species are located, including small trees that will never reach the canopy during their life cycle (Prado Júnior *et al.* 2015), in addition to shrubs, palms, arborescent embryos, seedlings and herbs (Oliveira *et al.* 2001).

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Understory species are influenced by different factors, which can be modified according to the seasonality of the environmental conditions, and consequently alter plant ecophysiology (Davis *et al.* 1999; Silva *et al.* 2010; Lage-Pinto *et al.* 2015). Among the abiotic factors that most influence the ecophysiological responses of understory species are water availability (Palhares *et al.* 2010; Flexas *et al.* 2012; Marengo *et al.* 2014), luminosity (Almeida *et al.* 2004; Vieira 2013; Leal 2016) and temperature (Lemos-Filho 2000; Marengo & Lopes 2009; Taiz & Zeiger 2013).

Water availability is one of the main limiting environmental factors for photosynthesis, because soil water deficiency results in the gradual reduction of photosynthesis by greater resistance to CO<sub>2</sub> fixation due to the closure of the stomata (Nepstad *et al.* 2002; Mendes 2009). In addition to water availability, luminosity may also limit the growth and ecophysiological development of understory plants. In tropical forests, for example, irradiance is quite variable, with less than 10 μmol m<sup>-2</sup> s<sup>-1</sup> in the understory and more than 1000 μmol m<sup>-2</sup> s<sup>-1</sup> in moderate clearings (Mendes 2009).

Floristic structure and composition and canopy openings, as well as small openings caused by canopy leaf fall during the dry season, may influence the ecophysiology of understory species (Frazer *et al.* 1999; Pezzopane *et al.* 2002; 2005; Balch *et al.* 2013; Mendes *et al.* 2013a). In this sense, some ecophysiological variables, such as the leaf area index (LAI), visible sky fraction VSF) and photosynthetically active radiation (PAR), of understory species can be used as indices to infer the degree of light available in the understory (Mendes *et al.* 2013b). A variety of different techniques have been used to analyze the structure of the canopy and the transmission of light, such as the use of hemispheric photographs (Bianchini *et al.* 2001; Guariguata & Kattan 2002; Zhang, *et al.* 2005; Monte *et al.* 2007; Silva *et al.* 2009; Rody *et al.* 2014; Moraes *et al.* 2016), as well as LAI meters for attenuation of solar radiation (Welles & Norman 1991; Kunz *et al.* 2007), among others.

*Erythroxylum simonis* (Erythroxylaceae) is typical of the understory and is endemic to the Northeast Region of Brazil, where it occurs in the states of Paraíba, Pernambuco, Sergipe, Ceará and Rio Grande do Norte. It is found in humid Atlantic Forest and in *brejos de altitude* (Seasonal Semideciduous Forests) (Loiola *et al.* 2007; Loiola & Costa-Lima 2015). This species is of high significance in these regions, mainly with regard to the preservation of endemic genetic resources and as a source of food for fauna (Fabricante 2013). However, there is little information on the ecophysiology of understory species that would be useful in designing models that seek to predict carbon sequestration scenarios, as well as explain the dynamics of the community in the understory of seasonal tropical forests.

The objective of this study was to evaluate the effects of seasonality on the ecophysiology of *Erythroxylum simonis*. The hypothesis is that the species' ecophysiology is seasonally dependent, and exhibits lower values for physiological variables during the dry season as an economic strategy under water stress due low rainfall and higher light and temperature (caused by foliar deciduousness), which consequently decreases soil moisture.

## Materials and methods

### Study area

The study was undertaken in Parque Estadual Mata do Pau-Ferro, in the municipality of Areia located in the micro-region of Brejo and mesoregion of Agreste Paraibano, state of Paraíba (PB), Northeast Region of Brazil (6°58'12"S 35°42'15"W) (Fig. 1). The climate of the region is tropical and classified as Aw according to Peel *et al.* (2007), which is characterized as hot and humid with autumn-winter rains. The elevation of the region varies between 400 and 600



**Figure 1.** Geographic location of Parque Estadual Mata do Pau-Ferro, municipality of Areia, state of Paraíba, northeast Region of Brazil.

meters, with the mean annual temperature being 22°C and the annual rainfall 1.400 mm (Mayo & Fevereiro 1982; Barbosa *et al.* 2004; Oliveira *et al.* 2006; Silva *et al.* 2006).

The study area is a fragment of the extremely endangered Brejo de Altitude, a plant formation of the Atlantic Forest. The fragment in question encompasses approximately 600 hectares situated five kilometers from the seat of the municipality of Areia, PB. The local vegetation is partially degraded, with signs of disturbance mainly near the urban area, and with little of the original vegetation that covered the municipality remaining. The forest fragment is one of the few forest remnants of Brejos de Altitude in the Northeast Region of Brazil, and is one of the most representative.

### Data collection

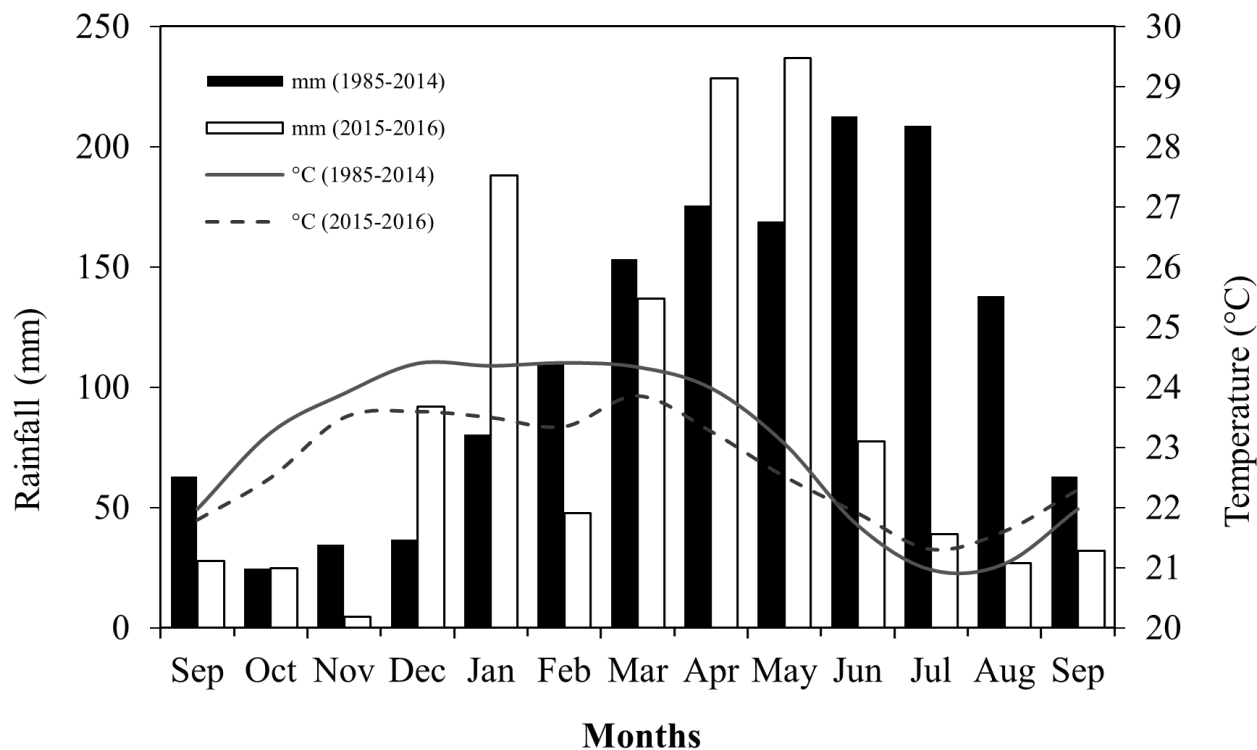
The months for data collection in each season were selected according to data from the ombrothermal diagram of the last 30 years for the city of Areia, PB (Fig. 2). Bimonthly readings were made in March, May and July for the rainy season and in September, November and January for the dry season.

For the collection of ecophysiological data, 10 adult individuals with diameters at chest height and mean heights of 18 cm and 3 m, respectively, were randomly selected. All individuals were tagged and georeferenced. To characterize the soil of the experimental area, a simple surface soil sample

(0-20 cm depth) was collected under the canopy of each individual, which were combined to form a composite sample that was submitted to chemical and physical (granulometric) analyses (Tab. 1).

In order to determine gas exchange, the rate of photosynthesis ( $A$ ) ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), internal  $\text{CO}_2$  concentration ( $C_i$ ) ( $\mu\text{mol mol}^{-1}$ ), transpiration ( $E$ ) ( $\text{mmol m}^{-2} \text{s}^{-1}$ ) and stomatal conductance ( $g_s$ ) ( $\text{mol m}^{-2} \text{s}^{-1}$ ) were measured. From these data the instantaneous water use efficiency (IWUE,  $A/E$ ) and instantaneous carboxylation efficiency (ICE,  $A/C_i$ ) were calculated (Zhang *et al.* 2001; Machado *et al.* 2005; Melo *et al.* 2009; Brito *et al.* 2012). Measurements were performed on the middle third of the plants on healthy, and fully expanded leaves using a portable infrared gas analyzer (IRGA) (ACD, model LCPro SD, Hoddesdon, UK). Readings of gas exchange were made between 10:00 am and 11:00 am. Relative chlorophyll content was measured using a Soil Plant Analysis Development chlorophyll meter (SPAD-502, Minolta, Japan), at four points on the middle third of the plants and averaged.

Leaf area index (LAI), visible sky fraction (VSF) and photosynthetically active radiation (PAR) above individual plants of *E. simonis*, located in the understory were estimated using digital hemispheric images with Digital Plant Canopy Imager - CI-110 (CID). The readings and the recording of images were made in diffuse light conditions (in the early morning or late afternoon or on days with uniformly cloudy



**Figure 2.** Rainfall and temperature at the Estação Meteorológica do Centro de Ciências Agrárias, Universidade Federal da Paraíba, municipality of Areia, state of Paraíba, Brazil, for the period from September 2015 to September 2016 and the normal average of the last 30 years (1985-2014).

**Table 1.** Chemical and granulometric properties of the soil at depth of 0-20 cm collected in Parque Estadual Mata do Pau-Ferro. Areia. PB.

pH in H <sub>2</sub> O	P	K	Na	H+Al	Al	Ca	Mg	BS	CEC	O.M.	Sand	Silt	Clay
	mg dm <sup>3</sup>		cmol dm <sup>3</sup>						g kg <sup>-1</sup>		g kg <sup>-1</sup>		
5	4.3	111.2	0.07	4.21	0.75	0.53	0.49	1.37	5.58	19.86	653	160	187

sky) in order to achieve the maximum possible contrast between leaves and sky (Whitford *et al.* 1995; Galvani & Lima 2014).

Soil samples were collected to determine moisture content at the time the ecophysiological variables were measured. Soil moisture (SM) was determined according to the gravimetric moisture equation recommended by Klein (2008): SM (%) = WM-DM. 100/DS, where, SM = soil moisture in %; WM = wet mass of sample (g); DM = dry mass of sample (g).

### Data analysis

To evaluate associations between environmental variables – Group I (LAI, VSF, PAR, SM, PREC and T) and ecophysiological variables – Group II (A, Ci, E, gs, A/E, A/Ci and SPAD) a multivariate analysis was performed employing canonical correlation analysis (CCA) and principle component analysis (PCA). For the analysis of the significance of canonical roots together, Wilks's Lambda multivariate test of significance was used (approximation of the F distribution). The differences between ecophysiological variables at different times of the year were tested by ANOVA with Tukey's test being used to compare means. All of the analyses were performed using SAS<sup>®</sup> 9.3.5 (Cody 2015).

## Results

### Influence of environmental factors on the ecophysiology of *E. simonis*

The analyzed ecophysiological variables correlated with the environmental variables according to the CCA, however, only the first and second canonical pair were significant, with R<sup>2</sup> values of 0.862 and 0.738, respectively (Tab. 2), indicating the effects of seasonality on the ecophysiology of *E. simonis*. In the first canonical pair, the most important environmental variables were rainfall and soil moisture (cc of 0.97 and 0.60, respectively), which were correlated with stomatal conductance, transpiration and photosynthetic rate (cc of 0.85, 0.62 and 0.56, respectively) (Tab. 3).

The principal components analysis (PCA) concentrated 49.1% of the total variability in the first two components (axes), with 28.55% in the first and 20.54% in the second (Fig. 3). Thus, it was possible to observe that stomatal conductance (gs) and transpiration (E) were strongly correlated with precipitation (PREC) and soil moisture content (SM) (Fig. 3). Along the main axis (PC1), the values of the eigenvectors of stomatal conductance and precipitation are positioned to the most extreme right (with

positive values), while LAI and PAR are positioned to the left (with negative values), which shows the separation of these two variables from the others analyzed (Fig. 3). Visible sky fraction, temperature, instantaneous water use efficiency and chlorophyll content contributed little to the total since they were located in the median portion of PC1 (Fig. 3).

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

Canonical function	R <sup>2</sup>	Fa	GL <sub>1</sub>	GL <sub>2</sub>	p-value
1	0.868	3.89	42	223.9	< 0.0001
2	0.738	2.20	30	194.0	0.001
3	0.500	1.01	20	163.4	0.454
4	0.282	0.41	12	132.57	0.954
5	0.119	0.13	6	102.0	0.992

Fa: approximate F value; GL<sub>1</sub>: degrees of freedom regarding treatments; GL<sub>2</sub>: degrees of freedom regarding error.

**Table 3.** Canonic correlations and canonical pair between groups I and II characteristics.

Variables	Canonical Pair
<b>Group I</b>	
Leaf area index (LAI)	-0.34
Visible sky fraction (VSF)	0.29
Photosynthetically active radiation (PAR)	-0.02
Soil moisture (SM)	0.60
Precipitation (PREC)	0.97
Temperature (T)	0.16
<b>Group II</b>	
Rate of photosynthesis (A)	0.56
Internal CO <sub>2</sub> concentration (Ci)	0.40
Transpiration (E)	0.62
Stomatal conductance (gs)	0.85
Instantaneous water use efficiency (IWUE)	-0.14
Instantaneous carboxylation efficiency (ICE)	0.38
Relative chlorophyll content (SPAD)	0.19
R <sup>2</sup>	0.86
Significance	**

\*\*Significant at 1% of probability by chi square test; R = canonic correlation.

### Evaluation of physiological characteristics at different times

Photosynthetic rate (A) varied from 0.625 μmol m<sup>-2</sup> s<sup>-1</sup> (November) to 1.357 μmol m<sup>-2</sup> s<sup>-1</sup> (May) (Fig. 4A). The internal concentration of CO<sub>2</sub> (Ci) decreased in the dry season, mainly in the month of November, ranging from 227.4 μmol m<sup>-2</sup> s<sup>-1</sup> (November) to 368.0 μmol m<sup>-2</sup> s<sup>-1</sup> (May) (Fig. 4B). The results for transpiration (E) followed the same trend as stomatal conductance, with significant differences

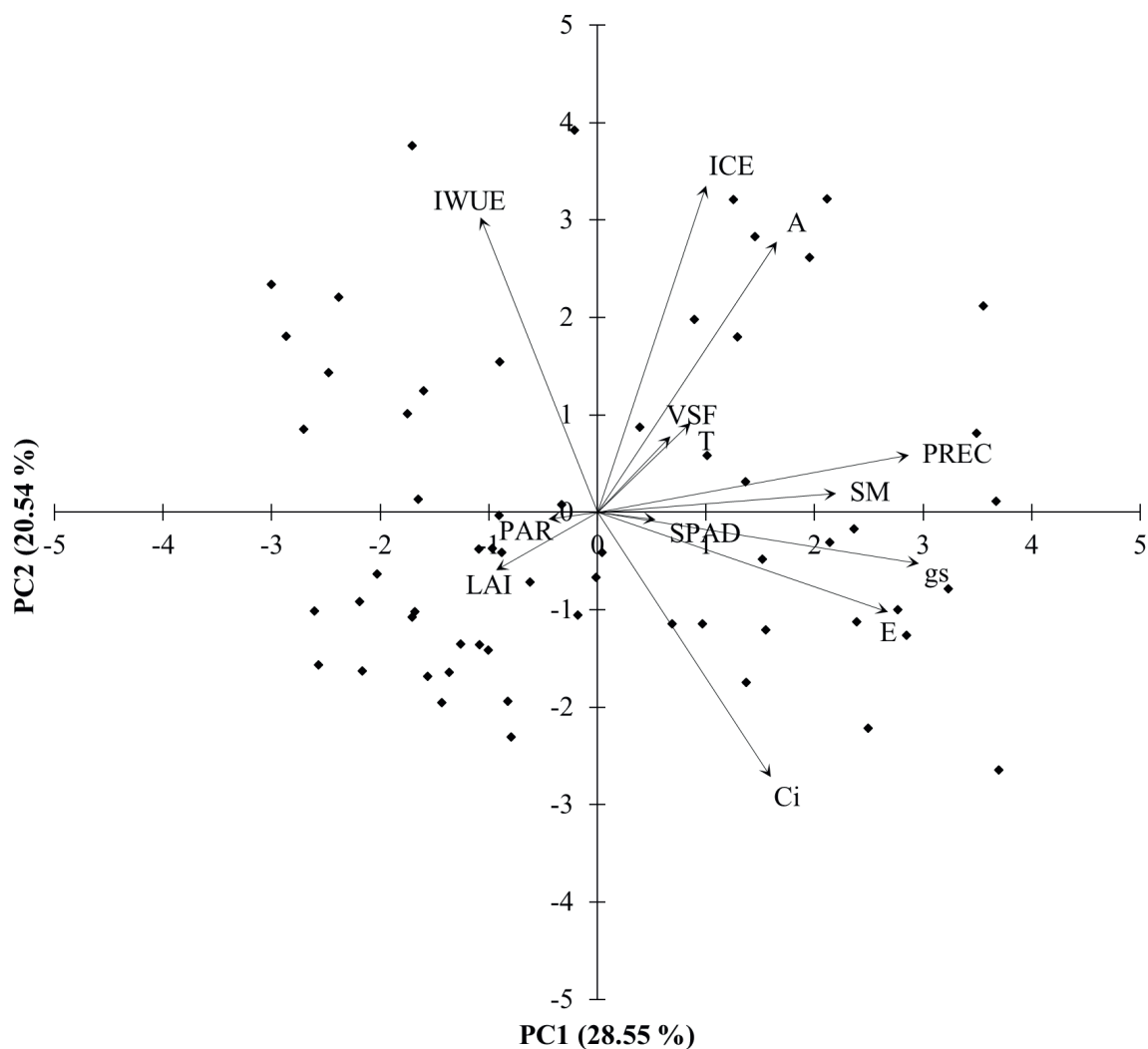


between the seasons ( $p < 0.001$ ), being 73% higher in the rainy season than in the dry season [varying from  $0.221 \text{ mmol m}^{-2} \text{ s}^{-1}$  (November) to  $1.357 \text{ mmol m}^{-2} \text{ s}^{-1}$  (May)] (Fig. 4C). Stomatal conductance ( $g_s$ ) also exhibited significant differences among months ( $p < 0.001$ ), with lowest values in the dry season, varying from  $0.02 \text{ mol m}^{-2} \text{ s}^{-1}$  (September) to  $0.127 \text{ mol m}^{-2} \text{ s}^{-1}$  (May) (Fig. 4D). Instantaneous water use efficiency (IWUE) differed significantly between the different study periods ( $p = 0.007$ ), where a reduction of 27% was observed between the highest value of  $3.830 [(\mu\text{mol m}^{-2} \text{ s}^{-1}) (\text{mmol m}^{-2} \text{ s}^{-1})^{-1}]$ , recorded in the rainy season in May, and the lowest value of  $0.900 [(\mu\text{mol m}^{-2} \text{ s}^{-1}) (\text{mmol m}^{-2} \text{ s}^{-1})^{-1}]$ , recorded in the beginning of the dry season in September (Fig. 4E). Finally, the instantaneous efficiency of carboxylation (ICE), calculated by the ratio  $A/C_i$ , did not show significant differences among the different months of the year ( $p = 0.165$ ). In January the plants had higher instantaneous efficiency of carboxylation;  $0.005 [(\mu\text{mol m}^{-2} \text{ s}^{-1})$

$(\mu\text{mol mol}^{-1})^{-1}]$ , resembling the values in May of  $0.0049 [(\mu\text{mol m}^{-2} \text{ s}^{-1}) (\mu\text{mol mol}^{-1})^{-1}]$  (Fig. 4F). Relative chlorophyll content (SPAD) was higher in the rainy season, with values 53% higher than in the dry season (Fig. 4G), with significant differences among seasons of the year ( $p < 0.001$ ).

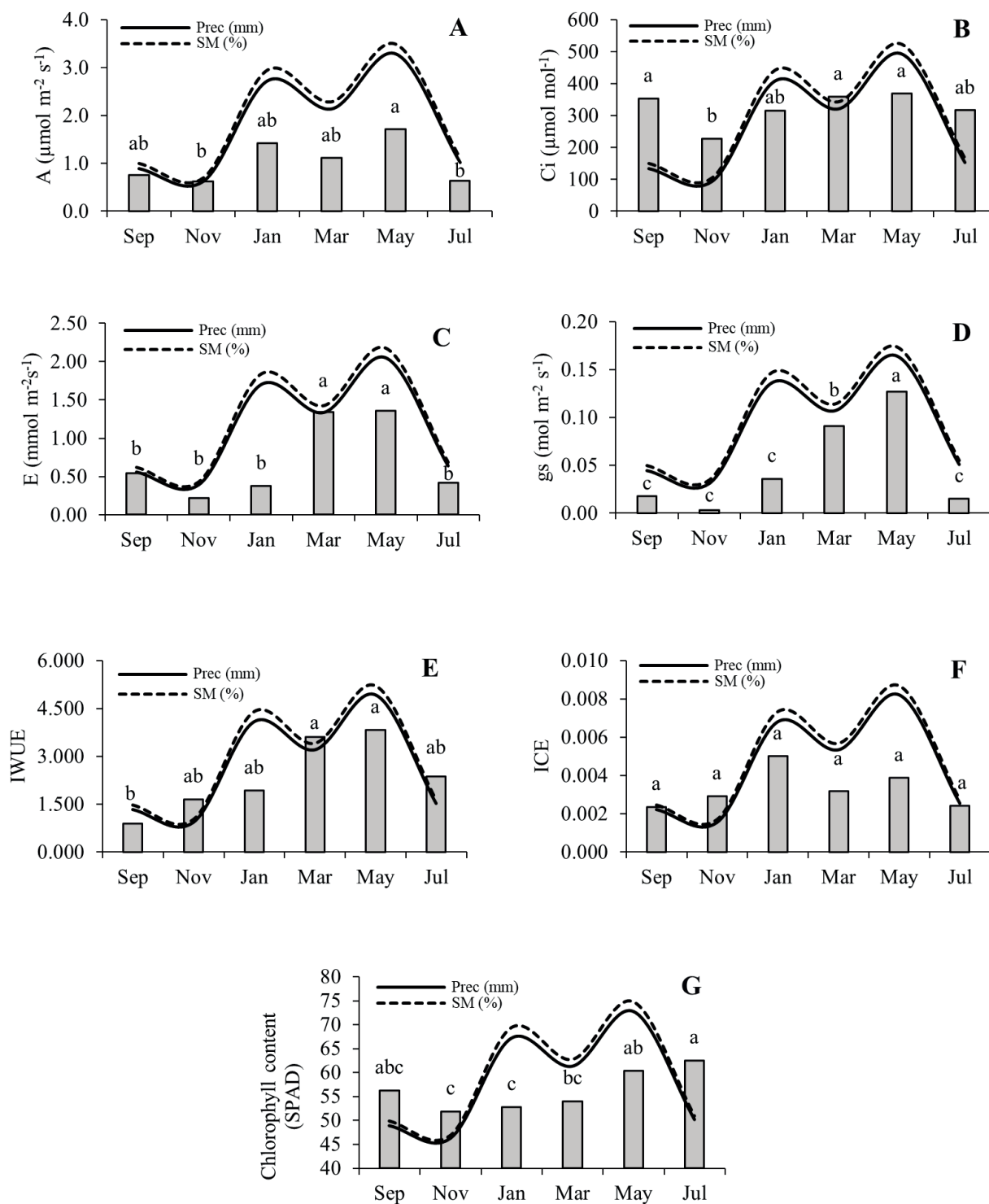
## Discussion

Precipitation and soil moisture can be considered the most important variables in relation to stomatal conductance, transpiration and photosynthetic rate of *E. simonis*, according to the results of the CCA (Vessoni 1998; Hair *et al.* 2005; 2009). There was a positive correlation of stomatal conductance and transpiration with rainfall and soil moisture, demonstrating the influence of water availability on the ecophysiological development of *E. simonis* (Larcher 2006; Marenco & Lopes 2009). However, it was not possible to explain the lack of response of gaseous



**Figure 3.** Principal Component Analysis (PCA; PCA1 and PCA2) among the variables of Group I and Group II. The abbreviations are provided in Table 3.





**Figure 4.** Means of physiological variables, together with rainfall (mm) and soil moisture (%) for *E. simonis*, measured at different times of the year (months), in Parque Estadual Mata do Pau-Ferro, municipality of Areia, state of Paraíba, Brazil: **A.** photosynthetic rate; **B.** internal  $\text{CO}_2$  concentration; **C.** transpiration; **D.** stomatal conductance; **E.** instantaneous water use efficiency; **F.** instantaneous carboxylation efficiency; and **G.** chlorophyll content (SPAD). \* Averages followed by the same letter do not differ among themselves by the Tukey test at 5% of probability.

changes to luminosity by the canopy structure indices (LAI and PAR) in the understory because LAI and PAR were constant throughout the study. On the other hand, seasonal variation in gas exchange may be modulated more by edaphic factors, mainly the availability of water in the soil, as observed in other forest species (Campelo *et al.* 2015), as well as herbaceous species (Holmes & Klein 1986).

The high water deficit found for the soil during the dry season (Allen & Pearcy 2000; Sendall *et al.* 2009; Tonello & Teixeira Filho 2012; Cunha *et al.* 2013) may have been responsible for the low photosynthetic rate observed during that period. A reduction in photosynthetic rate is related to a lower internal concentration of CO<sub>2</sub> (C<sub>i</sub>) and lower stomatal conductance (g<sub>s</sub>) resulting from the closure of stomata in response to abiotic stresses during the dry season (Sharkey 1990; Pallardy 2008; Dalmagro *et al.* 2011; Taiz & Zeiger 2013; Dalastra *et al.* 2014; Taiz *et al.* 2017). The lower the water availability the less ATP and NADPH generated and, as a result, less CO<sub>2</sub> is fixed. Consequently, photosystem II depends on water to generate chemical energy, which is used to fixate CO<sub>2</sub>. Therefore, seasonal variation results in lower efficiency of photosystem II, which is why seasonality effects on photosynthetic rate (A) during the dry season are caused by a non-stomatal factor.

The internal CO<sub>2</sub> concentration of plants is directly influenced by photosynthesis and is extremely important for the productivity of terrestrial ecosystems (Mello *et al.* 2015). During the process of CO<sub>2</sub> assimilation plants absorb carbon dioxide and transform it into biomass, using water and sunlight, and release O<sub>2</sub> into the atmosphere (Taiz *et al.* 2017). Consequently, photosynthesis has a direct influence on the amount of carbon stocked in vegetal biomass (Ribeiro *et al.* 2010; Simkin *et al.* 2015; Lawson *et al.* 2016).

Stomatal closure reduces the internal concentration of CO<sub>2</sub> (C<sub>i</sub>) in the leaf mesophyll due to diffusive CO<sub>2</sub> resistance in the leaves, with a consequent reduction in the photosynthesis rate (A) (Lawlor 2002; Loreto *et al.* 2003; Dias & Marengo 2007; Dalastra *et al.* 2014). In this sense, water availability and C<sub>i</sub> may represent limiting factors for photosynthesis, especially due to the restriction to gas conduction in the leaf (Kerbaudy 2008; Wehr *et al.* 2016; Aguiar-González *et al.* 2016).

Variation in chlorophyll level among different seasons may be attributed to the sensibility of this pigment to increased water stress, which may result in the reduction of plant defenses, especially during the dry season, which is in agreement with the results found by other researchers (Smirnoff 1995; Larcher 2006; Kiani *et al.* 2008; Hayatu & Mukhtar 2010; Moura *et al.* 2016; Kargar *et al.* 2017).

In this sense, water deficit reduces the photosynthetic rate by closing stomata, which decreases the efficiency of the carbon fixation process, thereby decreasing the formation and expansion of leaf area and accelerating senescence and leaf abscission (Kozłowski & Pallardy 1996; Larcher 2006; Dutra *et al.* 2012; Taiz & Zeiger 2013; Taiz *et al.* 2017). In

addition, the reduction of transpiration during the dry season represents a mechanism that helps reduce the rapid exhaustion of soil water by plants (Larcher 2006). This physiological strategy to avoid excessive loss of water by transpiration can be considered a mechanism that favors the growth of leaves in drier seasons (Kozłowski & Pallardy 1996; Silva *et al.* 2008; Scalon *et al.* 2011; Campelo *et al.* 2015).

Inversely, water surplus during the rainy season contributed to higher photosynthetic rates (Larcher 2006; Tatagiba *et al.* 2008; 2015; Llusia *et al.* 2016; Zhang *et al.* 2017), due to greater stomatal opening resulting from the water surplus in the soil, which may have also influenced the higher relative chlorophyll content and higher transpiration values in this season. The high values for photosynthetic rate can be explained by less strict and necessary stomatal control, since the atmosphere and the soil remain with good water availability; that is, the presence of a water surplus (Taiz *et al.* 2017). Consequently, the availability of an adequate amount of water in the soil during the rainy season (while in the dry season there was not enough water in the soil) allowed individuals of *E. simonis* to exhibit high rates of transpiration.

Instantaneous water use efficiency is determined by the relationship between the rate of photosynthesis and transpiration (A/E), where the values measured relate the amount of carbon the plant receives per unit of water lost (Jaimez *et al.* 2005). Based on this principle, the increases observed in IWUE, notably from September to July, are a reflection of increases in photosynthetic rate in individuals of *E. simonis*. Therefore, Larcher (2006), Melo *et al.* (2010), Taiz & Zeiger (2013) and Taiz *et al.* (2017) stated that gas exchange is influenced by environmental conditions. In this sense, the observed decreases in instantaneous water use efficiency in the driest months may be related to lower water availability.

Instantaneous carboxylation efficiency did not show significant differences among the different months of the year. The high values of internal CO<sub>2</sub> concentration associated with increased stomata conductance may indicate an increase in instantaneous carboxylation efficiency (Silva 2012; Silva *et al.* 2015), however, this was not the case in the present study where ICE values remained constant throughout the months of evaluation. For Machado *et al.* (2005), ICE bore little resemblance to internal CO<sub>2</sub> concentration and the rate of assimilation of carbon dioxide.

## Conclusions

Seasonality was observed to influence the ecophysiology of *E. simonis*, with a greater influence of rainfall and soil moisture on stomatal conductance, transpiration and photosynthetic rate of *E. simonis*. On the other hand, with water stress during the dry season the species exhibited distinct physiological responses, with lower photosynthetic



rates due to the closure of stomata as a physiological strategy to avoid excessive water loss.

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