

**Trocas gasosas e eficiência fotossintética em espécies de sub-bosque em Mata Atlântica**  
**Gas exchanges and photosynthetic efficiency in sub-forest species from Atlantic Forest**  
**Intercambios de gases y eficiencia fotosintética en especies de sotobosque en el Bosque Atlántico**

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**Resumo**

A disponibilidade de luz é um dos fatores que mais limitam a fotossíntese de árvores juvenis no sub-bosque. O estudo foi realizado no Parque Estadual Mata do Pau-Ferro, localizado na cidade de Areia, PB. O objetivo deste estudo foi avaliar como ocorrem as trocas gasosas em indivíduos de *Psychotria colorata* (Willd. Ex Roem & Schult.), *Senna georgica* Irwin & Barneby, *Himatanthus phagedaenicus* (Mart.) Woodson, *Solanum swartzianum* Roem. & Schult, *Psychotria carthagenensis* Jacq.e *Psychotria hoffmannseggiana* (Willd. Ex Schult.). A taxa de fotossíntese (*A*), transpiração (*E*), condutância estomática (*G<sub>s</sub>*), concentração interna de

CO<sub>2</sub> (*C<sub>i</sub>*) temperatura da folha na temperatura do ar (°C) e carbono interno (*C<sub>i</sub>*), eficiência instantânea do uso da água (*EUA*) (*A/E*), eficiência intrínseca do uso da água (*EiUC*) (*A/Gs*) e eficiência intrínseca da carboxilação (razão *A/C<sub>i</sub>*). As taxas de fotossíntese máxima (*A*), fotossíntese (*E*) e condutância estomática (*Gs*) mostraram-se influenciadas pela hora do dia, pois não houve interferência de fatores externos nos padrões diurnos das trocas gasosas; fatores endógenos, provavelmente devido ao ritmo circadiano. O parâmetro das trocas gasosas das espécies sub-florestais responde diferentemente, nas pequenas variações nos níveis de luminosidade do sub-bosque.

**Palavras-chave:** Características fotossintéticas; Variação diurna; Taxas de carboxilação.

### Abstract

The availability of light is one of the factors that most limits the photosynthesis of juvenile trees in the understory of the forest. The study was carried out in the Mata do Pau-Ferro State Park, located in the city of Areia, PB. The objective of this study was to evaluate how gas exchanges occur in individuals of *Psychotria colorata* (Willd. Ex Roem & Schult.), *Senna georgica* Irwin & Barneby, *Himatanthus phagedaenicus* (Mart.) Woodson, *Solanum swartzianum* Roem. & Schult, *Psychotria carthagenensis* Jacq. e *Psychotria hoffmannseggiana* (Willd. ex Schult.) in the understory of a remnant of Mata Atlântica. The rate of photosynthesis (*A*), transpiration (*E*), stomatal conductance (*Gs*), internal CO<sub>2</sub> concentration (*C<sub>i</sub>*) leaf temperature-air temperature (°C), and internal carbon (*C<sub>i</sub>*), instantaneous efficiency of water use (*EUA*) (*A/E*), Intrinsic efficiency of water use (*EiUC*) (*A/Gs*) and the intrinsic efficiency of carboxylation (ratio *A/C<sub>i</sub>*). The rates of maximum photosynthesis (*A*), photosynthesis (*E*) and stomatal conductance (*Gs*) were shown to be influenced by the time of day, as there was no interference of external factors in the diurnal patterns of gas exchange, variations are due to endogenous factors, probably due to the circadian rhythm. The parameter of the gas exchange of sub-forest species responds differently, in the small variations in the luminosity levels of the forest understory

**Keywords:** Photosynthetic characteristics; Diurnal variation; Carboxylation rate.

### Resumen

La disponibilidad de luz es uno de los factores que más limitan la fotosíntesis de árboles jóvenes en el sotobosque. El estudio se realizó en el Parque Estatal Mata do Pau-Ferro, ubicado en la ciudad de Areia, PB. El objetivo de este estudio fue evaluar cómo se produce el intercambio de gases en individuos de *Psychotria colorata* (Willd. Ex Roem & Schult.), *Senna georgica* Irwin & Barneby, *Himatanthus phagedaenicus* (Mart.) Woodson, *Solanum swartzianum* Roem. & Schult, *Psychotria carthagenensis* Jacq. e *Psychotria hoffmannseggiana* (Willd. Ex Schult.). La tasa de fotosíntesis (*A*), transpiración (*E*), conductancia estomática (*Gs*), concentración

interna de CO<sub>2</sub> (*C<sub>i</sub>*) temperatura de la hoja a temperatura del aire (°C) y carbono interno (*C<sub>i</sub>*), eficiencia instantánea del uso del agua (*EUA*) (*A/E*), eficiencia de uso intrínseco del agua (*EiUC*) (*A/G<sub>s</sub>*) y eficiencia de carboxilación intrínseca (relación *A / C<sub>i</sub>*). Las tasas de fotosíntesis máxima (*A*), fotosíntesis (*E*) y conductancia estomática (*G<sub>s</sub>*) fueron influenciadas por la hora del día, ya que no hubo interferencia de factores externos en los patrones diurnos de intercambio de gases; factores endógenos, probablemente debido al ritmo circadiano. El parámetro de intercambio de gases de las especies sub-forestales responde de manera diferente, en las pequeñas variaciones en los niveles de luz del sotobosque.

**Palabras clave:** Características fotosintéticas, Variación diurna, Tasas de carboxilación.

## 1. Introduction

The Atlantic forest is recognized worldwide as the second largest tropical forest in the Americas (Myers et al., 2000). Initially, its geographical extension stretched along the Brazilian coast, passing through eastern Paraguay and northeast Argentina in its southern portion (Tonello & Filho, 2012).

The forest has currently 8% of its original area with a lower percentage of natural forest remnants and non-anthropized areas. Despite the scenario, which is the Atlantic Forest, it is one of the biomes with the greatest biodiversity in fauna and flora (Graipel et al., 2016).

The Atlantic Forest of Northeast Brazil hosts several pioneer species, which are divided into the portions of Ombrophylous Forest, Semidecidual and Decidual Seasonal Forest, occupying a currently area of about 2.21% of its original territory. These fragments are present in the states of Alagoas, Bahia, Ceará, Paraíba and Pernambuco (Alves et al., 2015).

The knowledge of plant ecophysiology and species interactions with each other is essential, because through the knowledge of the structure and dynamics of forest formations, their management and regeneration will be effectively carried out (Chaves et al., 2013).

The growth and development of different species in the same area causes dynamic interactions in the plant community, which change with time. In areas where there is the arboreal component, there is a continuous increase in height, canopy projection and leaf area index, which modify the distribution of the existing resources in the system (Muller et al., 2014).

The concept of understory vegetation seems to be broader, including small trees, which during their life cycle do not reach the canopy (Tabarelli et al., 1993), young individuals of canopy tree species, shrubs, seedlings and herbs, being of vital importance for the establishment and development of the species that will constitute the other strata of the forest (Oliveira & Amaral, 2005). Despite the importance of the understory vegetation in the plant community, there is still little consensus regarding the methodology used for its characterization and sampling.

The light intensity is one of the main factors for plant growth and development, responsible for changes in stomatal conductance, remaining high until the leaf water potential is reduced, inducing stomata closure (Sesma et al., 2009). This reduction in the stomatal conductance decreases leaf water loss and restricts CO<sub>2</sub> entry in these organs, which decreases photosynthetic carbon assimilation (Costa & Marengo, 2007).

The objective of this work was to evaluate the occurrence of gas exchange in individuals of *Psychotria colorata* (Willd. Ex Roem & Schult.), *Senna georgica* Irwin & Barneby, *Himatanthus phagedaenicus* (Mart.) Woodson, *Solanum swartzianum* Roem. & Schult, *Psychotria carthagenensis* Jacq. and *Psychotria hoffmannseggiana* (Willd. ex Schult.) in the sub-forest of a remnant of Atlantic Forest.

## 2. Methodology

The study was carried out at Mata do Pau-Ferro State Park, located in Areia, PB. The local altitude is approximately 637 m, standing out as the remnant of “Brejo de Altitude” most representative of the state of Paraíba. It is georeferenced by the coordinates 6° 58' 12" S; 35° 42' 15" W at the municipality of Areia, PB. According to the Brazilian phytogeographic classification, it is a fragment of Seasonal Semi deciduous Forest (Ibge, 2012).

In this present study, six understory species were used: *Psychotria colorata* (Willd. Ex Roem & Schult.), *Senna georgica* Irwin & Barneby, *Himatanthus phagedaenicus* (Mart.) Woodson, *Solanum swartzianum* Roem & Schult, *Psychotria carthagenensis* Jacq and *Psychotria hoffmannseggiana* (Willd. Ex Schult.). The sample composition consisted of 8 plants (repetitions) of each species, totaling 48 individuals. Gas exchange measurements were taken on completely expanded leaves, with adequate phytosanitary appearance, without signs of senescence, in positions of higher incidence of canopy irradiance and in the middle third canopy in the understory. Data were collected in one leaf per individual. The fully expanded leaves inserted in the third node

from the apex of the plants were selected, between 9:00 and 11:00 am, as it is considered the most favorable period for gas exchange (Perez & Moraes, 1991).

Measurements for each gas exchange on each leaf were performed for approximately 3-5 minutes. Species with height ranging from 1 to 3 meters were selected taking into account their relative abundance in the forest understory. These species are used in various ways, as can be seen from Chart 1.

**Chart 1:** Families and importance of the studied species.

Species	Botanic family	Use and importance	Reference
<i>Psychotria colorata</i>	Rubiaceae	It is traditionally used by Amazonian people for the treatment of ear and abdominal pain.	Moura; Maruo, 2014.
<i>Senna georgica</i>	Fabaceae	Native to the northeastern flora, cerrado, and caatinga. It is characterized by shrubs and small tree of 2-5 m. they are geographically distributed throughout most of Latin America.	Flora do Brasil, 2020
<i>Himatanthus phagedaenicus</i>	Apocynaceae	Native, it is not endemic, present in the states of Acre, Amazonas, Pará, Rondônia, Roraima, has domains in Terra Firme Forest, Lowland Forest.	<i>Himatanthus</i> in Flora do Brasil, 2020.
<i>Solanum swartzianum</i>	Solanaceae	Exclusive species from South America, with distribution in Venezuela. In Brazil, registered for the states of Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, Sao Paulo, Roraima Paraná, Santa Catarina and Paraiba.	(Carvalho, 1996).
<i>Psychotria carthagenensis</i>	Rubiaceae	The genus <i>Psychotria</i> is the largest in this family, with approximately 1600 species.	(Almeida; Alves 2000).
<i>Psychotria hoffmannseggiana</i>	Rubiaceae	Distributed in Central America, Colombia, Venezuela, Guyana, Suriname French Guiana, Ecuador, Peru, Bolivia and Brazil. In Brazil, it is present from the Amazon Basin to the Midwest and Center-South of the country.	(Margalho, Rocha Secco, 2009); (Delprete, 2010).

The portable infrared gas analyzer - IRGA (LCi model, ADC BioScientific, England) determined photosynthesis rate ( $A$ ), transpiration ( $E$ ), stomatal conductance ( $G_s$ ), internal  $CO_2$  concentration ( $C_i$ ) leaf temperature and temperature. air ( $^{\circ}C$ ), and internal carbon ( $C_i$ ).

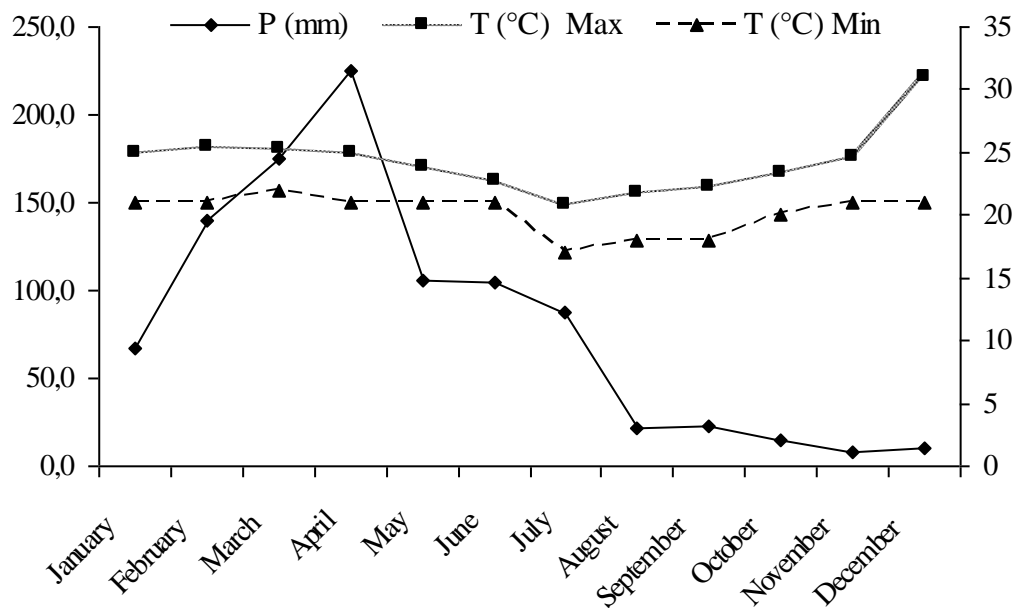
With these values, the instantaneous water use efficiency (US) ( $A/E$ ), intrinsic water use efficiency ( $EiUC$ ) ( $A/g_s$ ) and the intrinsic carboxylation efficiency ( $A/C_i$  ratio) were calculated

according to (Machado et al., 2005, Melo et al., 2009, Brito et al., 2012). The obtained data were submitted to the analysis of variance by the F test, and the averages compared to each other by the Tukey test at 5% probability using the computer program *Sisvar*® (Ferreira, 2000).

### 3. Results and Discussions

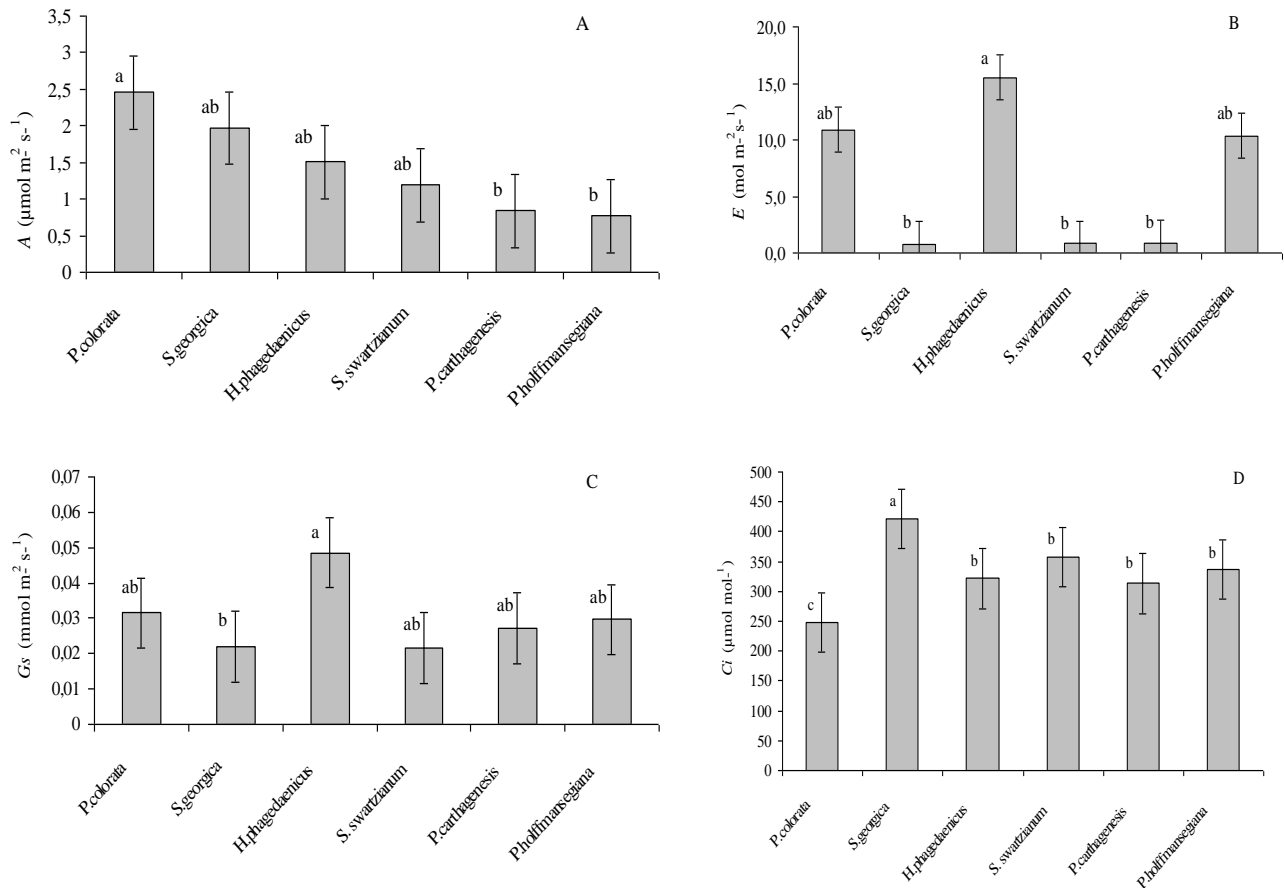
The average precipitation of the study period (November to December 2017) was 23 mm, where the highest precipitation was in April (224 mm) starting to decay from July. In the understory, the relative humidity was always above 68% and the minimum and maximum temperatures were 21°C and 28°C, respectively (Figure 1). However, soil moisture during the study period was 12%.

**Figure 1.** Precipitation and maximum and minimum temperature (Tmax, T min) during the year 2017 in the forest understory measured during data collection



Statistical analysis found that there was a significant difference ( $p < 0.05$ ) between species under study in gas exchange, as they are different species, these results would be expected. Based on the results obtained, the highest photosynthesis rate ( $A_{max}$ ) value was  $2.5 \mu\text{mol m}^{-2} \text{s}^{-1}$  found in *P. colorata*, however the lowest values were recorded in *P. carthagenensis* e *P. hoffmannsegiana* species. differing statically, with values of 0.83 and  $0.77 \mu\text{mol m}^{-2} \text{s}^{-1}$  respectively (Figure 2A).

**Figure 2.** (A) CO<sub>2</sub> assimilation rate (A) ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), (B) transpiration (E) ( $\mu\text{mol de m}^{-2} \text{s}^{-1}$ ) (C) stomatal conductance (Gs) ( $\text{mmol m}^{-2} \text{s}^{-1}$ ) internal concentration of CO<sub>2</sub> (Ci) ( $\mu\text{mol mol}^{-1}$ ) in different understory species.



\*\* Means followed by the same lower case letter do not differ between species (F test at 5%).

The highest values of transpiration rate (E) were observed for *H. phagedaenicus* seedlings  $15.5 \text{ mmol.m}^{-2}.\text{s}^{-1}$ , and with lower transpiration rate were found in *S. georgica*, *S. swartzianum* and *P. carthagenensis* species, probably the species *S.* are sensitive to light. When under stress, plants reduce stomatal conductance and transpiration and increase water use efficiency (Dalastra et al., 2014), probably in *S. georgica*, *S. swartzianum* and *P. carthagenensis* species. Under these conditions, the photosynthesis rate also ends up being reduced (Ferraz et al., 2012).

The stomatal conductance (Gs) the *H. phagedaenicus* resulted in higher Gs values, with approximately  $0.048 \text{ mol. m}^{-2} .\text{s}^{-1}$ . According to Tonello; Teixeira Filho et al. (2012) water deficiency causes loss of guard cell turgidity, resulting in reduced stomatal conductance, which

prevents excessive water loss through perspiration. Thus, it was observed in the species *H. phagedaenicus* that the rate of transpiration is proportional to the stomatal conductance.

Transpiration that is directly related to photosynthesis, through the stomata functioning. This relationship is possible because at the same time that stomata offer resistance to the diffusion of water from the leaf to the atmosphere, stomatal closure constitutes a barrier to the acquisition of CO<sub>2</sub> (Percy & Pftisch, 1991). Thus, the reduction in stomatal conductance aims to decrease water loss, reducing photosynthetic rates.

According to Mendes et al. (2017), research conducted on tree species in response to environmental factors in central Amazonia, found that there was significant difference between species in photosynthesis saturated by CO<sub>2</sub> ( $A_{max}$ ), stomatal conductance ( $G_s$  [2000]) with an average of 8.3  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and 0.12  $\text{mol m}^{-2} \text{s}^{-1}$  respectively.

The internal CO<sub>2</sub> concentration (421.6  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was observed in *S. geórgica*, (Table 1D), while the lowest value occurred in *P. colorata* for the others, (*H. phagedaenicus*, *S. swartzianum*, *P. carthagenesis*, *P. holffmansegiana*) did not differ statistically with average values of 321.6; 357.4; 313.2; 336.3  $\mu\text{mol m}^{-2} \text{s}^{-1}$  respectively.

The photosynthetic response to temperature is an important behavior of the physiological dynamics of trees, at high temperatures increase the transpiration rates, which can cause stomata closure, thus reducing the amount of CO<sub>2</sub> assimilated by plants. Photosynthesis values in the studied species are lower than those found by Mendes & Marengo (2010) who report  $A_{max}$  values between 7 and 9  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for species under natural conditions in the same study area. This indicates that low-irradiance-adapted leaves of understory plants allocate a small amount of assimilates and nitrogen for protein synthesis of the Rubisco enzyme (Mendes et al., 2017).

Figure 3B shows the results of the difference between leaf temperature and air temperature ( $T_{\text{foliar}} - T_{\text{air}} \text{ } ^\circ\text{C}$ ) that showed no statistically significant differences, except for *S. georgica* species that found 27  $^\circ\text{C}$ .

Temperature is a limiting factor for plant growth and development, so plant metabolism is modified when subjected to high temperatures, providing changes in stomatal conductance, inhibiting leaf expansion (Taiz et. al., 2017) because there is no high temperature inside the forest.

The highest values of intrinsic water efficiency ( $A/g_s$ ) were obtained in *P. colorata* and *S. georgica* species with averages of 79.03 and 98.65  $\mu\text{mol mol}^{-1}$  respectively. The species *H.*



*phagedaenicus*, *P. holffmansegiana* and *P. holffmansegiana* resulted in the lowest values with averages 34.03; 39.98 and 25.02 ( $\mu\text{mol mol}^{-1}$ ).

The high photosynthetic rate, associated with lower  $G_s$  and  $E$  values, are characteristic of plants tolerant to lower soil water availability, which is reflected by the higher  $EIUA$  and  $USA$  (Ma et al., 2004) in the present research we can observe the species *S. georgica* (Figure 3B)

Regarding the carboxylation efficiency ( $A/C_i$ ) there was a progressive and marked reduction in the plants *S. georgica*, *H. phagedaenicus*, *S. swartzianum*, *P. carthagenensis* and *P. holffmansegiana* (Figure 3C). For this variable, the highest carboxylation efficiency was found in *P. colorata* species with an average of  $0.010\mu\text{mol m}^{-2} \text{s}^{-1}$ .

In environments with limited availability of resources (water and nutrients), this efficiency parameter becomes essential for the proper functioning of plants and serves as indicators to monitor the full establishment of plants in the field, as well as to demonstrate the physiological plasticity of the plants species in relation to abiotic factors (Santos Júnior et al., 2006, Funk & Vitousek, 2007, Li et al., 2008, Silva et al., 2008).

#### 4. Conclusion

There is gas exchange in individuals of *Psychotria colorata* (Willd. Ex Roem & Schult.), *Senna georgica* Irwin & Barneby, *Himatanthus phagedaenicus* (Mart.) Woodson, *Solanum swartzianum* Roem. & Schult, *Psychotria carthagenensis* Jacq. and *Psychotria hoffmannseggiana* (Willd. ex Schult.) in the sub-forest of a remnant of Atlantic Forest. and the individuals responds differently the slight variations in the understory light levels of the forest.

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