

Carbon uptake in response to climatic seasonality and time of day in Amazonian trees from different forest strata: the effect of shading on morning photosynthesis

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ABSTRACT: This study examined the effect of time of day and climatic seasonality on photosynthetic traits of canopy leaves from Amazonian trees of different forest strata. Photosynthetic traits and the F_v/F_m ratio were measured in the morning, at midday and in the afternoon, both in the dry and rainy seasons. Microclimatic data were obtained and the degree of shading estimated based on sunshine hours a tree received. The evaluated species and height of trees were: *Coussapoa orthoneura* (27.2 m tall), *Mabea angularis* (17.1 m), *Goupia glabra* (12.5 m) and *Inga paraensis* (8.4 m). In the dry season, in three of the four evaluated trees, light-saturated photosynthesis (A_{sat}) was higher in the morning than in the afternoon. Whereas, in the rainy season, A_{sat} was higher at midday or in the afternoon than in the morning in *Mabea* and *Inga*. In most trees, light and CO_2 -saturated photosynthesis (A_{max}) varied between times of day and climatic seasonality. In general, there was only a slight decline in the F_v/F_m ratio during the daylight hours, with the F_v/F_m ratio recovering to early morning values overnight. Morning irradiance was 34% lower in the rainy season than in the dry season, and in both seasons the morning temperature was about 3 °C below the daily mean. Diurnal and seasonal variations of A_{sat} reflect the effect of stomatal conductance, as the F_v/F_m ratio consistently recovers overnight. In shaded trees, the morning photosynthesis is lower than in those that receive more sunlight, particularly in the rainy season when the morning irradiance is the lowest.

Key words: morning temperature, net photosynthesis, stomatal conductance, F_v/F_m ratio.

Ganho de carbono em resposta à sazonalidade climática e horário do dia em árvores amazônicas de diferentes estratos florestais: o efeito do sombreamento na fotossíntese matutina

RESUMO: O estudo examinou o efeito do horário do dia e sazonalidade climática nas características fotossintéticas em folhas da copa de árvores amazônicas de diferentes estratos florestais. Características fotossintéticas e a razão F_v/F_m foram medidas pela manhã, ao meio-dia e à tarde, tanto na estação seca quanto na chuvosa. Os dados microclimáticos foram obtidos e o grau de sombreamento estimado com base nas horas de sol que a árvore recebeu. As espécies e altura das árvores avaliadas foram: *Coussapoa orthoneura* (27,2 m), *Mabea angularis* (17,1 m), *Goupia glabra* (12,5 m) e *Inga paraensis* (8,4 m). Na época seca, em três das quatro árvores avaliadas, a fotossíntese saturada por luz (A_{sat}) foi maior pela manhã que à tarde. Enquanto que na época chuvosa A_{sat} foi maior ao meio dia ou à tarde que pela manhã em *Mabea* e *Inga*. Na maioria das árvores, a fotossíntese saturada por luz e CO_2 (A_{max}) variou entre os horários do dia e com a sazonalidade climática. Em geral, houve apenas um pequeno declínio na razão F_v/F_m durante os horários do dia, com o F_v/F_m recuperando para os valores do início da manhã durante a noite. A irradiância matutina foi 34% menor na época chuvosa que na seca, e em ambas as épocas, a temperatura matutina foi cerca de 3 °C abaixo da média diária. Variações diurnas e sazonais de A_{sat} refletem o efeito da condutância estomática, uma vez que a razão F_v/F_m se recupera consistentemente durante a noite. Em árvores sombreadas, a fotossíntese matutina é menor que naquelas que recebem mais luz solar, principalmente na época chuvosa, quando a irradiância matutina é mais baixa.

Palavras-chave: condutância estomática, fotossíntese líquida, razão F_v/F_m , temperatura matutina.

INTRODUCTION

Light, temperature and availability of water are important factors that affect photosynthesis. During periods of water stress stomatal conductance limits photosynthesis, while excessive light intensity may cause photoinhibition of photosynthesis (OSMOND, 1994; DEMMIG-ADAMS & ADAMS, 2018; FERNANDO & MARENCO, 2023). Leaf temperature greatly affects diurnal variation in carbon assimilation (MIAO et al., 2021; WITTEMANN et

al., 2022). In tropical trees, such as *Calophyllum longifolium* Willd., *Ficus insipida* Willd., *Ochroma pyramidale* (Cav. ex Lam.) Urb., excessive temperature (35-45 °C) leads to a decrease in photosynthetic rates (SLOT & WINTER, 2016), whereas in the Amazonian tree *Guarea carinata* Ducke carbon uptake increases with a rise in temperature from 25 to 31 °C (MENDES & MARENCO, 2017). Besides light and temperature, other factors that affect photosynthetic rates are tree height and leaf age, as higher photosynthetic rates are observed in fully mature expanded leaves than in

young or old leaves (ALBERT et al., 2018). Tree size can affect carbon assimilation in several ways. For instance, largest trees can receive more light, but on the other hand, hydraulic conductance and stomatal conductance of trees can decrease with tree height, which may negatively affect carbon uptake in the upper-crown of sun-exposed leaves (SCHÄFER et al., 2000; FERNÁNDEZ-DE-UÑA et al., 2023).

The measuring of the maximum photochemical efficiency of PSII (the F_v/F_m ratio) is a tool often used to monitor the physiological status of a plant in response to abiotic stresses (KALAJI et al., 2016). Taking the F_v/F_m ratio of an unstressed leaf as the base line (~ 0.83 ; BJÖRKMAN & DEMMIG, 1987), the decrease of F_v/F_m ratio during midday, as often observed under full sunlight, indicates the occurrence of dynamic photoinhibition; while the failure of the F_v/F_m values to recover overnight may indicate the occurrence of chronic photoinhibition (OSMOND, 1994; LONG et al., 1994; DEMMIG-ADAMS & ADAMS, 2018). It was hypothesized that photosynthetic rates from trees of different forest strata vary in a manner that reflects the effect of variations in the physical environment. Thus, this study examined the effect of time of day and climatic seasonality on photosynthetic traits of canopy leaves from Amazonian trees of different forest strata.

MATERIALS AND METHODS

The study was conducted in the Central Amazon at the Tropical Silviculture Experimental Station (ZF2), a research area belonging to the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil. The region is characterized by a dense *terra-firme* forest. Mean temperature is about 26 °C and relative humidity 78%, while annual precipitation often ranges from 2,450 to 2,970 mm (DIAS & MARENCO, 2016; MARENCO et al., 2024). There is a mild dry season (June to October), being the months of July to September the driest period of the year (precipitation < 100 mm per month). The soil is an oxisol with low fertility, clay texture, and acidic pH (3.9–4.0 in water, MAGALHÃES et al., 2014).

Precipitation, air temperature, relative humidity, and photosynthetically active radiation (PAR) were recorded daily in August (2006) and February–March (2007) above the forest canopy, at the top of a 40-m tall observation tower located at same study site (02°35'21"S, 60°06'53"W). A light sensor (LI-190SA, Li-Cor, Lincoln, NE, USA) and relative humidity (RH, %) sensor (Humitter 50y, Vaisala

Ov, Finlandia) were connected to a datalogger (LI-1400, Li-Cor) to record data at 15-minute intervals (DIAS & MARENCO, 2016), while air temperature (T_{air}) was measured (at 10-minute intervals) using a TR52 temperature sensor (Thermo recorded TR-52; T&D Co, Nagano, Japan). Daily PAR ($\text{mol m}^{-2} \text{day}^{-1}$) was obtained by integrating the instantaneous PAR values over the whole daylight period. A standard rain gauge located at the same observation tower was used for collecting rainfall data. In the study, four trees from different forest strata and accessible from the previously mentioned observation tower were used (Table 1), and for the sake of simplicity, we will refer to them by their genus name. The degree of shading the upper canopy of a tree received from other trees (or the observation tower itself) was visually estimated by observing the amount of time it received direct sunlight. It was classified in three levels, depending on the number of hours a tree received direct sunlight. Low: direct sunlight for ≥ 6 h, middle: 4–6 h, and high: ≤ 4 h of direct sunlight.

Photosynthetic traits and chlorophyll fluorescence were measured on the upper leaves of the trees, in August of 2006 (dry season) and in February–March of 2007 (rainy season). Due to the apparent solar movement, radiation that impinged on the leaf surface varied daily, and overall most of the time the trees received more direct sunlight in the morning, while they were shaded in the afternoon.

Diurnal and seasonal changes in photosynthetic traits were measured with a portable infrared gas analyzer photosynthesis system (LI-6400, Li-Cor Inc., NE, USA). We used three mature healthy leaves per tree. Light-saturated photosynthesis (A_{sat}) and light and CO_2 -saturated photosynthesis (A_{max}), stomatal conductance (g_s), and maximum photochemical efficiency of PSII (F_v/F_m ratio) were measured three times a day, in the morning (06:00–09:59 h), midday (10:00–14:00 h) and in the afternoon (14:01–18:00 h). Light-saturated photosynthesis (A_{sat}) was measured at light intensity of $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ and ambient CO_2 concentration ($380 \mu\text{mol mol}^{-1}$). The light and CO_2 -saturated photosynthesis (A_{max}) was measured at light intensity of $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ and CO_2 concentration of $1,000 \mu\text{mol mol}^{-1}$.

The F_v/F_m ratio was determined on five intact leaves per tree using a portable fluorometer (PEA, MK2, 9600, Hansatech, Norfolk, UK). The maximal fluorescence (F_m) was induced by applying a saturation pulse (650 nm) of $3,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ on a 4-mm diameter foliar disc. The variable fluorescence (F_v) was obtained as the maximal (F_m) minus the minimal fluorescence (F_0). The F_v/F_m ratio was measured at

Table 1 - Description, degree of shading, and forest strata of trees used in the study. DBH: diameter at breast height. The degree of shading was classified as: Low, direct sunlight for ≥ 6 h; middle, 4-6 h, and high shading, ≤ 4 h under direct sunlight.

Family	Tree	Height (m)	DBH (cm)	Forest strata	Degree of shading
Urticaceae	<i>Coussapoa orthoneura</i> Standl.	27.2	24.0	Upper	Low
Euphorbiaceae	<i>Mabea angularis</i> Hollander	17.1	27.9	Middle	High
Goupiaceae	<i>Goupia glabra</i> Aubl.	12.5	20.0	Middle	Middle
Fabaceae	<i>Inga paraensis</i> Ducke	8.4	17.5	Lower	High

hourly interval from 6 am to 6 pm on 15-min dark-adapted leaves, both in August and February-March, and it was computed, as described by BJÖRKMAN & DEMMIG (1987), i.e.: $F_v/F_m = (F_m - F_0)/F_m$.

The experiment was conducted using a completely randomized design in a 2×3 factorial arrangement, with three leaves per tree (one tree/species) for gas-exchange parameters, and five leaves per tree, for the F_v/F_m ratio. The factors were the seasons (dry and rainy) and the times of day (morning, midday and afternoon). Prior to statistical analyzes the data were tested for normality (Shapiro-Wilk test), and then submitted to ANOVA. In all analyses, we used a type 1 error (α) = 0.05 to define statistical significance. Statistica 10.0 (StatSoft, Inc. Tulsa OK, USA) was used for data analyzes. Mean values of each variable were expressed with their standard error (SE).

RESULTS AND DISCUSSION

During the days of data collection, the mean temperature was 26.3 °C in August of 2006 (dry season) and 24.4 °C in February-March (rainy

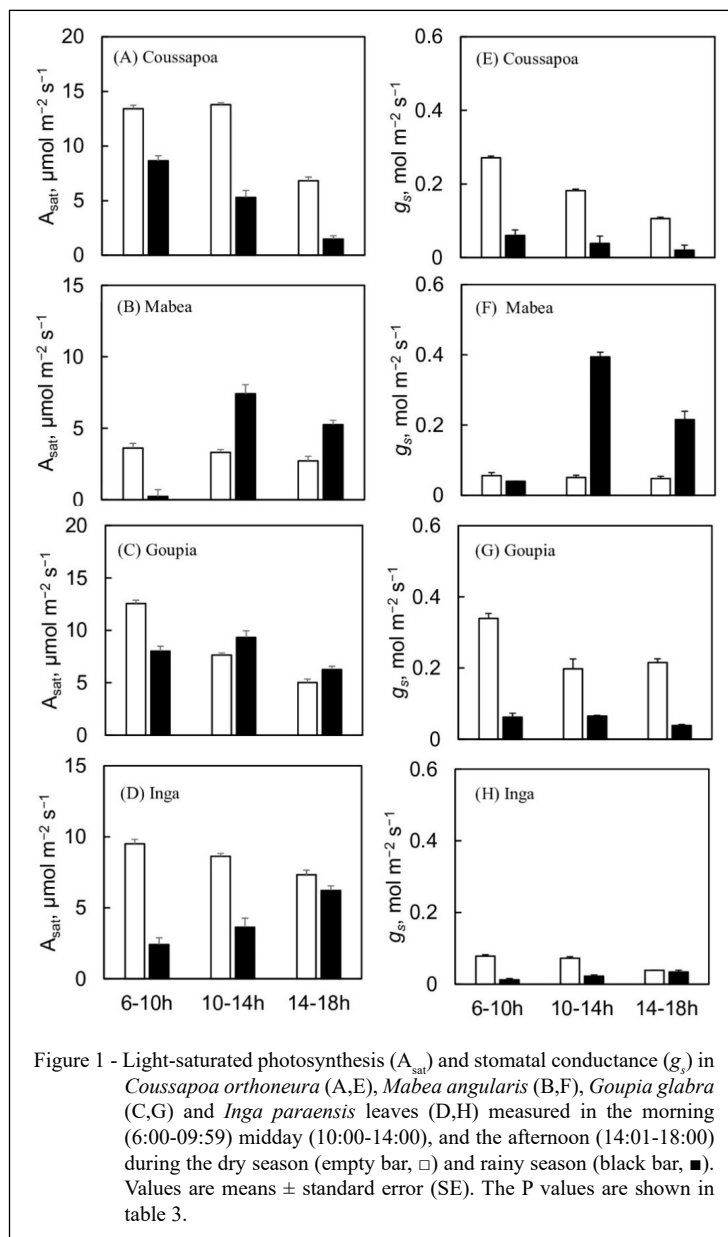
season) (Table 2). While the mean of PAR was 31.9 $\text{mol m}^{-2} \text{day}^{-1}$ in the dry season and 24.4 $\text{mol m}^{-2} \text{day}^{-1}$ in the rainy season. It is important to note that before 10 am, the PAR values were 34% lower in the rainy season than in the dry season, and that over seasons the morning temperatures were about 3 °C below the daily mean (22.4 °C versus the mean value of 25.4 °C, Table 2). Rainfall was very low in August of 2006 (53.6 mm), and also low in February of 2007 with 146.2 mm month^{-1} (Table 2).

Light-saturated photosynthesis (A_{sat}) varied between climatic seasons and time of day in Amazonian trees from different forest strata (Figure 1, Table 3). In general, A_{sat} followed the variation in stomatal conductance measured under ambient CO_2 (Figure 1, Table 3). High morning A_{sat} values (13–15 $\mu\text{mol m}^{-2} \text{s}^{-1}$) were observed during the dry season, in *Coussapoa* and *Goupia* (Figure 1A and 1C, Table 3), and over trees, the lowest A_{sat} mean value was recorded in *Mabea* during the morning hours of the rainy season (0.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Figure 1B). Likewise, low morning A_{sat} values were recorded in *Inga* during the rainy season (Figure 1D). *Coussapoa* and *Inga* had higher A_{sat} values in

Table 2 - Air temperature (T , °C), relative humidity (RH, %) and photosynthetically active radiation (PAR) recorded during the days of data collection, at different periods of time in the month of August of 2006 (dry season) and February-March of 2007 (rainy season).

-----August (dry season)-----				--February - March (rainy season)--		
Time	T_{air} (°C)	RH (%)	PAR (mol m^{-2})	T_{air} (°C)	RH (%)	PAR (mol m^{-2})
6:00-09:59	22.28 $\pm$ 0.04	88.34 $\pm$ 1.23	6.88 $\pm$ 0.13	22.50 $\pm$ 0.03	98.02 $\pm$ 1.10	4.56 $\pm$ 0.06
10:00-14:00	27.68 $\pm$ 0.77	67.40 $\pm$ 1.74	18.45 $\pm$ 0.03	23.87 $\pm$ 0.26	83.11 $\pm$ 3.32	13.87 $\pm$ 0.06
14:01-18:00	31.48 $\pm$ 0.31	67.77 $\pm$ 2.99	6.57 $\pm$ 0.11	26.80 $\pm$ 0.10	86.88 $\pm$ 1.95	5.99 $\pm$ 0.07
Mean (T_{air} , RH) or total PAR ($\text{mol m}^{-2} \text{day}^{-1}$)	26.33 $\pm$ 0.31	81.15 $\pm$ 0.24	31.91 $\pm$ 0.07	24.41 $\pm$ 0.15	93.38 $\pm$ 1.00	24.42 $\pm$ 0.05

During the study period, rainfall was 53.6 mm in August (2006) and 146.2 mm in February (2007), and over the year 2006-2007: Precipitation of the dry season was 101.78 mm month^{-1} (mean of June-October/2006), and the rainy season was 293.74 mm month^{-1} (mean of November/2006-May/2007). Mean of annual rainfall during 2006-2007 was 2,543,0 mm year^{-1} .



the dry season than in the rainy season. *Goupia* also had high morning A_{sat} values during the dry season; however, in the rainy season the higher A_{sat} values of *Goupia* were observed at midday than in the morning or the afternoon (Figure 1C; $P < 0.001$, Table 3).

The trees that received more sunlight (*Coussapoa* and *Goupia*) had the highest morning A_{sat} values. Whereas the *Mabea* tree that received less direct sunlight (i.e. most of the day under shade, Table 1) had the lowest morning A_{sat} .

In *Coussapoa*, A_{sat} was similar in the morning-midday in the dry season, but declined

by 50% in the afternoon (from 14 to about $7 \mu\text{mol m}^{-2} \text{s}^{-1}$, Figure 1A). During the rainy season, A_{sat} of *Coussapoa* gradually declined throughout the day, down to $1.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the afternoon.

In the dry season, A_{sat} decreased by 23% in *Inga*, in the afternoon (Figure 1D). In this same tree, however, A_{sat} gradually increased throughout the day in the rainy season. *Goupia* and *Inga* had the same trend in the dry season, with A_{sat} decreasing over daytime. A_{sat} of *Mabea* did not vary diurnally in the dry season. In the rainy season, however, the A_{sat} of *Mabea* was the lowest in the morning, reached the

Table 3 - Summary of analysis of variance, there are given the F values (with P values in parenthesis) of the effect of climatic seasonality (season) and time of day (time) on evaluated photosynthetic parameters in *Coussapoa orthoneura*, *Mabea angularis*, *Goupia glabra* and *Inga paraensis* leaves. Abbreviations: A_{sat} : Light-saturated photosynthesis, g_s : stomatal conductance, A_{max} : Light and CO_2 -saturated photosynthesis.

Specie	Parameter	Season	Time of day	Season x time
Coussapoa	A_{sat} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	236.9 (<0.001)	101.1 (<0.001)	9.0 (<0.001)
	g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	614.0 (0.001)	90.2 (0.03)	33.9 (0.10)
	A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	48.7 (<0.001)	4.3 (0.015)	22.5 (<0.001)
Mabea	A_{sat} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	0.07 (0.80)	8.22 (0.003)	15.72 (<0.001)
	g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	259.3 (<0.001)	81.7 (<0.001)	84.3 (<0.001)
	A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	22.3 (<0.001)	38.0 (<0.001)	3.64 (0.03)
Goupia	A_{sat} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	1.8 (0.18)	46.4 (<0.001)	27.0 (<0.001)
	g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	196.2 (0.001)	12.7 (<0.001)	10.2 (<0.001)
	A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	48.7 (<0.001)	13.4 (<0.001)	33.0 (<0.001)
Inga	A_{sat} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	67.8 (<0.001)	1.1 (0.33)	14.1 (<0.001)
	g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	86.0 (<0.001)	0.05 (0.95)	6.8 (0.002)
	A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	0.27 (0.60)	4.16 (0.02)	1.77 (0.17)

maximum around midday (i.e., 10-14 h with $6.7 \mu\text{mol m}^{-2} \text{s}^{-1}$), and then decreased toward the afternoon ($5.5 \mu\text{mol m}^{-2} \text{s}^{-1}$, Figure 1B).

In addition to intrinsic genetic factors, the light environment in which a tree grows greatly influences leaf traits and carbon assimilation (MARENCO et al., 2017; VIALET-CHABRAND et al., 2013). *Coussapoa* and *Goupia* had higher g_s values in the dry season than in the rainy season (Figure 1E and G). While in *Mabea* the highest g_s values were recorded in the rainy season at midday, with small variations in g_s values in the dry season over time (Figure 1F). In general, the lowest g_s values were recorded in *Inga* (Figure 1H). Variations in stomatal conductance led to variation in photosynthetic rates, as mentioned above, since stomatal conductance is a key factor for photosynthesis (LLOYD & FARQUHAR, 2008; FERNANDO & MARENCO, 2023).

In periods of high evaporative demand, often associated with a rise in temperature and a decrease in air humidity, trees with different access to soil water can show large differences in stomatal conductance (MEINZER et al., 1993). Stomatal limitation to carbon assimilation occurs because it is through the stomatal pores that CO_2 enters cellular spaces, and they often close under high vapor pressure deficit –VPD (SHIRKE & PATHRE, 2003; LLOYD & FARQUHAR, 2008) to reduce excessive transpiration. In this respect, it has been found that VPD is more important than the isolated effect of temperature or irradiance on midday depression of photosynthesis and stomatal conductance (SHIRKE

& PATHRE, 2003). The high photosynthetic rates recorded in the dry season suggest: first, that in the previous rainy season the soil had stored enough water to meet the evaporative demand of trees. Second, that the stem-stored water was sufficient to meet the early morning transpiration (SCHULZE et al., 1985). While the decline of photosynthesis at midday and in the afternoon can be ascribed to stomata closing to avoid excessive transpiration, as mentioned previously.

The low morning photosynthetic rates observed in *Inga*, but particularly in *Mabea*, during the rainy season deserve an explanation. This finding can be explained by observing, the rather low morning temperatures (22.4°C), degree of shading and PAR values recorded before 10 am in rainy season (Table 1 and Table 2). The combined effect of a high degree of shading (as observed in *Mabea*) and a low morning PAR values—as recorded in the rainy season delays the warming of the canopy, which affects stomatal opening and thereby carbon assimilation. In some trees, such as, *Populus deltoides* W.Bartram ex Marshall; *Platanus occidentalis* L., and *Fraxinus americana* L., stomatal conductance increases when night temperatures increase from 10 to 20°C (DREW & BAZZAZ, 1982). Likewise, in several Amazonian tree species, stomatal conductance and photosynthesis have been observed to increase with a rise in temperature in the range of 22 to 30°C (MARENCO et al., 2014; MENDES & MARENCO, 2017). This is an important finding, as there is little information on the effect of shading on morning photosynthetic rates of rainforest tropical

trees during the rainy season under natural conditions. In addition, low temperature can lead to a decrease in photosynthetic rates because of the effect of low root temperature on water uptake, as both water viscosity and root resistance increase at low root temperature, as suggested by DELUCIA (1986).

Light and CO₂-saturated photosynthesis ($A_{\max}$) varied among climatic seasonality and time of day in Amazonian trees from different forest strata (Figure 2, Table 3), with high values observed in *Coussapoa* (mean of 22 $\mu\text{mol m}^{-2} \text{s}^{-1}$, Figure 2A), followed by *Goupia* and *Inga* (17 $\mu\text{mol m}^{-2} \text{s}^{-1}$, Figure 2C and D). The lowest $A_{\max}$ values were measured in *Mabea* in the morning (Figure 2B, Table 3) can be attributed to the combined effect of low morning temperatures and the effect of shading, which may affect leaf temperature, as mentioned before. In addition to the effect of temperature on stomatal conductance, temperature can affect photosynthesis by modulating the activity of photosynthetic enzymes (e.g. Rubisco and other enzymes of the Calvin cycle) and the electron transport chain (LLOYD & FARQUHAR, 2008).

In both seasons, the F_v/F_m ratio slightly declined over time ($P < 0.05$, Figure 3). The exception was noted in *Coussapoa*, in which the F_v/F_m ratio remained almost constant during the day in dry season ($P = 0.33$, Figure 3A). Overall, the largest effect of daytime was observed in *Mabea* (Figure 3B, $P < 0.001$). Taking the value recorded early in the morning as the base line, a slight decline in the F_v/F_m ratio was also observed in *Coussapoa* early in the afternoon in the rainy season (Figure 3A). In *Mabea*, the F_v/F_m showed a gradual decline since the beginning of the light period, with the lowest F_v/F_m value (~ 0.60) being observed at midday, in the rainy season (Figure 3B). Furthermore, there was difference in the F_v/F_m ratio between climatic seasons in almost all species (Figure 3). The exception was observed in *Goupia*, in which the F_v/F_m ratio followed the same trend in both seasons (Figure 3C).

The diurnal decline in F_v/F_m ratio during daylight hours indicates the occurrence of photoprotection (also termed dynamic photoinhibition), a set of mechanisms, which include the qE quenching (associated with pH changes of the thylakoid lumen and chloroplast stroma) and qZ quenching, related to the xanthophyll cycle. By these mechanisms, among others, the excess of absorbed light is dissipated as heat (DEMMIG-ADAMS & ADAMS, 2006; DEMMIG-ADAMS & ADAMS, 2018). Since in both seasons, the F_v/F_m ratio recovered to pre-morning values overnight, it can be concluded that in both seasons chronic photoinhibition – as defined by OSMOND (1994) did not occur.

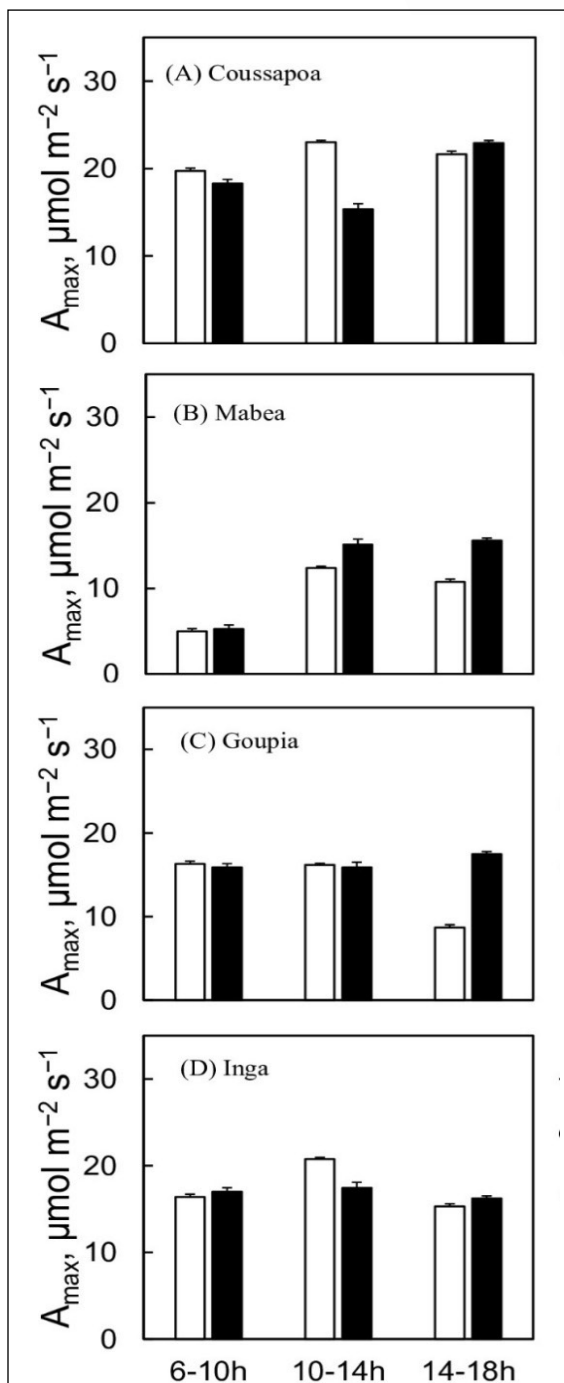
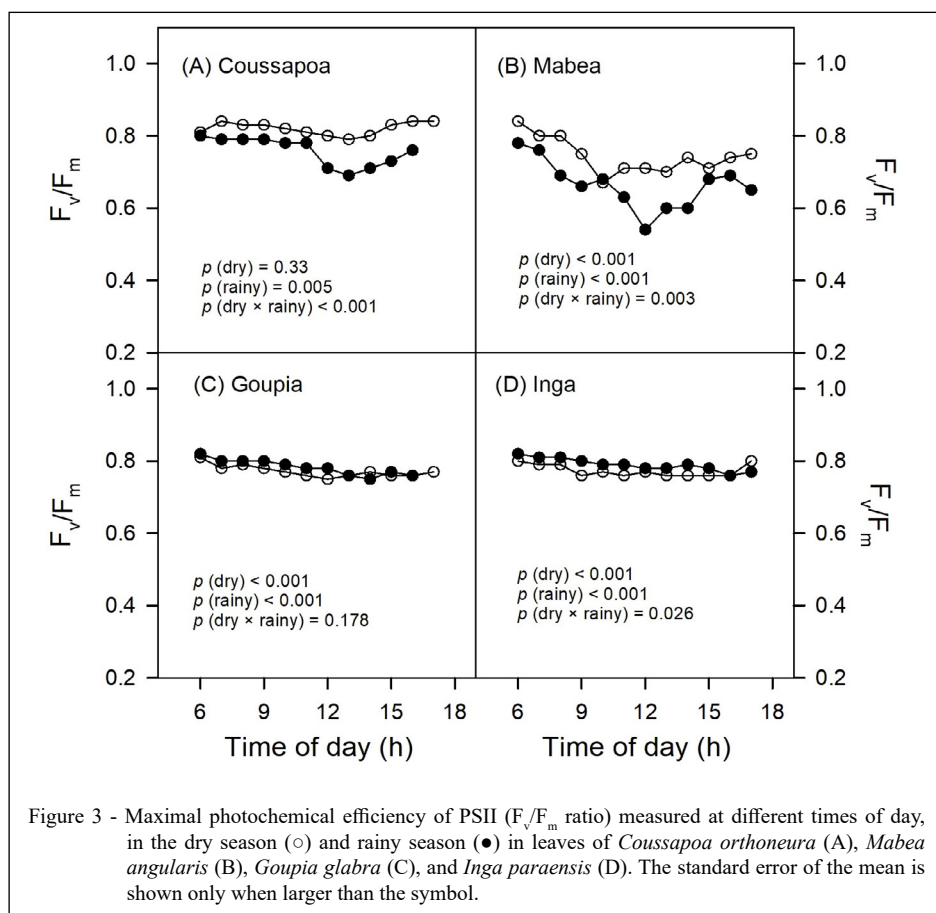


Figure 2 - Light and CO₂-saturated photosynthesis ($A_{\max}$) in *Coussapoa orthoneura* (A), *Mabea angularis* (B), *Goupia glabra* (C) and *Inga paraensis* leaves (D) measured in the morning (6:00-09:59) midday (10:00-14:00), and the afternoon (14:01-18:00) during the dry season (empty bar, □) and rainy season (black bar, ■). Values are means $\pm$ standard error (SE). The P values are shown in table 3.



The F_v/F_m ratio decreased during the rainy season in *Coussapoa* and *Mabea* (Figure 3A and 3B), whereas in *Inga*, the F_v/F_m ratio slightly increased in the rainy season (Figure 3D). In *Goupia*, on the other hand, there was no effect of climatic seasonality on the F_v/F_m ratio ($P = 0.18$, Figure 3C). Variations in the F_v/F_m values between seasons in *Coussapoa* and *Mabea*, and, to a lesser extent, in *Inga* may indicate changes in the concentration of components of the xanthophyll cycle.

A limitation of this study is the absence of true replications, as the data were collected from leaves of the same tree over time, and from one tree/species. On the other hand, the diurnal variation of gas-exchange and chlorophyll fluorescence from the upper canopy of Amazonian trees is only occasionally reported, and as far as we know there is little information on the effect of shading and early morning temperature on the morning upper canopy photosynthesis of Amazonian trees. In this regards, this paper provides information on this important area of tree physiology.

CONCLUSION

The diurnal and seasonal decline in light saturated photosynthesis reflects the effect of stomatal conductance. Irrespective of climatic seasonality, trees show a slight decrease in the F_v/F_m ratio during the day, which consistently recovers overnight. The exception was *Coussapoa* (dry season), in which the F_v/F_m ratio remains constant overtime. Altogether these results clearly show that the evaluated trees did not suffer from chronic photoinhibition. The degree of shading and morning sunlight intensity appear to affect morning photosynthesis, particularly in the rainy season, when irradiance is lower than in the dry season. This is an important finding that deserves further research in the future.

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DECLARATION OF CONFLICT OF INTEREST

We have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

RAM conceived the research. RAM and DPD performed the data analysis. RAM and DPD performed the data and experimental validation. RAM wrote the manuscript with the contribution of DPD.

DECLARATION OF USE OF ARTIFICIAL INTELLIGENCE

The authors did not used artificial intelligence in the preparation of this manuscript.

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