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Scientific Article

Density of photosynthetically active photons and its influence on the physiological aspects of *Alternanthera brasiliana*

Densidade de fótons fotossinteticamente ativos e sua influência nos aspectos fisiológicos de *Alternanthera brasiliana*

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ABSTRACT - The photosynthetically active photon flux density plays a crucial role in regulating the photosynthetic performance and physiological processes of plants. However, its influence on the physiological aspects of *Alternanthera brasiliana* is not yet well understood. In this perspective, this study aimed to investigate the effects of different photon flux densities on gas exchange and chlorophyll *a* fluorescence and to identify the PPFD that promotes greater CO_2 assimilation and increased electron transport rate in *A. brasiliana*. The experimental design was completely randomized, with six replications. The treatments consisted of photosynthetically active photon flux densities (0, 25, 50, 75, 100, 125, 150, 175, 200, 400, 600, 800, 1,000, 1,200, 1,400, 1,600, 1,800, and 2,000 µmol m^{-2} s^{-1}) evaluated at three times of the day (8:00 a.m., 12:00 p.m. and 4:00 p.m.). The physiological processes of *A. brasiliana* exhibited significant variations in response to photon flux density and environmental conditions throughout the day. An increase in PPFD to 2,000 µmol m^{-2} s^{-1}, observed at 8 a.m., resulted in the maximization of gas exchange and chlorophyll *a* fluorescence variables. At 12 p.m., a period characterized by the highest temperature (35.01 °C) and lowest relative humidity (44.95%), a PPFD of 1,800 µmol m^{-2} s^{-1} promoted higher CO_2 assimilation and an increase in the electron transport rate. These findings highlight the crucial role of photon flux density in regulating the physiological processes of the species.

Keywords: Amaranthaceae. Gas exchange. Chlorophyll fluorescence. Light intensity. Photosynthesis.

RESUMO - A densidade de fluxo de fótons fotossinteticamente ativos desempenha um papel crucial na regulação do desempenho fotossintético e dos processos fisiológicos das plantas. No entanto, sua influência sobre os aspectos fisiológicos de *Alternanthera brasiliana* ainda é pouco compreendida. Nessa perspectiva, este estudo buscou investigar os efeitos de diferentes densidades de fluxo de fótons sobre as trocas gasosas e a fluorescência da clorofila *a*, e identificar a PPFD que promove maior assimilação de CO_2 e aumento na taxa de transporte de elétrons em *A. brasiliana.* O delineamento experimental foi inteiramente casualizado, com seis repetições. Os tratamentos foram compostos por densidades de fluxo de fótons fotossinteticamente ativos (PPFD) (0; 25; 50; 75; 100; 125; 150; 175; 200; 400; 600; 800; 1.000; 1.200; 1.400; 1.600; 1.800 e 2.000 µmol m^{-2} s^{-1}) avaliados em três horários do dia (8 a.m., 12 p.m. e 4 p.m.). Os processos fisiológicos de *A. brasiliana* apresentaram variações significativas em resposta à densidade de fluxo de fótons e às condições ambientais ao longo do dia. Um aumento da PPFD para 2.000 µmol m^{-2} s^{-1}, observado às 8h, resultou na maximização das trocas gasosas e das variáveis de fluorescência da clorofila *a*. Já às 12h, período caracterizado pela maior temperatura (35,01ºC) e menor umidade relativa do ar (44,95%), uma PPFD de 1.800 µmol m^{-2} s^{-1} favoreceu uma maior assimilação de CO_2 e um aumento na taxa de transporte de elétrons. Esses resultados ressaltam o papel crucial da densidade de fluxo de fótons na regulação dos processos fisiológicos da espécie.

Palavras-chave: Amaranthaceae. Trocas gasosas. Fluorescência da clorofila. Intensidade luminosa. Fotossíntese.

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INTRODUCTION

Alternanthera brasiliana (L.) Kuntze is a species in the Amaranthaceae family and is popularly known as Brazilian joyweed. Although it is used in traditional medicine to treat infections and aid in wound healing, it also has several other potential therapeutic applications (ALENCAR FILHO et al., 2020). Given its importance, understanding the physiological responses of *A. brasiliana* to environmental variations is crucial to advancing knowledge about this species' adaptive strategies.

Abiotic factors, such as temperature, luminosity, humidity, and nutrient availability, play a central role in regulating physiological processes in plants. Among several abiotic factors affecting plant photosynthesis, light is essential to plant carbon metabolism (SHAFIQ et al., 2021). Light supplies the energy needed for photosynthesis and serves as a crucial signal for regulating plant growth and morphology (AMMAR et al., 2020; YANG et al., 2020; RIBEIRO et al., 2022a).

The photosynthetic photon flux density (PPFD) represents the quantity of light available for photosynthesis. This density varies throughout the day, and this causes foliar and physiological adjustments in plant species. However, both insufficient and excessive light intensity can affect plant growth, development, and productivity. In several plant species, the variation in light distribution is directly influenced (COÊLHO et al., 2023).

Plants can adjust to different conditions, including variations in light availability, due to different physiological mechanisms and leaf characteristics (RIBEIRO et al., 2022b; COÊLHO et al., 2023). This acclimatization to light is essential for understanding the mechanisms involved in plants' adaptability in different environments. Light exhibits varying patterns of activation in different plant species (REIS et al., 2015).

In this context, the amount of light incident on species and environments should be studied to assess the degree of leaf acclimatization in plants. We hypothesize that there is a reduction in CO_2 assimilation at times of lower light and temperature throughout the day. Therefore, the aims of this study were (i) to assess gas exchange and chlorophyll *a* fluorescence over the course of the day, and (ii) to determine the PPFD that enhances CO_2 assimilation and electron transport rate in *A. brasiliana*.

MATERIAL AND METHODS

The study was conducted on adult plants of *A. brasiliana* situated in the educational garden of the Federal Rural University of the Semi-Arid Region, in Mossoró, Northeast Brazil (5°12′26"S, 37°19′02"W, at an altitude of 24 meters). The climate of the area is classified as BSh (ALVARES et al., 2013), with an average annual temperature of 27.8 °C, 555 mm of rainfall, and a relative humidity of 68.9% (CLIMATE-DATA, 2023).

The *A. brasiliana* plants were propagated by cuttings and were approximately 8 years old at the time of analysis period. Planting was carried out in three rows, each 2 meters long, with a spacing of 25 cm between the rows. To ensure adequate plant development, a drip irrigation system was implemented, which provided 10 mm of water per plant daily, distributed in two shifts (early morning and late afternoon).

The experimental design was a completely randomized setup with six replications. A total of 18 different photosynthetically active photon flux densities (PPFDs) (0, 25, 50, 75, 100, 125, 150, 175, 200, 400, 600, 800, 1,000, 1,200, 1,400, 1,600, 1,800, and 2,000 μmol $m^{-2} s^{-1}$) were tested at three different times: 8 a.m., 12 p.m., and 4 p.m.

Gas exchange was assessed with a portable infrared gas analyzer (IRGA) (LI-COR, model LI-6400XT). Internal temperature (InT), external temperature (ExT), internal relative humidity (InRH), and external relative humidity (ExRH) were tracked in the controlled environment during physiological evaluations using a digital thermo-hygrometer (Minipa, model MT-241A). Additionally, photosynthetically active radiation (PAR) was measured with a natural light sensor attached to the IRGA.

The following parameters were measured: net CO_2 assimilation rate (A) (μmol m^{-2} s^{-1}), stomatal conductance (gs) (mol m^{-2} s^{-1}), transpiration (E) (mmol m^{-2} s^{-1}), internal CO_2 concentration (Ci) (μmol mol^{-1}), vapor pressure deficit (VPD) (kPa), and the ratio of internal to external carbon (Ci/Ca). Chlorophyll *a* fluorescence was analyzed using a fluorometer (LI-COR, model LI-6400-40 LCF) attached to the IRGA. The leaves were exposed to a saturating flash of actinic light and a far-red light pulse. From this, we determined initial fluorescence (F_o'), maximum fluorescence (F_m'), variable fluorescence (F_v'), quantum efficiency of the PSII antenna (F_v'/F_m'), ratio of variable to initial fluorescence (F_v'/F_o'), effective quantum efficiency of PSII (ΦPSII), photochemical quenching (qP), non-photochemical quenching (qN), and electron transport rate (ETR).

Gas exchange and chlorophyll *a* fluorescence evaluations in relation to photosynthetic photon flux density were conducted at various times of the day over the course of a week. Measurements were taken from fully expanded, undamaged leaves from the middle third of the plants, with four leaves per plant analyzed. The measurement protocol in the IRGA chamber included: relative humidity between 50-60%, an air flow rate of 300 μmol s^{-1}, CO_2 concentration of 400 μmol mol^{-1}, and an artificial light sensor placed in a 2 cm² leaf chamber.

Response curves for gas exchange and chlorophyll *a* fluorescence in relation to PPFD were generated by decreasing the intensity from 2,000 to 200 μmol m^{-2} s^{-1} in 200 μmol m^{-2} s^{-1} increments. For values below 200 μmol m^{-2} s^{-1} down to 0, measurements were taken in 25 μmol m^{-2} s^{-1} intervals to determine the apparent quantum efficiency (Φ [μmol CO_2/μmol photons]).

The data were analyzed using polynomial regression with the R® v. 4.1.1 software (R CORE TEAM, 2024). Additionally, Pearson's linear correlation analysis was conducted to examine the relationship between environmental and physiological variables, with correlation values categorized according to the degree of dependence as outlined by Steel and Torrie (1980).

RESULTS AND DISCUSSION

For the environmental variables, differences were observed as a function of the evaluation times (Figure 1). The peak photosynthetically active radiation (PAR) was recorded at 12 p.m., with a value of 480.34 μmol m^{-2} s^{-1}, while the minimum was recorded at 4 p.m., 70.10 μmol m^{-2} s^{-1}. The highest internal and external temperatures were also observed at 12 p.m. [35.01 ºC (InT) and 32.96 ºC (ExT)], whereas the lowest temperatures were recorded at 8 a.m. [29.29 ºC (InT) and 26.76 ºC (ExT)]. Regarding internal and external humidity, the minimum data were observed at 12 p.m. [48.90% (InRH) and 44.95% (ExRH)], and the maximum values were observed at 4 p.m. [75.53% (InRH)] and 8 a.m. [69.10% (ExRH)].

In the study region, the highest PAR values observed at 12 p.m. are attributed to the higher transmission of solar radiation that occurs currently. Thus, the 12 p.m. time would allow for a higher PAR while promoting reduced internal and external humidity and increased temperatures. Nevertheless, elevated temperatures coupled with decreased relative humidity may reduce water permeability in the plant due to alterations in cuticle components, such as waxes (COÊLHO et al., 2023). This would directly imply the efficiency of the photosynthetic apparatus; for this reason, studying the photosynthetic photon flux density (PPFD) at various times throughout the day is crucial.

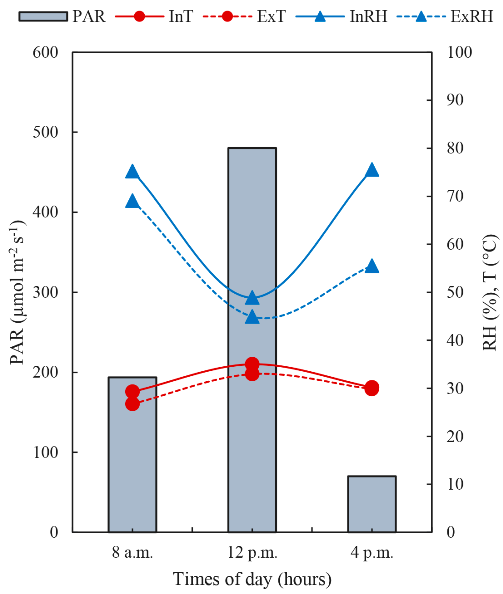

Figure 1. Photosynthetically active radiation (PAR), internal (InT) and external (ExT) air temperatures, and internal (InRH) and external (ExRH) relative humidity, throughout the day.

The net CO_2 assimilation rate (A) increased with PPFD at different times of the day (Figures 2A, 2B, and 2C). The highest A value (14.97 µmol m^{-2} s^{-1}) was recorded at 12 p.m. with a PPFD of 1,800 µmol m^{-2} s^{-1} (Figure 2B). At 8 a.m., the peak A value (8.88 µmol m^{-2} s^{-1}) was observed at a PPFD of 2,000 µmol m^{-2} s^{-1} (Figure 2A). At 4 p.m., the assimilation rate was lower compared to the other times, reaching a maximum of 5.68 µmol m^{-2} s^{-1} at a PPFD of 1,600 µmol m^{-2} s^{-1} (Figure 2C).

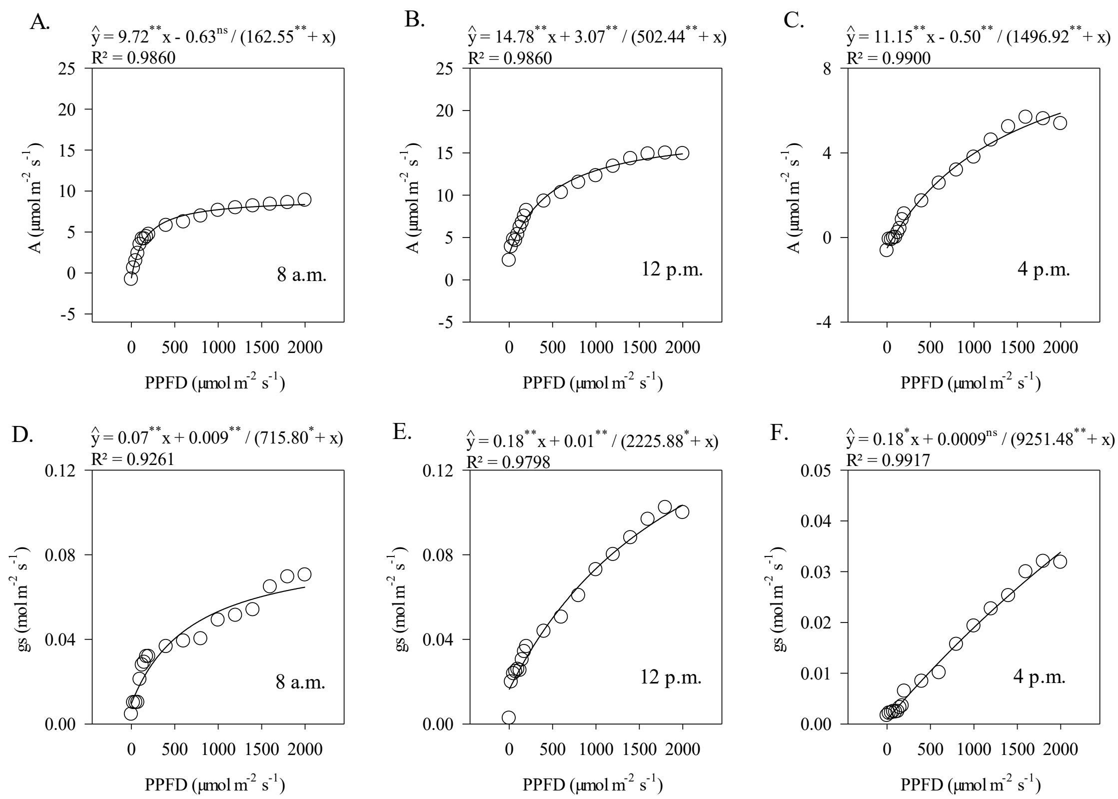

Figure 2. CO_2 assimilation rate (A) and stomatal conductance (gs) in *Alternanthera brasiliana* plants as related to photosynthetic photon flux density (PPFD) at various times of the day [8 a.m. (A, D), 12 p.m. (B, E), and 4 p.m. (C, F)].

Light intensity, under ideal conditions, favors the process of chemical energy conversion during photosynthesis and stimulates the stomatal opening for CO_2 capture. Plants, however, can respond quickly to changes in light intensity, with photosynthesis increasing with the density of the photosynthetic photon flux until the leaves are saturated (LUO; KEENAN, 2020). This could explain the higher net assimilation of CO_2 for a PPFD of 1,800 µmol m^{-2} s^{-1} at 12 p.m., as a higher PPFD suggests evidence of light saturation by plants. In the case of 4 p.m., the time of lower radiation and temperature, the assimilation of CO_2 was lower, which proves our hypothesis that under lower luminosity and temperature, there is a reduction in this physiological variable. However, a higher PPFD can potentially promote greater assimilation than a lower PPFD.

Stomatal conductance (gs) was also observed as a function of the increase in PPFD (Figures 2D, 2E, and 2F). The peak value (0.102 mol m^{-2} s^{-1}) was recorded at 12 p.m., with a PPFD of 1,800 µmol m^{-2} s^{-1} (Figure 2E). At 8 a.m. and 4 p.m., the highest values were 0.071 mol m^{-2} s^{-1} and 0.032 mol m^{-2} s^{-1}, corresponding to PPFDs of 2,000 and 1,800 µmol m^{-2} s^{-1}, respectively (Figures 2D and 2F).

Low stomatal conductance (gs) indicates a major limitation to photosynthetic efficiency, and its variability plays a crucial role in determining plant productivity and adaptability across various environments (WANG et al., 2022). Considering these points, a higher gs observed at 12 p.m. for a PPFD of 1,800 µmol m^{-2} s^{-1} suggests an improvement in the maintenance of photosynthesis for this time. At very high temperatures, gs can increase to prevent overheating of the leaves. Typically, declines in the photochemical activity of the species are associated with reduced stomatal conductance, which limits the influx of CO_2 into the cells (RIBEIRO; COÊLHO, 2021; RIBEIRO et al., 2024).

The transpiration rate (E) was higher at 12 p.m., reaching a maximum value of 3.49 mmol m^{-2} s^{-1} at PPFD of 2,000 µmol m^{-2} s^{-1} (Figure 3B). Similarly, at 8 a.m., a higher value (1.42 mmol m^{-2} s^{-1}) was found at the same PPFD (Figure 3A). At 4 p.m., E was lower than at the other times studied, with a maximum of 0.59 mmol m^{-2} s^{-1} for the PPFD of 1,600 µmol m^{-2} s^{-1} (Figure 3C).

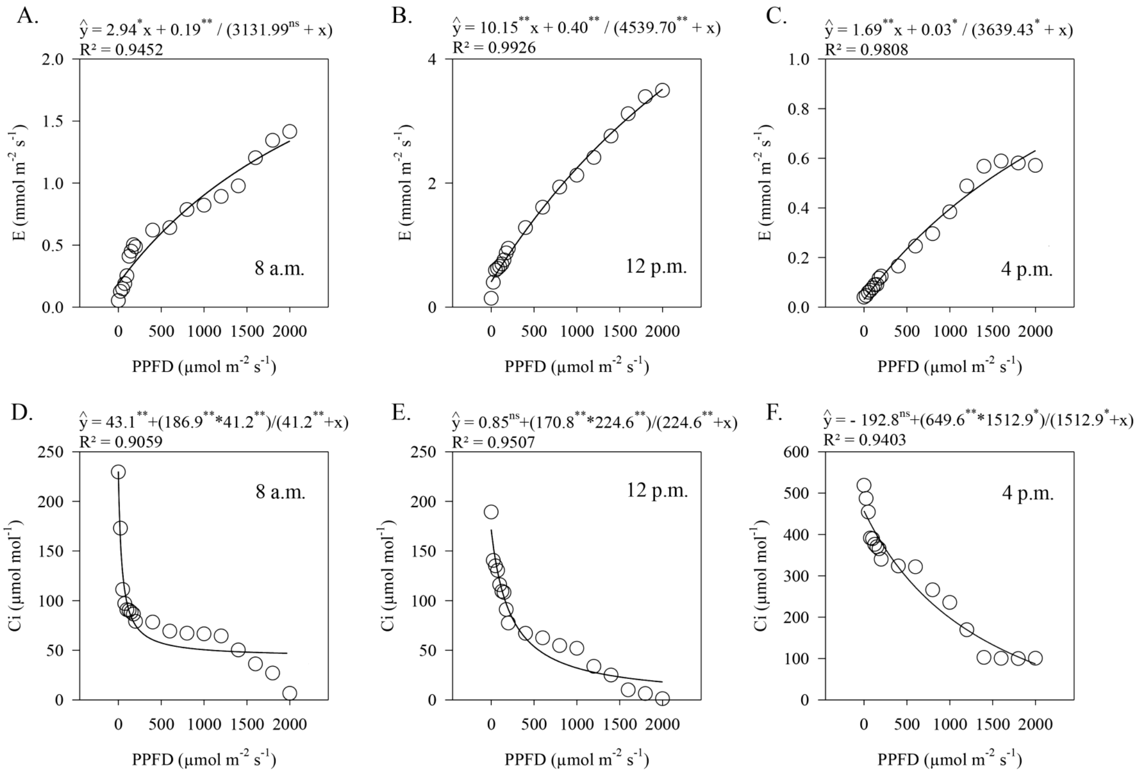

Figure 3. Transpiration (E) and internal CO_2 concentration (Ci) in *Alternanthera brasiliana* plants relative to photosynthetic photon flux density (PPFD) at various times of the day [8 a.m. (A, D), 12 p.m. (B, E), and 4 p.m. (C, F)].

Although the plants with higher PPFD obtained higher transpiration, it can be inferred that this did not lead to stomatal closure because it would lead to a reduction in A and gs, which was not observed in this study. As the temperature tends to reduce the concentration of vapor in the outside air, the transpiration rate may be higher at higher temperatures. Increases in crop transpiration rates driven by higher vapor pressure deficit (VPD) can penalize productivity (KIMM et al., 2020). Plant transpiration is primarily regulated by variations in stomatal opening and the difference in water vapor pressure between the plant and the surrounding atmosphere. When stomata are open, transpiration rates can increase, helping to cool the plant. From this perspective, it is suggested that *A. brasiliana* plants, at a higher PPFD and warmer time of the day, adapted to the imposed conditions, regulating leaf temperature through transpiration.

As for the internal concentration of CO_2 (Ci), this variable was reduced as the PPFD was increased at all times studied (Figures 3D, 3E, and 3F). The maximum Ci (518.62 µmol mol^{-1}) was observed at 4 p.m. at the PPFD of 0.00 µmol m^{-2} s^{-1} (Figure 3F), followed by the values 229.56 and 189.22 µmol mol^{-1} corresponding to the hours of 8 a.m. and 12 p.m., at the same PPFD (Figures 3D and 3E). Thus, the reduction in Ci was 55.74 and 63.52% at 8 a.m. and 12 p.m. when compared to 4 p.m. for the PPFD of 0.00 µmol m^{-2} s^{-1}.

Baligar et al. (2021) state that plants that tolerate reduced PPFD have more significant potential to survive longer. In their results, these authors also found a lower Ci under higher PPFD. Ci refers to the concentration of carbon dioxide within the intercellular spaces in leaves. Therefore, a lower Ci in the plant suggests a lower availability of internal CO_2. This implies that, at a higher PPFD, the rate of CO_2 consumption by photosynthesis was high, surpassing the rate of CO_2 input. Conversely, a lower PPFD (0.00 µmol m^{-2} s^{-1}) and at a time of lower PAR (4 p.m.) higher Ci is obtained; possibly, under these conditions, the photosynthetic activity decreased, and there was lower CO_2 consumption, increasing Ci. Fernandes, Cairo, and Novaes (2015) point out that increases in Ci are related to the CO_2 that reaches the mesophyll cells and is not fixed in the carboxylation phase of RuBisCO.

The maximum values obtained for the variable VPD were observed at the PPFD of 2,000 µmol m^{-2} s^{-1} at different times of the day (Figures 4A, 4B, and 4C). VPD was intensely higher (3.20 kPa) at 12 p.m. (Figure 4B), followed by 4 p.m. (2.68 kPa) (Figure 4C), and to a lesser extent (0.91 kPa) at 8 a.m. (Figure 4A). VPD is a variable that is influenced by relative humidity and temperature. Thus, high temperatures and low relative humidity keep the VPD high, justifying the highest value observed at 12 p.m. However, a PPFD of 2,000 µmol m^{-2} s^{-1} appears to intensify this increase. Up to a specific limit, high VPD directs transpiration, but after exceeding it, plants partially close their stomata. Elevated VPD can decrease the photosynthetic rate by decreasing the stomatal opening and reducing carbon fixation (DING et al., 2022).

For the ratio between internal and external carbon (Ci/Ca), the lowest values were recorded at the PPFD of 2,000 µmol m^{-2} s^{-1} at different times of the day (Figures 4D, 4E, and 4F). Therefore, the maximum values were found at the PPFD of 0.00 µmol m^{-2} s^{-1}, obtaining Ci/Ca ratios of 1.43, 0.62, and 0.42 for the 4 p.m., 8 a.m., and 12 p.m., respectively. Thus, in percentage terms, the 12 p.m. time reduced the Ci/Ca ratio by 70.24%, and the 8 a.m. time reduced the Ci/Ca ratio by 56.42% compared to 4 p.m.

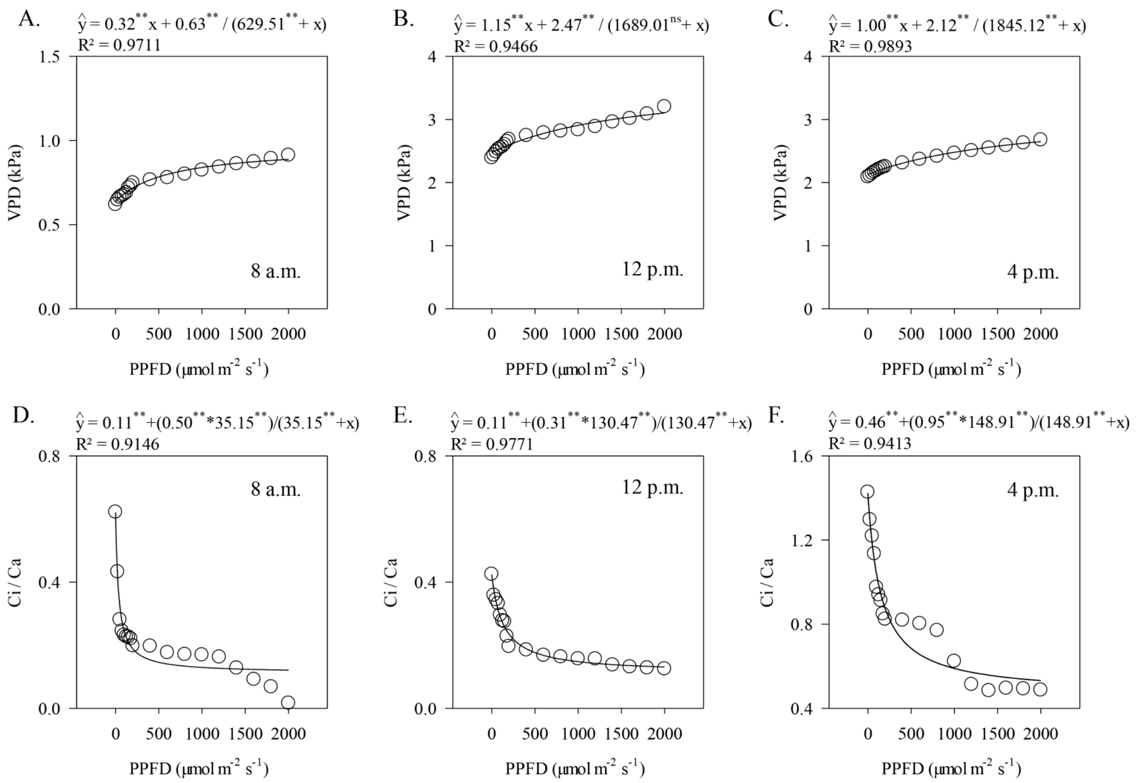

Figure 4. Vapor pressure deficit (VPD) and the ratio of internal to external leaf carbon (Ci/Ca) in *Alternanthera brasiliana* plants relative to photosynthetic photon flux density (PPFD) at various times of the day [8 a.m. (A, D), 12 p.m. (B, E), and 4 p.m. (C, F)].

When stomata close, CO_2 entry is restricted, leading to a reduction in the CO_2 available in the mesophyll and consequently lowering the Ci/Ca ratio (SANTOS et al., 2020). However, the lower Ci at the PPFD of 2,000 µmol m^{-2} s^{-1} was not a consequence of the lower gs because, as seen in this study, there was no reduction in gs due to higher PPFD. This implies that Ci is inversely proportional to the CO_2 demand required by photosynthesis (FAUSET et al., 2019). It is presumed that at a higher PPFD, there was an increase in the demand for CO_2, decreasing the Ci and, consequently, the Ci/Ca ratio.

In the chlorophyll *a* fluorescence variable, the initial fluorescence (F_o') was highest (560.02) at 4 p.m. with a PPFD of 0.00 µmol m^{-2} s^{-1} (Figure 5C). At 12 p.m., the maximum F_o' (473.15) was recorded at the PPFD of 0.00 µmol m^{-2} s^{-1} (Figure 5B), and at 8 a.m., the highest value (253.34) was observed at the PPFD of 0.00 µmol m^{-2} s^{-1} (Figure 5A). For the maximum fluorescence (F_m'), increments were observed as the PPFD increased, with a maximum value of 2099.71, recorded at 12 p.m. at the PPFD of 2,000 µmol m^{-2} s^{-1} (Figure 5E). Subsequently, at 4 p.m. with a maximum of 1211.00, at the same PPFD (Figure 5F), and at 8 a.m. with 900.14 also at the PPFD of 2,000 µmol m^{-2} s^{-1} (Figure 5D).

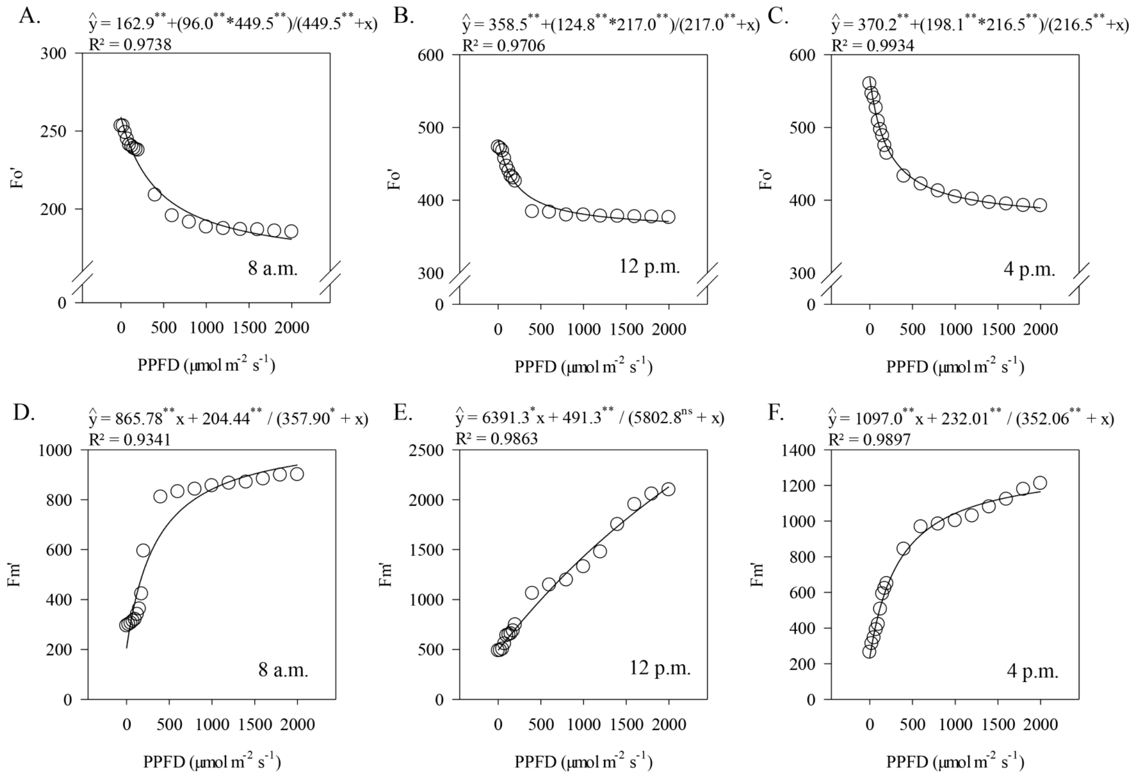

Figure 5. Initial fluorescence (F_o') and maximum fluorescence (F_m') in *Alternanthera brasiliana* plants relative to photosynthetic photon flux density (PPFD) at various times of the day [8 a.m. (A, D), 12 p.m. (B, E), and 4 p.m. (C, F)].

F_o' reflects the oxidation state of quinone A (QA), a primary electron acceptor in the photosystem II (PSII) reaction center. Consequently, an increase in this measure could be linked to stress conditions experienced by the plants, which were observed under lower PPFD (COÊLHO et al., 2023). At the same time, an increase in QA oxidation means that more electrons are being taken out, which can lead to a decrease in the production of NADPH and ATP during electron transport. On the other hand, the decrease in F_m' characterizes QA photoreduction deficiencies, which could be linked to the inactivation of PSII in the thylakoid membranes, directly impacting the electron flow between photosystems. Thus, the increase in F_o' implies a modification in the reaction center of PSII, an interruption in the transfer of absorbed light energy, and an increase in F_m' increase in photosynthetic activity. From this perspective, our results indicate that, at lower PPFD, electron transport rates are inhibited (KALAJI et al., 2017).

Variable fluorescence (F_v') exhibited similar patterns at various times of the day, with its highest values observed at a PPFD of 2,000 µmol m^{-2} s^{-1} (Figures 6A, 6B, and 6C). However, the highest F_v' (1723.55) was observed at 12 p.m. (Figure 6B), and at the other times (4 p.m. and 8 a.m.), the highest indices recorded were 818.52 and 714.83, respectively (Figures 6B and 6A). Regarding the quantum efficiency of the PSII antenna (F_v'/F_m'), different results were observed between the times due to the photon flux density (Figures 6D, 6E, and 6F). The maximum values recorded were 1.43 at 12 p.m. at the PPFD of 1,800 µmol m^{-2} s^{-1} (Figure 6E), 0.79 at 8 a.m. at PPFD of 2,000 µmol m^{-2} s^{-1} (Figure 6D), and 0.48 at 4 p.m. at PPFD of 800 µmol m^{-2} s^{-1} (Figure 6F). These results show that the plant responded positively to higher light intensities.

The results demonstrate a higher quantum efficiency of the PSII antenna at 12 p.m. at a higher PPFD. This behavior may have occurred because plants adapt photosynthesis in response to prevailing conditions. Therefore, a higher radiation (Figure 1) observed at this time could induce a greater sensitivity of the PSII. Vishnupradeep et al. (2022) report that, under stress conditions, the quantum efficiency of PSII decreases, which may be linked to photoinhibition due to alterations in the integrity and functionality of PSII reaction centers. The same was stated by Mousavi, Karami, and Maggi (2022), who pointed out that plant stress is associated with a decreased quenching capacity by phytochemicals within the PSII. From this perspective, in our study, higher PPFDs did not cause stress in the plants but boosted increases in chlorophyll *a* fluorescence variables.

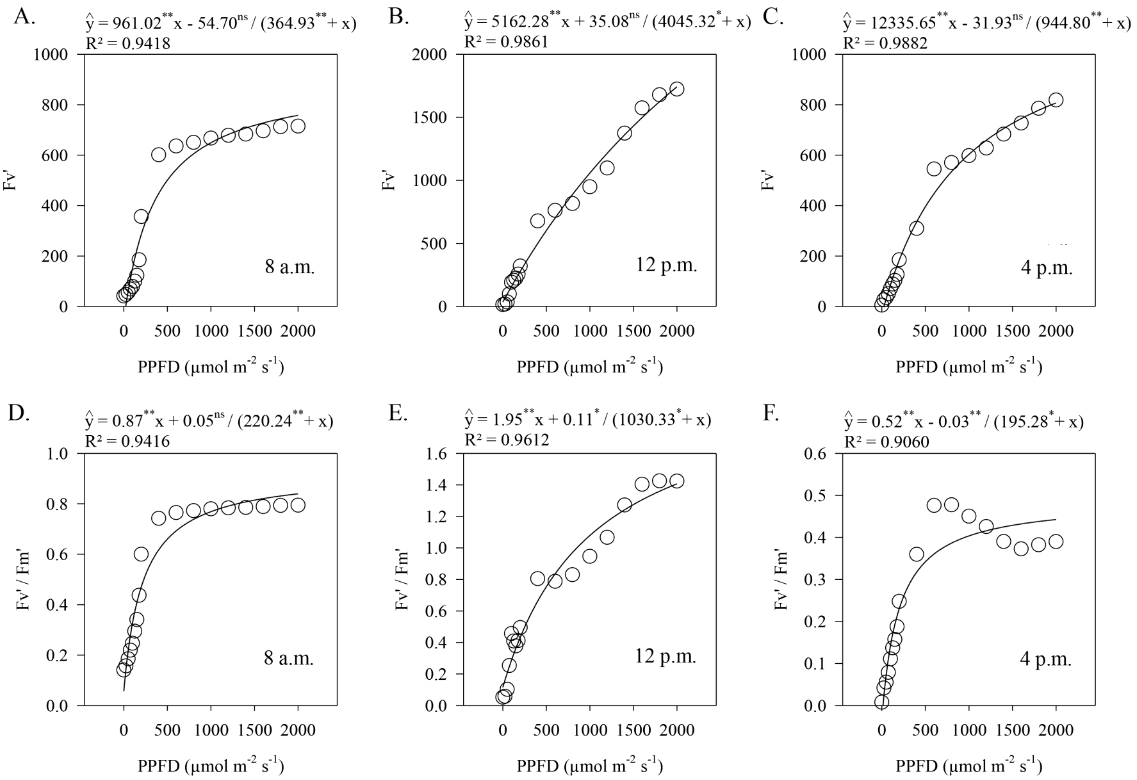

Figure 6. Variable fluorescence (F_v') and the quantum efficiency of the PSII antenna (F_v'/F_m') in *Alternanthera brasiliana* plants relative to photosynthetic photon flux density (PPFD) at various times of the day [8 a.m. (A, D), 12 p.m. (B, E), and 4 p.m. (C, F)].

The ratio of variable to initial fluorescence (F_v'/F_o') rose with increasing PPFD across all times observed (Figures 7A, 7B, and 7C). However, the maximum value (4.82) was recorded at 12 p.m. at the PPFD of 2,000 µmol m^{-2} s^{-1} (Figure 7B). At 8 a.m., the highest record was 3.86 (Figure 7A), and at 4 p.m., the highest record was 2.09 (Figure 7C), both at the PPFD of 2,000 µmol m^{-2} s^{-1}.

The F_v'/F_o' ratio is a crucial indicator of stress, as it reflects the balance between absorbed and dissipated energy (COÊLHO et al., 2023). Thus, the increase in the F_v'/F_o' ratio implies an improvement in the plant's photosynthetic efficiency since there is a greater ability to transfer energy through PSII.

Regarding the effective quantum efficiency of PSII (ΦPSII), the highest value obtained was 0.71 at 4 p.m. at the PPFD of 1,800 µmol m^{-2} s^{-1} (Figure 7F). At 12 p.m., the maximum ΦPSII recorded was 0.55 at the PPFD of 2,000 µmol m^{-2} s^{-1} (Figure 7E), and at 8 a.m., the maximum ΦPSII reached 0.37, also at the PPFD of 2,000 µmol m^{-2} s^{-1} (Figure 7D). Specifically, ΦPSII is expressed as the efficiency of converting absorbed light into photochemical energy. This suggests that, as this efficiency increases, a more significant proportion of the absorbed light is used to initiate photochemical reactions. However, the excess of light energy in the PSII leads to decreases in the quantum efficiency of this photosystem due to better energy dissipation (LAI et al., 2022).

The photochemical dissipation (qP) always showed significant increases up to the PPFD of 600 µmol m^{-2} s^{-1}, from which the values became practically constant (Figures 8A, 8B, and 8C). However, the maximum values found were 0.95 at 4 p.m. at the PPFD of 2,000 µmol m^{-2} s^{-1} (Figure 8C), 0.92 at 12 p.m. at the PPFD of 2,000 µmol m^{-2} s^{-1}, and 0.48 at 8 a.m. at the PPFD of 1,800 µmol m^{-2} s^{-1}.

The qP value represents the fraction of photosynthetic electrons transferred after light absorption by pigments in the reaction center antenna, indicating the opening of the photosystem II reaction center. This dissipated energy reflects the plant's capacity to release more electrons from the PSII quinone receptor, leading to increased consumption of ATP and NADPH (JARDIM et al., 2021). Therefore, a lower qP reflects the reduced state of PSII's first stable electron acceptor, QA, providing an estimate of PSII's ability to utilize light energy to reduce NADP+.

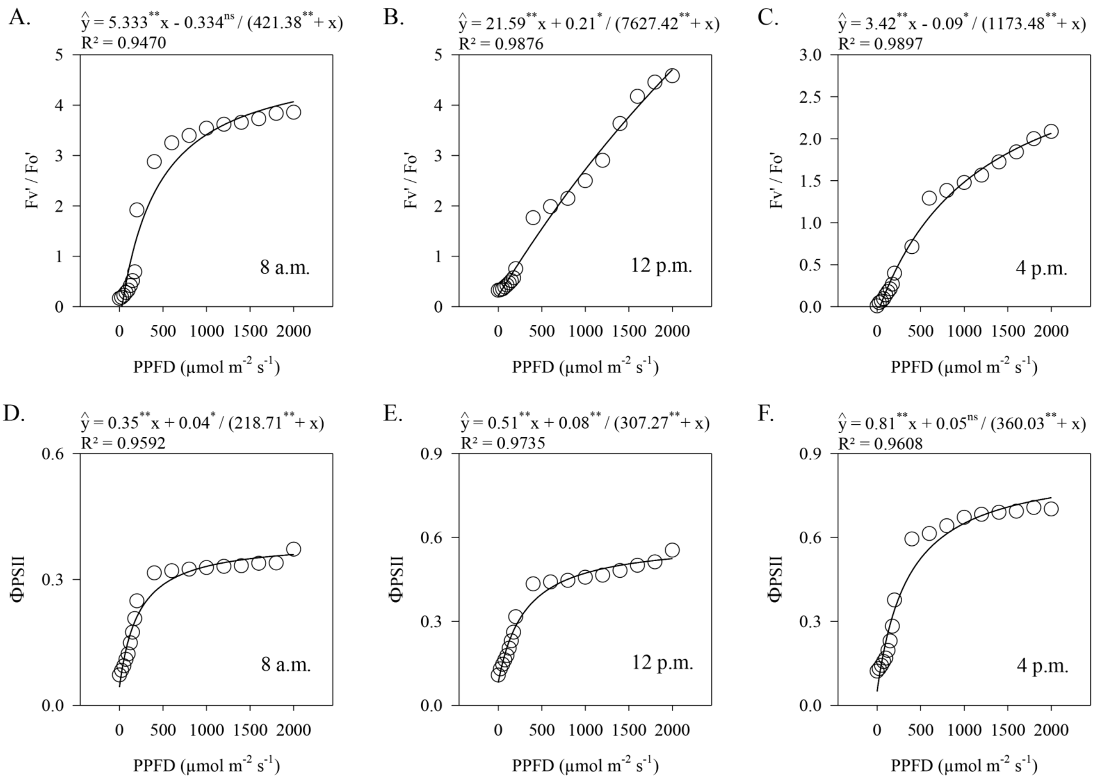

Figure 7. Ratio of variable to initial fluorescence (F_v'/F_o') and the effective quantum efficiency of PSII (ΦPSII) in *Alternanthera brasiliana* plants relative to photosynthetic photon flux density (PPFD) at various times of the day [8 a.m. (A, D), 12 p.m. (B, E), and 4 p.m. (C, F)].

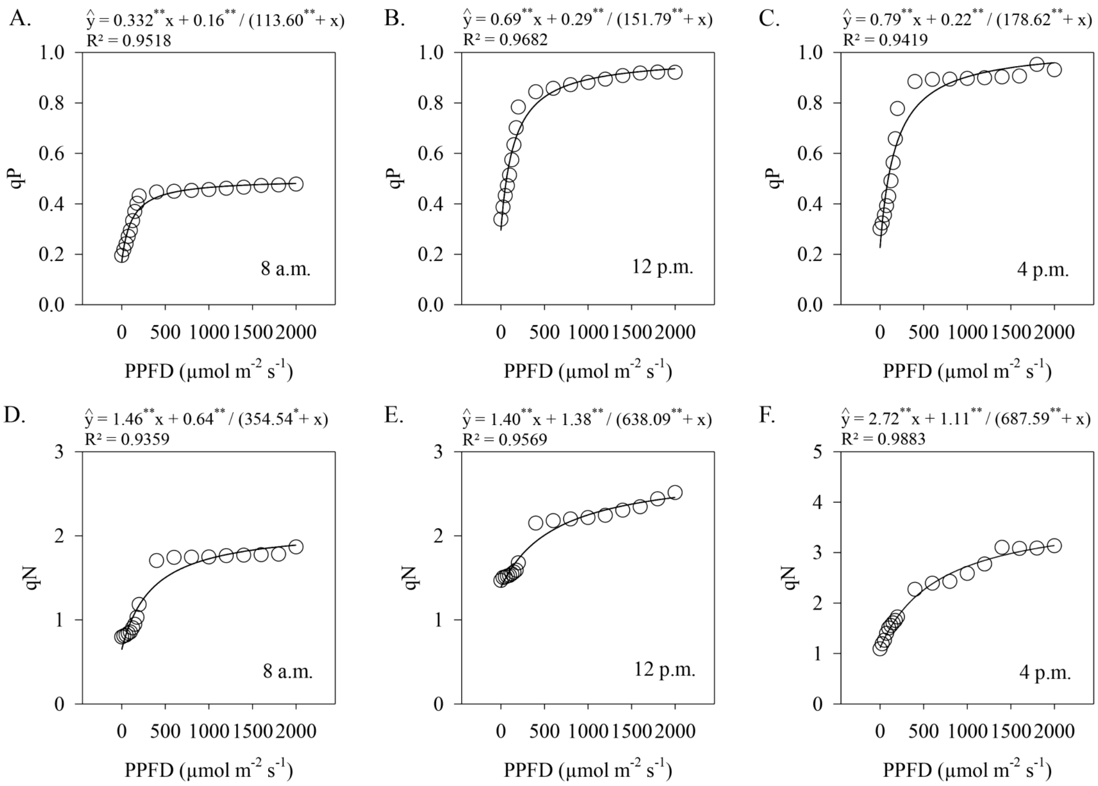

Figure 8. Photochemical dissipation (qP) and non-photochemical dissipation (qN) in *Alternanthera brasiliana* plants relative to photosynthetic photon flux density (PPFD) at various times of the day [8 a.m. (A, D), 12 p.m. (B, E), and 4 p.m. (C, F)].

For non-photochemical dissipation (qN), increases were observed due to the increased PPFD at all times studied (Figures 8D, 8E and 8F). The maximum qN (3.13) was obtained at 4 p.m. at the PPFD of 2,000 μmol m^{-2} s^{-1} (Figure 8F). The highest values for this variable at the other times (12 p.m. and 8 a.m.) corresponded, respectively, to 2.51 (Figure 8E) and 1.87 (Figure 8D) at the PPFD of 2,000 μmol m^{-2} s^{-1}.

The qN indicates heat dissipation efficiency due to the increase in the proton gradient between the lumen and the chloroplast stroma. Thus, an increase in this variable may indicate a photoprotective response of the plant in which a more significant amount of captured energy is released as heat (HAN et al., 2023).

The electron transport rate (ETR) was also affected by increasing PPFD at various times (Figures 9A, 9B, and 9C). The peak ETR was observed at 12 p.m. with a PPFD of 1, 600 μmol m^{-2} s^{-1} (Figure 9B). At 4 p.m., the maximum ETR was 99.09 with a PPFD of 2,000 μmol m^{-2} s^{-1} (Figure 9C), and at 8 a.m., the highest value was recorded at a PPFD of 1,400 μmol m^{-2} s^{-1} (Figure 9A).

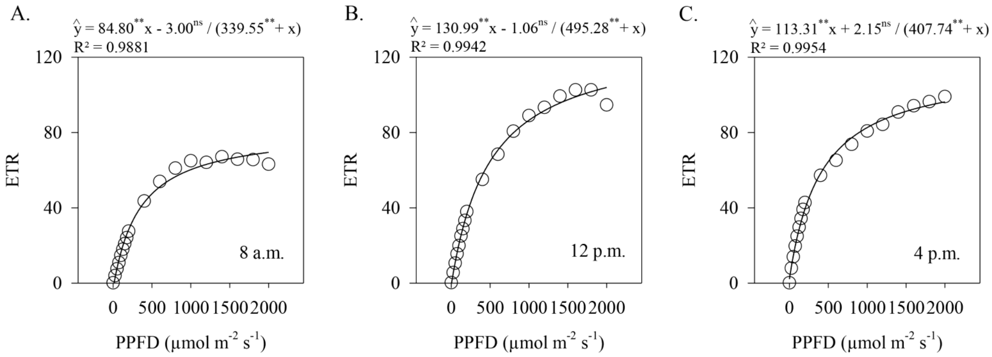

Figure 9. Electron transport rate (ETR) in *Alternanthera brasiliana* plants relative to photosynthetic photon flux density (PPFD) at various times of the day [8 a.m. (A), 12 p.m. (B), and 4 p.m. (C)].

The increase in ETR with higher PPFD suggests a rise in the dissipation of absorbed light (KALAJI et al., 2017). Observing elevated electron transport rates during high temperatures and light intensities may reflect enhanced resource use in the photochemical phase, leading to higher photosynthetic rates (SMITH; KEENAN, 2020).

A strong positive correlation was observed between stomatal conductance (gs) and transpiration (E), as well as between E and net CO_2 assimilation (A). Maximum fluorescence (F_m'), variable fluorescence (F_v'), and the quantum efficiency of the PSII antenna (F_v'/F_m') were all highly correlated with A, gs, and E (Figure 10). Photochemical dissipation (qP) showed a very strong correlation with the effective quantum efficiency of PSII (ΦPSII) and non-photochemical dissipation (qN). The electron transport rate (ETR) was strongly correlated with both F_m' and F_v'. External temperature (ExT) had a high correlation with vapor pressure deficit (VPD) and internal temperature (InT), while photosynthetically active radiation (PAR) showed a very strong correlation with InT.

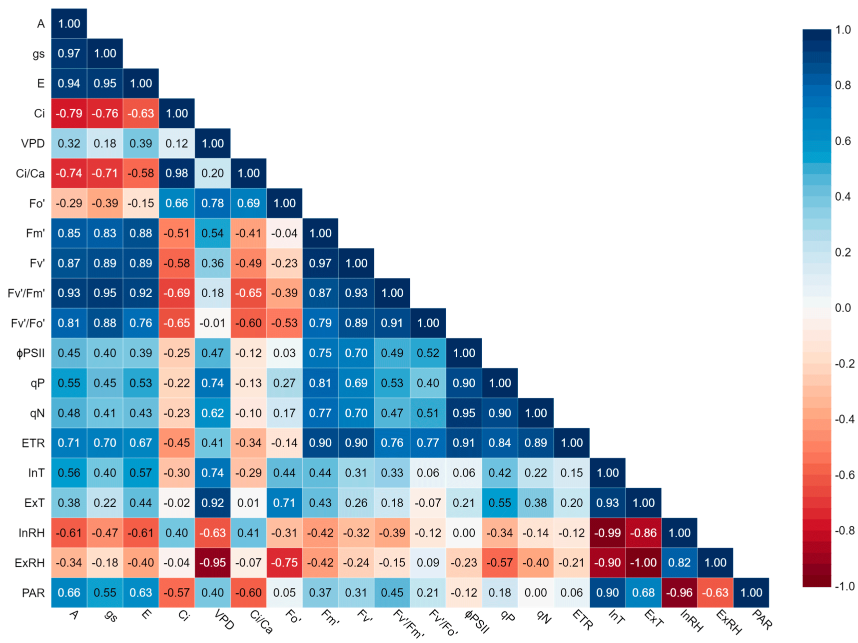

Figure 10. Pearson's correlation analysis between environmental and physiological variables.

CONCLUSIONS

The physiological processes of *A. brasiliana* were influenced by PPFD and environmental conditions throughout the day.

At 12 p.m., a PPFD of 1,800 μmol m^{-2} s^{-1} promoted higher CO_2 assimilation and an increased electron transport rate.

At 8 a.m., a PPFD of 2,000 μmol m^{-2} s^{-1} positively affected gas exchange and chlorophyll *a* fluorescence.

The species shows an adaptive capacity to varying light conditions, highlighting the importance of light intensity in optimizing its physiological performance.

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