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Scientific Article

Photosynthetic performance or behavior in 'Keitt' mango under diurnal environmental fluctuations

Desempenho fotossintético em manga 'Keitt' sob flutuações ambientais diurnas

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ABSTRACT – Abiotic factors, such as temperature and irradiance, induce different physiological responses in plants throughout the day. In fruit trees, unfavorable weather conditions affect net CO_2 assimilation and fruit quality. Therefore, the objectives of this study were to evaluate the photosynthetic behavior of mango (*Mangifera indica* L.) cv. 'Keitt' throughout the day by analyzing gas exchange and chlorophyll *a* fluorescence, determine the predominance of abiotic factors (temperature, relative humidity, and radiation) on these physiological responses and identify the photosynthetic photon flux density (PPFD) that promotes higher CO_2 assimilation and electron transport rate. The experiment was conducted in a greenhouse in a completely randomized experimental design, in which 18 different flux densities of photosynthetically active photons (PPFD) (0 – 2000 µmol m^{-2} s^{-1}) were tested at three different times throughout the day (8 a.m., 12 p.m., and 4 p.m.). Each combination of flux density and time was repeated six times, and in each repetition, two plants per plot were considered. Ecophysiological (net photosynthesis rate, stomatal conductance, transpiration, and internal CO_2 concentration) and environmental (temperature, relative humidity, and photosynthetically active radiation) variables were analyzed. Gas exchange and chlorophyll fluorescence of mango cv. 'Keitt' were negatively affected by conditions of high temperature and photosynthetically active radiation. PPFD between 1600 and 2000 µmol m^{-2} s^{-1} provided a higher net photosynthesis rate and electron transport rate in mango cv. 'Keitt' at 8 a.m.

Keywords: *Mangifera indica*. Abiotic stresses. Photosynthesis. Photoinhibitory damage. Phenotypic plasticity.

RESUMO – Fatores abióticos, como temperatura e irradiância, induzem diferentes respostas fisiológicas nas plantas ao longo do dia. Em árvores frutíferas, condições climáticas desfavoráveis afetam a assimilação líquida de CO_2 e a qualidade dos frutos. Portanto, os objetivos deste estudo foram avaliar o comportamento fotossintético da mangueira (*Mangifera indica* L.) cv. 'Keitt' ao longo do dia por meio da análise de trocas gasosas e fluorescência da clorofila *a*, determinar a predominância dos fatores abióticos (temperatura, umidade relativa e radiação) sobre essas respostas fisiológicas, e identificar a densidade de fluxo de fótons fotossinteticamente ativos (DFFFA) que promove maior assimilação de CO_2 e taxa de transporte de elétrons. O experimento foi conduzido em casa de vegetação em delineamento experimental inteiramente casualizado, no qual 18 diferentes densidades de fluxo de fótons fotossinteticamente ativos (DFFFA) (0 – 2000 µmol m^{-2} s^{-1}) foram testadas em três horários diferentes ao longo do dia (8h, 12h e 16h). Cada combinação de densidade de fluxo e tempo foi repetida seis vezes, e em cada repetição, duas plantas por parcela foram consideradas. Variáveis ecofisiológicas (taxa líquida de fotossíntese, condutância estomática, transpiração e concentração interna de CO_2) e ambientais (temperatura, umidade relativa e radiação fotossinteticamente ativa) foram analisadas. As trocas gasosas e a fluorescência da clorofila da manga cv. 'Keitt' foram afetadas negativamente por condições de alta temperatura e radiação fotossinteticamente ativa. O DFFFA na faixa entre 1600 e 2000 µmol m^{-2} s^{-1} proporcionou uma maior taxa de fotossíntese líquida e taxa de transporte de elétrons na manga cv. 'Keitt' às 8h.

Palavras-chave: *Mangifera indica*. Estresses abióticos. Fotossíntese. Dano fotoinibitório. Plasticidade fenotípica.

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INTRODUCTION

Constant climate change has intensified scientific interest in understanding the effects of abiotic factors on the development of fruit trees. The main factors affecting these crops are the availability of water and nutrients, relative humidity, temperature and light (BACELAR et al., 2024). When at inadequate levels, these elements can induce stress conditions capable of causing significant physiological changes in plants, compromising their growth, yield and fruit quality (ZHANG et al., 2021).

As one of the most consumed fruits in the world, mango plays an essential role in the world economy and food areas (TIRADO-KULIEVA et al., 2022). Mango (*Mangifera indica* L.) is widely grown worldwide and can provide diverse value-added products (LEBAKA et al.,2021). In addition, it is considered an essential source of vitamins and minerals, with many antioxidant properties.

In fruit species such as mango, light distribution in the canopy directly influences fruit quality (ZHANG et al., 2021). Lebaka et al. (2021) state in their study that the production success of mango depends on its establishment under abiotic conditions suitable for its development. In this context, the availability of light directly influences this crop's physiological, morphological, and productive characteristics.

Light intensity and quality directly influence the production of secondary metabolites in plants (MURTHY et al., 2024). These compounds play a crucial role in protecting against photooxidative stress caused by high-light conditions and in defining sensory and nutritional characteristics that determine the commercial quality of fruits (PIEPER et al., 2024).

The photosynthetic photon flux density (PPFD) corresponds to the amount of light available for photosynthesis; this density varies throughout the day, and this causes a leaf and physiological adjustment in plant species (LIU et al., 2024). This acclimatization to light is essential to understanding the mechanisms involved in the adaptability of plants in distinct environments.

Research on PPFD simulates possible temporal variations in light intensity, seeking to understand plants' response mechanisms (JIANG et al., 2024). In mango trees, Zhang et al. (2021) associated environmental fluctuations simulated by PPFD with stomatal regulation modeling and demonstrated the involvement of PPFD in gas exchange and, consequently, in photosynthetic efficiency.

The effects of photon flux density on plant physiology have been widely addressed in several crops, but there is still a significant lack of specific information on this variable in mango trees (LAHAK et al., 2024). Little is known about how different light intensities affect the species' physiological and biochemical processes, especially in photosynthetic efficiency. Investigating these aspects is essential to understand how mango trees respond to variations in light availability and, thus, optimize management practices that ensure fruit quality and crop yield. We hypothesized a reduction in CO_2 assimilation at times of higher luminosity and temperature in mango seedlings throughout the day. Thus, the objectives of this study were (i) to evaluate the photosynthetic responses (or plasticity) through gas exchange and chlorophyll *a* fluorescence analyses at different times of the day, (ii) to assess the predominance of abiotic factors (temperature, relative humidity, and radiation) on photosynthetic behavior, and (iii) to identify the PPFD that promotes greater assimilation of CO_2 and increases in the electron transport rate in mango cv. 'Keitt'.

MATERIAL AND METHODS

Study location and soil characterization

The research was conducted on three-year-old mango plants (*Mangifera indica* L.) cv. 'Keitt' grown in a greenhouse of the Federal University of Paraíba, in the city of Areia, state of Paraíba, in northeastern Brazil (6°57'59"S and 35°42'57"W). This region is located in the mesoregion of Agreste Paraibano and the microregion of Brejo Paraibano, with an average temperature of about 22 °C and an average rainfall of approximately 1,400 mm per year (RIBEIRO et al., 2018). The climate is categorized as "As" type, characterized as tropical, with a hot and dry summer and rainfall during the winter (ALVARES et al., 2013).

The experiment was carried out in August 2019, during which meteorological information about the environment was recorded daily. The average temperature was 25.2 °C and relative humidity was 52.5%. These climatic data were obtained using a digital thermo-hygrometer.

Plastic pots with a capacity of 50 dm³ were used to cultivate the plants obtained from seeds. The pots were filled with local soil and commercial substrate (3:1). The commercial substrate used was Carolina Soil® (Carolina Soil do Brasil Ltda.), which is composed of Sphagnum peat, vermiculite, dolomitic gypsum, limestone, NPK fertilizer, coconut or wood fiber, and carbonized rice husk. The physicochemical characteristics of the soil used in the experiment were as follows: pH (H_2O): 5.35; P: 109.0 mg dm^{-3}; K^+: 201.1 mg dm^{-3}; Na^+: 0.62 cmol$_c$ dm^{-3}; $H^+ + Al^{3+}$: 3.05 cmol$_c$ dm^{-3}; Al^{3+}: 0.00 cmol$_c$ dm^{-3}; Ca^{2+}: 2.2 cmol$_c$ dm^{-3}; Mg^{2+}: 3.6 cmol$_c$ dm^{-3}; sum of bases: 7.82 cmol$_c$ dm^{-3}; cation exchange capacity: 10.2 cmol$_c$ dm^{-3}; base saturation: 60.2%; organic matter: 32.10 g kg^{-1}; sand: 550 g kg^{-1}; silt: 255 g kg^{-1}; and clay: 205 g kg^{-1}. Daily, the plants were irrigated using the gravimetric method to maintain the field capacity at approximately 80%.

Experimental design

The experiment was conducted in a completely randomized experimental design, in which 18 different flux densities of photosynthetically active photons (0, 25, 50, 75, 100, 125, 150, 175, 200, 400, 600, 800, 1000, 1200, 1400, 1600, 1800, and 2000 µmol m^{-2} s^{-1}) were tested at three different times throughout the day (8 a.m., 12 p.m. and 4 p.m.). The analyses were performed on August 3, 2019, during a single data collection session. Each combination of flux density and time was repeated six times, and in each repetition, two plants per plot were considered, totaling 12 individuals evaluated at each time of data collection.

Climate and ecophysiological variables

During the execution of the physiological analyses, the internal temperature (InT), external temperature (ExT), relative humidity of the internal air (InRH), and relative humidity of the external air (ExRH) were recorded in the protected environment. These measurements were performed with a digital thermo-hygrometer (Minipa model MT-241A). Photosynthetically active radiation (PAR) was captured using a natural light sensor integrated into portable infrared gas analyzer (IRGA) (LICOR, model LI-6400XT).

Gas exchange evaluations were conducted using the IRGA. The net assimilation rate of CO_2 (A) (µmol m^{-2} s^{-1}), stomatal conductance (gs) (mol m^{-2} s^{-1}), transpiration (E) (mmol m^{-2} s^{-1}), and internal CO_2 concentration (Ci) (µmol mol^{-1}) were analyzed. Chlorophyll fluorescence readings were performed using a fluorometer (LI-COR, model LI-6400-40 LCF) coupled to the IRGA. Initial fluorescence (F_0'), maximum fluorescence (F_m'), photochemical quenching (qP), and electron transport rate (ETR) were obtained with the leaves subjected to a saturating flash of atypical irradiation and a pulse of light in the far-red region.

The measurements were performed on healthy leaves, free from damage, pests, or diseases, and fully expanded in the median third of the plants, with four leaves analyzed per individual. The IRGA sensor was always positioned on the adaxial (upper) surface of the leaf, in the central region of the leaf blade, avoiding main veins. In the measurement protocol in the IRGA chamber, the following parameters were maintained: relative humidity between 50 and 60%; airflow of 300 µmol s^{-1}; CO_2 concentration of 400 µmol mol^{-1}; and artificial light sensor in leaf chamber of 2 cm².

To obtain the response curves of gas exchange and chlorophyll fluorescence as a function of the flux density of photosynthetically active photons (PPFD), PPFD was gradually reduced from 2000 to 200 µmol m^{-2} s^{-1}, in decrements of 200 µmol m^{-2} s^{-1}. Below 200 µmol m^{-2} s^{-1} through 0, PPFD was varied at intervals of 25 µmol m^{-2} s^{-1} to determine the apparent quantum efficiency (Φ [µmol CO_2/ µmol photons]). The apparent quantum efficiency was calculated by fitting a linear equation in the range where A variation as a function of PPFD was linear, i.e., $A = a + \Phi.Q$, where a and Φ are fitting coefficients and Q represents PPFD. The value of the luminous compensation point Γ (µmol m^{-2} s^{-1}) was determined at the intersection of the line with the X-axis. The response curve of A as a function of PPFD was fitted by the rectangular hyperbola function, $A = Amax.Q/a + Q$, where Amax is the maximum rate of photosynthesis and a is a fitting coefficient of the equation.

Data analysis

The data were subjected to a nonlinear regression analysis and fitted by the rectangular hyperbola function, whose fit was assessed based on the significance of the coefficients of the equations, using Student's t-test. In addition, a principal component analysis (PCA) and a Pearson linear correlation analysis were performed to investigate the relationship between environmental variables (PAR, InT, ExT, InRH, and ExRH) and ecophysiological variables (A, gs, E, Ci, F_0', F_m', qP and ETR). All analyses were conducted using the R® software version 4.3.1 (R DEVELOPMENT CORE TEAM, 2023).

RESULTS AND DISCUSSION

The plants were subjected to different increasing intensities of light, temperature, and humidity (Figure 1). At 12:00 p.m., the highest value of photosynthetically active radiation (PAR) was recorded, accompanied by the highest internal (39 °C) and external (37°C) temperatures. At 4:00 p.m., PAR and temperatures decreased, with 30 °C (internal) and 32 °C (external). Internal and external relative humidity reached their lowest values at noon, with 33% and 40%, respectively (Figure 1).

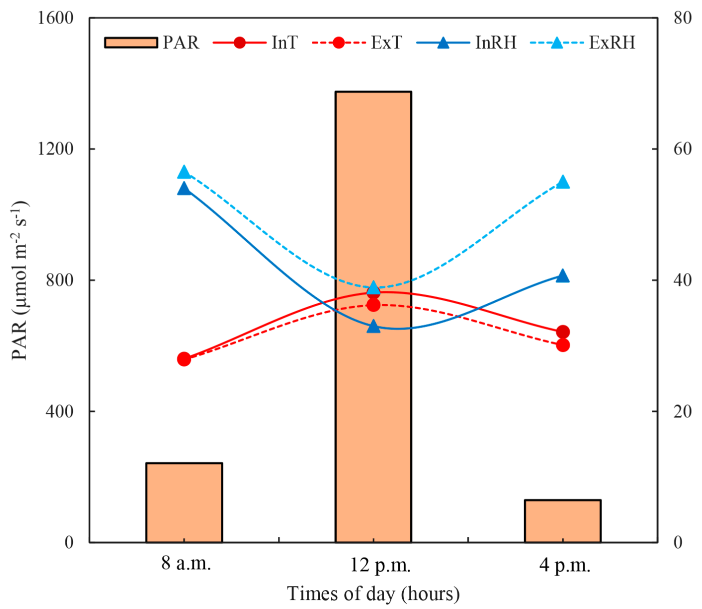

Figure 1. Photosynthetically active radiation (PAR), internal (InT) and external (ExT) temperature, and internal (InRH) and external (ExRH) relative humidity of the environment during ecophysiological analyses.

The influence of abiotic components can occur through the isolated action of each factor or by the combined action so that the interference caused directly affects the physiological processes (ROYCHOWDHURY et al., 2023). The results obtained indicate that, at the time of highest photosynthetically active radiation (PAR), it was also possible to observe records of higher temperature and lower relative humidity. The observed variation throughout the day in photosynthetically active radiation determines the availability of energy for photosynthesis, affecting all components involved in the photosynthetic process (PROUTSOS et al., 2022). With increasing temperature, plants may exhibit morphophysiological changes that induce a state of acclimatization; these changes include characteristic modifications such as increased wax production, changes in leaf angle and thickness, and changes in cuticle composition

(TRIVEDI et al., 2022). There are some studies that evidence that conditioned heat stress at hotter hours of the day alters membrane fluidity, transpiration rate through stomatal conductance, and net photosynthesis (QIU et al., 2025). Notably, abiotic factors directly influence the most critical vital process of plant development, photosynthesis. The combination of high temperatures associated with low relative humidity, as observed in the present study at the time of 12 p.m., may limit the enzymatic activity of Ribulose-1,5-bisphosphate carboxylase oxygenase, increasing its oxygenase activity and causing photorespiration (JAHAN et al., 2021).

The photosynthetic characteristics were recorded over a period to evaluate carbon assimilation in response to increased luminosity in plants by means of net photosynthesis curves (A) in response to increased PPFD (Figure 2). It was observed that the gradual increase of light influenced the net fixation of CO_2 at all evaluation times (8 a.m., 12 p.m., and 4 p.m.), especially between the values of 1600 and 1800 µmol of photons m^{-2} s^{-1}. Thus, at 8 a.m., the saturation values for A reached approximately 10 µmol CO_2 m^{-2} s^{-1} at PPFD values of 1600 µmol of photons m^{-2} s^{-1} (Figure 2A). At the time of 12 p.m., higher saturation of net photosynthesis was recorded when the plants were subjected to 6.5 µmol CO_2 m^{-2} s^{-1} at PPFD of 1800 µmol of photons m^{-2} s^{-1} (Figure 2B). The evaluation performed at 4 p.m. showed an increase of A by about 8 µmol CO_2 m^{-2} s^{-1} at PPFD of 1800 µmol of photons m^{-2} s^{-1} (Figure 2C). Net photosynthesis decreased when plants were exposed to PPFD values of 2000 µmol of photons m^{-2} s^{-1} photons at all evaluation times (Figures 2A, 2B, and 2C).

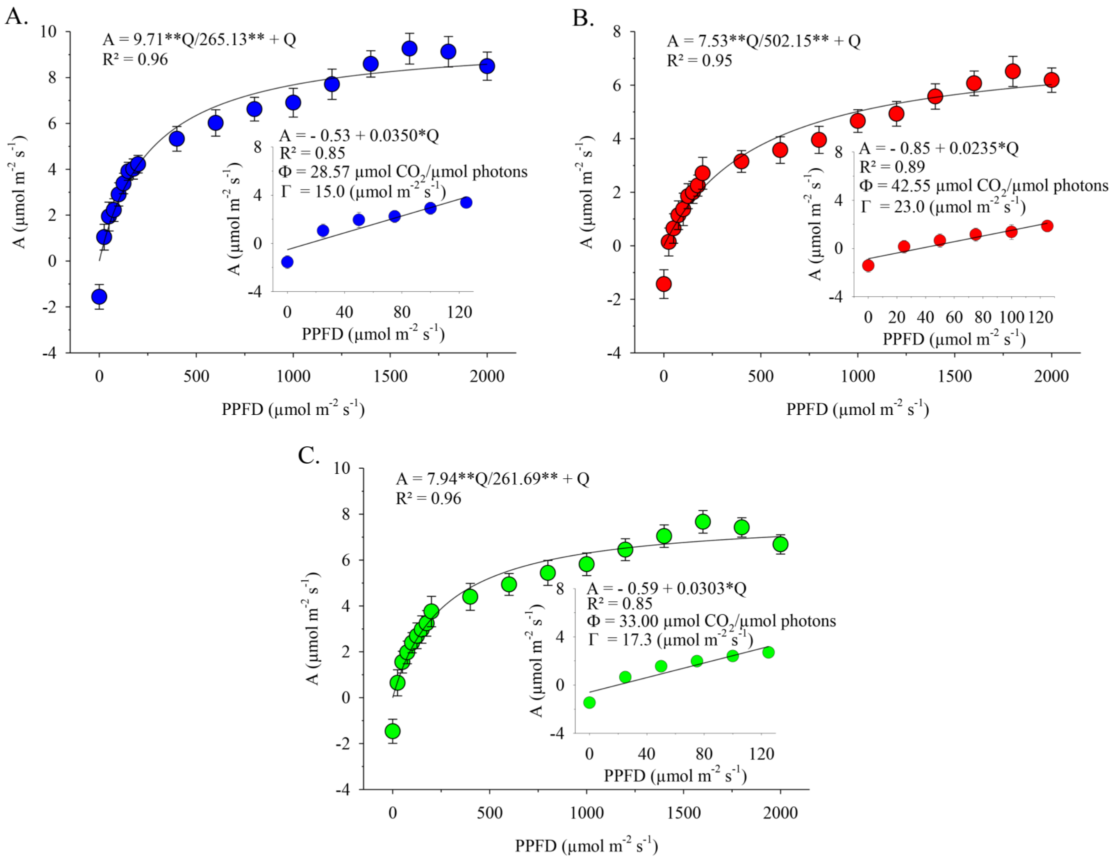

Figure 2. Curves of (A) net photosynthesis at 8 a.m. (A), 12 p.m. (B), and 4 p.m. (C) in response to increased luminosity (PPFD – Photosynthetically active photon flux density) in mango (*Mangifera indica* L.) cv. 'Keitt'.

The results obtained indicate that the increase of light favored net photosynthesis (A), but this variable was reduced as the plants reached a point of light saturation. The perception of light interception required for A is initially observed from the stomatal conductance as the opening of the stomata is mediated primarily by abiotic signals such as light, temperature, and relative humidity (KOSTAKI et al., 2020). The reduction in A observed at the time of 12 p.m. can be attributed to the increase in temperature observed in this period, as the reduction of leaf turgor due to the water efflux promotes stomatal closure and a decrease in the photosynthetic rate (YANG et al., 2020). On the other hand, the increase in A values may be related to the stomatal opening induced by light. Peng et al. (2025) in their study state that throughout the day, plants are subjected to changes in the quantity and quality of light that alter stomatal motion and net photosynthesis. Furthermore, the reduction in net photosynthesis (A) observed at higher PPFD values may also indicate the onset of photoinhibition. This process is triggered when light absorption by leaves exceeds the capacity of the photosynthetic apparatus to use it efficiently, resulting in damage to photosystem II (PSII) and the generation of reactive oxygen species (ROS), which compromise photosynthetic efficiency and carbon assimilation (KHAN et al., 2025). Photoinhibition is a common physiological response in plants exposed to high light intensities, especially when associated with other abiotic stresses, such as extreme temperatures, drought, and salinity (DIDARAN et al., 2024).

The parameters of gas exchange determined based on the daily course showed an increase in the assimilation of carbon from the plant when exposed to a high pulse of light saturation. The results show higher values of stomatal conductance and transpiration rate in the plants during the morning at 8 a.m. (0.21 and 3.80 mol m^{-2} s^{-1}, respectively). In the afternoon, at 4 p.m., it is observed that the values of these parameters decrease, which is associated with the partial closure of the stomata with the decrease of the luminosity levels (Figures 3A and 3B). However, larger increments of these parameters (gs and E) at all evaluation times were observed in response to the increase in PPFD in the range of 1600 µmol of photons m^{-2} s^{-1}. The intercellular concentration of CO_2 (Ci) during the morning (8 a.m.) remained constant (Figure 3C). On the other hand, throughout the afternoon (12 p.m. and 4 p.m.), this variable showed a significant reduction with the increase in luminosity.

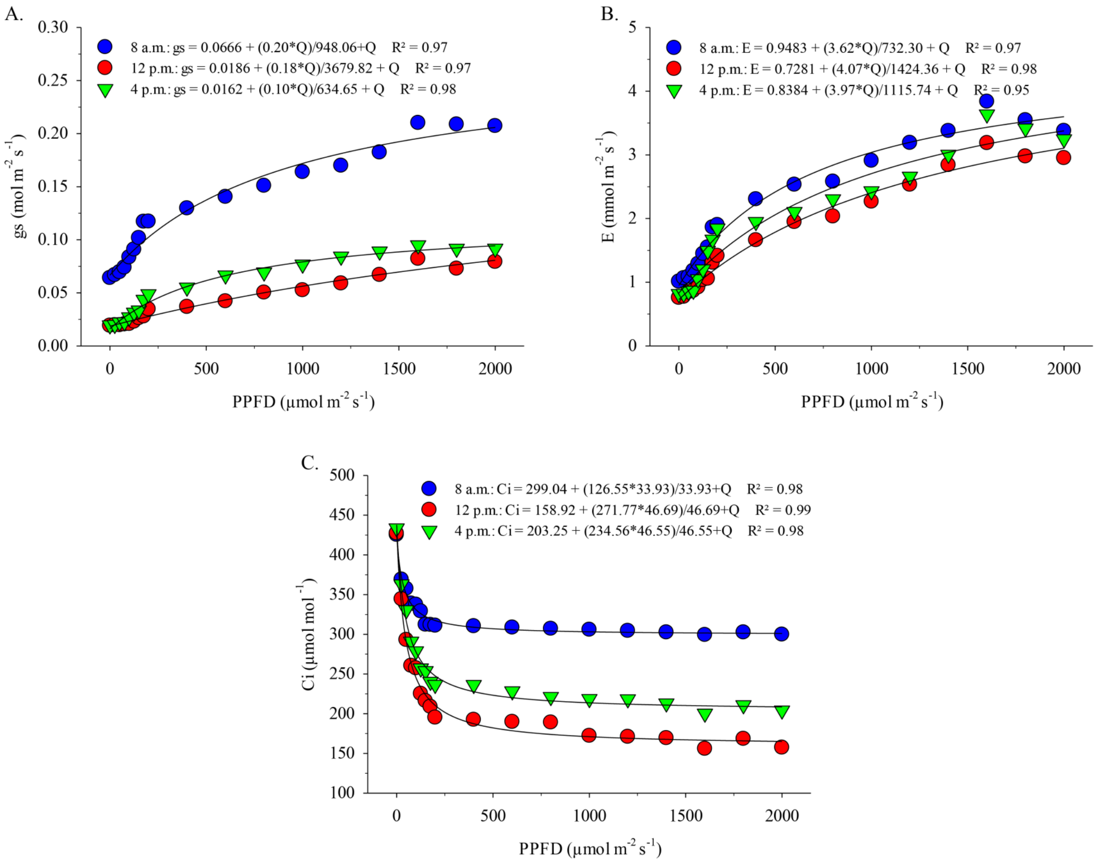

Figure 3. Curves of (A) stomatal conductance (gs), (B) transpiration (E), and (C) intercellular concentration of CO_2 (Ci) at different times of the day (8 a.m., 12 p.m., and 4 p.m.) in mango (*Mangifera indica* L.) cv. 'Keitt' in response to increased luminosity (PPFD – Photosynthetically active photon flux density).

Stomatal conductance (gs) records at the 8 a.m. time confirm the need for daytime opening of the stomata for CO_2 diffusion to the leaf mesophyll. In addition, the results found for gs directly influence the transpiration rate since the dynamic behavior of the stomata is essential for the regulation of water availability. Regarding the responsive increase of A, gs, and E due to the luminosity level, previous studies have already indicated the importance of light variation in photosynthetic induction and stomatal conductance (TAYLOR; WALTER; KROMDIJK et al., 2024). The increase in transpiration rate associated with greater stomatal opening is necessary for the cooling of leaves at times with high temperatures, which is an adaptation capacity of plants to maintain thermal homeostasis (HOČEVAR; VULETA; MANITAŠEVIĆ JOVANOVIĆ, 2025). Stomatal regulation plays an essential role in the absorption of CO_2 required by photosynthesis and transpiration. Low gs results in the limitation of A, while a high gs favors A with a higher cost of water loss by transpiration. The internal concentration of CO_2 is inversely proportional to the CO_2 demand required by photosynthesis, so a reduction in gs provides the maintenance of Ci (BATISTA et al., 2024).

Photosynthetic parameters in mango cv. 'Keitt' under different light intensities were analyzed over time to observe the behavior of initial fluorescence (F_0'), maximum fluorescence (F_m'), photochemical quenching (qP), and electron transport rate (ETR) through daily analyses. The initial fluorescence (F_0') was elevated during the three hours (8 a.m., 12 p.m., and 4 p.m.) when plants were subjected to low PPFD; however, with the increase in luminosity, there was a reduction of this parameter in all periods (Figure 4A). The values of F_m', qP and ETR exhibited similar trends, increasing at all times until they reached the maximum points in 2000 µmol of photons m^{-2} s^{-1}, except for the electron transport rate (ETR), which reached this point when plants were exposed to 1800 µmol of photons m^{-2} s^{-1} (Figures 4B, 4C, and 4D).

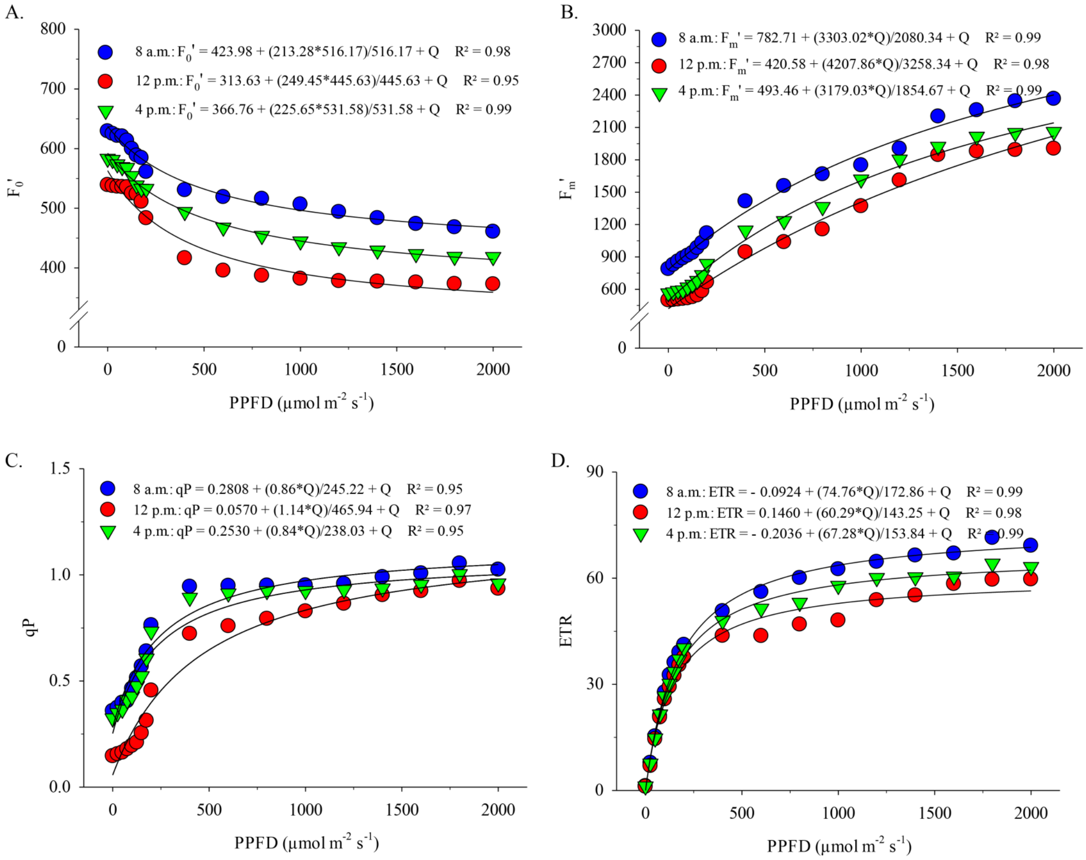

Figure 4. Curves over time of (A) initial fluorescence (F_0'), (B) maximum fluorescence (F_m'), (C) photochemical quenching (qP), and (D) electron transport rate (ETR) in mango (*Mangifera indica* L.) cv. 'Keitt' in response to increased luminosity (PPFD – Photosynthetically active photon flux density).

Luminous intensity influences thylakoid membrane integrity, and photosystems I and II, and the parameters evaluated are related to the dissipation of energy absorbed by photons, electron transfer, and the temperature (JAHAN et al., 2021). In general, the effects of stresses caused by abiotic factors cause a reduction in PSII activity and consequently interfere with photosynthetic metabolism. The evaluation of parameters related to chlorophyll fluorescence is essential for the analysis of the responses of factors such as light intensity, water, and thermal stress (SWOCZYNA et al., 2022). The observed variation in chlorophyll fluorescence parameters and photosynthetic performance can be explained by the inhibition of electron transport. Our results showed that mango in the treatments with lower PPFD had higher records of F_0' and lower values of F_m', qP, and ETR. The increase in ETR associated with a higher PPFD suggests the increase in the dissipation of absorbed light, and the reduction in F_m' at low PPFD may have occurred due to the inhibition of electron transport rates (WANG et al., 2022). From these results, it is possible to affirm that this species shows better photosynthetic performance under conditions of higher photon density. However, there is a threshold of light saturation where, in this condition, photoinhibition can occur.

Internal (InRH) and external (InRH) relative humidity are positively correlated with most ecophysiological variables, while internal (InT) and external (ExT) temperature and photosynthetically active radiation (PAR) are negatively correlated with all ecophysiological variables (Figure 5). The rate of net photosynthesis (A), electron transport rate (ETR), maximum fluorescence (F_m'), photochemical quenching (qP), and stomatal conductance (gs) are strongly positively correlated with each other, while internal CO_2 concentration (Ci) and initial fluorescence (F_0') showed a negative correlation with the other ecophysiological variables (Figure 5).

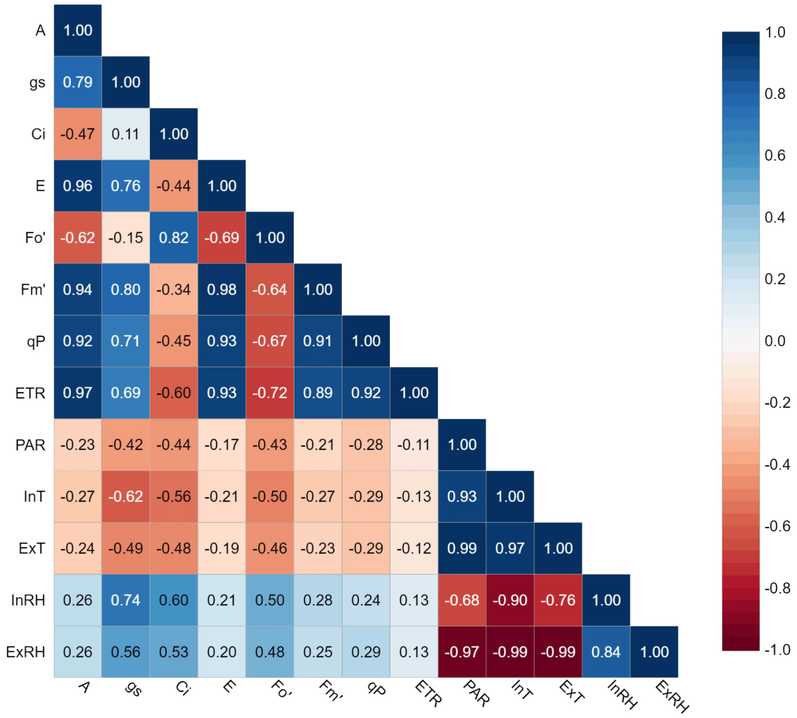

Figure 5. Pearson's correlation between ecophysiological and climatic aspects in mango (*Mangifera indica* L.) cv. 'Keitt' as a function of photosynthetically active photon flux density (PPFD) at different times of the day.

The results obtained in the Pearson correlation indicate that the positive correlation of internal (InRH) and external (ExRH) relative humidity with the ecophysiological variables suggests that in more humid environments, the photosynthetic efficiency of the mango tree is favored, as there is a greater stomatal opening (gs) under these conditions. In contrast, the negative correlation found between internal (InT) and external (ExT) temperatures and photosynthetically active radiation (PAR) with ecophysiological variables suggests that warmer conditions with greater luminosity can cause thermal and light stress, reducing photosynthetic efficiency (PSHYBYTKO, 2024). Thus, the greater or lesser gs in the mango tree is mediated mainly by abiotic factors (relative humidity, temperature and radiation), which modulate photosynthetic efficiency (KISHORE et al., 2023). The positive correlation between A, ETR, F_m’, qP and gs highlights the essentiality of stomatal regulation in photosynthetic parameters since greater stomatal conductance provides an increase in electron transport in mango trees (KISHORE et al., 2023). On the other hand, the negative correlation of internal CO_2 concentration (Ci) and initial fluorescence (F_0’) with the other variables may demonstrate limitations in CO_2 assimilation that can be caused by stress conditions (MOUSTAKAS; CALATAYUD; GUIDI, 2021).

CONCLUSION

The mango cultivar ‘Keitt’ showed phenotypic plasticity with diurnal climate variations. Photosynthetic performance was highest in the early morning hours, especially around 8 a.m., when photosynthetically active radiation (PPFD) between 1600 and 2000 μmol m^{-2} s^{-1} favored maximum rates of net photosynthesis. Throughout the day, the increase in temperature and radiation resulted in a saturation point and possible onset of photoinhibition, reflected in reduced photosynthesis under higher light intensities. Even under these conditions, the cultivar maintained high levels of photosynthetic activity and responses of physiological mechanisms that promote adaptation to tropical environments with high irradiance and thermal variations.

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