PAB Pesquisa Agropecuária Brasileira 60 years

ISSN 1678-3921

Journal homepage: www.embrapa.br/pab

For manuscript submission and journal contents, access: www.scielo.br/pab

Plant Physiology/ Original Article

Photosynthesis, growth, and leaf nutrients of mahogany and jatoba seedlings acclimated to direct sunlight

Abstract – The objective of this work was to evaluate how the mahogany and jatoba species, with different growth rates, respond to full sunlight acclimatization during their juvenile stage. Three- and eight-month-old seedlings of mahogany and jatoba, respectively, were grown under low light and exposed to six independent full sunlight acclimation times for 30 days: 0.0 hour (control), 1.5 hour (11h15–12h45), 3.0 hours (10h30–13h30), 6.0 hours (9h00–15h00), 9.0 hours (7h30–16h30), and 12.0 hours (6h00–18h00). Then the plants were transferred to outdoor conditions the whole day for 120 days. Leaf gas exchange, leaf traits, plant growth, biomass allocation, and leaf nutrient contents were evaluated. In both species, photosynthetic rates increase with the length of full sunlight exposure, associated with an increase in stomatal conductance. The variable fluorescence/maximal fluorescence ratio decreases after exposure to acclimation times of 6.0, 9.0 and 12 hours, particularly in mahogany. Mahogany presents greater growth rates and leaf production than jatoba when exposed to full sunlight. Macronutrient concentrations, except of nitrogen and phosphorus, are higher in jatoba than in mahogany. Mahogany, a fast-growing species, acclimates to full sunlight primarily through the production of new leaves, while jatoba, a slow-growing species, acclimates to full sunlight based on its leaf traits, especially on its low specific leaf area (high leaf thickness).

Index terms: *Hymenaea courbaril*, *Swietenia macrophylla*, leaf gas exchange, specific leaf area, stomatal density.

Fotossíntese, crescimento e nutrientes foliares de mudas de mogno e jatobá aclimatadas à luz solar direta

Resumo – O objetivo deste trabalho foi avaliar como as espécies mogno e jatobá, com diferentes taxas de crescimento, respondem à aclimatação à luz solar plena durante o estágio juvenil. Mudas de mogno e jatobá, com três e oito meses de idade, respectivamente, foram cultivadas sob baixa luminosidade e expostas a seis tempos independentes de aclimatação à luz solar plena por 30 dias: 0,0 hora (controle), 1,5 hora (11h15–12h45), 3,0 horas (10h30–13h30), 6,0 horas (9h00–15h00), 9,0 horas (7h30–16h30) e 12,0 horas (6h00–18h00). A seguir as plantas foram transferidas a local aberto por 120 dias, o dia todo. Foram avaliadas trocas gasosas foliares, características foliares, crescimento da planta, alocação de biomassa e teores de nutrientes foliares. Em ambas as espécies, as taxas fotossintéticas aumentam com o tempo de exposição à luz solar plena, associado a um aumento na condutância estomática. A razão fluorescência variável/fluorescência máxima diminui após exposição ao

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Received
November 11, 2024

Accepted
April 01, 2025

How to cite
AZEVEDO, G.F. da C.; DIAS, D.P.; MARENCO, R.A. Photosynthesis, growth, and leaf nutrients of mahogany and jatoba seedlings acclimated to direct sunlight **Pesquisa Agropecuária Brasileira**, v.60, e03962, 2025. DOI: https://doi.org/10.1590/S1678-3921.pab2025.v60.03962.

tempo de aclimatação de 6,0, 9,0 e 12 horas, particularmente no mogno. O mogno apresenta maiores taxas de crescimento e produção de folhas do que o jatobá quando exposto à luz solar plena. As concentrações dos macronutrientes, exceto de nitrogênio e fósforo, são maiores no jatobá do que no mogno. O mogno, uma espécie de crescimento rápido, se aclimata à luz solar plena principalmente com base na produção de novas folhas, enquanto o jatobá, uma espécie de crescimento lento, se aclimata à luz solar plena com base em suas características foliares, especialmente sua baixa área foliar específica (alta espessura foliar).

Termos para indexação: *Hymenaea courbaril*, *Swietenia macrophylla*, trocas gasosas foliares, área foliar específica, densidade estomática.

Introduction

Understanding the ecophysiological and silvicultural aspects of tree species used for reforestation, conservation, and degraded lands reclamation is crucial, yet limited. This knowledge is particularly relevant given the large variation in photosynthetic performance among trees (Magalhães et al., 2014; Marenco et al., 2017) and ongoing effects of climate change. Thus, in tropical conditions, it becomes essential to study the effect of exposure to solar radiation and water shortage, on tree physiology, as they are primary factors influencing tree survival, growth, and development (Kaur & Asthir, 2017; Gjindali et al., 2021; Ribeiro et al., 2023). For shade-acclimated seedlings, for instance, sudden prolonged exposure to full sunlight causes photoinhibition of photosynthesis and, in extreme cases, irreversible leaf tissue damage due to photooxidative stress (Magalhães et al., 2009; Gjindali et al., 2021).

As sessile organisms, trees must adapt to changes in environmental conditions throughout their lifetime. During its ontogeny, for instance, a tree often experiences significant shifts in irradiance, transitioning from severe shading in the forest understory to full sunlight as it grows toward the canopy. Since individual plants cannot undergo genetic changes across generations like a population, their morphological and physiological modifications during development rely on phenotypic plasticity. The extent of these ecophysiological adjustments, however, varies considerably among species, depending on their acclimation potential which determines diverse biochemical and anatomical responses to microclimatic variability (Marenco et al., 2017).

Mahogany (*Swietenia macrophylla* King) is a fast-growing, light-demanding species with light wood density of approximately 0.5 g cm^{-3} (Free et al., 2014; Arisandi et al., 2023). Its stem diameter at breast height (DBH) growth rate varies with tree size, ranging from 5 mm yr^{1}, for a 40 cm DBH tree, to 20 mm yr^{-1} for a 90 cm DBH tree (Forero-Montaña et al., 2021). This species can reach 50 m in height and 2 m in DBH, though trees as tall as 60 m have been reported (Susilowati et al., 2018).

Jatoba *(Hymenaea courbaril* L.), in contrast, is a slow-growing species characterized by a high wood density of 0.76 to 0.95 g cm^{-3}. Similar to mahogany, its radial growth rate varies with tree size. The fastest diameter growth (4 to 6 mm year^{1}) occurs in medium size trees (25 to 45 cm DBH); whereas the smallest (10 cm DBH) and largest trees (>100 cm DBH) grow very slowly, at about 2 mm year^{1} (Grogan & Schulze, 2012).

Although considerable research has been conducted on mahogany and jatoba, how these important tropical trees respond to sudden exposure to full sunlight remains largely unclear. Such abrupt exposure can arise during natural canopy gap formation or when trees are transplanted from greenhouses or nurseries to open fields. Light acclimation can be assessed by measuring a leaf's maximum quantum yield, known as the variable fluorescence/maximal fluorescence (F_v/F_m) ratio, which has a maximum baseline of approximately 0.83 in non-stressed, dark-adapted leaves. Very low F_v/F_m values, or around 0.2 to 0.3, may indicate photoinhibition, also termed chronic photoinhibition, if the ratio fails to recover overnight (Magalhães et al., 2009; Didaran et al., 2024).

Besides, the photoinhibitory quenching (qI) associated with chronic photoinhibition, the excess of light energy absorbed by a leaf, such as the one not used in photochemical reactions, can be dissipated by several nonphotochemical mechanisms, energy quenching (qE), related to lumen/stroma ΔpH, and qZ, related to the xanthophyll cycle (Asthir, 2015; Nawrocki et al., 2021). However, if the photoprotective mechanisms fail to prevent the production of reactive oxygen species (ROS), photooxidative stress can lead to extreme damage and ultimately leaf death (Magalhães et al., 2009; Asthir, 2015).

The objective of this work was to assess how mahogany and jatoba, species with different growth rates, respond to full sunlight acclimatization during their juvenile stage, with expected variations in photosynthesis, growth, and leaf nutrient.

Materials and Methods

The experiment was carried out at the V8 Campus of Instituto Nacional de Pesquisas da Amazônia (INPA), in the municipality of Manaus, in the state of Amazonas, Brazil (03°05'30"S, 59°59'35"W, at 93 m of altitude). This region has a tropical equatorial climate (Af) according to Köppen-Geiger's classification, with a mean annual temperature of 26.9°C and a mean annual rainfall of 2,256 mm, data registered from 1931 to 2020 (INMET, 2025).

For this experiment, seedlings of mahogany and jatoba were grown from seeds. Mahogany seeds originated from mother trees at INPA V8 Campus in Manaus. Jatoba seeds were collected from trees at INPA Estação Experimental de Fruticultura Tropical in Manaus (02°37'S, 60°02'W).

After germination, three-month-old mahogany seedlings and eight-month-old jatoba seedlings were kept under greenhouse conditions until the experiment started; the jatoba plants were older due to their slower growth rate. In the greenhouse, the conditions were: 0.8 mol m^{-2} day^{-1} of photosynthetic active radiation (PAR), 27°C, and 80% of relative humidity (RH). Plants were cultivated in 10 L polyethylene bags containing substrate composed of 60% forest soil from the upper 20-cm-soil layer, 30% organic matter, and 10% humus. This substrate was amended with a slow-release fertilizer of 1.7 g kg^{-1} substrate, containing 16% N, 8% P, 12% K, 2% Mg, 4% S, and trace of micronutrients.

When the seedlings of both species reached 12 cm in height, they were exposed for 30 days to six independent full sunlight acclimation times: 0.0 hour (control), 1.5 hour (11h15–12h45), 3.0 hours (10h30–13h30), 6.0 hours (9h00–15h00), 9.0 hours (7h30–16h30), and 12.0 hours (6h00–18h00). Then the plants were transferred to outdoor conditions the whole day for 120 daays, for a total experimental period of 150 days. In the acclimation area, shade of existing trees provided morning and late afternoon sun protection. Following their daily-predetermined light acclimation treatment, plants were then returned to the greenhouse. PAR, temperature, and relative humidity (RH) were recorded at 15-minute intervals using specific sensors: LI-191SA (LI-Cor, Lincoln, NE, USA) and Humitter 50U-50Y (Vaisala Oyj, Vantaa, Finland) connected to a LI- 1400 data logger (LI-Cor Lincoln, NE, USA) during the experimental period from July 2010 to December 2011. At the end of the 30-day acclimation period, leaf gas exchange was measured.

An LI-6400 XT portable gas-exchange system (LI-Cor, Lincoln, NE, USA) was used to measure light-saturated photosynthesis ($P_{N\text{-}sat}$), stomatal conductance (g_s), and leaf transpiration (E). Measurements were taken on two fully expanded leaves from the upper half of the stem of each plant. For gas exchange and F_v/F_m measurements, recently fully expanded leaves were used when available. Data were collected daily between 8h and 14h, after the pre-defined acclimation periods. During gas exchange measurements, conditions were maintained at a temperature of 27±1ºC, RH of 70±2%, a light intensity or light saturation of 1,000 µmol m^{-2} s^{-1} and 380 ppm CO_2. Water use efficiency (WUE), calculated as $P_{N\text{-}sat}/E$ ratio, and the intrinsic WUE (WUEi), determined by $P_{N\text{-}sat}/g_s$ ratio, were also obtained. Additionaly, the relative leaf chlorophyll content (SPAD) values were assessed using a SPAD-502 meter (Konica Minolta, Tokyo, Japan).

Fluorescence parameters, including initial fluorescence (F_0) and maximal fluorescence (F_m) were determined on intact leaves using a PEA MK2-9600 portable fluorometer (Hansatech Instruments, Norfolk, UK) during the whole experimental period. The software of the instrument calculated F_0 by extrapolating the initial data points (8–24) to time zero, the start of illumination. The F_m value was obtained by applying a saturation pulse (650 nm) of 3,000 µmol m^{-2} s^{-1} to a 4-mm diameter leaf disc. Subsequently, the variable fluorescence (F_v) and the F_v/F_m ratio were computed, as follows:

$$\frac{F_v}{F_m} = \frac{[F_m - F_0]}{F_m}$$

At the end of the whole experimental period (150 days) we measured, specific leaf area SLA), stomatal density and stomatal size, as well as leaf nutrient content. Plant height (H), measured from base to

DOI: 10.1590/S1678-3921.pab2025.v60.03962

apex, and diameter (D), measured at 5 cm from the ground level, were monthly recorded during the whole experimental period. Stem diameter was assessed using digital calipers. Monthly leaf production was assessed by counting the number of leaflets per plant. To determine biomass (dry matter), plant organs, such as leaves, stems, and roots, were oven-dried at 72°C to a constant mass for approximately 72 hours. Leaf area was measured with an LI-3050 leaf area meter (LI-Cor, Lincoln, NE, USA). Specific leaf area (SLA) was measured from leaves collected at the end of the 120-day full sunlight exposure, as mentioned above. The relative growth rate (RGR) was calculated as the slope of the natural logarithm (ln) of whole-plant dry mass over time, using the following equation:

$$\mathrm{RGR}(\mathrm{mg\ g^{-1}\ dia^{-1}}) = 1000 \times \frac{\ln \mathrm{TDM}_2 - \ln \mathrm{TDM}_1}{\mathrm{t}_2 - \mathrm{t}_1}$$

where, TDM_1 and TDM_2 denote the whole-plant dry mass in grams. The difference between the beginning and end (t_1 - t_2) of the experimental periods represents the time interval in days. A factor of 1,000 was used to convert g to mg g^{-1} day^{-1}.

Stomatal density and stomatal size, which is estimated from guard cell length, were measured on two leaves per plant and five plants per species. Clear nail polish impressions, four per leaf, were taken from both the upper and lower leaf surfaces and used to determine stomatal density and size under a light microscope (Leica DM500, Leica Microsystems, Wetzlar, Germany). Stomatal density was assessed at 400 times magnification, with a field of view diameter of 0.495 mm, while stomatal size was measured at 1,000 times magnification on a sample of 15–20 stomata per leaf. An optical reticle with an accuracy of 1 µm, mounted on the eyepiece, was used for determining stomatal size and was calibrated against a micrometer slide (Nachet, Paris, France).

Plant material was oven-dried at 72°C to constant mass, for approximately 72 hours, and then ground for mineral concentration determination. Leaf nitrogen was quantified using the classic Kjeldahl method. Calcium and magnesium concentrations were measured by Avanta Sigma atomic absorption spectrophotometry (GBC Scientific Equipment, Dandenong, Australia), while potassium was determined by B462 flame photometry (Micronal, São Paulo, SP, Brazil). Phosphorus levels were analyzed using the ammonium molybdate method, with absorbance measured at 660 nm with a Helios β spectrophotometer (Thermo Spectronic, Rochester, NY, USA).

The experiment utilized a completely randomized design in 2 × 6 factorial arrangement with five replicates. The factors were species, with two levels, and acclimation times, with six levels. Prior to statistical analysis, data were tested for normality using the Shapiro-Wilk's test, at an α of 0.05, and log-transformed [log (x+1)] when necessary. Subsequently, data were subjected to ANOVA, and means were compared using the Fisher-LSD's test. All statistical analyses were performed using SigmaPlot 11.0 (Systat Software, San Jose, CA, USA), at 5% probability.

Results and Discussion

During the experimental period, the outdoor area used for acclimation treatments exhibited a mean PAR of 17.9 mol m^{-2} day^{-1}, an average temperature of 27.5°C and a relative humidity (RH) of 73.8%. For both species, the 30-day acclimation periods positively impacted light-saturated photosynthesis ($P_{\text{N-sat}}$) (Figures 1 A and B). However, the effect of acclimation time varied between species. Although both species initially displayed similar photosynthetic rates after 0.0–1.5 hours of full sunlight exposure, mahogany achieved higher $P_{\text{N-sat}}$ values than jatoba during the highest acclimation period.

When plants with shade leaves are exposed to full sunlight, they typically acclimate by producing smaller, thicker leaves that are better adapted to high light conditions and exhibit increased photosynthetic capacity (Magalhães et al., 2009; Gjindali & Johnson, 2023). This acclimation process involves a gradual decrease in the plant's investment in light-harvesting complexes, coupled with a simultaneous increase of the concentration of enzymes associated with the Calvin cycle (Poorter et al., 2019; Gjindali et al., 2021). Furthermore, shade leaves exposed to high irradiance increase their photosynthetic capacity through morphological changes, such as developing thicker leaves and leaf blades with more cell layers than those grown in shade (Gjindali & Johnson, 2023).

The positive effect of the acclimation period on $P_{\text{N-sat}}$ was associated with an increase in stomatal conductance, which was observed to be greater in light-acclimated plants than in control plants (Figures 1 C and D). There is a positive correlation between photosynthesis and stomatal conductance, as the internal CO_2 concentration depends on the aperture of the stomatal pore (Suwannarut et al., 2023; Fernando & Marenco, 2023). Moreover, leaves produced during the acclimatization treatments, in both mahogany and jatoba, exhibited higher stomatal density and smaller stomata with shorter guard cell length than control plants. These morphological changes may have affected the velocity of stomatal opening and closing (Marenco et al., 2017).

Water use efficiency (WUE) in mahogany (Figure 2 A) greatly increased with longer acclimation times, which was not observed in jatoba (Figure 2 B). The intrinsic water use efficiency (WUE_i) in mahogany (Figure 2 C) varied considerably, consistent with the impact of acclimation time on both $P_{N\text{-}sat}$ and g_s. Despite this intra-species variation, overall WUE_i was similar both between species (p=0.16) and acclimation times (p=0.56) (Figure 2 D). The observed increase in WUE in mahogany plants between 9 and 12 hours

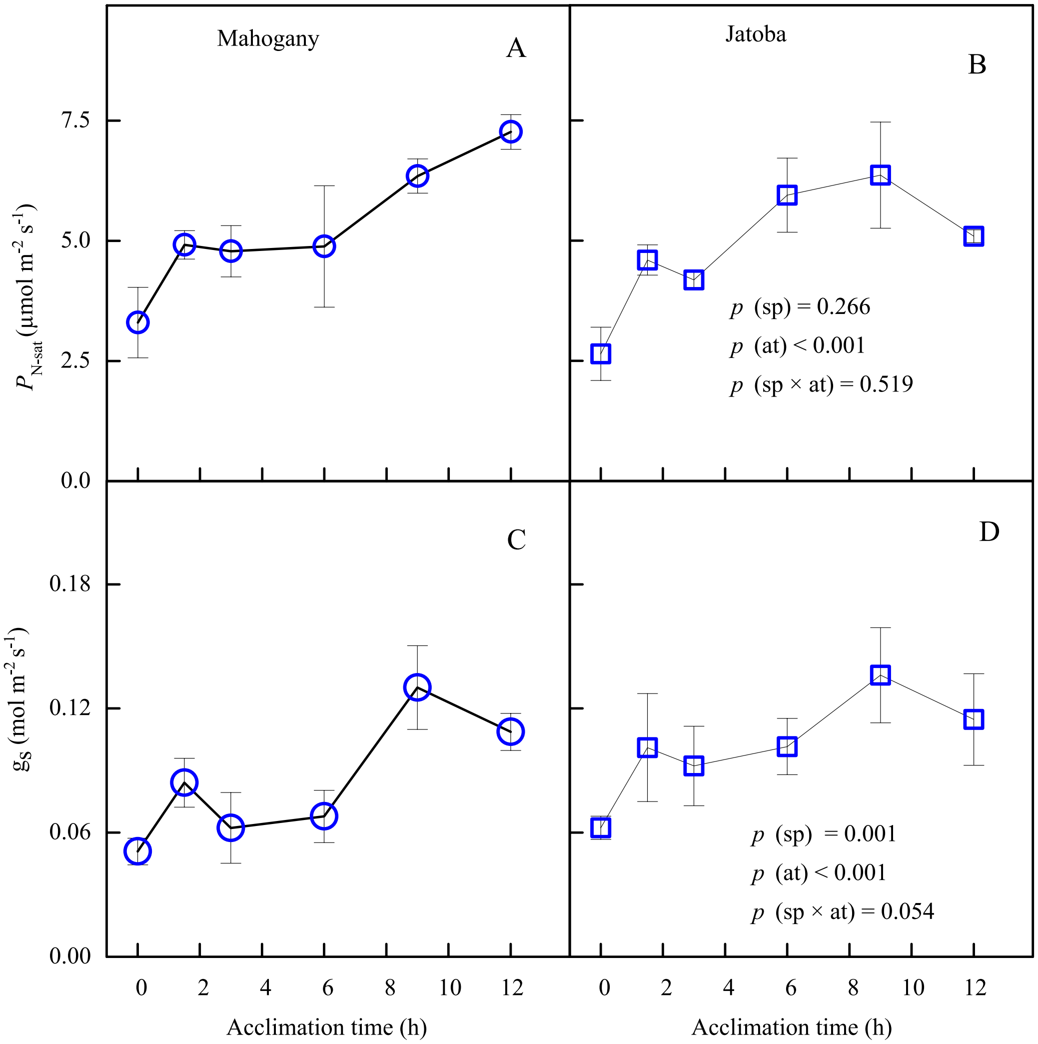

Figure 1. Light saturated photosynthesis ($P_{N\text{-}sat}$) and stomatal conductance (g_s) in seedlings of four-month-old mahogany (A and C) and nine-month-old jatoba (B and D) as a function of the acclimation time under full sunlight for 30 days. *p* (sp), probability for the effect of species; *p* (at), probability for the effect of the acclimation time; *p* (sp × at), effect of the interaction: species × acclimation time.

of acclimation time was attributed to the production of new acclimated leaves with greater photosynthetic capacity. This enhancement in WUE is significant, as water availability is a critical factor influencing photosynthetic rates and crop productivity; thus, species with higher WUE values can perform better in environments with less rainfall (Zhou et al., 2019). Additionally, WUE is often targeted for improving crop performance. However, it should be noted that a higher WUEi frequently comes at the expense of a reduced carbon assimilation (Lawson & Blatt, 2014), as an increase in WUEi is typically associated with a decrease in stomatal conductance.

During the first weeks after the exposure to full sunlight, the F_v/F_m values decreased, with the effect of acclimation treatments being more pronounced in mahogany (Figure 3). Specifically in mahogany, the F_v/F_m ratio significantly decreased when the seedling were exposed to full sunlight for more than 3 hours per day, reaching values as low as 0.2 by the end of the first two weeks (Figure 3 B). In contrast, in jatoba, the F_v/F_m value only occasionally decreased below 0.6 (Figure 3 D), which indicates the absence of chronic photoinhibition (Magalhães et al., 2009; Gjindali & Johnson, 2023).

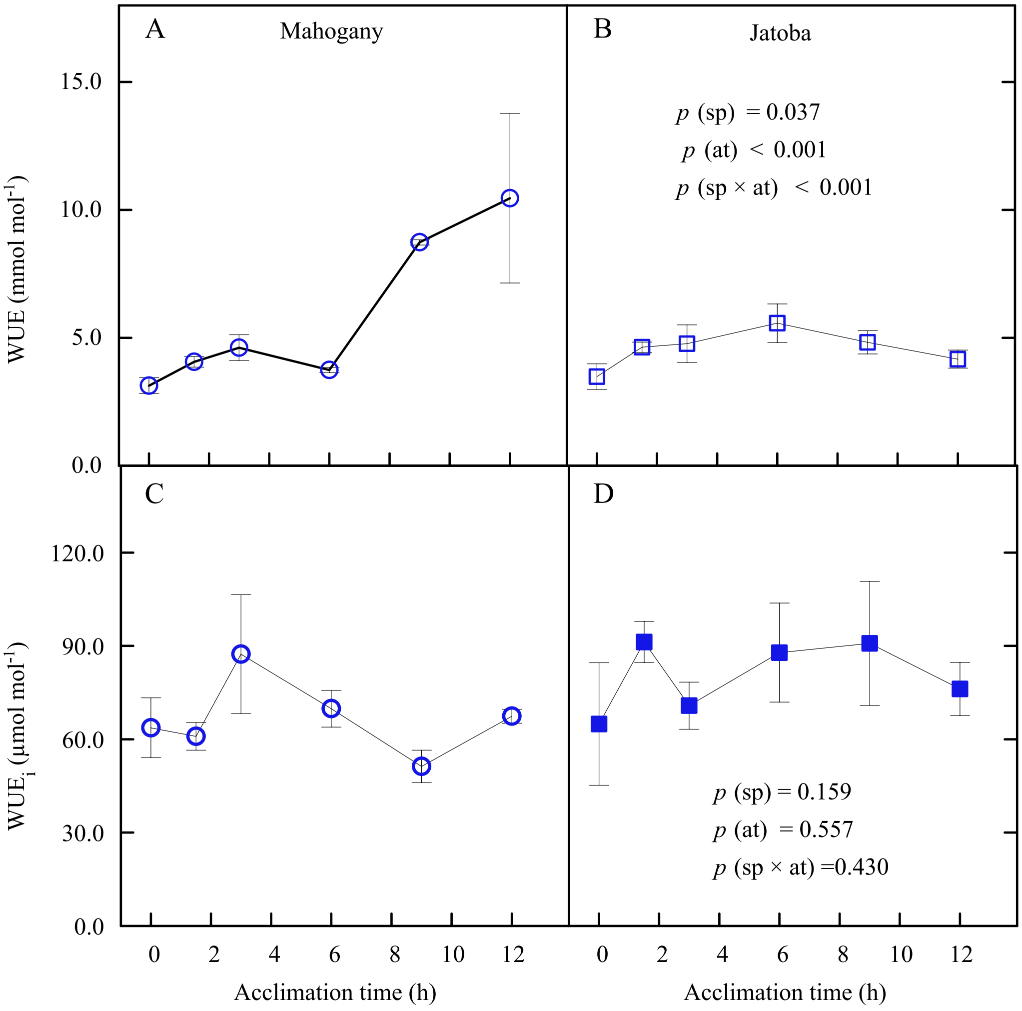

Figure 2. Water use efficiency (WUE) and intrinsic water use efficiency (WUE_i) in seedlings of four-month-old mahogany (A and C) and nine-month-old jatoba (B and D) as a function of the acclimation time under full sunlight for 30 days. *p* (sp), probability for the effect of species; *p* (at), probability for the effect of the acclimation time; *p* (sp × at), effect of the interaction: species × acclimation time.

Since photosynthesis rapidly responds to changes in light intensity, as irradiance increases, non-photochemical quenching (NPQ) mechanisms are quickly activated (Asthir, 2015; Gjindali et al., 2021). This rapid activation is vital for plants, so to prevent photo-oxidative damage and to adapt to changes in their light environment, plants develop direct and indirect mechanisms to detect and respond to excess light (Didaran et al., 2024). An increase in photosynthetic capacity reduces susceptibility to photodamage by enhancing photochemical activity, concurrently, elevated carotenoid concentrations, such as pigments associated with the xanthophyll cycle, contribute to improve NPQ efficiency (Asthir, 2015; Gjindali et al., 2021).

The activation of qE and the state transition quenching (qT) occurs on the scale of seconds to minutes, while the photoinhibitory quenching (qI) occurs on the scale of hours to days (Asthir, 2015; Gjindali et al., 2021). This rapid, short-term response to variations in light intensity complements the photosynthetic changes resulting from plant acclimation to irradiance, which occurs on time scales of weeks to months (Luo & Keenan, 2020). The sudden decrease of the F_v/F_m ratio down to very low values, approximately 0.2 to 0.3, indicates photoinhibition after exposure of

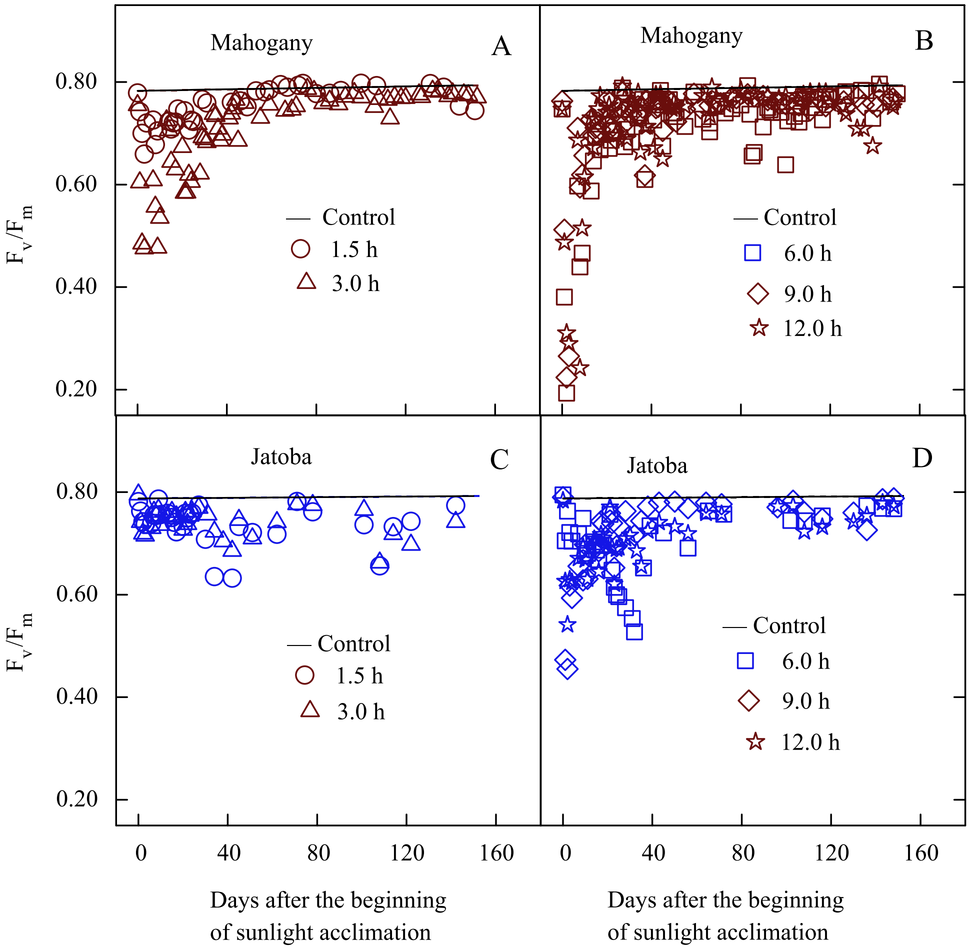

Figure 3. The F_v/F_m ratio in seedlings of mahogany (A and B) at three to eight months old over the measurement period and jatoba (C and D) at eight to 13 months old as a function of time. The seedlings were initially exposed to the acclimation times for 30 days, then they were transferred to outdoor conditions the whole day for 120 days. The acclimation treatments are: circle, 1.5 hour; triangle, 3.0 hours; square, 6.0 hours; diamond, 9.0 hours; and star, 12.0 hours. *p* (sp), probability for the effect of species; *p* (at), probability for the effect of the acclimation time; *p* (sp × at), effect of the interaction: species × acclimation time.

shade-grown leaves of tropical trees to full sunlight (Magalhães et al., 2009).

Exposure of shade leaves to full sunlight can lead to excessive concentrations of reactive oxygen species, which may cause severe photooxidative stress and ultimately leaf death (Magalhães et al., 2009; Gjindali et al., 2021). Under such challenging conditions, successful acclimation to intense light may rely on multiple strategies, such as the production of new leaves, as observed in *Minquartia guianensis* (Magalhães et al., 2009), as well as an increase in leaf thickness and energy dissipation via non-photochemical mechanisms, as noted in several tropical tree species (Cifuentes & Moreno, 2022). Consistent with these strategies, a high production of leaves was observed in mahogany, reaching approximately 30 leaflets per month (Figure 6), when compared to jatoba. Furthermore, specific leaf area was intrinsically lower in jatoba than in mahogany.

F_v/F_m ratio values around 0.2 were also observed in *M. guianensis* by Magalhães et al. (2009). These values were associated with photo-oxidation of the leaf tissue, which evolved from chlorotic spots to necrotic spots within a week from the initial exposure to full sunlight. Thus, it can be inferred that any increase in F_v/F_m during acclimation period occurred in newly produced leaves. Photodamage and photo-oxidation occur when the amount of light absorbed by the leaf exceeds its energy requirements to drive photosynthesis and when the photoprotective mechanisms fail to prevent the detrimental effect of excessive ROS production (Gjindali et al., 2021).

Jatoba seedling survived all acclimation times, spanning 0 to 12 hours under full sunlight. In contrast,

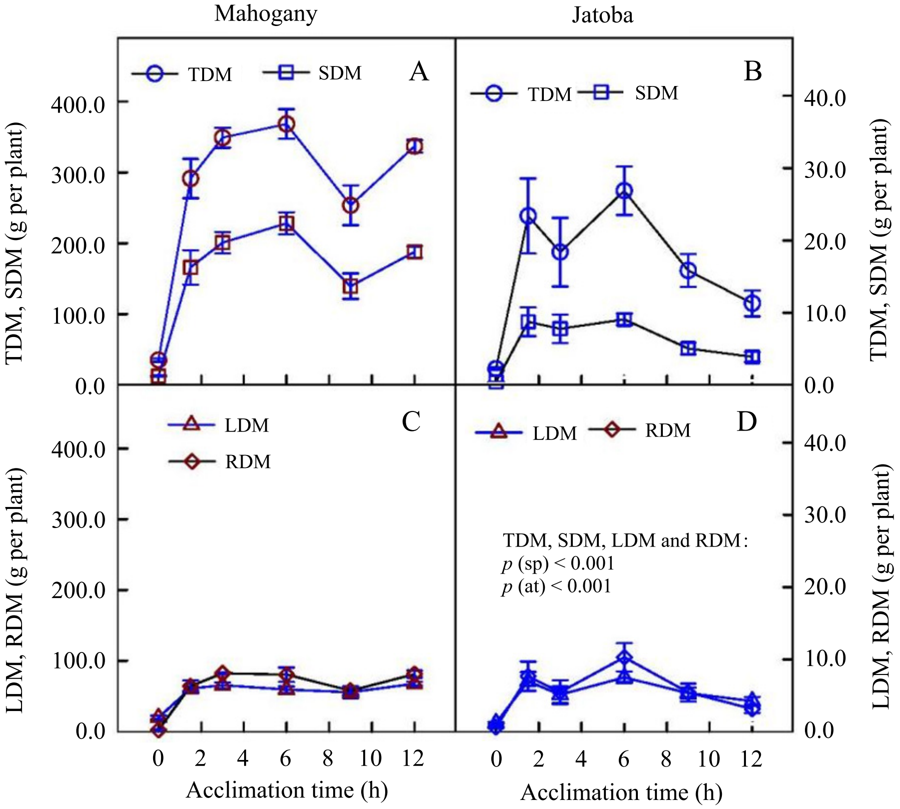

Figure 4. Total dry matter (TDM), stem dry matter (SDM), leaf dry matter (LDM), and root dry matter (RDM) as a function of the acclimation time in seedlings of eight-month-old mahogany (A and C) and 13-month-old jatoba (B and D). *p* (sp), probability for the effect of species; *p* (at), probability for the effect of the acclimation time; *p* (sp × at), effect of the interaction: species × acclimation time. The seedlings were initially exposed to the acclimation times for 30 days, then they were transferred to outdoor conditions the whole day for 120 days. Note that the y-scales are different.

two out of the five mahogany plants collapsed after three or more hours of full sunlight exposure. Although the total plant biomass was greater in mahogany than in jatoba (Figure 4 A and B), both species, when exposed to sunlight, allocated most of the biomass to the stems, with a similar proportion directed to leaves and roots.

In both species, light acclimation increased the dry matter of all plant organs (Figure 4 A and D). However, the increase in dry mass was more evenly distributed in jatoba compared to mahogany, which notably invested more in its stem than in its leaves and roots (Figure 4 A). This pattern is consistent with the higher growth rates observed in mahogany than in jatoba (Figure 5 A and B).

Specific leaf area (SLA) was higher in mahogany than in jatoba. In both species, the largest SLA values were observed in control plants, which were not exposed to full sunlight (Figure 5 C). The shoot/root ratio was higher in mahogany than in jatoba (Figure 5 D), largely due to mahogany's greater stem biomass allocation compared to jatoba, this difference was especially pronounced in control plants. Furthermore, both monthly leaf production and the relative growth rate (RGR) were higher in mahogany than in jatoba. In both species, the larger values for these parameters were observed in plants exposed to full sunlight (Figure 6 A and B).

SLA reflects leaf thickness and density; consequently, thick leaves typically exhibit low SLA values. This is particularly important for jatoba, as the exposure to direct sunlight resulted in only a moderate decrease in F_v/F_m. This observation indicates that leaf thickness inferred from SLA is a relevant factor for this species in mitigating photooxidative stress caused by high irradiance in shade-acclimated leaves. Indeed, the structural modifications of a leaf are among the

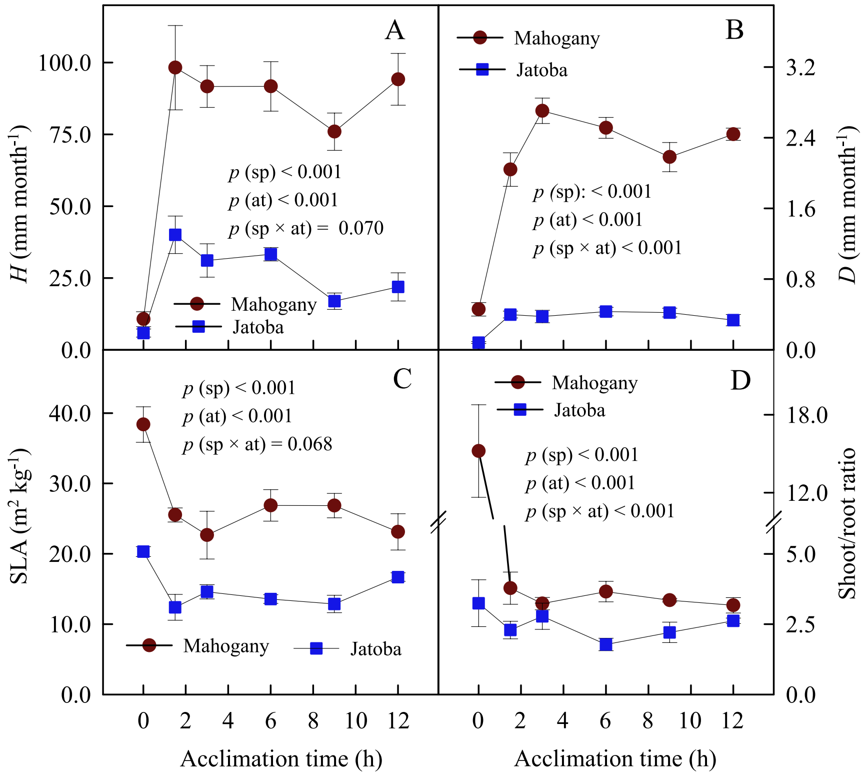

Figure 5. Height growth rate (*H*) (A) and diameter growth rate (*D*) (B), specific leaf area (SLA) (C), and shoot/root ratio (D) in seedlings of eight-month-old mahogany (circle) and 13-month-old jatoba (square) as a function of the acclimation times. *p* (sp), probability for the effect of species; *p* (at), probability for the effect of the acclimation time; *p* (sp × at), effect of the interaction: species × acclimation time. The seedlings were initially exposed to the acclimation times for 30 days, then they were transferred to outdoor conditions the whole day for 120 days.Note that the y-scales are different.

most relevant mechanisms for acclimation to changing light conditions. Increased leaf thickness is usually associated with an increased number of chloroplasts per unit leaf area and more cell layers (Gjindali & Johnson, 2023).

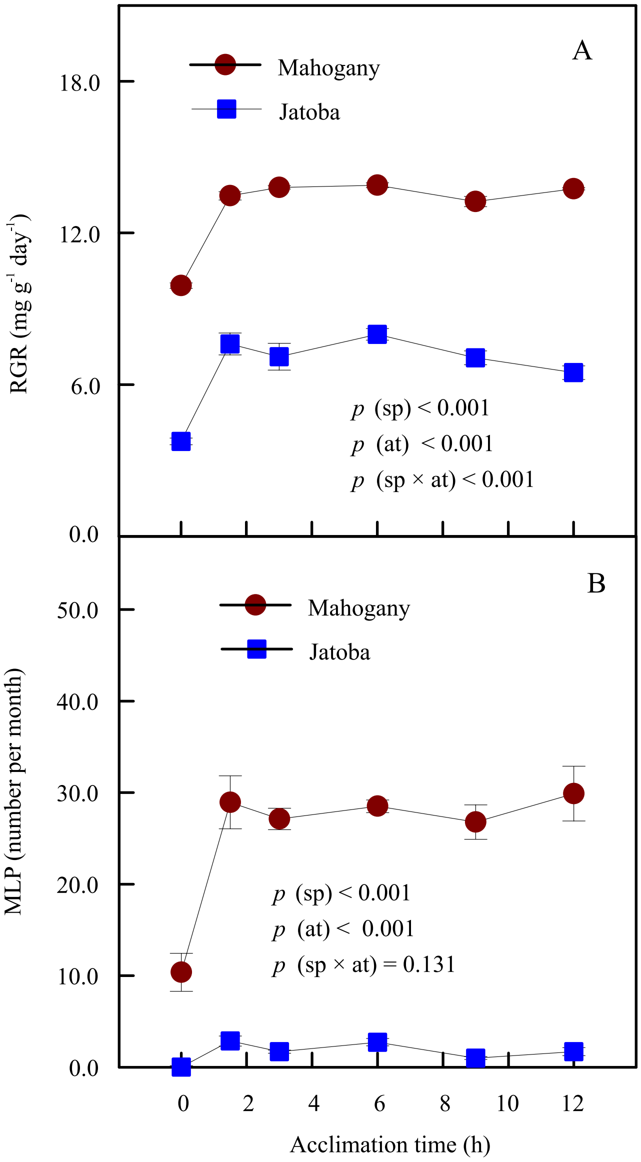

Figure 6. Relative growth rate (RGR) (A) and monthly leaflet production (MLP) (B) in seedlings of eight-month-old mahogany and 13-month-old jatoba as a function of the acclimation times. p (sp), probability for the effect of species; p (at), probability for the effect of the acclimation time; p (sp × at), effect of the interaction: species × acclimation time. Further information as described in Figure 5.

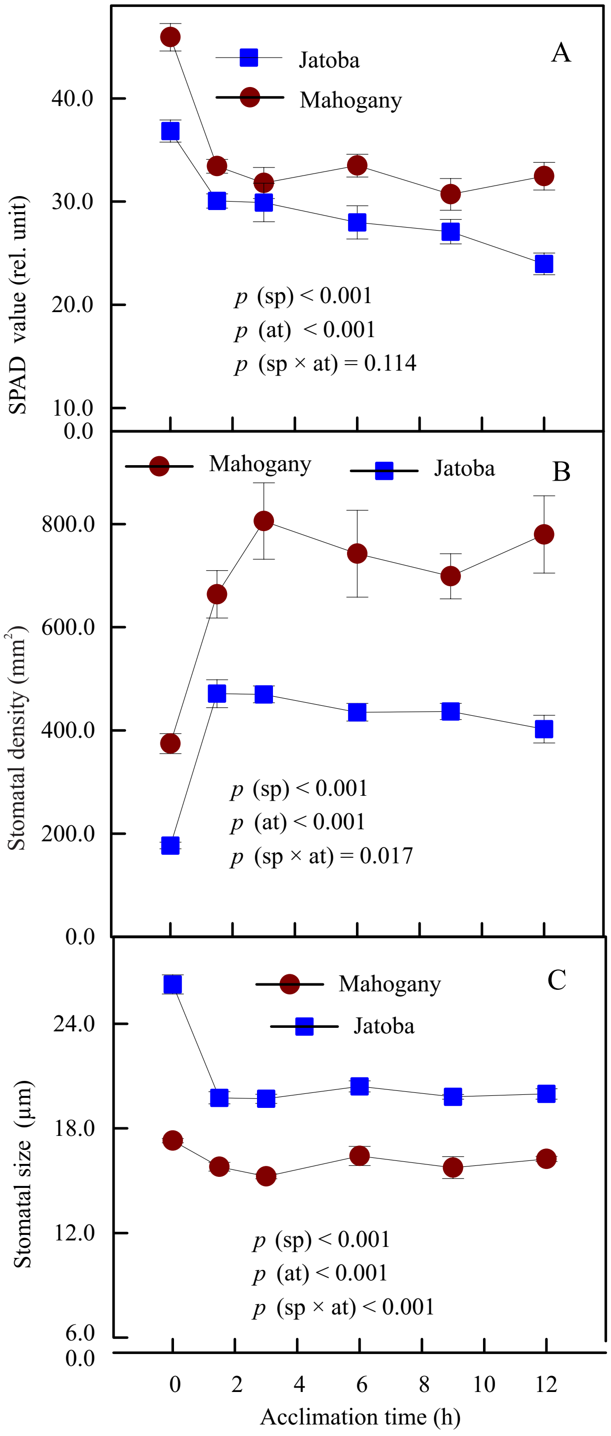

Figure 7. SPAD value (A), stomatal density (B), and stomatal size (estimated from guard cell length) (C) in seedlings of eight-month-old mahogany (circle) and 13-month-old jatoba (square) as a function of the acclimation times. p (sp), probability for the effect of species; p (at), probability for the effect of the acclimation time; p (sp × at), effect of the interaction: species × acclimation time. Further information as described in Figure 5.

Under high irradiance, the grana thylakoid to stroma thylakoid ratio typically decreases, and hence, chlorophyll content per unit leaf area often increases in sun leaves (Lichtenthaler & Babani, 2022). This trend was not observed in this experiment. Compared with control plants, leaves exposed to full sunlight were relatively younger, and chlorophyll content increased with leaf age (Pereyra et al., 2014). This explains the higher SPAD values measured in shade leaves of control plants (Figure 7 A).

Stomatal density followed a similar trend to that of SLA. However, remarkable changes were observed in plants acclimated to direct light. In contrast to SLA, stomatal size was greater in jatoba than in mahogany. Conversely, stomatal density was higher mahogany than in jatoba (Figure 7 B and C), which seems to be an acclimation mechanism to increased irradiance. These findings suggest that mahogany has greater leaf plasticity than jatoba in response to changes in irradiance, performing well under high light conditions by producing new leaves.

Macronutrient concentrations, with the exception of nitrogen and phosphorus, were higher in jatoba than in mahogany (Figure 8). Acclimation time led to a reduction in most macronutrients in both species. An exception was observed in the magnesium (Mg) concentration of mahogany, which did not follow this general reduction trend.

High leaf thickness, a xeromorphic feature induced by environmental factors like water stress or high irradiance, is commonly associated with more lignified sclerenchyma and epicuticular waxes (Bieras & Sajo, 2009). These structural traits can influence leaf nutrient concentration per unit leaf mass. Consequently, jatoba may present less nutrient per unit leaf mass than mahogany due to the presence of more lignified tissues.

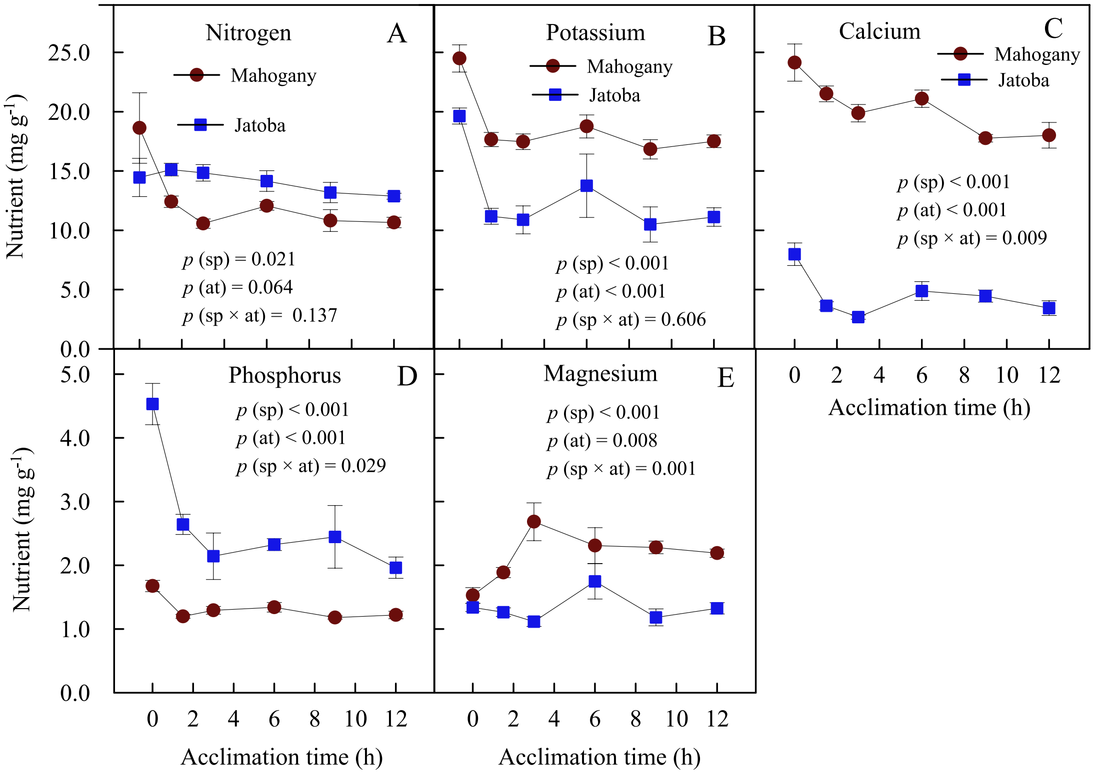

Figure 8. Leaf nitrogen (A), potassium (B), calcium (C), phosphorus (D), and magnesium (E) in seedlings of eight-month-old mahogany (circle) and 13-month-old jatoba (square) as a function of the acclimation time. *p* (sp), probability for the effect of species; *p* (at), probability for the effect of the acclimation time; *p* (sp × at), effect of the interaction: species × acclimation time. Further information as described in Figure 5.

The lower concentrations of nitrogen (N) and phosphorus (P) in mahogany's thinner leaves compared to jatoba's thicker leaves (Figure 8 A and D) can be attributed to differences in leaf production rates. Mahogany produced leaves at twice the rate of jatoba (Figure 6), and both elements are critical for leaf production. N is a key component of proteins, and P is essential for cellular energy. As both species received the same amount of nutrients, it is likely that the available N and P in mahogany was in relatively lower amounts to meet the needs for leaf production. Interestingly, this effect was not observed for other elements, like potassium (K), calcium (Ca), and Mg (Figure 8 B, C, and E), indicating that the relative amounts were sufficient to meet the demands of both species.

With the same amount of P applied to both species, the P content in mahogany was about half of that found in jatoba, which can be attributed to a dilution effect resulting from mahogany's high leaf production. Notably, this lower P concentration did not affect photosynthesis, because most cellular P is stored in vacuoles and are mobilized from them to meet the P requirement for enzyme reactions in the cytosol (Hawkesford et al., 2012). Leaf nutrient concentrations, particularly P and K, measured in this experiment are higher than those often reported for Amazonian trees in their natural environment (Marenco et al., 2024). This difference is not unexpected, as the substrate for plant growth in this potted experiment was amended, as previously described.

The exposure to full sunlight significantly affects plant responses, influencing their morphology, chemistry, physiology, growth, and reproduction (Poorter et al., 2019). The results of this study show that changes in leaf traits are crucial for seedlings to flourish under full sunlight. This is important given that seedling establishment is a critical phase during plant growth in reforestation projects. Adjusting leaf traits, such as stomatal density and size in response to increased light intensity can be used in biotechnology projects. This approach may enhance plant acclimation capability in response to physical environment modifications, including increased temperatures, water deficits, and atmospheric dryness, a relevant consideration in the current global climate change scenario.

Conclusions

1. Seedlings of mahogany (*Swietenia macrophylla*) and jatoba (*Hymenaea courbaril*) exhibit distinct strategies for acclimation to sunlight.
2. Mahogany, a fast-growing species, acclimates to full sunlight primarily through the production of new leaves.
3. Jatoba, a slow-growing species, acclimates to full sunlight based on its leaf traits, especially its low specific leaf area, which indicates high leaf thickness.
4. Stomatal density and stomatal size are highly responsive to changes in light conditions in both species. Consequently, stomatal conductance and light-saturated photosynthesis increase in both species as a result of light acclimation.
5. Macronutrient concentrations, except nitrogen and phosphorus, are higher in jatoba than in mahogany.

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Chief editor: Edemar Corazza
Edited by: Célia Tremacoldi

Data availability statement

Data available upon request: research data are only available uponreasonable request to the corresponding author.

Declaration of use of AI technologies

No generative artificial intelligence (AI) was used in this study.

Conflict of interest statement

The authors declare no conflicts of interest.

Acknowledgments

To Instituto Nacional de Pesquisas da Amazônia (INPA), Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM), and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), for support (grant number: 306801/2025-6); and to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), for financing, in part, this study (Finance Code 001).

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