

Ecophysiological Response to Increased Photosynthetic Photon Flux Density (PPFD) in *Handroanthus chrysanthus* (Jacq.) S.O. Grose and *Swietenia macrophylla* King Seedlings Under Amazonian Conditions

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Abstract

Handroanthus chrysanthus and *Swietenia macrophylla* are ecologically and economically significant tree species whose populations have declined due to high demand for their timber, adversely affecting their natural regeneration. This study aimed to evaluate the ecophysiological response to increased photosynthetic photon flux density (PPFD) in *H. chrysanthus* and *S. macrophylla* seedlings under Amazonian conditions. Assimilation measurements (A) were performed using a portable iFL-LCpro-SD system. The evaluation of A in response to increased PPFD ranged from 25 to 1800 $\mu\text{mol m}^{-2}\text{s}^{-1}$. Water use efficiency (WUE) was calculated as the ratio between A and the transpiration rate (E). *S. macrophylla* exhibited a significantly higher maximum photosynthetic assimilation rate (A_{max} , $9.4 \pm 0.52 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) compared to *H. chrysanthus* ($6.18 \pm 0.17 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $p < 0.05$), indicating greater carbon fixation efficiency. *S. macrophylla* showed a maximum WUE (WUE_{max}) of $13.17 \pm 0.24 \mu\text{mol mmol}^{-1}$ at 600 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFD, while *H. chrysanthus* reached its WUE_{max} ($6.16 \pm 0.23 \mu\text{mol mmol}^{-1}$) at 750 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFD. These results suggest that *S. macrophylla* exhibits higher WUE under high irradiance conditions, potentially due to more efficient stomatal regulation and an optimized balance between carbon fixation and water loss via transpiration.

Keywords: gas exchange, light intensity, photosynthesis, reforestation



Respuesta ecofisiológica al incremento de la densidad de flujo de fotones fotosintéticos (PPFD) en plántulas de *Handroanthus chrysanthus* (Jacq.) S.O. Grose y *Swietenia macrophylla* King bajo condiciones amazónicas

Resumen

Handroanthus chrysanthus y *Swietenia macrophylla* son especies arbóreas de gran importancia ecológica y económica cuyas poblaciones se han visto reducidas debido a la alta demanda de su madera, lo que afecta negativamente su regeneración natural. Este estudio tuvo como objetivo evaluar la respuesta ecofisiológica al incremento de la densidad de flujo de fotones fotosintéticos (PPFD) en plántulas de *H. chrysanthus* y *S. macrophylla* bajo condiciones amazónicas. Las mediciones de asimilación (A) se realizaron utilizando un sistema portátil iFL-LCpro-SD. La evaluación de A en respuesta al aumento de PPFD abarcó un rango de 25 a 1800 $\mu\text{mol m}^{-2} \text{s}^{-1}$. La eficiencia en el uso del agua (WUE) se calculó como la relación entre A y la tasa de transpiración (E). *S. macrophylla* presentó una tasa máxima de asimilación fotosintética (A_{max}) significativamente mayor ($9,4 \pm 0,52 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) en comparación con *H. chrysanthus* ($6,18 \pm 0,17 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $p < 0,05$), lo que indica una mayor eficiencia en la fijación de carbono. *S. macrophylla* alcanzó su WUE máxima (WUE_{max}) de $13,17 \pm 0,24 \mu\text{mol mmol}^{-1}$ a 600 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ de PPFD, mientras que *H. chrysanthus* alcanzó su WUE_{max} ($6,16 \pm 0,23 \mu\text{mol mmol}^{-1}$) a 750 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ de PPFD. Estos resultados sugieren que *S. macrophylla* presenta una mayor eficiencia en el uso del agua bajo condiciones de alta irradiancia, posiblemente debido a una regulación estomática más eficiente y un balance optimizado entre la fijación de carbono y la pérdida de agua por transpiración.

Palabras clave: intercambio gaseoso, intensidad lumínica, fotosíntesis, reforestación

Resposta ecofisiológica ao aumento da densidade de fluxo de fótons fotossintéticos (PPFD) em plântulas de *Handroanthus chrysanthus* (Jacq.) S.O. Grose e *Swietenia macrophylla* King sob condições amazônicas

Resumo

Handroanthus chrysanthus e *Swietenia macrophylla* são espécies arbóreas de grande importância ecológica e econômica, cujas populações têm diminuído devido à alta demanda por sua madeira, impactando negativamente sua regeneração natural. Este estudo teve como objetivo avaliar a resposta ecofisiológica ao aumento da densidade de fluxo de fótons fotossintéticos (PPFD) em plântulas de *H. chrysanthus* e *S. macrophylla* sob condições amazônicas. As medições de assimilação (A) foram realizadas utilizando um sistema portátil iFL-LCpro-SD. A avaliação de A em resposta ao aumento de PPFD variou de 25 a 1800 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. A eficiência no uso da água (WUE) foi calculada como a razão entre A e a taxa de transpiração (E). *S. macrophylla* apresentou uma taxa máxima de assimilação fotossintética (A_{max}) significativamente maior ($9,4 \pm 0,52 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) em comparação com *H. chrysanthus* ($6,18 \pm 0,17 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $p < 0,05$), indicando maior eficiência na fixação de carbono. *S. macrophylla* alcançou sua eficiência máxima no uso da água (WUE_{max}) de $13,17 \pm 0,24 \mu\text{mol mmol}^{-1}$ a 600 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ de PPFD, enquanto *H. chrysanthus* atingiu sua WUE_{max} ($6,16 \pm 0,23 \mu\text{mol mmol}^{-1}$) a 750 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ de PPFD. Esses resultados sugerem que *S. macrophylla* apresenta maior eficiência no uso da água sob condições de alta irradiância, possivelmente devido a uma regulação estomática mais eficiente e um equilíbrio otimizado entre a fixação de carbono e a perda de água por transpiração.

Palavras-chave: troca gasosa, intensidade luminosa, fotossíntese, reflorestamento

1. Introduction

Handroanthus chrysanthus and *Swietenia macrophylla* are tree species of substantial ecological and economic relevance in Neotropical forests (Héctor et al., 2024; Herrera-Feijoo et al., 2023). Both species are currently listed in Appendix II of CITES, indicating that although they are not immediately threatened with extinction, their international trade must be regulated to prevent unsustainable exploitation (Ministerio del Ambiente, Agua y Transición Ecológica, 2024). *H. chrysanthus*, commonly known as the yellow trumpet tree, is valued for its hard

and durable timber, widely used in construction and furniture manufacturing (Kübler et al., 2020). Its mass flowering events in Ecuadorian dry forests also hold notable cultural and touristic importance, particularly within community-based ecotourism initiatives (Sánchez Amboage et al., 2016). In contrast, *S. macrophylla* (mahogany) is globally recognized for its high-quality wood and long-standing commercial demand (He et al., 2020).

The incorporation of these species into ecological restoration programs carries important ecological and socio-economic implications. From an ecological perspective, their establishment contributes to the recovery of forest structure, enhancement of ecosystem functions, and conservation of biodiversity in degraded tropical landscapes. From a socioeconomic standpoint, the sustainable production of premium timber from restored or managed systems offers significant economic opportunities, particularly for rural and Indigenous communities that depend on forest resources (de Oliveira Neves et al., 2024). Nevertheless, historical overharvesting and inadequate management strategies have jeopardized natural population resilience, threatening both the ecological sustainability of these species and the economic benefits associated with their high-value timber.

The Ecuadorian Amazon region, characterized by its high biodiversity and ecological complexity, offers unique environmental conditions that influence the growth and development of these species' seedlings (García-Quintana et al., 2020; Ureta-Leones et al., 2024). The photosynthetic photon flux density (PPFD) is a critical environmental factor affecting photosynthesis, water use efficiency, and, consequently, plant growth (Jin et al., 2024; Rosati et al., 2020). Studies on the ecophysiological response of seedlings to increasing PPFD are essential to understand how these species adapt to variations in light availability, particularly in Amazonian ecosystems where tree canopy cover significantly alters understory irradiance (Amaral et al., 2023; Debiasi et al., 2024; Yan et al., 2015).

Photosynthesis is the fundamental process through which plants convert light energy into chemical energy, enabling biomass production and plant growth (Dumais et al., 2025; Trugman & Anderegg, 2025). Understanding how *H. chrysanthus* and *S. macrophylla* respond to different PPFD levels is crucial for developing management strategies (planting zonation according to light requirements, canopy management to optimize incident PPFD, among others) that optimize their establishment and growth in ecological restoration programs. Moreover, this knowledge can aid in selecting appropriate sites for reforestation and implementing silvicultural practices that promote the natural regeneration of these species.

In this context, the objective of this research was to evaluate the ecophysiological response to increasing PPFD in *H. chrysanthus* and *S. macrophylla* seedlings under Amazonian conditions, as a contribution to forest restoration programs.

2. Materials and Methods

2.1 Study Area

The research was conducted at the Centro Experimental de Investigación y Producción Amazónica (CEIPA), 1°14'17.6" S 77°53'07.7" W) of the Universidad Estatal Amazónica, located in Arosemena Tola, Napo province, Ecuador (Figure 1). The center spans 2,848 hectares, of which at least 2,500 hectares are native forest. The region is characterized by a warm and humid climate, with an average annual temperature ranging between 24 and 25 °C. Average annual precipitation reaches 4,000 mm, with altitudes ranging from 580 to 990 meters above sea level and a relative humidity of 80% (Ureta-Leones et al., 2024). Seedlings of *H. chrysanthus* and *S. macrophylla* were cultivated under controlled nursery conditions at CEIPA for a period of four months. During this phase, standardized silvicultural practices were applied, including regular irrigation, phytosanitary control, and the use of enriched substrates, ensuring uniform and healthy initial development. These conditions minimized

environmental variability and ensured the physiological quality of the seedlings prior to field establishment. The planting site was selected based on the presence of remnant populations of the study species. Within a one-hectare area, a plantation was established using the enrichment method. The assessment of photosynthetic parameters was conducted when the seedlings were eight months old. *H. chrysanthus* had an average height of 60 ± 5 cm and a root collar diameter of 4 ± 0.7 cm, while *S. macrophylla* reached an average height of 50 ± 9 cm and a root collar diameter of 4 ± 0.3 cm. Both species grew in a shaded environment beneath the forest canopy, under which their ecophysiological performance was assessed.

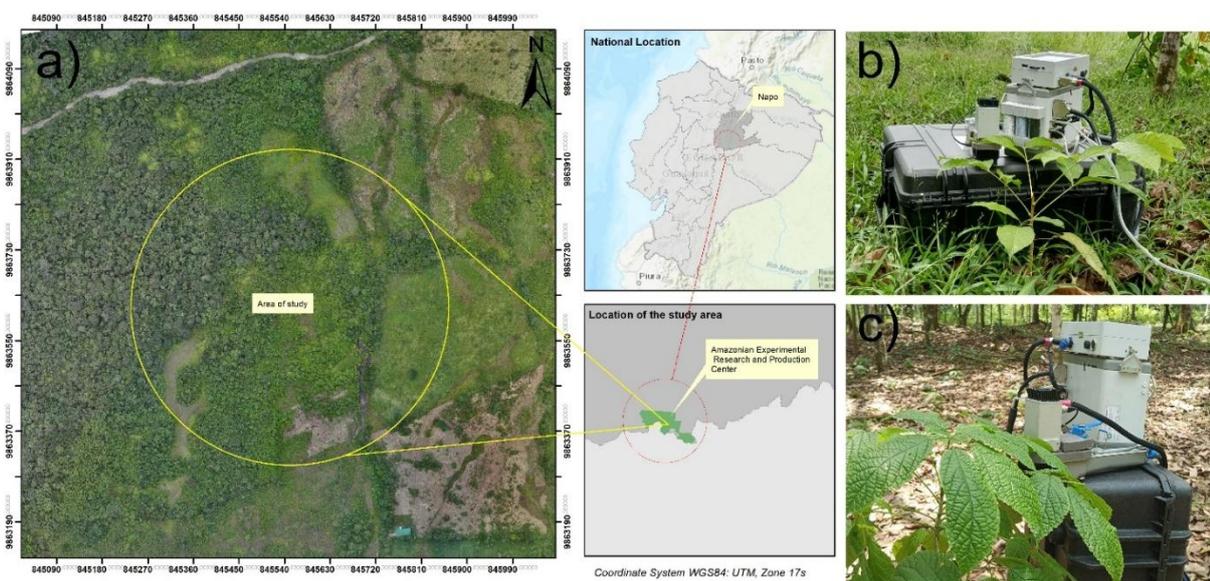


Figure 1. Location map of the Centro Experimental de Investigación y Producción Amazónica: a) Study area; b) Photosynthetic parameter measurements of *S. macrophylla*; c) Photosynthetic parameter measurements of *H. chrysanthus*

2.2 Photosynthetic Parameter Measurements

Photosynthetic assimilation measurements in *H. chrysanthus* and *S. macrophylla* seedlings were performed using a portable integrated system for photosynthesis and chlorophyll fluorescence measurement (iFL - LCpro-SD) with fully programmable microclimate control, developed by Opti-Sciences Inc. and ADC BioScientific Ltd. (UK). This device is equipped with a high-intensity white actinic light source, predominantly blue spectrum, which allows chloroplast migration similar to natural conditions. The iFL system can emit a maximum light intensity of $2,000 \mu\text{mol m}^{-2} \text{s}^{-1}$. It also incorporates a leaf absorption measurement system using an RGB sensor that evaluates leaf reflectance and transmittance. Additionally, an infrared (IR) temperature sensor covers approximately 80% of the chamber area, enabling the recording of various variables (Table 1).

Table 1. Definition of the abbreviations for photosynthetic parameters

| Abbreviation | Definition | Units |
|---------------------------|---|--|
| PPFD | Photosynthetic Photon Flux Density | $\mu\text{mol m}^{-2} \text{s}^{-1}$ |
| A | Photosynthetic Assimilation | $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ |
| A_{max} | Maximum Photosynthetic Assimilation | $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ |
| C_i | Intercellular CO_2 Concentration | $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ |
| E | Transpiration Rate | $\text{mmol m}^{-2} \text{ s}^{-1}$ |
| Gs | Stomatal Conductance | $\text{mol m}^{-2} \text{ s}^{-1}$ |
| Γ^* | Compensation Point | $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ |
| R_d | Daytime Respiration | $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ |
| ETR | Electron Transport Rate | $\mu\text{mol m}^{-2} \text{ s}^{-1}$ |
| ETR_{max} | Maximum Electron Transport Rate | $\mu\text{mol m}^{-2} \text{ s}^{-1}$ |

2.3 Light Compensation Point

Measurements to determine the light compensation point were conducted in situ. Owing to the presence of compound leaves, measurements were performed on a single leaflet per plant, using five randomly selected replicates per species. The procedure followed the methodology proposed by Laisk (1997), incorporating modifications introduced by the authors (see Table 2). The experiment involved generating three A/Ci curves under different light intensity levels. At each level, CO₂ concentration was progressively increased, with temperature maintained at 25 °C and relative humidity at 80% (Table 2). The light compensation point is defined as the lowest light intensity at which a plant's photosynthetic rate equals its respiration rate. At this point, the amount of oxygen produced by photosynthesis equals the amount consumed in respiration, and the amount of CO₂ absorbed during photosynthesis equals the amount released by respiration (Schmiege et al., 2023).

Table 2. Characteristics of the Laisk protocol

| N° | Time* (min) | PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) | CO ₂ concentration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) | Humidity (%) | Temperature (°C) |
|----|----------------|--|---|-----------------|---------------------|
| 1 | 4 | 200 | 115 | 80 | 25 |
| 2 | 2 | 200 | 160 | 80 | 25 |
| 3 | 2 | 200 | 205 | 80 | 25 |
| 4 | 2 | 200 | 250 | 80 | 25 |
| 5 | 4 | 400 | 115 | 80 | 25 |
| 6 | 2 | 400 | 160 | 80 | 25 |
| 7 | 2 | 400 | 205 | 80 | 25 |
| 8 | 2 | 400 | 250 | 80 | 25 |
| 9 | 4 | 600 | 115 | 80 | 25 |
| 10 | 2 | 600 | 160 | 80 | 25 |
| 11 | 2 | 600 | 205 | 80 | 25 |
| 12 | 2 | 600 | 250 | 80 | 25 |

* Modified Laisk protocol values; PPFD: Photosynthetic Photon Flux Density.

2.4 Photosynthetic Response to Increasing PPFD

Photosynthesis measurements in response to varying PPFD intensities were conducted following the guidelines of Ávila-Lovera and Tezara (2018) and Cao et al. (2024), incorporating modifications to the measurement duration. For the analysis, 25 healthy seedlings per species (*H. chrysanthus* and *S. macrophylla*) were selected. Measurements were performed on a single leaflet per plant, ensuring that only undamaged and morphologically intact leaflets were evaluated. Measurements were conducted in the morning (08:00-11:00) under clear sky conditions. Experimental conditions were controlled at 25 °C, 80% relative humidity, and a CO₂ concentration of 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$. PPFD was gradually increased from 25 to 1800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ across 12 levels (25, 50, 100, 150, 250, 450, 600, 750, 1000, 1250, 1500, and 1800 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Each measurement lasted four minutes, resulting in a total assessment time of 48 minutes per seedling.

2.5 Determination of Water Use Efficiency Coefficients at the Leaf Level

Water use efficiency (WUE) is defined as the ratio between net photosynthesis (A) and the transpiration rate (E), mathematically expressed as $WUE = A / E$, in units of $\mu\text{mol CO}_2 (\text{mmol H}_2\text{O})^{-1}$. This parameter is fundamental for understanding the adaptive strategies of plants in environments with variable water and light availability. In this study, the determination of coefficients related to WUE was based on the approach proposed by Jin et al. (2024). According to this model, four key coefficients were calculated from the area under the WUE curve for each of the analyzed species: water potential coefficient (WPC), water loss coefficient (WLC), strategic water

use coefficient (WSC), and total water use coefficient (WTC). This procedure was performed using SigmaPlot 15.0 software, enabling precise quantification of the ecophysiological response of seedlings under different PPFD intensities (Figure 2).

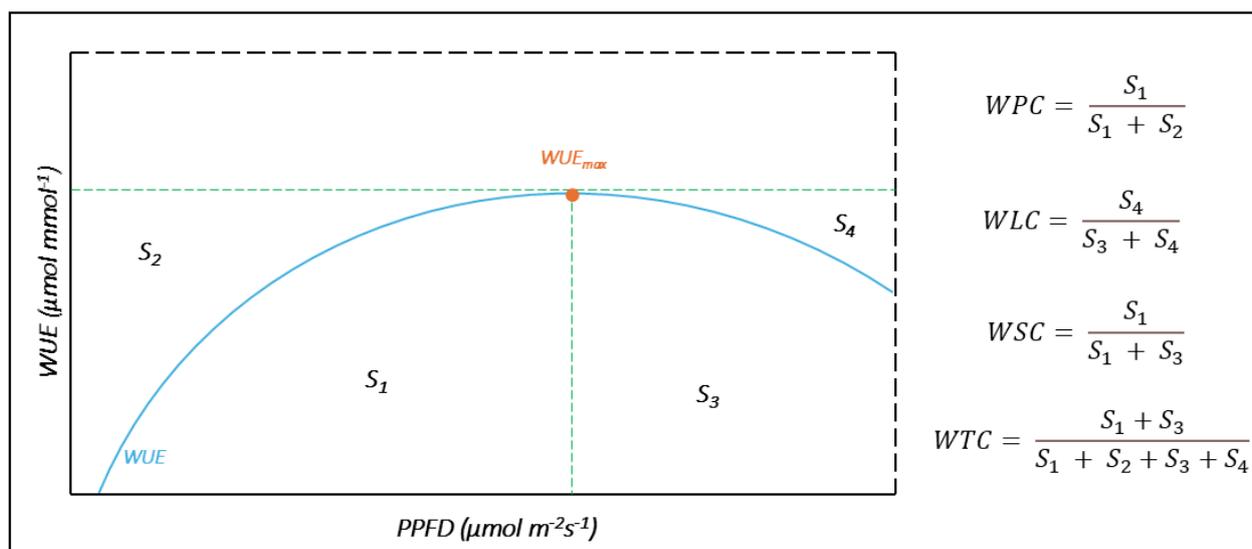


Figure 2. Categorized areas under the WUE curve for coefficient estimation

WUE_{max}: Maximum Water Use Efficiency; WUE: Water Use Efficiency; WPC: Water Potential Coefficient; WLC: Water Loss Coefficient; WSC: Strategic Water Use Coefficient; WTC: Total Water Use Coefficient.

2.6 Data Processing and Analysis

The photosynthetic parameters of *H. chrysanthus* and *S. macrophylla* were evaluated using descriptive statistics. Significant differences ($P < 0.05$) between species were assessed through a one-way ANOVA, followed by Tukey's HSD post hoc test to identify pairwise differences, using OriginLab 2024 software. To examine the photosynthetic response curves under varying PPFD levels (A/PPFD and ETR/PPFD), the data were fitted to the Rectangular Hyperbola model using SigmaPlot 15.0 (Kieffer et al., 2024).

3. Results

3.1 Determination of the Compensation Point (Γ^*)

Figures 3a and 3b highlight important differences in the ecophysiological adaptation of *H. chrysanthus* and *S. macrophylla* under Amazonian conditions. The compensation point (Γ^*) of *H. chrysanthus* ($151.0 \pm 17.27 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was higher than that of *S. macrophylla* ($117.0 \pm 2.34 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), indicating that the former requires higher CO_2 concentrations to achieve a net carbon balance. Regarding daytime respiration (R_d), *H. chrysanthus* exhibited a higher value ($1.85 \pm 0.07 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) compared to *S. macrophylla* ($1.39 \pm 0.02 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Conversely, the lower Γ^* and R_d values of *S. macrophylla* underscore its efficiency under low irradiance and low CO_2 concentrations, favoring its survival in the understory.

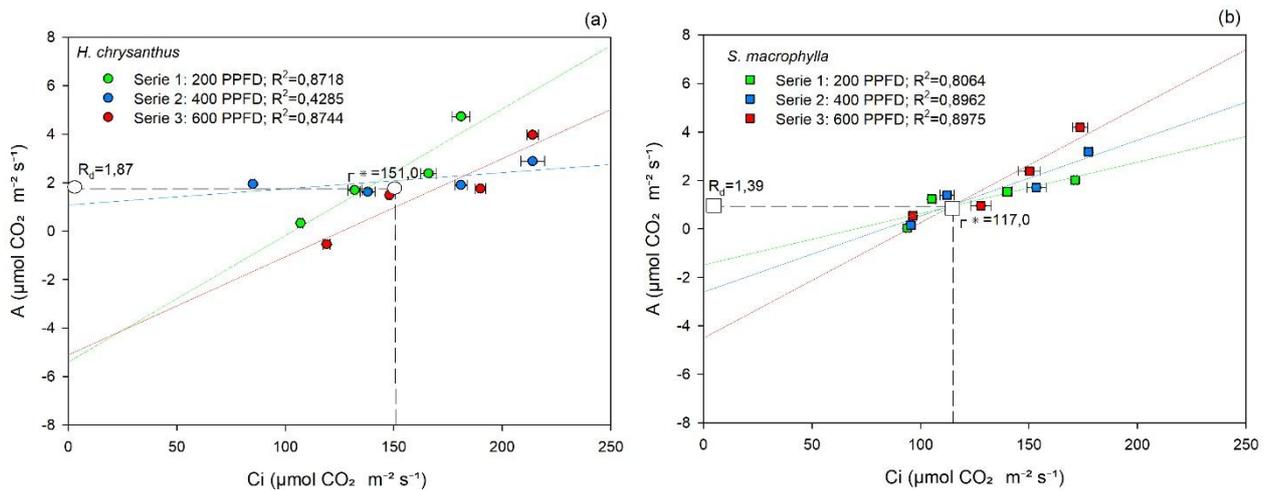


Figure 3. Compensation point means of the studied species: a) *H. chrysanthus*; b) *S. macrophylla*

Photosynthetic assimilation (A); Intracellular CO₂ concentration (Ci); CO₂ compensation point (Γ^*); Daytime respiration (R_d); Photosynthetic Photon Flux Density (PPFD $\mu\text{mol m}^{-2}\text{s}^{-1}$). Error bars at each data point indicate the corresponding standard error of the mean (SEM).

3.2 Photosynthetic Response to Increasing PPFD

Figures 4a and 4b present the photosynthetic assimilation curves in response to increasing PPFD. Under low light intensity conditions (25-600 $\mu\text{mol m}^{-2}\text{s}^{-1}$), no significant differences were found between *S. macrophylla* and *H. chrysanthus* ($P > 0.05$). However, beyond 750 $\mu\text{mol m}^{-2}\text{s}^{-1}$, *S. macrophylla* showed a significantly superior response, with a photosynthetic rate that continued to increase steadily, indicating a high capacity to efficiently utilize light without exhibiting photoinhibition.

In contrast, *H. chrysanthus* reached its maximum photosynthetic assimilation rate ($5.85 \pm 0.18 \mu\text{mol CO}_2 \text{m}^{-2}\text{s}^{-1}$) at 750 $\mu\text{mol m}^{-2}\text{s}^{-1}$, followed by a decline in photosynthetic activity, evidencing photoinhibition. This phenomenon suggests that *H. chrysanthus* is better adapted to intermediate irradiance levels, whereas *S. macrophylla* exhibits greater ecophysiological plasticity, enhancing its performance under high light conditions. These results are critical for selecting species in reforestation programs based on the light characteristics of the site.

Figures 4c and 4d show the electron transport rate (ETR) in response to different PPFD intensities, which allows evaluating the efficiency of electron flow in chloroplasts –a critical process for energy generation in the light phase of photosynthesis. Beyond 450 $\mu\text{mol m}^{-2}\text{s}^{-1}$ PPFD, *S. macrophylla* exhibited a significantly higher ETR ($90.33 \pm 1.05 \mu\text{mol m}^{-2}\text{s}^{-1}$, $P < 0.05$) compared to *H. chrysanthus* ($63.56 \pm 1.61 \mu\text{mol m}^{-2}\text{s}^{-1}$).

This result suggests that *S. macrophylla* possesses a greater capacity to handle electron flows under high irradiance conditions, optimizing the generation of ATP and NADPH, which are essential for carbon fixation in the dark phase. On the other hand, the lower ETR of *H. chrysanthus* indicates limitations in electron transport under high light intensities, which may be related to reduced tolerance to intense light. These differences reflect contrasting ecophysiological strategies that should be considered when selecting species for restoration programs based on the light conditions of the site.

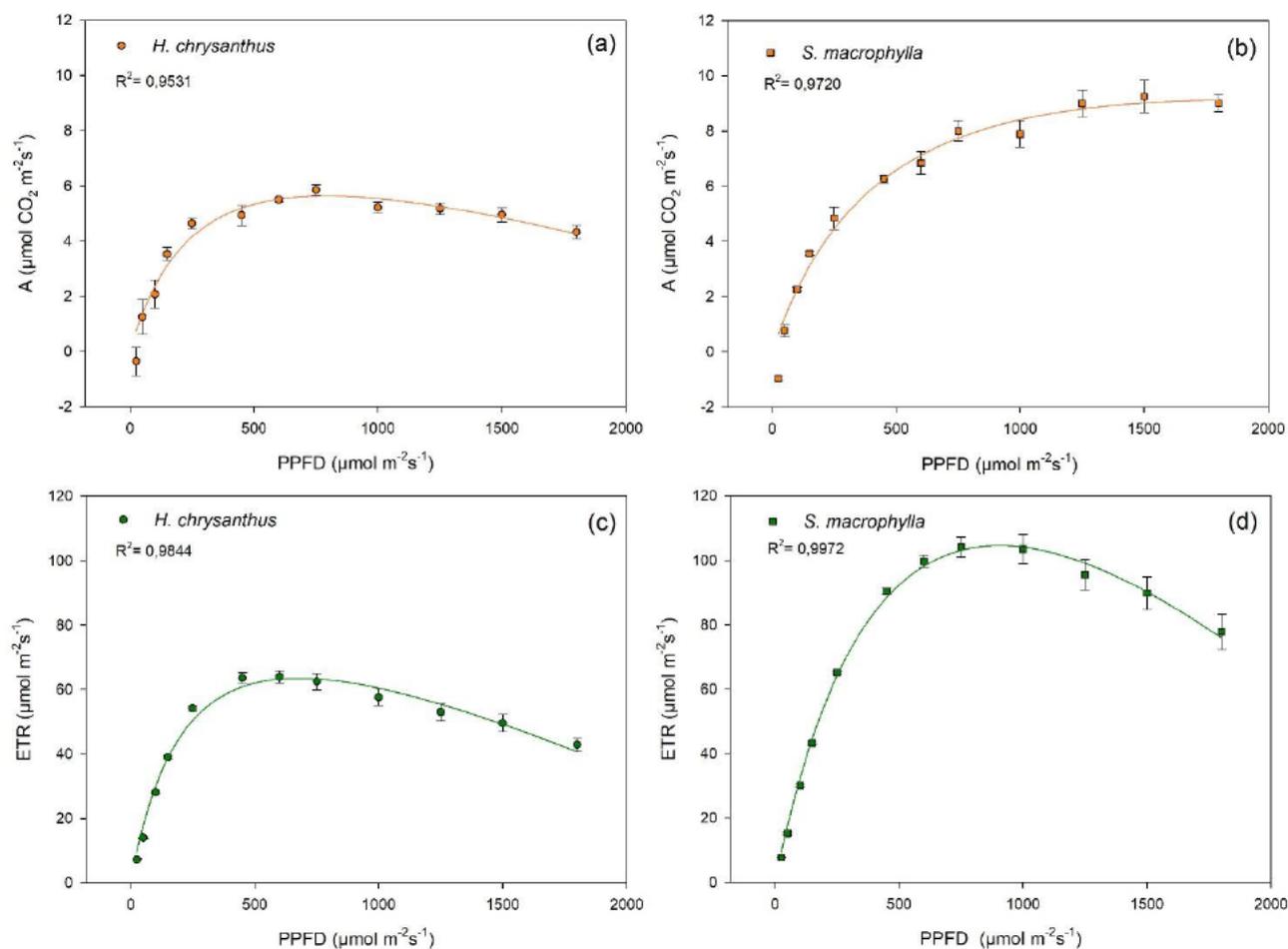


Figure 4. Mean response curves of photosynthetic assimilation and electron transport under different light intensities for each species: a) and c) *H. chrysanthus*; b) and d) *S. macrophylla*

Photosynthetic assimilation (A); Electron transport rate (ETR); Photosynthetic photon flux density (PPFD). Error bars at each data point indicate the corresponding standard error of the mean (SEM).

S. macrophylla exhibited a significantly higher maximum photosynthetic assimilation rate (A_{max}) ($9.4 \pm 0.52 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) compared to *H. chrysanthus* ($6.18 \pm 0.17 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $p < 0.05$) (Table 3), indicating greater efficiency in carbon fixation. This advantage may be associated with the superior adaptation of *S. macrophylla* to high irradiance conditions, enabling it to maximize the use of available light energy. In terms of stomatal conductance (Gs), *S. macrophylla* also demonstrated higher values ($G_s = 0.15 \text{ mol m}^{-2} \text{ s}^{-1}$, $p < 0.05$) compared to *H. chrysanthus* ($G_s = 0.10 \text{ mol m}^{-2} \text{ s}^{-1}$) (Table 3). This indicates a greater capacity of *S. macrophylla* to efficiently regulate stomatal opening, facilitating CO_2 uptake for photosynthesis while minimizing water loss – a critical trait in Amazonian conditions where water balance is crucial.

Furthermore, the maximum electron transport rate (ETR_{max}) of *S. macrophylla* was reached at an irradiance of $750 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFD, while *H. chrysanthus* achieved its ETR_{max} at $600 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFD (Table 3). This suggests that *S. macrophylla* has a greater capacity to handle high light intensities without experiencing photoinhibition, making it better suited to open environments or forest gaps.

In terms of transpiration (E), *H. chrysanthus* exhibited a significantly higher value ($1.14 \pm 0.03 \text{ mmol m}^{-2} \text{ s}^{-1}$) compared to *S. macrophylla* ($0.75 \pm 0.04 \text{ mmol m}^{-2} \text{ s}^{-1}$, $p < 0.05$) (Table 3). This result suggests that *H. chrysanthus* experiences greater water loss through transpiration, potentially linked to an adaptive strategy to maintain optimal leaf temperatures under high light conditions. On the other hand, no significant differences were

observed between the species in intracellular CO₂ concentration (Ci), indicating that despite differences in transpiration, both species maintain similar efficiency in CO₂ diffusion to carboxylation sites.

Table 3. Photosynthetic parameters of the studied species

| Photosynthetic parameters | <i>H. chrysanthus</i> | <i>S. macrophylla</i> |
|--|--------------------------|----------------------------|
| A _{max} (μmol CO ₂ m ⁻² s ⁻¹) | 6.18 ^b ± 0.17 | 9.4 ^a ± 0.52 |
| E (mmol m ⁻² s ⁻¹) | 1.14 ^a ± 0.03 | 0.75 ^b ± 0.04 |
| Gs (mol m ⁻² s ⁻¹) | 0.10 ^b ± 0.01 | 0.15 ^a ± 0.01 |
| Ci (μmol CO ₂ m ⁻² s ⁻¹) | 337 ^a ± 8 | 357 ^a ± 13 |
| ETR _{max} (μmol m ⁻² s ⁻¹) | 64 ^b ± 1.79 | 104.83 ^a ± 3.79 |

Maximum Photosynthetic Assimilation (A_{max}); Transpiration rate (E); Stomatal conductance (Gs); Intracellular CO₂ concentration (Ci); Maximum electron transport rate (ETR_{max}). Different superscript letters indicate significant differences ($p < 0.05$) between species.

3.3 Water Use Efficiency (WUE)

Figures 5a and 5b illustrate the WUE curves determined from photosynthetic parameters in response to increasing PPFD. Under low light intensity conditions (25-100 μmol m⁻² s⁻¹), no significant differences in WUE were observed between *S. macrophylla* and *H. chrysanthus* ($P > 0.05$). However, starting at 150 μmol m⁻² s⁻¹, *S. macrophylla* showed a significantly superior response, reaching a maximum water use efficiency (WUE_{max}) of 13.17 ± 0.24 μmol mmol⁻¹ at 600 μmol m⁻² s⁻¹ PPFD. In contrast, *H. chrysanthus* achieved its WUE_{max} at 750 μmol m⁻² s⁻¹ PPFD, with a considerably lower value (6.16 ± 0.23 μmol mmol⁻¹) (Table 4). These results suggest that *S. macrophylla* exhibits greater water use efficiency under high irradiance conditions, likely due to more efficient stomatal regulation and an optimized balance between carbon fixation and water loss through transpiration. Conversely, *H. chrysanthus* demonstrates a lower WUE_{max}, indicating relatively greater water loss under high light intensities, possibly associated with a growth strategy that is more dependent on water resources.

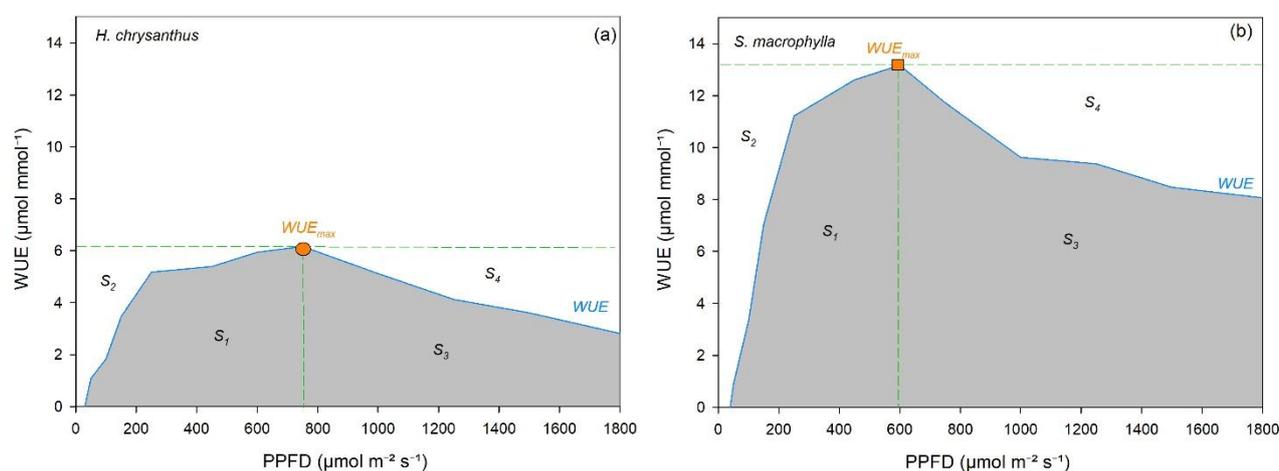


Figure 5. Water use efficiency in response to increasing photosynthetic photon flux density: a) *H. chrysanthus*; b) *S. macrophylla*

WUE_{max}: Maximum water use efficiency; WUE: water use efficiency; PPFD: Photosynthetic Photon Flux Density.

Regarding the water potential coefficient (WPC), water loss coefficient (WLC), strategic water use coefficient (WSC), and total water use coefficient (WTC), no significant differences were observed (Table 4), suggesting that the compensatory mechanisms are similar between the species.

Table 4. Water use efficiency coefficients

| Coefficients | <i>H. chrysanthus</i> | <i>S. macrophylla</i> |
|---|--------------------------|---------------------------|
| WUE _{max} (μmol mmol ⁻¹) | 6.16 ^b ± 0.23 | 13.17 ^a ± 0.24 |
| WPC | 0.74 ^a ± 0.01 | 0.74 ^a ± 0.00 |
| WLC | 0.29 ^a ± 0.04 | 0.26 ^a ± 0.18 |
| WSC | 0.37 ^a ± 0.07 | 0.32 ^a ± 0.00 |
| WTC | 0.72 ^a ± 0.03 | 0.73 ^a ± 0.01 |

WUE_{max}: Maximum water use efficiency; WPC: Water potential coefficients; WLC: Water loss coefficient; WSC: Strategic water use coefficient; WTC: Total water use coefficient. Different superscript letters indicate significant differences ($p < 0.05$) between species.

4. Discussion

The ecophysiological differences between seedlings of *H. chrysanthus* and *S. macrophylla* reflect distinct adaptive strategies in response to variable environmental conditions in Amazonian ecosystems. The higher compensation point observed in *H. chrysanthus* indicates a greater dependence on elevated CO₂ concentrations to sustain a positive net carbon balance (Espinosa et al., 2018). In contrast, *S. macrophylla* exhibits a lower compensation point, which may imply a higher energetic cost associated with cellular maintenance in the absence of light. This trait could be linked to a rapid growth strategy adapted to highly illuminated environments and is characterized by enhanced photosynthetic efficiency under low CO₂ concentrations (Jhou et al., 2017). Moreover, the higher respiratory cost (R_d) in *H. chrysanthus* may reflect a growth strategy suited to high-light and high-CO₂ environments, whereas *S. macrophylla* shows a lower R_d , indicative of a more efficient metabolism that facilitates adaptation to shaded conditions (Azevedo & Marengo, 2012; Leyerer & Katzensteiner, 2025). In *H. chrysanthus*, the absence of regression line intersection suggests a less flexible photosynthetic response to variations in light and CO₂, potentially reflecting a higher respiratory burden. Conversely, *S. macrophylla* demonstrates greater photosynthetic adaptability, as evidenced by the convergence of its regression lines, which points to a more efficient strategy under diverse environmental conditions. Collectively, these findings underscore the functional differentiation between these species and their capacity to occupy distinct ecological niches within the Amazonian ecosystem.

In terms of A_{max} , *S. macrophylla* showed significantly higher values compared to *H. chrysanthus*. This difference suggests greater photosynthetic efficiency in *S. macrophylla*, possibly due to better adaptation to high irradiance conditions. Previous studies have indicated that *S. macrophylla* exhibits high phenotypic plasticity, allowing it to adjust its photosynthetic capacity in response to variations in light availability (Cordeiro et al., 2009; Sembada et al., 2024). Consistent with these patterns, stomatal conductance (G_s) was also higher in *S. macrophylla* compared to *H. chrysanthus*. Higher G_s facilitates greater CO₂ uptake for photosynthesis but may also increase water loss through transpiration (Melo et al., 2025). However, *S. macrophylla* demonstrated superior WUE, reaching a maximum value of $13.17 \pm 0.24 \mu\text{mol mmol}^{-1}$ at $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, while *H. chrysanthus* achieved its WUE_{max} of $6.16 \pm 0.23 \mu\text{mol mmol}^{-1}$ at $750 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD. These findings suggest that *S. macrophylla* possesses more efficient mechanisms for balancing carbon acquisition and water conservation, which is crucial in environments with fluctuating water availability (Kabala et al., 2024; Song et al., 2025).

Regarding ETR, *S. macrophylla* reached its ETR_{max} at an irradiance of $750 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, while *H. chrysanthus* achieved its ETR_{max} at $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD. An ETR_{max} at higher light intensities indicates a greater capacity to handle high light energy fluxes without experiencing photoinhibition (Oluborode et al., 2025). This suggests that *S. macrophylla* can maintain high photosynthetic activity under high irradiance conditions due to its greater efficiency in dissipating excess energy and protecting photosynthetic components (Dai et al., 2024; Tang et al., 2024). In line with these physiological differences, transpiration (E) was significantly higher in *H. chrysanthus* compared to *S. macrophylla*. Higher transpiration rates may indicate a foliar cooling strategy to

prevent overheating under high irradiance but could also lead to greater water loss, which might be disadvantageous under water stress conditions (Liu et al., 2025; Zhang et al., 2025). Conversely, the lower transpiration in *S. macrophylla* suggests a more conservative water-use strategy, potentially conferring an advantage in environments with limited water availability (Zhao et al., 2025).

No significant differences were found between the species in intracellular CO₂ concentration (C_i), indicating that both species maintain similar carboxylation efficiency. However, differences in G_s and WUE suggest that stomatal regulation strategies and water balance differ between the species, which could influence their performance under varying environmental conditions (Kabala et al., 2024).

The WPC values were high in both species, indicating an adaptive strategy oriented towards active water conservation. Similarly, the high WTC values reflect efficient water management, even under light stress conditions. Conversely, the low WLC values indicate a high water retention capacity under high irradiance, minimizing water loss through transpiration. Finally, the low WSC values suggest a physiological focus on the simultaneous optimization of light and water use, regardless of resource availability or intensity (Jin et al., 2024; Valladares & Niinemets, 2008; Xu et al., 2009). These coefficients showed no significant differences between species, suggesting that while there are differences in photosynthetic and transpiration responses, the general water-use strategies are similar between *S. macrophylla* and *H. chrysanthus* (Jin et al., 2024). These results underscore the importance of ecophysiological strategies in the adaptation of seedlings to environments with variable light and water availability.

The observed differences in the ecophysiological responses of these species have important implications for ecological restoration programs. *S. macrophylla*, with its greater photosynthetic and water-use efficiency, may be more suitable for areas with high irradiance and variable water availability. Conversely, *H. chrysanthus*, with its higher transpiration rate, may require sites with greater water availability to ensure successful establishment and growth. Nevertheless, these recommendations must be interpreted with caution, as a methodological limitation of this study is that measurements were conducted exclusively on seedlings growing under the forest canopy. While this approach provides valuable insights into plant performance in shaded microenvironments, it does not capture the full spectrum of physiological responses that may occur under direct light exposure. Considering the pronounced heterogeneity of Amazonian ecosystems, future research should include experimental designs that evaluate plants subjected to higher irradiance levels. Such studies would allow contrasting the physiological responses observed here and provide a more comprehensive understanding of species-specific adaptive strategies across diverse light environments.

5. Conclusions

Seedlings of *S. macrophylla* exhibited a higher A_{max} and a lower R_d rate compared to *H. chrysanthus*, indicating greater carbon-use efficiency under high irradiance conditions. In contrast, *H. chrysanthus* showed greater photoinhibition at intensities above 750 μmol m⁻² s⁻¹ PPFD, reflecting lower tolerance to intense light.

The WUE coefficients did not show significant differences between species, suggesting that while there are differences in photosynthetic and transpiration responses, the general water-use strategies are similar for both species. However, *S. macrophylla* exhibited higher G_s, indicating better regulation of gas exchange, optimizing photosynthesis while minimizing transpiration compared to *H. chrysanthus*.

The results indicate that *S. macrophylla* exhibits greater ecophysiological plasticity, adapting more effectively to changes in light availability, whereas *H. chrysanthus* requires specific irradiance conditions to optimize its

photosynthetic performance during the seedling stage. These differences should be considered in ecological restoration programs to maximize the survival and establishment of both species in Amazonian ecosystems.

Transparency of Data

Available data: The entire data set that supports the results of this study was published in the article itself.

Author Contribution Statement

| | D Ureta-Leones | A Medina-Gahona | Y Arteaga-Crespo | Y García-Quintana | A López-Alban | B Alvarado-Sarango |
|------------------------------|----------------|-----------------|------------------|-------------------|---------------|--------------------|
| Conceptualization | | | | | | |
| Investigation | | | | | | |
| Methodology | | | | | | |
| Supervision | | | | | | |
| Writing – original draft | | | | | | |
| Writing – review and editing | | | | | | |

References

- Amaral, G. C., Pezzopane, J. E. M., de Souza Nóia Júnior, R., Fonseca, M. D. S., Martínez, M. F., de Oliveira Gomes, V., Toledo, J. V., Pezzopane, J. R. M., & Martín, R. T. (2023). Climate change and the growth of Amazonian species seedlings: An ecophysiological approach to *Euterpe oleracea*. *New Forests*, 54(2), 269-287. <https://doi.org/10.1007/s11056-022-09921-1>
- Ávila-Lovera, E., & Tezara, W. (2018). Water-use efficiency is higher in green stems than in leaves of a tropical tree species. *Trees*, 32(6), 1547-1558. <https://doi.org/10.1007/s00468-018-1732-x>
- Azevedo, G. F. C., & Marengo, R. A. (2012). Growth and physiological changes in saplings of *Minquartia guianensis* and *Swietenia macrophylla* during acclimation to full sunlight. *Photosynthetica*, 50(1), 86-94. <https://doi.org/10.1007/s11099-012-0001-2>
- Cao, Y., Li, J., Li, S., & Zhou, B. (2024). The effects of long-term precipitation exclusion on leaf photosynthetic traits, stomatal conductance, and water use efficiency in *Phyllostachys edulis*. *Forests*, 15(5), Article 849. <https://doi.org/10.3390/f15050849>
- Cordeiro, Y. E. M., Pinheiro, H. A., dos Santos Filho, B. G., Corrêa, S. S., e Silva, J. R. R., & Dias-Filho, M. B. (2009). Physiological and morphological responses of young mahogany (*Swietenia macrophylla* King) plants to drought. *Forest Ecology and Management*, 258(7), 1449-1455. <https://doi.org/10.1016/j.foreco.2009.06.054>
- Dai, Y., Guo, Z., Guo, X., Deng, R., Li, L., Fan, T., Cui, K., & Pan, T. (2024). Plastic particles and fluorescent brightener co-modify *Chlorella pyrenoidosa* photosynthesis and a machine learning approach predict algae growth. *Journal of Hazardous Materials*, 477, Article 135406. <https://doi.org/10.1016/j.jhazmat.2024.135406>
- de Oliveira Neves, F., Salgado, E. G., & Lira, J. M. S. (2024). Energetic sustainability in the Amazon region: Exploring impacts, environmental solutions, and rebound effect analysis. *Environmental Development*, 51, Article 101043. <https://doi.org/10.1016/j.envdev.2024.101043>

- Debiasi, T. V., Calzavara, A. K., Gomes, D. G., Andreas, I. R., Rondina, A. B. L., Duarte, K. E., Pereira, R. M., Batista, B. L., Pimenta, J. A., Seabra, A. B., Centeno, D. C., Gaspar, M., & Oliveira, H. C. (2024). Influence of light intensity on the responses of seedlings of neotropical tree species to nitrogen source. *Environmental and Experimental Botany*, 228, Article 106007. <https://doi.org/10.1016/j.envexpbot.2024.106007>
- Dumais, D., Raymond, P., & Champagne, E. (2025). Translocated southern seedlings perform as well as local provenances: Insights from an ecophysiological monitoring under varying cutting modalities. *New Forests*, 56(1), 1-25. <https://doi.org/10.1007/s11056-024-10089-z>
- Espinosa, C. I., Camarero, J. J., & Gusmán, A. A. (2018). Site-dependent growth responses to climate in two major tree species from tropical dry forests of southwest Ecuador. *Dendrochronologia*, 52, 11-19. <https://doi.org/10.1016/j.dendro.2018.09.004>
- García-Quintana, Y., Arteaga-Crespo, Y., Torres-Navarrete, B., Robles-Morillo, M., Bravo-Medina, C., & Sarmiento-Rosero, A. (2020). Ecological quality of a forest in a state of succession based on structural parameters: A case study in an evergreen Amazonian-Andean forest, Ecuador. *Heliyon*, 6(7), Article e04592. <https://doi.org/10.1016/j.heliyon.2020.e04592>
- He, T., Marco, J., Soares, R., Yin, Y., & Wiedenhoef, A. C. (2020). Machine Learning Models with Quantitative Wood Anatomy Data Can Discriminate between *Swietenia macrophylla* and *Swietenia mahagoni*. *Forests*, 11(1), Article 36. <https://doi.org/10.3390/f11010036>
- Héctor, E., Cevallos, D., Corozo, L., Macías, F., & Fosado, O. (2024). Development of a protocol for the micropropagation of two forest species threatened with extinction in Ecuador. *Plant Cell, Tissue and Organ Culture*, 159(2). <https://doi.org/10.1007/s11240-024-02864-9>
- Herrera-Feijoo, R. J., Torres, B., López-Tobar, R., Tipán-Torres, C., Toulkeridis, T., Heredia-R, M., & Mateo, R. G. (2023). Modelling climatically suitable areas for mahogany (*Swietenia macrophylla* King) and their shifts across neotropics: The role of protected areas. *Forests*, 14(2), Article 385. <https://doi.org/10.3390/f14020385>
- Jhou, H. C., Wang, Y. N., Wu, C. S., Yu, J. C., & Chen, C. I. (2017). Photosynthetic gas exchange responses of *Swietenia macrophylla* King and *Melia azedarach* L. plantations under drought conditions. *Botanical Studies*, 58(1), Article 57. <https://doi.org/10.1186/s40529-017-0212-8>
- Jin, C., Zha, T., Bourque, C. P., Di, K., Zhang, W., Jiao, Y., Fan, Z., & Hu, Z. (2024). Water use efficiency in tropical plants based on a set of newly created leaf photosynthesis-related parameters. *The Science of the Total Environment*, 957, Article 177657. <https://doi.org/10.1016/j.scitotenv.2024.177657>
- Kabala, J. P., Niccoli, F., Altieri, S., Liyaqat, I., & Battipaglia, G. (2024). Distinct responses of climate-growth and iWUE in *Fagus sylvatica* L. at two low elevation sites in southern Italy. *Journal of Forestry Research*, 36(1), 1-17. <https://doi.org/10.1007/s11676-024-01788-6>
- Kieffer, C., Kaur, N., Li, J., Matamala, R., Fay, P. A., & Hui, D. (2024). Photosynthetic responses of switchgrass to light and CO₂ under different precipitation treatments. *Global Change Biology Bioenergy*, 16, Article e13138. <https://doi.org/10.1111/gcbb.13138>
- Kübler, D., Hildebrandt, P., Günter, S., Stimm, B., Weber, M., Muñoz, J., Cabrera, O., Zeilinger, J., Silva, B., & Mosandl, R. (2020). Effects of silvicultural treatments and topography on individual tree growth in a tropical mountain forest in Ecuador. *Forest Ecology and Management*, 457, Article 117726. <https://doi.org/10.1016/j.foreco.2019.117726>
- Laisk, A. (1997). Kinetics of photosynthesis and photorespiration in C3 plants. *Nauka*, 198, 243-251.
- Leyerer, L., & Katzensteiner, K. (2025). Effects of substrate on ecophysiology of young silver fir and Norway spruce growing on shallow calcareous soils. *Forest Ecology and Management*, 578, Article 122477. <https://doi.org/10.1016/j.foreco.2024.122477>

- Liu, C., Peltoniemi, M., Alekseychik, P., Mäkelä, A., & Hölttä, T. (2025). A coupled model of hydraulic eco-physiology and cambial growth - accounting for biophysical limitations and phenology improves stem diameter prediction at high temporal resolution. *Plant, Cell & Environment*, 48(2), 1344-1365. <https://doi.org/10.1111/pce.15239>
- Melo, A., Nicodemos, J., Lopes, R. F., & Santos, M. G. (2025). Seasonal balance of whole plant non-structural carbohydrates in a deciduous species with green stem in a dry tropical forest. *Journal of Arid Environments*, 227, Article 105324. <https://doi.org/10.1016/j.jaridenv.2025.105324>
- Ministerio del Ambiente, Agua y Transición Ecológica. (2024). *Sistematización del estudio poblacional de especies forestales CITES: Swietenia macrophylla (ahuano) y Cedrela odorata (cedro)*. Universidad Técnica Particular de Loja.
- Oluborode, J., Chadzinikolau, T., Formela-Luboińska, M., Ye, Z. P., & Robakowski, P. (2025). Adaptive significance of age- and light-related variation in needle structure, photochemistry, and pigments in evergreen coniferous trees. *Photosynthesis Research*, 163(1), Article 3. <https://doi.org/10.1007/s11120-024-01125-2>
- Rosati, A., Wolz, K. J., Murphy, L., Ponti, L., & Jose, S. (2020). Modeling light below tree canopies overestimates net photosynthesis and radiation use efficiency in understory crops by averaging light in space and time. *Agricultural and Forest Meteorology*, 284, Article 107892. <https://doi.org/10.1016/j.agrformet.2019.107892>
- Sánchez Amboage, E., Sánchez Cevallos, R. E., Bustamante Sánchez, N. S., & Mora Jácome, V. L. (2016). Turismo experiencial a través del florecimiento de los guayacanes del sur de Ecuador: Un análisis desde su comunicación. In J. R. Araújo, V. A. Martínez Fernández, M. M. Rodríguez, I. P. Rivera, J. Y. Quichimbo & E. Sánchez Amboage (Eds.), *De los medios y la comunicación de las organizaciones a las redes de valor* (pp. 566-579). Universidad Técnica Particular de Loja. <https://dialnet.unirioja.es/servlet/articulo?codigo=6075397&info=resumen&idioma=ENG>
- Schmiege, S. C., Sharkey, T. D., Walker, B., Hammer, J., & Way, D. A. (2023). Laisk measurements in the nonsteady state: Tests in plants exposed to warming and variable CO₂ concentrations. *Plant Physiology*, 193(2), 1045-1057. <https://doi.org/10.1093/plphys/kiad305>
- Sembada, A. A., Faizal, A., & Sulistyawati, E. (2024). Photosynthesis efficiency as key factor in decision-making for forest design and redesign: A systematic literature review. *Ecological Frontiers*, 44(6), 1128-1139. <https://doi.org/10.1016/j.ecofro.2024.07.008>
- Song, H., Zhong, T., Zhu, J., & Yan, T. (2025). Higher risk of hydraulic dysfunction and carbohydrate depletion of declining *Larix principis-rupprechtii* trees. *Ecological Processes*, 14(1), 1-10. <https://doi.org/10.1186/s13717-024-00567-9>
- Tang, X., Zhao, J., Zhou, J., Zhu, Q., Sheng, X., & Yue, C. (2024). Elevated CO₂ Shifts Photosynthetic Constraint from Stomatal to Biochemical Limitations During Induction in *Populus tomentosa* and *Eucalyptus robusta*. *Plants (Basel)*, 14(1), Article 47. <https://doi.org/10.3390/plants14010047>
- Trugman, A. T., & Anderegg, L. D. L. (2025). Source vs sink limitations on tree growth: From physiological mechanisms to evolutionary constraints and terrestrial carbon cycle implications. *The New Phytologist*, 245(3), 966-981. <https://doi.org/10.1111/nph.20294>
- Ureta-Leones, D., Arteaga-Crespo, Y., García-Quintana, Y., & Arellano-Reinoso, K. (2024). Respuesta fotosintética de *Guadua angustifolia* Kunth y *Bambusa vulgaris* Schrad. ex J.C. Wendl. a diferentes intensidades de luz. *Revista Cubana de Ciencias Forestales*, 12(3), Article e869. http://scielo.sld.cu/scielo.php?script=sci_arttext&pid=S2310-34692024000300007&lng=en&tng=es
- Valladares, F., & Niinemets, Ü. (2008). Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics*, 39, 237-257. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173506>

- Xu, F., Guo, W., Xu, W., Wei, Y., & Wang, R. (2009). Leaf morphology correlates with water and light availability: What consequences for simple and compound leaves? *Progress in Natural Science*, 19(12), 1789-1798. <https://doi.org/10.1016/j.pnsc.2009.10.001>
- Yan, J., Zhu, C., Liu, W., Luo, F., Mi, J., Ren, Y., Li, J. & Sang, T. (2015), High photosynthetic rate and water use efficiency of *Miscanthus lutarioriparius* characterize an energy crop in the semiarid temperate region. *Global Change Biology Bioenergy*, 7, 207-218. <https://doi.org/10.1111/gcbb.12118>
- Zhang, S., Wang, X., Huang, Z., Bao, Y. T., Jiang, J., & Liu, Z. (2025). *Quercus acutissima* exhibits more adaptable water uptake patterns in response to seasonal changes compared to *Pinus massoniana*. *Forest Ecosystems*, 12, Article 100255. <https://doi.org/10.1016/j.fecs.2024.100255>
- Zhao, N., Lu, S., Li, S., Li, B., Yu, X., & Xu, X. (2025). Enhancing the water use efficiency model predictions for *Platycladus orientalis* and *Quercus variabilis*: Integrating the dynamics of carbon dioxide concentration and soil water availability. *The Science of the total environment*, 959, Article 178179. <https://doi.org/10.1016/j.scitotenv.2024.178179>