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ORIGINAL ARTICLE – Silviculture

Optimizing *Copaifera langsdorffii* Seedling Production Through Light-mediated Phenotypic Plasticity in Nursery Environments

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Abstract

Copaifera langsdorffii thrives in variable light conditions, prompting investigation of this adaptive advantage. We evaluated morphological and physiological traits contributing to phenotypic plasticity in response to nursery light environments, aiming to improve seedling quality and inform light-based management strategies. Morphological adjustments, especially in stem and root growth, were the primary response to light variation, with high light promoting root development and higher DQI values. The greatest plasticity occurred between high and medium light. As light decreased, morphological plasticity declined while physiological adjustments became more prominent, suggesting a hierarchical acclimation strategy. For nursery management, we recommend high light conditions (full sunlight) to produce robust seedlings with enhanced root development (27% higher root allocation) and superior quality indices (DQI = 0.40), while medium light (50% shade) and low light conditions (75% shade) should be avoided due to reduced seedling quality despite physiological acclimation. Assisting with best practices and seedling nursery management.

Keywords: Dickson Quality Index, Red:Far-red ratio, Relative Distance Plasticity Index, Multivariate Plasticity Index, Nursery management.

1. INTRODUCTION AND OBJECTIVES

The Brazilian Cerrado is a savanna-like biome with significant challenges for plant establishment, including high temperatures, limited water, nutrient-poor soils, and frequent fires (Rossatto & Franco, 2017). *Copaifera langsdorffii* Desf. (Fabaceae) is a widespread species demonstrating remarkable acclimation to different environmental conditions (Melo et al., 2018; Siqueira et al., 2023). This species, commonly known as 'copaíba', is ecologically important as a keystone species in Cerrado ecosystems, providing wildlife food resources and contributing to forest succession. Additionally, *C. langsdorffii* has significant economic value due to its medicinal oleoresin, high-quality timber, and carbon sequestration potential (Oliveira & Santos, 2018). Understanding *C. langsdorffii*'s resilience mechanisms is crucial for conservation and reforestation efforts in degraded areas. As demand for high-quality seedlings increases, so does the need for efficient nursery practices (Nascimento et al., 2022). Precision technologies, such as controlled light availability, offer promising avenues for optimizing seedling production (Barbosa et al., 2022).

Light availability critically drives plant growth and development, influencing seedling characteristics through physiological and morphological processes (Rossatto et al., 2018; Gommers, 2020; Yu et al., 2020; Fagundes et al., 2021). Light shifts significantly affect seedling success (Valladares et al., 2016; Umaña et al., 2021; Mielke et al., 2023), including during nursery-to-field transitions. Plants rely on photoreceptors, especially phytochromes, to perceive and respond to varying light availability (Cerqueira et al., 2023). Phytochromes detect red to far-red light ratios (R:Fr), converting photons into biochemical signals triggering adjustments to optimize growth under varying light conditions (Freitas et al., 2022; Song et al., 2023; Nie et al., 2024).

Under high light availability (high R:Fr), plants reduce light-harvesting pigments and enhance photoprotective mechanisms (Rossatto et al., 2018; Mendonça et al., 2020; Song et al., 2023). Seedlings prioritize root growth for water access and display higher stomatal conductance and photosynthetic rates (Naves et al., 2018; Mendonça et al., 2020; Yu et al., 2020; Bartieres et al., 2023). Conversely, in low light (low R:Fr), plants increase leaf area, allocate more biomass aboveground, and enhance light-harvesting efficiency with higher chlorophyll content (Valladares et al., 2016; Mendonça et al., 2019; Olguin et al., 2020; Freitas et al., 2022), though lower net carbon assimilation may occur (Naves et al., 2018; Rossatto et al., 2018).

Plasticity varies among species, with niche-generalist species exhibiting higher plasticity than niche-specific species (Pennacchi et al., 2021). Considering *C. langsdorffii* is a niche-generalist species, we hypothesize high phenotypic plasticity enabling adaptation across light conditions. We predict *C. langsdorffii* will prioritize morphological adjustments over physiological ones under high light, but rely more on physiological plasticity under low light where photosynthesis is limited, suggesting hierarchical responses with morphological plasticity primary under favorable conditions and physiological plasticity prominent under shade (Linné et al., 2021; Barbosa et al., 2022). This hypothesis, based on resource allocation theory (Pigliucci, 2003; Pennacchi et al., 2021), suggests plants prioritize morphological adjustments before physiological modifications. Studies confirm this pattern in trees (Valladares et al., 2007; Poorter et al., 2019), with morphological changes preceding physiological ones when necessary. We investigate morphological-physiological adjustments in *C. langsdorffii* seedlings under varying light conditions to inform nursery management. By optimizing light intensity and R:Fr ratio, we aim to enhance seedling quality for improved restoration success.

2. MATERIALS AND METHODS

2.1. Experimental design and growth conditions

The experiment was conducted at the Plant Physiology Laboratory greenhouse facilities of the Federal University of Lavras, Minas Gerais, Brazil (21°14'S, 45°00'W, 918 m altitude) from January to May 2013. The local climate is classified as Cwa (humid subtropical) according to Köppen's classification, with dry winters and rainy summers. During the experimental period, the average temperature was 23.5°C (±2.8°C) and relative humidity averaged 68% (±12%).

Seeds of *C. langsdorffii* were collected from multiple trees in a natural Cerrado area (coordinates 21°11'04" S, 44° 56' 44" W to 21°18'12"S, 44° 59' 14" W) during October-November 2012, encompassing both *stricto sensu* and gallery forest fragments. After collection, all seeds were pooled together, dried, and cleaned according to standard protocols. Seeds were visually inspected and homogenized based on size and appearance to minimize variation in initial vigor, with damaged or malformed seeds discarded.

From this homogenized seed pool, 90 seeds of similar size and appearance were randomly selected, with 30 seeds allocated to each light treatment. This bulk sampling approach, while not controlling for maternal effects, ensured a representative genetic sample from the local *C. langsdorffii* population and simulated practical conditions encountered in commercial nursery operations where seed source tracking is not typically implemented. Seedlings were cultivated under light treatments for 120 days after emergence.

Thirty days after emergence, six seedlings from each treatment (n=6) were selected based on objective criteria: height between 8-12 cm, stem diameter between 2-3 mm, and 4-6 fully expanded leaves. Statistical analysis confirmed no significant differences among selected seedlings within treatments (p>0.08), ensuring comparable initial conditions. The experiment followed a completely randomized design with three light treatments:

1.High Light (HL): seedlings in greenhouse covered with low-density clear plastic, allowing full sunlight penetration.

2.Medium Light (ML): seedlings in greenhouse with clear plastic and Sombrite® shade net undercover, providing 50% reduction in incident solar radiation.

3.Low Light (LL): seedlings in greenhouse with clear plastic and Insulfilm® shade film undercover, providing 75% reduction in visible spectrum (400-700nm) and 50% in red and near-infrared spectrum.

Percentage reductions were determined through comparative measurements using the USB-650 RED TIDE spectroradiometer (Ocean Optics Inc., Dunedin, FL, USA). Environmental parameters monitored throughout the experiment included photosynthetic photon flux density measured every 30 minutes using a LI-COR Quantum Sensor Q41031 (LI-COR Inc., Lincoln, NE, USA) coupled to datalogger Li 1400; solar radiation incidence (200-850nm) measured with USB-650 RED TIDE spectroradiometer; and air temperature and relative humidity measured with Extech Thermo-hygrometer RHT10 (Extech Instruments Corp., Nashua, NH, USA). Vapor Pressure Deficit was calculated according to Jones (1992).

Visible light intensity, photosynthetic photon flux density, air temperature and vapor pressure deficit were higher in high light, followed by medium and low light treatments. The R:Fr ratio was higher for high and medium light but low for the low light treatment (Figure 1 and Table 1).

Clear plastic protected seedlings from precipitation changes while allowing light treatments. Citropote® containers in buckets maintained 65-70% moisture, monitored with ML2x Tetra Probe (Delta-T Devices Ltd., Cambridge, UK) every 7 days. Irrigation occurred every three days; fertilization six times with quarter-strength solution (Malavolta, 1997).

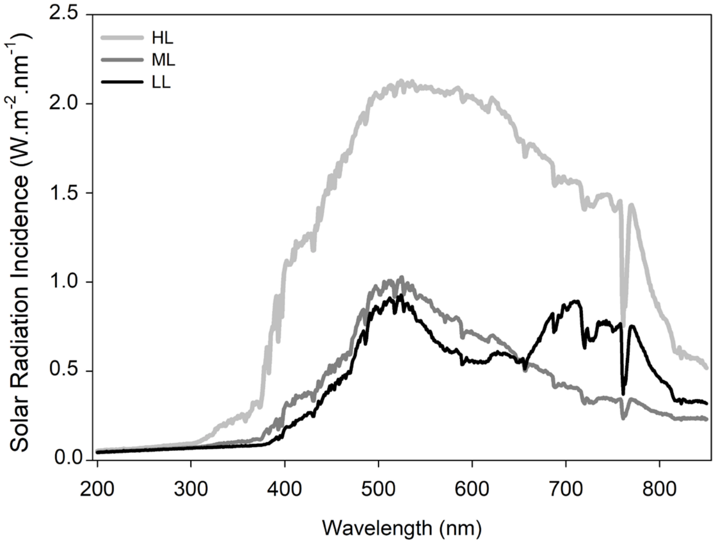

Figure 1. Spectral distribution of incident solar radiation ($W{\cdot}m^{-2}{\cdot}nm^{-1}$) at midday across the three light environments used in the experiment: High Light (light-gray line), Medium Light (dark-gray line), and Low Light (black line). Each line represents the mean of 10 measurements taken under clear-sky conditions. The spectral curves illustrate the reduction and filtering effects imposed by the shading materials in each treatment, particularly in the visible (380nm -700nm) and near-infrared regions (780nm – 850nm).

2.2. *Growth, biomass partitioning and seedling quality*

The growth and biomass measurements were performed on six seedlings per treatment (n = 6), totaling 18 experimental units. The following growth traits were measured for each seedling at the end of the 120-day growth period:

Plant height (H): Measured from the base of the stem to the apical meristem, in centimeters.

Stem diameter (D): Measured 1 cm above the container rim in millimeters.

Following these measurements, seedlings were harvested, and leaves, stems and roots were separated and oven-dried at 70°C for 72 hours to determine dry biomass. The following biomass parameters were then calculated:

Leaf, stem, and root dry matter (LDM, SDM and RDM, respectively): Measured in grams.

Total dry matter (DM): Sum of leaf, stem, and root dry matter in grams.

Biomass partitioning: Percentage of total dry matter allocated to leaves (LB), stems (SB), and roots (RB).

Root-to-shoot ratio (R/S): Calculated as root dry matter divided by shoot dry matter (stem + leaf dry matter).

The Dickson Quality Index (DQI) (Dickson et al., 1960) was calculated using the growth and biomass partitioning variables in order to measure the quality of the seedling in the light treatments. DQI was calculated according to the Equation 1.

$$DQI = \frac{DM}{\frac{H}{D} + \frac{SDM}{RDM}} \tag{1}$$

where DM is the seedling total dry matter in grams, H is the stem high in centimeters, D is the stem diameter in millimeters, and the stem dry matter (SDM) and the root dry matter (RDM) in grams. The higher values of DQI indicate high quality at time of planting based on either physiological or morphological characteristics of the seedlings (Dickson et al., 1960).

Table 1. Experimental parameters of High light (HL), Medium Light (ML), and Low Light (LL) throughout the experimental period (120 growing days after emergence). Values are the daily averages ± standard error. The n=120 for VPD -Vapor pressure deficit; PPFD -photosynthetic photon flux density; T - air temperature; and RH - relative humidity. The n = 16 for the θ - water volumetric content. The n = 10 for UVC Intensity (Ultraviolet C Intensity from 201nm to 259nm); UVB Intensity (Ultraviolet B Intensity from 261nm -319nm); UVA Intensity (Ultraviolet A Intensity from 321nm -379nm); Violet Intensity (381nm – 439nm); Blue Intensity (441nm – 499nm); Green Intensity (501nm – 559nm); Yellow Intensity (561nm – 599nm); Orange Intensity (601nm – 639nm); Red Intensity (641nm – 699nm); Far-red Intensity (701nm – 779nm); Near infrared Intensity (NIR – 780nm-850nm); Total Intensity (200nm - 850nm); Visible Light Intensity (VIS 380nm - 700nm); Red:Far-red Ratio; 660nm:730nm Ratio. Values followed by different letter show significant differences among treatments (in the line) according to one-way ANOVA F-test (P<0.05).

Environmental Variable	Light Availability		
	HL	ML	LL
VPD (kPa)	1.36 ± 0.05^a	0.88 ±0.03^b	0.88 ±0.03^b
PPFD (µmol.m^{-2}.s^{-1})	592.5±64.7^a	280.7±24.1^b	158.0±21.^{6}c
T (°C)	27.2 ± 0.3^a	23.5 ± 0.3^b	23.6± 0.3^b
RH (%)	63.0 ± 0.8^b	70.0 ± 0.8^a	70.2 ± 0.9^a
θ (m^3 m^{-3})	0.140±0.014^a	0.140±0.022^a	0.150±0.015^a
UVC Intensity (W.m^{-2})	3.6±2.4^a	3.2±1.3^a	3.1±1.4^a
UVB Intensity (W.m^{-2})	5.5±2.5^a	4.2±1.3^a	4.0±1.3^a
UVA Intensity (W.m^{-2})	15.1±2.6^a	6.3±1.5^b	4.8±1.8^b
Violet Intensity (W.m^{-2})	64.4±22.2^a	18.4±3.8^b	12.2±4.1^b
Blue Intensity (W.m^{-2})	106.3±24.1^a	41.1±4.4^b	33.3±5.3^c
Green Intensity (W.m^{-2})	125.3±21.2^a	56.9±7.0^b	45.6±6.3^c
Yellow Intensity (W.m^{-2})	82.4±32.6^a	31.1±5.4^b	21.2±4.2^c
Orange Intensity (W.m^{-2})	79.4±21.2^a	27.1±2.1^b	23.0±2.7^c
Red Intensity (W.m^{-2})	104.5±31.0^a	30.9±3.2^c	44.5±3.7^b
Far-red Intensity (W.m^{-2})	112.8±18.5^a	27.6±5.0^c	60.8±4.5^b
NIR Intensity (W.m^{-2})	52.2±10.1^a	18.0±2.2^c	34.1±3.1^b
Total Intensity (W.m^{-2})	751.8±195.4^a	264.9±38.2^b	285.6±37.4^b
VIS Intensity (W.m^{-2})	562.3±130.1^a	205.6±25.9^b	184.8±26.3^c
Red:Far-red Ratio	0.92±0.07^a	1.12±0.13^a	0.73±0.12^b
660nm:730nm Ratio	1.2±0.2^a	1.6±0.3^a	0.8±0.1^b

2.3. *Chlorophyll content, chlorophyll a fluorescence, and gas exchange measurements*

The morphological and physiological trait measurements were taken 120 days after emergence. Physiological measurements including chlorophyll content, fluorescence parameters, and gas exchange traits were performed on two fully expanded leaves per seedling, of the up third of the seedling, totalizing 2 x 6 =12 replicates per treatment (n = 12). All the measurements were performed between 09:00 AM and 11:00 AM. Leaf chlorophyll content was estimated using a portable chlorophyll meter (atLEAF+, FTGreen LLC, Wilmington, DE, USA). Four measurements were taken per replicate, and the mean value was used for analysis.

Chlorophyll *a* fluorescence traits were determined using a portable fluorometer (MINI-PAM, Heinz Walz GmbH, Effeltrich, Germany). Measurements were performed under ten incrementally increasing levels of actinic light intensity to determine the following traits: Photochemical yield (ΦPSII), Electron Transport Rate (ETR), Photochemical quenching (qP).

Gas exchange traits were measured using an infrared gas analyzer (IRGA model LI-6400XT, LI-COR Inc., Lincoln, NE, USA) under the following chamber-controlled conditions: photosynthetic photon flux density of 600 µmol m^{-2} s^{-1}, temperature of 30°C, relative humidity of 60%, and leaf-to-air vapor pressure deficit of approximately 1.8 kPa. The following traits were measured: Net photosynthesis (A), Stomatal conductance (gs), Transpiration rate (E), Internal carbon dioxide concentration (Ci), Intrinsic water use efficiency (WUEi), and Instantaneous carboxylation efficiency (A/Ci).

2.4. *Quantification of the phenotypic plasticity*

Were calculated using all measurements from six seedlings per treatment (n = 6). To assess the degree to which morphological and physiological traits were modified by light treatments, we calculated two indices of phenotypic plasticity:

Relative Distance Plasticity Index (Valladares et al., 2006): The RDPI quantifies the trait-specific extent of phenotypic differences between individuals grown under different light conditions. It was calculated using the following equation (Eq.2):

$$RDPI = \frac{\Sigma \frac{dij \rightarrow i'j'}{xi'j' + xij}}{n} \qquad (2)$$

where *j* and *j'* represent individual plants, *i* and *i'* represent different light conditions, $dij \rightarrow i'j' / (xi'j' + xij)$ is the relative distance between pairs of individuals exposed to different light conditions, and *n* is the total number of distances calculated.

Multivariate Plasticity Index (Pennacchi et al., 2021): The MVPi provides an integrated measure of phenotypic plasticity across multiple traits. It was calculated using Canonical Variance Analysis based on Euclidean distances of standardized trait values. The following traits were included in the MVPi calculation:

Physiological traits: ΦPSII, ETR, qP, A, gs, E, Ci, WUEi, and A/Ci.

Biomass partitioning traits: LB, SB, RB, and R/S ratio.

Plasticity indices were calculated using data from six seedlings per treatment (n = 6) for both morphological and physiological traits.

2.5. *Statistical analysis*

Prior to analysis, all data was tested for normality using the Kolmogorov-Smirnov test and homogeneity of variances using Levene's test. Data that met the assumptions of normality and equal variance were analyzed using one-way Analysis of Variance to determine the effects of light treatment on measured traits. When significant differences ($p<0.05$) were detected, Tukey's Honestly Significant Difference post-hoc test was employed to make pairwise comparisons between treatment means. Data that do not met the assumptions of normality and equal variance was analyzed using the Kruskal-Wallis Rank Analysis of Variance to determine the effects of light treatment on measured traits. When significant differences ($p<0.05$) were detected, Dunn's post-hoc test was employed to make pairwise comparisons between treatment means. All statistical analyses were conducted using SISVAR software (Ferreira, 2011).

To explore the relationship between phenotypic plasticity and plant performance, we calculated the correlation between the Multivariate Plasticity Index and normalized differences in biomass and growth variables between treatments at 120 days after emergence, following the approach described by Pennacchi et al. (2021) and using the Pearson Product Moment Correlation Coefficient (r) ($p<0.05$). The normalized differences in biomass and growth traits were estimated as the module of the difference of the variables divided by the higher value.

3. RESULTS

3.1. *Growth, biomass allocation and seedling quality*

Light availability significantly influenced the growth; the biomass allocation patterns and the quality of the seedlings of *C. langsdorffii*. While total dry matter (1.70g ±0.13g, p = 0.127), stem dry matter (0.22g ± 0.02g, p = 0.089) and leaf dry matter (0.49g ± 0.04g, p = 0.156) did not differ significantly between light treatments after 120 growing-days, according to one-way ANOVA followed by Tukey's test (means ± standard errors, n = 18), we observed clear shifts in plant morphology and biomass partitioning that affected seedling quality (Figure 2).

Plants grown under low and medium light exhibited significantly greater stem elongation, resulting in increased plant height. For stem diameter, plants under high and low light conditions showed statistically similar values (Figure 2B), both being significantly lower than those under medium light. Furthermore, low light led to a shift in biomass allocation, with a greater proportion of biomass allocated to leaves and a corresponding decrease in allocation to roots compared to plants grown under high light. Interestingly, only plants grown under medium light showed a significant increase in biomass allocated to stems. The observed decrease in root dry matter and root-to-shoot ratio under low light further supports a shift in carbon allocation away from belowground structures.

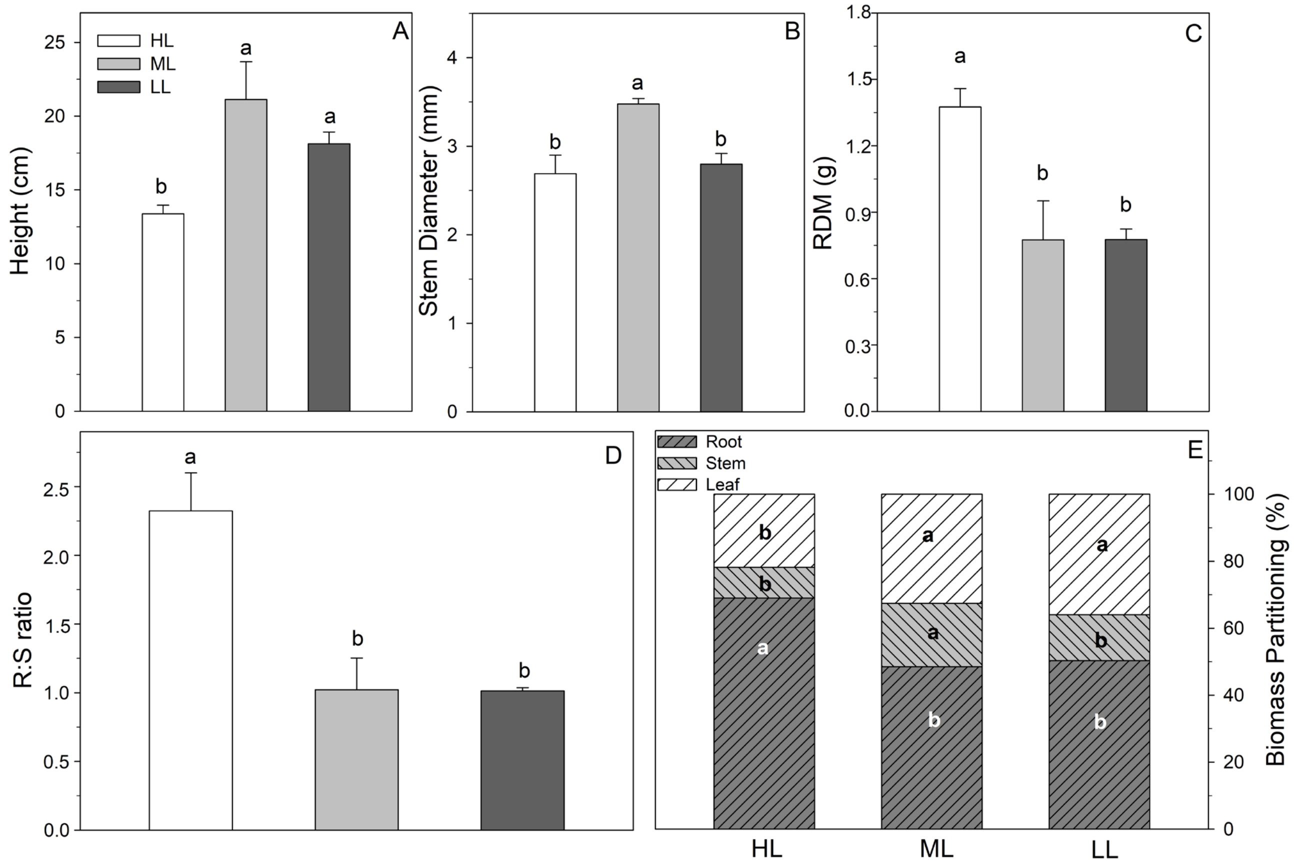

Figure 2. Height (A), Stem diameter (B), Root dry matter - RDM (C), Root-to-shoot ratio- R:S ratio (D), and Biomass partitioning into root, stem, and leaf of *C. langsdorffi*i seedlings grown under High (HL – white bars), Medium (ML - light-gray bars), and Low (LL -dark bars) light at 120 days after emergence. Values followed by the same letter do not show significant differences according to one-way ANOVA followed by Tukey's test (R:S ratio and RDM) or Kruskal-Wallis Rank Analysis of Variance followed by Dunn's test ($p<0.05$). Values are the means ± standard error (n= 6).

Those growth and biomass partitioning patterns resulted in higher and similar DQI ($p<0.01$) in high (0.40 ± 0.05) and low (0.33 ± 0.03) light in relation to medium light (0.26 ± 0.03) according to one-way ANOVA followed by Tukey's test. While the DQI values suggest differences in seedling quality, it is important to note that this index should be interpreted in conjunction with other morphological and physiological parameters. When considering the complete set of measured traits, particularly root development and physiological performance, high light conditions produced the most balanced seedlings for field establishment.

3.2. Leaf physiological traits

Light availability significantly influenced the photosynthetic performance of *C. langsdorffii* seedlings. Seedlings grown under high light exhibited higher values of ΦPSII, ETR, and qP compared to those under medium light ($p < 0.05$). However, statistical analysis indicated that values under low light did not differ significantly from either high or medium light, suggesting a convergence in photochemical performance under shaded conditions. In contrast, seedlings exposed to medium and low light exhibited a marked increase in chlorophyll content, reflecting a typical acclimation response to reduced irradiance (Figure 3).

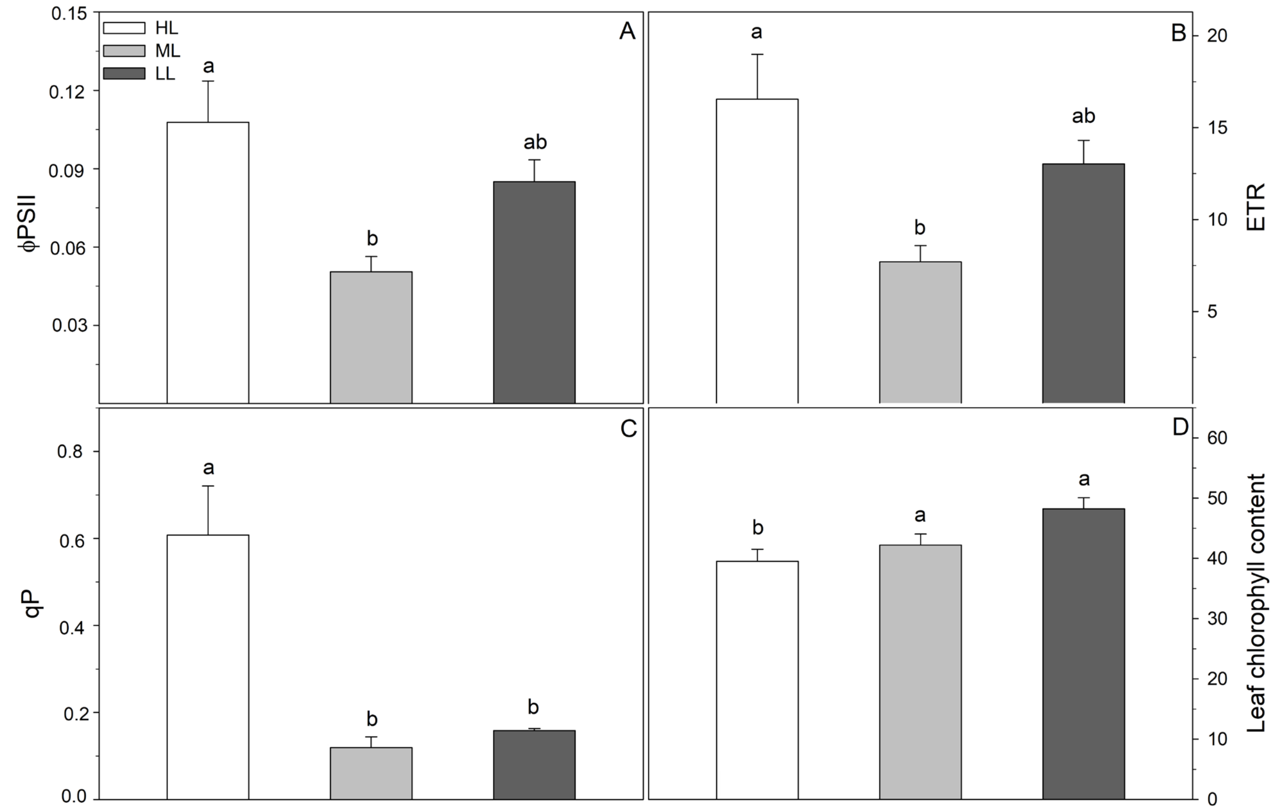

Figure 3. Photochemical yield- ΦPSII (A), Electron transport rate-ETR (B), Photochemical quenching- qP (C), and leaf chlorophyll content (D) of *C. langsdorffi*i seedlings grown under High (HL – white bars), Medium (ML - gray bars), and Low (LL -dark bars) light availability at 90 and 120 days after emergence. Values followed by the same letter do not show significant differences according to one-way ANOVA followed by Tukey's test ($p<0.05$). Values are the means ± standard error ($n = 12$).

Gas exchange traits were also significantly affected by light availability. Seedlings grown under medium light exhibited the highest photosynthetic rates, associated with a combination of reduced internal CO_2 concentration (Ci), elevated stomatal conductance (gs), and greater carboxylation efficiency (A/Ci) (Figure 4). In contrast, the carbon balance in leaves was compromised under low light, with reductions in both net photosynthesis and carboxylation efficiency. Despite showing higher transpiration rates, seedlings under medium light maintained greater intrinsic water use efficiency (WUEi) compared to those under high or low light.

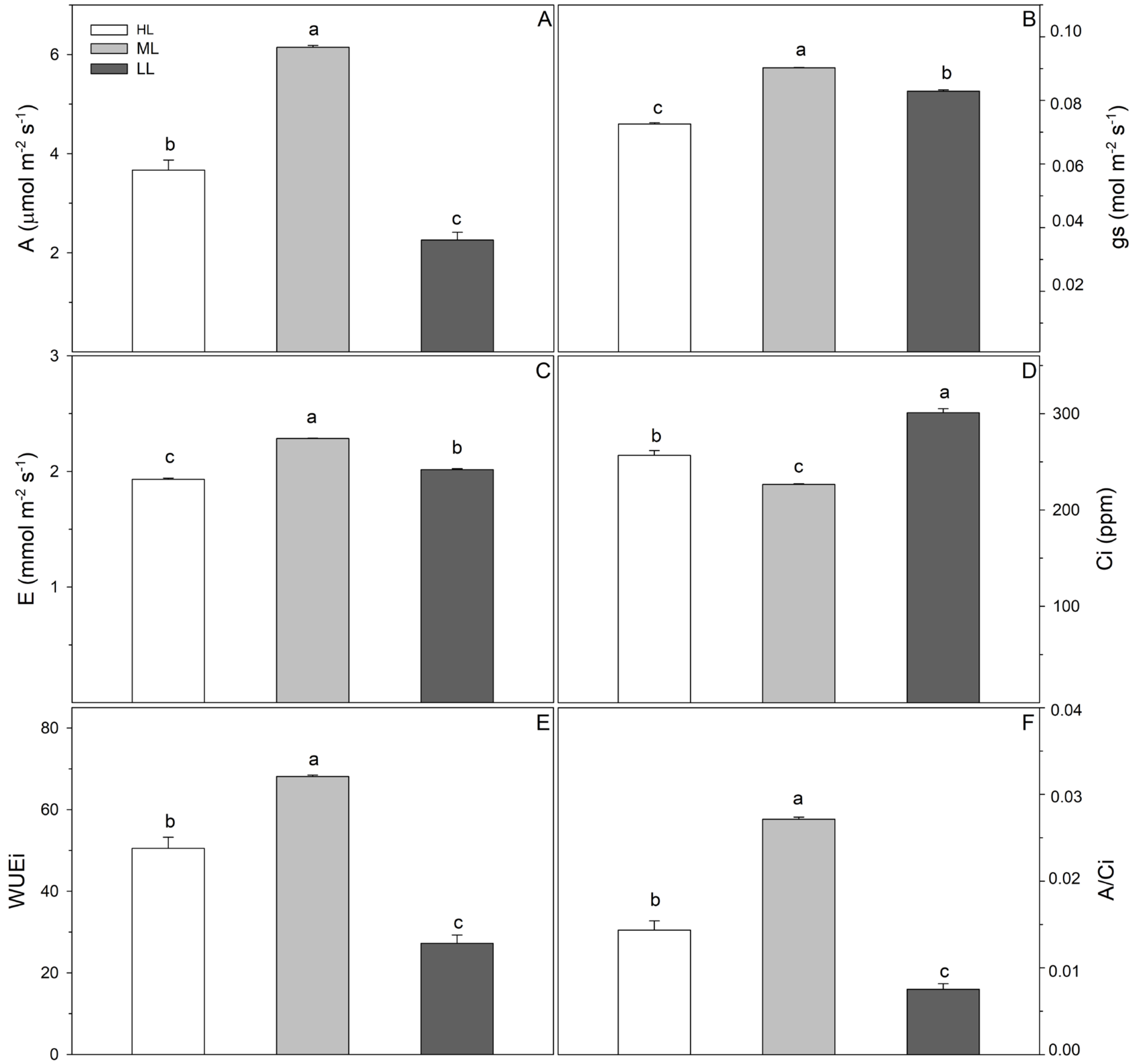

Figure 4. Net photosynthesis- A (A), stomatal conductance- gs (B), transpiration- E (C), internal carbon dioxide concentration- Ci (D), intrinsic water use efficiency- WUEi (E), and instantaneous carboxylation efficiency- A/Ci (F) of *C. langsdorffii* seedlings grown under High (HL – white bars), Medium (ML - gray bars), and Low (LL -dark bars) light availability at 90 and 120 days after emergence. Values followed by the same letter do not show significant differences according to one-way ANOVA followed by Tukey's test (Ci and A/Ci) or Kruskal-Wallis Rank Analysis of Variance followed by Dunn's test ($p<0.05$). Values are the means ± standard error (n= 12).

3.3. *Phenotypic plasticity in response to light*

The Relative Distance Plasticity Index (RDPI) provided insights into traits exhibiting highest plasticity to light variation. High-to-medium light transitions elevated RDPI values for root-to-shoot ratio and photochemical quenching (qP), indicating pronounced plasticity. Traits such as stem diameter, internal CO_2 concentration (Ci), leaf chlorophyll content, stomatal conductance (gs), and transpiration showed lower RDPI values (Figure 5).

Photochemical quenching (qP) consistently showed high RDPI values in both high-to-medium and high-to-low light transitions, suggesting robust plastic response. Root-to-shoot ratio exhibited increased RDPI in both high-to-medium and medium-to-low contrasts, reinforcing irradiance sensitivity. RDPI values for A/Ci, net photosynthesis (A), and intrinsic water use efficiency (WUEi) were particularly high in medium-to-low transitions, indicating enhanced physiological plasticity under low light.

The Multivariate Plasticity Index (MVPi) quantified overall phenotypic divergence. Highest MVPi (7.76 ± 0.40) occurred between high and medium light ($p<0.05$; one-way ANOVA, Tukey's test), indicating the most substantial phenotypic shift. High-to-low (6.49 ± 0.25) and medium-to-low (6.57 ± 0.19) comparisons showed no significant difference ($p>0.05$), suggesting similar global responses to low light regardless of previous conditions.

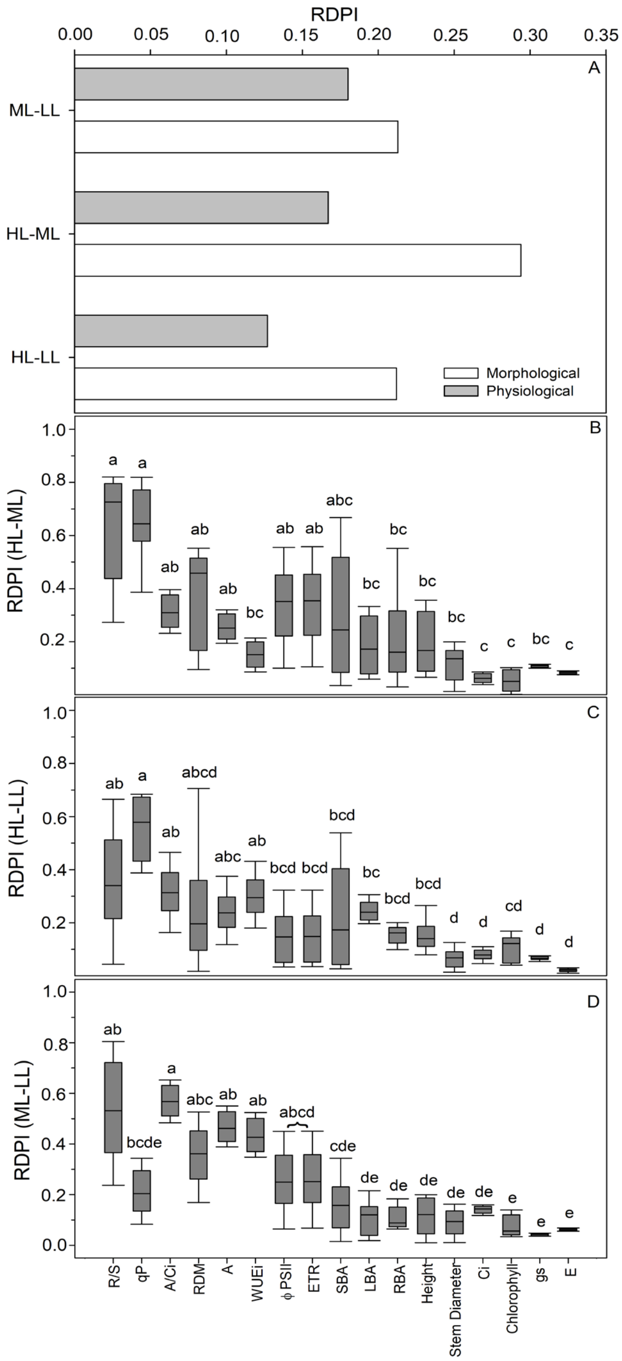

Figure 5. Relative Distance Phenotypic Index (RDPI) of the overall morphological and of the overall physiological traits of high-to-medium (HL-ML), high-to-low (HL-LL), and medium-to-low (ML-LL) (A). The RDPI observed for the individual traits of high-to-medium (B) high-to-low (C), and medium-to-low (D) light availability of *C. langsdorffi*i seedlings at 120 days after emergence. Values followed by the same letter do not show significant differences according to Kruskal-Wallis Rank Analysis of Variance followed by Dunn's test ($p<0.05$). Values are the means ± standard error (n= 6 for the growth and biomass allocation traits, and n = 12 for the leaf physiological traits).

Furthermore, we found a positive correlation between MVPi and the normalized difference in the plant growth and biomass variables, particularly important and significant ($p<0.05$) for plant height ($r=0.882$), stem diameter ($r=0.751$) and root dry matter ($r=0.659$). This finding suggests that a greater phenotypic plasticity is linked with higher stem growth and root biomass production in *C. langsdorffii* seedlings.

Taken together, our results indicate that *C. langsdorffii* exhibits a light-dependent shift in its phenotypic plasticity strategy. Morphological adjustments — mainly in stem elongation and root biomass allocation — predominated in the high-to-medium light comparison. In contrast, physiological adjustments, particularly in photosynthetic traits, became more prominent under the medium-to-low light contrast, likely as an acclimation mechanism to preserve photosynthetic efficiency under reduced irradiance.

4. DISCUSSION

4.1. Morphological adjustments to light

Our findings reveal key morphological and physiological mechanisms underpinning *C. langsdorffii*'s capacity to adjust to varying light availability. These adaptive modifications are essential for plants to occupy diverse positions along light gradients (Freitas et al., 2022; Mielke et al., 2023). The observed stem elongation under shaded conditions aligns with shade avoidance syndrome under low R:Fr conditions (Jesus et al., 2021; Freitas et al., 2022). This response maximizes light capture efficiency in shade environments (Yang & Kim, 2020; Huang et al., 2021), but could potentially increase susceptibility to wind damage or herbivory when outplanted (Fernández-Milmanda & Ballaré, 2021).

Under high light availability, *C. langsdorffii* seedlings invested significantly more in root biomass, likely to enhance water uptake and offset increased transpiration rates (Freitas et al., 2022; Reis et al., 2023). This pattern is consistent with observations from Brazilian savanna, where plants prioritize root over shoot growth as adaptation to seasonal drought (Mendonça et al., 2020; Fagundes et al., 2021). Increased root biomass may enhance survival under high temperatures and limited water availability typical of restoration sites. Such morphological plasticity represents a crucial adaptive mechanism for woody species across diverse light environments (Valladares et al., 2016; Silverio et al., 2024).

Our results revealed diminished morphological plasticity under low light, coupled with increased physiological plasticity, suggesting strategic resource allocation shifts. While morphological adjustments dominate in high-to-medium light transitions, physiological mechanisms become crucial under low light with low R:Fr ratios. This hierarchical response highlights the importance of considering spectral quality when managing nursery light. Manipulating R:Fr through supplemental lighting or spectrally-selective shade materials could optimize seedling physiology for low-light conditions, potentially improving outplanting success.

4.2. Physiological adjustments to light

The complex interplay between photochemical efficiency and photosynthetic capacity in *C. langsdorffii* seedlings underscores light quality's importance in modulating physiological responses. While high light enhanced photochemical traits, as documented for this species (Rodrigues et al., 2019; Barbosa et al., 2022), it did not proportionally increase photosynthetic rates. This decoupling suggests additional limiting factors, such as stomatal constraints or elevated photorespiration (Mendonça et al., 2019; Rosa et al., 2021), particularly given reduced stomatal conductance under high light.

Increased chlorophyll content under shade represents classic acclimation to maximize light harvesting (Huang et al., 2021). Plants under medium light exhibited elevated chlorophyll and enhanced photosynthesis, suggesting optimal balance. However, under lowest light with low R:Fr, impaired photosynthesis occurred despite increased chlorophyll, highlighting *C. langsdorffii*'s sensitivity to spectral quality. This reinforces the need for spectral manipulation in nurseries to optimize performance under reduced light (Naves et al., 2018; Cerqueira et al., 2023). Considering both light quantity and spectral composition can enhance seedling physiological performance even under space-constrained shading.

4.3. Phenotypic plasticity and nursery technological application

Phenotypic differences in *C. langsdorffii* seedlings between high and medium light were driven predominantly by morphological rather than physiological adjustments. As light decreased, biomass allocation shifted towards shoot growth, optimizing light capture. This investment in aboveground structures under reduced light aligns with findings from other tree species (Naves et al., 2018).

Conversely, biomass allocation towards belowground structures under high light reflects adaptive acclimation to enhance water and nutrient uptake, consistent with Cerrado species' responses to high light (Freitas et al., 2022). This pattern could prove advantageous for seedlings in sites susceptible to seasonal water shortages (Bartieres et al., 2023).

Our results revealed decreased morphological plasticity under low light, as pronounced changes occurred in high-to-medium light transitions, with minimal differences under low light. This diminished morphological plasticity coincided with increased physiological plasticity. Physiological plasticity represents plants' response to environmental perturbations challenging homeostasis (Garcia et al., 2021; Pennacchi et al., 2021; Silverio et al., 2024). Increased physiological plasticity under low light indicates stress, where morphological adjustments alone proved insufficient to maintain photosynthetic performance under low R:Fr conditions.

The high phenotypic plasticity of *C. langsdorffii* offers opportunities for optimizing nursery practices. Understanding how light quantity and spectral quality influence development allows tailored light regimes. Manipulating R:Fr ratio could enhance seedling quality under reduced light, ensuring adequate photomorphogenic signals (Cerqueira et al., 2023).

Future research should refine light management strategies to optimize Dickson Quality Index parameters and maximize establishment success, contributing to precision nursery technologies

4.4. *Methodological considerations and results limitations*

Our pooled sampling strategy incorporates genetic variation (Valladares et al., 2007; Silverio et al., 2024) into our experimental design. While limiting our ability to identify family-specific responses, it strengthens the generalizability of our conclusions. Future studies could employ half-sib designs to explore provenance-specific plasticity responses to light.

Several constraints affect result interpretation: The 120-day evaluation period represents only initial seedling development; discrete light treatments revealed threshold responses, particularly between high and medium conditions; and controlled greenhouse conditions cannot replicate complex environmental interactions in natural settings where light fluctuates and interacts with water availability, temperature, and soil nutrients (Cerqueira et al., 2023; Bartieres et al., 2023). Future research opportunities include longer evaluation periods, continuous light gradients, and multi-factor designs to further elucidate *C. langsdorffii*'s environmental adaptability.

4.5. *Implications for nursery management*

Our findings provide practical guidelines for optimizing *C. langsdorffii* seedling production. Nurseries should prioritize high light conditions, which promote enhanced root development and superior seedling quality (DQI = 0.40 ± 0.05). This low-cost investment yields better field performance while maintaining cost-effective production.

We discourage shade use, as it results in inferior seedling quality despite increased chlorophyll content. The metabolic cost of physiological adjustments under shade doesn't compensate for reduced light availability (Linné et al., 2021; Cerqueira et al., 2023).

For implementation, we recommend precision management with quantifiable parameters: PPFD > 1000 μmol m^{-2} s^{-1} during peak daylight and R:Fr ratios > 1.15. These can be achieved through strategic nursery design, appropriate container spacing, reflective surfaces, and spectrally-neutral covering materials that maintain natural solar spectrum.

5. CONCLUSIONS

This study confirms that *Copaifera langsdorffii* exhibits hierarchical phenotypic plasticity, with morphological adjustments predominating under high light and physiological mechanisms under low light. Seedlings in full sunlight prioritized root development and achieved superior quality indices (DQI = 0.40), while those under low light showed physiological adjustments but reduced quality. The highest plasticity occurred between high and medium light, indicating a threshold response.

For nursery management, we recommend high light conditions for producing quality seedlings with enhanced root development and field performance. Shade conditions should be avoided despite the species' acclimation capacity, as they result in lower seedling quality.

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DATA AVAILABILITY

All data supporting the findings of this study are available upon request from the corresponding author, Prof. Dr. João Paulo Rodrigues Alves Delfino Barbosa.

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