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Original Article

Campomanesia xanthocarpa (Myrtaceae: Myrtoideae) seedlings reveal morpho-physiological plasticity under shade conditions

Mudas de *Campomanesia xanthocarpa* (Myrtaceae: Myrtoideae) demonstram plasticidade morfofisiológica à sombra

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Abstract

Plants exposed to different light intensities generate physiological, morphological, and anatomical changes conducting to plasticity. Thus, this characteristic establishes the ability of plants to present phenotypic adjustments by the same genotype under different environmental conditions. The objective of this study was to verify the morphophysiological alterations in *Campomanesia xanthocarpa* (Mart.) O. Berg (guabiroba) seedlings cultivated in different shading levels. The seedlings were grown for 21 months under full sun or 30%, 50%, and 80% under shading. Growth, photosynthetic pigments, gas exchange rate, chlorophyll fluorescence, and leaf anatomy were evaluated. In all the treatments subjected to shading, plasticity mechanisms involved structural and physiological changes such as an increase in leaf area and chlorophyll content (total and Chl *a*), reduction in leaf thickness, and increased gas exchange and quantum yield of photosystem II. The guabiroba seedlings can be cultivated in full sun or different shading environments; even under high shading intensity (80%), the plants showed vigor similar to those produced in a sunny environment. These results confirmed our hypothesis about guabiroba acclimation capacity to shading, noteworthy information for nurseries, orchards, agroforestry systems, or forest restoration in a wide range of light environments.

Keywords: Guabiroba tree, acclimation, chlorophyll content, CO_2 assimilation, quantum yield.

Resumo

Plantas submetidas a diferentes intensidades luminosas sofrem alterações fisiológicas, morfológicas e anatômicas que conduzem à plasticidade, o que permite que as plantas apresentem ajustes fenotípicos pelo mesmo genótipo em diferentes condições ambientais. O objetivo deste estudo foi verificar as alterações morfofisiológicas que definem a tolerância à sombra de *Campomanesia xanthocarpa* (Mart.) O.Berg (guabirobeira). As mudas foram cultivadas por 21 meses a pleno sol ou à 30%, 50% e 80% de sombreamento. Foram avaliados caracteres de crescimento, pigmentos fotossintéticos, taxa de troca gasosa, fluorescência da clorofila e anatomia foliar. Em todos os tratamentos submetidos ao sombreamento, os mecanismos de plasticidade da guabirobeira envolveram aumento da área foliar e do teor de clorofila (total e Chl *a*), redução da espessura da folha e aumento de trocas gasosas e do rendimento quântico do fotossistema II. A produção de mudas de guabirobeira pode ser feita a pleno sol ou em diferentes ambientes de sombreamento, pois mesmo sob alta intensidade de sombreamento (80%), as mudas apresentaram vigor semelhante às produzidas em ambiente a pleno sol. Esses resultados confirmaram nossa hipótese sobre a capacidade de aclimatação de *Campomanesia xanthocarpa* ao sombreamento, informação importante para o cultivo da espécie em viveiros, pomares, sistemas agroflorestais e para a restauração florestal em diferentes ambientes de luz.

Palavras-chave: Guabirobeira, aclimatação, teor de clorofila, assimilação de CO_2, rendimento quântico.

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1. Introduction

Understanding how to achieve more vigorous seedlings of forest tree species is essential for forest restoration and orchard cultivation for human fruit consumption. For this, the definition of an adequate shade environment to obtain good quality plants in nurseries is initially as crucial as later handling in the field. In the meantime, plants can display physiological, biochemical, morphological, and anatomical changes by the same genotype under different light environmental gradients, known as phenotypic acclimation or plasticity (Taiz et al., 2014). Such adjustments mainly lead to photosynthesis regulation to keep the positive carbon balance and allow species establishment under sunlight restrictions (Feng et al., 2019). However, morpho-physiological and architectural traits combinations permit plants to tolerate shadow, explaining the response in different geographical conditions and characteristics of species-specific and intraspecific variability (Valladares and Niinemets 2008; Lusk and Jorgensen 2013; Laforest-Lapointe et al., 2014; Laanisto and Niinemets 2015; Ameztegui et al., 2017).

The guabiroba tree [*Campomanesia xanthocarpa* (Mart.) O. Berg], hereafter only guabiroba, is a native species of the Myrtaceae that occurs in the Atlantic Forest Biome in the South and Southeast regions of Brazil (Oliveira et al., 2020). Considerable annual fruit production (Danner et al., 2010) and wide guabiroba recognition by wild fauna species (Fuzessy et al., 2022) permit the distinction of this tree as a significant forest restoration species. Besides, the guabiroba and other *Campomanesia* species are considered human health promoters employed in treating several diseases (Viecili et al., 2014; Alves et al., 2020; De Sousa et al., 2019; Pacheco et al., 2020; Regginato et al., 2021).

To define appropriate light availability in guabiroba nurseries and intercropping in natural areas and agroforestry systems, it is essential to evaluate morpho-physiological adjustments under different light saturation levels. In addition, tolerance investigation in sunlight limitation is crucial because this explains species coexistence and ecological succession in forests, i.e., reflecting vital environmental strategies for light and carbon acquisition (Lusk and Jorgensen 2013; Ameztegui et al., 2017). In Brazil, significant variation has been naturally found under several shading levels in guabiroba (throughout coexistence in high density of seedlings, juveniles, and reproductive individuals) (Krupek and Lima 2012; Felker et al., 2017; Oliveira et al., 2020). Furthermore, guabiroba shade tolerance studies under semi-controlled conditions have been published (Bartieres et al., 2020; 2021; Silverio et al., 2020). Notwithstanding, these articles evaluate a few light regimes, and leaf anatomy was not assessed in seedlings. Hence, we hypothesized in this study that guabiroba seedlings develop morpho-physiological changes to tolerate both three levels of shade intensity and full sunlight, keeping photosynthesis rate and growth similar among them.

2. Material and Methods

2.1. Experimental conditions

For the experiment establishment, seeds were collected from a single ten-year-old guabiroba (*Campomanesia xanthocarpa*) to minimize the genetic variation bias in a total sun environment. Plant material was located in Pato Branco, Paraná, Brazil (26°11´55 S; 52°41´26 W; 820 m a.s.l.). The seedlings were grown in 2 L pots, kept in a nursery with natural temperature and humidity, and under a 50% shade screen for 12 months. Then, the seedlings with apparent but not curled roots and well-developed stems, branches, and leaves (approximately 20 cm in height and 0.5 cm in stem diameter, measured 5 cm aboveground) were transplanted into 40 L pots. These pots contained a mixture of soil (63%), commercial substrate (31.5%), and vermiculite (5.5%). The pots with the seedlings were placed under full sun and three shadding intensities (30%, 50%, and 80%), where 12 guabiroba plants in each treatment were included. The three shade intensities were generated by wooden structures surrounded, on all sides, by black mesh screens corresponding to each treatment (following the manufacturer's directions). The plants received daily irrigation and manual weed control; two fertilizations with 20 g per plant of NPK formulation (8-28-16) were supplemented 12 and 18 months after the treatments' establishment. All evaluations were performed 21 months after the beginning of the experiment under different light environments. After this time, the seedlings' roots were apparent at the bottom of the pots.

2.2. Growth parameters

Plants' growth was assessed based on the difference between height and diameter measured when the experiment was installed, compared to 21 months later. The leaf area of 100 leaves in four plants per treatment was measured using LI-3100 meter (Li-Cor, Inc.). Above and belowground plant tissue was dried in an oven at 60 ºC for three days. Dickson's quality index (DQI) = [total dry mass / (RSS + RSR)] was calculated, where RSS is the ratio between the shoot height and stem diameter, and RSR is the ratio between the shoot dry mass and root dry mass (Dickson et al., 1960). The dry weight was measured using all 12 plants for each treatment. Because it is a destructive analysis, this measure was determined after all other evaluations.

2.3. Pigments

The photosynthetic molecules (chlorophyll *a*, chlorophyll *b*, and carotenoids) from two leaves of all plants per treatment were analyzed. Fully expanded leaves capable of intercepting the maximum radiation (without overlapping with other leaves) were collected from the upper third of each plant. Two 0.6 cm diameter discs were detached from each leaf, immersed in dimethyl sulfoxide (DMSO) (5.0 ml), and maintained for 18 hours (this time was considered adequate in our previous tests) in the dark and a water bath at 65 °C until they were translucent. The absorbance readings were performed on a UV/VIS spectrophotometer (Shimadzu UV-1800) at 480 nm, 649.1 nm, and 665.1 nm for carotenoids, chlorophyll *a*, and chlorophyll *b*, respectively. Finally, pigment concentrations were calculated (Wellburn, 1994).

2.4. Gas exchanges

Gas exchanges were assessed using an infrared gas analyzer (IRGA) model LC-pro (ADC Bio Scientific Ltda., UK) between 8:30 a.m. and 10:30 a.m. on a sunny day, 21 months after treatments establishment. Three leaves were evaluated in five plants per treatment. The leaves were fully expanded, with the capacity to receive the maximum radiation (without overlapping with other leaves) and located in the upper third of each plant. Photosynthetically active radiation (PAR), net CO_2 assimilation rate (A), transpiration rate (E), stomatal conductance (Gs), intercellular CO_2 concentration (Ci), and carboxylation efficiency (EiC) were measured. The instantaneous carboxylation efficiency was calculated using = A/Ci.

2.5. Chlorophyll fluorescence

Chlorophyll *a* fluorescence was determined using a fluorometer (Multi-ModeChlorophyll Fluorometer®, Model OS5p). The evaluations were performed between 9:00 a.m. and 10:00 a.m. on three fully expanded leaves and adapted to the ambient light of five plants per treatment. Each sample was exposed to a light saturation pulse, obtaining the results of initial fluorescence (F'), maximum fluorescence (Fm), maximum quantum yield of PSII (Y), and relative electron transport rate (ETR).

2.6. Leaf anatomy

Three leaves were collected in four plants per treatment for leaf anatomy measurement. The leaves were fixed in FAA_{50} (formaldehyde, glacial acetic acid, 50% ethanol, 1: 1: 18 vol) for an entire day, washed in 50% ethanol, and stored in 70% ethanol (Johansen 1940). The samples were cut into three fragments, each segment 0.5 cm^2 in diameter, obtained from the central part of the leaf laminae. Then, disks were dehydrated in an ethyl series (80%, 90%, and 95%) and included in methacrylate (Historesina, Leica Instruments). Cross-sections with 8.0 µm thickness were made, stained with 0.12% toluidine blue in 5% borax, and the slides were mounted in Incolor 500® stained varnish (Paiva et al., 2006). A photomicroscope (Zeiss Axiolab) with a digital camera (Sony Cybershot 7.2mb) was employed to digitalize images. ANATI QUANTI software (Aguiar et al., 2007) was operated for image visualization. Abaxial (BE) and adaxial epidermis (DE), spongy (SP), and palisade parenchyma (PP) and lamina thickness were measured in nine measurements per sample.

2.7. Data analysis

Data normality test (Shapiro Wilk) and homogeneity of variance test (Bartlett) were applied, and Box-Cox transformation was used when necessary. Furthermore, ANOVA ($p \leq 0.05$) in a completely randomized design was performed, and the Scott-Knott clustering test ($p \leq 0.05$) was used to compare the means of treatments. All analyses were processed in the R environment (R Core Team 2020).

3. Results

3.1. Growth parameters

There were significant height and diameter growth in guabiroba seedlings under 50% shading compared to the other treatments (Figure 1). Under the highest shadow intensity (80%), the plants presented significant height growth compared to plants' growth in total sunlight and 30% shading. However, this treatment (80%) showed less diameter increase than all other treatments, demonstrating the etiolation effect. Furthermore, the highest shade level seedlings also had a higher total dry matter production than the other treatments. In contrast, dry root matter did not display significant differences between 80% and 0% shaded treatments. Due to these growth adjustments, there were no statistically significant differences among these treatments in DQI (Figure 1).

3.2. Pigments

The chlorophyll *a* and total chlorophyll content were lower in guabiroba seedlings submitted to the full sun than the shaded ones. There were no statistically significant differences in chlorophyll *b* and carotenoid content between the four treatments assessed (Figure 2).

3.3. Gas exchanges

Gas exchange results were more significant in seedlings under 50% shade, with higher net CO_2 assimilation rate (A) and stomatal conductance (Gs). At the same time, the lowest values were observed in guabiroba seedlings grown in full sun (Figure 3). Seedlings submitted to the three shaded levels had a higher transpiration rate (E) and instantaneous carboxylation efficiency (EiC) than plants grown in total sunlight (Figure 3). Therefore, to compensate for the lower PAR values, leaves under shade increased their photosynthetic capacity, mainly guabiroba seedlings grown under 50% shading. No statistically significant differences among treatments for CO_2 intercellular concentration (Ci) were found (Figure 3).

3.4. Chlorophyll fluorescence

The results showed that the greater values of initial (F') and maximum (Fm) fluorescence and quantum yield of the photosystem II (Y) were detected in plants under the three shade levels compared to those under full sun conditions. However, the seedlings' electron transport rate (ETR) was higher under full sunlight. This suggests that the guabiroba showed acclimation strategies to the limited availability of light, optimizing the photosynthetic apparatus after 21 months (Figure 4).

3.5. Leaf anatomy

The palisade, spongy parenchyma, and leaf blade were thicker in guabiroba seedlings under full sun treatment than the shaded ones (Figure 5). Nevertheless, both adaxial and abaxial epidermis thickness did not differ among treatments. Leaves of the seedlings under the highest shade intensity (80%) were thinner due to the parenchyma's thickness compared to the other treatments (Figure 5).

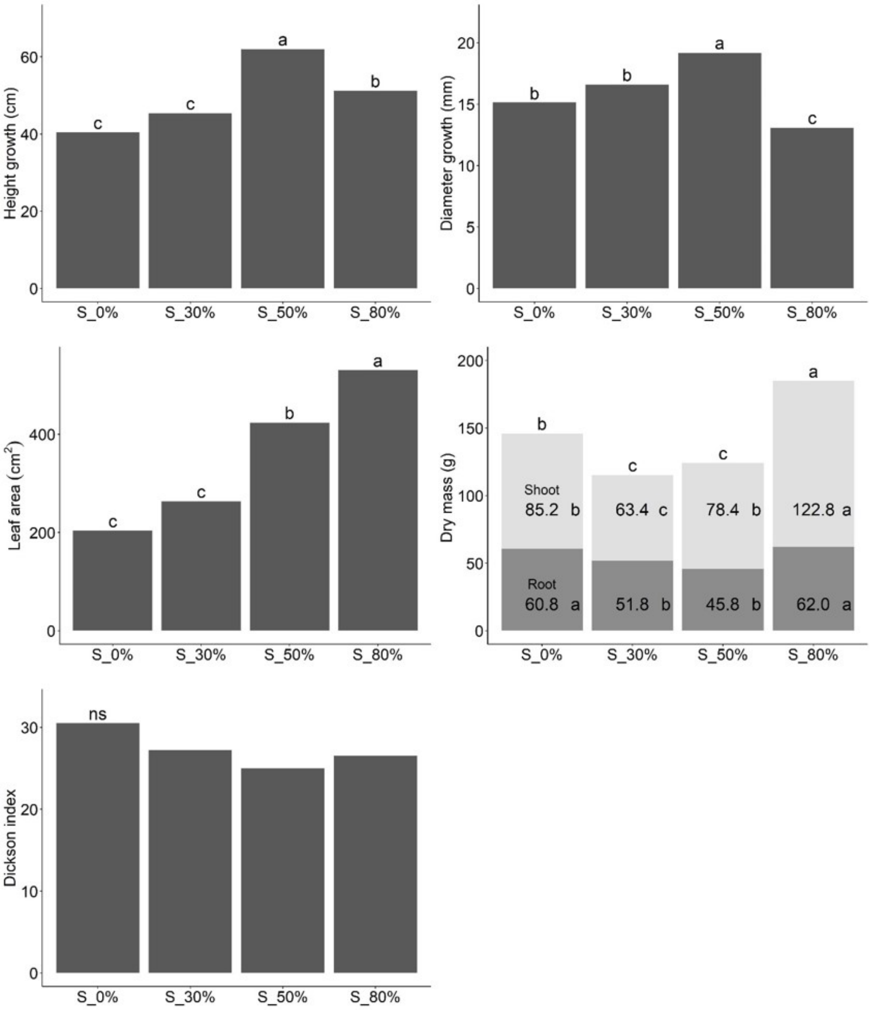

Figure 1. Growth variables of *Campomanesia xanthocarpa* seedlings grown under shade gradient. Non-shaded (S_0%), 30% (S_30%), 50% (S_50%), and 80% (S_80%) of shading. Leaf area and root dry biomass data were modified employing Box-Cox transformation. Total and sub-divided bars represent each treatment's averages and contain letters that may differ from each other by the Scott-Knott test (p≤0.05). When containing 'ns' are no significant differences among the treatments' averages (p>0.05).

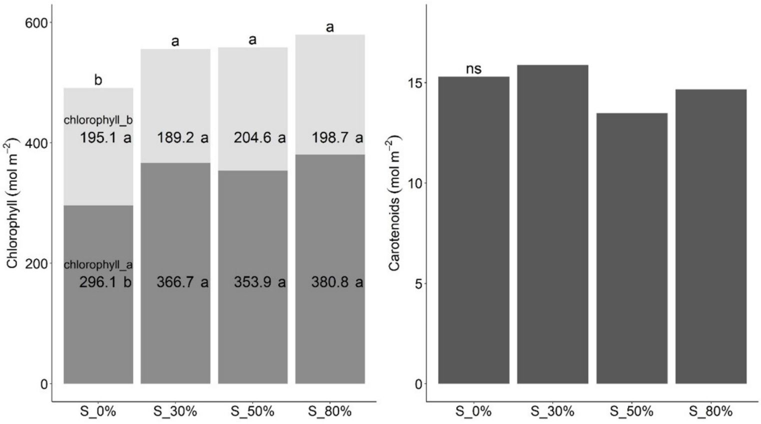

Figure 2. Photosynthetic pigments content of *Campomanesia xanthocarpa* leaves under shade gradient. Non-shaded (S_0%), 30% (S_30%), 50% (S_50%), and 80% (S_80%) of shading. Total and sub-divided bars represent each treatment average, and letters may differ from each other by the Scott-Knott test (p≤0.05). When containing 'ns' are no significant differences among the treatments' averages (p>0.05).

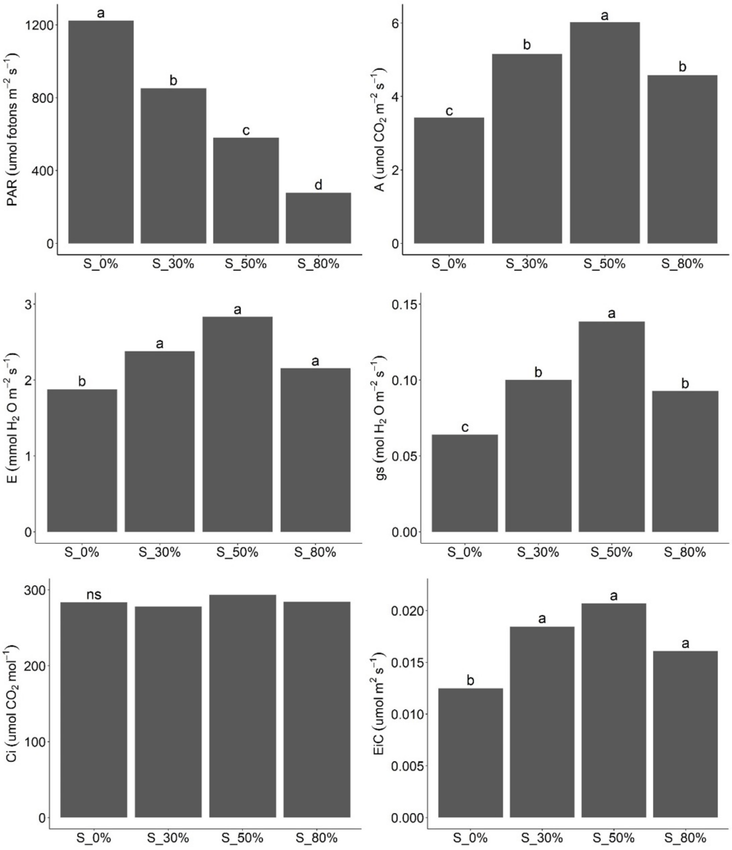

Figure 3. Gas exchange variables of *Campomanesia xanthocarpa* leaves under shade gradient. Non-shaded (S_0%), 30% (S_30%), 50% (S_50%), and 80% (S_80%) of shading. Bars represent each treatment average, and letters may differ from each other by the Scott-Knott test ($p \leq 0.05$). When containing 'ns' are no significant differences among the treatments' averages ($p > 0.05$). Photosynthetically active radiation (PAR); net CO_2 assimilation rate (A); transpiration rate (E); stomatal conductance (Gs); intercellular CO_2 concentration (Ci); and carboxylation efficiency (EiC).

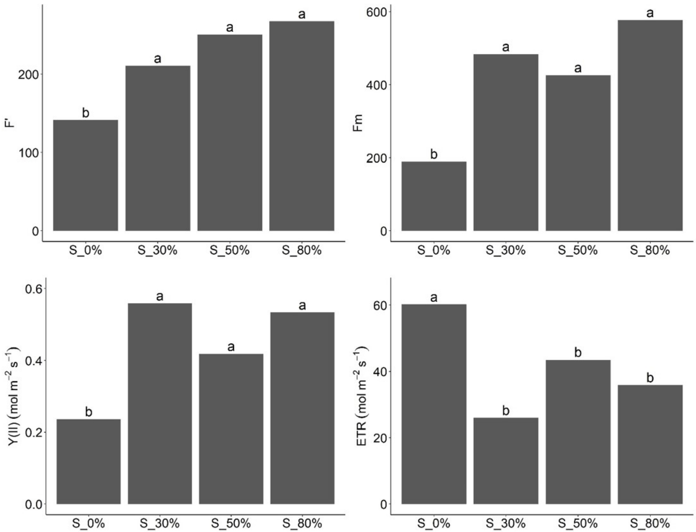

Figure 4. Chlorophyll fluorescence variables from *Campomanesia xanthocarpa* leaves under shading gradient. Non-shaded (S_0%), 30% (S_30%), 50% (S_50%), and 80% (S_80%) of shading. Bars represent each treatment average and contain letters that may differ from each other by the Scott-Knott test ($p \leq 0.05$). Initial (F') and maximum (Fm) fluorescence; Photosystem II quantum yield (Y(II)); and electron transport rate (ETR).

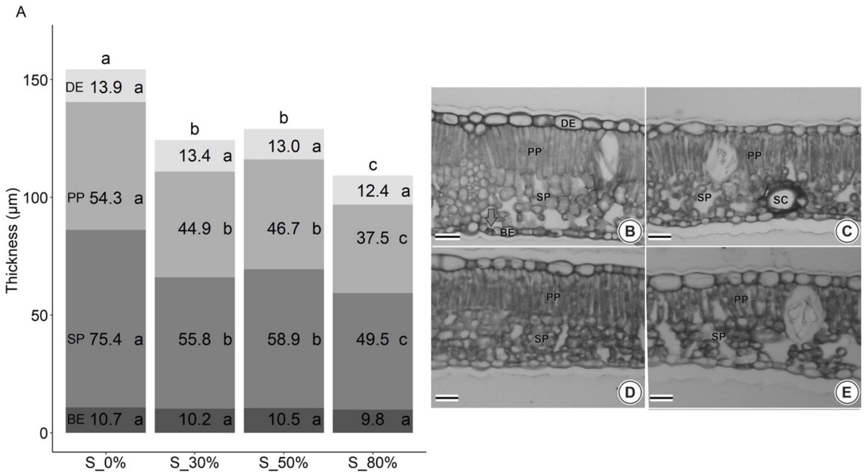

Figure 5. Leaf thickness (A) and cross sections (B, C, D, and E))) of leaf blade by light microscopy in seedlings of *Campomanesia xanthocarpa* under shadding gradient. Non-shaded (S_0%), 30% (S_30%), 50% (S_50%), and 80% (S_80%) of shading. Left figure (A): Different letters indicate significant differences between averages of each treatment by the Scott-Knott test ($p \leq 0.05$). Right figure: B. Full sunlight: palisade parenchyma one layered. C-E. Reduction in leaf thickness on 30% (C), 50% (D), and 80% (E) of shade, respectively. Abbreviatures: DE (adaxial epidermis), BE (abaxial epidermis), SP (spongy parenchyma), PP (palisade parenchyma), SC (secretory cavities). The gray arrow indicates the stomata. Bars = 100 µm.

4. Discussion

Guabiroba seedlings under light restriction had several acclimation responses to attain the same vigor (measured as DQI) compared to plants in a non-shaded environment. Under the three different shade levels, chlorophyll *a* content and gas exchange increased, and thinner leaf modifications were significantly exhibited in guabiroba seedlings. Thus, these changes improved light uptake and transportation under lower PAR, as a survival mechanism for maintaining growth in an environment with lower light availability (Valladares and Niinemets, 2008).

In addition to better absorption, leaves exposed to shade treatments increased the quantum yield of photosystem II (Y). Although a lower quantity of light reached in photosystems, plants in the shade invest the sun's energy to produce photochemical products more efficiently than the seedling under complete solar light (Zhang et al., 2003). The reduced quantum yield of photosystem II in the non-shade treatment indicated that despite high PAR, not all sunlight absorbed was transformed into photochemical products, but this solar energy was dissipated as heat; it is well known that the excessive energy dissipation prevents photosynthetic apparatus disturbance in the thylakoids (Taiz et al., 2014). In addition to this, the higher ETR observed in species grown in full sunlight conditions in the Atlantic Forest demonstrates no damage in the reaction centers in photosystem I (Dos Anjos et al., 2012; Cerqueira et al., 2018; Silva et al., 2022). Our results regarding photosynthetic efficiency under shade treatments were congruent with previous research on the guabiroba plants (Bartieres et al., 2021).

Besides the modifications previously indicated, guabiroba plants under shading had an increase in Gs and E, likely due to the lower temperature and higher humidity that shadow environments often display (Amissah et al., 2015). These conditions, associated with elevated EiC, resulted in greater CO_2 assimilation in guabiroba seedlings under shade than in full sunlight. Contrastingly, guabiroba plants grown in shade-free environments showed lower gas exchange without compromising biomass accumulation and seedlings' vigor. Higher irradiance and temperatures might be responsible for reducing both Gs and E to avoid excessive water loss by leaves (Bartieres et al., 2020). A lower EiC in total sunlight conditions might be associated with a reduction in the CO_2 absorption rate in the intercellular spaces due to the partial closing of the stomata. The reduced EiC observed in this treatment is most likely due to photorespiration generated by high irradiance and leaf temperature (Zhang et al., 2003), although more research is needed to confirm this effect in guabiroba seedlings. Thus, the CO_2 assimilation rate (A) in the leaves in full-sunlight treatment was reduced per unit leaf area. Nevertheless, this modification without drastic impact on guabiroba seedlings growth, mainly compared to the biomass accumulation in the intermediate shaded levels (30% and 50%).

All these shade adaptations positively affected biomass accumulation because guabiroba seedlings grown under 80% shading had greater biomass accumulation than those under the non-shaded treatment. This can be explained by the larger leaves in this condition compared to other treatments. Results found in previous studies (Martins et al., 2014; Bartieres et al., 2020), explain that leaf expansion in native forest species is facilitated by shading. Leaves were thinner in the shaded treatments, mainly in the more intense shading treatment (80%). Better photosynthetic performance in the basal leaves might contribute to the higher root dry mass accumulation, the main drain of the plant's underground section. The increase in light efficiency is related to the possibility of luminosity getting through the canopy (Li et al., 2014).

In plants grown under shade, leaf area adjustment permits them to absorb significant solar energy and allow a better photon distribution through the mesophyll (Krupek and Lima 2012; Earles et al., 2017). Besides, the guabiroba seedlings that grew under deep shade presumably offset low PAR with no reduced root biomass investment (Amissah et al., 2015) and required more significant allocation in stem and leaf biomass fraction (Modrzyński et al., 2015). The significant biomass investment, in root and shoot in 80% shade treatment, was due to the greater photosynthetic efficiency as a result of leaf structure modifications.

Even though there was no positive effect on biomass accumulation in the intermediate shaded levels (30% and 50%), morphophysiological and anatomical modifications were fundamental for the guabiroba seedlings's quality in these environments. The compensations due to the different light regimes, especially in the biometric variables, resulted in similar seedlings' vigor in all treatments. Such vigor was measured by the Dickson Quality Index (DQI), indicating the suitable balance between above and underground biomass (Dickson et al., 1960). Similar growth adjustment modifications, such as height and stem diameter in response to 50% of shading, have been reported in guabiroba seedlings (Bartieres et al., 2020; Silverio et al., 2020).

Our results demonstrated that leaf anatomy changes aided in the guabiroba seedlings acclimation to total sunlight condition. In this treatment, the mesophyll (palisade and spongy parenchyma) thickness was responsible for the guabiroba leaf thickness; a similar effect has been observed in other Myrtaceae species (Da Costa et al., 2020; Moura et al., 2022). Inside sun leaves, palisade parenchyma contributes to the propagation efficiency and homogeneity of light, whilst spongy parenchyma promotes increases in the CO_2 diffusion (Barbosa-Campos et al., 2018; Karabourniotis et al., 2021). These mechanisms boost photosynthesis efficiency in plants subjected under high irradiance environments, preventing light absorption excess (Wimalasekera 2019).

In this study, morphological and physiological adjustments in guabiroba seedlings under shade reveal species' plasticity and tolerance even in deep shade (80%) conditions. The leaf area and chlorophyll concentration boost are noteworthy because they increased the low PAR interception available under shade. Finally, even in low light circumstances, guabiroba seedlings displayed increased gas exchange and quantum yield in photosystem II, i.e., increased efficiency in photochemical and biochemical photosynthetic variables, indispensable to producing good quality seedlings in these light regimes.

5. Conclusions

The guabiroba (*Campomanesia xanthocarpa*) seedlings developed morpho-physiological plasticity and tolerance under light limitations. Therefore, seedlings might be produced in a wide range of light intensities, either under shaded or sunny conditions, since plants grown under light restriction presented a quality index similar to the ones grown in sunlight conditions. These results confirm our initial hypothesis. Therefore, guabiroba seedlings can be cultivated among other species at agroforestry systems or forest restoration.

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