

Original Article

Morpho-physiological adjustments reveal *Araucaria angustifolia* [(Bert.) O. Kuntze] plasticity of saplings under shade regimes

Ajustes morfofisiológicos revelam plasticidade de mudas de *Araucaria angustifolia* [(Bert.) O. Kuntze] sob regimes de sombreamento

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Abstract

This study aimed to investigate the morpho-physiological adaptations of *Araucaria angustifolia* saplings under different shade conditions. Saplings were grown for 21 months under full sunlight (S0%) and three shade levels: 30%, 50%, and 80% (S-30%, S-50% and S-80%, respectively). Growth, light-harvesting pigments (chlorophyll and carotenoids), chlorophyll fluorescence, and anatomical leaf structure were analyzed. Plants in S-0% and S-30% showed higher stem diameter, total and root dry mass, Dickson quality index, chlorophyll *a*/chlorophyll *b* ratio, carotenoids content, and electron transport rate. Conversely, shaded plants (S-50% e S-80%) exhibited physiological adaptations, compensating for the decreased light supply by primarily increasing the amount of chlorophyll and the quantum efficiency of photosystem II and reducing the thickness of their leaves. These results indicate that, despite the physiological plasticity to shade in *Araucaria*, the saplings grow better under a high-irradiance environment or low-shade condition (S-30%). In this sense, shaded cultivation of this species should be avoided in nurseries and reforestations due to the significant total dry mass reduction. This study highlights the importance of optimal light intensity to promote the growth of this endangered species.

Keywords: Brazilian pine, dry biomass, leaf structure, photosynthetic pigments, reforestation.

Resumo

O objetivo deste estudo foi investigar as adaptações morfofisiológicas de mudas de *Araucaria angustifolia* sob diferentes condições de sombreamento. As mudas foram cultivadas durante 21 meses em pleno sol (S0%) e em três níveis de sombreamento: 30%, 50% e 80% (S-30%, S-50% e S-80%, respectivamente). Foram analisadas variáveis de crescimento, pigmentos de captação de luz (clorofila e carotenoides), fluorescência da clorofila e a estrutura anatômica da folha. As mudas sob S0% e S30% apresentaram maior diâmetro do caule, massa seca total e radicular, índice de qualidade de Dickson, relação clorofila *a*/clorofila *b*, teor de carotenoides e taxa de transporte de elétrons. Plantas sob S-50% e S-80% apresentaram adaptações fisiológicas, compensando a diminuição da disponibilidade de luz principalmente aumentando a quantidade de clorofila *a* e a eficiência quântica do fotossistema II, e reduzindo a espessura da folha. Esses resultados indicam que, apesar da plasticidade fisiológica da araucária à sombra, as mudas crescem mais em ambientes de alta irradiação ou baixo sombreamento (S-30%). Assim, plantios sombreados desta espécie devem ser evitados em viveiros e reflorestamentos devido à significativa redução do acúmulo de massa seca. Este estudo destaca a importância da intensidade ideal de luz para melhorar o crescimento de mudas desta espécie que está ameaçada de extinção.

Palavras-chave: pinheiro brasileiro, biomassa seca, estrutura da folha, pigmentos fotossintéticos, reflorestamento.

1. Introduction

The Mixed Ombrophilous Forest, belonging to the Atlantic Forest biome, is a vast ecosystem located mainly in the southern Brazilian region but with fragments in southeastern Brazil, Argentina, and Paraguay, spanning a subtropical climate area above 500 m a.s.l. (Hueck, 1972).

This ecoregion, also known as 'Araucaria Forest', is named based on the dominant tree species, the conifer *Araucaria angustifolia* (Bert.) O. Kuntze (Gymnosperm, Araucariaceae family) that towers over the understory forest layer (Eisenlohr and Oliveira-Filho, 2014). *Araucaria* or 'Brazilian

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pine' plays a critical role in local food security, as its seeds, named 'pinhão', are rich in starch (energy source) and widely cooked in broad autochthonous preparations in the origin area. Therefore, 'pinhão' represents economic, social, and ecological importance because it is also a food supply for humans and wildlife alike (Adan et al., 2016). The relevance of its species has also been demonstrated by its scientific research that has increased over the last 10 years (Castrillon et al., 2023).

Until the late 19th century, Araucaria Forest covered almost 20 million hectares, which has undergone massive fragmentation and degradation due to human activities (Hueck, 1972). The intense deforestation in the 20th century reduced the original area to less than 3%, leading to the critically endangered status of *A. angustifolia* species (Brasil, 2014). Furthermore, the remaining small fragments of Araucaria Forest have undergone genetic diversity reduction (Medina-Macedo et al., 2016) and the regeneration of species in old forests has displayed severe restriction due to minimal irradiation available to young trees (Souza et al., 2008). Efforts to avoid species extinction include producing and planting araucaria during the reforestation process (Sasso et al., 2021; Duarte et al., 2002). Nevertheless, sapling mortality in field plantations remains a significant problem for *A. angustifolia* reforestation (Maran et al., 2016). Testing the light intensity in nurseries to produce high-quality saplings is essential to maximize the survival rate of samplings and support replantation. In this context, species conservation and restoration programs have benefited greatly from research on plant physiology and structural responses under irradiance regimes (Olguin et al., 2020; Tang et al., 2015).

Araucaria is a long-lived pioneer species that relies heavily on open-canopy sites to grow and colonize the dominant layer in forest because juvenile individuals are only found in open areas (Souza et al., 2008). Araucaria has lower plasticity to shade in the forest, due to the species seeking out incident light, generating an etiolation effect in these environments (Olguin et al., 2020). Notwithstanding, araucaria responds quickly to canopy reopening, enhancing its photosynthesis efficiency and growth rate (Sasso et al., 2021). Studies on *A. angustifolia* have mainly evaluated the shade effect by comparing merely one shade level versus full sunlight conditions (Franco and Dillenburg, 2007; Olguin et al., 2020; Sasso et al., 2021). Nonetheless, assessing various shade levels is essential to clarify and quantify the shade stress in the growth traits of araucaria saplings. The research carried out by Duarte and Dillenburg (2000) showed no differences in araucaria shoot biomass and chlorophyll content under three shade regimes (0, 55%, and 90%) after five months of germination. On the contrary, another study demonstrated that araucaria saplings growth differs between high light (100% of available irradiance) and full darkness 160 days after germination (Dillenburg et al., 2010). That research stated that early observations do not evaluate adequately the araucaria responses to shade, because seed-stored reserves influenced species growth in that period. Therefore, short-term evaluations may not display consistent results related to irradiance treatments because they represent no critical light requirement period

for araucaria growth. In addition, physiological effects and leaf anatomy were poorly analyzed in the previous studies.

During growth-limiting resources or stress factors (e.g. light restriction), plants respond using structural and physiological mechanisms, known as 'acclimation', and the degree of this adjustment is referred to as 'plasticity' (Stotz et al., 2021). In general terms, light-adapted species, such as *A. angustifolia*, are more plastic when compared to natural shade-tolerant ones (Longuetaud et al., 2013). Under low light intensity, these species have arranged several morpho and physiological adjustments, to maximize light capture (Landi et al., 2020). Light-demanding species, such as the conifers, acquire the scape strategy, using the photosynthetic products in height growth (Poorter et al., 2012), physiological modifications, and foliar plasticity, maximizing light interception (Greenwood et al., 2009; Schmiede et al., 2021). Conversely, under high radiation situations sunlight-adapted species use a photoprotection mechanism (Kothari et al., 2021), avoiding the photoinhibition process. During forest restoration programs, these morpho-physiological parameters, are essential for suitable species selection (Lima et al., 2021).

Evaluating shade regimes over a long-term assessment that covers growth, physiology, and anatomical attributes in araucaria saplings is critical to improve reforestation operations in the Mixed Ombrophilous Forest. This study aimed to investigate the morpho-physiological changes degree of *A. angustifolia* saplings across a range of light gradients, 21 months after treatment establishment. We hypothesize that araucaria saplings exhibit morpho-physiological adaptations to shaded levels, which generate adjustments in the photosynthetic mechanisms. Our research is an important contribution to achieve the best light intensity for optimizing reforestation efforts in the Araucaria Forest, and it contributes to the knowledge of plant responses to different light intensities.

2. Materials and methods

2.1. Study conditions

The study was carried out in a seedling nursery in Pato Branco, Southwest region of Paraná, Brazil. The climate is Cfa type (subtropical, without dry season, with an average temperature below 18 °C in the coldest month and above 22 °C in the warmest one), according Köppen classification (Alvares et al., 2013).

Araucaria angustifolia seeds were obtained from one tree located in Pato Branco and planted in plastic bags containing a mixture of commercial substrate and soil in a 1:3 ratio. After emergence, the saplings were kept for nine months in the nursery, under a 50% shading screen (Sasso et al., 2021).

2.2. Treatments establishment

The araucaria saplings were then transferred into containers (40 L) containing a mixture of soil, substrate, and vermiculite in a 3:1.5:0.5 ratio. The chemical analysis of the final composite mixture indicated a pH (CaCl₂) of 5.0, 6.1% of organic matter, 14.2 and 80.2 mg dm⁻³ of P

and K, respectively; and 5.7 and 5.6 $\text{cmol}_c \text{dm}^{-3}$ of Ca and Mg, respectively. Twelve saplings of homogeneous size in each treatment were subjected to four light intensity levels: in full sunlight (S-0%), and 30% (S-30%), 50% (S-50%), and 80% (S-80%) of shade, by covering the plants with the respective black shading screen. The plants were irrigated daily using drip irrigation, maintaining soil moisture to field capacity, and received two applications of the NPK 8-28-16 fertilizer, with 20 g per plant at 12 and 18 months after shading treatments application. Besides, periodically, weed control was carried out manually.

2.3. Growth evaluations

Plant height was evaluated in each sapling and light intensity level, considering the measurement from the collar to the apex. The stem diameter at 5 cm above the substrate level was obtained with a caliper. Height and diameter of the stem were measured on the first day and 21 months after the establishment of treatments and the difference between them were calculated.

At the end of the experiment (21 months) the following characteristics were evaluated: i) average leaf area was estimated using the LI-3100 meter (Li-Cor, Inc) in 100 leaves per plant in twelve plants per treatment; ii) shoot, root, and total dry mass (weight; determined in an oven at 60 °C until constant weight mass) in all twelve plants per treatment. We also calculated the shoot/root dry mass ratio (shoot-root ratio) and stem height/diameter ratio (height-diameter quotient) for Dickson quality index (DQI), obtained by the Equation 1 (Dickson et al., 1960):

$$DQI = \left[\frac{\text{weight}}{(\text{height-diameter quotient} + \text{shoot-root ratio})} \right] \quad (1)$$

2.4. Pigment analysis and chlorophyll a fluorescence

Chlorophyll *a* and *b*, and carotenoid contents were quantified at the end of the experiment. Fully expanded leaves were collected from the upper third of the plants, and then, in the laboratory, two leaf discs with 0.6 cm diameter (0.56 cm^2 total area) was removed from each leaf. These disks were immersed in 5.0 mL of dimethyl sulfoxide for 18 hours and kept in a water bath at 65 °C under darkness conditions. Absorbance readings were taken on a spectrophotometer (SHIMADZU, UV 1800, Japan) at 470 nm, 649.1 nm, and 665.1 nm for carotenoids, chlorophyll *a*, and chlorophyll *b*, respectively. After that, the pigment concentration of each one was determined according to Wellburn (1994). In addition, Chl*a*:Chl*b* ratio was determined by the rate between chlorophyll *a* and chlorophyll *b*.

Chlorophyll *a* fluorescence was determined using a Model OS5p modulated portable fluorometer (Opti-Sciences, Hudson, USA), between 9:00 and 10:00 am on a sunny day. Determinations were performed on the adaxial surface of fully expanded leaves in optimal phytosanitary conditions in the upper third plants portion. For each light level, five plants were selected, and three leaves per plant were used in this evaluation. The parameters of photosynthetic active radiation (PAR), effective quantum

yield of photosystem II [$Y_{(II)}$] and relative electron transport rate (ETR) were obtained through fluorometer analysis.

2.5. Anatomical leaf structure

To evaluate leaf anatomy, we collected three leaves from five plants per treatment at the end of the experiment. The leaves were immersed in FAA50 solution (composed of formaldehyde, acetic acid, and 50% ethanol in a 1:1:18 ratio) for 24 hours (Johansen, 1940). Afterward, they were rinsed with 50% ethanol and stored in 70% ethanol. The leaf samples were then sectioned into 0.5 cm^2 fragments, taken from the central region of the leaf blade. These fragments were dehydrated using a series of ethyl alcohol concentrations (80%, 90%, and 95%), and embedded in methacrylate (Historesin, Leica Instruments). Cross-sections of 8.0 μm thickness were prepared and stained with 0.12% toluidine blue solution in 5% borax, both in w/v. The glass slides were then mounted and, to digitalize the images, a photomicroscope (Zeiss Axiolab) with a digital camera (Sony Cybershot) was used. The ANATI QUANTI software (Aguar et al., 2007) was employed to measure the thickness of total leaf, and its sections (mesophyll, abaxial, and adaxial epidermis).

2.6. Statistical analysis

In order to compare different light intensities in araucaria saplings, the data were subjected to analysis of variance, following a completely randomized design, and 12 replicates for each shade treatment. Normality of the deviations (Shapiro-Wilk test) and homogeneity of variance (Bartlett test) were evaluated. Leaf area data, Chl*a*: Chl*b* and shoot:root ratio did not fit the assumptions and were then transformed by the Box-Cox test (Venables and Ripley, 2002). A comparison of the means by the Scott-Knott test ($p \leq 0.05$) was also performed. All statistical analyses were processed using software R (R Core Team, 2022).

3. Results

3.1. Growth evaluations

The height growth of araucaria saplings at 21 months was higher in S-50% and S-80% (Table 1). In terms of stem diameter, the S-0% treatment resulted in saplings that were almost 1.9× wider than S-80%. Notably, plants exposed to full sunlight exhibited the largest leaf area when compared with shade treatments.

Regarding the total dry mass, saplings maintained in the S-0% and S-30% treatments had higher values than those in higher shade levels (Table 1). There was a reduction of 67% in total dry mass in plants subjected to S-80% compared to S-0%. Furthermore, the saplings in S-30% showed similar shoot and root dry mass compared to S-0% treatment. Conversely, saplings submitted to the higher shade levels (50% and 80%) exhibited a greater dry mass allocation to the shoot than the roots. As a result, S-0% saplings showed the highest Dickson quality index, which dropped in the shadow treatments, with an index

reduction of 17.16%, 52.14%, and 80.2% in S-30%, S-50%, and S-80%, respectively.

3.2. Pigment analysis and chlorophyll a fluorescence

Leaves exposed to the S-0% treatment had higher chlorophyll *a* content (Table 2). However, chlorophyll *b* contents were higher at S-0% and S-80%, compared to the two intermediate shade levels (S-30% and S-50%). The carotenoid concentration was higher in saplings kept at S-0%, differing significantly from the other treatments (Table 2). Notably, there was an average reduction of 15.9% in carotenoid content in plants exposed to any shade level compared to that subjected to full sunlight.

In the case of chlorophyll fluorescence, we detected differences in PAR in the three different shade levels, representing a reduction of 34%, 58%, and 87%, in S-30%,

S-50%, and S-80% respectively, when compared to full sunlight conditions. Simultaneously, the saplings subjected to S-80% had a combination of higher effective quantum yield of photosystem II [$Y_{(II)}$] with a lower electron transport rate (ETR) (Table 2). Saplings in S-0% had the opposite behavior to S-80% treatment, when comparing $Y_{(II)}$ and ETR characteristics.

3.3. Anatomical leaf structure

The mesophyll (ME) and total leaf thickness were greater in araucaria saplings exposed to total irradiance compared to those in shaded conditions (Table 3). Besides, the thickness of the adaxial and abaxial epidermis was higher in S-0% and S-30% (Figure 1). The reduction in total leaf thickness was approximately 27.3% in leaves exposed to S-80% when compared with those subjected to the full irradiance.

Table 1. Growth evaluations of *Araucaria angustifolia* saplings under shade gradient 21 months after treatment establishment. Full sunlight (S-0%), and 30% (S-30%), 50% (S-50%), and 80% (S-80%) of shading.

Treatment	Height (cm)	Stem diameter (mm)	Leaf area (cm ²)	Total dry mass (g)	Shoot dry mass (g)	Root dry mass (g)	Shoot:root ratio dry mass	Dickson Quality Index
S-0%	53.3 b	20.9 a	29.0 a	461.8 a	334.0 a	127.8 a	2.7 b	76.9 a
S-30%	54.4 b	18.1 a	24.1 b	451.7 a	326.9 a	124.8 a	2.7 b	63.7 b
S-50%	62.5 a	14.9 b	23.9 b	294.1 b	225.1 b	69.0 b	3.2 a	36.8 c
S-80%	62.3 a	11.1 b	21.9 b	151.8 c	119.3 c	32.5 c	4.0 a	15.2 d

Leaf area and shoot:root ratio was transformed by Box-Cox. Different letters differ by the Scott-Knott test ($p \leq 0.05$). Plant height and stem diameter were considered between the difference from the 1st and 21st months after experiment establishment.

Table 2. Pigments content and fluorescence of chlorophyll *a* characteristics of *Araucaria angustifolia* leaves under shade gradient, in full sunlight (S-0%), and 30% (S-30%), 50% (S-50%), and 80% (S-80%) of shading.

Treatment	Chl <i>a</i>	Chl <i>b</i>	Chl <i>a</i> :Chl <i>b</i> ratio	Carotenoids	PAR	ETR	$Y_{(II)}$
	(mol m ⁻²)				(mol m ⁻² s ⁻¹)		
S-0%	531.7 a	201.4 a	2.65 a	21.9 a	322.1 a	42.8 a	0.26 c
S-30%	473.4 b	178.3 b	2.66 a	19.0 b	212.0 b	31.1 b	0.46 b
S-50%	428.0 c	166.8 b	2.57 b	18.2 b	134.8 c	33.1 b	0.44 b
S-80%	498.2 b	192.5 a	2.59 b	18.0 b	43.2 d	11.2 c	0.63 a

Chl*a*:Chl*b* ratio was transformed by Box-Cox. Different letters differ by the Scott-Knott test ($p \leq 0.05$). Chlorophylls (Chl), photosynthetic active radiation (PAR), effective quantum yield of photosystem II ($Y_{(II)}$); and electron transport rate (ETR).

Table 3. Total and section leaf thickness (μm) of *Araucaria angustifolia* saplings under shade gradient 21 months after treatment establishment. Full sunlight (S-0%), and 30% (S-30%), 50% (S-50%), and 80% (S-80%) of shading.

Treatment	Total leaf	BE	ME	DE
S-0%	654.3 a	36.4 a	577.4 a	40.5 a
S-30%	591.0 b	33.1 a	517.2 b	36.9 a
S-50%	545.8 b	26.5 b	492.5 b	26.8 b
S-80%	475.5 c	26.7 b	422.0 c	26.8 b

Different letters indicate significant differences between the averages of each treatment by Scott-Knott test ($p \leq 0.05$). Abbreviations: BE (abaxial epidermis); ME (mesophyll); DE (adaxial epidermis).

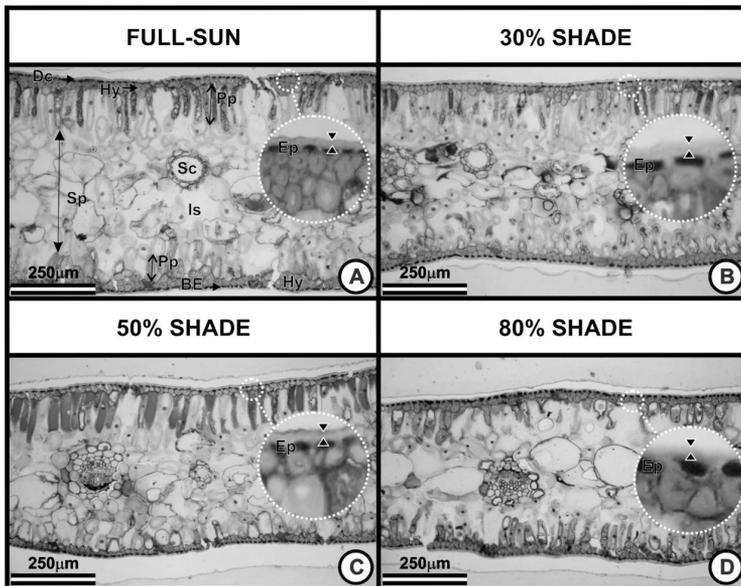


Figure 1. Structural leaf anatomy (cross sections) by light microscopy in saplings of *Araucaria angustifolia* saplings under shade gradient 21 months after treatment establishment. Full sunlight (S-0%), and 30% (S-30%), 50% (S-50%), and 80% (S-80%) of shading. Abbreviations: BE (abaxial epidermis); DC (adaxial cuticle); Hy (hypodermis); Pp (palisade parenchyma); Sc (secretory cavities); Sp (spongy parenchyma); Is (intercellular space); Ep (adaxial epidermis), highlighted in the circles to show thickness reduction as increased shade level.

4. Discussion

In this research, employing four differential light intensities (shade 0%, 30% 50%, and 80%), we demonstrate that the most suitable growth and development of *A. angustifolia* saplings are under full sunlight. The saplings exposed at S-0% had the highest total, shoot, and root dry mass. In addition, related responses of the larger leaf area in sunlight plants were connected to the higher chlorophyll content and electron transport rate. On the other hand, saplings under medium and higher shade (S-50% and S-80%) had lower mass accumulation, which would render plants less competitive for belowground resources, causing a reduction in the whole plant size, including a reduction in stem diameter and leaf area, besides generating a fine leaf mesophyll layer.

Araucaria saplings in the medium and major shade levels portrayed the greatest shoot height, but this did not determine its higher shoot biomass due to smaller stem diameter and leaf area, resembling an etiolation effect. Major heights presented by plants subjected to shade occur in response to the greater investment in cell elongation because this involves an important adaptation mechanism and a fast escape strategy in high-light demand species (Modrzyński et al., 2015). The higher diameter/height and root/shoot dry mass ratios growth determined that saplings in S-0% had better vigor, which the highest Dickson Quality Index (IQD) represented in this treatment. This index is one of the best quality indicators considering several morphological and growth traits simultaneously. Thus, the risk of selecting the highest saplings is reduced during transplanting selection of *araucaria*, as this population may not succeed in field survival (Sasso et al., 2021).

In growth terms, our results agree with previous research, demonstrating that the most significant growth,

particularly in biomass accumulation, is attained in sunlight conditions in *A. angustifolia* (Duarte and Dillenburg, 2000; Olguin et al., 2020; Sasso et al., 2021; Franco and Dillenburg, 2007). Nevertheless, we demonstrated that even in a slight shade regime (S-30%) *A. angustifolia* vigor might be substantially reduced, confirming that this species is strongly adapted to a high irradiation environment.

At the S-0% condition, the largest amount of chlorophyll *a* and *Chla*: *Chlb* ratio demonstrated the remarkable ability of *araucaria* to capture light and transfer the energy to photosystem reaction centers, being common physiological attributes in high-light demanding species (Dörken and Lepetit, 2018; Duarte and Dillenburg, 2000). Other studies have portrayed chlorophyll content increase in juvenile *araucaria* saplings (75 days after sowing) under 90% of shading compared to full sunlight (Franco and Dillenburg, 2007), while the irradiance level during the growth did not affect chlorophyll concentration or the ratio between chlorophyll *a* and chlorophyll *b* (Duarte and Dillenburg, 2000).

The discrepancies in the chlorophyll content between the previous study and our results might be due to the treatment period of light exposition and the age of the saplings. It is important to consider that seed reserves can influence physiological measurements before 100 days (Dillenburg et al., 2010), masking the shade effects in *araucaria* saplings. That is why it is important to carefully choose the measurement period in *araucaria* species if the interest is to assess the shade effect. An increase in chlorophyll *a* and *b* content under S-80% suggests the shade response amplification under a low light intensity, which has been described in light-demanding conifers such as Scots pine (Ranade et al., 2019). Thus, these species seek to maximize their capture light capacity while maintaining

a slow growth in shaded conditions (Tang et al., 2015; Modrzyński et al., 2015). However, we are concerned that time-frequency in the chlorophyll *a* and *b* assessment should be measured, to understand the dynamics of these concentrations. Further research into the dynamics of these pigments under different time-lapse and light intensities is necessary in araucaria saplings.

In addition, the higher carotenoid content in the treatment S-0% likely played a key role in dissipating energy to prevent photoinhibition damage as a tolerance plant mechanism against high irradiance (Goh et al., 2012). Also, the leaves exposed to total light availability were thicker than leaves in the shaded treatments, which should avoid photoinhibition too, as photosynthetic cells are protected by the upper multi-layer of palisade parenchyma cells in the mesophyll (Lopes et al., 2019). The greater epidermis thickness of *A. angustifolia* leaves exposed to full luminosity acts as a protective barrier against excess irradiation as well, a strategy of non-tolerant species to shading. On the other hand, thinner epidermis in the leaves under 50% and 80% shade reduces energy investment in this tissue and maximizes the light capture (Craven et al., 2010).

In the case of photosynthetic apparatus, the plants under the largest shade (S-80%) maximized the photosystem II efficiency, verified by the $Y_{(II)}$ value in this treatment. This result might be connected to the increased chlorophyll *b* content, which optimizes light use in photosystem II. $Y_{(II)}$ represents the effective absorbed light in PSII, a useful indicator of different environmental stresses (He et al., 2021; Murchie and Lawson, 2013). In natural light conditions, $Y_{(II)}$ presents values above 0.3 (He et al., 2021; Scott et al., 2016). In the case of ETR, this attribute was higher in the plants under full sunlight exposition due to the higher radiation intensity, explained by the high photon absorption in light-demanding conifers (Greenwood et al., 2009; Ranade et al., 2019). The higher $Y_{(II)}$ verified in saplings under S-80% shows an acclimatization effect of these plants to the low light incident radiation. This indicates a PSII efficiency, from the fraction of light absorbed by chlorophyll to the energy in photosystem II that was used in the photochemical activity (Cazzaniga et al., 2013). In full sunlight, the lower $Y_{(II)}$ values reflected the high number of excited chlorophylls until the saturation of ETR, and the energy excess presumably was dissipated by heat, as it was not being fully used in photosynthesis (Murchie and Lawson, 2013). Similar results in $Y_{(II)}$ increase and ETR reduction under light intensity decrease have been shown in *Ginkgo biloba* (Yang et al., 2021). In contrast, to *Tabebuia roseoalba* and *Handroanthus heptaphyllus*, both Brazilian shade-tolerant forest species, the high irradiance reduces their photosynthetic performance, probably due to stomatal closure under higher irradiation and temperature to reduce water loss, demonstrating a light stress avoidance mechanism (Ribeiro et al., 2022).

Therefore, with these results, it is feasible to infer that shading dramatically reduces the quality of araucaria saplings. The most significant adaptations observed in response to shade were the increase of chlorophyll content and the highest quantum efficiency of photosystem II under the deepest shade condition. Hence, despite of araucaria saplings under lower radiation conditions

displaying photosynthetic modifications, it is not enough to maintain the same vigor compared to sampling growth under the highest light intensity. This suggests adjustments in light absorption efficiency and resource conservation under shading, supporting the idea of shading avoidance in this high-light-demanding species (Duarte et al., 2002; Franco and Dillenburg, 2007). Notwithstanding, further investigation is necessary to determine if any physiological truncation exists in the PSI or Krebs cycle, elucidating the dramatical decline in biomass observed in araucaria samplings under deep shade conditions. Here, we hypothesized that juvenile araucaria may respond to shade stress with morphological and physiological adjustments, and our results highlight araucaria plasticity afterward light restrictions.

Higher quality araucaria saplings (with 21 months) were obtained in the highest irradiance scenario. As Olguin et al. (2020) reported, the morpho-physiological changes observed in araucaria saplings under different light intensities in pot experiments can be associated with results observed in forest gaps. Therefore, our results indicate that araucaria saplings may be cultivated in high-light environments, considering several situations, such as nurseries, afforestation, and forest restorations, which is recommended for obtaining the reforestation success of this threatened species.

5. Conclusion

In this research, we demonstrated that the high shade environments reduce the growth quality of *A. angustifolia* saplings, despite greater height growth (etiolation) and physiological adjustments in PSII. Furthermore, our results also showed that araucaria saplings can be cultivated in full sunlight conditions in nurseries and forests, as they demonstrate high irradiance tolerance through traits such as higher dry mass and leaf area, as well as the increase in chlorophyll content and ETR. These results have practical implications for forest professionals and tree growers and demonstrate efforts to improve reforestation practices to increase the success of araucaria sapling cultivation.

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