Morphophysiological adjustments to shade of jaboticaba tree saplings[1]

Amanda Pacheco Cardoso Moura[2], Bruna Valéria Gil[2], Anelise Tessari Perboni[3], Fabrícia Lorrane Rodrigues Oliveira[4], Bruno Francisco Sant'Anna-Santos[4], Moeses Andrigo Danner[2]*

10.1590/0034-737X202269040003

ABSTRACT

We aimed to verify the morphophysiological changes in jaboticaba tree (*Plinia peruviana* (Poir.) Govaerts) saplings under shade gradient to improve knowledge on the appropriate light environmental conditions for the saplings production and field homogeneous or intercropping cultivation of this species. The saplings were grown under full sun and artificial shade levels (30%, 50%, and 80%). Growth, photosynthetic pigments, gas exchanges, chlorophyll fluorescence, and leaf anatomy characters were evaluated. Our results showed that jaboticaba tree saplings growth was improved under full sun and 30% of shade. Under 50% and 80% shade the saplings demonstrate phenotypic plasticity, such as larger and thinner leaves. Chlorophyll fluorescence, chlorophyll content, and quantum yield of photosystem II were higher under higher shade level, but the CO_2 assimilation rate was not different between light conditions. These changes are typically found in shade-tolerant plants and is related to perform photosynthesis more efficiently in highly variable light conditions. Despite that, we recommend that cultivation be carried out under full sun or up to 30% shade to maximize jaboticaba tree saplings growth in nurseries and orchards.

Keywords: *Plinia peruviana*; light gradient; acclimatization; photosynthesis; leaf anatomy.

INTRODUCTION

Plant species are subjected to a varied range of light intensity in natural forests, which stimulates the development of plasticity mechanisms to ensure survival and growth along this range, but the changes also interfere in the species' management requested in nurseries and orchards. For example, high light intensity can damage the photosynthetic apparatus, and plants need avoid this damage developing more thickness leaves and increasing the carotenoids content, both to survive and efficiently use high light available to increase the photosynthesis and growth rate (Laanisto & Niinemets, 2015). On the other hand, under low light intensity, plant growth reduction may occur unless they develop mechanisms to maximize light uptake, such as increasing the leaf area, the chlorophyll content, and the efficiency light use in the photosystem II reaction center (Santos *et al.*, 2015; Mathur *et al.*, 2018). These plants mechanisms can be better understood submitting the saplings to artificial shade, because its behavior is related to natural conditions (Olguin *et al.*, 2020).

Despite the behavior under shade to be important knowledge for forest species, the light requirement of jaboticaba tree (*Plinia peruviana* (Poir.) Govaerts) is not conclusive for this species, having both full sun no climax and shade-tolerant climax classification (Toniato & Oliveira-Filho, 2004; Souza *et al.*, 2015), probably due to wide light range in natural forest stands in which its species occured. Furthermore, few studies show morphophysiological changes due to shade in the Myrtoideae group (Ajalla *et al.*, 2014; Lemos *et al.*, 2018), and not specific studies in *Plinia sp.* were found. Thereby, we hypothesize that jaboticaba saplings would have their grown favored under high light availability, although they could have some

Submitted on May 26th, 2021 and accepted on November 22nd, 2021.

[1]This work was partially supported by Brazilian agencies CAPES, and CNPq throughout fellowships and grant allocation.

[2]Universidade Tecnológica Federal do Paraná, Programa de Pós-Graduação em Agronomia, Pato Branco, Paraná, Brazil. amandapmoura@gmail.com; brunnagil@hotmail.com; moesesdanner@utfpr.edu.br

[3]Universidade Tecnológica Federal do Paraná, Dois Vizinhos, Paraná, Brazil. aneliseperboni@utfpr.edu.br

[4]Universidade Federal do Paraná, Departamento de Botânica, Curitiba, Paraná, Brazil. fabricia.lorrane@gmail.com; brunofrancisco@ufpr.br

*Corresponding author: moesesdanner@utfpr.edu.br

shading tolerance traits such as changes in leaf anatomy and photosynthesis efficiency and could have similar growth independently of shade level.

Jaboticaba tree is a native species of South America and mainly occurs in the Brazilian Atlantic Forest and some similar forests in Paraguai and Argentina (Stadnik *et al.*, 2020). The fruits (jaboticabas) could be considered a functional food due to high levels of polyphenols and has significant potential for medical purposes and the food industry (Morales *et al.*, 2016; Moura *et al.*, 2018). However, there are few records of commercial plantations in Brazil, which are concentrated in the few orchards, and there are some fruit sales records throughout harvesting in natural forests (Danner *et al.*, 2010). Therefore, understanding morphological and physiological changes under light gradient conditions in this native fruit species, especially at juveniles' stage, is important as it indicate the appropriate environment to achieve vigorous saplings.

We aimed to verify the morphophysiological changes in jaboticaba tree (*Plinia peruviana*) saplings under shade gradient to improve knowledge on the appropriate light environmental conditions for the saplings production in nurseries and in homogeneous or intercropping field to improve cultivation in orchards.

MATERIAL AND METHODS

Seeds collected from one jaboticaba tree (*Plinia peruviana*) in Clevelândia, Paraná, Brazil (26º26'17" S; 52º19'20" W; 963 m a.s.l) were used for seedlings production, which were grown in pots (2.0 L) in a nursery with 50% shade until twelve-month-old. The saplings were transplanted into pots (40.0 L) filled with a mixture of soil, commercial substrate, and vermiculite (3:1.5:0.5; v:v:v), which had following chemical attributes: pH in water = 5.2; organic matter = 53.1, P = 14.2 and K = 85.3 mg kg^{-1}; Al^{3+} = 0.03, Ca = 5.5 and Mg = 4.4 cmol$_{(c)}$ dm^{-3}; CTC = 17.8; and V(%) = 68.6. The plants were submitted to four light levels gradient, that is full sun, 30%, 50%, and 80% shade, with 12 replications (plants) of each treatment. The shade environments were built with wood structures completely surrounded by black mesh screens, with their respective three shade levels. The plants received daily irrigation, monthly manual weed control, and two fertilizations with 20 g per plant of NPK formulation (8-28-16), at 12 and 18 months after transplantation, and at 21 months all evaluations were performed.

Saplings growth evaluation were performed in all saplings by the difference between the height and diameter measured at the transplantation into shade levels and at 21st month. Individual leaf area measures in 100 leaves of four plants for each treatment were carried out, using the LI-3100 meter (Li-Cor, Inc.). We also measured the shoot and root dry matter after oven-dried in all saplings at 60 °C until reach a constant weight (~7 days). Dickson's quality index (DQI) = [total dry mass / (RSD + RSR)] was calculated, where RSD is shoot height and stem diameter ratio, and RSR is shoot dry matter and root dry matter ratio (Dickson *et al.*, 1960).

Photosynthetic pigments were evaluated in two expanded leaves in each twelve saplings of each treatment. From each leaf, two 0.6 cm diameter leaf discs were removed and immersed in 5.0 mL of dimethyl sulfoxide (DMSO) and kept in the dark and in a water bath at 65 °C until it becomes translucent (~18 hours, time set in preliminary range tests). Absorbance readings for carotenoids (480 nm), chlorophyll *a* (649.1 nm), and chlorophyll *b* (665.1 nm) were performed in a UV/VIS spectrophotometer (Shimadzu UV-1800) and pigments amount were calculated following Wellburn (1994).

Gas exchanges were evaluated using an infrared gas analyzer (IRGA) model LC-pro (ADC BioScientific Ltda., UK). The measured characters were photosynthetically active radiation (PAR), CO_2 assimilation rate (A), transpiration rate (E), stomatal conductance (gs), and intracellular CO_2 concentration (Ci). Through these data, the instantaneous carboxylation efficiency (EiC) was estimated by A/Ci. All measurements were performed in five saplings per treatment on the three upper-latest fully expanded leaves, from 9 to 11 am on a sunny day.

Chlorophyll fluorescence characters was determined using a fluorometer (Multi-ModeChlorophyll Fluorometer®, Model OS5p). These evaluations were conducted in the same leaves and conditions of gas exchanges analysis. Each leaf was exposed to a high-intensity light saturation pulse and the initial fluorescence (F'), maximum fluorescence (Fm), PSII maximum quantum yield ($Y_{(II)}$), and relative electron transport rate (ETR) were obtained.

Leaf anatomy analyses were performed in three leaves of five saplings per treatment, the same leaves of gas exchanges analysis, which were collected and fixed in FAA_{50} (formol:acetic acid:alcohol 50%, 1:1:18 v:v:v) for 24 h (Johansen, 1940). The samples were cut into 5.0 cm^2 fragments from the middle region of the leaf, dehydrated in a crescent ethylic series (80%, 90%, and 95%), and included in methacrylate (Historesin, Leica Instruments). Transverse cuts (8.0 µm) were stained with toluidine blue, and the slides were mounted in glass varnish Incolor 500® (Paiva *et al.*, 2006). The images were digitalized using a photomicroscope (Zeiss Axiolab model) with a digital camera attached (Sony Cybershot 7.2mb model). Besides qualitative analysis, the thickness of the adaxial and abaxial epidermis, the palisade and spongy parenchyma, and leaf blade were measured in nine records per sample, using the ANATI QUANTI software (Aguiar *et al.*, 2007).

All data were subjected to the Shapiro-Wilk's normality test and Bartlett's variance homogeneity test. The Box-

Cox procedure was used by transform variables that did not found the normality and variance homogeneity assumptions. Further, all variables were submitted to the variance analysis in a completely random design and the Scott-Knott clustering test was applied. All analyzes were performed and graphs were plotted on the R platform (R Development Core Team, 2020).

RESULTS

The highest values of diameter, shoot and root dry matter were found under full sun and 30% shade compared to other treatments, demonstrating more quickly development of plants. Consequently, the higher Dickson's quality index was found in these two treatments. On the other hand, there is no different effect of shade levels in height growth, whereas the leaf area was increased in the saplings under 50% and 80% shade (Figure 1), that demonstrate morphological changes and etiolation in plants to improve light uptake in low light environment.

Chlorophyll-*a*, chlorophyll-*b*, and total chlorophyll content were higher in saplings under three shade levels than plants under full sun, demonstrating improve in photosynthetically pigments to try to keep carbon fixation in saplings. On the other hand, higher carotenoid amounts were detected in saplings under full sun and 30% shade compared to other shade treatments (Figure 2), to protect photosynthesis apparatus against high light level.

Even though the photosynthetically active radiation (PAR) to be different among the light levels, did not have a significant effect on any gas exchanges variables (Figure 3). These also demonstrate the jaboticaba tree saplings changes to acclimatization under light environment range trying to keep carbon fixation and growth.

Higher values of initial fluorescence (F'), maximum fluorescence (Fm), and quantum yield of photosystem II (YII) were found in the saplings under 80% shade. These variables values were decreasing according it was enhancing the light available. On the other hand, the electron transport rate (ETR) was higher in saplings under

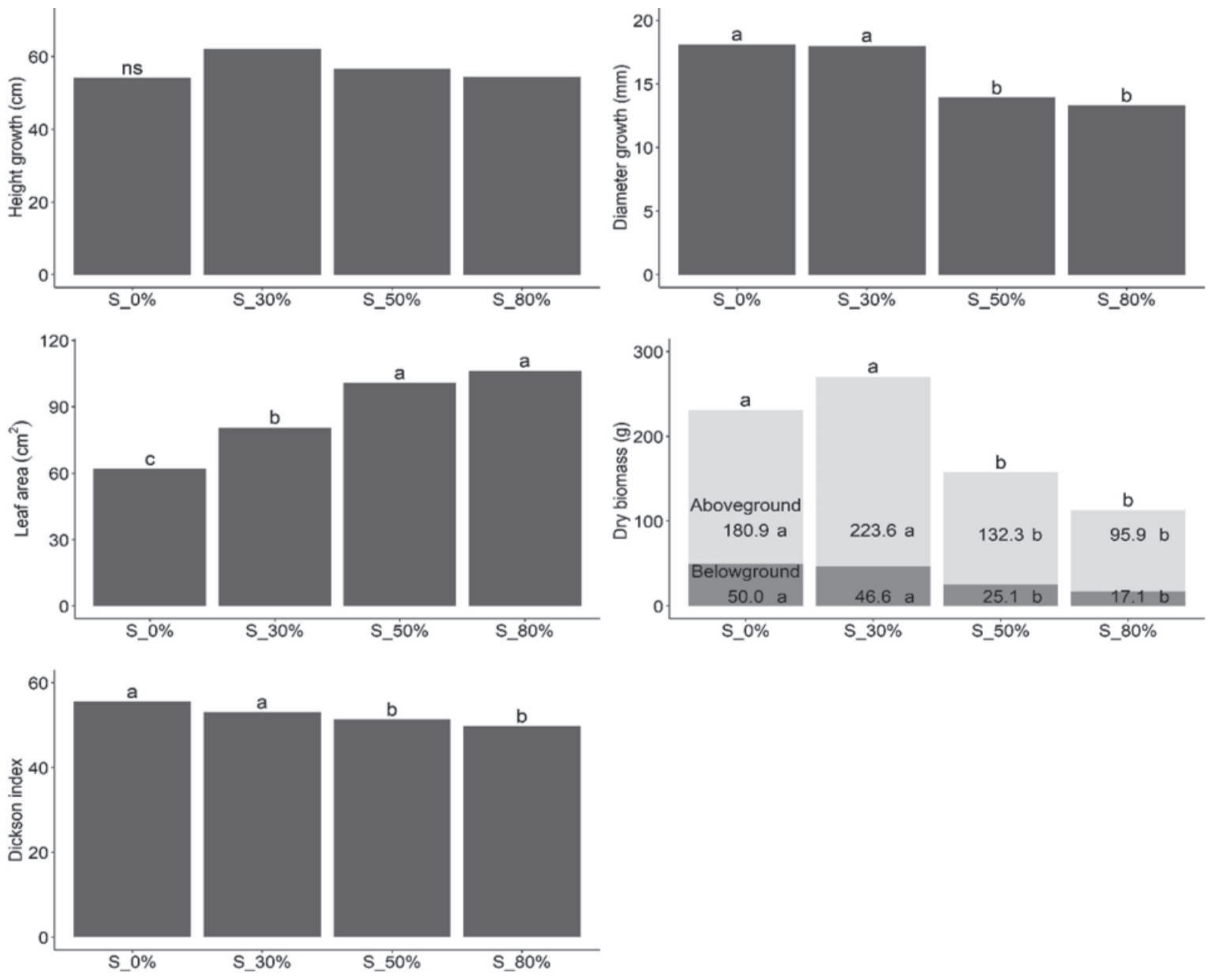

Figure 1: Growth parameters of *Plinia peruviana* saplings under shade gradient, in full sun (S_0%) and 30% (S_30%), 50% (S_50%) and 80% (S_80%) shade. Averages containing different letters differ from each other by the Scott-Knott test ($p \leq 0.05$). Leaf area data were transformed by BoxCox.

full sun and 30% shade (Figure 4), that are explain carbon balance in saplings together gas exchanges results.

All leaf tissues (abaxial and adaxial epidermis, spongy and palisade parenchyma, and total leaf thickness) presented lower thickness when exposed to 50% and 80% shade. This effect demonstrates a change conducting to more efficiently light uptake and less tissues protect required when sapling' leaves were subjected to low light level. Combined with that, the leaves of *Plinia peruviana* have dorsiventral mesophyll with three layers of palisade parenchyma on the adaxial surface and one layer of spongy parenchyma on the abaxial surface. Also, there are secretory cavities under the adaxial epidermis. The leaves under full sun and 30% shade have similar leaf structures with each other. On the other hand, under 50% and 80% shade, the reduction in total leaf thickness, and the lower differentiation between the second and third layers of palisade parenchyma were evident (Figure 5).

DISCUSSION

The jaboticaba tree saplings growth was favored under full sun and 30% shade, as well a higher Dickson Quality Index was found under these environments. The plants were more vigorous, meaning a greater balance in height and diameter growth and in allocation between shoot and root dry mass accumulation (Dickson *et al.*, 1960).

On the other hand, saplings under 50% and 80% shade developed larger leaves with higher chlorophyll content compared to seedlings grown in full sun, as a strategy for maximizing light capture. This occurred due to the increase in chlorophyll *b* in jaboticaba tree shaded (30, 50, and 80%), in order to absorb light more efficiently. The addition of chlorophyll *b* resulted in a reduction of the chlorophyll *a:b* ratio in saplings. This response, associated with an increase in the leaf area, is a typical mechanism of plant tolerance to the shaded environment (Gommers *et al.*, 2013, Mathur *et al.*, 2018).

In plants under full sun and 30% shade, a higher carotenoids concentration was observed, an accessory pigment of the photosystem with an important role in modulating the absorption and dissipation of light (Barros *et al.*, 2012). Higher content of carotenoids in response to increased irradiance was also observed in *Cariniana estrellensis*, being accompanied by greater dissipation of energy in the form of heat. The ability to dissipate the excess energy related to carotenoids is photoprotective mechanisms, avoid damage to photosystem II, allowed optimum energy use to maintain efficient biomass accumulation (Portela *et al.*, 2018). Furthermore, the lower leaf area values of seedlings in full sun and 30% of shading can be interpreted as an adaptive response of the species to greater exposure to solar radiation, which protects the photosynthetic apparatus against high light intensity (Zimmermann *et al.*, 2019).

The highest PAR levels were associated with better development of the jaboticaba tree saplings, indicating that this species requires a higher amount of light, such as many other forest species (Feltrin *et al.*, 2016). Despite this, there was no significant difference for the gas exchange variables under different light levels evaluated. This response was also observed in *Pueraria phaseoloides* (Tuffi-Santos *et al.*, 2015), when subjected to shading levels. It should be noted that the result of the present study reflects *A* per unit of leaf area in the upper

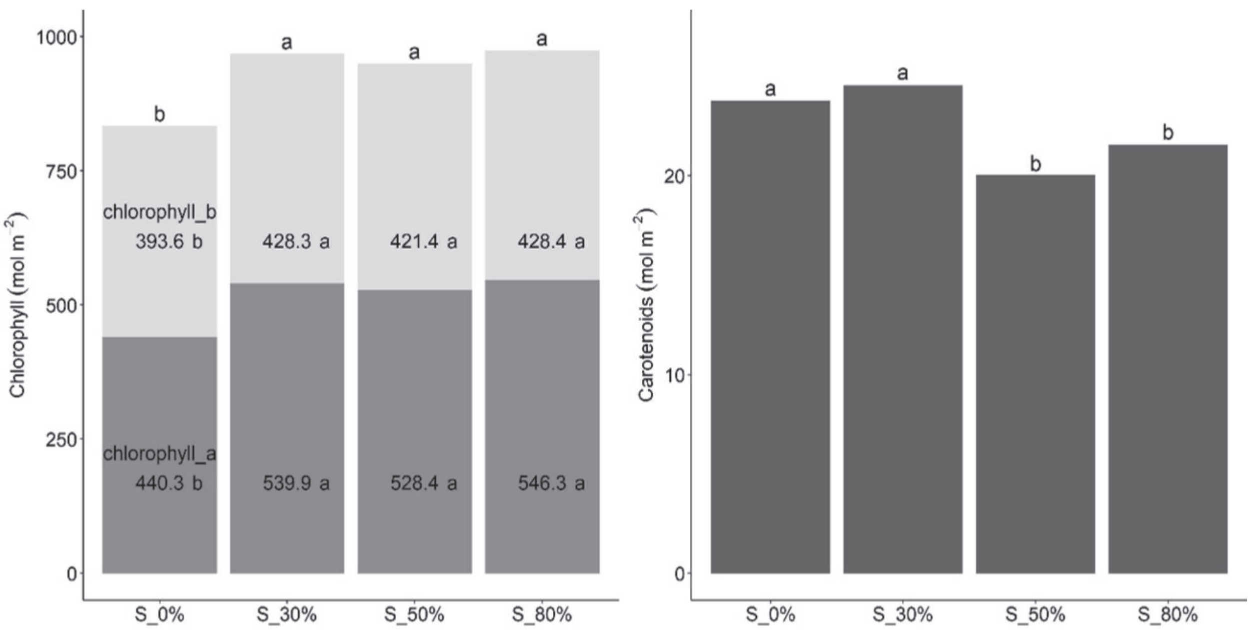

Figure 2: Photosynthetic pigments content of *Plinia peruviana* leaves under shade gradient, in full sun (S_0%) and 30% (S_30%), 50% (S_50%) and 80% (S_80%) shade. Averages containing different letters differ from each other by the Scott-Knott test ($p \leq 0.05$).

part of the jaboticaba trees. Thus, the greater accumulation of sapling biomass in treatments of full sun and 30% shading may have occurred, possibly, due to greater light penetration in the middle and lower third of the saplings in these two cultivation environments, in relation to the others (Rezai *et al.*, 2018).

It was noted that the leaves of jaboticaba tree saplings showed phenotypic plasticity, i.e. changes in the size and thickness of the leaves as the light environment changed. Under the higher shade (50% and 80%) it was observed decrease in the thickness of all leaf tissues and, consequently, in the total leaf thickness. The thinner leaves on shade-grown plants allow for better diffuse light distribution across the plant canopy allowing photosynthesis to occur more efficiently throughout the entire plant (Brodersen & Vogelmann, 2010). On the other hand, the increase of palisade and spongy parenchyma thickness in full sun and 30% shade was responsible for homogenization of the distribution and better use of light, minimizing the damage caused by the high light supply (Barbosa-Campos *et al.*, 2018).

Changes in chlorophyll fluorescence were observed, which higher values for F', Fm, and Y(II) were found under 50% and 80% shade, but the lesser ETR was observed in these treatments. Light capture was increased under shading conditions, which can be seen by the increase of Y(II) in treatments 50 and 80% shaded. This indicates that although the photosystems were receiving little light, their efficiency in capturing it for the photochemical effect was greater than in full sun treatment (Alagupalamuthirsolai *et al.*, 2018). With high PAR in treatments of full sun and 30% shading, much of the light absorbed by the photosystem was not converted into photochemical energy, being possibly dissipated in the form of heat (Dos

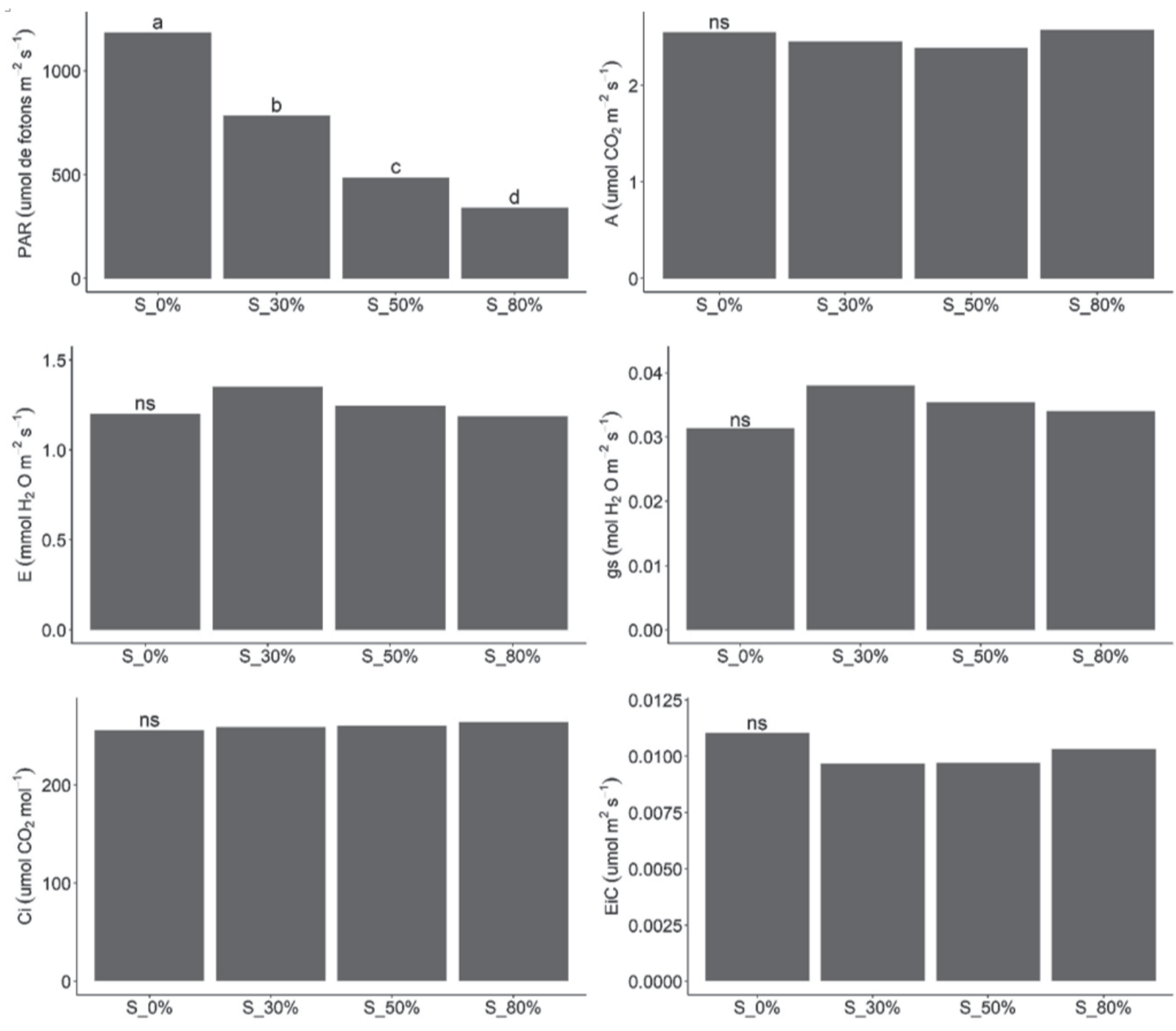

Figure 3: Gas exchange parameters of *Plinia peruviana* leaves under shade gradient, in full sun (S_0%) and 30% (S_30%), 50% (S_50%) and 80% (S_80%) shade. Averages containing different letters differ from each other by the Scott-Knott test (p d" 0.05). PAR: photosynthetically active radiation; A: net CO_2 assimilation rate; E: transpiration rate; gs: stomatal conductance; Ci: intercellular CO_2 concentration; EiC: carboxylation efficiency.

Anjos *et al.*, 2012). The dissipation of excess energy prevents damage to the photosynthetic apparatus and the ETR, higher in saplings at full sun and 30% shading, shows that electron transport was efficient at high PAR.

We observed that the jaboticaba tree saplings could acclimate to different light levels, evidencing the species' plasticity. Although our experiment was conducted in pots and artificial shade, they could be considered a good

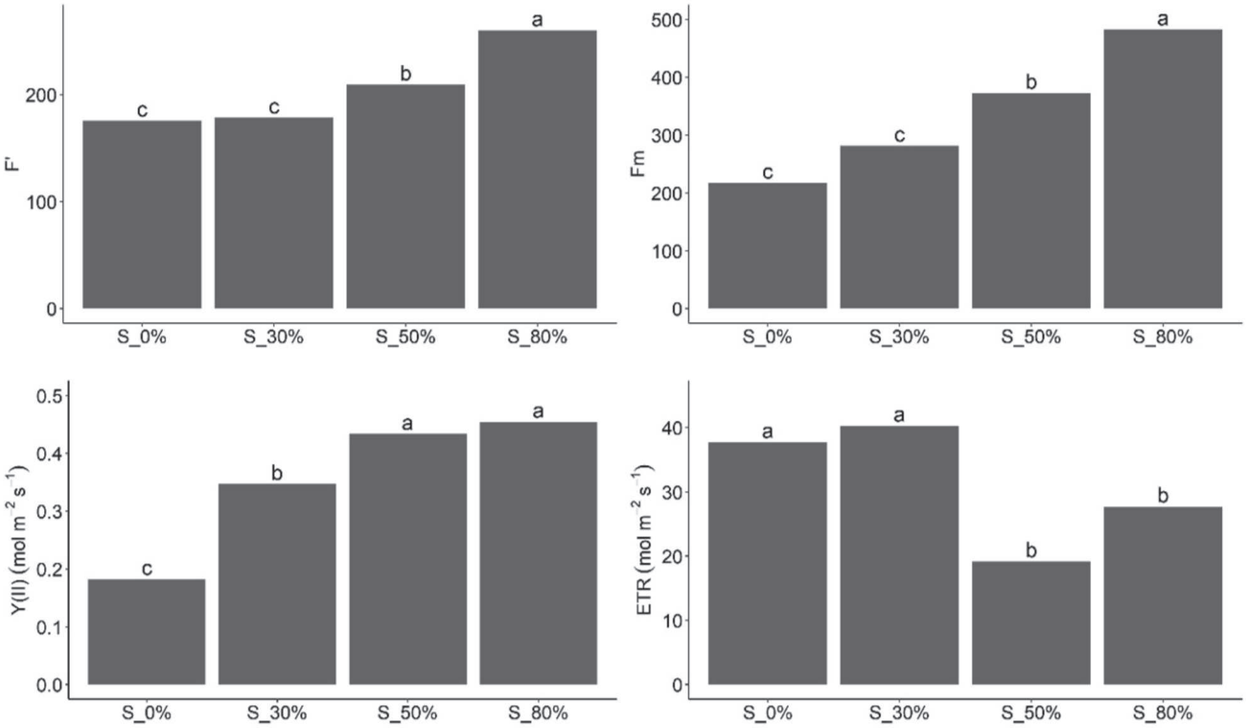

Figure 4: Fluorescence of chlorophyll parameters from *Plinia peruviana* leaves under shading gradient, in full sun (S_0%) and 30% (S_30%), 50% (S_50%) and 80% (S_80%) of shade. Averages containing different letters differ from each other by the Scott-Knott test ($p \leq 0.05$). F': initial fluorescence; Fm: maximum fluorescence; Y(II): quantum yield of photosystem II; ETR: electron transport rate.

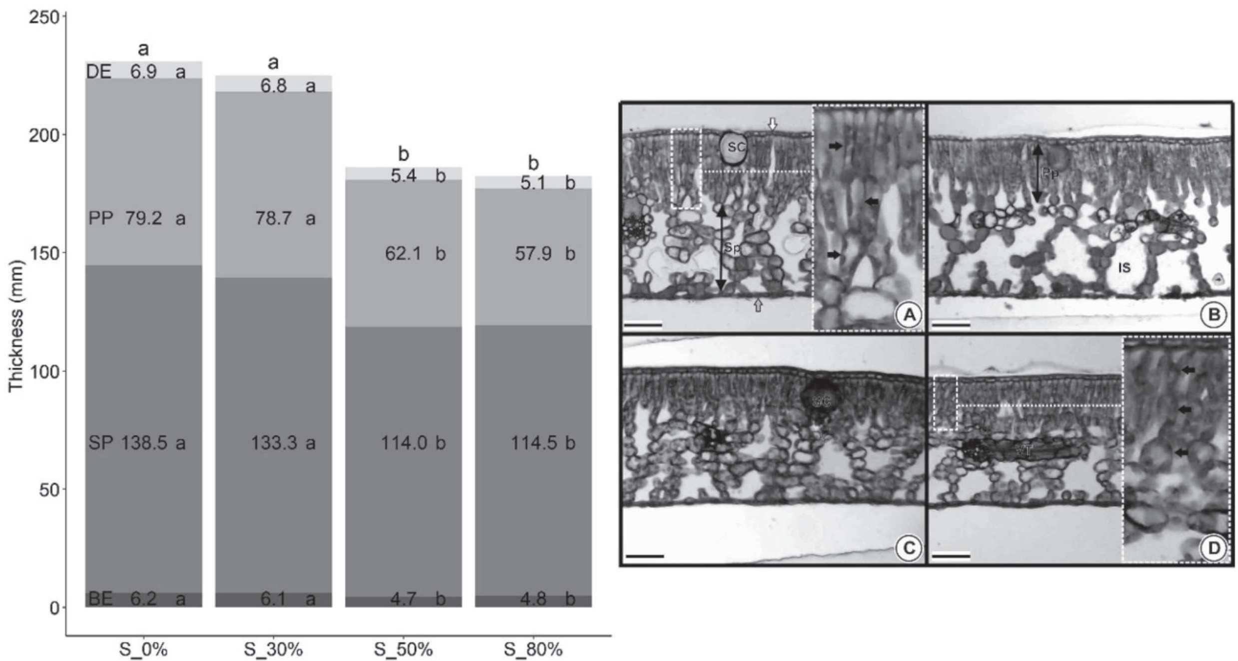

Figure 5: Thickness of leaf portions (left) and structural leaf anatomy (right) of *Plinia peruviana* leaves under full sun (S_0% and A) and 30% (S_30% and B), 50% (S_50% and C) and 80% (S_80% and D) shade. Averages containing different letters differ from each other by the Scott-Knott test ($p \leq 0.05$). BE: abaxial epidermis; SP: spongy parenchyma; PP: palisade parenchyma; DE: adaxial epidermis; Xy (xylem); Ph (phloem); Tricome (Tr); arrowhead (stomatas).

indicator for verifying species' plasticity, consistent with results founded under forest gaps (Olguin *et al.*, 2020). This phenotypic plasticity gives the possibility to realize new planting even under full sun and inside a highly shaded forest. Despite that, the saplings will have their development favored under full sun or up to 30% shade, and these light environments must be used to maximize their growth in nurseries and orchards.

CONCLUSIONS

We observed that jaboticaba tree saplings have acclimatization mechanisms to light environments, indicating that they can be grown under both full sun until deep shade. Jaboticaba saplings develop morphological and physiological acclimatization under a deep shade, such as larger leaves, increased chlorophyll content, chlorophyll fluorescence, and quantum yield of photosystem II, and reduction of leaf tissue thickness. However, to improve the quality of jaboticaba tree saplings in nurseries and growth in the orchards, we recommended that the planting be done under full sun or up to 30% shade due to enhanced growth and biomass accumulated. Also, we recommended future researches to discover the behavior of jaboticaba tree saplings under natural light conditions in forest environment and the effect on species' regeneration.

ACKNOWLEDGEMENTS, FINANCIAL SUPPORT AND FULL DISCLOSURE

We would to thanks CAPES and CNPq for fellowships and grant allocation.

The authors declare that there is no any conflict of interests in carrying the research and publishing the manuscript.

REFERENCES

Aguiar TV, Sant'Anna-Santos BF, Azevedo AA & Ferreira RS (2007) Anati Quanti: Software de análises quantitativas para estudos em anatomia vegetal. Planta Daninha, 25:649-659.

Ajalla ACA, Vieira MC, Volpe E & Zárate NAH (2014) Crescimento de mudas de *Campomanesia adamantium* (Cambess.) O. Berg (guavira), submetidas a três níveis de sombreamento e substratos. Revista Brasileira de Fruticultura, 36:449-458.

Alagupalamuthirsolai M, Ankegowda S & Krishnamurthy K (2018) Effect of different shade levels on growth, physiology and biochemical characteristics of small cardamom (*Elettaria cardamomum* Maton). Current Journal of Applied Science and Technology, 28:01-09.

Barbosa-Campos MT, Castro SAB, Kuster VC, Santos LN, Lemos-Filho JP & Vale FHA (2018) How the long-life span leaves of *Ouratea castaneifolia* Engl. (Ochnaceae) differ in distinct light conditions. Revista Brasileira de Botânica, 41:403-414.

Barros FV, Goulart MF, Telles SBS, Lovato MB, Valladares F & Lemos-Filho JP (2012) Phenotypic plasticity to light of two congeneric trees from contrasting habitats: Brazilian Atlantic Forest versus Cerrado (Savanna). Plant Biology, 14:208-215.

Brodersen CR & Vogelmann TC (2010) Do changes in light direction affect absorption profiles in leaves? Functional Plant Biology, 37:403-412.

Danner MA, Citadin I, Sasso SAZ & Tomazoni JC (2010) Diagnóstico ecogeográfico da ocorrência de jabuticabeiras nativas no Sudoeste do Paraná. Revista Brasileira de Fruticultura, 32:746-753.

Dickson A, Leaf AL & Hosner JF (1960) Quality appraisal of white spruce and white pine seedling stock in nurseries. The Forestry Chronicle, 36:10-13.

Dos Anjos L, Oliva MA & Kuki KN (2012) Fluorescence imaging of light acclimation of Brazilian Atlantic forest tree species. Photosynthetica, 50:95-108.

Feltrin RP, Will RE, Meek CR, Masters RE, Waymire J & Wilson DS (2016) Relationship between photosynthetically active radiation and understory productivity across a forest-savanna continuum. Forest Ecology and Management, 374:51-60.

Gommers CMM, Visser EJW, Onge KRS, Voesenek LACJ & Pierik R (2013) Shade tolerance: when growing tall is not an option. Trends in Plant Science, 18:65-71.

Johansen DA (1940) Plant microtechnique. New York, McGraw-Hill Book Company. 790p.

Laanisto L & Niinemets Ü (2015) Polytolerance to abiotic stresses: how universal is the shade-drought tolerance trade off in woody species? Global Ecology and Biogeography, 24:571-580.

Lemos VDOT, Lucena EMPD, Bonilla OH, Edson-Chaves B, Castro MAD & Sampaio VDS (2018) Ecological anatomy of *Eugenia luschnathiana* (O. Berg) Klotzsch ex BD Jacks. (Myrtaceae) leaves in the Restinga region, state of Ceará. Revista Brasileira de Fruticultura, 40:e-696.

Mathur S, Jain L & Jajoo A (2018) Photosynthetic efficiency in sun and shade plants. Photosynthetica, 56:354-365.

Morales P, Barros L, Dias MI, Santos-Buelga C, Ferreira ICFR, Asquieri ER & Berrios JJ (2016) Non-fermented and fermented jabuticaba (*Myrciaria cauliflora* Mart.) pomaces as valuable sources of functional ingredients. Food Chemistry, 208:220-227.

Moura MHC, Cunha MG, Alezandro MR & Genovese MI (2018) Phenolic-rich jaboticaba (*Plinia jaboticaba* (Vell.) Berg) extracts prevent high-fat-sucrose diet-induced obesity in C57BL/6 mice. Food Research International, 107:48-60.

Olguin FY, Paula A, Pinazo M, Gortari F & Vera J (2020) Morphological and physiological plasticity in seedlings of *Araucaria angustifolia* and *Cabralea canjerana* is related to plant establishment performance in the rainforest. Forest Ecology and Management, 460:e117867.

Paiva JGA, Fank-de-Carvalho SM, Magalhães MP & Graciano-Ribeiro D (2006) Verniz vitral incolor 500®: uma alternativa de meio de montagem economicamente viável. Acta Botanica Brasilica, 20:257-264.

Portela FCS, Macieira BPB, Zanetti LV, Gama VN, Silva DM, Milanez CRD & Cuzzuol GRF (2018) How does *Cariniana estrellensis* respond to different irradiance levels? Journal of Forestry Research, 30:31-44.

R Development Core Team (2020) R: A language and environment for statistical computing. Available at: https://www.R-project.org/. Accessed on: May 20th, 2020.

Rezai S, Etemadi N, Nikbakht A, Yousefi M & Majidi MM (2018) Effect of light intensity on leaf morphology, photosynthetic capacity, and chlorophyll content in sage (*Salvia officinalis* L.). Horticultural Science and Technology, 36:46-57.

Santos AS, Tuffi-Santos LD, Sant'Anna-Santos BF, Tanaka FAO, Silva LF & Santos A (2015) Influence of shading on the leaf morphoanatomy and tolerance to glyphosate in *Commelina benghalensis* L. and *Cyperus rotundus* L. Australian Journal of Crop Science, 09:135-142.

Souza TV, Torres IC, Steiner N & Paulilo MTS (2015) Seed dormancy in tree species of the Tropical Brazilian Atlantic Forest and its relationships with seed traits and environmental conditions. Brazilian Journal of Botany, 38:243-264.

Stadnik A, Caldas DKD & Souza MC (2020) Plinia in Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro. Available at: http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB37142. Accessed on: March 30th, 2021.

Toniato MTZ & Oliveira-Filho AT (2004) Variations in tree community composition and structure in a fragment of tropical semideciduous forest in southeastern Brazil related to different human disturbance histories. Forest Ecology and Management, 198:319-339.

Tuffi-Santos LD, Da Cruz LR, Santos AS, Sant'anna-Santos BF, Santos I, Oliveira AM, Barros RE, Santos MV & Faria RM (2015) Phenotypic plasticity of *Neonotonia wightii* and *Pueraria phaseoloides* grown under different light intensities. Anais da Academia Brasileira de Ciências, 87:519-528.

Wellburn AR (1994) The spectral determination of chlorophylls a and b, as well as total carotenoids, using various solvents with spectrophotometers of different resolution. Journal of Plant Physiology, 144:307-313.

Zimmermann APL, Fleig FD, Tabaldi LA & Aimi SC (2019) Morphological and physiological plasticity of saplings of *Cabralea Canjerana* (Vell.) Mart. in different light conditions. Revista Árvore, 43:e430103.