Revista Brasileira de
Engenharia Agrícola e Ambiental
v.17, n.11, p.1201–1209, 2013
Campina Grande, PB, UAEA/UFCG – http://www.agriambi.com.br
Protocolo 271.12 – 09/11/2012 • Aprovado em 02/08/2013

Morphological and photosynthetic adaptations of *Tabebuia aurea* seedlings in the nursery

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ABSTRACT

Tabebuia aurea (Benth. & Hook. f. ex S. Moore) (Bignoniaceae) is a boreal species common in Brazil. It is used for ornamental parks and along sidewalks. Its timber is also used for furniture. The objective of this study was to evaluate the effect of nursery shading on the growth and photosynthesis of *T. aurea* and their photosynthetic adaptation after being transferred to direct sunlight. The *T. aurea* seedlings were grown under 0, 50, 70 or 95% shade. The photosynthetic active radiation and leaf gas exchange were measured over two distinct periods: 51 (young seedlings) and 70 days after having been sown under each shade treatment. Immediately after the measurements were taken, the seedlings were transferred into full sunlight and the measurements were repeated two times after 15 min and 3 days under ambient sunlight. *T. aurea* seedlings showed satisfactory growth up to 50% shade in the nursery, which could be verified both by growth measurement and by total biomass accumulation. Shading greater than 70% reduced the number of leaves, the leaf area and the stem diameter in relation to plants exposed to full sunlight. The results suggest that *T. aurea* seedlings should be grown under full sunlight or under shading up to 50% to maximize their growth in the nursery and to minimize stress when transferring the seedlings to their final planting sites.

Key words: Bignoniaceae, nursery, Atlantic Forest, leaf gas exchange

Adaptações morfológica e fotossintética de plântulas de *Tabebuia aurea* no viveiro

RESUMO

Tabebuia aurea (Benth. & Hook. f. ex S. Moore) (Bignoniaceae) é uma espécie arbórea comum no Brasil, utilizada para fins ornamentais de calçadas e parques cuja madeira é usada para fabricação de móveis. O objetivo deste estudo foi avaliar o efeito do sombreamento no crescimento e na fotossíntese de mudas de *T. aurea* e sua adaptação fotossintética após transferência ao sol pleno. As plântulas de *T. aurea* foram cultivadas sob 0, 50, 70 e 95% de sombreamento. Sob cada condição de sombreamento foram avaliadas a radiação fotossinteticamente ativa e as trocas gasosas das folhas aos 51 (plântulas jovens) e após 70 dias após a semeadura das sementes sem o uso de luz artificial; logo em seguida as plântulas foram transferidas para o sol pleno e nova medidas foram feitas após 15 min e 3 dias da transferência para a nova condição. As plântulas de *T. aurea* apresentaram crescimento satisfatório até o nível de 50% de sombreamento no viveiro que pôde ser verificado tanto pelo crescimento como pelo acúmulo de biomassa total. O sombreamento acima de 70% reduziu o número de folhas, área foliar e o diâmetro do coleto em relação às plantas expostas ao pleno sol. Os resultados sugerem que plântulas de *T. aurea* devem ser cultivadas em sol pleno ou com sombreamento de até 50% para maximizar o crescimento no viveiro e minimizar o estresse de transferência das mudas para o local de plantio definitivo.

Palavras-chave: Bignoniaceae, produção de mudas, Floresta Atlântica, plântulas, trocas gasosas foliar

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INTRODUCTION

Extensive deforestation has changed the land cover of the region that was once the heart of Brazil's Atlantic rainforest. The forest once stretched over 1 million square kilometers along Brazil's coastal region with extensions inland. Today, only 7% of that original forest remains (Wuethrich, 2007). Despite continued forest conversion and degradation, forest cover is increasing in countries across the globe. New forests are regrowing on former agricultural land, and forest plantations are being established for commercial and restoration purposes (Chazdon, 2008).

In a human-impacted landscape, the new forest will not match the original forest in terms of species composition. The re-introduction of the original species is essential to increase biodiversity. For example, the dominance of a single N_2-fixing tree species in a legume mixture caused faster biomass accumulation and higher N concentrations in the biomass and litter than a diverse mixture with a low density of N_2 fixers (Siddique et al., 2008).

Establishing a self-sustainable reforested area with adequate biodiversity is the main goal of any reforestation program. Thus, knowledge of the ecophysiological behavior of the species to be used is crucial (Endres et al., 2010; Souza et al., 2010). In agroforestry, environmental limitations to plant growth are fairly common (Vilela & Ravetta, 2000). Light, water, temperature and soil conditions typically influence plant growth and development (Felfili et al., 1999). Among these factors, low light levels can limit photosynthesis, resulting in reduced growth, while excessive light can damage the photosynthetic apparatus. Light can also influence other physiological processes, both quantitatively and qualitatively. For this reason, environments that are either shaded or that receive full sunlight can inhibit the photosynthetic process simply because there is too little or too much light (Zhang et al., 2003).

Measurements of photosynthetic and morphological responses to light may reveal the tolerance of species to light intensity and have been useful in agriculture, ecology, forestry and horticulture (Aleric & Kirkman, 2005). Efficient photosynthetic activity is necessary for the high production of plant biomass. Nevertheless, abiotic and physiologically controlled factors (e.g., stomatal conductance and transpiration) can strongly influence photosynthetic activity (Gonçalves et al., 2005).

The species *Tabebuia aurea* (Benth. & Hook. f. ex S. Moore) is native to Brazil, occurring in very humid regions (the Amazon, Pantanal and Atlantic Forest) as well as more arid regions (the caatinga and cerrado). Its timber is used for furniture, and the tree is also used as an ornamental species, in reforestation, in parks and along sidewalks (Lorenzi, 2002).

Scientific articles related to shading typically consist of experimental studies on the growth of seedlings under different light levels that aim to understand the behavior of plant species during the process of reforestation and the requirements for the growth of seedlings in nurseries. Several native species have been used in shading studies, including many tropical tree species (Fonseca et al., 2002; Aguiar et al., 2005; Lima Jr. et al., 2006). However, little is known about the photosynthetic acclimation of seedlings grown in nurseries to reforestation areas (Aleric & Kirkman, 2005; Lima Jr. et al., 2005; Endres et al., 2010), and a significant photosynthetic depression can occur when seedlings acclimated to shade are suddenly exposed to full sunlight (Zhang et al., 2003).

The objective of this study was to evaluate the effect of nursery shading on the growth and photosynthesis of *T. aurea* seedlings (Benth. & Hook. f. ex S. Moore) (Bignoniaceae) and their photosynthetic adaptation after being transferred into direct sunlight. In this paper, it was describe how different light intensities can alter seedling morphology and leaf gas exchange. The photosynthetic adaptation of seedlings exposed to full sunlight after being acclimated to shading is also described.

MATERIAL AND METHODS

The experiment was conducted at Maceio, Alagoas State, Brazil, at the geographic coordinates 07º 35’ 43.8” S and 45º 46’0 8” W, at 60 m above sea level.

Seeds were collected from Craibeira trees [*T. aurea* (Benth. & Hook. f. ex S. Moore)] and immediately sown in a 1 x 3 m bed under a *Syzygium cumini* tree. The Environment Institute of Alagoas (IMA) identified the botanical material, and one exsiccate of the trees from which the seeds were collected was deposited in the institute herbarium, under the number MAC21433.

Seedlings (5 cm in height) were transferred to individual polyethylene bags with 3.5 dm^3 of soil, which was composed of 60%, loamy soil, 20% sand and 20% cattle manure. After the soil was prepared, no further fertilization was conducted until the end of the experiment.

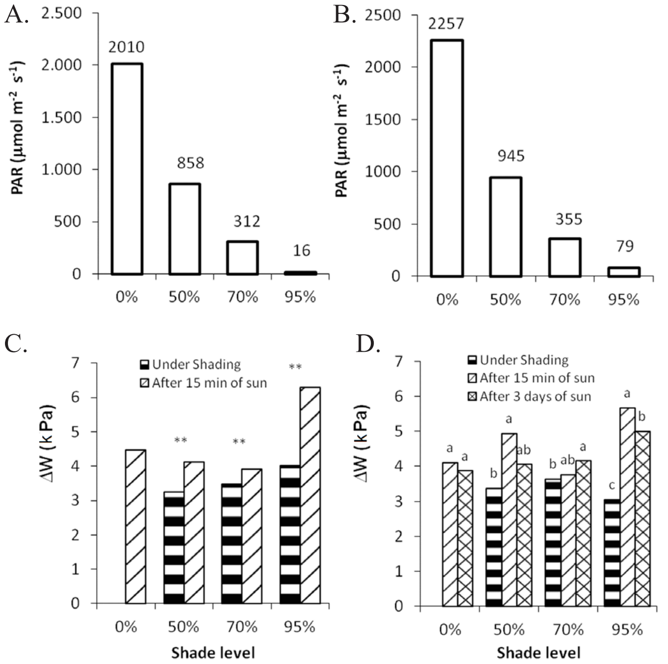
Ten days after being sown, 30 seedlings (replicates) were transferred to each shade treatment, as follows: no shading, with seedlings exposed to direct sunlight; seedlings arranged under a black polypropylene net with 50% shading; seedlings arranged under a black polypropylene net with 70% shading; seedlings arranged under a *Syzygium cumini* canopy with ~ 95% shading.

The photosynthetic active radiation (PAR) under each shade net was measured over two distinct periods with a PAR sensor (LCi, ADC, Hoddesdon, UK) between 10:00 a.m. and 12:00 a.m. (Figure 1).

The black polypropylene nets do not always supply the ideal shading levels indicated by the manufacturer (Figure 1). The 70% shade net reduced the PAR by 85%, while the 50% shade net reduced the luminosity by 61%. The values, which were measured between 10:00 a.m. and 12:00 p.m., may change during the day or over the course of the year due to the sun angle. The 95% shade treatment was conducted under a *Syzygium cumini* canopy, which may have increased the red light in relation to net shading. However, it should be noted that the light treatments were very different, making the light quality effects negligible.

The seedlings were irrigated three times a day for the first 20 days after being sown and twice a day after that until the end of the experiment.

The seedling height and leaf number per shoot were measured every 10 days from the 11th until the 70th day after sowing.



Columns in the same shading level are significantly different at $P < 0.05$ (*) and at $P < 0.01$ (**) by t-test ($N = 8$) and columns in the same shading level followed by different letters indicate significant differences ($N = 8$, Tukey test, $P < 0.05$)

Figure 1. Photosynthetic active radiation (PAR) under different shade net measured from 10:00 to 12:00 at geographic coordinates 07°35´43.8´´S and 45°46´08´´W on 02/03/2005 (A) and 19/03/2005 (B) and leaf-to-air vapor pressure deficit (Δw) on 02/03/2005 (C) and 19/03/2005 (D) of the *Tabebuia aurea* grown under different shading levels and then the seedlings were transferred to full sunlight, measured 15 min later and then only measured again 3 days later

The leaf gas exchange was measured for eight seedlings (replicates) under each shading treatment (without artificial light) at 51 (young seedlings) and 70 days after sowing. Then, the seedlings were transferred to full sunlight for 15 min, and the measurements were repeated under ambient sunlight (over 2,000 µmol m^{-2} s^{-1}). After three days under ambient light, the same leaves were measured again to quantify their photosynthetic acclimation to the new light regime, simulating the transfer of seedlings from the nursery to the field. This three-day acclimation to full sunlight was not done in the young seedlings to avoid damaging them.

Leaf gas exchange was measured by an infrared gas analyzer (IRGA) (LCi, ADC, Hoddesdon, UK) on the first expanded leaf after two minutes of equipment acclimation on the leaf. The following parameters were obtained: photosynthesis (A), transpiration (E), stomatal conductance (gs), internal and external leaf CO_2 concentration ratio (Ci/Ca), instantaneous water use efficiency (A/E), leaf-to-leaf chamber temperature difference (Tf-Tc) and instantaneous carboxylation efficiency (A/Ci). The leaf-to-air vapor pressure deficit (Δw) was calculated from the air temperature, air humidity and leaf temperature, considering the leaf mesophyll air space as saturated with water vapor. The IRGA measurements were taken between 10:00 a.m. and 12:00 p.m. under the light conditions described above (Figs. 1A and B). The values of leaf-to-air vapor pressure deficit ranged from 3.1 to 7.1 kPa (Figs 1C and D), the leaf chamber temperature ranged from 34 to 42 °C and the ambient CO_2 concentration ranged from 365 to 378 vpm.

Seventy days after sowing, the seedlings were collected, and their collar diameters were measured. The root, leaf and stem were separated, and their dry masses were determined after drying them in a forced-air circulation oven at approximately 70 ºC until constant weights were achieved. Before drying, the leaves were scanned, and the leaf area was estimated by the Quant v.1.0.1 software. From the dry mass and leaf area data for each seedling, the following parameters were obtained:

$$\text{Stem ratio}(\%) = \frac{\text{Stem dry mass}}{\text{Seedling total mass}} \times 100 \tag{1}$$

$$\text{Leaf ratio}(\%) = \frac{\text{Leaves dry mass}}{\text{Seedling total mass}} \times 100 \tag{2}$$

$$\text{Root ratio}(\%) = \frac{\text{Root dry mass}}{\text{Seedling total mass}} \times 100 \tag{3}$$

$$\text{Leaf area ratio}(\%) = \frac{\text{Leaves area}}{\text{Seedling total mass}} \left(\text{mm}^2\ \text{g}^{-1}\right) \tag{4}$$

$$\text{Specific leaf area}(\%) = \frac{\text{Leaf area}}{\text{Leaf dry mass}} \left(\text{mm}^2\ \text{g}^{-1}\right) \tag{5}$$

The results were statistically analysed as a randomized design with 30 replications per treatment for morphological characteristics and with eight replications per treatment for the leaf gas exchange data. The data were submitted to analysis of variance using the F-test, and the means were compared by Tukey test at 0,05 and t-test. No data transformation was necessary. Pearson's coefficient of correlation (r) was used to quantify the relationship between physiological parameters. All statistical analysis were performed using Statistica 6.0 from StatSoft, Inc.

RESULTS AND DISCUSSION

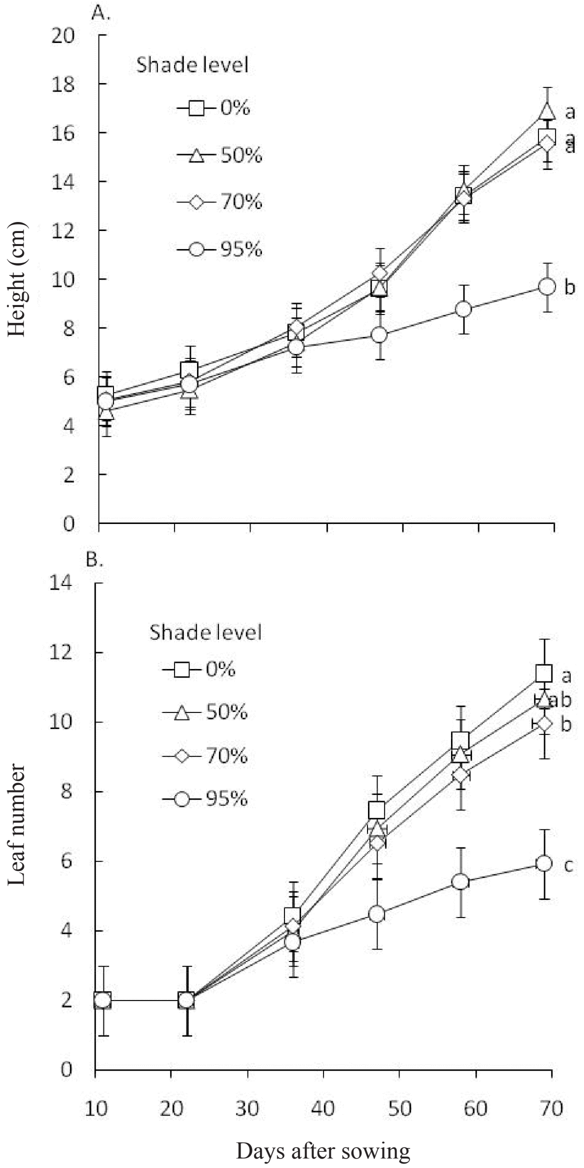
Shading strongly influenced the gas exchange of the plants, as shown by the positive correlations between PAR and stomatal conductance, PAR and transpiration, PAR and photosynthesis as well as PAR and instantaneous water use efficiency (Tab. 1). These correlations disappeared when the plants were placed under direct sunlight. The plants exposed to direct sunlight for three days showed negative correlations between PAR and photosynthesis as well as between PAR and instantaneous water use efficiency, possibly indicating photoinhibition and a subsequent decrease in CO_2 assimilation because the plants were not acclimated to high irradiance conditions. Similar results were observed in *Lycoris radiata* var. Radiata plants grown under 0 to 1,500 µmol m^{-2} s^{-1} (Zhou et al., 2010).

Shading of up to 70% did not affect the height of *T. aurea* plants. However, under 95% shade, the plant height was

Table 1. Pearson´s correlation coefficient between physiological parameters in *Tabebuia aurea* seedlings grown under shade and after transferring them to 15 min and 3 days in sunlight

	E	g_s	A	Ci/Ca	A/E	T_f-T_c	Δw
A) Grown under shade							
PAR	0.67**	0.80**	0.93**	-0.90**	0.93**	0.59**	0.23^{ns}
E		0.91**	0.82**	-0.79**	0.75**	-0.10^{ns}	0.76**
g_s			0.90**	0.81**	0.83**	0.08^{ns}	0.44*
A				-0.97**	0.98**	0.40^{ns}	0.40^{ns}
Ci/Ca					-0.99**	-0.42*	-0.46*
A/E						0.47*	0.34^{ns}
T_f-T_c							-0.31^{ns}
B) Grown under sun							
PAR	-0.04^{ns}	0.02^{ns}	-0.06^{ns}	-0.10^{ns}	-0.03^{ns}	0.72**	0.14^{ns}
E		0.82**	0.67**	0.87**	-0.18^{ns}	-0.69**	-0.03^{ns}
g_s			0.92**	0.78**	0.32^{ns}	-0.46^{ns}	-0.53*
A				0.52*	0.60*	-0.41^{ns}	-0.72**
Ci/Ca					-0.27^{ns}	-0.61*	-0.05^{ns}
A/E						0.20^{ns}	-0.92**
T_f-T_c							-0.02^{ns}
C) Shade grown and exposure to 15 min in sun							
PAR	0.36^{ns}	0.36^{ns}	0.23^{ns}	0.11^{ns}	0.00^{ns}	-0.31^{ns}	-0.09^{ns}
E		0.91**	0.75**	-0.04^{ns}	0.03^{ns}	-0.99**	0.08^{ns}
g_s			0.88**	-0.19^{ns}	0.34^{ns}	-0.87**	-0.26^{ns}
A				-0.61**	0.68**	-0.69**	-0.55**
Ci/Ca					-0.84**	-0.01^{ns}	0.65**
A/E						0.05^{ns}	-0.95**
T_f-T_c							-0.17^{ns}
D) Shade grown and exposure to 3 days in sun							
PAR	-0.38^{ns}	-0.39^{ns}	-0.46*	0.49*	-0.53**	0.09^{ns}	0.64**
E		0.98**	0.92**	-0.55**	0.74**	-0.34^{ns}	-0.83**
g_s			0.93**	-0.56**	0.75**	-0.42*	-0.84**
A				-0.81**	0.93**	-0.27^{ns}	-0.89**
Ci/Ca					-0.96**	-0.06^{ns}	0.70**
A/E						-0.18^{ns}	-0.85**
T_f-T_c							0.31^{ns}

Abreviations: photosynthetic active light (PAR), transpiration (E), stomatal conductance (gs), photosynthesis (A), leaf internal and external CO_2 concentration ratio (Ci/Ca), instantaneous water use efficiency (A/E), leaf-to-leaf chamber temperature difference (T_l-T_c), leaf-to-air vapour pressure deficit (Δw). *, $P < 0.05$; **, $P < 0.01$; and ^{ns} not significant $P < 0.05$



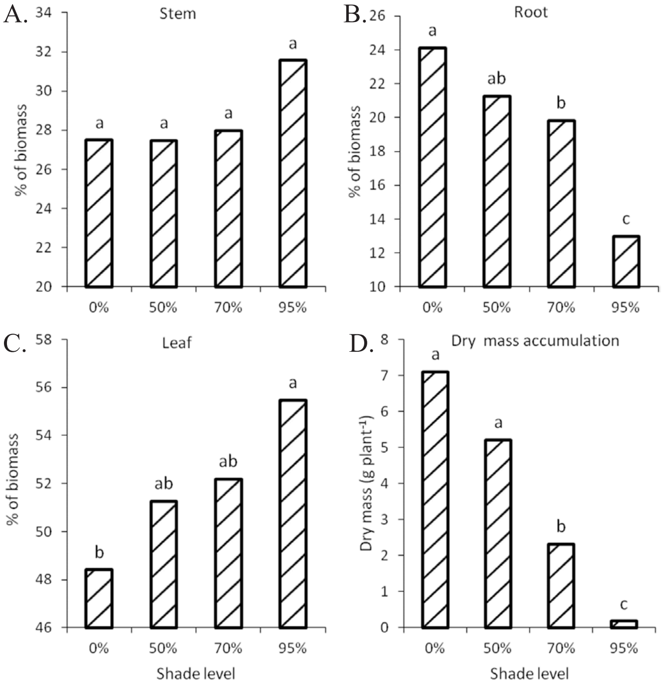
The data is means with standard error bars (N = 30). Values taken from 70 days after being sown followed by different letters indicate significant differences (Tukey test, $P < 0.05$)

Figure 2. Height (A) and leaf number (B) of the *Tabebuia aurea* seedling's grown under different shading net

reduced by approximately 40% (Figure 2A). The stem heights of *Tabebuia chrysotricha* and *Tabebuia avellanedae* Lorentz Griseb grown under different light intensities have also been shown to be reduced 130 and 90 days after planting, respectively, especially in plants grown in 95% shade (Endres et al., 2010). Furthermore, Almeida et al. (2005) found a significant height reduction of 31% in *Jacaranda puberula* Cham at 120 days after planting when grown under 50% shade. However, no reductions were observed in the height of *Caesalpinia echinata* Lam. (Aguiar et al., 2005) grown under up to 80% shade, in *Psidium cattleianum* grown under up to 70% shade (Ortega et al., 2006) or in *Bombacopsis glabra* (Pasq.) A. Robyns grown under up to 50% shade (Scalon et al., 2003) at 720, 120 and 124 days after planting, respectively. However, some plants grew taller under shade conditions, such as *Hymenaea parvifolia* (Silva et al., 2007), *Croton urucurana* Baill. (Alvarenga et al., 2003), *Simarouba amara* Aubl. (Azevedo et al., 2010) and *Trema micrantha* (L.) Blume (Fonseca et al., 2002).

Shading also negatively affected the number of leaves of *T. aurea*, especially at 95% shade, with a reduction of 44% (Figure 2B). Despite not affecting plant height (Figure 1A), 70% shade reduced the number of leaves compared to plants exposed to full sunlight (Figure 2B). Changes in the number of leaves were not observed in *Hymenaea parvifolia* (Silva et al., 2007) under up to 70% shade at 105 days after planting, *Simarouba amara* Aubl under up to 70% shade at 182 days after germination (Azevedo et al., 2010) or *Caesalpinia echinata* Lam under up to 80% shade analysed at 12, 18 and 24 months after germination (Aguiar et al., 2005). Moreover, Fonseca et al. (2002) found reductions in the number of leaves in *Trema micrantha* (L.) Blume grown under 48% shade at 120 days after germination, while Endres et al. (2010) reported a significant increase in the number of leaves in *Tabebuia chrysotricha*, especially those grown under 70% shade at 130 days after planting.

Shading caused an increase in the biomass allocation to the shoot at the expense of the root system in *T. aurea* (Figure 3). The allocation of dry mass in the shoots ranged from 76 (full sunlight) to 87% (95% shade) (Figure 3A and C). Endres et al. (2010) reported similar results in *Tabebuia chrysotricha*. The higher biomass allocation to the shoot was primarily due to the higher allocation of biomass in the leaves, ranging from 48% (full sunlight) to 55% (95% shade) (Figure 3C), and no significant change was observed in the allocation of biomass to the stem (Figure 3A). Ortega et al. (2006) showed reductions greater than 60% in the dry mass of shoots in *Psidium cattleianum* seedlings, especially when grown at 70% shade at 120 days after transplanting.



Columns followed by different letters indicate significant differences (N = 30, Tukey test, P < 0.05)

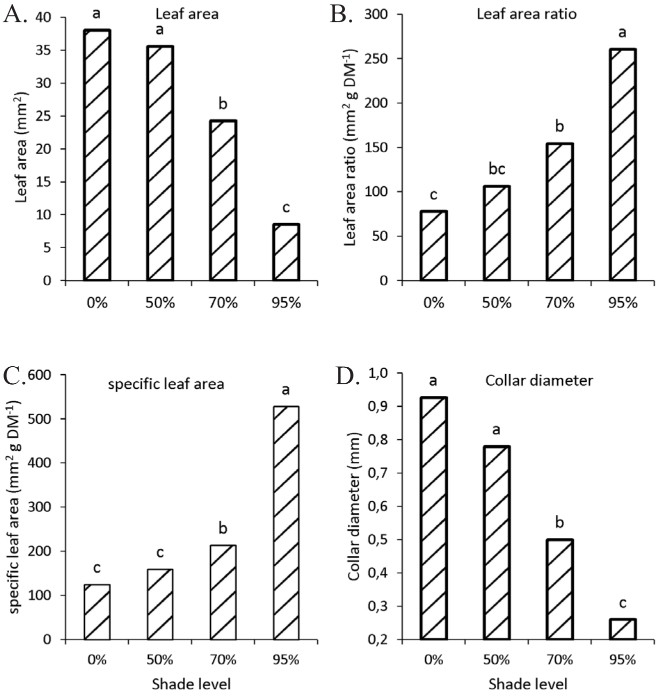
Figure 3. Proportional allocation of dry mass to stem (A), root (B) and leaf (C) and total biomass accumulation (D) of the *Tabebuia aurea* grown under different shading level

The dry mass allocation to the root system of *T. aurea* ranged from 13% (under 95% shade) to 24% (under full sunlight, Figure 3B). Silva et al. (2007) and Endres et al. (2010) observed reductions in the dry mass of the root systems of *Hymenaea parvifolia* and *Tabebuia chrysotricha* plants, respectively, under 70% shade, while Dantas et al. (2009) observed no significant differences in the dry masses of roots in seedlings of *Caesalpinia pyramidalis* Tul. grown under 75% shade at 100 days after sowing. The lower allocation of biomass to the roots as a result of shading, as occurred in this study, may reduce water and nutrient absorption, causing plants to loose their capacity to support higher rates of photosynthesis and transpiration in environments with more light (Carvalho et al., 2006). Furthermore, the dry matter allocation is an important process considering that biomass allocation plasticity to different organs may be crucial to the establishment of a seedling in a new environmental condition, for example, shading caused by other trees (Endres et al., 2010).

Total dry matter accumulation decreased dramatically under 70% shade (Figure 3D). Plants grown under 95% shade showed a total dry mass accumulation equivalent to 2.53% of the biomass of plants exposed to ambient sunlight. Similar results were found in seedlings of *Tabebuia chrysotricha* grown under 70% shade at 130 days after planting (Endres et al., 2010), in *Psidium cattleianum* grown under 30% shade at 120 days after planting (Ortega et al., 2006), in *Trema micrantha* (L.) Blume grown under 48% shade at 120 days after germination (Fonseca et al., 2002) and in *Simarouba amara* Aubl. (Simaroubaceae) grown under 70% shade at 182 days after germination (Azevedo et al., 2010).

The leaf area of *T. aurea* decreased dramatically under 70% and higher levels of shade (Figure 4A). Similar results were observed in *Jacaranda puberula* Cham. (Almeida et al., 2005) and in *T. chrysotricha* (Endres et al., 2010) under more than 70% shade. Ortega et al. (2006), however, observed no change in leaf area in *Psidium cattleianum* seedlings grown under 30 to 70% shade at 120 days after transplanting. The same finding was reported by Dantas et al. (2009) in *Caesalpinia pyramidalis* Tul. subjected to 75% shade. However, increased leaf area due to shading was observed in *Hymenaea parvifolia* grown under 50% shade (Silva et al., 2007) as well as *Croton urucurana* Baill. (Alvarenga et al., 2003) and *Simarouba amara* Aubl. (Azevedo et al., 2010) both grown under 70% shade.

The increase in leaf area may be one of the mechanisms used by plants to increase the photosynthetic surface, ensuring more efficient photosynthetic performance under low light intensity and thus compensating for the low rate of net CO_2 assimilation per unit of leaf area, a characteristic of shaded leaves (Gordon, 1969). However, in plants subjected to environments with more light, the leaf area is decreased, which is beneficial to the plant given that less leaf material is exposed to potential damages



Columns followed by different letters indicate significant differences (N = 30, Tukey test, P < 0.05)

Figure 4. The mean leaf area (A), leaf area ratio (B), specific leaf area (C) and collar diameter (D) of the *Tabebuia aurea* grown under different shading levels

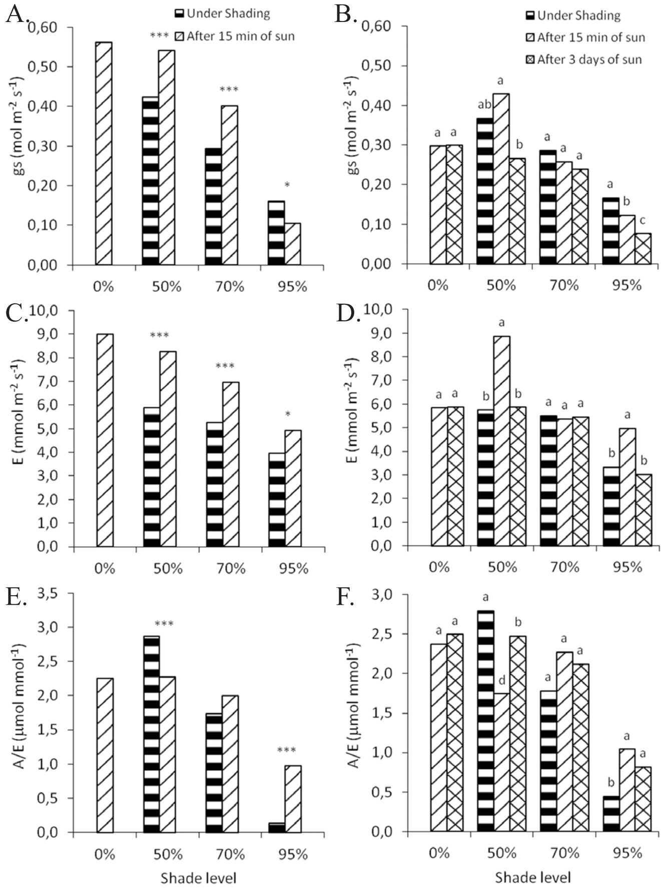
caused by excess light (Claussen, 1996). Nevertheless, in this study, it was observed that the greater the shade, the smaller the leaf area, indicating that other factors may have hindered the development of the plant.

The ratio of *T. aurea* leaf area, i.e., the usable area of the plant for photosynthesis (Benincasa 2003), showed significant increases at 70% and greater levels of shade (Figure 4B). Similar results were observed by Silva et al. (2007) in *Hymenaea parvifolia*, Dantas et al. (2009) in *Caesalpinia pyramidalis* Tul. and Endres et al. (2010) in *T. chrysotricha*. Plants grown under 95% shade (under the *Syzygium cumini* canopy) showed a dramatic increase in leaf area ratio (Figure 3B) and specific leaf area (Figure 3C). Part of this phenology could be attributed to changes in the light spectrum caused by the tree shading in this treatment and not just the lower light level (Endres et al., 2010).

The specific leaf area of *T. aurea* increased significantly under 70% and higher levels of shade, reaching values 4.2 times greater (under 95% shade) than those observed in plants grown under direct sunlight. Similar results were found in *T. chrysotricha* (Endres et al., 2010) when it was grown under more than 70% shade. However, Dantas et al. (2009) found no significant differences in the specific leaf area of *Caesalpinia pyramidalis* Tul grown under up to 75% shade.

Collar diameter showed significant reductions from 70% shading, becoming more evident at 95% shading. This reduction was superior to 70% compared to plants grown in full sunlight. Almeida et al. (2005) also found a reduction in collar diameter in *Jacaranda puberula*, as did Fonseca et al. (2002) in *Trema micrantha* (L.) Blume plants, Aguiar et al. (2005) in *Caesalpinia echinata* Lam. seedlings and Endres et al. (2010) in *T. chrysotricha* seedlings subjected to different levels of shading. In contrast, Ortega et al. (2006), Scalon et al. (2003) and Silva et al. (2007) observed no significant difference in collar diameter in seedlings of *Psidium cattleianum, Bombacopsis glabra* (Pasq.) A. Robyns and *Hymenaea parvifolia*, respectively, under shade. According to Kozlowski (1962), the increased shade decreases photosynthesis and, consequently, the amount of photoassimilates and growth regulators, causing a reduction in stem diameter. In addition, this author suggested that photosynthesis, apparently, is more directly related to growth in diameter than growth in height. In fact, the correlation between total biomass accumulation and stem diameter in *T. aurea* was high ($r = 0.94$; $p < 0.01$), indicating that this parameter can be a good indicator of the acclimation of *T. aurea* plants to the environment.

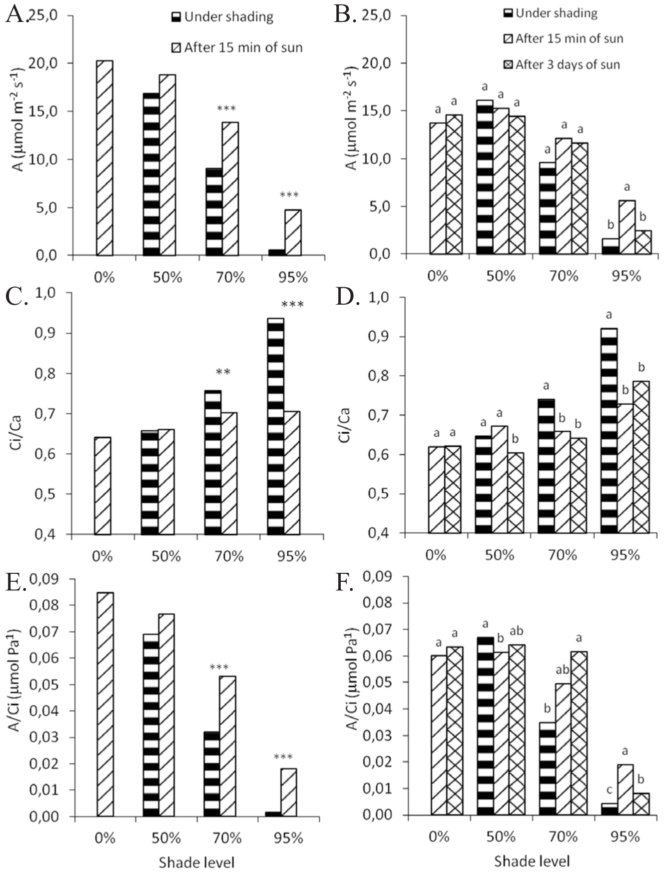
Shading caused severe changes in gas exchange in *T. aurea* seedlings (Figure 5 and 6). *T. aurea* stomatal conductance ranged from 0.1 to 0.56 mol H_2O and from 0.08 to 0.38 mol H_2O according to environmental conditions at 51 and 70 days after planting, respectively (Figure 5A and B). In 50% shade, *T. aurea* seedlings seemed to have the best stomatal conductance at 70 days after planting (Figure 5B). More intense shade inhibited stomatal conductance, which may be due to the observed increase in leaf to air vapor pressure deficit Δw (Figure 1). In general, there was an increase in gs when seedlings were transferred into direct sunlight, and it declined again after three days of exposure to natural light conditions. Reductions in gs have also been observed in seedlings of *T. chrysotricha* (Endres et al., 2010), *Paeonia suffruticosa* (Zhang et al., 2003) and Cupania *vernalis* Camb. (Sapindaceae) (Lima Jr. et al., 2006) exposed to natural light conditions after periods of 130, 60 and 150 days, respectively, under shade. Stomatal conductance was strongly correlated with PAR ($r = 0.80$; $p < 0.01$) under shade but was not correlated with PAR under full sunlight (Table 1).



Columns in the same shading level are significantly different at $P < 0.05$ (*) and at $P < 0.01$ (**) by t-test (N = 8) and columns in the same shading level followed by different letters indicate significant differences (N = 8, Tukey test, $P < 0.05$)

Figure 5. The leaf stomatal conductance (A, B), transpiration (C, D) and instantaneous water use efficiency (E, F) of the *Tabebuia aurea* grown under different shading levels and then the seedlings were transferred to full sunlight, measured 15 min later and then only measured again 3 days later. Figures 5A, 5C and 5E measure 51 days of having been sown. Figures 5B, 5D and 5F measure 70 days of having been sown

T. aurea transpiration decreased with increasing shading, especially at 51 days after planting, with a recovery trend in the three shading levels after 15 min of exposure to sunlight (Figure 5C). Similar to the findings for stomatal conductance under 50% shade, *T. aurea* seedlings had maximal transpiration 70 days after planting (Figure 5D) after 15 min of exposure to sunlight (Figure 5D). However, after three days of exposure to sunlight, these values were reduced to values similar to those found for plants subjected to shading. Transpiration was correlated with PAR ($r = 0.67$; $p < 0.01$) only under shade. A high correlation between transpiration and stomatal conductance was also observed of both under shade ($r = 0.91$; $p < 0.01$) and under different light intensities ($r = 0.82$; $r = 0.91$; $r = 0.98$; Table 1),



Columns in the same shading level are significantly different at P < 0.05 (*) and at P < 0.01 (**) by t-test (N = 8) and columns in the same shading level followed by different letters indicate significant differences (N = 8, Tukey test, P < 0.05)

Figure 6. The leaf stomatal conductance (A), transpiration (B), leaf internal and external CO_2 concentration ratio (C), photosynthesis (D), instantaneous carboxylation efficiency (E), instantaneous water use efficiency (F) and leaf-to-leaf chamber temperature difference (g) of the *Tabebuia aurea* grown under different shading levels and then the seedlings were transferred to full sunlight, measured 15 min later and then only measured again 3 days later

showing that with decreasing light availability, transpiration and conductance are highly interdependent.

Zhang et al. (2003) observed reductions in the transpiration of *Paeonia suffruticosa* subjected to 40 and 95% shading. However, changes in the transpiration rate due to shading were not observed at 130 days after planting in *T. chrysotricha* grown under up to 95% shade (Endres et al., 2010) or at 150 days after planting in *Cupania vernalis* Camb. (Sapindaceae) grown under up to 70% shade (Lima Jr. et al., 2006). Thus, in environments with different lighting conditions, plants can show great plasticity in relation to different irradiance levels, altering some features of leaf anatomy. These alterations may be directly related to inherent characteristics of gas exchange, such as photosynthetic rate, stomatal conductance and transpiration, therefore favoring a better development of seedlings under different environmental conditions (Lima Jr. et al., 2006).

In *T. aurea* plants, liquid/net photosynthesis was strongly influenced by shade, which is reflected in the high ratio of PAR to photosynthesis in seedlings grown under shade (r = 0.93; Table 1, Figures. 6A and B). The transfer of seedlings into direct sunlight for 15 min increased photosynthesis in seedlings that had been grown under 70 and 95% shade at 51 days after planting and only in those that had been grown under 95% shade at 70 days after planting. At both times (51 and 70 days after planting), the stomatal conductance of seedlings grown under 95% shade decreased and photosynthesis increased when the seedlings were exposed for 15 min to full sunlight. In addition, there was a reduction in internal and external leaf CO_2 concentration ratio under these conditions (Figure 5C), showing that stomatal conductance did not limit photosynthesis in conditions of intense shading.

Other authors have also found decreases in photosynthetic activity. Alvarenga et al. (2003) found that photosynthetic activity decreases as shading increased up to 70% in young plants of *C. urucurana* Baill. Similar results were found by Welander & Ottosson (2000) in *Quercus robur* under the same light conditions, by Mu et al. (2010) in *Triticum aestivum* L. from 22% of the incident solar radiation, by Zhou et al. (2010) in *Lycoris radiata* var. *radiata* under 85% shade and by Endres et al. (2010) in *T. chrysotricha* seedlings, especially under 95% shade. In *Lindera melissifolia*, however, the highest photosynthetic rates were observed when the plants were grown under 58% shade; yet, when irradiance was reduced by 81% (shading) net/liquid photosynthesis decreased significantly (Aleric & Kirkman, 2005).

After three days of exposure to full sunlight, seedlings that had been grown under shade showed no increase in photosynthesis (Figure 6B). Moreover, the positive correlation between PAR and photosynthesis (r = 0.93) was negative in plants that had been grown under shade (r = -0.46) after their transfer into full sunlight for three days, indicating possible damage to the photosynthetic apparatus.

Thus, *T. aurea* attempts to increase its photosynthetic efficiency under low light intensity (e.g., in 50% shade), but when it is transferred into full sunlight, the combination of high PPFD and temperature may damage PSII in leaves of this species, as has been shown in *L. radiata* var. *radiata* (Zhou et al., 2010).

CONCLUSIONS

1. The shade level in a nursery should be chosen based not only on the maximum growth of seedlings in the nursery but also on the adaptation of the seedlings to transplanting at the reforestation site. Thus, *T. aurea* seems to have satisfactory growth under 50% shade in the nursery. This species also shows a great capacity for regulating biomass allocation, especially regarding its leaves, to survive even under extreme shading conditions (95% shade).

2. The transfer of seedlings to sunlight caused drastic physiological changes, especially in the leaves. Both stomatal conductance and photosynthesis were strongly dependent on PAR when the seedlings were shaded. Based on morphological and physiological characteristics, it can be concluded that *T. aurea* is a heliophytic species that should be grown in full sunlight or under up to 50% shade to maximize growth in the nursery and minimize stress when transferring seedlings to the final planting site.

ACKNOWLEDGEMENTS

Thanks are due to FAPEAL (Fundação de Amparo a Pesquisa do Estado de Alagoas) and to CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) for financial assistance.

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