Morphological and physiological responses to shade in seedlings of *Parkia gigantocarpa* Ducke and *Schizolobium parahyba* var. *amazonicum* (Huber ex Ducke) Barneby (Leguminosae)

Respostas morfofisiológicas em mudas de *Parkia gigantocarpa* Ducke e *Schizolobium parahyba* var. *amazonicum* (Huber ex Ducke) Barneby (Leguminosae) ao sombreamento

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Resumo

O presente estudo teve como objetivo avaliar as respostas morfofisiológicas e a tolerância a diferentes intensidades de sombreamento de duas mudas arbóreas amazônicas. Mudas de *P. gigantocarpa* e *S. parahyba* foram distribuídas nas intensidades de sombreamento: pleno sol, baixa, moderada e alta (0, 23, 67 e 73% de sombreamento, ou 2000, 1540, 660 e 540 µmol m^{-2} s^{-1}, respectivamente) obtidas com telas de polietileno. Avaliou-se índice SPAD, condutância estomática (*gs*), transpiração (*E*), fotossíntese (*A*), produção de biomassa, área foliar específica (SLA) e alocação de biomassa. A *gs*, *E*, *A* e produção de biomassa foram maiores a pleno sol, em *P. gigantocarpa*, e ao baixo sombreamento, em *S. parahyba*. Com o aumento do sombreamento as mudas de *P. gigantocarpa* elevaram o índice SPAD (teor de clorofila) e a SLA; enquanto que as de *S. parahyba* aumentaram a alocação de biomassa para as folhas. Assim, como estratégia da sua plasticidade fenotípica, as espécies em estudo demonstraram distintas respostas morfofisiológicas ao sombreamento. Embora as mudas de *P. gigantocarpa* tenham apresentado melhor desenvolvimento a pleno sol e as de *S. parahyba* sob baixa intensidade de sombreamento, ambas as espécies sobreviveram às diferentes intensidades de sombreamento, sendo tolerantes a sombra e hábeis a programas de reflorestamento.

Palavras-chave: espécies florestais, área foliar específica, fotossíntese, índice SPAD.

Abstract

The present study aimed to evaluate the morphological and physiological responses and shade tolerance in two Amazonian tree seedling species under different shade intensities. Seedlings of *P. gigantocarpa* and *S. parahyba* were allocated to the following shade intensities: full sun, low, moderate and high (respectively, 0%, 23%, 67% and 73% of shade, or 2000, 1540, 660 and 540µmol.m^{-2}.s^{-1}) obtained with polyethylene screens in a nursery seedling production. We measured the SPAD index, stomata conductance (*gs*), transpiration (*E*), photosynthesis (*A*) and biomass production. We also calculated the specific leaf area (SLA) and biomass allocation. The highest values of *gs, E, A,* and biomass production were found under full sun, in *P. gigantocarpa*, and at low shade intensity, in *S. parahyba*. In *P. gigantocarpa,* the SPAD index (chlorophyll content) and SLA increased under increasing shade intensity; while in *S. parahyba,* the increase in shade intensity increased biomass allocated to leaves. Thus, as a strategy of its phenotypic plasticity, the studied species responded differently to shade intensity. Although *P. gigantocarpa* seedlings developed best under full sun and *S. parahyba* seedlings performed better under low shade intensity, both species survived the different shade intensities, being shade tolerant and adapted to reforestation programs.

Keywords: forest species, specific leaf area, photosynthesis, SPAD index.

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INTRODUCTION

Light is one of the most important environmental factors for plant development. Its intensity, duration and quality can change leaf structure and interfere with plant development, influencing many important processes in plants (KOZLOWSKI et al., 1991; SCHLUTER et al., 2003; UNEMOTO et al., 2010). According to Dias-Filho (1999), in tropical forests, light availability is among the major environmental factors that influence growth, reproduction and survival in plants. This is because in the closed canopy areas availability of solar irradiance is lower than in open areas and gaps, making the sunlight (sunfleck) penetration essential to natural regeneration and plant development (MERCES et al., 2013).

In addition, forest understories are dynamic environments in light availability, because of light gaps through trees, branch fall and opening gaps, which are subsequently filled by new plants and crowns development from adjacent trees (BLOOR; GRUBB, 2004; VALLADARES; NIINEMETS, 2008). Therefore, it is essential to know the light requirements of tropical tree species to produce seedlings with high morphological and physiological quality, aiming at the success of reforestation programs.

In fact, shade tolerance of forest seedlings is essential for forest regeneration, structure and dynamics (BLOOR; GRUBB, 2004; VALLADARES; NIINEMETS, 2008). Phenotypic plasticity is the seedling's ability to respond to environmental (e.g., light) variations and can be exhibited in plant morphological and physiological processes, being limited by ontogeny or environmental stresses (BLOOR; GRUBB, 2004; VALLADARES; NIINEMETS, 2008). According to Valladares and Niinemets (2008), in the case of low light availability, plant plasticity enhances light capture and photosynthetic efficiency. Therefore, morphological and physiological parameters such as chlorophyll content, stomata conductance, transpiration, photosynthesis, specific leaf area and biomass allocation, are commonly measured in studies on the adaptation of plant species to different light intensities (e. g.; MATOS et al., 2011; DUTRA et al., 2012; LENHARD et al., 2013).

Leguminous nitrogen-fixing trees facilitate natural regeneration, especially in degraded soils (BLOOR; GRUBB, 2004). In the Amazon region, species commonly used in reforestation programs are tree legumes such as *Schizolobium parahyba* var. *amazonicum* (Huber ex Ducke) Barneby (paricá) and some species of the genus Parkia, such as *Parkia gigantocarpa* Ducke (faveira-atanã) (BRIENZA JUNIOR et al., 2008). Both are light wood species used in construction of houses and shipbuilding, liners, sticks, plywood, toys, light boxes, doors, firewood and cellulose (LOUREIRO et al., 2000).

S. parahyba belongs to the subfamily Caesalpinioideae; it is a fast-growing pioneer Amazonian trees species, of primary and secondary forest, found in high floodplain areas (DUCKE, 1949). *P. gigantocarpa* belongs to the subfamily Mimosoideae; it is an Amazonian tree species naturally found on sandy soils and clay (LOUREIRO et al., 2000). Both species are considered shade intolerant (GOMES et al., 2010), but are being recommended for planting under different environmental conditions (BRIENZA JUNIOR et al., 2008).

The knowledge of the natural ability of each species is important for the development of an appropriate silviculture, especially when considering the growing demand for forest seedlings for degraded area recovery and the profit for wood industry. However, little is known about the Amazonian tree species, particularly *P. gigantocarpa*.

Thus, in order to expand knowledge on the responses of Amazonian tree species to environmental stresses and, assuming that shade affects the morphological and physiological behavior of these species. This study aimed to evaluate the morphological and physiological responses of seedlings of the Amazonian tree species *P. gigantocarpa* and *S. parahyba* var. *amazonicum* under different shade intensities and to associate these responses to shade tolerance, with the intent of providing technical support for reforestation programs.

MATERIAL AND METHODS

The experiment was conducted in a semi-controlled environment, at the seedling nursery production unit of Embrapa Amazônia Oriental (01°28′40″S, 48°26′59″W) in Belém, PA, Brazil. The mean air temperature and relative humidity, measured in an agro-meteorological station close to the experimental unit, during the experimental period, were 27±2.8°C and 81±0.68% (mean ± s.d.).

Seeds of *Parkia gigantocarpa* Ducke were donated by Cikel Brasil Verde Madeiras Ltda. and seed *Schizolobium parahyba* var. *amazonicum* (Hu-

ber ex Ducke) Barneby used in the study were collected from trees grow in the city of Paragominas, PA (02°59′45″S, 47°21′10″W) in the eastern Amazon region.

Prior to sowing, seeds of both species were subjected to mechanical scarification with emery to break dormancy (CRUZ; CARVALHO, 2006). Seeds were sown in plastic trays filled with a substrate composed of sand and sawdust (1:1). Six days after germination, seedlings were transplanted to black polyethylene bags (15 x 25 cm) with substrate made from a mixture of surface forest soil and sheep manure (3:2) (Table 1). Seedlings of both species were acclimated for 14 days under 75% shade. Fifteen days after germination, all seedlings were fertilized with 3g of NPK (10-28-20) per bag.

After acclimatization (20 days after germination), the seedlings of both species were distributed in the following light environments (treatments): full sun, low, moderate and high shade intensities (respectively, 0%, 23%, 67% and 73% of shade, or 2000, 1540, 660 and 540 µmol m^{-2} s^{-1}, at canopy height, measured at 11am, local time, on a cloudless day) obtained with polyethylene screens (Sombrite). Both species remained for 60 days under these treatments. Plants were irrigated once a day, until water saturation of the substrate. At the end of the experiment, (80 days after germination) we measured the SPAD index of three leaves per plant (youngest leaves, fully formed), yielding an average value of these measurements. We used a portable chlorophyll meter (SPAD-502. Konica Minolta Sensing, INC. Japan).

Stomata conductance (*gs*), transpiration (*E*) and net photosynthesis (*A*) were measured 80 days after germination, between 9:00 and 10:00 AM in fully developed and expanded leaves (one leaf per plant), with an infrared gas analyzer (IRGA) (model LCpro, ADC Bioscientific Ltd., UK) under natural CO_2 conditions and a constant photosynthetic active radiation of 500 µmol m^{-2} s^{-1} (obtained by an artificial light source coupled to the IRGA chamber). This light level was chosen to mimic the lowest light level used in the experiment. All gas exchange parameters were calculated on a leaf area basis.

Specific leaf area (SLA, the ratio of leaf area to leaf dry mass) was determined over leaf disks (three disks per plant) of either 1.12 cm^2 or 1.65 cm^2, dried at 60 °C until constant mass. Seedlings were harvested and divided into leaves, support tissue (stem and petiole) and roots (obtained by washing the substrate with water). Plant dry mass was obtained by drying the plant material in an oven at 60 °C until constant mass. The biomass allocation pattern was estimated as the leaf, stem and root mass ratios (respectively, the ratio between total leaf, stem and petiole or root dry mass per plant and total dry mass per plant). All of the above growth and biomass allocation parameters were calculated according to Hunt (1990).

The experimental design for each species was completely randomized with four treatments (shade intensities) and five replications (one experimental unit = one plant). Data were subjected to analysis of variance and means, with statistical differences, were compared by Tukey test at 5%. All computation of the data was performed by the statistical pack ace STATISTICA 7.

RESULTS AND DISCUSSION

In *P. gigantocarpa* the highest SPAD values were found under full sun and at high shade intensity (Figure 1). In *S. parahyba*, SPAD values were higher in seedlings grown under full sun (Figure 2). According to Salla et al. (2007), SPAD values can accurately estimate the amount of total chlorophyll in tree species. In the present study, the chlorophyll content (i.e. SPAD values) in seedlings of *P. gigantocarpa* and *S. parahyba* did not follow the expected response observed in tree species, which tend to increase under more intense shade (MATOS et al., 2011; FERREIRA et al., 2012; PIEREZAN et al., 2012).

For Kramer and Kozlowski (1979), in the presence of light chlorophylls are continuously synthesized and degraded. Degradation is caused by photo-oxidation and tends to increase under higher solar radiation. In the present study, the higher chlorophyll content in *P. gigantocarpa* and *S. parahyba* under full sun suggests that the higher solar radiation did not significantly in-

Table 1.   Chemical characteristics of the substrate used to produce *P. gigantocarpa* and *S. parahyba* seedlings nursery.
Tabela 1.   Atributos químicos do substrato utilizado na produção de mudas de *P. gigantocarpa* e *S. parahyba* em viveiro.

pH (H$_2$O)	P	K	Na	Ca	Ca+Mg	Al	H+Al	N	Ca/Mg
	mg dm^{-3}			cmolc dm^{-3}				(%)	g Kg
6,7	12,97	35	33	6.9	9.6	0,0	1.49	0.37	34.38

creased chlorophyll degradation in the studied species. This response may be explained by the adaptation of these pioneer species to high light environments (DUCKE, 1949; LOUREIRO et al., 2000). In *P. gigantocarpa*, high shade plants also showed high SPAD values, suggesting a higher plasticity in chlorophyll content as a compensatory mechanism for carbon acquisition (VALLADARES; NIINEMETS, 2008).

The SLA values found in this study for both species were similar to those reported by Ovington and Olson (1970) for different tropical tree species. The increase in SLA in *P. gigantocarpa* under high shade intensity (Figure 1) is a common response in forest tree species (e.g.; OLIVEIRA; GUALTIERI, 2011; CAMARGO; MARENCO, 2012). This trait is associated with an increase in the efficiency of light capture (LARCHER, 2006).

In this species an eco-physiological plasticity by increased in SLA with increase shade intensity was found (VALLADARES; NIINEMETS, 2008). According to Claussen (1996), decreased SLA (thicker or denser leaf) in lighted environments is beneficial to the plant as it exposes less vegetal material per unit of area to solar radiation, due to self-shading of chloroplasts.

The absence of response of SLA to the treatments observed in *S. parahyba* (Figure 2), corroborates with the results of Matos et al. (2011) and Dutra et al. (2012) who studied seedlings of *Jatropha curcas* L. and *Copaifera langsdorffii* Desf., respectively.

Biomass production in *P. gigantocarpa* was higher in plants grown under full sun and moderate shade intensity (Figure 1). In *S. parahyba*, the highest biomass production occurred at low and medium shade intensities (Figure 2). Under high shade intensity, both *P. gigantocarpa* and *S. parahyba* showed the lowest biomass production. Shading also reduced biomass production in *Jatropha curcas* (MATOS et al, 2011) and *Anadenanthera colubrina* (FERREIRA et al, 2012). This is an expected response of pioneer tree species. According to Salisbury and Ross (1992), this occurs because species intolerant to low light conditions have high light compensation points; therefore, as light intensity decreases carbon consumption by respiration will surpass carbon produced by photosynthesis decreasing biomass production.
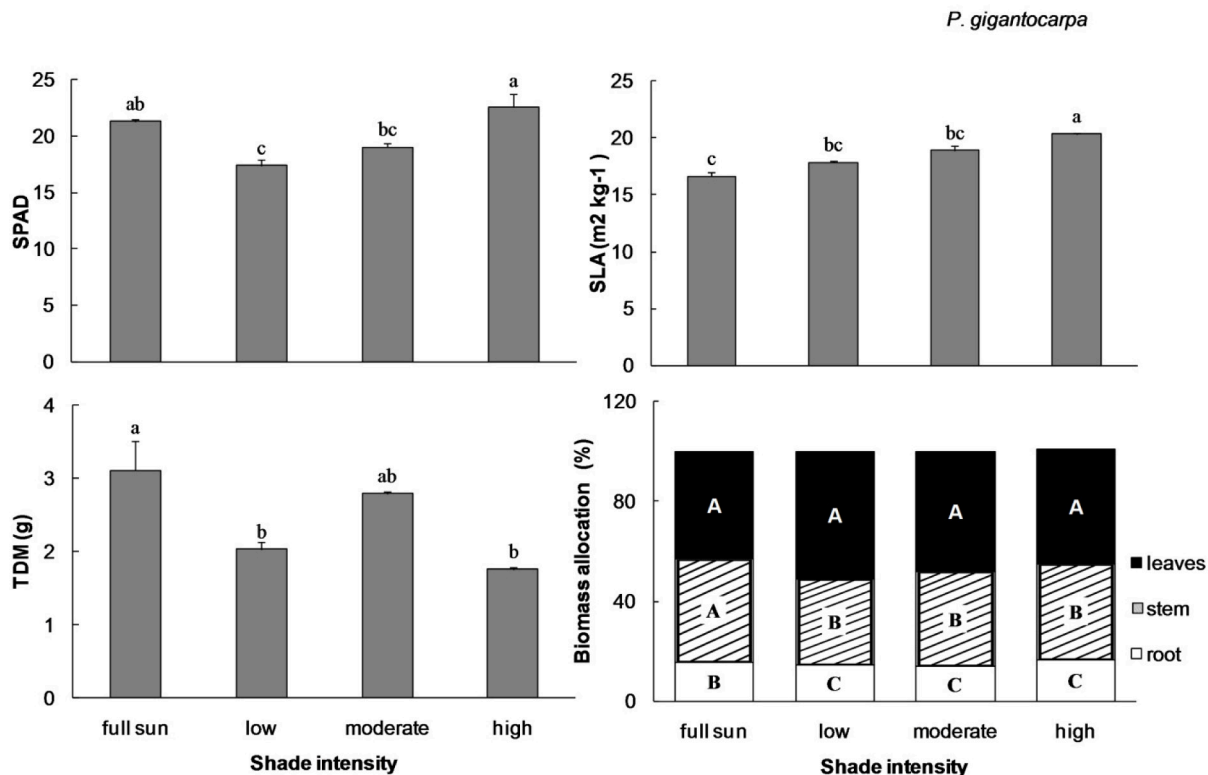

Figure 1. SPAD values, specific leaf area (SLA), Total dry matter (TDM) and biomass allocation of *Parkia gigantocarpa* under different shade intensities. Date are means ± standard error (n=5). Columns with different letters are significantly different among treatments (P < 0.05, Tukey test). Different upper-case letters within columns indicate significant differences among plant organs (P < 0.05, Tukey test).

Figura 1. Valores de SPAD, área foliar específica (SLA), massa seca total (TDM) e alocação de biomassa de *Parkia gigantocarpa* cultivadas sob diferentes intensidades de sombreamento. Média ± erro padrão (n=5). Colunas com letras diferentes apresentam diferenças significativas dentre tratamentos (P < 0.05, teste de Tukey). Diferentes letras maiúsculas dentre colunas indicam diferença significativa dentre órgãos vegetais (P < 0.05, teste de Tukey).
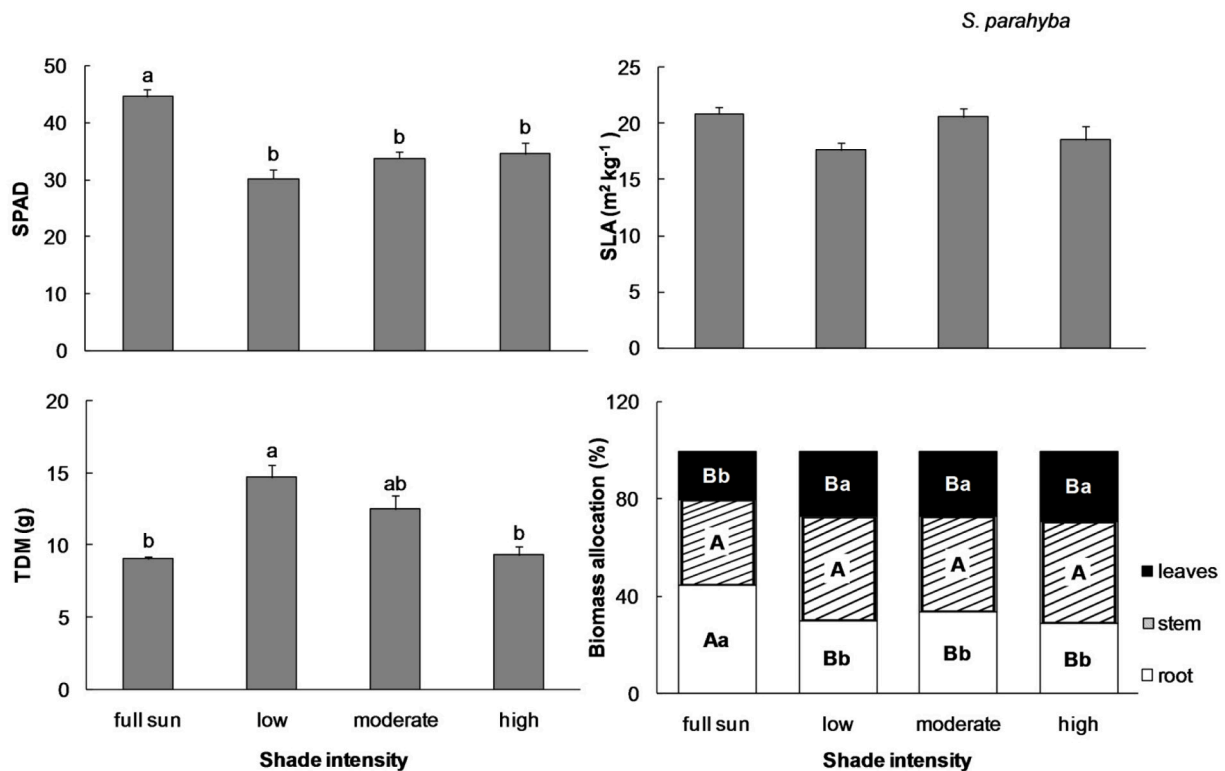
Figura 2. SPAD values, specific leaf area (SLA), total dry matter (TDM) and biomass allocation of *Schizolobium parahyba* under different shade intensities. Data are means ± standard error (n=5). Columns with different letters are significantly different among treatments (P < 0.05, Tukey test). Different upper-case letters within columns indicate significant differences among plant organs (P < 0.05, Tukey test).

Figure 2. Valores de SPAD, área foliar especifica (SLA), massa seca total (TDM) e alocação de biomassa de *Schizolobium parahyba* cultivadas sob diferentes intensidades de sombreamento. Média ± erro padrão (n=5). Colunas com letras diferentes apresentam diferenças significativas dentre tratamentos (P < 0.05, teste de Tukey). Diferentes letras maiúsculas dentre colunas indicam diferença significativa dentre órgãos vegetais (P < 0.05, teste de Tukey).

Independent of the light treatments, in *P. gigantocarpa* biomass was preferentially allocated do leaves (Figure 1), while in *S. parahyba* stems were the preferential allocation site (Figure 2). Both species followed the expected pattern of tropical species, with preferential biomass allocation to shoot (POORTER et al., 2012). The biomass increase in stems in *S. parahyba* is expected, as stems are the preferred carbon sink during the vegetative stage, particularly in fast-growing species (LARCHER, 2006; POORTER et al., 2012).

In *S. parahyba,* the increase in shade intensity tended to increase biomass allocation to leaves (Figure 2). This may be viewed as a shade-induced plasticity response, increasing the amount of photosynthetic tissue as a compensatory mechanism for light capture (POORTER et al., 2012). Under full sun, *S. parahyba* increased biomass allocation to roots, a light-induced plasticity response seeking greater water and nutrients absorption, due to higher transpiration demand and soil dryness, sustaining higher rates of photosynthesis and transpiration in environments with higher solar irradiance (POORTER et al., 2012).

The highest values of stomata conductance and transpiration were measured in *P. gigantocarpa* under full sun and in *S. parahyba* under low shading (Table 2). As expected for pioneer species, for both species, the photosynthetic rates were higher under full sun and at low shading (Table 2).

Gas exchange rates tended to be higher in *P. gigantocarpa* under full sun and in *S. parahyba* at low shade intensity, showing positive correlation with biomass production. These responses may indicate that these light environments were appropriate for these species. Similarly to the present study, photosynthetic rate increased in *Cupania vernalis* Camb., when grown at higher levels of solar radiation (LIMA-JUNIOR et al., 2005).

The positive correlation among *gs, E* and *A*, under low shade in *P. gigantocarpa* and under full sun in *S. parahyba*, may be because gas exchange during the day varied depending on several factors, such as leaf water potential, which on reaching lower values abruptly reduces stomata conductance, while maintaining photosynthesis high for a longer period (COSTA; MARENCO, 2007). This also occurs when the stomata opening is not uniform (MARENCO et al., 2006).

Table 2. Stomata conductance (gs), transpiration (E) and net photosynthesis rates (A) of *Parkia gigantocarpa* and *Schizolobium parahyba* under different shade intensities.
Tabela 2. Condutância estomática (gs), transpiração (E) e taxa fotossintética (A) de *P. gigantocarpa* e *S. parahyba* cultivadas sob diferentes intensidades de sombreamento.

Species	Shade Intensity	gs (mol m^{-2} s^{-1})	E (mmol m^{-2} s^{-1})	A (µmol m^{-2} s^{-1})
P. gigantocarpa	Full Sun	0.067 (± 0.004) a	1.48 (± 0.07) a	3.39 (± 0.36) a
	Low	0.027 (± 0.006) b	0.58 (± 0.13) b	2.98 (± 0.63) a
	Moderate	0.010 (± 0.000) b	0.12 (± 0.03) b	0.75 (± 0.14) b
	High	0.017 (± 0.002) b	0.24 (± 0.05) b	1.79 (± 0.19) b
S. parahyba	Full Sun	0.120 (± 0.008) b	2.057 (± 0.15) b	5.62 (± 0.18) a
	Low	0.208 (± 0.051) a	3.423 (± 0.56) a	6.43 (± 0.06) a
	Moderate	0.072 (± 0.011) b	1.686 (± 0.11) b	4.89 (± 0.33) b
	High	0.075 (± 0.021) b	1.424 (± 0.39) b	4.42 (± 0.55) b

*Values are means ± standard error (n = 5). Means followed by different letters in each column are significantly different (P < 0.05, Tukey test).

*Valores de média ± erro padrão (n=5). Colunas com letras diferentes apresentam diferenças significativas (P < 0.05, teste de Tukey).

Net photosynthesis showed a negative correlation with biomass production under low shade in P. gigantocarpa and under full sun in S. parahyba. A possible explanation for this response may be because, in addition to photosynthesis, biomass production results from the interaction of various physiological processes, such as respiration rate, leaf area and the efficiency of translocation and allocation of assimilates (MARENCO; LOPES, 2005).

CONCLUSION

As a strategy of its phenotypic plasticity, the studied species responded morphological and physiological differently to shade intensity. In *P. gigantocarpa*, the SPAD index (chlorophyll content) and SLA increased under increasing shade intensity; while in *S. parahyba*, the increase in shade intensity increased biomass allocated to leaves. Although *P. gigantocarpa* seedlings developed best under full sun and *S. parahyba* seedlings performed better under low shade intensity, both species survived the different shade intensities, being shade tolerant and adapted to reforestation programs.

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