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Initial development of carapa guianensis aubl. plants under different shading levels: a two-year study on growth and physiological variables

Carapa guianensis Aubl. (andiroba in Brazil) is an Amazonian multi-use tree. Due to an increased early growth (caused by large seeds reserves), no conclusive data on light preferences during initial development are available. This two-year greenhouse experiment aimed to evaluate growth and physiological variables under four levels of shading (0%, 30%, 50% and 70%). In the very-early stage of Carapa guianensis development (= 15 months), the growth in height, leaf number did not give conclusive results. Nevertheless, the shoot diameter and the relative chlorophyll content (SPAD) significantly indicated more efficient carbon gain by photosynthesis in high shade conditions (70%). After 15 months, significant changes suggested photoinhibition and high plasticity: i) gas exchange measurements (photosynthetic activity, stomatal conductance and transpiration) showed lower values under sun conditions, ii) the 50%-shade resulted in the highest dry matter increase (regarding leaves, stem and roots), iii) the Shoot-Root Ratio varied from 1.88 under sun exposure up to 4.73 under shade conditions. Although plantations of Carapa guianensis are often performed under open conditions, this study indicates that this species can give a higher return regarding biomass under shaded conditions, at least during the initial phase of establishment.

Keywords: Biomass; Shade; Tropical trees; Plant response.

Desenvolvimento inicial de plantas de Carapa guianensis aubl. em diferentes níveis de sombreamento: um estudo de dois anos sobre variáveis de crescimento e fisiológicas

A carapa guianensis Aubl. (andiroba no Brasil) é uma árvore multiuso da Amazônia. Devido ao aumento do crescimento inicial (causado por grande semente), não há dados conclusivos sobre as preferências de luz desta espécie durante seu desenvolvimento inicial. Assim, o objetivo desta experimentação em greenhouse de dois anos foi avaliar o crescimento e variáveis fisiológicas desta espécie sob quatro níveis de sombreamento. Na fase precoce do desenvolvimento de Carapa guianensis (= 15 meses), o crescimento em altura e número de folhas não apresentou resultados conclusivos. Porém, a evolução do diâmetro do caule o teor relativo de clorofila (SPAD) indicaram maior ganho de carbono pela fotossíntese com sombreamento. Após 15 meses, mudanças significativas nas medições sugeriram fotoinibição e alta plasticidade: i) as medições de troca de gases (atividade fotossintética, condutância estomacal e transpiração) mostraram valores mais baixos no pleno sol, ii) o sombreamento de 50% resultou no maior aumento da matéria seca (folhas, caule e raízes), iii) a razão parte aérea:raiz variou de 1,88 no pleno sol até 4,73 em condições de sombreamento. Este estudo indica que esta espécie pode proporcionar maior retorno em condições de sombra na fase inicial de seu estabelecimento.

Palavras-chave: Biomassa; Sombreamento; Árvores tropicais; Resposta da planta.

Topic: **Ciências Florestais**

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INTRODUCTION

Among the Amazonian trees, the *Carapa guianensis* Aubl. -commonly known as Andiroba (Brazil); crabwood (England); roba-mahogany (United States of America); karapa, british-guiana-mahogany (Guyana); bois-caille, carape-blanc, carape-rouge, Andiroba-carapa (French Guiana)- has considerable economic, social and cultural relevance for the populations of the Amazonian region (FERRAZ et al., 2002; MENDONÇA et al., 2007). This neotropical species belongs to Meliaceae family and is widely distributed in the Amazon region (KENFACK, 2011). It can be found in *terra firme*, along riversides and in seasonally flooded forests (DANTAS et al., 2016). According to the region, it can reach high local population density (>1 tree/ha) in comparison to other tree species in natural stands (SHANLEY et al., 2011).

Individual trees may reach 50 m in height and up to 65 cm in diameter at breast height (DBH) (MARTINS et al., 2012). The *Carapa guianensis* is a multi-use tree. Its wood is appreciated on the national and international market for carpentry, veneer and plywood for furniture (FERRAZ, 2003; FRAN et al., 2014). Seed oil has anti-inflammatory and insect repellent activities, is traditionally used in popular medicine, and increasingly applied in cosmetic products (e.g. FERRARI et al., 2007; MENDONÇA et al., 2007). Brazilian Ministry of Environment included *Carapa guianensis* as a priority species for sustainable development (BRASIL, 2009). It is also listed in the National List of Medicinal Plants of Interest by the Ministry of Health (AMARAL et al., 2013).

Carapa guianensis has very large seeds with 25 g to 32 g in average (MCHARGUE et al., 1983; FERRAZ et al., 2002). Germination is hypogeal, initial growth in height is fast and first leaves are developed with a stem height of about 40 cm (FERRAZ et al., 2002). Thus, *Carapa guianensis* seedlings have to be planted early to the final destination to reduce costs. On the other side, the large seedlings are in the initial phase very vulnerable, as lignification of the stem occurs later. Direct seeding is not advised, as animals highly consume seeds, even when still attached to the seedling (FAO, 1971).

Several reports were published about plantations of *Carapa guianensis* into open fields with full sun exposure (e.g. SOUZA et al., 2006; SEEDSOURCE, 2007). The species is also used to recover degraded areas (CAMARGO et al., 2002). Other studies suggest the plantation of *Carapa guianensis* for an enrichment of secondary forests (YARED et al., 1981) or agroforestry systems (FERNANDES, 1985). Volpato et al. (1972) conducted an experimental forestry plantation during eight years under three shading conditions. These authors concluded that cultivation of *Carapa guianensis* in open-areas is possible for seed production. For wood production, they recommended providing shaded conditions (as enrichment plantations) to the *Carapa guianensis* plantations.

Besides, several studies also reported the performance of *Carapa guianensis* seedlings and small trees under full sun exposed conditions, citing here, by instance: photosynthetic performance under water stress (GONÇALVES et al., 2009; AZEVEDO, 2013; SANTOS et al. 2022); physiological leaf traits related to seasonal growth (CAMARGO et al., 2012); relative chlorophyll content related to leaf characteristics (MARENCO et al., 2009);

Regarding light stress, Camargo et al. (2012) evaluated the shade impact on *Carapa guianensis* leaf traits, comparing leaves grown in the sun and shade. Leaf anatomy of eight months old *Carapa guianensis* plants was assessed under four shade conditions (ARAGÃO et al., 2014). In this study, the authors reported no significant difference in the stomatal density. However, the stomata size and the leaf thickness reduced with shade. Only one study was found concerning seedling growth in the nursery, where no difference in height, leaf number and shoot/root ratio was detected after three months under 25% and 50% shading and full sun exposure (AZEVEDO et al., 1997).

Carapa guianensis is described as a species with physiological plasticity (GONÇALVES et al., 2009), leaf anatomical plasticity (ARAGÃO et al., 2014) and potential for acclimation to changing climate conditions (CAMARGO et al., 2012). However, these earlier works do not permit considerations about more general aspects of growth and development and preference to light levels. Due to the high initial input by large seeds reserves, a more extended study period may be necessary to deduce conclusive data.

This study aimed to determine the best light conditions for growth and development of young *Carapa guianensis* plants, which have reached the minimum size for transplant to the field. As the initial phase of growth and development is very critical, several biometric and physiological growth parameters were analyzed during a two-year study, in a shading experiment in the nursery, where water stress was reduced. This work will contribute to improve the understanding of this economic important multi-use species and improve the implementation of silvicultural plantations.

MATERIALS AND METHODS

Fieldwork was carried out in the plant nursery (open area) in the municipality of Santarém, Pará State, Brazil (-2.42°, -54.74°, 51 m). The climate is tropical humid, according to Köppen classification (Alvares et al., 2013). The nearest meteorological station of the Brazilian National Meteorological Institute in Belterra (-2.63°, -54.95°, 26 km from the nursery) provided climatic data. During the two-year study (April 2011-April 2013), the monthly temperature laid between 25 °C and 27 °C with high relative humidity (≥83%). The average annual rainfall was 1,920 mm. In the rainy season (between December and April), precipitation ranged from 150 mm to 310 mm, during dry season inferior to 120 mm and felt below 40 mm in the driest months (August and September). In the months with less rainfall (between August and December), insolation was high with more than 180 $h.month^{-1}$.

Seeds of *Carapa guianensis* Aubl. were collected during natural dispersal from trees. The seeds were sown immediately in vermiculite. In April 2011, sixteen seedlings were selected. They had achieved an average height of 37±7 cm between insertion of the cotyledons and apex. At this stage of development, seed reserves were exhausted, and we manually removed the remaining attached seeds. We transplanted the plants into plastic pots with a capacity of 7.0 L. Each pot was filled with potting media composed of Amazonian dark soil [soil rich in nutrients according to Homburg (2007)] and rice straw in a 5:1 ratio. After an acclimation of one month, the base data were taken before the plants were randomly submitted to four shading levels: under full sun (0%) and black polypropylene screens providing 30%, 50% and 70% shading.

Each shading level received four pots. All plants were watered twice daily during the period from April 2011 to April 2013.

The study can be split into two periods: during the first one, measurements are related to initial growth; during the second period, we performed measurements associated with the plant physiology (Figure 1). Table 1 lists the variables and the respective abbreviations.

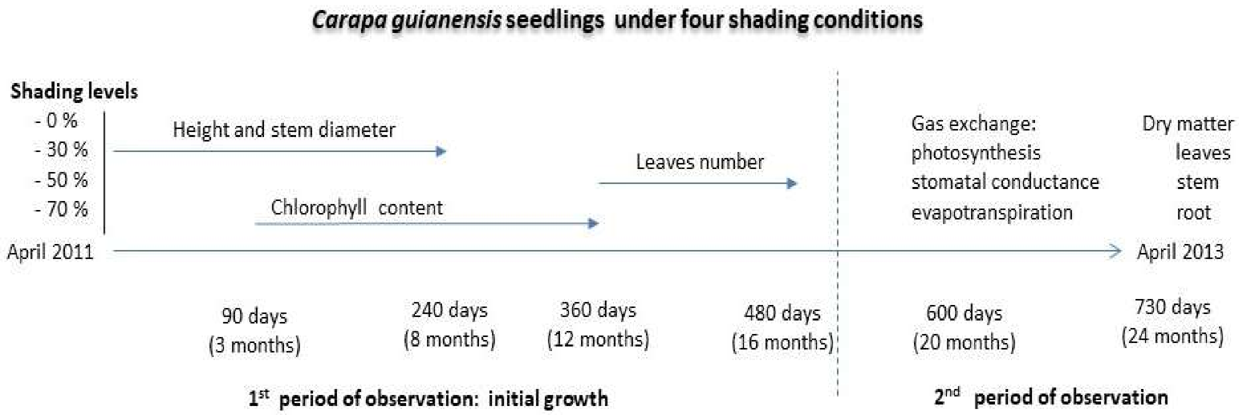

Figure 1: Flow chart of the two-year experiment with *Carapa guianensis* plants.

The first study period (until month 15) included monthly assessment of plant height and stem diameter (7 cm above the insertion of the cotyledons) of all plants for 240 days (8 months). We estimated the relative chlorophyll content on mature and healthy leaflets with a portable meter (SPAD-502®, Minolta Corporation) based on four measurements per plant. Several measures were performed between day 90 and day 360 (every 30 days). The number of compound leaves was monthly hand-counted between day 360 and day 480.

During the second study period (month 20 to 24), we measured gas exchange on day 600, between 06:00 a.m. and 11:00 a.m. with a portable infrared gas analyser (IRGA®, model LCpro). We assessed the gas activity on the three largest leaflets of each plant. The variables observed in this study were photosynthesis rate, stomatal conductance, and evapotranspiration rate (Table 1).

Table 1: List of assessed variables**.**

Variable	Unit	Abbreviation	Study period
Diameter (7 cm above soil)	mm	D7cm	First
Leaf number		LN	First
Plant height	cm	Height	First
Relative chlorophyll content		SPAD	First
Dry matter of leaves	g	DML	Second
Dry matter of stem	g	DMS	Second
Dry matter of roots	g	DMR	Second
Evapotranspiration	$mmol.m^{-2}.s^{-1}$	Ev	Second
Leaves in percentage of TDM	%	Leaves%	Second
Photosynthesis activity	$\mu mol \cdot m^{-2} \cdot s^{-1}$	PA	Second
Roots in percentage of TDM	%	Root%	Second
Shoot/Root Ratio		SRR	Second
Stem in percentage of TDM	%	Stem%	Second
Stomatal conductance	$mmol.m^{-2}.s^{-1}$	SC	Second
Total Dry Matter	g	TDM	Second

After two years of growth, we assessed the dry matter of all plants. We carefully separated the leaves from the stem and cleaned the roots from the substrate under current water. The plant parts were dried in paper bags in an oven at 65 °C until a constant weight of dry matter in repeated measurements. We weighed plant parts with a digital balance (0.01 g). Table 1 lists the variables measured and their abbreviations.

The data were analyzed with standard statistical descriptors such as mean and standard deviation. Regarding the assessment of the data homogeneity, we used the one-way analysis of variance (ANOVA) to consider whether data from the different shade condition have a common mean for each studied variable. For each parameter, we examined the differences between the means over each zone through the Tukey's range test at $p \leq 0.01$ (LARK, 2008).

RESULTS AND DISCUSSION

During the first eight months, seedlings increased between 26 and 32 cm in height, with no difference between the shade conditions (Figure 2a). However, the DBH increase was higher with shade than without shade (Figure 2b). Initial diameter of the shoot was 7.18±0.48 mm on average. In eight months, the diameter increased 2.20 mm in the sun, while all the shades condition resulted in increments between 2.90 mm (30% shade) and 3.37 mm (70% shade), still with no difference between shade conditions.

Relative chlorophyll content (SPAD Index) had significantly higher values under all shade conditions, (ranging from 43.11 (30%-shade) to 47.48 (70%-shade) in comparison to open conditions (36.76). During the following months, these values were slightly reduced remaining the statistical difference between shading and full sun exposure during the studied period (Figure 2c). SPAD Index was highest for all conditions at the first measurement (90 days after the beginning of the experiment). The reduction of chlorophyll content during the following months may be related with the hotter season and more insolation (Figures 2a and 2c). Analyzing average SPAD index over the whole study, full sunlight (0%) presented the lowest mean (34.07±1.41), and shading resulted in an averaged SPAD index above 40.00, with the highest SPAD index (48.48±2.28) recorded under 70%-shade.

The SPAD Index is a non-destructive method to specify the relative content of chlorophyll within the leaf sample (SÜß et al., 2015). It is based on leaf absorbance in red (650 nm) and near-infrared (940 nm) regions, transformed into a SPAD value. The SPAD Index is positively correlated with the results obtained with other methods of chlorophyll measurements. However, the relation is nonlinear (MONJE et al., 1992). Chlorophyll content, especially Chlorophyll b, increases under shade conditions to improve photosynthesis (while the ratio Chl a/Chl b ratio decreases). Almeida et al. (2005) reported that in comparison to full sun exposure, the 50%-shade treatment risen from 1.54 to 1.96 times the total chlorophyll content of young plants of four tropical tree species. We also observed it in the present study with *Carapa guianensis* plants: the relative chlorophyll content remained significantly higher under all shade conditions. This indicates a preference for shade conditions.

Regarding the number of leaves per plant (Figure 2d), 30%-shade provided a higher quantity with 13±1 leaves in average, whereas all other conditions resulted in an average leaf number of 10±1 over the same period.

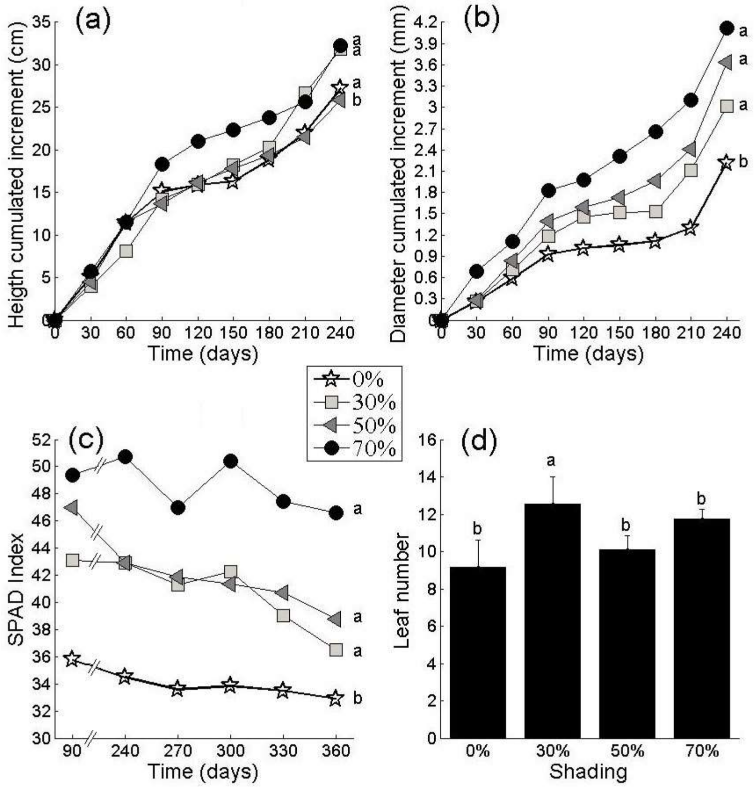

Figure 2: Initial growth of *Carapa guianensis* plants: a) Cumulated increment in height, b) Cumulated increment in diameter, c) Chlorophyll content – SPAD Index, d) Average number of composed leaves between months 11 and 15. Means with the same letter are not significantly different by Tukey's test at p ≤ 0.05.

Gas exchange measurements in the second period revealed a positive effect of shading (Figures 3a, 3b and 3c) on the *Carapa guianensis* plants in comparison to direct sun exposure. The response was similar for all three physiological variables. Direct sunlight (0%) provided the lowest photosynthetic rate (2.35±0.92 μmol.m^{-2}.s^{-1}), lowest stomatal conductance (0.05±0.01 mmol.m^{-2}.s^{-1}) and lowest transpiration (1.21±0.27 mmol.m^{-2}.s^{-1}). We found no statistical differences between the shadings. However, the 30%-shade treatment furnished the highest quantitative values with 4.29±2.09 μmol.m^{-2}.s^{-1}, 0.09±0.04 mmol.m^{-2}.s^{-1}, and 1.69±0.49 mmol.m^{-2}.s^{-1} for the photosynthetic rate, the stomatal conductance, and the transpiration, respectively.

Dry matter, after two years, showed significant variations (Figure 4a). The highest total biomass (361.0 g) was achieved with 50%-shade, 3.1 times the weight obtained in direct sunlight (117.8 g) and shading of 30% and 70% resulted in a 2.3 fold increase. Regarding dry matter allocation, the investment in the stem remained the highest one under all conditions. It was also significantly higher under the shading conditions (152-208 g) than under direct sun exposure (68 g). Under shade, the investment in leaves (74 g in average) was higher than in the roots (55 g in average), different to full sun exposure, where the allocation in roots biomass (41 g) was higher than in dry leaf matter (9 g). Despite the weak difference in leaf number observed in the first period (Figure 2d), after two years, the dry leaf matter remained higher under all shade conditions (47-71 g) than under full sun exposure (9 g). The 50%-shade treatment resulted in the highest value (71 g).

The distribution of above and below biomass allocation significantly differed when the plants received shade. Under these conditions, between four to five times more dry matter was allocated in the above biomass (SRR of 4.7, 4.1 and 4.6 for the 30%-, 50%- and 70%-shade treatments, respectively), whereas, under full sun exposure, the investment in the root system increased and resulted in an SRR of 1.9 (Figure

4b).

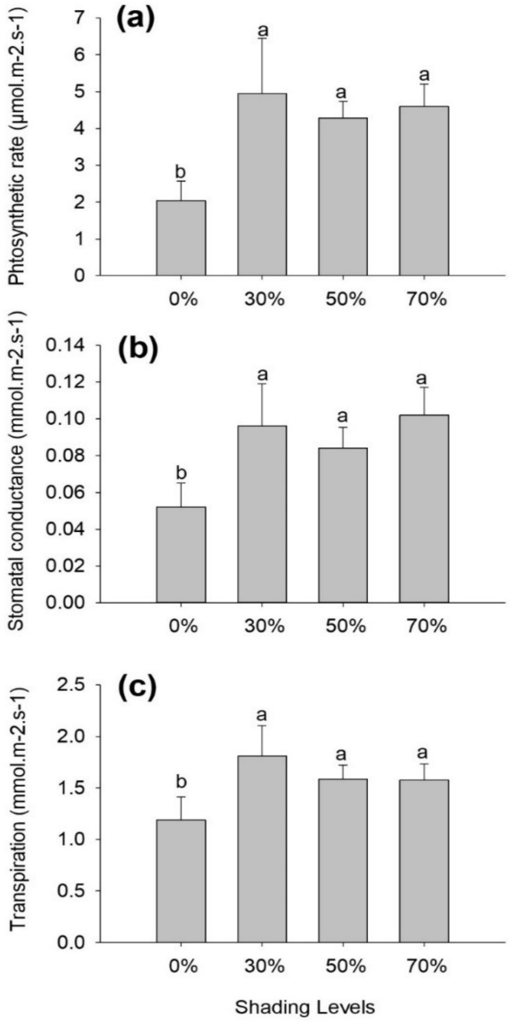

Figure 3: Gas exchange measurements of *Carapa guianensis* plants after 20 months*:* a) Photosynthetic activity, b) Stomatal conductance, c) Transpiration. Means with the same letter are not significantly different by Tukey's test at p ≤ 0.05.

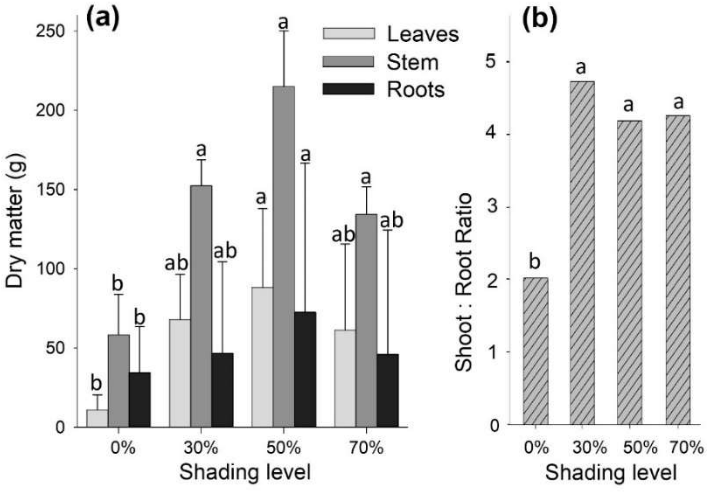

Figure 4: Dry matter allocation of *Carapa guianensis* plants: a) Dry matter of leaves, stems and roots, b) Shoot/Root Ratio. Means with the same letter of the same plant part are not significantly different by Tukey's range test at p ≤ 0.05.

Shading and light reduction influence plant growth. It may result into an alteration of investment in the different plant parts. Generally, under shading, a higher investment in height is expected compared to plants grown under open conditions where lateral growth such as branches is stimulated. This is known for many tree species, citing here, for example, acariquara *(Minquartia guianensis,* MAGALHÃES et al., 2009), chichá (*Sterculia foetida,* CAMARA et al., 2007) sansão-do-campo (*Mimosa caesalpiniaefolia Benth.*, CAMARA et al., 2007) and araucária (*Araucaria angustifolia* (Bertol.) Kuntze, FRANCO et al. 2007).

Carapa guianensis is considered as species with physiological plasticity (GONÇALVES et al., 2009; SANTOS et al., 2022) and potential for acclimation to changing environmental conditions (CAMARGO et al., 2012; SANTOS et al., 2022). Several studies were achieved with plantations or experiments under full sun exposure (e.g. CAMARGO et al., 2002; SOUZA et al., 2006). The present study confirms the high plasticity of this species as shown by the alteration of Shoot-Root Ratio from 1.88 under sun exposure to 4.12-4.73 under shade. On the other side, the study also reveals that plants produced much more biomass under shade than with full sun exposure.

Regarding the growth variables, we only detected the positive effect of shade in the second period of observation. In an previous nursery study with *Carapa guianensis*, Azevedo et al. (1997) did also not detect a significant difference in shoot lengths after 90 days when comparing the influence of 0%, 25% and 50% of shading treatments. However, these authors reported that the shoot diameter significantly increased with the 25%-shade. We also noted it in the present study: all shade treatments increased shoot diameter considerably after 240 days.

Some plants produce more leaves under shade, citing here, for example, *Dipteryx odorata* (Aubl.) seedlings (UCHIDA et al., 2000). However, in a nursery study with *Carapa guianensis* seedlings, Azevedo et al. (1997) reported no difference in leaf number. It is noteworthy to mention that this species has compound leaves, and the leaflets number increases with development (FERRAZ et al., 2002). In this study, leaf number and not leaflet number was assessed. The variation of leaf number in each shading was small, and the standard deviation remained inferior to two leaves. Thus, the leaf number did probably not reflect the real investment in photosynthetic active leaf area. Assessing dry matter after two years revealed that leaf biomass was highest with 50%-shade.

The physiological variables of gas exchange confirmed this tendency: all of them revealed that the plants suffer more stress under full sun exposure than under shade. Light stress can induce various responses, including the formation of sun-type chloroplasts with the adaptation of the photosynthetic apparatus and alteration of chloroplast ultrastructure (LICHTENTHALER et al., 1999). Exposure of plants to irradiances far above the light saturation point of photosynthesis can result into photoinhibition. If the light excess is moderate, the quantum efficiency of photosynthesis can decrease without reducing the maximum photosynthetic rate. Nevertheless, an excessive light will also lessen the photosynthetic rate (TAIZ et al., 2010). Seen in this study with the *Carapa guianensis* seedlings exposed to full sun where the photosynthetic rate was significantly lower under sun-exposed conditions.

Stomatal conductance allows measuring the transpiration at the leaf level. It is a function of stomatal density, aperture and size. It can be used as an indicator of plant water status and stomatal conductance or transpiration rate can be estimated from leaf temperature measurements. When plant water status is adequate, leave temperature is appreciably less than the air temperature, through the cooling effect of evaporation. As stomata are partially close in response to increasing plant water stress, the energy balance of the plant is altered: less heat is dissipated through the evaporation of water, and consequently leaf temperature increases (TAIZ et al., 2010). In this study, stomatal conductance and transpiration measurements indicate, that even with irrigation twice a day, the *Carapa guianensis* plants suffered water stress, which reduced stomatal conductance and transpiration in the sun-exposed conditions. Similar results for stomatal conductance (between 4.1 and 5.3 µmol.m^{-2}.s^{-1}) and transpiration (about 1.3-1.5 mmol.m^{-2}.s^{-1}) were obtained by Gonçalves et al. (2009) under comparable conditions in a nursery with *Carapa guianensis* plants. Differently from our study, these authors only examined plants under full sun exposure. Thus, the stress reduction by shading was not verified. Even so, the authors confirmed the high plasticity of *Carapa guianensis* seedlings during a recovery after 21 days water stress.

It is known that light sensitivity may change during development. For instance, with *Neobalanocarpus heimii*, at initial plant development, Sherzad et al. (2017) reported higher production of total dry mass under shade than under full sun. These authors showed that photoinhibition was a temporary process and the plants could acclimate to direct sunlight after establishment. This may also be the case of *Carapa guianensis* seedlings.

CONCLUSIONS

In the very-early stage of *Carapa guianensis* development (≤ 15 months), no conclusive results about the impact of shading have been observed regarding the growth in height and leaf number, except for the shoot diameter and the chlorophyll content, that were significantly lower under full sun exposure (indicating less efficient carbon gain through photosynthesis).

After 15 months, significant changes suggested photoinhibition and high plasticity: i) gas exchange measurements (photosynthetic activity, stomatal conductance and transpiration) showed lower values under sun conditions, ii) the 50%-shade resulted in the highest dry matter increase, iii) the Shoot-Root Ratio varied from 1.88 under sun exposure up to 4.73 under shade.

Further similar studies should measure the leaflets number instead of leaves number, as the higher number of leaves under the 30%-shade significantly observed in the 15th-first months did not match with a higher leaf dry matter at the end of the experiment. Although plantations of *Carapa guianensis* are often performed under open conditions, we recommend providing a 50%-shaded condition to the young plants to give higher return regarding biomass.

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