Photosynthetic light response curves in *Eucalyptus benthamii* and *Eucalyptus dunnii* clones

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Abstract

The photosynthetic light-response curve reflects the instantaneous response of the net photosynthetic rate to different gradients of photosynthetically active radiation. Genetic materials can respond differently to light and consequently alter productivity. Thus, this work aimed to compare clones of *Eucalyptus benthamii* and *Eucalyptus dunnii* by checking the CO_2 assimilation rate due to the increase in photosynthetically active radiation. The evaluations were carried out in mini-stumps implanted in a clonal mini-garden system. The CO_2 assimilation rate curves were determined with the aid of a portable photosynthesis meter. The curves of CO_2 assimilation rate (*A*) in response to the increase in photosynthetically active radiation (*PAR*) were evaluated at values of 1500, 1000, 700, 450, 250, 120, 50 and 0 $\mu mol\ m^{-2}\ s^{-1}$ for clones of *E. benthamii* and *E. dunnii*. The three *Eucalyptus* clones evaluated showed a similar behavior of the *A/PAR* curve, showing a high demand for photosynthetically active radiation. In general, the three clones were very similar in terms of CO_2 assimilation rate due to the increase in photosynthetically active radiation.

Keywords: photosynthetically active radiation, quantum efficiency of photosynthesis, respiration.

Introduction

Eucalyptus is ranked globally among the most economically important trees (Bayle et al., 2019). They exhibit traits such as fast growth (Lorentz and Minogue, 2015) and high water and light use efficiency (Maier et al., 2017) that contribute to their candidacy as an excellent biofuel crop (Gonzalez et al., 2011). *Eucalyptus* plants are classified as C3 – carbon dioxide fixation and follow a C3 pentose phosphate cycle (Machado et al., 2011). Most eucalypt species are native to Australia and Indonesia and are adapted to tropical and subtropical environments. However, some species have developed frost tolerance through advancements in biotechnology or adaptation (Stanturf et al., 2013). Two species, in particular *Eucalyptus benthamii* and *Eucalyptus dunnii*, has been shown to exhibit competitive frost tolerance when compared to members of the same genus (Arnold et al., 2015).

In Brazil, these two species are well adapted to southern Brazil. However, in many places in this region it is common to have many cloudy days (Aguiar et al., 2018), which can significantly decrease the growth of species, whether in the field or in a nursery. Light absorption capacity is thought to be a major factor limiting growth at tree scale across a broad range of environmental contexts and management (Binkley et al., 2013). However, the positive effect of light absorption on gross primary productivity and biomass production can be obscured by other limiting factors (Will et al., 2001). The effect of light absorption on forest productivity is expected to vary among genotypes, soil, climate and management conditions (Forrester et al., 2018).

In order to better understand and predict the productivity of different genetic materials, studies involving photosynthetic capabilities can facilitate this process. Photosynthesis is the process used by plants to transform less than 5% of the solar radiation into the energy needed to drive carbon dioxide fixation and to form the organic matter of plant tissues, and to promote plant growth (Solarte et al., 2010). Photosynthesis is critical for support of life systems on the Earth. Each plant species has its own optimal light intensity range, soil conditions, and other environmental needs for photosynthesis (Liao et al., 2020).

The radiation used in photosynthesis ranges between 400 to 700 nm of the solar radiation spectrum and is known as photosynthetically active radiation (*PAR*) (Azcón-Bieto et al., 2008). The *PAR* intercepted and absorbed by the leaves, and the efficiency of the conversion of carbohydrates into chemical energy are key factors to understanding plant growth (Woittiez et al., 2017). One way to study these factors is with light saturation curves, which represent the response of the net photosynthetic rate to the *PAR*.

The photosynthetic light-response curve reflects the instantaneous response of the net photosynthetic rate (*Pn*) to different gradients of photosynthetically active radiation (*PAR*). It can provide measures of many photosynthetic indicators, such as the maximum *Pn* (*Pmax*), dark respiration

rate (Rd), apparent quantum yield (AQY), light compensation point (LCP) and light saturated point (LSP), for analysing plant photosynthetic activity (Coble et al., 2016). Therefore, our work aimed to compare clones of *Eucalyptus benthamii* and *Eucalyptus dunnii* by checking the CO_2 assimilation rate due to the increase in photosynthetically active radiation.

Results and Discussion

In average, there was no difference between the evaluated clones (Figure 1b) in photosynthetically active radiation (*PAR*), whereas the general average obtained was 13.22 µmol CO_2 m^{-2} s^{-1}.

The three *Eucalyptus* clones showed very similar *A/PAR* curves (Figure 2), showing a pattern of higher increase in CO_2 *A* assimilation rate (µmol CO_2 m^{-2} s^{-1}) up to approximately 1000 µmol m^{-2} s^{-1} of photosynthetically active radiation (*PAR*). For all clones there was a high increase in *A* assimilation rate mainly up to 450 µmol m^{-2} s^{-1} as we raised *PAR*.

Dark respiration (Rd) values ranged from 2.15 µmol CO_2 m^{-2} s^{-1} for clone C (*E. dunnii*) to 2.76 µmol CO_2 m^{-2} s^{-1} for clone A (*E. benthamii*), representing an increase of 22%. Clone B had a Rd value closer to clone A (also from *E. bethamii*). For maximum photosynthesis (A_{max}), *E. benthamii* clones (clones A and B) showed higher values compared to clone C, with a difference of less than 5%.

The quantum efficiency of photosynthesis (AQY) ranged between 0.0719 and 0.0810 µmol CO_2 µmol of photons^{-1}. The highest value obtained for clone A, with a difference of 12% higher in relation to the other clone of *E. benthamii* (B). Regarding the light compensation point (φ), the *E. benthamii* clones obtained the highest values, close to 35 µmol of photons m^{-2} s^{-1}, while the *E. dunnii* clone C presented a value lower than 30 µmol of photons m^{-2} s^{-1}.

The three *Eucalyptus* clones showed a similar behavior of the *A/PAR* curve, showing a high demand for photosynthetically active radiation (greater than 800 µmol m^{-2} s^{-1}). This result demonstrates that in the presence of light clones highly respond to photosynthetic production. Many species also exhibit such as behavior. Berry and Goldsmith (2020) reported that *Heliocarpus americanus* L., *Cecropia polyphlebia* Donn. Sm. and *Ficus* spp require at least 800 µmol m^{-2} s^{-1} to reach to the maximum photosynthetic capacity. Other species such as *Meliosma vernicosa* Liebm. and *Conostegia rufescens* Naudin reached the maximum photosynthetic capacity with only 400 µmol m^{-2} s^{-1}.

Working with *Eucalyptus grandis* (W. Hill ex Maiden) and the hybrid between *E. grandis* x *Eucalyptus camaldulensis* (Dehnh.), Shem et al. (2009) obtained a limitation of 800 µmol m^{-2} s^{-1} for the species, and values lower than this were assumed to limit assimilation. In this same study, the maximum photosynthesis obtained for *E. grandis* was 19.2 µmol m^{-2} s^{-1} and for the hybrid *E. grandis* x *Eucalyptus camaldulensis*, 24.6 µmol m^{-2} s^{-1}. It is important to highlight that Shem et al. (2009) studied 3-year-old field plantations, while our results are from younger plants planted in a mini-clonal garden for minicutting production, periodically pruned with continuous fertilization. It is noteworthy that there are no studies on the need for light in a nursery environment for the production of mini-cuttings. The authors consider this variation between species due to differences between them in the light absorption properties of leaves. The same is applied to our study, however with less accentuated differences between the two species (*E. benthamii* and *E. dunnii*).

In general, the three clones presented very similar pattern in *A/PAR* curve. However numerically, clone A of *E. benthamii* presented a higher A_{max}, about 4.3% higher than clone C, demonstrating a possible greater potential for mass accumulation. However, the Rd value of about 28.5% higher in clone A compared to C can neutralize this higher A_{max}, or even, in the final carbon balance fixed in a 24h cycle, it can be negative. The higher Rd can also mean higher capacity/potential to relocate the starch accumulated by photosynthesis in the leaves. The maximum net photosynthetic rate (A_{max}) is an important parameter of plant growth rate, describing the maximum net light plant potential, and reflecting the maximum potential of plants can turn the CO_2 from the atmosphere into organic matter in the unit area (Xiong et al., 2012).

Dark respiration reflects a condition, in which with no absorption of light radiation by leaves, the amount of CO_2 released by respiration exceeds that of CO_2 fixed in photosynthesis (Larcher, 2004). Differences in dark respiration rate have been used as criteria for discriminating varieties with low respiration rates and high biomass accumulation capacity (Wilson and Jones, 1982). Working with *Eucalyptus pauciflora* (Sieb. ex Spreng), Atkin et al. (2000) found values like the present study for Rd, obtaining 2.48 µmol CO_2 m^{-2} s^{-1} at a temperature of 30 ºC. However, this value was reduced with temperature, reaching 0.64 µmol CO_2 m^{-2} s^{-1} at 15 ºC. Our study was carried out in a greenhouse where daytime temperatures are approximately between 25 and 30 ºC. Average values of dark respiration for the plants of the three provenances of *Eucalyptus cloeziana* F. Muell. ranged from 0.61 to 1.86 µmol m^{-2} s^{-1} (Ngugi et al., 2003).

Numerically, clone A had the greatest potential for radiation response (0.081). This shows that for each mole of photon absorbed by the clone leaves, 0.081 moles of CO_2 are fixed via photosynthesis. Compared to clone C, it would be 9.46% more efficient. The decline of *AQY* implies that the conversion efficiency of low-light energy was decreased (Liang et al., 2016). Our values are higher compared to an 18-month-old *Eucalyptus cloeziana* plantation, whose apparent quantum efficiency of photosynthesis (*AQY*) was 0.04 to 0.06 µmol of CO_2 µmol photons^{-1} (Ngugi et al., 2003). In addition to the effect of species observed in this study compared to *Eucalyptus cloeziana*, the cultivation environment must also be mentioned, in which the mini-stumps are conducted aiming at the maximum production of mini-cuttings, with temperature, humidity and nutrition control, with greater response to radiation.

The compensation point reflects the number of moles of photons that are needed for the carbon balance in the leaves to be equal to zero, which is photosynthesis equal to respiration. The clone C was numerically smaller, about 22.28%, compared to clone A. This means that clone C (*E. dunnii*) presents a more characteristic photosynthetic apparatus adapted to shading conditions, which may reflect in the lower A*max* and *Rd*, since the saturation of photosynthesis by light occurs more quickly, and usually shade plants present lower Rd. Plants with lower light compensation point have stronger adaptability to environment light (Xiong et al., 2012).

There are several factors that can affect the photosynthetic rate, such as nutritional management, genetic effect, climate,
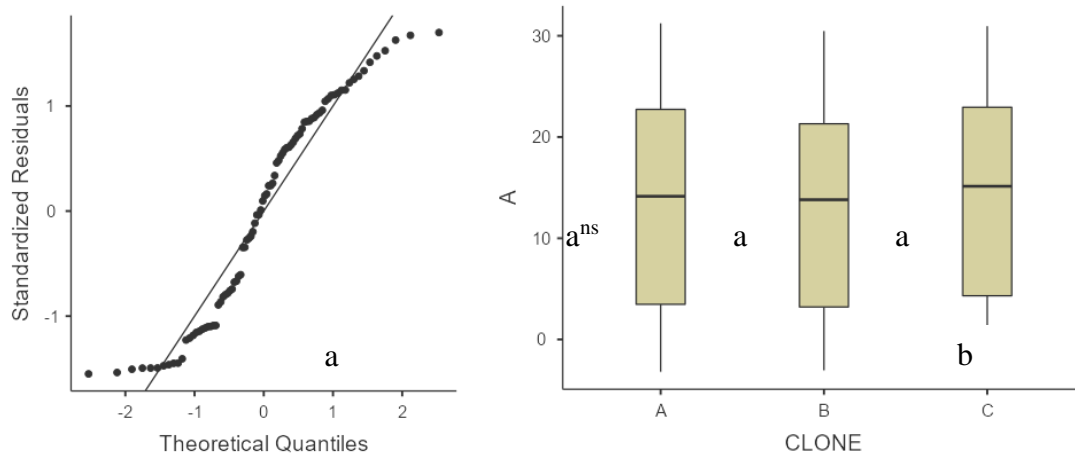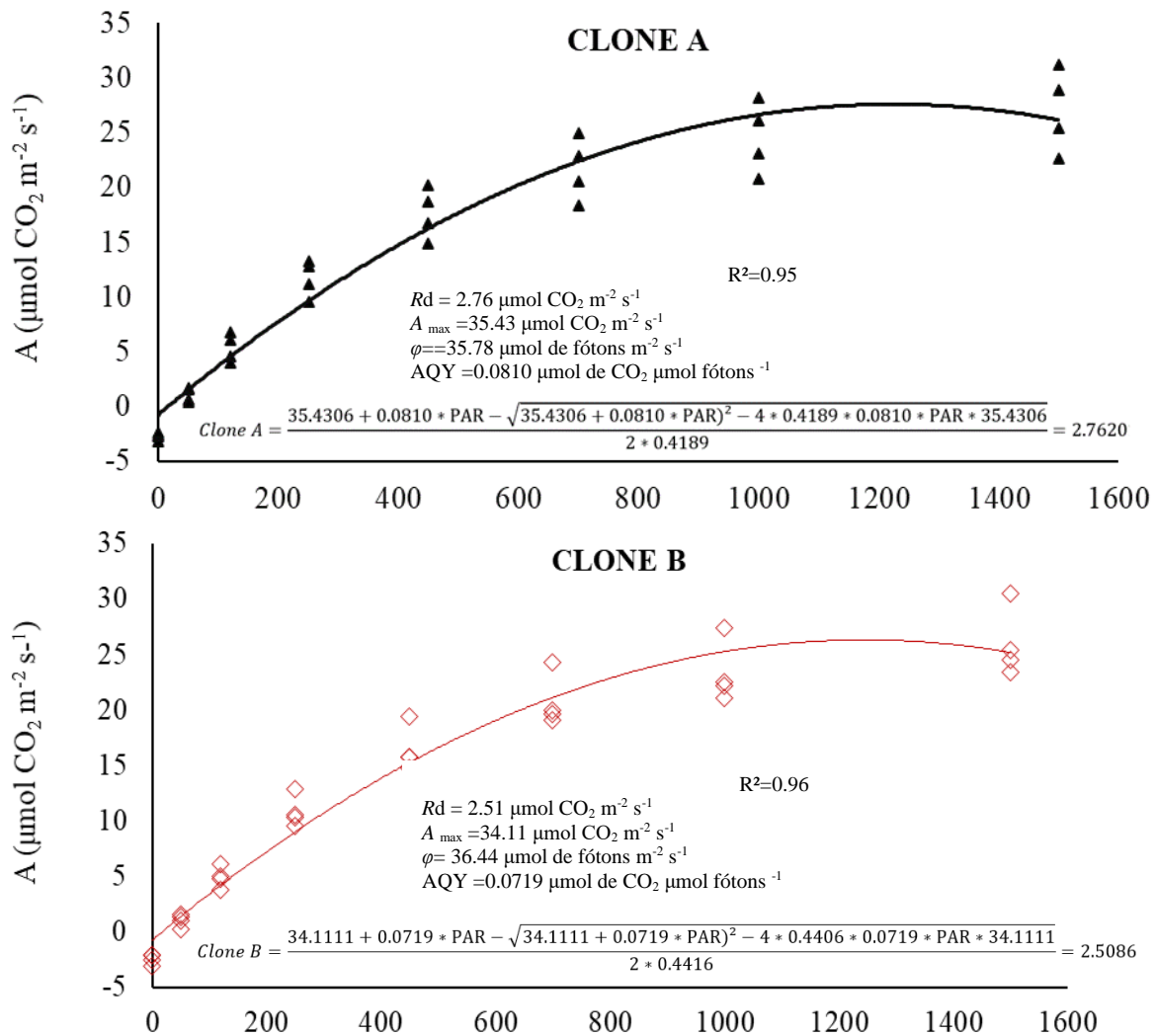
Figure 1. Standardized residuals (a) and (b) A assimilation rate (μmol CO_2 m^{-2} s^{-1}) em different *Eucalyptus* clones. [ns] - not significant at 5% error by Tukey's test.
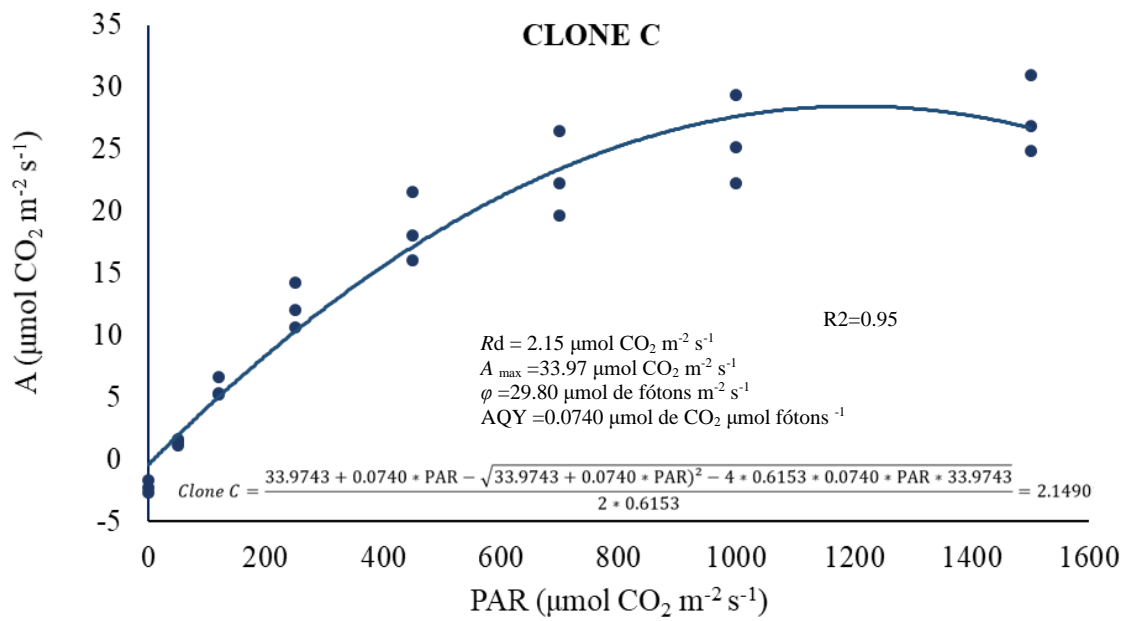

CLONE A

$R^2=0.95$

Rd = 2.76 μmol CO_2 m^{-2} s^{-1}
A_{max} =35.43 μmol CO_2 m^{-2} s^{-1}
φ==35.78 μmol de fótons m^{-2} s^{-1}
AQY =0.0810 μmol de CO_2 μmol fótons $^{-1}$

$$Clone\ A = \frac{35.4306 + 0.0810 * PAR - \sqrt{(35.4306 + 0.0810 * PAR)^2 - 4 * 0.4189 * 0.0810 * PAR * 35.4306}}{2 * 0.4189} = 2.7620$$

CLONE B

$R^2=0.96$

Rd = 2.51 μmol CO_2 m^{-2} s^{-1}
A_{max} =34.11 μmol CO_2 m^{-2} s^{-1}
φ= 36.44 μmol de fótons m^{-2} s^{-1}
AQY =0.0719 μmol de CO_2 μmol fótons $^{-1}$

$$Clone\ B = \frac{34.1111 + 0.0719 * PAR - \sqrt{(34.1111 + 0.0719 * PAR)^2 - 4 * 0.4406 * 0.0719 * PAR * 34.1111}}{2 * 0.4416} = 2.5086$$

CLONE C

$$Clone\ C = \frac{33.9743 + 0.0740 * PAR - \sqrt{(33.9743 + 0.0740 * PAR)^2 - 4 * 0.6153 * 0.0740 * PAR * 33.9743}}{2 * 0.6153} = 2.1490$$

$R^2 = 0.95$

$Rd = 2.15\ \mu mol\ CO_2\ m^{-2}\ s^{-1}$
$A_{max} = 33.97\ \mu mol\ CO_2\ m^{-2}\ s^{-1}$
$\varphi = 29.80\ \mu mol\ de\ fótons\ m^{-2}\ s^{-1}$
$AQY = 0.0740\ \mu mol\ de\ CO_2\ \mu mol\ fótons\ ^{-1}$

Figure 2. Liquid CO_2 assimilation curves (A) in response to the increase in photosynthetically active radiation (PAR) ranging between 0 and 1.500 $\mu mol\ m^{-2}\ s^{-1}$ in three *Eucalyptus* clones (clones A and B - *Eucalyptus benthamii* and clone C - *Eucalyptus dunnii*). Where: AQY = apparent quantum yield ($\mu mol\ de\ CO_2\ \mu mol\ fótons\ ^{-1}$); φ= light compensation point ($\mu mol\ de\ fótons\ m^{-2}\ s^{-1}$); A_{max}= maximum net photosynthetic rate ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$); Rd= dark breath rate ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$).
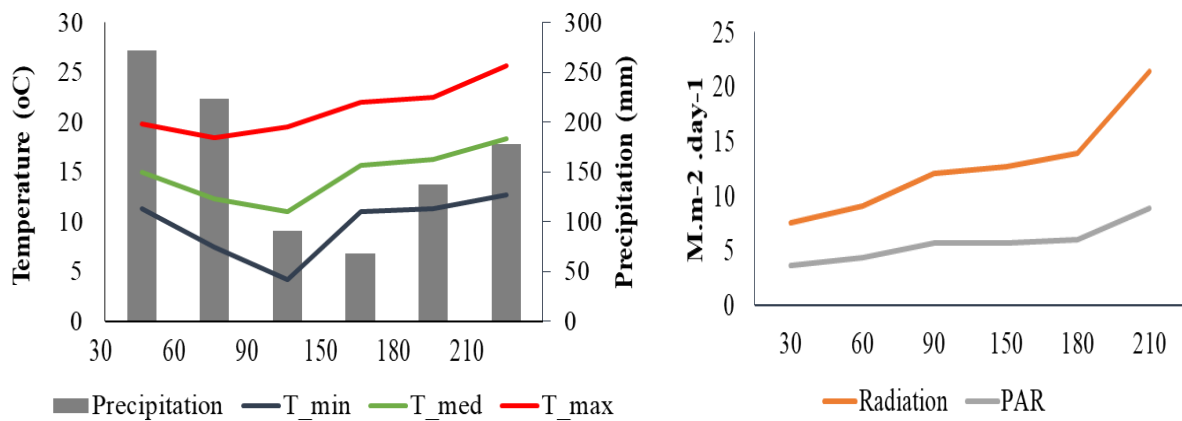

Figure 3. Summary of meteorological variables of the month in that was evaluated the experiment.
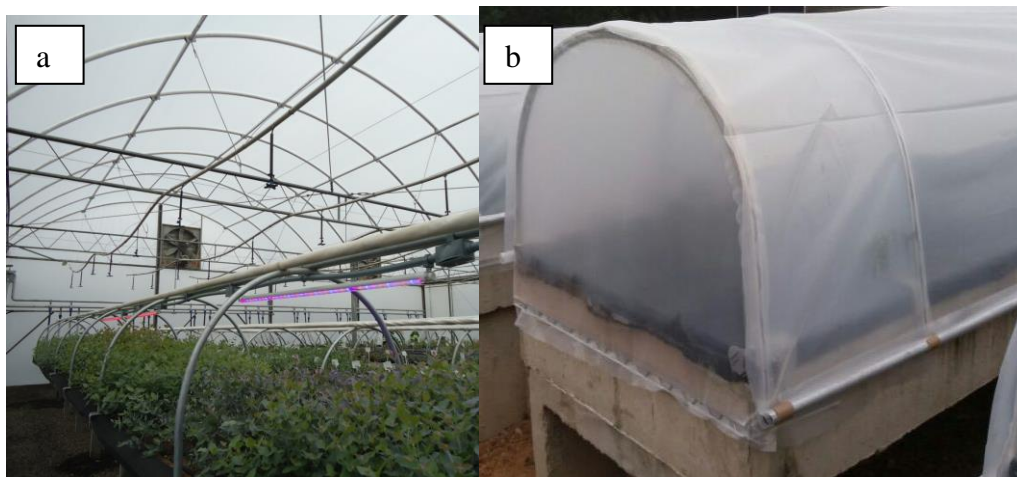

Figure 4. Partial view of the experimental greenhouse, showing an uncovered (a) and covered (b) plastic incubator.

among others, modifying the productive potential of the species (Woittiez et al., 2017). Studies have shown that there is a relationship between photosynthesis and productivity (Romero et al., 2007). Consequently, conditions that limit the components of photosynthesis (water, sunlight, CO_2, nutrients, chlorophyll and leaf area) negatively affect this process, resulting in less growth and less resistance to pests and diseases (Cayón, 1999).

In general, the three clones are very similar in terms of CO_2 assimilation rate due to the increase in photosynthetically active radiation, with little superiority for the *E. benthamii* clones. Thus, acclimatization and development studies with field monitoring are necessary to achieve a better understanding of the light needs of each genetic material.

Materials and methods

Conduction of study

This study was conducted in the greenhouse of a Forestry company located at Otacílio Costa, Santa Catarina state, Brazil. The area has a temperate climate of type Cfb (Alvares et al., 2013). In this area, cloudy days prevail throughout the year, especially in fall and winter, reducing the availability of light for the mini-stumps, meaning that a highly controlled environment is required for optimizing the performance of mini-stumps and the production of shoots for mini-cuttings (Aguiar et al., 2018).

Meteorological data

Meteorological variables (Figure 3) were recorded daily from an automatic station available at Forestry company. The meteorological variables were correlated with the amount of mini-cuttings produced and with the photosynthetic variables. The following variables were used: minimum, mean and maximum temperature (°C); relative humidity (%); precipitation (mm); radiation (M m^{-2} day^{-1}); and photosynthetic active radiation (*PAR*) (M m^{-2} day^{-1}).

Plant material and experimental design

The experiment was installed in March 2017 and conducted in a plastic incubator with mini-stumps of two clones of *E. benthamii* (referred as A and B) and one clone of *E. dunnii* (clone C). The incubator (Figure 4) had 16.6 in length, 0.8 m of width and a height of 0.8 m, located inside a greenhouse with plastic cover. The plastic of the greenhouse and incubator was transparent with a thickness of 150 microns, diffusing light transmission and protection against ultraviolet rays. The incubator was open during the day and closed at night. Humidity inside the incubator was generally greater than 80% at night (closed) and variable during the day (open). Photoperiod in this region varied from approximately 10 h in winter to 14 h in summer.

Mini-stumps were grown in a substrate consisting of a layer of sand covering a narrow layer of crushed stone, making up a total depth of 30 cm. The mini-stumps were originated from cuttings of each of the clones evaluated. Mini-stumps were planted in consecutive lines spaced 10x10 cm apart. Each clone was represented by eight lines, each one having eight mini-stumps planted in sand. Four plots per clones were planted in the incubator. Mini-stumps were adapted to the incubators, receiving daily irrigation with a balanced nutrient solution for continuous production of mini-cuttings. The nutrient solution was prepared with the same concentrations described in our previous work (Aguiar et al., 2018): 165 mg L^{-1} N, 32.7 mg L^{-1} P, 255 mg L^{-1} K, 200 mg L^{-1} Ca, 40 mg L^{-1} Mg, 52 mg L^{-1} S, 0.4 mg L^{-1} B, 0.05 mg L^{-1} Zn, 0.06 mg L^{-1} Cu, 1.6 mg L^{-1} Fe, 1.04 mg L^{-1} Mn, and 0.02 mg L^{-1} Mo. In winter, two events of fertigation were conducted per day, while in summer the frequency was increased to three or four events. Each fertigation lasted between 2 and 4 minutes.

The incubator was also equipped with LED lamps with red/rose light or a mixture of red and blue light (red/blue). The specifications of each type of lamps were: (i) red lamp - 36", 1W, AC85 − 265 V, red/rose = 660:730= 1:1, LED quantity: 36 pcs; (ii) red/blue - 36", 1W, AC85 − 265 V, red/blue = 660:450 = 2:1, LED quantity: 36 pcs. The lamps were placed at the top of the incubator, at a height of 0.8 m. The mini-stumps were exposed to the artificial light for 14 h (between 6 a.m. and 10 p.m.) on a daily basis. Eight replicates of each clone were not exposed to artificial light (control treatment). To separate light-exposure treatments, eight more lines of mini-stumps (borders) were planted between lamps (a space with no direct exposure to any lamp). For the present experiment (*A/PAR* curves) only the control treatment was used.

Evaluated variables and statistical analysis

One year after the installation of the light experiment in the clonal minigarden (in February 2018) with the aid of a portable photosynthesis meter, the CO_2 assimilation rate curves were determined. The portable meter is model 6400XT (Li-Cor, Biosciences), equipped with a light source type LI-6400-02B and operating in an open system. The CO_2 assimilation rate curves (*A*, µmol CO_2 m^{-2} s^{-1}) were evaluated at values of 1500, 1000, 700, 450, 250, 120, 50 and 0 µmol m^{-2} s^{-1}, for clones A and B (*E. benthamii*) and clone C (*E. dunnii*) in response to the increase in photosynthetically active radiation (PAR).

The evaluations were carried out between the hours of 8 and 12h, on the third pair of leaves, starting from the apex, using 4 repetitions. From the data, the response curve of *A* was adjusted as a function of *PAR*, adjusting the non-rectangular hyperbolic function, given by the equation:

$$A = \{[A_{max} + (\alpha * PAR) - [(A_{max} + (\alpha * PAR))^2 - (4 * \alpha * \theta * PAR * A_{max})]^{0.5}] / (2\vartheta)\} - Rd + \varepsilon, \text{ where:}$$

- *A* is the assimilation of photosynthesis - µmol CO_2 m^{-2} s^{-1}
- A_{max} is maximum photosynthesis - µmol CO_2 m^{-2} s^{-1}
- *Rd* is respiration in the dark - µmol CO_2 m^{-2} s^{-1}
- α is apparent quantum yield of *A*;
- θ is one dimensional convexity;
- and ε is the standard error.

Statistical analyses were performed using the statistical package "Jamovi" for Windows Version 1.6.23. The least significant difference between mean values was calculated using Tukey's multiple range test at the 5% significance level.

Conclusion

The three *Eucalyptus* clones evaluated showed a similar behavior of the *A/PAR* curve, showing a high demand for photosynthetically active radiation. Regarding the light compensation point (*φ*), *E. benthamii* clones obtained the highest values (close to 35 µmol of photons m^{-2} s^{-1}).

The clones are very similar in terms of CO_2 assimilation rate due to the increase in photosynthetically active radiation little superiority for *E. benthamii* clones.

References

Aguiar NS, Navroski MC, Miranda L, Mota CS, Estopa RA, Nicoletti, MF, Konzen ER (2018) The canopy coverage is correlated with the number of shoots produced by *Eucalyptus* clones in a clonal mini-garden. Canadian Journal of Forest Research. 48:1411–1416.

Alvares CA, Stape JL, Sentelhas PC, De Moraes Gonçalves JL, Sparovek G (2013) Köppen's climate classification map for Brazil. Meteorologische Zeitschrift. 22: 711–728.

Arnold, R, Li B, Luo J, Bai F, Baker T (2015) Selection of cold-tolerant *Eucalyptus* species and provenances for inland frost-susceptible, humid subtropical regions of southern China. Australian Forestry. 78:180–193.

Atkin OK, EvanS JR, Ball MC, Pons TL (2000) Leaf Respiration of Snow Gum in the Light and Dark. Interactions between Temperature and Irradiance. Plant Physiology. 122:915–923.

Azcón-Bieto, J Bou IF, Aranda X, Casanovas NG (2018) Photosynthesis, environmental factors and climate change. pp. 247-263. In: Azcón-Bieto, J. & M. Talon. (eds.). Fundamentals of plant physiology and biochemistry. 2nd ed. McGraw-Hill-Interamerican, Madrid, Spain.

Bayle G (2019) Ecological and social impacts of *Eucalyptus* tree plantation on the environment. Journal of Biodiversity Conservation and Bioresource Management. 5:93-104.

Berry ZC, Goldsmit GR (2020) Diffuse light and wetting differentially affect tropical tree leaf photosynthesis. New Phytologist. 225: 143–153.

Binkley D, Laclau JP, Sterba H (2013) Why one tree grows faster than another: patterns of light use and light use efficiency at the scale of individual trees and stands. Forest Ecology and Management. 228: 1-4.

Cayón G (1999) Notes on physiology of growth and development of oil palm (*Elaeis guineensis* Jacq.). Palmas. 20: 43-54.

Coble AP, VanderWall B, Mau A, Cavaleri MA (2016) How vertical patterns in leaf traits shift seasonally and the implications for modeling canopy photosynthesis in a temperate deciduous forest. Tree physiology. 36:1077-1091.

Forrester DI. et al. (2018) Effects of crown architecture and stand structure on light absorption in mixed and monospecific *Fagus sylvatica* and *Pinus sylvestris* forests along a productivity and climate gradient through Europe. Journal of Ecology. 106:746-760, 2018.

Gonzalez R, Treasure T, Phillips R, Gonzales R, Saloni D, Wrigth J (2011) Exploring the potential of Eucalyptus for energy production in the Southern United States: Financial analysis of delivered biomass. Part I. Biomass Bioenergy. 35:755-766, 2011.

Larcher W (2004) Carbon utilization and dry matter production. Physiological plant ecology, 4.ed. Berlin: Springer. 506p.

Liang GTS, Zhang Y, Guo J, Yang R, Li H, Fang XC, Zhang GC (2018) The effects of para-hydroxybenzoic acid treatment on photosynthetic parameters of *Populus × euramericana*"Neva". Photosynthetica. 56:505–511.

Liao L, Rong, Y, QiuX, Dong T, Wang Z (2020) Photosynthetic model for citrus cultivar Huangguogan. Semina: Ciências Agrárias. v. 41: 61-72.

Lorentz KA, Minogue PJ (2015) Exotic *Eucalyptus* plantations in the southeastern US: Risk assessment, management and policy approaches. Biological Invasions. 17:1581-1593.

Machado DN, Novais RF, Silva IR, Loureiro ME, Milagres JJ, Soares EMB (2011) Enriquecimento e alocação de ^{13}c em plantas de eucalipto. Revista Brasileira de Ciência do Solo. 35:857-866.

Maier CA, Albaugh J, Cook RI, Hall K, McInnis D, Johnsen KA, Johnson J, Rubilar RA, Vose JM. (2017) Comparative water use in short-rotation *Eucalyptus benthamii* and *Pinus taeda* trees in the Southern United States. Forest Ecology and Management**.** 397:126–138.

Ngugi MR, Hunt MA, Doley D, Ryan P (2003) Photosynthetic light and temperature responses of *Eucalyptus cloeziana* and *Eucalyptus argophloia*. Australian Journal of Botany. v.51:573-583.

Romero HM, Ayala IM, Ruíz R (2007) Ecofisiología de la palma de aceite. Revista Palmas. 28 (especial):176-184.

Shem K, Catherine M, Ong C (2009) Gas exchange responses of *Eucalyptus*, *C. africana* and *G. robusta* to varying soil moisture content in semi-arid (Thika) Kenya. Agroforest Syst. 75:75:239.

Solarte, M, Pérez-Martínez L, Melgarejo LM Ecofisiología vegetal. pp. 97-120. 2010. In: Melgarejo L.M. (ed.). Experimentos en fisiología vegetal. Universidad Nacional de Colombia, Bogotá, Colombia.

Stanturf JA, Vance, E, Fox, T, Kirst M (2013) *Eucalyptus* beyond its native range: Environmental issues in exotic bioenergy plantations. International Journal of Forestry Research, Article ID 463030.

Will LE, Barron GA, Burkes EC, Schiver B, Teskey RO (2001) Relationship between intercepted radiation, net photosynthesis, respiration, and rate of stem volume growth of *Pinus taeda* and *Pinus elliottii* stands of different densities. Forest Ecology and Management. 154:155-163.

Wilson D, Jones JG (1982) Effect of selection for dark respiration rate of mature leaves on crop yields of *Lolium perenne* cv. 523. Annals of Botany. 49:313-320.

Woittiez L, Wijk MT, Slingerlanda M, Noordwijkac M. Gillera KE (2017) Yield gaps in oil palm: A quantitative review of contributing factors. European Journal of Agronomy. 83:57-77.

Xiong CY, Zeng W, Xiao FM (2012) An analysis of photosynthetic parameters among Schima superba provenances. Acta Ecologica Sinica. 32:3628-3631.