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ORIGINAL ARTICLE

How does water deficit induce changes in primary and secondary metabolism in *Corymbia citriodora* seedlings?

Como a deficiência hídrica induz alterações no metabolismo primário e secundário em mudas de *Corymbia citriodora*?

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Abstract

Corymbia citriodora is a species of commercial importance planted by small - and medium-sized producers. It produces good quality wood and has been attracting the attention of the forestry market. The occurrence of abiotic stresses will be more and more frequent, caused by climate change, which can limit plant development. Water deficit is the main factor in the reduction of eucalyptus productivity. This research aimed to evaluate the effects of water stress on the development of *C. citriodora* plants. The seedlings were grown in pots and submitted to five irrigation regimes (20, 35, 50, 65, and 80% of the maximum soil water retention capacity) for 110 days in a greenhouse. Plant growth, gas exchange, leaf water potential, chlorophyll, carotenoid, proline, and lipid peroxidation by malondialdehyde (MDA) content were evaluated at the end of this period. The decrease in water availability may have provided a reduction in cell number, increasing the concentration of pigments, proline, and MDA, and a reduction in leaf water potential, gas exchange, and plant growth. *C. citriodora* seedlings showed a significant reduction in growth when grown at levels below 50% of the maximum soil water retention capacity.

Keywords: Seedling development; Oxidative stress; Eucalyptus; Drought sensitivity; Gas exchange.

Resumo

Corymbia citriodora é uma espécie de importância comercial, plantada por pequenos e médios produtores, que produz madeira de boa qualidade e vem atraindo a atenção do mercado florestal. A ocorrência de estresses abióticos será cada vez mais frequente, podendo ser ocasionada pelas mudanças climáticas, o que pode limitar o desenvolvimento de plantas, sendo o déficit hídrico o principal fator de redução da produtividade do eucalipto. O objetivo dessa pesquisa foi avaliar os efeitos do estresse hídrico no desenvolvimento de plantas de *C. citriodora*. As mudas foram cultivadas em vasos e submetidas a cinco regimes de irrigação (20, 35, 50, 65 e 80% da capacidade máxima de retenção de água no solo) durante 110 dias em casa de vegetação. Ao final desse período foram avaliados o crescimento das plantas, as trocas gasosas, potencial hídrico foliar, teores de clorofila, de carotenoides, de prolina e a peroxidação lipídica pelo conteúdo de Malondialdeído (MDA). Observou-se que a diminuição da disponibilidade hídrica pode ter proporcionado redução no número celular, aumentando a concentração de pigmentos, prolina e MDA e redução no potencial hídrico foliar nos parâmetros de trocas gasosas e crescimento nas plantas. As mudas de *C. citriodora* apresentaram redução significativa no crescimento quando cultivadas em níveis inferiores a 50% da capacidade máxima de retenção de água no solo.

Palavras-chave: Desenvolvimento de mudas; Estresse oxidativo; Eucalipto; Sensibilidade à seca; Trocas gasosas.

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INTRODUCTION

The genus *Eucalyptus* comprises the most important cultivated forest species in Brazil and occupies 75.8% of the 9.93 million hectares of forest plantations for industrial purposes (Indústria Brasileira de Árvores, 2022). This genus has advantages compared to native species and other exotic species, having undergone constant processes of genetic improvement since its introduction in Brazil (Gonçalves et al., 2017). *Corymbia citriodora* (Hook.) K.D. Hill & L.A.S. Johnson is an economically important species in the world, used for the production of solid wood, energy, treated wood (fence posts and poles), and civil construction (Associação Brasileira dos Produtores de Florestas Plantadas, 2010). The species C. *citriodora* belonged to the genus *Eucalyptus*; in 1995 a more detailed study on the species of eucalyptus, showed differences, resulting in the genus *Corymbia* (Hill & Johnson, 1995). Essential oils are extracted from the leaves and are widely used in the chemical and pharmaceutical industry (Lin et al., 2019).

Forest species have a long cycle and, compared to agricultural crops; therefore, they are more subject to multiple biotic and/or abiotic stresses. Water deficiency is the main cause of abiotic stress in agricultural and forestry crops, with no one single mechanism related to drought tolerance; which involves, for example, complex physiological, biochemical, and anatomical interactions of plants (Matos et al., 2014; Martins et al., 2018; Nóia Júnior et al., 2020).

Water deficit can change primary and secondary metabolism in plant species. Primary metabolism affects water relations and gas exchanges, and it can affect certain cellular components and functional integrity at a more pronounced level (Souden et al., 2020), leading to changes in secondary metabolism. Thus, water stress changes primary metabolism, causing stomatal closure with a decrease in CO_2 absorption and a reduction in photosynthetic rate (Nóia Júnior et al., 2020; Ripoll et al., 2016), which can result in a significant increase in reactive oxygen (ROS) (Fanciullino et al., 2014; Mittler, 2017), negatively affecting plant growth, development, and productivity, especially in arid and semi-arid regions (Pulavarty et al., 2016; Suzuki & Katano, 2018).

Knowledge of the mechanisms involved in plant drought tolerance is essential for the development of sustainable silviculture and the selection of plants with a higher probability of success in the face of climate change (Martins et al., 2020). However, although several studies with eucalyptus species can be found in the literature, those with *C. citriodora* are scarce, mainly evaluating the physiological and biochemical responses of plants under water stress. In this sense, we hypothesize that *C. citriodora* plants develop mechanisms that induce physiological and biochemical responses to tolerate water stress under different conditions of water availability and, thus, this study aimed to evaluate the effects of water stress on the behavior of *C. citriodora* plants grown in pots.

MATERIAL AND METHODS

C. citriodora seeds collected from remaining trees from a 40-year-old open pollination progeny test installed in the municipality of Jaboticabal, State of São Paulo (21°15' S, 48°19' W, 605 m asl) were used for seedling production. The regional climate is Cwa, according to the Köppen climate classification (Alvares et al., 2013). The progeny test underwent an individual phenotypic selection, leaving the best 150 trees. Fruits harvested from 15 of these trees were dried in a semi-shaded environment for later seed extraction, manual processing, and homogenization in a single seed lot.

The experiment was carried out in a greenhouse from December 2018 to March 2019, totaling 110 days of duration, with *C. citriodora* seedlings subjected to five water regimes. The greenhouse was covered with a 150-μm thick transparent plastic film with sides covered with screens capable of intercepting 30% of sunlight. Maximum and minimum temperatures and relative air humidity were monitored inside the greenhouse during the experimental period (Figure 1).

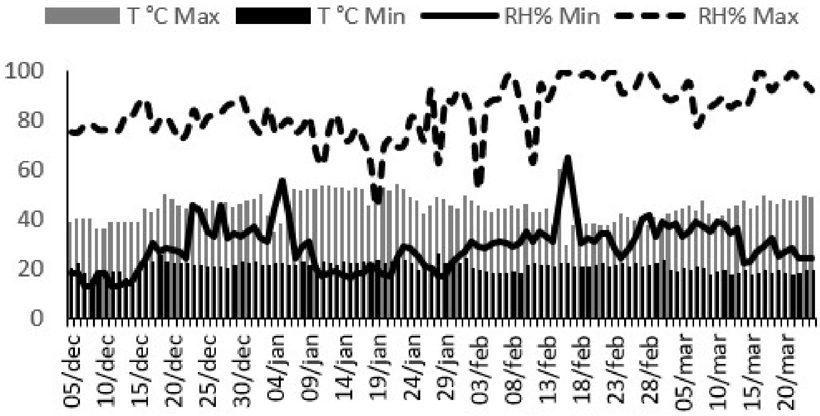

Figure 1. Daily maximum (T °C Max) and minimum (T °C Min) temperatures and maximum (RH% Max) and minimum (RH% Min) relative humidity obtained inside the greenhouse during the experimental period (December 2018 to March 2019).

Seedlings were produced from seeds germinated in 50-cm^3 tubes filled with Plantmax® substrate and sand. The surplus seedlings were later eliminated, leaving only those most central with the best development. The seedlings remained in tubes for 90 days, when they reached an adequate size for planting in pots.

The seedlings were planted in plastic pots filled with 7 kg of a soil sample from the Jaboticabal region, classified as a very clayey-textured typical eutrophic Red Latosol (Santos et al., 2018), whose chemical characterization analysis is shown in Table 1. The dried and sieved soil was properly corrected to raise the base saturation of 60% using a 3:1 Ca to Mg ratio. Phosphate fertilization was performed in the same procedure by applying 100 mg P dm^{-3}, using simple superphosphate, based on the crop requirements, as proposed by Gonçalves et al. (1997).

Table 1 – Chemical characterization of the soil used in the experiment.

pH	OM	P-resin	K	Ca	Mg	H+Al	SB	T	V
$CaCl_2$	g dm^{-3}	mg dm^{-3}			mmol$_c$ dm^{-3}				%
5.6	4.0	4.0	1.8	9.0	3.0	12.0	13.8	25.8	53.0

OM – organic matter; SB – sum of bases; T – cation exchange capacity, V – base saturation.

The seedlings were acclimatized for seven days (totaling 97 days) after planting in the pots and before the establishment of water regimes, which consisted of daily maintenance of soil moisture at 20% (IR1), 35% (IR2), 50% (IR3), 65% (IR4), and 80% (IR5) of the maximum water retention capacity by the substrate, also called field capacity (Silva et al., 2014).

The treatments corresponding to soil moisture levels were maintained for 110 days when the experiment was completed. The evapo-transpirated water was replaced daily by the gravimetric method, aiming to replace the amount of water sufficient to maintain the desired moisture. The design was randomized blocks, with eight replications of two plants per pot, totaling 80 plants in 40 pots.

Gas exchange and leaf water potential – The net assimilation rate (*A*, μmol CO_2 m^{-2} s^{-1}), transpiration (*E*, mmol H_2O m^{-2} s^{-1}), stomatal conductance (*gs*, mol H_2O m^{-2} s^{-1}), and intracellular CO_2 (*Ci*, μmol mol^{-2}) were evaluated at 2-hour intervals, between 8:00 and 16:00 h, for 110 days after the establishment of water regimes using with an LCPro+ infrared gas analyzer (IRGA) (ADC BioScientific® Ltd.) coupled to an artificial light source set to provide a photosynthetically active photon flux of 1000 μmol m^{-2} s^{-1} and under ambient CO_2 concentration (400 ± 10 μmol m^{-2} s^{-1}). The evaluations were performed on fully expanded leaves in the upper third of the canopy. Leaf water potential was determined in the predawn and at noon on leaves detached from the plant and placed in a pressure chamber, using the method established by Scholander et al. (1965).

Photosynthetic pigments – Carotenoid and chlorophyll contents were determined following the methodology described by Lichtenthaler (1987). For this, leaf discs with 0.025 to 0.030 g of fresh mass were collected from one plant of each replication per treatment, placed in an Eppendorf with 2 mL of 80% acetone, and maintained for 48 hours under cooling at temperatures ranging from 6 and 10 °C, with subsequent reading in a spectrophotometer at 470, 647, and 663 nm. The analysis results were interpolated in a standard curve to determine the amount of these compounds (mg g^{-1} of leaf fresh mass).

Organic solutes – Malondialdehyde (MDA) and proline contents were determined at the end of the experiment, i.e., 110 days after the establishment of water regimes, in plant samples collected from one plant per pot, in the eight replications.

The MDA content was estimated by the content of thio-barbituric acid reactive substances (TBARS). The MDA concentration was determined using 0.2 g of leaves macerated in trichloroacetic acid (TCA) and then centrifuged at 10,000 rpm for 15 minutes at −4 °C. TBA (thio-barbituric acid) was added to the supernatant. The mixture was placed in a dry bath at 95 °C for 30 minutes and then the solution was clarified. The concentration of MDA equivalents was calculated using an extinction coefficient of 1.55×10^{-5} mol^{-1} cm^{-1}, with readings at 535 and 600 nm and results expressed in μmol mg^{-1} of fresh mass (Gratão et al., 2012).

Proline content quantification was performed following the methodology of Bates et al. (1973) by the procedure that consists of manual homogenization in a porcelain mortar using 0.5 g of fresh plant material with 10 mL of 3% sulfosalicylic acid and filtering. Proline contents were calculated for the standard curve and based on fresh mass, expressed in μmol proline g^{-1} fresh mass.

Biometry, leaf area, and plant mass – The following variables were determined at the end of the experiment: plant height (cm), measured with a ruler graduated in mm; collar diameter (mm), determined with a digital caliper; the number of leaves, determined by manually counting the number of leaves per plant; leaf area (cm^2), determined with the Li-Cor 3100 leaf area analyzer; and dry mass of plant components (g), determined on an analytical balance (0.001 g) after submitting leaves, stem + branches and roots to drying in an air circulation oven at 65 ± 3 °C until constant mass. Plant biomass was determined in four replications per treatment.

Data analysis – The data were subjected to analysis of variance, followed by polynomial regression to express the evaluated characteristics as a function of water regimes. The analyses were performed using the AgroEstat® software (Barbosa & Maldonado Júnior, 2015) and plots were constructed using the Origin® software.

RESULTS AND DISCUSSION

A significant variation was observed in the net assimilation rate (A, μmol CO_2 m^{-2} s^{-1}), transpiration (E, mmol H_2O m^{-2} s^{-1}), stomatal conductance (gs, mol H_2O m^{-2} s^{-1}), and intracellular CO_2 (Ci, μmol mol^{-2}) as a function of irrigation regimes (Figure 2). These characteristics increased as water availability became higher, presenting a quadratic behavior for net assimilation rate and intracellular CO_2 and a linear behavior for transpiration and stomatal conductance. In percentage terms, stomatal conductance was more impaired by the decrease in water availability in the substrate, reaching a reduction of 64% in the IR1 regime relative to IR5 than the transpiration (54% reduction) and the net assimilation rate (reduction of 35%).

Soil water availability directly affects gas exchange and leaf water potential, and this relationship is influenced by climate conditions (Tonello & Teixeira Filho, 2012). Plants under more intense water deficit cannot absorb water from the soil in the same magnitude that they lose it through transpiration, resulting in stomatal closure with a decrease in conductance and reduction in water potential (Xavier et al., 2019), which are strategies for the plant to maintain turgor and prevent evapotranspiration.

The most restrictive irrigation regimes (IR1 and IR2) provided a reduction in gas exchange, but more significantly in stomatal conductance (*gs*) and transpiration rate (*E*), relative to the net assimilation rate (*A*), increasing water use efficiency. A decrease in stomatal conductance may occur at the initial stage of water deficit and, therefore, the amount of CO_2 entering the stomata can decrease to levels that do not meet the demands of photosynthesis, which leads to a reduction in the net assimilation rate (Song et al., 2020). The maximum temperature of around 40 °C causes another (heat) stress in plants, which can contribute to changes in physiological adaptations.

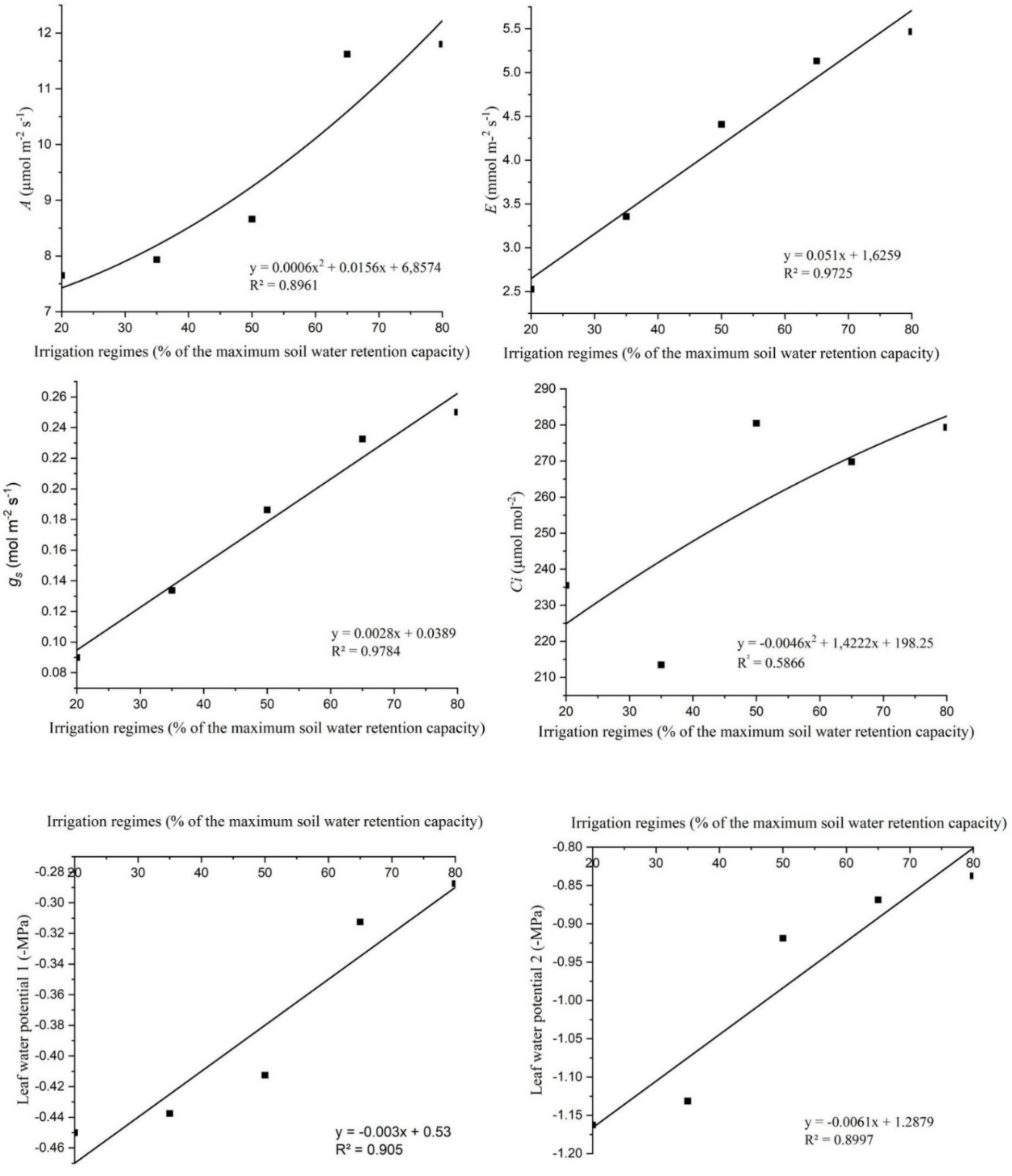

Figure 2. Net assimilation rate (*A*, μmol m^{-2} s^{-1}), transpiration (*E*, mmol m^{-2} s^{-1}), stomatal conductance (*gs*, mol m^{-2} s^{-1}), intracellular CO_2 (*Ci*, μmol mol^{-2}), leaf water potential 1 (in the predawn period, −MPa), and leaf water potential 2 (at noon, −MPa) in *C. citriodora* plants submitted to five irrigation regimes (IR1, IR2, IR3, IR4, and IR5, that is, 20, 35, 50, 65, and 80% of the maximum substrate water retention capacity, respectively), evaluated at 110 days after the establishment of water regimes.

Leaf water potential, both in the predawn and at noon, increased as the water availability was higher, but the values observed at noon were lower than those observed in the predawn (Figure 2). Irrigation regimes IR1 and IR2 provided the lowest rates of internal CO_2 concentration (*Ci*) and stomatal conductance (*gs*), indicating higher stress by the plants. The gas exchange measured throughout the day indicates that the net assimilation rate (*A*), stomatal conductance (*gs*), and transpiration (*E*) were maximum between 8:00 and 10:00 h, with a reduction throughout the day (Figure 3), but more expressively at the water regimes that are more restrictive to plant growth (IR1 and IR2). Intracellular CO_2 concentration was also maximum between 8:00 and 10:00 h, decreasing until 14:00 h, with an increase at 16:00 h for all water regimes. One of the most important strategies for plants to deal with water deficit is the stomatal closure, which is a way to reduce water loss and improve the water use efficiency (Hsieh et al., 2010). Xavier et al. (2019) studied two commercial genotypes of *E. urophylla* x *E. grandis* and stated that the recurrent reduction in water availability affected leaf water potential and gas exchange in seedlings.

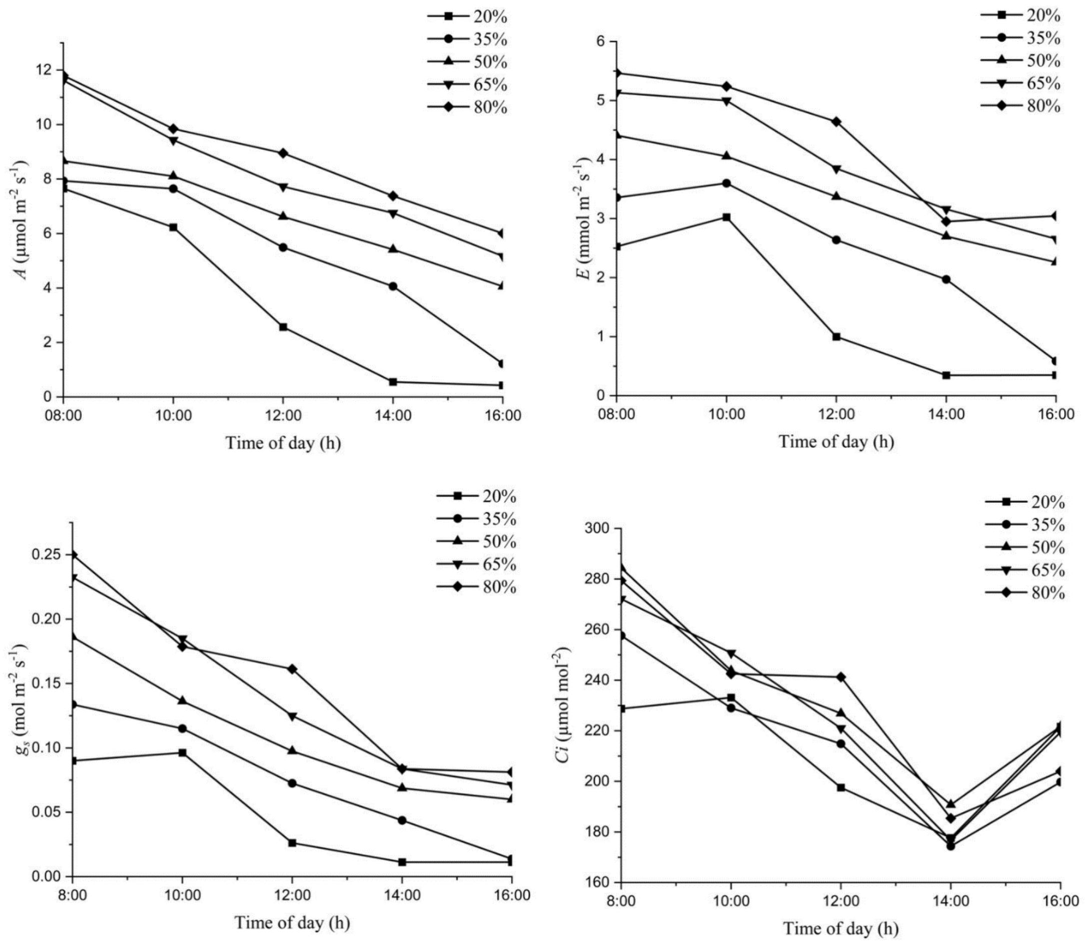

Figure 3. Net assimilation rate (*A*, μmol m^{-2} s^{-1}), transpiration (*E*, mmol m^{-2} s^{-1}), stomatal conductance (*gs*, mol m^{-2} s^{-1}), and intracellular CO_2 (*Ci*, μmol mol^{-2}) in *C. citriodora* plants submitted to five irrigation regimes (IR1, IR2, IR3, IR4, and IR5, that is, 20, 35, 50, 65, and 80% of the maximum substrate water retention capacity, respectively), evaluated at 110 days after the establishment of water regimes.

The assessments of gas exchange throughout the day showed a relationship between *A*, *E*, *Ci*, and *gs*, with higher values at the beginning of the day, even at milder temperatures and higher water availability, and a gradual reduction in these characteristics, especially at times of higher evaporative demand. Osakabe et al. (2014) stated that plants have lower leaf water potential, and lower values of *A*, *E*, *gs*, and *Ci* under water deficit, reducing CO_2 assimilation and, consequently, providing lower biomass production. Cano et al. (2014) observed that a decrease in *gs* leads to a reduction in *Ci* in plants under water deficit, limiting photosynthesis. Also, Zhong et al. (2017) observed that drought can markedly reduce *gs*, causing a decrease in *Ci*.

Ci represents the intracellular carbon that can be used by the plant for photosynthesis (Tominaga et al., 2018). However, this variable can be affected by external factors such as temperature and water scarcity. In fact, the *Ci* at 16:00 h in our experiment presented an increase compared to that at 14:00 h, which may have occurred due to a decrease in temperature. Plants may have closed their stomata at times with higher temperature incidence, causing reduced CO_2 absorption. Temperatures above 33 °C were recorded repeatedly in the greenhouse.

Chlorophyll a, chlorophyll b, and chlorophyll a+b contents (Figure 4) adjusted to a decreasing quadratic equation with increasing water availability, but with a trend to stabilize from water regime 3 (IR3). The lowest carotenoid content values were also observed in less restrictive water regimes for plant growth (IR3, IR4, and IR5), similar to the results obtained for chlorophyll contents (Figure 4).

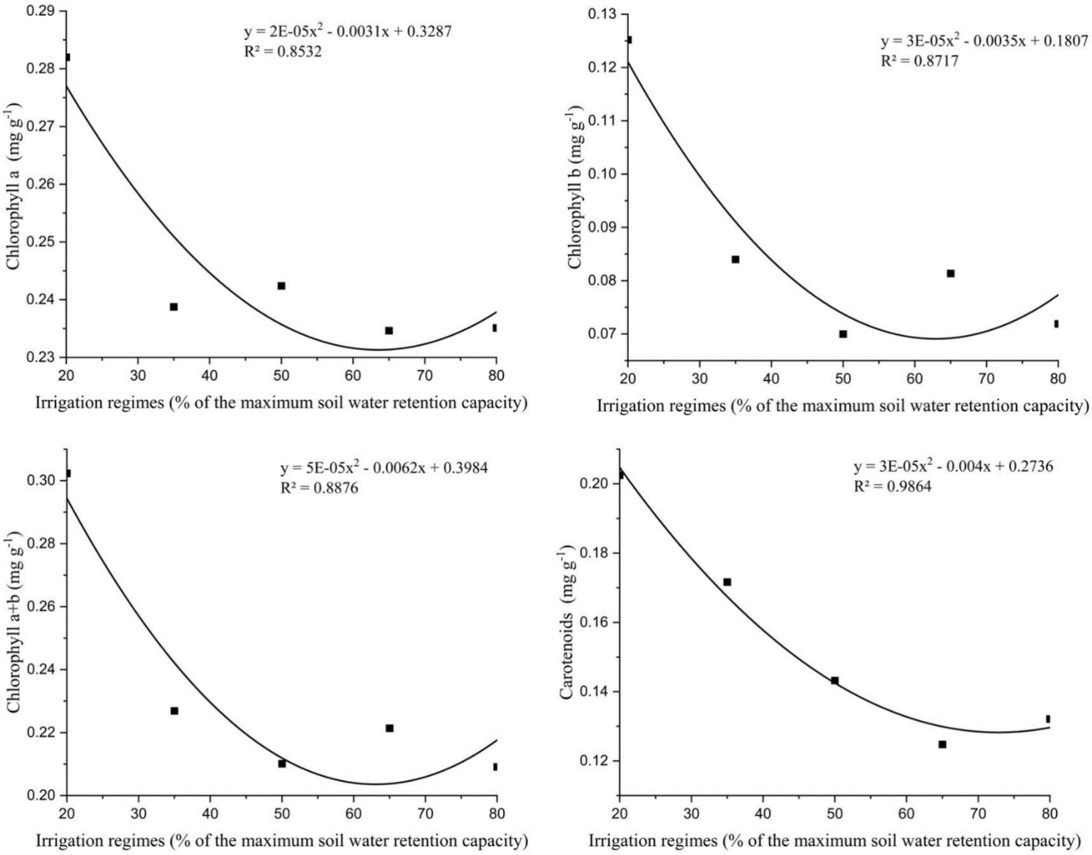

Figure 4. Content (mg g^{-1}) of chlorophyll a (Chl-a), chlorophyll b (Chl-b), chlorophyll a+b (Chl a+b), and carotenoids (Cx+c) in *C. citriodora* plants submitted to five irrigation regimes (IR1, IR2, IR3, IR4, and IR5, that is, 20, 35, 50, 65, and 80% of the maximum substrate water retention capacity, respectively), evaluated at 110 days after the establishment of water regimes.

Higher chlorophyll and carotenoid contents were found under a lower water availability (RI1), which agrees with the results obtained by Jesus et al. (2015) with *E. globulus* plants submitted to water deficit. Chlorophyll is the main element of pigment-protein complexes and plays an important role in photosynthesis (Chen et al., 2018). The increased chlorophyll content under water deficit may be related to a decrease in leaf area, with a protective role of carotenoids or other mechanisms, which protect these pigments from degradation to protect photosynthetic capacity (Jesus et al., 2015), and a reduction of cell expansion can lead to the concentration of the accumulation of chlorophyll and carotenoids.

The increase in water stress increased lipid peroxidation, expressed by MDA content (Figure 5), which showed a linear reduction with the increase in water availability. IR1 provided an increase of 31.57% in MDA content compared to IR5. The lower photosynthetic capacity related to more restrictive water regimes (IR1 and IR2), as well as the increase in MDA and proline contents, indicates that the lower water availability favored an increase in reactive oxygen species (ROS) levels. Plants under oxidative stress show an accumulation of MDA, resulting from lipid oxidation (Pompelli et al., 2010; Silva et al., 2010; Arcoverde et al., 2011; Jesus et al., 2015; Yalcinkaya et al., 2019). It indicates that both the enzymatic and non-enzymatic antioxidant defense system was affected by water deficit, which may be associated with reduced photosynthesis and increased total chlorophyll contents recorded in this experiment.

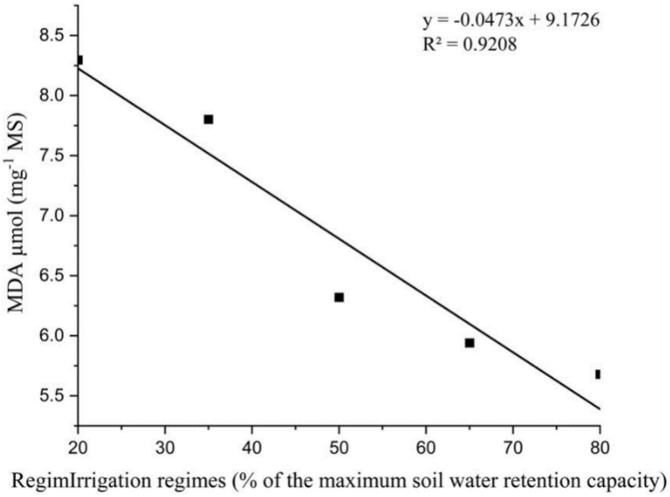

Figure 5. MDA (malondialdehyde) content in *C. citriodora* plants submitted to five irrigation regimes (IR1, IR2, IR3, IR4, and IR5, that is, 20, 35, 50, 65, and 80% of the maximum substrate water retention capacity, respectively), evaluated at 110 days after the establishment of water regimes.

The highest MDA contents were observed under lower water availability (IR1 and IR2), in agreement with the results obtained by Berenguer et al. (2018) in seedlings of *E. globulus* Labill. and *E. globulus* x *E. cypellocarpa*, and Jesus et al. (2015) in seedlings of *E. globulus*, indicating the occurrence of oxidative stress under limited water availability.

Proline contents were also higher in the more restrictive water regimes for plants, but with a trend to stabilize in the two regimes with higher water availability (Figure 6). IR1 provided an increase in the content of the stress indicator (proline) by 47.32% relative to IR5.

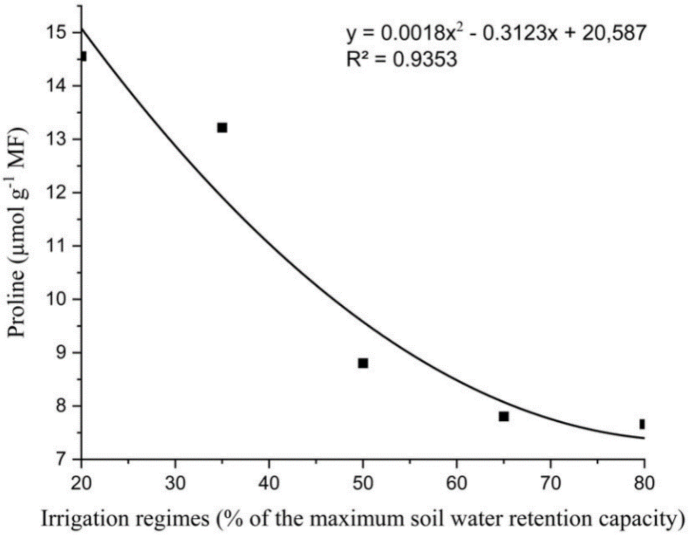

Figure 6. Proline content in *C. citriodora* plants submitted to five irrigation regimes (IR1, IR2, IR3, IR4, and IR5, that is, 20, 35, 50, 65, and 80% of the maximum substrate water retention capacity, respectively), evaluated at 110 days after the establishment of water regimes.

Proline, which is a compatible osmolyte, also accumulated in plants with lower water availability, as observed for MDA contents, in agreement with Hongying et al. (2009) and Kaur & Asthir (2015), who observed that this osmolyte tends to accumulate in plants under abiotic stresses. These results agree with those found by Cha-um et al. (2014), who studied eight eucalyptus genotypes subjected to water deficit and observed an increase in proline concentration. According to Cha-um & Kirdmanee (2010), the increase in proline contents is one of the most sensitive biochemical indicators in plants under water deficit. The increase in proline and MDA contents indicates that the defense system was not enough to mitigate stress.

The growth variables were favored with the increase in water availability, except for the number of leaves, whose variation was not significant (Figures 7-8). Height, diameter at soil level (DSL), root dry mass (RDM), and leaf area (LA) showed a linear increase, while stem + branch dry mass (S+BDM) and leaf dry mass (LDM) showed a quadratic response with a trend to stabilize in the three regimes with the highest water availability (IR3, IR4, and IR5). *Eucalyptus* growth is strongly related to water availability (Stape et al., 2010; Silva et al., 2016a; Otto et al., 2017; Araujo et al., 2019), with water deficit being more critical when it reaches plants at the first growth stages, significantly affecting shoot and root biomass production (Hsiao & Xu, 2000).

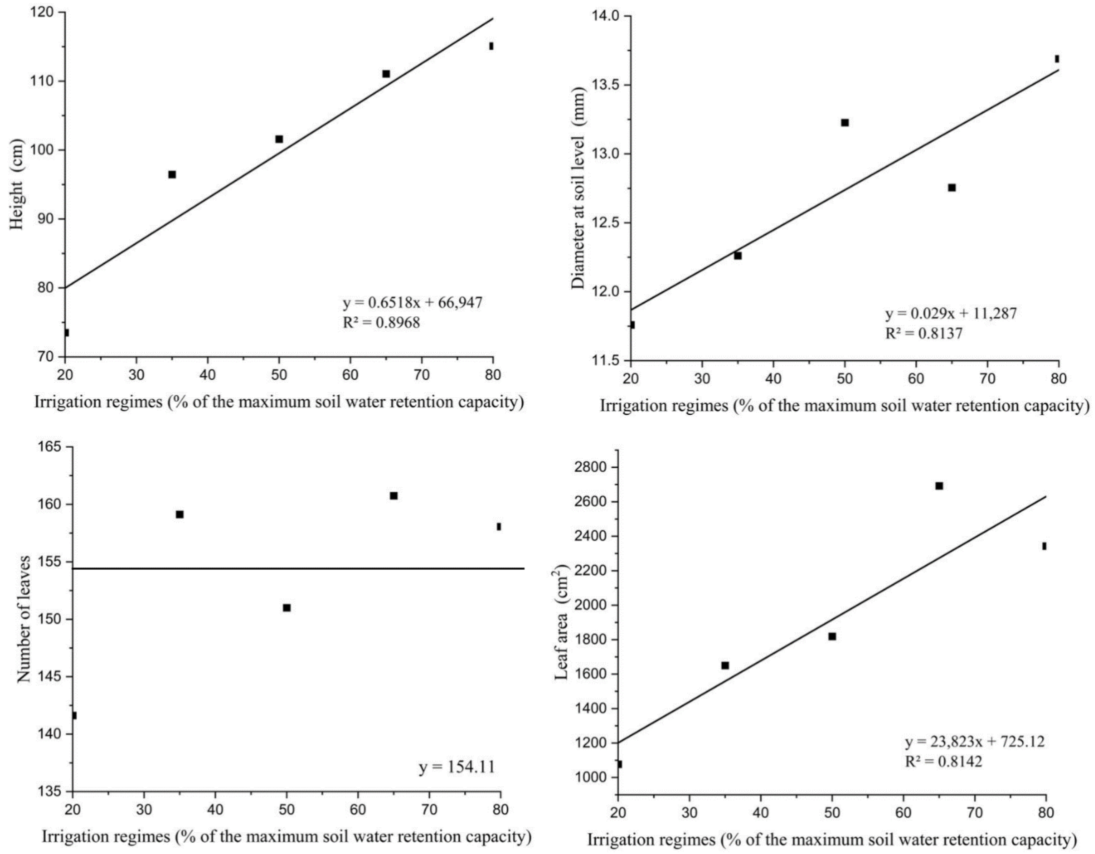

Figure 7. Behavior of height (cm), diameter at soil level (mm), number of leaves, and leaf area (cm^2) of *C. citriodora* plants submitted to five irrigation regimes (IR1, IR2, IR3, IR4, and IR5, that is, 20, 35, 50, 65, and 80% of the maximum substrate water retention capacity, respectively), evaluated at 110 days after the establishment of water regimes.

Plants are influenced by the environment, adapting to adversities, which may interfere with biomass (Chen et al., 2020), water scarcity can cause a reduction in the size of the leaf area, the size of the leaf area can be a strategy for survival (Meier & Leuschner, 2008). Although the number of leaves did not differ between irrigation regimes, there was a reduction in the leaf area with an increase in water restriction, which indicates less leaf expansion in the regimes of lower water availability. Plants decrease leaf area as a response to water deficiency, which reduces transpiration, decreasing water loss (Nóia junior et., 2019).

This reduction in leaf area occurred more intensely than the reduction in the net assimilation rate, corroborating the statement by Nóia Júnior et al. (2020) that leaf expansion is reduced before photosynthesis is affected. A study carried out with 16 taxa of eucalyptus in seedlings aged 70 days submitted to two water regimes (20 and 60% of soil water retention capacity) showed changes in growth and physiological parameters between taxa and water regimes (Silva et al., 2016b).

The mean percentage of reduction in the different studied characteristics, specifically water regime IR1 compared to IR5, reached 36% for height and 14% for collar diameter. Root dry mass (RDM) and leaf dry mass (LDM) accumulations were the most affected characteristics with the induced water deficit, with values of around 80 and 60%, respectively. *Eucalyptus* plants have a large leaf area at the seedling stage or beginning of establishment in the field, which changes at more advanced ages. Thus, leaf area and leaf dry mass at this stage are among the characteristics most affected by water stress (Nóia Júnior et al., 2020), as observed in our study. Increasing water use efficiency and reducing biomass is a strategy to reduce the effects of water stress. *Eucalyptus* plants can mitigate the impact of water scarcity with a higher root system development (Christina et al., 2017).

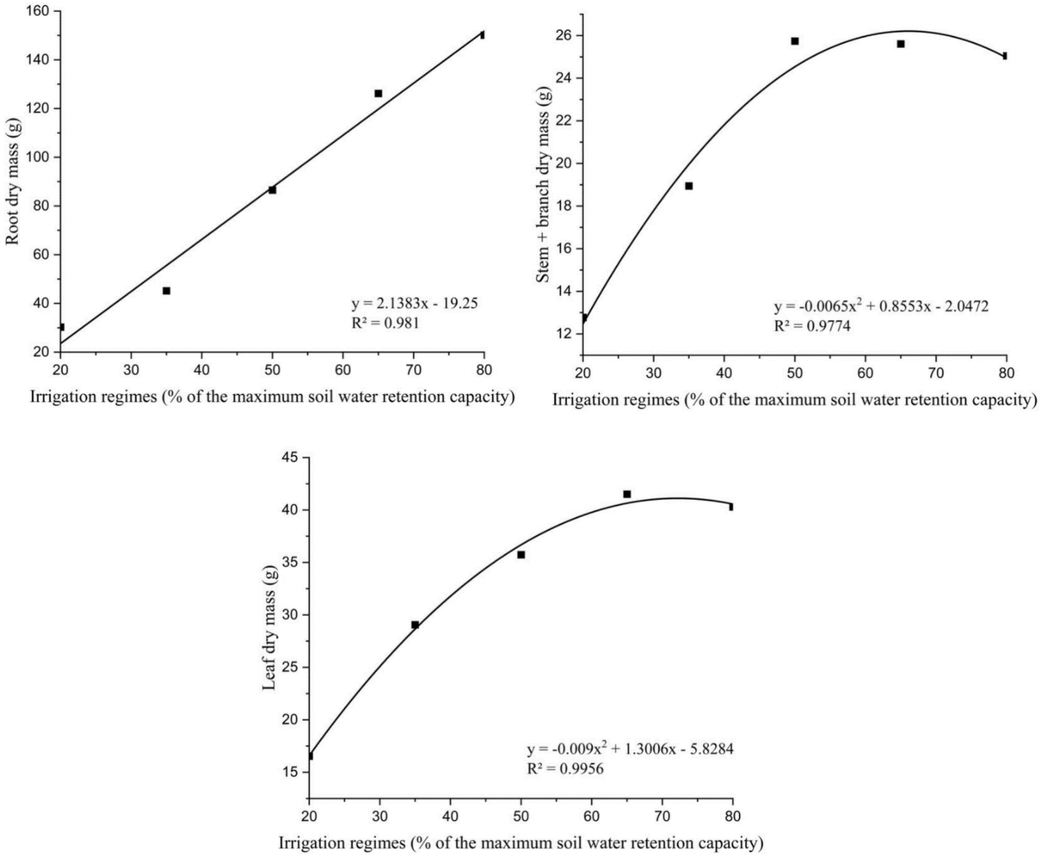

Figure 8. Behavior of root dry mass (g), stem + branch dry mass (g), and leaf dry mass (g) of *C. citriodora* plants submitted to five irrigation regimes (IR1, IR2, IR3, IR4, and IR5, that is, 20, 35, 50, 65, and 80% of the maximum substrate water retention capacity, respectively), evaluated at 110 days after the establishment of water regimes.

RDM was also compromised in about 70 and 42% in IR1 and IR2 relative to IR5, denoting high sensitivity even under less intense water stress. Leaf area, with a 54% reduction in IR1 compared to IR5, was the third most affected characteristic by the low water availability despite the number of leaves not being affected. *C. citriodora* plants showed a significant reduction in growth and biomass accumulation when cultivated at levels below 50% of the maximum soil water retention capacity. The photosynthetic apparatus and, consequently, gas exchange are compromised under this condition, causing the intensification of lipid peroxidation (Nóia Júnior et al., 2020; Correia et al., 2014).

CONCLUSION

Water stress affects the primary and secondary metabolism of *Corymbia citriodora* plants at the initial phase of establishment, reducing stomatal conductance, transpiration, and photosynthesis and increasing the contents of chlorophyll, carotenoids, MDA, and proline, with a decrease in growth. Seedlings subjected to irrigation regimes below 50% of maximum water retention capacity by the substrate had their physiological and growth parameters affected.

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