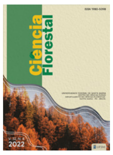

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Artigos

Photosynthetic and enzymatic metabolism of *Ormosia arborea* (Vell.) Harms under different water availabilities

Metabolismo fotossintético e enzimático de *Ormosia arborea* (Vell.) Harms sob diferentes disponibilidades hídricas

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ABSTRACT

In this research, we hypothesized that *Ormosia arborea* (Vell.) Harms seedlings should grow better and achieve greater levels of gas exchange when grown in soils with higher water availability. Thus, this study was developed to assess the metabolic responses of the seedlings to different levels water availability. Irrigation was performed on alternate days, at water holding capacities (WHC) of 25%, 50%, 75%, and 100%. The metabolic responses were analyzed at 15, 50, 85, and 120 days after starting treatments. The *O. arborea* plants grown in conditions of higher water availability (75% and 100% WHC) had higher leaf water potential and chlorophyll content, in addition to higher values for chlorophyll *a* fluorescence and gas exchange, than those grown in other conditions. Water deficit caused by low levels of water availability (25% or 50% WHC) reduces leaf water potential, chlorophyll *a* fluorescence, and gas exchange. As a strategy to tolerate stress, seedlings tend to invest in their antioxidant system, as shown by the high levels of activity of the enzymes Superoxide dismutase (SOD), Peroxidase (POD), and Catalase (CAT). Although the seedlings may be tolerant to cultivation under 50% WHC, the best functioning of the photosynthetic apparatus occurred under WHC of 75%.

Keywords: Antioxidant enzymes; Chlorophyll *a* fluorescence; Hydric stress; Photosynthesis

RESUMO

Nesta pesquisa, hipotetizamos que as mudas de *Ormosia arborea* (Vell.) Harms crescem melhor e alcançam maiores níveis de troca gasosas quando cultivadas em solos com maior disponibilidade de água. Assim, este estudo foi desenvolvido para avaliar as respostas metabólicas das mudas a diferentes níveis de disponibilidade hídrica. A irrigação foi realizada em dias alternados, nas capacidades de retenção de água (CRA) de 25%, 50%, 75% e 100%. As respostas metabólicas foram analisadas aos 15, 50, 85 e 120 dias após o início dos tratamentos. As plantas de *O. arborea* cultivadas em condições de maior disponibilidade hídrica (75% e 100% CRA) apresentaram maior potencial hídrico foliar e teor de clorofila, além de maiores valores para a fluorescência da clorofila *a* e trocas gasosas do que aquelas cultivadas em outras condições. O déficit hídrico causado por baixos níveis de disponibilidade hídrica (25% ou 50% CRA) reduz o potencial hídrico foliar, a fluorescência da clorofila *a* e as trocas gasosas. Como estratégia para tolerar o estresse, as mudas tendem a investir em seu sistema antioxidante, como demonstrado pelos altos níveis de atividade das enzimas Superóxido dismutase (SOD), Peroxidase (POD) e Catalase (CAT). Embora as mudas possam ser tolerantes ao cultivo com menos de 50%, o melhor funcionamento do aparato fotossintético ocorreu sob 75% de CRA.

Palavras-chave: Enzimas antioxidantes; Fluorescência da clorofila *a*; Estresse hídrico; Fotossíntese

1 INTRODUCTION

The increasing destruction of phytophysiognomies in the *Cerrado* region of Brazil has led to stronger environmental policies to promote the recovery and conservation of ecosystems (SARMENTO; VILLELA, 2010), however, implementing these policies requires technical expertise to facilitate better understanding of the propagation and behavior of native species in the region in the face of environmental change. However, this knowledge is still under development and is often diffuse, especially in relation to the physiological responses of plants to adverse situations, particularly in relation to water availability.

In most cases, plants under stress conditions respond by decreasing turgidity and leaf water potential, reducing stomatal conductance, photosynthesis and transpiration, and changing the quantum efficiency of the photosystem and chlorophyll *a* fluorescence, leading to a decline in the rate of growth (JALEEL *et al*., 2009; CAMPELO *et al.,* 2015; BENTO *et al.,* 2016; ROSA *et al.,* 2017). Another response to conditions of water deficit is the production of reactive oxygen species (ROS). As a defense mechanism, plants develop antioxidant enzyme systems against free radicals, for example, superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX) (CARNEIRO *et al.,*2011).

Knowledge of the responses of species under the influence of different water conditions is fundamental, starting right from the first few months of growth, when the seedlings are highly susceptible to environmental variations (ROSA *et al.,* 2017)

Ormosea arborea (Vell.) Harms (Fabaceae - Papilionoideae) is a species often found in riparian forests, recommended for planting in degraded areas to allow ecosystem recovery. Morphophysiological adjustments indicate phenotypic plasticity and potential for survival in temporarily flooded areas (JUNGLOS *et al.,* 2018). Information on the development of this species under water deficit is scarce, which would make it possible to better understand the interactions caused by water stress in the physiological processes and in the development of the seedlings of this species.

For this reason, our hypothesis was that its seedlings should grow better and achieve greater levels of gas exchange when grown in soils with higher water availability. Thus, this study was developed to assess the metabolic responses of the seedlings to different levels of water availability.

2 MATERIALS AND METHODS

2.1 Plant and cultivation material

This study was carried with *Ormosia arborea* (Vell.) Harms seedlings that were six months old. The experiment was conducted in greenhouse, coated with Sombrite® with a 30% reduction in luminosity and a low-density plastic cover to prevent rain from falling on the plant containers. The 5-liter containers were filled with a substrate consisting of sifted Dystroferric Red Latosol and sand at a proportion of 1:1(v:v).

The containers were irrigated in order to maintain 25%, 50%, 75% or 100% of the water-holding capacity (WHC). The mass of all containers was measured using a precision scale (0.001 g), with individualized irrigation performed on alternate days using sufficient quantities of tap water to reach the pre-established mass for each treatment. The plants were maintained in the pots for 15 days at the different levels of water availability before the experiment was initiated.

The experiment had a duration of 120 days. Metabolic responses were evaluated at 15, 50, 85, and 120 days after the beginning of the treatments, using four representative seedlings for each repeat.

2.2 Evaluations

Leaf water potential (Ψω) was obtained from readings performed on individual leaves belonging to the third pair of fully expanded leaves using a pressure chamber (Portable Plant water status console).

Index of chlorophyll (SPAD) was obtained using a Konica Minolta, SPAD 502 chlorophyll analyzer.

Chlorophyll *a* fluorescence was obtained by means of a portable fluorometer (Opti-Sciences Chlorophyll Fluorometer), with measurement of the potential quantum efficiency of photosystem II (Fv/Fm).

Gas exchange measurements were performed every two days. The following parameters were quantified: photosynthetic rate (*A* μmol m^{-2} s^{-1}), leaf transpiration (*E* mmol m^{-2} s^{-1}), stomatal conductance (*gs* mol m^{-2} s^{-1}), and internal CO_2 concentration (*Ci* μmol mol^{-1}) using an LCi PRO infrared gas analyzer (IRGA). The assessments were performed on two leaves from three seedlings from each treatment. The leaves were fully expanded and marked so that all measurements were performed on the same leaf. The following relationships were calculated from the gas exchange data: instantaneous water use efficiency (*WUE*), intrinsic water use efficiency (*IWUE*) and carboxylation efficiency of ribulose-1.5-bisphosphate carboxylase oxygenase

(Rubisco) (*A/Ci*). The evaluation was performed using four seedlings per treatment, in the morning, between 08:00 and 11:00 h, in fully expanded leaves that were previously marked, and all measurements were performed on the same leaves, and only the data measured under a photosynthetic photon flux (PPF) higher than 700 mmol m^{-2} s^{-1} was considered.

Activity of the antioxidant enzymes was obtained after harvesting the leaves and roots of *O. arborea* from each treatment, the material was frozen in liquid nitrogen. From each sample, 1 g was macerated in 6 mL of a solution comprising 0.3 g of polyvinylpyrrolidone (PVP) diluted in 100 mL of potassium phosphate buffer (0.2M). Then, the samples were centrifuged at 4000 rpm for 20 minutes at 4°C and the supernatant was used as an enzyme extract. Quantification of the activity of the enzymes catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD) was performed according to Broetto's methodology (2014).

2.3 Experimental design and statistical analysis

The statistical design was completely randomized in a 4 x 4 factorial scheme (4 levels of water availability x 4 evaluation times), with each treatment consisting of 10 seedlings. All data were submitted to variance analysis at 5% probability of error. If significant, they were then adjusted with regression equations, using the SISVAR computer program (FERREIRA, 2011).

3 RESULTS AND DISCUSSION

3.1 Water potential, chlorophyll index and chlorophyll *a* fluorescence

Seedlings at all levels of water availability showed reductions in water potential (Ψw) over the course of the experiment, and the seedlings under water deficit (WHC of 25% or 50%) had greater reductions, reaching values of -1.7 and -1.3 MPa, respectively, at 120 days (Figure 1A). The Ψw value indicates the difference between the hydric condition of a plant in a given system and a reference value. Thus, when the value is close to zero, the plant becomes more hydrated.

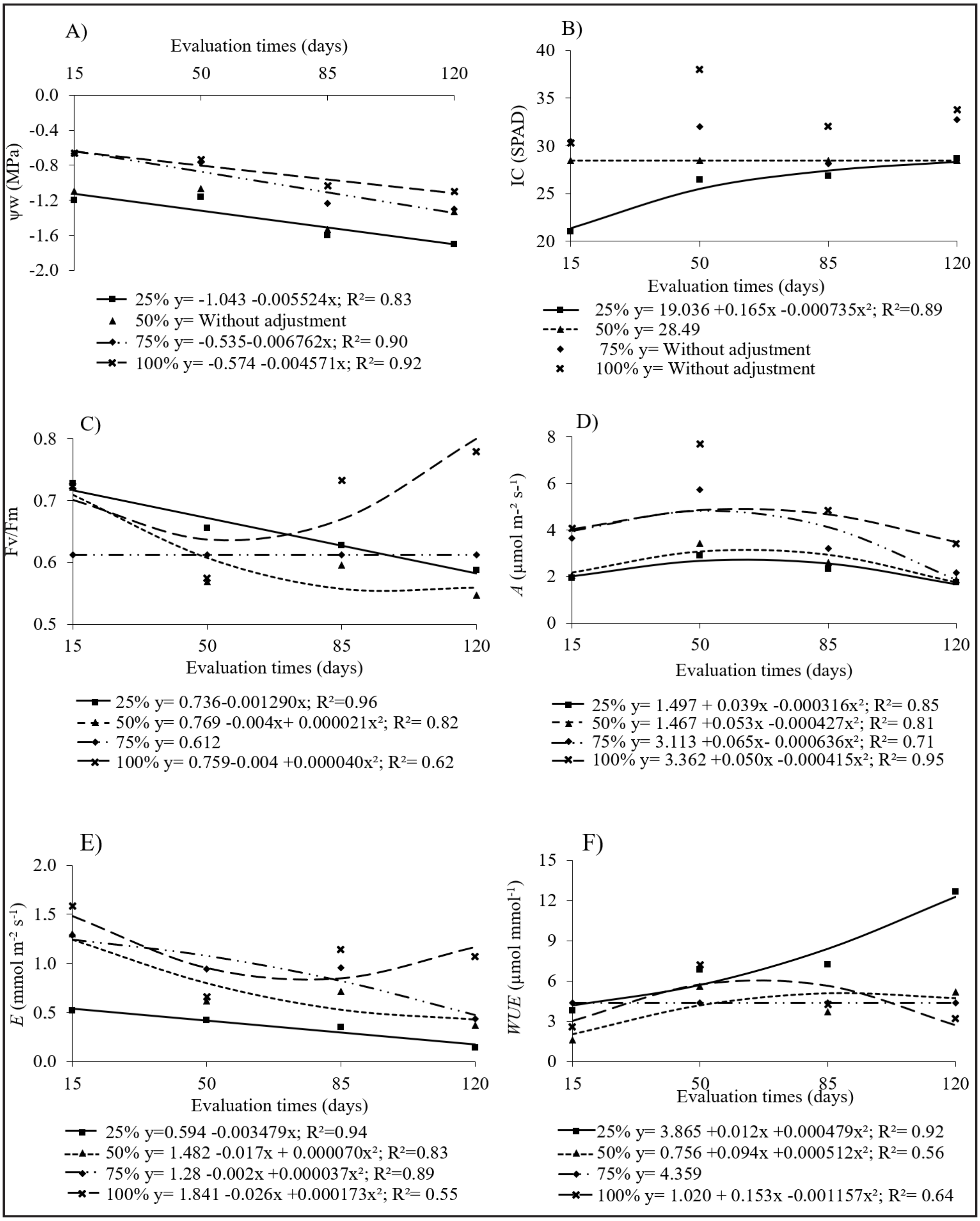
Similarly to water potential, the chlorophyll contents of the plants grown under 25% and 50% WHC were lower than those of plants under other treatments (28.34 and 28.49 SPAD, respectively) (Figure 1B). Even though the treatments with higher water availability did not show linear or quadratic adjustment, it was possible to observe that their values were high (Figure 1B). SPAD reduction can probably be attributed to lower pigment synthesis, but leaf yellowing was not observed under water deficit. In general, plants subjected to water stress show a marked decrease in photosynthetic pigment content (ASHARAF; HARRIS, 2013; BENTO *et al.*, 2016).

A reduction in the potential quantum efficiency of photosystem II (Fv/Fm) of plants cultivated at 25% WHC was observed, and plants at 50% reached a minimum value of this ratio at 107 days after starting treatment (0.549). The best results were reached at 100% WHC at 120 days (0.800) (Figure 1C). In this period, the Fv/Fm values observed for seedlings grown at WHCs of 25% and 50% (0.582 and 0.559, respectively) were below the critical limit suggested in the literature, which can range from 0.75 to 0.80 (CAMPELO *et al.*, 2015; BENTO *et al.*, 2016). These changes in Fv/Fm in plants subjected to conditions of water stress have been reported by several authors as indicators of stress, since the reduction in water availability enables the photoinhibitory processes in the PSII reaction centers (LAGE-PINTO *et al.*, 2012).

3.2 Gas exchange

The maximum values of photosynthetic rate (*A*) were observed in the seedlings grown under 75% WHC at 51 days (4.81 μmol $m^{-2}s^{-1}$) and 100% WHC at 61 days (4.91 μmol m^{-2} s^{-1}), whereas the lowest capacities (25% and 50% WHC) resulted in values of 2.71 and 3.14 μmol $m^{-2}s^{-1}$, respectively (Figure 1D). At the end of the 120 days, a decline in the photosynthetic rate of the seedlings under all WHCs was observed.

Figure 1 – Leaf water potential; index of chlorophyll; chlorophyll a fluorescence; and gas exchange in *Ormosia arborea* (Vell.) Harms depending on different water retention capacity and evaluation times



Source: Authors (2019)

In where: Water potential of the leaves – Ψw (A); index of chlorophyll (SPAD) – IC (B); potential quantum efficiency of photosystem II (Fv/Fm) (C); Photosynthetic rate - *A* (D); transpiration – *E* (E); water use efficiency - *WUE* (F) in *Ormosia arborea* (Vell.) Harms depending on different water retention capacity (WRC) and evaluation times (days).

Water deficit usually leads to a decrease in the rate of photosynthesis, although tolerance levels may vary between different plant species. We highlight that the leaf water potential observed with a WHC of 25% was greater than the value considered critical for several species (-1.5 MPa) (BENTO *et al.,* 2016), followed by the WHC of 50%.

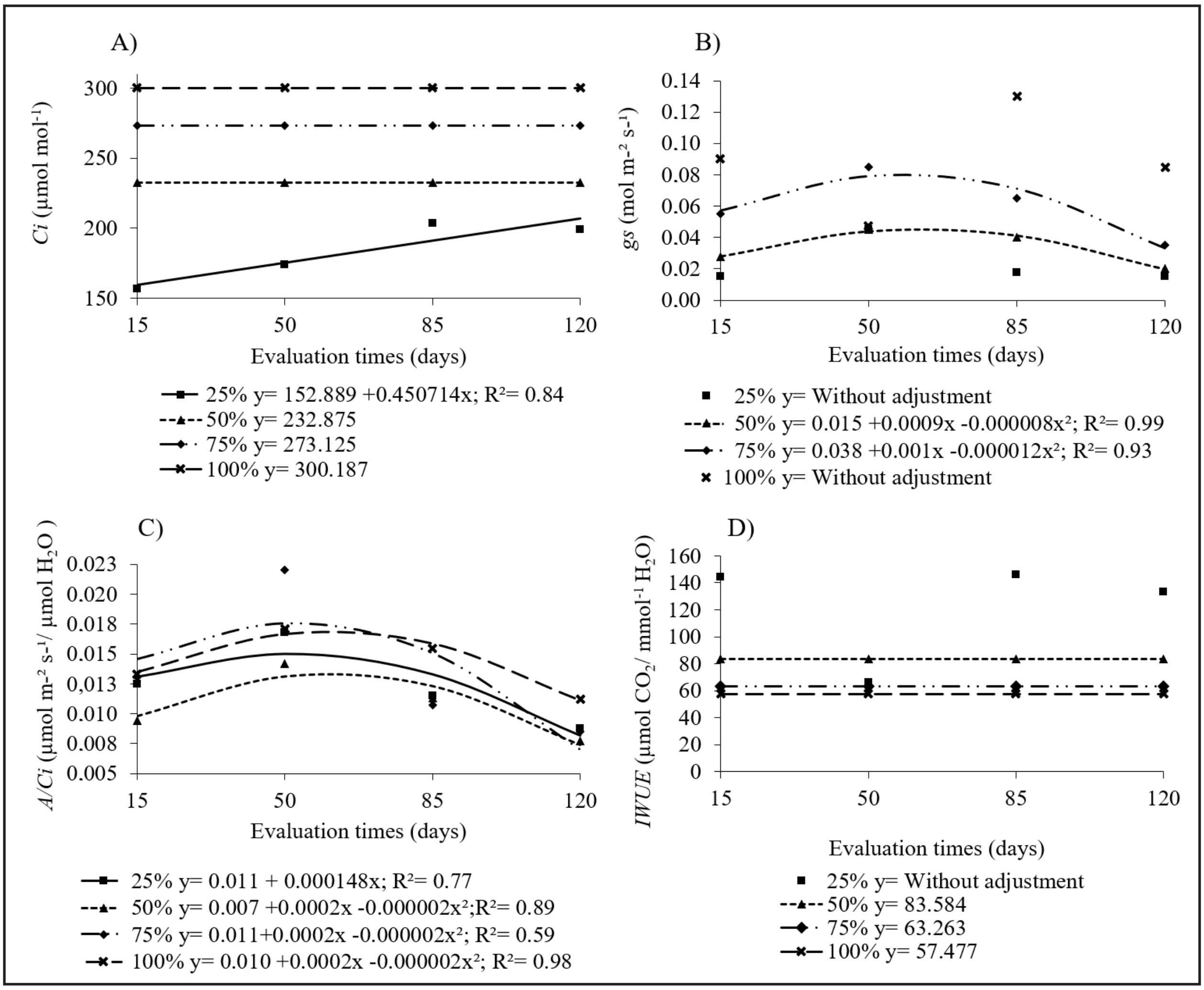
The lowest values of transpiration (*E*) too were observed in seedlings grown at 25% and 50% WHC after 120 days (1.676 and 1.755 mmol m^{-2} s^{-1}, respectively), whereas seedlings with greater water availability (100% WHC) had a value of 3.472 mmol m^{-2} s^{-1} (Figure 1E).

Regarding instantaneous water use efficiency (*WUE*), the seedlings under 100% WHC showed a maximum value of 6.49 μmol $mmol^{-1}$at approximately 66 days, followed by the WHC of 75% (5.40 μmol $mmol^{-1}$). However, at 120 days, the highest value was observed in seedlings at 25% WHC (12.28 μmol $mmol^{-1}$) (Figure 1F), which is attributed to the reduced transpiration rate in this condition.

The internal CO_2 concentration (*Ci*) was negatively affected by reduced WHC (25% and 50% WHC) (Figure 2A). For the seedlings grown under 50%, 75%, and 100% WHC, values did not vary over the course of the assessments (232.87, 273.12, and 300.18 μmol mol^{-1}, respectively).

Similarly to the other characteristics, stomatal conductance remained lower in plants grown under 25% and 50% WHC conditions (0.020 and 0.019 mol m^{-2} s^{-1}, respectively, at 120 days) than those grown under other conditions. A maximum at 71 days after starting treatment was observed for 75% WHC (0.424 mol m^{-2} s^{-1}). Even though the data did not fit the equations tested, a WHC of 100% provided higher mean values (Figure 2B).

Figure 2 – Internal CO2; stomatal conductance; carboxylation efficiency; intrinsic water use efficiency – IWUE (D) in *Ormosia arborea* (Vell.) Harms depending on different water retention capacity and evaluation times



Source: Authors (2019)

In where: Internal CO_2 concentration – *Ci* (*A*); stomatal conductance – *gs* (B); carboxylation efficiency of ribulose RUBISCO - *A/Ci* (C); intrinsic water use efficiency – *IWUE* (D) in *Ormosia arborea* (Vell.) Harms depending on different water retention capacity (WRC) and evaluation times (days).

The greatest reductions in *E* and *gs* were also recorded for the lowest levels of water availability, and at the end of 120 days, the best results were obtained by the highest WHCs (75% and 100%). These results were expected for *O. arborea* as it is a typical riparian forest species, and thus may increase photosynthetic performance at higher levels of water availability. Water stress, even when moderated, affects

A and *gs*. As this stress becomes more severe, the dehydration of mesophyll cells inhibits photosynthesis and water-use efficiency generally decreases. Therefore, during the dry season a major restricition in transpiration is presumed to occur, with decreases in photosynthetic activity being observed in seedlings of woody species, and with photosynthesis values tending to be closer to zero (MARIANO *et al.*, 2009; CAMPELO *et al.*, 2015).

The reduction in values of *E* due to water deficit conditions was probably a direct consequence of the reduction in *gs*, thus reducing water use. Ferraz *et al.* (2012) explained that, in general, plants under water stress tend to adopt conservation mechanisms, reducing *gs* and *E*, and increasing *WUE*, so that the rate of photosynthesis is also reduced. According to Machado *et al.* (2009), these responses can be considered a successful plant strategy in response to low water availability. The fact that these efficiency values are related to CO_2 assimilation, as well as to transpiration and stomatal conductance, makes them very useful parameters for irrigation projects aimed at conserving water.

The highest values of instantaneous carboxylation efficiency of Rubisco *(A/Ci)* were attained at the higher levels of water availability (75% and 100% WHC), which had maximum values of 0.018 μmol mol^{-1} at 58 days and 0.015 μmol mol^{-1} at 50 days into the experiment, respectively. After 85 days, a decrease was observed for all treatments (Figure 2C).

Regarding intrinsic water use efficiency (*IWUE*), a behavior similar to that of *WUE* was observed, which was higher in the seedlings with the lowest water availability (25% and 50% WHC) than in those with higher water availability. The increase in *IWUE* was probably due to the reduction in *gs*, which was proportionally higher than the reduction in *A* (Figure 2D).

It should be noted that, at the assessment at 85 days after starting treatment, the reduction in the rate of photosynthesis and in the instantaneous carboxylation efficiency of Rubisco was probably due to the decrease in humidity and the increase in temperature during this period (data not shown).

The behavior of *O. arborea* seedlings suggests that when there is low water availability, partial closure of the stomata reduces the output of water molecules through transpiration more than CO_2 fixation by photosynthesis (POMPELLI *et al.*, 2010; BENTO *et al.*, 2016). This reduction in transpiration at low levels of water availability is a strategic way for the plant to deal with limited water by avoiding loss through evaporation during the water deficit.

However, due to stomatal closure, CO_2 assimilation and quantum yield of photosystem II (MARIANO *et al.*, 2009; CECHIN *et al.*, 2010) decrease, thus resulting in the lowest photosynthetic rates in plants grown at the lowest levels of water availability.

The lower *gs* at lower levels of water availability suggests the presence of chemical signals in plants, such as abscisic acid, which under dry conditions controls stomatal opening in many species (HIRAYAMA; SHINOZAKI, 2010; OLIVEIRA; GUALTIERI; BOCCHESE, 2011). This response is considered a strategy by plants to reduce excess loss of water by transpiration (ALBUQUERQUE *et al.*, 2013) and it contributes to the maintenance of water potential in the leaves, preventing the drying of tissues.

The decrease in *Ci* observed at lower levels of water availability occurs because the partial closure of stomata – governed by the dehydration of the guard cells or by hormonal responses – restricts water loss through transpiration in leaves, leading to a decrease in the entry and assimilation of CO_2 and thus restricting the photosynthetic process (BENTO *et al.*, 2016; ROSA *et al.*, 2017).

This reduction in photosynthesis can be aggravated by the lower *A/Ci* observed at lower levels of water availability, associated with greater resistance of the mesophyll due to stomatal closure, restricting CO_2 absorption in chloroplasts and increasing the oxygenase activity of Rubisco, and consequently, photorespiration. We observed in the literature that drought reduces the metabolism of the mesophyll by decreasing the activation and activity of Rubisco, decreasing its efficiency (BENTO *et al.,* 2016; ROSA *et al*., 2017).

Liu *et al.* (2014) observed in their review that a reduction in photosynthesis is attributed as much to stomatal limitation as to non-stomatal limitations. In the latter case, photosynthesis may decrease due to various causes, such as: reduction in the content and activity of the enzyme ribulose-1.5- biphosphate carboxylase oxygenase (which can be observed in the present study when assessing the *A/Ci* ratio), inhibition of photosynthetic electron transport, photosynthetic phosphorylation, regeneration of ribulose 1.5-bisphosphate, metabolic disorders of active oxygen, and increases of ethylene and other endogenous hormones.

Generally, the maintenance of relatively high rates of photosynthesis, associated with lower values of stomatal conductance and leaf transpiration, is characteristic of plants that are responding to low water availability in the soil, reflected by higher values of *IWUE* and *WUE* (BENTO *et al.*, 2016; ROSA *et al.*, 2017).

3.3 Antioxidant activity

With respect to antioxidant activity, an increase in the activity of the enzyme superoxide dismutase (SOD) was observed in the aerial parts and roots of the *O. arborea* seedlings. The SOD values were higher in the aerial parts of the seedlings cultivated at 25% WHC than in those subjected to the other treatments. For the roots, time was the only significant factor and enzyme activity increased independently of WHC (Fig. 3A and B).

The activity of the enzyme peroxidase (POD) in shoots (aerial parts) decreased in seedlings at all levels of water availability, with the lowest values at 75% and 100% WHC, up to 85 days during the experiment. Seedlings at 50%, 75%, and 100% WHC, however, plateaued at the end of the assessments. In the roots, enzymatic activity increased during all treatments, with the greatest values at 25% and 50% WHC (2.384 and 2.059 µKat µg Prot^{-1}) at 120 days, respectively) (Fig. 3C and D). The water retention capacity of 75% was the cultivation condition that provided the lowest increase of pod at 120 days. We emphasize that the roots of O.arborea were more sensitive to water stress than the leaves.

The activity of the enzyme catalase (CAT) increased at the end of 120 days, both for the aerial parts and the roots at the lowest level of water availability (25% WHC) (Fig. 3E and F). As observed in the aerial parts of *O. arborea* seedlings, there was greater CAT activity in the root system at a WHC of 25%. Such behavior may be related to the environmental changes recorded during these periods, such as the decrease in relative air humidity and the changes in temperatures recorded toward the end of the assessment period (data shown).

The similarity in POD activities at the end of the assessments of plants grown at WHC percentages of 50%, 75%, and 100% was probably due to the decrease in relative air humidity that occurred during this period. The results observed in this study confirm our hypothesis that seedlings require a greater availability of water and can be grown under WHC of 75% and 100% without compromising the quality of the seedlings (data not shown).

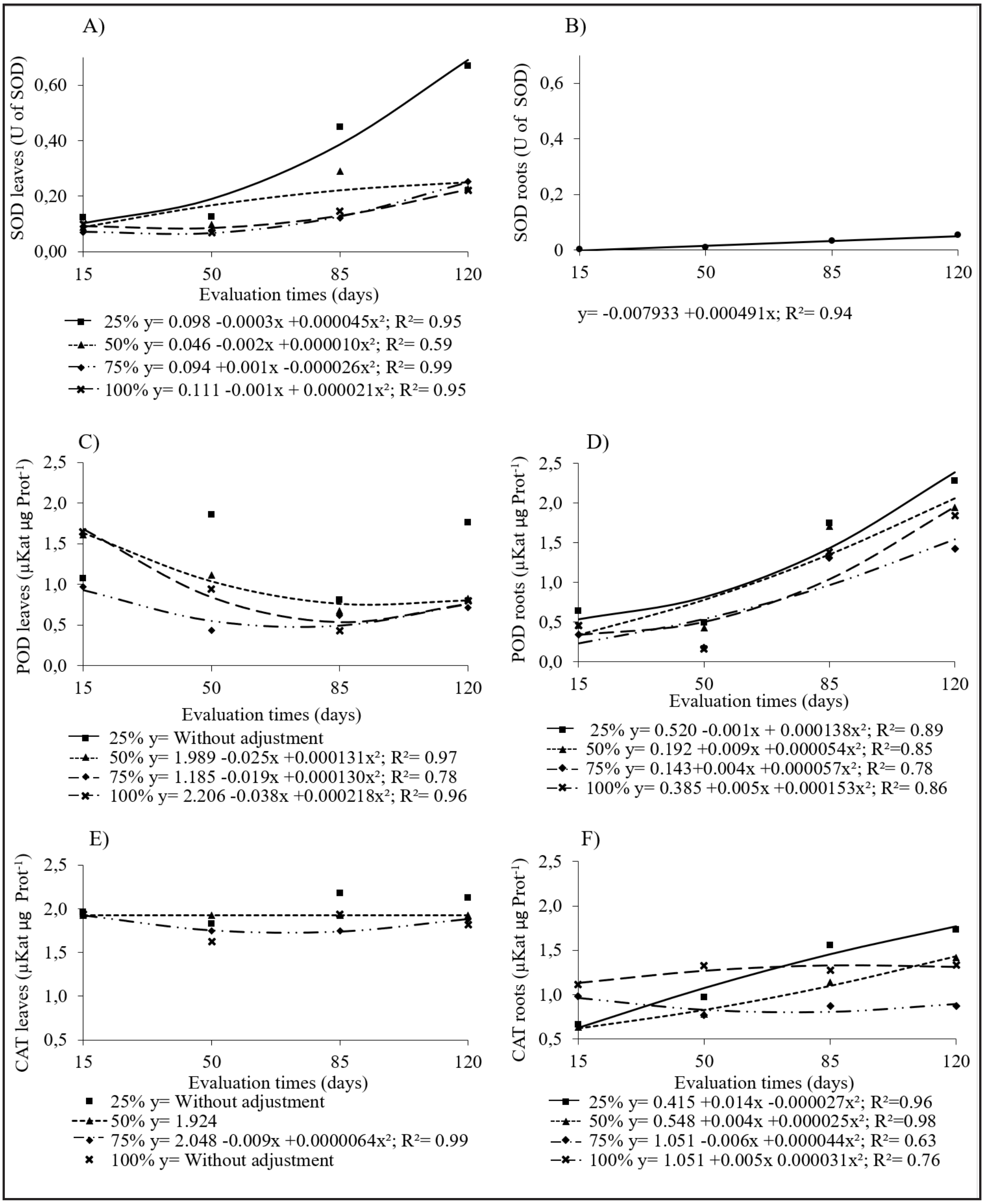
The superoxide radical produced under stress conditions is toxic and has a half-life of less than one second. It is generally rapidly dismuted by SOD to H_2O_2, a relatively stable product which can be eliminated by the action of catalase (CAT), which transforms it into O_2 and water, or by the action of peroxidase (POD), which oxidizes ascorbate and thus transforms it into monodehydroascorbate.

These metalloenzymes constitute an important primary defense of cells against the superoxide radicals generated under stress conditions, and an increase in SOD activity may confer tolerance to oxidative stress (JALEEL *et al*., 2009).

Increases in the enzymatic activity of SOD, POD, and CAT in the aerial parts and root systems of *O. arborea* seedlings, as verified in the present work, suggest that water restriction, represented by WHC of 25% and 50%, caused oxidative stress.

The increased antioxidant activity observed in *O. arborea* may be an indicator of tolerance to periods of water restriction, because, to minimize water loss, a plant's metabolism is initially reduced due to stomatal closure. However, it is known that this alteration leads to an increase in oxidative stress (ARCOVERDE *et al*., 2011), which is ameliorated by the action of SOD as the first line of defense to this damage, which may indicate that this enzyme plays an important role in the metabolism of O_2 when plants suffer some type of stress (BASU *et al*., 2010).

Figure 3 – Activity of the antioxidant enzymes in leaves and roots in *Ormosia arborea* (Vell.) Harms depending on different water retention capacity and evaluation times



Source: Authors (2019)

In where: Enzimatic activity in leaves and roots of superoxide dismutase (SOD leaves and roots) (A, B) and roots (SOD roots) (B); of peroxidase (POD leaves and roots) (C, D); of catalase (CAT leaves and roots) (E, F) in *Ormosia arborea* (Vell.) Harms depending on different water retention capacity (WRC) and evaluation times (days).

The decrease in Ψw negatively affected chlorophyll content, chlorophyll *a* fluorescence, and gas exchange, and resulted in increases in the activity of antioxidant enzymes. The leaf Ψw decreases with a decline in water availability in the soil, leading to a loss of turgescence and also inducing stomatal closure; these responses differ from species to species (BENTO *et al.*, 2016; ROSA *et al.*, 2017).

4 CONCLUSION

In conclusion, the water deficit caused by low levels of water availability (25% or 50% WHC) reduces leaf water potential, chlorophyll *a* fluorescence, and gas exchange. As a strategy to tolerate stress, seedlings tend to invest in their antioxidant system, as shown by the high levels of activity of the enzymes SOD, POD, and CAT. Although the seedlings may be tolerant to cultivation under 50% WHC, the photosynthetic apparatus functions best at a WHC of 75%.

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