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Original Article

Do *Dipteryx alata* Vogel seedlings recover the quality and the photosynthetic and antioxidant responses in the post-flooding?

Mudas de *Dipteryx alata* Vogel recuperam a qualidade e as respostas fotossintéticas e antioxidantes no pós-alagamento?

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Abstract

D*ipteryx alata* Vogel is a tree species widely found in Cerrado, settling preferentially in well drained soils. Studies related to ecophysiology of *D. alata* may contribute to the decision making about using seedlings of this species in projects aimed at the recovery of degraded areas where seasonal flooding happens. This study aimed to assess the effects of flooding on photosynthetic and antioxidant metabolism and quality of *D. alata* seedlings cultivated or not under flooding during four assessment periods (0, 20, 40, and 60 days), followed by 100 days after the end of each assessment period (0+100, 20+100, 40+100, and 60+100 days), allowing verifying the potential for post-flooding recovery. Flooded plants showed lower photosynthetic efficiency than non-flooded plants, regardless of the periods of exposure. However, this efficiency was recovered in the post-flooding, with values similar to that of the non-flooded seedlings. Moreover, the damage to F_V/F_M was evidenced by an increase in the period of exposure to flooding, but recovery was also observed at this stage of the photosynthetic metabolism. Seedling quality decreased under flooding, not varying between periods of exposure, but remained lower although the increase observed in the post-flooding period, with no recovery after flooding. The occurrence of hypertrophied lenticels associated with physiological changes and an efficient antioxidant enzyme system might have contributed to the survival and recovery of these seedlings. Thus, this species is sensitive to flooding stress but capable of adjusting and recovering metabolic characteristics at 100 days after the suspension of the water stress, but with no recovery in seedling quality. Thus, we suggested plasticity under the cultivation condition and determined that the time of 100 days is not enough for the complete resumption of growth.

Keywords: baru, water stress, gas exchange, reactive oxygen species, plasticity, tolerance.

Resumo

Dipteryx alata Vogel é uma arbórea de ampla ocorrência no Cerrado, se estabelecendo preferencialmente em solos bem drenados. Estudos referentes à ecofisiologia de *D. alata* em podem contribuir para a tomada de decisão sobre o uso de mudas dessa espécie em programas de recuperação de áreas degradadas sujeitas a alagamento temporário. Objetivamos com essa pesquisa avaliar os efeitos do alagamento no metabolismo fotossintético e antioxidante, além da qualidade de mudas dessa espécie, cultivadas ou não sob alagamento durante quatro períodos de avaliação (0, 20, 40 e 60 dias) seguidos de 100 dias após o término de cada período (0+100, 20+100, 40+100, 60+100 dias), possibilitando verificar o potencial de recuperação pós-alagamento. Observamos que as plantas alagadas apresentaram menor eficiência fotossintética e danos em F_V/F_M entretanto houve recuperação dessas características no pós alagamento. A qualidade das mudas reduziu sob alagamento não variando entre os períodos de exposição e embora tenha aumentado no pós-alagamento manteve-se menor não se recuperando. A ocorrência de lenticelas hipertrofiadas associadas a alterações fisiológicas e um eficiente sistema enzimático antioxidante devem ter contribuído para a sobrevivência e recuperação metabólica dessas mudas. Diante disso, sugerimos que a espécie é sensível ao estresse por alagamento, mas capaz de se ajustar e recuperar as características metabólicas 100 dias após a suspensão deste estresse hídrico, no entanto a qualidade da mudas não apresentou recuperação, assim, sugerimos plasticidade diante da condição de cultivo e ressaltamos que o tempo de 100 dias não é suficiente para a completa retomada do crescimento.

Palavras-chave: baru, estresse hídrico, trocas gasosas, espécies reativas de oxigênio, plasticidade, tolerância.

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1. Introduction

The impacts of climate change on plants are alarming and cause effects capable of altering the characterization of biomes. Physiological, morphological, and biochemical changes emerge as responses of adaptation and acclimatization to abiotic stresses, which can be defined as any growth alteration within the natural habitat of plants that disturbs its metabolic homeostasis (Redman et al., 2011; Harfouche et al., 2014; Kosová et al., 2018). Global climate change is associated with variations in precipitation and flooding events, that is why it is important to study how they affect plant growth and distribution under this stressful condition.

The waterlogging of the soil generates different impacts on trees, with some species dying rapidly whereas others are able to adapt and survive in such conditions (Silva et al., 2010). Flooding stress reduces the oxygen supply to submerged plant tissues so that plants have strategies to compensate for anaerobic soil conditions (Wittmann et al., 2013). Tree species demonstrate a variety of morphophysiological responses to deal with prolonged periods of flooding, such as the development of adventitious roots, aerenchyma, and hypertrophied lenticels, in addition to reducing gas exchange and increasing carbohydrate reserves in the roots (Pimentel et al., 2014; Argus et al., 2015; Marcílio et al., 2019).

High production of reactive oxygen species (ROS), such as hydrogen peroxide and superoxide and hydroxyl radicals, which promote oxidative damage to lipids and proteins in membranes and nucleic acids (Irfan et al., 2010; Delmastro and Piganelli, 2011), is also common under these conditions. However, the elimination of excess ROS and prevention of its formation are possible through an antioxidant enzyme system (Pradedova et al., 2011; Contin et al., 2014; Voesenek and Bailey-Serres, 2015).

Several enzymes are involved in ROS detoxification, such as superoxide dismutase, peroxidase, catalase, and ascorbate peroxidase, and plants with higher activities of this antioxidant system are possibly more resistant to oxidative damage (Hernandez et al., 2010; Alves et al. 2013; Souza et al., 2013; Larré et al., 2016), favoring their recovery potential after stress.

In this scenario, phenotypic plasticity can be determined as the advantage a species has in response to a changing environment, i.e., a new climate condition, being adaptive when it reaches similar or higher values for a given physiological characteristic compared to its initial environment with no abiotic stresses (Becklin et al., 2016).

Forests are important to mitigate the effects caused by climate change and the use of plant species selected for extreme environmental conditions is essential in projects aimed at the recovery of degraded areas (Contin et al., 2014). Thus, the knowledge of their ecophysiological responses is required, considering that tolerance or susceptibility to stress, i.e., the ability to survive or not under an unfavorable condition, respectively, can directly imply the success of these programs (Contin et al., 2014; Bozinovic and Pörtner, 2015).

Baru (Dipteryx alata Vogel, Fabaceae) is a tree species that has gained prominence for its potential use in the recovery of degraded areas (Sano et al., 2016). Its occurrence and distribution occur mainly in the Brazilian Cerrado, composing a global biodiversity hotspot (Bonanomi et al., 2019) where seasonal floods and long periods of drought are common (Vourlitis et al., 2017) typical of the Cerrado and Pantanal region (Ratter et al., 1996; Salis et al., 2006).

Seeing that Nabout et al. (2010) in their review and Sano et al. (2016) found that this species preferably has its establishment in well-drained soils as in dense savanna formations and in dry forests, and we did not find in the literature any record of the species in flooded regions of the species' occurring biomes, we hypothesize that excess water may limit its development. We also hypothesize that this species does not tolerate long periods of flooding, but adjustments in photosynthetic and antioxidant metabolism may contribute to recovering seedlings after flooding suspension. Therefore, we aimed to assess the effect of different times of exposure to flooding and the potential for recovery of *D. alata* seedlings.

2. Material and Methods

2.1. Plant material and implementation of the experiment

D. alata seeds were collected from matrices which were distributed in remaining areas of the Cerrado, in the regions of Dourados and Nova Alvorada do Sul, in Mato Grosso do Sul, Brazil and later they were taken to the Federal University of Grande Dourados, where they were selected according to their uniformity. A voucher specimen is deposited in the herbarium of Dourados city under the voucher number 5993.

Based on pre-tests, seedlings were produced in nurseries with a Sombrite® screen with 30% shade where they were kept until the end of the experiment. Sowing was carried out in expanded polystyrene trays containing Distroferric Red Latosol (sieved) soil and sand at a proportion of 2:1 under daily irrigation. Seedlings with 54 days after sowing were transplanted into pots with eight liters capacity with soil, sand and adding Carolina® commercial substrate (2:1:1 v:v:v). The experimental unit consisted of a pot with two seedlings.

The first phase of the experiment consisted of two water regimes and four assessment periods. The water regimes were represented by non-flooded plants, which were used as controls and irrigated with a sufficient amount of water to reach 75% of the soil water capacity (SWC) (Souza et al., 2000). The other group consisted of flooded seedlings, which were placed in a pool (pot + seedlings) and a water depth of approximately 5 cm was maintained above the substrate surface. The pool was cleaned weekly using a hose to prevent the proliferation of insect larvae.

The four assessment periods (0, 20, 40, and 60 days) represented the periods of exposure of seedlings to flooding compared to the non-flooded seedlings (control). The time of 0 days was characterized by seedling assessments under the same conditions before flooding begins, that it is initial time. Twelve flooded seedlings were taken at each assessment period, and part of them was destined for the flooding effect assessment and the other part was drained naturally and maintained at 75% SWC to be assessed in the next phase (second phase), called post-flooding recovery periods.

The recovery period, that is, the second part of the study, consisted of assessing the seedlings at 100 days after interrupting each flooding period, being characterized as 0+100, 20+100, 40+100, and 60+100 days, as well as non-flooded seedlings (control), which were also assessed in the same periods.

Temperature and relative humidity data during all experimental periods were obtained from the Weather Station of Embrapa Western Agriculture, Dourados, MS, Brazil (Figure 1).

2.2. Analysis and sampling

2.2.1. Survival of seedlings, Lenticels and Adventitious Roots

Morphological changes were detected visually, consisting of the development of lenticels and adventitious roots. Survival was assessed based on seedling dryness and mortality.

2.2.2. Gas exchanges

Using an infrared gas analyzer (IRGA), brand ADC and model LCi PRO (Analytical Development Co. Ltda, Hoddesdon, UK), plants were evaluated with regard to the leaf net photosynthesis – *A* (μmol m^{-1} s^{-1}), stomatal conductance – *gs* (mol m^{-2} s^{-1}) and instantaneous Rubisco carboxylation efficiency –*A/Ci* (μmol μmol mol^{-1}). The evaluations were carried out by the average reading of two leaves of each repetition (totaling eight readings and four averages) in the morning from 8 to11 am on completely expanded and previously marked leaves, which means all measurements were always taken from these marked leaves, considering data measured under photosynthetic photon flux equal to 1500 μmol m^{-2} s^{-1}.

2.2.3. The potential quantum efficiency of photosystem II – F_V/F_M

It was obtained using a portable fluorometer model OS-30p (Opti-SciencesChlorophyllFluorometer, Hudson, USA) from 8 to 11 am on the same leaves used to evaluate gas exchanges, which were submitted to a 30 min dark adaptation period using leaf-clip holders, so that all reaction centers in that foliar region acquired the "open" condition, indicating the complete oxidation of the photosynthetic electron transport system.

2.2.4. Seedling growth

The growth was evaluated in four seedlings, and root length (cm) was measured by the largest root with a ruler graduated in millimeters and the Dickson's Quality Index (DQI) according to the mathematical expression of Dickson et al. (1960) in which:

$$\text{DQI} = \left[\text{total dry matter/}\left(\begin{array}{l}\text{height/diameter ratio +}\\ \text{shoot dry matter/ root dry matter ratio}\end{array}\right)\right] \quad (1)$$

2.2.5. Total proteins in leaves (mg)

Total proteins were quantified according to the methodology from Bradford (1976) using fresh leaves from four seedlings consisting in four repetitions. Absorbance readings were performed in triplicates at the wavelength of 595 nm using a spectrophotometer (Metash Visible Spectrophotometer - model V5000).

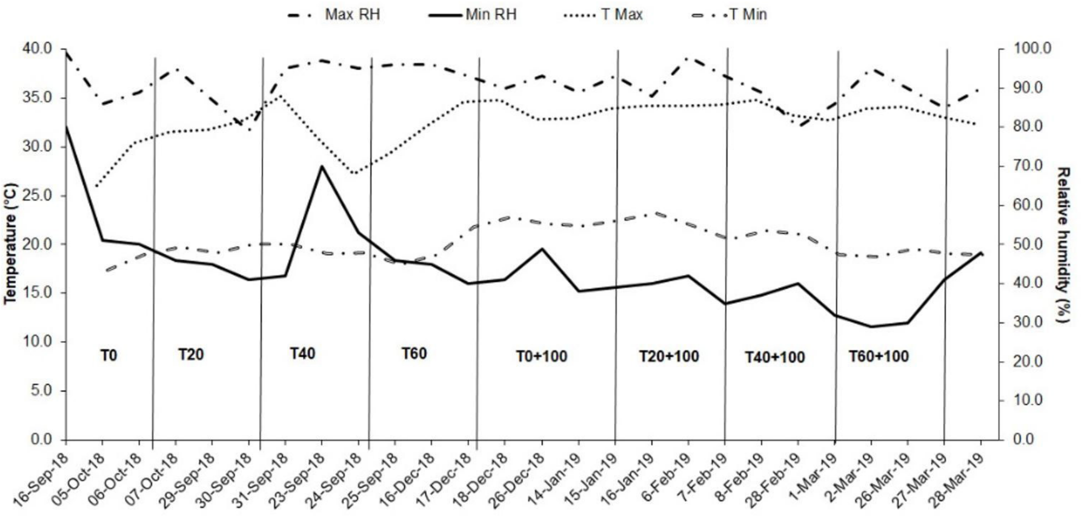

Figure 1. Relative humidity and relative temperature during the periods of flooding (T0, T20, T40 and T60) and recovery (T0 + 100, T20 + 100, T40 + 100 and T60 + 100). RH max = maximum relative humidity (%), UR min = minimum relative humidity (%), T max = maximum temperature (°C), T min = minimum temperature (°C).

2.2.6. *Enzymes activity in leaves (mg protein^{-1})*

The peroxidase (POD) activity (mg protein^{-1}) was obtained by preparing the extract with fresh leaves from four seedlings, the activity was determined by the direct spectrophotometric method, converting guaicol to tetraguaiacol at 470 nm (Hammerschmidt et al., 1982) using an ELISA microplate reader (Expert Plus model).

The superoxide dismutase (SOD) activity (mg protein^{-1}) was measured according to Giannopolitis and Ries (1977), using fresh leaves from four seedlings to prepare the extract. The absorbance readings were performed in triplicates at the wavelength of 560 nm using a spectrophotometer (Metash Visible Spectrophotometer - model V5000).

2.3. *Statistical analysis*

At each phase the experiment was conducted in a completely randomised design with four replications, in a 2x4 factorial scheme (two water regimes and four periods) for evaluation periods and recovery periods. The data collected were submitted to analysis of variance with 5% significance, when detected differences, the averages relating to water regimes in each evaluation period were compared by the Bonferroni T test (5%) and the periods were adjusted by regression equations, using the statistical program SISVAR 5.6 (Ferreira, 2019). In the absence of interaction between the factors, we present the single effect of each significant treatment. The two phases of the experiment, being independent, were not compared with each other.

3. Results

3.1. *Survival of seedlings, Lenticels, Adventitious Roots*

We verified that even with flooding sensitivity, *D. alata* seedlings showed 100% survival during both periods of exposure to flooding and post-flooding. Lenticel development was evident at the base of stems submerged in flooded *D. alata* seedlings during all assessment periods and initially detected at 14 days after flooding (Figure 2). These structures remained evident at 100 days after flooding, presenting a dehydrated aspect.

Adventitious roots were not formed during the periods of assessment and recovery. Also, the seedlings showed 100% survival during the periods of exposure to flooding and post-flooding even with sensitivity to flooding.

3.2. *Gas exchanges*

The leaf net photosynthesis (*A*) (Figure 3A) and instantaneous Rubisco carboxylation efficiency (*A/Ci*) (Figure 3C) of flooded plants remained reduced compared to the control seedlings in the assessment periods with values that did not vary during 60 days of flooding. On the other hand, no significant difference was observed between the previously flooded seedlings and the control for these physiological characteristics in the recovery periods (Fig. 3BD).

The flooded seedlings also maintained low *gs* values, which showed no variation between assessment periods. However, control seedlings had a maximum value of 0.069

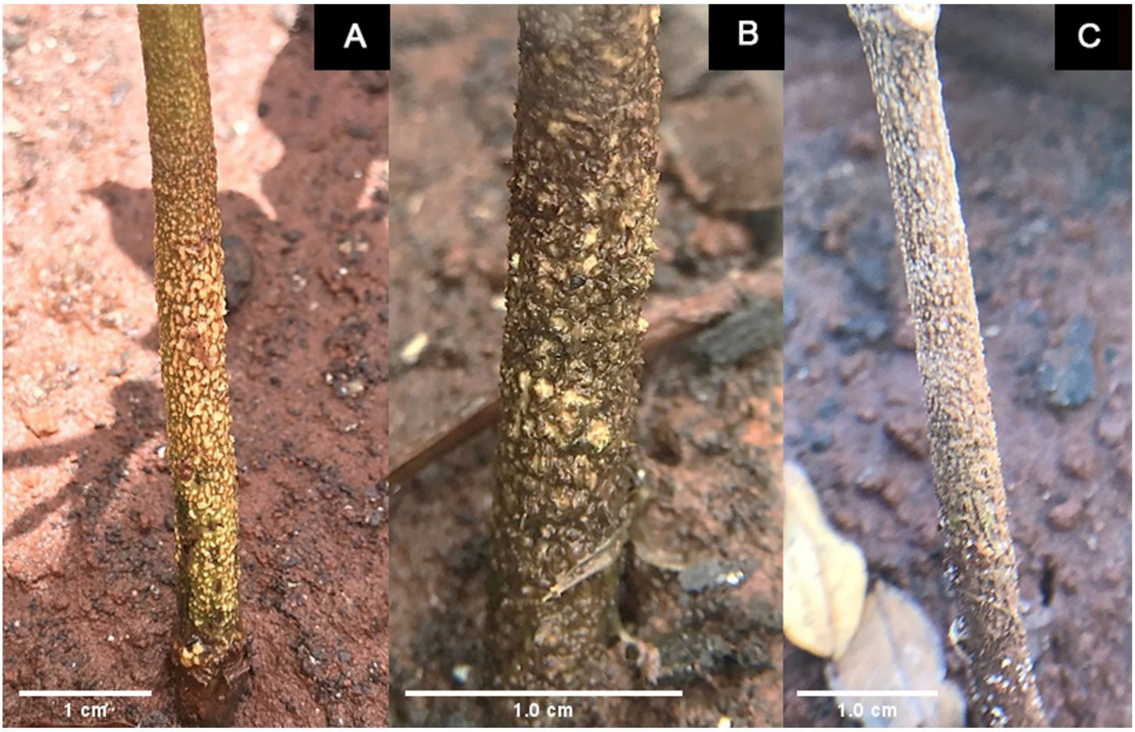

Figure 2. Presence of hypertrophied lenticels in the bases of *D. alata* flooded seedlings stems during the evaluation periods of 20 days (A), 40 days (B) and 60 days (C) in flooded plants. Photos: Autores.

mol m^{-2} s^{-1} at 35 days, with subsequent reduction, but still higher than flooded seedlings (Figure 3E). This reduction is related to the low relative humidity during the period, characterized by the assessment days from 11/23/2018 to 12/17/2018 (Figure 1). Plants previously flooded for up to 60 days in the recovery periods showed values similar to

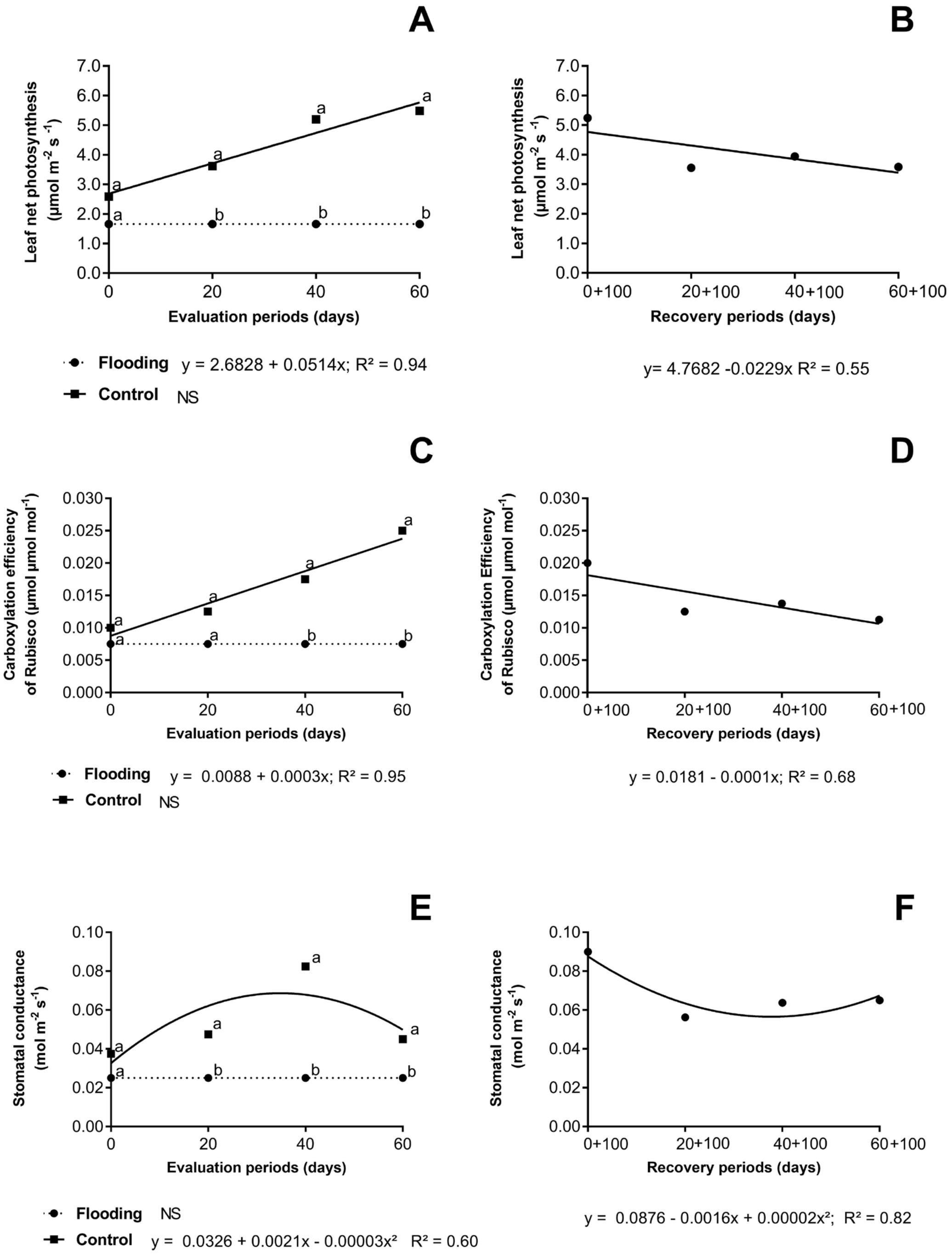

Figure 3. Gas exchange in *D. alata* seedlings. Photosynthetic rate - A (µmol m^{-2} s^{-1}) in seedlings under flooding and control for up to 60 evaluation days (A) and depending on the recovery periods for this characteristic, 100 days after each evaluation (B); Instant efficiency of the Rubisco –A / Ci (µmol m^{-2} s^{-1}) carboxylation under flooding and control seedlings for up to 60 evaluation days (C) and depending on the recovery periods for this characteristic, 100 days after each evaluation (D); Stomatal conductance - gs (mol m^{-2} s^{-1}) in seedlings grown under flooding and control for up to 60 evaluation days (E) and depending on the recovery periods for this characteristic, 100 days after each evaluation (F). Same lower case letters do not differ by Bonferroni t test ($p \geq 0.05$) for water regimes. NS = not significant.

those of the control plants, with a minimum *gs* of 0.055 mol m^{-2} s^{-1} (Figure 3F).

3.3. The potential quantum efficiency of photosystem II – F_V/F_M

Flooded plants had the lowest F_V/F_M values and we found that the reductions were accentuated due to the time of exposure to this stress condition (Figure 4). No significant difference was found between previously flooded plants and control plants during the recovery periods, in which we observed a general average for F_V/F_M of 0.679.

3.4. Seedling growth

The maximum root length was observed at 43 days (42.89 cm), with a subsequent decrease, being higher in the control plants (Figure 5A). The minimum root growth in the recovery periods was 51.83 cm and we observed a recovery trend from seedlings previously flooded for 40 days (Figure 5B).

Control and flooded seedlings had no significant difference regarding the Dickson quality index (DQI) in the assessment periods for up to 40 days (Figure 5C). However, control seedlings showed higher quality at 60 days. The same behavior was observed in the next phase, that is, the recovery periods (Figure 5D).

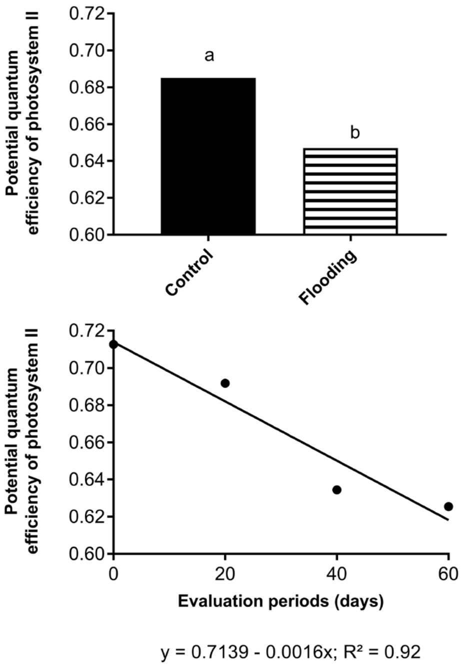

Figure 4. Potential quantum efficiency of photosystem II- FV / FM in D. *alata* seedlings depending on water regimes and evaluation periods, in isolation. Lower case letters compare the means by the Bonferroni t test ($p \geq 0.05$) for water regimes.

3.5. Total proteins in leaves (mg)

We verified a reduction in protein synthesis under both irrigation conditions, but more pronounced under flooding, in which seedling leaves presented lower total proteins, suggesting stress. Flooded seedlings had a minimum total protein value of 13.70 mg and control seedlings reached a value of 21.46 mg at 46 and 37 days, respectively. However, an increase in this value was observed from 40 days, suggesting a trend to adjust to growing conditions (Figure 6A), which can be confirmed by the values in the recovery periods when seedlings had no significant differences between water regimes (Figure 6B). The decrease in total proteins in control plants in the initial assessment periods can be associated with abiotic stresses (Figure 6A), such as low relative humidity during (Figure 1) and/ or post-transplant stress.

3.6. Enzymes activity in leaves (mg protein^{-1})

Flooded seedlings showed higher peroxidase (POD) enzyme activity in their leaves in the assessment periods at 24 days, reaching the maximum value of 2.54 mg protein^{-1}, while control seedlings presented the maximum activity of 1.50 mg protein^{-1} at 21 days (Figure 7A). However, the difference in activity decreased from 40 days and the reduced values presented no statistical difference from control seedlings at 60 days (Figure 7A). Moreover, seedlings previously flooded for 60 days did not differ from the control during the recovery period, but the data did not fit the tested mathematical models (Figure 7B).

We observed that the superoxide dismutase (SOD) activity in the leaves of flooded plants was higher than that found in control plants during the assessment periods, reaching a maximum value of 150.50 mg protein^{-1} at 56 days (Figure 7C). However, we observed in the recovery periods that only seedlings previously flooded for 60 days reduced the activity of this enzyme and recovered values similar to those of control plants (Figure 7D).

4. Discussion

Our results disagree with the hypothesis that *D. alata* does not tolerate flooding and demonstrate that this species, although sensitive to flooding during 60 days of flooding, it has phenotypic plasticity that favors its survival and potential for post-flooding recovery. Thus, morphological adjustments in photosynthetic and antioxidant metabolism allowed recovering seedlings after flooding. We emphasize that the species is promising for projects aimed at recovering degraded areas subject to temporary flooding.

Based on the analyzed characteristics, we verified that *D. alata* seedlings are sensitive to flooding, with lenticel development, increased activity of the leaf antioxidant enzyme system, and adjustments in gas exchanges, which alleviated the stressful flooding effect and favored the recovery of seedlings, which showed 100% survival .

Stomatal and non-stomatal causes were attributed to reduced photosynthesis during flooding (Liu et al., 2014). Stomatal causes are associated with the possible closure

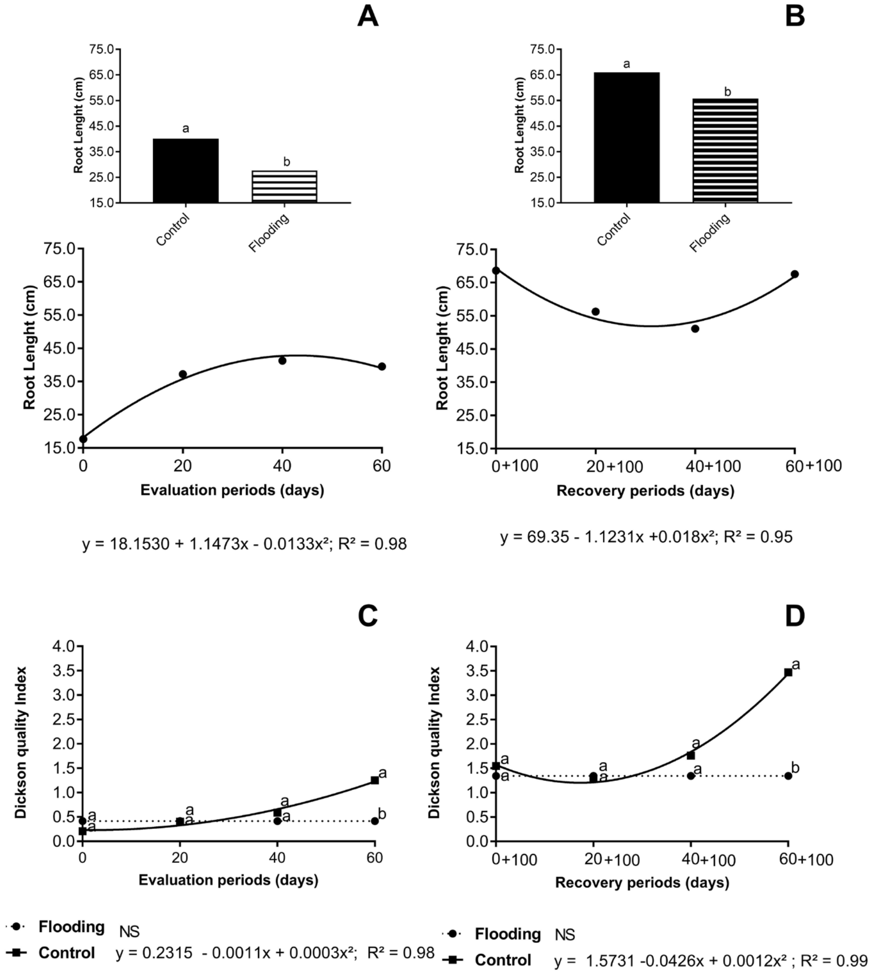

Figure 5. Growth e quality of *D. alata* seedlings. Root length (cm) as a function of water regimes and assessment periods, alone, (A) and as a function of water regimes and recovery periods, 100 days after each assessment, alone (B); Dickson's quality index (IQD) of seedlings grown under flooding and control for up to 60 evaluation days (C) and depending on the water regimes and recovery periods for this characteristic, 100 days after each evaluation (D). Same lower case letters do not differ by Bonferroni t test ($p \geq 0.05$) for water regimes. NS = Not significant.

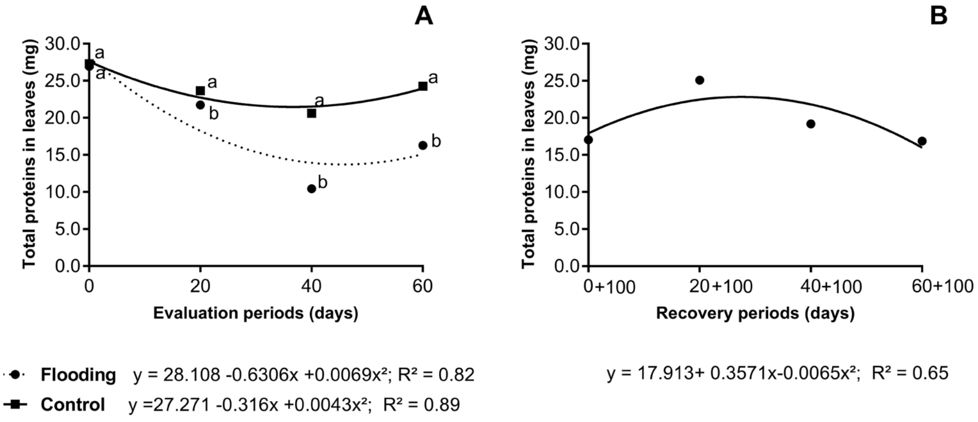

Figure 6. Total leaf proteins (mg) of *D. alata* seedlings. Due to flooding and control for up to 60 evaluation days (A) and due to the recovery periods for this characteristic, 100 days after each evaluation (B). Same lower case letters do not differ by Bonferroni t test ($p \geq 0.05$) for water regimes.

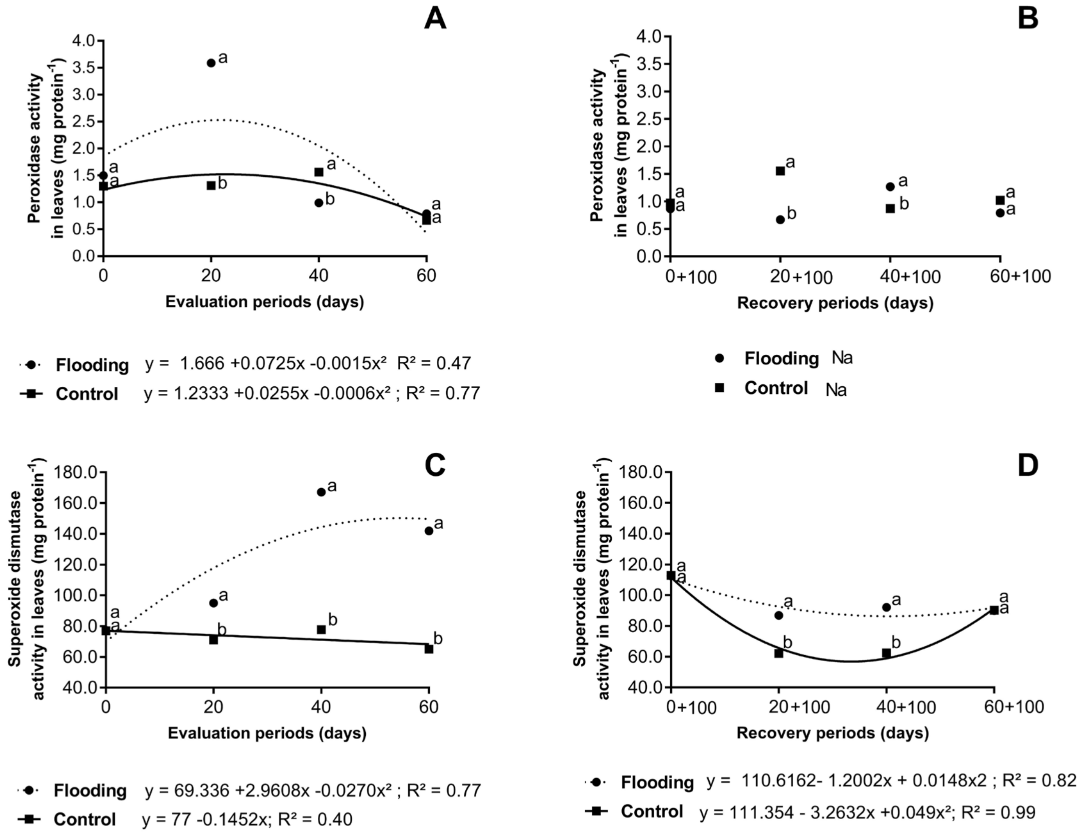

Figure 7. Enzymatic activity in *D. alata* seedlings. Peroxidase (POD) due to flooding and control for up to 60 days of evaluation (A) and depending on water regimes and recovery periods for this characteristic, 100 days after each evaluation (B). Superoxide dismutase (SOD) due to flooding and control for up to 60 days of evaluation (C) and depending on water regimes and recovery periods for this characteristic (D). Same lower case letters do not differ by Bonferroni t test ($p \geq 0.05$) for water regimes. Na = Not adjusted.

of stomata, which was not assessed in this study but is associated with a reduction in *gs*, which hindered the entry of CO_2 and caused reductions in the ribulose-1,5-bisphosphate carboxylase/oxygenate (Rubisco) activity (non-stomatal cause) (Dalmolin et al., 2013; Liu et al., 2014; Vidal et al., 2019), reducing photosynthetic metabolism, which was verified in this study.

Although low *gs* values right after flooding were found in the literature in both susceptible and tolerant species to stress, recovery often occurs in the latter. Therefore, the reduction in *gs* is a fundamental indicator of the survival of flooded plants, as it controls excess transpiration when water intake is affected (Kissmann et al., 2014). In this context, we verified that the survival of *D. alata* seedlings in this work was total.

Plants considered tolerant or adapted to stress can acclimatize even when their roots are under conditions of limited oxygen availability to maintain stomatal conductance and leaf net photosynthesis at stable levels to allow their survival. Thus, plant growth and development may be interrupted as an escape from stress because, under these conditions, the energy reserves are destined for metabolism in response to plant survival and protection, such as the formation of morphological and anatomical structures (e.g., lenticels and adventitious roots), (Dolferus, 2014; Li et al., 2015; Junglos et al., 2018; Queiroz-Alves et al., 2019) as verified in this work with *D. alata* seedlings.

These last structures were not found during the assessed period in *D. alata* seedlings, but the presence of lenticels, essential in gas exchange under hypoxia and anoxia conditions, favoring the increase in O_2 uptake, is an indication of phenotypic plasticity. Not necessarily, all of these changes must occur at the same time for a plant to be considered tolerant or with high phenotypic plasticity (Sauter, 2013; Queiroz-Alves et al., 2019).

Under flooding, root respiration underwent an immediate drop due to oxygen deficiency, with reductions in ATP production, limiting the energy supply for root and shoot growth (Zanandrea et al., 2010). On the other hand, this growing interruption is related to metabolic changes during the flooding period, which shows an increased production of the ethylene hormone, considered an important signal of water stress, allowing energy reserves to be used for the formation of organs, tissues, or structures that assist plant survival during stress, such as hypertrophied lenticels (Voesenek and Sasidharan, 2013; Dolferus, 2014), which may have led to lower growth of *D. alata* roots as the exposure to flooding increased. Based on the fact that photosynthetic characteristics have been recovered, we believe that periods higher than 100 days after flooding could allow the recovery of this characteristic too, but further studies are necessary.

The Dickson quality index (DQI), considered an indicator of seedling vigor and assessed in several species before being transplanted to the field (Fonseca et al., 2002), indicated that *D. alata* seedlings had no increased quality with an increase in the time of exposure to flooding despite all the physiological, biochemical, and morphological changes. This behavior was also observed in the recovery phase, and previously flooded seedlings maintained a lower DQI during the 100 days after flooding.

The reduction in the potential quantum efficiency of photosystem II (F_V/F_M) reflects the photoinhibitory impairment caused by flooding (Liu et al., 2014), as observed in *D. alata* seedlings flooded in the different assessment periods, but followed by recovery after the suspension of the stress factor, as no significant difference was observed between treatments at this stage. Changes in the xanthophyll cycle that correspond to reductions in photosynthesis may be associated with the ability to withstand the photodamage (Qiu et al., 2003; Yu et al., 2015).

The reduction of total protein in the leaves of seedlings under flooding is a response commented on in the literature. Bertolde et al. (2014) reported that O_2 deficiency due to flooding causes changes in gene transcription, protein synthesis/degradation, and plant cell metabolism. The low availability of ATP generated by inhibition of the mitochondrial electron transport chain is accompanied by an inhibition of energy-consuming processes associated with cell division and growth, including synthesis of DNA, proteins, ribosomes, and cell wall (Voesenek and Bailey-Serres, 2015).

On the other hand, protein synthesis can also be compromised due to the activation of the anaerobic metabolism, which can cause a high ROS production, affecting cell survival and causing the oxidation of lipids, membrane proteins, and nucleic acids (Voesenek and Sasidharan, 2013).

Moreover, the decrease in F_V/F_M also contributes to the ROS occurrence, such as superoxide anions and H_2O_2, which damage chloroplast structures and, consequently, harm *A* (Yu et al., 2015). The balance between an increase in ROS production and the ability to respond to flood stress through the rapid activation of the antioxidant defense system is related to tolerance or adaptation to this limiting condition (Larré et al., 2016).

Peroxidase and catalase have an important function in controlling the intracellular concentration of hydrogen peroxide (H_2O_2), considered one of the ROS that most cause cell damage (Bansal and Srivastava, 2015). Therefore, the increase in its activity can be considered response of protection from stress. However, seedlings had a reduction in POD activity with an increase in the time of exposure to flooding, suggesting that another antioxidant mechanism, such as catalase, could contribute to this protection, but we were unable to obtain data on this enzyme activity.

The enzyme SOD is considered as the first barrier against stress since it performs the function of removing the superoxide ion ($O2^{\bullet-}$) and catalyzing its dismutation to oxygen and hydrogen peroxide, which can be decomposed by several pathways, such as catalase and peroxidase (Liu and Jiang, 2015). The increase in the activity of antioxidant enzymes observed during flooding reinforces ROS production and the activity of these enzymes in the fight against ROS, which we believe contributed to the recovery of F_V/F_M in the post-flooding.

In this study, we did not quantify the products of the activity of these antioxidant enzymes, which could be evaluated in future studies, as well as the activity of the catalase enzyme to complement the understanding of the physiological behavior of this species under flooding.

We also suggest that further studies should be carried out to test recovery periods higher than 100 days after flooding, considering the high recovery potential of seedlings under flooding although with the compromised quality and length of roots.

5. Conclusion

The occurrence of hypertrophied lenticels associated with physiological changes and an efficient antioxidant enzyme system must have contributed to the survival and recovery of seedlings. We suggest that the species is sensitive to flooding stress but capable of adjusting and recovering metabolic characteristics at 100 days after flooding suspension. However, seedling quality is compromised, with no recovery. Therefore, we suggested plasticity under this condition of cultivation and determined that 100 days is not enough for the complete resumption of growth.

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