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Original Article

Water-retaining polymer in *Dipteryx alata* seedlings: strategy to mitigate the effect of water deficit

Polímero hidroretentor em mudas de *Dipteryx alata*: estratégia para mitigar o efeito do déficit hídrico

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Abstract

Water deficit is a stressful condition that negatively affects photosynthetic metabolism and plant growth. In an attempt to alleviate the effect of low water availability, the use of water-retaining polymer (hydrogel) has proven to be a viable strategy. We aimed to evaluate the effect of the hydrogel on photosynthetic metabolism and antioxidant protection in *Dipteryx alata* Vogel. seedlings under water deficit and on potential recovery in post-stress. The seedlings grown under the following water regimes: i) control – irrigated daily, ii) water deficit – suspension of irrigation, and iii) water deficit + hydrogel – addition of polymer in the time of transplanting. Assessments were carried out at photosynthesis close to zero and at recovery (resumption of irrigation after). We observed decreased in gas exchange and growth of seedlings subjected to water deficit in photosynthesis close to zero, but those with hydrogel maintained high values, in addition to a more efficient recovery. Although the hydrogel did not contribute to chlorophyll *a* fluorescence, it favored enzymatic regulation similar to control plants, especially peroxidase in leaves and roots, and superoxide dismutase in roots. *D. alata* responds to water deficit activating protective mechanisms through physiological and antioxidants adjustments that ensure its survival when exposed to water deficit and its recovery post-stress, indicating phenotypic plasticity. The hydrogel contributes positively to the photosynthetic, enzymatic, and quality maintenance of *D. alata* seedlings during and after stress.

Keywords: antioxidant enzymes, chlorophyll *a* fluorescence, hydrogel, photosynthetic metabolism, phenotypic plasticity.

Resumo

O déficit hídrico é uma condição estressante que afeta negativamente o metabolismo fotossintético e o crescimento das plantas. Na tentativa de amenizar o efeito da baixa disponibilidade hídrica, o uso de polímero hidroretentor (hidrogel) tem demonstrado ser uma estratégia viável. Objetivamos avaliar o efeito do hidrogel sobre o metabolismo fotossintético e de proteção antioxidante em mudas de *Dipteryx alata* Vogel sob déficit hídrico e no potencial de recuperação pós-estresse. As mudas foram cultivadas sob os seguintes regimes hídricos: i) controle – irrigadas diariamente, ii) déficit hídrico – suspensão da irrigação e iii) déficit hídrico + hidrogel – adição do polímero no momento do transplantio. As avaliações foram realizadas em fotossíntese próximo a zero e na recuperação (retomada da irrigação). Observamos redução das trocas gasosas e crescimento das mudas submetidas ao déficit hídrico na fotossíntese próximo a zero, mas aquelas com hidrogel mantiveram os valores elevados, além de uma recuperação mais eficiente. Embora o hidrogel não tenha contribuído na fluorescência da clorofila a, favoreceu a regulação enzimática semelhante as plantas controle, especialmente da peroxidase nas folhas e raízes e superóxido dismutase nas raízes. *D. alata* responde ao déficit hídrico ativando mecanismos de proteção por ajustes fisiológicos e antioxidantes que asseguram sua sobrevivência quando expostas ao déficit hídrico e sua recuperação no pós-estresse, indicando plasticidade fenotípica. O hidrogel contribui positivamente na manutenção fotossintética, enzimática e de qualidade das mudas de *D. alata* durante e após o estresse.

Palavras-chave: enzimas antioxidantes, fluorescência da clorofila *a*, hidrogel, metabolismo fotossintético, plasticidade fenotípica.

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1. Introduction

Global climate change has been a cause for concern in several sectors such as forestry, and has become one of the most discussed topics among professionals working in plant ecophysiology. From this perspective, water is one of the most limiting factors on plant morphophysiology, especially considering that several areas are subject to seasonal droughts, affecting seedling establishment in afforestation and reforestation areas.

Lower soil water availability impairs photosynthetic metabolism and production of photoassimilates in plants, which affects their growth and quality (Saracho et al., 2021; Yang et al., 2023; Haghpanah et al., 2024). However, when exposed to adverse conditions, plants may exhibit adjustment mechanisms, whether morphophysiological or biochemical, in order to ensure their survival (Santos et al., 2023). However, according to these authors, resilience varyng on the plasticity potential of each species, and the plant may adjust and recover or enter a state of exhaustion and cell death.

Therefore, establishing strategies that can solve this unfavorable environmental situation has been the focus of research, and the water-retaining polymer (hydrogel) has gained prominence as a product with the potential to mitigate the effects of water deficit. The product's composition contains a polymer chain with polyacrylamide, which, when in contact with water, has the capacity to absorb and expand 300 to 400 times its initial particle size (Kaur et al., 2023; Ma et al., 2023), favoring hydraulic conductivity (Santos et al., 2021), becoming a source for water supply in periods with lower water availability in the soil.

Among the promising species in silvicultural systems, *Dipteryx alata* Vogel., known as "baru" (Fabaceae), in addition to the ecological benefits such as shading and refuge for wild animals, its fruits have appreciable characteristics for human consumption and in agro-industrial products. Although *D. alata* occurs in several phytophysiognomies, Jesus et al. (2022) and Silva et al. (2022) found that when exposed to water deficit, the seedlings decreased their quality as a result of damage to the functioning of photosynthetic apparatus.

We hypothesized that (i) *D. alata* is responsive to water deficit, activating morphophysiological and antioxidant protection mechanisms, (ii) that addition of hydrogel may be a strategy to alleviate the stressful effect and possible damage to the photosynthetic apparatus, and (iii) the seedlings have the recovery potential when normal water supply is resumed. We aimed to evaluate the effect of hydrogel on photosynthetic metabolism and antioxidant protection in *D. alata* seedlings under water deficit and recovery potential post-stress.

2. Material and Methods

2.1. General conditions

The experiment was developed in a greenhouse with top and side coverage with black nylon mesh with 30% shading and additional protection with 150 µm plastic coverage to avoid rainfall, at the Faculty of Agricultural Sciences (22° 11' 51.5" S, 54° 56' 04.3" W), of Federal University of Grande Dourados (UFGD), Dourados – MS, Brazil.

Ripe fruits of *D. alata* were collected from five matrices distributed in remaining areas of Cerrado (21º 49' 19.6" S and 53º 14' 43.1" W), in the municipality of Nova Andradina, MS, Brazil. The seeds were selected for integrity and uniformity. To obtain seedlings, sowing was carried out in 50 × 190 mm tubes containing Oxisols corresponding to Dystroferric Red Latosol, commercial substrate and coarse sand in the proportion of 1:1:1 (v/v).

At 35 days after sowing, when they reached 15 cm in height, the seedlings were transplanted into pots with a capacity of 7 liters, with a mixture of Dystrophic Red Latosol + and coarse sand (3:1, v/v) and a nursery with 30% shade and daily irrigation during 45 days, characterizing the period of 1st acclimatization.

2.2. Water regimes and evaluation periods

D. alata seedlings were subjected to three water regimes: i) control - irrigation was carried out daily, maintaining 70% of the water retention capacity in the substrate according to the methodology of Souza et al. (2000), ii) water deficit (WD), characterized by the suspension of irrigation (SI) and iii) WD + hydrogel: addition of 20 mL of water-retaining polymer at the time of transplanting the seedlings, remaining for another 25 days in 2nd acclimatization and subsequent SI.

The hydrogel was prepared using the Forth Gel® at a dose of 4 g L^{-1} of water as recommended by the manufacturer, leaving it to stand for 45 min until it presented the appearance of a hydrated gel, and of the product was added at the time of seedling transplantation to each stress + hydrogel pot close the plant roots. Forth Gel® is composed of potassium polyacrylic polyacrylamide copolymer, CEC 532.2600 ($mmol_c$ dm^3) and water retention capacity of 1,526.690%.

The evaluations were carried out in two periods: P0 = period in which the seedlings subjected to stressful conditions reached photosynthesis (*A*) close to zero, which occurred 17 days after the suspension of irrigation. Photosynthesis was monitored every two days, considering favorable weather conditions. The second period was characterized as recovery (REC), resuming irrigation of all seedlings after P0, maintaining the WHC of 70%, until the seedlings previously subjected to stressful conditions presented *A* values ≥ 70% of that of the control seedlings, which occurred 13 days after P0, that is, 30 days.

The experimental design used was completely randomized, and the treatments were arranged in a subplot scheme, with the plots consisting of the evaluation periods (P0 and REC) and the subplots of the water regimes (control, WD, and WD + hydrogel), with three replicates, with each experimental unit consisting of a pot with two seedlings each.

2.3. Assessments

The evaluations of gas exchange, chlorophyll index, and chlorophyll *a* fluorescence were performed on fully expanded leaves located in the middle third, between 8 and 11 am, with photosynthetically active radiation > 900 µmol photons m^{-2} s^{-1}.

a) Chlorophyll *a* fluorescence: the leaves were subjected to dark conditions with leaf clips during 30 min. After this period, the initial fluorescence emission (F_0) and photochemical potential quantum efficiency of photosystem II (F_v/F_m) were determined using a portable OS p 30 fluorometer (Opti-Sciences Chlorophyll Fluorometer, Hudson, USA). The absorbed energy conversion efficiency (F_v/F_0) and the maximum basal yield of non-photochemical processes (F_0/F_m) were calculated.
b) Gas exchange: the CO_2 assimilation rate – photosynthesis (*A*, µmol CO_2 m^{-2} s^{-1}), transpiration (*E*, mmol H_2O m^{-2} s^{-1}), stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}) and intercellular CO_2 concentration (C_i, mol CO_2 m^{-2} s^{-1}) were quantified using a portable infrared gas analysis (IRGA) system – LCI Pro-SD ADC Bio Scientific Ltd, and subsequently the intrinsic carboxylation efficiency of Rubisco (A/C_i, µmol mol CO_2 m^{-2} s^{-1}) and water use efficiency (*A*/*E* – *WUE*, µmol CO_2 mmol H_2O m^{-2} s^{-1}) were calculated.
c) Enzymatic activity: 1 g samples of leaves and roots were previously frozen in liquid N, and 0.3 g of material was macerated in 6 mL of a solution containing 0.3 g of polyvinylpyrrolidone (PVP) diluted in 100 mL of potassium phosphate buffer (0.2 M). It was centrifuged at 12,000 rpm for 20 minutes and the supernatant was used as an enzymatic extract to determine superoxide dismutase (SOD) (µg FW^{-1}) and peroxidase (POD) (µg FW^{-1} $protein^{-1}$) activity according to the methodologies of Giannopolitis and Ries (1977) and Broetto (2014), respectively.
d) Growth and quality: plant height was measured with a ruler graduated in millimeters, using the distance between the collar and the inflection of the highest leaf as the evaluation standard, and stem diameter (mm) using a digital caliper. The seedlings were removed whole from the pots, separated into shoots and roots, and the length of the largest root (cm) was measured with a ruler. The leaf area (cm^2) was determined using an area integrator (LI-COR, 3100 C – Area Meter). To obtain dry biomass, the shoots and roots were stored in an oven with forced air circulation at 60 ± 5 °C for 72 hours, with results expressed in g per plant. The Dickson quality index was calculated using the proposal of Dickson et al. (1960).
e) Phenotypic plasticity: the phenotypic plasticity index (PPI) was calculated for F_v/F_m, *A*, and DQI, in which the values of the seedlings subjected to WD without and with hydrogel were used, comparing them individually with the control, as proposed by Valladares et al. (2006). According to these authors, the values vary from 0 to 1, and the higher the value, the more plastic the characteristic evaluated.

3. Data Analysis

The data were subjected to analysis of variance, and when significant (F test, $p \leq 0.05$), the means of the isolated effects and interactions in function of water regimes were compared by the Tukey test and the evaluation periods by F test, both $p \leq 0.05$ ± standard error. For the phenotypic plasticity data, no statistical analysis was performed, presenting them in a descriptive manner (Santos et al., 2023).

3.1. Results and discussion

D. alata seedlings are responsive and sensitive to water deficit (WD), since drastically reduced photosynthetic metabolism and increased the activity of antioxidant enzymes as a protective mechanism, negatively affecting growth, especially in the recovery period. However, the use of water-retaining polymer alleviated the stressful effect of WD on gas exchange and some growth characteristics during the stress period, in addition to favoring recovery more efficiently, confirming our initial hypothesis.

Among the parameters of chlorophyll *a* fluorescence evaluated, all except the maximum basal yield of non-photochemical processes were influenced by the interaction between the factors under study (Figure 1). In general, the values of F_0 increased and those of the photochemical potential quantum efficiencies in the PSII (F_v/F_m) and absorbed energy conversion (F_v/F_0) decreased under WD, regardless of the use of the hydrogel, differing statistically from the control seedlings. In REC, all seedlings resumed photochemical activities similar to the control. The maximum basal yield of non-photochemical processes (F_0/F_m) was higher in seedlings under WD regardless of the hydrogel and the evaluation periods.

Low soil water availability negatively affects plant tissue water status and, consequently, water photolysis and hydrogen pumping, an important process in electron transfer and energy substrate production (Santos et al., 2021; Silva et al., 2022). This response promoted a decreased in F_v/F_m and an increase in F_0/F_m, indicating energy dissipation and inefficiency of photochemical activities in PSII, regardless of use of hydrogel.

The mitigating effect of the hydrogel on photochemical responses varies between species as reported by Santos et al. (2021), in which the addition of the polymer contributed to the activities in the PSII reaction centers of *Campomanesia xanthocarpa* O. Berg. seedlings under WD by favoring hydraulic conductivity, but according to Silverio et al. (2024) it contributed little in *Eugenia myrcianthes* Nied seedlings. Conversely, in our study with *D. alata*, even though it did not contribute to mitigating damage to the photochemical apparatus, this damage was reversible, since the photochemical yield values increased after normal water supply.

Regarding gas exchange, we observed interaction between water regimes and evaluation periods, with a decreased in the photosynthetic rate (*A*) under WD (0.90 µmol CO_2 m^{-2} s^{-1}) at P0, while those with water-retaining polymer maintained *A* values that did not differ statistically (8.86 µmol CO_2 m^{-2} s^{-1}) from the control in this same period (Figure 2A). In REC, seedlings previously subjected to stress conditions, regardless of the use of hydrogel, presented *A* values (> 7.00 µmol CO_2 m^{-2} s^{-1}) statistically similar to the control.

The response pattern of intrinsic carboxylation efficiency (A/C_i) was similar to that of *A* at P0, while in REC, the seedlings previously subjected to WD with hydrogel had higher values that differed statistically even from the

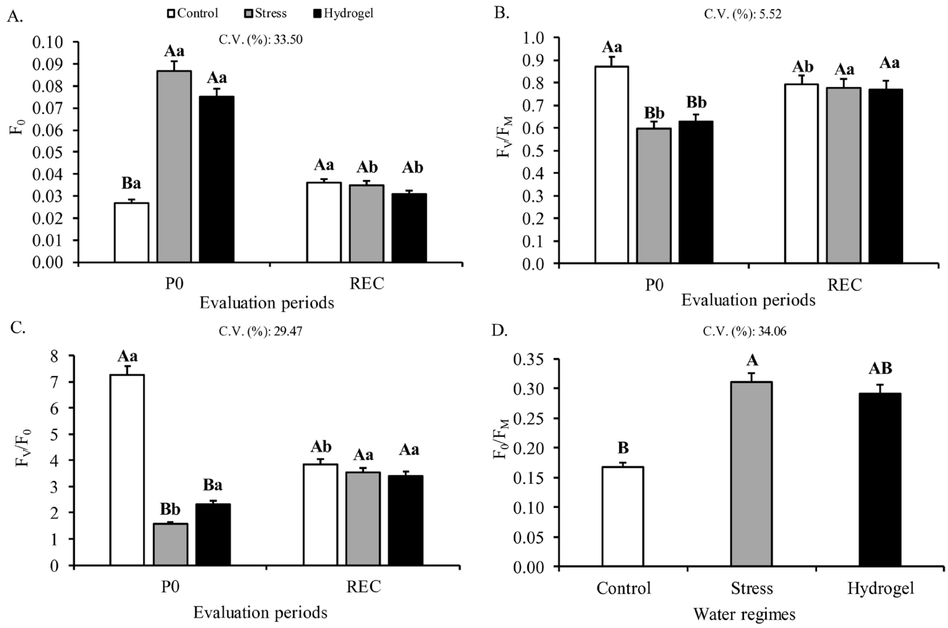

Figure 1. Initial fluorescence – F_0 (A), photochemical potential quantum efficiency in photosystem II – F_v/F_m (B), absorbed energy conversion efficiency – F_v/F_0 (C) and maximum basal yield of non-photochemical processes – F_0/F_m (D) in *Dipteryx alata* seedlings grown under different water regimes (control, stress, and hydrogel) and two evaluation periods (P0 and REC). Capital letters compare water regimes by Tukey's test and lowercase letters compare evaluation periods by F test, all at $p \leq 0.05$ ± standard error.

control (Figure 2B). Although the values of photochemical activities were impaired during the stress period, regardless of the hydrogel, this impairment was not reflected in CO_2 assimilation when the plants were subjected to hydrogel, demonstrating that the water made available in the water-retaining polymer favored the regeneration of Rubisco in the carboxylation.

Similarly, Beltramin et al. (2020) observed that *Schinus terebinthifolia* Raddi seedlings also maintained higher photosynthesis values even under WD, maintaining higher cellular water content. We suggest that with the addition of the hydrogel, the plants maintained higher *WUE* and turgor, which contributed to the efficiency of CO_2 assimilation and carboxylation.

We verified a decreased in stomatal conductance (g_s) in seedlings subjected to WD (0.03 mol H_2O m^{-2} s^{-1}), but those with hydrogel maintained higher values (0.11 mol H_2O m^{-2} s^{-1}), both at P0 (Figure 2C). In REC, all seedlings previously subjected to WD, regardless of use of hydrogel, resumed the g_s values, not differing statistically from the control. We observed an increase in the intercellular CO_2 concentration (C_i) in seedlings subjected to WD without hydrogel at P0 (344.33 mol CO_2 m^{-2} s^{-1}), differing from the other conditions in this period, while in REC seedlings with hydrogel presented lower values (251.66 mol CO_2 m^{-2} s^{-1}) of C_i (Figure 2D).

The *E* and *WUE* values showed the same response pattern at P0, in which the values decreased in seedlings under WD without hydrogel (0.59 mmol H_2O m^{-2} s^{-1} and 1.70 µmol CO_2 mmol H_2O m^{-2} s^{-1}), differing statistically from the other conditions in the same period. However, in REC, seedlings previously subjected to WD with hydrogel had lower and higher *E* and *WUE* values, respectively (Figures 2E and 2F). The increase in gas exchange values, especially *A*, g_s, A/C_i, and *WUE*, and the decreased in C_i suggest that *D. alata* seedlings have potential for ecological resilience through physiological plasticity.

Water deficiency promotes the overproduction of reactive oxygen species that degrade cellular structures and the photosynthetic apparatus (Takahashi et al., 2020; Samanta et al., 2024), which justifies the increase in C_i as a response to the inefficiency of Rubisco carboxylation in our study with *D. alata* under WD without hydrogel, reinforcing the sensitivity and responsiveness of species to this adverse condition, as also reported by Jesus et al. (2022) and Silva et al. (2022).

The activity of peroxidase (POD) and superoxide dismutase (SOD) in leaves was influenced by the interaction between the factors under study, while in the roots it was influenced by the factors alone (Figure 3). The POD activity was more pronounced in the leaves than in the roots, in which in the leaves, the highest values (0.90 µg FW^{-1} protein $^{-1}$) occurred in the seedlings under WD without hydrogel at P0, differing from the other conditions in this same period. However, in REC the values reduced (< 0.040 µg FW^{-1} $protein^{-1}$) and did not differ from the other conditions. In the roots, the highest values also occurred in the seedlings under WD without hydrogel, but regarding the evaluation periods, it was higher in REC.

SOD in leaves was higher (> 50 µg FW^{-1}) in seedlings exposed to WD regardless of use of hydrogel at P0, and in REC the values of seedlings previously subjected to WD did not vary statistically compared to the control. In the evaluation periods, the highest SOD value occurred at P0.

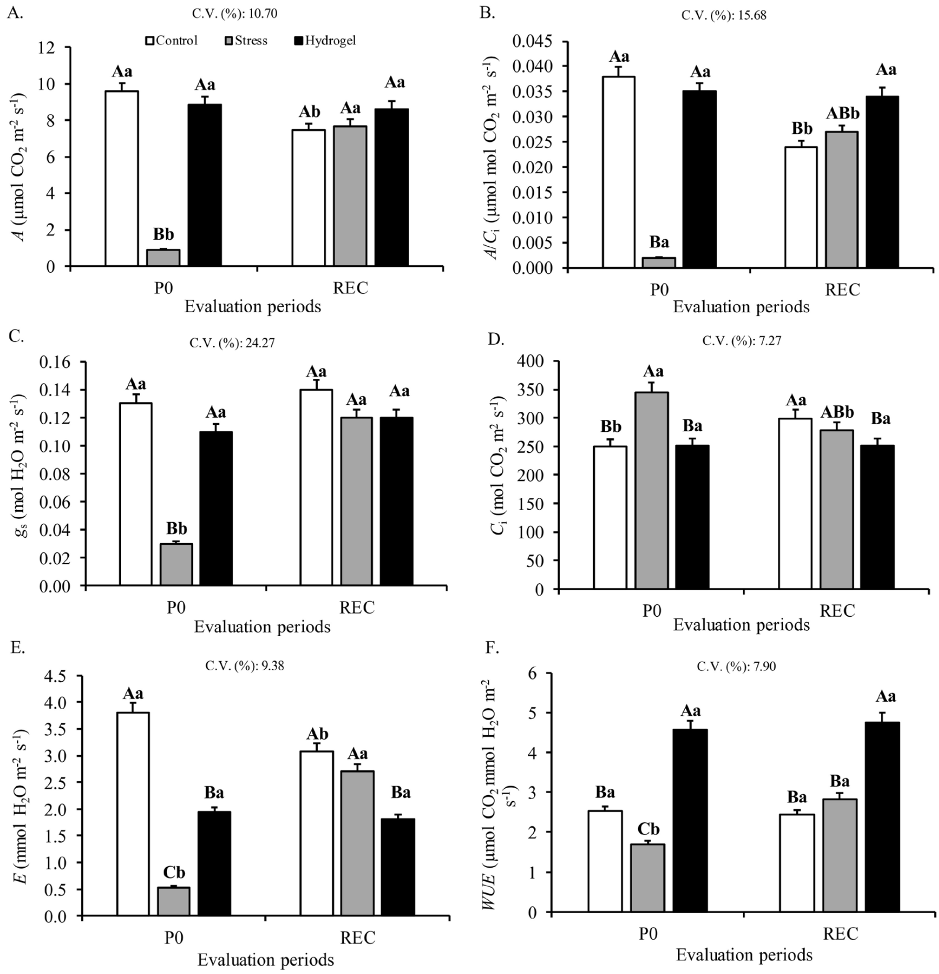

Figure 2. Photosynthetic rate – *A* (A), intrinsic carboxylation efficiency – A/C_i (B), stomatal conductance – g_s (C), intercellular CO_2 concentration – C_i (D), transpiration – *E* (E) and water use efficiency – *WUE* (F) in *Dipteryx alata* seedlings grown under different water regimes (control, stress, and hydrogel) and two evaluation periods (P0 and REC). Capital letters compare water regimes by Tukey's test and lowercase letters compare evaluation periods by F test, all at $p \leq 0.05$ ± standard error.

Plants have different mechanisms to adapt at adverse conditions. One of the most common responses to stress is an increase in the activity of antioxidant enzymes such as SOD and POD, which act to combat reactive oxygen species, alleviating oxidative stress and its damage to the cellular structure (Naeem et al., 2024; Silverio et al., 2024). Although there was an increase in SOD and POD as a defense mechanism against stress, plants with hydrogel only increased SOD, with no need to increase POD, that is, directing energy to maintain other metabolic processes such as *A* and A/C_i values.

The plant height and root dry mass was did not influenced by the factors under study ($p > 0.05$). The shortest root length (32.58 cm) occurred in seedlings with hydrogel, regardless of evaluation period (Figure 4A), owing the water is easily available in the polymer in the rhizosphere these plants, not requiring area expansion. For stem diameter and leaf area, the lowest values (4.12 mm and 216.51 cm^2) occurred in seedlings under WD without hydrogel, respectively, differing statistically from the control and hydrogel seedlings (Figures 4B and C). Under water deficit, plants generally reduce turgor, leaf expansion capacity, and photosynthesis (Haghpanah et al., 2024), similar to that observed in our study with *D. alata*.

Regarding shoot dry mass, we observed effect of isolated factors, with lower values under WD without hydrogel and at P0 (1.66 and 1.79 g per plant) (Figure 4D) reflecting the lower values of leaf area and photosynthesis, demonstrating lower production and accumulation of photoassimilates. The Dickson quality index (DQI) was influenced by the interaction, in which at P0 the seedlings under WD regardless of use of hydrogel reduced their quality, while at REC the seedlings with hydrogel had an increase and did not differ from the control, while those without hydrogel remained low (Figure 4E).

The phenotypic plasticity index (PPI) for *A* and DQI showed greater variation than F_v/F_m in function of water regimes, especially *A* under WD without hydrogel at P0, while those with hydrogel had little need to invest in plasticity in the same period (Figure 5).

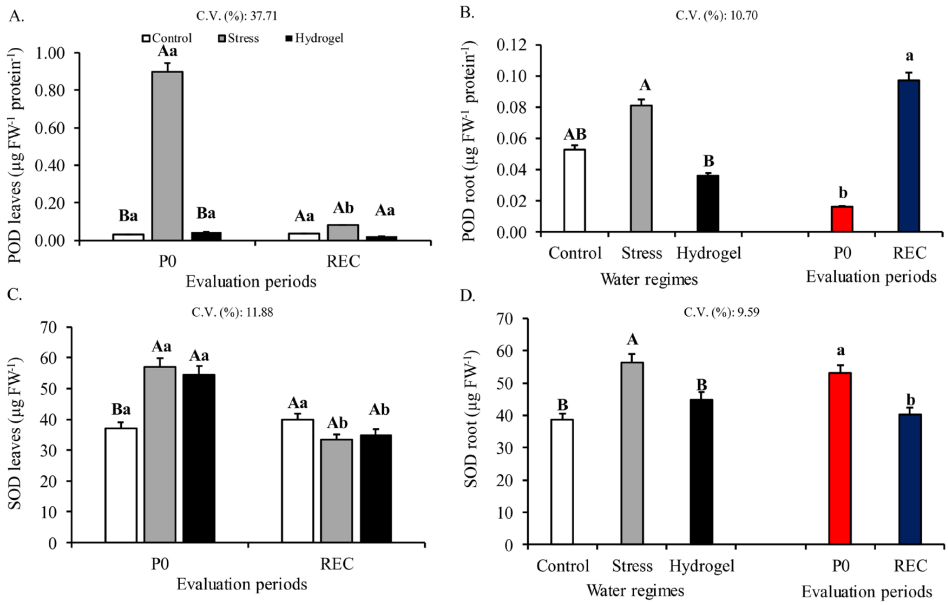

Figure 3. Peroxidase – POD in leaves (A) and roots (B) and superoxide dismutase – SOD activities in leaves (C) and roots (D) in *Dipteryx alata* seedlings grown under different water regimes (control, stress, and hydrogel) and two evaluation periods (P0 and REC). Capital letters compare water regimes by Tukey's test and lowercase letters compare evaluation periods by F test, all at $p \leq 0.05$ ± standard error.

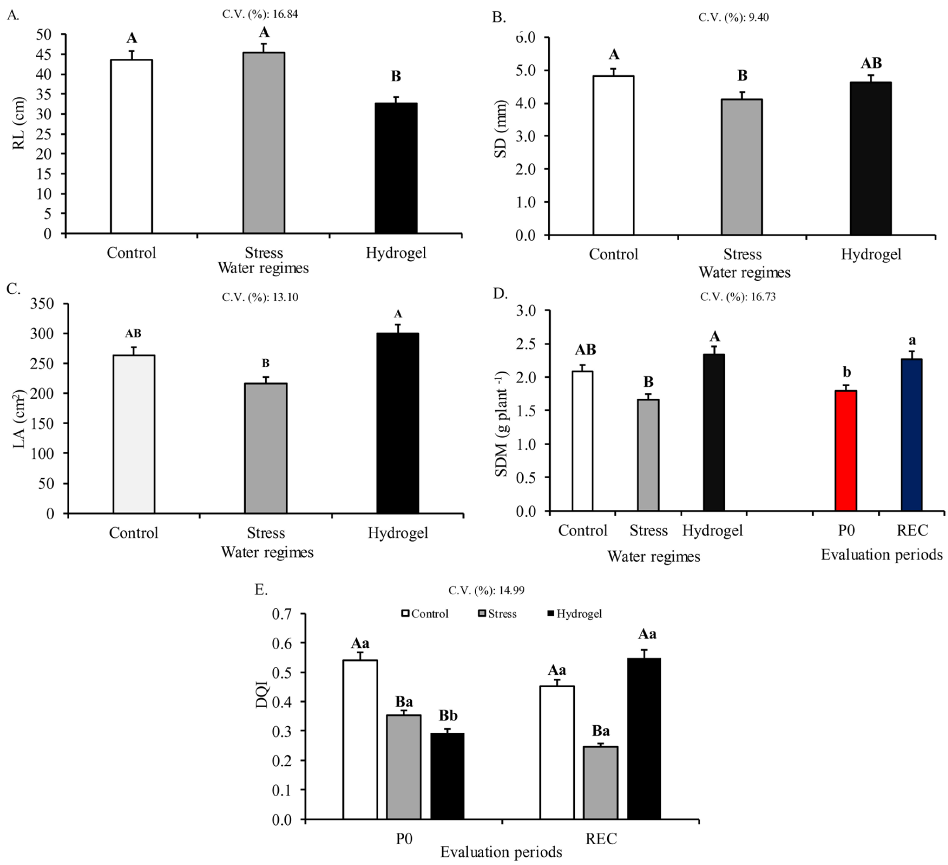

Figure 4. Root length – RL (A), stem diameter – SD (B), leaf area – LA (C), shoot dry mass – SDM (D) and Dickson quality index – DQI (E) in *Dipteryx alata* seedlings grown under different water regimes (control, stress, and hydrogel) and two evaluation periods (P0 and REC). Capital letters compare water regimes by Tukey's test and lowercase letters compare evaluation periods by F test, all at $p \leq 0.05$ ± standard error.

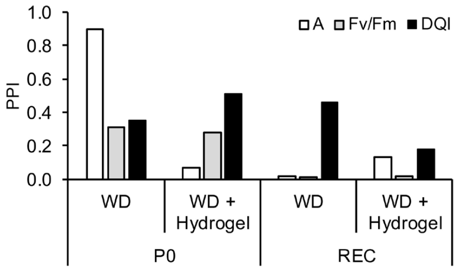

Figure 5. Phenotypic plasticity index (PPI) values for photosynthetic rate (*A*), photochemical potential quantum efficiency in photosystem II (F_v/F_m) and Dickson quality index (DQI) in *Dipteryx alata* seedlings subjected to water deficit (WD) without or with hydrogel, evaluated in two periods (P0 and REC).

However, the PPI for F_v/F_m was similar regardless of the use of hydrogel in both P0 and REC, reinforcing the low participation of the hydrogel in mitigating the stressful effect on the PSII reaction centers. Overall, in REC the PPI values for all characteristics decreased, except for DQI under WD without hydrogel, which remained high, that is, even when resuming the normal water supply, the production of photoassimilates was impaired.

The increase in PPI represents a strategy of the plant to adjust to a certain stressful condition, aiming at its survival, and as lower the value, the certain characteristic is closer to the control seedlings, as observed in those with hydrogel at P0. Conversely, increase in PPI for DQI indicates that seedlings with the polymer had higher values even than the control seedlings, reinforcing the role of water-retaining polymer in the recovery in a more efficient manner.

In general, the use of water-retaining polymers is a promising practice for this species, especially in areas of afforestation or reforestation, which are generally subject to seasonal or prolonged droughts, and is a strategy to contribute to inducing tolerance to this stressful drought condition. From a practical point of view, for a rural producer, research institutions or sustainable actions, the use of hydrogel, in addition to mitigating the deficit by supplying and retaining water in the soil, also helps the growth of seedlings, especially in the initial establishment phases.

4. Conclusions

Dipteryx alata seedlings are responsive and sensitive to water deficit, decreasing photosynthetic metabolism and growth potential. The water-retaining polymer alleviates the stressful effect of water deficit on gas exchange and dynamics of antioxidant enzyme activity and help in the potential more efficient post-stress recovery.

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Data Availability Statement

Research data is available in the body of the article.

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