BRAZILIAN
JOURNAL OF
BIOLOGY®

ISSN 1519-6984 (Print)
ISSN 1678-4375 (Online)

Original Article

Does silicon help to alleviate water deficit stress and in the recovery of *Dipteryx alata* seedlings?

O silício auxilia no alívio do estresse hídrico e na recuperação de mudas de *Dipteryx alata*?

M. S. Silva[a], S. P. Q. Scalon[a], C. C. Santos[a], J. M. Silverio[a], J. K. V. Santos[a] and D. M. Dresch[a]
[a]Universidade Federal da Grande Dourados – UFGD, Faculty of Agricultural Sciences, Dourados, MS, Brazil

Abstract

Water deficit to causes serious problems in the growth and development of plants, impairing their metabolism. Thus, it is necessary to use agents that can mitigate plant damage. This study assesses the potential of silicon to mitigate water deficit stress in *Dipteryx alata* Vogel seedlings and to help in their recovery after the resumption of irrigation. The study analyzed four water regimes: (I) Continuous irrigation; (II) Water deficit without Si; (III) Water deficit + 0.75 mL Si; and (IV) Water deficit + 1.50 mL Si. Seedlings were evaluated in four periods: (1) (T0 – time zero) at the beginning of the experiment, before irrigation suspension; (2) (P0) when the photosynthetic rates (*A*) of seedlings under irrigation suspension reached values close to zero, period in which irrigation was resumed; (3) (REC) when *A* reached values close to those of seedlings under continuous irrigation, characterizing the recovery period; and (4) (END) 45 days after REC, when seedlings were kept under continuous irrigation, similar to the control. Application of 0.75 mL Si alleviates damage to the photosynthetic apparatus of *D. alata* seedlings that remain longer under water deficit, and contributes to faster physiological recovery after the resumption of irrigation. *D. alata* seedlings have recovery potential after the stress period, regardless of Si application.

Keywords: attenuation, baru, chlorophyll *a* fluorescence, gas exchange, water stress.

Resumo

O déficit hídrico vem ocasionando sérios problemas no crescimento e desenvolvimento das plantas, fazendo com que ocorram danos no seu metabolismo. Assim, faz necessário o uso de agentes que possam mitigar os danos ocasionados nas plantas. Objetivamos neste estudo verificar o potencial do silício de mitigar os efeitos estressantes do déficit hídrico em mudas de *Dipteryx alata* Vogel, e auxiliar na recuperação após a retomada da irrigação. Foram estudados quatro regimes hídricos: (I) Irrigação contínua; (II): Déficit hídrico + Si 0; (III): Déficit hídrico + 0.75 mL de Si e (IV): Déficit hídrico + 1.50 mL de Si. As mudas foram avaliadas em quatro períodos: (1) (T0 – tempo zero) início do experimento, período antes de iniciar a suspensão da irrigação, (2) (F0) quando os valores da taxa fotossintética nas mudas sob suspensão da irrigação chegaram próximos à zero, quando ocorreu a retomada da irrigação; (3) (REC) quando os valores de *A* alcançaram valores próximos ao das mudas sob irrigação contínua, caracterizando o período de recuperação e (4) (FINAL) 45 dias após a REC quando as mudas foram mantidas sob irrigação contínua, semelhante ao controle. A aplicação de 0.75 mL de Si alivia os danos ao aparato fotossintético das mudas de *D. alata* por maior período sob déficit hídrico, e contribui na recuperação fisiológica de maneira mais rápida após a retomada da irrigação. As mudas de *D. alata* apresentam potencial de recuperação após o período de estresse, independente da aplicação de Si.

Palavras-chave: atenuação, baru, fluorescência da clorofila *a*, trocas gasosas, estresse hídrico.

1. Introduction

World climate change has affected soil water availability in several regions, especially in tropical and subtropical regions (Saud et al., 2014; Fei et al., 2017). Water deficit is a limiting factor for the initial growth and development of plants, which can impair their physiological and biochemical processes (Saud et al., 2014). Moreover, water deficit reduces the water and osmotic potential, decreasing hydraulic resistance in the xylem vessels as well as cell turgor, thus compromising the photosynthetic capacity (Ahmed et al., 2013; Nunes et al., 2019).

In this context, the search for techniques to mitigate water deficit damage in tree seedlings has increased. In recent years, silicon (Si) has gained prominence in terms of its potential to mitigate multiple abiotic stresses, especially water deficit, in different crop species (Adrees et al., 2015; Rizwan et al., 2015; Wang et al., 2017). However, reports on tree species are scarce.

---

*e-mail: marcyyo@outlook.com
Received: December 9, 2021 – Accepted: January 18, 2022

Silicon is a beneficial nutrient for plant development. The element plays an important role in photosynthetic metabolism and morphoanatomical aspects (Liang et al., 2015a), as it increases the cell wall rigidity and mechanical resistance of plants (Kim et al., 2016). Furthermore, Si can increase the activity of antioxidant enzymes capable of reducing reactive oxygen species (ROS) (Torabi et al., 2015; Tripathi et al., 2017), relieving oxidative stress.

Among the species of socioeconomic and environmental importance, baru (*Dipteryx alata* Vogel., Fabaceae) is a tree fruit species native to central Brazil. It occurs in areas of Cerrado and Cerradão, in the transition between the biomes atlantic forest and Cerrado (Honorio et al., 2019). The Cerrado, located in the central region of Brazil, is characterized by vegetation that range from grasslands, savanna, and forest formations (Capuzzo et al., 2012). It is also considered as a big biodiversity center and one of the world hotspots (Costa et al., 2015a). The species grows mostly in well-drained soils and has commercial value due to the use of its wood in civil construction and its fruits in the preparation of candies, jellies, or consumed in natura (Costa et al., 2015b). The species has also a great importance to traditional peoples and communities of the Cerrado, since the extractivism of the baru nut helps them to generate income and it can promote the Cerrado conservation (Arakaki et al., 2009; Santos et al., 2012; Freitas et al., 2018).

Its seedlings can be used in the recovery of degraded areas and for the enrichment of native forests or agroforestry systems. However, this species is explored in native areas, and information on its biology and management for sustainable use is scarce (Ajalla et al., 2012), which makes it an endangered species due to predatory extraction (Honorio et al., 2019).

In this study, we hypothesized that water deficit impairs the photosynthetic metabolism and the growth of seedlings of this species, but foliar application of silicon can help to alleviate stress and maintain metabolic stability and seedling quality.

This study assesses the potential of silicon to mitigate the effects of water deficit, to stabilize the photosynthetic metabolism and growth of *D. alata* seedlings, and to help in their recovery after the resumption of irrigation.

2. Materials and Methods

2.1. General conditions

We conducted the experiment from November 2019 to January 2020 at the Faculty of Agricultural Sciences of the Federal University of Grande Dourados (UFGD), in Dourados city, Mato Grosso do Sul (MS) State, Brazil. The experiment took place in a nursery under 30% shading, using a black nylon mesh (Sombrite®) with an additional plastic top and side cover to protect against rainfall.

Ripe *D. alata* fruits were collected from several matrices in the Cerrado area, in the region of the Itamarati settlement (22º 11’ 24.731” S and 55º 35’ 37.370” E), in Ponta Porã city, Mato Grosso do Sul State. The fruits were manually processed, and the extracted seeds were sown directly in 8-L plastic pots filled with Dystroferric Red Latosol + coarse sand (3:1, v/v). The seeds were irrigated daily at 70% of the water holding capacity for 75 days, moment when the seedlings presented an average height of 20 cm.

2.2. Experimental design

The seedlings were separated into four groups based on the following water regimes: R1) Continuous irrigation – I: 75% of the substrate water holding capacity was maintained using the gravimetric method (Souza et al., 2000); R2) Water deficit – II, characterized by suspension of irrigation; R3) Water deficit II + 0.75 mL Si; R4) Water deficit II + 1.50 mL Si. Silicon was applied in the morning via foliar spraying until dripping (20 mL per plant), and seedling irrigation was suspended on the same day.

The silicon used consisted of the foliar fertilizer Sifol®, which is a source of silicon and potassium, with 12% of its weight containing 168 g/L Si and 15% of its weight containing 210 g/L K_2O. The product is fluid-type and has an electrical conductivity of 2.93 mS cm^{-1}, density of 1.40 g L^{-1}, and pH 10.96. The K values according product doses were balanced.

The seedlings were evaluated in four periods: (1) (T0 – time zero) at the beginning of the experiment, before irrigation suspension; (2) (P0) when the photosynthetic rates of seedlings under irrigation suspension reached values close to zero, period in which irrigation was resumed; (3) (REC) when *A* reached values close to those of seedlings under continuous irrigation, characterizing the recovery period; and (4) (END) 45 days after REC, when seedlings were kept under continuous irrigation, similar to the control.

The experimental design was completely randomized with treatments arranged in a subplot scheme. The plots consisted of the combination of water regimes with silicon, and the subplots consisted of the four evaluation periods. The experiment had three replicates, with two plants per pot in each experimental unit.

2.3. Characteristics evaluated

a) Gas exchange: photosynthetic rate (*A*; µmol CO_2 m^2 s^{-1}), stomatal conductance (g_s; mol H_2O m^{-2} s^{-1}), intercellular CO_2 concentration (C_i; µmol CO_2 m^2 s^{-1}), and leaf transpiration rate (*E*; mol H_2O m^{-2} s^{-1}) were quantified using an infrared gas analyzer - IRGA (ADC, LCi PRO; Analytical Development Co. Ltd., Hoddesdon, UK). From these data, Rubisco carboxylation efficiency (A/C_i; µmol CO_2/mmol H_2O) and water use efficiency (*WUE*; µmol CO_2/mmol H_2O) were calculated. Evaluations were conducted between 8 and 11 a.m., selecting four previously marked seedlings per treatment;

b) Chlorophyll *a* fluorescence: readings were taken between 8 and 11 a.m., subjecting the leaves to a dark condition for 30 minutes. The procedure included the use of adapter clips so that all reaction centers had an “open” configuration, indicating complete oxidation of the photosynthetic electron transport system. After this period, initial (F_0) and maximum fluorescence (F_M) of chlorophyll *a*, potential quantum efficiency of photosystem II (F_V/F_M), absorbed energy conversion efficiency (F_V/F_0), and basal quantum production of nonphotochemical processes (F_0/F_M) were measured using a portable chlorophyll fluorometer model OS-30p (Opti-Sciences, Hudson, USA);

c) Chlorophyll index: determined using a Soil Plant Analysis Development (SPAD-502) portable chlorophyll meter (Konica-Minolta, Tokyo, Japan). Readings were taken in the morning, using fully expanded leaves from the middle third;

d) Leaf relative water content (RWC; %): determined according to methodology the Slavick (1979);

e) Plant growth: leaf area (cm^2) was determined with a LI-COR® leaf area integrator (LI 3100, Nebraska – USA). Seedling quality index was calculated according to Dickson et al. (1960).

2.4. Statistical analysis

Data were subjected to analysis of variance (ANOVA). Significant means (F test, $p < 0.05$) as a function of water regimes, evaluation periods, and interactions were submitted to the Tukey test ($p < 0.05$) using the statistical program SISVAR 5.3 (Ferreira, 2019).

3. Results

The significant interaction of treatments, here represented association water regimes and silicon for the characteristics of *A*, C_i, *E*, *gs*, A/C_i, *WUE*, F_0/F_M, F_0 and RWC, while F_V/F_M, F_V/F_0 and DQI were influenced by the factors alone (Table 1). The SPAD index was not influenced by the factors under study.

During the suspension of irrigation, *D. alata* seedlings under water deficit treated with 1.50 mL Si reached P0 (0.59 μmol CO_2 m^{-2} s^{-1}) at 16 days, while seedlings grown without Si and with 0.75 mL Si reached P0 at 18 and 20 days of water restriction, with values of 0.43 and 0.48 μmol CO_2 m^{-2} s^{-1}, respectively (Figure 1).

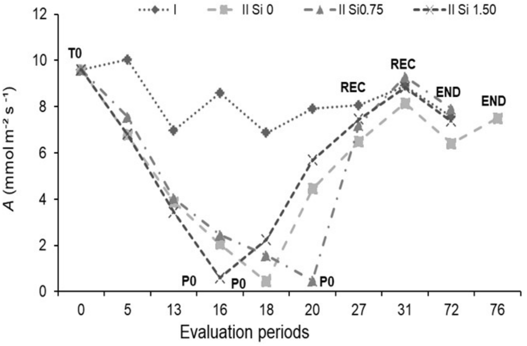

Figure 1. Dynamics of photosynthesis (*A*) in *D. alata* seedlings produced under different water regimes (I: Irrigated; II: combined intermittent irrigation without and with 0.75 and 1.50 Si) in different evaluation periods (T0: zero time; P0: photosynthesis close to zero; REC: recovery: END: end of evaluations).

Table 1. Analysis of variance (ANOVA) results to test the effect of Silicon on water deficit during the evaluation periods and its interaction in *D. alata* seedlings.

Characteristics	Treatments		Evaluation periods (EP)		Interaction (T x EP)	
	F	***P***	***F***	***p***	***F***	***P***
A	24.058	<0.0001	151.183	<0.0001	17.088	<0.0001
C_i	5.021	0.0041	10.233	<0.0001	3.685	0.0014
E	8.496	<0.0001	70.800	<0.0001	4.985	<0,0001
g_s	22.620	<0.0001	112.781	<0.0001	7.827	<0.0001
A/C_i	17.904	<0.0001	102.788	<0.0001	11.820	<0.0001
WUE	4.571	0.0068	14.834	<0.0001	7.976	<0.0001
F_V/F_M	2.986	0.0456	12.033	<0.0001	1.338	0.2568
F_0/F_M	6.564	0.0014	41.365	<0.0001	3.101	0.0086
F_M	0.721	0.5466	21.521	<0.0001	0.406	0.9228
F_V/F_0	5.694	0.0030	46.945	<0.0001	1.700	0.1299
SPAD	1.301	0.2910	2.308	0.0952	0.620	0.7711
Leaf Area	1.209	0.3222	17.939	<0.0001	0.447	0.8988
RWC	1.331	0.2752	36.238	<0.0001	3.137	0.0047
DQI	5.398	0.0040	5.164	0.0050	0.983	0.4727

Note: treatments with water suspension + Silicon, in *D. alata* seedlings produced under different water regimes (I: Irrigated; II: combined intermittent irrigation without and with 0.75 and 1.50 mL Si) at different evaluation times (T0: time zero; P0: photosynthesis close to zero; REC: recovery: END: end of evaluations). Photosynthetic rate - *A*, intracellular CO_2 concentration - C_i, transpiration - *E*, stomatal conductance - g_s, Rubisco intrinsic carboxylation efficiency - A/C_i, water use efficiency - *WUE*; Potential quantum efficiency of photosystem II - F_V/F_M, basal quantum production of non-photochemical processes - F_0/F_M, maximum chlorophyll-a fluorescence - F_M, absorbed energy conversion efficiency - F_V/F_0, initial fluorescence - F_0; Soil Plant Analysis Development – SPAD; Leaf Area, Relative Leaves Water Content - RWC and Dickson Quality Index - DQI.

In the REC, seedlings treated with Si had *A* values close to those of the control seedlings 11 days after the resumption of irrigation (27th day of the experiment), while untreated seedlings only recovered 15 days after the resumption of irrigation (31st day). In the END stage, all seedlings presented *A* values similar to those of the control seedlings, end untreated seedlings took 4 days longer to recover in relation to those treated with Si.

At 16 days of water suspension, *D. alata* seedlings grown with 1.50 mL Si reached a photosynthetic rate (*A*) of 0.59 µmol CO_2 m^{-2} s^{-1} at P0 (Figure 2a). In turn, those grown with 0.75 mL Si maintained higher values of *A* (2.93 µmol CO_2 m^{-2} s^{-1}), although they did not differ from seedlings under water deficit grown without Si in the same period. These values did not vary as a function of Si doses in the REC and END stages.

In the P0 stage, seedlings grown with 1.50 mL Si had higher intercellular CO_2 concentration (C_i) (311.25 µmol CO_2 m^{-2} s^{-1}) and lower Rubisco carboxylation efficiency (A/C_i) (0.002 µmol CO_2 m^{-2} s^{-1}), while seedlings that received 0.75 mL Si had better results. In the REC and END stages, the values of these variables were similar between treatments regardless of silicon use and water regimes (Figure 2b and 2e).

During P0, seedlings under water deficit had lower transpiration values (*E*), regardless of Si use (Figure 2c). In the END stage, in turn, seedlings grown with 0.75 mL Si had lower *E* (2.54 mmol m^{-2} s^{-1}). Moreover, seedlings grown under water deficit had lower *gs* during P0, regardless of Si use. During REC, seedlings that received 0.75 mL Si had *gs* values similar to those of control seedlings (Figure 2d).

Seedlings under water deficit grown without Si and with 0.75 mL Si had higher *WUE* values (1.83 and 1.67 µmol CO_2 m^{-2} s^{-1}, respectively) in P0, differing from those that received 1.50 mL Si in the same period of evaluation. During REC, the values of treated seedlings were similar to those of control seedlings. In the END stage, seedlings grown with 0.75 mL Si had higher *WUE* (3.12 µmol CO_2 m^{-2} s^{-1}) (Figure 2f).

Seedlings under water deficit grown without Si had lower potential quantum efficiency of photosystem II (F_V/F_M) (0.740). However, the application of 0.75 mL Si increased F_V/F_M (0.761) which did not differ from the control seedlings (Figure 3a). During P0, the F_V/F_M value was reduced (0.723) (Figure 3d). After the reestablishment of irrigation in (REC and END) the plants were able to normalize their photochemical activity, where they reached a value higher than the control.

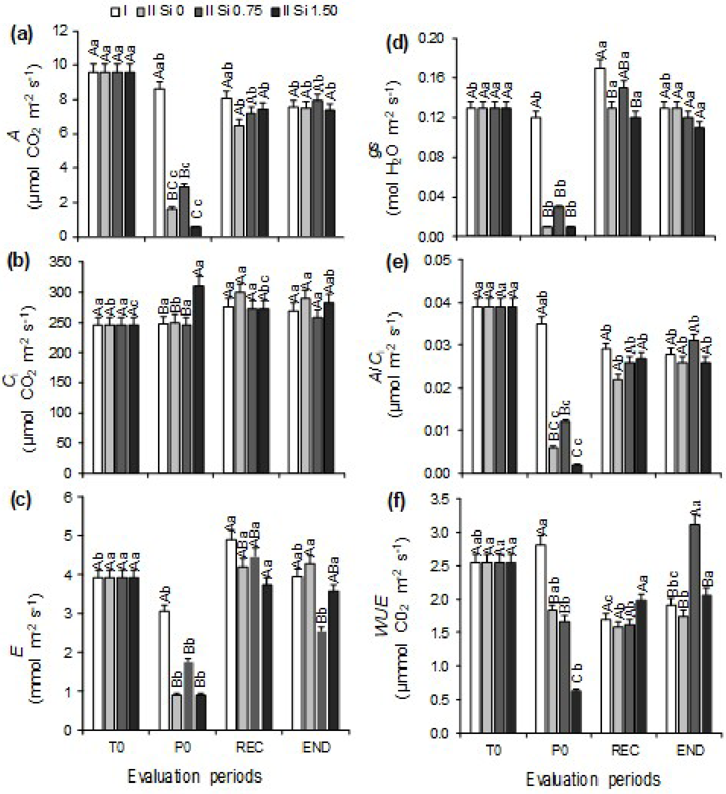

Figure 2. Photosynthetic rate – *A* (a), intracellular CO_2 concentration – C_i (b), transpiration – *E* (c), stomatal conductance – g_s (d), intrinsic Rubisco A/C_i carboxylation efficiency (e) and efficiency of water use – *WUE* (f) in *D. alata* seedlings produced under different water regimes (I: Irrigated; II: combined intermittent irrigation without and with 0.75 and 1. Si) in different evaluation periods (T0: zero time; P0: photosynthesis close to zero; REC: recovery: END: end of evaluations). Capital letters compare water regimes within each assessment period (Tukey; $p < 0.05$); Lowercase letters compare the evaluation periods within each water regime. (Tukey; $p < 0.05$).

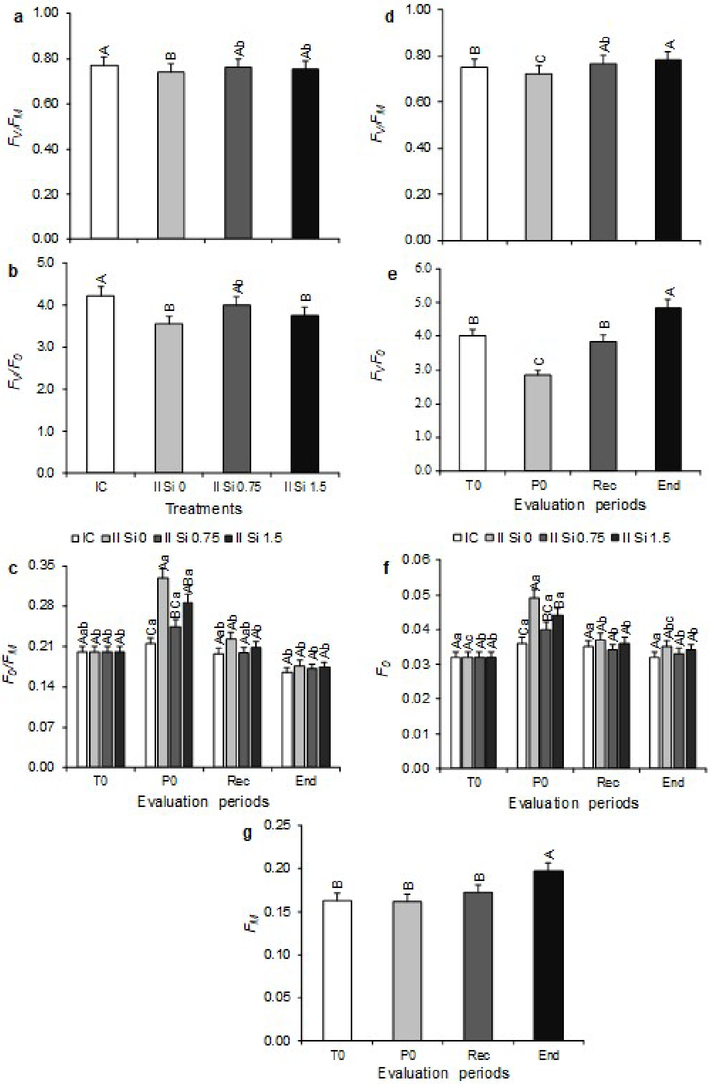

Figure 3. Potential quantum efficiency of photosystem II - F_V/F_M (a and d), absorbed energy conversion efficiency - F_V/F_0 (b and e), basal quantum production of non-photochemical processes - F_0/F_M (c), maximum chlorophyll-*a* fluorescence - F_M (f) and initial fluorescence - F_0 (g) in *D. alata* seedlings produced under different water regimes (I: Irrigated; II: combined intermittent irrigation without and with 0.75 and 1.50 Si) in different evaluation periods (T0: time zero; P0: photosynthesis close to zero; REC: recovery: END: end of evaluations). Capital letters compare water regimes within each assessment period (Tukey; $p < 0.05$); Lowercase letters compare the evaluation periods within each water regime. (Tukey; $p < 0.05$).

The highest values of absorbed energy conversion efficiency (F_V/F_0) were observed in control seedlings cultivated under continuous irrigation and in those produced with 0.75 mL of Si with values of (4.22 and 3.99) (Figure 3b). During P0, the stressed seedlings presented a lower value of (F_V/F_0) (3.85), after reirrigation, the seedlings recovered (REC) the value of F_V/F_0, where they did not differ from the seedlings of the initial time (Figure 3e).

During P0, the F_0/F_M ratio and F_0 values were higher in seedlings grown without Si, and lower in seedlings treated with 0.75 mL Si (Figure 3c and 3f). In the REC and END stages, the values of previously stressed seedlings remained close to those of control seedlings and seedlings treated with Si.

The stressed seedlings showed higher F_m values in the (END) evaluations with a mean (0.197) (Figure 3g). After irrigation was resumed (REC and END), previously stressed *D. alata* seedlings recovered.

The leaf area of seedlings under water deficit did not vary from that of control seedlings as a function of Si application in any of the evaluation periods (Figure 4a), averaging 209.32 cm^2. As for WRC, seedlings under water deficit grown without Si and with 1.50 mL Si had lower values, while those treated with 0.75 mL Si (68.16%) did not differ from control seedlings (Figure 4b). In the REC and END stages, the RWC of all seedlings were similar and did not vary between treatments. This demonstrates recovery of this characteristic after the resumption of irrigation.

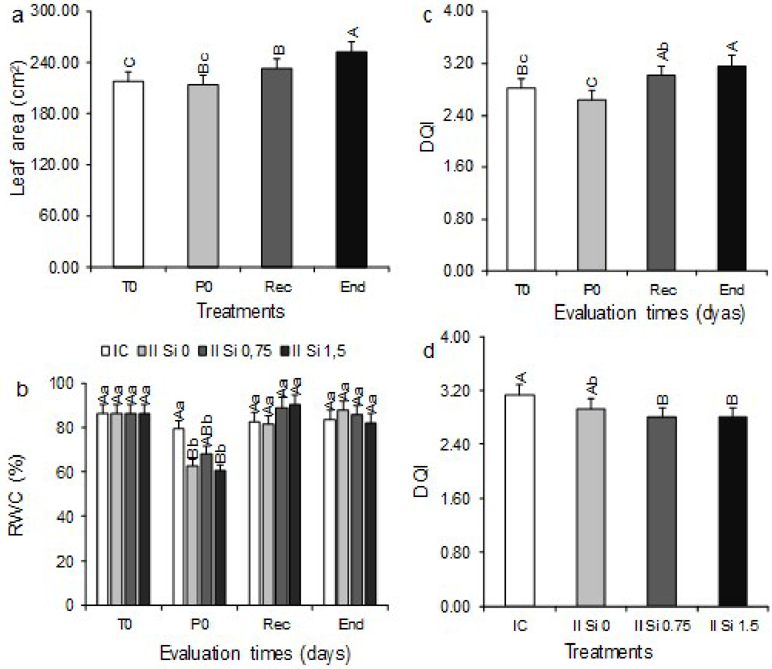

Figure 4. Leaf area (a), relative water content of WRC leaves (b) and Dickson quality index DQI (c and d) in *D. alata* seedlings produced under different water regimes (I: Irrigated; II: combined intermittent irrigation without and with 0.75 and 1.50 of Si) in different evaluation periods (T0: time zero; P0: photosynthesis close to zero; REC: recovery: END: end of evaluations). Capital letters compare water regimes within each assessment period (Tukey; $p < 0.05$); Lowercase letters compare the evaluation periods within each water regime (Tukey; $p < 0.05$).

The seedlings treated with Si had Dickson quality index (DQI) values that did not differ statistically from the control seedlings during their evaluation, and lower values in the seedlings without Si (Figure 4c). During P0, the DQI value was lower under stress conditions, after reirrigation in the REC and END period, all seedlings had similar values of DQI (Figure 4d).

4. Discussion

We accept the hypotheses that water deficit changes the light energy absorption capacity and gas exchange of *D. alata* seedlings, and that seedlings under deficit water treated with silicon, especially at a dose of 0.75 mL, have better physiological and initial growth performance (Table 1).

D. alata seedlings were sensitive to water deficit since low water availability caused several physiological damages to the plants, reducing tissue relative water content and stomatal conductance (*gs*). This negatively affected gas exchange, increasing C_i and reducing CO_2 assimilation rate, thereby reducing A/C_i. This behavior may be due to the increased production of reactive oxygen species, which were not presented in this study. According to the literature, reactive oxygen species compromise the integrity of the photosynthetic apparatus (Pereira et al., 2012; Vítolo et al., 2012). When used in adequate doses (here represented by the dose of 0.75 mL), silicon alleviated the effects of water deficit in the seedlings, minimizing damage to the photosynthetic apparatus. In addition, during REC, seedlings treated with 0.75 mL Si had faster *A* recovery than the seedlings of other treatments.

We emphasize that the dose of 0.75 mL contributed to the reduction of *A* to be smaller under water deficit. This demonstrates the potential of this element as a water stress mitigating agent, provided that it is applied in adequate doses. Silicon increases the ability to scavenge reactive oxygen species by regulating the activity of antioxidant defense enzymes in plants under abiotic stresses (Kim et al., 2016; Tripathi et al., 2017). This reduces oxidative damage and favors membrane integrity (Maghsoudi et al., 2016) as well as leaf metabolism (Shi et al., 2016) in different species such as *Solanum lycopersicum* and *Triticum aestivum* L.

Other authors mention the beneficial effects of silicon on photosynthesis for different species under drought, suggesting that Si can improve the water status of plants (Zhu and Gong, 2014; Etesami and Jeong, 2018). Although leaf RWC decreased at times of greater water deficit (P0) in *D. alata* seedlings, with the resumption of irrigation seedlings treated with Si recovered turgor with significantly higher values in relation to seedlings grown without Si.

The faster and more accentuated reduction of *A* with 1.50 mL Si possibly indicates a stressed effect, which was confirmed by some of the chlorophyll *a* fluorescence parameters under study. Moraes et al. (2011) treated sugarcane with increasing doses of potassium silicate and observed that foliar application of doses higher than 40 g L^{-1} caused a phytotoxic effect for the species, reducing leaf area.

The application of 0.75 mL Si has promoted numerically higher values of A, E, gs, and A/C_i in relation to the application of 1.50 mL Si. However, we suggest that Si contributed little to the maintenance of gas exchange during the stress period (P0), as treated plants did not differ statistically from plants that did not receive fertilizer.

We emphasize that even with little contribution to P0, the application of 0.75 mL Si contributed positively to the increase of g_s and *WUE* in the REC and END stages, respectively. This indicates the prolonged effect of this element on leaf metabolism and its water relationships. The fact that *D. alata* seedlings respond poorly to silicon may be due to the ability of this species to accumulate Si. Most studies in the literature address Si-accumulating plants, while fewer studies address non-Si-accumulating plants (Zhang et al., 2018). The results of the present study indicate that Si can mitigate the deleterious effects of water stress in non-Si-accumulating plants.

Moreover, the literature shows positive results of Si application in increasing gas exchange in *Glycine max* L., *Triticum aestivum* L., and *Oryza sativa* L. (Shen et al., 2010; Gong and Chen, 2012; Song et al., 2014). These results differ from those of the present study in *D. alata* seedlings, suggesting the need for more studies with tree species.

Chlorophyll *a* fluorescence parameters such as Fv/F_M and Fv/F_0 decreased in *D. alata* seedlings during water deficit (P0). Song et al. (2014) state that the decrease in photochemical efficiency of photosystem II under water restriction may be due to the reduction in chlorophyll content. Other species, such as *Jatropha curcas* L. (Moura et al., 2016), *Hymenaea courbaril* L. (Freitas et al., 2018) and *Campomanesia xanthocarpa* (Mart.) O. Berg (Bartieres et al., 2021) also showed a reduction in Fv/F_M and Fv/F_0 when grown under water deficit.

Silicon application, especially at the dose of 0.75 mL Si, contributed to the stability of the photochemical processes of photosynthesis, as it alleviated the negative effects of water deficit. Similarly, tomato seedlings (*Solanum lycopersicum* L.) (Zhang et al., 2018) had better results when treated with silicon even during water deficit.

Silicon improves physiological functions in plants and regulates the positive distribution of minerals in leaves, stems, and roots. It may further protect plants from water stress while decreasing the production of ROS, which in turn reduces the oxidative stress of plants, as already reported for some species (Tripathi et al., 2016; Hasanuzzaman et al., 2017; Tripathi et al., 2017). Furthermore, silicon increases water absorption by the roots (Liu et al., 2014) and stimulates the accumulation of osmolytes (Ming et al., 2012). However, it is noteworthy that most of these responses occurred in grasses that are Si-accumulating species (Zhu and Gong, 2014).

The higher yields of nonphotochemical processes (F_0/F_M) and F_0 in seedlings under water deficit grown without Si and with 1.50 mL Si are due to the low use of light energy by the plants, which compromised the transfer of electrons to the center of reaction. The increase in these variables indicates a stressful condition, reducing photochemical activities (especially Fv/F_M and gas exchange) in *D. alata* seedlings. These damages in PSII activities affect the photosynthetic capacity (A) of plants due to the reduction of leaf water potential (Cruz et al., 2009), interfering with seedling quality (DQI). Silicon application favored photochemical stability by promoting membrane integrity and decreasing its permeability (Liang et al., 2015b). Kim et al. (2017) report that by modulating antioxidant defense systems, Si can also alleviate oxidative stress in plants under adverse conditions.

The reduction in leaf area of *D. alata* seedlings during P0 indicates that the time that the plants were subjected to stress negatively affected the absorption of light and, consequently, the metabolic and physiological functions of the plants under water stress conditions. After rehydration, the leaf area was established, causing the resumption of metabolic and physiological activities of the seedlings.

Stability in the leaf area (LA) of *D. alata* seedlings under all water regimes in P0 is due to the fact that this species has a slow initial growth, and the time in which the seedlings were subjected to stress was not enough for an increase in this variable.

The same responses for LA were observed in seedlings of *Schinus terebinthifolia* Raddi (Beltramin et al., 2020), *Cedrela odorata* L. (Silva et al., 2021), and *Campomanesia xanthocarpa* O. Berg. (Santos et al., 2021), where these species had reduction in LA under low water availability.

Although growth characters did not decrease, seedlings grown without Si and with 1.50 mL Si had lower RWC. This demonstrates the sensitivity of the species to these growing conditions. The lowest values of this variable indicate loss of turgor, negatively affecting the production of photoassimilates. However, the dose of 0.75 mL Si contributed to the maintenance of RWC and greater *WUE*, especially in the P0 and END stages, consequently stabilizing other metabolic processes.

As in the literature, the present study proved in *D. alata* that low water availability in the substrate negatively affects the leaf water potential (Cruz et al., 2009), this impairs metabolic processes, decreasing the production of photoassimilates and reducing initial growth, thereby reducing seedling quality (DQI). However, Si contributes to the osmotic adjustment and water potential gradient (Sonobe et al., 2010; Chen et al., 2018). The element is deposited in the form of amorphous silica, forming a protective barrier over the stomatal pore (Ahmed et al., 2013; Fátima et al., 2019). Thus, even under water deficit, the application of 0.75 mL Si regulated seedling growth, both in P0 and in REC. This is because Si reduces tissue lignification and can facilitate cell wall loosening and extensibility as well as increase plant growth under stress conditions (Maksimović et al., 2007).

We emphasize that after the resumption of irrigation (REC) until the END stage, *D. alata* seedlings previously subjected to water deficit presented values of all characteristics under study similar to those of control seedlings, regardless of Si application. This behavior suggests that this species has physiological plasticity, which is an important and desirable response since the species occurs in areas under stress conditions caused by large variations in temperature, water, and light availability.

We therefore suggest that *D. alata* seedlings have a high resilience capacity due to physiological plasticity. This behavior is important in projects for the recovery of degraded areas since anthropized areas usually show fluctuations in terms of soil water availability, and this resilience contributes to the potential for survival of this species.

5. Conclusions

Application of 0.75 mL Si alleviates damage to the photosynthetic apparatus of *D. alata* seedlings that remain longer under water deficit, and contributes to faster physiological recovery after the resumption of irrigation.

D. alata seedlings have recovery potential after the stress period, regardless of Si application.

Acknowledgements

Coordination for the Improvement of Higher Education Personnel (CAPES).

References

ADREES, M., ALI, S., RIZWAN, M., ZIA-UR-REHMAN, M., IBRAHIM, M., ABBAS, F., FARID, M., QAYYUM, M.F. and IRSHAD, M.K., 2015. Mechanisms of silicon-mediated alleviation of heavy metal toxicity in plants: a review. *Environmental Science and Pollution Research International*, vol. 22, no. 11, pp. 8148-8162. http://dx.doi.org/10.1007/s11356-015-4496-5. PMid:25874438.

AHMED, M., KAMRAN, A., ASIF, M., QADEER, U., AHMED, Z.I. and GOYAL, A., 2013 [viewed 9 December 2021]. Silicon priming: a potential source to impart abiotic stress tolerance in wheat: a review. *Australian Journal of Crop Science* [online], vol. 7, no. 4, pp. 484-491. Available from: https://www.cropj.com/ahmed742013484491.pdf

AJALLA, A.C.A., VOLPE, E., VIEIRA, M.C. and ZÁRATE, N.A.H., 2012. Production of baru (*Dipteryx alata* Vog.) seedlings under three levels of shading and four textural classes of soil. *Revista Brasileira de Fruticultura*, vol. 34, no. 3, pp. 888-896. http://dx.doi.org/10.1590/S0100-29452012000300031.

ARAKAKI, A.A., SCHEIDT, G.N., PORTELLA, A.C., ARRUDA, E.J. and COSTA, R.B., 2009. O baru (*Dipteryx alata* Vogel.) como alternativa de sustentabilidade em área de fragmento florestal do Cerrado, no Mato Grosso do Sul. *Revista Interações*, vol. 10, no. 1, pp. 31-39. http://dx.doi.org/10.20435/interações.v10i1.400.

BARTIERES, E.M.M., DRESCH, D.M., REIS, L.C., PEREIRA, Z.V., MUSSURY, R.M. and SCALON, S.P.Q., 2021. Shading minimizes the effects of water deficit in *Campomanesia xanthocarpa* (Mart.) O. Berg seedlings. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 83, pp. e244718. http://dx.doi.org/10.1590/1519-6984.244718. PMid:34161459.

BELTRAMIN, F.A., SILVA, W.C., SANTOS, C.C., SCALON, S.P.Q. and VIEIRA, M.C., 2020. Water-retaining polymer mitigates the water deficit in *Schinus terebinthifolia*: photosynthetic metabolism and initial growth. *Engenharia Agrícola*, vol. 40, no. 6, pp. 684-691. http://dx.doi.org/10.1590/1809-4430-eng.agric.v40n6p684-691/2020.

CAPUZZO, J.P., ROSSATTO, D.R. and FRANCO, A.C., 2012. Differences in morphological and physiological leaf characteristics between *Tabebuia aurea* and *T. impetiginosa* is related to their typical habitats of occurrence. *Acta Botanica Brasílica*, vol. 26, no. 3, pp. 519-526. http://dx.doi.org/10.1590/S0102-33062012000300002.

CHEN, D., WANG, S., YIN, L. and DENG, X., 2018. How does silicon mediate plant water uptake and loss under water deficiency? *Frontiers in Plant Science*, vol. 9, pp. 281. http://dx.doi.org/10.3389/fpls.2018.00281. PMid:29556247.

COSTA, A.C., REZENDE-SILVA, S.L., MEGGUER, C.A., MOURA, L.M.F., ROSA, M. and SILVA, A.A., 2015a. The effect of irradiance and water restriction on photosynthesis in young jatobá-do-cerrado (*Hymenaea stigonocarpa*) plants. *Photosynthetica*, vol. 53, no. 1, pp. 118-127. http://dx.doi.org/10.1007/s11099-015-0085-6.

COSTA, E., DIAS, J.G., LOPES, K.G., BINOTTI, F.F.S. and CARDOSO, E.D., 2015b. Shading screens and substrates for *Dipteryx alata* Vog. seedling production. *Floresta e Ambiente*, vol. 22, no. 3, pp. 416-425. http://dx.doi.org/10.1590/2179-8087.071714.

CRUZ, M.C.M., SIQUEIRA, D.L., SALOMÃO, L.C.C. and CECON, P.R., 2009. Chlorophyll a fluorescence in leaves of 'Ponkan' mandarin and the 'Tahiti' acid lime submitted to water stress. *Revista Brasileira de Fruticultura*, vol. 31, no. 3, pp. 896-901. http://dx.doi.org/10.1590/S0100-29452009000300037.

DICKSON, A., LEAF, A.L. and HOSNER, J.F., 1960. Quality appraisal of white spruce and white pine seedling stock in nurseries. *Forestry Chronicle*, vol. 36, no. 1, pp. 10-13. http://dx.doi.org/10.5558/tfc36010-1.

ETESAMI, H. and JEONG, B.R., 2018. Silicon (Si): review and future prospects on the action mechanisms in alleviating biotic and abiotic stresses in plants. *Ecotoxicology and Environmental Safety*, vol. 147, pp. 881-896. http://dx.doi.org/10.1016/j.ecoenv.2017.09.063. PMid:28968941.

FÁTIMA, R.T., JESUS, E.G., GUERRERO, A.C., ROCHA, J.L.A. and BRITO, M.E.B., 2019. Silicon fertilization as atenuant of water stress in lettuce growth and gas exchanges. *Revista Engenharia na Agricultura*, vol. 27, no. 2, pp. 170-178. http://dx.doi.org/10.13083/reveng.v27i2.892.

FEI, S., DESPREZ, J.M., POTTER, K.M., JO, I., KNOTT, J.A. and OSWALT, C.M., 2017. Divergence of species responses to climate change. *Science Advances*, vol. 3, no. 5, e1603055. http://dx.doi.org/10.1126/sciadv.1603055. PMid:28560343.

FERREIRA, D.F., 2019. Sisvar: a computer analysis system to fixed effects Split plot type designs. *Revista Brasileira de Biometria*, vol. 37, no. 4, pp. 529-535. http://dx.doi.org/10.28951/rbb.v37i4.450.

FREITAS, V.M.B., SCALON, S.P.Q., DRESCH, D.M., BASTOS, S.S. and SOUZA, A.P.R., 2018. Influence of exogenous application of abscisic acid in gas exchanges of *Hymenaea courbaril* L. (Fabaceae) seedlings subjected to water deficit. *Floresta*, vol. 48, no. 2, pp. 163-172. http://dx.doi.org/10.5380/rf.v48i2.53076.

GONG, H. and CHEN, K., 2012. The regulatory role of silicon on water relations, photosynthetic gas exchange, and carboxylation activities of wheat leaves in field drought. *Acta Physiologiae Plantarum*, vol. 34, no. 4, pp. 1589-1594. http://dx.doi.org/10.1007/s11738-012-0954-6.

HASANUZZAMAN, M., NAHAR, K., ANEE, T.I. and FUJITA, M., 2017. Exogenous silicon attenuates cadmium-induced oxidative stress in *Brassica napus* L. by modulating ASA-GSH pathway and glyoxalase system. *Frontiers in Plant Science*, vol. 8, pp. 1061. http://dx.doi.org/10.3389/fpls.2017.01061. PMid:28674552.

HONÓRIO, A.B.M., LOPES, M.B.S., SIEBENEICHLER, S.C., SOUZA, C.M. and LEAL, T.C.A.B., 2019. Growth analysis and physiological parameters in *Dipteryx alata* Vogel seedlings. *Pesquisa Aplicada & Agrotecnologia*, vol. 12, no. 1, pp. 41-52. http://dx.doi.org/10.5935/PAeT.V12.N1.04.

KIM, Y.H., KHAN, A.L., WAQAS, M. and LEE, I.J., 2017. Silicon regulates antioxidant activities of crop plants under abiotic-induced oxidative stress: a review. *Frontiers in Plant Science*, vol. 8, pp. 510. http://dx.doi.org/10.3389/fpls.2017.00510. PMid:28428797.

KIM, Y.H., KHAN, A.L., WAQAS, M., SHAHZAD, R. and LEE, I.J., 2016. Silicon-mediated mitigation of wounding stress acts by up-regulating the rice antioxidant. *Cereal Research Communications*, vol. 44, no. 1, pp. 111-121. http://dx.doi.org/10.1556/0806.43.2015.031.

LIANG, Y., NIKOLIC, M., BÉLANGER, R., GONG, H. and SONG, A. 2015a. *Silicon in agriculture: from theory to practice.* 1st ed. Dordrecht: Springer, pp. 233-235.

LIANG, Y., NIKOLIC, M., BÉLANGER, R., GONG, H. and SONG, A. 2015b. *Silicon in agriculture: from theory to practice.* Dordrecht: Springer. Silicon-mediated tolerance to other abiotic stresses, pp. 161-179. http://dx.doi.org/10.1007/978-94-017-9978-2_8.

LIU, P., YIN, L., DENG, X., WANG, S., TANAKA, K. and ZHANG, S., 2014. Aquaporin-mediated increase in root hydraulic conductance is involved in silicon-induced improved root water uptake under osmotic stress in (*Sorghum bicolor* L.). *Journal of Experimental Botany*, vol. 65, no. 17, pp. 4747-4756. http://dx.doi.org/10.1093/jxb/eru220. PMid:24879770.

MAGHSOUDI, K., EMAM, Y. and PESSARAKLI, M., 2016. Effect of silicon on photosynthetic gas exchange, photosynthetic pigments, cell membrane stability and relative water content of different wheat cultivars under drought stress conditions. *Journal of Plant Nutrition*, vol. 39, no. 7, pp. 1001-1015. http://dx.doi.org/10.1080/01904167.2015.1109108.

MAKSIMOVIĆ, J.D., BOGDANOVIĆ, J., MAKSIMOVIĆ, V. and NIKOLIC, M., 2007. Silicon modulates the metabolism and utilization of phenolic compounds in cucumber (*Cucumis sativus* L.) grown at excess manganese. *Journal of Plant Nutrition and Soil Science*, vol. 170, no. 6, pp. 739-744. http://dx.doi.org/10.1002/jpln.200700101.

MING, D.F., PEI, Z.F., NAEEM, M.S., GONG, H.J. and ZHOU, W.J., 2012. Silicon alleviates PEG-induced water-deficit stress in upland rice seedlings by enhancing osmotic adjustment. *Journal Agronomy & Crop Science*, vol. 198, no. 1, pp. 14-26. http://dx.doi.org/10.1111/j.1439-037X.2011.00486.x.

MORAES, W.B., JESUS JUNIOR, W.C., MORAES, W.B., ARAUJO, G.L., SOUZA, A.F. and SILVA, M.V., 2011. Application of potassium silicate and leaf growth of sugarcane. *Agrária*, vol. 6, no. 1, pp. 59-64. http://dx.doi.org/10.5039/agraria.v6i1a902.

MOURA, A.R., NOGUEIRA, R.J.M.C., SILVA, J.A.A. and LIMA, T.V., 2016. Water relations and organic solutes in young plants of *Jatropha curcas* L. under different water regimes/Relacoes hidricas. *Ciência Florestal*, vol. 6, no. 2, pp. 345-354. http://dx.doi.org/10.5902/1980509822735.

NUNES, A.M.C., NUNES, L.R.L., RODRIGUES, A.J.O. and UCHÔA, K.S., 2019. Silicon in tolerance to water stress in tomatoes. *Revista Científica Rural*, vol. 21, no. 2, pp. 239-258. http://dx.doi.org/10.30945/rcr-v21i2.2658.

PEREIRA, W.P., MELO FILHO, P.A., ALBUQUERQUE, M.B., NOGUEIRA, R.J.M.C. and SANTOS, R.C., 2012. Biochemical changes in peanut genotypes submitted to moderate water stress. *Revista Ciênca Agronomica*, vol. 43, no. 4, pp. 766-773. http://dx.doi.org/10.1590/S1806-66902012000400019.

RIZWAN, M., ALI, S., IBRAHIM, M., FARID, M., ADREES, M., BHARWANA, S.A., ZIA-UR-REHMAN, M., QAYYUM, M.F. and ABBAS, F., 2015. Mechanisms of silicon-mediated alleviation of drought and salt stress in plants: a review. *Environmental Science and Pollution Research International*, vol. 22, no. 20, pp. 15416-15431. http://dx.doi.org/10.1007/s11356-015-5305-x. PMid:26335528.

SANTOS, C.C., SILVERIO, J.M., SCALON, S.P.Q. and VIEIRA, M.C., 2021. Hydrogel and water regimes in the chlorophylL- *A* fluorescence and growth of *Campomanesia xanthocarpa* (Mart.) O. Berg. seedlings. *Engenharia Agrícola*, vol. 41, no. 3, pp. 330-337. http://dx.doi.org/10.1590/1809-4430-eng.agric.v41n3p330-337/2021.

SANTOS, G.G., SILVA, M.R., LACERDA, D.B.C.L., MARTINS, D.M.O.M. and ALMEIDA, R.A.A., 2012. Aceitabilidade e qualidade físico-química de paçocas elaboradas com amêndoa de baru. *Pesquisa Agropecuária Tropical*, vol. 42, no. 2, pp. 159-165. http://dx.doi.org/10.1590/S1983-40632012000200003.

SAUD, S., LI, X., CHEN, Y., ZHANG, L., FAHAD, S., HUSSAIN, S., SADIQ, A. and CHEN, Y., 2014. Silicon application increases drought tolerance of kentucky bluegrass by improving plant water relations and morphophysiological functions. *TheScientificWorldJournal*, vol. 2014, 368694. http://dx.doi.org/10.1155/2014/368694. PMid:25054178.

SHEN, X., ZHOU, Y., DUAN, L., LI, Z., ENEJI, A.E. and LI, J., 2010. Silicon effects on photosynthesis and antioxidant parameters of soybean seedlings under drought and ultraviolet-B radiation. *Journal of Plant Physiology*, vol. 167, no. 15, pp. 1248-1252. http://dx.doi.org/10.1016/j.jplph.2010.04.011. PMid:20713250.

SHI, Y., ZHANG, Y., HAN, W., FENG, R., HU, Y., GUO, J. and GONG, H., 2016. Silicon enhances water stress tolerance by improving root hydraulic conductance in *Solanum lycopersicum* L. *Frontiers in Plant Science*, vol. 7, pp. 196. http://dx.doi.org/10.3389/fpls.2016.00196. PMid:26941762.

SILVA, M.S., SCALON, S.P.Q., SILVÉRIO, J.M., SANTOS, J.K.V., SANTOS, C.C. and DRESCH, D.M., 2021. Do hydro-retainer polymers attenuate damage from water fluctuations in leaf metabolism and the quality of *Cedrela odorata* seedlings? *International Journal of Agriculture and Biology*, vol. 26, no. 6, pp. 209-216. http://dx.doi.org/10.17957/IJAB/15.1826.

SLAVICK, B., 1979. *Methods of studying plant water relations*. Berlin: Springer-Verlag, 449 p.

SONG, A., LI, P., FAN, F., LI, Z. and LIANG, Y., 2014. The effect of silicon on photosynthesis and expression of its relevant genes in rice (*Oryza sativa L.*) under high-zinc stress. *PLoS One*, vol. 9, no. 11, e113782. http://dx.doi.org/10.1371/journal.pone.0113782. PMid:25426937.

SONOBE, K., HATTORI, T., AN, P., TSUJI, W., ENEJI, A.E., KOBAYASHI, S., KAWAMURA, Y., TANAKA, K. and INANAGA, S., 2010. Effect of silicon application on *Sorghum* root responses to water stress. *Journal of Plant Nutrition*, vol. 34, no. 1, pp. 71-82. http://dx.doi.org/10.1080/01904167.2011.531360.

SOUZA, C.C., OLIVEIRA, F.A., SILVA, I.F. and AMORIM NETO, M.S., 2000. Evaluation of methods of available water determinaton and irrigation management in “terra roxa” under cotton crop. *Revista Brasileira de Engenharia Agrícola e Ambiental*, vol. 4, no. 3, pp. 338-342. http://dx.doi.org/10.1590/S1415-43662000000300006.

TORABI, F., MAJD, A. and ENTESHARI, S., 2015. The effect of silicon on alleviation of salt stress in borage (*Borago officinalis* L.). *Soil Science and Plant Nutrition*, vol. 61, no. 5, pp. 788-798. http://dx.doi.org/10.1080/00380768.2015.1005540.

TRIPATHI, D.K., SINGH, S., SINGH, V.P., CHAUHAN, D.K., DUBEY, N.K. and PRASAD, R., 2016. Silicon as a beneficial element to combat the adverse effect of drought in agricultural crops. In: P. AHMAD, ed. *Water stress and crop plants: a sustainable approach*. Chichester: Wiley, pp. 682-694. http://dx.doi.org/10.1002/9781119054450.ch39.

TRIPATHI, D.K., SINGH, S., SINGH, V.P., PRASAD, S.M., DUBEY, N.K. and CHAUHAN, D.K., 2017. Silicon nanoparticles more effectively alleviated UV-B stress than silicon in wheat (*Triticum aestivum*) seedlings. *Plant Physiology and Biochemistry*, vol. 110, pp. 70-81. http://dx.doi.org/10.1016/j.plaphy.2016.06.026. PMid:27470120.

VÍTOLO, H.F., SOUZA, G.M. and SILVEIRA, J.A.G., 2012. Cross-scale multivariate analysis of physiological responses to high temperature in two tropical crops with C3 and C4 metabolism. *Environmental and Experimental Botany*, vol. 80, pp. 54-62. http://dx.doi.org/10.1016/j.envexpbot.2012.02.002.

WANG, M., GAO, L., DONG, S., SUN, Y., SHEN, Q. and GUO, S., 2017. Role of Silicon on plant-pathogen interactions. *Frontiers in Plant Science*, vol. 8, pp. 701. http://dx.doi.org/10.3389/fpls.2017.00701. PMid:28529517.

ZHANG, Y., SHI, Y., GONG, H., ZHAO, H., LI, H., HU, Y. and WANG, Y., 2018. Beneficial effects of silicon on photosynthesis of tomato seedlings under water stress. *Journal of Integrative Agriculture*, vol. 17, no. 10, pp. 2151-2159. http://dx.doi.org/10.1016/S2095-3119(18)62038-6.

ZHU, Y. and GONG, H., 2014. Beneficial effects of silicon on salt and drought tolerance in plants. *Agronomy for Sustainable Development*, vol. 34, no. 2, pp. 455-472. http://dx.doi.org/10.1007/s13593-013-0194-1.