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Original Article

The role of silicon in the mitigation of water stress in *Eugenia myrcianthes* Nied. seedlings

O papel do silício na mitigação do estresse hídrico em mudas de *Eugenia myrcianthes* Nied.

C. C. Santos[a*], S. P. Q. Scalon[a], A. C. Foresti[a], L. C. Reis[a] and D. M. Dresch[a]

[a]Universidade Federal da Grande Dourados, Faculdade de Ciências Agrárias, Dourados, MS, Brasil

Abstract

Silicon (Si) is a beneficial element that can mitigate effects of water stress on photosynthetic metabolism and plant growth. Thus, the aimed was to evaluate the effect of Si in mitigating the stressful effect of water deficit and flooding in *Eugenia myrcianthes* Nied. seedlings. The seedlings received three silicon doses (0, 2, and 4 mmol) and were subjected to two water regimes (I – continuous irrigation and S – water fluctuation, characterized as water stress obtained by two cycles of water regimes: irrigation suspension and flooding). Each cycle was ended when the seedlings had a photosynthetic rate close to zero (P0) when the stressful irrigation condition was normalized until the photosynthetic rate reached the values of the control seedlings (REC). The evaluations were carried out in five periods: T0 – initial seedling condition; 1st and 2nd P0; and 1st and 2nd REC. The *E. myrcianthes* seedlings reached P0 at 22 and 50 days under water deficit and flooding, respectively. Water stress caused damage to photochemical activities in photosystem II. *E. myrcianthes* is a species sensitive to water stress, but capable of adjusting to water fluctuation, and the application of 2 mmol Si contributed to the regulation of gas exchange, photochemical yields, and growth of this species at the deficit and flooding phases. We emphasize that *E. myrcianthes* seedlings have potential for resilience due to physiological plasticity, regardless of the silicon application.

Keywords: water deficit, flooding, photosystem II, physiological plasticity, gas exchange.

Resumo

O silício (Si) é um elemento benéfico que pode mitigar os efeitos do estresse hídrico sobre o metabolismo fotossintético e crescimento das plantas. Assim, objetivou-se avaliar o potencial do Si na mitigação do efeito estressante do déficit hídrico e alagamento em mudas de *Eugenia myrcianthes* Nied. As mudas receberam aplicação de três doses de silício: 0, 2 e 4 mmol e foram submetidas a dois regimes hídricos: (I) - irrigação contínua e (E) flutuação hídrica, caracterizada como estresse hídrico obtido por dois ciclos de regimes hídricos: suspensão da irrigação e alagamento. Cada ciclo foi encerrado quando as mudas apresentaram taxa fotossintética próxima de zero (F0), momento que a condição de irrigação estressante foi normalizada até que a taxa fotossintética alcançasse os valores das mudas controle (REC). As avaliações foram realizadas em cinco períodos: T0 – condição inicial das mudas; 1ª e 2ª F0; 1ª e 2ª REC. As mudas de *E. myrcianthes* atingiram F0 aos 22 e 50 dias sob déficit hídrico e alagamento, respectivamente. O estresse hídrico promoveu danos nas atividades fotoquímicas no fotossistema II. *E. myrcianthes* é uma espécie sensível ao estresse hídrico, mas capaz de se ajustar à flutuação hídrica e a aplicação de 2 mmol de Si contribuiu na regulação das trocas gasosas, rendimentos fotoquímicos e crescimento dessa espécie na fase de déficit e alagamento. Ressaltamos que mudas de *E. myrcianthes* apresentam potencial de resiliência por plasticidade fisiológica independente da aplicação de silício.

Palavras-chave: déficit hídrico, alagamento, fotossistema II, plasticidade fisiológica, trocas gasosas.

1. Introduction

Given the global climate change scenario, several phytoecological regions present water fluctuations at different times of the year, promoting a stressful effect on the vegetation in these areas. Several species show morphophysiological and growth changes and oxidative damage in the photosynthetic apparatus under these adverse conditions, that is, due to deficit or flooding (Barbosa et al., 2014; Foyer, 2018).

Studies aimed at mitigating the deleterious effects of water stress on the photosynthetic apparatus have increased over the years. Silicon (Si) has been a promising agent for reducing damage caused by multiple abiotic stresses

*e-mail: cleber_frs@yahoo.com.br
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(Shen et al., 2014; Coskun et al., 2016; Frew et al., 2018) to which the plants may be exposed.

In the plant, Si provides higher structural rigidity of the tissue, favors osmotic adjustment (Yin et al., 2013; Lima et al., 2019), and increases photosynthetic and water use efficiency (Cooke and Leishman, 2016; Thorne et al., 2020; Cassol et al., 2021), regulating physiological processes. The beneficial effect of Si is associated with the fact that this element promotes an increase in photosynthetic pigments and gene and phytohormone expressions, in addition to the activity of antioxidant enzymes and amino acids capable of relieving or delaying oxidative stress (Chen et al., 2011; Parveen et al., 2019).

However, information on the use of Si associated with the mitigating effect of water stress for forest and fruit species is still insufficient. *Eugenia myrcianthes* Nied. (Myrtaceae) is among the species of remarkable bioecological importance, whose leaves and fruits have antioxidant compounds (Takao et al., 2015). It is a pioneer and deciduous species, usually found in moist and well-drained soils (Lorenzi, 2009). Its seedlings can be used to recover degraded areas and/or enrich agroforestry systems.

Considering the habitat where *E. myrcianthes* is found naturally and the mitigating potential of Si, we seek to answer the following questions: i) Are *E. myrcianthes* seedlings sensitive to water deficit and/or flooding? ii) Does silicon attenuate the stressful effect of water fluctuations on the photosynthetic apparatus of this species? and iii) Does *E. myrcianthes* have the ability to resume metabolism and growth after normal water supply? Thus, this study aimed to evaluate the photosynthetic metabolism and growth of *E. myrcianthes* seedlings under water fluctuation and the effect of silicon in mitigating water stress and seedling recovery.

2. Material and Methods

2.1. General conditions and obtaining seedlings

Ripe fruits of *E. myrcianthes* were collected from random mother plants in a remaining area of Cerrado. Subsequently, the processing was performed manually, immersing the seeds in 2% sodium hypochlorite for 5 minutes, with sowing carried out in 72-cell expanded polystyrene trays filled with commercial substrate Tropstrato® with chemical attributes: pH $CaCl_2$ = 5.75; P (g dm^{-3}) = 65.70; K = 1.60 $cmol_c$ dm^{-3}; Ca = 23.80 $cmol_c$ dm^{-3}; Mg = 12.40 $cmol_c$ dm^{-3}; Al = 0.00 $cmol_c$ dm^{-3}; H + Al = 4.20 $cmol_c$ dm^{-3}; SB = 39.80 $cmol_c$ dm^{-3}; CEC = 42.10 $cmol_c$ dm^{-3}; and base saturation (V%) = 64.80.

Transplanting was carried out when the seedlings had an average height of 10.0 cm (45 days after emergence) into 7-L plastic pots filled with Dystroferric Red Latosol + sand (3:1, v/v), irrigated daily to maintain 70% of water retention capacity (WRC) in the substrate (pre-test based), and 30% shading for 30 days, characterizing the acclimatization period.

2.2. Si application, water regimes, and evaluation periods

Initially, the seedlings receive the application of three silicon doses (0, 2, and 4 mmol) based pre-test, using silicon oxide (SiO_2 – 92% Si) as a source, via spraying on the abaxial and adaxial surfaces of leaves, in the morning, until drip point (20 mL per plant) pre-test based.

Subsequently, the seedlings were divided into two groups based on the following water regimes: (I) continuous irrigation (control) – performed daily, keeping 70% WRC in the substrate, according to Souza et al. (2000), and (S) stress – water fluctuation obtained by two cycles of water regimes: the first cycle with irrigation suspension followed by a second cycle with flooding. In the first cycle, the seedlings were grown under a 150-micron plastic cover to protect against rainfall. In the second cycle, the seedlings were stored in a plastic pool with a capacity of 1000 L, with a water depth of 5.0 cm above the substrate level.

Each cycle was ended when the seedlings had a photosynthetic rate close to zero (P0) when the stressful irrigation condition was normalized until the photosynthetic rate reached the values of the control seedlings (REC).

The evaluations of morphophysiological characteristics were carried out in five periods: T0 – zero time: characterized as the initial plant condition, that is, one day before the submission of the plants to different water regimes; 1st P0 (22 days): 1st REC (23–45 days), with the resumption of irrigation until the plants under stress had *A* values close to those under continuous irrigation; 2nd P0 (46–96 days) when the pots were removed from this water condition, leaving them under natural drainage for seven days, followed by the second resumption of irrigation; 2nd REC (97–116 days), considering the criteria described in the 1st REC.

2.3. Evaluated morphophysiological characteristics

Gas exchanges: the CO_2 assimilation rate (photosynthesis) – *A*, stomatal conductance – g_s, intercellular CO_2 concentration – C_i and transpiration – E were evaluated in two fully expanded leaves located in the middle third using an LCIPro-SD portable photosynthesis analyzer (IRGA, Model ACD BioScientific Ltd.); subsequently, the carboxylation efficiency of Rubisco (A/C_i) and water use efficiency – *WUE* (A/E) were calculated. The evaluations were carried out between 8 and 10 am, considering photosynthetically active radiation > 850 μmol photons m^{-2} s^{-1}.

Chlorophyll *a* fluorescence: the same leaves were subjected to a dark condition, using leaf-clips for 30 minutes. The initial chlorophyll *a* fluorescence (F_0) and the potential photochemical quantum efficiency in photosystem II (F_v/F_m) were determined after this period, using a portable fluorometer under a flash of 1,500 μmol m^{-2} s^{-1}. Subsequently, the conversion efficiency of absorbed energy (F_v/F_0) and the maximum yield of non-photochemical processes (F_0/F_m) were calculated.

Relative water content (RWC): determined following the methodology of Turner (1981).

Photosynthetic pigments: the contents of chlorophyll *a*, *b*, and total and carotenoids were quantified using 1 g of leaf, according to the methodology of Arnon (1949) and Lichtenthaler and Wellburn (1983).

Initial growth: the number of fully expanded leaves (NL), leaf area (LA), using area meter (LI-COR, 3100C, Nebraska, USA), and the largest root length (RL) were quantified. The material was then stored in a forced-air circulation oven at 60 ± 5 °C until constant total dry mass (DMT). Seedling quality standard (DQI) was calculated using the morphometric data of the shoot and biomass production, as proposed by Dickson et al. (1960).

2.4. Experimental design and statistical analysis

The experimental design was completely randomized, with three replications. The treatments were arranged in a subplot scheme. A double factorial was grouped in the plots between water regimes and silicon doses, consisting of six treatments (I 0 Si, I 2 Si, I 4 Si, S 0 Si, S 2 Si, and S 4 Si), while the evaluation periods (T0, 1st P0, 1st REC, 2nd P0, and 2nd REC) were grouped in the subplots. Each experimental unit consisted of a pot and two plants in each pot.

The data were subjected to principal component analysis (PCA) using vectors of variance and covariance, eliminating the characteristics with factor loads of scores < 0.20. Subsequently, Pearson's linear correlation analysis (r) ($p < 0.05$) and similarity between treatments and times were performed, based on the Euclidean distance of the hierarchical groups. Statistical analyses were performed using the software PAST 3.21.

3. Results

E. myrcianthes took 22 and 50 days to reach P0 values when submittted to water deficit (1st P0) and flooding (2nd P0), respectively. Regarding physiological recovery, at 1st and 2nd REC, values photosynthetic rate (*A*) normalized at 22 and 19 days after irrigation resumption, respectively. In general, the components of photosynthetic metabolism of *E. myrcianthes* seedlings were negatively affected by both the deficit and flooding, with a reduction in the *A* under these water conditions (1st and 2nd P0), especially in the seedlings without Si, while those who received 2 mmol Si showed values *A* (Figure 1).

The 1st P0 and 2nd P0 presented *A* values of stressed seedlings not treated with Si of 0.38 and 0.73 µmol CO_2 m^{-2} s^{-1}, respectively, while those that received 2 mmol Si, despite having reduced, showed values 5 times higher (2.01 and 3.46 µmol CO_2 m^{-2} s^{-1}, respectively) during these same periods and water regime (S), demonstrating the mitigating effect of the silicon dose in reducing the photosynthetic rate. After the resumption of irrigation (REC), all seedlings had a pronounced increase in *A* and other aspects of gas exchange compared to those that received 2 mmol Si, both under continuous irrigation and those subjected to water stress relative to those not treated with Si.

The characteristics chlorophyll *b* and root length were excluded from the principal component analysis (PCA) due to their low representativeness, that is, they showed a load < 0.20, with an overall mean of 9.42 µg cm^2 and 54.12 cm, respectively. The highest positive factor loads of the scores in decreasing order were observed in g_s, *A*, F_v/F_m, and A/C_i in PC 1 and DMT, DQI, LA, NL, and C_i in PC 2 (Table 1), that is, these characteristics presented the highest qualitative experimental representativeness, i.e., importance for seedlings.

We observed that 71.71% of the variability was explained by PCA, with 49.37 and 22.34% constituting PC 1 and PC 2, respectively (Figure 2). The highest values of C_i and F_0/F_m occurred in seedlings grown under stress without Si (0 mmol) and with 4 mmol Si, while those that received 2 mmol Si had the lowest values of these characteristics. The seedlings had better and greater characteristics of the chlorophyll a fluorescence (F_v/F_m and F_v/F_0), gas exchange (*A*, *E*, g_s, A/C_i, and *WUE*), RWC, and growth when grown under continuous irrigation, regardless of the Si dose and those stressed with 2 mmol Si. Also, all seedlings normalized the values of all characteristics at the final recovery (R) phase (2nd REC), regardless of the treatment.

On the other hand, the characteristics of potential photochemical quantum efficiency in photosystem II (F_v/F_m), photosynthetic rate (*A*), relative water content (RWC), and photosynthetic pigments were more representative in seedlings grown with 2 mmol Si both in the cultivation under continuous irrigation and in the cultivation subjected

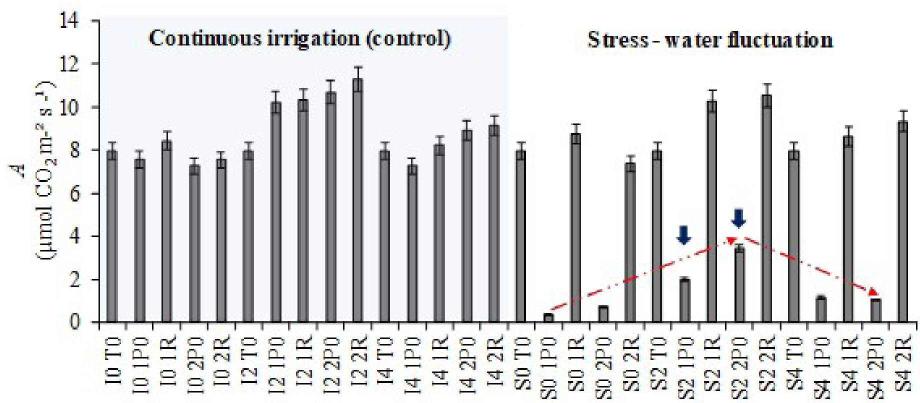

Figure 1. Photosynthetic rate (*A*) of *Eugenia myrcianthes* Nied. seedlings grown under water regimes (continuous irrigation, deficit – 1st P0, and flooding – 2nd P0), with silicon doses (0, 2, and 4 mmol). I: continuous irrigation; S: stress; P0: photosynthesis close to zero; R: recovery.

Table 1. Factor loads of the characteristics evaluated in *Eugenia myrcianthes* Nied. seedlings grown under water regimes and silicon doses (0, 2, and 4 mmol).

Characteristic	PC 1	PC 2	PC 3	PC 4	PC 5
A	**0.2849**	-0.1647	-0.0235	0.1627	0.0118
C_i	-0.1402	**0.2931**	-0.0452	-0.1397	-0.4391
E	0.2575	-0.0487	-0.1940	-0.2361	0.3633
g_s	**0.2855**	0.0884	-0.1410	-0.0028	-0.1449
WUE	0.0545	-0.2080	0.2299	0.5418	-0.3693
A/C_i	**0.2684**	-0.2253	0.0096	0.1120	0.1321
Chl *a*	0.2462	0.0807	-0.0209	-0.3554	-0.0198
Chl *b*	0.1684	-0.0744	0.3971	-0.3247	-0.0995
Chl T	0.2458	0.0012	0.2311	-0.4048	-0.0724
Car	-0.1277	-0.2214	-0.4273	0.0969	0.2370
F_v/F_m	**0.2834**	-0.1516	-0.0618	-0.0283	-0.0720
F_0	-0.2599	-0.0416	0.2773	-0.0238	0.3541
F_m	-0.1004	-0.2706	0.3952	-0.0426	0.3418
F_v/F_0	0.2752	-0.1786	-0.0107	0.0182	-0.1341
F_0/F_M	-0.2667	0.1905	-0.0004	-0.0139	0.1558
NL	0.1891	**0.3245**	0.0813	0.1511	0.1791
RL	0.0901	0.1895	0.4860	0.2243	0.0575
LA	0.1927	**0.3362**	-0.0681	0.1000	0.1335
RWC	0.2484	-0.2166	-0.0479	0.1929	0.1485
DMT	0.1781	0.3610	-0.0548	0.1908	0.1209
DQI	0.1773	0.3524	0.0563	0.1638	0.2215

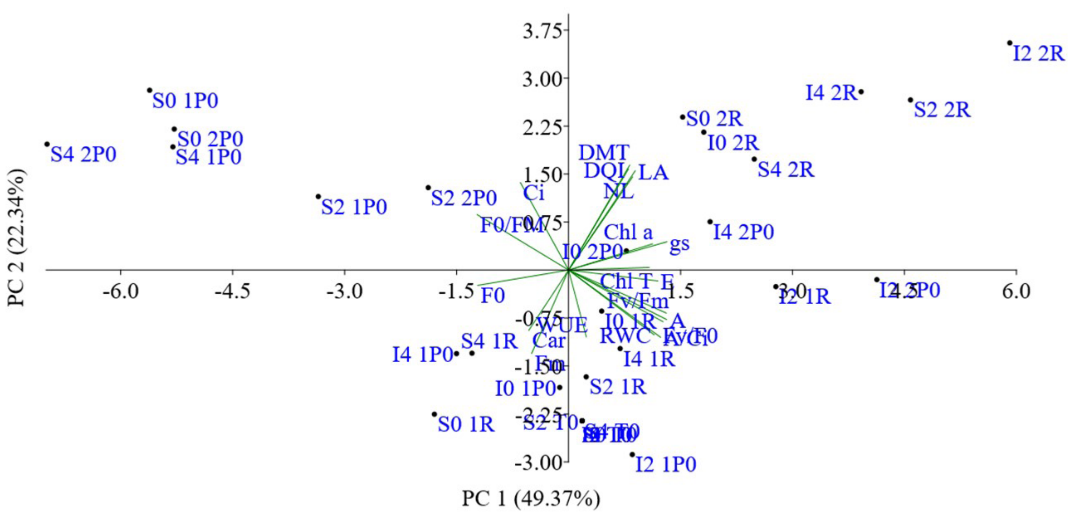

Figure 2. Principal component analysis (PCA) of the characteristics evaluated in *Eugenia myrcianthes* Nied. seedlings grown under water regimes (continuous irrigation, deficit – 1st P0, and flooding – 2nd P0) and silicon doses (0, 2, and 4 mmol). I: continuous irrigation; S: stress; P0: photosynthesis close to zero; R: recovery.

to stress under irrigation fluctuation (deficit and flooding) and at the recovery phase.

We found a correlation between most of the evaluated characteristics ($p < 0.05$), both positive and negative (Figure 3). The highest positive intensities occurred between the photosynthetic rate (A) and the characteristics A/C_i (r = 0.97), RWC (r = 0.93), and F_v/F_m and F_v/F_0 (both with r = 0.85). A positive correlation of high magnitude was also observed

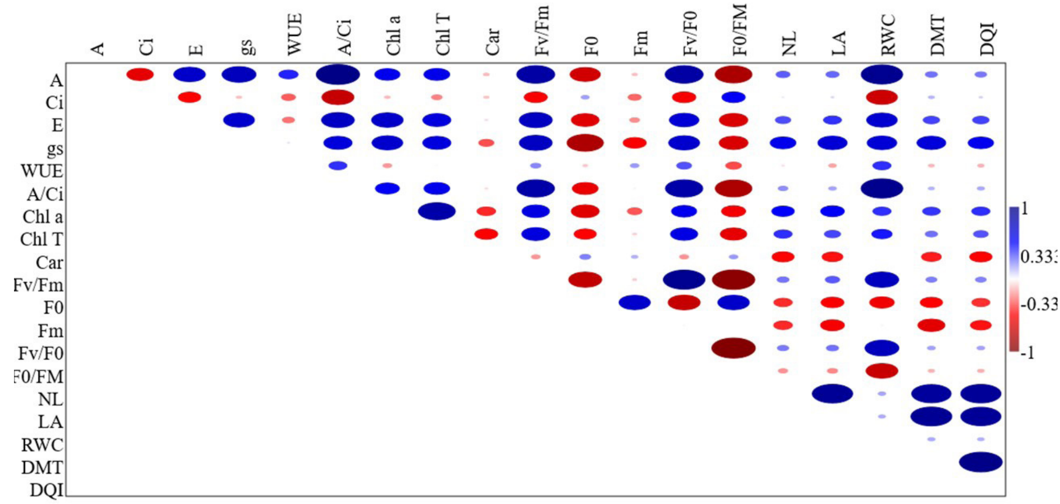

Figure 3. Pearson's linear correlation (r) of the characteristics evaluated in *Eugenia myrcianthes* Nied. seedlings grown under water regimes (continuous irrigation, deficit – 1st P0, and flooding – 2nd P0) and silicon doses (0, 2, and 4 mmol).

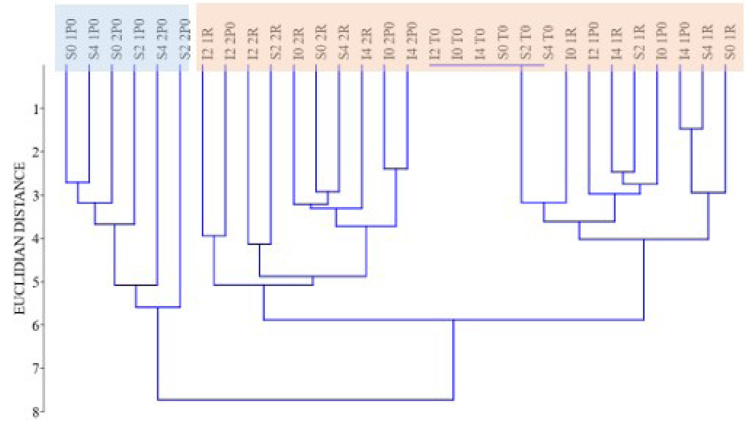

Figure 4. Hierarchical groups based on the Euclidean distance of the characteristics evaluated in *Eugenia myrcianthes* Nied. seedlings grown under water fluctuations (deficit – 1st P0 and flooding – 2nd P0) and silicon doses (0, 2, and 4 mmol). I: continuous irrigation; S: stress; P0: photosynthesis close to zero; R: recovery.

between the growth characteristics NL (r = 0.90), LA (r = 0.90), and DMT (r = 0.96) with DQI. However, correlations of medium to high negative magnitude occurred between F_0 with *A* (r = −0.67) and *gs* (r = −0.81) and between F_0/F_m with *A*, A/C_i, F_v/F_m, and F_v/F_0, presenting r values of −0.82, −0.82, −0.95, and −0.97, respectively.

The smallest Euclidean distances in the cluster analysis (cophen. corr.: 0.80) occurred in seedlings in all treatments of T0, regardless of the Si dose (0.00), followed by those cultivated under continuous irrigation in the 1st P0 and stressed in REC, both with the application of 4 mmol Si (I4 1P0 and S4 1R, respectively) (1.46) (Figure 4). A similarity (a distance of 2.70) was observed between stress without Si and 4 mmol Si in the 1st P0 (S0 1P0 and S4 1P0, respectively), differing from the stress treatment with 2 mmol Si in the 1st P0 (S2 1P0). In general, seedlings under stress (deficit and flooding) presented values close to each other and distant from those irrigated daily, and those that received 2 mmol Si were presented in isolated subgroups of the other treatments, in addition to the influence of the evaluation periods.

4. Discussion

The reduction in *A* and other components of gas exchange in *E. myrcianthes* seedlings is associated with the stressful effect of water fluctuations. However, they were more sensitive to the deficit than flooding, as they took 50 days to reach 2nd P0 in the 2nd cycle of stress, while it only took 22 days in the first cycle under deficit. We suggest that seedlings of this species have a higher capacity to adjust to flooding or that previous water stress, caused by water deficit. Intermittent stresses triggers memory to stress, which favors protective and adjustment responses and the preservation of plants under extreme climate conditions, reflecting on their resilience (Walter et al., 2013).

The highest values of gas exchange, especially the *A*, are due to the highest photochemical yields, represented here by the potential photochemical quantum efficiency in PSII (F_v/F_m) and conversion of absorbed energy (F_v/F_0), demonstrating that the effects in the reaction centers reflected in the production of photoassimilates (Figure 2), here represented by DMT, especially in the 1st and 2nd REC.

However, the best gas exchange, chlorophyll a fluorescence, photosynthetic pigments, RWC and DQI for *E. myrcianthes* with Si application, especially at a dose of 2 mmol (Figures 1-2) in the two cycles of stress and recovery, demonstrate the mitigating effect of water stress, proving our initial hypothesis. Si contributes to increasing the activity of antioxidant metabolism enzymes and amino acids that help to alleviate oxidative stress and repair damage to membranes (Liang et al., 2003; Shen et al., 2014), increasing carboxylation efficiency of Rubisco (A/C_i), stabilizing photosynthetic metabolism in *E. myrcianthes* seedlings through increased gas exchange and photochemical yields in PSII reaction centers.

The normalization of values of the characteristics regarding the photosynthetic metabolism after the resumption of continuous irrigation, that is, in the 1st and 2nd REC, indicate physiological plasticity, a desirable aspect as it increases the resilience of *E. myrcianthes* in areas subject to water stress, especially fluctuations over the year in phase seedlings.

Moreover, stressed seedlings treated with 2 mmol at the flooding phase (2nd P0) showed higher values of *A* (Figures 1-2), demonstrating a prolonged effect of Si as a stress mitigation agent. The Si deposited in the leaf tissue in the form of monosilicic acid (H_4SiO_4) in the epidermal cells and xylem vessels forms a sub-cuticle over the stomatal pore, favoring osmotic adjustment (Epstein, 1999; Yin et al., 2013; Luyckx et al., 2017), and the application of 2 mmol Si favored the regulation of g_s and *E*, which is reflected in the higher *WUE* and RWC of *E. myrcianthes* seedlings.

However, we emphasize that the dose of 4 mmol Si on stressed plants contributed less effectively to mitigate the negative effects of stress than 2 mmol, indicating that it is an overdose for this species. We reinforce this conclusion based on PCA since the stressed plants without Si and with 4 mmol Si had similar scores, also a stressful condition, and that promoted an increase in C_i and maximum non-photochemical yield (F_0/F_m) (Figures 2-3).

We believe that the highest applied dose possibly led to an excessive deposition on the stomatal pore, which reduced CO_2 intake and assimilation, especially at the stress phase. We observed that the literature has no specific information on Si doses for each species, especially tree and fruit species, justifying the importance of evaluating the appropriate dose for each of them.

In this sense, seedlings not treated and with 4 mmol Si under stressful conditions (1st and 2nd P0) showed damage to the reaction centers as F_0 and F_0/F_m increased, dissipating energy in the electron transport chain, negatively affecting *A* and A/C_i (Figures 2-3). Flooding and water deficit promotes cellular damage that reduces ATP production (Voesenek and Bailey-Serres, 2015; Phukan et al., 2016), directing the energy towards reactive oxygen species production (Quijano et al., 2016; Foyer, 2018), compromising leaf metabolism. In this context, low water availability conditions lead to changes in the chloroplast ultrastructure, degrading pigments and reducing electron transport between acceptors (Urban et al., 2017; Dahal and Vanlerberghe, 2018), as occurred in our study.

However, Si favored the photochemical stability of *E. myrcianthes* seedlings by increasing the synthesis of chlorophylls (Figure 2), especially at the stress phase. This element contributes to the plant architecture, leaving the leaves more erect and rigid (Tubana et al., 2016; Lima et al., 2019), favoring solar interception and reflecting a higher production of photoassimilates, increment in leaves, and photosynthetic area (leaf area) and biomass production (DMT), a result different from that of seedlings not treated with Si.

In general, seedlings that presented higher vegetative characters had a higher quality standard (DQI), resulting from the higher balance between robustness and photoassimilate partitioning. Based on our results, we accept the hypothesis that *E. myrcianthes* is a species sensitive to water stress, but capable of adjusting to water fluctuation and that the application of 2 mmol Si contributed to the regulation of gas exchange, photochemical yields, and growth of this species at the deficit and flooding phase (Figure 4).

We emphasize that *E. myrcianthes* seedlings have the potential for resilience due to physiological plasticity regardless of the silicon application. In future perspectives, new studies should be carried out with the species to obtain more information, especially regarding antioxidant metabolism and leaf tissue anatomy; in addition to developing studies in field condition afteter transplanting seedlings.

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