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Original Article

Does silicon and salicylic acid contribute in the morphophysiology of *Schinus terebinthifolia* seedlings under flooding?

O silício e ácido salicílico contribuem na morfofisiologia de mudas de *Schinus terebinthifolia* sob alagamento?

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Abstract

Flooding can damage the photosynthetic apparatus and initial growth of *Schinus terebinthifolia*. We aimed this study evaluates the potential of silicon (Si) and salicylic acid (SA) as mitigating agents on the ecophysiological responses and initial growth of *S. terebinthifolia* subjected to flooding periods. Seedlings were grown under the following conditions: 1) control (non-flooded): daily irrigation, 2) Flooded (F): storage of seedlings in a 500 L plastic pool, keeping the water depth at ± 2.0 cm above the substrate level, 3) F + 1.0 mM Si, 4) F + 2.0 mM Si, 5) F + 1.5 mM SA, and 6) F + 3.0 mM SA, and evaluated to 15 and 30 days. We observed that flooded seedlings formed hypertrophied lenticels on the stem on the 7th day as a stress adjustment strategy. *S. terebinthifolia* is sensitive to flooding, although it maintains a stable gas exchange for up to 15 days in this condition. The applications of 1.0 mM Si mitigated the pronounced decrease of gas exchange by 30 days. Using 1.0 mM Si and 3.0 mM SA contributed for integrity of the photosynthetic apparatus and to photochemical activities in the reaction centers, in addition favors to higher seedling biomass and quality under flooding. Foliar application of Si and SA is promising practice for photosynthetic metabolic and initial growth of *S. terebinthifolia* seedlings under flooded stress.

Keywords: gas exchange, hypertrophied lenticels, root adventitious, plasticity, photosystem II.

Resumo

O alagamento pode promover danos ao aparato fotossintético e crescimento inicial de *Schinus terebinthifolia*. Objetivamos nesse estudo avaliar o potencial do silício (Si) e ácido salicílico (AS) como agentes de mitigação sobre as respostas ecofisiológicas e crescimento inicial de *S. terebinthifolia* submetidas a períodos de alagamento. As mudas foram cultivadas sob as seguintes condições: 1) controle (não alagado): irrigação diariamente, 2) Alagado (A): acondicionamento das mudas em piscina plástica de 500 L, mantendo uma lâmina d'água ± 2,0 cm acima do nível do substrato, 3) A + 1,0 mM Si, 4) A + 2,0 mM Si, 5) A + 1,5 mM AS e 6) A + 3,0 mM AS. Observamos que as mudas alagadas formaram lenticelas hipertrofiadas no caule a partir dos 7 dias como estratégia de ajuste ao estresse. *S. terebinthifolia* é sensível ao alagamento, embora mantenha estável as trocas gasosas por 15 dias nessa condição. A aplicação de 1.0 mM de Si mitigou o decréscimo pronunciado das trocas gasosas por 30 dias. O uso de 1,0 mM Si e 3,0 mM SA contribuíram para a integridade do aparato fotossintético e atividades fotoquímicas nos centros de reação, além de favorecer maior produção de biomassa e qualidade das mudas sob alagamento. A aplicação foliar de Si e AS é uma prática promissora para o metabolismo fotossintético e crescimento inicial de mudas de *S. terebinthifolia* sob estresse por alagamento.

Palavras-chave: trocas gasosas, lenticelas hipertrofiadas, raízes adventícias, plasticidade, fotossistema II.

1. Introduction

Brazilian pink pepper (*Schinus terebinthifolia* Raddi - Anacardiaceae), a pioneer species, is a fruit tree found in several countries, including Brazil, in its different phytophysiognomies. Adult plants of this species can reach up to 10 m height and have small reddish fruits that are attractive to avifauna (Lorenzi, 2008); can also be used in gastronomy and drinks prepare. In addition, the species is widely used in Brazil for landscaping in urban areas. Moreover, as the species shows rapid growth, its seedlings can be inserted in integrated production systems such as agroforestry and forest restoration of disturbed and/or degraded areas.

However, many regions with different phytophysiognomies in the Cerrado biome, such as areas close to gallery or

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riparian forests or floodplains, are subject to water stress due to soil flooding from an increase in the water table depth because to climate change or anthropogenic actions (Rosa et al., 2015; Santos et al., 2023); this can cause stress for the species inserted in these localities. The reduction in O_2 concentration (anoxia) in the soil becomes limiting to photosynthetic metabolism and plant growth, especially because the plants under study present high metabolic demands (Gonçalves et al., 2013). Morphoanatomical changes such as formation of adventitious roots and hypertrophic lenticel, and these changes lead to the ecological adaptation of species (Linné et al., 2023). These demands lead to higher energy expenditure; thus, the metabolic and morphological differentiation of seedlings may be hindered due to oxidative stress according to time of exposure to stress.

In this sense, it is necessary to establish practices, such as preconditioning of seedlings through foliar application of silicon (Si) and salicylic acid (SA), that can alleviate the damage to the photosynthetic apparatus and contribute positively to the physiological plasticity and/or tolerance induce under adverse conditions, here in our study represented by temporary flooding.

The use of Si, generally in the form of silicate, attenuates the effects of water stress in plants by increasing water use efficiency and improving metabolic pathways (Etesami and Jeong, 2018; Silva et al., 2019a; Santos et al., 2022b). In the plant, Si acts by providing greater tissue rigidity (Lima et al., 2019), increasing nutritional and photosynthetic efficiency and stomatal regulation due to hormonal signals (Santos et al., 2022b). Furthermore, this element correlates with phytohormone signaling, gene expression, and other benefits to the antioxidant system of plants (Manivannan and Ahn, 2017; Neves et al., 2019), as a protective mechanism against to stressed conditions.

SA, a phytohormone of a phenolic nature, is important elicitor for maintaining photochemical activities in photosystem II, and gas exchange contributed for photosynthetic performance, in addition of acting on growth and increasing antioxidant enzymes so as to mitigate the harmful effects of reactive oxygen species (ROS) (Silva et al., 2019b; Santos et al., 2023). Moreover, it delays the degradation of protein D_1 and the functional damage on photosystem II (PSII), promoting electron transfer stability in reaction centers (Hou et al., 2019; Poór et al., 2019; Santos et al., 2022a). In the literature, 2 mmol of Si alleviated effect of water stress in *Eugenia myrcianthes* Nied. seedlings (Santos et al., 2022b) and application of SA stimulated the growth of *Hymenaea courbaril* L. under flooding (Santos et al., 2023).

Considering the fact that *S. terebinthifolia* is found in different phytophysiognomies with moist and drained soils, this study seeks to answer the following questions: i) Are *S. terebinthifolia* seedlings sensitive to flooding? ii) Do morphoanatomical changes attenuate flooding stress? iii) Does priming with Si and SA contribute to mitigate the damage to the photosynthetic apparatus under stress conditions? iv) Do doses of products and time of exposure to flooding influence the plasticity of this species? We aimed this study evaluates the potential of silicon and salicylic acid as mitigating agents on the ecophysiological responses and initial growth of *S. terebinthifolia* under flooding periods.

2. Materials and Methods

2.1. Fruits collection and seedlings formation

Ripe fruits of *S. terebinthifolia* (Access Registration No. A9CDAAE – CGEN – MMA) were collected of ten matrices (Figure 1a-1b) located in the Horto Medicinal Plant (22º11'43.7"S and 54º56'08.5"W, 452 m), in Faculty of Agrarian Sciences, at the Universidade Federal da Grande Dourados (UFGD), Dourados, Mato Grosso do Sul, Brazil. After manual processing for seed extraction and selection, the sowing was performed in 128-cell expanded polystyrene trays, filled with Tropstrato® with daily irrigations.

The seedlings were transplant with height 10 cm for plastic pots with a capacity of 2 kg filled (Figure 1c) with Dystrophic

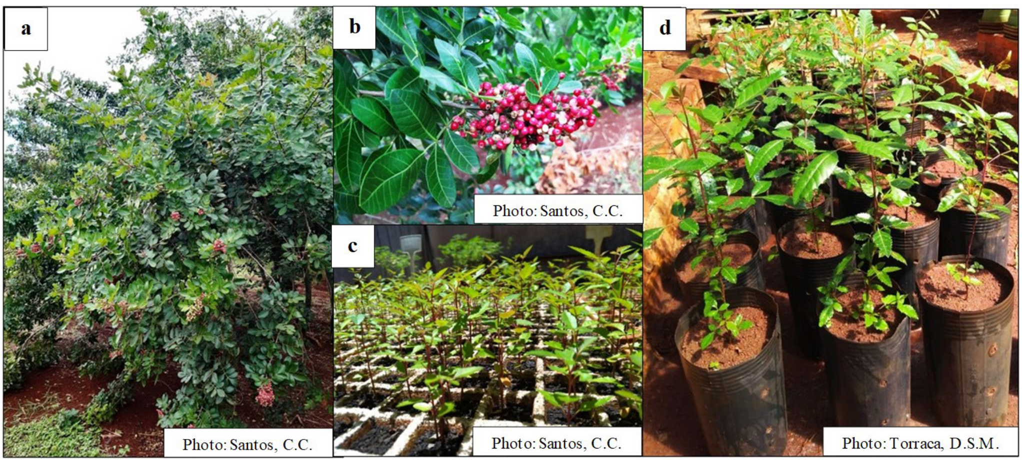

Figure 1. Adult plants (a), fruits (b) and seedlings (c-d) of *Schinus terebinthifolia*.

Red Latosol [Santos et al. (2018), Brazilian Classification] of clayey texture, corresponding to Oxisols soil USDA classification staying for 30 days after transplant with daily irrigations and 50% shading, characterizing the acclimatization period, with height of 20.0 cm (Figure 1d).

2.2. Water regimes, and Si and SA application

We performed the experiment in a nursery, using black nylon (Sombrite®) to provide 30% shading. Initially, the two products were applied via foliar spraying onto the abaxial and adaxial surfaces until drip point (10.0 mL per plant, based pre-test), at 24-h intervals, three days prior to submitting the seedlings to flooding. Potassium silicate (K_2SiO_3; 12% Si and density 1.40 g L^{-1}, and the balancing of K) and salicylic acid (P.A.) were used as sources of Si and SA, respectively. In syrup preparation (solution), 1.0 mL L^{-1} of the LI 700 adjuvant were used to favor the adherence of the products in the leaves.

The seedlings were subjected to six grown conditions (treatments): 1) control (non-flooded): daily irrigation, maintaining 75% of the water retention capacity of the substrate according methodology Souza et al. (2000); 2) Flooded (F): storage of seedlings in a 500 L plastic pool, keeping the water depth at ± 2.0 cm above the substrate level; 3) F + 1.0 mM Si; 4) F + 2.0 mM Si; 5) F + 1.5 mM SA, and 6) F + 3.0 mM SA. The environmental and water conditions are shown in Table 1.

2.3. Evaluated characteristics

Nondestructive evaluations were conducted in two distinct periods, at 15 and 30 days after submitting the seedlings to the different treatments; destructive evaluations were conducted only in the latter period (30 days). To carry out the evaluations, the seedlings were removed one at a time for measurements and were placed again in the flooding condition.

Table 1. Environmental conditions and water of flooding in two evaluations periods for production of *Schinus terebinthifolia* seedlings.

Environmental conditions	Evaluations periods (days)	
	15	30
Photosynthetically active radiation (µmol photons m^2 s^{-1})	913.92	852.37
Atmospheric CO_2 concentration (ppm)	437.12	447.91
Minimum temperature (ºC)	23.7	25.5
Maximum temperature (ºC)	23.9	26.3
Minimum relative air humidity (%)	43	65
Maximum relative air humidity (%)	50	71
Water (flooding)		
Electrical conductivity (µS cm^2)[1]	0.076	0.073
Temperature (ºC)[2]	19.9	22.3

[1]Portable conductivity meter TDS & EC – Meter Hold. [2]Infra Red thermometer Raytek.

Survival. Count of the number of live seedlings, having as criterion the presence of fully expanded green leaves and photosynthesis ≥ 0.75 µmol CO_2 m^2 s^{-1}.

Morphological adaptative structures. Visual observations and records on the emission of hypertrophied lenticels and adventitious roots during experimental period were performed.

Gas exchange. CO_2 assimilation rate – photosynthesis (A; µmol CO_2 m^{-2} s^{-1}), intercellular CO_2 concentration (C_i; mmol CO_2 mol air^{-1}), stomatal conductance (g_s; mol H_2O m^{-2} s^{-1}), and transpiration (E; mmol H_2O m^{-2} s^{-1}) were measured in third fully expanded leaf using a portable photosynthesis meter (LCI Pro-SD, ADC BioScientific Ltd.), between 8 and 10 am. Subsequently, water use efficiency ($WUE= A/E$; µmol CO_2/mmol H_2O) and instantaneous Rubisco carboxylation efficiency (iCE= A/C_i; µmol CO_2/mmol CO_2) were calculated.

Chlorophyll indices. Using the third fully expanded leaf of each seedling, chlorophyll *a*, *b*, and total chlorophyll ($a + b$) were determined using a portable chlorophyll meter ClorofiLOG CFL 1030 (Falker – FCI), between 8 and 10 am.

Photochemical processes in photosystem II. Leaves were submitted to the dark condition, with leaf clips for 30 minutes. Absorbed energy conversion efficiency (F_v/F_0) and maximum basal yield of non-photochemical processes (F_0/F_m) calculated with values using a portable fluorometer (OS-30p; Opti-Sciences Chlorophyll Fluorometer, Hudson, NY, USA) at 1,500 µmol m^{-2} s^{-1} light intensity to analyze the quantum efficiency photochemical potential on photosystem II (F_v/F_m).

Initial growth and quality index. Plant height was determined using a millimeter ruler, and was considered as the distance from the ground to the inflexion of the highest leaf. The number of expanded leaves were also recorded. The seedlings were collected and separated into leaves, stems, and roots. Leaf area was determined using an area integrator (LI-COR, 3100 C - Area Meter), and the length of the largest root was measured. Using growth and dry weight data Dickson quality index (DQI) was calculated according to Dickson et al. (1960).

2.4. Experimental design and statistical analysis

The experimental design was completely randomized in a subplot scheme, where evaluation periods corresponded to plots, and treatments were considered as subplots for nondestructive evaluations. Each treatment had three replications (n= 3), and each experimental unit consisted of three pots containing one seedling each. The data were submitted to the Shapiro-Wilk test to verify normal distribution, and submitted to analysis of variance (ANOVA) and, when significant by the F test ($P \leq 0.05$), the means were compared by the Bonferroni t test ($P \leq 0.05$) for evaluation periods (flooding time), and by the Scott-Knott test for treatments ($P \leq 0.05$) ± standard deviation (SD). Statistical analyzes were performed using the SISVAR software.

3. Results

We verified that *S. terebinthifolia* seedlings presented 100% survival at 15 and 30 days of flooding. At 7 days of flooding, the seedlings began to present hypertrophic lenticels on the stems (Figure 2a). Morphoanatomical structures increased at 15 and 30 days (Figure 2b-2c), especially in seedlings that received applications of Si and SA.

Gas exchange was influenced by the interaction between treatments and flooding periods (Figure 3). The photosynthetic rate (*A*) of *S. terebinthifolia* seedlings at 15 days remained high under flooding (F) and in seedlings flooded and treated with silicon (F + 1.0 mM Si), with values of 11.01 and 12.83 µmol CO_2 m^{-2} s^{-1}, respectively. Noteworthy, these seedlings did not differ statistically from non-flooded seedlings (12.08 µmol CO_2 m^{-2} s^{-1}), while *A* decreased in the other treatments in the same evaluation period (Figure 3a).

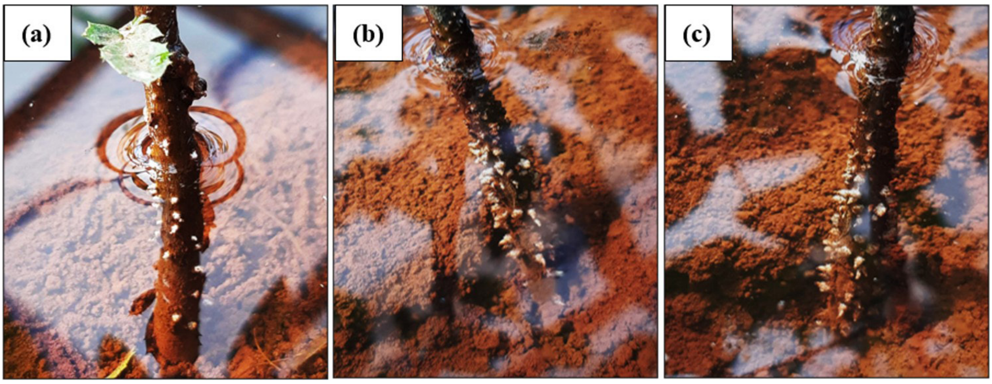

Figure 2. Visual aspects of hypertrophied lenticels in *Schinus terebinthifolia* seedlings at 7 (a), 15 (b) and 30 (c) days of flooding.

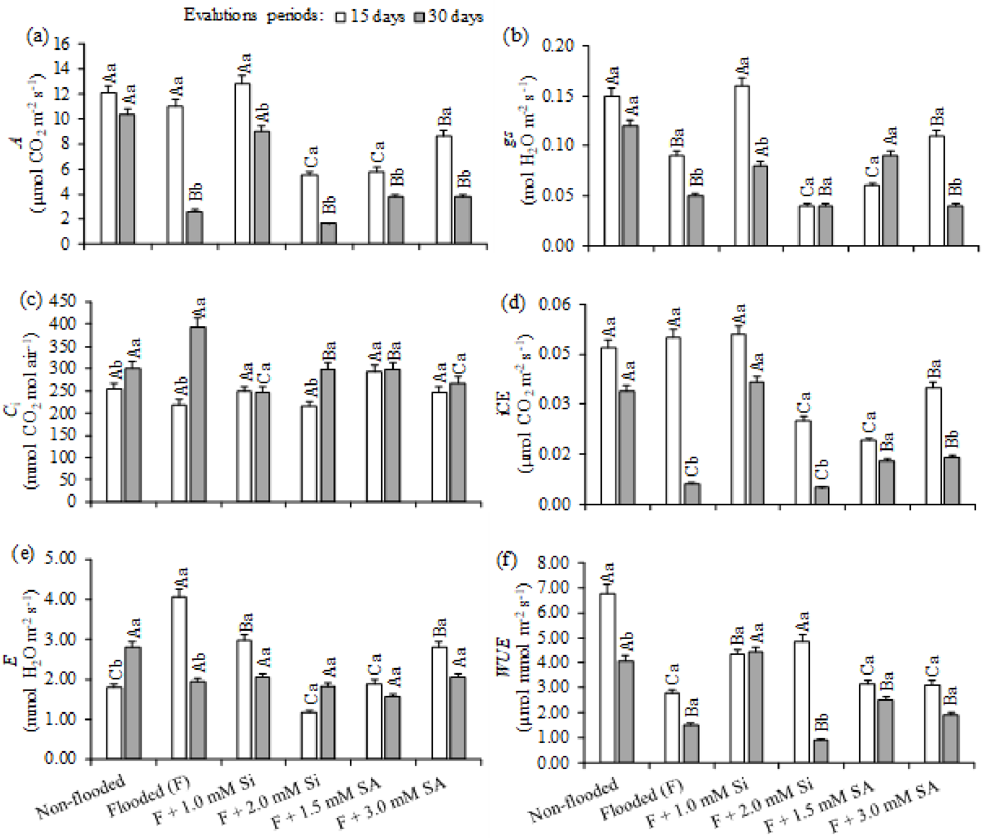

Figure 3. Photosynthesis – *A* (a), stomatal conductance – g_s (b), intercellular CO_2 concentration – C_i (c), instantaneous Rubisco carboxylation efficiency – iCE (d), transpiration – *E* (e) and water use efficiency – *WUE* (f) in *Schinus terebinthifolia* seedlings under control (non-flooded) and flooded associated at use of Si and SA, under two evaluations periods (15 and 30 days). Capital letters compared treatments within each evaluation period ± SD (Scott-Knott test; $P \leq 0.05$). Uppercase letters compared evaluation periods within each treatment ± SD (Bonferroni *t* test; $P \leq 0.05$) (*n*= 3).

Flooded seedlings that received 1.0 mM Si maintained a high value of *A* (9.02 μmol CO_2 m^{-2} s^{-1}) in comparison to flooded seedlings with and without applications of the other doses of Si and SA, at 30 days. With the application of 1.0 mM Si, the seedlings maintained 79% of the photosynthetic rate in comparison to non-flooded seedlings (control). With this same dose (1.0 mM Si), the seedlings maintained 56 and 64% of *A* in relation to those with lower values (2.62 and 1.68 μmol CO_2 m^{-2} s^{-1}), i.e., under F and F + 2.0 mM Si, respectively, all in comparison to the control, in the 30-day period.

The responses of seedlings to stomatal conductance (g_s) resembled their responses to *A,* i.e., at 15 days, the values remained high in seedlings under F + 1.0 mM Si, being similar to those of non-flooded seedlings, while the other seedlings had their values reduced in this period (Figure 3b). At 30 days, seedlings under F + 1.0 mM Si and F + 1.5 mM SA maintained the same values of g_s (0.09 mol H_2O m^{-2} s^{-1}) than non-flooded seedlings. Noteworthy, at 15 and 30 days, seedlings under F + 2.0 mM Si presented lower values of g_s (0.04 mol H_2O m^{-2} s^{-1} in both periods).

Intercellular CO_2 concentration (C_i) did not vary as a function of treatments at 15 days. However, at 30 days, the C_i value in flooded seedlings without any treatment increased more (393 mmol CO_2 mol air^{-1}) than in the other treatments. Seedlings treated otherwise maintained lower values of this variable in the same period (Figure 3c), especially those under F + 1.0 mM Si (247.5 mmol CO_2 mol air^{-1}).

For the 15-day period, instantaneous Rubisco carboxylation efficiency (iCE) decreased in seedlings under F + 2.0 mM Si, F + 1.5 mM SA, and F + 3.0 mM SA, with values of 0.025, 0.019, and 0.035 μmol CO_2 m^{-2} s^{-1}, respectively (Figure 3d). However, at 30 days, seedlings that received applications of 1.0 mM Si maintained the iCE values; seedlings treated with 1.5and 3.0 mM SA showed a reduction in these values, being lower in the F + 3.0 mM SA treatment; and those grown under flooding (F) and under F + 2.0 mM Si showed the lowest values. At 15 days, flooded seedlings (F) showed the highest transpiration value (*E*) (4.05 mmol H_2O m^{-2} s^{-1}), and those treated with F + 2.0 mM Si (Figure 3e) the lowest value (1.17 mmol H_2O m^{-2} s^{-1}). However, at 30 days, flooded seedlings and those under flooding + application of Si and SA maintained values similar to those of non-flooded seedlings.

Regarding the water use efficiency (*WUE*) in the 15-day period, only seedlings under F + 2.0 mM Si showed a value (4.86 H_2O m^{-2} s^{-1}) close to that of non-flooded seedlings (6.78 H_2O m^{-2} s^{-1}), differing statistically from the other treatments (Figure 3f). At 30 days, *WUE* reduced in relation to those obtained at 15 days, except when seedlings were grown under F + 1.0 mM Si. In this case, the values remained close and did not differ statistically, being 4.32 and 4.41 mmol H_2O m^{-2} s^{-1}, respectively. It is noteworthy that these values remained similar to that of control plants at 30 days (Figure 3f).

The lowest value of the quantum efficiency photochemical potential on PS II (F_v/F_m) was 0.729 in flooded seedlings, while in the other treatments the values remained high (Figure 4a). On the other hand, the efficiency of conversion of absorbed energy (F_v/F_0) was influenced by the evaluation periods, with a greater value at 15 days of flooding (3.952) (Figure 4b). As for the maximum basal yield of non-photochemical processes (F_0/F_m), the seedlings showed higher values when subjected to flooding (F) or F + 2.0 mM Si (0.255 and 0.235, respectively) (Figure 4c), and at 30 days (0.236) (Figure 4d).

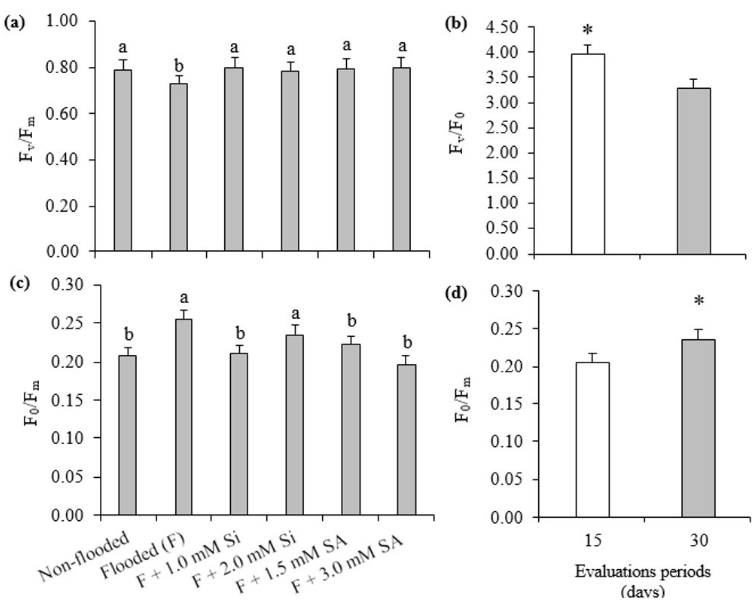

Figure 4. Quantum efficiency photochemical potential on photosystem II (F_v/F_m) (a), absorbed energy conversion efficiency (F_v/F_0) (b), maximum basal yield of non-photochemical processes (F_0/F_m) (c-d) in *Schinus terebinthifolia* seedlings under control (non-flooded) and flooded associated at use of Si and SA, under two evaluations periods (15 and 30 days). Different letter did not differ statistically ± SD (Scott-Knott test; $P \leq 0.05$) *± SD (Bonferroni *t* test; $P \leq 0.05$) (*n*= 3).

Plant height, number of leaves, chlorophyll *b*, and total chlorophyll were influenced by the treatments, regardless of evaluation period (Figure 5). Seedlings under flooding (F) and F + 1.5 mM SA had a lower height (26.15 and 29.65 cm, respectively) (Figure 5a). However, for seedlings flooded with the two doses of Si and with 3.0 mM SA, height values did not differ statistically from those of non-flooded seedlings. Flooded seedlings (F) showed the lowest number of leaves (14.5), and flooded seedlings with the application of Si and SA, especially with 1.0 mM Si and 1.5 mM SA, maintained values close to those of non-flooded seedlings (Figure 5b).

The flooding had little influence on the synthesis of chlorophyll pigments, but the application of 1.0 mM Si and 3.0 mM SA increased the values of these indices. The highest levels of chlorophyll *b* (20.61 and 21.88 FCI) and total chlorophyll (57.10 and 61.95 FCI) occurred in seedlings under F + 1.0 mM Si and F + 3.0 mM SA, respectively. In the other treatments the values were lower, but did not differ from that of non-flooded seedlings (Figure 5c-5d).

Leaf area of seedlings grown under F and F + 1.5 mM SA (91.66 and 187 cm^2, respectively) was lower, while in the other treatments the values did not differ, with an increase in seedlings under F + 1.0 mM Si (398 cm^2) (Figure 6a). Root length (RL) was shorter in seedlings subjected to flooding (F) and F + 2.0 Mm Si (18.66 and 24.35 cm, respectively), and the largest growth (47 cm) occurred under F + 1.0 mM Si. The RL values in F + 1.5 mM SA and F + 3.0 mM SA were equal to that of non-flooded seedlings (Figure 6b).

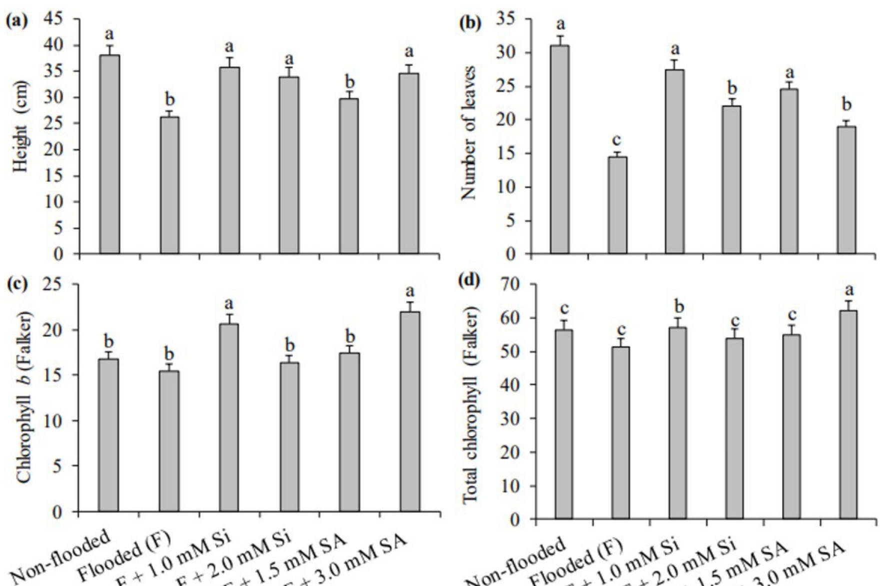

Figure 5. Plant height (a), number of leaves (b), chlorophyll *b* (c) and total chlorophyll (d) in *Schinus terebinthifolia* seedlings under control (non-flooded) and flooded associated at use of Si and SA. Different letter differ statistically ± SD (Scott-Knott test; $P \leq 0.05$) (n= 3).

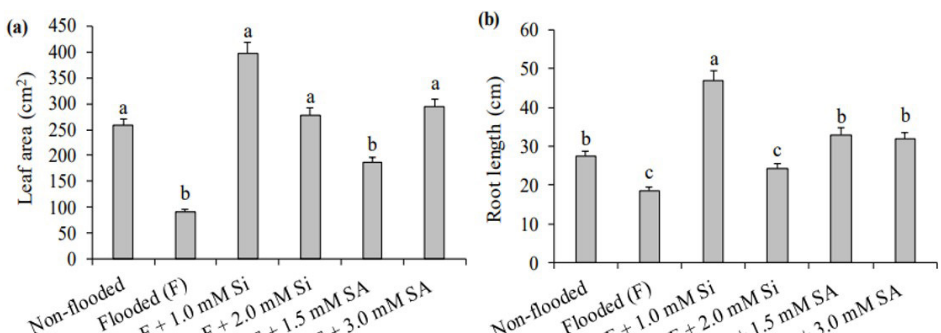

Figure 6. Leaf area (a) and root length (b) in *Schinus terebinthifolia* seedlings under control (non-flooded) and flooded associated at use of Si and SA. Different letter differ statistically (Scott-Knott test; $P \leq 0.05$) (n= 3).

In addition, the flooded roots of *S. terebinthifolia* changed from purple to darkened hue (Figure 7), indicating oxidation. We highlight that the flooded seedlings that received 1.0 mM Si and 3.0 mM SA presented adventitious roots (Figure 7c-7f, respectively). Seedlings presented higher shoot dry weight when grown under F + 1.0 mM Si and F + 3.0 mM SA (3.52 and 3.90 g, respectively) (Figure 8a). However, under F + 2.0 mM Si and F + 1.5 mM SA, the values did not differ from those of non-flooded seedlings. Treatment F + 1.0 mM Si provided higher root dry weight (1.27 g), but seedlings grown under F + 2.0 mM Si and under flooding with two doses of SA did not differ from non-flooded seedlings (Figure 8b).

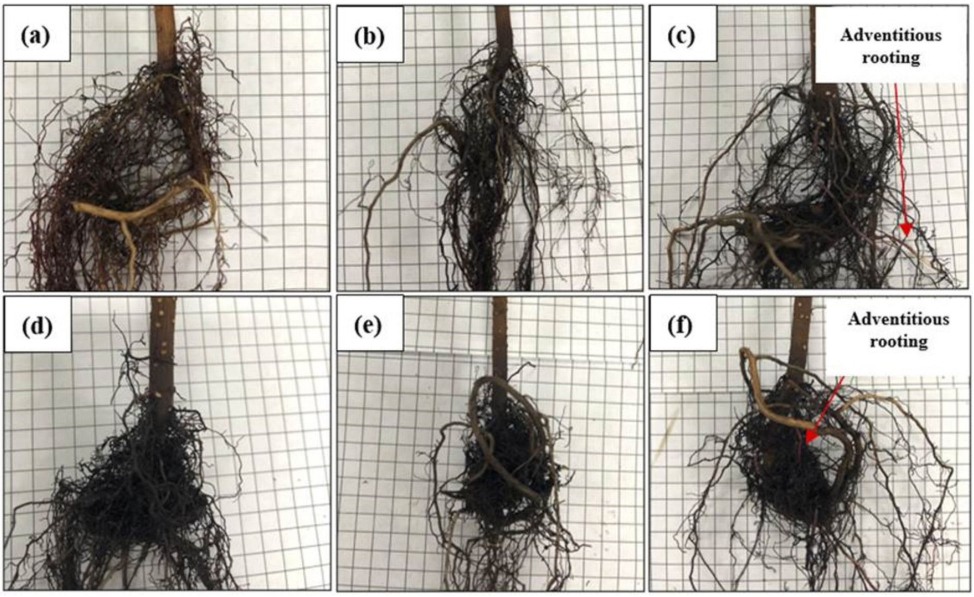

Figure 7. Visual aspect of roots *Schinus terebinthifolia* seedlings. (a) Control – non-flooded, (b) flooded, (c) F + 1.0 mM Si, (d) F + 2.0 mM Si, (e) F + 1.5 mM SA and (f) F + 3.0 mM SA.

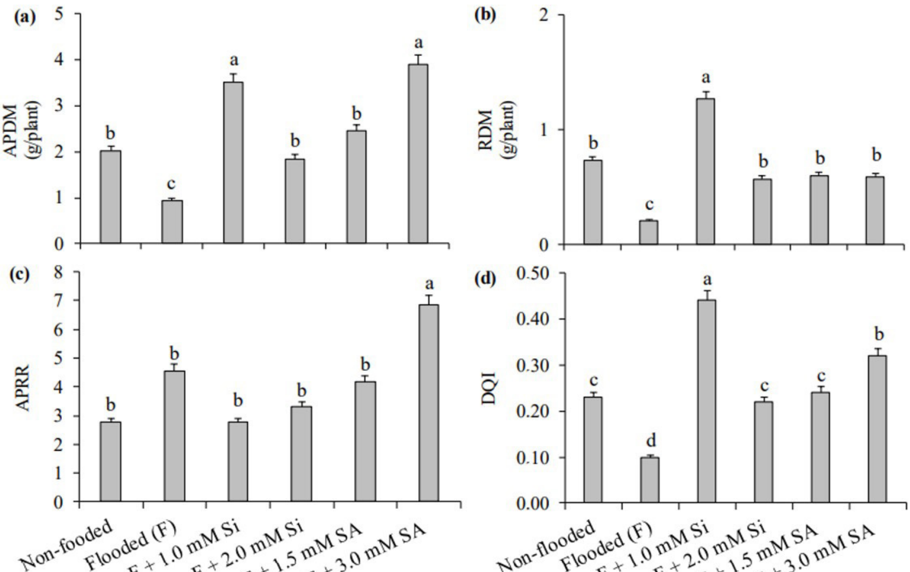

Figure 8. Aerial part dry mass – APDM (a), root dry mass – RDM (b), aerial part/root ratio – APRR (c) and Dickson quality index – DQI (d) in *Schinus terebinthifolia* seedlings under control (non-flooded) and flooded associated at use of Si and SA. Different letter differ statistically ± SD (Scott-Knott test; $P \leq 0.05$) (n= 3).

The seedlings presented higher shoot/root ratio (APRR) (6.83) when cultivated under F + 3.0 mM SA, while those grown in the other conditions showed lower values, which did not differ (Figure 8c). In general, seedlings flooded with Si and SA presented higher values of DQI than non-flooded seedlings. In this regard, the treatment F + 1.0 mM Si promoted the highest increase, leading to a DQI value of 0.44 (Figure 8d).

4. Discussion

Although *S. terebinthifolia* seedlings had 100% survival, flooding reduced their photosynthetic activity and initial growth, demonstrating that this species is sensitive to this condition. Notwithstanding, applications of Si and SA alleviate these negative effects, suggesting tolerance induction after foliar application, proving our initial hypothesis. Seedling responses vary depending on product doses and evaluation periods, i.e., flooding intensity (flooding time).

Morphological adaptation, such the emergence of adventitious roots and lenticels, contributes to the ecological plasticity of the species under flooding (Linné et al., 2023), favoring their potential for resilience, favor gas exchange between the internal tissues and the external environment. However, adaptive responses to flooding vary with the species. For example, Santos et al. (2023) observed that *Hymenaea courbaril* L. seedlings did not have morphological adaptations and reduced gas exchange, but tolerated 30 days flooding.

Seedlings treated with Si and SA present well-developed lenticels, which correlates with the priming effect of applying these products before stress conditions. This induces the signaling of enzymes, which, in turn, speed up damage repair (Etesami and Jeong, 2018; Hou et al., 2019). Thus, these seedlings possibly already had an activated signaling mechanism when subjected to flooding, and emitted adaptive structures more quickly than those that had not yet been preconditioned, suggesting tolerance induction.

A stability after 15 days of flooding indicates physiological plasticity of this species to short periods of stress through morphological adjustments such as the appearance of hypertrophied lenticels that favored metabolic adjustments. However, as the plant is exposed to stress, metabolic processes decrease or destabilize (Santos et al., 2023). The reduction in *A* can be attributed both to stomatal closure and to the decline in the photochemical phase of photosynthesis, increasing C_i (Rosa et al., 2018; Santos et al., 2022b, 2023). With an increased exposure to flooding, ROS production can occur due to the activity of the alcohol dehydrogenase enzyme, largely increasing the activity of fermentative enzymes, obtaining of energy in this condition occurs mainly through alcoholic fermentation (Borella et al., 2019), reducing the photosynthetic capacity of plants.

The mitigation of the sharp decrease of *A* with 1.0 mM Si is due to the fact that this element contributes to the protection of the photosynthetic apparatus. Although we did not evaluate in this study, foliar application of Si possibly favored the activity of antioxidant enzymes that repair cell damage by detoxification of ROS, increasing the functionality of the chloroplast ultrastructure and the synthesis of photosynthetic pigments (Etesami and Jeong, 2018), therefore stabilizing metabolic processes. According to Santos et al. (2022b) foliar application of Si mitigated the effect of flooding about photosynthetic metabolism in *Eugenia myrcianthes* Nied. seedlings.

Foliar application of Si reduces transpiration while regulating gas exchange and CO_2 uptake, also improving photosynthetic efficiency (Xie et al., 2015). However, high doses of this element can promote an excessive deposition in stomatal pores, causing depletion of gas exchange and stomatal limitations (Santos et al., 2022b). Similarly, *Physocarpus amurensis* Maxim and *P. opulifolius* also had a reduction in the photosynthetic rate to values close to zero after 16 days of flooding (Zhang et al., 2017).

The increase in C_i represents that most of the CO_2 is stored instead of being assimilated, indicating enzymatic inefficiency of Ribulose-1,5-bisphosphate-carboxylase/oxygenase (RuBisCO), compromising the other metabolic processes and the production of photoassimilates. Lower values of iCE may reflect the damage caused by prolonged conditions of lack of O_2 in the substrate, collapsing the photosynthetic apparatus of seedlings exposed to flooding for longer, therefore compromising the Rubisco activity (Rosa et al., 2018; Santos et al., 2023).

Application of Si and SA promotes the efficiency of iCE, since both this nutrient and the phytohormone favor the protection of the photosynthetic apparatus from free radicals due to the greater action of antioxidant enzymes such as catalase, superoxide dismutase, and others (Nazar et al., 2015). Thus, our results show the benefit of Si and SA for *S. terebinthifolia* as a strategy to mitigate stomatal and nonstomatal limitations; however, the appropriate dose of each product should be checked.

The lowest *E* correlates with the smallest g_s in the same cultivation condition. According to Linné et al. (2023), who observed woody forestry species under flooding conditions, this is due to the appearance of hypertrophied lenticels altering photosynthetic rates for certain periods; another hypothesis is the reduction of transpiration due to inefficiency of stomatal control. The maintenance of *WUE* values at 30 days indicates stability both in CO_2 assimilation and in leaf transpiration, reinforcing the beneficial effect of these doses on water regulation. Rosa et al. (2018) observed that higher values of WUE indicate greater physiological plasticity in the face of the abiotic adversities to which the species are exposed.

SA and Si, regardless of dose, prevented enzyme inhibition and membrane breakdowns, delaying both the degradation of protein D1 and the damage to reaction centers, especially because these products are associated with the signaling of antioxidant metabolism enzymes (Ghassemi-Golezani and Lotfi, 2015; Mimouni et al., 2016), promoting the stability of the photochemical processes of PSII.

Under a higher period of exposure to adverse conditions, represented here by 30 days of flooding, there was a reduction in the potential light collection and subsequent transfer to the antenna complex. According to Zhang et al. (2017) this correlates with the F_v/F_m ratio of the most sensitive components in the transport chain of electrons;

the higher the ratio, the better the performance of the metabolic processes of photosynthesis.

These results reinforce that under these conditions there is a significant reduction in energy use. Under flooding, electron transfer instability occurs due to chloroplast damage promoted by increased C_i and higher expenditure of ATP and NADPH, since most of the light energy converted into chemical energy is directed to ROS or dissipated in the form of fluorescence (Zhang et al., 2018; Linné et al., 2023; Santos et al., 2023).

The height values of seedlings flooded with Si and SA indicate stability in the production of photoassimilates and investment in morphological characters. The Si can positively affect the absorption of nutrients such as N and other cations that contribute to plant growth (Etesami and Jeong, 2018). Regarding SA, this result can be attributed to its participation in several metabolic processes, especially optimization of water use and regulation of metabolic processes, resulting in an increase in growth (Saracho et al., 2021; Santos et al., 2022a).

The increase in growth indicators in plants treated with Si and/or SA demonstrates the mitigating effects of these elements on abiotic stress disorders, thus enabling plants to tolerate stress (Melo-Filho et al., 2019; Silva et al., 2019a, b). *S. terebinthifolia* seedlings subjected to water stress with application of SA developed better when cultivated under water saturation (100% daily irrigation capacity) and under water deficit by 12 days, reinforcing the potential of SA to mitigate stressful effect (Saracho et al., 2021).

Carvalho et al. (2016) suggests that the increment in height is an increase was a response to the flooding condition as a strategy to keep the leaves above the water level, as observed for *Peltophorum dubium* (Sprengel) Taub. seedlings after 15 days of flooding, similar to what was observed for *S. terebinthifolia* seedlings. The reduction in number of leaves under flooding as a response to the increase in ethylene in the leaf tissue, promoting leaf abscission (Medri et al., 2011). As for chlorophyll indices, flooding had little influence, but the foliar application of 1.0 and 3.0 mM of Si and SA, respectively, favored the maintained synthesis of photosynthetic pigments.

The increase in LA may be associated with greater stability in water relations, as observed in g_s and *WUE*, contributing to the increase in the number of leaves and, consequently, in vegetative growth. When plants present metabolic adjustments to internal water use, the effect of ethylene is reduced, thus reducing leaf abscission (Carvalho et al., 2016), and SA acts stimulating vegetative growth (Santos et al., 2023).

The reduction in root growth probably correlates with the higher energy expenditure and lower ATP production of plants under flooding. However, Kim et al. (2016) state that silicon attenuated the effects on plant biomass, as Si correlates with hormonal signaling and favors the increase of antioxidant enzymes that repair the damage generated by ROS, stabilizing enzymatic activities. The authors then reported a decrease in membrane disorders and reduction of oxidative stress, favoring growth in Si-treated plants.

The oxidation of flooded roots is due to the fact that under anoxia/hypoxia there is an excessive production of ethanol due to the increased enzymatic activity associated with anaerobic respiration. That is, low supply of O_2 accelerates glycolysis, and anaerobic respiration leads to excess acid production by lactate dehydrogenase to compensate for the low energy production in respiration (Lobo and Joly, 2000; Vidal et al., 2019).

The adventitious roots in seedlings with 1.0 mM Si and 3.0 mM SA demonstrate once again that preconditioning favors the signaling of seedling metabolism to adverse conditions through morphological adjustments. It also shows that these products contribute to increase photoassimilates and biomass production, leading to higher values in relation to flooded seedlings without preconditioning. The adventitious roots, in addition to contributing to gas exchange due to anoxia, favor the absorption of nutrients, being considered a mechanism of adjustment to the stress condition (Zhang et al., 2017).

In *Caesalpinia peltophoroides* Benth. seedlings, Henrique et al. (2010) observed that flooded plants had reduced biomass due to leaf abscission and metabolic destabilization, which reduces photoassimilates production; this behavior is similar to that observed in *S. terebinthifolia* seedlings. The increase in DQI reflects greater vegetative traits and biomass production under flooded with Si and SA, contributing to high quality seedlings.

Based on our results, although flooded seedlings without Si and SA showed 100% survival, similar to other treatments, these had lower growth rates and photosynthetic metabolism, which will possibly compromise its initial establishment in areas subject to temporary flooding. In these assumptions, the use of elicitors agents, represented by foliar application with silicon and salicylic acid contributed positively to the integrity of the photosynthetic device and quality of seedlings, increasing the physiological plasticity and tolerance induction of *S. terebinthifolia*, proving to be a promising technique for seedling production.

5. Conclusions

Schinus terebinthifolia seedlings presented hypertrophied lenticels in response to flooding favored the tolerate this condition for up to 15 days without drastically reducing photosynthetic rate and photochemical yields. Foliar application of silicon and salicylic acid at dose of 1.0 mM and 3.0 mM, respectively, contributes in the morphophysiology of *S. terebinthifolia* under flooding by 30 days.

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