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Salicylic acid on gas exchange and growth of *Hymenaea courbaril* L. seedlings under flooding¹

Ácido salicílico nas trocas gasosas e crescimento de mudas de *Hymenaea courbaril* L. sob alagamento

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HIGHLIGHTS:

*Flooding damages the gas exchange of *Hymenaea courbaril* seedlings.*

*Foliar application of salicylic acid stimulates the initial growth and quality of *H. courbaril* seedlings.*

Physiological variables present greater phenotypic plasticity than growth characteristics.

ABSTRACT: Flooding is a stressful condition that causes damage to the photosynthetic apparatus, negatively affecting the growth of seedlings of fruit species, including *Hymenaea courbaril* L. Studies on physiological management, such as exogenous application of phytohormones, to alleviate abiotic stress have increased. The objective of this study was to evaluate the effect of foliar application of salicylic acid (SA) on *H. courbaril* seedlings subjected to flooding. The seedlings received foliar application of four concentrations of SA (0, 100, 200, and 400 mg L⁻¹) and were subjected to two water regimes: a) control - non-flooded and irrigated daily and b) flooded - seedlings were placed in a plastic pool, keeping the water depth at ± 5.0 cm above the substrate level. After 35 days, we evaluated the gas exchange, initial growth, quality, and potential ecological resilience of the seedlings. All flooded seedlings survived, but had reduced photosynthesis, carboxylation of Rubisco efficiency, and water-use and stomatal conductance when they received 100-300 mg L⁻¹ SA. The seedlings that received between 100 and 300 mg L⁻¹ SA had greater growth, quality, and phenotypic plasticity. Foliar application of SA did not mitigate the effect of flooding on gas exchange but contributed to the growth of *H. courbaril* seedlings.

Key words: *Hymenaea courbaril* L. ('Jatobazeiro'), photosynthetic metabolism, phenotypic plasticity, physiological adjustments, abiotic stress

RESUMO: O alagamento é um fator estressante e promove danos ao aparato fotossintético, afetando negativamente o crescimento de mudas de espécies frutíferas, dentre elas a jatobazeiro. Estudos sobre o manejo fisiológico, tal como aplicação exógena de fitohormônio, para aliviar o estresse abiótico tem aumentado. Assim, objetivou-se com esse estudo avaliar o efeito da aplicação foliar de concentrações de ácido salicílico (AS) em mudas de *H. courbaril* submetidas ao alagamento. As mudas receberam aplicação via foliar de quatro concentrações de AS: 0, 100, 200 e 400 mg L⁻¹, e submetidas a dois regimes hídricos: a) controle: - não alagadas e irrigadas diariamente e b) alagamento - acondicionamento das mudas em piscina com lâmina d'água (5.0 cm) acima do nível do substrato. Decorridos 35 dias avaliamos as trocas gasosas, crescimento inicial, qualidade e o potencial de resiliência ecológica das mudas. Observou-se que todas as mudas alagadas sobreviveram, mas tiveram redução da fotossíntese, eficiência instantânea de carboxilação da Rubisco e de uso da água e condutância estomática e quando receberam aplicação entre 100-300 mg L⁻¹ de AS. As mudas que receberam aplicação das concentrações entre 100 e 300 mg L⁻¹ de AS tiveram maiores características de crescimento, qualidade e plasticidade fenotípica. A aplicação foliar de ácido salicílico não mitigou o efeito do alagamento sobre as trocas gasosas, mas contribuiu no crescimento das mudas de *H. courbaril*.

Palavras-chave: Jatobazeiro, metabolismo fotossintético, plasticidade fenotípica, ajustes fisiológicos, estresse abiótico

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INTRODUCTION

Among the native fruit trees in the Cerrado, *Hymenaea courbaril* L. ('Jatobazeiro', Fabaceae) is a tree species found in several phytogeographic domains, such as Amazon, Caatinga, Cerrado, Atlantic Rain Forest, and Pantanal, which vary under different edaphoclimatic conditions (Pinto et al., 2020). *H. courbaril* fruits can be consumed in natura or in the form of flour, and are attractive to wild fauna. *H. courbaril* seedlings have the potential to be inserted into silvopastoral systems and to enrich forests (Oliveira et al., 2020).

Owing to climate change and anthropism, many regions are subject to flooding during certain periods. Under these conditions, there is usually a reduction in gas exchange owing to stomatal closure and membrane damage (León et al., 2021; Santos et al., 2022a; Linné et al., 2023). A plant's response to abiotic stress factors is associated with the intensity of exposure and its phenotypic plasticity, which confers its potential for ecological resilience.

Cultivation management techniques that can mitigate the possible damage caused by flooding on plant metabolism have been developed. Among the promising alternatives, foliar application of salicylic acid (SA), a phenolic phytohormone, can alleviate the negative effects of abiotic stresses by contributing to the antioxidant system, metabolic regulation, and plant growth (Saracho et al., 2021; Foresti et al., 2022; Santos et al., 2022b).

For *H. courbaril*, the ecophysiological information on flooding is insufficient, and this knowledge will help in the decision-making for seedling production of this species. Thus, we hypothesized that these seedlings are sensitive to flooding, but that the application of SA alleviates the stress effects on their physiology and initial growth. The objective of this study was to evaluate the effects of foliar application of SA on *H. courbaril* seedlings subjected to flooding.

MATERIAL AND METHODS

The experiment was carried out under an agricultural nursery condition with top and side coverage of black screen to provide 30% shade at the Faculdade de Ciências Agrárias (22° 11' 51.5" S, 54° 56' 04.3" W), Universidade Federal da Grande Dourados, Dourados, MS, Brazil.

The experimental design used was completely randomized, with treatments arranged in a subdivided plot scheme, in which the water regimes were allocated in the plots and the SA concentrations in the subplots, with four replications ($n = 4$), each consisting of a pot with two seedlings in each plot. Ripe fruits of *H. courbaril* were collected from matrices in the remaining areas of the Cerrado. Subsequently, we manually processed and sanitized the seeds in 2% sodium hypochlorite for 5 min. The seeds were scarified with emery to overcome tegumentary dormancy and immersed in water for 24 hours before soaking (Souza et al., 2015).

Sowing was performed in polyethylene tubes with a volume of 290.0 cm³ filled with commercial substrate Tropstrato had the following attributes: pH CaCl₂, 5.75; P, 65.70 mg dm⁻³; K, 1.60 cmol_c dm⁻³; Ca, 23.80 cmol_c dm⁻³; Mg, 12.40 cmol_c dm⁻³;

Al, 0 cmol_c dm⁻³; H + Al, 4.20 cmol_c dm⁻³; the sum of bases, 39.80 cmol_c dm⁻³; cation exchange capacity, 42.10 cmol_c dm⁻³; and base saturation (V%), 64.80, and irrigation was performed daily according to Souza et al. (2000).

At 15 days after emergence, the seedlings were transplanted into 7.0 L plastic pots, previously filled with an Oxisol soil (United States, 2014) that corresponds to a Distroferric Red Latosol in the Brazilian Soil Classification System (EMBRAPA, 2018) and coarse sand (3:1, v/v) with chemical attributes: pH CaCl₂ = 5.67; P = 27.92 mg dm⁻³; K = 0.63 cmol_c dm⁻³; Ca = 8.55 cmol_c dm⁻³; Mg = 2.04 cmol_c dm⁻³; Al = 0 cmol_c dm⁻³; H + Al = 2.37 cmol_c dm⁻³; the sum of bases = 11.22 cmol_c dm⁻³; CEC = 13.59 cmol_c dm⁻³; S = 4.22 mg dm⁻³; B = 0.48 mg dm⁻³; Fe = 52.13 mg dm⁻³; Cu = 3.90 mg dm⁻³; Mn = 78.60 mg dm⁻³; Zn = 1.75 mg dm⁻³; organic matter = 20.82 g dm⁻³; and base saturation (V%) = 82.6.

The substrate was maintained 70% of the water retention capacity (WRC) (Souza et al., 2000) until plant reached an average height of 20.0 cm for 30 days (acclimatization).

The seedlings received foliar application of four concentrations of SA: 0, 100.0, 200.0, and 400.0 mg L⁻¹ (Saracho et al., 2021). The SA (99% P.A.) was diluted in 20 mL of ethyl alcohol, and subsequently, this solution was diluted in distilled water and 1.0 mL L⁻¹ of the LI 700 adjuvant was added to the solution to facilitate adherence to the leaves, as the leaves of this species are waxy. Applications were performed in the morning on the abaxial and adaxial surfaces until the drip point (10.0 mL per plant based on pre-test) by isolating them from the plants at the time of application to avoid drift, on alternate days, for 10 days prior to submitting seedlings to different water regimes.

Subsequently, the seedlings were divided into two water regimes: (a) control: non-flooded and irrigation daily, maintaining 70% of the WRC (Souza et al., 2000), and (b) flooded: storage of seedlings in a 1,500 L plastic pool, keeping the water depth at 5.0 cm above the substrate level, and the water presented average values of 0.071 μS cm⁻¹ and 22.3 °C of electrical conductivity and temperature, respectively (Figure 1). We cleaned the pool and changed the water to prevent proliferation of insect larvae.

After 35 days, the seedlings were subjected to different water regimes, and when the seedlings flooded with or without SA application showed photosynthesis values close to zero, the following physiological and growth characteristics were evaluated:

Survival (%) was calculated considering the number of live seedlings that presented fully expanded green leaves.

Gas exchange: Using fully expanded leaves in the middle third of the seedlings, the CO₂ assimilation rate (photosynthesis) (A; μmol CO₂ m⁻² s⁻¹), intercellular CO₂ concentration (C_i; mmol CO₂ mol⁻¹), stomatal conductance (g_s; mol H₂O m⁻² s⁻¹), and transpiration (E; mol H₂O m⁻² s⁻¹) were quantified using portable photosynthesis meter LCIPro-SD (IRGA- Infra Red Gas Analyzer) (Model ADC BioScientific Ltd.). Subsequently, water-use efficiency (WUE; μmol CO₂ mmol⁻¹ H₂O) and instant carboxylation (μmol CO₂ mmol⁻¹ CO₂ m⁻² s⁻¹) were calculated using the A/E and A/C_i ratios, respectively. The evaluations were performed between 8:00 and 11:00 a.m., with average



Figure 1. Visual aspects of *H. courbaril* seedlings on the bench (control) and in the pool (flooded) during the development of the experiment.

values of photosynthetically active radiation of $852.37 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, atmospheric CO_2 concentration of 447.91 ppm , temperature of $25.9 \text{ }^\circ\text{C}$ and relative humidity of air of 68% .

Stomatal limitation value (SL): was calculated according to Song et al. (2020) using the following Eq. 1:

$$\text{SL} = 1 - \left(\frac{C_i}{C_a} \right) \quad (1)$$

where:

C_a - atmospheric CO_2 concentration; and,
 C_i - intercellular CO_2 concentration. C_i and C_a - data were quantified using the IRGA, LCIPro-SD (ADC BioScientific Ltd.) between 8:00 and 11:00 a.m.

Initial growth and seedling quality index: The length of the largest root of the seedlings (cm) was evaluated using a millimeter ruler, and the leaf area (cm^2) was measured using an area integrator (LI-COR, Model 3100 LC; Nebraska, USA). Seedling quality standards (DQI) was calculated according to Dickson et al. (1960) using the following Eq. 2:

$$\text{DQI} = \frac{\text{TDM}}{(\text{HDR} + \text{APRR})} \quad (2)$$

where:

DQI - Dickson's Quality Index;
 TDM - total dry mass;
 HDR - height/diameter ratio; and,
 APRR - shoot/root dry weight ratio. To obtain the dry weight, the different plant organs were placed in Kraft paper bags and subjected to drying in a forced air circulation oven at $60 \pm 5 \text{ }^\circ\text{C}$ for 72 hours.

The ecological resilience potential was estimated using the phenotypic plasticity index (PPI) of A and DQI, according to the proposal of Valadares et al. (2006), using the following Eq. 3:

$$\text{PPI} = \frac{(M - m)}{M} \quad (3)$$

where:

M - value of the highest average; and,
 "m" - value of the lowest average. In this study, we calculated the PPI using the highest and lowest values between the non-flooded seedlings (control) without SA and those of the flooded seedlings without and with the SA concentrations, presenting the results only for characterization, not applying statistical analysis.

In this study, we calculated the PPI using the highest and lowest values between the non-flooded seedlings (control) without SA and those of the flooded seedlings with and without SA concentrations, presenting the results only for characterization, not applying statistical analysis.

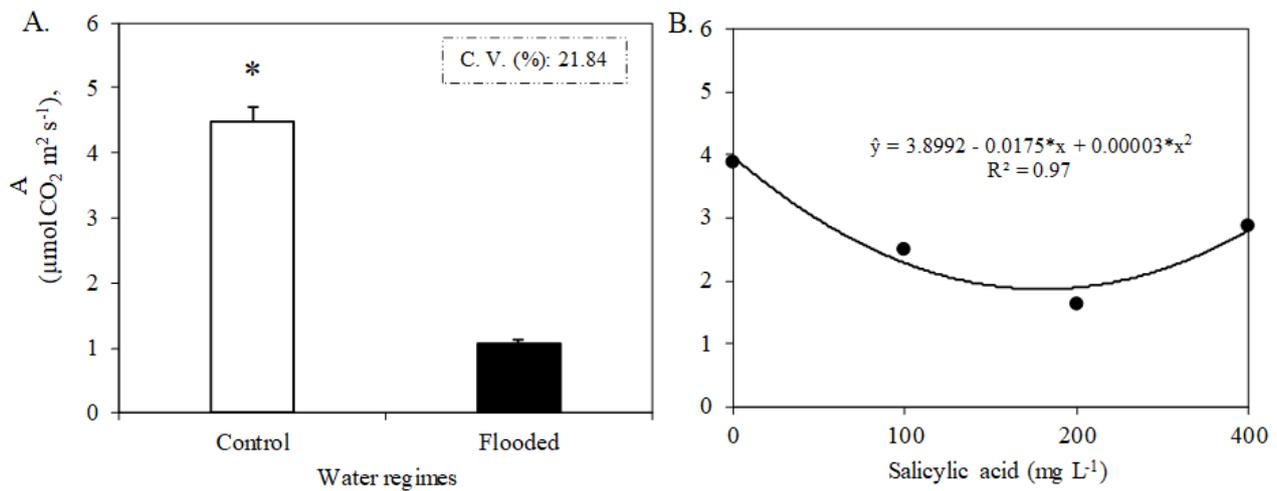
The data were subjected to normal distribution using the Bartlett and Shapiro-Wilk tests. The data, except PPI, were subjected to analysis of variance (ANOVA), and when significant according to the F test ($p \leq 0.05$), the means and interactions were compared using the F test for water regimes (control and flooded) and by regression analysis using linear and quadratic models with a coefficient of determination ≥ 0.60 for SA concentrations ($p \leq 0.05$), using the SISVAR software version 5.3.

RESULTS AND DISCUSSION

H. courbaril seedlings had reduced gas exchange under flooding, indicating sensitivity; however, they tolerated this stressful condition owing to their physiological plasticity, with 100% seedling survival under flooding as a function of SA concentration. On the other hand, we reject the hypothesis that foliar application of SA would mitigate the stressful effect on the photosynthetic apparatus, since its application, especially at concentrations between $100.0\text{-}300.0 \text{ mg L}^{-1}$, accentuated the reduction of gas exchange of seedlings in both water regimes, but otherwise, they stimulated growth.

The CO_2 assimilation rate (A) was influenced by the factors under study in isolation, with lower values (1.08 and $1.34 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in flooded seedlings (Figure 2A) and with the application of 291.66 mg L^{-1} SA (Figure 2B). Under flooding, the production of reactive oxygen species (ROS) promotes membrane damage (Park & Lee, 2019; León et al., 2021), negatively affecting the integrity of the photosynthetic apparatus.

As for SA, the results of this study with *H. courbaril* differ from those in the literature, which reports that this phytohormone plays a role in metabolic regulation and alleviation of stress factors in the photosynthetic apparatus (Foresti et al., 2022; Santos et al., 2022b), as its application accentuated the reduction of A in *H. courbaril* seedlings.



* - Significant at $p \leq 0.05$

Figure 2. CO_2 assimilation rate (A) in *Hymenaea courbaril* L. seedlings grown under different water regimes (A) and with salicylic acid concentrations (B)

However, at a dose higher than 200.0 mg L^{-1} , the seedlings may have adjusted to the flooding condition, as there was no significant difference in flooded and control seedlings when treated with SA, and there was a tendency to increase the photosynthetic rate (Figure 2B).

The instant carboxylation efficiency (A/C_i), intercellular CO_2 concentration (C_i), stomatal conductance (g_s), transpiration (E), water-use efficiency (WUE), and stomatal limitation (SL) were influenced by the interaction between water regime and SA concentration (Figure 3). The reduction in A/C_i was observed in the flooded seedlings without the effect of SA concentrations compared to the control seedlings. In contrast, in the non-flooded seedlings, we observed a quadratic adjustment with the minimum value ($0.0256 \mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) at 140.0 mg L^{-1} SA (Figure 3A).

Thus, the increase in photosynthetic rate in seedlings treated with a dose higher than 200.00 mg L^{-1} SA cannot be attributed to the carboxylation efficiency of the Rubisco enzyme, as it did not show an upward trend with increasing dose. Other factors contributed to these values to be similar, but they were also not stomatal, since g_s also did not change and the stomatal limitation increased with the dose above 200.0 mg L^{-1} ; however, the C_i was reduced.

The C_i values without SA were higher in the flooded seedlings, and when SA was applied, there was no difference between the control and flooded seedlings with 353.15 and $349.71 \text{ mmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ when receiving 255.14 and 180.50 mg L^{-1} SA, respectively (Figure 3B).

The g_s in the flooded seedlings was lower than that in the non-flooded seedlings and was not influenced by the SA concentrations, with an average value of $0.013 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$, whereas in the control seedlings, a maximum value ($0.145 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$) was observed with 320.0 mg L^{-1} SA (Figure 3C). According to Jesus et al. (2021) this reduction is directly related to lower permeability and hydraulic conductivity of the root in the condition of O_2 deficiency, which is similar to the results observed in our study for *H. courbaril* seedlings.

The maximum E value ($2.71 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$) occurred in control seedlings that received 302.50 mg L^{-1} SA, whereas under flooding, the minimum value ($0.31 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$) occurred

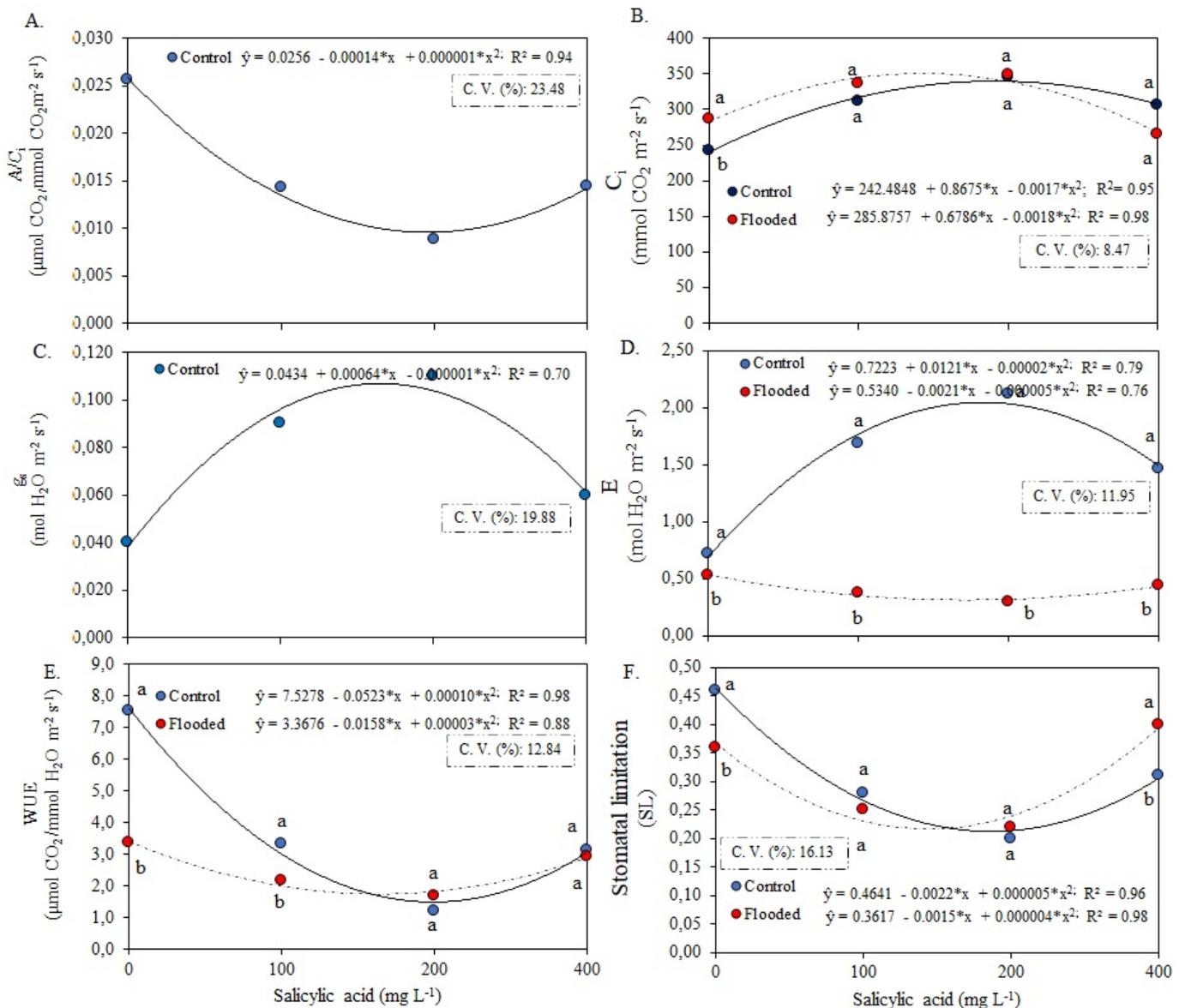
with 210.00 mg L^{-1} SA (Figure 3D). It is highlighted that E was lower in the flooded seedlings than in the control, regardless of SA concentration, a response related to the lower g_s observed under the same conditions as a water regulation mechanism. However, this protection mechanism impaired CO_2 entry and the maintenance of lower A/C_i , and consequently, lower A.

Both WUE and SL were reduced under flooding with minimum values when they received 263.30 mg L^{-1} SA (Figure 3E) and 187.5 mg L^{-1} SA (Figure 3F), respectively, after which the seedlings had to be adjusted to flooding as they tended to increase these characteristics. The WUE did not vary in both water regimes for seedlings treated with concentrations from 200.0 mg L^{-1} , whereas the SL of seedlings treated with 100.0 and 200.0 mg L^{-1} SA did not vary in either water regime; however, for seedlings flooded and treated with 400.0 mg L^{-1} , the SL was significantly higher than that of the control seedlings. Without SA application, the flooded seedlings had a lower SL than the control (Figure 3F), indicating lower A/C_i efficiency and increased C_i under these conditions.

The roots of the seedlings under flooding showed a darkened hue compared to the control seedlings, indicating oxidation (Figure 4A), a result of fermentative metabolism due to O_2 deficiency rather than aerobic respiration (Sousa & Sodek, 2002). Flooding seedlings and those that received 207.15 mg L^{-1} SA showed greater root lengths (22.37 and 27.01 cm , respectively) (Figures 4C and D).

Leaf area (LA) was influenced only by SA concentrations, presenting a quadratic adjustment with a maximum value of 260.76 cm^2 in seedlings that received an application of 215.17 mg L^{-1} SA (Figure 4B). Possibly this increase is owing to the fact that SA contributes to nitrogen metabolism (Khan et al., 2015), which favors vegetative growth. Similarly, *Schinus terebinthifolia* Raddi. seedlings also had a higher LA when they received exogenous foliar application of SA at a dose of 200.0 mg L^{-1} (Saracho et al., 2021).

The flooded seedlings and those that received 207.15 mg L^{-1} SA had the longest root lengths - RL (22.37 and 27.01 cm , respectively) (Figures 4C and D). Generally, plants under flooding tend to have lower RL due to rotting and root disruption, but for *H. courbaril*, our results suggest that the



* - Significant at $p \leq 0.05$; ns - Not significant ($p > 0.05$); Different letters between water regimens at the same dose differ statistically at $p \leq 0.05$

Figure 3. Instant carboxylation efficiency - A/C_i (A), intercellular CO_2 concentration - C_i (B), stomatal conductance - g_s (C), transpiration - E (D), water-use efficiency - WUE (E), and stomatal limitation - SL (F) in *Hymenaea courbaril* L. seedlings grown under different water regimes associated with salicylic acid concentrations

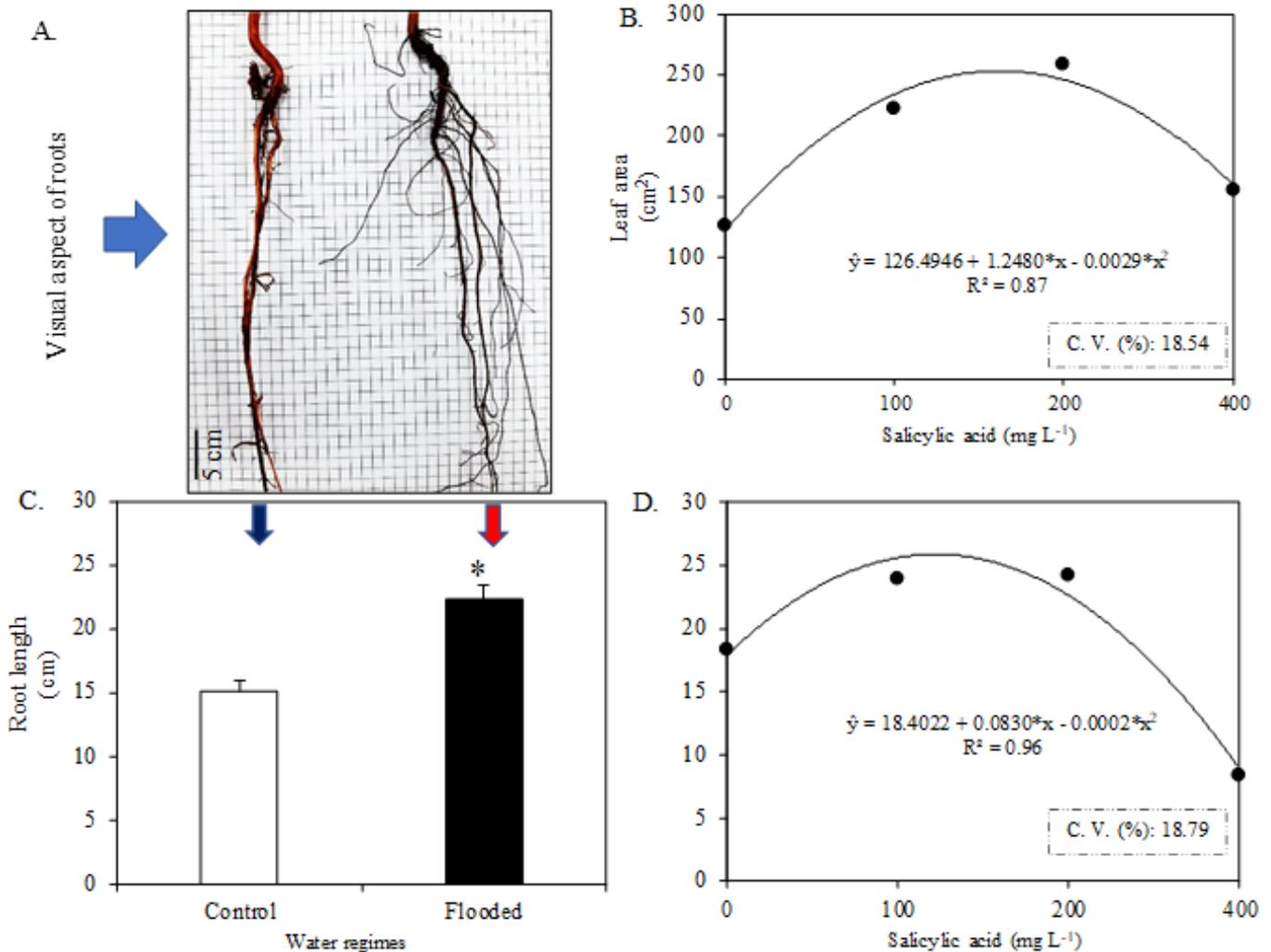
species has the ability to adjust its root system to this condition, considering the exposure time to flooding. Based on the results of this study, it is suggested that SA acts as a growth regulator in both leaf and root areas, as observed in the literature (Bagautdinova et al., 2022; Foresti et al., 2022), but at a dose lower than 200.0 mg L^{-1} .

It is observed that *H. courbaril* seedlings presented higher DQI values (0.43 and 0.45) when receiving 230.0 and 275.0 mg L^{-1} SA under control and flooding, respectively (Figure 5A), correlating with better aspects regarding their vigor when they received application between 100-300.0 mg L^{-1} SA in both water regimes (Figure 5B). According to Santos et al. (2022b) the DQI evaluation is used to verify seedling vigor, as it combines information on the robustness and accumulation of photoassimilates, making it desirable to obtain higher values of this characteristic. According to Fonseca et al. (2002), the minimum value should be 0.20, and the results observed for the *H. courbaril* seedlings were superior, indicating good

quality. However, these values may vary with species, age, and ecological succession group, among other factors (Santos et al., 2022b).

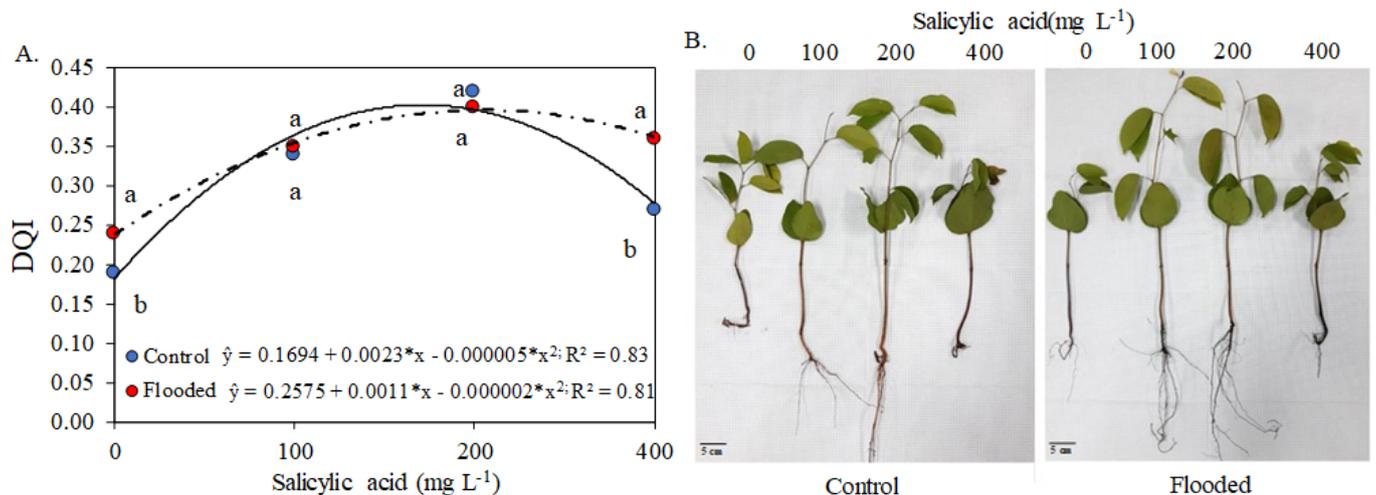
The results of our study are atypical. Although SA did not contribute to the maintenance of A , A/C_i , and WUE under flooding, especially at concentrations of 100-300 mg L^{-1} , its application may have contributed to non-stomatal factors and favored an energy compensation strategy, that is, there was an increase in the characteristics of LA and RL, which provided a greater accumulation of photoassimilates and DQI of the seedlings even under flooding with the same concentrations, promoting greater morphophysiological rusticity of seedlings to this adverse condition.

In addition, it has been reported that plants under stressful conditions normally present an increase in proline content as a mechanism of osmoprotection against ROS and osmotic adjustment (Delauney & Verma, 1993). Although this amino acid was not evaluated in this study, we suggest that there was



* Significant at $p \leq 0.05$

Figure 4. Visual aspects of roots (A), leaf area (B), and root length (C, D) of *Hymenaea courbaril* L. seedlings grown under different water regimes and/or with salicylic acid concentrations



* - Significant at $p \leq 0.05$; ^{NS} - Not significant ($p > 0.05$); Different letters between water regimes at the same dose differ statistically at $p \leq 0.05$

Figure 5. Dickson's Quality Index - DQI (A) and visual aspect (B) of *Hymenaea courbaril* L. seedlings grown under different water regimes associated with salicylic acid concentrations (B)

an increase in proline under these crop conditions, which contributes to protection and osmotic adjustment, favoring tissue turgidity, thus maintaining growth even with lower production of photoassimilates.

Variable results were observed regarding the species in response to SA, although there are few studies on tree and fruit species, especially from the same botanical family. For *E. myrcianthes* assimilation CO₂ rate increases, while seedling

growth did not change (Foresti et al., 2022). In *Psidium guajava* L., SA concentrations did not influence gas exchange or fruit growth (Lacerda et al., 2022). Thus, further studies should be conducted with tree and fruit species to verify the potential effect of SA in mitigating abiotic stress.

Higher values of plasticity indices of A and DQI were observed in seedlings that received application of 100.0 and 200.0 mg L⁻¹ SA compared to the other seedlings (Table 1). According to Valadares et al. (2006) this index varies on a scale of 0 to 1.00; the higher the value, the greater the plasticity of the characteristic. For *H. courbaril* seedlings, physiological characteristics were more adjustable than growth characteristics, which can be explained by the faster expression of metabolic responses to stressful conditions.

The lower PPI value of A and DQI in the flooded seedlings without SA suggests that their quality standard is close to that of the control seedlings. The plasticity of a species is a desirable characteristic because it provides species flexibility by adjusting to different environmental conditions, particularly under abiotic stress. Considering the responses of *H. courbaril* seedlings in this study, we asked: Is the species sensitive to flooding?

It is emphasized that because *H. courbaril* is also found in riparian or gallery forest vegetation (Pinto et al., 2020), the species presented good tolerance to temporary flooding, represented here for 35 days, owing to its plasticity, especially for physiological adjustments, which ensured 100% survival and maintenance of seedling growth even with reduced foliar metabolism, presenting a visual aspect similar to that of the control seedlings. These results suggest that this species has potential for ecological resilience under abiotic stress conditions.

Other species also had potential for ecological resilience owing to their physiological plasticity to flooding, including *Dipteryx alata* Vogel. (Linné et al., 2023) and *Copaifera langsdorffii* Desf. (Cremon et al., 2020), which presents adjustments and survival.

We emphasize that SA application at certain concentrations contributes to obtaining high-quality seedlings compared to those without SA, regardless of water regime, becoming a promising practice in nursery farming and in planning projects for the recovery of degraded areas or areas with temporary flooding.

It is noteworthy that plant responses to SA are dose dependent, so very low concentrations are insufficient to trigger responses, the intermediates induce expression of genes linked to resistance, and high concentrations can trigger cell death due to oxidative stress (Kuai et al., 2015; Zhang & Li, 2019);

Table 1. Phenotypic plasticity index (PPI) of CO₂ assimilation rate (A) and Dickson quality index (DQI) in *Hymenaea courbaril* L. seedlings under flooding with salicylic acid (SA) concentrations

Flooded treatments	PPI (0.00 to 1.00)	
	A (μmol CO ₂ m ⁻² s ⁻¹)	DQI
Flooded (F) without SA	0.71	0.25
F + 100 mg L ⁻¹ SA	0.90	0.53
F + 200 mg L ⁻¹ SA	0.85	0.51
F + 400 mg L ⁻¹ SA	0.78	0.43

these concentrations are dependent, among other factors, on the species and developmental stage of the plant, and climate conditions (Radojčić et al., 2018). SA-induced tolerance to water stress occurs mainly because of the increased activity of the antioxidant system, osmotic adjustment, and synthesis of secondary metabolites (Muñoz-Espinoza et al., 2015; Li et al., 2017).

CONCLUSIONS

1. *Hymenaea courbaril* seedlings are sensitive to flooding as they reduce gas exchange;
2. Foliar application of SA did not mitigate the effect of flooding on gas exchange; however, concentrations of 100-300.0 mg L⁻¹ contributed to seedling growth and quality.
3. *Hymenaea courbaril* is able to adjust physiologically through its plasticity, conferring potential for ecological resilience.

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