



## Potassium Silicate and Salicylic Acid as Mitigation Strategies in *Talisia esculenta* Seedlings Exposed to Water Stress

João Lucas da Costa Santos de Almeida<sup>1</sup>, Silvana de Paula Quintão Scalon<sup>2\*</sup>, Cleberton Correia Santos<sup>2</sup>, Wálles Matos Cerqueira<sup>3</sup>, Vanda Maria de Aquino Figueiredo<sup>2</sup>, Jéssica Aline Linné<sup>2</sup>, Juliana Milene Silverio<sup>2</sup>, Lucas Coutinho Reis<sup>2</sup>, Andressa Caroline Foresti<sup>2</sup>, Daiane Mugnol Dresch<sup>2</sup>

<sup>1</sup> Federal Institute of Education, Science and Technology of Mato Grosso do Sul, Ponta Porã, MS, Brazil

<sup>2</sup> Plant Nutrition and Metabolism Laboratory, Faculty of Agricultural Science, Federal University of Grande Dourados, Dourados, MS, Brazil

<sup>3</sup> Department of Botany, Federal University of Paraná, Curitiba, PR, Brazil

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\*Corresponding author's email: [silvanascalon@ufgd.edu.br](mailto:silvanascalon@ufgd.edu.br)

### ABSTRACT

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Our objective was to evaluate strategies to mitigate the effects of water deficit and anaerobic stress (flooding) on *Talisia esculenta* Radlk seedlings treated with potassium silicate ( $K_2SiO_3$ ) or salicylic acid (SA). In the first experiment, seedlings were subjected to water restriction (WR) for 15 and 35 days, and in the second experiment, they were exposed to flooding (FL) for 15, 30, and 45 days. In both experiments, seedlings were grown under three conditions, i.e., normal irrigation, WR, or FL, either without treatment or with foliar application of SA ( $200 \text{ mg L}^{-1}$ ) or  $K_2SiO_3$  ( $10.0 \text{ mL L}^{-1}$ ). Under WR, seedlings showed reduced photosynthetic metabolism and chlorophyll indices, alongside an increase in leaf proline content, but growth was not compromised. Both SA and  $K_2SiO_3$  alleviated the effects of water restriction at 15 days and supported seedling tolerance under these conditions. Under FL, seedlings developed hypertrophied lenticels but exhibited reduced photosynthetic activity.  $K_2SiO_3$  proved more effective than SA in mitigating the effects of flooding for up to 45 days, whereas SA failed to sustain growth under flooding conditions. Seedling survival differed markedly between stress types. Under WR, survival was only 30% compared to 100% under FL, when no  $K_2SiO_3$  or SA was applied. However, with WR, application of  $K_2SiO_3$  raised survival to 80%, far exceeding the 40% survival observed with SA treatment. Overall, *T. esculenta* demonstrated resilience to water stress, and  $K_2SiO_3$  in particular showed strong potential to mitigate its effects, offering a promising strategy for seedling production under short-term adverse conditions.

### Introduction

*Talisia esculenta* (A. St.-Hil.) Radlk. (Sapindaceae) is a native forest fruit species of Brazil, with its natural distribution across the Amazon region, the Atlantic Forest, and the Cerrado of Mato Grosso do Sul State, and it also occurs in Bolivia and Paraguay (Guarim Neto et al., 2003; Bueno et al., 2018; Rodrigues et al., 2018). In the Brazilian Northeast, its fruits are harvested directly from domestic cultivations or naturally occurring trees, without organized cultivation, and are sold in street markets

and along highways. Beyond its fruit value, the wood of *T. esculenta* is used in civil construction, particularly for interior applications such as ceilings, frames, doorframes, flooring, and carpentry. The species holds ecological, economic, and medicinal importance, being recommended for reforestation and the recovery of riparian forests (Guarim Neto et al., 2003; Umetsu et al., 2011; Lorenzi, 2016). However, many of the phytophysiognomies where *T. esculenta* occurs are increasingly affected by soil

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water fluctuations driven by global climate change and anthropogenic pressures. As a result, atypical climatic seasonality has been observed, with alternating periods of drought and flooding. Despite this, little is known about the morphophysiological responses of *T. esculenta* to such adverse conditions, particularly in relation to water deficit and flooding stress.

In general, under water deficit or flooding, plants reduce stomatal opening and conductance to minimize water loss. This response, however, also limits CO<sub>2</sub> entry, decreases the photochemical efficiency of photosystem II (PSII), increases the production of reactive oxygen species (ROS), and impairs photosynthetic and respiratory capacity, ultimately restricting growth (Cremon et al., 2020; Barbosa et al., 2021; Santos et al., 2023; Samanta et al., 2024). Under flooding, plants often form hypertrophied lenticels and adventitious roots as adaptive mechanisms to adverse conditions, supporting survival (Barbosa et al., 2021; Linné et al., 2023).

Given these challenges, interest has grown in identifying strategies that mitigate the harmful effects of water deficit or flooding on seedlings. In this regard, previous studies highlight the beneficial roles of silicon—particularly in the form of potassium silicate (Santos et al., 2023a; Foresti et al., 2024)—and salicylic acid (Saracho et al., 2021; Santos et al., 2022; 2023b) in regulating plant metabolism and promoting growth under abiotic stress.

According to Santos et al. (2023a) and Paula et al. (2024), foliar application of these agents enhances antioxidant protection metabolism and favors the repair of membrane damage. These authors also reported that Si and K contribute to osmotic adjustment and stomatal pore protection, thereby improving water use efficiency. In addition, Aires et al. (2022) observed that exogenously applied SA supported plant maintenance under water deficit, while Santos et al. (2023b) demonstrated that this phytohormone stimulated growth under flooding.

However, for *T. esculenta*, information linking water stress—whether by deficit or flooding—to the role of such treatments remains limited. Based on this gap,

we hypothesized that (1) K<sub>2</sub>SiO<sub>3</sub> and SA mitigate drought stress in *T. esculenta*, and (2) flooding tolerance is enhanced by these foliar treatments. Therefore, our objective was to evaluate the effects of SA and K<sub>2</sub>SiO<sub>3</sub> in mitigating water stress in *T. esculenta* seedlings.

## Materials and Methods

### Plant propagation

The study was conducted from March to May 2021 in the nursery of the Faculty of Agricultural Sciences at the Federal University of Grande Dourados (UFGD), located in Dourados, MS, Brazil. Ripe fruits were collected from ten matrix trees growing in a pasture area near forest fragments in the rural zone of the municipality of Glória de Dourados (22°22'35" S, 54°08'59" W, 396 m a.s.l.). Fruits were manually processed, and seeds were disinfected in 2.0% sodium hypochlorite solution (active chlorine) for 5 min, rinsed under running water, and sown in 50 × 190 mm tubes filled with Carolina Soil® commercial substrate. The substrate had the following characteristics: electrical conductivity of 0.4 mS cm<sup>-1</sup>, maximum moisture content of 60% m<sup>-1</sup>, density of 130 kg m<sup>-3</sup>, water retention capacity of 350% m m<sup>-1</sup>, and was composed of peat, vermiculite, and limestone.

The tubes were maintained in a greenhouse with a 50% shading cloth cover and irrigated three times daily using microsprinklers and automatic nebulizers. At 60 days after sowing, when seedlings reached an average height of 13 cm, they were transplanted into 7-kg capacity pots filled with a mixture of Oxisols (USDA classification; Dystroferic Red Latosol, Brazilian classification) and coarse sand in a 3:1 (v v<sup>-1</sup>) ratio. The soil texture consisted of 440 g kg<sup>-1</sup> sand, 70 g kg<sup>-1</sup> silt, and 490 g kg<sup>-1</sup> clay. The chemical attributes of the soil are presented in Table 1.

Each pot received two seedlings, which were maintained in the nursery under 30% shading for 30 days as an acclimatization period. Afterward, the seedlings were transferred to an area covered on the top and sides with 150-micron plastic to prevent precipitation.

**Table 1.** Chemical analysis of the substrate used in the *Talisia esculenta* experiment under different water conditions.

pH <sup>1</sup> H <sub>2</sub> O	pH <sup>2</sup> CaCl <sub>2</sub>	H+Al <sup>3</sup>	Ca <sup>4</sup> exchangeable	Mg <sup>5</sup> exchangeable	K <sup>6</sup> exchangeable	CEC <sup>7</sup> pH 7	p <sup>8</sup> Mehlich	O.M. <sup>9</sup> (Oxidation)	V <sup>10</sup>
cmol <sub>c</sub> dm <sup>-3</sup>						(mg dm <sup>-3</sup> )		(%)	
5.09	4.46	2.63	1.50	0.70	0.06	4.89	0.71	6.38	46.22

<sup>1</sup>pH in water; <sup>2</sup>pH in calcium chloride; <sup>3</sup>Hydrogen + aluminum; <sup>4</sup>Calcium-exchangeable forms; <sup>5</sup>Magnesium-exchangeable forms; <sup>6</sup>Potassium-exchangeable forms (Mehlich I); <sup>7</sup>Cation exchange capacity (pH 7.0); <sup>8</sup>Phosphorus-exchangeable forms (Mehlich I); <sup>9</sup>Organic matter (K<sub>2</sub>Cr<sub>2</sub>O<sub>7</sub>); <sup>10</sup>Base saturation.

### Treatments

Foliar applications of potassium silicate ( $K_2SiO_3$ ) and salicylic acid (SA) were done in the morning, on the abaxial and adaxial leaves up to dripping point (10 mL per plant, based pre-test). Foliar application was done only 1 d before submission to water regimes. The sources used were potassium silicate, with 12% by weight ( $168 \text{ g L}^{-1}$ ) of Si and 15% by weight ( $210 \text{ g L}^{-1}$ ) of  $K_2O$ , electrical conductivity of  $2.93 \text{ mS cm}^{-1}$ , density  $1.40 \text{ g L}^{-1}$ , pH 10.96, fluid physical nature. The salicylic acid used was pure (pa), both diluted in distilled water. Considering that most of the studies with  $K_2SiO_3$  and SA available in the literature evaluated cultivated species or vegetables, the doses of  $K_2SiO_3$  and SA in the present research were based on Paula et al. (2024) and Santos et al. (2022), respectively, which evaluated tree species. As the ideal doses in both stress conditions have not yet been determined, in this experiment we decided to use the same doses.

The seedlings at time zero presented the following average values: leaf area=  $39.2 \text{ cm}^2$ , photosynthesis (A)=  $5.65 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , quantum efficiency of photosystem II ( $F_v/F_m$ )= 0.707, and Dickson quality index (DQI)= 0.06. After the application of  $K_2SiO_3$  and SA, the seedlings were divided in two lots to conduct two experiments:

**Experiment I:** the seedlings were exposed to the following treatments: T1: CK (control)= irrigation carried out daily, maintaining 70% of water retention capacity (WRC) in the substrate according Souza et al. (2000), T2: CK +  $200 \text{ mg L}^{-1}$  SA, T3: CK +  $10.0 \text{ mL L}^{-1}$   $K_2SiO_3$ , T4: WR (water restriction), T5: WR +  $200 \text{ mg L}^{-1}$  SA, and T6: WR +  $10.0 \text{ mL L}^{-1}$   $K_2SiO_3$ . The design used was completely randomized, with treatments arranged in a split-plot scheme, with treatments being allocated to the plots and the evaluation periods (15 and 35 d) to the subplots, with five replications, with each experimental unit consisting of a pot with two plants each.

**Experiment II:** the seedlings were exposed to the following treatments: T1: CK (control)= irrigation carried out daily, maintaining 70% of WRC according Souza et al. (2000), T2: CK +  $200 \text{ mg L}^{-1}$  SA, T3: CK +  $10.0 \text{ mL L}^{-1}$   $K_2SiO_3$ , T4: FL (flooded), T5: FL +  $200 \text{ mg L}^{-1}$  SA, T6: FL +  $10.0 \text{ mL L}^{-1}$   $K_2SiO_3$ . Flooding was simulated using 1,500 L plastic pools with a water depth of approximately 5 cm above the surface of the substrate. The pools were cleaned weekly to prevent the proliferation of insect larvae.

The design was completely randomized and the treatments were arranged in a split-plot scheme with treatments being allocated to the plots, and evaluation periods (15, 30, and 45 d) to the subplots, with five replications, each experimental unit consisting of a pot with two plants each.

### Assessments

Survival was assessed based on counting the seedlings that had expanded green leaves and the potential to maintain metabolism and growth. Morphological changes, chlorosis and senescence, were considered when evaluating the general condition of the plants. For flooded plants, the appearance of hypertrophied lenticels was also observed. The evaluations of gas exchange, photochemical processes, and chlorophyll indices were carried out in the morning, between 8 and 11 am, in expanded leaves located in the middle third, previously marked from the beginning to the end of the experiment, with mature intermediate leaves of similar age being evaluated on one plant from each replication. The determination of chlorophyll *a* and *b* indices was carried out fully, using a portable chlorophyll meter (Falker CFL 1030).

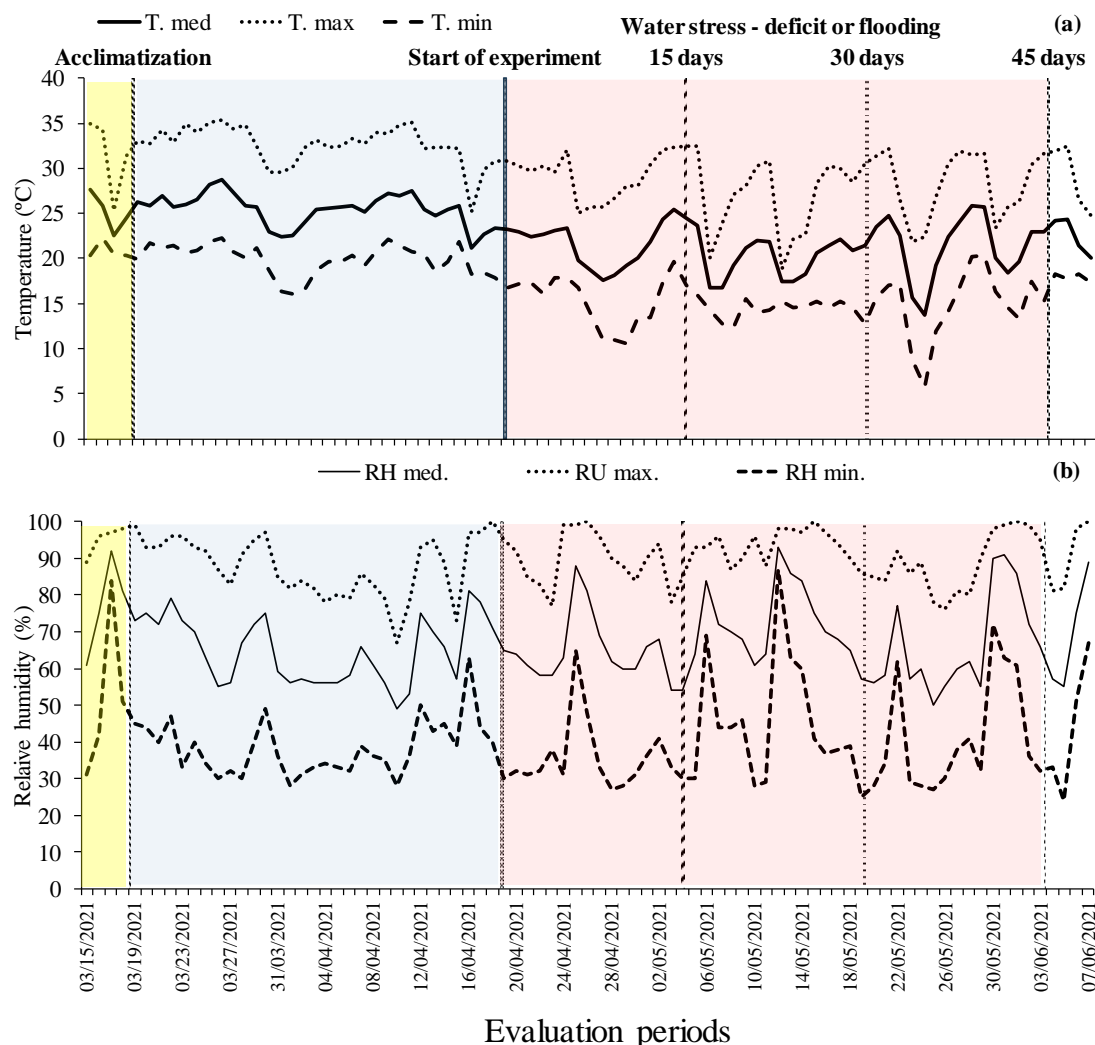
The assimilation rate of  $CO_2$  (A,  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) and carboxylation efficiency of Rubisco ( $A/C_i$ ,  $\mu\text{mol m}^{-2} \text{ s}^{-1} \mu\text{mol mol}^{-1}$ ) were quantified using a portable infrared gas analyzer (IRGA) system—LCI PRO - SD (Analytical Development Co. Ltd, Hoddesdon, UK). The evaluations were carried out under a photosynthetic photon flux of  $1,500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , considering favorable climatic conditions.

The leaves were subjected to dark conditions for 30 min, using leaf clips to induce complete oxidation of the photosynthetic electron transport system of the reaction centers. Then, they were exposed to a 1 second flash, with an intensity of  $1,500 \mu\text{mol m}^{-2} \text{ s}^{-1}$  and the quantum efficiency of photosystem II ( $F_v/F_m$ ). The absorbed energy conversion efficiency ( $F_v/F_0$ ) was determined using a portable continuous excitation fluorometer OS-30p (Opti-Sciences Chlorophyll Fluorometer, Hudson, USA).

The relative water content in leaves (RWC) was determined using leaf discs obtained from a cylinder pouter, which were weighed fresh, saturated and dried for subsequent calculation according to Turner (1981). The leaf area (LA) was determined using an area integrator (LI-COR, 3100 C – Area Meter – Nebraska). Using the biomass data and growth, the Dickson Quality Index (DQI) was calculated according to Dickson et al. (1960).

The proline amino acid quantification was adapted according to Bates et al. (1973) and Colton-Gagnon et al. (2014) using the sulfosalicylic acid method, in which the dried leaves were macerated in liquid N to obtain the extract. The absorbance reading was taken at 520 nm using a spectrophotometer.

The temperature and relative humidity in the nursery were obtained from the database of the Embrapa Agropecuária Oeste Meteorological station, Dourados/MS during the experiment (Fig. 1), with variations between 35 and 19 °C for maximum and minimum, respectively.



**Fig. 1.** (a) Data of temperature; and (b) relative humidity averages during the assessments, Dourados – MS, 2021. Source: EMBRAPA, 2021.

### Statistical analysis

The data from both experiments were subjected to analysis of variance (ANOVA), and effects were considered significant at  $P \leq 0.05$  according to the F test. For Experiment I, treatment means were compared using the Scott–Knott test, while evaluation periods (15 and 35 days) were analyzed with the Bonferroni  $t$  test ( $P \leq 0.05$ ), with results expressed as means  $\pm$  standard error. For Experiment II, treatment means were compared using the Scott–Knott test, and flooded periods (15, 30, and 45 days) were compared using Tukey’s test ( $P \leq 0.05$ ), also expressed as means  $\pm$  standard error. All statistical analyses were performed with SISVAR software, version 5.6 (Ferreira, 2011).

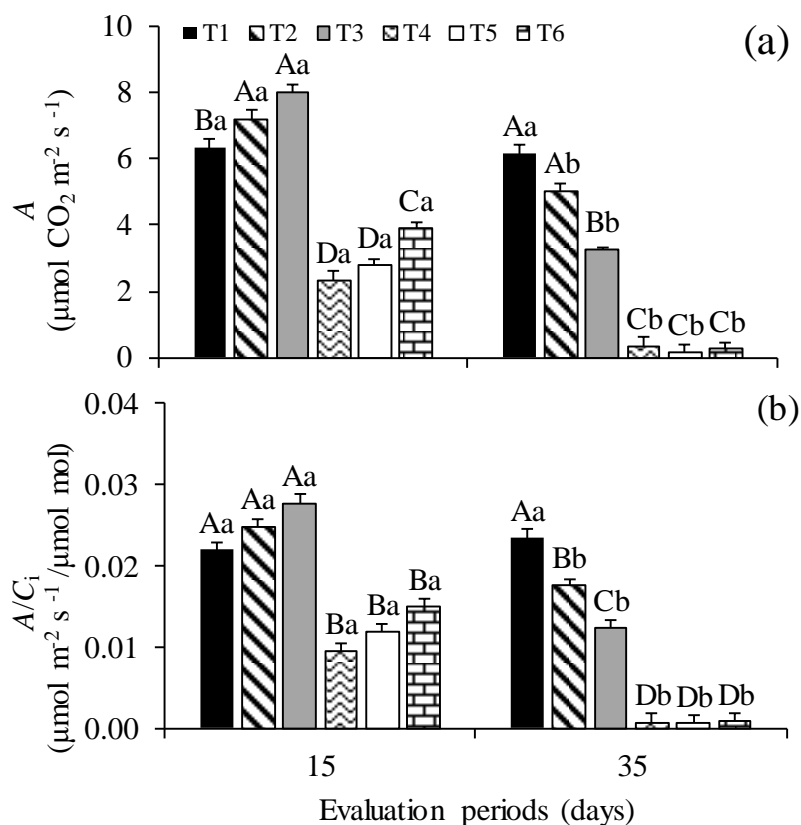
### Results

In general, the characteristics of *T. esculenta* seedlings were influenced by the interaction between the use of potassium silicate and salicylic acid both

under water-deficit and flooding in the evaluation periods.

### Exp. I: Foliar application of $K_2SiO_3$ and SA in *T. esculenta* seedlings under water-deficit Survival, photosynthetic metabolism, and chlorophyll a and b

*T. esculenta* seedlings grown under CK, regardless of foliar treatment, exhibited 100% survival, whereas survival under WR, WR + SA, and WR +  $K_2SiO_3$  was 30%, 40%, and 80%, respectively. At 15 days, seedlings subjected to WR showed a reduced photosynthetic rate (A) (Fig. 2a). However, those treated with  $K_2SiO_3$  maintained higher values ( $3.90 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) compared to the other WR seedlings. By 35 days, all seedlings under WR, regardless of foliar application of SA or  $K_2SiO_3$ , exhibited a marked decrease in A, with values approaching 1 (mean  $1.62 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ).



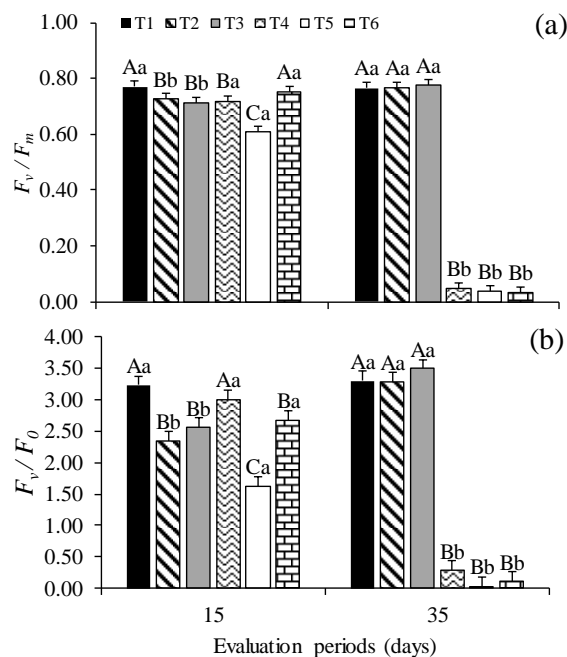
**Fig. 2.** (a) Photosynthetic rate –  $A$ ; (b) and Rubisco carboxylation efficiency –  $A/C_i$  in *Talisia esculenta* seedlings under water regimes (C= control; WR= water restriction) associated with salicylic acid (SA) and potassium silicate ( $K_2SiO_3$ ), evaluated at 15 and 35 d after subjected to water regimes. Capital letters compare the effect of treatments within each evaluation period (Scott-Knott test,  $P \leq 0.05$ )  $\pm$  standard error. Lowercase letters compare the evaluation periods within each treatment (Bonferroni t-test,  $P \leq 0.05$ )  $\pm$  standard error. T1: C; T2: C + 200 mg L<sup>-1</sup> SA; T3: C + 10.0 mL L<sup>-1</sup>  $K_2SiO_3$ ; T4: WR; T5: WR + 200 mg L<sup>-1</sup> SA; T6: WR + 10.0 mL L<sup>-1</sup>  $K_2SiO_3$ .

The highest carboxylation efficiency ( $A/C_i$ ) was also observed in CK seedlings at 15 d (Fig. 2b), but at 35 d the CK seedlings treated with SA and  $K_2SiO_3$  reduced the  $A/C_i$ . However, seedlings under WR presented the lowest averages, close to zero. The quantum efficiency of photosystem II ( $F_v/F_m$ ) was lower at 15 d in seedlings with SA, whereas those treated with  $K_2SiO_3$  showed values similar to those of CK seedlings.  $F_v/F_m$  was lower at 35 d in all seedlings exposed to water-deficit, with no significant variation among treatment groups (Fig. 3a). However, at 15 d, the seedlings in WR with foliar application of  $K_2SiO_3$  had higher values when compared to the other seedlings in the same water regimen.

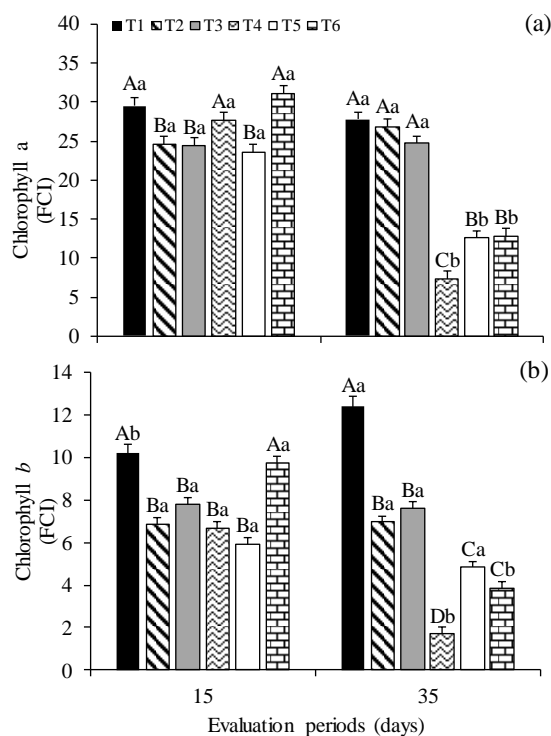
Regarding the efficiency of absorbed energy conversion ( $F_v/F_0$ ) at 15 d, the values varied, but were lower in seedlings under WR + SA. At 35 d, all seedlings under WR showed the lowest values, regardless of treatments (Fig. 3b).

In general, chlorophyll *a* and *b* indices (Fig. 4a and b) were higher at 15 d in CK seedlings and in those treated with WR +  $K_2SiO_3$ . At 35 d, there was a decrease in values, especially under water-deficit. In CK seedlings, treatments with SA and  $K_2SiO_3$  contribute to a reduction in chlorophylls, but in seedlings under WR and treated with SA and  $K_2SiO_3$  the values were higher. The seedlings showed higher chlorophyll indices at 35 d when receiving foliar application of SA and  $K_2SiO_3$  compared to untreated ones (WR).

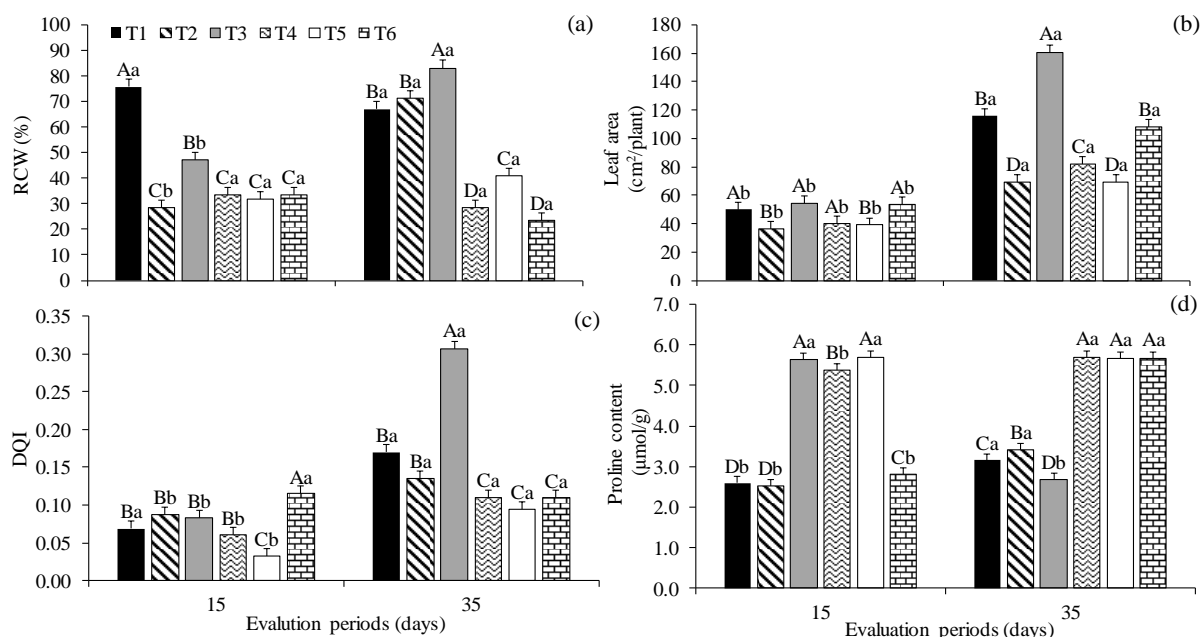
The relative water content (RWC) in the leaves was higher in the CK seedlings at 15 d, but at 35 d the seedlings treated with CK +  $K_2SiO_3$  showed higher RWC (Fig. 5a). At 35 d, seedlings under WR showed lower values, although the WR + SA seedlings showed higher values than the others in the same water regimen.



**Fig. 3.** (a) Photosystem II quantum efficiency ( $F_v/F_m$ ); and (b) energy conversion efficiency ( $F_v/F_0$ ) in *Talisia esculenta* Radlk seedlings under water regimes (C= control; WR= water restriction) associated with salicylic acid (SA) and potassium silicate ( $K_2SiO_3$ ), evaluated at 15 and 35 d after exposed to water regimes. Capital letters compare the effect of treatments within each evaluation period (Scott-Knott test,  $P \leq 0.05$ )  $\pm$  standard error. Lowercase letters compare the evaluation periods within each treatment (Bonferroni t-test,  $P \leq 0.05$ )  $\pm$  standard error. T1: C; T2: C + 200 mg L<sup>-1</sup> SA; T3: C + 10.0 mL L<sup>-1</sup>  $K_2SiO_3$ ; T4: WR; T5: WR + 200 mg L<sup>-1</sup> SA; T6: WR + 10.0 mL L<sup>-1</sup>  $K_2SiO_3$ .



**Fig. 4.** (a) Chlorophyll a; and (b) chlorophyll b in *Talisia esculenta* Radlk seedlings under water regimes (C= control; WR= water restriction) associated with salicylic acid (SA) and potassium silicate ( $K_2SiO_3$ ), evaluated at 15 and 35 d after exposed to water regimes. Capital letters compare the effect of treatments within each evaluation period (Scott-Knott test,  $P \leq 0.05$ )  $\pm$  standard error. Lowercase letters compare the evaluation periods within each treatment (Bonferroni t-test,  $P \leq 0.05$ )  $\pm$  standard error. T1: C; T2: C + 200 mg L<sup>-1</sup> SA; T3: C + 10.0 mL L<sup>-1</sup>  $K_2SiO_3$ ; T4: WR; T5: WR + 200 mg L<sup>-1</sup> SA; T6: WR + 10.0 mL L<sup>-1</sup>  $K_2SiO_3$ .



**Fig. 5.** Relative water content in the (a) leaf; (b) leaf area; (c) Dickson quality index; and (d) proline content in the leaves in *Talisia esculenta* Radlk seedlings in function of water regimes (C= control; WR= water restriction) associated with salicylic acid (SA) and potassium silicate ( $K_2SiO_3$ ), evaluated at 15 and 35 d after application and submission. Capital letters compare the effect of treatments within each evaluation period (Scott-Knott test,  $P \leq 0.05$ )  $\pm$  standard error. Lowercase letters compare the evaluation periods within each treatment (Bonferroni t-test,  $P \leq 0.05$ )  $\pm$  standard error. T1: C; T2: C + 200 mg L<sup>-1</sup> SA; T3: C + 10.0 mL L<sup>-1</sup>  $K_2SiO_3$ ; T4: WR; T5: WR + 200 mg L<sup>-1</sup> SA; T6: WR + 10.0 mL L<sup>-1</sup>  $K_2SiO_3$ .

Leaf area values showed small variations at 15 d and did not follow the expected pattern. However, at 35 d, irrigated seedlings that received  $K_2SiO_3$  showed higher values, differing from the other conditions (Fig. 5b). In addition, seedlings under WR +  $K_2SiO_3$  showed values that did not differ statistically from irrigated CK. This result shows the beneficial effect of  $K_2SiO_3$  in mitigating water deficit damage and its potential to maintain leaf turgor and consequently leaf area. The Dickson Quality Index (DQI) of *T. esculenta* seedlings differed statistically and was higher in seedlings under WR +  $K_2SiO_3$  at 15 d, and after 35 d, the beneficial effect of  $K_2SiO_3$  was observed only in CK +  $K_2SiO_3$  seedlings (Fig. 5c). The proline contents in leaves were influenced by interactions between the factors under study, with higher proline under CK +  $K_2SiO_3$ , WR, and WR + SA. At 35 d, we found increased proline in all seedlings under WR (Fig. 5d).

### Exp. II: Foliar application of $K_2SiO_3$ and SA in *T. esculenta* seedlings under flooding

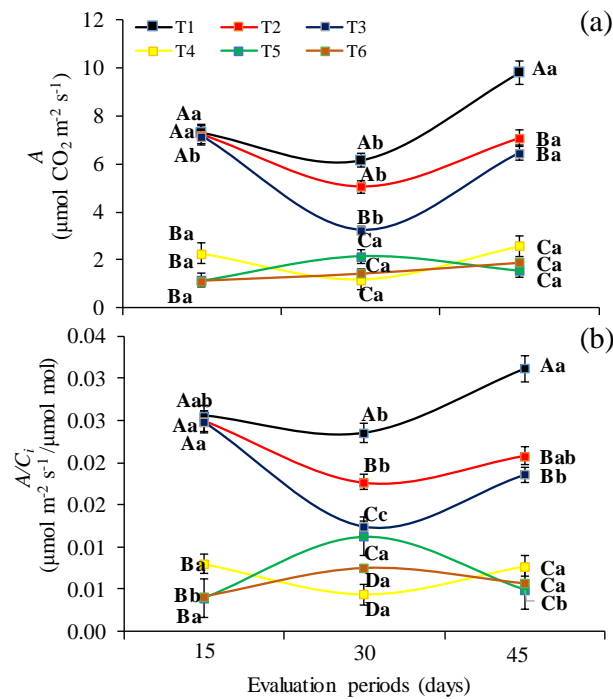
#### Survival, photosynthetic metabolism, and chlorophyll a and b

Quantitative assessments of the water were not performed. Since the pool water was changed weekly to prevent insect proliferation, no changes in odor or drastic color shifts were observed, with the color varying only from light gray to light brown. Overall,

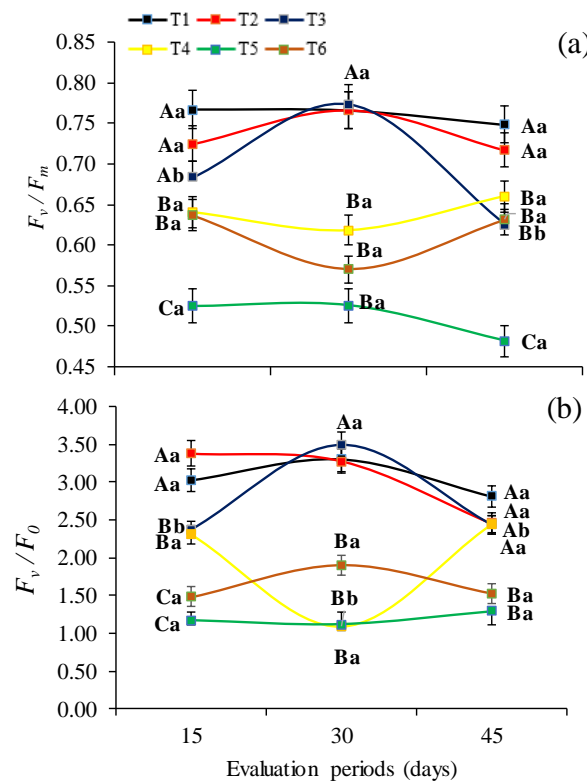
100% of the seedlings survived under flooding (FL), regardless of foliar application of  $K_2SiO_3$  or SA. Seedlings grown under flooded conditions exhibited a lower photosynthetic rate (A), independent of the evaluation period and the application of SA or  $K_2SiO_3$ , with no significant differences observed among treatments (Fig. 6a).

The carboxylation efficiency of Rubisco ( $A/C_i$ ) was similar to A, decreasing with flooding regardless of evaluation period (Fig. 6b). However, at 30 d, the seedlings treated with SA maintained higher  $A/C_i$  values than the other flooded seedlings. The quantum efficiency of photosystem II ( $F_v/F_m$ ) decreased under flooding in seedlings treated with SA (Fig. 7a). The absorbed energy conversion efficiency ( $F_v/F_0$ ) decreased under flooding (Fig. 7b) and did not vary between seedlings treated with SA or  $K_2SiO_3$  at 15 and 45 d, thereby remaining lower than the value recorded in seedlings treated with SA at 30 d.

Foliar application of SA and  $K_2SiO_3$  on plants that were associated or not with flooding led to a reduction in the chlorophyll a and b indices in seedlings, with the highest values observed in the CK seedlings. Chlorophyll a and b reduced significantly after 45 d of flooding and chlorophyll b was more affected by the presence of SA after 15 d of flooding (Fig. 8a and b).

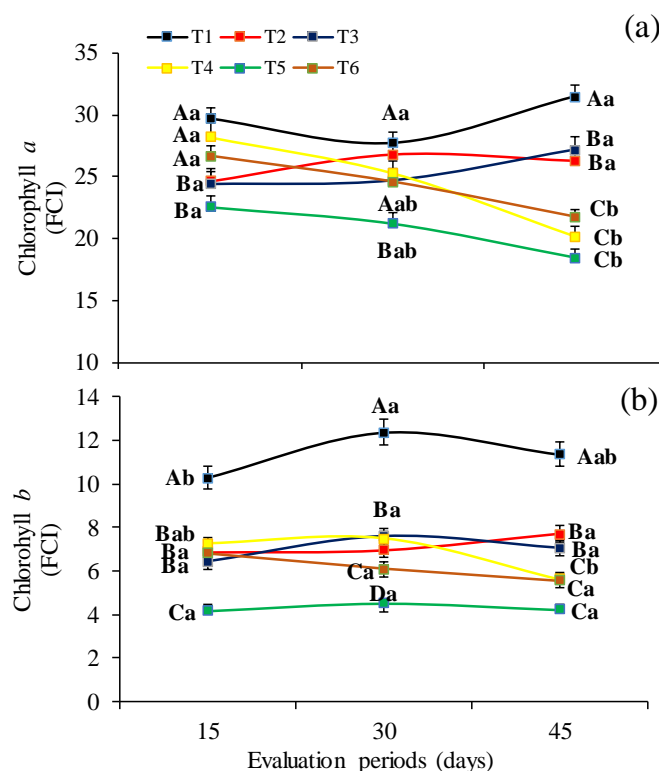


**Fig. 6.** (a) Photosynthetic rate –  $A$ ; and (b) Rubisco carboxylation efficiency –  $A/C_i$  (in *Talisia esculenta* Radlk seedlings in function of water regimes (C= control; F= flooded) associated with salicylic acid (SA) and potassium silicate ( $K_2SiO_3$ ), evaluated at 15, 30 and 45 d after application and submission. Capital letters compare the effect of treatments within each evaluation period (Scott-Knott test,  $P \leq 0.05$ )  $\pm$  standard error. Lowercase letters compare the evaluation periods within each treatment (Tukey's test,  $P \leq 0.05$ )  $\pm$  standard error. T1: (control)= irrigation carried out daily, maintaining 70% of water retention capacity; T2: C + 200 mg  $L^{-1}$  SA; T3: C + 10.0 mL  $L^{-1}$   $K_2SiO_3$ ; T4: F (flooded); T5: F + 200 mg  $L^{-1}$  SA; T6: F + 10.0 mL  $L^{-1}$   $K_2SiO_3$ .



**Fig. 7.** (a) Quantum efficiency of photosystem II ( $F_v/F_m$ ); and (b) absorbed energy conversion efficiency ( $F_v/F_0$ ) in *Talisia esculenta* Radlk seedlings in function of water regimes (C= control; F= flooded) associated with salicylic acid (SA) and

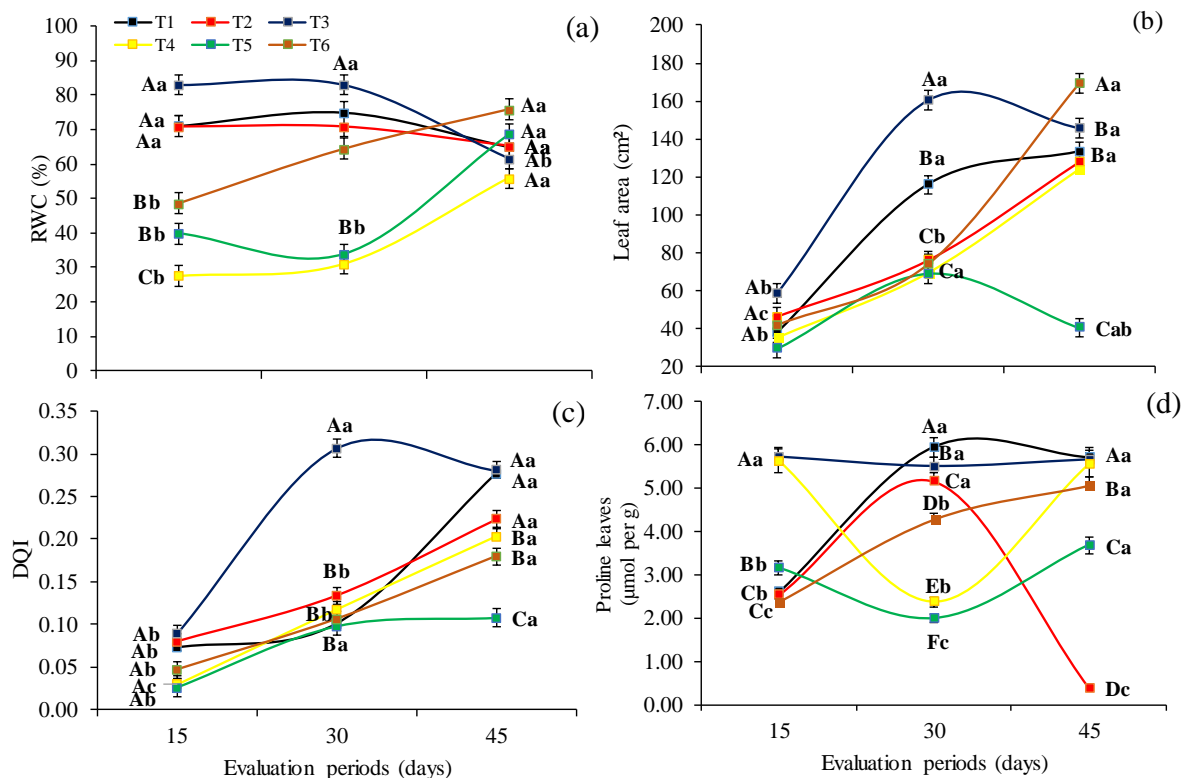
potassium silicate ( $K_2SiO_3$ ), evaluated at 15, 30 and 45 d after application and submission. Capital letters compare the effect of treatments within each evaluation period (Scott-Knott test,  $P \leq 0.05$ )  $\pm$  standard error. Lowercase letters compare the evaluation periods within each treatment (Tukey's test,  $P \leq 0.05$ )  $\pm$  standard error. T1: (control) = irrigation carried out daily, maintaining 70% of water retention capacity; T2: C + 200 mg  $L^{-1}$  SA; T3: C + 10.0 mL  $L^{-1}$   $K_2SiO_3$ ; T4: F (flooded); T5: F + 200 mg  $L^{-1}$  SA; T6: F + 10.0 mL  $L^{-1}$   $K_2SiO_3$ .



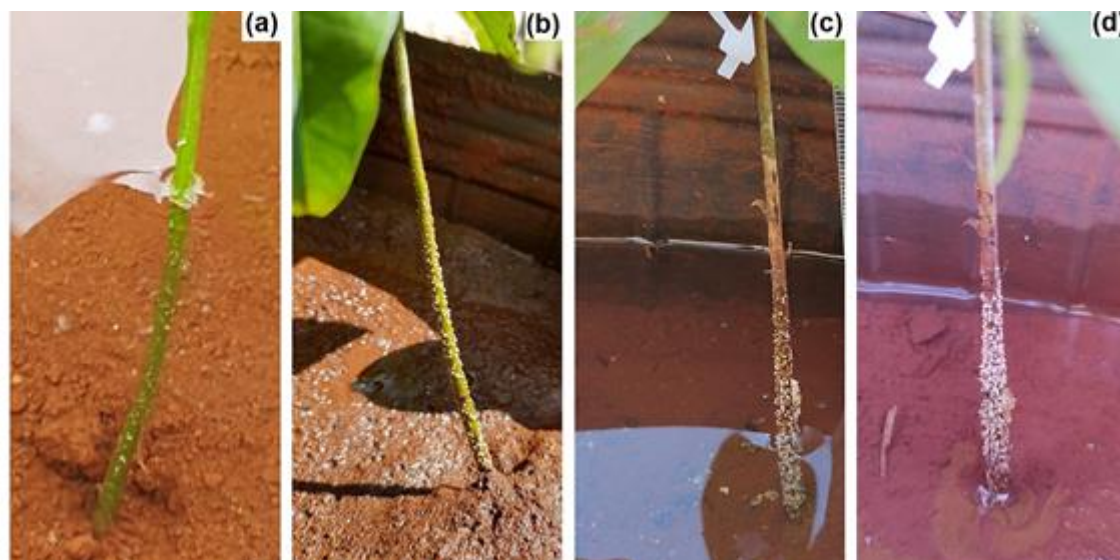
**Fig. 8.** (a) Chlorophyll *a*; and (b) chlorophyll *b* in *Talisia esculenta* Radlk seedlings in function of water regimes (C = control; F = flooded) associated with salicylic acid (SA) and potassium silicate ( $K_2SiO_3$ ), evaluated at 15, 30 and 45 d after application and submission. Capital letters compare the effect of treatments within each evaluation period (Scott-Knott test,  $P \leq 0.05$ )  $\pm$  standard error. Lowercase letters compare the evaluation periods within each treatment (Tukey's test,  $P \leq 0.05$ )  $\pm$  standard error. T1: (control)= irrigation carried out daily, maintaining 70% of water retention capacity; T2: C + 200 mg  $L^{-1}$  SA; T3: C + 10.0 mL  $L^{-1}$   $K_2SiO_3$ ; T4: F (flooded); T5: F + 200 mg  $L^{-1}$  SA; T6: F + 10.0 mL  $L^{-1}$   $K_2SiO_3$ .

The relative water content (RWC) in the leaves of *T. esculenta* seedlings also decreased with the flooding. However, foliar application of SA and  $K_2SiO_3$  kept the WRC in leaves higher at 15 d of flooding. At 30 d, the seedlings treated with  $K_2SiO_3$  showed values significantly the same as the CK seedlings. At 45 d, the RWC of the leaves did not vary between treatments (Fig. 9a). The leaf area of *T. esculenta* seedlings did not vary significantly between treatments after 15 d of flooding. However, at 30 d, the CK + SA and all flooded seedlings showed a reduction in leaf area, as did the FL + SA seedlings at 45 d. Potassium silicate showed greater efficiency in leaf area at 30 d in CK seedlings and at 45 d in FL +  $K_2SiO_3$  seedlings. Root length initially presented higher values in FL seedlings for 15 d. However, it did not vary between treatments in the other periods (Fig. 9b).

The Dickson Quality Index (DQI) of *T. esculenta* initially did not differ at 15 d. However, at 30 d, seedlings from the CK treatment using  $K_2SiO_3$  showed better DQI (0.30). At 45 d, the quality of seedlings was lower under flooding and was even lower in the seedlings treated with SA (Fig. 9c). The proline content in the leaves did not show a clear pattern of response; at 30 d the levels were significantly higher in FL +  $K_2SiO_3$  followed by CK +  $K_2SiO_3$ . At 45 d, the proline content decreased in all treatments, being lower in both CK and FL seedlings that received SA or  $K_2SiO_3$  (Fig. 9d). The seedlings showed the appearance of lenticels (Fig. 10) after 7 d of flooding, regardless of the application of  $K_2SiO_3$  or SA. An increase in the intensity of the presence of lenticels was observed due to the visual appearance of white coloration on the stem of the plants through time of exposure to flooding, suggesting physiological plasticity up to 45 d of flooding.



**Fig. 9.** (a) Relative water content – RWC; (b) leaf area; (c) Dickson quality index; and (d) proline content in leaves in *Talisia esculenta* Radlk seedlings. In function of water regimes (C= control; F= flooded) associated with salicylic acid (SA) and potassium silicate ( $K_2SiO_3$ ), evaluated at 15, 30 and 45 d after application and submission. Capital letters compare the effect of treatments within each evaluation period (Scott-Knott test,  $P \leq 0.05$ )  $\pm$  standard error. Lowercase letters compare the evaluation periods within each treatment (Tukey's test,  $P \leq 0.05$ )  $\pm$  standard error. T1: (control) = irrigation carried out daily, maintaining 70% water retention capacity; T2: C + 200 mg L<sup>-1</sup> SA; T3: C + 10.0 mL L<sup>-1</sup>  $K_2SiO_3$ ; T4: F (flooded); T5: F + 200 mg L<sup>-1</sup> SA; T6: F + 10.0 mL L<sup>-1</sup>  $K_2SiO_3$ .



**Fig. 10.** Lenticels in *Talisia esculenta* Radlk seedlings produced under flooded conditions at (a) 7 d; (b) 15 d; (c) 30 d; and (d) 45 d. Source: Almeida, J. L. C. S.

## Discussion

We observed that *T. esculenta* seedlings were more sensitive to water restriction (WR) than to flooding

(FL). Without the application of  $K_2SiO_3$  or SA, survival under WR was only 30%, compared to 100% survival under FL. Under WR, however, foliar

application of  $K_2SiO_3$  increased survival to 80%, a much higher rate than seedlings treated with SA, which showed only 40% survival. The higher survival rate under FL can be attributed, in addition to other unevaluated factors, to the occurrence of hypertrophied lenticels, which appeared after the 7th day of flooding. Junglos et al. (2018) reported that lenticel formation is an adaptive event mediated by ethylene through hypoxia/anoxia-induced signaling. Hypertrophied lenticels facilitate gas exchange and oxygen diffusion from aerial parts to the root system, while also assisting in the elimination of potentially toxic metabolites such as methanol and acetaldehyde, along with excess ethylene produced under low-oxygen conditions. These structures are generally associated with flood tolerance and enhance the survival of plants exposed to hypoxia or anoxia. Their presence in *T. esculenta* seedlings may have contributed to improved cellular oxygenation and the maintenance of aerobic respiration (Li et al., 2015).

Both water deficit and flooding impaired the photochemical and biochemical processes of photosynthesis. These negative effects are largely attributed to the overproduction of reactive oxygen species (ROS) and membrane damage (Samanta et al., 2024; Chauhan et al., 2023). Water restriction reduced leaf area expansion and seedling quality (DQI). Although flooding also decreased leaf area, its effect on DQI was minimal, except at 45 days in seedlings treated with SA, which showed higher leaf area but lower DQI, suggesting that SA may have exacerbated the stress effects of flooding.

We further emphasize that although photosynthetic pigments decreased under both forms of water stress, chlorosis was observed only in seedlings subjected to prolonged flooding. Importantly, leaf abscission did not occur under any cultivation condition. Under WR, the severity of negative effects increased with longer exposure. Foliar application of  $K_2SiO_3$  had a mitigating effect during shorter exposure (15 days), improving parameters such as A, A/Ci, Fv/Fm, Fv/Fo, and chlorophyll indices a and b, thereby alleviating stress and helping to maintain higher DQI values during longer exposure. The pronounced reduction in A observed under WR at 35 days may be linked to significant declines in relative water content (RWC) and Rubisco carboxylation efficiency (A/Ci), the latter already evident by 15 days. The rapid reduction in A/Ci highlights the high sensitivity of *T. esculenta* seedlings to WR, leading to increased Ci (data not shown), reduced carboxylation, and decreased photoassimilate production. Notably, chlorophyll indices were only reduced after 35 days. Together, these factors contributed to the reduced photosynthetic efficiency of seedlings under prolonged WR. Finally, the elevated proline content in all treatments compared with CK seedlings under prolonged WR confirms the

stressful nature of this condition and indicates that neither SA nor  $K_2SiO_3$  functioned effectively as protective agents against long-term WR.

The results observed for seedlings grown under WR partially confirm our initial hypothesis. However, the effects of  $K_2SiO_3$  and SA were insufficient to mitigate the damage caused by prolonged water restriction, although seedlings under WR +  $K_2SiO_3$  maintained higher photosynthetic rate, chlorophyll b index, and DQI up to 15 days. We suggest that silicon has potential to alleviate some of the negative effects of short-term WR. These findings align with previous studies (Santos et al., 2022; Santos et al., 2023a; Paula et al., 2024), which report that silicon activates antioxidant enzymes and amino acids that help relieve or delay oxidative stress, promote membrane repair, and increase photosynthetic pigment content. According to these authors, Si and K contribute to osmotic adjustment and stomatal protection, thereby improving water-use efficiency. By contrast, foliar application of SA at the evaluated dose may have accentuated stress in *T. esculenta* seedlings for some of the traits evaluated.

Under FL, seedlings exhibited reductions in photosynthetic metabolism and leaf RWC by 15 days, followed by declines in DQI at 30 days and chlorophyll content at 45 days, accompanied by visible chlorosis. At 45 days, the relatively high RWC may be associated with reduced water loss through transpiration and lower stomatal conductance (not measured in this study), reflecting the physiological plasticity of this species. However, these traits also limited  $CO_2$  uptake, thereby reducing A. Similarly, Santos et al. (2023b) reported decreased gas exchange in *Hymenaea courbaril* L. seedlings, with no alleviation by foliar application of SA under flooding conditions.

We confirmed that foliar application of  $K_2SiO_3$  increased leaf area at 45 days of flooding, but this effect was not accompanied by increases in pigments or photosynthetic rate. It is noteworthy that DQI did not differ significantly between flooded seedlings with or without foliar application of SA or  $K_2SiO_3$ . The significant increase in proline content at 30 days suggests the activation of protective mechanisms that may have supported seedling growth and quality. In this context, abscisic acid, ROS, and proline act as signaling molecules that trigger antioxidant defenses. Proline, in particular, protects and activates antioxidant enzymes such as SOD and POD, along with other detoxification pathways (not evaluated in this study). Moreover, proline catabolism can provide additional energy during post-stress recovery, supporting renewed plant growth—an aspect that warrants further investigation (Junglos et al., 2018; Bastos et al., 2022).

Similar to the results under water restriction, the findings for flooded seedlings partially support our initial hypothesis. The application of  $K_2SiO_3$

provided beneficial effects on some traits up to 45 days of flooding, whereas SA negatively affected several characteristics, including chlorophyll index, chlorophyll *a* fluorescence, leaf area, DQI, and proline content. A decline in energy conversion efficiency ( $F_v/F_0$ ) was observed in seedlings subjected to both water deficit and flooding when treated with SA, already evident in the earliest evaluations. This reduction, together with the decline in potential quantum efficiency of photosystem II ( $F_v/F_m$ ), directly contributed to lower photosynthetic rate (A). Since photochemical processes drive energy production, reductions in  $F_v/F_m$  limit energy availability and consequently decrease Rubisco carboxylation efficiency (Foresti et al., 2024). The reduced chlorophyll *a* fluorescence values thus reflect the stressful effects on *T. esculenta* seedlings.

Although PSII photochemical activity declined, it did not show a pronounced drop throughout flooding exposure, except in seedlings treated with SA. Chlorophyll *a* fluorescence is widely used as a tool to investigate stress physiology, as it indicates emission patterns and photochemical yield (Santos et al., 2020). Reference  $F_v/F_m$  values generally range from 0.75 to 0.85, representing an intact photosynthetic apparatus; values below this threshold are associated with reduced electron transport capacity between PSII acceptors (Reis et al., 2020; Santos et al., 2020) and thus signal stress conditions in seedlings.

Interestingly, previous studies (Santos et al., 2022; Santos et al., 2023) reported that foliar application of SA and Si improved chlorophyll indices and sustained PSII photochemical processes in other species. In this context, energy allocation strategies may help plants cope with water stress, and the use of compounds such as  $K_2SiO_3$  and SA could contribute to mitigating the adverse impacts of water stress on photosynthesis and energy production in *T. esculenta* seedlings. Nevertheless, we believe that the doses tested in the present study may not have been appropriate for this species. For instance, Figueiredo et al. (2023), working with the same species, found positive effects of both Si and SA on mitigating water deficit when applying considerably lower concentrations ( $0.5\text{--}1.0\text{ g L}^{-1} K_2SiO_3$  and  $50\text{--}100\text{ mg L}^{-1}$  SA).

Water stress, whether caused by soil water scarcity or flooding, leads to destructive changes in the biochemical and physiological processes of plants, ultimately reducing growth (Attia et al., 2021; Desoky et al., 2021; Mansour et al., 2021). For *T. esculenta* seedlings, however, cultivation under water restriction did not result in drastic reductions in growth or quality, in contrast to seedlings flooded for 45 days and treated with SA, which exhibited pronounced declines.

Supporting the idea of stress induction, previous studies report that the amino acid proline typically accumulates in plants under stressful conditions, functioning as an osmoregulatory mechanism (Liu et al., 2011; Silva et al., 2019). Proline mitigates stress damage by reducing the harmful effects of reactive oxygen species, thereby alleviating the consequences of water stress (Merwad et al., 2018). In *T. esculenta* seedlings, proline accumulation was observed under both water deficit and flooding, regardless of treatment, suggesting that these seedlings exhibit a degree of physiological flexibility in adjusting to environmental stress. Although proline functions as an important osmoregulatory molecule (Batista-Silva et al., 2019; Alvarez et al., 2022), its accumulation was not a decisive factor in determining tolerance or sensitivity of this species to water stress.

Among the reported benefits of  $K_2SiO_3$  and SA in conferring stress tolerance is their ability to maintain relative water content (RWC) in leaves and preserve chlorophyll indices, thereby sustaining photosynthetic activity. However, such benefits were not consistently observed in *T. esculenta* seedlings, in contrast to other tree species. For example, *Inga vera* Willd. (Santos et al., 2023), *Eugenia myrcianthes* (Foresti et al., 2024), and *Schinus terebinthifolia* Raddi (Saracho et al., 2021; Santos et al., 2023b) all showed attenuation of water stress when treated with silicon, potassium silicate, or salicylic acid.

The use of  $K_2SiO_3$  provides an advantage in maintaining relative water content (RWC), as it helps preserve leaf turgidity by forming a protective layer over the stomatal pore (Santos et al., 2022). In this regard, both Si and K alleviate plant water stress through osmotic adjustment, reducing the accumulation of reactive oxygen species and improving water-use efficiency (Pereira et al., 2019; Saracho et al., 2021). Similarly, SA, a phytohormone, strengthens the antioxidant defense system, reduces reactive oxygen species, enhances water-use efficiency, and stimulates protein synthesis, thereby contributing to biomass accumulation and improved drought tolerance (Saracho et al., 2021).

Based on our results, we confirmed the stressful effects of both water deficit and flooding on *T. esculenta* seedlings. Nonetheless, the higher survival observed under WR +  $K_2SiO_3$  and the total survival under flooding, regardless of treatment, may be explained by other factors not evaluated in this study—such as increased activity of antioxidant enzymes and protective compounds—that could have been stimulated by the treatments and contributed to preserving cell membrane integrity and seedling survival. We also noted that stress responses intensified with longer exposure.

Given that foliar application of  $K_2SiO_3$  and SA showed limited effects on the photochemical and biochemical processes of photosynthesis and on leaf RWC, we suggest that their efficacy in *T. esculenta* may have been temporary, or that responses are dose- and/or species-dependent. Even so, it is important to highlight that both compounds mitigated some of the negative impacts of water restriction on photosynthetic metabolism, particularly during shorter stress exposure. Moreover,  $K_2SiO_3$  and SA are low-cost products that are readily available in agricultural stores or through online vendors, making them accessible tools for nurseries or institutions engaged in ecological restoration and reforestation projects.

The results of this study differ from reports on other species, where more consistent benefits were observed. Although the dose of  $10.0 \text{ mL L}^{-1} K_2SiO_3$  tested here yielded limited results in *T. esculenta*, it can be considered a starting point for future investigations. Furthermore, since this study did not evaluate the activity of antioxidant enzymes, lipid peroxidation (MDA), or other metabolic markers, we recommend that future research address these aspects and also test responses under field conditions. Such studies would broaden understanding of the physiological behavior of this species under water restriction and flooding and may lead to more effective and lasting strategies for mitigating water stress.

## Conclusion

Water stress negatively affected photosynthetic metabolism and chlorophyll index while increasing proline content in the leaves of *T. esculenta* seedlings. Water deficit reduced seedling quality after 30 days of exposure, whereas under flooding this reduction occurred only after 45 days. Foliar application of  $K_2SiO_3$  alleviated the effects of water deficit on photosynthetic rate and seedling quality after 15 days and mitigated the impact of prolonged flooding stress (45 days) on chlorophyll *a* fluorescence, chlorophyll index, leaf area, and DQI. In contrast, the use of SA at the applied dose was ineffective and even detrimental to photosynthetic metabolism, chlorophyll index, and seedling quality under both water stress conditions. Overall, foliar applications of  $K_2SiO_3$  and SA mitigated some negative effects of water deficits on photosynthetic metabolism, particularly during shorter periods of stress exposure.

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## Author Contributions

Investigation, JLCSA, SPQS, CCS, and WMC; Formal analysis and Writing – original draft, JLCSA, CCS, VMAF, JAL, JMS, LCR, and ACF; Writing – review and editing, JLCSA, SPQS, and CCS; Resources, SPQS and CCS. All authors have read and agreed to the published version of the manuscript.

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## Conflict of Interest

The authors indicate no conflict of interest in this work.

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