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# Potassium silicate and light availability affect photochemical efficiency and morphology of *Alibertia edulis*

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Received January 30, 2023 Accepted July 27, 2023 ABSTRACT: Light stress damages the photochemical apparatus and affects seedling growth of forest species. Using potassium silicate (K<sub>2</sub>SiO<sub>3</sub>) can mitigate these deleterious effects and contribute to the acclimatization and robustness of seedlings. This study evaluated the effect of K2SiO3 and shading levels on the photochemical and growth of Alibertia edulis (Rich) A. Rich seedlings. The experiment was arranged under three light conditions based on shading levels of 0 % (full sun), 30 %, and 70 %. Four doses of K2SiO3 applied through foliar spray were tested: 0.0, 2.5, 5.0, and 10.0 mL L<sup>-1</sup>. Cultivation under full sun and under 70 % of shade was stressful for A. edulis, while cultivation under 30 % of shade improved plant growth. Increasing application of K<sub>2</sub>SiO<sub>3</sub> in seedlings under full sun damaged the reaction center, causing lower photochemical yields, but increased the photochemical efficiency of photosystem II under 30 % of shade. Using K<sub>2</sub>SiO<sub>3</sub> contributed to leaf water regulation while applying 10.0 mL L<sup>-1</sup> increased chlorophyll indices, leaf area, physiological indices, and the quality of seedlings cultivated under full sun and 30 % of shade. Using 10.0 mL L<sup>-1</sup> K<sub>2</sub>SiO<sub>3</sub> mitigated the negative effects of light stress under full sun. It provided high photochemical efficiency, morphology aspects, and Dickson quality index A. edulis seedlings in environments with high or moderate light availability.

Keywords: Chlorophyll-a fluorescence, K<sub>2</sub>SiO<sub>3</sub>, photosystem II, seedling quality, shading

# Introduction

Alibertia edulis (Rich) A. Rich is a fruit tree native to Brazil, belonging to the family Rubiaceae. Adult plants can reach approximately 8 m in height. Regarding the successional group, the species is classified as early secondary (Leles et al., 2011), and it occurs in transition forests, lowland forests, Cerrado biome, "Cerradão", swamp forests, and gallery forests (Campos Filho, 2009), all with different light gradients.

Light availability is a determinant environmental factor in the capacity of plants in silvicultural activities since the plants can be inserted in open areas, clearings, understories, or dense forests in different vegetation and/or agroforestry systems. Thus, high or low light intensity can be a stressful condition affecting the production of photoassimilates since it correlates with the thylakoid structure (Petrova et al., 2020), mesophilic conductance, and carboxylation efficiency of RuBisCO (Mendes et al., 2017), and overall photosynthesis. On the other hand, some species can acclimatize to these conditions, adjusting their metabolism through receptors that control the expression of cell division genes and the formation of meristematic tissues (Anpo et al., 2019).

The use of agents that mitigate the adverse effects of environmental stress in species of arboreal interest is relevant, such as silicon (Si), a beneficial element generally used in the form of potassium silicate ( $K_2SiO_3$ ), contributing positively to induce plant tolerance to adverse conditions (Hashemi et al., 2010; Conceição et al., 2019; Aras et al., 2020); however, not many studies have investigated the association of the use of  $K_2SiO_3$  agents with light conditions for *A. edulis*.

Silicon is absorbed via mass flow as monosilicic acid ( $H_4SiO_4$ ) and when translocated by the xylem (Epstein, 1999; Ma and Yamaji, 2006), it is deposited in the form of hydrated amorphous silica on the epidermal cell walls, increasing adaxial epidermis and trichome thickness and stomatal functionality (Gao et al., 2022). Potassium (K) is an essential element in osmotic adjustment and regulation of turgor (Ahanger et al., 2017; Nobre et al., 2023), favoring leaf metabolism and nutrition (Lima et al., 2021).

Considering the successional classification of *A. edulis*, we hypothesized that foliar application of  $K_2SiO_3$  contributes to the maintenance of water balance, stabilizing the photochemical activities in the PSII reaction centers, alleviating the photo inhibitory and stressful effect under different light gradients. Thus, this study discusses the potential of potassium silicate to mitigate the effects of light stress on the morphophysiological responses of *A. edulis* seedlings.

# **Materials and Methods**

#### Collection of seeds and plant growth conditions

Ripe fruits of *A. edulis* (Access Registration No. A9CDAAE – CGEN-MMA) were collected from matrices located in the Brazilian Cerrado (18°07′03″ S, 54°25′07″ W, altitude 452 m). The exsiccate (N° 4649) was deposited at Herbarium DDMS, of Universidade Federal da Grande

Dourados (UFGD). After manual processing for seed extraction, sowing was performed in 128-cell expanded polystyrene trays filled with Tropstrato<sup>®</sup> with daily irrigations in a greenhouse.

When they reached an average height of 6.0 cm, the seedlings were transplanted to 5-kg plastic pots filled with Oxisol soil (United States – USDA Classification) correspondent to Dystrophic Red Latosol of clayey texture staying (Brazilian Classification), for 30 days with daily irrigations and 50 % shade, characterizing the acclimatization period. The Oxisols presented the following chemical attributes according to the methodology in Silva (2009): CaCl<sub>2</sub> pH: 6.2; P: 1.7 mg dm<sup>-3</sup>; Ca: 6.7 cmol<sub>c</sub> dm<sup>-3</sup>; K: 1.0 cmol<sub>c</sub> dm<sup>-3</sup>; Mg: 1.8 cmol<sub>c</sub> dm<sup>-3</sup>; Al: 0.12 mmol<sub>c</sub> dm<sup>-3</sup>; Cationic exchange capacity: 42.4 mmol<sub>c</sub> dm<sup>-3</sup>, and bases per saturation: 60.5 %.

# $\rm K_2SiO_3$ application, shading levels, and experimental design

Four doses of  $K_2SiO_3$  (12 % Si and 15 %  $K_2O$ ; density: 1.40 g L<sup>-1</sup>) were applied to the seedlings through foliar spray: 0.0, 2.5, 5.0, and 10.0 mL L<sup>-1</sup>, corresponding to 0.00, 0.42, 0.84, and 1.68 g Si L<sup>-1</sup> and 0.00, 0.52, 1.05, 2.10 g K<sub>2</sub>O L<sup>-1</sup>. Two mL of LI 700 adjuvant were added to the K<sub>2</sub>SiO<sub>3</sub> solution to favor adherence. The plants were collected from an environment protected from rainfall for 24 h.

Subsequently, the pots were arranged under three light availabilities ( $22^{\circ}11'43.7"$  S,  $54^{\circ}56'08.5"$  W, altitude 452 m) based on shading levels of 0 % (full sun), 30 %, and 70 %, with average photosynthetically active radiation of 988.27, 690.58, and 280.75 µmol photons m<sup>-2</sup> s<sup>-1</sup>, respectively. Shading was simulated using black nylon fabric with the corresponding levels of light retention. K<sub>2</sub>SiO<sub>3</sub> doses were applied in two periods ( $1^{st}$ : zero time;  $2^{nd}$ : after 45 days, with 7.0 and 8.5 cm height, four and six leaves, and 30 and 75 days after emergence – DAE, respectively), both on the abaxial and adaxial surfaces of the leaves, until drip point (10 mL per plant, based pre-test).

The experimental design was in randomized blocks, installing three blocks per treatment, with the treatments arranged in a subplot scheme. Plots consisted of the shading levels, while subplots corresponded to the  $K_2SiO_3$  doses, with three replicates. The experimental unit consisted of three plastic pots with two plants each. During the experimental period, cultural treatments consisted of daily irrigations and weeding when necessary.

#### Evaluated morphophysiological characteristics

Evaluations were performed in the leaves located on the third pair of fully expanded, considered physiologically mature, between 8 and 10 h. At 60 days after transplanting (90 DAE), the seedlings were evaluated for the following characteristics:

a) Growth: considering plant height – H (cm) (distance from the ground to the inflexion of the highest leaf), measured with a centimeter ruler; stem diameter – SD (mm) ( $\pm$  1.0 cm > substrate level), measured with a digital caliper, and analyzed as a function of the height/ diameter ratio (HDR). The number of expanded leaves (NL) was also counted. The seedlings were harvested, and the roots were washed to remove excess substrate. They were then separated into leaves, stems, and roots. Leaf area (LA, cm<sup>2</sup>) was measured with an area integrator (LI-COR, 3100 C - Area Meter), and the length of the largest root - RL (cm) was measured.

b) Chlorophyll indices: chlorophyll a, b, and total chlorophyll (a + b) were measured using a portable chlorophyll meter ClorofiLOG<sup>®</sup> (Falker CFL 1030).

c) Chlorophyll-*a* fluorescence: the leaves were adapted to the dark condition for 30 min using leaf clips and, soon after the initial (F<sub>0</sub>), variable (F<sub>v</sub>) and maximum (F<sub>m</sub>) emission of chlorophyll-*a* fluorescence, the maximum quantic photochemical efficiency of photosystem II – PSII (F<sub>v</sub>/F<sub>m</sub>) was measured using a portable fluorometer (OS-30p; Opti-Sciences Chlorophyll Fluorometer) at 1,500 µmol m<sup>-2</sup> s<sup>-1</sup> light intensity. Absorbed energy conversion efficiency (F<sub>v</sub>/F<sub>0</sub>) and maximum non-photochemical performance (F<sub>0</sub>/F<sub>m</sub>) (Rohácek, 2002) were calculated.

d) Leaf water balance: four leaf discs with a known area were obtained from each seedling from the different treatments using a borer. They were weighed in a millesimal precision scale (0.0001 g) and the fresh weight was obtained. Subsequently, the discs were placed in a container with distilled water for 24 h, and the saturated mass was obtained. The discs were placed in an oven at  $60 \pm 5$  °C, until constant dry weight. From these data, the relative water content (RWC) (Turner, 1981) and deficit water saturation ( $\Delta W_{sat}$ ) (Larcher, 2004) were calculated.

e) Physiological indices: from the data on kiln-dried masses ( $60 \pm 5$  °C) and leaf area, the leaf area ratio (LAR) and specific leaf area (SLA) were calculated (Hunt, 2017).

f) Seedling quality standard: Dickson quality index (DQI) was obtained from the data on height/diameter ratio, shoot/root ratio, and total dry weight (Dickson et al., 1960).

#### Statistical analysis

The data were submitted to analysis of variance (ANOVA) and, when significant (F test,  $p \le 0.05$ ), the means for the light availabilities were compared by the Tukey test  $\pm$  standard deviation ( $p \le 0.05$ ). The potassium silicate doses and interaction between the factors were analyzed through the regression analysis ( $p \le 0.05$ ). All analyses were performed using SISVAR software.

# Results

In general, *A. edulis* seedlings had a visual aspect with good vigor under 30 % of shade and with increasing doses of  $K_2SiO_3$ , while seedlings under full sun increased their growth with foliar application of  $K_2SiO_3$  (Figure 1). Plant height and the number of leaves were influenced by shading levels individually (Figures 2A and 2C), and the highest values (11.80 cm and 13 leaves, respectively) occurred in seedlings under 30 % of shade. The lowest stem diameter and the highest HDR occurred in seedlings grown under 70 % shade (Figures 2B and 2D).

Leaf area was influenced by the factors under study individually, with the highest values occurring under 30 % of shade (109.25 cm<sup>2</sup>) (Figure 3A) and increased linearly with 10.0 mL K<sub>2</sub>SiO<sub>3</sub> (111.08 cm<sup>2</sup>) (Figure 3B). Root length (RL) was influenced by the interaction between shading levels and potassium silicate (Figure 3C). Maximum RL was 12.35 cm in seedlings produced under 30 % of shade with 4.70 mL K<sub>2</sub>SiO<sub>3</sub>. Under full sun (0 %), the highest values (11.40 and 11.66 cm) occurred without and with 10.0 mL of K<sub>2</sub>SiO<sub>3</sub>, respectively. Under 70 % shade, the K<sub>2</sub>SiO<sub>3</sub> did not significantly affect root length (p > 0.05), which averaged 11.33 cm.

Chlorophyll indices presented the same response and the isolated effect of shading levels and  $K_2SiO_3$ . For the shading levels, the highest indices of chlorophyll *a*, *b*, and total chlorophyll were 29.7, 9.36, and 38.07 Falker in seedlings under 30 % of shade (Figures 4A, 4C, and 4E, respectively). In addition, the seedlings had higher chlorophyll *a* (33.11), *b* (9.70), and total chlorophyll (42.91) (Figures 4B, 4D, and 4F) when applying 10.0 mL of  $K_2SiO_3$ .

Chlorophyll-a fluorescence and indicators photochemical processes of PSII were influenced by

the interaction between shading levels and  $K_2SiO_3$  doses (Figures 5A-5F). Seedlings under full sun showed an increase in initial fluorescence –  $F_0$  and maximum nonphotochemical yield –  $F_0/F_m$  (0.050 and 0.551, respectively) and a decrease in variable fluorescence –  $F_{v_i}$  quantum photochemical efficiency of PSII –  $F_v/F_m$ , and conversion of absorbed energy –  $F_v/F_0$  with values of 0.043; 0.406; and 0.808, respectively, all due to the increasing doses of  $K_2SiO_3$ .

The relative water content (RWC) and the water saturation deficit  $(\Delta W_{Sat})$  of A. edulis seedlings were influenced by the interaction between shading levels and K<sub>2</sub>SiO<sub>3</sub> doses. The maximum RWC calculated was 68 % in seedlings produced under full sun (0 % shade) with 5.19 mL K<sub>2</sub>SiO<sub>3</sub>. Under 30 % of shade, the maximum value was 67.98 % with 5.79 mL K<sub>2</sub>SiO<sub>3</sub> (Figure 6A). The  $\Delta W_{Sat}$  in full sun (0 % shade) adjusted to the quadratic model, with the highest values, 39 % and 40 %, obtained with and without 10.0 mL of K<sub>2</sub>SiO<sub>3</sub>, respectively (Figure 6B). The results under 30 % of shade were similar, and at the same K<sub>2</sub>SiO<sub>3</sub> doses, the highest calculated values were 44.73 % and 38.71 %, respectively. For the RWC and  $\Delta W_{Sat}$  of seedlings under 70 % shade, no statistical effect of  $K_2SiO_3$  (p > 0.05), with an average of 64.5 and 34.5 %, respectively.

The specific leaf area was influenced only by shading levels, with a higher value (288.70 cm<sup>2</sup> g<sup>-1</sup>) in seedlings under 70 % shade (Figure 7A). The leaf area ratio was influenced by the factors under study individually, with the highest values (155.80 and 126.77 cm<sup>2</sup> g<sup>-1</sup>) obtained under 70 % shade (Figure 7B) and without K<sub>2</sub>SiO<sub>3</sub> (Figure 7C), respectively.

For DQI, the treatment with 70 % of shade did not significantly affect the quality standard of *A. edulis* seedlings due to  $K_2SiO_3$  doses (p > 0.05), with an average



Figure 1 – Visual aspect of Alibertia edulis seedlings grown with potassium silicate (K<sub>2</sub>SiO<sub>3</sub>) under different shading levels.



Figure 2 – Height (A), stem diameter (B), number of leaves (C), and HDR = height/diameter ratio (D) in *Alibertia edulis* seedlings grown under different shading levels. Different letters differ from each other ± SD (Tukey test; *p* ≤ 0.05).



**Figure 3** – Leaf area (A, B) and root length (C) in *Alibertia edulis* seedlings produced with potassium silicate ( $K_2SIO_3$ ) under different shading levels. Different letters differ from each other ± SD (Tukey test;  $p \le 0.05$ ) (A). \*Significant at  $p \le 0.05$  (B-C).

of 0.045 (Figure 7D). On the other hand, seedlings under full sun presented slightly higher DQI than those under 30 % of shade (0.16 and 0.15, respectively), both with 10.0 mL of  $K_2SiO_3$ .

# Discussion

A. edulis seedlings responded differently through morphophysiological adjustments according to the

shading levels, with environments of 0 % and 70 % of shade considered stressful for this species. Applying  $K_2SiO_3$  improved chlorophyll indices and photochemical functionality and potentiated the increase in biomass that reflected higher DQI, with varying responses depending on each light environment.

Although the application of  $K_2SiO_3$  increased energy expenditure under certain light conditions,  $K_2SiO_3$  has a compensatory effect in the production of



Figure 4 – Chlorophyll *a* (A-B), Chlorophyll *b* (C-D), and total chlorophyll indices (E-F) in leaves of Alibertia edulis seedlings grown with potassium silicate ( $K_2SiO_3$ ) or different shading levels. Different letters differ from each other ± SD (Tukey test;  $p \le 0.05$ ) (A-C-E). \*Significant at  $p \le 0.05$  (B-D-F).

photoassimilates, mainly under high and moderate light availability, proving our initial hypothesis. In general, the improvement of morphophysiological characteristics in seedlings grown under 30 % shade correlates with the fact that *A. edulis* is an early secondary species (Leles et al., 2011). This was an adequate and non-stressful light condition in which the application of  $K_2SiO_3$  potentiated the production of the species.

The lower values of H, SD, and LA under full sun are mechanisms to reduce water loss through transpiration because of less exposure of the canopy to high temperatures due to high irradiance. Under full sun, auxin also has less preservation, limiting its production and transport to the meristematic region, resulting in short internodes (Fiorucci and Fankhauser, 2017) and leading to smaller plants. On the other hand, the lowest value under 70 % of shade indicates phenotypic plasticity under extreme light conditions. In addition, because they are in a condition of lower light incidence and low production of photosynthetic pigments, plants have little leaf area to optimize available resources.

On the other hand, chlorophyll synthesis decreases under excessive shading (represented here by 70 % of shade) in *A. edulis*, reflecting lower production of photoassimilates and consequently lower vegetative

expansion of *A. edulis* seedlings. However, the preference and responses of tree species for light gradients vary according to their successional classification. For example, seedlings of *Parkia gigantocarpa* Ducke (Lopes et al., 2015) and *Anadenanthera peregrina* (L.) Speg (Santos et al., 2020) grow taller under full sun environments because these species are heliophilous. In contrast, seedlings of *Azadirachta indica* A. Juss (Azevedo et al., 2015) and *Euterpe oleracea* Mart. (Araújo et al., 2019) respond positively to shaded environments.

The higher SD under 70 % of shade favors soil moisture, which explains its lower value in this luminous condition, possibly improving the transport of water and nutrients, contrary to observations in seedlings under 0 % and 30 % of shade. Under greater light availability, the evaporation of substrate water and leaf transpiration may be higher, requiring higher solute translocation capacity.

However, the increase in SD can be monitored as a function of height; otherwise, seedlings have an aspect of stagnation, as observed in the HDR of seedlings under 70 % of shade. Different light intensities can cause morphophysiological changes; thus, a slight reduction of light exposure can increase the leaf area (Garrett et al., 2020). This occurred for seedlings under 30 % of shade, indicating an efficient use of light. On



**Figure 5** –  $F_0$  = Initial (A),  $F_m$  = maximum (B),  $F_v$  = variable (C),  $F_v/F_m$  = chlorophyll-a fluorescence, photochemical efficiency of photosystem II (D),  $F_v/F_0$  = absorbed energy conversion efficiency (E), and  $F_0/F_m$  = maximum nonphotochemical yield (F) in leaves of *Alibertia edulis* seedlings grown with potassium silicate under different shading levels. \*Significant at  $p \le 0.05$ .

the other hand, excessive shading reduced LA due to less photosynthetically active radiation, resulting in less photoassimilates per unit area, negatively affecting seedling production, represented by the DQI.

Leaf area reduction under 0 % of shade correlates with the mechanism of mitigating water loss through transpiration (Pinto et al., 2016), reflecting the smallest number of leaves. The increase in LA with the application of  $K_2SiO_3$  correlates with the stimulation of cytokinin synthesis by  $K_2SiO_3$ , promoting cell division (Steiner et al., 2016; Markovich et al., 2017) and increasing the photosynthetic area.

Plants use mechanisms to maintain their metabolic efficiency under stress conditions, such as high irradiance. The first stimulus is the signaling of abscisic acid, which increases root length and reduces leaf area (Daszkowska-Golec, 2016). This contributes to the ecological adaptation of species, as observed in *A. edulis*. However, as turgidity increases, hormonal signaling is reduced due to the stability of water relations in the tissue (Sack et al., 2017), resulting in shorter root lengths with the application of dose close 5.0 mL  $K_2SiO_3$  doses.

Under stress conditions, such as excessive light, reactive oxygen species (ROS) like hydrogen peroxide  $(H_2O_2)$  and superoxide  $(O_2^-)$  are produced. These compounds impair several metabolic processes, affecting the chloroplast structure, promoting chlorophyll photo-oxidation (Ksas et al., 2015; Saleem et al., 2020), and reducing chlorophyll indices, especially total chlorophyll. However, under 70 % of shade, the lower incident photosynthetically active radiation reduces the stimulus to synthesize of these pigments, thus reducing



Figure 6 – RWC = Relative water content (A) and  $\Delta W_{sat}$  = water saturation deficit (B) in leaves of *Alibertia edulis* seedlings grown with potassium silicate under different shading levels. \*Significant at  $p \le 0.05$ .



Figure 7 – SLA = Specific leaf area (A), LAR = Leaf area ratio (B-C), and DQI = Dickson quality index (D) in *Alibertia edulis* seedlings produced with potassium silicate under different shading levels. Different letters differ from each other  $\pm$  SD (Tukey test;  $p \le 0.05$ ) (A-B). \*Significant at  $p \le 0.05$  (C-D).

these indices in this cultivation condition. Chlorophyll values confirm that *A. edulis* seedlings are plastic in contrasting light environments; they adjust to each growing condition. These results reinforce the ecological classification of the species in initial secondary since it had higher values under 30 % of shade.

Regarding the effect of  $K_2SiO_3$  on the pigments absorbed by the leaves,  $K_2SiO_3$  contributes to making them more erect (Ma and Yamaji, 2006), promoting better use of incident radiation and thereby triggering the increase in chlorophyll indices, as observed in *A. edulis* seedlings.

The increase in  $F_0$  under full sun conditions (0 % of shade) suggests that excessive incident light exceeded the capacity of its use in photochemical processes; that

is, the treatment exceeded the point of light saturation, leading to photoinhibition in *A. edulis*. In this condition, part of the energy excess is directed to ROS biosynthesis, such as  $H_2O_2$  and  $O_2^-$ , which can degrade lipids and proteins, such as  $D_1$  (Goh et al., 2011), damaging the photochemical apparatus and increasing the dissipation of energy. In general, although there are reference values in the literature, the values of the characteristics of chlorophyll a fluorescence and photochemical processes associated to the photosystem are variable due to several factors, such as species, genetics, plant age, and degree of ecological succession.

Thus, the greater availability of electrons, followed by their low utilization capacity in this condition, justifies the lower Fv values and higher energy values dissipated without use. In other words, maximum nonphotochemical yield  $(F_0/F_m)$  reduces the maximum photochemical efficiency of PSII  $(F_v/F_m)$  at the expense of less energy conversion  $(F_v/F_0)$  in the antenna complex and reaction centers.

Silicon in K<sub>2</sub>SiO<sub>3</sub> induces the activity of antioxidant metabolism enzymes, such as catalase and superoxide dismutase (Zanetti et al., 2016), which were not shown in this study. In addition, potassium contributes to the osmotic adjustment, turgor regulation, and cellular cytoplasmic content (Ahanger et al., 2017; Nobre et al., 2023). Nevertheless, increasing doses of K<sub>2</sub>SiO<sub>3</sub> further reduced the photochemical yield of A. edulis when grown under full sun, possibly due to the higher energy expenditure in K<sub>2</sub>SiO<sub>3</sub> absorption associated to light stress. For the plant to absorb K<sub>2</sub>SiO<sub>3</sub> a mineral element, the force generated by the electric gradient must be greater than the force by the chemical gradient to allow the proton pump H +  $ATP_{ase}$  to hydrolyze ATP and export H<sup>+</sup> to the apoplast, which requires high ATP expenditure (Fernandes et al., 2018).

Under the full sun condition, considered stressful, the seedlings present an unfavorable energy balance since expenditure is enhanced not only by the greater energy dissipation caused by photoinhibition, but also by  $K_2SiO_3$  absorption, damaging the reaction centers due to metabolic destabilization. However, this damage to the photochemical apparatus does not mean that gas exchange parameters are also negatively affected since they can be reversible (dynamic photoinhibition) (Li et al., 2020). These parameters were re-established in the biochemical phase of photosynthesis through metabolic adjustments and a compensatory effect in the production of photoassimilates.

On the other hand, the application of 10.0 mL of  $K_2SiO_3$  in seedlings under 30 % of shade led to distinct responses and improved photochemical properties of PSII, especially  $F_v/F_m$  (0.686) and  $F_v/F_0$  (3.192). This shading level improves the conditions for the seedlings of this species to take advantage of the light energy absorbed since the species prefer moderate shading (Leles et al., 2011). Moreover,  $K_2SiO_3$  enhanced the photochemical activities due to its benefits to metabolism, mainly the increase of chlorophylls, improving the integrity of the reaction centers and the photochemical yields of PSII.

In seedling cultivation under 70 % of shade, even without  $K_2SiO_3$  application, the plants have a high capacity to use available electrons  $(F_v)$ , providing high conversion efficiency of energy absorbed  $(F_v/F_0)$ , which works as a strategy to enhance photochemical processes  $(F_v/F_m)$  and keep them stable, as the seedlings are exposed to less light availability.

The increase in shading levels favors the regulation of the RWC of plants since, in shaded environments, there is usually lower substrate water evaporation and leaf transpiration due to lower temperature (Monteiro et al., 2016). This occurred for seedlings under 70 % of shade in this study. Although seedlings grown under full sun generally had lower RWC due to the opposite shading situation, applying  $K_2SiO_3$  promoted higher RWC and lower  $\Delta W_{Sat}$  under full sun for *A. edulis*. This demonstrates the beneficial effect of this application on regulating water relations by forming a double layer on the stomatal pore and osmotic adjustment (Chung et al., 2020), improving water use efficiency.

In our study, the benefits of Si in plant shoots for chlorophylls, leaf area, and RWC of *A. edulis* seedlings correlate with a reduction of the transpiration rate due to the formation of a double layer over the stomatal pore, improving water use efficiency (Ma and Yamaji, 2006; Chung et al., 2020), photochemical of photosynthesis, and plant growth. In addition, Si positively influences plant architecture, making leaves more upright, improving light interception, and stabilizing hormone and enzyme levels while regulating antioxidant metabolism (Hossain et al., 2007).

Although the seedlings showed lower photochemical yield  $(F_v/F_m)$  with increasing  $K_2SiO_3$  doses under full sun,  $K_2SiO_3$  promoted a compensatory effect on biomass production, as evaluated by the DQI. The adaptive mechanisms of *A. edulis* seedlings under 70 % of shade were proven by the increase in SLA, optimizing the use of light per unit of biomass (Liu et al., 2016; Santos et al., 2023). Under a higher shading level, the plant needs a larger photosynthetically active area to produce the same number of photoassimilates (Santos et al., 2023).

Applying  $K_2SiO_3$  optimizes the leaf area for biomass production due to its beneficial effects on the plant, such as increased chlorophyll index. *A. edulis* LAR decreased with increasing doses of  $K_2SiO_3$ , reinforcing the importance of  $K_2SiO_3$  application in the stability of leaf metabolism. The increase in the DQI of *A. edulis* seedlings is due to the better development conditions provided to the plants. This is reflective sufficient and non-stressful light conditions and the beneficial effects of Si.

Our results show that using  $K_2SiO_3$  benefits *A. edulis* seedlings under full sun, even though it is not a pioneer species. In this sense, when associated to this practice (e.g., in seedling production in a nursery), *A. edulis* has greater ecological resilience to abiotic adversities. It has the potential to be introduced in fully anthropized areas or agroforestry borders. It may be exposed to high irradiance, especially in the initial growth phase, when seedlings need high vigor to establish themselves in the acclimatization phase.

On the other hand, the production or insertion of *A. edulis* seedlings under intense shading is not indicated, regardless of using  $K_2SiO_3$ , since they show reduced growth, which may hinder initial establishment. Future studies should analyze other possible agents that mitigate environmental stress, aiming to understand better the behavior of native and fruit tree species in the face of global climate changes and anthropic actions, considering the *in situ* and *ex situ* conservation of biodiversity.

A. edulis seedlings are sensitive to extremes of light availability. Cultivation under full sun (0 % shade) or intense shading (70 %) are considered stressful conditions for this species. Using potassium silicate at a dose of 10.0 mL L<sup>-1</sup> mitigated the negative effects of light stress caused by full sun and increased the quality of seedlings under 30 % of shade. It is thus a promising alternative to produce seedlings of this species, as it favors the production of robust and high-quality seedlings.

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#### References

- Ahanger MA, Tomar NS, Tittal M, Argal S, Agarwal RM. 2017. Plant growth under water/salt stress: ROS production; antioxidants and significance of added potassium under such conditions. Physiology and Molecular Biology of Plants 23: 731-744. https:// doi.org/10.1007/s12298-017-0462-7
- Anpo M, Fukada H, Wada T. 2019. Plant Factory Using Artificial Light: Adapting to Environmental Disruption and Clues to Agricultural Innovation. Elsevier, Cambridge, MA, USA. https:// doi.org/10.1016/C2017-0-00580-3
- Aras S, Keles H, Esitken A. 2020. Silicon nutrition counteracts salt-induced damage associated with changes in biochemical responses in apple. Bragantia 79: 1-7. https://doi. org/10.1590/1678-4499.20190153
- Araújo JM, Andrade Neto RC, Oliveira JR, Lunz AMP, Almeida UO. 2019. Shading and slow release fertilizer effects on the growth characteristics of assai seedlings (*Euterpe oleracea*). Floresta e Ambiente 26: 1-10. https://doi.org/10.1590/2179-8087.001918
- Azevedo GTOS, Novaes AB, Azevedo GB, Silva HF. 2015. Development of Indian neem seedlings under different levels of shading. Floresta e Ambiente 22: 249-255. https://doi. org/10.1590/2179-8087.091414
- Campos Filho EM. eds. 2009. Plant the Xingu and Araguaia Trees: Identification Guide = Plante as Árvores do Xingu e Araguaia: Guia de Identificação. ISA, São Paulo, SP, Brazil (in Portuguese).

- Chung YS, Kim K, Hamayun M, Kim Y. 2020. Silicon confers soybean resistance to salinity stress through regulation of reactive oxygen and reactive nitrogen species. Frontiers in Plant Science 10: 1-11. https://doi.org/10.3389/fpls.2019.01725
- Conceição SS, Oliveira Neto CF, Marques EC, Barbosa AVC, Galvão JR, Oliveira TB, et al. 2019. Silicon modulates the activity of antioxidant enzymes and nitrogen compounds in sunflower plants under salt stress. Archives of Agronomy and Soil Science 65: 1237-1247. https://doi.org/10.1080/03650340.2018.1562272
- Daszkowska-Golec A. 2016. The role of abscisic acid in drought stress: how ABA helps plants to cope with drought stress. In: Hossain MA, Wani SH, Bhattacharjee S, Burritt D, Tran Lam-Son P. eds. How ABA helps plants to cope with drought stress. Springer, Geneva, Switzerland. https://doi.org/10.1007/978-3-319-32423-4\_5
- Dickson A, Leaf AL, Hosner JF. 1960. Quality appraisal of white spruce and white pine seedling stock in nurseries. Forestry Chronicle 36: 10-13. https://doi.org/10.5558/tfc36010-1
- Epstein E. eds. 1999. Silicon. Annual Review of Plant Physiology and Plant Molecular Biology 50: 641-664.
- Fernandes MS, Souza SR, Santos LA. 2018. Nutrient uptake = Absorção de nutrientes. In: Fernandes MS. ed. Plant mineral nutrition = Nutrição mineral de plantas. 2ed. Sociedade Brasileira de Ciência do Solo, Viçosa, MG, Brazil (in Portuguese).
- Fiorucci A, Fankhauser C. 2017. Plant strategies for enhancing access to sunlight. Current Biology 27: 931-940. https://doi. org/10.1016/j.cub.2017.05.085
- Gao H, Wu X, Yang X, Sun M, Liang J, Xiao Y, et al. 2022. Silicon inhibits gummosis by promoting polyamine synthesis and repressing ethylene biosynthesis in peach. Frontiers in Plant Science 28: e986688. https://doi.org/10.3389/fpls.2022.986688
- Garrett ATA, Peres FSB, Inoue MT, Garcia FAO. 2020. Adaptation of cedro-vermelha, tarumã-azeitona, ingá-doce, branquilhobravo and ocotea-guaicá seedlings to shading levels. Floresta e Ambiente 27: 1-8. https://doi.org/10.1590/2179-8087.005917
- Goh C, Ko S, Koh S, Kim Y, Bae H. 2011. Photosynthesis and environments: photoinhibition and repair mechanisms in plants. Journal Plant of Biology 55: 93-101. https://doi. org/10.1007/s12374-011-9195-2
- Hashemi A, Abdolzadeh A, Sadeghipour HR. 2010. Beneficial effects of silicon nutrition in alleviating salinity stress in hydroponically grown canola, *Brassica napus* L., plants. Soil Science and Plant Nutrition 56: 244-253. https://doi. org/10.1111/j.1747-0765.2009.00443.x
- Hossain MT, Soga K, Wakabayashi K, Kamisaka S, Fujii S, Yamamoto R, et al. 2007. Modification of chemical properties of cell walls by silicon and its role in regulation of the cell wall extensibility in oat leaves. Journal of Plant Physiology 164: 385-393. https://doi.org/10.1016/j.jplph.2006.02.003
- Hunt R. 2017. Growth analysis, individual plants. Encyclopedia of Applied Plant Sciences 1: 421-429. https://doi.org/10.1016/ B978-0-12-394807-6.00226-4
- Ksas B, Becuwe N, Chevalier A, Havaux M. 2015. Plant tolerance to excess light energy and photooxidative damage relies on plastoquinone biosynthesis. Science Reports 5: 1-16. https:// doi.org/10.1038/srep10919
- Larcher W. eds. 2004. Plant Ecophysiology = Ecofisiologia Vegetal. RiMa, São Carlos, SP, Brazil (in Portuguese).

- Leles PSS, Abaurre GW, Alonso JM, Nascimento DF, Lisboa AC. 2011. Growth of tree species in different planting spacing for forest recovery. Scientia Forestalis 39: 231-239 (in Portuguese, with abstract in English).
- Li YT, Li Y, Li YN, Liang Y, Sun Q, Li G, et al. 2020. Dynamic light caused less photosynthetic suppression, rather than more, under nitrogen deficit conditions than under sufficient nitrogen supply conditions in soybean. BMC Plant Biology 20: e339. https://doi.org/10.1186/s12870-020-02516-y
- Lima GS, Soares MGS, Soares LAA, Gheyi HR, Pinheiro FWA, Silva JB. 2021. Potassium and irrigation water salinity on the formation of sour passion fruit seedlings. Revista Brasileira de Engenharia Agrícola e Ambiental 25: 393-401. https://dx.doi. org/10.1590/1807-1929/agriambi.v25n6p393-401
- Liu Y, Dawson W, Prati D, Haeuser E, Feng Y, van Kleunen M. 2016. Does greater specific leaf area plasticity help plants to maintain a high performance when shaded? Annals of Botany 118: 1329-1336. https://doi.org/10.1093/aob/mcw180
- Lopes MJS, Dias-Filho MB, Menezes Neto MA, Santos JUM, Cruz ED, Dias HSS. 2015. Morphological and physiological responses to shade in seedlings of *Parkia gigantocarpa* Ducke and *Schizolobium parahyba* var. *amazonicum* (Huber ex Ducke) Barneby (Leguminosae). Scientia Forestalis 43: 573-580.
- Ma JF, Yamaji N. 2006. Silicon uptake and accumulation in higher plants. Trends in Plant Science 11: 392-397. https://doi. org/10.1016/j.tplants.2006.06.007
- Markovich O, Steiner E, Kouřil Š, Tarkowski P, Aharoni A, Elbaum R. 2017. Silicon promotes cytokinin biosynthesis and delays senescence in Arabidopsis and Sorghum. Plant, Cell & Environment 40: 1189-1196. https://doi.org/10.1111/pce.12913
- Mendes KR, Marenco RA, Nascimento HCS. 2017. Maximum carboxylation velocity of rubisco and maximum rate of electron transport in sapling in response to variations in environmental factors in central Amazonia. Ciência Florestal 27: 947-949. https://doi.org/10.5902/1980509828666
- Monteiro EB, Silva AC, Souza AP, Tanaka AA, Ferneda BG, Martim CC. 2016. Water requirements and crop coefficients of tropical forest seedlings in different shading conditions. Revista Brasileira de Engenharia Agrícola e Ambiental 20: 709-715. https://doi.org/10.1590/1807-1929/agriambi.v20n8p709-715
- Nobre RG, Filho RAR, Lima GS, Linhares ELR, Soares LAA, Silva LA, et al. 2023. Gas exchange and photochemical efficiency of guava under saline water irrigation and nitrogen-potassium fertilization. Revista Brasileira de Engenharia Agrícola e Ambiental 27: 429-437. https://dx.doi.org/10.1590/1807-1929/ agriambi.v27n5p429-437
- Petrova N, Paunov M, Stoichev S, Todinova S, Taneva SG, Goltsev V, et al. 2020. Thylakoid membrane reorganization, induced by growth light intensity, affects the plants susceptibility to drought stress. Photosynthetica 58: 369-378. https://doi.org/10.32615/ps.2019.165

- Pinto JRS, Dombroski JLD, Santos Junior JH, Souza GO, Freitas RMO. 2016. Growth of *Mimosa caesalpiniifolia* Benth., under shade in the northeast semi-arid region of Brazil. Revista Caatinga 29: 384-392. https://doi.org/10.1590/1983-21252016v29n215rc
- Rohácek K. 2002. Chlorophyll fluorescence parameters: the definitions, photosynthetic meaning, and mutual relationships. Photosynthetica 40: 13-29. https://doi. org/10.1023/A:1020125719386
- Sack L, John GP, Buckley TN. 2017. ABA accumulation in dehydrating leaves is associated with decline in cell volume not turgor pressure. Plant Physiology 176: 489-493. https://doi. org/10.1104/pp.17.01097
- Saleem MH, Rehman M, Fahad S, Tung SA, Iqbal N, Hassan A, et al. 2020. Leaf gas exchange, oxidative stress, and physiological attributes of rapeseed (*Brassica napus* L.) grown under different light-emitting diodes. Photosynthetica 58: 836-845. https://doi. org/10.32615/ps.2020.010
- Santos CC, Jorge HPG, Dias LGF, Vieira MC. 2020. Shading levels and substrates affect morphophysiological responses and quality of *Anadenanthera peregrina* (L.) Speg seedlings. Floresta e Ambiente 27: 1-9. https://doi.org/10.1590/2179-8087.011919
- Santos CC, Goelzer A, Silva OB, Santos FHM, Silverio JM, Scalon SPQ, et al. 2023. Morphophysiology and quality of *Alibertia edulis* seedlings grown under light contrast and organic residue. Revista Brasileira de Engenharia Agrícola e Ambiental 27: 375-382. https://doi.org/10.1590/1807-1929/agriambi. v27n5p375-382
- Silva FC. eds. 2009. Manual of Chemical Analysis of Soil, Plants and Fertilizers = Manual de Análises Químicas do Solo, Plantas e Fertilizantes. 2ed. Embrapa Informação Tecnológica, Brasília, DF, Brazil (in Portuguese).
- Steiner E, Livne S, Kobinson-Katz T, Tal L, Pri-Tal O, Mosquna A, et al. 2016. The putative O-linked N-acetylglucosamine Transferase spindly inhibits class I TCP proteolysis to promote sensitivity to cytokinin. Plant Physiology 171: 1485-1494. https://doi.org/10.1104/pp.16.00343
- Turner NC. 1981. Techniques and experimental approaches for the measurement of plant water status. Plant and Soil 58: 339-366. https://doi.org/10.1007/BF02180062
- Zanetti LV, Milanez CRD, Gama VN, Aguilar MAG, Souza CAS, Campostrini E, et al. 2016. Leaf application of silicon in young cacao plants subjected to water deficit. Pesquisa Agropecuária Brasileira 51: 215-223. https://doi.org/10.1590/ S0100-204X2016000300003