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Photosynthesis and growth of the sweet sorghum supplemented with silicon

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***Abstract*— Silicon is a major element in plants, being essential for some species and beneficial for others, with important role in plant metabolism. Several families of monocotyledons have the ability to absorb high amounts of this compound, being considered silicon accumulators. This is the case of sweet sorghum (Sorghum bicolor L. Moench), a plant with C_4 carbon metabolism, with high photosynthetic activity, and great potential for ethanol production; its residual biomass can also be used for energy cogeneration in sugarcane production systems. The aim of this work was to evaluate the effect of silicon, in the form of sodium metasilicate, on sweet sorghum plants cultivated under hydroponic conditions and without stress of biotic or abiotic origin. There is a linear increase in silicon content in leaves, stalks and roots as a function of increasing doses of this element in the substrate. Silicon supplementation in sweet sorghum increases photosynthesis rates, water use efficiency and leaf biomass. The best dose of silicon for maximum photosynthetic efficiency is 70 mg L^{-1} of Si in the nutrient solution.*

I. INTRODUCTION

Silicon (Si) plays an important role in plant-environment relations, as it can promote better ability of plants to withstand climatic, edaphic and biological adversities, with the possibility of increase in both production quality and quantity. The use of Si in agriculture becomes particularly interesting as it is considered a natural antistress agent. Silicate fertilizers can enhances plant resistance to abiotic stresses, including extreme temperatures, salinity, drought, heavy metal toxicity, nutritional imbalance. Silicon fertilization can also increase resistance to various fungal diseases as well as some pests. Some mechanisms of Si that can alleviate biotic and abiotic stresses in plants include: regulation of the activities of antioxidant enzymes; polyamines and phytohormones, as well as lignin biosynthesis; maintenance of plant water balance; increase in mineral nutrient uptake and assimilation; structural alterations; formation of physical and chemical barriers and improvement of the gas exchange attributes (Haynes, 2017; Luyckx et al., 2017; Etesani; Jeong, 2018).

Ethanol production from sugarcane places Brazil as a world reference in the use of bioenergy. In the off season of sugarcane, there is reduced availability of ethanol, with price increases and risk of shortage. The growing demand for alcohol as fuel has driven the search for alternatives to increase agricultural production of distilleries and industrial yields, reducing production costs and increasing viability of these production plants. An alternative is the use of sweet sorghum (*Sorghum bicolor* L. Moench), either in the off season or as a complement to sugarcane availability. This plant has technical and economic potential for ethanol and residual biomass production for energy cogeneration, considering pilot plantations data collected since the 1980’s and the available agricultural and industrial technology (Durães, 2011; Durães et al., 2012).

Sorghum is a crop able to achieve high photosynthetic rates, with potential to respond to Si fertilization (Meena et al., 2014). Application of 200 ml L^{-1} of potassium silicate in pots with soil, increased water leaf potential, leaf area index, net assimilation and relative growth rates, and chlorophyll content (SPAD index), compared to a treatment with the same K (potassium chloride) level, under both normal and water stress conditions (Ahmed et al., 2011, 2014). Studies with sorghum show increased content of this element in its tissues and a positive response to growth and resistance to some stresses of biotic and abiotic origin - drought and salt tolerance (Yin et al., 2014; 2016) and heavy metal mitigation as Al (Bath et al., 2019), for example.

Although many annual crops potentially respond to silicate fertilization, especially in silicon poor soils, few studies have been done with sorghum, notably sweet sorghum. Thus, the aim of this work was to assess the effect of increasing doses of sodium silicate under hydroponic conditions on the production of sweet sorghum dry mass and photosynthesis rates.

II. MATERIAL AND METHODS

The experiment was carried out in a greenhouse at Embrapa Agropecuária Oeste, in Dourados, Mato Grosso do Sul, Brazil, in 2017. Sorghum plants, variety BRS 511, were submitted to increasing levels of Si in Johnson's nutrient solution, modified (Epstein; Bloom, 2006), with pH adjusted to 6.0. The experiment was installed in completely randomized design with five treatments – (1) 0 mg L^{-1}; (2) 10 mg L^{-1}; (3) 25 mg L^{-1}; (4) 50 mg L^{-1} and (5) 100 mg L^{-1} (equivalent to 0, 0.36, 0.89, 1.78 and 3.60 mmol) of Si in the form of sodium metasilicate (PA), with five replications, totaling 25 experimental units (one plant per pot of four liters of nutrient solution).

At stage V13, prior to booting (period from elongation start to beginning of flag leaf blade opening), physiological parameters were measured with an infrared gas analyzer (IRGA) – Lcpro-SD (ADC Bioscientific, Hoddesdon, England) in the middle of the leaf blade of the third leaf with visible auricle from the apex. We set up the IRGA to work with environmental conditions throughout the analysis: CO_2 concentration = environment (~378 ppm); air relative humidity = follow environment (65 - 78%); temperature = follow environment (28 – 33 ºC); light intensity = environment (~1100 – 1200 µmol m^{-2} s^{-1}); reading stabilization timing = 135 s.

Readings were taken in the beginning of the morning, between 07:30 hs and 09:30 hs. Although the experiment was conducted in completely randomized design, we used blocks for the IRGA assessments aiming to compensate the day progress (systematic increase in light level and temperature) on readings, as this is a known cause of error. For this, we assessed the blocks in order (B1 - B5). Into each block, treatments were ordered as follows: for blocks 1 and 3, treatments were orderly assessed (T1 - T5); blocks 2 and 4 were assessed on opposite order of treatments (T5 - T1), while block 5 was assessed randomly.

The measured or calculated variables were: photosynthetic rate (A) - assesses the incorporation rate of carbon (C) in biomass, in mol m^{-2} s^{-1}; transpiration rate (E) - measures the loss of water through the stomata in mol H_2O m^{-2} s^{-1}; stomatal conductance (Gs) - the flow through the stomata, in mol m^{-1} s^{-1}; gradient of CO_2 (ΔC) - carbon dioxide gradient between the outer and the inner parts of the leaf, in µmol mol^{-1}; internal concentration of CO_2 (Ci) - carbon dioxide content within the mesophyll available for photosynthesis, in µmol mol^{-1}; water use efficiency (WUE) - the relationship between plant CO_2 assimilation and water loss in the same time interval, in µmol CO_2 mol^{-1} H_2O.

After IRGA measurements, plants were collected by separating leaves, stalks and roots, and prepared for dry mass measurement after drying in air-circulating over at 65 ºC for three days. Silicon contents in plant tissues were performed according to Korndörfer et al. (2004). The data was submitted to regression analysis (Ferreira, 2014) and presented in comprehensive graphs, with treatment significance and regression adjustment coefficients.

III. RESULTS AND DISCUSSION

The supplementation of Si to sorghum plants provided increased leaf dry mass of about 17% when 100 mg L^{-1} of Si was supplied. On the other hand, there was no variation in shoot or total biomass (shoot + roots), as there was a tendency of reduction in stalk mass, although not statistically significant (Figure 1). There was increase in sweet sorghum leaf: stalk mass ratio, due to the increased leaf dry mass reported. This represents an increase in the photosynthetic apparatus not translated to increased yield ability, since there was no significant variation in stalk mass.

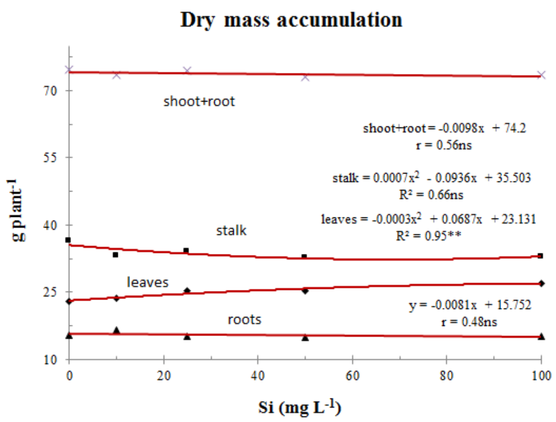

Fig. 1. Dry mass accumulation in sweet sorghum plants at stage V13, submitted to increasing levels of Si in nutrient solution.

Higher leaf production with silicate supplementation may be related to higher specific leaf weight or leaf area index (Ahmed et al., 2011). Ahmed e Aslam (2011) reported increase in foliar biomass with or without induction of water stress in sorghum. As occurred in our experiment, there was a higher mass ratio between leaves and stem, obtained with addition of the Si to the substrate (Figure 2). The increase in leaf biomass in this study may be related to the fact that Si increases the cytokinin biosynthesis in sorghum, as demonstrated by Markovich et al. (2017). Studies show that the cytokinin produced in the roots promotes leaf growth (Salisbury; Ross, 2012).

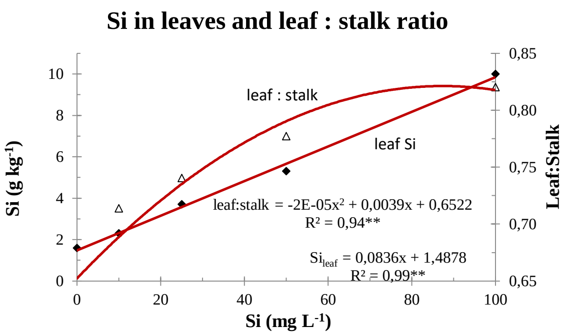

Fig. 2. Leaf : stalk ratio and Si content in leaves of sweet sorghum plants at stage V13, submitted to increasing levels of Si in nutrient solution.

The stomatal conductance (Gs) was not impacted by Si supplementation to plants. It is controlled by a series of internal and external factors, with water availability being one of the main ones. Under hydroponic cultivation and similar environment for all treatments, stomatal conductance remained with little variation as a function of Si level in the substrate and plant.

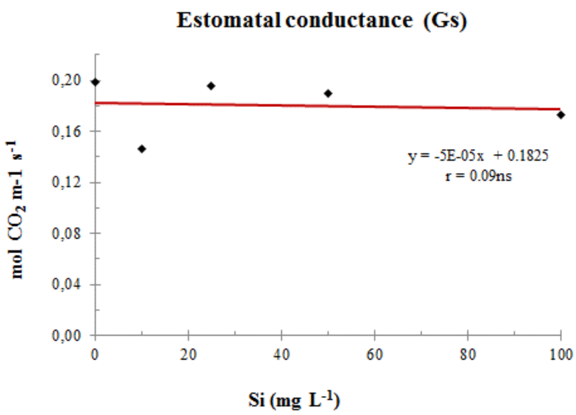

Fig. 3. Stomatal conductance (Gs) in sweet sorghum plants at stage V13, under increasing levels of Si in nutrient solution.

On the other hand, Si supplementation increased the CO_2 gradient (ΔC) between the outer and the inner leaf environments, as consequence of the stomatal resistance to gas diffusion (Figure 4). The higher absorption and incorporation of carbon in the sorghum biomass is corroborated by the drop in the internal CO_2 concentration (Ci) as stomatal conductance (Gs) was not altered (Figure 5).

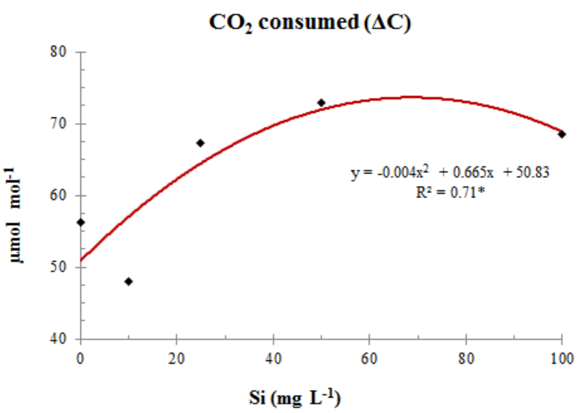

Fig. 4. CO_2 gradient (ΔC) between the outer and the inner leaf environments in sweet sorghum plants at stage V13, under increasing levels of Si in nutrient solution.

This higher incorporation of C in plant biomass promoted by Si is a function of the increased photosynthesis rates (A) with its application (Figure 6). As there was little variation in transpiration (E) with increasing doses of Si on the substrate (Figure 7), water use efficiency (WUE) was increased (Figure 8). This means that the proportion of CO_2 incorporated into the biomass was greater than the amount of water lost over the same time period. Silicon helped improving plant water status by probably allowing shorter periods of stomatal opening, due to a higher ΔC.

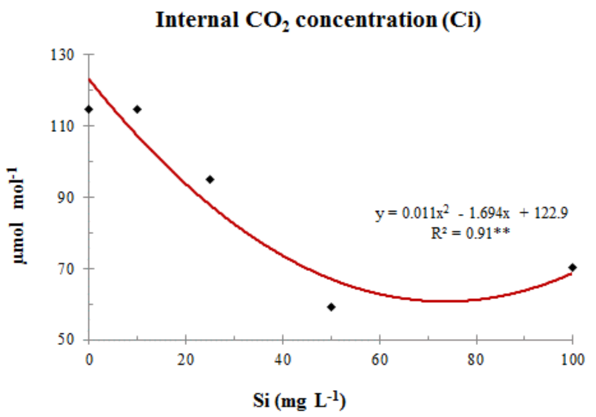

Fig. 5. Internal CO_2 concentration (Ci) in sweet sorghum plants at stage V13, under increasing levels of Si in nutrient solution.

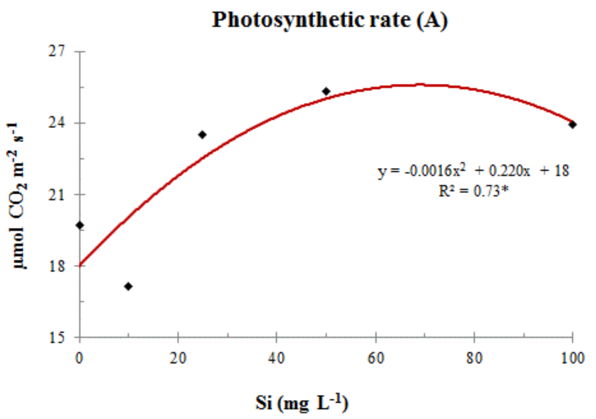

Fig. 6. Photosynthetic rate (A) in sweet sorghum plants at stage V13, under increasing levels of Si in nutrient solution.

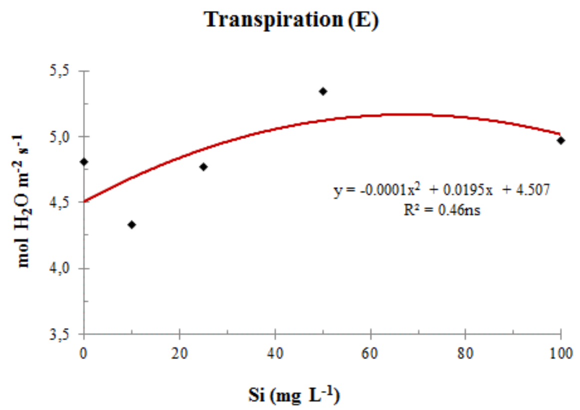

Fig. 7. Transpiration (E) in sweet sorghum plants at stage V13, under increasing levels of Si in nutrient solution.

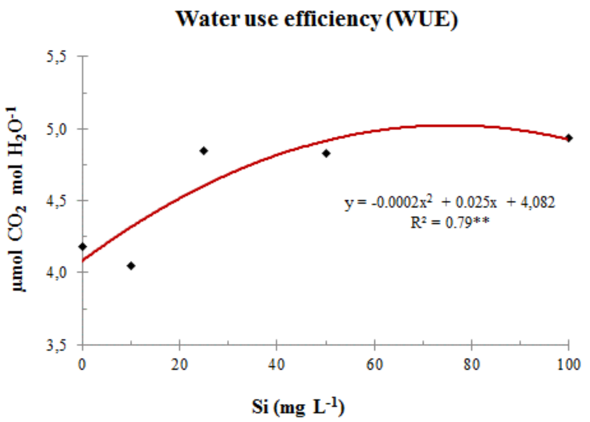

Fig. 8. Water use efficiency (WUE) in sweet sorghum plants at stage V13, under increasing levels of Si in nutrient solution.

The photosynthetic rate depends on the carbon gradient and the rate of CO_2 influx to leaf mesophyll. Taking into account the curves adjusted to the physiological parameters, it seems that the maximum values for CO_2 gradient (ΔC) and water use efficiency (WUE) would be obtained with 83 and 63 mg L^{-1} of Si in nutrient solution, respectively, with an average of 73 mg L^{-1} Si (Figure 4 and Figure 8). This concentration is close to that obtained for the photosynthetic rate, which was 69 mg L^{-1} Si (Figure 6).

Thus, it can be stated that the best dose of Si in the nutrient solution for maximum photosynthetic efficiency is approximately 70 mg L^{-1} Si in solution or a Si foliar content of 7.3 g kg^{-1} (Figure 2). In this case, the maximum photosynthetic rate was 25.6 µmol CO_2 m^2 s^{-1} or 40.5 mg CO_2 dm^2 h^{-1}. Photosynthetic rates vary widely among species, with sorghum being one of those with the highest values, reaching rates between 50 and 60 mg CO_2 dm^2 h^{-1}, depending on environmental and cultivation conditions (Fageria et al., 1997).

Other authors evaluated in some crops, such as rice, the effects of Si on photosynthesis-related parameters, where research shows significant increases in photosynthesis (Gong, 2011; Li et al., 2011). However, sorghum-related studies are scarce. Resende et al. (2014) investigated the effect of Si on anthracnose (*Colletotrichum sublineolum*) infected sorghum plants, reporting that the photosynthetic performance (A, Gs and E) was significantly higher in Si supplied plants. Ali et al. (2013) postulate that the benefits of Si in photosynthetic parameters may be linked to both indirect effects, such as increased disease resistance, and direct effects, in this case linked to improved plant nutritional balance.

In plants subject to water stress, for example, the effect of Si on maintenance of photosynthetic rates is much greater, probably due, at least in part, to the decrease in transpiration rates (Ma; Takahashi, 2002). In sorghum with irrigated or non-irrigated treatment, Si significantly increased leaf water potencial and photosynthesis (Ahmed et al., 2011). Avila et al. (2020) studied the effects of Si in plants of sorghum with two different soil water levels. The silicate treatments increased leaf water potential in plants grown at field capacity and under water deficiency. In the same way, plants grown at field capacity with Si supplementation, showed higher chlorophyll content, photosynthesis and instantaneous carboxylation efficiency. As in our research, stomatal conductance and transpiration were not influenced by Si under ideal conditions of moisture in the substrate. On the other hand, under water deficiency, Si treatments increased these parameters. This higher tolerance of sorghum to water stress can be due to an active osmotic adjustment in roots, triggered by Si supplementation (Sonobe et al., 2011).

Although most studies show the effect of silicon on plants under stress, researches show the direct impact of Si extends to more fundamental metabolic processes. Several genes non-related to stress, associated with primary metabolic processes or unknown functions, are activated or affected by fertilization with Si, as demonstrated for example, by Fauteux et al. (2005), Brunings et al. (2009), Chain et al. (2009), Fleck et al. (2011), Van Bockhaven et al. (2015), and Markovich et al. (2017). These genes are associated with glycolysis, cell wall biosynthesis, amino acid and ethylene metabolism, cytokinin pathway, defence hormones like jasmonic and salicylic acids, among others. As our study, Detmann et al.(2012) obtained an increase in the photosynthetic efficiency on unstressed rice plants. The authors, analysing photosynthetic gas exchange parameters alongside transcriptomic and metabolomic profiling, concluded that Si stimulated the amino acid remobilization by alteration of primary metabolism.

There was no effect on total dry mass accumulation in the vegetative phase, but significant intensification of photosynthetic activity coupled to increased leaf dry mass. Thus, it is possible to suggest the role of Si in stimulating the translocation of photoassimilates from sources (leaves) to sink (panicles), according to the results obtained. As example, Takahashi et al. (1966) and Detmann et al. (2012) report in rice an increase in grain yield. This is related to the fact that Si increases photoassimilation of carbon, subsequently allowing greater carbon remobilization to the seeds (Meena et al., 2014).

IV. CONCLUSION

The silicon supplementation in sweet sorghum increased its content in leaves, stalk and roots, but elevated the dry mass only in leaves. Likewise, there was an increase in photosynthesis, which is related to an increase in the CO_2, consumed due to higher incorporation rate of carbon in biomass and in the water use efficiency. The evidence of the results obtained in this research, suggests a possible role of Si in stimulating the translocation to the grains of soluble organic compounds, synthesized during photosynthesis.

Therefore, it is suggested to focus future researches on the subject, to verify the effect of Si, without stressful conditions, on grain production in sorghum.

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