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ORIGINAL PAPER

Silicon Mitigates Manganese Deficiency Stress by Regulating the Physiology and Activity of Antioxidant Enzymes in Sorghum Plants

Raimundo Leonardo Lima de Oliveira[1] · Renato de Mello Prado[2] · Guilherme Felisberto[1] · Mirela Vantini Checchio[1] · Priscila Lupino Gratão[2]

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Abstract
Silicon (Si) may mitigate different nutritional stresses in cultivated plants associated with a higher activity of enzymatic compounds, which act in the reduction of oxidative stress. Thus, this study aimed to evaluate the effects of Si supplied via root (nutrient solution) and leaf spraying to mitigate manganese (Mn) deficiency, considering the biochemical and physiological aspects of grain sorghum plants. The experiments were carried out in a greenhouse under a hydroponic system. Initially, a test was performed to evaluate the source and concentration of Si for leaf spraying of sorghum plants. Subsequently, the study was carried out with the following treatments: without Si, Si via leaf spraying, and Si via root on the omission and presence of Mn. Stabilized sodium and potassium silicate (SiNaKE) was applied in three leaf sprayings (1.0 g L^{-1} Si) and in the nutrient solution (2.0 mmol L^{-1} Si). Mn-deficient plants without Si presented higher concentrations of hydrogen peroxide (H_2O_2), malondialdehyde (MDA), and lower activity of superoxide dismutase (SOD), with reflections on the decrease of photosynthesis, leaf area, and shoot dry matter. Silicon mitigated the effects of stress due to Mn deficiency in sorghum plants, and the application via root of the beneficial element was more effective than leaf spraying. This benefit of Si was evidenced by the higher activity of superoxide dismutase, reducing oxidative stress, with reflections on photosynthesis, leaf area, manganese use efficiency, and dry matter production of plants.

Keywords Beneficial element · Nutritional stress · Si sources · *Sorghum bicolor* L

1 Introduction

Studies indicate that silicon (Si) has potentiated benefits on growth, dry matter, and photosynthesis of sorghum plants (Chen et al. 2016; Flores et al. 2018; Yin et al. 2013, 2016) and in other accumulating species, even in the absence or presence of stress (Camargo et al. 2017; Kleiber et al. 2015; Mahdieh et al. 2015; Moradtalab et al. 2018; Soratto et al. 2012). Si can reduce the effects of nutritional stresses, such as the deficiency of manganese and iron indicated in cucumber (Bityutskii et al. 2014; Pavlovic et al. 2016), potassium in sorghum (Chen et al. 2016), and phosphorus in wheat plants (Kostic et al. 2017).

Manganese (Mn) deficiency is common in alkaline soils in several regions of the world causing damage to various grains, including sorghum production (George et al. 2014; Hernandez-Apaolaza 2014). This occurs because Mn deficiency can often manifest latently without the presence of visual symptoms (Schmidt et al. 2013). In plants, Mn deficiency causes physiological disturbances due to the oxidative stress by an increase of reactive oxygen species (ROS), characterized by the increased hydrogen peroxide (H_2O_2) concentration, forming malondialdehyde (MDA) (Zhao et al. 2014), with consequences on the reduction of chlorophyll content, reduction of leaf area and photosynthetic activity, lower root growth, and reduction of dry matter of plants (Moradtalab et al. 2018; Saidi et al. 2012).

The use of Si is an option to mitigate the effects of Mn deficiency because it is a beneficial element that can reduce the nutritional stress, especially in Si-accumulating plants such as sorghum (Chen et al. 2016; Yin et al. 2013). Si is

✉ Raimundo Leonardo Lima de Oliveira
raimundoleonardo22@gmail.com

1 São Paulo State University (Unesp), Jaboticabal 14884-900, Brazil

2 State University of São Paulo (Unesp), Jaboticabal 14884-900, Brazil

absorbed as monosilicic acid (H_4SiO_4) by roots when supplied via nutrient solution, being the concentration of 2.0 mmol L^{-1} widely used as it is considered adequate for plant cultivation and without risk of polymerization of the element (Barreto et al. 2016, 2017; Song et al. 2011).

Another form of Si supply, which has grown in agriculture, would be the supply via leaf spraying. However, there are no indications about the concentration and the most adequate Si source to be used in sorghum, which is cause for concern. It is expected that the beneficial effects of Si on plants will be more evident in the plants that accumulate more Si, provided constantly via nutrient solution when compared with leaf spraying, which is provided at most in three periods or applications during the vegetative development of crops (Crusciol et al. 2013; Flores et al. 2018; Soratto et al. 2012).

Therefore, Si supply in plants under stress induces the defense system, increasing the activity of antioxidant enzymes, such as ascorbate peroxidase (APX) and superoxide dismutase (SOD), which acts in the reduction and production of ROS, such as the thermal stress in corn (Moradtalab et al. 2018) and saline stress in sorghum (Kafi et al. 2011), avoiding chlorophyll degradation (Ahmed et al. 2011; Gonzalo et al. 2013; Wang et al. 2012) and favoring the photosynthesis and dry matter of plants (Camargo et al. 2017; Moradtalab et al. 2018). Considering the improvement in the physiological aspects, Si supply can also promote higher root growth and contribute to improve the nutritional status of Mn-deficient plants, as well as increase the efficiency of micronutrient use and favor shoot biomass production (Hattori et al. 2003; Moradtalab et al. 2018).

In Mn-deficient plants, Si supply can promote Mn remobilization, which would be bound to the apoplast and cell walls of roots, increasing the nutrient distribution in the plant, reducing oxidative stress, and mitigating the symptoms of nutritional deficiency (Bityutskii et al. 2014; Hattori et al. 2003; Moradtalab et al. 2018; Pavlovic et al. 2013). However, the beneficial effect of Si under different forms of supply on the enzymatic activity of Mn-deficient sorghum plants and the benefits that it may provide for plant physiology are unknown.

To increase the knowledge on this subject, it is pertinent to evaluate the hypothesis that Si application, especially via nutrient solution in relation to leaf spraying in sorghum plants, would be effective in mitigating Mn deficiency by regulating the enzyme activity of the antioxidant system, improving plant physiology. To meet this hypothesis, this study aimed to evaluate the effects of Si supplied via root (nutrient solution) and leaf spraying to mitigate Mn deficiency, considering the biochemical and physiological aspects of grain sorghum plants.

2 Material and Methods

A preliminary experiment was initially conducted to study the best concentration of Si and the foliar application source for the element on sorghum plants. In this study, the treatments consisted of a 4 × 4 factorial, in random blocks with three replications. Four Si sources were used: stabilized sodium and potassium silicate (114.91 g L^{-1} of Si, 18.9 g L^{-1} of K_2O, and pH value of 11); nano-silicon Bindzil® 15/750 AkzoNobel® (77.12 g L^{-1} of Si, 750 m^2 g^{-1} of specific area, 1.1 g L^{-1} of density, pH value of 10.5, and 4.0 nm of average particle size); stabilized silicic acid (14.04 g L^{-1} of Si and pH value of 2); and potassium silicate Diatom® (128.00 g L^{-1} of Si, 126 g L^{-1} of K_2O, and pH value of 11); at four concentrations: 0, 0.5, 1.0, and 1.5 g L^{-1} of Si.

The four foliar applications of Si were conducted at three phenological stages of development of the sorghum plant, V_4 and V_8 (four and eight leaves completely expanded respectively) and R_1 (onset of flowering). On the second experiment, the treatments consisted of a 3 × 2 factorial, with the following treatments: no Si, foliar Si, and radicular Si in the presence of Mn at a concentration of 12.6 μMol L^{-1} and in the absence of Mn, on the nutrition solution, with three replications. For the treatments that received Si application, stabilized sodium and potassium silicate were used (SiNaKE) (113.40 g L^{-1} of Si, 18.9 g L^{-1} of K_2O, and pH value of 11), at a concentration of 1.0 g L^{-1}, through foliar application, at three stages of development of sorghum plants, V_5 and V_9 (with five and nine leaves completely expanded, respectively), and the last application was made on the onset of flowering (R_1).

For the radicular treatment, Si was supplied at a concentration of 2.0 mmol L^{-1} during the entire experiment. On both experiments, grain sorghum from cultivar Dekalb 540 was grown in 7.0-dm^3 vases filled with vermiculite, with three plants per vase. The nutrition solution used was Hoagland and Arnon (1950), with the iron source changed from Fe-EDTA to Fe-EDDHMA.

2.1 Grain Production

On the first experiment, when the panicles were at harvest point, the panicle of sorghum plants was collected in order to determine the grain production by the vase, correcting the water content to 130 g kg^{-1} (Brasil 2009).

2.2 Leaf Area

The leaf area was determined to measure the length and the maximal width of the foliar limb of all leaves, with the help of a millimetric ruler and an adjustment factor. For the sorghum culture, the factor used was 0.75, as described by Stickler et al. (1961).

2.3 Si Accumulation, Mn, and Mn Use Efficiency

The shoot of the plants (culm and leaves) was collected and washed with a detergent solution and deionized water,

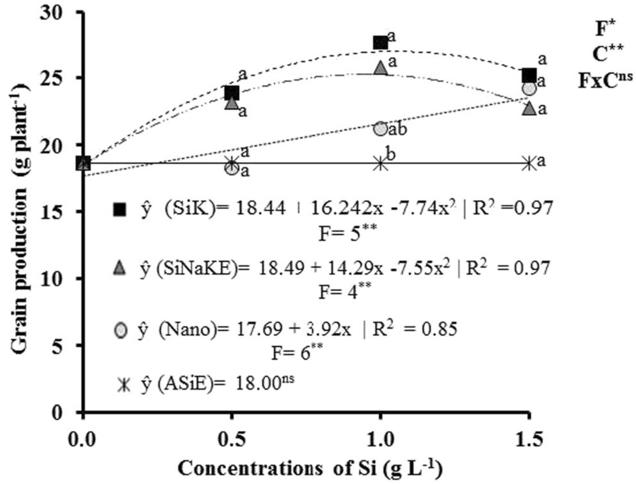

Fig. 1 Sorghum grain production plants exposed to alternative sources (Nano, nano-silicon; ASIE, stabilized silicic acid; SiNaKE, sodium silicate and potassium stabilized; and SiK, potassium silicate) and leaf Si concentrations. Double asterisks and single asterisk are significant at 1 and 5% probability and ns means not significant; different letters in the same concentration differ from each other, by the Tukey test at 5% probability

then, the samples were placed in paper bags and dried in a forced air circulation greenhouse at 65 ± 2 °C until a constant mass was reached, to determine the dry mass of the shoot. The shoot of the sorghum plants was ground on a Wiley mill for chemical analysis, determining the Si content according to the methodology described by Korndorfer et al. (2004).

The Si accumulation was calculated, as a result of the dry mass product and the element content, expressed in mg by the plant. The Mn content was also determined, according to the methodology described by Bataglia et al. (1983). Then, the Mn accumulation was determined, as a result of the dry mass product and the element content. The Mn use efficiency was obtained, from the total dry matter^2 produced by the plant, divided by the total content of the nutrient on the plant, according to Siddiqi and Glass (1981).

2.4 Photosynthesis Rate

The photosynthesis (Pn) physiological variable was evaluated on the fourth leaf developed at flowering, measured with an IRGA apparatus (infrared gas analyzer, model LI-6400XT, LI-COR®, Lincoln, NE, USA). The gas exchanges were measured in the presence of natural light inside the greenhouse.

2.5 Determining the Lipid Peroxidation and Hydrogen Peroxide Concentration

The lipid peroxidation was determined by the estimation of the content of thiobarbituric acid reactive substances (TBARS), as described by Heath and Packer (1968). Two hundred milligrams of plant tissue was measured and ground with polyvinylpolypyrrolidone at 20% (PVPP) and 0.1% of trichloroacetic acid (TCA). After centrifuging at 11,000×*g* for 15 min, the supernatant was added to a solution of 20% of TCA and 0.5% of trichloroacetic acid (TBA) and incubated a bain-marie at 95 °C, for 30 min. After being removed from the dry bath, the material was placed on ice for 10 min and then centrifuged for 5 min, at 11,000×*g*. The malondialdehyde (MDA) concentration was determined on a spectrophotometer with wavelength of 535 and 600 nm. The data were calculated using an extinction coefficient of 1.55×10^{-5} mol^{-1} cm^{-1} (Gratão et al. 2012). The MDA results were expressed in nMol g^{-1} of fresh matter.

The H_2O_2 content was estimated following the method suggested by Alexieva et al. (2001). Two hundred milligrams of plant tissue was weighted, homogenized in trichloroacetic acid (TCA) at 0.1%, and centrifuged at 11.000×*g* for 15 min. The supernatant was added to the potassium phosphate buffer 100 mM (pH 7.50) and the potassium iodide solution 1.0 M. Then, the material was incubated on ice for 1 h, the absorbance read at 390 nm, and the H_2O_2 content was determined using an H_2O_2 concentration curve known as the standard curve. The H_2O_2 results were expressed in μMol g^{-1} of fresh matter.

2.6 Determining the Ascorbate Peroxidase Activity and Superoxide Dismutase

The ascorbate peroxidase (APX) activity was also determined, and it was measured in a spectrophotometer, in a reaction containing potassium phosphate buffer 50 mM (pH 7.0), ascorbate 0.5 mM, EDTA 0.1 mM, and H_2O_2 0.1 mM (Gratão et al. 2012). The APX activity was determined by monitoring the ascorbate oxidation rate at 290 at 30 nm. The APX activity was expressed in nMol of ascorbate min^{-1} mg^{-1} of protein.

Determined according to Giannopolitis and Ries (1977), using a spectrophotometer, the enzyme activity was measured through its ability to inhibit the photochemical reduction of nitro blue tetrazolium chloride (NBT), performed in a reaction chamber (box), lighted by a fluorescent lamp of 15 W, at 25 °C. The reaction solution was constituted by 50 mM of potassium phosphate buffer (pH 7.8), 50 mM of methionine, 1.0 mM of NBT, 10 mM of EDTA, 0.1 mM of riboflavin, and 50 μL of the extracted and unfrozen sample. Then, the solution was added to glass tubes and placed inside the box for 5 min. The measurement was taken using a spectrophotometer at 560 nm, and the results, expressed in U SOD mg^{-1} of protein.

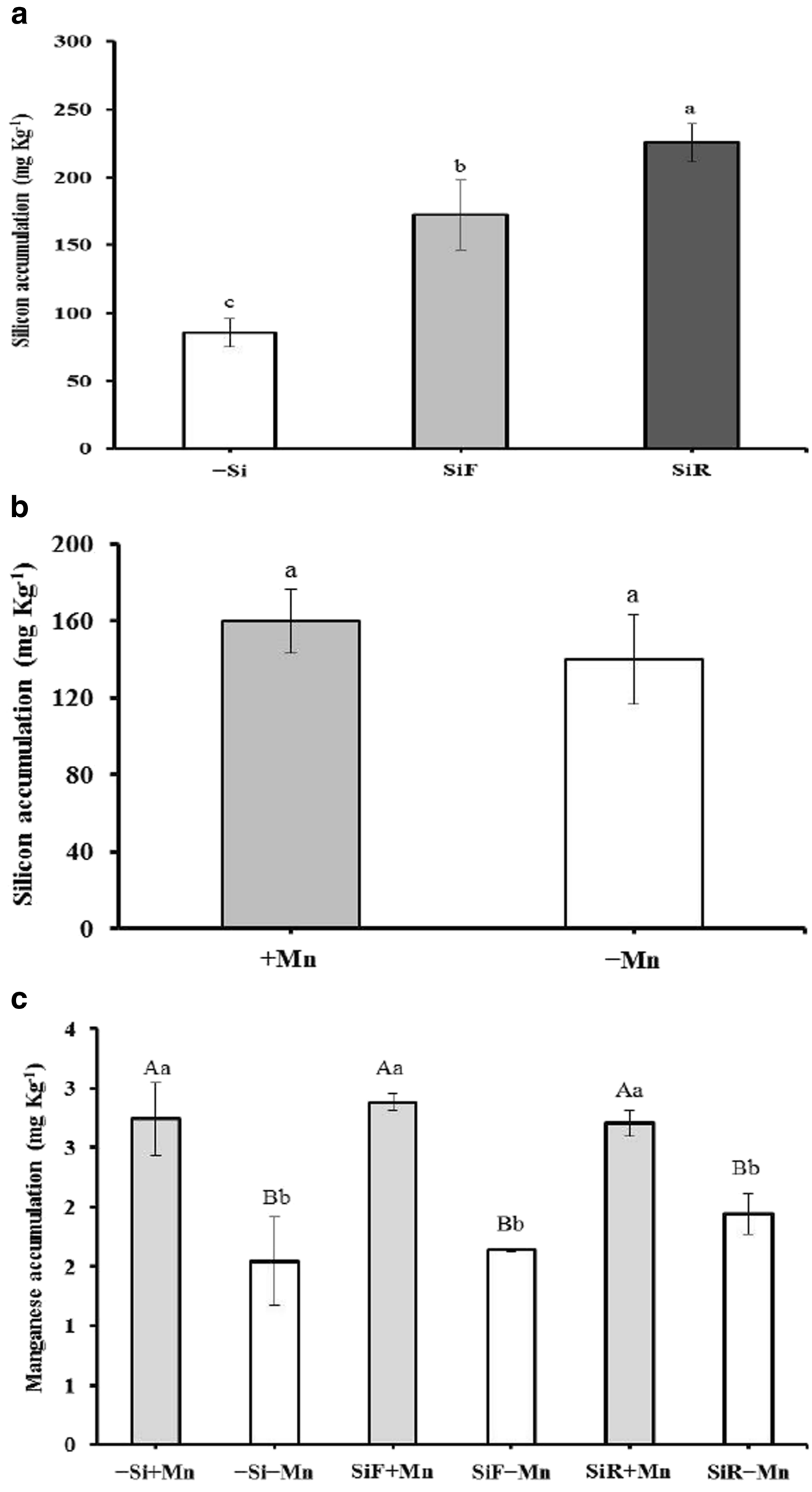

Fig. 2 Accumulation of silicon (A and B) in sorghum plants as a function of the treatments: −Si, without silicon, SiF, leaf silicon; SiR, root silicon; with (+Mn) and without (−Mn). Accumulation of manganese (C) as a function of the treatments: −Si + Mn, without Si with Mn; −Si − Mn, without Si and Mn; SiF + Mn, Si leaf with Mn; SiF − Mn, Si leaf without Mn; SiR + Mn, Si root with Mn; and SiR − Mn, Si root without Mn. In the interaction graph (C), the uppercase letters compare the application forms within each level of Mn and the lowercase letters compare the presence or absence of Mn within each application form. Different letters shown in the error bars indicate significant differences between the treatments, by the Tukey test at 5% probability

2.7 Statistical Analysis

The data obtained were subject to the analysis of variance, using the *F* test, and, to compare the means, Tukey's test was used, at 5% of probability. A polynomial regression study was also conducted to evaluate the Si concentrations, using the statistical program AgroEstat (Barbosa and Júnior 2016).

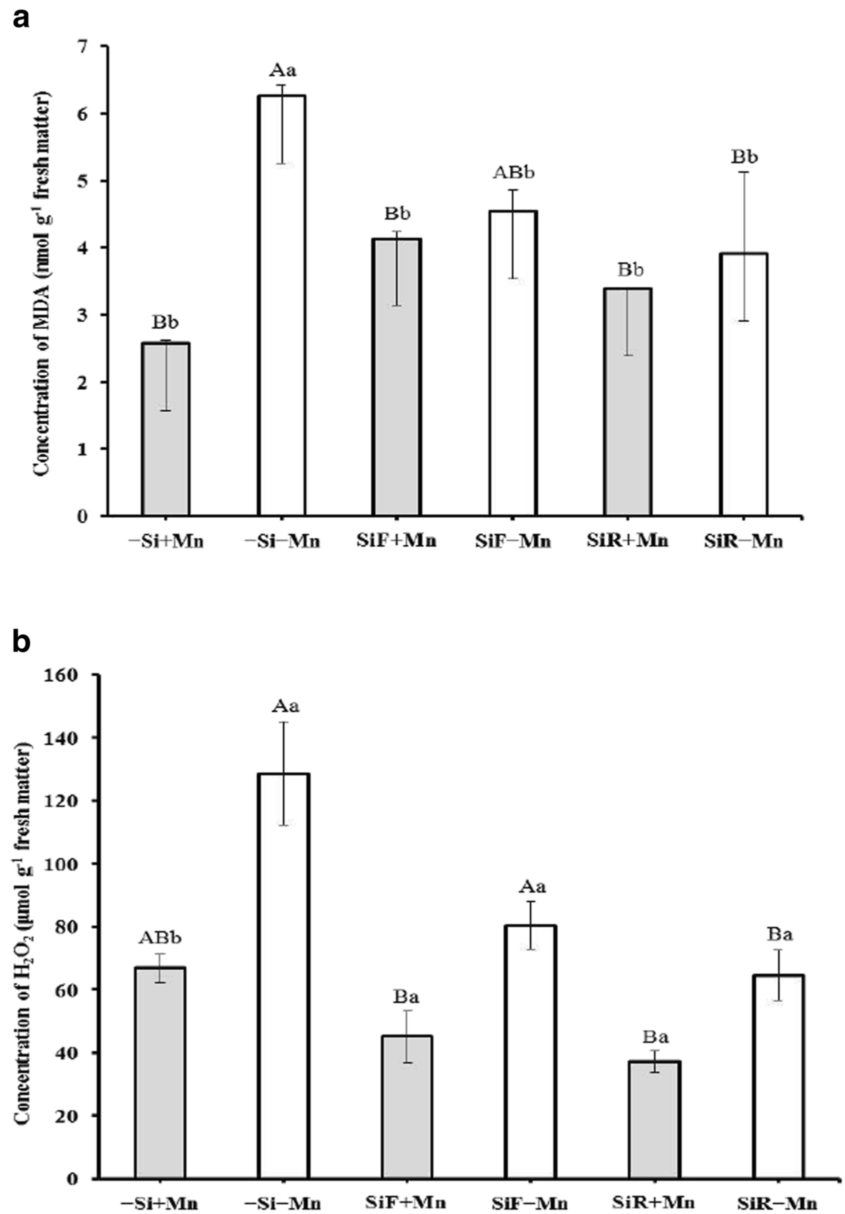

Fig. 3 Concentration of malondialdehyde (A) and hydrogen peroxide (B) on leaves of sorghum plants. –Si + Mn, without Si with Mn; −Si − Mn, without Si and Mn; SiF + Mn, Si leaf with Mn; SiF − Mn, Si leaf without Mn; SiR + Mn, Si root with Mn; and SiR − Mn, Si root without Mn. In the interaction graphs (A and B), the uppercase letters compare the application forms within each level of Mn and the lowercase letters compare the presence or absence of Mn within each application form. Different letters shown in the error bars indicate significant differences between the treatments, by the Tukey test at 5% probability

3 Results

3.1 Grain Yield

Leaf application of Si by using potassium silicate (SiK) and SiNaKE sources at concentrations of 1.05 and 0.95 g L^{-1} Si was responsible to promote an increase in grain yield of 9.0 and 7.0 g per plant, which corresponds to 50 and 39%, respectively, when compared with the control treatment. Grain yield using SiNaKE, SiK, and nano-silicon (Nano) sources at a concentration of 1.0 g L^{-1} Si was similar, but the first two sources differed from stabilized silicic acid (ASiE) (Fig. 1).

3.2 Si and Mn Accumulation

Root Si supply via nutrient solution stood out when compared with the leaf spraying due to an increase of this beneficial element in the shoot of sorghum plants (Fig. 2A). In manganese-deficient (−Mn) and manganese-sufficient (+Mn) plants, no effect was observed on Si accumulation (Fig. 2B).

In Mn deficiency, root Si supply via nutrient solution or leaf spraying did not influence the accumulation of this micronutrient and did not differ from plants without Si. As expected, Mn-sufficient plants showed a higher micronutrient accumulation when compared with deficient plants (Fig. 2C).

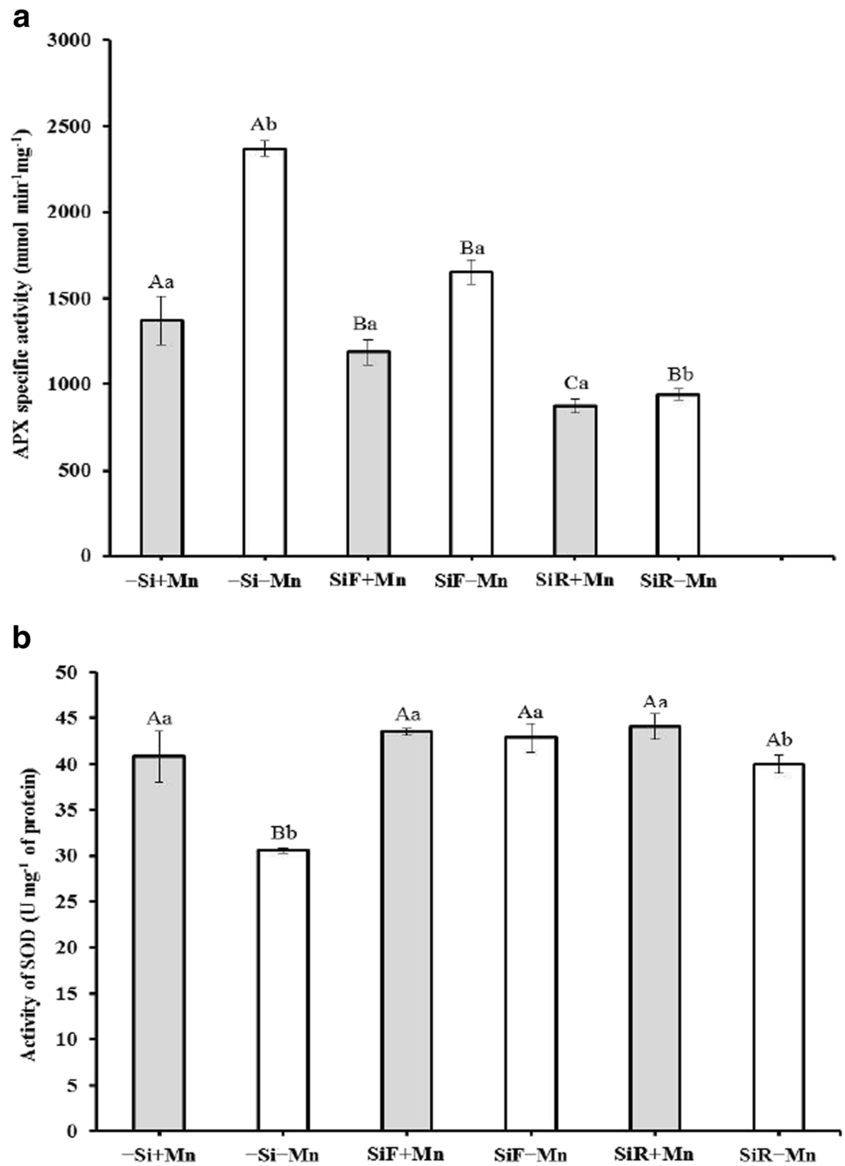

Fig. 4 Specific activity of ascorbate peroxidase (A) and superoxide dismutase (B) on leaves of sorghum plants. –Si + Mn, without Si with Mn; −Si – Mn, without Si and Mn; SiF + Mn, Si leaf with Mn; SiF − Mn, Si leaf without Mn; SiR + Mn, Si root with Mn; and SiR − Mn, Si root without Mn). In the interaction graphs (A and B), the uppercase letters compare the application forms within each level of Mn and the lowercase letters compare the presence or absence of Mn within each application form. Different letters shown in the error bars indicate significant differences between the treatments, by the Tukey test at 5% probability

3.3 MDA and H_2O_2 Concentrations and Enzymatic Activity of SOD and APX

The highest MDA concentrations in the leaves were observed in treatments under Mn deficiency, with no Si addition or only Si via leaf spraying (Fig. 3A). However, Si supply especially via root in the nutrient solution in Mn-deficient plants decreased MDA content, not differing from Mn-sufficient plants. Mn-deficient plants with no Si addition and with Si supplied via leaf had the highest H_2O_2 concentrations, not differing from each other. On the other hand, plants supplied with Si via root or Mn-sufficient plants had the lowest H_2O_2 concentrations (Fig. 3B).

Manganese-deficient plants without Si addition presented a higher APX activity, differing from Mn-sufficient plants. On the other hand, deficient plants that received Si had a lower APX activity, especially those supplied with Si in the nutrient solution (Fig. 4A). In addition, the treatment with Mn-deficient plants without Si addition showed a lower SOD activity, differing from Mn-sufficient plants (Fig. 4B). However, deficient plants with Si supply via leaf or directly in the nutrient solution did not differ from Mn-sufficient plants with and without Si, promoting a decrease in APX activity and increase of SOD activity, with a lower H_2O_2 and MDA content in the plants (Fig. 3A, B).

3.4 Photosynthetic Activity

Manganese-deficient plants without Si addition had a decreased photosynthetic rate in relation to Mn-sufficient plants (Fig. 5). This effect of Mn deficiency was reversed with Si addition via root, as it increased the photosynthetic rate, not differing from treatments with Mn.

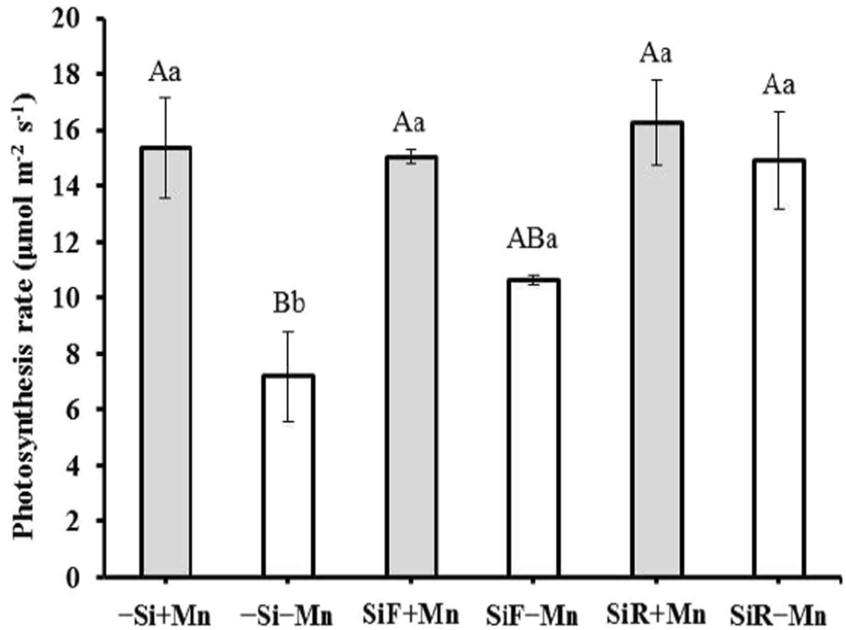

Fig. 5 Photosynthesis rate in sorghum plants. –Si + Mn, without Si with Mn; −Si − Mn, without Si and Mn; SiF + Mn, Si leaf with Mn; SiF − Mn, Si leaf without Mn; SiR + Mn, Si root with Mn; and SiR − Mn, Si root without Mn). In the interaction graph, the uppercase letters compare the application forms within each level of Mn and the lowercase letters compare the presence or absence of Mn within each application form. Different letters shown in the error bars indicate significant differences between the treatments, by the Tukey test at 5% probability

3.5 Mn Use Efficiency, Leaf Area, and Shoot Dry Matter

Treatments without Si addition with sufficiency and deficiency of Mn and the treatment with Mn deficiency and Si addition only via leaf spraying led to a lower Mn use efficiency by the plant, not differing from each other (Fig. 6A). However, the treatment with Mn deficiency, submitted to Si application via root, promoted an increase in Mn use efficiency, not differing from treatments with Mn that received Si.

In addition, a reduction in the leaf area of sorghum plants cultivated under Mn deficiency without Si and with Si application via leaf was also observed when compared to treatments with Mn sufficiency provided in the nutrient solution (Fig. 6B). In Mn-deficient plants, Si addition, especially via root, increased the leaf area of sorghum plants, not differing from treatments with Mn sufficiency with or without Si supply.

Dry matter results were similar to those of leaf area because treatments submitted to Mn deficiency without Si addition or with Si application, but via leaf spraying, did not differ from each other and showed the lowest values of shoot dry matter of sorghum plants (Fig. 6C). However, this effect was reversed because the treatment with Mn deficiency with Si addition applied via nutrient solution increased plant dry matter production, not differing from treatments with Mn sufficiency.

4 Discussion

The important role of leaf spraying of Si was evidenced in the increase of sorghum grain production, standing out the Si concentration close to 1.0 g L^{-1}, which was similar to the Nano, SiNaKE, and SiK sources. Studies have indicated the beneficial effect of the leaf spraying of Si at a concentration of 2.5 g L^{-1} as potassium silicate but in corn plants (De Sousa et al. 2010). Therefore, Si concentration via an adequate leaf spraying depends on the species, being sorghum plants less demanding than corn plants.

The second experiment showed that the highest Si absorption by sorghum plants occurs through the root when compared with the leaf spraying. This occurs because the plant is Si accumulator and presents a high absorption of this element through the root (Ahmed et al. 2011; Yin et al. 2013), which was constantly supplied in the nutrient solution, but only at some periods through leaf spraying, reducing the plant capacity to accumulate this element.

In the absence and presence of Mn, Si supply via root or leaf spraying did not alter the micronutrient accumulation by the plant. It indicates that Si did not influence the Mn absorption process. However, some studies have observed that corn seedlings not treated with Si and submitted to thermal stress at root zone showed a limitation in Mn absorption, leading to a lower micronutrient accumulation (Moradtalab et al. 2018). This effect was reversed with Si supply via root, providing a higher accumulation of the micronutrient in the leaf, improving the nutritional status, and promoting an increase of root and shoot dry matter in plants.

Manganese deficiency in plants, without Si addition, induced stress as it increased H_2O_2 and MDA concentration when compared with plants supplied with this micronutrient (Fig. 3A, B), which was also found in sorghum (Kafi et al. 2011), rice (Song et al. 2011), and corn (Zhao et al. 2014). This was mainly due to a decrease in the enzyme activity of the antioxidant system of plants, evidenced by a reduction in

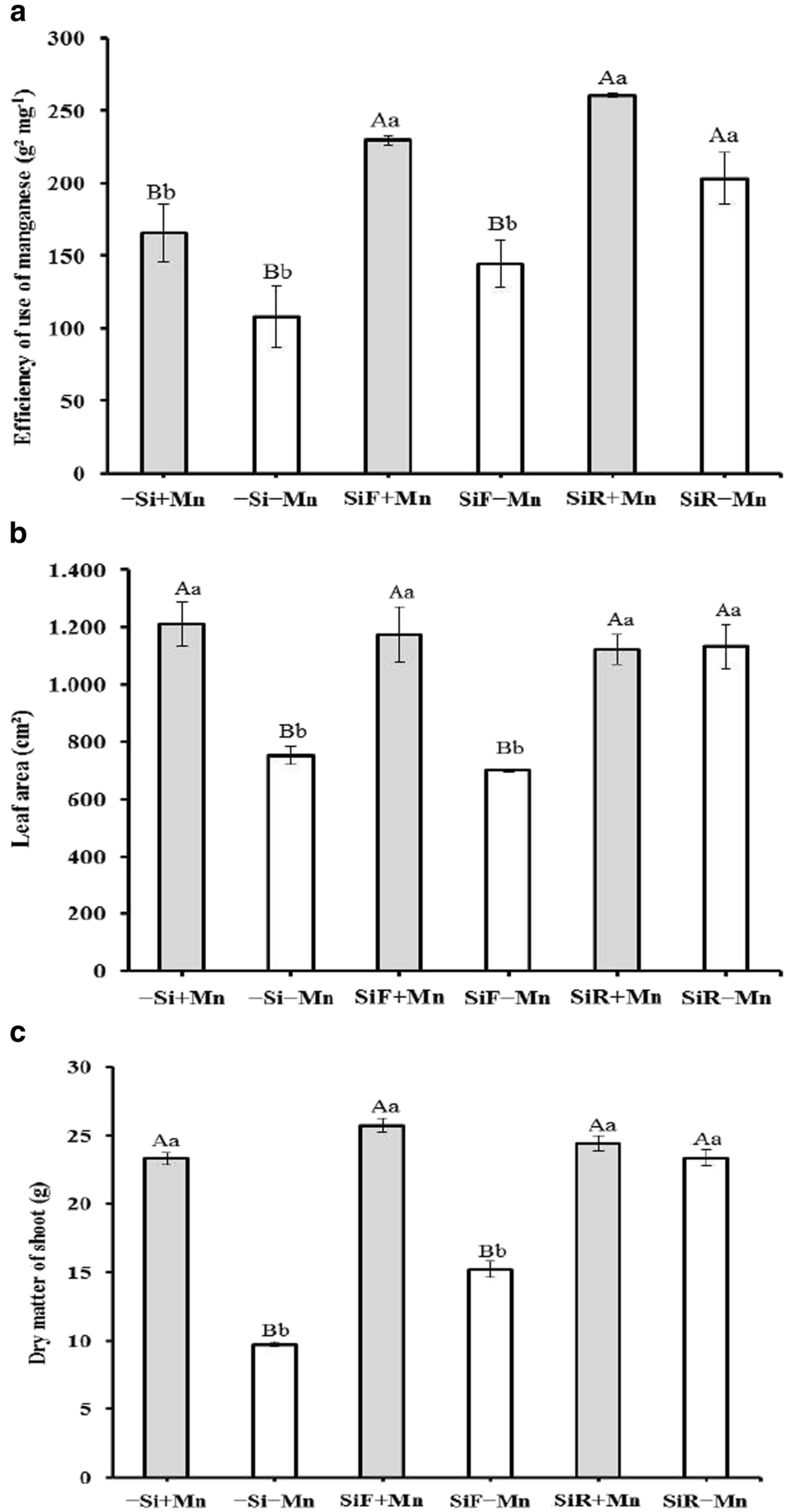

Fig. 6 Efficiency of manganese (A), leaf area (B) and shoot dry matter (C) in sorghum plants. –Si + Mn, without Si with Mn; −Si − Mn, without Si and Mn; SiF + Mn, Si leaf with Mn; SiF – Mn, Si leaf without Mn; SiR + Mn, Si root with Mn; and SiR − Mn, Si root without Mn). In the interaction graphs (A, B, and C), the uppercase letters compare the application forms within each level of Mn and the lowercase letters compare the presence or absence of Mn within each application form. Different letters shown in the error bars indicate significant differences between the treatments, by the Tukey test at 5% probability

SOD activity in plants under stress (Houmani et al. 2016; Zhao et al. 2014; Wang et al. 2012).

Manganese deficiency reduces SOD activity, as this micronutrient is a constituent of the enzyme (Mn-SOD) (Saidi et al.

2012; Wang et al. 2012). In addition, the low activity of this enzyme (Fig. 3C), involved in the plant defense against oxidative stress, contributes to the accumulation of ROS, in excess. This induces oxidative damages to cellular components and pigments, promoting an increase in MDA concentration (Tewari et al. 2013), which was reduced with Si supply in deficient plants because it provided an increase in SOD activity, reducing the damages (Moradtalab et al. 2018).

In this sense, many studies are in accordance with the present study, standing out the role that Si exerts in the mitigation of abiotic stresses. This is due to an increase in the activity of enzymatic and non-enzymatic compounds, which would act to decrease ROS and, consequently, H_2O_2 and MDA concentrations (Fig. 3A, B), which are signs of oxidative stress (Farooq et al. 2016; Hasanuzzaman et al. 2017; Kim et al. 2017; Liang et al. 2007).

The high oxidative stress of Mn-deficient plants led to a low photosynthetic rate when compared with Mn-sufficient plants (Fig. 4). In addition, the nutritional deficiency may promote leaf chlorosis due to a decrease of photosynthetic pigments and degradation of chlorophylls. This is due to a higher ROS accumulation, decreasing the production and allocation of assimilates necessary for root development and, consequently, a decrease in the absorption and distribution of Mn to the shoot, affecting the photosynthetic activity (Moradtalab et al. 2018; Papadakis et al. 2007).

When damaging the formed structures of pigments and proteins, Mn deficiency decreases light absorption of chloroplasts, inhibiting the synthesis of chlorophylls, and the energy transfer between amino acids in the pigment-protein complex of photosystem (PS II), affecting the transport of energy between chlorophylls and evolution of oxygen in the chloroplast (Gong et al. 2010). Rubisco activities and its gene expressions in the plant are also inhibited by micronutrient deficiency, affecting CO_2 assimilation and hence the entire photosynthetic process (Gong et al. 2011; Schmidt et al. 2016).

Because of the low photosynthetic rate observed in Mn-deficient plants without Si addition, there was a loss in the leaf area and shoot dry matter production of sorghum plants. These losses due to Mn deficiency in agricultural crops, including sorghum, have been widely reported in the literature (Bityutskii et al. 2014; Gong et al. 2010, 2011; Moradtalab et al. 2018; Qu et al. 2012; Schmidt et al. 2013).

However, even in Mn-deficient plants, but in the absence of Si, stress effects were alleviated due to a decrease in H_2O_2 concentration by using Si via leaf or root, as well as in MDA concentration with Si supply via root. This beneficial effect of Si occurs due to the higher SOD activity, an antioxidant enzyme that reacts with ROS, decreasing its concentration in cells (Bityutskii et al. 2014; Führs et al. 2009; Miao et al. 2010; Moradtalab et al. 2018). The reduction of oxidative stress favored an increased photosynthetic rate, mainly in plants that received Si via nutrient solution. The beneficial effect of Si on Mn-deficient plants on increasing photosynthetic rate has been described in Mn-deficient cucumber plants (Bityutskii et al. 2014) and Fe-deficient soybean plants (Muneer and Jeong 2015).

The higher photoassimilate production in Mn-deficient plants that received Si, especially via nutrient solution, induced an increased Mn use efficiency by plants. Silicon supply via root also tends to provide a higher root growth due to the higher amount of photoassimilates by favoring the photosynthesis (Hattori et al. 2003; Moradtalab et al. 2018).

Therefore, this higher conversion of the absorbed Mn into dry matter occurred due to an increase in the photosynthetic rate, which may also be involved with a higher internal Mn distribution in the plant to the shoot (Hernandez-Apaolaza 2014; Moradtalab et al. 2018), clearly illustrating the beneficial role of Si and its effects on the nutritional efficiency of sorghum plants. With a higher nutritional efficiency of Mn, plants deficient of this nutrient were able to increase their growth, as verified through the increase in leaf area and shoot dry matter production. It may also be associated with an increase in the enzyme activity (Mn-SOD), which is involved in the reduction of oxidative stress, thus mitigating Mn deficiency and confirming the hypothesis of this study.

5 Conclusion

Silicon mitigated the effects of stress due to manganese deficiency in sorghum plants and its application via root was more effective than leaf spraying. The benefit of silicon was evidenced by the higher activity of superoxide dismutase, reducing oxidative stress, with reflections on photosynthesis, leaf area, manganese use efficiency, and dry matter production of plants.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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