



## Research article

# Silicon attenuates sodium toxicity by improving nutritional efficiency in sorghum and sunflower plants

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## ARTICLE INFO

## Keywords:

*Helianthus annuus*  
Ionic stress  
Nutrient uptake efficiency  
Nutrient utilization efficiency  
Salinity stress  
*Sorghum bicolor*

## ABSTRACT

Salt stress is known to negatively affect the fundamental processes in plants, reducing their growth and yield. The role of Silicon (Si) to protect the sorghum and sunflower plants against salinity stress was assessed. The objective of this study was to evaluate the effects of different forms of Si application on the uptake and use efficiency of macronutrients and micronutrients in sorghum and sunflower plants under salinity stress under greenhouse conditions. Two experiments were conducted using sorghum and sunflower under greenhouse conditions. Four Si levels were applied to plants: no Si application; foliar application of 28.6 mmol.L<sup>-1</sup>; root application of 2.0 mmol.L<sup>-1</sup>; and combined Si application with both via nutrient solution and foliar spraying. Each Si treatment was applied in the absence and presence of NaCl (100 mM). Thirty days after treatments, sodium (Na<sup>+</sup>) and Si accumulation, nutrient uptake and use efficiency, and the roots and total plant dry weight were measured. Salinity stress induced nutritional imbalance and decreased dry weight production in both plant species. Our results showed that Si application alleviated the salinity stress by decreased Na<sup>+</sup> uptake and increased nutritional efficiency, thereby favoring the total plant dry weight in sorghum by 27% and sunflower by 41%. This occurred when Si was applied either via root or in combination via root and foliar application, respectively. Collectively, our findings indicate that Si application can attenuate the deleterious effects of salt stress and increase yield in sorghum and sunflower plants in a sustainable manner.

## 1. Introduction

Salinity is one of the main abiotic stresses limiting crop growth and yield globally, particularly in semi-arid climate areas (Ahmad et al., 2018; D'Imperio et al., 2018; Sattar et al., 2016). This is due to water deficit induced by high osmolarity of the soil solution (Munns, 2002) and ionic toxicity associated with nutritional imbalance and metabolic disorders (Grattan and Grieve, 1999), because of the toxic effects of salts in the protoplasm (Silva et al., 2007). Therefore, salt (NaCl) stress may induce nutritional deficiency (Bandehagh et al., 2011; Kosová

et al., 2011).

Salinity induces changes in the uptake, transport, and redistribution of nutrients in a plant, which can cause physiological inactivation of a certain nutrient and increase the internal need of the plant for that nutrient (Munns et al., 2016). Salinity stress decreases growth in sorghum (Almodares et al., 2014; Avci et al., 2017; Nxele et al., 2017) and sunflower (Kumari et al., 2016; Taher et al., 2018). Salinity stress-induced damage can be explained by decreased nutritional efficiency of some or all nutrients. However, the results obtained in these species are incipient and decreased use efficiency has only been reported for

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<sup>1</sup> Silicon (Si); sodium (Na<sup>+</sup>); no Si treatment (0); foliar Si application at 28.6 mmol. L<sup>-1</sup> treatment (F); root Si application at 2.0 mmol. L<sup>-1</sup> treatment (R); combined root application and foliar Si treatments (F + R); root dry weight (RDW); total plant dry weight (TDW); nitrogen uptake efficiency (NUpE); phosphorus uptake efficiency (PUpE); potassium uptake efficiency (KUpE); calcium uptake efficiency (CaUpE); magnesium uptake efficiency (MgUpE); sulfur uptake efficiency (SUpE) iron uptake efficiency (FeUpE); manganese uptake efficiency (MnUpE); zinc uptake efficiency (ZnUpE); copper uptake efficiency (CuUpE); nitrogen utilization efficiency (NUtE); phosphorus utilization efficiency (PUtE); potassium utilization efficiency (KUtE); calcium utilization efficiency (CaUtE); magnesium utilization efficiency (MgUtE); sulfur utilization efficiency (SUtE); iron utilization efficiency (FeUtE); manganese utilization efficiency (MnUtE); zinc utilization efficiency (ZnUtE); copper utilization efficiency (CuUtE).

<https://doi.org/10.1016/j.plaphy.2019.07.010>

Received 13 May 2019; Received in revised form 6 July 2019; Accepted 8 July 2019

Available online 09 July 2019

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nitrogen (N) in sunflower under salinity stress (Zeng et al., 2015). In other annual crops, salinity decreases the use efficiency of some isolated nutrients such as N in mungbean (Nazar et al., 2011) and cotton (Zhang et al., 2012); and phosphorous (P) (Zribi et al., 2014), zinc (Zn) (Seilsepour, 2006), and calcium (Ca) in wheat and tomato plants (Caines and Shennan, 1999).

Si has been shown to alleviate various types of abiotic stress (e.g., cold, drought, heat, salinity, and mineral deficiency or toxicity) and biotic stress (e.g., plant diseases and other pests) (Adrees et al., 2015; Bakhat et al., 2018; Debona et al., 2017; Etesami and Jeong, 2018; Kim et al., 2017; Olivera et al., 2019; Rizwan et al., 2015). One approach to mitigate salinity stress in sorghum and sunflower plants is root Si supplementation (Ashraf et al., 2015; Conceição et al., 2018; Liu et al., 2015; Yin et al., 2016, 2013). Additionally, there are recent reports suggesting that foliar Si supplementation alleviates salinity stress in wheat, okra, and mungbean plants (Abbas et al., 2017; Sattar et al., 2019, 2017). This is because Si application, especially via the root, helps maintain nutrient balance, sequester toxic ions, and decrease  $\text{Na}^+$  uptake (Alsaedi et al., 2019; Ashraf et al., 2015; Liang et al., 2007; Ma, 2004; Malhotra and Kapoor, 2019; Rizwan et al., 2015; Sattar et al., 2016; Zhu et al., 2015; Zhu and Gong, 2014).

However, in sorghum and sunflower plants under salinity stress, it is unknown whether the beneficial effects of Si are just due to decreased  $\text{Na}^+$  uptake or to the improvement of nutrient uptake and use efficiency. Higher dry mass production of plants grown with Si supplementation in saline environments can be attributed to higher nutrient uptake and use efficiency. In species that have a low root uptake of Si such as sunflower, Si accumulation through foliar application of Si can be used to attenuate salinity stress. Meanwhile, species that absorb a high quantity of Si through the roots do not require foliar application. Information on the relative benefits of these two strategies and their level of salinity stress attenuation is limited.

Therefore, we hypothesized that Si application can be an efficient treatment to minimize the nutritional imbalance caused by salinity in sorghum and sunflower plants, by decreasing uptake of  $\text{Na}^+$  and especially by increasing the uptake and use efficiency of macronutrients and micronutrients. We also hypothesized that the beneficial effects of Si in alleviating salinity stress in non-Si-accumulating species such as sunflower can be maximized by supplying Si via nutrient solution to the roots and foliar application. Whereas, in Si-accumulating species, such as sorghum, the benefits of Si application can be achieved by supplying Si via nutrient solution alone. In this study, we evaluated the effects of Si in different application forms on salinity stress by measuring macronutrient and micronutrient uptake and use efficiency in sorghum (Si-accumulating) and sunflower (non-Si-accumulating).

## 2. Material and methods

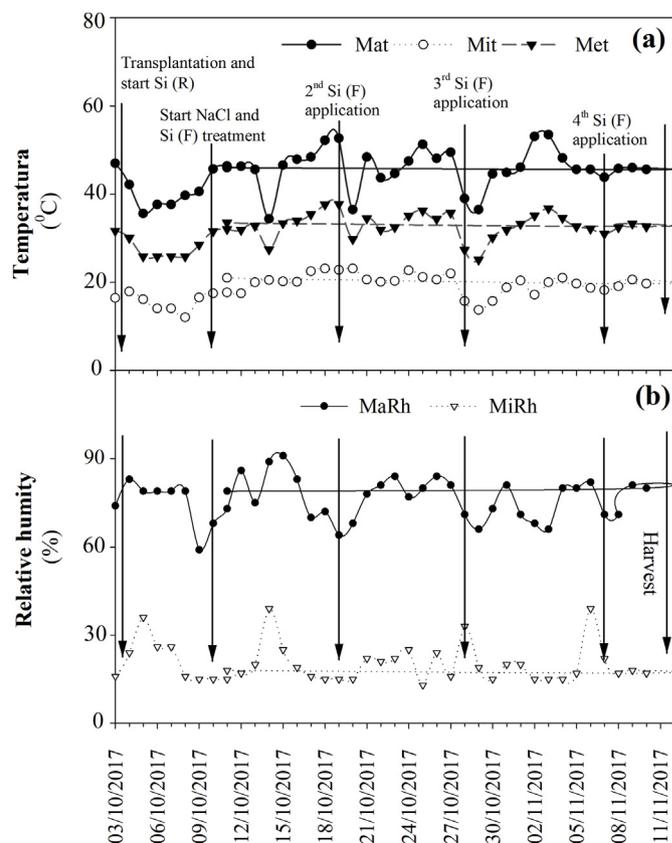
### 2.1. Growing conditions and plant material

The experiments were carried out at the “Julio de Mesquita Filho,” State University of São Paulo (UNESP) in a glass greenhouse. The plants were maintained at a temperature of  $28.6 \pm 3.7^\circ\text{C}$  (Fig. 1a) and a relative humidity of  $65.7\% \pm 25\%$  (Fig. 1b).

The plant species studied were sorghum (*Sorghum bicolor* L. ‘Moench’ Dekalb 540) and the yellow dwarf sunflower (*Helianthus annuus* L. ‘Double Sungold’). The seeds of these plants were placed in trays for germination and irrigated three times daily with 300 mL of deionized water.

### 2.2. Experimental design

The experiments were carried out in randomized blocks with a factorial design ( $2 \times 4$ ) for each crop. We tested two levels of NaCl, the absence (0; no added NaCl) and presence of 100 mM NaCl. The plants were subjected to the following four levels of Si treatments: control no



**Fig. 1. Experimental greenhouse conditions.** Climatological variables in the experimental glass greenhouse during the experiments. Maximum temperature (Mat); minimum temperature (Mit); mean temperature (Met) (a); maximum relative humidity (MaRh); and minimum relative humidity (MiRh) (b).

Si (0); foliar application of  $28.6 \text{ mmol.L}^{-1}$  Si (F); root application of  $2.0 \text{ mmol.L}^{-1}$  Si in nutrient solution (R); and combined of Si application through root nutrient solution ( $2.0 \text{ mmol.L}^{-1}$ ) and foliar spraying ( $28.6 \text{ mmol.L}^{-1}$ ) (F + R). Overall, there were eight combination treatments and five replicates per treatment. The experimental unit consisted of a  $4.0\text{-dm}^3$  polyethylene vessel filled with washed sand, with a perforated bottom and nutrient solution collector, containing either two sorghum plants or four sunflower plants.

### 2.3. Nutrient solution

The sorghum and sunflower seedlings were transplanted 15 days after emergence. After transplanting, the nutrient solution of Hoagland and Arnon (1950) was supplied to the plants, starting at 25% ionic strength to acclimatize the plants, increasing to 50% by two weeks, and to 75% by the end of the experiment (35 days). The pH of Hoagland nutrient solution was monitored daily and maintained at  $5.0 \pm 0.8$  using 1 N hydrochloric acid (HCl) solution.

### 2.4. Si and NaCl treatments

The plants were subjected to osmotic shock seven days after transplantation to hydroponic culture; the plants were acclimatized via the application of  $\sim 2.0 \text{ dS m}^{-1}$  salinity on the first day. After seven days of acclimatization, the plants were exposed to the desired level of salinity ( $\sim 10.0 \text{ dS m}^{-1}$ ) caused by addition of 100 mM NaCl and this was maintained until the end of the experiment. Si for foliar application was diluted in deionized water and spraying fully developed leaves at stages S2–S4 for sorghum (Vanderlip and Reeves, 1972) and stages V4–V8 in sunflower (Schneider and Miller, 1981). Si was supplied at

2.0 mmol.L<sup>-1</sup> concentration in Hoagland nutrient solution by bathing the roots, and the solution was available to the roots throughout the experimental period. The source of Si in the nutrient solution and foliar application was stabilized sodium and potassium silicate (SiNaKE), with a total Si content of 113.4 g.L<sup>-1</sup> Si, comprising 94.2 g.L<sup>-1</sup> Si in sodium silicate form (Na<sub>2</sub>SiO<sub>3</sub>) and 19.2 g.L<sup>-1</sup> Si in potassium silicate form (K<sub>2</sub>SiO<sub>3</sub>). The Na<sup>+</sup> and K<sup>+</sup> levels were equilibrated among all the treatments. The pH of the solution for foliar application was maintained at 7.5 ± 0.8 using 1 N HCl solution, to liberate monosilicic acid, the only form assimilated by plants. The plants were maintained under the following conditions: relative humidity of > 60%; and temperature of 20°C–27 °C.

### 2.5. Determination of plant dry weight

After collection, the plants were washed with distilled water to remove residues. The plants were then washed with detergent solution (0.2%), hydrochloric acid solution (0.1%), and finally deionized water (Prado, 2008). The roots, leaves, and stems were placed in paper sacks and dried in a forced ventilation oven at a constant temperature of 65 °C until they reached a constant weight, and then the dry mass was measured.

### 2.6. Determination of nutrient content, uptake, and utilization efficiency

The content of Na<sup>+</sup> was measured in the root and shoot, and the content of N, P, potassium (K), Ca, magnesium (Mg), sulfur (S), copper (Cu), iron (Fe), zinc (Zn), manganese (Mn), and Si was measured in the shoot; the content of all macronutrients and micronutrients is expressed as mg. kg<sup>-1</sup> of dry matter. The Si content was evaluated in the shoot as described by Kraska and Breitenbeck (2010). The Na<sup>+</sup> and nutrient content was determined as described by Bataglia et al. (1983). Total macronutrient and micronutrient accumulation was calculated as the N, P, K, Ca, Mg, S, Cu, Fe, Zn, and Mn content per plant dry weight (g per plant) (Lawlor, 2002). Nutrient uptake efficiency, calculated as total nutrient accumulation divided by root dry weight (RDW) (g of each element g<sup>-1</sup> RDW), was determined (Swiader et al., 1994). Nutrient utilization efficiency was calculated as the total plant dry weight (TDW) divided by the N, P, K, Ca, Mg, S, Cu, Fe, Zn, and Mn content (g TDW mg<sup>-1</sup> of each element) (Siddiqi and Glass, 1981).

### 2.7. Statistical analysis

Data obtained were analyzed after testing normality and homogeneity of variance with Kolmogorov–Smirnov and Levene's tests, respectively. Once parametric assumptions were confirmed, the two-way analysis of variance was carried out using the SAS software version v9.2. Means were compared by least significant differences with a 5% significance level (P < 0.05).

## 3. Results

### 3.1. Accumulation of Na<sup>+</sup> and Si

We found significant and interactive effects of salinity and Si application on Na and Si accumulation in both cultures (Fig. 2). Salinity stress significantly increased Na<sup>+</sup> accumulation in the roots and shoots of sorghum and sunflower plants (Fig. 2a–d). In sorghum plants, the R and F + R treatments decreased Na<sup>+</sup> accumulation in the roots and shoots compared with that under the F and 0 treatments (Fig. 2a, c). In sunflower plants, Na<sup>+</sup> accumulation in the roots and shoots decreased only under the F + R treatment (Fig. 2b, d).

In both plant species, Si accumulation was similar in the absence and presence of NaCl under all the Si application treatments (Fig. 2e and f), indicating that NaCl does not influence Si uptake. Si accumulation in the shoots of sorghum plants under the Si (R) and Si (F + R)

treatments was higher than under the Si (F) treatment, whereas in this one was higher than under the control (0) (Fig. 2e). In sunflower plants cultivated under saline conditions, the highest accumulation of Si occurred in the Si (F + R) treatment compared with that in the other treatments.

### 3.2. Si increased nutrient uptake efficiency

There was a significant and interactive effect of salinity and Si on the uptake efficiency of macronutrients in both plant species (Fig. 3). Sorghum plants showed increased uptake efficiency of N, P, K, Ca, Mg, and S in the presence of NaCl compared with that in the absence of NaCl (Fig. 3a, c, e, g, i, k). Under salinity stress, the Si (R) and Si (F + R) treatments promoted higher uptake efficiency of all the nutrients than that under the F and 0 treatments (Fig. 3a, c, e, g, i, k).

Sunflower plants presented increased uptake efficiency of N, K, Ca, Mg, and S when they were cultured in the absence of NaCl, whereas the uptake efficiency of P increased in the presence of NaCl (Fig. 3b, d, f, h, j, l). In plants under salinity stress, there was greater uptake efficiency of all the nutrients under the Si (F + R) treatment than that under the other treatments (Fig. 3b, d, f, h, j, l).

A significant and interactive effect of NaCl and Si on uptake efficiency of micronutrients was observed in young sorghum and sunflower plants (Fig. 4). The uptake efficiency of Fe, Mn, Zn, and Cu in sorghum plants was higher under the NaCl treatment than that under non-NaCl treatment (Fig. 4a, c, e, g). In sorghum plants under salinity stress, the Si (R) and Si (F + R) treatments increased the uptake efficiency of all micronutrients compared with that of the Si (F) and Si (0) treatments (Fig. 4a, c, e, G). In sunflower plants under salinity treatments, there was a decrease in the uptake efficiency of all studied micronutrients. However, only the Si (F + R) treatment increased the uptake efficiency of micronutrients in sunflower plants grown under salinity stress compared with that of plants grown under the other treatments (Fig. 4b, d, f, h).

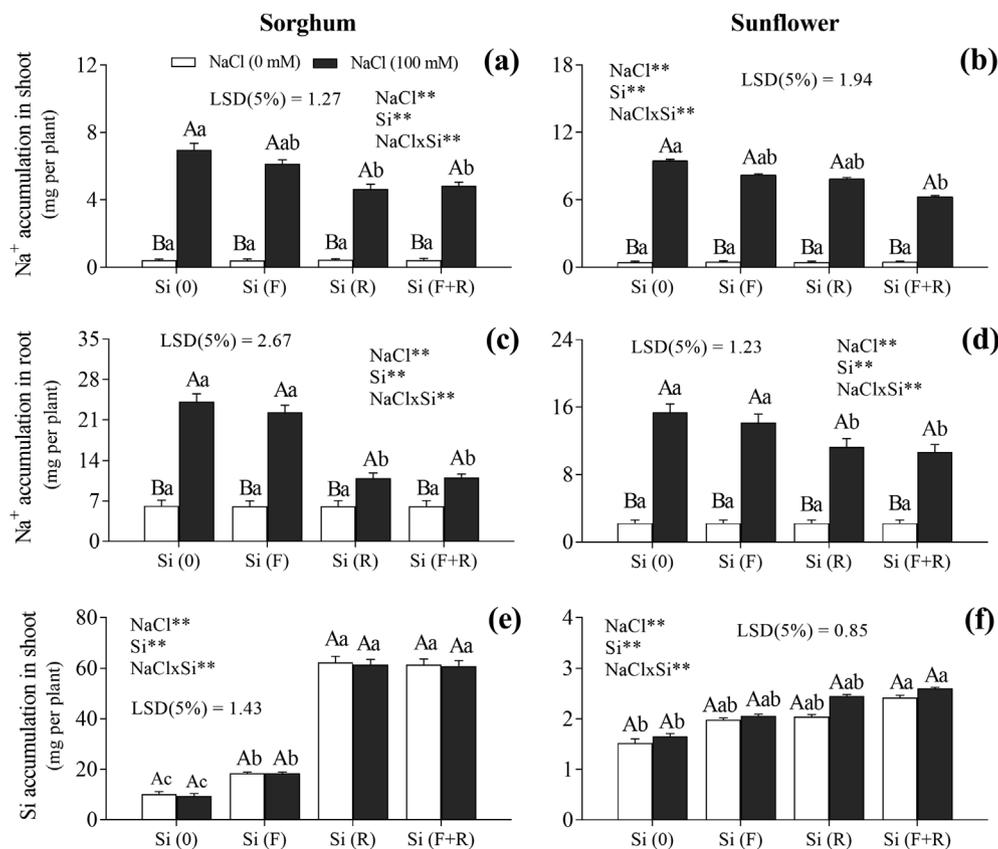
### 3.3. Si increased nutrient utilization efficiency

There was a significant and interactive effect of salinity and Si on the utilization of macronutrients in the two species (Fig. 5). In both sorghum and sunflower plants, the use efficiency of N, P, K<sup>+</sup>, Ca, Mg, and S was lower with the NaCl treatments than without the NaCl treatment (Fig. 5). In sorghum plants, the Si (R) and Si (F + R) treatments increased the use efficiency of macronutrients (K, N, Ca, Mg, P, and S) compared with that of the Si (F) and control treatments (Si (0)) (Fig. 5a, c, e, g, i, k). In sunflower plants, all the Si treatments increased the use efficiency of N, P, K, Ca, Mg, and S compared with the control (Si (0)), especially the Si (F + R) treatment (Fig. 5b, d, f, h, j, l).

The use efficiency of Fe, Mn, Zn, and Cu was higher in sorghum and sunflower plants grown without NaCl than in plants stressed with NaCl (Fig. 6). The use efficiency of micronutrients Fe, Mn, Zn, and Cu in sorghum plants under salt stress was increased by the Si (R) and Si (F + R) treatments compared with that by the Si (F) and Si (0) treatments (Fig. 6a, c, e, g). Salt-stressed sunflower plants had higher use efficiencies of Fe, Mn, Zn, and Cu with all the Si application treatments (R, F, and F + R) than those with the Si (0) treatment, and the highest results were achieved with the Si (F + R) treatment (Fig. 6b, d, f, h).

### 3.4. Dry matter production

A comparison of means revealed that interaction between Si and NaCl stress was significant on the root and total plant dry weight (TDW) production in sorghum and sunflower plants (Fig. 7). The RDW and TDW of the two plant species decreased when cultivated with NaCl (Fig. 7a and b). In sorghum plants grown under salinity stress, the Si (R) and Si (F + R) treatments increased the RDW and TDW compared with that of the Si (F) and Si (0) treatments (Fig. 7a). However, in sunflower



**Fig. 2.** Na<sup>+</sup> and Si accumulation in sorghum and sunflower plants. Na<sup>+</sup> accumulation in the shoots of sorghum (a) and sunflower plants (b) and in the roots of sorghum (c) and sunflower plants (d), and Si accumulation in the shoots of sorghum (e) and sunflower plants (f), in the absence and presence of NaCl (0 and 100 mM) combined with different Si treatments; no added Si [Si (0)]; foliar Si application at 28.6 mmol L<sup>-1</sup> [Si (F)]; root Si application at 2.0 mmol L<sup>-1</sup> [Si (R)]; combination of root and foliar Si application [Si (F + R)]. Different small letters indicate significant differences among the Si application treatments at each level of NaCl, and different capital letters indicate significant differences among the NaCl treatments for each level of Si, according to Student's *t*-test at ( $P < 0.05$ ). The values are mean  $\pm$  standard error (SE) from five replicates (Mean  $\pm$  SE;  $n = 5$ ); least significant difference [LSD]. \*\* Significant at ( $P < 0.01$ ) of probability. The vertical bars represent the SE of the mean.

plants under salinity stress, all the three modes of Si application (F, R, and F + R) increased the RDW and TDW compared with that of the Si (0) treatment (Fig. 7b).

#### 4. Discussion

The salinity treatment we used increased Na<sup>+</sup> uptake in the root and shoot of sorghum and sunflower plants without affecting Si accumulation (Fig. 2). Si decreased Na<sup>+</sup> accumulation in the roots and shoots of both cultures, especially when Si was supplied via nutrient solution to the roots (Fig. 2a, b, c, d). This was because Si application, especially via the root, increased Si accumulation in the shoots of both plant species (Fig. 2e and f). We observed that sorghum accumulated more Si in the shoots than sunflower did independent of salinity. This is because gramineous plants specifically express Si transporters, and therefore absorb a high amount of Si, whereas legumes do not express these transporters and have mechanisms to exclude Si (Ahmed et al., 2014; Kumar et al., 2017; Liang et al., 2005; Ma et al., 2001).

It has been observed that Si when supplied to the roots as nutrient solution can alleviate salinity stress in sorghum (Yin et al., 2016, 2013) and sunflower (Ashraf et al., 2015; Conceição et al., 2018). This effect has been reported in other species, such as rice (Yeo et al., 1999), wheat (Liang, 1999; Zhu and Gong, 2014), and sugarcane (Ashraf et al., 2010), and the authors observed decreased transpirational flow and Na<sup>+</sup> uptake (Li et al., 2015).

Salinity increased the uptake efficiency of N, P, K, Ca, Mg, S, Fe, Mn, Zn, and Cu in sorghum plants, but decreased it in sunflower plants (Figs. 3 and 4). The increased nutrient uptake efficiency in sorghum plants can be attributed to the drastic reduction in root growth under salinity stress, which has also been observed in other studies (Avci et al., 2017; Nxele et al., 2017). In sunflower plants, decreased nutrient uptake efficiency under salinity stress has been reported by Sánchez and Delgado (1996) and Zribi et al. (2014). The decreased uptake efficiency of N, P, K, Ca, Mg, S, Fe, Mn, Zn, and Cu in sunflower plants

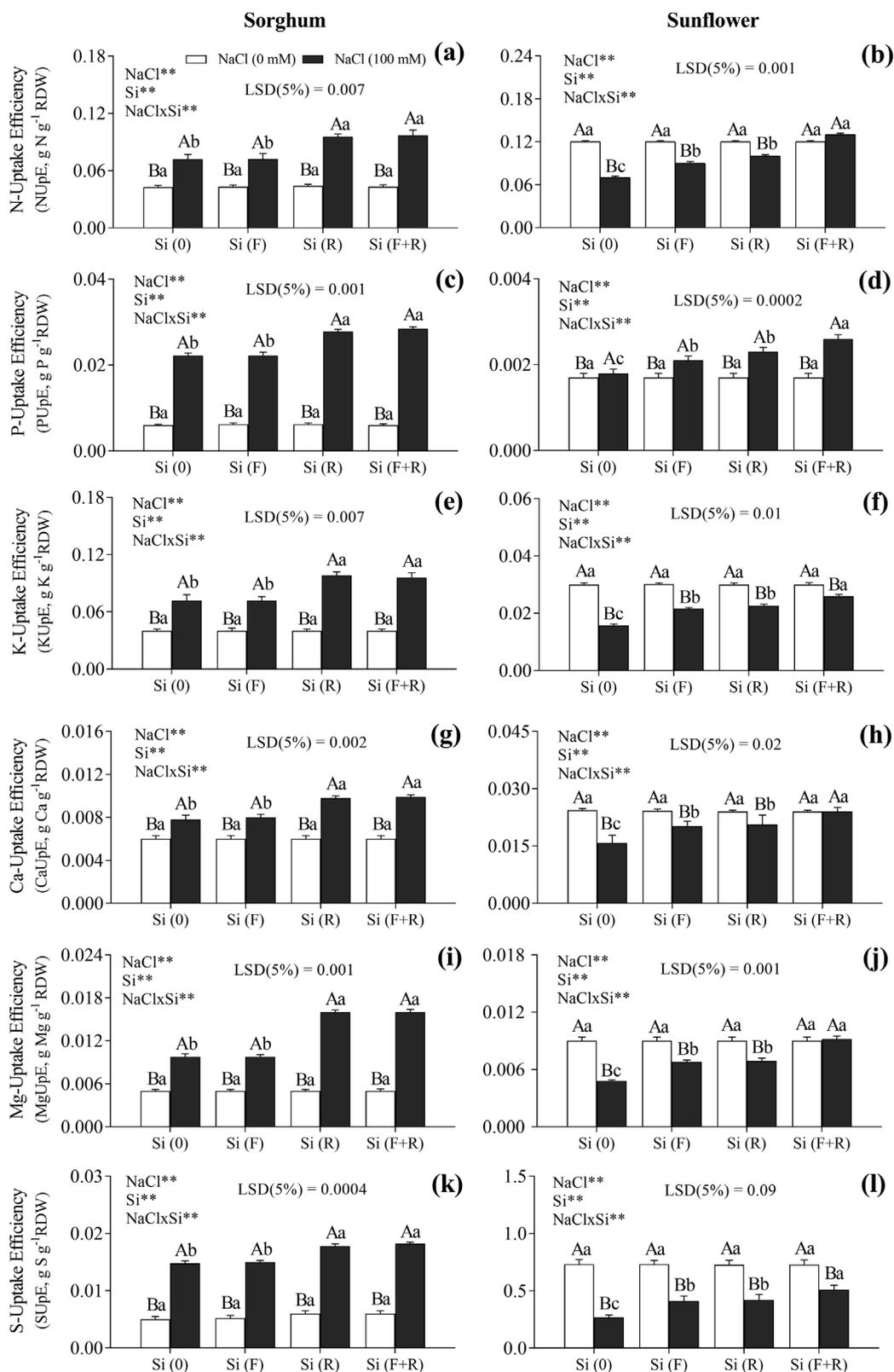
under salinity stress may have been caused by Na<sup>+</sup> competing with cations, a process which is associated with toxic effects such as generation of reactive oxygen species that can degrade enzymes or nutrient uptake transporters (Cakmak, 2002; Santos, 2004).

In the present study, the Si (R) treatment in sorghum plants and the Si (F + R) treatment in sunflower plants were efficient in alleviating salt stress because they increased the uptake efficiency of N, P, K, Ca, Mg, S, Fe, Mn, Zn, and Cu (Figs. 3 and 4). We observed that in sorghum with Si supplied exclusively to the roots via nutrient solution, there was a significant benefit under salinity stress, which is consistent with the findings of a previous study (Hossain et al., 2002). This reinforces that the beneficial effects of Si are more pronounced in monocotyledonous species than in dicotyledonous species.

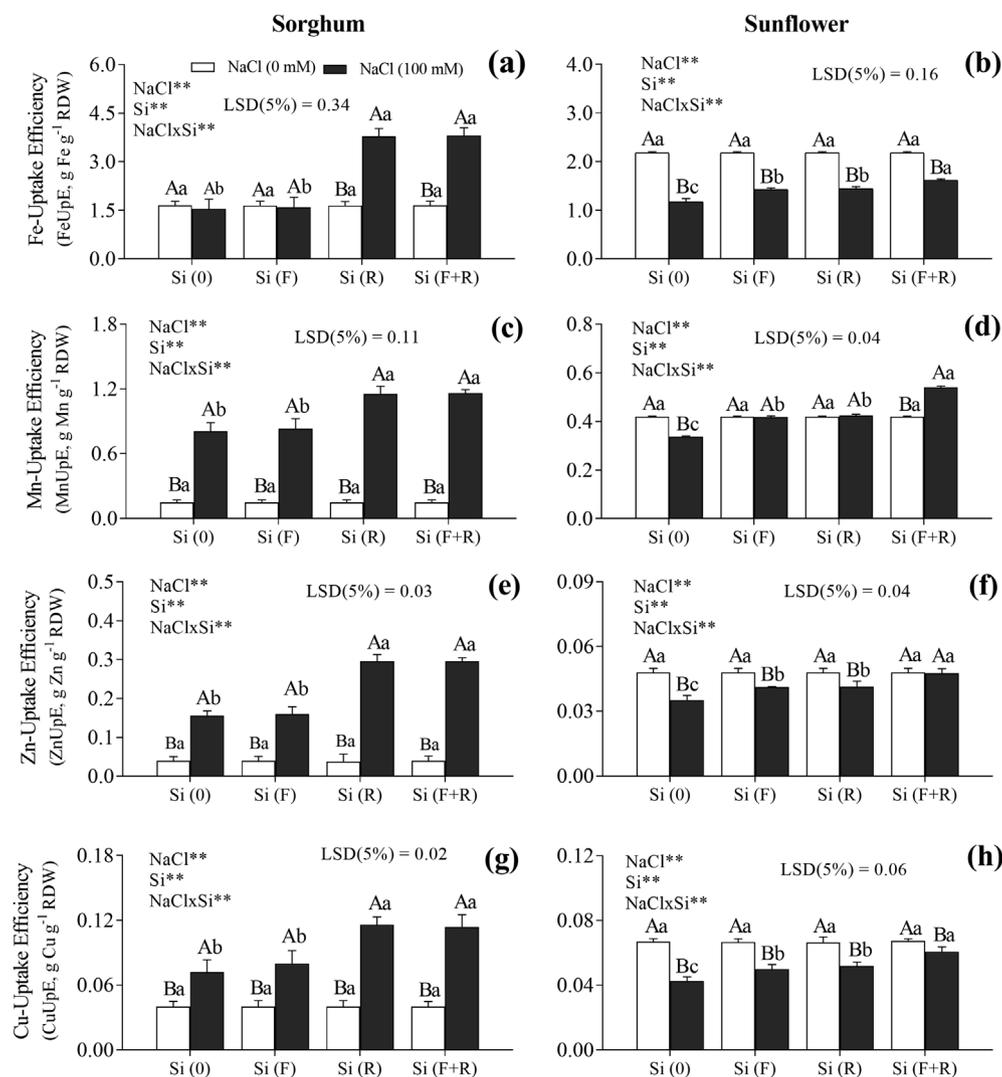
On the other hand, in sunflower plants, the importance of Si supplied through foliar application was apparent, with Si attenuating the deleterious effects of salinity stress by decreasing Na<sup>+</sup> accumulation in the roots and shoots, and by increasing the uptake efficiency of all the nutrients, which were not observed in sorghum plants with foliar Si application. Therefore, this novel finding indicates that in non-Si-accumulating plants such as sunflower foliar application is a feasible method to reduce salinity-induced damage.

The beneficial effect of Si on nutrient uptake in plants grown under salinity stress has been reported for K in sorghum (Yin et al., 2013), sunflower (Ashraf et al., 2015; Conceição et al., 2018), corn (Sattar et al., 2016), rice (Farooq et al., 2015), barley (Liang et al., 2005), alfalfa (Wang and Han, 2007), sweet pepper (Tantawy et al., 2015), and cucumber (Alsaedi et al., 2019, 2018).

Similarly, under saline conditions, Si application increased the accumulation of Mg, K, P, and Ca in Egyptian clover (Abdalla, 2011), and increased the shoot concentration of Ca in cucumber, cowpea, and kidney bean (Khoshgoftarmansh et al., 2014; Murillo-Amador et al., 2007). Similar results of increase in nutrient uptake with Si application has been reported (Hellal et al., 2005) in faba beans. In moringa (*Moringa oleifera* L.) and aloe plants under salt stress, Si application



**Fig. 3.** Uptake efficiency of macronutrients under Si and NaCl treatments. Nitrogen uptake efficiency (NUPe) in sorghum (a) and sunflower plants (b), phosphorus uptake efficiency (PUPe) in sorghum (c) and sunflower plants (d), potassium uptake efficiency (KUPe) in sorghum (e) and sunflower plants (f), calcium uptake efficiency (CaUPe) in sorghum (g) and sunflower plants (h), magnesium uptake efficiency (MgUPe) in sorghum (i) and sunflower plants (j), and sulfur uptake efficiency (SUPe) in sorghum (k) and sunflower plants (l). Treatments and statistics as in Fig. 2.



**Fig. 4.** Uptake efficiency of micronutrients under the Si and NaCl treatments. Iron uptake efficiency (FeUpE) in sorghum (a) and sunflower plants (b), manganese uptake efficiency (MnUpE) in sorghum (c) and sunflower plants (d), zinc uptake efficiency (ZnUpE) in sorghum (e) and sunflower plants (f), and copper uptake efficiency (CuUpE) in sorghum (g) and sunflower plants (h). Treatments and statistics as in Fig. 2.

increased the P, K, Ca, and Mg content (Hussein and Abou-baker, 2014; Xu et al., 2015).

It has been reported that Si supplementation increased the Ca and Mg content in the leaf and root of tomato plants under saline conditions (Li et al., 2015). In alfalfa plants, Si application increased the Ca and Mn content in the root, while decreased the Ca content in the shoots (Wang and Han, 2007). It has also been reported that Si application maintained a high P content in salt-stressed canola plants (Farshidi et al., 2012). Similarly, an increase in N uptake in cucumber plant under salt stress has been reported (Alsaeedi et al., 2019).

On the other hand, application of Si can increase the Mn content under saline condition in the shoots of alfalfa, while decreased the Cu content in the shoots (Wang and Han, 2007). Similarly, it has been reported that Si supply maintained the Fe content in canola plants (Farshidi et al., 2012). Salt stress decreased the use efficiency of N, P, K, Ca, Mg, S, Fe, Mn, Zn, and Cu in some plant species (Caines and Shennan, 1999; Ho et al., 1995; Khoshgofarmanesh et al., 2005; Reich et al., 2017; Seilsepour, 2006; Zeng et al., 2015; Zhang et al., 2012; Zribi et al., 2014).

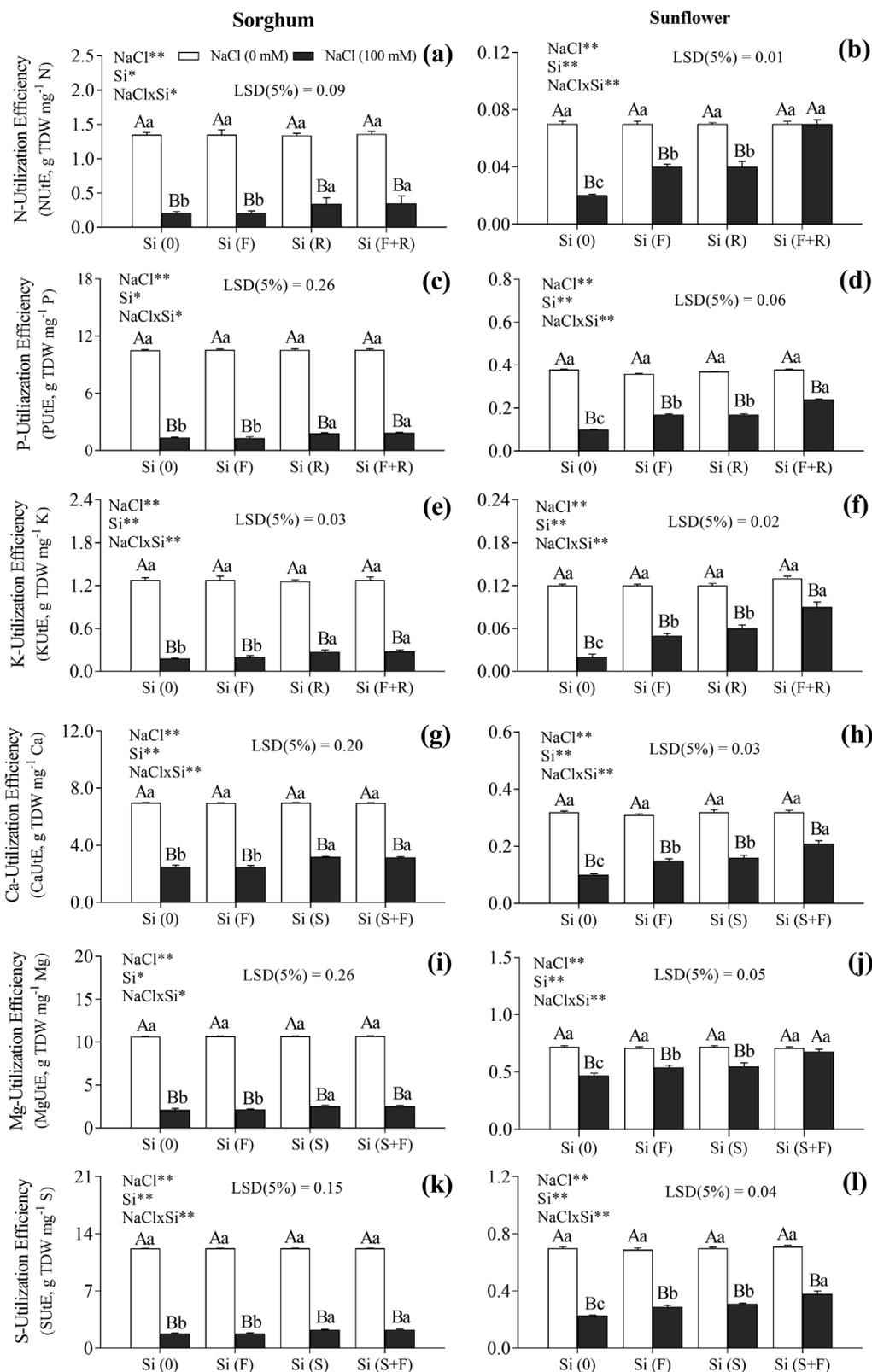
In sorghum plants grown in NaCl solution, the Si (R) and Si (F + R) treatments were beneficial and increased the nutrient utilization efficiency, whereas in sunflower plants all the Si treatments increased the nutrient utilization efficiency of macros and micronutrients, especially

when applied the Si (F + R) treatment (Figs. 5 and 6). The higher nutrient utilization efficiency observed with Si application in both cultures under salinity stress may be related to the reduction in  $\text{Na}^+$  accumulation in the root and shoot (Fig. 2a–d), thereby allowing greater nutrient uptake and higher nutrient uptake efficiency. This would favor nutrient use in plants, as reflected by the higher nutrient utilization efficiency.

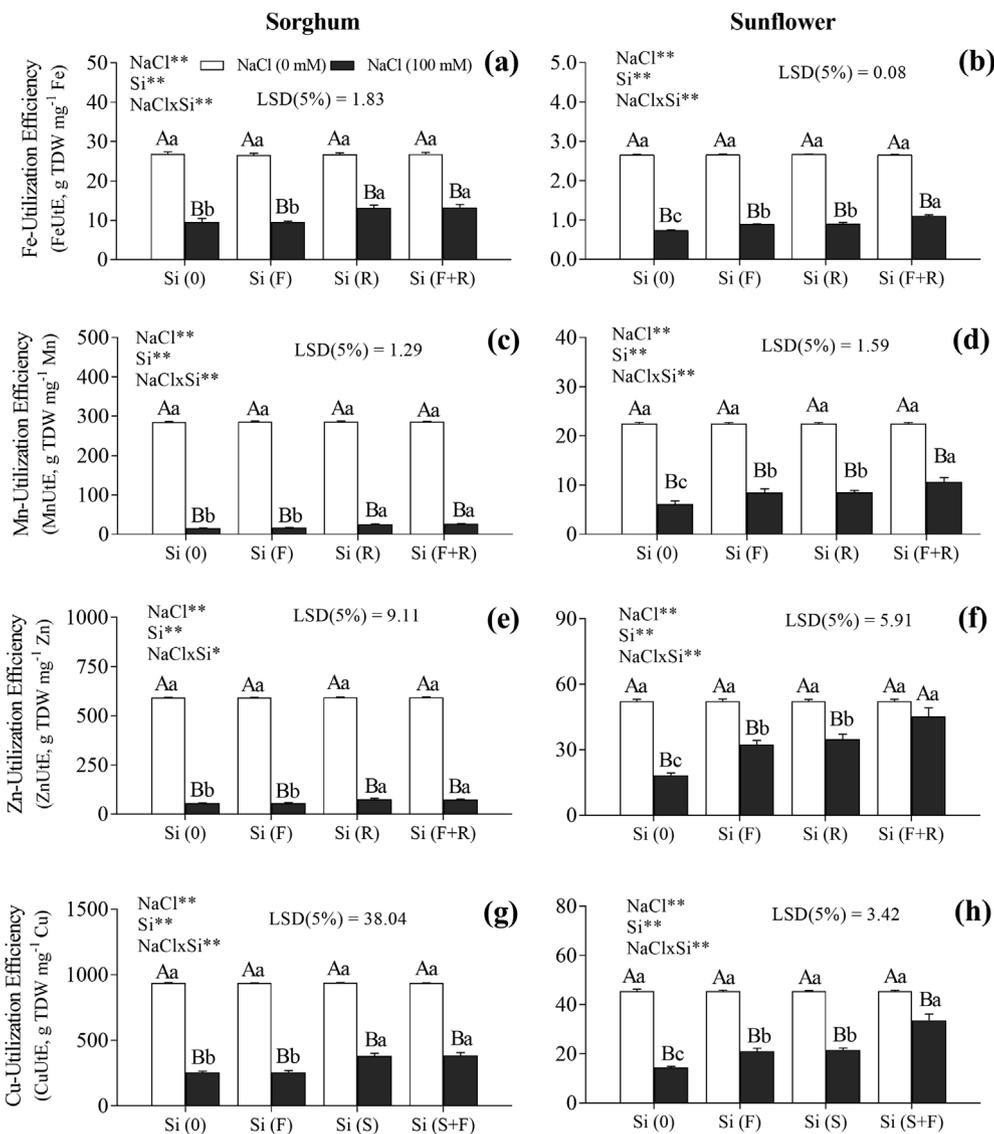
Salinity, without Si application, inhibited TDW in sorghum and sunflower plants, due to increased  $\text{Na}^+$  accumulation in the root and shoot and reduced uptake and use efficiency of most nutrients. These effects of salinity stress on TDW are consistent with the findings of previous studies in sorghum (Avci et al., 2017; Nxele et al., 2017) and sunflower plants (Kumari et al., 2016; Taher et al., 2018).

In sorghum plants, the Si (R) and Si (F + R) treatments had similar effects on RDW and TDW; both attenuated salinity by increasing the RDW by 33% and TDW up to 27% compared with that of the control (Si (0)) (Fig. 7a,c), which is similar to the findings of Yin et al. (2013) in sorghum. Therefore, it is apparent that Si attenuates the deleterious effects of salinity stress by increasing the uptake and use efficiency of both macronutrients and micronutrients.

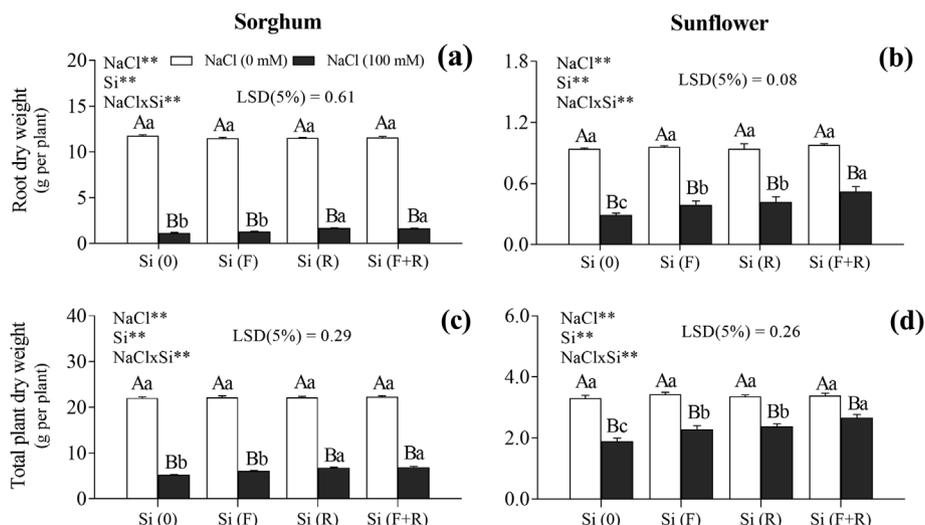
In sunflower plants, all Si treatments increased the RDW and TDW, the combined application of Si (S + F) performing better than the exclusive Si (F) and (F + R) treatments (Fig. 7b,d). The Si (F + R)



**Fig. 5.** Utilization efficiency of macronutrients under the Si and NaCl treatments. Nitrogen utilization efficiency (NUE) in sorghum (a) and sunflower plants (b), phosphorus utilization efficiency (PUE) in sorghum (c) and sunflower plants (d), potassium utilization efficiency (KUE) in sorghum (e) and sunflower plants (f), calcium utilization efficiency (CaUE) in sorghum (g) and sunflower plants (h), magnesium utilization efficiency (MgUE) in sorghum (i) and sunflower plants (j), and sulfur utilization efficiency (SUE) in sorghum (k) and sunflower plants (l). Treatments and statistics as in Fig. 2.



**Fig. 6.** Utilization efficiency of micronutrients under the Si and NaCl treatments. Iron utilization efficiency (FeU<sub>TE</sub>) in sorghum (a) and sunflower plants (b), manganese utilization efficiency (MnU<sub>TE</sub>) in sorghum (c) and sunflower plants (d), zinc utilization efficiency (ZnU<sub>TE</sub>) in sorghum (e) and sunflower plants (f), and copper utilization efficiency (CuU<sub>TE</sub>) in sorghum (g) and sunflower plants (h). Treatments and statistics as in Fig. 2.



**Fig. 7.** Root and total plant dry weight production under the Si and NaCl treatments. Root dry weight production in sorghum (a) and sunflower plants (b); total dry weight production (TDW) in sorghum (c) and sunflower plants (d). Treatments and statistics as in Fig. 2.

treatment is promising for salinity stress attenuation, as evidenced by increasing the RDW by 79% and TDW by 41% compared with that of the control treatment (Si (0)). This effect was because the Si (F + R) treatment reduced Na<sup>+</sup> accumulation in the roots and shoots and increased the uptake and use efficiency of macronutrients and micronutrients. Ashraf et al. (2015) and Alsaeedi et al. (2019) also found that supplementation of Si in nutrient solution to the roots attenuates salinity stress and increases TDW in sunflower plants.

Therefore, the benefits of Si in salinity stress alleviation occur via the maintenance of nutrient balance, which is associated with decreased sodium uptake, as reported in several studies (Ashraf et al., 2015, 2010; Liang et al., 2007; Ma, 2004; Rizwan et al., 2015; Sattar et al., 2016; Zhu et al., 2015; Zhu and Gong, 2014) and proven in the present study.

Finally, our hypotheses were verified, indicating that Si is beneficial for salinity stress alleviation in sorghum and sunflower plants due to improved nutritional efficiency, and this translates into increased TDW. Additionally, it is possible to potentiate the beneficial effects of Si in different species by modifying the mode of application.

## 5. Conclusions

Si contributes to the attenuation of salinity stress in sorghum and sunflower plants by improving nutritional efficiency. This is because Si decreases Na<sup>+</sup> uptake and increases nutrient uptake and use efficiency, thereby favoring root and total dry matter production. These beneficial effects of Si can be effectively implemented in non-Si-accumulating plants (e.g., sunflower) through Si application to the roots via nutrient solution as well as foliar application, and in Si-accumulating plants (e.g., sorghum), through Si application only to the roots via nutrient solution. The findings of this study provide insights into attenuating the harmful effects of salt stress in sorghum and sunflower plants through Si application, and could potentially lead to sustainable increase in crop yield.

## Authors contributions

RMP and DAC planned and designed the study. ACH, DAC, GSSD, and GF evaluated and performed the experiments. ACH, RMP, and DAC analyzed and interpreted the data and drafted the manuscript; all the authors read and approved the final version of the manuscript.

## Declarations of interest

None.

## Acknowledgments

We wish to thank the São Paulo State University (UNESP), for providing the necessary facilities for this study, and also the GENPLANT research for their help and assistance during the experiments. The authors are grateful to the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) [Finance Code 001, 2017-0]; and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPQ) [142490, 2018-0] for providing the PhD fellowship for the first author.

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