SÃO PAULO STATE UNIVERSITY – UNESP
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SILICON APPLICATION ALLEVIATES THE EFFECTS OF SALT STRESS IN SORGHUM AND SUNFLOWER PLANTS

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DADOS CURRICULARES DO AUTOR

ALEXANDER CALERO HURTADO – nascido em 23 de outubro de 1980 em Sancti Spiritus, Cuba, filho de Ermitaño Calero Ramos e Ismari Hurtado Borroto. Ingressou no curso de Engenharia Agronômica da Universidad Central "Marta Abreu" De las Villas em 2000 onde se tornou Engenheiro Agrônomo em 2005. Durante o período de graduação desenvolveu experimentos na área de Fitotecnia. Ingressou no curso de pós-graduação em Agronomia (Agricultura Sustentável), nível Mestrado na Universidad de Cienfuegos "Carlos Rafael Rodríguez", Cienfuegos em 2008, onde conduziu a dissertação na linha de pesquisa de Fitopatologia e obtendo o título de Mestre em Agricultura Sustentável em 2010. No período de setembro de 2005 a fevereiro de 2017 desempenhou a função de Professor auxiliar na Universidade de Sancti Spiritus "José Martí Pérez". No período de junho a setembro de 2012 realizou um estágio de investigação na Kwantlen Polytechnic University- Surrey Campus, como parte do projeto "Students for Development", com Bolsa da agencia Canadian lnternational Development Agency (CIDA). Em março de 2017 iniciou o curso de pós-graduação em Agronomia (Produção Vegetal), nível Doutorado da UNESP - Câmpus de Jaboticabal, com bolsa da CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior). Fez parte do Grupo de Estudos em Nutrição de Plantas da Unesp (Genplant) e desenvolveu pesquisas com Nutrição de Plantas, correspondentes com a tese de doutorado.

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TOPICS

SILICON APPLICATION ALLEVIATES THE EFFECTS OF SALT STRESS IN SORGHUM AND SUNFLOWER PLANTS

ABSTRACT – The effect of silicon (Si) on physiological and nutritional mechanisms to attenuate salt stress depends on the species and the mode of supply of the beneficial element. The objective of this study was evaluated whether supplied Si in different mods-manner attenuates the deleterious effects of salt stress based on the biochemical, physiological and nutritional responses of two distinct species, sorghum (accumulator of Si) and sunflower (intermediate accumulator of Si) under greenhouse conditions. Two pots experiments were carried out in a randomized block in a factorial scheme (2 × 4) with two factors, include salinity which was applied to the root medium as sodium chloride (NaCl), with the control and salt-stress groups (0 and 100 mmol L^{-1} NaCl), and the plants from each group were combined with the following Si-treatment groups: control (no Si), foliar application (28.6 mmol L^{-1}), root application (2 mmol L^{-1}), and combined foliar and root applications. Stabilized sodium and potassium silicate (SiNaKE) were used to maintain the Si levels. We tested the effects of different methods of Si applications in the response of mineral and water uptake, lipid peroxidation, proline concentration, enzymatic antioxidants activities, root diameter, leaf area, uptake and use efficiency of macronutrients and micronutrients in sorghum and sunflower plants under salinity stress conditions. Forty days after cultivation, in the stage S4 for sorghum and V8 for sunflower, the plants were harvested. Salinity stress decreased all the biological parameters. Si application resulted in higher K^+ accumulation, and lower Na^+ accumulation and lipid peroxidation levels in sorghum and sunflower leaves compared with untreated plants. In addition, Si increased the leaf relative water content, modified the proline content, enhanced enzymatic antioxidants activities, root diameter, leaf area, nutritional efficiency, and roots, shoots, and whole dry matter. These increases were more prominent under salinity stress, when Si was applied via nutrient solution in sorghum plants and the combined foliar and root applications of Si in sunflower plants. Our results also suggest that foliar Si spraying may be important in the biochemical and physiological activities for growth and development of both salt-stressed sorghum and sunflower plants.

Keywords: *Helianthus annuus*, *Sorghum bicolor*, beneficial element, enzymatic activity, nutritional efficiency, oxidative stress, proline, salinity

APLICAÇÃO DE SILÍCIO ATENUA OS EFEITOS DO ESTRESSE SALINO EM PLANTAS DE SORGO E GIRASSOL

RESUMO – O efeito do silício (Si) nos mecanismos fisiológicos e nutricionais para atenuar o estresse salino depende da espécie e do modo de suprimento do elemento benéfico. Em este estudo foi avaliado se o Si fornecido de diferentes modos atenua os efeitos deletérios do estresse salino com base nas respostas bioquímicas, fisiológicas e nutricionais de duas espécies distintas, sorgo (acumulador de Si) e girassol (acumulador intermediário de Si) em casa de vegetação. Dois experimentos para cada cultura foram realizados em blocos casualizados em esquema fatorial (2 × 4) tendo na solução nutritiva na ausência e na presença de 100 mmol L^{-1} NaCl e com fornecimento de Si em quatro formas diferentes: aplicação via foliar (28,6 mmol L^{-1}), aplicação radicular (2 mmol L^{-1}), aplicação foliar e radicular combinadas, e controle (sem Si). O Si foi utilizado na forma de silicato de sódio e potássio estabilizado (SiNaKE). Avaliaram-se o acúmulo de Si peroxidação lipídica, concentração de prolina, atividade enzimática antioxidante, diâmetro das raízes, área foliar, eficiências de absorção e uso dos macronutrientes e micronutrientes em plantas de sorgo e girassol. Aos quarenta dias após início dos tratamentos realizou-se a coleta das plantas no estágio S4 para sorgo e V8 para girassol. O estresse salino prejudicou todas as variáveis biológicos nas duas culturas. A aplicação de Si resultou em maiores acúmulos de K^+ e diminuiu o acúmulo de Na^+ e a peroxidação lipídica nas folhas de sorgo e de girassol em comparação com as plantas não tratadas. Além disso, o Si aumentou o conteúdo relativo da água nas folhas, modificou o conteúdo de prolina, aumentou a atividade das enzimas antioxidantes, diâmetro das raízes, área foliar, a eficiência nutricional e a massa seca das raízes, parte aérea e a planta inteira. Esses benefícios foram mais proeminentes sob salinidade, quando o Si foi aplicado via solução nutritiva em plantas de sorgo e a aplicação combinada de Si via foliar e radicular em plantas de girassol. Nossos resultados também sugerem que a aplicação foliar de Si pode ser importante nas atividades bioquímicas e fisiológicas beneficiando o crescimento e o desenvolvimento das plantas de sorgo e girassol estressadas por sal.

Palavras-chave: *Helianthus annuus*, *Sorghum bicolor*, elemento benéfico, atividade enzimática, eficiência nutricional, estresse oxidativo, prolina, salinidade.

CHAPTER 1 – General considerations

1. Introduction

Salinity referring to soil and/or irrigation water is the main obstacle towards maximizing the productivity and sustainability of agricultural crops, throughout the entire world and particularly in arid and semi-arid regions (Siddiqui et al., 2017). The detrimental effect of salinity on plant growth is a consequence for two main effects; osmotic pressure and toxicity resulted from ionic imbalance in plant cell and thereby affect the physiochemical processes that take place inside the plant (Munns and Gilliham, 2015; Hussain et al., 2016). Osmotic and ionic effects, are harmful to growing plants because they can cause changes in cell membrane characteristics, water status, enzyme activities, protein synthesis and gene expression (Qados, 2015). The accumulation of Na^+ and Cl^- in the protoplasm disrupts the ionic homeostasis of cells, which is essential for many physiological, biochemical and molecular processes (Munns et al., 2016).

Plants have evolved a variety of defense mechanisms to survive in saline environments. For example, osmotic adjustment involves an increase in the concentration of compatible osmolytes, such as proline, to maintain cell turgidity (An et al., 2013; Iqbal et al., 2014). Proline has antioxidant activity, activates detoxification systems, contributes to cellular homeostasis by protecting the redox balance, functions as protein precursor, and is an energy source for the stress recovery process (Reddy et al., 2015; Mansour and Ali, 2017). Overproduction of proline in plants may improve salt tolerance of plants (Shahbaz and Ashraf, 2013). Proline can now be regarded as nonenzymatic antioxidants that microbes, animals, and plants require to mitigate the adverse effects of reactive oxygen species (ROS) (Gill and Tuteja, 2010).

Results from several studies show that salinity induces excess production and accumulation of ROS including superoxide radical (O_2^-), hydroxyl radical (OH•), singlet oxygen ($1O_2$), and hydrogen peroxide (H_2O_2) can be produced in saline conditions to a high levels and accumulate in the chloroplasts and other organelles, leading to a disruption in the metabolism within plant cells through lipid peroxidation (LPO), protein oxidation and enzyme inhibition (Khoshgoftarmanesh et al., 2014).

The enzymatic antioxidant system includes a variety of enzymes, including superoxide dismutase (SOD, EC 1.15.1.1), catalase (CAT, EC 1.11.1.6), and ascorbate peroxidase (APX, EC 1.11.1.11). During the scavenging process, the primary reaction was catalyzed by SOD causing the dismutation of O_2^- into H_2O_2 and O_2. Yet H_2O_2 is also toxic to cells and has to be further detoxified by CAT and/or peroxidases such as guaiacol peroxidase (GPX) and APX into H_2O and O_2 (Singh et al., 2015; Soundararajan et al., 2017b).

An important strategy for reducing the effect of salinity in plants consists in using silicon (Si), especially in roots supplementation (Farooq et al., 2015; Muneer and Jeong, 2015; Soundararajan et al., 2017b), foliar applications (Abbas et al., 2015; Sattar et al., 2016, 2018), or both associating the foliar spraying with root application (Calero et al., 2019). It has been widely reported that Si application may increase salt tolerance in many important agricultural crops such as sorghum (Yin et al., 2013; Liu et al., 2015; Yin et al., 2016) and sunflower (Ashraf et al., 2015; Conceição et al., 2019).

It is well documented that oxidative damage caused by saline stress was ameliorated by a supply of Si that helped maintain redox homeostasis (Allen, 1997). Additionally, Si increased cell membrane H^+-ATPase activity, thus enhancing cell K^+ uptake, which in turn activated K^+ channels and transporters (Liang, 1999; Liang et al., 2006b, 2005a). Conversely, Si reduced transpiration and Na^+ uptake (Gurmani et al., 2013a; Li et al., 2015; Coskun et al., 2016). Si increases K^+ uptake and water content of tissues (Zhu et al., 2015; Abdel- Latef and Tran, 2016; Ahmad et al., 2019) and reduces LPO by eliminating ROS generation via increased activity of antioxidant enzymes (Liu et al., 2015; Coskun et al., 2016; Alsaeedi et al., 2018).

Furthermore, Si supplementation increases the ATP-synthase in the leaf chloroplasts (Muneer et al., 2014) and activates important genes associated with salt-stress responses, antioxidant synthesis, and Si transport (Muneer and Jeong, 2015). Si may enhance plant tolerance to salt stress by increasing the uptake and translocation of mineral elements in plants, as shown previously in faba bean (*Vicia faba* L.) (Hellal et al., 2012), moringa (*Moringa oleifera* L.) (Hussein and Abou-baker, 2014), tomato (Li et al., 2015), and cucumber (Alsaeedi et al., 2018).

An alternative to supplying Si to the soil for roots to absorb, is foliar spraying, which has the advantage over soil or nutrient solution applications because foliar spraying uses lower quantities of Si and can be applied in different phenological phases of crop growth. Further, there are no reports on the effects of the combined foliar and root applications of Si, to address chemical imbalance in plants under saline stress that have different Si uptake capacities; namely, Si- accumulators sorghum (foliar content of Si > 10 g kg^{-1}), and Si-intermediate accumulators such as sunflower (foliar content of Si 1- 5 g kg^{-1}) (Ma 2004; Hodson et al. 2005).

In species like sunflower, which show little uptake of Si via the roots, saline stress could be assuaged using an alternative method; that is, the combined foliar and root applications of Si. However, in Si accumulating species that absorb large quantities of the element via the roots, the complementary application of Si via foliar spraying would likely be of little benefit to counter the effects of salinity. Knowledge of the best Si supply strategy in saline environments can help minimize nutritional imbalance and favor the growth of distinct species with variable Si uptake capacity.

Therefore, we judged convenient to test the following hypotheses: (1) Si supplementation attenuates salt stress in sorghum and sunflower plants by decreasing Na^+ accumulation LPO through the modifications of enhancing K^+ accumulation, leaf relative water content (RWC), and plant biomass production; (2) Si mitigates salt stress by increasing the activities of SOD, CAT, and APX, which are involved in the regulation of lipid peroxidation; (3) Si application can be an efficient treatment to minimize the nutritional imbalance caused by salinity in sorghum and sunflower plants, by decreasing uptake of Na^+ and especially by increasing the uptake and use efficiency of macronutrients and micronutrients; and (5) the combined foliar and root applications of Si attenuates salinity effects in intermediate Si-accumulating plants (e.g., sunflower), but not in high Si-accumulating plants (e.g., sorghum). Therefore, we evaluated whether supplied Si in different mods-manner attenuates the deleterious effects of salt stress based on the biochemical, physiological and nutritional responses of two distinct species, sorghum (accumulator of Si) and sunflower (intermediate accumulator of Si).

2. Literature review

2.1 Soil salinity

Salinity is one of the major abiotic factors, limiting crop production worldwide. Approximately 7% of the world's total land area, 20% of the world's cultivated land area and nearly 50% of the world's irrigated land area are affected by salinity (Kibria et al., 2017). In Brazil, although the information on the salt affected areas is not well defined, it is estimated that 20 to 25% of irrigated areas in the Northeast region face problems of soil salinization (Pessoa et al., 2016). Part of these degraded saline areas, which are unsuitable for conventional crops, can be used to grow alternative plants to serve as a source of food, fuel, fodder, fiber, resin, essential oils and pharmaceutical products, and also for landscape reintegration (Bessa et al., 2017).

Salinity is one of the environmental factors that most limits crop growth and productivity, especially in arid and semi-arid regions, under rain-fed conditions, where low rainfall and high evapotranspiration during vegetation periods restricts the growth of crop plants (Hussain et al., 2016; Ahmad et al., 2018).

There are several classification systems for salt-affected soils in the world, for example the USDA system, the USSR system and the Australian system (Chhabra, 1996). The USDA system classifies soils in three distinct categories (saline, sodic and saline–sodic soils). Saline soils have an electrical conductivity of the saturated paste (ECe) >4 dS m^{-1}, ESP<15 or SAR<13 and pH<8.5. Sodic soils have an ESP>15 or SAR>13. Soils that have both detrimental levels of neutral soluble salts (ECe>12 dS m^{-1}) and a high-proportion of sodium ions (ESP>15 or SAR>13) are classified as saline–sodic soils (Brady and Weil, 2013) (Table 1).

Table 1. Classification of salt-affected soils.

Salt-affected soil classification	EC (dS m^{-1})	pH	Sodium uptake ratio	Soil physical condition
Saline	>4.0	<8.5	<15	Normal
Saline–sodic	>4.0	<8.5	>15	Normal
Sodic	<4.0	>8.5	>15	Poor

EC, electrical conductivity. Fonte: Brady and Weil (2013).

Salt-affected soils can be classified according to how the salinity developed: primary salinity which occurs naturally where the soil parent material is rich in soluble salts, or geochemical processes result in salt-affected soil. Secondary salinity is salinization of land and water resources due to human activities. Human activities which can induce salinization include poor irrigation management; insufficient drainage; improper cropping patterns and rotations; chemical contamination (Dudley, 1994).

2.2 Salt stress in plants

Salt stress is one of the most important factors limiting plant growth and yield worldwide (Fahad et al., 2015). However, since salt injury depends on species, variety, growth stage, environmental factors, and nature of the salts, it is difficult to define saline soils precisely (Yadav et al., 2011). Therefore, salinization of arable land is becoming more widespread and thus decreasing the yield from formerly productive soil throughout the world. Although the term salinity implies high concentration of salts in soil, NaCl constitutes the most part in soil salinity and this explains why all plants have evolved some mechanisms to regulate NaCl accumulation or exclusion (Türkan and Demiral, 2009).

Salinity inhibits plant growth in three principle ways: by ion toxicity (mainly of Na^+ and Cl^-), osmotic stress, and nutritional disruption (Munns, 2002, 2011). To understand the physiological mechanisms responsible for the salinity tolerance of species, it is necessary to know whether their growth is being limited by the osmotic effect of the salt in the soil, or the toxic effect of the salt within the plant (Munns and Tester, 2008).

Salt stress imparts stern restrictions in the metabolic stability of plants by causing ion imbalance resulting in impeded transportation of essential ions and solutes (Al-Huqail et al., 2017). Among the key physiological and biochemical processes impaired by high salinity include transpiration, photosynthesis, protein synthesis, etc., (Asrar et al., 2017). This is induced by over-production and accumulation of ROS. The reasons causing an oxidative stress mainly include: (i) an imbalance between ROS generation and detoxification due to disturbance of ‘normal’ cell physiology; (ii) ROS biosynthesis de novo as a constituent part of stress signaling and immunity response needed for defense and adaptation (Demidchik, 2015).

Apart from the restrictions in the uptake of mineral nutrients and the hindrances in key physiological processes, greater accumulation of toxic ions leads to excessive generation of ROS thereby leading to oxidative damage to cells (Siddiqui et al., 2017). The key toxic ROS include singlet oxygen, superoxide ions, hydroxyl ion and hydrogen peroxide which can easily target important biomolecules like membrane lipids and proteins, nucleic acids, etc. (Asrar et al., 2017; Demidchik, 2015).

Toxic ions, predominantly sodium (Na^+) and chloride (Cl^-), accumulate in the protoplasm and causing ionic imbalance and metabolic and nutritional disorders, while decreasing plant growth (Munns, 2011). Excess Na^+ in the soil decreases K^+ concentration in the plant, especially in roots (Agarie et al., 1998). This is due to the combined action of decreasing inflow and increasing efflux of K^+ (Apse and Blumwald, 2007) mediated by transporters and K^+ channels located in the plasmalemma (Voigt et al., 2009). Therefore, Na^+ accumulation in the cell is partly a result of competition between Na^+ and K^+ for the active sites of the enzymes and ribosomes (Tester and Davenport, 2003), whereby essential metabolic processes might be hampered (Munns et al., 2016).

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 (Grattan and Grieve, 1999; Munns et al., 2016). Further, a high cytosolic Na^+ concentration induces changes in the absorption and metabolism of calcium (Ca^{2+}). Na^+ replaces Ca^{2+} on cell membranes (Rengel, 1992) and cell wall (Nilsen and Orcutt, 1996), hence decreasing their permeability, which in turn reduces their elasticity (Neumann et al., 1994) and worsens salinity damage to the plant. Moreover, a low Ca^{2+} concentration in the plant interrupts stress-signal transduction processes that would otherwise attenuate plant damage (Türkan and Demiral, 2009).

An excess accumulation of Na^+ in plant tissues tends to increase Na^+/K^+ ratio, thereby altering cellular ionic and nutritional homeostasis (Apse and Blumwald, 2007; Munns et al., 2016). The resulting decrease in cellular metabolic efficiency can induce symptoms that start with chlorosis and develop into early leaf senescence (Hanin et al., 2016; Munns et al., 2016), and ultimately, plant death (Shi et al., 2002). Further, overall salinity decreases the equilibrium between cations and anions, osmoregulation and many other essential metabolic processes (Hasanuzzaman et al., 2018). This disruption of homeostasis occurs at the cellular level and throughout the whole plant, causing molecular damage, restricting growth and perhaps even leading to plant death (Luma et al., 2016).

2.3 Osmoprotectant proline

Plants have evolved a variety of defense mechanisms to survive in saline environments. Salinity stress detrimental to plant metabolism through ion toxicity, osmotic stress, and oxidative stress (Munns, 2011; Ahmad et al., 2019). The response to osmotic stress initially involves osmotic adjustments. Osmotic adjustment is critical for keeping cell turgor, which allows the maintenance of plant metabolic activity and in turn plant growth and yield (Munns et al., 2016).

One of the cellular responses to saline conditions is the alteration of metabolism and production of compatible solutes, which are distributed among different organisms. Compatible compounds can be highly accumulated in different species without disturbing their intracellular metabolism (Liang et al., 2018). Plants synthesize proline, soluble sugars, glycine, betaine, and other osmolytes to promote osmotic balance at the cellular level (Monsour e Ali, 2017). Among quaternary amino acid derivatives, glycinebetaine and proline are the most common solutes involved in plants under salinity conditions (Mansour and Ali, 2017; Liang et al., 2018).

Proline accumulation is one of the most prominent changes in plant metabolism in response to salt stress. Some reports have demonstrated that proline is significantly higher in response to saline environments, and this accumulation has been thus suggested to correlate with plant salt tolerance (Liang et al., 2018).

Accumulation of proline has been reported to be generally higher in non-tolerant plants than in salt tolerant plant species (An et al., 2013; Iqbal et al., 2014) suggestive of proline role in plant stress tolerance. Similarly, under salinity conditions proline concentration was higher in sunflower (Conceição et al., 2019) and in sorghum plants (Freitas et al., 2019). Proline has been suggested in the earlier studies to contribute to osmotic homeostasis, and eventually salt acclimation. As proline accumulates normally in the cytoplasm for osmotic adjustment in response to salinity stress (Mansour and Ali, 2017; Liang et al., 2018).

It is interesting to note that proline in these low concentrations enhances adaptation to high salinity in a variety of plant species. Proline has been shown to have antioxidant activity, activates detoxification systems, contributes to cellular homeostasis by protecting the redox balance, functions as protein precursor, an energy source for the stress recovery process (Reddy et al., 2015; Mansour and Ali, 2017; Liang et al., 2018). Also, proline can protect the plasma membrane by enhancing activities of various antioxidant systems to minimize membrane lipid and protein oxidation resulted from salinity-induced oxidative stress (An et al., 2013).

Further, proline protects the photosynthetic apparatus and proteins by functioning as ROS scavenger, showing through the antioxidant activity, and thus kept better plant growth under saline conditions (Mansour and Ali, 2017).Therefore, the beneficial effect of proline concentrations on plants might be because the existing proline can be degraded and used as a source of carbon and nitrogen in plants recuperating from salt stress (An et al., 2013; Reddy et al., 2015). Considering the above argument, it is clear that proline contributes to osmotic adjustment, protective functions and ion homeostasis. Consequently, proline can help as a selection criterion for the tolerance of numerous species under salinity conditions despite its debatable role.

2.4 Silicon in plants

Although Si is not considered as an essential element, it is beneficial to the plant growth. Its effect is more evident under abiotic and biotic stress conditions (Coskun et al., 2019). Nevertheless, debates regarding essentiality must consider that food products derived from Si-exposed plants offer greater bone strength and improved nervous and immune system functions in human beings (Farooq and Dietz, 2015). Silicon is taken up by plants in the form of monosilicic acid (Si_4OH_4), a prevalent and uncharged monomeric molecule, when the solution pH is below 9 (Ma et al. 2006).

The first report of the identification of Si transporters in plants was in rice (Ma et al., 2001). This Si root uptake involves specific low silicon (*LSi1*) channel identified for the first time in rice by Ma and Yamaji, (2006). Si can be then translocated to the shoots thanks to two other Si transporters, i.e., *LSi2* [which allows Si efflux outside the Casparian strip in the roots (Ma et al., 2007)] and *LSi6* expressed only in leaves (Kaur and Greger, 2019). Subsequently, Si is polymerized and accumulates in amorphous forms in plant tissues (SiO_2-nH_20) (Bauer et al., 2011; Raven, 2003).

The process of Si polymerization converts silicic acid to colloidal silicic acid and finally to silica gel with increasing silicic acid concentration (Ma and Takahashi, 1993; Ma and Yamaji, 2015). More recently, transporters were also exposed in other plants including cucumber (Liang et al., 2005a), barley (Chiba et al., 2009), wheat (Montpetit et al., 2012), and pumpkin (Mitani et al., 2011).

The beneficial effects of Si are significantly hampered by the uptake ability of plants. However, vascular plants accumulate large ranges of Si, from 0.1 to 15% of dry weight (Epstein, 1999), and agricultural crops are frequently classified into three main groups (weak, medium, and strong Si accumulators) according to their Si contents. Thus, dicotyledon species with low Si contents (around 0.1% of dry weight) are classified as “low Si accumulators.” Monocotyledon crops are considered either as “intermediate accumulators” if Si content is between 1–3% of dry weight (as rye, oats, or wheat) or as “strong accumulators” if their Si content reach 5% of dry weight (as cultivated rice) (Deshmukh and Bélanger, 2016; Epstein, 1999; Hodson et al., 2005; Liang et al., 2007).

More recently, it has been reported that both active and passive mechanisms are operating in Si uptake and transport in the same Si-accumulator such as rice, sorghum and maize and intermediate type species such as sunflower and wax gourd with their contribution being dependent upon plant species and external Si concentrations (Liang et al., 2006). The content of Si in plants is equivalent to or more than the major nutrients N, P, and K, which are supplied through fertilizers (Epstein, 1999; Meena et al., 2014).

In general, some research suggests that the use of Si in agricultural is a sustainable strategy for the attenuation of detrimental effects of salt stress (Rizwan et al., 2015; Etesami and Jeong, 2018; Kim et al., 2017; Zargar et al., 2019). Overall, the inclusion of Si is important for plant growth and numerous reports and reviews illustrated the Si dependent modulations of antioxidant enzymes, nutrient contents, homeostasis in reactive oxygen species. However very few studies have dealt with the Si-mediated molecular regulation of genes in plants under abiotic and biotic stresses (Muneer et al., 2014; Muneer and Jeong, 2015; Yin et al., 2016).

Silicon nutrition resulted in the improvement of growth and development (Eneji et al., 2008; Liu et al., 2015; Soundararajan et al., 2017b), increase in yield (Epstein, 1999; Abbas et al., 2017; Rohanipoor et al., 2013), and management of macro and micro nutrients (Tripathi et al., 2014; Alsaeedi et al., 2018; Yaghubi et al., 2019). Likewise, Si inclusion in tissue nutrient solution resulted in the enhancement of axillary shoot induction (Manivannan and Ahn, 2017), attenuation of hyperhydricity (Soundararajan et al., 2017a), and root morphogenesis (Asmar et al., 2013).

2.5 Importance of silicon in mitigates the detrimental effects of salinity

Si ameliorated attenuation of salinity stress in plants through the regulation of photosynthesis, root developmental changes, redox homeostasis equilibrium, and regulation of nutrients have been demonstrated (Liu et al., 2019).

In general, Si-mediated salinity stress resistance mechanism can be attributed to the following physiological improvements in plants; enhancement of growth and biomass (Soundararajan et al., 2018), management of nutrients (Rizwan et al., 2015), maintenance of structural rigidity (Schoelynck et al., 2010), increased photosynthesis efficiency (Khan et al., 2018), lodging resistance (Epstein, 1999), balancing the ion homeostasis (Alsaeedi et al., 2018; Yaghubi et al., 2019), activation of antioxidant system in plants (Soundararajan et al., 2017), elicitation of secondary metabolites related to stress resistance (Manivannan and Ahn, 2017), and regulation of genes involved in various physiological processes (Muneer and Jeong, 2015). Thus, the numerous merits of Si have been introduced in several crops to increase the productivity and stress tolerance.

Si has been proven to foster progression and biomass, yield, and quality of a broad range of crops including monocotyledonous crops, some dicotyledonous crops, and some vegetable and fruit crops under salinity conditions (Etesami and Jeong, 2018), which actively take up and accumulate high amounts of Si in their tissue (Liang et al., 2006a, 2007). Many studies have reported that different application methods via the soil and foliar spraying can reduce salt stress in plants. Some details of these studies are given below.

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2.5.1 Root Si supplementation

Plants will absorb Si in the form of Si_4OH_4 from soil or nutrient solutions and by the leaves. The maximum solubility of Si_4OH_4 in solution is on the concentration at 2 mM, and its concentration in soil solutions usually varies between 0.1 and 0.6 mM (Coskun et al. 2019). It has been extensively reported that Si supplementation decreased Na^+ uptake by plants under salt stress (Tuna et al., 2008; Rizwan et al., 2015; Xu et al., 2015). These studies were reported in several plant species such as rice (Gong et al., 2006; Gurmani et al., 2013b; Shi et al., 2013), wheat (Liang, 1999; Ali et al., 2009; Gurmani et al., 2013a), and cucumber (Liang et al., 2006, 2007). Si increases plant resistance to salt stress by decreased Na^+ uptake via the Na^+-H^+ exchangers *HvSOS1* in the plasma membrane and *HvNHX1* in the tonoplast, respectively and increasing K^+ ion uptake (via K^+-H^+ symporters such as *HvHAK1*) (Rizwan et al., 2015).

The decreasing of Na^+ uptake might be attributed to Si-mediated stimulation of the root plasma membrane H^+-ATPase activity under salt stress as previously reported in barley (Liang et al. 2005, 2006) and aloe (Xu et al. 2015). This increase in K^+ uptake and decrease in Na^+ uptake and translocation might be due to deposition of Si in roots which could decrease Na^+ bypass flow previously found in rice (Yeo et al., 1999; Gong et al., 2006; Gurmani et al., 2013b) and wheat (Gurmani et al., 2013a). Several studies described the Si-mediated increase in K^+ uptake and decrease in Na^+ translocation towards shoots in wheat plants under salt stress (Tuna et al., 2008; Tahir et al., 2011).

Si application (1.44 g kg^{-1} soil) with SiO_2 via soil, increased SOD, POD, CAT, APX, and GSH activities in sorghum under salinity stress in filed conditions, and Si (1.92 g kg^{-1} soil) increased the membrane stability index, soluble sugar and total phenol contents, CAT, SOD and total antioxidant activity (Kafi et al., 2011). Similarly, Nabati et al. (2013) reported that Si (1.92 g kg^{-1} soil) as SiO_2 via soil, attenuated detrimental effects of salinity by increased photosynthetic rate, transpiration rate, quantum yield, total pigments, and dry matter accumulation in sorghum plants.

It has been reported that Si supplementation (0.83 mM) with metasilicic acid in root medium decreased Na^+ concentration, proline levels and increased relative water content, sucrose and fructose in sorghum under salt stress (Yin et al., 2013). Similarly, Si application (1.67 mM) as sodium silicate via nutrient solution decreased root H_2O_2 levels and enhanced root hydraulic conductance (Lp), increased upregulated transcript levels of several aquaporin genes, water uptake, and stimulated the activities of antioxidant enzymes in salt-stressed sorghum plants (Liu et al., 2015).

More recently, Yin et al. (2016) reported that Si application (0.83 mM) in the form of metasilicic acid via the root medium attenuated salt stress effects in sorghum seedlings by decreasing Na^+ accumulation and increased polyamines and decreased ethylene. It has been widely reported that Si application may increase salt tolerance in several Si accumulators plant species such as barley (Liang et al., 2005b, 2006a), wheat (Gurmani et al., 2013a; Bybordi, 2014), rice (Gong et al., 2006; Gurmani et al., 2013a; Kim et al., 2014), and maize (Xie et al., 2015; Khan et al., 2018; Moradtalab et al., 2018).

Silicon application (2 mM) as sodium silicate via nutrient solution enhanced both the protein content and the activities of enzymatic, SOD, POD, and CAT, and non-enzymatic, AA and GSH, and decreased lipid peroxidation in sunflower seedlings under salinity stress (100 mM) (Ali et al., 2013). Similarly, Si supplementation (50 mg kg^{-1} soil) with sodium silicate applied to the soil, decreased Na^+ accumulation and increased K^+ concentration, K^+/Na^+ ratio, relative water content, and membrane stability index are the main factors contributing to improved adaptation capability of sunflower to NaCl stress (Ashraf et al., 2015).

Recently, Flam-Shepherd et al. (2018) observed that Si (1.67 mM) as sodium silicate via nutrient solution, increased growth and lowered Na^+ concentration in shoots of rice cultivars under salt stress conditions. The authors concluded that, while Si can reduce Na^+ translocation via bypass flow in some (but not all) rice cultivars, it does not affect unidirectional Na^+ transport or Na^+ cycling in roots, either across root cell membranes or within the bulk root apoplast. Similarly, Si (2 mM) as sodium silicate via the root medium ameliorated salt-induced damages in salt-stressed rice cultivars by altering ascorbate-glutathione cycle (Das et al., 2018).

Si supplementation (2.0 mM) as silicic acid in nutrient solution increased vegetative growth, stem, leaf dry matter weight and the pH of the tomato juice, and decreased the number of fruits with blossom-end rot in salt-stressed tomato seedlings (Korkmaz et al., 2018). Similarly, Soundorajaran et al. (2018) reported that Si addition (1.8 mM) as potassium silicate on roots medium decreased the content of malondialdehyde, O_2^-, and H_2O_2, enhanced activity of antioxidant enzymes such as SOD, CAT, APX, and GPX, and increased protein on roots to overcome the salinity stress in *Rosa hybrida* plants. Application of Si (4 mM) as potassium silicate on root medium promoted higher growth, gas exchange, tissue water and membranes stabilities, and K^+ content, had limited MDA and Na^+ content and reduced electrolyte leakage in salt stressed wheat plants (Alzahrani et al., 2018).

It has been reported that the Si addition at 1 mM with nano-silicon oxide (nano-SiO_2) in nutrition solution decreased of Na^+ concentration, lipid peroxidation, and reactive oxygen species production and improved shoot and root growth, K^+ concentration, antioxidant activities, non-enzymatic compounds in salt-stressed soybean seedlings (Farhangi-Abriz and Torabian, 2018).

Similarly, Si supplementation at 2 mM with metasilicic acid on root medium attenuated both osmotic and oxidative stress in salt-stressed maize plants by decreasing Na^+ accumulation and improving water-use efficiency, ion accumulation, photosynthetic rate, enzyme activities, and phenolic compounds (Khan et al., 2018).

Silicon use in doses of 1.0 and 1.5 mM using silicic acid as source, applied via nutrient solution, significantly increased the shoots and roots weight, content of photosynthetic pigments, accumulation of nitrates and decreased the peroxidation of membrane lipids and malondialdehyde concentration in salt stressed wheat seedlings and leaves (Sienkiewicz-Cholewa et al., 2018). Correspondingly, the addition of Si (2.5 mM) as sodium silicate on root medium significantly decreased the MDA content and enhanced water relations, chlorophyll contents and antioxidant activity of SOD, CAT and POD the activities of SOD in salt–stressed maize plants (Fialová et al., 2018).

Silicon supplied (1.5 mM) to the root medium in the form of orthosilcici acid accumulates less Na^+ in both root apex and cortex, by increased presence of *ZmSOS1* and *ZmSOS2* in the root apex and cortex facilitating Na^+ exclusion, and in the root stele for enhanced Na^+ loading into the xylem. Also, Si down-regulated the expression of *ZmHKT1* in the root stele, which further decreased Na^+ unloading from the xylem. Consequently, Si increased accumulation of Na^+ in leaves, but also enhances sequestration of Na^+ into the vacuoles thereby decreasing Na^+ accumulation in the chloroplasts on maize plants under salt stress conditions (Bosnic et al., 2018).

More recently, Si at 2 mM, modulated nitrogen metabolism and antioxidant enzyme activities in sunflower plants in order to attenuate the harmful effects of salinity observed that Si (2 mM) in the form of sodium silicate via nutrient solution decreased the levels of H_2O_2, lipid peroxidation, and electrolyte leakage and enhanced the antioxidant enzymes (SOD, CAT, APX and GR), the accumulation of K^+ and Ca^{2+} and decreased Na^+ in Si-supplemented mung bean plants under NaCl stress (Conceição et al., 2019).

So far, mechanisms of Si-mediated attenuation of salt stress in plants is poorly understood at the molecular and genetic levels; more genetic experiments are required to determine linkage relationships between Si and salt stress to study the expression level of genes related to transport, deposition, and translocation of Na^+ and Si in different plant species.

Some results suggest that foliar Si application showed significant increases in the Si contents of the leaves compared to non-treated plants (Laane, 2018)

2.5.2 Foliar application of Si

The use of foliar sprays with Si compounds is relatively new. Foliar Si sprays increase growth and yield and decrease of detrimental effects of salinity stresses. Foliar sprays with Si are effective to attenuate salt stress, regardless of source, compound, and concentrations applied. High Si concentration as foliar spraying should guarantee the greatest uptake and accumulation of the element by the leaves of plants. Therefore, it is important to use the best source and the concentration of Si in the solution to use via foliar spraying. Recently foliar sprays with the source of stabilized sodium and potassium silicate at a concentration of ~1 g L^{-1} (28.6 mmol L^{-1}) performing high Si accumulation in sorghum plants (Oliveira et al., 2019). It has been reported that the Si applied to leaves as foliar spray attenuates salinity stress (Abbas et al., 2015; 2017; Sattar et al., 2016, 2018).

Among the most important mechanisms of plant resistance to salt stress is to decrease Na^+ uptake and accumulation by plants (Rizwan et al., 2015). It has been reported that foliar application of Si (17 mmol L^{-1}) enhanced the ratios of fatty acid unsaturation, in glycolipids and phospholipid and elevated amounts of membrane lipids in salt-stressed strawberry plants (Wang and Galletta, 1998). Supporting evidence for this includes reports that foliar Si spraying (1000 ppm SiO_2) reduced Na^+ concentration and increased K^+ concentration, K:Na ratio, chlorophyll and carotene, pod yield, seed number per plant, chlorophyll contents, and yield of faba bean under salt stress (Hellal et al., 2012).

Foliar Si spraying (300 ppm SiO_2) with potassium silicate decreased Na^+ uptake and increased P, K, Ca, and Mg concentrations in salt-stressed moringa (*Moringa oleifera* L.) plants (Hussein and Abou-baker, 2014). Similarly, foliar application of Si (4 mmol L^{-1}) as potassium silicate decreased Na^+ uptake, increased potassium and consequently improved plant weight, 100-seed weight, seed yield, ear length, and photosynthesis rate has been observed in salt-stressed wheat (*Triticum aestivum* L.) plants (Bybordi, 2014).

It has been reported that the foliar Si spraying (150 mg L^{-1}) with silicic acid decreased Na^+ uptake and lipid peroxidation and increasing relative water content, proline, glycine betaine, total free amino acids, photosynthetic rate, stomatal conductance, transpiration rate, water use efficiency, number and size of stomata, and SOD, POD, and CAT activities has been observed in salt-stressed okra (*Abelmoschus esculentus* L.) plants (Abbas et al. 2015). As well as, Shahid et al. (2015) reported that foliar spray of Si (150 mg L^{-1}) with potassium silicate decreased lipid peroxidation, electrolyte leakage, and H_2O_2 content by strengthening the enzymatic and nonenzymatic (proline and glycine betaine) antioxidant defense system and increased growth, gas exchange attributes, and productivity of pea (*Pisum sativum* L.) under salt stress conditions.

Foliar spray with Si (1 mM) with potassium silicate on *Cynodon dactylon* (L.) Pers., *Festuca arundinacea* (Schreb.) and *Lolium perenne* (L.) ameliorated the adverse effects of salinity by decreased Na^+ concentration and increased chlorophyll content, proline content, K^+ concentration, shoot length and shoot number in all turfgrasses (Esmaeili et al., 2015). More recently, Abbas et al. (2017) reported that the foliar application of Si (150 mg L^{-1}) as silicic acid increased leaf area and leaf area index, Ca and Mg concentrations and enhancing the turgor potential, relative water contents, activity of APX and POD, and nitrate reductase levels and activity in salt stressed okra plants. Similarly, Sattar et al. (2017) foliar Si spraying (50 mM) with silicic acid improved the plant growth, water relations, photosynthetic attributes, transpiration rate and chlorophyll contents in salt-stressed wheat seedlings.

In salt-stressed soybean plants, foliar Si sprays (1 mM) with silica nanoparticles (nano-SiO_2) decreased Na^+ concentration, lipid peroxidation, and reactive oxygen species production and increased K^+ concentration, antioxidant activities, non-enzymatic compounds (Farhangi-Abriz and Torabian, 2018). As well, foliar application of Si (70 mg L^{-1}) in the form of potassium silicate increased the activity antioxidant enzymes such as SOD, CAT and guaiacol peroxidase in strawberry plants under salt stress conditions (Park et al., 2018). Amer and El-Emary (2018) reported that foliar Si spraying (nano-silica concemntration 300 mg L^{-1}) increased the chlorophyll content, nitrogen uptake and nitrogen use efficiency of maize and faba bean growing under salinity conditions.

On the other hand, foliar Si spraying (50 mM) (without Si source mentioned) improved the morphology, water relations, photosynthetic pigments and gas exchange parameters, and the activity of SOD, CAT, and POD in salt-stressed wheat seedlings under salinity (Sattar et al., 2018). More recently, Yavaş et al. (2019) (without Si source mentioned) evaluated the foliar Si spraying increased the steviol glycoside contents, rebaudioside-A, stevioside accumulation, and the fresh weight in salt-stressed *Stevia rebaudiana* plants.

In conclusion developing more detailed knowledge about the interactions between plant and foliar Si application, would facilitate a better under-standing of attenuating salinity stress and maybe would allow better predictions concerning the plant response.

2.6 Importance of sorghum and sunflower crops

2.6.1 *Sorghum bicolor*

The estimate of world sorghum (*Sorghum bicolor* L.) productivity in the 2018/19 harvest is 1.49 t ha^{-1}, of which Brazil is responsible for the productivity of 3,008 kg / ha, making it the 9th largest producer of grain sorghum in the world (Conab, 2019). *S. bicolor* constitutes the major source of proteins, calories and minerals for millions of people, principally in Africa and Asia (Ahmed and Babiker, 2011; Dicko et al., 2006). However, the human consumption of sorghum in Brazil is not significant and its production is destined mainly for animal feed. In Brazil, sorghum cultivation expanded starting in 1971, initiated by seed and feed companies, as a promising alternative to use to corn, because it is more rugged and highly adaptable to variable climatic conditions (Mariguele and Silva, 2002). The sorghum average yield per hectare in 2016 was 1193.1kg ha^{-1}) (FAO, 2018) which is still relatively low.

Sorghum belongs to the Poaceae family, a species originating from the central region of the African continent. *S. bicolor* can be classified as sweet, grain and forage type (Almodares and Hadi, 2009). Sorghum is an important industrial crop that was moderately tolerant of drought and salt stress (Nxele et al., 2017). This cereal is mainly considered as a subsistence crop because of its unique tolerance to drought and adaptation to dry tropical and subtropical ecosystems throughout the world. It is cultivated in arid and semi-arid areas of the world because of its ability to grow under water limited conditions (Avci et al., 2017; Nxele et al., 2017).

Recent development studies about the genetic mechanism of sorghum showed that it is an important cellulose-providing crop (Kausar and Gull, 2019). The cultivation of sorghum in drought and salinity hit areas for food sources is needed to exploit new genotypes of sorghum cultivars (Cui et al., 2018). Salinity stress decreases growth in sorghum (Avci et al., 2017; Nxele et al., 2017).

2.6.2 *Helianthus annuus*

The sunflowers of the genus *Helianthus* comprise some 67 species, all native to the Americas; the majority of them are found in the United States. Most sunflower (*Helianthus annuus* L.) historians agree that the present cultivated sunflower in North America stems from materials reintroduced from Russia after the crop became widely grown there (Strasburg and Rieseberg (2008). Sunflower is one of the most important oilseed crops in the world, because its grains have high oil content (38% to 50%), primarily used for the production of high-quality oil (Birck et al., 2017). The production of sunflower increases the supply of protein meal for animal feeding, which enables an increase of protein production, more specifically meat, eggs and milk (Leite et al., 2007). Grain production systems in Brazil have peculiarities, since two to three different crops are grown in a special arrangement (simultaneously), in the same area and year. In spite of the small cultivated area in Brazil of 62.3 thousand hectares, sunflower is used in succession or rotation with other grain crops such as soybean or maize, showing an enormous potential for expansion and can be cultivated from latitudes 33°S to 5°N, especially in the Brazilian Cerrado biome (Castro and Leite, 2018).

Sunflower cultivation in succession with soybean as a second summer crop can also reduce environmental impacts because of the more efficient usage of production factors, such as land use and sharing of agricultural inputs, machinery, infrastructure and workforce (Birck et al., 2017). The success of establishing the sunflower is associated with the adequate management of soil fertility, use of cultivars adapted to different environments, plant arrangement, seed quality and adequate phytosanitary management, among other factors (Castro and Leite, 2018).

This plant is usually preferred in arid and semi-arid regions under rain-fed conditions, where low rainfall and high evapotranspiration during vegetation periods restricts the growth of crop plants (Kaya et al., 2019). Sunflower is a species that is moderately susceptible to salinity and suffers progressive reduction of agronomic parameters with increasing concentration of salts in the root medium (Rauf, 2008; Kaya et al., 2019). The effect of salinity in decreasing plant growth has been extensively reported by several authors regarding sunflower (Taher et al., 2018; Kaya et al., 2019).

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CHAPTER 2 – Silicon application in different methods attenuates salinity stress on the growth of sorghum and sunflower plants through the modifications of mineral and water uptake, proline, and enzymatic antioxidants activities [1]

Abstract

Salt stress is a major environmental factor, which negatively affects plant growth and productivity. Recent research has suggested that the application of silicon (Si) exerts beneficial effects against salt stress in sorghum and sunflower plants by adequate regulation of the antioxidant system, mineral nutrients, and other mechanisms. However, it remains unclear whether these effects can also be achieved through the foliar application of Si and whether Si application affects Si-accumulating (sorghum) and intermediate -Si-accumulating (sunflower) plant species differently. Accordingly, in this study, we aimed to elucidate the relationship between salinity and different methods of Si application in attenuating the negative effects of salt stress, based on the biological responses of two distinct species of Si accumulators under greenhouse conditions. Two pots experiments were designed as a factorial design (2 × 4) based on a randomized block design with the control and salt-stress groups (0 and 100 mmol L^{-1} NaCl) were established, and the plants from each group were assigned to the following Si-treatment groups: control (no Si), foliar application (28.6 mmol L^{-1}), root application (2 mmol L^{-1}), and combined foliar and root applications. Our results showed the harmful effects of saline stress were attenuated by Si treatments in both plant species which decreased Na^+ uptake and lipid peroxidation and increased K^+ uptake, relative leaf water content, antioxidant enzyme activities, root diameter, leaf area and shoot dry matter. These results were more prominent when Si was applied via nutrient solution in the sorghum plant and the combined foliar and root applications of Si in sunflower plants. In addition, foliar Si spraying alone constitutes an efficient alternative to attenuate the effects of salinity in both species when Si is not available in the rooting medium. These results suggest that Si application may be involved in defensive mechanisms, with positive effects on the growth of sorghum and sunflower plants under salt stress.

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Keywords: salt stress; foliar application; *Helianthus annuus*; leaf silicon; *Sorghum bicolor.*

1 Introduction

Salinity is an abiotic stress that limits the yield of agronomic crops that are important for the production of both food and industrial products (*Munns,* 2011; *Munns and Gilliham,* 2015). Therefore, understanding the mechanisms of adaptation of the plant to salt stress is important, especially when attempting to improve plant productivity in saline environments (*Munns and Gilliham,* 2015; *Negrão et al.,* 2017).

Low rainfall, which results in water deficit, is a common occurrence in salt environments. Sorghum (*Sorghum bicolor* L. Moench) exhibits moderate to high tolerance to drought stress (*Masojídek* et al., 1991), whereas sunflower (*Helianthus annuus* L.) has been reported to exhibit low to moderate tolerance to drought stress (*Kaya et al.,* 2019; *Rauf,* 2008). Therefore, sunflower and sorghum represent potential options for cultivation in salt environments, provided that their tolerance levels can be enhanced.

Plants have evolved a variety of defense mechanisms to survive in saline environments. For example, osmotic adjustment involves an increase in the concentration of compatible osmolytes, such as proline (Pro), to maintain cell turgidity (*An et al.,* 2013; *Iqbal et al.,* 2014). Pro has antioxidant activity, activates detoxification systems, contributes to cellular homeostasis by protecting the redox balance, functions as protein precursor, and is an energy source for the stress recovery process (*Mansour and Ali*, 2017; *Reddy et al.,* 2015). Pro has also been shown to minimize the damage caused by reactive oxygen species (ROS), and thus, protects the photosynthetic apparatus by reducing lipid peroxidation (LPO) (*Mansour and Ali*, 2017).

Salt stress induces the production of ROS, which alter and modify the functionality of macromolecules. Therefore, plants have also developed antioxidant systems that decrease ROS generation (*Kibria et al.,* 2017). The enzymatic antioxidant system includes a variety of enzymes, including superoxide dismutase (SOD, EC 1.15.1.1), catalase (CAT, EC 1.11.1.6), and ascorbate peroxidase (APX, EC 1.11.1.11). Indeed, SOD constitutes the first line of enzymatic defense against ROS and converts superoxide radicals (O_2^-) into H_2O_2. Subsequently, H_2O_2 is converted into

H_2O by CAT and APX, thereby preventing lipid peroxidation by ROS (*Amirjani,* 2012; *Singh et al.,* 2015).

Salinity attenuators, such as K, Se, and Si, have been studied to determine the mechanisms by which they minimize the effects of salt stress on plants (*Hasanuzzaman et al.,* 2018; *Sattar et al.,* 2017; *Shekari et al.,* 2017); one of the more frequently used attenuators that mitigate salt stress is Si (*Etesami and Jeong,* 2018; *Liu et al.,* 2019). It has been widely reported that Si attenuates the salt stress through via to the soil and nutrient solution, including sorghum (*Calero et al.,* 2019; *Liu et al.,* 2015; *Yin et al.,* 2016, 2013) and sunflower (*Ashraf et al.,* 2015; *Calero et al.,* 2019; *Conceição et al.,* 2019) or by via foliar spray were also previously reported in okra (*Abbas et al.,* 2015; *Sattar et al.,* 2017), wheat (*Sattar et al.,* 2018, 2017) , strawberry (*Park et al.,* 2018), maize and faba bean (*Amer and El-Emary,* 2018), and sunflower plants (*Calero et al.,* 2019).

Si attenuates the effects of salinity on plants in several ways, such as by maintaining the water retention capacity of leaves, reducing oxidative stress, relieving ionic toxicity via the biosynthetic regulation of solutes, and increasing transpiration (*Zhu and Gong,* 2014). The effect of Si on the attenuation of Na^+ toxicity is the most widely studied mechanism, and Si has been shown to both reduce Na^+ uptake and increase K^+ uptake in a variety of species, including barley (*Liang et al.,* 2005b), mungbean (*Ahmad et al.,* 2019), and cucumber (*Alsaeedi et al.,* 2018).

At the cellular level, the accumulation of Si might reduce cytoplasmic Na^+ concentration and increase K^+ concentration, thereby stimulating H^+-ATPase enzymes in the plasma membrane (*Liang et al.,* 2006b, 2005b). This stimulatory effect of Si on H^+-ATPase activity in the plasma membrane has been reported in barley plants cultivated under salt stress (*Liang,* 1999). Si increases K^+ uptake and water content of tissues (*Ahmad et al.,* 2019; *Zhu et al.,* 2015) and reduces LPO by eliminating ROS generation via increased activity of antioxidant enzymes (*Coskun et al.,* 2019; *Liu et al.,* 2015). Furthermore, Si supplementation increases cytochrome *b6/f* complex and ATP-synthase in the leaf chloroplasts (*Muneer et al.,* 2014). Similarly, Si application activates important genes associated with salt-stress responses (*leDREB-1*, *leDREB-2*, and *leDREB-3*), antioxidant synthesis (*leAPX*, *leSOD*, and *leCAT* genes), and Si transport (*leLsi-1*, *leLsi-2*, and *leLsi-3*) (*Muneer and Jeong,* 2015).

Considerable literature supports that Si application in root growing media is an efficient means of mitigating the adverse effects of salt stress on plants; most of those studies have focused on Si uptake by plant roots (*Ashraf et al.,* 2015; *Conceição et al.,* 2019; *Liu et al.,* 2015; *Yin et al.,* 2016). In intermediate Si-accumulating plants, such as sunflower (*Hodson et al.,* 2005; *Liang et al.,* 2006a), the combined application of Si would be ineffective in plants, such as sorghum, that already absorb high concentrations of Si through their roots (*Liang et al.,* 2007). However, until now, the biological effects of Si, when applied via foliar or combined methods, in salt-stressed plants with contrasting Si-absorbing capacities, such as sorghum and sunflower, have been restricted in the literature.

The foliar Si spraying increases the uptake and accumulation of Si by the leaves and might increase salt tolerance. Studies in okra have shown that the foliar application of Si (150 mg L^{-1}) increases the salt tolerance of plants by increasing antioxidant enzyme activities and consequently reducing lipid peroxidation (*Abbas et al.,* 2017, 2015). As a result of the relatively low concentrations of Si provided by foliar application (<1.0 kg ha^{-1}) and the beneficial effects of combined applications, it might be possible to increase salt tolerance and reduce salt damage in a range of crop species. Knowledge of the best Si-supply strategy might provide an additional approach for salinity-stress attenuation in plants that take up low concentrations of Si through their roots.

Therefore, in this study, our main our main hypotheses are as follows. (1) Si applications in different methods could regulate the salinity stress induced changes for adequate physiological and biochemical adaptations against salt stress; (2) the combined foliar and root applications of Si is more promissory to attenuates salinity effects in intermediate Si-accumulating plants (e.g., sunflower), but in high Si-accumulating plants (e.g., sorghum) the root application of Si is enough; and (3) the foliar application of Si alone can be attenuate the harmful effects of NaCl stress in both plant species. Thus, the purpose of the present study was to evaluate the effect of different methods of Si applications in attenuating the negative effects of salt stress, based on the biological responses of two distinct species, sorghum (accumulator of Si) and sunflower (intermediate accumulator of Si).

2 Material and methods

2.1 Plant material and growth conditions

The present study was conducted in a glass greenhouse at the ‘Julio de Mesquita Filho’ State University of São Paulo (UNESP), using sorghum (*Sorghum bicolor* (L.) Moench ‘Dekalb 540’) and dwarf sunflower (*Helianthus annuus* L. ‘Double Sungold’). The seeds of both plant species were grown in vermiculite (3:1) and irrigated with only deionized water three times per day for 16 days. The plants were grown under natural light conditions, with day/night temperatures of 26°C/18°C (± 2.5°C), 10 h day/14 h night photoperiod, and 65%–75% relative humidity.

Nutrient solution was provided as a source of water and fertilizer (*Hoagland and Arnon*, 1950). A 25% (50 mL per pot) ionic strength solution was used to acclimatize the plants, but the concentration was increased to 50% by 2 weeks (100 mL per pot) and to 75% (150 mL per pot) by the 40-day experimental period. The pH of the nutrient solution was monitored daily and maintained at 5.0 ± 0.8, using 1N hydrochloric acid (HCl) before applying to the plants. The amount of water lost by evapotranspiration was replaced by a nutrient solution in all experimental periods.

2.2 Si and NaCl and NaCl applications to sorghum and sunflower plants

During 40 days of cultivation, two experiments were carried out and eight treatments was arranged factorial (2 × 4) based on a randomized block design with five replicates (n = 5) for each experiment, giving a total of 80 pots (40 for each crop). Two levels of salinity were applied via the nutrient solution (0 and 100 mmol L^{-1} NaCl) combined with different Si availability: no Si, control (0 mmol L^{-1} Si), Si(L), foliar Si application (28.6 mmol L^{-1}); Si(S), root Si application (2 mmol L^{-1}); and Si(L+S), combined foliar and root applications of Si. Treatments were started by adding sodium chloride (NaCl) and stabilized sodium and potassium silicate (SiNaKE) was used to maintain the Si concentration in the treatments (foliar application, root application, and combined foliar and root application).

The SiNaKE source, used for delivering the Si treatments, was applied via the nutrient solution and foliar applications, and contained 4.05 mol L^{-1} of Si derived from stabilized sodium silicate (Na_2SiO_3, 3.36 mol L^{-1}) and potassium silicate (K_2SiO_3, 0.69 mol L^{-1}). Na^+ and K^+ in the nutrient solution were balanced among all treatments, including the control, by subtracting additional Na^+ and K^+ introduced by SiNaKE and then adding Na^+ balanced by NaCl and K^+ by potassium chloride (KCl). Each experimental unit consisted of a 4-dm^3 polyethylene vessel that was filled with washed sand, with a perforated bottom and nutrient solution collector. These units contained either two sorghum plants or two sunflower plants. The pots were rearranged within each block every 3 d.

The plants of both species were acclimatized via nutrient solution application with an electric conductivity (EC) of approximately 1.8 dS m^{-1} on the first day. After 7 days of adaptation, salt treatment level was maintained in the corresponding pots by adding NaCl (EC ~10 dS m^{-1}) every day through the nutrient solution. The foliar spraying of Si was applied four times for both plant species; the first and second sprayings contained approximately 0.12 mL of the solution per plant, and the third and fourth sprayings contained approximately 0.24 mL of the solution per plant. It was carried out by spraying on fully developed leaves at the phenological stages S2-S4 in sorghum (*Vanderlip and Reeves,* 1972) and stages V4-V8 in sunflower (*Schneiter and Miller,* 1981). Si was supplied at a concentration of 2 mmol L^{-1} in Hoagland nutrient solution by bathing the roots, and the solution was applied to the roots throughout the 40-day experimental period. We considered the following conditions for performing the foliar application of Si: the pH was neutralized with dilute HCl (1 N) before applying Si to plants, relative humidity was > 60%, and ambient temperature was between 20°C and 27°C.

2.3 Determination of plant growth parameters

After 40 days of cultivation, in the stage S4 for sorghum and V8 for sunflower, the plants were harvested. The harvested plants were divided for biochemical analysis and for determining the biometric parameters and ion accumulation. After harvesting the plants, they were sequentially washed in distilled water, a detergent solution (0.2%), HCl solution (0.1%), and deionized water (*Prado,* 2020). Samples for biochemical estimations and ion accumulation were collected in three replicates and each replicate/sample was assayed twice. The leaves and stems were then transferred on to paper sacks and dried to a constant weight using a forced ventilation oven (TE 394-3, Tecnal, Piracicaba, São Paulo, Brazil) at 65°C. The leaf area (LA) and root diameter (RD) were measured using the Delta-T Devices LTD image analysis system (Delta-T Devices Ltd, Cambridge, England). The roots were stained in methylene blue for approximately 2 min, transferred to a tray of water, and then photographed using the Delta-T scan Delta-4 and Hewlett Packard model 5C scanner (Delta-T Devices Ltd, Cambridge, England).

2.4 Determination of concentration and accumulation of Si, Na^+, and K^+

Finely pulverized shoot samples were digested with a di-acid mixture of nitric acid (HNO_3) and perchloric acid ($HClO_4$) in a 3:1 ratio for Na^+ and K^+ concentration analysis. The concentration of Na^+ and K^+ in the digested mixture was estimated by flame photometry (Jencon PFP 7; JENCONS-PLS, Bedfordshire, England). The Na^+ and K^+ concentration in the plant shoots was evaluated as described by *Bataglia et al.* (1983).

The Si concentration was evaluated as described by *Korndörfer et al.* (2004). Briefly, 0.1 g of tissue was ground to a fine powder and added to a polyethylene tube (100 mL). Two milliliters of hydrogen peroxide (H_2O_2) was added and stirred (magnetic stirrer) for a few seconds. After cooling (~1 h), 5 mL of sodium hydroxide solution (1 g NaOH/mL H_2O) was added to the tube and shaken thoroughly. The capped tube was then placed in a Maria bath for 1 h. After liberating the gas, the tube was placed in an autoclave and heated for 1 h at 123°C and 1.5 atm (20 psig). After cooling (~1 h), 45 mL of distilled water was added to each tube. After further cooling (~1 h), 1 mL of the digested plant material mixture was added to 19 mL of distilled water.

Hydrochloric acid (1 mL of 1:1 mixture of HCl and H_2O) was added to the tube along with ammonium molybdate solution (2 mL, 100 g L^{-1} at pH 7.0), shaken, and allowed to stand for 5–10 min. Briefly, 0.1 g of tissue was ground to a fine powder and added to a polyethylene tube (100 mL). Two milliliters of hydrogen peroxide (H_2O_2) were added and stirred (magnetic stirrer) for a few seconds. After cooling (~1 h), 5 mL of NaOH solution (1 g NaOH/mL H_2O) was added to the tube and shaken to mix thoroughly. The capped tube was then placed in a Maria bath for 1 h. After liberating the gas, the tube was placed in an autoclave and heated for 1 h at 123°C and 1.5 atm (20 psig). After cooling (~1 h), 45 mL of distilled water was added to each tube. After further cooling (~1 h), 1 mL of the digested plant material mixture was added to 19 mL of distilled water.

Hydrochloric acid (1 mL of 1:1 mixture of HCl and H_2O) was added to the tube along with ammonium molybdate solution (2 mL, 100 g L^{-1} at pH 7.0), shaken, and allowed to stand for 5–10 min. Two milliliters of oxalic acid were added to the tube and shaken. After 2 min, a yellow color developed, which was measured between 10 and 15 min at 410 nm by using a spectrophotometer (SP-1105, Ningbo Hinotek Technology, Shanghai, China). Finally, the absorbance was compared with that of a standard calibration curve of known Si concentrations prepared with soluble Si combined with the above-mentioned reagents that were added to the tube and shaken. Based on the concentrations of Na^+, K^+, and Si in the shoots of both plant species and their respective shoot dry masses, the accumulation of these elements was calculated [mg per plant shoot biomass (SB)].

2.5 Determination of lipid peroxidation

Lipid peroxidation was estimated as the total concentration of thiobarbituric acid-reactive substances in leaf, as described by *Cakmak and Horst* (1991). The homogenate was centrifuged at 15 000 × *g* for 15 min, and 1.5 mL of the supernatant was added to 2.5 mL 0.5% (w/v) thiobarbituric acid in 20% trichloroacetic acid. The mixture was incubated in boiling water for 20 min, and the reaction stopped by placing the reaction tubes in an ice bath. Then the samples were centrifuged at 10,000 × *g* for 10 min to yield a clear solution. The absorbance of the supernatant was read at 532 nm using a spectrophotometer (Beckman DU 640, San Diego, California, U.S.A.). The reading at 600 nm was subtracted to remove non-specific absorption. The amount of LPO was calculated from the extinction coefficient 155 mM^{-1} cm^{-1} and expressed as nmol g^{-1} fresh weight (FW).

2.6 Determination of proline concentration

The Pro concentration in the leaves was determined as described by *Bates et al.* (1973). Briefly, lyophilized plant material (0.1 g) was homogenized in 10 mL of 3% aqueous sulfosalicylic acid, and the resulting homogenate was filtered through Whatman #2 filter paper (Whatman™, GE Healthcare, USA). The filtrate (2 mL) was then reacted with 2 mL of acid-ninhydrin ($C_9H_6O_4$) and 2 mL of glacial acetic acid ($C_2H_4O_{24}$) in a test tube for 1 h at 100°C, after which the reaction was terminated by transferring the tube to an ice bath. After cooling (~1 h), the reaction mixture was extracted with 4 mL toluene, and absorbance was measured at 520 nm with a Beckman DU 640 spectrophotometers (San Diego, California, USA). A standard curve for Pro was obtained using Pro dissolved in 3% sulfosalicylic acid (0.5–10 µg mL^{-1}), and the Pro concentration in the extracts was calculated on a dry weight (DW) basis using the standard curve.

2.7 Determination of relative water content

The RWC of the plant leaves was determined using six leaf disks (0.5 cm of diameter) obtained from the middle of fully developed leaves. The FW of the leaf samples was measured, and then the leaves were immersed in distilled water in a Petri dish. After 6 h, the leaves were removed and blotted dry, and then the turgid weight (TW) of the leaf disks was measured. The samples were then dried to a constant weight in an oven at 65°C and the DW was measured. Finally, the leaf RWC was calculated using the following formula (*Barrs and Weatherley,* 1962):

$$\text{RWC (\%)} = [(\text{FW} - \text{DW}) / (\text{TW} - \text{DW})] \times 100$$

2.8 determination of protein extraction and antioxidant enzyme activities

The leaf samples (0.5 g) were macerated in liquid nitrogen using a pestle and mortar. The powdered sample was then mixed in 3 mL of 50 mM potassium phosphate buffer (PBS, pH 7.5), containing the following reagents: 0.1 mM EDTA, 5 mM 2-mercaptoethanol, and 20% polyvinylpyrrolidone (PVP). The homogenate was centrifuged at 10 000 × *g* for 30 min, and the resulting supernatant was stored at -80°C to analyze antioxidant enzyme activities (*Azevedo et al.,* 1998). The total protein concentration in the samples was estimated using Bradford's method (*Bradford,* 1976) and a standard curve for bovine serum albumin (BSA).

Superoxide dismutase (SOD; EC 1.15.1.1) activity (U SOD mg^{-1} protein) was measured by mixing 0.5 g of powdered sample with 3 mL of 50 mM PBS (pH 7.0), containing the following reagents: 0.1 mM EDTA, 10 mM methionine, 2 µm riboflavin, 0.075 mM nitro blue tetrazolium chloride (NBT), and 20 µL enzyme extract, with a total volume of 3 mL. The mixture was allowed to react for 5 min in a closed chamber under illumination with a fluorescent lamp (15 W) at 25°C, and the absorbance of the solution at 560 nm was measured using a Beckman DU 640 spectrophotometers (*Giannopolitis and Ries,* 1977). Catalase (CAT; EC 1.11.1.6) activity (µmol H_2O_2 mg^{-1} min^{-1} protein) was measured by mixing 0.5 g of powdered sample with 3 mL of 50 mM PBS (pH 7.0) containing 12 mM H_2O_2, with a final volume of 2 mL. The activity was calculated as the decomposition of H_2O_2, as indicated by absorbance at 240 nm at 25°C with a Biochrom

Libra S70 spectrophotometer (Harvard Bioscience, Shanghai, China) (*Havir and McHale,* 1987). Ascorbate peroxidase (APX; EC 1.11.1.11) activity (μmol H_2O_2 mg^{-1} min^{-1} protein) was measured by mixing 0.5 g of powdered sample with 3 mL of 50 mM PBS containing 0.1 mM H_2O_2, 0.5 mM ascorbate, and 25 μL enzyme extract, with a final volume of 2 mL. The APX activity was calculated as the rate of ascorbate oxidation, as indicated by the absorbance at 290 nm at 28°C using a Biochrom Libra S70 spectrophotometer (*Nakano and Asada,* 1981).

2.9 Statistical analysis

The experiments were repeated twice, with similar results. The data presented in this paper were from one typical experiment and subjected to statistical analysis by factorial analysis to test the main effects of the four levels of Si, two levels of NaCl, and their interactions (Si × NaCl). The normality of the data was tested using the Shapiro–Wilk test $P < 0.05$, and unequal variances was determined by Fisher's exact test at $P < 0.05$. The data were then subjected to a two-way analysis of variance (ANOVA) using the Statistical Analysis System (SAS version 9.2) software. The mean values were compared by Tukey's multiple range test at ($P < 0.05$). All figures are illustrated using GraphPad Prism v8.0 (GraphPad Inc, San Diego, CA, USA).

3 Results

3.1 Influence in the accumulation of Si, Na^+, and K^+ after Si and NaCl treatments

The ANOVA revealed a significant interaction ($P < 0.001$) between NaCl and Si on the accumulation of Si, Na^+, and K^+ in shoots of sorghum and sunflower plants ((Figure. 1a-f)). Salt stress (100 mmol L^{-1} NaCl) had a negligible effect on the accumulation of Si in shoots of sorghum and sunflower plants, however, it was not statistically different ($P < 0.01$) ((Figure 1a,b)). The Si accumulation in shoots of both plant species showed an increasing pattern in Si-applied via nutrient solution [Si(S)] and the combined application of Si between via foliar spraying and nutrient solution [Si(L+S)] under non-salt and salt- stressed plants as compared to the others Si treatments ($P < 0.01$). Similarly, the Si accumulation in Si-supplied via foliar spraying [Si(L)] revealed a slight increase in shoots of sorghum and sunflower plants relative to the non-Si treatment under non-salt and salt- stress conditions ((Figure. 1a,b)). The shoot Si accumulation was absolutely increased in both plant species in an application methods-dependent manner when Si was applied to plants.

Na^+ accumulation in the shoots of both plant species after treatment of 30 d were increased significantly by salt application (100 mmol L^{-1} NaCl) in the rooting medium, while Si supplementation drastically decreased it and showed a significant difference ($P < 0.01$) ((Figure. 1c,d)). Shoot Na^+ accumulation in salt-stressed sorghum plants decreased by ~39% in the Si(S) and Si(L+S) treatments compared with the non-Si treatments ($P < 0.01$). On the other hand, foliar application of Si [Si (L)] decreased shoot Na^+ accumulation by ~13% in salt-stressed sorghum plants compared with non-Si treated plants ((Figure. 1c)). In salt-stressed sunflower plants, the Na^+ accumulation in the shoots was lower in the all Si treatments compared to the non-Si treatment. In particular, the Si(L+S) treatment decreased shoot Na^+ accumulation by 51% compared with compared with non-Si treated plants under salinity conditions. The Na^+ accumulation by sunflower plants under NaCl stress was similar in the Si(L) and Si(S) treatments ($P < 0.01$) ((Figure. 1d)).

K^+ accumulation in the shoots of both plant species was decreased markedly by salt stress (100 mmol L^{-1} NaCl), regardless of Si treatment ((Figure. 1e,f)). In salt-stressed sorghum plants, both Si(S) and Si(L+S) treatments resulted in 13% higher K^+ accumulation in the shoot than that in the others Si treatments ((Figure. 1e)). In salt-stressed sunflower plants, all Si treatments increased K^+ accumulation, especially, the Si(L+S) treatment increased shoot K^+ accumulation by 15% relative to the non-Si treatment under salt stress ($P < 0.01$). The K^+ accumulation was similar and higher in the Si(L) and Si(S) treatments compared with non-Si treatment under NaCl stress ((Figure. 1f)). Under non-saline conditions, Si had no effect on K^+ accumulation. Our results showed that salt stress not affect the accumulation of Si in shoots of both plant species. Si application in different methods can be decrease Na^+ uptake and increase the K^+ accumulation in shoots of both plant species. This supports the idea that changes in mineral accumulation were triggered by the different methods of Si application.

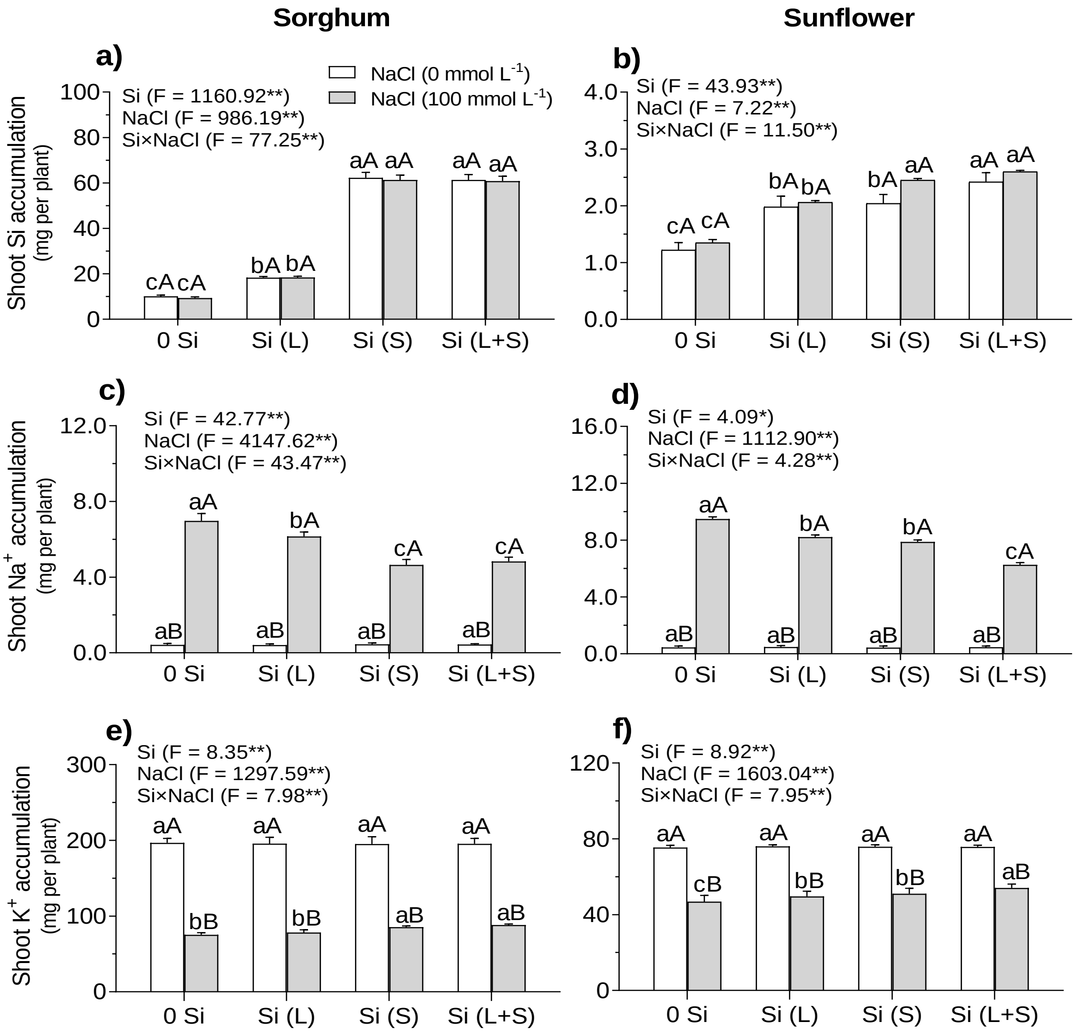

Figure 1: Effect of Si application on the accumulation of Si, Na^+, and K^+ in the shoots of sorghum and sunflower plants. Shoot Si accumulation in sorghum (a) and sunflower plants (b), shoot Na^+ accumulation in sorghum (c) and sunflower plants (d), and shoot K^+ accumulation in sorghum (e) and sunflower plants (f) grown under two different levels of NaCl (0 and 100 mmol L^{-1}) combined with different Si availability: no Si, control (0 mmol L^{-1} Si); Si(L), foliar Si application (28.6 mmol L^{-1}); Si(S), root Si application (2 mmol L^{-1}); and Si(L+S), combined foliar and root applications of Si. Different lowercase letters indicate significant differences among Si treatments under the same NaCl level and different uppercase letters indicate significant differences between non-salt and salt treatments at the same level of Si, according to the Tukey test. Values are the means of five replicates ± standard deviation (SD). (F values from ANOVA: $*P < 0.05$; $**P < 0.01$). Si × NaCl, Si–NaCl interaction. Stack bars show the standard error (SE) based on the average of five replicates.

3.2 Influence of lipid peroxidation after Si and NaCl treatments

Salt stress markedly increased LPO in the leaves of sorghum and sunflower plants and showed a significant interaction (*P* < 0.001) between NaCl and Si ((Figure. 2a,b)). In salt-stressed sorghum plants, the application of Si [Si(L), Si(S), and Si(L+S)] resulted in 29% lower LPO in the leaves compared with the non-Si treatment ((Figure. 2a)). In leaves of salt-stressed sunflower plants, the LPO was decreased by all Si treatments than that in the others treatments; especially the Si(L+S) treatment decreased LPO by 26% compared to the non-Si-treated plants under salt stress (*P* < 0.01). However, the LPO was similar and decreased by 15% in the Si(L) or Si(S) treatments compare with non-Si treatment under NaCl stress ((Figure. 2b)).

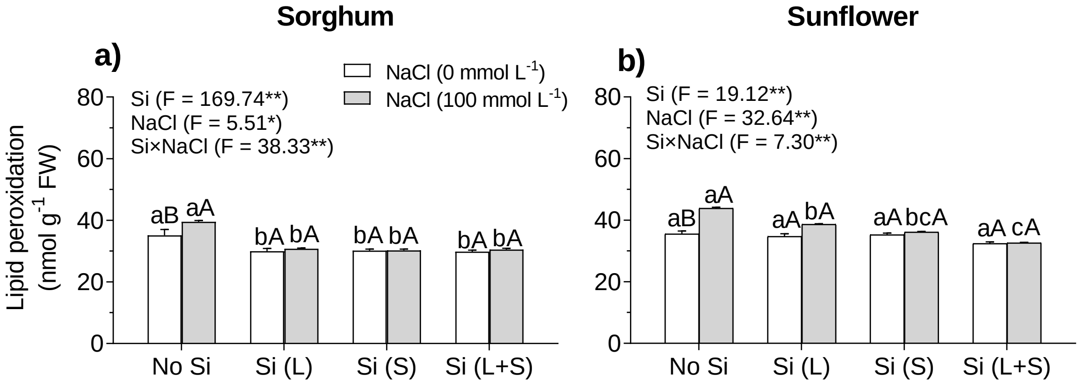

Figure 2: Effect of Si application on lipid peroxidation in the leaves of sorghum and sunflower plants. Lipid peroxidation in sorghum (a) and sunflower leaves (b) grown in two levels of NaCl (0 and 100 mmol L^{-1}) combined with different Si availability: no Si, control (0 mmol L^{-1} Si); Si(L), foliar Si application (28.6 mmol L^{-1}); Si(S), root Si application (2 mmol L^{-1}); and Si(L+S), combined foliar and root applications of Si. Different lowercase letters indicate significant differences among Si treatments under the same NaCl level and different uppercase letters indicate significant differences between non-salt and salt treatments at the same level of Si, according to the Tukey test. Values are the means of five replicates ± SD; (F values from ANOVA: **P* < 0.05; ***P* < 0.01). FW, fresh weight; Si × NaCl, Si–NaCl interaction. Stack bars show the SE based on the average of five replicates.

3.3 Influence of Proline concentration after Si and NaCl treatments

Salt stress (100 mmol L^{-1} NaCl) markedly enhanced Pro concentration in the leaves of sorghum and sunflower plants and showed a significant Si × NaCl interaction

(P < 0.001) ((Figures. 3a,b)). Under non-salt conditions, the Si(L+S) treatment decreased the Pro concentration in leaves of sorghum plants than that other Si treatments, but the Pro concentration was not affected in the leaves of sunflower plants (P < 0.01) ((Figures 3a,b)). In salt-stressed sorghum plants, the Pro concentration was 89% higher in the Si(L) treatment compared to the others Si treatments (P < 0.01). However, the Pro concentration decreased by 71% in the Si(S) and Si(L+S) treatments compared to the non-Si treatment under NaCl stress (P < 0.01) ((Figure. 3a)). In salt-stressed sunflower plants, the Pro concentration was increased by ~90% in all Si treatments compared with non-Si-treated plants ((Figure. 3b)).

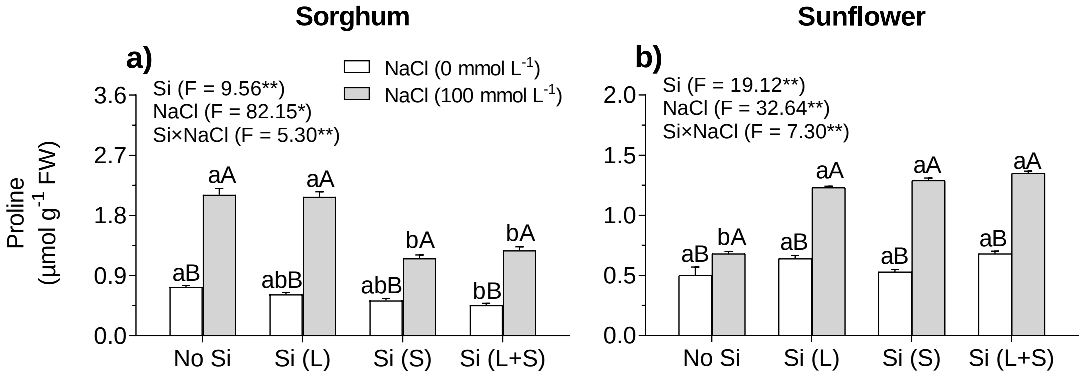

Figure 3: Effect of Si application on the free proline concentration in the leaves of sorghum and sunflower plants. Free proline concentration in sorghum (a) and sunflower leaves (b) grown under two different levels of NaCl (0 and 100 mmol L^{-1}) combined with different Si availability: no Si, control treatment (0 mmol L^{-1} Si); Si(L), foliar Si application (28.6 mmol L^{-1}); Si(S), root Si application (2 mmol L^{-1}); and Si(L+S), combined foliar and root applications of Si. Different lowercase letters indicate significant differences among Si treatments at the same NaCl level and different uppercase letters indicate significant differences between non-salt- and salt treatments at the same level of Si, according to the Tukey test. Values are the means of five replicates ± SD. (F values from ANOVA: *P < 0.05; **P < 0.01); fresh weight; Si × NaCl, Si–NaCl interaction. Stack bars show the SE based on the average of five replicates.

3.4 Influence of relative water content after Si and NaCl treatments

Leaf water status was prejudiced by salinity, as confirmed by the lower RWC values observed in treatments with 100 mmol L^{-1} NaCl in the leaves of sorghum and sunflower plants, with significant Si × NaCl interaction (P < 0.01) (Figure. 4a,b). In sorghum, the Si(S) and Si(L+S) treatments resulted in higher leaf RWC compared with the others Si treatments in the both non-salt and salt conditions (Figure. 4a). In sunflower, under non-salt stress, Si application did not affect the leaf RWC (Figure. 4b). However, in salt-stressed sunflower plants, the leaf RWC was higher in the Si(L+S) treatment than that in the others Si treatments (*P* < 0.01) (Figure. 4b).

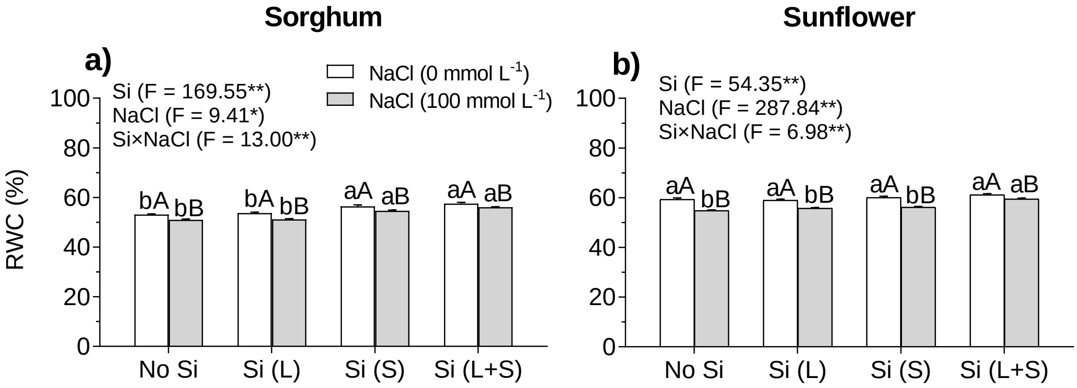

Figure 4: Effect of Si application on the relative water content (RWC) in sorghum and sunflower plants. RWC of sorghum (a) and sunflower (b) leaves grown with different levels of NaCl (0 and 100 mmol L^{-1}) combined with different Si availability: no Si, control treatment (0 mmol L^{-1} Si); Si(L), foliar Si application (28.6 mmol L^{-1}); Si(S), root Si application (2 mmol L^{-1}); and Si(L+S), combined foliar and root applications of Si. Different lowercase letters indicate significant differences among Si treatments at the same NaCl level and different uppercase letters indicate significant differences between non-salt and salt treatments at the same level of Si, according to the Tukey test. Values are the means of five replicates ± SD. (F values from ANOVA: **P* < 0.05; ***P* < 0.01). Si × NaCl, Si–NaCl interaction. Stack bars show the SE based on the average of five replicates.

3.5 Influence of Antioxidant enzyme activity after Si and NaCl treatments

The ANOVA revealed a significant interaction (*P* < 0.001) between NaCl and Si was observed on the activities of SOD, CAT, and APX in the leaves of sorghum and sunflower plants ((Figure. 5a-f)). Si supplementation did not alter SOD activity in the leaves of non-salt stressed sorghum plants ((Figure. 5a)). Meanwhile, under non-salt conditions, the SOD activity decreased in all Si [Si(L), Si(S), and Si(L+S)] treatments and showed a significant difference (*P* < 0.011) than in non-Si-treated plants under non-salt stress ((Figure. 5b)). Salt stress markedly decreased SOD activity by 33% in the leaves of sorghum plants and by 16% in leaves of sunflower plants after 30 d compared to the non-NaCl treatment ((Figure. 5a,b)). However, in salt-stressed sorghum plants, all Si [Si(L), Si(S) and Si (L+S)] treatments increased the SOD activity by ~76% than that non-Si-treatments under salt stress ($P < 0.01$) ((Figure. 5a)). In salt-stressed sunflower plants, the SOD activity increased by 23% in all Si [Si(L), Si(S) and Si(L+S)] treatments compare with non-Si-treated plants under NaCl stress ((Figure. 5b)).

In the leaves of sorghum plants grown under non-salt conditions, the CAT activity was lower in the Si(S) and Si(L+S) treatments than that in the others Si treatments ((Figure. 5c)). Salt stress (100 mmol L^{-1} NaCl) drastically decreased the CAT activity by 19% in the leaves of sorghum plants compared with non-salt-stressed plants under non-Si treatment. Meanwhile, the CAT activity was increased by 57% in the salt-stressed sorghum plants by the Si(S) and Si(L+S) treatments compared with others Si treatments ($P < 0.014$) ((Figure. 5c)). Under non-saline conditions, Si had no effect on CAT activity among the different Si treatments. Thus, under salt stress, the CAT activity was higher by Si(L+S) treatment compared to the others Si treatments. Similarly, the CAT activity was similar and increased by 66% in the Si(L) or Si(S) treatments compared to non-Si treatment under salt stress ((Figure. 5d)).

Under non-salt conditions, the APX activity in the leaves of sorghum plants was lower in the Si(L), Si(S), and Si(L+S) treatments compare with non-Si-treated plants under non-NaCl stress ((Figure. 5e)). Salt stress (100 mmol L^{-1} NaCl) significantly decreased the APX activity by 51% in the leaves of sorghum and by 30% in sunflower plants relative to the non-Si treatment under salt stress ($P < 0.01$) ((Figure. 5e,f)). In salt-stressed sorghum plants, the APX activity was increased by 72% in the Si(L+S) treatment than that in the non-Si-treated plants under salt stress. The APX activity sowed equal significant and increased by 40% in the Si(L) and Si(S) treatments compare with non-Si-treated plants under NaCl stress ((Figure. 5e)). In the leaves of sorghum plants grown under non-salt conditions, the activity of APX was decreased by all Si treatments, especially the Si(L+S) treatment (Figure. 5f). However, in salt-stressed sunflower plants, the APX activity was 30% higher in the Si(L+S) treatments than in non-Si-treated plants under salt stress ($P < 0.012$). The activity of APX showed a similar effect in the Si(L) and Si(S) treatments under salt stress ((Figure. 5f)).

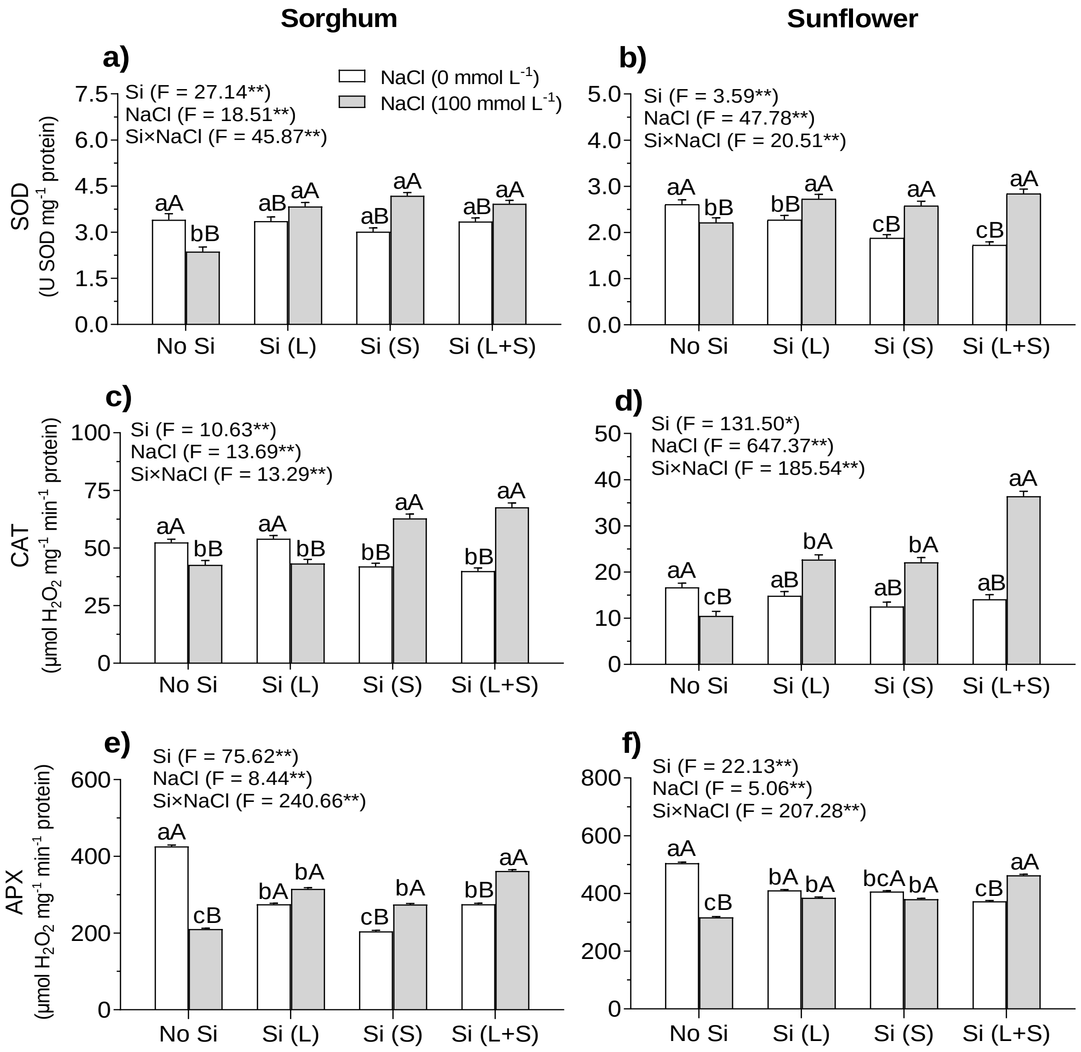

Figure 5: Effect of Si application on the enzymatic antioxidant activities in the leaves of sorghum and sunflower plants. Superoxide dismutase (SOD) activity in sorghum (a) and sunflower leaves (b); catalase (CAT) activity in sorghum (c) and sunflower leaves (d); and ascorbate peroxidase (APX) activity in sorghum (e) and sunflower leaves (f) grown under two different levels of NaCl (0 and 100 mmol L^{-1}) combined with different Si availability: no Si, control treatment (0 mmol L^{-1} Si); Si(L), foliar Si application (28.6 mmol L^{-1}); Si(S), root Si application (2 mmol L^{-1}); and Si(L+S), combined foliar and root applications of Si. Different lowercase letters indicate significant differences among Si treatments at the same NaCl level and different uppercase letters indicate significant differences between non-salt and salt treatments at the same level of Si, according to the Tukey test. Values are the means of five replicates ± SD. (F values from ANOVA: *$P < 0.05$; **$P < 0.01$). Si × NaCl, Si–NaCl interaction. Stack bars show the SE based on the average of five replicates.

3.6 Influence of Si and NaCl treatments on plant growth parameters

Our results indicated that there was a significant interaction ($P < 0.01$) between the NaCl and Si on the RD, LA, and SB of sorghum and sunflower plants ((Figures 6a-f)). Si supplementation had no effect on the RD of sorghum plants grown under non-salt conditions ((Figure. 6a)). RD in sorghum plants was significantly decreased (~16%) by NaCl stress after 30 d and this effect were reverted by Si application. The application of Si(L), Si(S), and Si(L+S) treatments increased the RD by 19% in salt-stressed sorghum plants compared with non-Si-treated plants under NaCl stress ($P < 0.01$) ((Figure. 6a)). Under non-salt conditions, the RD in sunflower plants was significantly increased in the Si(L+S) treatment compared to the others Si treatments ((Figure. 6b)). Meanwhile, the RD was ~22% higher in salt-stressed sunflower plants under the Si(S) and Si(L+S) treatments than that in the others Si treatments (Figure. 6c,d).

Under non-salt conditions, the LA of sorghum plants was greater in the Si(S) and Si(L+S) treatments than in the others Si treatments ((Figure. 6c)). Salt stress decreased the LA in sorghum and sunflower and showed significant difference ($P < 0.01$) ((Figure 6c,d)). However, the LA was increased by ~23% in salt-stressed sorghum plants by the Si(S) and Si(L+S) treatments increased compared with the others Si treatments ((Figure. 6c)).

In sunflower plants under non-salt conditions, the LA was greater in all Si [(L), (S), and (L+S)] treatments than in non-Si application. Nevertheless, in salt-stressed sunflower, the LA was increased by all Si [Si(L), Si(S), and Si(L+S)] treatments with the compared with non-Si-treated plants under salt stress, especially in the Si(L+S) treatment (52% increase). The LA was similar and increased by ~34% in the Si(L) and Si(S) treatments compared to non-Si-treated plants under NaCl stress ((Figure. 6d)).
Si application had no effect on the SB of sorghum plants under non-salt conditions ((Figure. 6e)), but in sunflower plants the SB was highest in the Si(L) treatment than that in the others Si treatments ($P < 0.01$) ((Figure. 6f)). Salt stress significantly decreased the SB in sorghum and sunflower plants (Figure. 6e,f). However, all Si [Si(L), Si(S), and Si(L+S)] treatments increased on average the SB by ~16% in sorghum plants and by ~27% in sunflower plants compared to non-Si-treated plants under salt stress conditions ((Figure. 6e,f)).

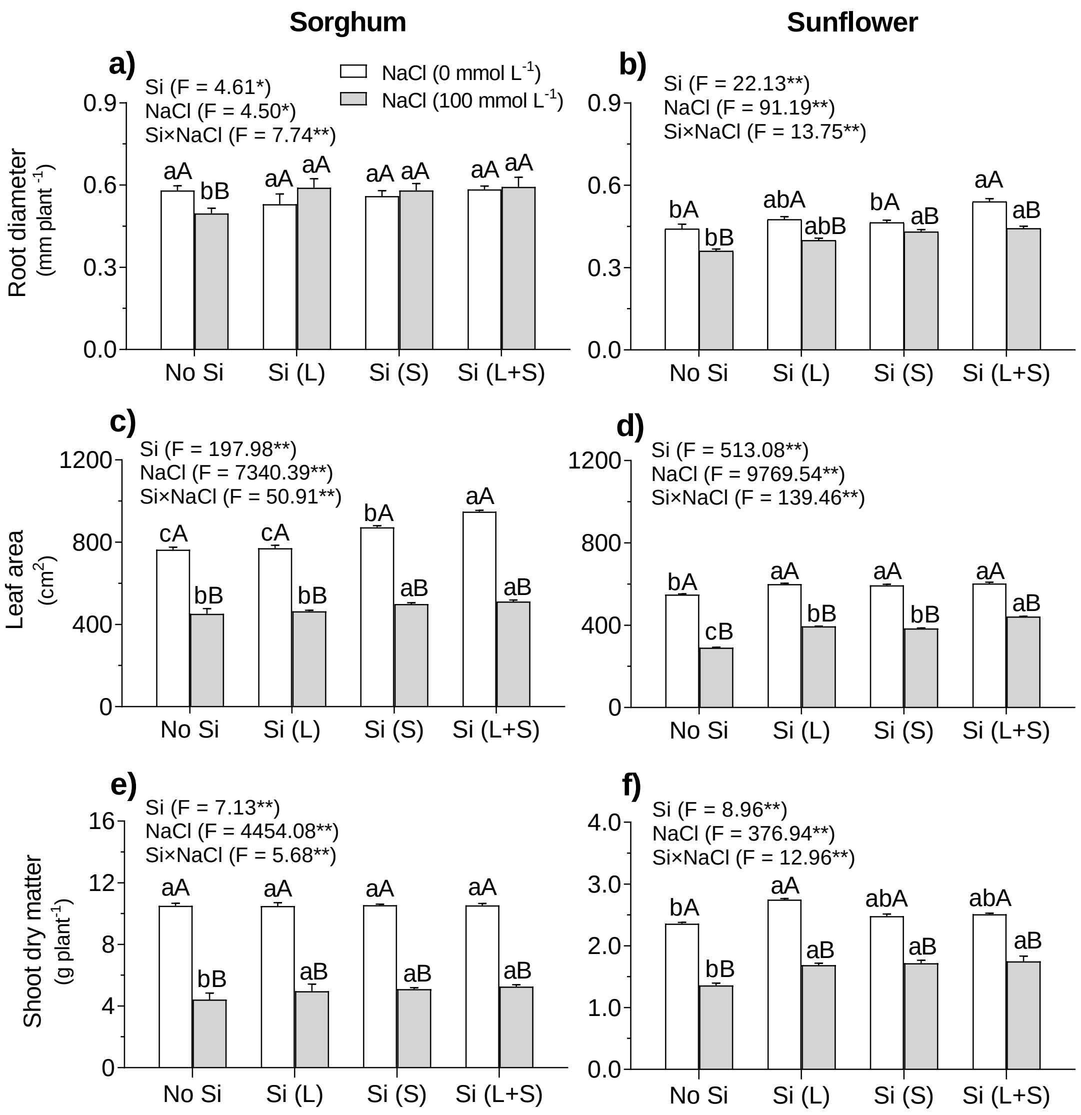

Figure 6: Effect of Si application on the plant growth parameters in sorghum and sunflower plants. The root diameter of sorghum (a) and sunflower plants (b), leaf area of sorghum (c) and sunflower plants (d), shoot dry matter of sorghum (e) and sunflower plants (f) grown under two different levels of NaCl (0 and 100 mmol L^{-1}) combined with different Si availability: no Si, control treatment (0 mmol L^{-1} Si); Si(L), foliar Si application (28.6 mmol L^{-1}); Si(S), root Si application (2 mmol L^{-1}); and Si(L+S), combined foliar and root applications of Si. Different lowercase letters indicate significant differences among Si treatments at the same NaCl level and different uppercase letters indicate significant differences between non-salt and salt treatments at the same level of Si, according to the Tukey test. Values are the means of five replicates ± SD. (F values from ANOVA: $^*P < 0.05$; $^{**}P < 0.01$). Si × NaCl, Si–NaCl interaction. Stack bars show the SE based on the average of five replicates.

4 Discussion

In the present study, our results show for the first time the effect of different methods of Si application on attenuating ionic, osmotic and oxidative stress under long-term exposure to salt stress in different Si-accumulating species, such as sorghum (accumulator of Si) and sunflower (intermediate-Si accumulator). Although there are numerous reports on Si-induced improvement in salt stress sorghum (*Liu et al.,* 2015; *Yin et al.,* 2016, 2013) and sunflower plants (*Ashraf et al.,* 2015; *Conceição et al.,* 2019), this is the first report that Si were applied via foliar spray and in the combined foliar and root applications on sorghum and sunflower plants.

Si accumulation in plants significantly varies among the plant species, because of the architecture of Si transporter system and prevalent environmental conditions. In the present study, we found that salt stress had no effect on the accumulation of Si in the shoots of sorghum and sunflower plants ((Figure. 1a,b)). Our results show that all methods of Si application increased accumulation of in shoots of both plant species. Under salt-stress conditions, the accumulation of Si by sorghum plants can be enhanced by root Si application alone or by combined foliar and root Si application ((Figure. 1a)). This was probably because of the high Si-uptake potential of sorghum roots, as it is a Si-accumulating plant (*Hodson et al.,* 2005; *Liang et al.,* 2006a). A recent study showed that both active and passive mechanisms operate in Si uptake and transport in Si-accumulating (sorghum) and intermediate Si-accumulating (sunflower) species (*Liang et al.,* 2007). However, we found that in salt-stressed sunflower plants, Si accumulation can be increased by all methods of Si application, especially the combined application of Si(L+S) accumulated significant amounts of Si ((Figure. 1b)), indicating that it is possible to increase the Si concentration in intermediate Si-accumulating plants under salt-stress conditions when both methods of Si application are combined, which are dependent on the plant species and external Si concentrations (*Liang et al.,* 2007). Similar findings showed increased significant amounts of Si under salt stress as well depicted this requirement for attenuation of NaCl toxicity (*Ahmad et al.,* 2019). These mechanisms can be promoted by Si supplementation under salt-stress conditions, activating important genes responsible for salt tolerance (*Muneer and Jeong,* 2015), thus, increasing Si accumulation and transportation by influx and efflux transporters such as *Lsi1* and *Lsi2* and *Lsi6 (Liu et al.,* 2019).

Present study clearly showed lower accumulation of Na^+ in the all Si treatments in salt-stressed sorghum and sunflower plants, in particular the application of Si (S) or the combined application of Si (S + F) in sorghum and the combined application of Si (S + F) in sunflower performing better than the exclusive application of Si (F) ((Figure. 1c,d)), thereby demonstrating the ability of Si to attenuate Na^+ accumulation, as reported previously (*Liu et al.,* 2015; *Sattar et al.,* 2017). In addition, we found that the shoot Na^+ accumulation was also decreased by exclusive foliar application of Si in both plant species ((Figure. 1c,d)). The Si-mediated reduction in Na^+ uptake by plants grown under salt-stress conditions might be owing to reduced transpiration, as Si is deposited in the cell walls of leaf tissues (*Matoh et al.,* 1986). Moreover, this reduction in Na^+ uptake and translocation might be attributed to the deposition of Si in the roots, which could decrease Na^+ bypass flow as shown in rice (*Gong et al.,* 2006; *Gurmani et al.,* 2013b; *Yeo et al.,* 1999), wheat (*Gurmani et al.,* 2013a), and sorghum (*Yin et al.,* 2013). However, in sunflower plants treated by combined application of Si(L+S), Na^+ accumulated was reduced to levels lower than those in the others Si treatments. These results are in agreement with the findings of *Gong et al.* (2006) who reported that the deposition of Si in the exoderm and root endoderm of rice, another Si accumulator, compromises the apoplastic transport of Na^+. Si application reduced Na^+ uptake and accumulation by polyamine metabolism that mediating some important metabolic processes related to ion chancel regulation in salt-stressed sorghum plants (*Yin et al.,* 2016). These outcomes are predictable with the recent discoveries that Si supplied in salt-stressed maize plants accumulate less Na^+ in both root apex and cortex. This was accompanied by increased expression of *ZmSOS1* and *ZmSOS2* in the root apex and cortex facilitating Na^+ exclusion (*Bosnic et al.*, 2018).

Ours results showed that the application of NaCl to sorghum and sunflower plants resulted in a strong reduction of K^+ accumulation, but K^+ accumulation was increased in sorghum plants treated by the application of Si (S) ((Figure. 1e)), and in sunflower plants treated by combined application of Si (L+S) ((Figure. 1f)). Root Si application has previously been shown to increase K^+ uptake in sunflower plants (*Ashraf et al.,* 2015), sorghum (*Yin et al*., 2013), rice (*Farooq et al.,* 2015), and cucumber (*Alsaeedi et al.,* 2018). However, Si application increased the selectivity between K^+ and Na^+ ions (*Liang et al.,* 1996). Furthermore, the cellular-level benefits of Si during ionic adjustment have been validated, i.e., Si reduces cytoplasmic Na^+ concentration and increases cytoplasmic K^+ concentration by stimulating H^+-ATPase enzymes in the plasma membrane (*Liang et al.,* 2006b, 2005a; *Xu et al.,* 2015). Si supplementation also improves the activity of ATP-synthase in the chloroplast under salt-stress conditions (*Muneer et al.,* 2014; *Muneer and Jeong,* 2015).

In the leaves of both sorghum and sunflower, salt stress induced LPO, consistent with the result of a previous study (*Davey et al.,* 2005). This effect is probably owing to the high accumulation of Na^+ ((Figure. 1c,d)), which induces toxicity by increasing ROS and, therefore, LPO (*Gill and Tuteja,* 2010). In salt-stressed sorghum plants, root application of Si and combined foliar and root Si application consistently reduced the LPO ((Figure. 2a)), but in sunflower plants, only the combined foliar and root application was effective ((Figure. 2b)). Overall, Si-mediated reduction in LPO has also been shown in rice (root application) (*Kim et al.,* 2014), *Rosa hybrida* (*Soundararajan et al.,* 2018), and okra (foliar spray) (*Abbas et al.,* 2015). These results suggest that maintenance of low levels of Na^+ might be partly owing to the decreased LPO caused by Si treatment. Moreover, Si-mediated also redox homeostasis is critical to retain ROS level and essential metabolic process of plants (*Liu et al*., 2019).

Salt stress increased the Pro concentration in both sorghum and sunflower leaves ((Figure. 3a,b)), consistent with the results of previous studies (*Shahbaz et al.,* 2011; *Siddiqui et al.,* 2014). Pro functions as a compatible osmolyte during osmotic adjustment, which can be considered as an adaptive mechanism to salt stress (*Iqbal et al.,* 2014). In the current study, we observed a significant increase in a free Pro concentration in salt treated sorghum plants compared to the non-salt treated plants ((Figure. 3a)), but this increase was reversed by the application of Si (S) or combined Si (L+S) treatments. The beneficial effect of Si applied via the nutrient solution on the decrease in Pro concentration has been shown in Si-accumulating plants such as sorghum (*Yin et al.,* 2013) and wheat (*Tuna et al.,* 2008). One possible explanation is that the Pro biosynthesis is a highly energy-demanding process, and reduced production of Pro could benefit the plant by saving more energy for coping with others metabolic processes (*Yin et al.,* 2013).

Conversely, in salt-stressed sunflower plants, the Pro concentration in the leaf increased by all methods of Si application ((Figure. 3b)). Si supplementation under salt-stress conditions favored the accumulation of Pro in the tissues of sunflower plants. This trend has also been reported previously in sunflower plants and might be related to salt-stress tolerance (*Conceição et al.,* 2019). However, the effect of Si on Pro concentration clearly varies between species, and Si might increase tolerance to salt stress in plants by increasing osmolyte concentration and adjusting osmotic potential (*Kim et al.,* 2017). Therefore, the beneficial effect of Si on plants might be because the existing Pro can be degraded and used as a source of carbon and nitrogen in plants recovering from stress, as well as a membrane stabilizer and also a free radical scavenger (*Mansour and Ali,* 2017; *Reddy et al.,* 2015).

In the present study, the attenuation of Na^+ toxicity and its helpful effects on RWC were observed following both root Si application and combined foliar and root Si application in sorghum leaves and combined foliar and root Si application in sunflower leaves ((Figure. 4a,b)). This can be explained by two hypotheses. The first is that Si application reduced the rate of transpiration and, therefore, the rate of water loss. Indeed, because Si is deposited in plant tissues and because a thick layer of silica is associated with cellulose in the epidermal cells, the accumulation of Si is likely to reduce water loss (*Kumar et al.,* 2017; *Li et al.,* 2015). In contrast, the second hypothesis is that Si increases the leaf RWC by decreasing Na^+ accumulation and by increasing the activity of antioxidant enzymes (e.g., SOD, CAT, and APX), thereby maintaining membrane integrity and cell and tissue turgidity. The second hypothesis was verified by the results of the present study ((Figure. 5a-d)) and is consistent with the results of a previous study (*Gomathi and Rakkiyapan,* 2011), which showed that plants increase salt tolerance by maintaining low levels of LPO and high membrane stability.

The results of the present study indicate that the SOD, CAT, and APX activities in both salt-stressed sorghum and sunflower plants could be increased by various Si application methods ((Figure 5a-f)), as shown previously in sorghum (*Liu et al.,* 2015) and sunflower (*Conceição et al.,* 2019). These enzymes play important roles in the elimination of ROS. Thus, enzymatic activity is enhanced by Si under salt stress, decreasing LPO caused by ROS generation (*Amirjani,* 2012; *Singh et al.,* 2015). Si supplementation via nutrient solution alone or foliar application increases the enzymatic activity under salt-stress conditions. These findings are in line with some previous reports, indicating the potential role of Si in attenuating the detrimental effects of salt stress on different plant species, such as okra (*Abbas et al.,* 2017, 2015), rice (*Abdel-Haliem et al.,* 2017), wheat (*Alzahrani et al.,* 2018; *Sattar et al.,* 2018), maize

(*Bosnic et al.,* 2018; *Khan et al.,* 2018), and mungbean (*Ahmad et al.,* 2019). Our results are consistent with the findings of previous studies showing that Si has been shown to play an important role in ROS detoxification by promoting the activities of antioxidant enzymes in tomato plants under salt stress (*Muneer and Jeong,* 2015). In addition, Si-induced attenuation of salt stress, via increased antioxidant enzyme activity, likely reduced ROS generation as Si application was also observed to decreased LPO ((Figure. 2a,b)), which is an important plant defense mechanism (*Coskun et al.,* 2019, 2016).

Our results showed the effect of Si on plant physiology and salt stress by assessing the growth variables of the two evaluated plant species. In sorghum, the effects of combined foliar and root Si application were similar to those observed following root Si application, i.e., both methods attenuated salt stress by increasing the RD, LA, and SB ((Figure. 6a-f)). These effects can be attributed to the increased leaf RWC, due to increased SOD, CAT, and APX activities, which mitigated the negative effects of salt stress, as indicated by the reduction in Pro concentration. Our results are consistent with the findings of previous studies of root Si application in sorghum (*Liu et al.,* 2015; *Yin et al.,* 2013) and other Si-accumulating species, such as sugar cane (*Ahraf et al.,* 2010; *Ashraf et al.,* 2010), corn (*Rohanipoor et al.,* 2013), and rice (*Kim et al.,* 2014). In the present study, the role of Si absorbed by sorghum roots during the attenuation of salt stress was indicated by an increase in the SB ((Figure. 6a)). However, foliar Si application attenuate salt stress and help to increase the plant growth by decreased the accumulation of Na^+ ((Figure 1c)), maintained lower LPO ((Figure 2a)), increased the Pro concentration ((Figure. 3a)), and the activities of SOD and APX ((Figure 5a,c)). These findings suggest that foliar Si application mitigate salt stress in sorghum, a Si-accumulating plant. These results are in agreement with our findings that revealed an up-regulation of the free Pro and the enzymatic antioxidants activities in salt-treated plants supplied with Si, which is according with previous works in Si-accumulating plant such as wheat (*Sattar et al.,* 2018, 2017).

Similar effects have been observed in sunflower plants, including increased RD, but only following combined foliar and root Si application ((Figure. 6b)). Indeed, the combined foliar spray and nutrient solution of Si treatment attenuated salt stress, as indicated by the increased RD, LA, and SB. This was probably because Si reduced the accumulation of Na^+ and LPO and increased the K^+ accumulation; leaf RWC; SOD, CAT, and APX activities; RD; and LA, which had a positive effect on the SB. Previous studies in sunflower have shown that root Si application can attenuate salt stress, by increasing growth and dry matter production (*Ashraf et al.,* 2015). Our results are consistent with that of a previous study in okra have shown the beneficial effects of foliar Si application on the growth of salt-stressed plants (Abbas et al., 2017, 2015). In the present study, the effect of combined foliar and root Si application constitutes an unprecedented result for sunflower, an intermediate Si-accumulating species. The beneficial supply of Si via the root is known to mitigate the effects of salinity by increasing dry matter production, and this has been shown in sunflower (*Ashraf et al.,* 2015; *Calero et al.,* 2019).

Thus, our results show that the beneficial effects of Si on salinity attenuation were the highest when Si is supplied via combined foliar and root application to intermediate Si-accumulating plants (e.g., sunflower) rather than to high Si-accumulating plants (e.g., sorghum). Further studies are necessary regarding Si application methods to reduce salt stress in intermediate Si-accumulating plant species, such as sunflower.

Conclusions

Si application reduced the negative effects of salt stress in both sorghum and sunflower plants. The adverse effects of salt stress were attenuated by combined foliar and root Si application in sunflower plants and root Si application in sorghum plants, as indicated by reduced Na^+ uptake and lipid peroxidation, modified proline concentration, and increased K^+ uptake, leaf RWC, antioxidant enzyme activity, root diameter, leaf area, and shoot biomass. Our results indicated that the combined foliar and root Si application was more important for the attenuation of salinity in intermediate Si-accumulating plants than in high Si-accumulating plants. These findings suggested that Si could actively mediate some important metabolic processes that enhance stress tolerance in plants that are Si accumulators and intermediate accumulators.

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CHAPTER 3 – Silicon attenuates sodium toxicity by improving nutritional efficiency in sorghum and sunflower plants[1]

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^{-1}; root application of 2.0 mmol.L^{-1}; 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^+) 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^+ 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.

Keywords: *Helianthus annuus*; ionic stress; nutrient uptake efficiency; nutrient utilization efficiency; salinity stress; *Sorghum bicolor*

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

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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 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 Na^+ uptake (Alsaeedi 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 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 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°C ± 3.7°C (Figure 1a) and a relative humidity of 65.7% ± 25% (Figure 1b).

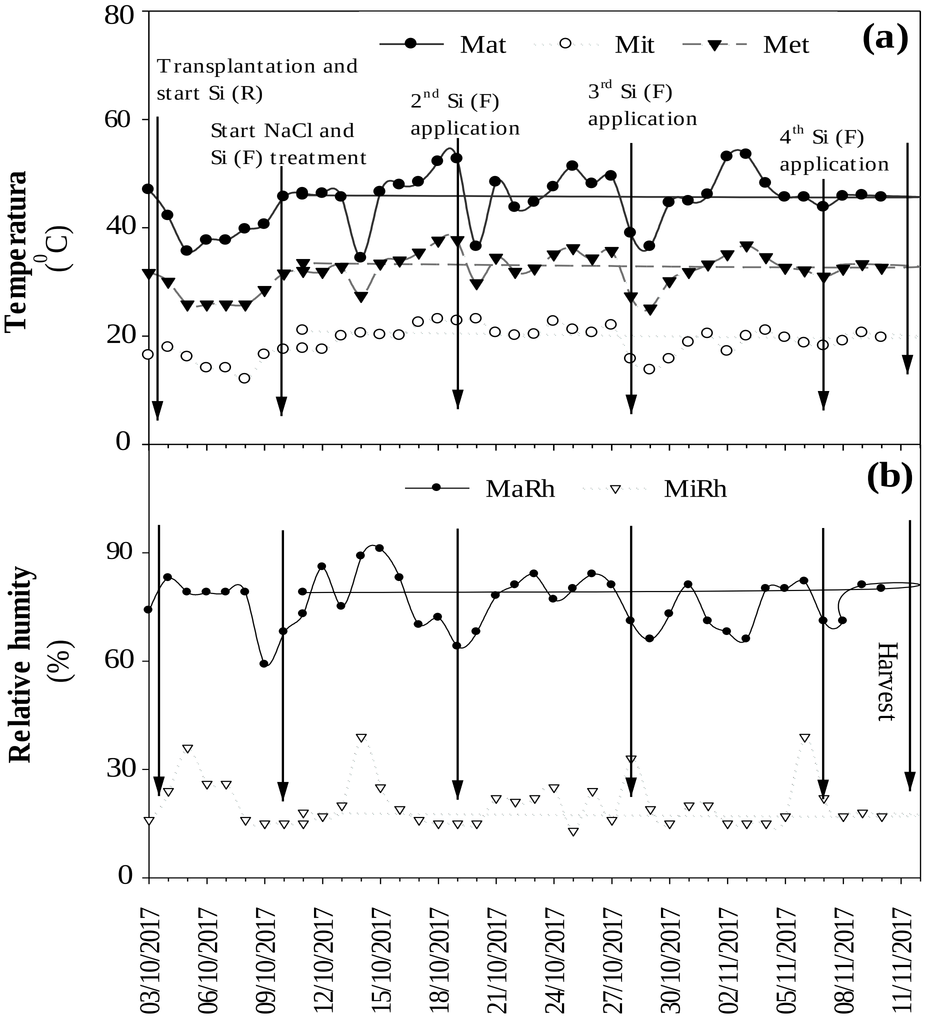

Figure 1. Experimental greenhouse conditions. Climatological variables in the experimental glass greenhouse during the experiments. Maximum temperature (Mat); minimum temperature (Mit); mean temperature (Met) (a); maximum relative humidity (MaRh); and minimum relative humidity (MiRh) (b).

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 × 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 Si (0); foliar application of 28.6 mmol.L^{-1} Si (F); root application of 2.0 mmol.L^{-1} Si in nutrient solution (R); and combined of Si application through root nutrient solution (2.0 mmol.L^{-1}) and foliar spraying (28.6 mmol.L^{-1}) (F + R). Overall, there were eight combination treatments and five replicates per treatment. The experimental unit consisted of a 4.0-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 ± 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 ~2.0 dS.m^{-1} salinity on the first day. After seven days of acclimatization, the plants were exposed to the desired level of salinity (~10.0 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 (Schneiter and Miller, 1981). Si was supplied at 2.0 mmol.L^{-1} 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^{-1} Si, comprising 94.2 g.L^{-1} Si in sodium silicate form (Na_2SiO_3) and 19.2 g.L^{-1} Si in potassium silicate form (K_2SiO_3). The Na^+ and K^+ 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^+ was measured in the root and shoot, and the content of N, P, potassium (K), Ca, magnesium (Mg), sulfur (S), cooper (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^{-1} of dry matter. The Si content was evaluated in the shoot as described by Kraska and Breitenbeck (2010). The Na^+ 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^{-1} 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^{-1} 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^+ 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^+ accumulation in the roots and shoots of sorghum and sunflower plants (Figure 2a-d). In sorghum plants, the Si(R) and Si(F + R) treatments decreased Na^+ accumulation in the roots and shoots compared with that under the F and 0 treatments (Figure 2a, c). In sunflower plants, Na^+ accumulation in the roots and shoots decreased only under the F + R treatment (Figure 2b, d).

In both plant species, Si accumulation was similar in the absence and presence of NaCl under all the Si application treatments (Figure 2e, 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 that under the Si (F) treatment, whereas in this one was higher than under the control (0) (Figure 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 (Figure 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 (Figure 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 (Figure 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 (Figure 3b, d, f, h, j, l).

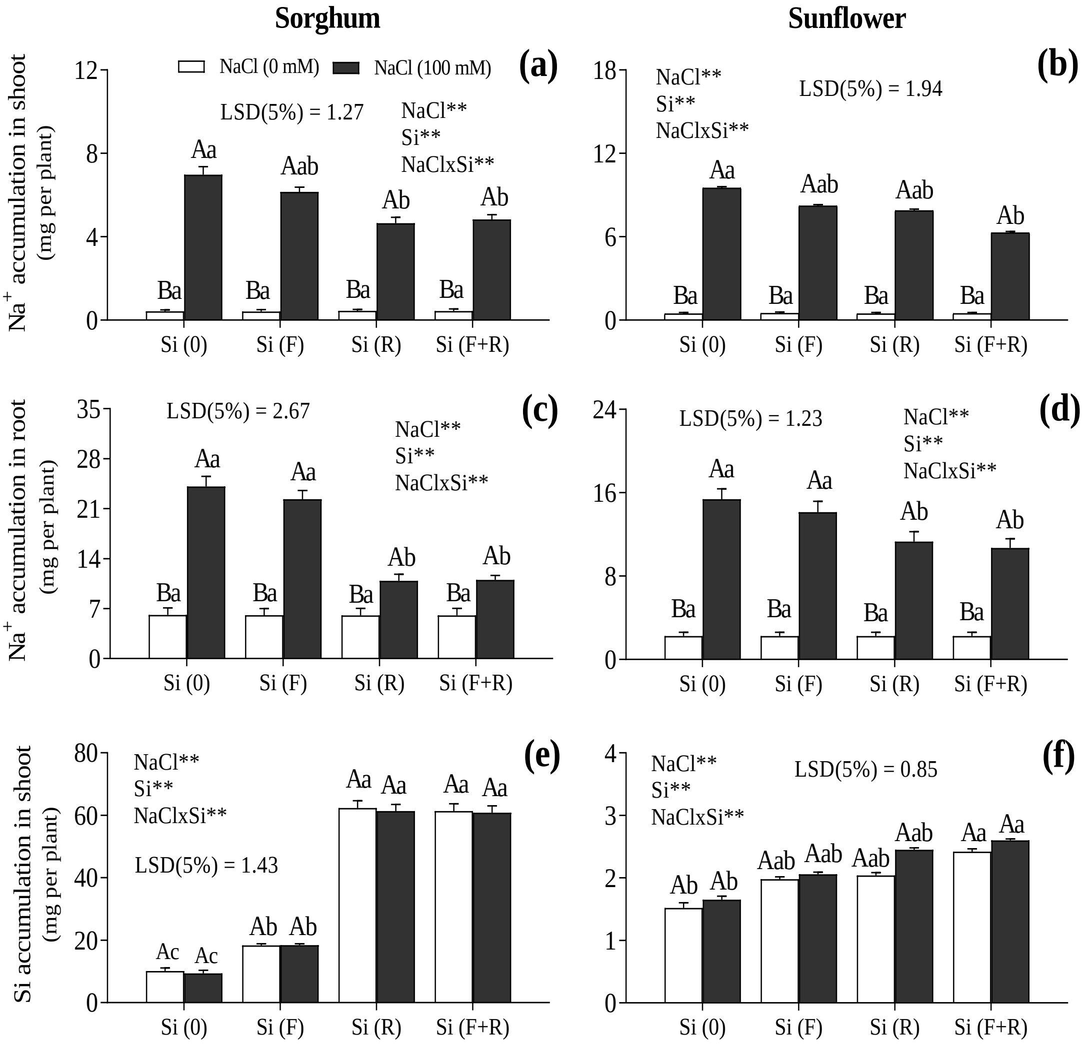

Figure 2. Na^+ and Si accumulation in sorghum and sunflower plants. Na^+ accumulation in the shoots of sorghum (a) and sunflower plants (b) and in the roots of sorghum (c) and sunflower plants (d), and Si accumulation in the shoots of sorghum (e) and sunflower plants (f), in the absence and presence of NaCl (0 and 100 mM) combined with different Si treatments; no added Si [Si (0)]; foliar Si application at 28.6 mmol L^{-1} [Si (F)]; root Si application at 2.0 mmol L^{-1} [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 ± standard error (SE) from five replicates (Mean ± SE; n = 5); least significant difference [LSD]. ** Significant at ($P < 0.01$) of probability. The vertical bars represent the SE of the mean.

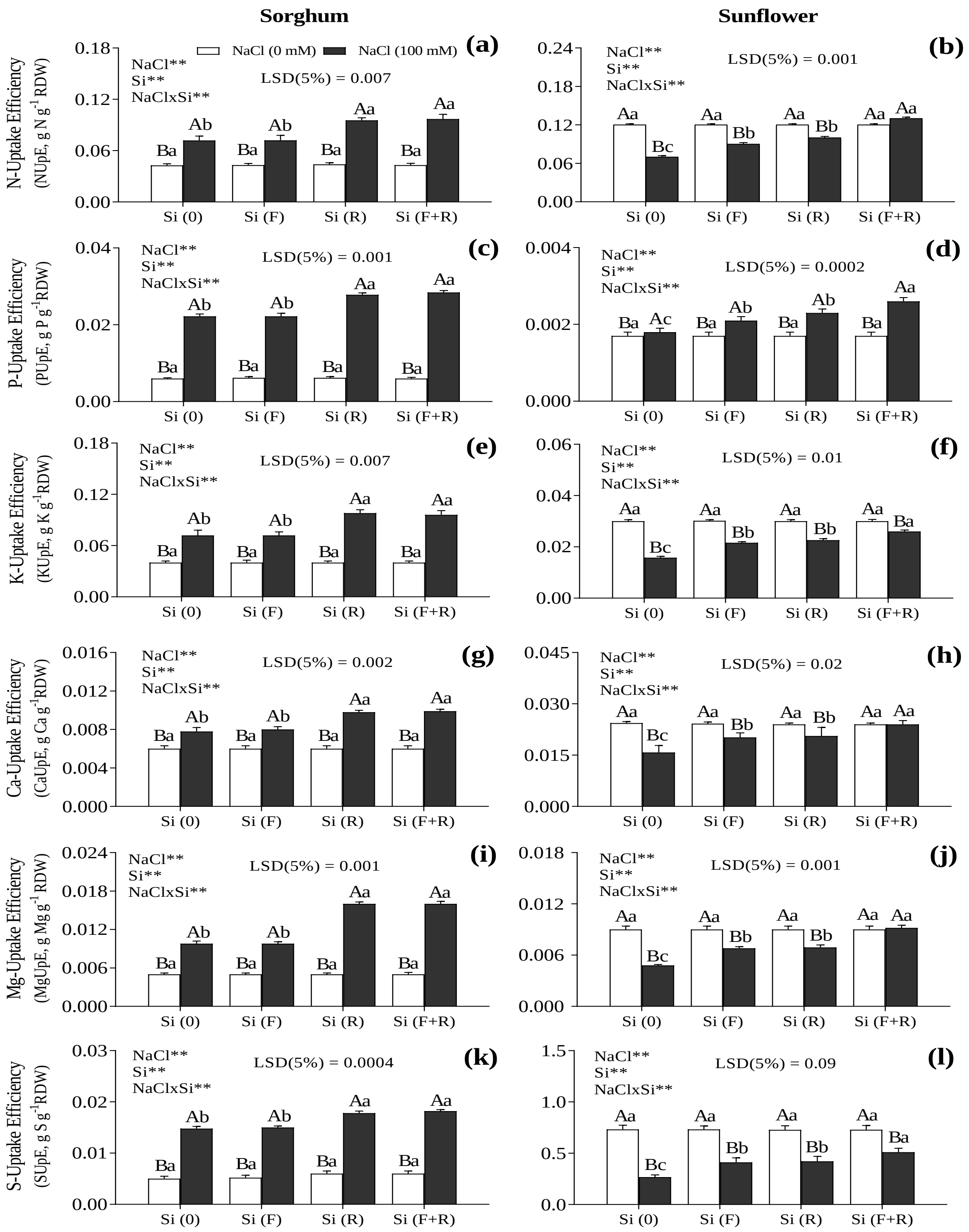

Figure 3. Uptake efficiency of macronutrients under Si and NaCl treatments. Nitrogen uptake efficiency (NUpE) in sorghum (a) and sunflower plants (b), phosphorus uptake efficiency (PUpE) in sorghum (c) and sunflower plants (d), potassium uptake efficiency (KUpE) in sorghum (e) and sunflower plants (f), 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

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 (Figure 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 (Figure 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 (Figure 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^+, Ca, Mg, and S was lower with the NaCl treatments than without the NaCl treatment (Figure 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)) (Figure 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 (Figure 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 (Figure 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 (Figure 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 (Figure 6b, d, f, h).

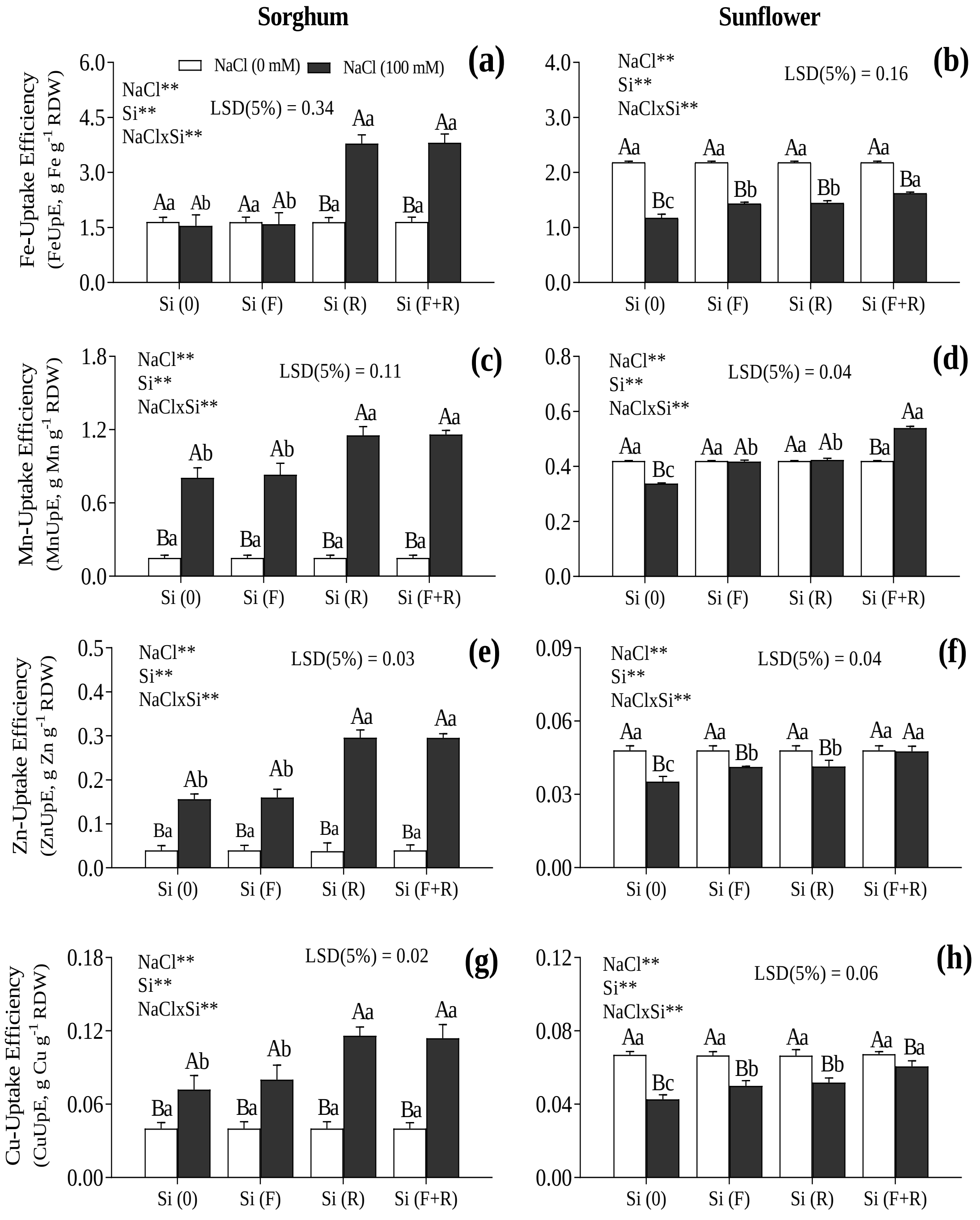

Figure 4. Uptake efficiency of micronutrients under the Si and NaCl treatments. Iron uptake efficiency (FeUpE) in sorghum (a) and sunflower plants (b), manganese uptake efficiency (MnUpE) in sorghum (c) and sunflower plants (d), zinc uptake efficiency (ZnUpE) in sorghum (e) and sunflower plants (f),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

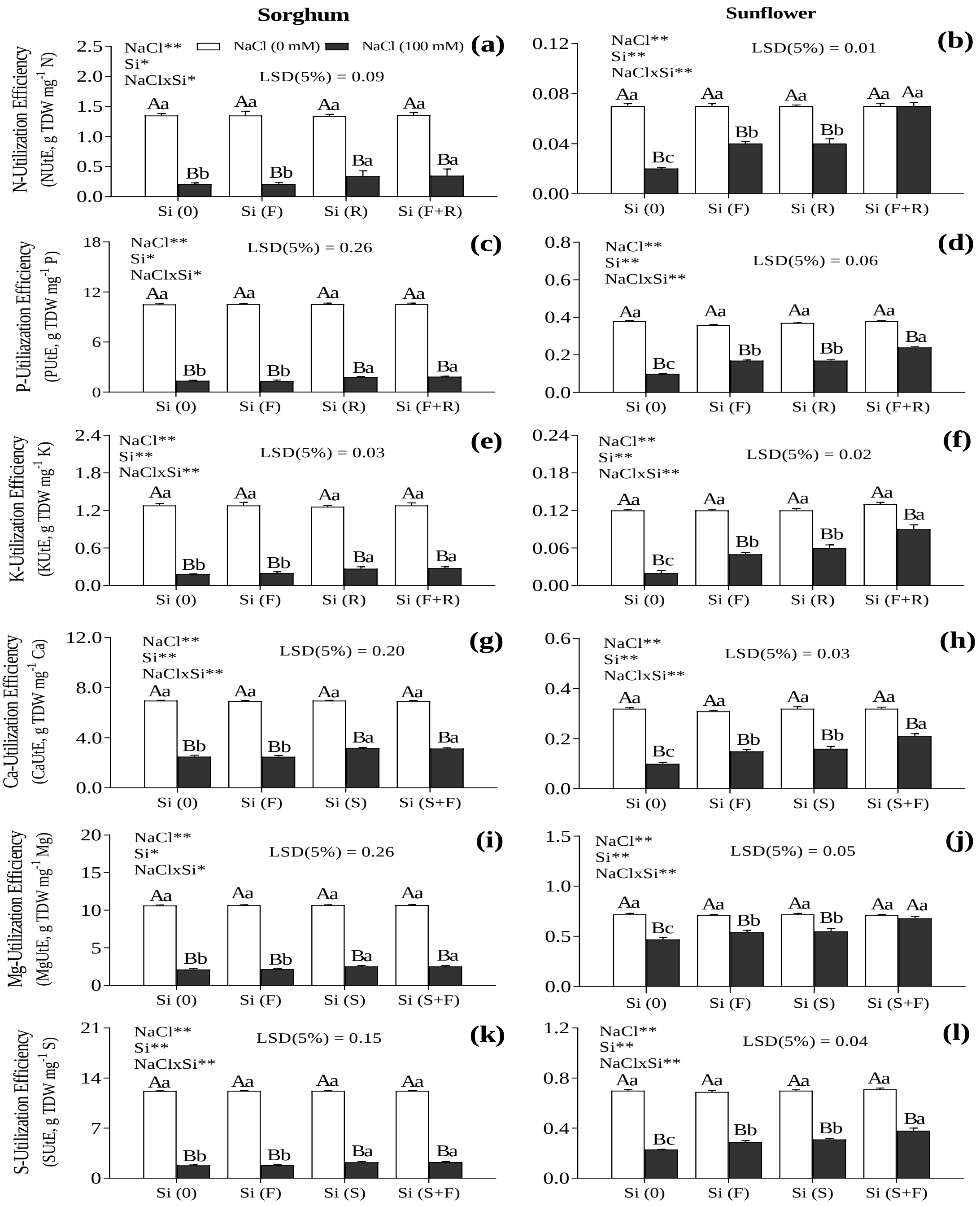

Figure 5. Utilization efficiency of macronutrients under the Si and NaCl treatments. Nitrogen utilization efficiency (NUtE) in sorghum (a) and sunflower plants (b), phosphorus utilization efficiency (PUtE) in sorghum (c) and sunflower plants (d), potassium utilization efficiency (KUtE) in sorghum (e) and sunflower plants (f), calcium utilization efficiency (CaUtE) in sorghum (g) and sunflower plants (h), magnesium utilization efficiency (MgUtE) in sorghum (i) and sunflower plants (j), and sulfur utilization efficiency (SUtE) in sorghum (k) and sunflower plants (l). Treatments and statistics as in Fig. 2

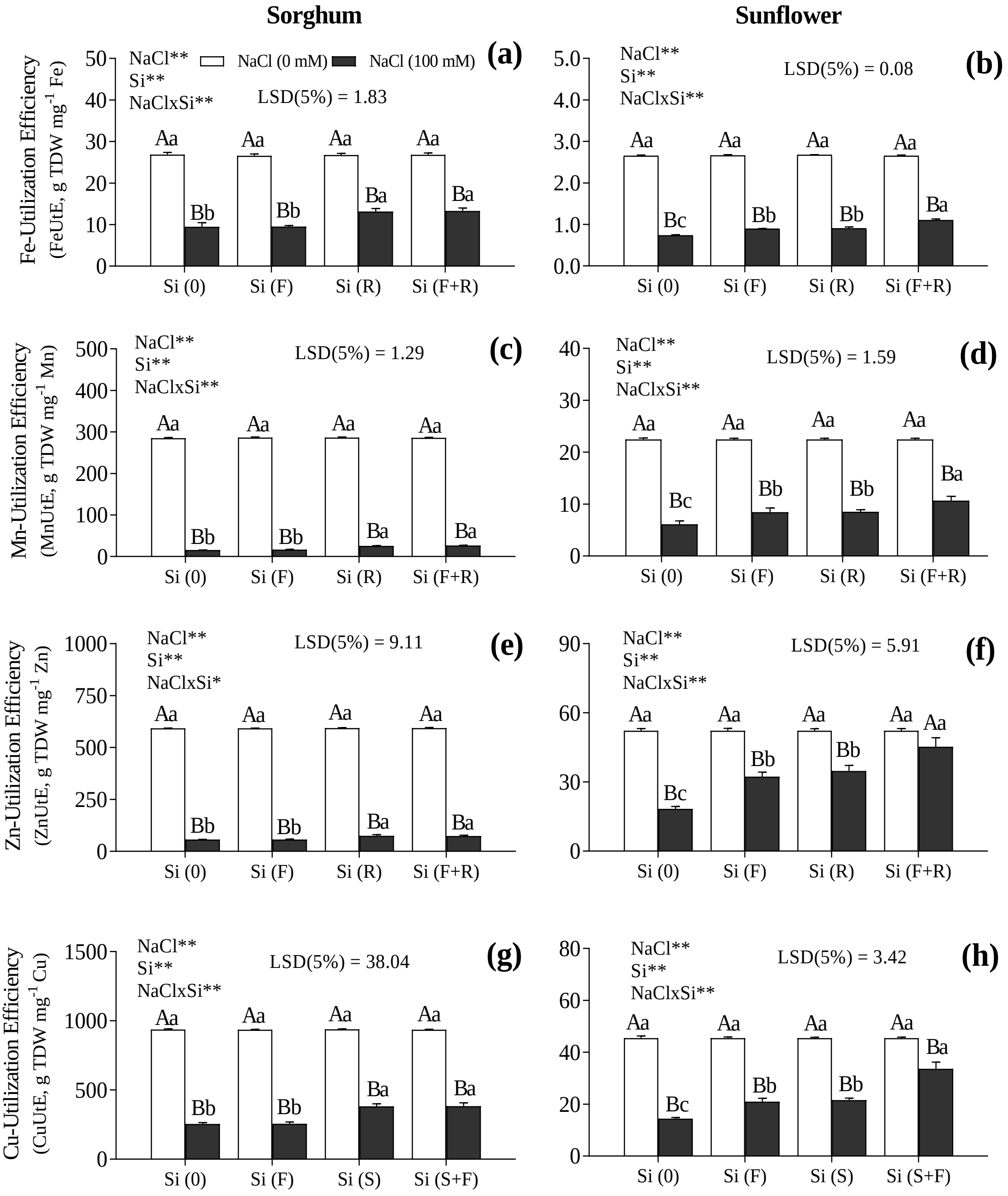

Figure 6. Utilization efficiency of micronutrients under the Si and NaCl treatments. Iron utilization efficiency (FeUtE) in sorghum (a) and sunflower plants (b), manganese utilization efficiency (MnUtE) in sorghum (c) and sunflower plants (d), zinc utilization efficiency (ZnUtE) in sorghum (e) and sunflower plants (f), and copper utilization efficiency (CuUtE) in sorghum (g) and sunflower plants (h). Treatments and statistics as in Fig. 2

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 (Figure 7a, 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 (Figure 7a). However, in sunflower 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 (Figure 7b).

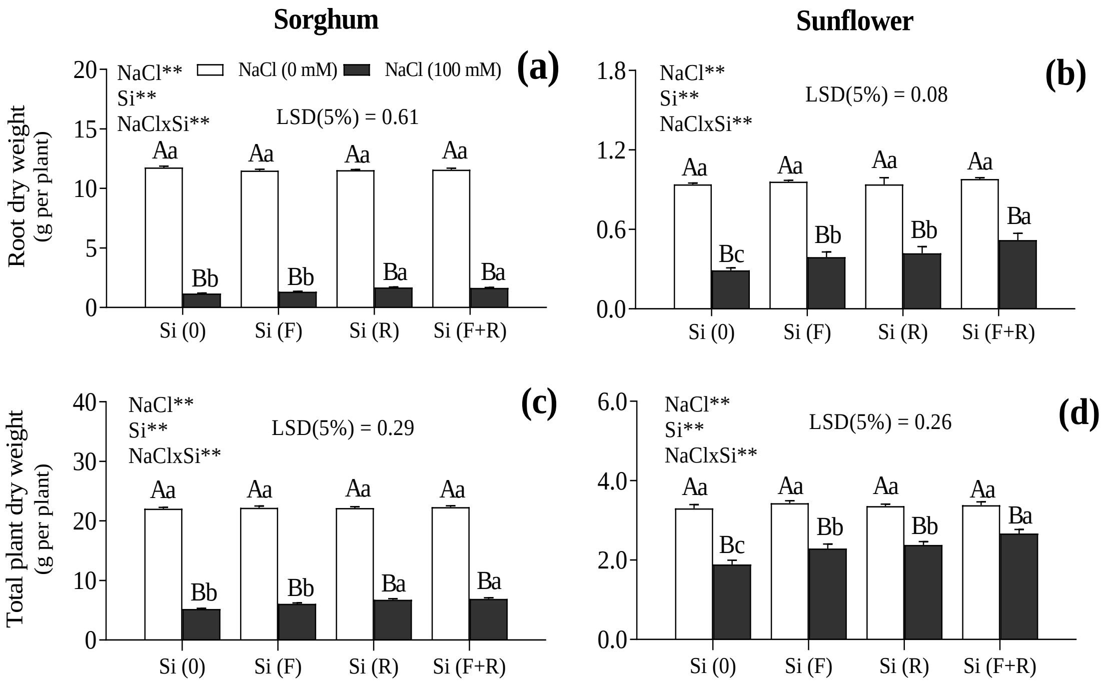

Figure 7. Root and total plant dry weight production under the Si and NaCl treatments. Root dry weight production in sorghum (a) and sunflower plants (b); total dry weight production (TDW) in sorghum (c) and sunflower plants (d). Treatments and statistics as in Fig. 2

4. Discussion

The salinity treatment we used increased Na^+ uptake in the root and shoot of sorghum and sunflower plants without affecting Si accumulation (Figure 2). Si decreased Na^+ accumulation in the roots and shoots of both cultures, especially when Si was supplied via nutrient solution to the roots (Figure 2a, b, c, d). This was because

Si application, especially via the root, increased Si accumulation in the shoots of both plant species (Figure 2e, 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^+ 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 (Figures 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^+ 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 (Figures 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^+ 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 (Alsaeedi 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 (Khoshgoftarmanesh 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 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; Khoshgoftarmanesh 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 Na^+ accumulation in the root and shoot (Figs. 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 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)) (Figure 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) 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^+ 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^+ 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.

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