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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 International 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).

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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).

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).

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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