Acta Sci. Pol. Hortorum Cultus, 19(2) 2020, 87–96

www.acta.media.pl ISSN 1644-0692 e-ISSN 2545-1405 DOI: 10.24326/asphc.2020.2.9

ORIGINAL PAPER

Accepted: 1.07.2019

DOES SILICON INCREASE THE TOLERANCE OF A SENSITIVE PEPPER GENOTYPE TO SALT STRESS?

Ozlem Altuntas[1]✉, Hayriye Yıldız Dasgan[2], Yelderem Akhoundnejad[2], Ibrahim Kutalmıs Kutsal[1]

[1] Malatya Turgut Özal University, Faculty of Agriculture, Department of Horticulture, Battalgazi, Malatya, Turkey

[2] Cukurova University, Faculty of Agriculture, Department of Horticulture, Adana, Turkey

ABSTRACT

We evaluated the growth performance, ion regulation, osmotic potential, and chlorophyll content of two pepper (*Capsicum annuum*) genotypes with different salinity tolerance levels (Karaisali is tolerant and Demre is sensitive to salinity) under saline conditions with the application of silicon (Si). Plants were grown in pots filled with vermiculite in control or saline conditions [150 mM sodium chloride (NaCl)] with or without 2 mM Si from potassium silicate for 60 days after sowing. Better growth effects due to Si application were observed in the sensitive pepper Demre than in Karaisali, particularly, the root and fruit growth were remarkably enhanced in Demre. Furthermore, Si application reduced sodium (Na) and chloride (Cl) concentrations and increased potassium (K) and calcium (Ca) concentrations in the leaves and roots. The reduction in Na concentration in the leaves due to Si application was 9% and 2% in Demre and Karaisali, respectively. Under saline conditions, the increase in K concentration due to Si application in the leaves was 11% and 14% in Demre and Karaisali, respectively. In addition, Si application resulted in an increase in K/Na ratios in the leaves by 22% and 17% in Demre and Karaisali, respectively, in the presence of 150 mM NaCl. The increase in Ca concentration in the roots due to Si application was 55% in Demre compared with only 9% in Karaisali. The addition of NaCl decreased the chlorophyll concentration in both the genotypes, but Si application increased it. This increase in chlorophyll concentration was higher in Demre than in Karaisali. Si application allowed both the genotypes to maintain higher osmotic potentials than those in untreated plants. As a result, it may be claimed that under salt stress, Si application has a more alleviative effect on the susceptible pepper genotypes (Demre) than on the tolerant one (Karaisali). This information could be useful for the practical application of Si under saline conditions.

Key words: *Capsicum annuum*, salt stress, silicon, plant growth, physiological parameters

INTRODUCTION

In agriculture, one of the major problems is the salinization of arable lands, which limits the agricultural production due to yield loss. Recent studies have reported that at least 20% of irrigated lands worldwide are salinized [Pitman and Läuchli 2002, Chinnusamy et al. 2005, Ashraf and Akram 2009]. Thus, it is inevitable to develop new techniques that ameliorate this salt stress. A conventional approach to overcome this problem is the cultivation of salt-tolerant plants. In addition, the application of some exogenous components, such as potassium (K) [Akram et al. 2007], calcium (Ca) [Awada et al. 1995], silicon (Si) [Rodrigues et al. 2003, Ma 2004], salicylic acid, jasmonic acid [Khan et al. 2012], and melatonin [Li et al.

✉ ozaltuntas01@gmail.com

2012] or of beneficial microorganisms, such as plant growth-promoting bacteria [Habib et al. 2016] and arbuscular mycorrhizal fungi [Evelin et al. 2009] can provide tolerance to plants by regulating ion metabolism or secreting hormones.

Si is an important element in agriculture because it improves plant growth, provides strength, and more importantly, ameliorates plant tolerance to various abiotic stresses [Abbas et al. 2015]. Si is not an essential element for higher plants [Liang et al. 2007], but external Si treatments can result in positive effects on plant growth under normal and stressful conditions, including biotic and abiotic stresses [Gao et al. 2006, Liang et al. 2007, Zhu and Gon 2014]. A number of possible mechanisms have been proposed through which Si may improve salt tolerance in plants: reducing the uptake and translocation of Na to shoots [Epstein 2001, Gong et al. 2003, Liang et al. 2003], increasing the selective uptake of K by the activation of H-ATPase in the membranes [Liang et al. 2005], mitigating against the toxic effects of sodium (Na) by enhancing the K/Na selectivity ratio [Liang et al. 1996], improving water status by enhancing the leaf water potential due to a silica-cuticle double layer formed on leaf epidermal tissue [Liang et al. 1999, Gong et al. 2003, Romero et al. 2006], increasing the photosynthetic activity and improving the ultrastructure of leaf organelles [Shu and Liu 2001], stimulating the antioxidant system [Zhu et al. 2004], reducing electrolytic leakage from the leaves [Liang et al. 1996], increasing endogenous hormone gibberellin (GA) and free salicylic acid (SA) levels and decreasing the abscisic acid (ABA) level [Hamayun et al. 2010].

One of the mechanisms of salt tolerance in plants is associated with ion regulation. A key factor that contributes to the high salt tolerance is the maintenance of higher K and Ca and lower Na and chlorine (Cl) levels in plant tissues. The genotypes that are tolerant to salt stress are capable of maintaining higher K/Na ratios in tissues [Mansour 2003, Zeng et al. 2003]. Thus, ensuring a reduced Na uptake and promoted K uptake would provide a higher K/Na ratio in plants to ameliorate the deleterious effects of salt stress. The parameters that are commonly used to determine salt tolerance level in plants include leaf K/Na and Ca/Na ratios and root Na and Cl concentrations [Dasgan et al. 2002]. Although many studies have reported about the role of Si in alleviating salt stress [Liang et al. 2005, Romero-Aranda et al. 2006, Abbas et al. 2015], no study has investigated the effects of Si application in pepper (*Capsicum annuum*) plants.

Pepper (*C. annuum* L.) is an important crop worldwide based on its economic importance as well as nutritional value. Pepper is very commonly consumed as a fresh vegetable and spice in Turkey. It is known that pepper plant is sensitive to salt stress. Excessive salinity of soil or irrigation water observed in many semi-arid to arid regions of the world inhibits pepper plant growth and yield. While a salinity level of 0–2 dS/m is acceptable, the salinity level of >3 dS/m results in decreased crop yield [Navarro et al. 2010].

This research aimed to investigate the role of Si in mitigating short-term salt stress in pepper plants in the early growth stage. The possible hypotheses were as follows: Si application improves the plant water status by diminishing the salt-induced osmotic stress, and Si reduces Na uptake and increases the K/N ratio in a salt-insensitive pepper genotype. To test the aforementioned hypotheses, fresh weight, chlorophyll content, osmotic potential, and ion accumulation under short-term salt stress were compared between tolerant and sensitive pepper genotypes in the presence or absence of Si application.

MATERIALS AND METHODS

Plant material and growth conditions. In the present study, two local pepper genotypes were used: Karaisali is tolerant and Demre is sensitive to salt stress [Altuntas et al. 2016]. The plants were grown in a climate chamber at the Department of Horticulture, Faculty of Agriculture, Cukurova University. Pepper seeds were germinated in a soilless growing system in vermiculite. When the seedlings reached the 4–5 leaves stage they were transplanted into pots filled with vermiculite. The composition of the nutrient solution (mg L^{-1}) was as follows: nitrogen (N) = 200, phosphorus (P) = 50, potassium (K) = 300, calcium (Ca) = 200, magnesium (Mg) = 55, sulfur (S) = 28, iron (Fe) = 5, manganese (Mn) = 0.5, zinc (Zn) = 0.25, boron (B) = 0.90, copper (Cu) = 0.12, and molybdenum (Mo) = 0.12. Half-strength Hoagland nutrient solution was used for plant nutrition. Pots with a capacity of 2 L were filled with vermiculite, and 15-day-old pepper seedlings were placed in each pot. Plants were grown in a growth chamber at 22/18°C with a 16 h photoperiod and 60% relative humidity for 60 days. The amount of photosynthetically active radiation received by the upper plant surfaces was 300 mol m^{-2} s^{-1}.

The study design was completely randomized with three replicates, each replicate contained three pots, and each pot contained three plants. Control plants were grown without salt ans Si. The salinity and Si treatments were initiated by adding NaCl and potassium silicate (K_2SiO_3) to the nutrient solution when the plants were 30-day-old, and this process was continued up to 60 days after sowing. To avoid osmotic shock, the salinity treatment was introduced in increments, with a daily increase of 50 mM in concentration until the final concentration of 150 mM was achieved. Si was applied by adding 2 mM K_2SiO_3 along with NaCl. Additional K which was introduced due to the addition of K_2SiO_3 was neutralized by the addition of potassium nitrate (KNO_3) in the nutrient solution. All measurements were performed at the end of the experiment, i.e. 30 days after the salt-stress condition. On day 31, the plants were harvested and their shoots, roots, and fruits were separated for determining the fresh weight of the biomass. The entire root system and representative leaves from the shoot were used for analyzing the K, Ca, Na, and Cl contents.

Ion content. Leaves and roots were washed once with tap water and twice with deionized water. They were then dried in a forced-air oven at 65°C for 48 h and ground through a 40-mesh sieve for elemental analysis. The samples were dry-ashed in a muffle furnace at 550°C for 6 h. The ash was then dissolved in 0.1 M hydrochloric acid (HCl) solution. Concentrations of K, Ca, and Na were determined using an atomic absorption spectrophotometer [Jones 2001]. The Cl concentration in tissue samples was determined using titrimetric analysis with silver nitrate ($AgNO_3$).

Osmotic potential. To determine the osmolality (c), 1 g of fresh weight from fully expanded leaves was homogenized in a mortar and mixed with distilled water to reach a final volume of 20 mL. After extraction using a millipore filter, the sap was utilized to determine the osmolality using a freezing point osmometer (Gonotec Osmomat 030, Germany). The osmotic potential was determined using the following formula according to the Van’t Hoff equation [Silva et al. 2010]: $\psi_s(\text{MPa}) = -c\ (\text{mos mol kg}^{-1}) \times 2.58 \times 10^{-3}$.

Chlorophyll measurements. A portable chlorophyll meter (SPAD-502, Minolta, Japan) was used to measure the leaf greenness or relative chlorophyll content of the fully matured leaves of all plants in each pot on the harvest day. For each plant, measurements were recorded at four locations on fully expanded fifth leaves from the top, and the average value was then calculated [Khan et al. 2003, Yıldırım et al. 2008].

Statistical analysis. Fresh weights of shoots, roots, and fruits, Na, K, Ca, Na, and Cl concentrations in the leaves and roots, and osmotic potential and chlorophyll content in the leaves were examined using analysis of variance. The least significant difference (LSD) was calculated at a 0.05 probability level for each parameter.

RESULTS

Plant growth. Compared with the control, the shoot fresh weight was significantly lower for both the genotypes when grown in saline conditions (Tab. 1). The reduction in shoot fresh weight was much lower in Demre than in Karaisali. Furthermore, Si application increased the shoot fresh weight in both the genotypes grown in either control or saline conditions, the shoot fresh weight increased by 32% and 15% under control conditions and 39% and 34% under saline conditions in Demre and Karaisali, respectively. The effect of Si application on shoot fresh weight was more pronounced in Demre than in Karaisali under saline conditions.

The effects of Si application on root fresh weight under both control and saline conditions were more remarkable in Demre than in Karaisali (Tab. 1). Si application resulted in an increase in the root fresh weight by 54% and 17% under control conditions and by 20% and 7% under saline conditions in Demre and Karaisali, respectively.

Plant fruits were harvested and weighed at the end of the experiment. Application of Si increased the fruit fresh weight under both control and saline conditions. However, under saline conditions, this increase was more remarkable in Demre than in Karaisali (Tab. 1).

Physiological parameters. The concentration of K was decreased in both roots and leaves, particularly in the leaves under saline conditions. The K concentration

Table 1. Fresh weight (FW) of two 60-day-old pepper genotypes that were grown for 30 days under control and saline conditions with or without silicone (Si) application (g plant^{-1})

Si	Genotype	NaCl (mM)	Shoot FW	Root FW	Fruit FW
Si (–)	Karaisali	0	33.93 ab	17.45 b	55.65 a
		150	12.10 cd	5.39 d	4.55 b
	Demre	0	24.03 bcd	10.01 c	53.87 bcd
		150	7.42 d	2.90 d	2.42 b
Si (+)	Karaisali	0	44.73 a	20.44 a	72.75 a
		150	16.26 cd	5.76 d	8.50 b
	Demre	0	27.62 bc	15.41 b	68.80 a
		150	10.35 cd	3.49 d	8.04 b

LSD test: the same letter within each column indicates no significant difference between the treatments ($P < 0.05$)

Table 2. Concentrations of potassium (K), calcium (Ca), sodium (Na), and chlorine (Cl) in the leaves of two pepper genotypes grown under control and saline conditions with or without silicon (Si) application (%)

Si	Genotype	NaCl (mM)	K	Ca	Na	Cl
Si (–)	Karaisali	0	3.63 a	1.23 a	0.29 c	0.22 c
		150	2.20 b	0.82 cd	2.05 b	2.26 b
	Demre	0	3.50 a	1.18 a	0.30 c	0.22 c
		150	2.03 b	0.76 d	2.99 a	3.21 a
Si (+)	Karaisali	0	3.58 a	1.24 a	0.30 c	0.20 c
		150	2.51 b	1.01 b	2.01 b	2.09 b
	Demre	0	3.51 a	1.20 a	0.33 c	0.17 c
		150	2.26 b	0.94 bc	2.73 a	3.01 a

LSD test: the same letter within each column indicates no significant difference between the treatments ($P < 0.05$)

Table 3. Concentrations of potassium (K), calcium (Ca), sodium (Na), and chlorine (Cl) in the roots of two pepper genotypes grown under control and saline conditions with or without silicon (Si) application (%)

Si	Genotype	NaCl (mM)	K	Ca	Na	Cl
Si (–)	Karaisali	0	1.85 a	0.76 b	0.49 c	0.68 d
		150	1.12 cd	0.40 d	1.34 a	2.04 b
	Demre	0	1.37 bc	0.70 b	0.51 c	0.18 e
		150	0.89 d	0.33 d	1.51 a	2.63 a
Si (+)	Karaisali	0	1.61 ab	0.87 a	0.46 c	0.65 d
		150	1.40 bc	0.54 c	1.11 b	1.66 c
	Demre	0	1.58 ab	0.74 b	0.48 c	0.13 e
		150	1.01 d	0.51 c	1.33 a	2.21 b

LSD test: the same letter within each column indicates no significant difference between the treatments ($P < 0.05$)

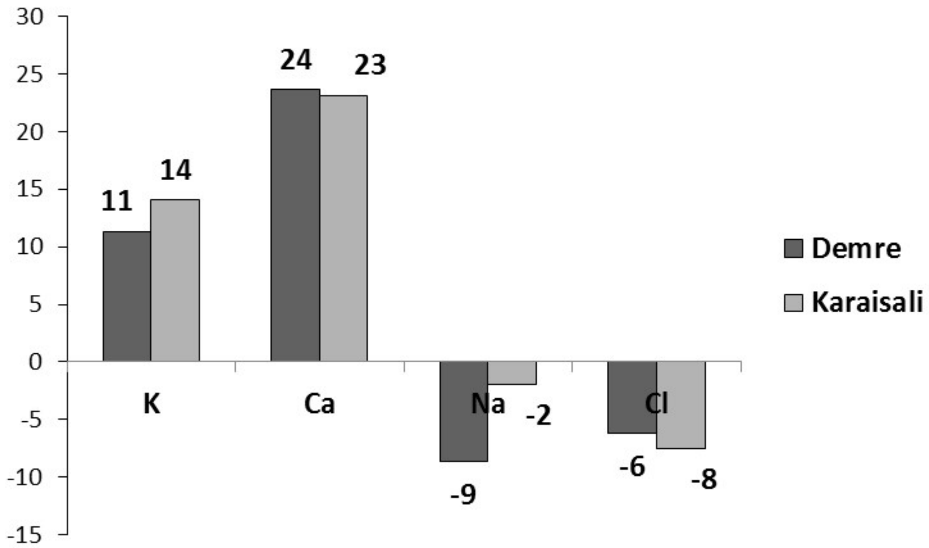

Fig. 1. Percent increase in potassium (K) and calcium (Ca) concentration and decrease in sodium (Na) and chlorine (Cl) concentration in the presence of 150 mM NaCl in the leaves of Demre and Karaisali peppers following the addition of silicon

in roots and leaves of both the genotypes was significantly higher ($P < 0.05$) under saline conditions with Si application than without Si application (except in the roots of Karaisali). The K concentration in the leaves of salt-treated plants was lower ($P < 0.05$) than that in untreated plants in the presence of Si, but a greater difference was observed in the K concentration of the leaves than that of the roots. Therefore, salt stress significantly reduced the K concentration in the leaves of both the genotypes when grown without Si (Tabs. 2 and 3). The K concentration was similar in the leaves of both the genotypes in the absence of Si and salt conditions. The sensitive genotype Demre lost more K than the tolerant Karaisali under saline contitins (73% and 65%, respectively). Application of Si increased the K concentration by 11% and 14% in the leaves of Demre and Karaisali under saline conditions, respectively (Fig. 1).

The Na concentration considerably increased under saline conditions. Si application significantly reduced the Na concentration in the leaves and roots, with a stronger effect in the roots. The Na concentration of the leaves decreased by 9% and 2% due to Si application under saline conditions in Demre and Karaisali, respectively (Fig. 1), however, in the roots, these values were 12% and 17%, respectively (Tabs. 2, 3 and Fig. 2). Notably, Si application in the tolerant Karaisali genotype resulted in less Na concentration in the roots, therefore, less Na was localized to the leaves. In terms of the K/Na ratio, stronger effects were observed in the roots than in the leaves. With Si application, the K/Na ratio under saline conditions (150 mM NaCl) increased by 22% and 17% in the leaves and by 31% and 52% in the roots in Demre and Karaisali, respectively (Tab. 4).

Under saline conditions, all plants showed higher Na and Cl concentrations in the leaves than in the roots. The Cl concentration was increased under saline conditions in both the leaves and roots, with a preferential allocation in the leaves. With Si application, the reduction in Cl concentration under saline conditions was 6% and 8% in the leaves (Tab. 2, Fig. 1) and 16% and 19% in the roots in Demre and Karaisali, respectively. Thus, the reduction in Cl concentration was more in the roots than in the leaves (Tab. 3, Figs. 1 and 2).

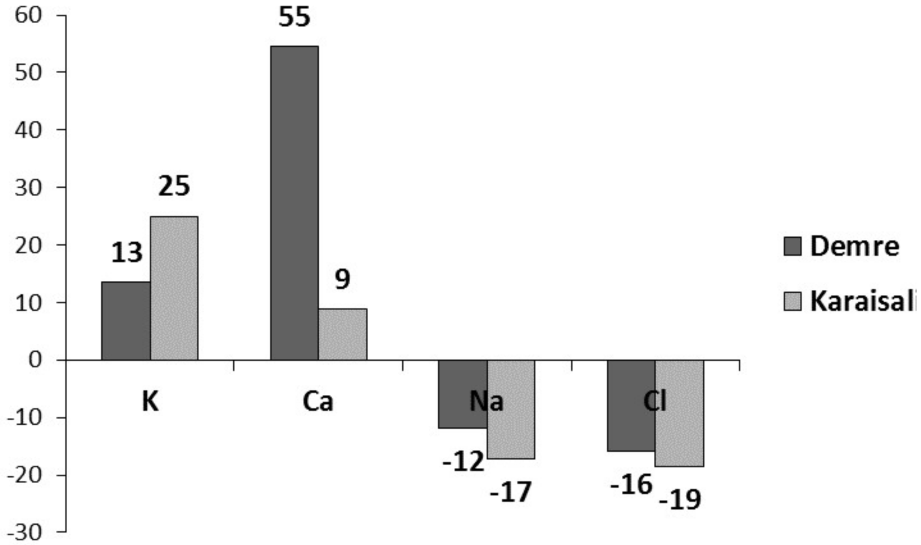

Fig. 2. Percent increase in potassium (K) and calcium (Ca) concentrations and decrease in sodium (Na) and chlorine (Cl) concentrations in the presence of 150 mM NaCl in the roots of Demre and Karaisali peppers following the addition of silicon

Salt treatment greatly reduced the Ca concentration in the leaves and roots in both the cultivars (Tabs. 2 and 3). With Si application, the Ca concentration increased by 24% and 23% under saline conditions in Demre and Karaisali, respectively, which was significantly more than that under saline conditions, this increase was significant in Demre (*P* = 0.05), but not Karaisali (Fig. 1). The increase in root Ca concentration under saline conditions with Si application was remarkably higher in Demre (55%) than that in Karaisali (9%) – Figure 2.

The osmotic potential was decreased due to salt stress in both the genotypes, however, Demre showed a greater decrease than Karaisali (Tab. 5). Si application enabled both the genotypes to maintain higher osmotic potentials than those of untreated plants. Under saline conditions with Si application, the osmotic potential was increased by 15% and 14% in Demre and Karaisali, respectively. These results demonstrated that Si application can alleviate the salt-induced plant-water imbalance (Tab. 5).

The chlorophyll concentration was significantly decreased due to salt stress in the pepper plants. Application of Si alleviated this salt-induced decrease in both the genotypes. Under saline conditions, Si application increased the chlorophyll concentration by 5.8% and 3.6% in Demre and Karaisali, respectively.

DISCUSSION

The addition of Si in the growth medium increased the fresh weights of shoots, roots, and fruits of both the pepper cultivars under both normal and saline conditions (Tab. 1). The effects of Si application were more pronounced in Demre than in Karaisali, the root and fruit growth rates were remarkably increased in Demre. In addition, salt-induced growth inhibition was reversed by Si supplementation (Tab. 1). This growth improvement is in agreement with previous studies that reported the beneficial effects of Si on the growth and yield of various cultivated plant species under salt-stress conditions [Zhu et al. 2004, Romero-Aranda et al. 2006, Ashraf et al. 2010a, 2010b]. Yin et al. [2013] reported that growth improvement in the presence of Si was related to maintaining a high photosynthetic rate which allowed a constant supply of assimilates to the growing tissue. In sorghum plants, the net photosynthetic rate, stoma-

Table 4. Shoot and root potassium to sodium (K/Na) ratios of two pepper genotypes grown under control and saline conditions with or without silicon (Si) application (%)

Si	NaCl (mM)	Shoot K/Na in Demre	Shoot K/Na in Karaisali	Root K/Na in Demre	Root K/Na in Karaisali
Silicon (−)	0	12.0	13.0	2.7	3.78
	150	0.68	1.07	0.58	0.83
Silicon (+)	0	11.0	18.0	3.3	3.5
	150	0.83	1.25	0.76	1.26

Table 5. Osmotic potential and chlorophyll content of two pepper genotypes grown under control or saline conditions with or without silicon (Si) application (%)

Si	Genotype	NaCl (mM)	Osmotic potential (MPa)	Chlorophyll (SPAD)
Si (−)	Karaisali	0	−1.23 de	68.63 a
		150	−2.06 b	58.43 c
	Demre	0	−1.60 cd	70.23 a
		150	−2.47 a	60.97 bc
Si (+)	Karaisali	0	−1.06 e	69.53 a
		150	−1.75 b	60.53 bc
	Demre	0	−1.28 de	72.80 a
		150	−2.09 b	64.50 b

LSD test**:** the same letter within each column indicates no significant difference between the treatments ($P < 0.05$)

tal conductance, and transpiration rates were increased by 30%, 42%, and 41%, respectively, with the addition of 0.8 mM Si following salt treatment compared with 100 mM NaCl treatment alone [Yin et al. 2013]. Hamayun et al. [2010] reported that Si significantly increased the growth attributes and effectively mitigated the adverse effects of salt stress in soybean plants. This improvement was attributed to the fact that Si improved the physio-hormonal attributes of soybean and mitigated the adverse effects of salt. Endogenous GAs, bioactive GA_1 and GA_4, and free SA levels in soybean leaves increased, whereas ABA levels decreased with Si application in salt-stressed plants. One mechanism by which Si induces salinity tolerance is the increase in K uptake [Liang et al. 1999]. The present results revealed a significant increase in K uptake in both the genotypes under saline conditions with Si application, especially in the tolerant cultivar Karaisali (Tabs. 2 and 3).

In this study, Si-enhanced salt tolerance was believed to be associated with a decrease in Na and Cl concentrations and increase in K and Ca concentrations in the shoots and roots, particularly in the roots (Tabs. 2 and 3). Si-enhanced salt tolerance may have originated from the efficacy of Si in maintaining the membrane integrity due to increased K and Ca concentrations in the tissues and cells of salt-stressed pepper plants [Liang 1999]. The increase in Ca concentration was higher than that in K concentration under saline conditions with Si application in the shoots and roots of both the cultivars, however, it was highest in the roots of Demre (Figs. 1 and 2). The increased uptake in Ca due to Si application under salt stress may enable the plants to tolerate salt stress. It is well known that plants are prone to Na-induced Ca deficiency [Liang 1999]. Generally, Si decreases the transpiration rate, and may result in a decrease in Ca concentration. However, in this study, Si application had no significant effect on Ca concentration in control pepper plants, but a significant increase in Ca concentration was observed under saline conditions. It is possible that Si does not reduce the transpiration rate in pepper plants.

The K uptake and transport is an active process associated with the ATP-driven H^+ pump in the plasma membranes [Marschner 1995]. One possible mechanism for the stimulating effect of Si on K uptake by plants under salt stress is the activation of H^+-ATPase in the membranes, which is consistent with an increased H^+-ATPase activity in salt-stressed plants with Si application [Liang 1999]. The increase in the H^+-ATPase activity due to Si resulted in a higher K uptake. Thus, a higher K concentration in the tissues may have caused a reduction in Na uptake and concentration in the tissues. Potassium plays a significant role in improving the plant water status and mitigating the toxic effects of Na. The K/Na ratio was lower under saline conditions in the absence of Si. Our results showed that the K/Na ratio was significantly increased in the root environment in the presence of Si, indicating an enhanced K/Na selectivity ratio in both the genotypes.

Under salt stress, Na suppresses the K uptake. The significant increase in Na concentration and decrease in K/Na ratio under high salt concentrations in the leaves, especially in the sensitive cultivar Demre, shows that Na was transported to the leaves in a greater proportion than K. Several studies have claimed that the uptake mechanisms for both K and Na are similar [Niu et al. 1995]. The K absorption–reduction trend was lower than leaf Na accumulation, especially in Demre (Tabs. 1 and 2). Application of Si alleviated the adverse effects of high salinity on plants and improved the K content in the leaves and roots. It also decreased the Na content and K/Na ratio in the leaves and roots. Si may be more useful in the roots than in the shoots of pepper plants (Figs. 1 and 2). Potassium is essential for cell expansion, osmoregulation, and cellular and whole-plant homeostasis, and a high K requirement was reported for stomatal opening and carbon dioxide (CO_2) supply for photosynthesis [Munns and Tester 2008].

In the present study, an osmotic adjustment may be achieved by an increase in K and Ca (osmolytes) concentrations in the tissues when the water content decreased under saline conditions (Tabs. 1 and 2). A high salt concentration around the roots resulted in enhanced osmotic stress, which induced difficulties in the root water uptake and caused a leaf water imbalance, eventually resulting in plant growth reduction [Boursiac et al. 2005, Munns and Tester 2008]. In the present study, Si alleviated the salt-induced osmotic stress by increasing the K and Ca uptake. Therefore, the amelioration of the water balance using Si application may contribute to an enhanced salt tolerance in plants.

Ion toxicity is the result of salt accumulation to toxic concentrations in the leaves. It also decreases chlorophyll concentration and accelerates leaf senescence, eventually leading to a reduced photosynthetic rate and leaf death [Munns and Tester 2008, Liu and Shi 2010]. In the present study, Si application decreased the Na concentration in the leaves (Tab. 2), furthermore, K and Ca concentrations and K/Na and Ca/Na ratios in the leaves were enhanced (Tab. 4). Correspondingly, the chlorophyll concentration in the leaves was maintained at a higher level in the Si-treated plants than in untreated plants, especially in Demre (Tab. 5), which suggested that Si application decreased the salt-induced ion toxicity.

CONCLUSION

In the present study, Si application significantly alleviated the salt-induced biomass reduction, indicating that Si enhances salt tolerance in pepper plants, especially in the salt-sensitive genotype Demre in terms of root and fruit growth. Pepper plants adapt to salt stress by decreasing the salt-induced ion toxicity, osmotic stress, and chlorophyll loss. The Na uptake and transportation into the shoots from the roots was greatly inhibited with Si application under salt stress, whereas the K and Ca concentrations in the shoots and roots in salinized plants were enhanced by Si application. Si probably limits Na and Cl absorption and enhances K and Ca inclusion. Consequently, maintaining high K/Na and Ca/Na ratios results in safe growth. Salt tolerance in the sensitive pepper Demre was increased by the addition of Si in terms of growth, ion regulation, osmotic adjustment, and chlorophyll content.

REFERENCES

Abbas, T., Balal, R.M., Shahid, M.A., Pervez, M.A., Ayyub, C.M., Aqueel, M.A., Javaid, M.M. (2015). Silicon-

-induced alleviation of NaCl toxicity in okra (*Abelmoschus esculentus*) is associated with enhanced photosynthesis, osmoprotectants and antioxidant metabolism. Acta Physiol. Plant., 37. DOI: 10.1007/s11738-014-1768-5

Akram, M.S., Athar, H.U.R., Ashraf, M. (2007). Improving growth and yield of sunflower (*Helianthus annuus* L.) by foliar application of potassium hydroxide (KOH) under salt stress. Pakistan J. Bot., 39, 769–776.

Altuntas, O., Dasgan, H.Y., Akhoundnejad, Y. (2016). Silicon nutrition ameliorates salt stress of *Capsicum annuum* L. by ion regulation. XVI Eucarpia Capsicum and Eggplant Meeting Kecskemet, Hungary 12–14 September 2016, Proceedings, 465–469.

Ashraf, M., Akram, N.A. (2009). Improving salinity tolerance of plants through conventional breeding and genetic engineering: an analytical comparison. Biotechnol. Adv., 27, 744–752.

Ashraf, M.R., Ahmad, R., Bhatti, A.S., Afzal, M., Sarwar, A., Maqsood, M.A., Kanwal, S. (2010a). Amelioration of salt stress in sugarcane (*Saccharum officinarum* L.) by supplying potassium and silicon in hydroponics. Pedosphere, 20, 153–162. DOI: 10.1016/S1002-0160(10)60003-3

Ashraf, M., Afzal, M., Ahmed, R., Mujeeb, F., Sarwarn, A., Ali, L. (2010b). Alleviation of detrimental effects of NaCl by silicon nutrition in salt-sensitive and salt-tolerant genotypes of sugarcane (*Saccharum officinarum* L.). Plant Soil, 326, 381–391. DOI: 10.1007/s11104-009-0019-9

Awada, S., Campbell, W.F., Dudley, L.M., Jurinak, J.J., Khan, M.A. (1995). Interactive effects of sodium chloride, sodium sulfate, calcium sulfate, and calcium chloride on snapbean growth, photosynthesis, and ion uptake. J. Plant Nutr., 18, 889–900. DOI: 10.1080/01904169509364946

Boursiac, Y., Chen, S., Luu, D.T., Sorieul, M., Dries, N. vanden, Maurel, C. (2005). Early effects of salinity on water transport in *Arabidopsis* roots. Plant Physiol., 139, 790–805. DOI: 10.1104/pp.105.065029

Chinnusamy, V., Jagendorf, A., Zhu, J. (2005). Understanding and improving salt tolerance in plants. Crop Sci., 45, 437–448. DOI: 10.2135/cropsci2005.0437

Dasgan, H.Y., Aktas, H., Abak, K., Cakmak, I. (2002). Determination of screening techniques to salinity tolerance in tomatoes and investigation of genotype responses. Plant Sci., 163, 695–703. DOI: 10.1016/S0168-9452(02)00091-2

Epstein, E. (2001). Chapter 1 Silicon in plants: Facts vs. concepts. Stud. Plant Sci., 8, 1–15. DOI: 10.1016/S0928-3420(01)80005-7

Evelin, H., Kapoor, R., Giri, B. (2009). Arbuscular mycorrhizal fungi in alleviation of salt stress: a review. Ann. Bot., 104, 1263–1280. DOI: 10.1093/aob/mcp251

Gao, X., Zou, C., Wang, L., Zhang, F. (2006). Silicon decreases transpiration rate and conductance from stomata of maize plants. J. Plant Nutr., 29, 1637–1647. DOI: 10.1080/01904160600851494

Gong, H.J., Chen, K.M., Chen, G.C., Wang, S.M., Zhang, C.L. (2003). Effect of silicon on growth of wheat under drought. J. Plant Nutr., 26, 1055–1063. DOI: 10.1081/PLN-120020075

Habib, S.H., Kausar, H., Saud, H.M. (2016). Plant growth-promoting Rhizobacteria enhance salinity stress tolerance in Okra through ROS-scavenging enzymes. BioMed Res. Intern., 2016, 6284547, pp. 10. DOI: 10.1155/2016/6284547

Hamayun, M., Sohn, E.Y., Khan, S.A., Shinwari, K., Khan, A.L., Lee, I.J. (2010). Silicon alleviates the adverse effects of salinity and drought stress on growth and endogenous plant growth hormones of soybean (*Glycıne max*). Pak. J. Bot., 42, 1713–1722.

Jones, J.B. (2001). Laboratory guide for conducting soil tests and plant analysis. In: Laboratory Guid for Conducting Soil Tests Plant Analysis, pp. 202.

Khan, M.I.R., Syeed, S., Nazar, R., Anjum, N.A. (2012). An insight into the role of salicylic acid and jasmonic acid in salt stress tolerance. In: Phytohormones Abiotic Stress Tolerance of Plants, Khan, N.A., Nazar, R., Iqbal, N., Anjum, N.A. (eds.). Springer, Berlin, 277–300.

Khan, W., Prithiviraj, B, Smith, D.L. (2003). Photosynthetic responses of corn and soybean to foliar application of salicylates. J. Plant Physiol., 160, 485–492. DOI: 10.1078/0176-1617-00865

Li, C., Wang, P., Wei, Z., Liang, D., Liu, C., Yin, L., Jia, D., Fu, M., Ma, F. (2012). The mitigation effects of exogenous melatonin on salinity-induced stress in Malushupehensis. J. Pineal Res., 53, 298–306. DOI: 10.1111/j.1600-079X.2012.00999.x

Liang, Y.C. (1999). Effects of silicon on enzyme activity and sodium, potassium and calcium concentration in barley under salt stress. Plant Soil, 209, 217–224.

Liang, Y.C., Qirong, S., Zhenguo, S. (1999). Effect of silicon on enzyme activity and sodium, potassium and calcium concentration in barley under salt stress. Plant Soil, 209, 217–224.

Liang, Y.C., Shen, Q.R., Shen, Z.G., Ma, T.S. (1996). Effects of silicon on salinity tolerance of two barley cultivars. J. Plant Nutr., 19(1), 173–183. DOI: 10.1080/01904169609365115

Liang, Y.C., Sun, W.C., Zhu, Y.G., Christie, P. (2007). Mechanisms of silicon-mediated alleviation of abiotic stresses in higher plants: a review. Environ. Pollut., 147, 422–428. DOI: 10.1016/j.envpol.2006.06.008

Liang, Y.C., Zhang, W.Q., Chen, J., Ding, R. (2005). Effect of silicon on H^+-ATPase and H^+-PPase activity, fatty acid composition and fluidity of tonoplast vesicles from roots of salt-stressed barley (*Hordeum vulgare* L.). J. Environ. Exper. Bot., 53, 29–37.

Liu, J., Shi, D. (2010). Photosynthesis, chlorophyll fluorescence, inorganic ion and organic acid accumulations of sunflower in responses to salt and salt–alkaline mixed stress. Photosynthetica, 48, 127–134. DOI: 10.1007/s11099-010-0017-4

Ma, J.F. (2004). Role of silicon in enhancing the resistance of plants to biotic and abiotic stresses. J. Soil Sci. Plant Nutr., 50, 11–18. DOI: 10.1080/00380768.2004.10408447

Mansour, M.M.F. (2003). Transport proteins and salt tolerance in plants. Plant Sci., 164, 891–900.

Marschner, P. (2012). Mineral nutrition of higher plants, 3rd ed. Elsevier, London.

Munns, R., Tester, M. (2008). Mechanisms of salinity tolerance. Annu. Rev. Plant Biol., 59, 651–681. DOI: 10.1146/annurev.arplant.59.032607.092911

Navarro, J.M., Garrido, C., Flores Martínez, V. (2010). The effect of salinity on yield and fruit quality of pepper grown in perlite. Span. J. Agric. Res., 8, 142–150.

Niu, X., Bressan, R.A., Hasegawa, P.M., Pardo, J.M. (1995). Ion homeostasis in NaCl stress environments. Plant Physiol., 109, 735–742. DOI: 10.1104/pp.109.3.735

Pitman, M.G., Läuchli, A. (2002). Global impact of salinity and agricultural ecosystems. In: Salinity: Environment Plants Molecules, Läuchli, A., Lüttge, U. (eds). Kluwer Academic Publishers, Dordrecht, 3–20.

Rodrigues, F.A., Vale, FX.R., Korndorfer, G.H., Prabhu, A.S., Datnoff, L.E., Oliveira, A.M.A., Zambolim, L. (2003). Influence of silicon on sheath blight of rice. Braz. J. Crop Prot., 22, 23–29. DOI: 10.1016/s0261-2194(02)00084-4

Romero-Aranda, M.R., Jurado, O., Cuartero, J. (2006). Silicon alleviates the deleterious salt effect on tomato plant growth by improving plant water status. J. Plant Physiol., 163, 847–855. DOI: 10.1016/j.jplph.2005.05.010

Shu, L.Z., Liu, Y.H. (2001). Effects of silicon on growth of maize seedlings under salt stress. Agro-Environ. Prot., 20, 38–40.

Silva, E.N., Ribeiro, R.V., Ferreira-Silva, S.L., Viégas, R.A., Silveira, J.A.G. (2010). Comparative effects of salinity and water stress on photosynthesis, water relations and growth of *Jatropha curcas* plants. J. Arid Envir., 74, 1130–1137.

Yıldırım, E., Turan, M., Güvanç, İ. (2008). Effect of foliar salicylic acid applications on growth, chlorophyll, and mineral content of cucumber grown under salt stress. J. Plant Nutr., 31, 593–612. DOI: 10.1080/01904160801895118

Yin, L., Wan, S., Li, J., Tanaka, K., Oka, M. (2013). Application of silicon improves salt tolerance through ameliorating osmotic and ionic stresses in the seedling of *Sorghum bicolor*. Acta Physiol. Plant., 35, 3099–3107. DOI: 10.1007/s11738-013-1343-5

Zeng, L., Poss, J., Wilson, C., Draz, A.S.E., Grieve, C.M. (2003). Evaluation of salt tolerance in rice genotypes by physiological characters. Euphytica, 129, 281–292.

Zhu, Y., Gong, H. (2014). Beneficial effects of silicon on salt and drought tolerance in plants. Agron. Sustain. Dev., 34, 455–472. DOI 10.1007/s13593-013-0194-1

Zhu, Z., Wei, G., Li, J., Qian, Q., Yu, J. (2004). Silicon alleviates salt stress and increase antioxidant enzymes activity in leaves of salt stressed cucumber (*Cucumis sativus* L.). Plant Sci., 167, 527–533. DOI: 10.1016/j.plantsci.2004.04.020