

# Silicon-induced Salinity Tolerance Improves Photosynthesis, Leaf Water Status, Membrane Stability, and Growth in Pepper (*Capsicum annuum* L.)

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**Abstract.** Salt stress is a major problem worldwide because it decreases yields of many important agricultural crops. Silicon is the second-most abundant element in soil and has numerous beneficial effects on plants, particularly in alleviating stress-related impacts. Pepper is an important crop in the Mediterranean region, but pepper varieties differ in their salinity tolerances. The objective of this research was to test the ability of silicon to mitigate effects of salt stress in both salt-sensitive and salt-tolerant cultivars. Salt damage was evaluated by measuring biomass, photosynthetic-related variables, leaf water potential, and membrane damage. We found that the addition of silicon solute to a growth medium was highly effective in improving plant growth by enhancing photosynthesis, stomatal conductance ( $g_s$ ), leaf water status, and membrane stability, which in turn led to higher biomass production in salt-stressed pepper plants, especially in a salt-sensitive cultivar. From an agronomic viewpoint, application of Si may provide economically relevant productivity improvements for salt-sensitive pepper genotypes grown under moderate salinity conditions and for salt-tolerant genotype grown under higher-salinity conditions.

Silicon (Si) is the second-most abundant element in the earth's crust (Manivannan et al., 2016). Its availability to plants is low (Hattori et al., 2005), and the forms of Si (monosilicic and polysilicic acid) are soluble and weakly adsorbed by plants (Matichenkov and Calvert, 2002). Silicon is absorbed and deposited in the cell walls of various organs in plants, such as in stems, roots, and leaves (Epstein and Bloom, 2005), where it forms colloidal complexes with macromolecules (Zhu et al., 2016). Silicon is also considered to be a beneficial element for plants (Epstein and Bloom, 2005), and some argue that it is essential (Ma, 2004). Whether essential or not, Si enhances water and solute transport, improves photosynthesis rates, and improves resistance to abiotic and biotic stresses (Ma, 2004).

Pepper (*Capsicum annuum* L.) is one of the most important cash crops grown in the

Mediterranean region because it is widely consumed and popular. Recent studies have shown that pepper can respond in a variety of ways to salinity stress. Indeed, salinity doses ranging from 0 to 2 dS/m are routinely tolerated.

However, higher-salinity doses, ranging from 8% to 15%, might create linear decreases in yield (Chartzoulakis and Klapaki, 2000; Navarro et al., 2002). Salt stress is one of the most important factors limiting plant growth and yield worldwide (Fahad et al., 2015). High salt concentrations in soils cause high osmotic potential within plant cells, which results in physiological drought in plants. Furthermore, higher concentrations of  $Na^+$  and  $Cl^-$  are toxic to plants because they create an ion imbalance in cells. As a result of this imbalance, levels of reactive oxygen species increase, while plant growth and yield decline (Liang et al., 2015). It has been widely reported that the application of Si to plants may increase salt tolerance among many important agricultural crops, such as wheat (Ahmad, 2014; Gurmani et al., 2013a), rice (Gong et al., 2006; Gurmani et al., 2013b; Kim et al., 2014), maize (Kochanová et al., 2014; Xie et al., 2015), barley (Liang et al., 2005), sorghum (Kafi et al., 2011; Yin et al., 2013), tomato (Liang et al., 2015; Muneer et al., 2014), and soybean (Lee et al., 2010). In this study, we investigate the effect of Si (grown under two salinity regimes) on two pepper cultivars, one salt-tolerant and the other salt-sensitive. We also determined whether the application of Si treatment increases the salt-tolerance of the salt-sensitive pepper cultivar.

## Materials and Methods

### *Plant material and growth conditions.*

Two locally grown pepper varieties were used in this study: Karaisali (a salt-tolerant cultivar) and Demre (a salt-sensitive cultivar) (Altuntas et al., 2016). Plants were grown in a climate chamber under controlled environmental conditions: a light/dark regime of 16/8 h, temperature was 24 °C day and 20 °C night at 60% to 65% relative humidity, and under lights with a photosynthetic photon flux density of  $\approx 300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at plant height.

Vermiculite was used as growing medium. Fifteen-day-old pepper seedlings were planted into 2-L capacity pots, three plants

Table 1. Dry weights and leaf area for two 60-day-old pepper genotypes grown for 30 d under saline and nonsaline conditions, with (+) or without (–) amendments of 2 mM Si.

Genotype	NaCl (mM)	Shoot dry wt (g/plant)	Root dry wt (g/plant)	Leaf area (cm <sup>2</sup> /plant)
K (Si+)	0	6.04 a <sup>2</sup>	2.81 a	512.87 a
	75	4.43 b	1.17 b	391.34 b
	150	2.98 c	0.86 c	290.09 d
D (Si+)	0	5.86 ab	1.21 ab	497.39 a
	75	4.16 b	0.97 b	331.11 c
	150	2.85 c	0.56 c	215.17 e
K (Si–)	0	5.47 ab	2.57 a	460.36 ab
	75	4.20 b	1.11 ab	333.63 c
	150	2.73 d	0.72 c	264.71 de
D (Si–)	0	5.37 ab	1.17 b	459.36 ab
	75	3.70 c	0.70 c	267.52 de
	150	2.38 d	0.48 d	202.75 f
<i>P</i> values for genotype * NaCl eosages		0.981	0.001	0.492
<i>P</i> values for genotype		0.024	0.001	0.002
<i>P</i> values for NaCl dosages		0.001	0.001	0.001

<sup>2</sup>Means followed by different letters within columns indicate significant differences  $P \leq 0.05$  using analysis of variance.

D = 'Demre' salt-sensitive pepper genotype; K = 'Karaisali' salt-tolerant pepper genotype.

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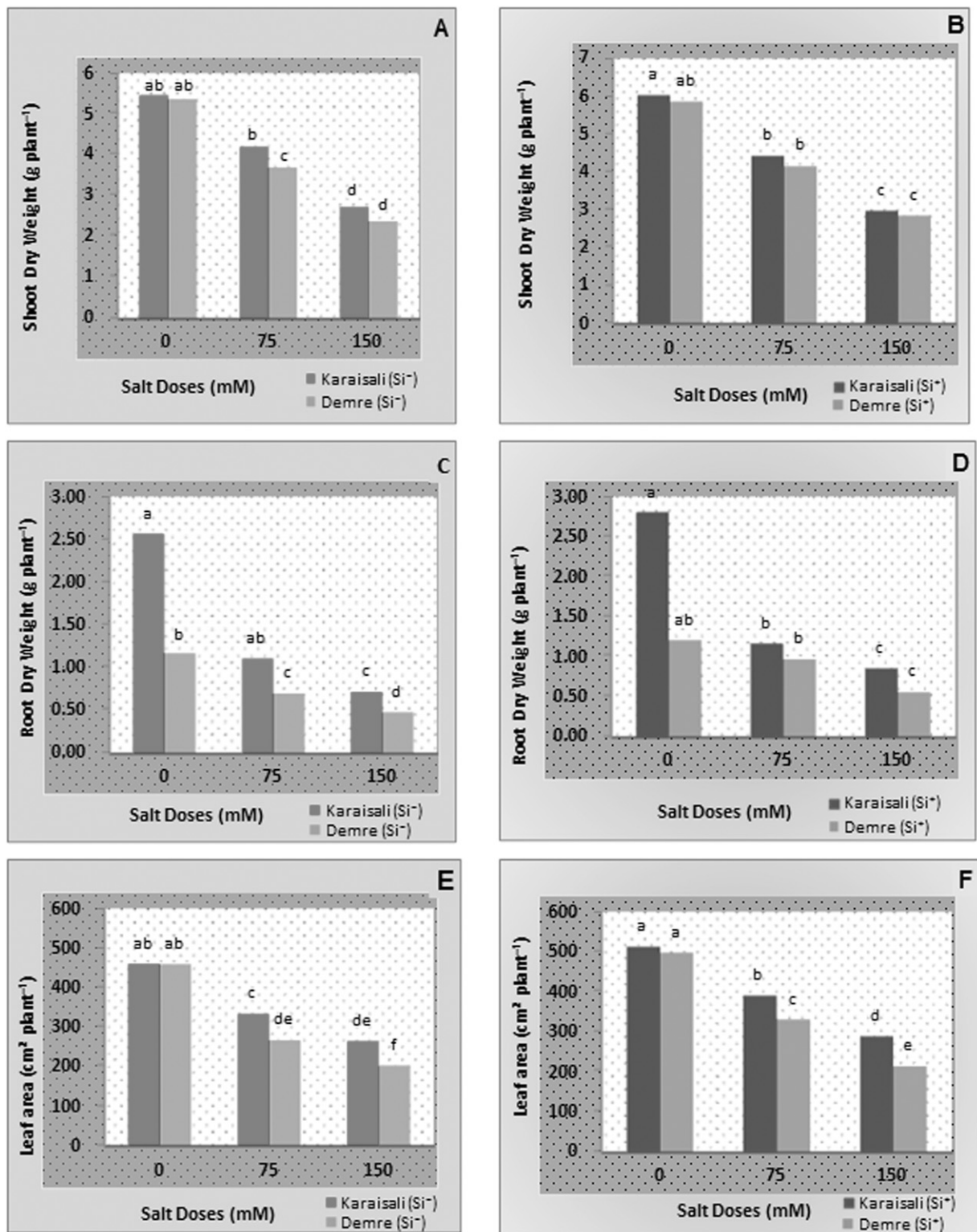


Fig. 1. (A) Shoot dry weight for two pepper genotypes 60 d after sowing (DAS) and 30 d under saline and nonsaline conditions, without (-) amendments of 2 mM Si. (B) Shoot dry weight for two pepper genotypes 60 DAS and 30 d under saline and nonsaline conditions, with (+) amendments of 2 mM Si. (C) Root dry weight for two pepper genotypes 60 DAS and 30 d under saline and nonsaline conditions, without (-) amendments of 2 mM Si. (D) Root dry weight for two pepper genotypes 60 DAS and 30 d under saline and nonsaline conditions, with (+) amendments of 2 mM Si. (E) Leaf area for two pepper genotypes 60 DAS and 30 d under saline and nonsaline conditions, without (-) amendments of 2 mM Si. (F) Leaf area for two pepper genotypes 60 DAS and 30 d under saline and nonsaline conditions, with (+) amendments of 2 mM Si.

per pot. The study design was completely randomized with three replicates (i.e., each replicate contained three pots). The plants were irrigated with half-strength Hoagland's

nutrient solution. The composition of the nutrient solution used was as follows (Molar):  $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ ,  $3.0 \times 10^{-3}$ ;  $\text{K}_2\text{SO}_4$ ,  $0.90 \times 10^{-3}$ ;  $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ ,  $1.0 \times 10^{-3}$ ;  $\text{KH}_2\text{PO}_4$ ,

$0.2 \times 10^{-3}$ ;  $\text{H}_3\text{BO}_3$ ,  $1.0 \times 10^{-5}$ ;  $10^{-4}$  M FeEDTA,  $\text{MnSO}_4 \cdot \text{H}_2\text{O}$ ,  $1.0 \times 10^{-6}$ ;  $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ ,  $1.0 \times 10^{-7}$ ;  $(\text{NH})_6\text{Mo}_7\text{O}_{24} \cdot 4\text{H}_2\text{O}$ ,  $1.0 \times 10^{-8}$ ;  $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ ,  $1 \times 10^{-6}$ .

Table 2. Photosynthetic rate, stomatal conductance, internal CO<sub>2</sub> and transpiration rate for two 60-day-old pepper genotypes grown for 30 d under saline and nonsaline conditions, with (+) or without (-) amendments of 2 mM Si.

Genotype	NaCl (mM)	Photosynthetic rate ( $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ )	Stomatal conductance ( $\text{mmol}/\text{m}^2/\text{s}$ )	Internal CO <sub>2</sub> ( $\mu\text{mol}\cdot\text{mol}^{-1}$ )	Transpiration rate ( $\text{mmol H}_2\text{O}/\text{m}^2/\text{s}$ )
K (Si+)	0	12.43 a <sup>r</sup>	0.27 a	265.67 a	4.12 a
	75	7.88 b	0.06 c	167.33 c	1.31 c
	150	6.75 c	0.05 c	137.67 cd	1.10 c
D (Si+)	0	12.07 a	0.20 a	251.00 a	3.64 ab
	75	7.65 b	0.06 c	157.33 c	1.28 c
	150	4.79 d	0.04 c	118.00 d	0.90 d
K (Si-)	0	12.00 a	0.25 a	242.33 a	3.29 ab
	75	7.07 b	0.05 c	155.00 c	1.01 cd
	150	5.89 cd	0.04 c	114.47 d	0.77 e
D (Si-)	0	11.73 a	0.15 b	222.00 ab	2.78 b
	75	6.28 c	0.05 c	145.33 c	0.92 d
	150	4.31 e	0.02 d	104.60 d	0.58 e
<i>P</i> values for genotype * NaCl dosages		0.954	0.984	0.991	0.990
<i>P</i> values for genotype		0.472	0.341	0.535	0.612
<i>P</i> values for NaCl dosages		0.943	0.995	0.853	0.993

<sup>r</sup>Means followed by different letters within columns indicate significant differences  $P \leq 0.05$  using analysis of variance.

D = 'Demre' salt-sensitive pepper genotype; K = 'Karaisali' salt-tolerant pepper genotype.

**Salt and silicon treatments.** Salinity and silicon treatments began when plants were 30 days old. Sodium chloride (NaCl) and potassium silicate (K<sub>2</sub>SiO<sub>3</sub>) were then added to the nutrient solution, which continued to 60 d after sowing. To avoid the osmotic shock of salinity stress, the salinity treatments were imposed incrementally by daily increasing the concentration by 50 mM until a final salinity concentration was achieved (either 75 mM or 150 mM). The silicon was applied into the nutrient solution (2 mM from K<sub>2</sub>SiO<sub>3</sub>) for the Si-treated treatments in concert with the additions of NaCl. The additional K introduced with the K<sub>2</sub>SiO<sub>3</sub> solution was subtracted from the KNO<sub>3</sub> (potassium nitrate) in the nutrient solution. All plant measurements were conducted at the end of the experiment (i.e., after 30 d of growth under a salt-stressed condition).

**Leaf gas exchange.** At 60 d after transplanting and 30 d under salt stress, one leaf per plant (fifth from the top to down) and nine leaves from each replicate were used for measuring of photosynthetic rate, transpiration rate and *g<sub>s</sub>*, using a portable photosynthesis analyser system (Li-6400; LI-COR Inc., Lincoln, NE) (conditions: block temperature = 25 °C, CO<sub>2</sub> reference = 360  $\mu\text{mol}\cdot\text{mol}^{-1}$  CO<sub>2</sub>, PAR = 1000  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , flow rate = 300  $\mu\text{mol}\cdot\text{s}^{-1}$ ).

**Leaf water potential.** Leaf water potential was measured on young, fully expanded leaves, nine leaves from each replicate, on the same day that observations of gas exchange parameters were made (on the third or fourth leaves from the plant apex). Measurements were made with a pressure chamber (Soil Moisture Equipment Corp., Goleta, CA) between 1000 and 1100 HR solar time (Pearcy et al., 1989).

**Membrane electrolyte leakage.** Both salinity and Si affect membrane characteristics. Therefore, electrolyte leakage was used to assess membrane permeability. Leakage was chosen as an indicator of the ability of cellular membranes to maintain integrity and/or recover from imposed stresses (Kocheva and Georgiev, 2003). Electrolyte leakage was measured by

taking five leaf discs (each one 10 mm in diameter) from a fully expanded leaf of salt-treated, Si-treated, and control plants. The leaf discs were placed in tubes containing 10 mL of deionized distilled water (Stevens et al., 2006) and after incubation for 5 h at 25 °C, the conductivity of the solution was measured using a portable conductivity meter (WTW and model Cond3110). The samples were then placed in a boiling-water bath (100 °C) for 10 min, and their EC was recorded as earlier (this measurement considered all cellular electrolytes combined). A membrane injury index (MII) was calculated from the conductivity data, using the following formula:

$$\text{MII} = 1 - (1 - T_1/T_2)/(1 - C_1/C_2) \times 100 [1],$$

where T<sub>1</sub> and T<sub>2</sub> are the initial and second measurements of salt- and Si-treated, leaf-disc conductivity, respectively, and C<sub>1</sub> and C<sub>2</sub> are the same measurements for the controls (Kocheva and Georgiev, 2003).

**Plant measurements.** The three treated plants from each replicate were sampled to determine change in biomass. For a dry weight (DW) determination, shoots and roots were dried at 70 °C for 48 h and then weighed. Leaf area was measured at the same time as other physiological measurements, using an area meter (LICOR 3100; LiCor Inc., Lincoln, NE), based on an average the value for three plant samples.

IBM SPSS Statistics 20 software was used for data analysis. The mean values of the growth and physiological parameters for the Si treatment in the saline conditions were compared using an analysis of variance test. The effects of silicon on the growth and physiological parameters were considered significant at  $P \leq 0.05$ .

## Results

Biomass, photosynthetic variables, and osmotic and membrane changes were measured 30 d after application of salt-stress treatments to evaluate growth impairment and general plant conditions.

**Plant growth.** Dry weight of plant shoots of both genotypes was reduced when grown with saline water (Table 1; Fig. 1A). The reduction in shoot DW was lower in the salt-sensitive 'Demre' than in the salt-tolerant 'Karaisali'. The addition of Si often increased the shoot DWs of both genotypes grown under either control or saline conditions. Dry weight of shoots for the control treatment (with the addition of Si) was 10.4% higher in 'Karaisali' and 9.1% higher in 'Demre' (Table 1; Fig. 1B). The effect of Si on shoot DW was more pronounced in the salinity treatment of 'Demre' than in 'Karaisali'. The percent increase in DW for 'Demre' (with Si amendments) was 12.4% under the 75 mM salinity regime and 19.7% under 150 mM salinity regime, whereas for 'Karaisali', percent DW increase was 5.5% under the 75 mM salinity and 9.2% under the 150 mM salinity.

The addition of supplementary Si caused the control root DW to increase by 9.3% in 'Karaisali' and 3.4% in 'Demre', whereas under 75 mM salinity, percent DW increases were 5.4% for 'Karaisali' and 38.6% for 'Demre' (Table 1; Fig. 1C and D). In contrast, under the 150-mM salinity treatment, percent DW increase was 19.4% for 'Karaisali' and 16.7% for 'Demre'. Therefore, the effect of Si amendment on root DW was much more substantial for 'Demre' exposed to the mild saline regime (75 mM) than it was for salt-tolerant 'Karaisali'.

The addition of Si increased the leaf area of both genotypes, whether grown under control or saline conditions. Increases in leaf area for the control (with Si amendments) were 11.4% in 'Karaisali' and 8.3% in 'Demre'. Leaf area for Si-treated plants increased much more in salt-sensitive 'Demre' subjected to the milder salinity treatment (75 mM) than it did for salt-tolerant 'Karaisali'. The percent increase in leaf area (for plants subjected to Si treatment) was 23.8% for 'Demre' under the 75 mM salinity and 6.1% under the 150 mM salinity, whereas the percent increase in leaf area for 'Karaisali' was 17.3% under the 75 mM and 9.6% under the 150 mM salinity treatment (Table 1; Fig. 1E and F).

Internal  $CO_2$ ,  $g_s$ , photosynthesis and transpiration rates. Higher salinities significantly lowered  $g_s$ , internal  $CO_2$ , photosynthesis, and transpiration rates. These rate

declines (without Si enhancements) were more acute in 'Demre' than Karaisali', as salinity declined from 75 to 150 mM (Table 2; Fig. 2). Salinity induced a striking inhibition

in photosynthetic activities in both pepper genotypes. The inhibitions under salinity treatments without Si in 'Demre' were higher by 47% under the 75 mM and higher by 63%

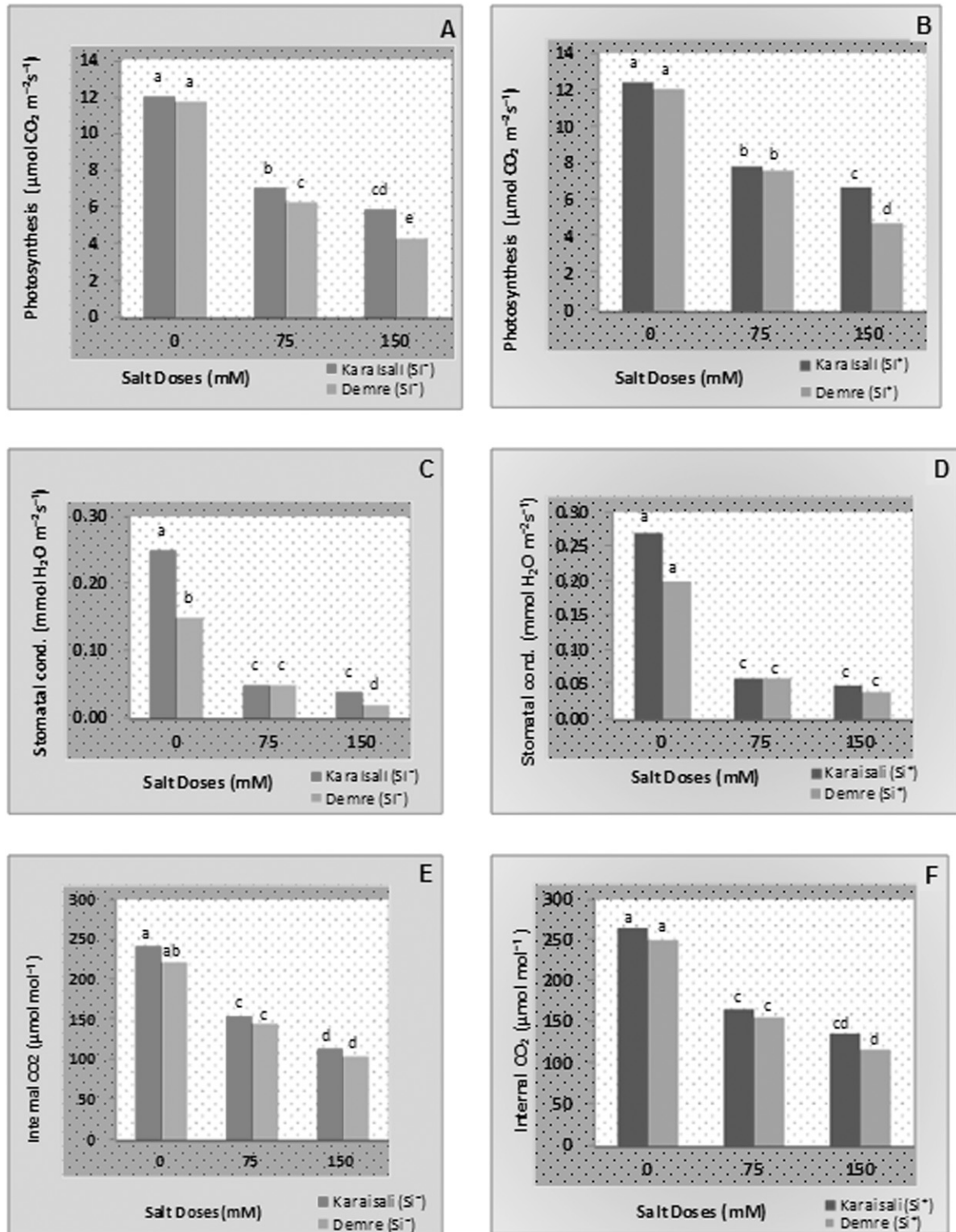


Fig. 2. (A) Photosynthetic rate for two pepper genotypes 60 d after sowing (DAS) and 30 d under saline and nonsaline conditions, without (-) amendments of 2 mM Si. (B) Photosynthetic rate for two pepper genotypes 60 DAS and 30 d under saline and nonsaline conditions, with (+) amendments of 2 mM Si. (C)  $G_s$  for two pepper genotypes 60 DAS and 30 d under saline and nonsaline conditions, with (+) amendments of 2 mM Si. (D)  $g_s$  for two pepper genotypes 60 DAS and 30 d under saline and nonsaline conditions, without (-) amendments of 2 mM Si. (E) Internal  $CO_2$  for two pepper genotypes 60 DAS and 30 d under saline and nonsaline conditions, without (-) amendments of 2 mM Si. (F) Internal  $CO_2$  for two pepper genotypes 60 DAS and 30 d under saline and nonsaline conditions, with (+) amendments of 2 mM Si.

under the 150 mM. For 'Karaisali', photosynthetic inhibition was higher by 41% under the 75 mM and higher by 51% under the 150 mM. Silicon application increased photosynthetic

rate under salinity treatments (Table 2; Fig. 2A and B). Photosynthetic rates were 21.8% higher under the 75 mM for 'Demre' and 11.5% higher for 'Karaisali'; photosyn-

thetic rates under the 150 mM salinity were 11.1% higher for 'Demre' and 14.6% higher for 'Karaisali'. Silicon's influence on the increased rate of photosynthesis was highest

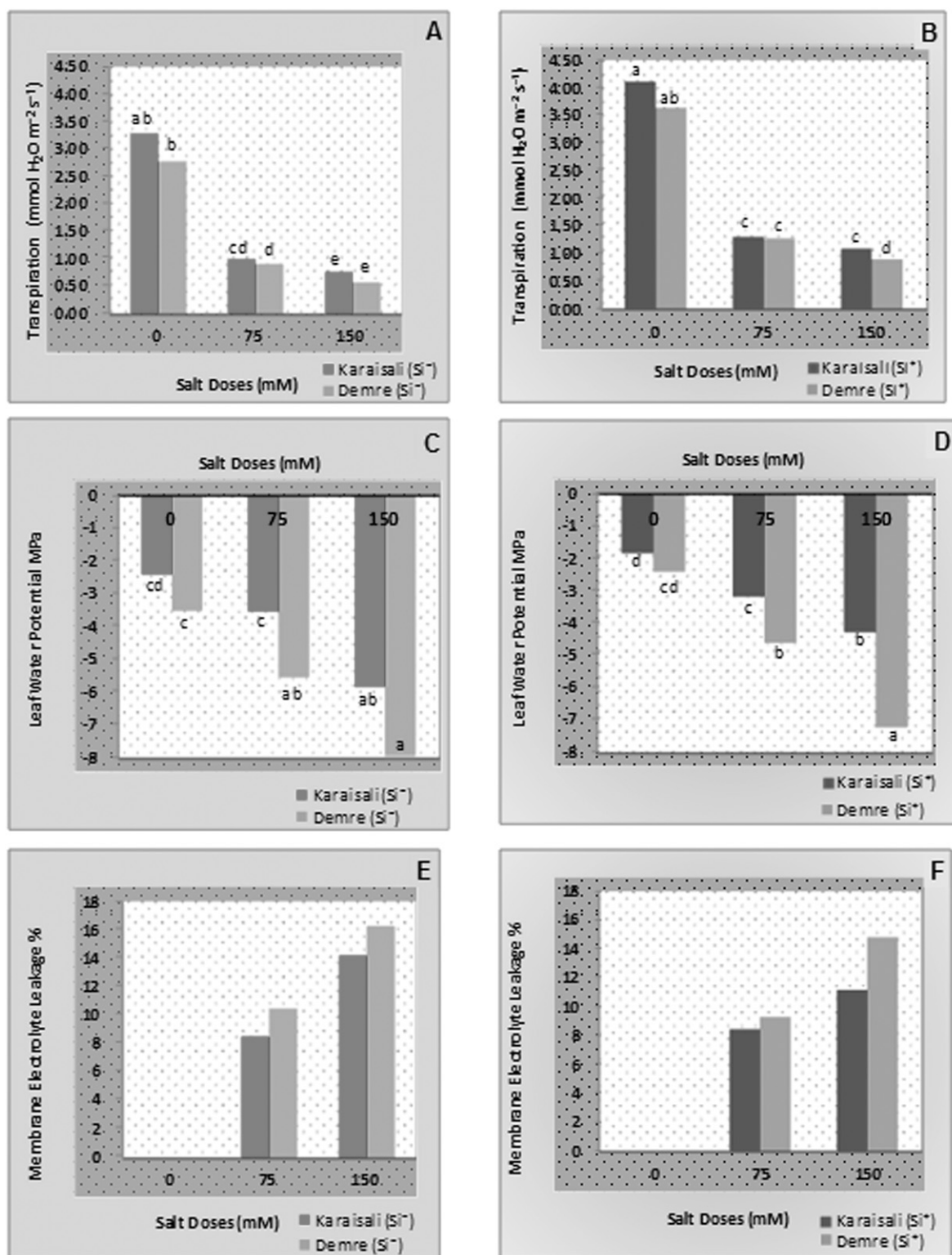


Fig. 3. (A) Transpiration rate for two pepper genotypes 60 d after sowing (DAS) and 30 d under saline and nonsaline conditions, without (–) amendments of 2 mM Si. (B) Transpiration rate for two pepper genotypes 60 DAS and 30 d under saline and nonsaline conditions, with (+) amendments of 2 mM Si. (C) Leaf water potential for two pepper genotypes 60 DAS and 30 d under saline and nonsaline conditions, without (–) amendments of 2 mM Si. (D) Leaf water potential for two pepper genotypes 60 DAS and 30 d under saline and nonsaline conditions, with (+) amendments of 2 mM Si. (E) Membrane electrolyte leakage for two pepper genotypes 30 d 60 DAS and under saline and nonsaline conditions, without (–) amendments of 2 mM Si. (F) Membrane electrolyte leakage for two pepper genotypes 60 DAS and 30 d under saline and nonsaline conditions, with (+) amendments of 2 mM Si.

under the mild salinity (75 mM) in 'Demre' (Table 2; Fig. 2A and B).

Salinity stress decreased  $g_s$  in both genotypes. However, in 'Demre', this reduction was more extreme (Table 2; Fig. 2C and D). At 75 mM salinity, application of Si increased  $g_s$  by 20% in both genotypes. However, under the more severe salinity-stressed condition (150 mM NaCl), the Si application treatment increased  $g_s$  by 100% in 'Demre' and 25% in 'Karaisali'. Silicon-improved  $g_s$  was highest in 'Demre' under the 75 mM salinity (100% increase) (Table 2; Fig. 2C and D).

Internal CO<sub>2</sub> concentrations in the salt-sensitive 'Demre' were increased by 8.3% in plants subjected to 75 mM salinity and 12.8% in plants subjected to 150 mM NaCl salinity, whereas CO<sub>2</sub> concentrations in 'Karaisali' increased by 8.0% and 20.3%, respectively (Table 2; Fig. 2E and F).

Lowered transpiration rates caused by salinity stress were also somewhat ameliorated by Si application. This improvement was more substantial in 'Demre' than in 'Karaisali' (Table 2; Fig. 3A and B). Silicon amendments increased the transpiration rate by 39.1% in 'Demre' and 29.7% in 'Karaisali' under the 75 mM NaCl, whereas transpiration rate increased by 55.2% in 'Demre' and 42.9% in 'Karaisali' under the 150 mM NaCl. The highest transpiration rate was recorded in 'Demre' under the 150 mM salinity (55% increase) (Table 2; Fig. 3A and B).

*Leaf water potential and electrolyte leakage (membrane injury).* Salinity at both concentrations (75 mM and 150 mM) decreased leaf water potential in both genotypes with potentials related to salt concentration (Table 3; Fig. 3). However, Si amendments ameliorated detrimental effects on reduction in leaf water potential in salt-stressed pepper plants. It seemed that 'Demre' fared better with Si additions under the 75 mM salinity, while 'Karaisali' fared better under the 150 mM salinity (Table 2; Fig. 3C and D). The Si amendments increased leaf water potential by 16.8% in 'Demre' and 11.2%

in 'Karaisali' under the 75 mM NaCl and 9.2% and 26.8% for 'Demre' and 'Karaisali', respectively, under the 150 mM NaCl. The amendment of Si resulted in the pepper plants retaining higher leaf water content, which improved  $g_s$  and photosynthesis under NaCl stress, which in turn resulted in higher dry mass production (Tables 2 and 3).

Leaf electrolyte leakage and leaf membrane injury under salinity stress was expected; the higher the salinity concentration was, the more damage occurred in both pepper genotypes. Membrane damage was less pronounced in the salt-tolerant genotype (Karaisali) (Table 3). As was the case for leaf water potential, the positive effect of Si in ameliorating membrane injury in salt-stressed plants occurred with 'Demre' (under the 75 mM salinity) and for 'Karaisali' (under the 150 mM salinity). Si amendments lessened leaf membrane injury in 'Demre' by 11.2% under the 75 mM NaCl salinity and 0.8% under the 150 mM NaCl, whereas salt-induced injury in 'Karaisali' was reduced 8.9% and 21.3%, respectively (Table 3; Fig. 3E and F).

## Discussion

Salinity stress in both NaCl concentrations tested severely altered plant growth, gas exchange attributes, leaf water status and membrane injury responses of both pepper genotypes [particularly the salt-sensitive 'Demre', and especially under the higher (150 mM) salinity]. The exogenous application of 2 mM Si significantly ameliorated NaCl toxicity in both genotypes. However, this influence was more pronounced for the salt-sensitive pepper at both salinity concentrations, especially in counteracting effects on biomass production and photosynthesis. Si additions either increased resistance to salt stress at 75 mM salinity or prevented a complete collapse at 150 mM salinity. Leaf area was reduced under salinity stress because in an attempt by the plant to minimize water loss via evapotranspiration. However, plants

subjected to salinity stress but provided amendments of Si, acquired higher leaf area and shoot and root biomass (dry). Enhancement of plant growth under salinity stress have also been reported for wheat (Gurmani et al., 2013a), rice (Gong et al., 2006; Gurmani et al., 2013b; Kim et al., 2014), maize (Kochanová et al., 2014; Xie et al., 2015), barley (Liang et al., 2005), sorghum (Kafi et al., 2011; Yin et al., 2013), tomato (Liang et al., 2015; Muneer et al., 2014), and soybean (Lee et al., 2010) with variations in responses.

Reduction in photosynthesis under salinity stress occurs because plants close their stomata to reduce water loss, which in turn leads to a reduction in leaf transpiration rates and a lowering of internal CO<sub>2</sub> concentrations in leaves (Table 2). Haghghi and Pessaraki (2013) reported that the improvement in photosynthesis, attributed to Si amendments to salinity-stressed plants, is primarily due to  $g_s$  changes rather than to an increase in chlorophyll content of leaves. According to Xu et al. (1994) and Parveen and Ashraf (2010), a reduction in the rate of photosynthesis is partly due to a decline in leaf water potential because photosynthetic functioning under salinity stress depends on adequate leaf water potential and maintenance of sufficient turgor pressure; however, Si alleviates salinity stress by improving plant water status. Abbas et al. (2015) have reported that okra plants subjected to salinity stress, and amended with Si, exhibited both an increase in  $g_s$  and an increase in the number and size of stomata. In our study, we found that the exogenous application of Si significantly enhanced  $g_s$ , leaf area and leaf water potential in salt-stressed plants and that these improvements were associated with increases in gas exchange in leaves, which consequently led to more efficient photosynthetic activity under salinity stress in both pepper genotypes, but especially in the more salt-sensitive 'Demre'. Transpiration rates were under salinity stress increased with amendments of Si in both pepper genotypes in our study. This may have been a consequence of a Si barrier being created on the outer layer of our pepper plants, which was not visible to us. This speculation is supported by other research (Ma and Yamaji, 2006), which found that Si can provide a physical barrier of silica gel on the outer layers of leaves, roots and vascular tissues of stems, which reduces evapotranspiration. Electrolyte leakage from leaf membranes in our pepper plants under salt stress was reduced by applying Si in solution. This may be explained by the fact that Si has the ability to maintain cells by improving the permeability of their plasma membranes, which improves access into the cell by antioxidative enzymes (Al-Aghabary et al., 2004).

The molecular and biochemical effects of Si are still under investigation. Abbas et al., (2015) reported that by applying a Si solution to plants under stressed conditions, plants produce various compatible solutes or osmolytes, such as proline, glycine betaine, total

Table 3. Leaf water potential and membrane electrolyte leakage for two 60-day-old pepper genotypes grown for 30 d under saline (+) and nonsaline (-) conditions, with and without amendments of 2 mM Si.

Genotype	NaCl (mM)	Leaf water potential (MPa)	Membrane electrolyte leakage (%) <sup>2</sup>
K (Si+)	0	-1.83 d <sup>3</sup>	—
	75	-3.17 c	8.48
	150	-4.27 b	11.20
D (Si+)	0	-2.40 cd	—
	75	-4.60 b	9.31
	150	-7.20 a	14.84
K (Si-)	0	-2.40 cd	—
	75	-3.53 c	8.55
	150	-5.83 ab	14.23
D (Si-)	0	-3.50 c	—
	75	-5.53 ab	10.49
	150	-7.93 a	16.29
<i>P</i> values for genotype * NaCl dosages		0.937	0.996
<i>P</i> values for genotype		0.017	0.575
<i>P</i> values for NaCl dosages		0.922	0.969

<sup>2</sup>Membrane electrolyte leakage calculated relative to the zero salt treatment (control).

<sup>3</sup>Means followed by different letters within columns indicate significant differences  $P \leq 0.05$  using analysis of variance.

D = 'Demre' salt-sensitive pepper genotype; K = 'Karaisali' salt-tolerant pepper genotype.

free amino acids, total soluble sugars, and antioxidant compounds (such as phenolics) that significantly enhance the osmotic adjustment capacity and antioxidant activity of salt-stressed plants. Sugars may act as osmoprotectants and have been found to increase in cucumber leaves and roots subjected to salt stress (Zhu et al., 2016). Silicon-influenced levels of enzymes are also involved in sugar synthesis and in starch degradation of sugars (Zhu et al., 2016). Proteomic studies in pepper (Manivannan et al., 2016) and in tomato subjected to salt stress (Muneer et al., 2014) have identified declines in levels of Rubisco and other proteins in the light harvesting complex and such declines were ameliorated by additions of Si solute. In a search for stress markers, Sadler et al. (2014) found that Rubisco was associated with salt tolerance. This may explain why an improvement in photosynthesis under saline conditions was restricted to the salt-sensitive genotype in our study.

We conclude that Si is highly effective in improving growth in salt-stressed pepper plants by enhancing photosynthesis, *gs*, leaf water status, and cell membrane stability, all of which lead to higher biomass production, especially in salt-sensitive pepper cultivars.

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