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ROLE OF SILICON IN MITIGATING THE ADVERSE EFFECTS OF SALT STRESS ON GROWTH AND PHOTOSYNTHETIC ATTRIBUTES OF TWO MAIZE (*ZEA MAYS* L.) CULTIVARS GROWN HYDROPONICALLY

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Abstract

An experiment was conducted in an aerated hydroponic system to examine the ameliorating effects of varying levels of silicon on growth and some key gas exchange characteristics in two maize cultivars subjected to salt stress. Various components of the experiment were two maize cultivars (Sahiwal-2002 and Sadaf), two salt treatments (0 and 150 m*M* NaCl) and nine Si levels (0, 0.4, 0.8, 1.2, 1.6, 2.0, 2.4, 2.8 and 3.2 m*M*) in Hoagland's nutrient solution (full strength). Salicic acid [$Si(OH)_4$] was used as a source of Si. After the application of Si and NaCl treatment plants were allowed to grow for 28 days. Exogenously applied varying concentrations of Si significantly improved the growth of both maize cultivars under saline regimes. However, more improvement was observed under non-saline conditions as compared with that under saline conditions. Exogenously applied Si levels in the rooting medium also improved some key plant gas exchange characterstics such as net CO_2 assimilation rate (A), stomatal conductance (g_s), transpiration (E), and leaf sub-stomatal CO_2 concentration (C_i) of both maize cultivars both under non-saline and saline regimes. Furthermore, the Si-induced growth improvement in the rooting medium was positively correlated with plant photosynthetic attributes. Of different exogenously applied Si levels, 0.8, 1.6 and 2.8 m*M* proved to be relatively more effective in enhancing the growth as well as gas exchange attributes as compared with other levels. Overall, exogenously applied Si was found beneficial for improving salt tolerance of maize plants.

Introduction

Although Si is not generally listed in the list of essential elements, it is considered as one of the important beneficial nutrient for plant growth (Liang *et al*., 2006). The amount of Si in soil may vary considerably from 1 % to 45 % (Sommer *et al*., 2006). However, Si is present in soil in different forms, but plants can easily absorb silicic acid $Si(OH)_4$ from soil. Silicic acid is generally found in the range of 0.1-0.6 m*M* in soils (Epstein, 1994).

Although Si is beneficial for plant growth it plays a vital role as a physico-mechanical barrier in most plants. Despite its deposition on cell walls (Marshner, 1995), its active involvement in a multitude of physiological and metabolic processes is also evident (Epstein, 1995, 1999; Moussa, 2006).

Plants deprived of Si often show poor development and reproduction, but it depends on the type of plant species. In general, plants belonging to family Gramineae accumulate much more silicon than that by other species belonging to other families. It has also been reported that most dicot plants absorb Si passively but legumes can efficiently exclude Si from their roots (Ma *et al*., 2001). However, in rice, a known Si accumulator, uptake and transport of Si takes place through active process (Ma *et al*., 2006).

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Salinity stress is one of the most devastating stressful environments for plant growth and production (Rus *et al*., 2000; Ashraf *et al*., 2008; Ashraf, 2009). One viable strategy of overcoming the salt-induced injurious effect on plant growth is the exogenous application of osmoprotectants and inorganic nutrients (Ashraf & Foolad, 2007). By adopting this strategy, Tuna *et al*., (2008) have recommended the supplements of Si to plants subjected to the salt affected soils, because in view of Epstein (1995) addition of Si has been considered beneficial for improving crop tolerance to both biotic and abiotic stresses (Epstein, 1994). The ameliorative role of Si to adverse effects of salinity has been examined in different crops e.g., rice (Yeo *et al*., 1999), barley (Liang *et al*., 2005), wheat (Ahmad *et al*., 1992), tomato (Al-Aghabary *et al*., 2004) and cucumber (Zhu *et al*., 2004). However, the information on the role of Si in allaying the salinity induced harmful effects on maize crop is not much in the literature. Thus, the present investigation was undertaken with the premier objective to provide some additional information that how far exogenously applied different concentrations of supplementary Si through root medium can allay the salt-induced harmful effects on growth and gas exchange characteristics of two maize cultivars at early growth stages.

Materials and Methods

A hydroponic experiment was conducted in the Botanic Garden of the University of Agriculture, Faisalabad, Pakistan during 2009 under natural environmental conditions. The seeds of two maize cultivars, Sahiwal 2002 and Sadaf, were obtained from the Maize and Millet Research Institute (MMRI), Yousafwala, Sahiwal, Pakistan. Four hundred seeds of each cultivar were sterilized in $HgCl_2$ solution (0.1%) for 10 min, and after rinsing the seeds with distilled water they were sown in plastic pots containing well washed river sand supplied with Hoagland's nutrient solution (full strength). The seeds were allowed to germinate for 8 days. Uniform sized (with two expanded leaves and one expanding leaf) two seedlings of each cultivar per replicate were transferred to a hydroponic system comprising plastic tubs fitted with a thermopore white sheet with holes, through which the plants were supported over the treatment solution. Silicon was applied as a slicic acid $Si(OH)_4$ through the root growing medium. Each pot was supplied with 2 L Hoagland's nutrient solution. Varying concentrations of silicon used were 0, 0.4, 0.8, 1.2, 1.6, 2.0, 2.4, 2.8 and 3.2 m*M* in Hoagland's nutrient solution 0 or 120 m*M* NaCl.

Salinity and silicon treatments were supplied by adding sodium chloride (NaCl) and silicic acid $Si(OH)_4$, respectively, to the nutrient solution after four days of transplantation to the hydroponic system. The pH of the treatment solution was maintained at 6.5 by using 0.01 N KOH or 0.01 N HCl. The treatment solutions in all pots were aerated 12 h daily and changed weekly. The plants remained subjected to salt or Si treatment for 28 days, after which time two plants/replicate of each treatment were harvested and properly rinsed with distilled water and blotted dry. The data for different morphological attributes such as shoot and root lengths were recorded. The plants were then oven-dried at 65^{o}C for 72 h and their dry biomass recorded.

Gas exchange parameters: Before harvesting the plants, some key gas exchange attributes were measured using a portable infrared gas analyzer (LCA-4; Analytical Development Company, Hoddesdon, UK). These measurements were made on the 2nd intact leaf from the top from 10.30 a.m. to 12.30 p.m. with specific specifications/ adjustments mentioned elsewhere (Ali *et al*., 2008).

Statistical analysis: The experiment was placed in a completely randomized design (CRD) with four replicates of each treatment. Analysis of variance of data for each attribute was computed using the Costat Computer Package (Version 6.303, PMB 320, Monterey, CA, 93940 USA). The least significant difference (LSD) test to assess the significant difference between the mean values was calculated as described in Snedecor & Cochran (1980).

Results

Data presented in Table 1; Fig. 1 show that imposition of salt stress to root growing medium significantly suppressed shoot fresh and dry masses of both maize cultivars. Exogenously applied different concentrations of silicon (Si) in the rooting medium significantly increased the shoot fresh and dry weights of both maize cultivars except at 0.4 and 1.2 m*M* of Si that showed no significant response. A maximal increase in shoot fresh and dry weights due to Si application was observed when Si was applied @ 0.8, 1.6 and 2.8 m*M* under stress and non-stress conditions.

Addition of NaCl to the root growing medium decreased the root fresh weights of both maize cultivars. Exogenously applied Si significantly affected the root fresh weights of both maize cultivars under saline regimes. Under non-saline conditions, exogenously applied Si increased the root fresh weight of both maize cultivars and the maximum increase was observed at 0.8 and 2.8 m*M* of silicon. However, under saline conditions, the response of both cultivars in increasing or decreasing root fresh weight due to exogenously applied silicon was not similar. In cv. Sahiwal-2002 root fresh weight under saline conditions increased significantly due to exogenous application of Si, but the reverse was true for cv. Sadaf.

Root dry weight like root fresh weight also decreased due to root zone salinity. Exogenous application of Si significantly increased the root dry mass of both maize cultivars under saline and non-saline regimes. Under non-saline conditions cv. Sahiwal-2002 showed more increasing response as compared with cv. Sadaf and the maximum increase was observed when Si was applied @ 0.8 and 1.6 m*M*. However, under saline conditions both cultivars showed a similar increasing response to all the exogenously applied Si levels in the rooting medium.

Data for shoot length of both maize cultivars presented in Fig. 2 show that root-zone salinity significantly reduced the shoot length of both maize cultivars. Exogenously applied Si in varying levels significantly increased the shoot length of both maize cultivars both under saline conditions. However, in contrast under non-saline conditions, both cultivars responded differently to exogenously applied silicon. For example in cv. Sahiwal-2002 the maximum increase in shoot length was observed when silicon was applied @ 2.8 m*M*, but this increase in shoot length in cv. Sadaf was maximum at 1.6 m*M* of silicon. However, under saline conditions both cultivars showed maximum increase in shoot length at 0.8 and 2 m*M* of Si (Fig. 2).

Of different gas exchange attributes, photosynthetic rate (*A*) decreased markedly due to salt stress but the reduction in this attribute was almost uniform in both cultivars. Exogenously applied Si in rooting media significantly enhanced plant photosynthetic rate under stress conditions, but the effective levels of Si were not similar under saline or non-saline conditions. Under non-saline conditions maximum increase in photosynthetic rate of both cultivars was observed at 0.8 and 1.6 m*M* of Si. However, under saline conditions, all Si levels were equally effective in increasing plant photosynthetic rate of both maize cultivars (Fig. 3).

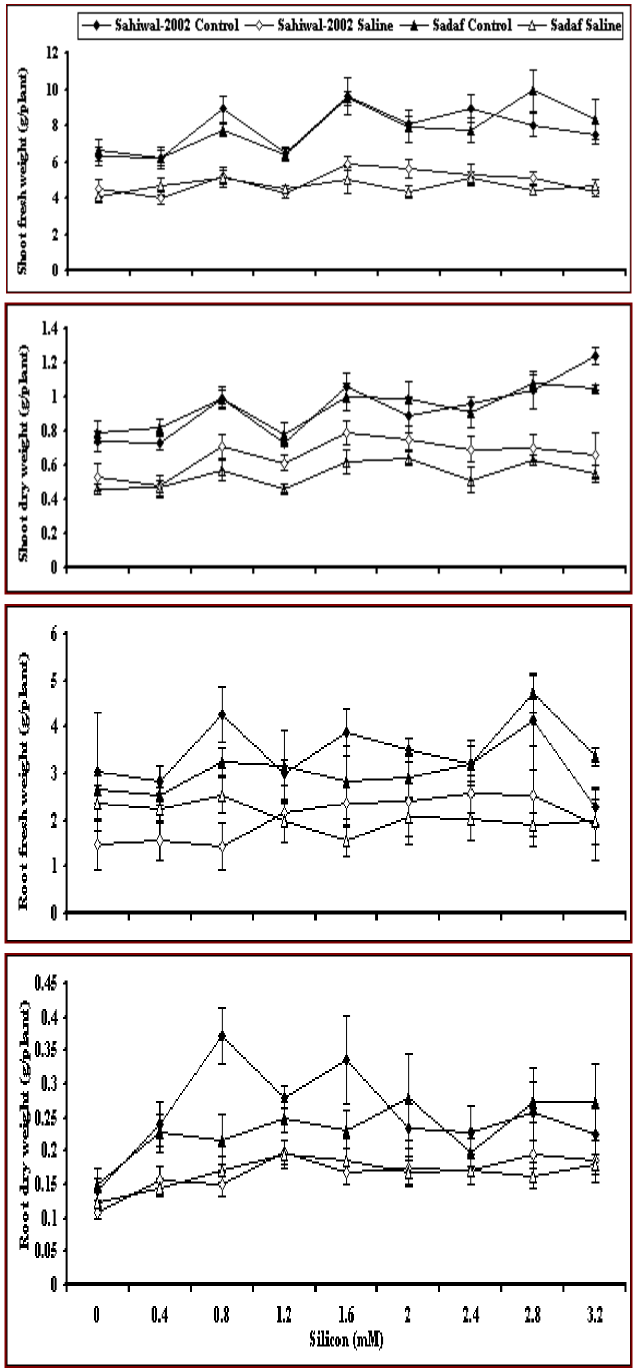

Fig. 1. Shoot and root fresh and dry weights of hydroponically grown two cultivars of maize (*Zea mays* L.) as influenced by different concentrations of silicon applied in the rooting medium under salt stress or non-stress conditions (n=4; Mean ± S.E).

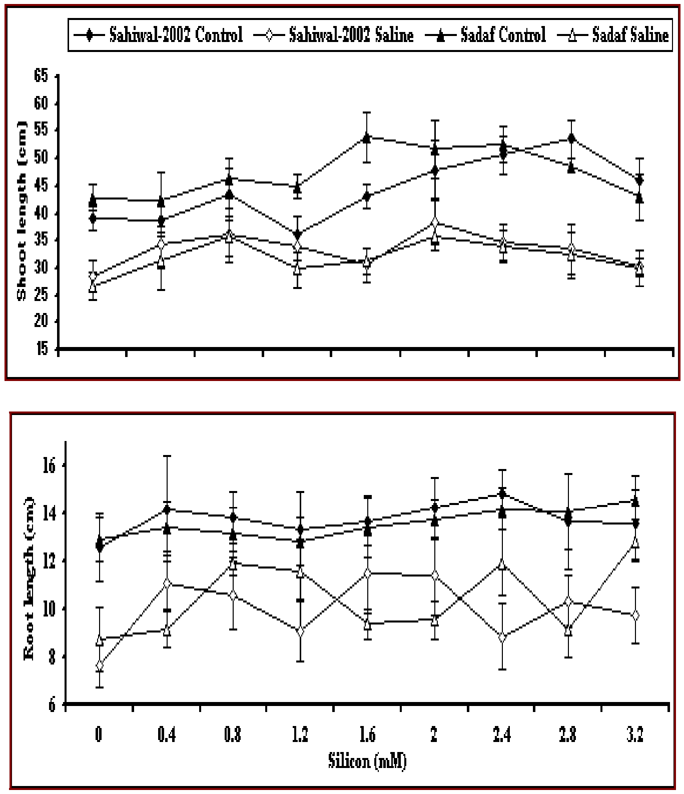

Fig. 2. Shoot and root lengths of hydroponically grown two cultivars of maize (*Zea mays* L.) as influenced by different concentrations of silicon applied in the rooting medium under salt stress or non-stress conditions (*n*=4; Mean ± S.E).

Data in Fig. 3 show that root-zone salinity significantly decreased the transpiration rate (*E*) of both maize cultivars. However, different levels of Si applied exogenously had significantly increased the transpiration of both maize cultivars under saline regimes, but this increasing effect was not observed under normal growth conditions. Under saline conditions, a maximal increase in *E* was observed at 1.6 and 2.4 m*M* levels of Si (Fig. 3).

Other gas exchange attributes such as *Ci* and g_s of both maize cultivars also decreased due to salt treatment. The cultivars did not show different performance in relation to these attributes. A significant increasing effect of exogenous application of Si on these gas exchange attributes was observed both under stressful environments. A maximum increase in these gas exchange attributes due to exogenously applied Si was observed at 0.8 and 1.6 m*M* (Fig. 3).

A significant salt-induced reduction in water use efficiency (*A*/*E*) was observed in both maize cultivars. Exogenously applied Si significantly increased the water use efficiency of both maize cultivars under salt treatments. The cultivars responded differently to exogenously applied different concentrations of Si in saline and non-saline conditions. The response of cv. Sahiwal-2002 in increasing plant *A*/*E* was maximum at 0.8, 2.0 and 2.8 m*M* of Si both under saline and non-saline conditions. However, this increasing trend in *A*/*E* in cv. Sadaf due to exogenously applied different levels of Si was different both under saline regimes as compared with that in cv. Sahiwal-2002 (Fig. 4).

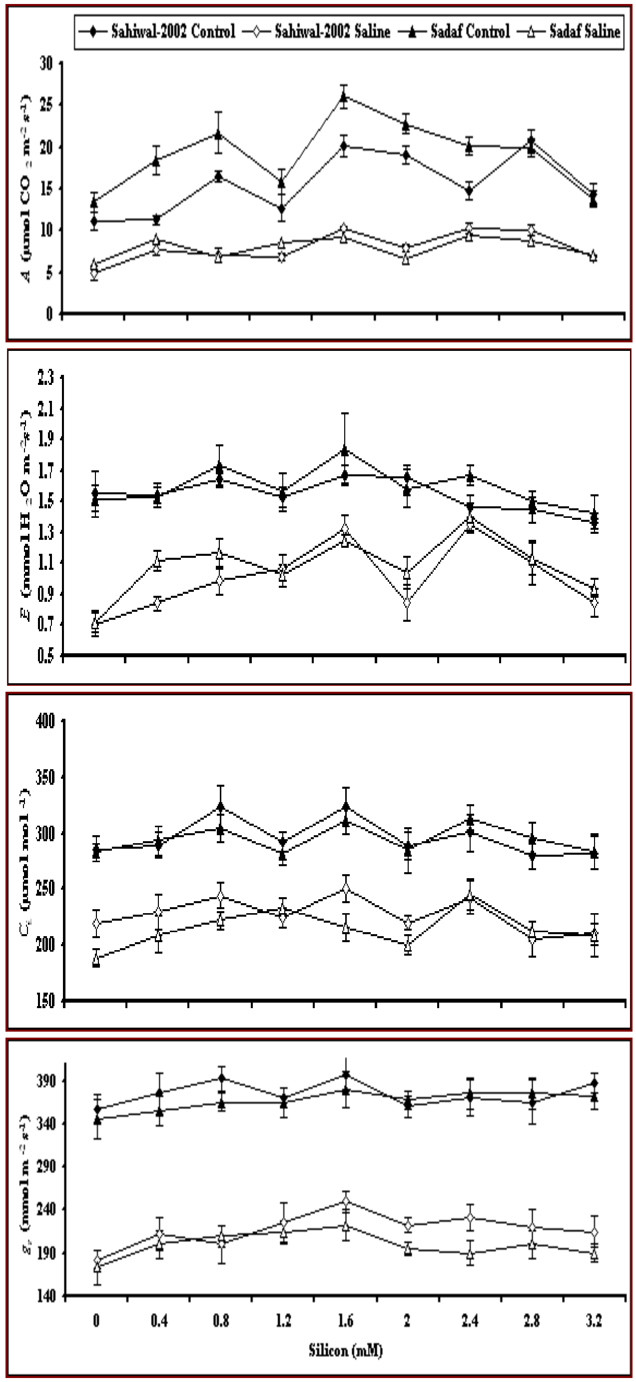

Fig. 3. Gas exchange attributes of hydroponically grown two cultivars of maize (*Zea mays* L.) as influenced by different concentrations of silicon applied in the rooting medium under salt stress or non-stress conditions (*n*=4; Mean ± S.E).

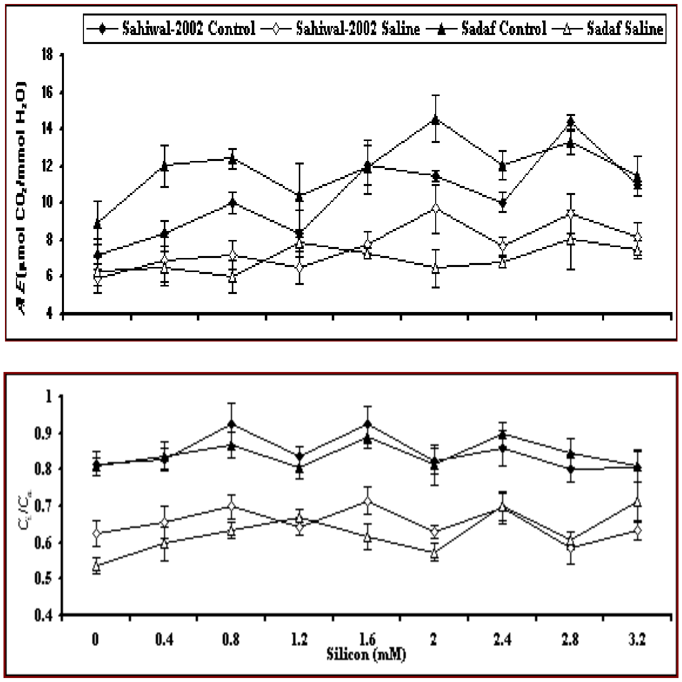

Fig. 4. *A*/*E* and C_i/C_a of hydroponically grown two cultivars of maize (*Zea mays* L.) as influenced by different concentrations of silicon applied in the rooting medium under salt stress or non-stress conditions (*n*=4; Mean ± S.E)

Ratio of leaf sub-stomatal CO_2 concentration to ambient CO_2 concentration (C_i/C_a) of both maize cultivars also decreased due to root zone salinity. The cultivars were not different with respect to this gas exchange parameter. This reducing effect of salinity on plant C_i/C_a ratio was significantly alleviated due to exogenously applied Si. A maximal increase in C_i/Ca ratio due to exogenous application of Si in both cultivars under salt treatments was observed at 0.8, 1.6 and 2.4 m*M* of Si (Fig. 4).

Overall, it was concluded that exogenously applied Si in the rooting medium reduced the inhibitory effects of salinity on plant growth and photosynthetic attributes and 0.8, 1.6 and 2.8 m*M* of Si were found to be more effective as compared with other levels used in this study.

Discussion

Although silicon (Si) is considered as a non-essential element (Taiz & Zeiger, 2006), however, from some earlier studies it is evident that, exogenous application of Si can promote growth of most plant species (Epstein, 1999). This increase in plant growth due to Si application not only takes places under normal growth conditions (Agurie *et al*., 1992; Hossain *et al*., 2002), but also under stressful conditions (Matichenkov *et al*., 2001; Rodrigues *et al*., 2003; Ma, 2004) This effect of Si on plant growth is dose- and crop-specific (Ali *et al*., 2009). Silicon affects plant growth under stressed conditions by affecting a variety of processes including the improvement in plant water status (Romero-Aranda *et al*., 2006), changes in ultra-structure of leaf organelles (Shu & Liu, 2001), up-regulation of plant defense system (Zhu *et al*., 2004) and mitigation of specific ion effect of salt (Tahir *et al*., 2006).

Table 1. Mean squares from analyses of variance of the data for growth and photosynthetic attributes of hydroponically grown two cultivars of maize (*Zea mays* L.) as influenced by different concentrations of silicon applied in the rooting medium under salt stress or non-stress conditions.

SOV	d.f	Shoot fresh wt.	Root fresh wt.	Shoot dry wt.	Root dry wt.
Salinity (S)	1	334.64 ***	14.21 ***	3.960 ***	0.179 ***
Varities (V)	1	0.22 ns	2.31 ns	0.110 **	0.004 ns
Silicon (Si)	8	10.21 ***	2.36 *	0.180 ***	0.015 ***
Inetraction					
S x V	1	0.90 ns	0.02 ns	0.120 **	0.004 ns
S x Si	8	2.99 **	3.10 **	0.040 *	0.007 *
V x Si	8	1.11 ns	1.69 ns	0.020 ns	0.003 ns
S x V x Si	8	1.44 ns	2.31 *	0.006 ns	0.006 ns
Error	108	0.99	0.93	0.013	0.003
SOV	**d.f**	**Shoot length**	**Root length**	***A***	***E***
Salinity (S)	1	7687.78 ***	493.95 ***	3984.87 ***	11.97 **
Varities (V)	1	12.11 ns	0.71 ns	104.46 ***	0.22 **
Silicon (Si)	8	190.91 ***	9.41 ns	92.49 ***	0.32 **
Inetraction					
S x V	1	143.12 ns	13.02 ns	113.61 ***	1.61 ns
S x Si	8	150.01 ***	5.76 ns	60.85 ***	0.16 **
V x Si	8	34.19 ns	12.25 *	10.01 **	0.03 ns
S x V x Si	8	41.39 ns	5.25 ns	8.97 **	0.08 **
Error	108	39.64	4.68	3.05	0.03
SOV	d.f	C_i	g_s	A/E	C_i/C_a
Salinity (S)	1	183512.28 ***	334.64 ***	474.64 ***	1.500 ***
Varities (V)	1	1024.00 ns	0.22 ns	10.23 *	0.008 ns
Silicon (Si)	8	2382.93 ***	10.21 ***	22.45 ***	0.019 ***
Inetraction					
S x V	1	486.20 ns	0.90 ns	49.87 ***	0.003 ns
S x Si	8	619.37 ns	2.99 **	17.08 ***	0.005 ns
V x Si	8	781.21 ns	1.11 ns	4.31 ns	0.006 ns
S x V x Si	8	367.32 ns	1.44 ns	5.88 *	0.003 ns
Error	108	507.88	0.98	2.54	0.004

In the present investigation, exogenously applied different concentrations of Si significantly increased the growth and morphological attributes (shoot and root length) of both maize cultivars in salt treatments. The most effective levels of silicon were found to be 0.8, 1.6 and 2.8 m*M*. This silicon-induced improvement in plant growth under salt stress may have been due to the significant role of Si in the improvement of plant water status (Romero-Aranda *et al*., 2006). Such beneficial effects of Si on plant biomass production under salt stress as well as non-saline conditions were also reported in some other plant species such as wheat (*Triticum aestivum*) (Tahir *et al*., 2006), mesquite (*Prosopis juliflora*) (Bradbury & Ahmad, 1990), and zinnia (*Zinnia elegans*) (Kamenidou *et al*., 2009), indicating the beneficial effects of Si application in alleviating salt-induced inhibitory effects on plant growth.

It is generally known that reduced photosynthetic rate leads to reduced plant growth in most plants. This decrease in plant photosynthesis under salt stress takes place due to closing of stomata that result in a decrease in leaf transpiration rate and reduced leaf internal CO_2 concentration. In the present study, imposition of salt stress in the root growing medium significantly reduced the photosynthetic efficiency (*A*), stomatal conductance (g_s), with a concomitant decrease in transpiration (*E*) and internal CO_2 concentration (C_i). However, exogenously applied Si significantly enhanced these plant photosynthetic attributes. Thus, these gas exchange attributes could have been the primary factors for Si induced growth improvement in maize under saline and non-saline conditions. The increase in photosynthetic attributes due to exogenous application of Si also increased the plant water-use efficiency (WUE). Such increasing effects of exogenously applied Si on different gas exchange attributes including net photosynthetic rate under saline regimes have earlier been examined in different wheat cultivars (Matichenkov *et al*., 2001; Matichenkov &. Kosobrukhov, 2004). They reported that this increase could be due to the role of silicon in controlling the enzyme activities, and its direct influence on the biochemical processes in plant tissues (Matichenkov & Kosobrukhov, 2004). Furthermore, Moussa (2006) showed that a significant increase in CO_2 -fixation rate and photosynthetic efficiency in different cultivars of maize due to the addition of Si to the root growing medium. The results of our study are similar to what has earlier been observed in barley and tomato (Liang, 1998; Al-Aghabary *et al*., 2004), in which silicon added to the saline growth medium improved photosynthetic activity.

Taken overall, exogenous application of varying levels of Si particularly low levels (0.8 and 1.6 m*M*) in the root growth medium can allay the salt-induced inhibitory effects on maize growth. This increase in plant growth was positively associated with the plant photosynthetic attributes.

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