African Journal of Biotechnology Vol. 11(3), pp. 642-649, 10 January, 2012
Available online at http://www.academicjournals.org/AJB
DOI: 10.5897/AJB11.3220
ISSN 1684–5315 © 2012 Academic Journals

Full Length Research Paper

Augmenting the salt tolerance in wheat (*Triticum aestivum*) through exogenously applied silicon

Anser Ali[1], Shahzad M. A. Basra[2], Javaid Iqbal[1], Safdar Hussain[1], M. N. Subhani, Muhammad Sarwar[1] and Muhammad Ahmed[3]

[1]University of Agriculture, Sub-Campus D.G. Khan, Faisalabad-38040, Pakistan.
[2]Department of Crop Physiology, University of Agriculture, Faisalabad-38040, Pakistan.
[3]Agriculture Adaptive Research Complex, Dera Ghazi Khan, Pakistan.

Accepted 19 December, 2011

Although silicon improves the salt tolerance in grasses, the mechanism involved is still ambiguous. Moreover in wheat, classified as Si-accumulator, silicon can alleviate the salt stress. Hence in this study, the effects of silicon using calcium silicate (150 mg/L) on the morphology, physiology and biochemistry of wheat genotypes (salt sensitive; Auqab-2000 and salt tolerant; SARC-5) differing in salt tolerance under saline (12 dS/m) and non-saline soil media (2 dS/m) were investigated. Silicon supplementation into the root medium significantly improved the K^+ and K^+:Na^+ ratio, leaf water potential and stomatal conductance, but reduced the Na^+. Plants harvested at maturity indicated a concomitant increase in number of tillers, number of grains per spike, grain and straw yield with Si application both under optimal and stressful conditions. The results suggest that Si application in soil medium is beneficial in profoundly affecting physiological phenomena and improving wheat growth under salt stress.

Key words: Wheat, salt stress, silicon, wheat growth, K^+:Na^+, water potential, stomatal conductance.

INTRODUCTION

Salinity is one of the major abiotic stresses (Rueda-Puente et al., 2007) that severely affects the growth and productivity of crop plants (Lopez et al., 2002). It changes the morphology, physiology and metabolism of plants (Hilal et al., 1998; Rhoades, 1993), ultimately diminishing growth and yield (Ashraf and Harris, 2004). Salt tolerance is a complex physiological trait (Tester and Davenport, 2003). Studies on salt tolerance normally point to limited beneficial and greater accumulation of toxic ions (Greenway and Munns, 1980). Practically the adverse effects of salinity are ameliorated through chemical, physical (engineering) and biological methods.

Exogenous application of nutrients under salt stress has been reported in many crops; for instance, K^+ in wheat (Raza et al., 2006; Akram et al., 2007), N in *Phaseolus vulgaris* (Wagenet et al., 1983) and Ca in snap bean (Awada et al., 1995). Furthermore, the use of some beneficial mineral nutrients that counteracted adverse effects of salt stress has been practiced. Silicon (Si), being a beneficial element, provides significant benefits to plants against various abiotic (e.g. salt, drought and metal toxicity) and biotic (plant diseases and pests) stresses (Liang et al., 2003; Ahmed et al., 2011; Ma, 2004).

The mechanisms responsible for salt tolerance in crop plants include exclusion, inclusion, compartmentation and homeostasis (Marschner, 1995; Saqib et al., 2005; Tahir et al., 2006), enhanced plant water status (Romero et al., 2006), immobilization of toxic Na^+ ion (Liang et al., 2003), reduced Na^+ and enhanced K^+ uptake (Yeo et al., 1999; Liang et al., 2005; Tahir et al., 2006) and higher K^+:Na^+ selectivity (Hasegawa et al., 2000). Consequently, better crop growth, physiological efficiency, balanced nutrition, and increased nutrient uptake is maintained in salinity-stressed plants (Murillo-Amador et al., 2007) by diluting

---

*Corresponding author. E-mail: uafanser@gmail.com. Tel: 00923017175236.

salts accumulated in saline environment (Matoh et al., 1986). Graminaceous plants manifest greater tissue Si accumulation than other species (Matichenkov and Kosobrukhov, 2004). Si is accumulated at a comparable rate to those of macronutrient elements (Epstein, 1999). Wheat is a member of Poaceae family and recently designated as Si accumulator and can alleviate salt-induced damages. Wheat, as a glycophytic plant, generally shows sensitivity to salinity since yield losses account for up to 45% (Qureshi and Barrett-Lennard, 1998). Wheat genotypes differ significantly in salinity tolerance (Munns, 2002; Flowers, 2004; Saqib et al., 2005) as salt tolerant plants accumulate less Na^+ than salt sensitive, which maintains the ionic balance within plant tissues (Tahir et al., 2006). These variations can be used to screen and develop more salt tolerant genotypes.

It is evident from the above that Si has a significant role in improving salinity tolerance. For this study on wheat, it was hypothesized that Si may be useful to enhance the salt tolerance of local wheat genotypes by profoundly changing morphological, physiological and biochemical aspects in wheat. Thus, the objectives were to study the; a) variation in salinity tolerance of two contrasting wheat genotypes, and b) change in some biochemical insights produced by exogenous supply of Si to wheat grown under salinity stress using soil media.

MATERIALS AND METHODS

The experiment was conducted in plastic pots containing soil medium. Two contrasting wheat genotypes (salt sensitive; Auqab-2000 and salt tolerant; SARC-5) were used for this experiment. The Si level (150 mg/kg) was used to investigate its effect on wheat under salt stress; 150 mg/kg of Si was selected as an optimized level in the previous experiment (Ali et al., 2009). The pots were filled with soil of known salinity level. Soil was taken from experimental field area of Institute of Soil and Environmental Sciences, University of Agriculture, Faisalabad, Pakistan. Ten kilogram of the prepared soil was filled in each of 24 plastic pots lined with polyethylene bags. In half of the pots, sodium chloride (NaCl) salt was used to develop salinity (12 dS/m), while the rest of the pots were kept as control having original EC (2 dS/m). Taking into account the acquired EC (2 dS/m) and saturation % of soil (32%), the required amount of NaCl was calculated for developing the required EC level (12 dS/m).

A basal dose of N at 100 mg/kg as urea, P at 90 mg/kg as single super phosphate and K at 120 mg/kg as potassium sulphate were mixed into soil prior to seed sowing. The remaining N was applied after the first irrigation. In each pots, 15 seeds were sown and thinned to five uniform plants/pot after seedling emergence at crown root stage. The whole Si was applied to the pots of the Si+ treatment at 150 mg/kg using calcium silicate solution. $CaCl_2$ solution was applied to the pots of the Si-deficient treatment to balance the same total of Ca as in the Si+ treatment in order to know the sole effect of Si. The pots were arranged according to factorial completely randomized design (CRD) with three replicates of each treatment.

Determination of Na^+ and K^+ from flag leaves

The oven dried and grinded material (0.1 g) of leaves was digested with mixture of 2 ml of sulfuric acid and hydrogen peroxide according to the method of Wolf (1980). Potassium and sodium in the digested material were determined with a flame photometer (Jenway, PFP-7).

Determination of Si from flag leaf

The leaves of harvested plants were oven dried and grinded in a Wiley mill into fine powder. Si concentration was measured at 650 nm wavelength with a UV visible spectrophotometer (Shimdzu, Spectronic 100, Japan), using calorimetric amino molybdate blue color method (Elliot and Synder, 1991).

Leaf area

Leaves were excised and the sub-sample of 10 g green lamina from detached leaves was used to record leaf area per plant on leaf area meter (LiCOR, 3100).

Water potential

Leaf water potential was measured at booting stage with water potential apparatus (Chas W. Cook and Sons, Birmingham B 42, ITT, England) following the method described by Scholander et al. (1964).

Stomatal conductance

The stomatal conductance was measured using an open system LCA-4 ADC portable infrared gas analyzer (Analytical Development Company, Hoddeson, England). Measurement of stomatal conductance (*g*s) was made on the youngest fully emerged leaf (normally 3rd leaf from top) of each plant.

Biological yield per plant

Five plants from each pot were harvested and left to dry under the sun, after which samples were weighed with spring balance and yield per plant was recorded.

Grain yield per plant

Five plants from each pot were harvested, and left for sun drying. After threshing samples, grain yield per plant was recorded on average basis.

Harvest index (%)

The harvest index for each pot was calculated using the following formula:

HI = (Grain yield / Biological yield) × 100

RESULTS

Effect of Si on plant water status and gaseous exchange

Significantly lower water potential was observed under

Table 1. Effect of Si on leaf area, plant water relations and ionic composition of wheat cultivars both under saline and non-saline conditions at $p \leq 0.05$.

Parameter	Genotype	Control (2 dS/m)		Saline (12 dS/m)	
		Si-	Si+	Si-	Si+
Leaf area (cm^2)	Auqab-2000	32.80^{c}	40.33^{a}	21.00^{f}	29.80^{d}
	SARC-5	27.40^{e}	34.73^{b}	21.70^{f}	26.67^{e}
Water potential (-MPa)	Auqab-2000	0.62^{cd}	0.48^{f}	1.14^{a}	0.63^{c}
	SARC-5	0.56^{e}	0.39^{d}	0.94^{b}	0.57^{de}
Stomatal conductance (µmol m^2 s^{-1})	Auqab-2000	0.42^{ab}	0.44^{a}	0.19^{f}	0.28^{d}
	SARC-5	0.38^{b}	0.37^{b}	0.24^{e}	0.34^{c}
K^+ (%)	Auqab-2000	1.41^{c}	1.76^{a}	0.39^{e}	1.09^{d}
	SARC-5	1.59^{b}	1.75^{a}	0.41^{e}	1.14^{d}
Na^+ (%)	Auqab-2000	0.48^{d}	0.37^{e}	1.89^{a}	0.65^{c}
	SARC-5	0.42^{de}	0.34^{e}	1.62^{b}	0.61^{c}
$K^+ : Na^+$	Auqab-2000	2.93^{c}	4.80^{a}	0.21^{e}	1.68^{d}
	SARC-5	3.78^{b}	5.16^{a}	0.25^{e}	1.89^{d}
Si (%)	Auqab-2000	1.09^{c}	1.26^{b}	0.09^{d}	1.13^{c}
	SARC-5	1.10^{c}	1.43^{a}	0.08^{d}	1.26^{b}

The values are means of three replicates. Si- and Si+ represent 0 and 150 mg kg^{-1} of Si, respectivelyg

saline conditions (12 dS/m) in comparison to non-saline conditions (2 dS/m) in both SARC-5 and Auqab-2000. The extent of reduction was lower in SARC-5 than Auqab-2000. Si applied (150 mg/kg) wheat plants maintained significantly higher water potential as compared to Si-deprived plants under saline and non-saline conditions in both cultivars. Comparing the cultivars, SARC-5 (salt tolerant) maintained higher water potential than Auqab-2000 (salt sensitive) both under saline and non-saline conditions (Table 1). Plants of both cultivars grown in saline soil had significantly ($p \leq 0.05$) lower stomatal conductance as compared to plants grown in non-saline soil. Si-amended wheat plants had significantly ($P < 0.05$) higher stomatal conductance as compared to those grown in the absence of Si only under salt stress conditions in both the cultivars. Under normal conditions, although non-significant but slightly increase in stomatal conductance was observed in both salt tolerant and salt sensitive cultivars. SARC-5 showed higher stomatal conductance than Auqab-2000 under saline conditions, where as reverse was true under non-saline conditions (Table 1).

Effect of Si on mineral composition of Wheat (K^+, Na^+ and Si)

The concentration of K^+ in flag leaf of wheat plants grown in the presence of NaCl was significantly lower in comparison to pots where salt was not added. Ca-silicate application significantly increased the K^+ concentration both under non-saline and saline conditions in both cultivars. Higher concentration of K^+ was observed in SARC-5 than Auqab-2000 cultivar under non saline conditions. Under saline conditions, however, there were no differences between cultivars (Table 1). Na^+ concentration in flag leaves of both cultivars under salt stress was observed to be significantly higher than non-saline conditions. Si amendment (150 mg/kg) reduced the Na^+ concentration in both the cultivars under saline and non-saline conditions when compared with Si-treatment. Higher concentration of Na^+ was recorded in Auqab-2000 than SARC-5 (Table 1). In addition, K^+:Na^+ was badly affected by salinity stress, indicating increased uptake of Na^+ than K^+. The data (Table 1) also shows that salt stress significantly reduced the K^+:Na^+ in comparison to non-saline conditions in both the cultivars.

Si supplementation enhanced K^+:Na^+ to a significant extent under saline and non-saline conditions in both the cultivars. K^+:Na^+ was higher in SARC-5 cultivar than Auqab-2000 both under non-saline and saline conditions. Si concentration in flag leaves of wheat was significantly decreased by NaCl stress in Auqab-2000 cultivar and SARC-5. Si supplementation at 150 mg/kg significantly increased the Si content in both cultivars under saline

Table 2. Effect of Si on grain yield and its components of wheat cultivars both under saline and non-saline conditions at $p \leq 0.05$.

Parameter	Genotype	Control (2 dS/m)		Saline (12 dS/m)	
		Si-	Si+	Si-	Si+
Plant height (cm)	Auqab-2000	70.29^{b}	77.39^{a}	55.45^{e}	58.80^{d}
	SARC-5	69.09^{b}	75.29^{a}	60.38^{d}	65.93^{c}
Number of tillers/plant	Auqab-2000	4.67^{b}	5.67^{c}	2.67^{a}	4.00^{dc}
	SARC-5	4.33^{c}	5.33^{ab}	3.00^{d}	4.33^{c}
Spike length (cm)	Auqab-2000	9.00^{a}	8.92^{a}	6.51^{b}	8.11^{a}
	SARC-5	8.91^{a}	9.10^{a}	6.63^{a}	8.24^{b}
Number of spikelets/spike	Auqab-2000	16.00^{a}	17.00^{b}	10.67^{a}	14.00^{cb}
	SARC-5	15.33^{ab}	15.00^{ab}	11.67^{c}	14.67^{b}
Number of grains/spike	Auqab-2000	39.67^{a}	41.00^{a}	25.33^{d}	31.67^{c}
	SARC-5	33.67^{bc}	35.33^{b}	27.33^{d}	33.00^{bc}
1000 Grain weight (g)	Auqab-2000	4.24^{ab}	4.67^{a}	3.24^{c}	3.53^{cc}
	SARC-5	3.83^{bc}	4.21^{ac}	3.32^{c}	3.66^{bc}
Biological yield (g/plant)	Auqab-2000	14.29^{ab}	14.76^{a}	9.62^{c}	13.10^{ab}
	SARC-5	12.96^{ab}	13.07^{ab}	10.07^{c}	12.38^{ab}
Grain yield (g/plant)	Auqab-2000	5.71^{a}	5.73^{a}	3.86^{b}	5.10^{a}
	SARC-5	5.34^{a}	5.30^{a}	3.94^{b}	5.16^{a}
Harvest Index	Auqab-2000	0.41^{a}	0.39^{a}	0.40^{a}	0.39^{a}
	SARC-5	0.41^{a}	0.41^{a}	0.39^{a}	0.42^{a}

The values are means of three replicates. Si- and Si+ represent 0 and 150 mg kg^{-1} of Si, respectively.

and non-saline conditions when compared with no Si application. Among the cultivars, more Si content was observed in SARC-5 than Auqab-2000 under saline conditions (Table 1).

Effect of Si on plant growth

Leaf area was significantly ($P \leq 0.05$) reduced by salt stress in both cultivars in comparison to optimal conditions. Leaf area increased significantly due to Si supplementation under saline and non-saline conditions in both the cultivars in comparison to treatment where Si was not supplied. Auqab-2000 produced more leaf area than SARC-5 in normal soil. Both cultivars were at par with each other in Si-amended saline soil (Table 2). Salinity stress reduced the shoot dry matter to a significant extent when compared with non-saline conditions. Application of Si significantly increased the shoot dry matter under saline conditions in both cultivars in comparison to plants where Si was not applied whereas; under non-saline conditions non-significant increase in dry matter was observed. Both cultivars were observed statically at par with each other both under saline and non-saline conditions (Table 2). Grain yield/ plant was significantly decreased by salt stress when compared with control conditions. Furthermore, the Si added had non-significant effect on grain yield under non-saline conditions in both cultivars when compared with plants where Si was not added. However, under saline conditions, significant increase in grain yield was observed (Table 2). Harvest index remained unaffected by Si application both under saline and non-saline conditions in both the cultivars. Under saline conditions, salt tolerant cultivar showed slightly higher harvest index as compared to Auqab-2000 (Table 2).

Various other parameters including plant height, spike length, number of tillers/plant, number of spikelets/spike, number of grains/spike were significantly reduced by salinity stress in comparison to and the magnitude of reduction was greater in SARC-5 than Auqab-2000 (Table 1). Plant height grown in the presence of Si had greater values as compared to plants grown without Si both under saline and non-saline conditions in both cultivars (Table 2). Nevertheless, non-significant increase in spike length, number of spikelets/spike and number of grains/spike was measured under non-saline conditions. The 1000 grain weight remained unaffected by Si application both under saline and non-saline conditions in both the cultivars (Table 2).

DISCUSSION

The response of plants to excessive salinity is multi-faceted and involves changes in plant's morphology, physiology and metabolism (Hilal et al., 1998), ultimately reducing the plant growth (Rhoades, 1993). In the present study, an important growth determinant, leaf area was significantly constrained by salt stress (EC = 12 dS/m) in Auqab-2000 and SARC-5 in the presence or absence of Si in comparison to non-stress (EC = 2 dS/m) conditions. In addition, salinity stress significantly deceased biological and grain yield. Similar cutback in these growth parameters in wheat due to salt stress in soil medium have been reported by Ahmad et al. (1992).

Silicon accumulates in plants at a rate comparable to those of macronutrient elements like calcium, magnesium and phosphorous (Epstein, 1999). In the current study, Ca-silicate application at 150 mg Si kg^{-1}soil significantly increased the Si content in flag leaves of wheat both under saline and non-saline conditions in comparison to treatment where Si was not applied. Previous reports and the current research suggested that Si deposition in plants is responsible for amelioration of salt stress. Plants grown in Si-supplied soil maintained higher leaf area compared to those where Si was not added under water stress conditions (Gong et al., 2003). In the present study leaf area increased significantly by Si supplementation at 150 mg/kg under saline and non-saline conditions in both cultivars in comparison to treatment where Si was not supplied. The beneficial effect of Si may be due to its hydrophilic nature that protected wheat plants from physiological drought induced by salt stress. Si application also increases yield in rice (Liang et al., 1994) in calcareous soils and improves the growth variables in legumes affected due to salt stress (Murillo-Amador et al., 2007). In the current study, Si amendment increased the biological and grain yield under saline and non-saline conditions in both cultivars. It can be suggested from current discussion that a significant and positive relationship exists between Si and grain yield under saline conditions. Comparing the genotypes, Auqab-2000 showed better performance than SARC-5 as exhibited by higher production of yield and yield contributing factors including leaf area as well under optimal conditions. However, the opposite trend was observed under saline conditions.

Salinity affects crop physiology by changing the water content of the plant cells (Sultana et al., 1999, Hasegawa et al., 2000). In the current study salinity also considerably lowered the leaf water potential and stomatal conductance in comparison to non-saline conditions in both SARC-5 and Auqab-2000. Si plays a pivotal role in the enhancement of plant water relations and gaseous exchange under stressful conditions. Si application in the root zone maintains transpiration, stomatal conductance, net photosynthesis in salinity stressed leguminous plants (Murillo-Amador et al., 2007) and enhances leaf water potential in wheat under drought and salinity stress (Liang et al., 1999), as a result, causes significant increase in dry matter yield of higher plants with improved water economy (Gong et al., 2003). This study confirms these reports because Si-application (150 mg/kg) helped to maintain significantly higher water potential as compared to control plants under saline and non-saline conditions in both cultivars. Besides, data shows a positive correlation between leaf Si accumulation and water potential. Liang et al. (1999) suggested that silica-cuticle double layer formed on leaf epidermal tissue is responsible for this increased water potential. Current findings confirm these results suggesting an induction of salt tolerance by Si owing by reducing transpirational losses.

In the present study, Si supplementation increased the stomatal conductance under saline conditions which ensured more gaseous exchange for higher photosynthesis. Sorghum also maintained an elevated stomatal conductance and photosynthesis when Si was applied in water stress (Hattori et al., 2005). Similarly, Gong et al. (2006) found an increase in stomatal conductance (from 138 to 150 mmol/m^2/s) in rice plants, 20% more as compared with control grown under saline and non-saline conditions. A significant ($p \leq 0.05$) positive regression co-efficient relationship was found between Si and stomatal conductance under saline conditions (Figure 1). It can be suggested that Si amendment increased the plant water content in rice plants. Moreover, by reducing the transpiration (Agurie et al*.,* 1992) the CO_2 intake was enhanced leading to higher photosynthetic rate. One of the important characteristics of salt tolerance is that the tolerant varieties maintain higher water potential under saline conditions. It helps the plants to dilute the toxic salts and maintaining turgidity required for growth. The salt tolerant cultivar, SARC-5, maintained higher water potential than sensitive (Auqab-2000) both under saline and non-saline conditions, thus confirming its salt tolerance.

Among major mechanisms responsible for salinity tolerance due to Si is an increased K^+ uptake (Liang et al., 1999) as depicted in the present study. The calcium silicate application at 150 mg Si kg^{-1}soil significantly increased the K^+ concentration both under non-saline and saline conditions. Lower Na^+ concentration in plant body

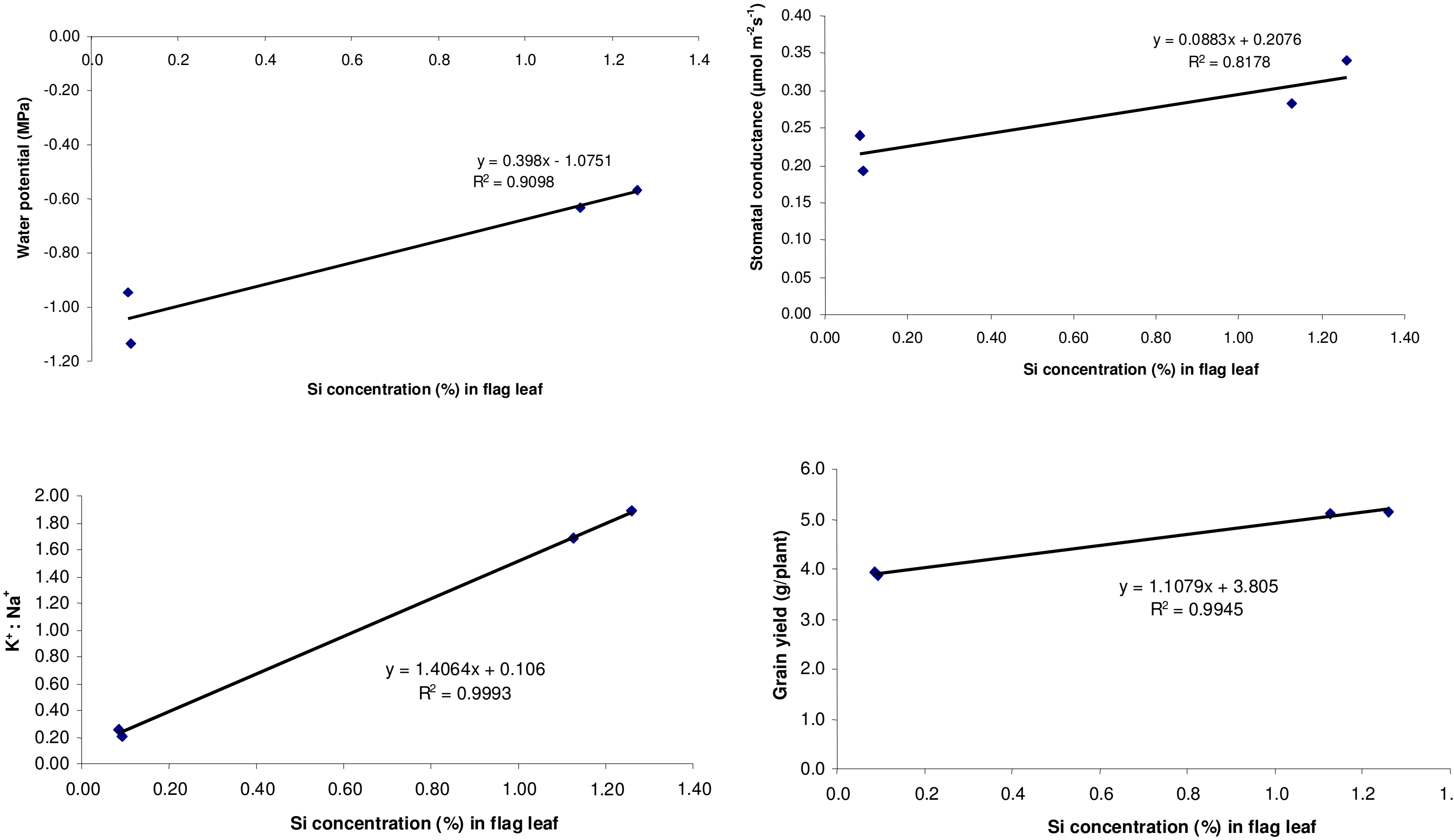

Figure 1. Schematic diagram showing regression coefficient relationship between Si and water potential, stomatal conductance, K^+:Na^+ in flag leaves and grain yield of wheat in saline culture.

is an indicator of salinity tolerance. The present study indicates that Na^+ concentration in flag leaves of both wheat cultivars was significantly reduced by Si application. Ma et al. (2001) suggested that the alleviation of Na^+ toxicity in corn is mainly due to the formation of Na^+ and Si complexes in solution rather than any physiological impact of Si on the plant. Si application reduces the Na^+ uptake that increases the stomatal conductance of salt-treated rice and ultimately net photosynthesis (Yeo et al., 1999). Hence, Ca-silicate application ameliorated the salt toxicity by both suppres-sing the Na^+-uptake and enhancing K^+ concentration and Si deposition in leaves leading towards increased K^+:Na^+. It was evident from our data that K^+:Na^+ was badly affected by salinity stress as compared to non-saline conditions indicating increased uptake of

Na^+ as compared to K^+. Si application into saline soil enhanced K^+:Na^+ to a significant extent under saline and non-saline conditions in both cultivars.

Furthermore, a significant positive correlation was found between Si and K^+:Na^+ (Figure 1). This might be due to the stimulated activity of H^+-ATPase on root plasma membrane and H^+-PPase activity on tonoplast of roots that improved the uptake and upward transport of K^+ and retarded the movement of Na^+ and improved the progress of Na^+/H^+ antiport, thus enhancing the K^+:Na^+ selectivity ratio in the shoots of salt stressed barley (Liang et al., 2005). Similarly, in cowpea and kidney bean, Si increased the K^+ and decreased Na^+ and Cl^- content (Murillo-Amador et al., 2007). The salt sensitive plants cannot lower the uptake of Na^+ and as a result plant absorbs higher Na^+, which is very toxic to most of the plants. The concentration of Na^+ was greater in Auqab-2000 as compared to SARC-5 under saline con-ditions. The K^+:Na^+ was highly observed in SARC-5 cultivar as compared to Auqab-2000 both under non-saline and saline conditions.

It is concluded from the current experiment that Si application significantly increased all growth variables including dry matter and grain yield of both wheat cultivars under normal as well as saline conditions. The major mechanism responsible for inducing salt tolerance in both cultivars was increased K^+ uptake and decreased Na^+ uptake that enhanced K^+:Na^+ selectivity ratio in leaves. The current results also show that higher water potential and stomatal conductance maintained by Si treated plants under salinity stress is one of the mechanisms for the improvement of crop growth. The current experiment, however, necessitate the exploration of these results working at field level.

REFERENCES

Agurie S, Agata W, Kubota F, Kaufman PB (1992). Physiological role of silicon in photosynthesis and dry matter production in rice plants. J Crop Sci. 61: 200-206.

Ahmed M, Fayyaz ul H, Khurshid Y(2011). Does silicon and irrigation have impact on drought tolerance mechanism of sorghum? Agricultural Water Management In Press, Corrected Proof. DOI: 10.1016/j.agwat..07.003.

Ahmad R, Zaheer SH, Ismail S (1992). Role of Si in salt tolerance of wheat (*Triticum aestivum* L.). Plant Sci. 85: 43-50.

Akram MS, Athar HR, Ashraf M (2007). Improving growth and yield of sunflower (*Helianthus annuus* L.) by foliar application of potassium hydroxide (KOH) under salt stress. Pak. J. Bot. 39: 2223-2230.

Ali A, Basra SMA, Ahmed R, Wahid A (2009). Optimizing silicon application to improve salinity tolerance in wheat. Soil Environ. 28(2): 136-144

Ashraf M, Harris PJC (2004). Potential biochemical indicators of salinity tolerance in plants. Plant Sci. 166: 3-6.

Awada S, Campbell WF, Dudley LM, Jurinak JJ, Khan MA (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.

Elliot CL, Snyder GH (1991). Autoclave-induced digestion for the calorimetric determination of silicon in rice straw. J. Agri .Food Chem. 39: 1118-1119.

Epstein E (1999a). Solution Culture Techniques. Measurement Techniques in Plant Sciences. In: Hashimoto. Y, Kramer PJ, Nomani H, Strain BR (eds.), Academic Press Inc, San Diego, USA. pp. 207-245.

Epstein E (1999b). Silicon. Annu Rev Plant Physiol Plant Mol Biol. 50: 641-664.

Flowers TJ (2004). Improving crop salt tolerance. J. Exp. Bot. 55: 307-319.

Gong HJ, Chen KM, Chen GC, Wang SM, Zhang CL (2003). Effect of silicon on growth of wheat under drought. J. Plant Nutr. 5: 1055-1063.

Gong HJ, Randall DP, Flowers TJ (2006). Silicon deposition in the root reduces sodium uptake in rice seedlings by reducing bypass flow. Plant Cell. Environ. 111: 1-9.

Greenway H, Munns R (1980). Mechanism of salt tolerance in non-halophytes. Annu. Rev. Plant Physiol. 31: 149-190.

Hasegawa P, Bressan RA, Zhu JK, Bohnert HJ (2000). Plant cellular and molecular responses to high salinity. Annu. Rev. Plant Mol. Biol. 51: 463-499.

Hattori T, Inanaga S, Araki H, An P, Morita S, Luxova M , Lux A (2005). Application of silicon enhanced drought tolerance in *Sorghum bicolor*. Physiol Plant. 123: 459-466.

Hilal M, Zenoff AM, Ponessa G, Moreno H, Massa ED (1998). Saline stress alters the temporal patterns of xylem differentiation and alternative oxidative expression in developing soyabean roots. Plant Physiol. 117: 695-701.

Liang YC, Ma TS, Li FJ, Feng YJ (1994). Silicon availability and response of rice and wheat to silicon in calcareous soils. Commun Soil Sci Plant Annal 25, 2285-2297.

Liang YC, Qirong, Zhenguo S (1999). Effect of silicon on enzyme activity and sodium, potassium and calcium concentration in barely under salt stress. Plant Soil, 209: 217-224.

Liang YC, Chen Q, Liu Q, Zhang W, Ding R (2003). Effects of silicon on salinity tolerance of two barley cultivars. J. Plant Physiol. 160: 1157-1164.

Liang YC, Zhang WQ, 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. Exp. Bot. 53: 29-37.

Lopez CML, H Takahashi, S Yamazaki (2002). Plant-water relations of kidney bean plants treated with NaCl and foliarly applied glycinebetaine. J. Crop Sci. 188: 73-80.

Ma JF (2004). Role of silicon in enhancing the resistance of plants to biotic and abiotic stresses. J. Soil Sci. Plant Nutri. 50: 11-18.

Ma JF, Miyake Y, Takahashi E (2001). Silicon as a beneficial element for crop plants. pp. 17-34. In: Silicon in Agriculture. (Eds. Datnoff LE and GH. Snyder. Elsevier, New York, USA.

Marschner H (1995). Mineral nutrition of higher plants. 2nd ed., Academic Press, San Diego, USA.

Matichenkov VV, Kosobrukhov AA (2004). Silicon effect on the plant resistance to salt toxicity. 13th International Soil Conservation Organization Conference. Conserving soil and water for society, Brisbane, July, 2004.

Munns R (2002). Comparative physiology of salt and water stress, Plant Cell Environ. 25: 239-250.

Murillo-Amador B, Yamada ST, Yamaguchi E, Rueda-Puente E, Avila-Serrano N, Garcia-Hernandez JL, Lopez-Aguilar R, Troyo-Dieguez E, Nieto-Garibay A (2007). Influence of calcium silicate on growth, physiological parameters and mineral nutrition in two legume species under salt stress. J. Agron. Crop Sci. 193: 413-421.

Qureshi RH, Barrett-Lennard EG (1998). Saline Agriculture for Irrigated Land in Pakistan: A Handbook. Australian Centre for International Agricultural Research, Canberra, Australia, p. 146.

Raza SH, Athar HR, Ashraf M (2006). Influence of exogenously applied glycinebetaine on the photosynthetic capacity of two differently adapted wheat cultivars under salt stress. Pak. J. Bot. 38: 341-351.

Rueda-Puente EO, Garcıa-Hernandez JL, Preciado-Rangel P, Murillo-Amador B, Tarazon-Herrera MA, Flores-Hernandez A, Holguin-Pena J, Aybar AN, Barron-Hoyos JM, Weimers D, Mwandemele O, Kaaya G, Larrinaga-Mayoral J, Troyo-Dieguez E (2007). Germination of *Salicornia bigelovii* ecotypes under stressing conditions of temperature and salinity and ameliorative effects of plant growth-promoting bacteria. J. Crop Sci. 193: 167-176.

Rhoades J D (1993). Practices to control salinity in irrigated soil. In:

Leith H, Al-Masoom A, (eds.). Towards the Rational Use of High Salinity Tolerant Plants. 2: 379-389.

Romero-Aranda MR, 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.

Saqib M, Zorb C, Rengel Z , Schubert S (2005). Na^+ exclusion and salt resistance of wheat (*Triticum aestivum*) are improved by the expression of endogenous vacuolar Na^+/H^+ anitporters in roots and shoots. Plant Sci. 169: 959-965.

Scholander PL, Hammel HT, Bradstreet ED, Hemminsoln EA (1964). Hydrostatic pressure and osmotic potential in leaves of mangroves and some other plants. Proc. Natl. Sci. USA. 52: 119-125.

Sultana N, Ikeda T, Itoh R (1999). Effect of NaCl salinity on photosynthesis and dry matter accumulation in developing rice grains. J. Environ. Exp. Bot. 42: 211-220.

Tahir MA, Rahmatullah, Aziz T, Ashraf M, Kanwal S, Muhammad A (2006). Beneficial effects of silicon in wheat under salinity stress-pot culture. Pak. J. Bot. 38: 1715-1722.

Tester M, Davenport R (2003). Na tolerance and Na transport in higher plants. Ann. Bot. 91: 503-527.

Wagenet RJ, Rodriguez RR, Campbell WF, Turner DL (1983). Fertilizer and salty water effects on Phaseolus. Agron. J. 75: 161-166.

Wolf B A (1980). Comprehensive system of leaf analysis and its use for diagnosing crop nutrient status. Commun. Soil Sci. Plant Anal. 13: 1035-1059.

Yeo AR, Flowers SA, Rao G, Welfare K, Senanayake N, Flowers TJ (1999). Silicon reduces sodium uptake in rice *(Oryza sativa L.)* in saline conditions and this is accounted for by reduction in transpirational bypass flow. Plant cell Environ. 22: 559-565.