Australian Journal of Crop Science AJCS

AJCS 7(4):484-491 (2013) ISSN:1835-2707

Silicon priming: a potential source to impart abiotic stress tolerance in wheat: A review

Mukhtar Ahmed[1], Atif Kamran[2], Muhammad Asif[2], Ummara Qadeer[1], Zammurad Iqbal Ahmed[1], Aakash Goyal[3*]

[1]Department of Agronomy, PMAS, Arid Agriculture University Pakistan
[2]Agricultural, Food and Nutritional Science, 4-10 Agriculture/Forestry Centre, Univ. of Alberta, Edmonton, AB T6G 2P5, Canada
[3]Bayer Crop Science, Saskatoon, Saskatchewan, S7N4N1

***Corresponding author: akgroyal@gmail.com**

Abstract

Water deficiency adversely affects a number of physiological and metabolic mechanisms in plants and probably, is a major yield limiting factor. This often put into perspectives, the challenge to produce higher crop yields than ever by conserving and efficiently using the depleting underground water and bringing the marginal water deficit lands under cultivation. A possible potential solution is to induce drought tolerance to mitigate this challenge. The drought resistance recently has drawn the future research focus mainly due to exhausting water table and distribution. Silicon priming is known to enhance crop tolerance against various environmental stresses by tailoring the plant water uptake and transport. Drought tolerance could be induced by modified physio-morphic features such as: adjustment for leaf water potential, stomatal frequency, stomatal size, osmotic adjustments. Silicon priming potentially can induce anatomical changes in cell wall with deposition of silica in the form of polymerized silicon dioxide (SiO_2) solid particles, alleviating the oxidative damage of functional molecules and improving anti-oxidative defense abilities. Silicon, actually, induces dehydration tolerance at tissue or cellular levels by improving the water status and hence, facilitates the plant to access photosynthates and this modified adaptability mechanism varies among species. In this review, we discuss the plant drought tolerance adjustments and role of silicon priming to withstand drought stress.

Keywords: silicon priming, drought tolerance, osmotic adjustment and dehydration.
Abbreviations: OA_Osmotic adjustment; CMS_Cell membrane stability; GA_3_gibberellic acid, SOD_Superoxide dismutase, POD_Peroxidase,CAT_Catalase, APX_Ascorbate peroxidase.

Introduction

Extreme environmental conditions like high temperature and low water exerts severe abiotic stress in the micro-environment of crops. Certain biochemical pathways enable the plants to tolerate the stress by water retention and ultimately protecting chloroplast and maintaining the ionic balance (Parida and Das 2005). Drought is one of the major environmental factors causing low productivity and growth (Peleg et al., 2011). The detrimental drought effects could be listed as the loss in yield and quality; and in certain scenarios the death of plant. Reportedly, the application of silicon is known to enhance crop tolerance against various environmental stresses by tailoring the plant water uptake and transport. This modified adaptability mechanism varies from specie to specie (Ma and Yamaji, 2006). Silicon, actually, induces dehydration tolerance at tissue or cellular levels by improving the water status (Gao et al., 2004, 2006). This in return, facilitates the plant photosynthetic access and availability to the plant. Ever increasing world population has always urged for more production of food, feed and fiber to maintain the planet worth for peaceful living. This urge is often challenged by changing climate and continuously depleting resources such as water, arable land, disease outbreaks and crop management issues. Therefore, it’s imperative to develop drought resistant varieties, and alternative strategies like silicon priming to solve the issue of food security. Anecdotal data reveal that drought is being the most common reason of severe food shortages. Drought has the foremost effect on agriculture as a result of which livestock is affected, due to feed shortage death of an animal can occur. Drought affect the land quality, causes soil erosion, famine, disturbs human health, malnutrition, and food borne diseases. Does the drought only affect the agriculture? Probably not, rather it has a wider social and economic impact, particularly in famine when everybody suffers black marketing and price hikes. The ultimate and long term solution to this challenge is to develop, manage and conserve the water resources and fulfill the crop water needs and/or by adopting drought tolerant varieties. Water stress is a serious risk to crop production. Crop yield losses due to water scarcity are much more adverse than other environmental stresses. Plants cannot survive without water. Water deficiency adversely has effects on number of physiological and metabolic mechanism in plants. Drought inhibits the growth at its first instance, as lack of water hampers the photosynthetic rates. Drought is the main factor hindering to reach a crop maximum theoretical yield (Mitra, 2001). It is one of the most limiting factors to the crop productivity. It has a differential effect on crop’s micro and macro-environment across a common field, different plant growth stages and the plant material to be harvested. Promising future researches need to be focused on a wide range of genetic, metabolic, environmental and physiological factors for improvement of drought resistance in crops (Araus et al., 2008). The drought resistance recently has drawn the future research focus due to exhausting water availability and distribution (Habash et al., 2009). This goal could only be promised by complete knowledge of genetic and molecular basis of drought resistance (Nachit and Elouafi, 2004). Blum, 2005 depicted that plant adopted various mechanisms to face drought e.g. osmotic adjustment, cell membrane stability, epicuticular wax, partitioning and stem reserve mobilization, manipulation and stability of flowering processes, seedling drought traits. Screening of such species will help to combat the drought conditions in Pakistan. Plant transpiration is the second drought victim to hamper the plant efficiency by decreasing transpiration that results in lowering wheat yield productivity to a greater extent. Carbon-dioxide assimilation and chlorophyll content were also influenced by drought (Monneveux et al., 2006). Chlorophyll contents were found to increase in leaves in short term water stress during the vegetative phase, whereas the reverse has been noticed (decrease in chlorophyll) during long term stress. Chlorophyll content, stomatal conductance, transpiration rate were known to strongly influence photosynthetic rate. Drought resulted to decrease in transpiration rate, stomatal conductance and photosynthetic rate of the seedlings of four spring wheat varieties while water use efficiency of leaves was increased (Chang-juan, 2012). Therefore, drought not only influences photosynthetic and transpiration rate, but also affects chlorophyll content and CO_2 assimilation rate to a considerable degree.

Drought tolerance in plants

Drought is a condition when an area faces a lack of precipitation and high evapotranspiration resulting to non-availability of minimum amount of water. Drought tolerance means a condition when plants are adapted to drought or arid condition by modifying physio-morphic features. These features include leaf water potential, stomatal frequency, stomatal size, osmotic adjustments (Ahmad et al., 2006). Water stress is a severe environmental and production constraint for a variety of food crops including wheat. Water is turning as a rare commodity and its severity has been predicted in the years to come. Drought alters all elements of the plant growth and the capability of plant to rehabilitate whereas different physiomorphic traits can amend the stress. These traits are genetically complex and are not simple to handle. Drought-induced loss in crop yield probably exceeds losses from all other causes, since both the severity and duration of the stress are critical. Drought stress affects the growth, phenology, water and nutrient relations, photosynthesis, assimilate partitioning, and respiration in plants. Proline and quaternary ammonium compounds e.g. glycinebetaine, choline, prolinebetaine are key osmolytes contributing towards osmotic adjustment (Huang et al., 2000 and Kavikishore et al., 2005). Furthermore, breeding for drought tolerance in crops is economical and considered to be an effective way of coping with drought stress (Blum, 1999). The pathway strategies in plant due to stress are elaborated below.

a) Osmotic adjustment

When a plant experiences the water stress, certain osmotically active compounds such as amino acids, ions and sugars inside the cell accumulate, which results in lowering osmotic potential of cell. It is reported to be an important mechanism in drought conditions (Yousifi et al., 2010). After the water accumulates in intercellular spaces, it will move inside the cell called as osmotic adjustment (OA). OA is the possible phenomena that will maintain the turgor and plant can survive in lack of water and facilitates root growth (Gonzalez et al., 2010). OA found as a positively related to grain yield in drought conditions in sorghum (Tangpremsri et al., 1995), wheat (Zivack et al., 2009), barley (Gonzalez et al., 2009), chickpea (Moinuddin and Khanna-Chopra, 2004), and pigeon pea (Subbarao et al., 2000). Verities with high OA are reported to have better grain yield than plants with low OA (Moinuddin and Khanna-Chopra, 2004). Although this adoptive mechanism seems beneficial, certain studies suggested to have negative (Kirkham, 1988) or no relation (Tangpremsri et al., 1995) with the grain yield.

b) Cell membrane stability

Cell membrane stability is ability of a cell to live in dehydration. This ability is particularly useful in OA. Osmotic adjustment coupled with cell membrane stability help plant to reduced water conditions during drought. Different crops have different tolerance to this stress depending upon the cell membrane stability (CMS). The tolerance depends upon CMS because it prevents electrolyte leakage in drought condition and maintains the cell activity in abiotic stresses like salinity (Ghoulam et al., 2002), drought (Blum 2011) and Yang et al., 2009), air pollution (Neves et al., 2009) and heat, cold (Arvin and Donnelly, 2008). Therefore CMS is considered to be one of the stress adaptive mechanisms under drought stress and is helpful in increasing yields as it maintains the cell activity in stress.

(c) Epicuticular wax

Epicuticular wax is the organic compounds of cuticle which covers the outer surface of plant tissues (Li et al, 2007). Epicuticular wax is very helpful for reducing leaf surface water losses. Species with thick cuticle layer retain more moisture and maintain leaf turgor for longer period of time in stress conditions due to reduced evapotranspiration. The wax composition of specie may differ for different parts of the same plant and may vary with season, locale, and the age of the plant (Eglinton and Hamilton, 1967).

(d) Partitioning and stem reserve mobilization

In drought conditions the process of photosynthesis is abridged and grain yield then have to rely upon stem reserves. The stem reserves buffer in stress condition and help in maintaining the grain yield by helping in photosynthesis and nutrient uptake during grain filling stage (Tahir and Nakata, 2005). The contribution of these assimilates to seed may be effected in severe stress conditions when photosynthesis is reduced and water, mineral uptake are limited (Arduini et al., 2006). In severe stress, the grain filling varies in different species, varieties and environment; and a large mobilization can occur in low soil fertility (Masoni et al., 2007). The partitioning and stem reserve mobilization starts from plant senescence, which transfers stored reserves from stems to seed (Ercoli et al., 2008). The previous study depicted that amount of reserve mobilization depends upon environment, genotype and cultural practices (Aynehband et al., 2011). A continuous rise in temperature during grain filling can cause a severe reduction in dry matter production (Alvaro et al., 2008). This mechanism encourages a decrease in gibberallic acid and

Table 1. Literature showing silicon role and plant response under stresses.

S.No	Silicon and plant responses under stress	References
1	Low-molecular-mass compounds as compatible solutes to cope stress	Hasegawa et al., 2000;
2	Reduction in the rate of leaf surface expansion under stress	Allakhverdiev et al.,2000
3	Biochemical pathways products and processes coup stress additively or synergistically	Iyengar and Reddy, 1996
4	High-complexity mechanisms involve changes that protects major metabolisms	Botella et al., 1994
5	Low-molecular-mass compounds to coup stress	Zhifang and Loescher, 2003
6	Proline the compatible solutes	Khatkar and Kuhad, 2000;
7	Glycine betaine (GB) to coup stress	Wang and Nil, 2000
8	Sugars the stress defenders	Kerepesi and Galiba, 2000
9	Polyols to coup stress	Bohnert et al., 1995
10	Nitrogen-containing compounds (NCC) accumualtes under stress such as amino acids, amides, imino acids, proteins, compounds, and polyamines.quaternary ammonium	Wang and Nil, 2000
11	Stress and lipid peroxides or reactive oxygen species (ROS)	Choudhury and Panda 2005
12	Si addition alleviated the reduction of antioxidative enzymes (superoxide dismutase (SOD) and ascorbate peroxidase (APX) in leaves; catalase (CAT) and APX in roots	Fan-rong et al.,2011
13	Si have multiple direct and indirect beneficial effects on plants	Ma et al. 2001
14	Si effects is pronounced in the plants under abiotic and biotic stresses	Epstein 1994,1999
15	silicon can reduce the toxicity of heavy metals	Song et al. 2009
16	Si promoted lignin deposition in cell walls	Ma et al., 2006
17	Si-increased antioxidant defense capacity	Song et al., 2009
18	Si promotes plant growth and alleviates abiotic stress	Liang, 2007
19	Si provides a wide variety of beneficial effects to plants	Marschner, 2002
20	Si functions as mechanical barrier against pathogen progress, or Si induces resistance components	Belanger et al.,2003
21	Silicon has positive effects on biomass production in plants like Poaceae	Eneji et al., 2008
22	Silicon is beneficial in pathogen, drought,pest resistance and metal tolerance	Fawe et al., 1998, Ma, 2004, Lanning, 1966; Cookson et al., 2007; Liang et al., 2007

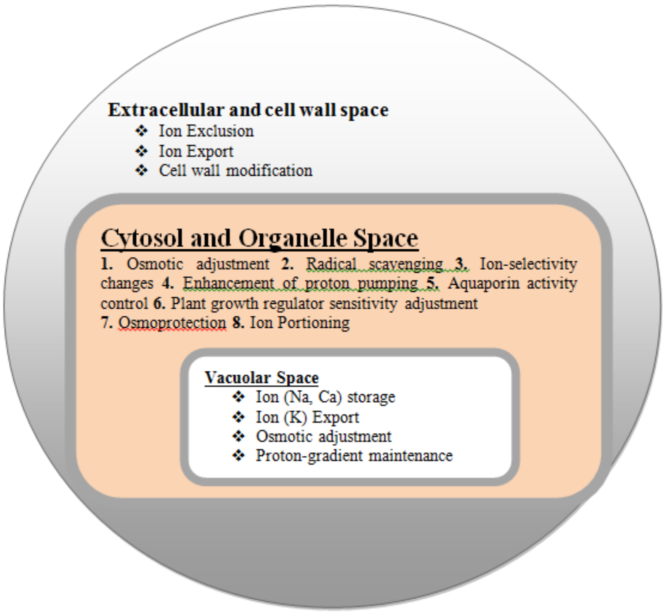

Fig 1. The diagrammatic representation of crop cell with three layers representing plasma membrane and tonoplast (reproduced from Bohnert and Jensen, 1996).

increase in abscisic acid concentration (Chinnusamy et al., 2004).

(e) Seedling drought traits

In drought conditions seedlings are planted deep to reach the receding water profile so that drought can be avoided and ultimately to help plant protected from high surface temperatures causing germination inhibition. Deep placed seeds will be able to capture more water from soil and exclude salts from root cells (Vadez et al., 2005).

Silicon and its Priming under abiotic stresses

The word priming refers to seed hydration or providing seed with moisture followed by its drying, so that the germination process begins. Priming hastens the germination, seedling emergence and early growth in such a way that soil moisture and nitrogen are engaged and utilized. Priming could be done with a number of chemicals including silicon, which is an effective barrier against water losses by cuticular transpiration and/or fungal infections. Silicon enables the plant to tolerate drought and increase uptake of water, which in return will help the plant to produce more dry mass and higher yield. Similarly priming with gibberellic acid (GA_3) enhanced the germination rate, reduced detrimental effects of salt stress, leaf water contents, leaf area and chlorophyll contents were increased (Ali et al., 2012). Silicon is one of the micronutrient element which is proved to be useful in seed plant species mainly graminae and cyperaceae especially during environmental stress (Hattori et al., 2005). In soil after oxygen silicon is present in maximum amount. Silicon is mostly present in the form of silica or silicates because of its high affinity to oxygen (Ma et al., 1989). Silicon can also be found in the form of silicic acid in soil (Chen et al., 2000) and is directly taken up as silicic acid (Ma et al., 2004).The absorption of silicon in the form of uncharged silicic acid and is then precipitated into the plant parts in the form of amorphous silica by an irreversible process (Ranganathan et al., 2006). Silicon is taken up as silicic acid when soil pH is below 9. Different plant species accumulate different amount of silicon e.g. rice accumulates maximum amount of Si (Ma et al., 2006). From soil solution silicon is transported to the cortical cells with the help of a transporter, the process is energy dependent because low temperature and metabolic inhibitions resist the transport. The silicon is transported from roots to shoots with the help of a xylem. In the case of wheat and rice, silicic acid polymerizes to silica gel, as concentration increases to 2 mM. In shoots silicon distribution is controlled by transpiration. More silicon is present in older tissues. Silicon is deposited beneath the cuticle layer, and this layer protects from biotic and abiotic stresses (Ma and Yamaji, 2006). Many studies have suggested positive effects of silicon on plant growth under stress. Si fertilization gave a positive response toward growth under water stress. To examine the effect of silicon on drought, water stress was applied in an experiment by sampling at booting and grain filling stage. Si was found to increase the water potential of water stressed plants at grain filling stage, whereas the effects were non-significant at booting stage (Gong et al., 2005). The same year Gong et al., 2005 stated that silicon application increased the amount of photosynthetic pigments and soluble proteins under drought. In the pot experiment with application of silicon and non-silicon treatment under drought condition, it was revealed that pots with silicon application have an improved water status as compared to pots with non-silicon treatment under

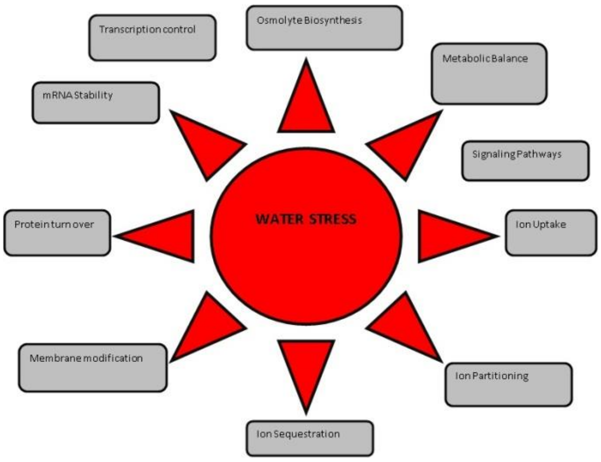

Fig 2. Plant cell organelles responses to water stress showing change in the cellular and metabolic processes (Modified from Bray, 1993).

drought conditions. Silicic acid is the only precursor in biota and plants that is taken in aqueous form and uncharged through their roots. The amount of silicon in plant is almost equivalent to macronutrients like magnesium (Mg), phosphorus (P), and calcium (Ca) (Epstein, 1999). Silicon may decrease the oxidative damage in plants facing the environmental stresses. Silicon priming could be indirectly useful in aspect that it facilitates the plant with increased growth and production by decreasing the chances of biotic and abiotic stresses like insect pest attack, diseases, drought and nutrient losses (Ma and Yamaji., 2006). A number of studies have shown silicon as nutrient that plays an important role in environmental stresses (Epstein., 1999). Silicon enhances the drought tolerance in crops because it diminishes the oxidative damage of functional molecules and exaggerating anti-oxidative defense abilities (Gong et al., 2005). Silicon was found beneficial in reducing the salt stresses as it increases dry mass, water contents, and transpiration rate which were reduced due to salt stress (Shu and Liu, 2001). Silicon was also found helpful in removing toxic substances like salts from plants by increasing water storage in plant tissues which in turn increases growth and contribute in dilution of solutes in plants (Romero-Aranda et al., 2006). Silicon helps in building cell strength and makes plant responding to environmental stresses (Cooke and Leishman, 2011). It is also beneficial in an aspect that it enhances the structural strength and increases tolerance against diseases and metal toxicity (Hodson et al., 1995). Silicon has also exhibited a positive effect in decreasing toxic effects in plants grown under salt stress (Tuna et al., 2008). Silicon potentially can induce anatomical changes in cell wall with deposition of silica in the form of polymerized silicon dioxide (SiO_2) solid particles, known as opalinephytoliths (Ma, 2004). Capacity to tolerate drought in plants is better with higher silicon deposition in roots endodermis (Lux et al., 2002). Gao et al. (2005) found that applying silicon increases the rate of water flow in xylem vessels which reduced the transpiration rate and resulted in enhanced water use efficiency in plants. Silicon is a bioactive element and it helps in relieving from biotic and abiotic stresses, and hence it gives resistance to plants to pathogenic fungi (Fautex et al., 2005). Plant biomass and yield of crops are adversely affected under drought stress because it greatly hampers various physiological and agronomical parameters. The experiment about silicon fertilization @ 50 mg/kg and 150 mg/kg of soil in three soil water content (50%, 75% and 100% of field capacity) improved wheat growth. Water deficiency in soil significantly reduced shoot biomass and spike weight of wheat plants. Silicon application significantly increases plant biomass, plant height and spike weight at all levels of water contents (Ahmad et al., 2007), however, the response of Si fertilization is higher under water deficient conditions than wet conditions. This phenomenon was verified by Hattori et al**.,** (2005) that Si application in sorghum decreases the dry weight under drought stress conditions whereas it had no effect on dry matter production under wet conditions. Application of certain chemicals or minerals can help plant in tolerating the stress e.g. phosphorus application is reported to improve osmotic adjustment in leaf tissues in bean and sorghum (Alkaraki et al., 1996), and roots tissues in white clover (Singh and Sale, 2000). Nitrogen fertilization increases nodule activity helping in improvement of drought tolerance (Purcell and King, 1996). Potassium application maintains osmotic adjustment in pearl millet (Ashraf et al., 2001). Enhanced phosphorous and potassium fertilization proved to be useful in increasing productivity in drought conditions. Some micronutrient elements have also been reported with a positive impact on drought tolerance. Drought effect on transpiration rate, water use efficiency (WUE), stomatal limitation value, net photosynthetic rate and many other parameters can minimized by Si application (Ahmed et al., 2011b). In the experiment two wheat (*Triticum aestivum* L.) cultivars, one drought-sensitive and other drought-tolerant were used to estimate the effect of Si on aforementioned parameters under water stress conditions. The net photosynthetic rates of the leaves of drought-stressed wheat were significantly enhanced by the silicon application. The treatment with 1.0 mmol/L Si was more effective in enhancing plant drought tolerance than the treatment with 0.1 mmol/L Si. Compared with control (with PEG alone) transpiration rate, water use efficiency stomatal limitation value and net photosynthetic rate were significantly enhanced, however, the stomatal conductance was significantly decreased by Si. Drought-stressed plants with Si application had significantly greater fresh weight, dry weight and leaf soluble protein content compared with drought-stressed plants without Si applied. Under mild and severe drought stress, supplying silicon could increase the plant biomass up to 31.1% to 33.3% and 23.7% to 40.5%, respectively, compared with the control (Li et al., 2007). Li et al (2007) observed that Si enhanced the net photosynthetic rate, chlorophyll content, enzymatic activities including superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), ascorbate peroxidase (APX) and restrained the increase of leaf plasma membrane permeability. Significant correlation between plant dry matter accumulation and diurnal photosynthetic cumulates was observed depicting the enhanced photosynthesis under silicon effect. Silicon supply was the main factor inducing the increased dry matter accumulation under drought stress (Ma, 2004). Silicon application also increases drought resistance in cucumber. The results suggested that in the absence of stress, silicon slightly enhanced the net photosynthetic rate, but significantly decreased the transpiration rate and stomatal conductance in cucumber plants. Silicon enhanced the net photosynthetic rate of cucumber plants under drought stress. Since silicon decreases the stomatal conductance, enhances the water holding capacity, and keeps the transpiration rate at a relatively steady rate during drought stress, the photosynthesis of the cucumber plants was sustained with increased biomass and water content in cucumber leaves. Silicon decreased the decomposition of chlorophyll in cucumber plants under drought stress. These findings demonstrated that silicon enhanced the resistance of the cucumber plants to drought. Si could ameliorate root growth of rye (*Secalecereale* L.) under drought; an experiment was conducted by Hattori et al., (2008) under two soil water regimes in pots. The rye with silicon application resulted in increased dry weight but it didn't affected shoot-root ratio in well watered conditions and lowered the ratio in dried conditions. In flooded conditions leaf water potential and water use efficiency were enhanced whereas water use efficiency, photosynthetic rate and stomatal conductance were not affected. Whereas under the dry condition, ryes with silicon application resulted in higher stomatal conductance, photosynthetic rate, water use and leaf water potential than non-silicon ones. Similarly Ahmed et al., (2011a) observed mild and severe drought stress, supplying silicon could increase the plant biomass. Silicon (Si) compounds fertilization and its subsequent accumulation in wheat (*Triticum aestivum* L.) has been studied by Joanna et al., 2007 in which all plants were given same conditions, but fertilized with various Si compounds (pyrolitic fine silica particles, sodium silicate, silica gel), and then above ground plant parts were analyzed via X-ray microanalysis (EDX) and atomic absorption spectroscopy (AAS) for silicon contents. Silicon was mainly deposited in the epidermis cells of the leaves and their cell walls. Poor growth of plants in water deficient conditions was significantly improved with Si application. In the same year, Ahmad et al., (2007) evaluated growth of wheat (CV. Inqlab-91) on different soil water regimes as affected by Si application. Silicon was added in soil @ 50 mg/kg and 150 mg/kg of soil. Plants were grown with three levels of soil water contents viz. 50%, 75% and 100% of field capacity. Water deficiency in soil significantly reduced shoot biomass and spike weight of wheat plants.

Conclusion

Significant number of studies has reported a strong and positive role of silicon to support a plant while responding to abiotic stresses. Modified physiological mechanism with improved water uptake and transport; alleviating the detrimental oxidative damage of functional molecules along with improved anti-oxidative defense abilities and better plant immunity to insects and pathogen are attributed to the silicon activity. However, a very precise role of silicon at tissue or cellular level for major food and fiber crops is still need to be discovered and practiced at a farm level for its commercial and economic worth.

References

Ahmad M, Akram Z, Munir M, Rauf M (2006) Physio-morphic response of wheat genotypes under rainfed conditions. Pak J Bot. 38(5):1697-1702

Ahmad, F, Rahmatullah T, Aziz MA, Maqsood A, Mukkram Tahir M, Kanwal S (2007) Effect of silicon application on wheat (*Triticum aestivum* L.) growth under water deficiency stress. Emir J Food Agric 19(2):01-07

Ahmed M, Hassen FU, Khurshid Y (2011a). Does silicon and irrigation have impact on drought tolerance mechanism of sorghum? Agric Water Mgt. 98: 1808– 1812

Ahmed M, Hassen FU, Qadeer U, Aslam MA (2011b) Silicon application and drought tolerance mechanism of sorghum. Afr J Agric Res. 6, 594–607

Ali HM, Siddiqui MH, Basalah MO, Al-Whaibi MH, Sakran AM, Al-Amri A (2012) Effects of gibberellic acid on growth and photosynthetic pigments of *Hibiscus* *sabdariffa* L. under salt stress. Afric J Biotech. 11 (4):800-804

Alkaraki GN, Clark RB, Sullivan CY (1996) Phosphorus nutrition and water stress effects on proline accumulation in sorghum and bean. J Plant Physiol 148: 745–751

Allakhverdiev SI, Sakamoto A, Nishiyama Y, Inaba M, Murata N (2000) Inactivation of photosystems I and II in response to osmotic stress in Synechococcus, contribution of water channels. Plant Physiol. 122: 1201–1208

Alvaro F, Isidro J, Villegas D, Garcia del Moral LF, Royo C (2008) Breeding eff ect on grain filling, biomass partitioning, and remobilization in Mediterranean durum wheat. Agron J 100:361-370

Araus JL, Slafer G, Royo C, Serret MD (2008) Breeding for yield potential and stress adaptation in cereals. Crit Rev Plant Sci 27, 377–412

Arduini I, Masoni A, Ercoli L, Mariotti M (2006) Grain yield, and dry matter and nitrogen accumulation and remobilization in durum wheat as affected by variety and seeding rate. Eur J Agron 25: 309-318

Arvin MJ, Donnelly DJ (2008) Screening potato cultivars and wild species to abiotic stresses using an electrolyte leakage bioassay. J Agric Sci Technol. 10:33-42

Ashraf M, Ahmad A, McNeilly T (2001) Growth and photosynthetic characteristics in pearl millet under water stress and different potassium supply. Photosynthetica 39: 389–394

Aynehband A, Valipoor M. and Fateh E (2011) Stem reserve accumulation and mobilization in wheat (*Triticum aestivum* L.) as affected by sowing date and N-P-K levels under Mediterranean conditions. Turk J Agric For 35:319-331

Belanger R, Benhamou N, Menzies J (2003) Cytological evidence of an active role of silicon in wheat resistance to powdery mildew (*Blumeria graminis* f. sp. *tritici*). Phytopathology 93(4):402-12

Blum A (2005) Drought resistance, water-use efficiency, and yield potential- are they compatible, dissonant, or mutually exclusive? Aust J Agri Res 56, 1159–1168

Blum A (2011) Plant Breeding for Water-Limited Environments, Drought Resistance and Its Improvement. Springer New York. ISBN - 978-1-4419-7491-4.pp 152. UR - http://dx.doi.org/10.1007/978-1-4419-7491-4_3.

Blum A, Zhang J, Nguyen HT (1999) Consistent differences among wheat cultivars in osmotic adjustment and their relationship to plant production. Field Crops Res 64:287–291

Bohnert HJ, Nelson DE, Jensen RG (1995) Adaptations to environmental stresses. Plant Cell 7: 1099–1111

Botella MA, Quesada MA, Kononowicz AK, Bressan RA, Pliego F, Hasegawa PM, Valpuesta V (1994) Characterization and in-situ localization of a salt-induced tomato peroxidase messenger-RNA. Plant Mol Biol. 25:105–114

Bray EA (1993) Molecular responses to water deficit. Plant Physiol. 103:1035-1040

Chang-juan S, Ju-xiang T, Wen-ping Y, Xin-liang Z, Xiu-juan R, Yi-zhuo L (2012) Comparison of photosynthetic characteristics of four wheat (*Triticum aestivum* L.) genotypes during jointing stage under drought stress. Afric J Agric Res. 7(8):1289-1295

Chen J, Russell DC, Cynthia AR, Robert S (2000) Silicon: The estranged medium element. University of Florida, USA. Bulletin 341, series of envi. Hort. Deptt.

Chinnusamy V, Schumaker K, Zhu JK (2004) Molecular genetic perspectives on cross-talk and specificity in abiotic stress signaling in plants. J Exp Bot 55: 225–236

Choudhury S, Panda S K (2005) Toxic effect, oxidative stress and ultrastructural changes in moss *Taxitheelium nepalense* (Schwaegr.) Broth. under lead and chromium toxicity. Water Air and Soil Pollution. 167**:**73-90.

Cookson LJ, Scown DK, McCarthy KJ, Chew N (2007) The effectiveness of silica against wood-boring vertebrates. Holzforschung. 61 (3):326-332

Cooke J, Leishman MR (2011) Is plant ecology more siliceous than we realise? Trends in plant Sci. 16(2):61-68

Eglinton G, Hamilton RJ (1967) Leaf epicuticular waxes. Science. 9:156(3780):1322-35

Eneji AE, Inanaga S, Muranaka S, Li J, Hattori T, An P, Tsuji W (2008) Growth and nutrient use in four grasses under drought stress as mediated by silicon fertilizers. J Plant Nutr. 31: 355–365

Epstein E (1994) The anomaly of silicon in plant biology. Proc Natl Acad Sci USA.91:11-17

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

Ercoli L, Lulli L, Mariotti M, Mosani A, Arduini I (2008) Postanthesis dry matter and nitrogen dynamics in durum wheat as aff ected by nitrogen supply and soil water availability. Eur J Agron 28: 138-147

Fan-rong Z, Fu-sheng Z, Bo-yin Q, You-nan O, Fei-bo1 WU, Guo-ping Z (2011) Alleviation of chromium toxicity by silicon addition in rice Plants. Agri Sci China. 10(8): 1188-1196

Fauteux F, Remus-Borel W, Menzies JG, Belanger RR (2005) Silicon and plant disease resistance against pathogenic fungi. FEMS Microbiology Letters 249:1–6

Fawe A, Abou-Zaid M, Menzies JG, Belanger RR (1998) Silicon-mediated accumulation of flavonoid phytoalexins in cucumber. Phytopathology. 88(5):396–401

Gao X, Zou C, Wang L, Zhang F (2004) Silicon improves water use efficiency in maize plants. J Plant Nutr 27(8): 1457-1470

Gao X, Zou C, Wang L, Zhang F (2006) Silicon decreases transpiration rate and conductance from stornata of maize plants. J Plant Nutr. 29:1637-1647

Ghoulam C, Foursy A, Fares K (2002) Effects of salt stress on growth, inorganic ions and proline accumulation in relation to osmotic adjustment in five sugar beet cultivars. Environ Exp Bot. 47:39–50

Gong HJ, Chen KM, Chen GC, Wang SM, Zhang CL (2005) Silicon alleviates oxidative damage of wheat plants in pots under drought. Plant Sci. 169: 313–321

Gonzalez A, Bermejo V, Gimeno BS (2010) Effect of different physiological traits on grain yield in barley grown under irrigated and terminal water deficit conditions. J Agric Sci. 148: 319–328

Gonzalez A, Martin I, Ayerbe L (2009) Yield and osmotic adjustment capacity of barley under terminal water-stress conditions. J Agron Crop Sci. 194: 81–91

Habash DZ, Kehel Z, Nachit M (2009) Genomic approaches for designing durum wheat ready for climate change with a focus on drought. J Exper Bot. 60(10): 2805–2815

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

Hattori T, Inanaga S, Araki H, An P, Morita S, Luxova M, Alexander L (2005). Application of silicon enhanced drought tolerance in *Sorghum bicolor.* Physiologia Plantarum.123 (4):459-466

Hattori T, Inanaga S, Araki H, An P, Morita S, Luxov M, Lux A (2005) Application of silicon enhanced drought tolerance in Sorghum bicolor. Physiologiya Plantarium. 123: 459–466

Hattori T, Sonobe K, Araki H, Inanaga S, An P, Morita S (2008) Silicon application improves water uptake by sorghum through the alleviation of stress-induced increase in hydraulic resistance. J Plant Nutr. 31:1482–1495

Hodson MJ, Evans DE (1995) Aluminium/silicon interactions in higher plants. J Exp Bot. 46: 161–171

Huang J, Hirji R, Adam L, Rozwadowski KL, Hammerlindl JK, Keller WA, Selvaraj G (2000) Genetic engineering of glycinebetaine production toward enhancing stress tolerance in 36 plants: metabolic limitations. Plant Physiol. 122:747–756

Humayun MS, DaCruz L, Dagnelie G, Mohand-Said S, Stanga P, Agrawal RN, Greenberg RJ Argus II Study Group (2010) Interim performance results from the second sight(R) ArgusTM II retinal prosthesis study. Invest Ophthalmol. Vis Sci. 51: 2022

Iyengar ERR, Reddy MP (1996) Photosynthesis in highly salt tolerant plants. In: Pesserkali, M. (Ed.), Handbook of photosynthesis. Marshal Dekar, Baten Rose, USA, pp. 897–909

Joanna M, Simone H, Werner GA, Gunter M, Rudiger F, Ernst B, Otto W (2007) Effect of silicon fertilizers on silicon accumulation in wheat. J Plant Nutr Soil Sci. 17: 769–772

Kavikishore PB, Sangam S, Amrutha RN, Srilakshmi P, Naidu KR, Rao KRSS, Sreenath R, Reddy KJ, Theriappan P, Sreenivasalu N (2005) Regulation of proline biosynthesis, degradation, uptake and transport in higher plants. Its implications in plant growth and abiotic stress tolerance. Current Sci. 88(3): 424-436

Kerepesi I, Galiba G. (2000) Osmotic and salt stress-induced alteration in soluble carbohydrate content in wheat seedlings. Crop Sci. 40: 482–487

Kirkham MB (1988) Hydraulic resistance of two Sorghum genotypes varying in drought resistance. Plant Soil. 105: 19–24

Lanning FC (1966) Relation of silicon in barley to disease cold and pest resistance. J Agric Food Chem. 14 (6), pp 636–638

Li S, Chen J, Zuo Q (2007) Influences of optimizing fertilization on the growth and yield of rice variety Wandao68. J Anhui Agric Sci. 35:8571–8573

Liang Y (2007) Mechanisms of silicon-mediated alleviation of abiotic stresses in higher plants: a review. Environ Pollut.147:422–8

Lux A, Luxova M, Hattori T, Inanaga S, Sugimoto Y (2002) Silicification in sorghum (*Sorghum bicolor*) cultivars with different drought tolerance. Physiol Plant. 115: 87–92

Ma JF, Yamaji N (2006) Silicon uptake and accumulation in higher plants. Trends Plant Sci. 11(8):392-397

Ma JA (2004) Role of silicon in enhancing the resistance of plants to biotic and biotic stresses. Soil Sci Plant Nutr.50: 11–18

Ma J, Nishimura K, Takahashi E (1989) Effect of silicon on the growth of rice plant at different growth stages. Soil Sci Plant Nutr. 35: 347-356

Ma JF, Tamai K, Yamaji N, Mitani N, Konishi S, Katsuhara M, Ishiguro M, Murata Y, Yano M (2006) A silicon transporter in rice. Nature. 440: 688–691

Marschner H (2002) Mineral nutrition of higher plants. San Diego, CA: Academic Press.

Masoni A, Ercoli L, Mariotti M, Arduini I (2007) Post-anthesis accumulation and remobilization of dry matter, nitrogen and phosphorus in durum wheat as affected by soil type. Eur J Agron. 26: 179-186

Mitra J (2001) Genetics and genetic improvement of drought resistance in crop plants. Current science. 80(6):758 – 763

Moinuddin, Khanna-Chopra R (2004) Osmotic adjustment in chickpea in relation to seed yield and yield parameters. Crop Sci. 44: 449–455

Monneveux P, Sanchez C, Beck D, Edmeades GO (2006) Drought tolerance improvement in tropical maize source populations: evidence of progress. Crop Sci. 46: 180–191

Nachit MM, Elouafi I (2004) Durum adaptation in the Mediterranean dryland: breeding, stress physiology, and molecular markers. In: Rao SC,Ryan J, eds. Challenges and strategies for dryland agriculture. CSSA Special Publication 32. Madison, Wisconsin, USA: Crop Science Society of America Inc., American Society of Agronomy Inc.203–218

Neves NR, Oliva MA, Centeno DC, Costa AC, Ribas RF, Pereira EG (2009) Photosynthesis and oxidative stress in the restinga plant species Eugenia uniflora L. exposed to simulated acid rain and iron ore dust deposition: potential use in environmental risk assessment. Sci Total Environ. 407 : 3740–3745

Parida AK, Das AB (2005) Salt tolerance and salinity effects on plants: a review. Ecotoxicology and Environmental Safety. 60(3): 324–349

Peleg Z, Reguera M, Tumimbang E, Walia H, Blumwald E (2011) Cytokinin-mediated source/sink modifications improve drought tolerance and increase grain yield in rice under water-stress. Plant Biotechol J. 9(7):747-58

Purcell LC, King CA (1996) Drought and nitrogen source effects on nitrogen nutrition, seed growth, and yield in soybean. J Plant Nutr 19: 969–993

Ranganathan S, Suvarchala V, Rajesh Y, Srinivasa Prasad M, Padmakumari A, Voleti S (2006) Effects of silicon sources on its deposition, chlorophyll content, and disease and pest resistance in rice. Biol Plant. 50:713–716

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

Shu LZ, Liu YH (2001) Effects of silicon on growth of maize seedlings under salt stress. Agro-Environ Prot. 20: 38–40

Singh DK, Sale PWG (2000) Growth and potential conductivity of white clover roots in dry soil with increasing phosphorus supply and defoliation frequency. Agron J. 92: 868–874

Song AL, Li ZJ, Zhang J, Xue GF, Fan FL, Liang YC (2009) Silicon-enhanced resistance to cadmium toxicity in *Brassica chinensis* L. is attributed to Si-suppressed cadmium uptake and transport and Si-enhanced antioxidant defense capacity. J Hazard Materials. 172: 74-83

Subbarao GV, Nam NH, Chauhan YS, Johansen C (2000) Osmotic adjustment,water relations and carbohydrate remobilization in pigeonpea under water deficits. J Plant Physiol. 157: 651–659

Tahir ISA, Nakata N (2005) Remobilization of nitrogen and carbohydrate from stems of bread wheat in response to heat stress during grain filling. J Agron Crop Sci. 191: 106-115

Tangpremsri T, Fukai S, Fischer KS (1995) Growth and yield of Sorghum lines extracted from a population for differences in osmotic adjustments. Aust J Agric Res. 46: 61–74

Tuna AL, Kaya C, Higgs D, Murillo-Amador B, Aydemir S, Gergon AR (2008) Silicon improves salinity tolerance in wheat plants. Environ Exp Bot. 62: 10-16

UNESCO (United Nations Educational, Scientific and Cultural Organization) (2000) Water Use in the World: Present Situation / Future Needs [online] Available from http://www.unesco.org>

Vadez V, Kashiwagi J, Krishnamurthy L, Serraj R, Sharma KK, Devi J, Bhatnagar-Mathur P, Hoisington D, Chandra S, Gaur PM, Nigam SN, Rupakula A, Upadhyaya HD, Hash CT and Rizvi SMH (2005) Recent advances in drought research at ICRISAT: Using root traits and rd29a::DREB1A to increase water use and water use efficiency in drought-prone areas. Poster presented at the Inter drought II conference, Rome 24-28 September

Valliyodan B, Nguyen HT (2006) Understanding regulatory networks and engineering for enhanced drought tolerance in plants. Plant Biol. 9:1–7

Wang Y, Nil N (2000) Changes in chlorophyll, ribulose biphosphate carboxylase–oxygenase, glycine betaine content, photosynthesis and transpiration in Amaranthus tricolor leaves during salt stress. J Hortic Sci Biotechnol. 75: 623–627

Yang F, Hu J, Li J, Wu X, Qian Y (2009) Chitosan enhances leaf membrane stability and antioxidant enzyme activities in apple seedlings under drought stress. Plant Growth Regul. 58: 131–136

Yousifi N, Slama I, Ghnaya T, Savoure A, Abdelly C (2010) Effects of water deficit stress on growth, water relations and osmolyte accumulation in *Medicago truncatula* and *M. laciniata* populations. Comptes Rendus Biologies. 333: 205–213

Zhifang G, Loescher WH (2003) Expression of a celery mannose 6- phosphate reductase in Arabidopsis thaliana enhances salt tolerance and induces biosynthesis of both mannitol and a glucosyl-mannitol dimmer. Plant Cell Environ. 26: 275–283

Zivack M, Repkava J, Olsavska K, Brestic M (2009) Osmotic adjustment in winter wheat varieties and its importance as a mechanism of drought tolerance. Cereal Res Commun. 37:569–572