

## SILICON-MEDIATED IMPROVEMENT IN TOLERANCE OF ECONOMICALLY IMPORTANT CROPS UNDER DROUGHT STRESS

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**Abstract.** Drought is considered as one of the significant threats to food security worldwide as it inhibits the growth, yield and quality of economically important crops. An increase in crop yield is considered a tremendous achievement as it will be helpful to meet the current growing demand for food in drought-stressed areas. Silicon (Si) is the second most abundant component in the soil. Recent research has revealed that Si can enhance plant tolerance against drought stress. In addition, application of Si can increase seed germination, underground and aboveground biomass, photosynthetic pigments, quality and yield of grains. Therefore, we have summarized the importance of Si in improving the drought tolerance in plants. Furthermore, we have explained the Si-mediated mechanisms which led to modifications in gas exchange properties, homeostasis of the nutrient element, synthesis of compatible solute, osmotic adjustments, antioxidant stimulation and enzymatic action in plants under drought stress. We believe that the current study will help in understanding the importance of Si application in plants under drought stress conditions.

**Keywords:** *seed germination, antioxidants enzymes, drought tolerance, gene expression, soil*

## Introduction

The increasing demand for food day by day is one of the significant challenges for agricultural scientists worldwide (Warner and Jones, 2017). On the other hand, the world's crop productivity is continually decreasing due to extreme climate changes and shrinking resources. In view of that, finding the new options to improve the crop productivity is a challenging task for all nations across the world (George et al., 2018; Lesk et al., 2016; Rizwan et al., 2018). Abiotic stresses (salt, drought, and extreme temperature stress) are the challenging problems for plant development and its productivity in many parts of the world (Khalil et al., 2016, 2018; Suzuki et al., 2014). Among these abiotic stresses, drought is one of the most harmful environmental factors which inhibit growth, yield and quality of economically important crops (Ali et al., 2016; Calvo-Polanco et al., 2016). Therefore, it is estimated to be one of the severe threats for future agricultural crop production (Khalil et al., 2018; Tayyab et al., 2018a). The negative impacts of drought stress on many plants have become the central debate in recent years (Tayyab et al., 2018a). Drought along with other abiotic stresses including heavy metal contamination not only restricts plant production but also poses severe threats to human health (Arshad et al., 2016; Noman and Aqeel, 2017). For example, Liu et al. (2017) revealed that under different growth stages, the translocation and redistribution of cadmium have a different influence for drought in peanut plants. It can affect the processes such as cell dehydration, the inhibition of cell expansion and division, stem elongation, leaf size, root proliferation, disturbed stomatal oscillations, water and nutrient absorption in plants (Kaushal and Wani, 2016; Khalil et al., 2018; Tayyab et al., 2018a). Furthermore, it also reduces photosynthesis (Khan et al., 2017; Zang et al., 2014), soil water potential, water use efficiency (WUE) (Kaushal and Wani, 2016), and induce oxygen deficiency by the production of reactive oxygen species (ROS) (Fukao et al., 2011). Consequently, combating the stress caused by drought is a serious matter to achieve food security in changing climate conditions around the world.

Si is found to be the second most abundant element in soil (Sommer et al., 2006). However, it comprises up to 10% dry weight of many plants. In the past, researchers could not find Si as an essential element for normal development and growth of the plant (Epstein, 1994; Hodson et al., 2005). However, concerning the Si efficiency on the plant's life cycle, Epstein and Bloom (2005) recommended that the proper need of Si element is significant for normal plant growth. Recently, numerous researches have demonstrated that Si mitigates the destructive effects of biotic stresses (pests and diseases) (Dann and Le, 2017; Yang et al., 2017) and abiotic stresses (drought, heavy metal toxicity and salinity) in plants (Biju et al., 2017; Hasanuzzaman et al., 2018; Tayyab et al., 2018b). These benefits are attributed to Si application; thus, Si can play a serious role in order to mitigate drought stress in plants. Moreover, sustainable agriculture has got great importance so it can be used as a high-quality fertilizer because of its non-corrosive and non-polluted nature. Si effect for plant growth and development in unfavorable climatic conditions has been reviewed by many researchers recently around the globe (Guntzer et al., 2012; Tayyab et al., 2018b; Van Bockhaven et al., 2012). Van Bockhaven et al. (2012) reviewed the role of Si for plant disease resistance. However, the mechanisms of Si-mediated mitigation of drought stress in plants are still debatable and need to be reviewed. Si application as a fertilizer for plants also has gained momentum recently. In order to enhance drought tolerance, Si application in term of soil amendment is expected to become a new approach in agricultural farming in the future. Therefore, we have reviewed the current status and progress in understanding the mechanisms of Si-mediated

drought tolerance in plants. The review unveils the various mechanisms involved in the plant's protection during drought stress as well as suggests guidelines for further research.

### History of silicon application

Si is widely distributed as silica or alumino-silicates – better known as rocks and sand. Si is not readily available for plants to use; instead plants can only absorb Si as a monosilicic acid (Marafon and Endres, 2013). Si is beneficial for plants, such as protecting against diseases, insects attacks, reinforcing nutrients and safeguarding under unfavorable conditions like drought, salt or heavy metals toxicity (Debona et al., 2017; Tayyab et al., 2018b). Kutschera and Niklas (2018) highlighted the function of Si in plant biology as “whether silicic acid is an indispensable substance for those plants that contain silica, whether it takes part in the nutritional processes, and what is the relationship that exists between the uptake of silicic acid and the life of the plant?” (Lewin and Reimann, 1969). In the 20<sup>th</sup> century, several trials were directed on Si to demonstrate its beneficial role in agriculture owing to its safe behavior and presence in nature. For the first time in the world, rice (*Oryza sativa*) soils in Japan were treated with Si in 1955 (Takahashi et al., 1990). Si fertilizers commonly contain neutral or slightly alkaline pH which has the neutralizing effect for acidic soils (Savant et al., 1999). Several kinds of Si fertilizers are applied in the field usually in the form of solids as well as liquids such as calcium silicates, calcium and magnesium silicates wollastonite, potassium silicate and sodium silicate.

### Silicon in soils

Si contributes to the second major element existing in soil (Sommer et al., 2006). Si reacts with oxygen and turns into silicates, i.e., feldspars and quartz (*Fig. 1*). Silicate formed by oxygen and pure Si is known as silica (i.e., quartz) whereas other silicates (i.e., feldspars) have some elements (sodium, potassium, aluminum, and calcium) including oxygen and Si. Soils are formed as the results of weathering of rocks made from alumino-silicates and silicates minerals. By biological and physical weathering silicate minerals release Si into soil solution that formulates silicic acid ( $H_4SiO_4$ ). Then, plant roots absorb silicic acid from soil solution (Epstein, 2009). The plant contains a significant amount of Si owing to its ubiquitous nature and abundance (Epstein, 1999). Si abundance and concentration fluctuates with the soil type. Typically, upper horizons frequently have low Si concentrations in the sandy soils (Marschner, 2011), whereas clay soils have higher phyllo-silicates quantities that release Si. The quartz ( $SiO_2$ ) mineral is abundantly present in sandy soils which are less prone to decomposition. The complexity of quartz mineral makes sandy soil more responsive to Si application than clayey soil (Dematté et al., 2011). In tropical and subtropical soils, Si commonly is found very low due to desilication because of leaching and some weathering processes (Epstein, 1999). Additionally, it is predicted that 210 to 224 million tons of Si have been removed by intensive arable cultivation throughout the world (Meena et al., 2014).

### Silicon uptake and accumulation in plants

Plants differ in their ability to uptaking the Si. Some plants can accumulate more Si in their leaves and those with more than 1.5% of their total dry biomass are known as

accumulators. Plants containing Si levels less than 0.5% in their leaves are considered as non-accumulators (Marafon and Endres, 2013). Variation of Si concentration in plants is attributed to their Si uptake capability and roots xylem loading (Ma et al., 2001a). The plasma membrane present in plant root cells might provide a path for uncharged monomeric  $H_4SiO_4$  uptake by diffusion. Thus,  $H_4SiO_4$  permeability coefficient of  $10^{-10}ms^{-1}$  throughout a plasma membrane (Raven, 2001), does not clarify experimentally measured Si contents in plants (Tamai and Ma, 2003). Passive and active transporters are involved in the Si uptake and transport from growth medium to xylem tissues (Mitani et al., 2005). This hypothesis was confirmed due to Si uptake inhibition as plants were exposed to metabolic inhibitors (i.e., 2,4- dinitrophenol, potassium cyanide) or low temperature (Mitani et al., 2005; Tamai and Ma, 2003). A low-affinity silicic acid transporter involves Si transportation from root medium to cortical cells. Kinetic studies for Si uptake in rice (*O. sativa*), tomato (*Solanum lycopersicum*) and cucumber (*Cucumis sativus*) confirmed that the density of transporters present in the plasma membrane is responsible for Si uptake changes (Mitani et al., 2005). Recently, *Lsi1*, *Lsi2*, and *Lsi6* genes are associated with Si uptake and distribution in rice (*O. sativa*), barley (*Hordeum vulgare*), maize (*Z. mays*), and cucumber (*C. sativus*) (Ma and Yamaji, 2015). Si-influx transporters (*Lsi1* and *Lsi6*) are associated with Si distribution in the tissues of root and shoot (Mitani et al., 2011). Whereas, putative anion transporter (*Lsi2*) is commonly expressed in roots endodermis (Ma et al., 2007). Ma et al. (2007) reported that *Lsi2* transporter activity is proton-driven and acts as a  $Si/H^+$  antiport.

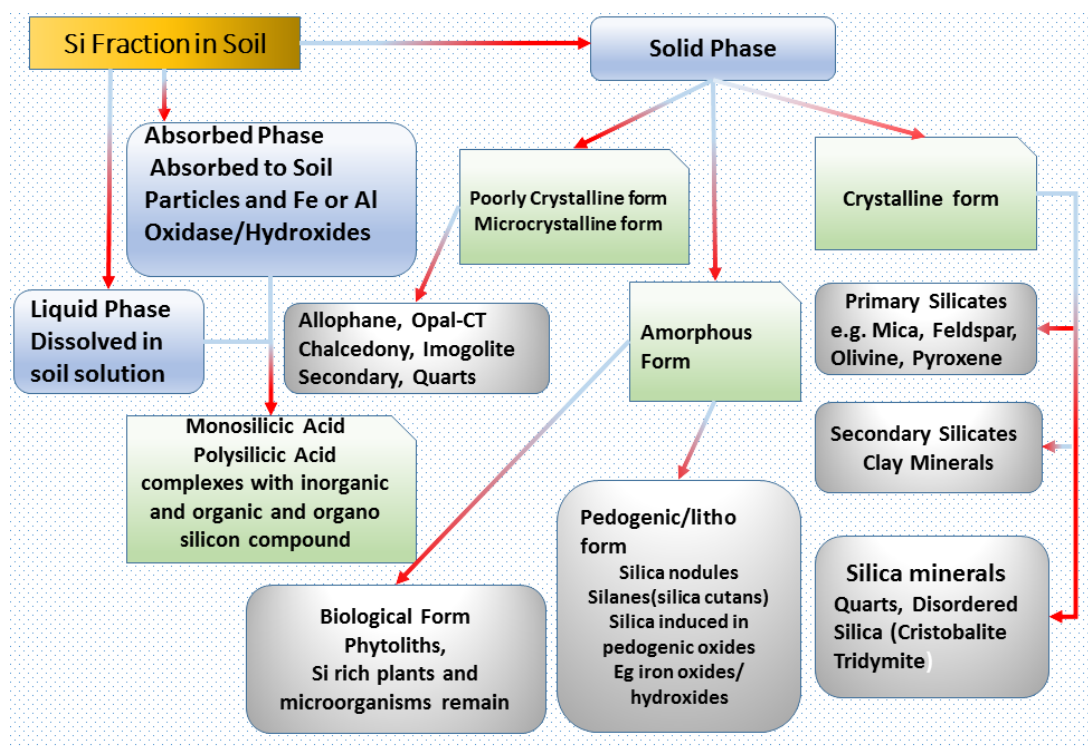
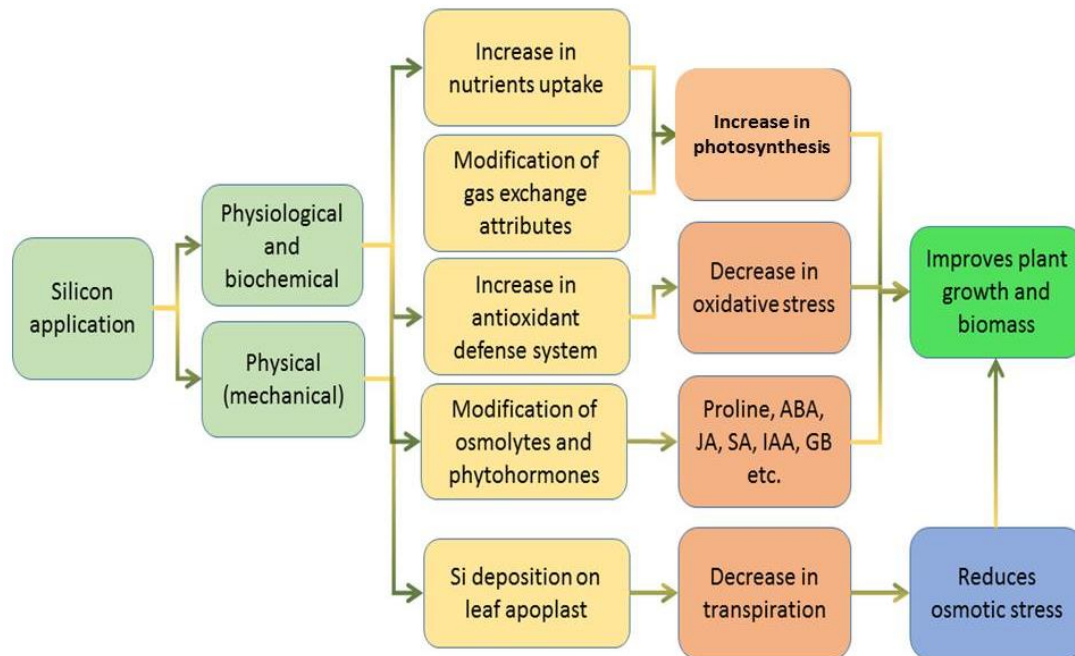


Figure 1. Various sources of silicon in the soil. (Modified from Zia, 2018)

## Silicon and drought stress

Drought commonly reduces plant growth and its yield in semiarid and arid regions throughout the world (Zandalinas et al., 2018). It adversely affects plant biomass and

growth of all crops cultivated in main fields as well (Kaushal and Wani, 2016). In contrast, various researchers have demonstrated that Si should consider being a practical approach to overcome these opposing effects stimulated by drought (Guo et al., 2017; Shi et al., 2014). The mechanisms in order to enhance drought tolerance in the plant by Si application at the morphological, physiological and biochemical levels are summarized below (see also Fig. 2).



**Figure 2.** The mechanism for the Si-mediated alleviation of drought stress tolerance in plants. (Modified from Rizwan et al., 2015; Tayyab et al., 2018b)

### ***Si-mediated improvement in seed germination under drought condition***

Drought stress negatively affects the seed germination leading to considerable reduction in crop yield (Guo et al., 2017; Shi et al., 2014). Until now, a little research was conducted to study the Si effects for seed germination under drought conditions (Ahmed et al., 2016; Hasanuzzaman et al., 2018). On the contrary, Si not only mitigates the adverse effect induced by drought stress on seed germination but also promotes seed development. For instance, seed priming with sodium silicate contributed to recovering wheat (*Triticum aestivum*) seed germination compared to untreated seeds (Hameed et al., 2013). The authors described that soaking of seeds for 8 h in aerated solutions of 20 mM, 40 mM and 60 mM sodium silicate resulted in 97% improvement in seed germination under water-deficit stress induced by 15% polyethylene glycol (PEG)-6000 (Hameed et al., 2013). Similarly, Ahmed et al. (2016) reported seeds priming with Si (silicic acid, sodium silicate, and silica gel) at different concentration (0.5%, 1.0%, and 1.5%) to explore its potential benefits for couple of wheat (*T. aestivum*) varieties. The authors have shown that silica gel can be used as an active priming practice at 1.5% concentration for better development of a plant under drought conditions. Likewise, calcium silicate employed in the soil in the same conditions enhanced seed germination of maize (*Z. mays*; 15 different cultivars) up to 80.96% under water stress (under rain-fed conditions) (Zargar and Agnihotri, 2013). Shi et al. (2014) reported that the Si

application improved the seed germination in four tomatoes (*S. lycopersicum*) cultivars under drought as compared to control (without Si). The authors investigated the effects of exogenous Si (0.5 mM) to tomato (*S. lycopersicum*) bud seedlings under water deficit stress simulated by 10% (w/v) PEG-6000 in four different cultivars ('Jinpengchaoguan', 'Zhongza No.9', 'Houpi L402' and 'Oubao318'), which significantly improved the seed germination by 21.9% - 38.2% (Shi et al., 2014). Similarly, in a recent study, Hasanuzzaman et al. (2018) revealed that application of Si is also an active practice for the alleviation of the destructive effects of drought on seed germination in *Brassica napus*. Furthermore, Si application improved the vigor of seedlings. These reports demonstrate that Si can be effective to mitigate the destructive effects of drought on seed germination of crop plants. However, the general mechanisms must be explored for well understanding of Si functions in seedlings under drought conditions.

### ***Silicon-mediated improvement in plant growth, biomass, and photosynthesis under drought stress***

Plant biomass and growth is severely reduced by drought (Amin et al., 2016; Noman et al., 2015), hence the application of Si under drought stress can be considered a practical approach to improve plant biomass and growth. Si should be used in conditions effective for its activity and approach to improve plant growth and biomass under drought stress (Hajiboland et al., 2017; Merwad et al., 2018). Si employed in wheat (*T. aestivum*) grown soil resulted in increased root biomass, shoots, spike weight and dry weight (Ahmad et al., 2007; Gong et al., 2003; Xu et al., 2017). Ratnakumar et al. (2016) reported that foliar application of Si (0, 8, 16, 32 ppm at different plant growth stages such as vegetative, booting and seed development stage) on wheat (*T. aestivum*) in the form of ortho-silicic acid improved the root length, density and growth. In another study shoot and root lengths were improved via seed priming by sodium silicate under PEG-6000-induced drought (Hameed et al., 2013). Similarly, Si supply improved roots and shoot fresh weight of Kentucky bluegrass (*Poa pratensis*) under water stress. The daily amount of water or Si solution was 250 mL per pot. For 14 d, plants were treated with 0, 0.1, and 1.0 mM Si solution for Si treatments and with distilled water for the control (Bae et al., 2017). Application of Si (seed priming) provided the better results of grain yield of wheat (*T. aestivum*) grown under drought in hydroponics in pots and field experiments (Ahmed et al., 2016; Gharineh and Karmollachaab, 2013; Pei et al., 2010). Seed priming combined with other sources of Si improved the grain yield and spike length of the wheat (*T. aestivum*) crop as compared to control without seed priming under drought (Ahmed et al., 2016). The authors used seeds of two wheat varieties, i.e., NARC-2009 and Chakwal-50 which were sown in pots after priming with distilled water and different concentration (0.5%, 1.0%, 1.5%) of Si sources (silicic acid, sodium silicate and silica gel). Maximum Si uptake at three leaves (0.028  $\mu\text{g g}^{-1}$  dry weight (DW), anthesis (0.072  $\mu\text{g g}^{-1}$  DW) and maturity (0.103  $\mu\text{g g}^{-1}$  DW) were recorded for silica gel (15%) (Ahmed et al., 2016). Similarly, the use of Si (potassium silicate) employed on sorghum (*Sorghum bicolor*) resulted in improved roots dry weight by 30% under drought (Ahmed et al., 2011). In a recent study, Si used as fertilizer in sugarcane field enhanced sugarcane (*Saccharum officinarum*) stalk yield, dry biomass and provided the best product under drought (de Camargo et al., 2017). Si applied in soil or through foliar application in the field (five sprays of 1.425 mM Si water solution), resulted in improved potato (*Solanum tuberosum*) yield and dry tuber weight just similar to well-irrigated potato (S.

*tuberosum*) plants (Pilon et al., 2014). Similarly, the application of Si improved the total root length, root surface area, volume and dry weight of rice (*O. sativa*) plants under drought (Ming et al., 2012). However, Nolla et al. (2012) and Moro et al. (2015) demonstrated rice (*O. sativa*) grain yield and plant height improvement by adopting the silicate in soil under drought conditions. Soybean (*Glycine max*) plant shoot length and dry and fresh weight were improved by use of Si under drought (Hamayun et al., 2010). The authors further explained that the adverse effects of PEG-induced drought were alleviated by adding and 200 mg L<sup>-1</sup> Si to the drought-stressed treatments (Hamayun et al., 2010). Diatomite application in soil provided effective results by improving growth parameter (shoots and roots length) and yield parameters (number of pods, fresh and dry weight of pod) in white lupine (*Lupinus albus L.*) under drought (Abdalla, 2011). Si increased leaf area index in numerous plant species, e.g., wheat (*T. aestivum*) and Fennel (*Foeniculum vulgare Mill*) under drought (Asgharipour and Mosapour, 2016; Gong et al., 2003). The application Si (300 kg of ha<sup>-1</sup>) increased the quantity of spikelet panicle and grain yield of rice; furthermore, dry matter recovery and yield had a positive linear relationship with shoot Si under drought (Ullah et al., 2017). The application of Si on two maize (*Z. mays*) varieties (hybrid P-33H25 and FH-810) increased the height of plant, stem diameter, number of leaves, cob length, the number of grain/cob, grain yield, and biological yield, which ultimately contributed to better growth and yield (Amin et al., 2016). The application of Si for tobacco (*Nicotiana Rustica L.*) has increased the biomass particularly aboveground parts in drought and control conditions (Hajiboland et al., 2017). Correspondingly, Si application on cowpea increased the yield per plant (Merwad et al., 2018).

Additionally, Si has also progressive influences on straw and grain quality of plants in drought conditions, but unfortunately, the studies are minimal. For example, Si (0.03 mM sodium selenite/1.5 mM potassium silicate) application has a direct relation to levels of phenolic compounds, amylose and flavonoid contents of rice grains. It also increased the lignin, cellulose, pectin, carbohydrates, proteins and fat contents of rice straw under drought conditions in a field experiment (Emam et al., 2014). So, it is necessary to clarify further mechanisms to improve the quality of cereals mediated by Si application under drought, especially at the molecular level. Drought stress is the primary driver which significantly reduces the photosynthesis in plants. On the other hand, various studies have exposed that by absorbing Si, photosynthetic pigments can be increased in various plant species (Hasanuzzaman et al., 2018; Merwad et al., 2018). The application of Si on wheat (*T. aestivum*) plants showed better result by improving the leaves chlorophyll content (Ma et al., 2016), and photosynthesis rate (Sattar et al., 2017). Likewise, Maghsoudi et al. (2016) demonstrated that Si leaf application increased photosynthesis pigments (chlorophyll a, b and total land carotenoids) and chlorophyll stability index (CSI) in different wheat (*T. aestivum*) cultivars under drought conditions. Similarly, Si foliar application on wheat increased leaf chlorophyll content (Ratnakumar et al., 2016). Si usage protected rapeseed (*B. napus*) leaves photosynthetic pigments (Hasanuzzaman et al., 2018), and increased total chlorophyll content of soybean (*G. max*) leaves under drought (Shen et al., 2010). Si was also observed to improve the allocation of light absorbed between PSII and PSI in the chloroplasts of tomato (*S. lycopersicum*) leaves and maintain the chloroplast membrane structure under drought (Cao et al., 2015). Moreover, Si (K<sub>2</sub>SiO<sub>3</sub> at the rate of 2.25 mM) increased photosynthesis and chlorophyll content of two cucumber cultivars (*C. sativus*) under drought (Ouzounidou et al., 2016).

In a recent study, Merwad et al. (2018) revealed that Si foliar application on cowpea (*Vigna unguiculata*) leaves improved chlorophyll (a, b, and total carotenoids) contents. Moreover, chlorophyll content and chlorophyll ratio (a:b) in chestnut leaves was improved under drought condition, when Si (Sili-K® solution containing 0.12% Si and 0.15% K) was repeatedly ( $\times 3$ ) sprayed onto leaves of potted chestnut plantlets and irrigation was suspended for 7 weeks (Zhang et al., 2013). Application of Si on two different rice cultivars (Curinga and IAC-202) enhanced the photosynthetic rate which was reduced by the lack of water (Moro et al., 2015). Soil or foliar applied Si enhanced chlorophyll (a and carotenoids) concentration and chlorophyll (a/b ratio) similar to well-irrigated potato (*S. tuberosum*) plants (Pilon et al., 2014). Si foliar application significantly increased the net photosynthesis rate, green leaf color of Blue Kentucky grass (*P. pratensis*) leaves (Saud et al., 2014), whereas enhanced photochemical efficiency and photosynthetic rate of Cacao (*Theobroma cacao*) leave under drought conditions (Zanetti et al., 2016).

### ***Impacts of Si application under drought stress***

Si use exhibited positive influences on seed germination, photosynthesis, plant growth and biomass under drought circumstances in the previous segment. These affirmative effects can be owing to various mechanisms such as enhancement of nutrient uptake by plants, by adjusting osmotic potential, by modifying the gaseous exchange attributes, decrease the oxidative stress and by an alteration in expressing of the gene in plants. Details of these mechanisms are given in (Fig. 2).

#### *Oxidative stress*

Dry conditions damage the photosynthetic pigments and disturb the balance between ROS production and antioxidants thus affect overall crop production (Kim et al., 2017). Through up-regulation of antioxidant activities of catalase (CAT), superoxide dismutase (SOD), and growth regulators (GR), Si treatment of wheat plants resulted in higher drought tolerance (Gong et al., 2005). Si supplements in wheat plants of wheat (*T. aestivum*) shown lesser contents of glutathione, lipid peroxidation and total flavonoid while raised content of ascorbate with Si application (Ma and Takahashi, 2002). Similarly, in tomato plants, Si supplementation upon polyethylene glycol (PEG) induced drought stress resulted in tolerance through increased activities of CAT and SOD along with the enhanced roots ability of water uptake (Shi et al., 2014). Moreover, Si reduced the activities of ascorbate peroxide (APX), under drought conditions in sunflower (*Helianthus annuus*) (Gunes et al., 2008b).

Drought stress produces ROS in plants triggering oxidative stress damage (Fukao et al., 2011; Noman et al., 2015). Various research communities revealed that Si supply increases the antioxidant enzymes activities while decreased oxidative damage stress in plants which can be adequate to the progression of plant drought tolerance (Bae et al., 2017; Hajiboland et al., 2017; Ma et al., 2016). Si application reduced the lipid peroxidation and hydrogen peroxide ( $H_2O_2$ ) of sunflower (*H. annuus*), chickpea (*Cicer arietinum*) (Gunes et al., 2007, 2008b), and lentil (*Lens culinaris*) plants leave under drought conditions (Biju et al., 2017). Similarly,  $H_2O_2$  and lipid peroxidation were reduced in rapeseed (*B. napus*) leaves (Hasanuzzaman et al., 2018), decreased  $H_2O_2$  contents in tobacco (*Nicotiana tabacum*) (Hajiboland et al., 2017), and wheat (*T. aestivum*) leaves (Gong et al., 2008; Ma et al., 2016). Xu et al. (2017) described that



usage of Si (potassium silicate 1.0 mM) significantly decreased H<sub>2</sub>O<sub>2</sub>, malondialdehyde (MDA) contents, and increased superoxide dismutase (SOD) activities in leaves of wheat during drought by Si supplementation (Gharineh and Karmollachaab, 2013). In addition, Pei et al. (2010) stated that the Si (1 mM)-supplying reduced H<sub>2</sub>O<sub>2</sub>, MDA in wheat (*T. aestivum*) leaves and Chinese liquorice (*Glycyrrhiza uralensis*), under drought conditions induced by 100 mM NaCl with 0, 10 and 20% of PEG-6000 (Zhang et al., 2017). Si supplementation in soil decreased the Lipid peroxidation (LP) in white lupin (*L. albus*) (Abdalla, 2011). Shi et al. (2014) demonstrated that Si addition improved superoxide dismutase (SOD), catalase activities (CAT), and H<sub>2</sub>O<sub>2</sub> in bud radicles than non-Si treated tomato (*S. lycopersicum*) seedlings. Similarly, Si supply enhanced antioxidant activity, including SOD, CAT and decreased H<sub>2</sub>O<sub>2</sub> & MDA contents in tomato (*S. lycopersicum*) (Cao et al., 2017). Additionally, Si application considerably enhanced peroxidase (POD) and SOD in the Canola (*B. napus*) plants activities (Habibi, 2014). Furthermore, the application of Si improved ascorbate peroxidase activity (APX) and glutathione (GSH) contents in Chinese liquorice (*Glycyrrhiza uralensis*) under drought than non-Si treatments (Zhang et al., 2017). The antioxidant enzyme's activity (e.g., SOD and CAT) was increased by Si application in wheat (*T. aestivum*) (Sattar et al., 2017), Cowpea (*V. unguiculata*) (Merwad et al., 2018) and in potato's plants (*S. tuberosum*) by foliar application of Si under drought (Pilon et al., 2014).

Moro et al. (2015) revealed that the use of Si was effective to increase rice SOD, CAT and APX activities and similarly, CAT, POD, SOD and H<sub>2</sub>O<sub>2</sub> were enhanced in soybean (*G. max*) (Shen et al., 2010) and Kentucky bluegrass (*P. pratensis*) during drought stress (Bae et al., 2017). Hasanuzzaman et al. (2018) noted that CAT, APX enhanced in rapeseed (*B. napus*) and similarly SOD activity of mango (*Mangifera indica*) leaves (Helaly et al., 2017). Moreover, SOD, CAT, APX, and POD were enhanced in the wheat (*T. aestivum*) (Tale and Haddad, 2011), chickpea (*C. arietinum*) shoot (Gunes et al., 2007) and tomato (*S. lycopersicum*) as compared to non-Si supplemented plants (Shi et al., 2014). Actions of SOD and POD decreased by the Si use and increased CAT activity of cucumber (*C. sativus*) plants than to Si-deficient plants (Ma et al., 2004). Impact of Si on the antioxidant enzyme of plants not only fluctuates with the changes of plant species but also depends on the plant stages of growth during drought (Gong et al., 2008). However, reports are limited on Si's functions on the antioxidant enzyme actions at various growth periods of the plant. For instance, the activities of APX, SOD and the CAT were not improved at the booting stage however improved the SOD while decreased APX activity at the filling stage of wheat (*T. aestivum*) during drought (Gong et al., 2008). Improvement of non-enzymatic antioxidants contents can provide best results to decrease the plant oxidative stress. Various reports revealed that levels of the nonenzymatic antioxidants of different species of plant could be affected by the Si application (Gong et al., 2005; Pei et al., 2010). For example, the Glutathione reductase (GSH) activity (Gong et al., 2005) and ascorbic acid (AA) concentration were improved through the use of the Si during drought conditions in wheat (*T. aestivum*) (Pei et al., 2010). In deduction, Si application reduced the oxidative stress and increased antioxidant enzymes activities.

### *Plant nutrients uptake*

The plants need sufficient quantity of the essential nutrients for proper development and growth, but nutrients uptake in plants is disturbed under drought conditions (Emam et al., 2014; Merwad et al., 2018; Ratnakumar et al., 2016). However, Si has positive

effects on nutrients uptake in plants under drought. For instance, by the application of Si, Potassium (K) and the total Phosphorus (P) level were enhanced straw of wheat (*T. aestivum*) seed (Ratnakumar et al., 2016), and rice (*O. sativa*) straw (Emam et al., 2014) and leaf P in wheat (*T. aestivum*) (Gong and Chen, 2012). Additionally, it was also effective to improve N, P and K of seed and shoot of cowpea (*V. unguiculata*) plants (Merwad et al., 2018). In addition, Calcium (Ca) and K content increase in wheat (*T. aestivum*) leaf and roots was observed (Kaya et al., 2006). Correspondingly, Kentucky Bluegrass (*P. pratensis*) (root, shoot and leaf) C: N ratio improved by the supply of Si under drought (Saud et al., 2014). Gunes et al. (2008a) noted that Si supply in soil enhanced the macronutrients (Ca, K, P, Mg) and the micronutrients (Cu, Fe, and Mn) uptake of sunflower (*H. annuus*) cultivar under drought. Exogenous Si supply was effective for wheat (*T. aestivum*) plant growth by modifying the nutrient uptake (Si, Na and Mg) (Xu et al., 2017), and improve (N, P, and K) uptake in different species of grass (Eneji et al., 2008). Contrarily, reports show that the nutrients uptake reduced in a plant with the supply of Si (Chen et al., 2011). For instance, in rice (*O. sativa*) plants Ca, K, Mg, and Fe contents were increased by drought, on the other hand, Si supply reduces these nutrients in plants (Chen et al., 2011).

### *Regulating osmotic potential*

Optimal water level plays a significant role in plants existence under drought. Generally, plants maintain a high water level through osmotic adjustment under dry stress circumstances (Blum, 2017). Although, high drought circumstances trigger a considerable reduction in water content of leaf including water potential in various plants (Abid et al., 2018; Paz-Kagan et al., 2017; Sattar et al., 2017). Various literature highlighted that Si supply extensively enhanced the water potential of plant's leaf and water content under a dry spell (Hasanuzzaman et al., 2018; Ming et al., 2012; Ratnakumar et al., 2016). For instance, supply of Si enhanced water contents in wheat (*T. aestivum*) (Ratnakumar et al., 2016; Sattar et al., 2017; Tale and Haddad, 2011), rapeseed (*B. napus*) (Hasanuzzaman et al., 2018), rice (*O. sativa*) (Ming et al., 2012), chickpea (*C. arietinum*) (Fawaz and Mohammad, 2013), sunflower (*H. annuus*) (Gunes et al., 2008b), cucumber (*C. sativus*) (Ma et al., 2004), and sorghum (*S. bicolor*) (Sonobe et al., 2010) under drought.

Application of Si enhanced the osmotic, relative water contents, turgor and water potential of wheat (*T. aestivum*) flag leaf (Sattar et al., 2017). Such as the water content of wheat (*T. aestivum*) was increased during drought (Ratnakumar et al., 2016). Si use improved the leaf relative water content in cowpea (*V. unguiculata*) (Merwad et al., 2018), rapeseed (*Brassica napus L.*) (Hasanuzzaman et al., 2018), Kentucky bluegrass (*P. pratensis*) (Saud et al., 2014) and maize (*Z. mays*) plants (Amin et al., 2014). On the other hand, under drought Si reduced the osmotic potential of roots in sorghum (*S. bicolor*) without interrupting water contents (Sonobe et al., 2010). Osmotic adjustment is consequence owing to soluble amino acids (alanine and glutamic acid) and sugars. Yin et al. (2014) revealed that Si reduced the proline content and osmotic potential of sorghum (*S. bicolor*) leaf whereas enhanced soluble sugar. Authors proposed that the osmotic adjustment does not contribute to Si mediated rise in drought tolerance in the sorghum (*S. bicolor*). The water content of leaf and the water potential improved by the supply of Si are accredited to a thickness of wheat (*T. aestivum*) leaves (Gong et al., 2003). Furthermore, leaf water potential enhancement might be triggered by Si

deposition in the leaves. Additionally, deposition of Si on leaf surface might reduce transpiration through controlling molecules of water (Keller et al., 2015).

#### *Regulation of osmolytes and phytohormones*

Osmolytes and phytohormones roles have been already well described for tolerance of plants at different stresses (Kurepin et al., 2017; Zhang et al., 2017). Various studies demonstrated about Si application improving plant tolerance against drought through modifications of osmolytes in different species of plants (Hamayun et al., 2010; Hasanuzzaman et al., 2018; Xu et al., 2017). Si was effective to enhance proline, a non-protein amino acid, but total sugar and soluble protein were decreased in potato (*S. tuberosum*) leaves (Crusciol et al., 2009). On a similar note, use of Si improved proline contents in the wheat (*T. aestivum*) (Gong et al., 2005), pepper (*Capsicum annuum*) (Pereira et al., 2013) and rapeseed (*B. napus*) plant (Hasanuzzaman et al., 2018). Proline is frequently measured as an osmotic protector which may be effective to support plants against drought. However, studies associated with Si supply effects on plants growth hormones are limited under drought condition. Si supply declined Jasmonic acid (JA) level but enhanced salicylic acid (SA) levels in shoots of soybean plant (Hamayun et al., 2010) and pepper (*C. annuum*) plants, nitrate reductase activity (Pereira et al., 2013). The study demonstrated that the Si could be effective to enhance tolerance against drought in the plant through improvement in nitrogen metabolism and signaling of phytohormones. Yin et al. (2014) revealed that the use of Si increased sorghum (*S. bicolor*) drought resistance through regulation of 1-aminocyclopropane-1-carboxylic acid and polyamine synthesis.

#### *Regulation of gene expression*

In the first report, Si supply was effective to enhance aquaporin genes expression under drought which prompted water uptake in sorghum (*S. bicolor*) roots (Liu et al., 2014). Also, the Si supply enhanced up-regulation of conjugated polyamines synthesis genes in sorghum (*S. bicolor*) during drought condition (Yin et al., 2014). Khattab et al. (2014) demonstrated that Si supply improved expression of the ring domain carrying protein (OsRDCP1), drought-related protein (OsCMO) and coding choline mono-oxygenase and dehydrin (OsRAB16b) in rice (*O. sativa*) plants of rice. So far, a mechanism of Si-mediated gene expression under alleviation of drought stress is poorly understood; therefore more efforts are required to uncover this aspect.

#### *Regulating gaseous exchange*

Leaf gas exchange attributes to deliver beneficial evidence on plant mechanisms in stressed conditions (Chen et al., 2011; Liu et al., 2014). Especially under drought conditions, the stomata regulate the water level of the plant by adjusting the rate of transpiration. Countless studies revealed that supply of the Si regulates plant's gaseous exchange attributes as plant are exposed to the drought (Hajiboland et al., 2017; Ming et al., 2012; Pereira et al., 2013; Saud et al., 2014). For example, the supply of diatomite in the soil provided a reduction in white lupine plants transpiration rate by improving stomatal conductance and the rate of photosynthesis (Abdalla, 2011). Similarly, Hattori et al. (2005) noted a higher transpiration rate and stomatal conductance in plants of sorghum (*S. bicolor*) during drought than without Si supply control plants. The authors concluded that maintenance of higher water level in sorghum (*S. bicolor*) plants was

because of higher water absorption in the existence of Si. Correspondingly, under drought Si use improved the transpiration and net photosynthesis rate in the rice (*O. sativa*) (Ming et al., 2012), pepper (*C. annuum*) plants (Pereira et al., 2013) and soybean (*G. max*) (Shen et al., 2010).

Furthermore, the use of Si enhanced rate of transpiration and the stomatal conductance in sorghum (*S. bicolor*) seedling (Liu et al., 2014). Gao et al. (2005) noted that Si supply improved WUE in the drought stress maize (*Z. mays*) through a reduction in transpiration rate of the leaf by stomata showed that the Si effects stomatal drive in the plant. Authors suggested that the rate of stomatal transpiration was decreased whereas stomatal density and morphology cannot clarify Si to decrease the rate of stomatal transpiration in maize (*Z. mays*) (Gao et al., 2006). Si use improved the rate of photosynthesis whereas the reduced rate of transpiration under drought condition in Tobacco (*N. Rustica*) (Hajiboland et al., 2017) and in plants of maize (Amin et al., 2014). Furthermore, the increase in WUE by Si supply was noted in chickpea (*C. arietinum*), (Fawaz and Mohammad, 2013), cacao (*Theobroma cacao*) grown in pots (Zanetti et al., 2016), wheat (*T. aestivum*) grown-up in the hydroponics (Ding et al., 2007) and wheat (*T. aestivum*) grown in field condition in drought (Gong and Chen, 2012). Gong et al. (2005) proposed that the use of Si on wheat (*T. aestivum*) was grown in the pots, shown an increased level in net CO<sub>2</sub> incorporation rate of the leaves during drought. The study is limited associated with the diurnal changes of plant gas exchanges characteristics with a supply of Si in drought. Gong and Chen (2012) revealed that Si use was effective for diurnal change in the net photosynthetic rate of leaf, the rate of transpiration and the stomatal conductance of plants of wheat (*T. aestivum*) in the field condition under drought. Likewise, Ma et al. (2004) noted Si mediated diurnal change in the gas exchange characteristic in plants of cucumber (*C. sativus*) in drought.

## Conclusion and perspective

Since 1999, many studies have been carried out to enlist benefits of Si for plant growth, but still, there is a lack of application of Si as a fertilizer for agronomic and horticulture benefits. Here is a dire need to create awareness about Si benefits among the masses and estimate its economic prospects. Therefore, the main aim of this review is to explain the mechanisms of the Si mediated mitigation of droughts in the plant. Available literature demonstrated that Si supplementation was sufficient to improve biomass, plant growth, seed germination, and photosynthesis drought stress condition. Si supply increased biomass and plant growth during a drought might be due to various mechanisms. This review can assist in well understanding mechanism of Si-arbitrated development in plants drought tolerance. Moreover, it could be effective to understand how crop production can be increased in drought stresses. We think that in the era of the 21<sup>st</sup> century where molecular tools are being incorporated at every step in all the field of studies, which genes are expressed under drought stresses in various plant species and which genes are playing their active part in plant growth improvement while Si usage and uptake by plant should be focused. This can take us to modify genetically economically significant crops to generate the drought stress tolerant cultivar which can be very beneficial in the future. Moreover, in all the studies, Si supplementation was in the form of potassium/calcium/sodium silicate. The need is to separate the Si from other anions and it can be applied at indigenous levels so that we may better understand the particular role of Si during plant development.

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