



# Role of silicon in plant stress tolerance: opportunities to achieve a sustainable cropping system

Sajad Majeed Zargar<sup>1</sup> · Reetika Mahajan<sup>2</sup> · Javaid A. Bhat<sup>2</sup> · Muslima Nazir<sup>1</sup> · Rupesh Deshmukh<sup>3</sup>

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## Abstract

Silicon (Si) being considered as a non-essential element for plant growth and development finds its role in providing several benefits to the plant, especially under stress conditions. Thus, Si can be regarded as “multi-talented” quasi-essential element. It is the most abundant element present in the earth’s crust after oxygen predominantly as a silicon dioxide (SiO<sub>2</sub>), a form plants cannot utilize. Plants take up Si into their root from the soil in the plant-available forms (PAF) such as silicic acid or mono silicic acid [Si(OH)<sub>4</sub> or H<sub>4</sub>SiO<sub>4</sub>]. Nevertheless, besides being abundantly available, the PAF of Si in the soil is mostly a limiting factor. To improve Si-uptake and derived benefits therein in plants, understanding the molecular basis of Si-uptake and transport within the tissues has great importance. Numerous Si-transporters (influx and efflux) have been identified in both monocot and dicot plants. A difference in the root anatomy of both monocot and dicot plants leads to a difference in the Si-uptake mechanism. In the present review, Si-transporters identified in different species, their evolution and the Si-uptake mechanism have been addressed. Further, the role of Si in biotic and abiotic stress tolerance has been discussed. The information provided here will help to plan the research in a better way to develop more sustainable cropping system by harnessing Si-derived benefits.

**Keywords** Silicon · Crop plants · Abiotic stress · Biotic stress · Sustainability

## Introduction

A major concern across the world is the (environmental) stresses that alter growth and development of plants. Both biotic and abiotic stresses cause a huge loss in crop yield and productivity. Crop yield stability and healthy growth under stressful conditions have always been a big challenge for the plant/agricultural science researchers. On the other hand, plants have evolved several mechanisms to survive under the

stress conditions; and healthy plants can sustain themselves or survive better under the stress. In other words, plant nutrition has an important role to maintain healthy growth as well as to enhance the stress tolerance. The role of micronutrients in providing tolerance to plant against various stresses has been demonstrated in several studies (Vanderschuren et al. 2013; Bradacova et al. 2016). Silicon (Si) is one such nutritive element which is gaining increasing attention due to its observed properties enhancing plant tolerance against biotic as well as abiotic stresses (Ma 2004). Ample amount of Si is present in the earth’s crust and it is considered as the second most abundant element after oxygen. However, most of the Si present in the soil is in the form of silicon dioxide (SiO<sub>2</sub>) that plants cannot uptake. Besides having abundant availability, the plant-available form (hereafter abbreviated, PAF) of Si (silicic acid) in the soil is mostly a limiting factor. Therefore, to improve Si-uptake and Si-derived benefits in plants, understanding the molecular basis of Si-uptake and transport within the tissues has great value.

Silicon is considered as a multi-talented micronutrient because of its versatile role in providing several benefits for plant growth particularly under stress conditions (Zargar

✉ Sajad Majeed Zargar  
smzargar@gmail.com

✉ Rupesh Deshmukh  
rupesh0deshmukh@gmail.com

<sup>1</sup> Division of Plant Biotechnology, Sher-e-Kashmir University of Agricultural Sciences and Technology of Kashmir, Shalimar, Srinagar, J&K 190025, India

<sup>2</sup> School of Biotechnology, Sher-e-Kashmir University of Agricultural Sciences and Technology of Jammu, Chatha, Jammu, J&K 180009, India

<sup>3</sup> Agri-Biotechnology Division, National Agri-Food Biotechnology Institute (NABI), Mohali, Punjab, India

et al. 2012). Some of the important roles that Si plays in plants are enhancing growth, yield and crop quality, photosynthesis, Nitrogen fixation and providing tolerance against abiotic and biotic stresses such as extreme temperature, UV radiation, metal toxicity, nutrient deficiency, drought, salinity, pathogen and fungus attack (Richmond and Sussman 2003; Ma 2004; Liang et al. 2007, 2015; Epstein 2009; Zargar et al. 2010, 2012; Cooke and Leishman 2011; Guntzer et al. 2012; Van Bockhaven et al. 2013). Earlier, Si was thought to be a non-essential element for plant growth (Sachs 1860; Arnon and Stout 1939) but numerous (over 100) studies performed during the last couple of decades confirmed the Si-derived benefits in several crop plants (Liang et al. 2015). Since the Si-derived benefits are more obvious under stress condition, it is widely considered as a quasi-essential element (Liang et al. 2015). Recently, the International Plant Nutrition Institute (IPNI) has declared Si as a nutritive element for plants (<http://www.ipni.net/nutrifacts-northamerican>). Moreover, the Association of American Plant Food Control Officials (AAPFCO) officially announced Si as a plant “beneficial substance” (<http://www.aapfco.org/>).

Silicon provides strength to the plant by making the plant tissues stronger and rigid (Marxen et al. 2015). Soluble Si can enhance resistance to diseases by interacting with several key compounds of the stress signaling system of the plant (Fawe et al. 1998; Rodrigues et al. 2004). Further, its accumulation leads to the production of phenolics and phytoalexins that provides tolerance against the various plant pathogens (Miyake and Takahashi 1982a, b; Datnoff et al. 1997). Priming of jasmonate-mediated antiherbivore defense responses via silicon in rice plant helps in providing defense against insects (Ye et al. 2013). As Si might have a role to play for attaining crop sustainability, biotechnology companies have developed the Si fluid ( $R_2SiO$ ) where R is any organic group that is used as a spreading agent instead of fertilizers (Vasanthi et al. 2012a, b). Recent farming systems mainly organic farming takes advantage of Si to overcome the problem of pesticide residues in food products (Vasanthi et al. 2012). Two review articles published earlier by our group gives details about the role of Si in both plants (as well as animal) growth and development, and its efficiency in providing tolerance against various environmental stresses (Zargar et al. 2010, 2012). In this review, we have focused on the recent advancements in Si research and its potential to attain crop sustainability.

### Plant available form of silicon in soil

Silicon is taken up by plants in the PAF such as silicic acid or mono silicic acid [ $Si(OH)_4$  or  $H_4SiO_4$ ]. The PAF-Si found in soil varies considerably ranging from 10 ppm to over 100 ppm (Liang et al. 2015). Soils with less than 20 ppm of

Si are considered as Si-poor and are mostly advised to supplement with Si-fertilizers. Among several natural sources, Wollastonite is one of the most preferred and affordable sources for Si-supplementation. Wollastonite is a naturally occurring metasilicate of calcium ( $CaSiO_3$ ), and contains a major portion of calcium (Ca, 34.3%) and Si (24.3%) with minor amounts of aluminum (Al), iron (Fe), manganese (Mn), magnesium (Mg), potassium (K), and sodium (Na) (Virta 2004; Maxim et al. 2008). Wollastonite is also mined for the production of ceramics, friction products, metallurgy, paints, and cementing material (Virta 2004). The other less preferred natural Si-sources includes minerals such as calcite, diopside, garnet, idocrase, and quartz. Additional sources used for Si supplementation in crop plants are steel slag, potassium silicate, sodium silicate and sugarcane bagasse, etc (Pereira et al. 2003; de Camargo et al. 2013; Tubana and Heckman 2015).

The monomeric form of silicic acid is the PAF of soil Si (Williams and Crerar 1985), whereas the polymeric form has a role in improving soil aggregation and water-holding capacity due to its property to link soil particles by creating silica bridges (Norton et al. 1984). Most of the Si present in soil is in an insoluble form and is of no use in agronomy and horticulture. Thus, for making the Si available to the plant, the soil is subjected to chemical and physical weathering. The weathering process of silicate minerals depends on environmental factors such as temperature and pH as well as the physicochemical characteristics of the minerals (Heaney et al. 1994; White and Brantley 1995; Gérard et al. 2002). Moreover, the concentration of Si in plants mainly depends on the concentration of silicic acid in soil solution (Ding et al. 2005; Henriot et al. 2008; Jones and Handreck 1967), and not on the concentration of total Si present in the soil (Brenchley and Maskell 1927).

### Uptake, transportation, and accumulation of Si in plants

Silicon in the form of silicic acid [ $Si(OH)_4$ ] or mono silicic acid [ $H_4SiO_4$ ] can cross the plasma membrane of root at physiological pH (Raven 2001). The concentration of silicic acid in soil solution below pH 9 ranges from 0.1 to 0.6 mM (Knight and Kinrade 2001). In the plant leaves, Si concentration varies from 0.1 to 10% on dry weight basis (Epstein 1999; Ma et al. 2001; Richmond and Sussman 2003). Silicon concentration varies significantly within and among plant species, and the variation of Si concentration within the species is lower than among the species (Broadley et al. 2011). The particular ability of the roots to uptake Si is considered to be the reason for the differences in Si accumulation in different plants (Ma and Yamaji 2006). Higher accumulation of Si was observed in Bryophyta, Lycopsida, and

Equisetopsids (Pteridophyta), whereas in Filicopsida (Pteridophyta), Gymnospermae and most Angiospermae there is a low Si concentration (Ma et al. 2001; Ma and Takahashi 2002; Hodson et al. 2005). However, a few taxa in Angiospermae namely Cyperaceae, Poaceae, and Balsaminaceae have > 4% Si accumulation, the Cucurbitales, Urticales and Commelinaceae have 2–4% Si accumulation, whereas Solanaceae (tomato), Fabaceae (faba bean) are Si excluder species (Ma and Takahashi 2002; Hodson et al. 2005). Based on the water uptake relation in higher plants, Si adsorption at the lateral roots is categorized in three possible ways: active (where Si-uptake is faster than water uptake), passive (where Si-uptake is similar to water uptake) and rejective (where Si-uptake is slower than water uptake) (Takahashi et al. 1990; Cornelis et al. 2011). Active transport of Si leads to a significant decrease in its concentration in the uptake solution while the Si concentration remains unchanged in uptake solution in passive transport. Passive transport of Si from soil via diffusion across the plasma membrane or via proteinaceous channels is an energy independent process present in all plant species, despite the Si accumulation ability of the plants (Raven 2003). Root uptakes silicic acid present in the soil via the apoplastic and symplastic route. The symplastic route of Si-uptake by roots depends on the presence of NIPs (Nod26-like intrinsic proteins) a class of the aquaporin (AQP) gene family. The Si-transporter AQPs have been identified in several monocot and dicot plant species (Ma et al. 2006; Chiba et al. 2009; Mitani et al. 2009a, b; Deshmukh et al. 2013). The Si-transporter AQPs have also been reported in the primitive plant species such as horsetail, which is known as the king of silicon accumulator (Grégoire et al. 2012; Vivancos et al. 2016).

Rice roots can uptake 90% of the Si present in the soil and translocate it to the shoots (Ma and Takahashi 2002). Research performed using rice mutants for Si-uptake have identified two different types of Si-transporters namely *OsLsi1* (Si-transporter AQPs, influx) and *OsLsi2* (efflux Si-transporters) (Ma et al. 2006, 2007). The influx Si-transporter AQPs, *OsLsi1* and *OsLsi6* (*OsLsi1* homolog) promotes passive transport of Si between the apoplast and plant cell across the plasma membrane. The *OsLsi1* gene belonging to the NIP-III subfamily of aquaporin facilitates Si influx from soil solution into the root cells (Ma et al. 2006). After uptake of Si by the root symplast through influx transporters (*OsLsi1*), efflux transporters (*OsLsi2*) facilitate Si release into the apoplast (xylem loading) from where the Si is translocated upwards to the shoots via transpiration stream. Hence, the *OsLsi2* gene (efflux Si-transporter) belonging to a putative anion-channel transporter is involved in Si transport out of the root cells towards the stele (Ma et al. 2007; Yamaji and Ma 2011). *Lsi2* is an active efflux transporter of Si which is driven by proton gradient and can transport soluble Si against the concentration gradient (Ma et al. 2011). It

is proposed that Si-uptake occurs in the mature roots than in the root tips as the expression level of *OsLsi1* gene was reported lower in the apical root region than the basal root region (Yamaji and Ma 2007). Plasma membranes of both the exodermal and endodermal root cells have *Lsi1* transport protein at the distal side; and casparian strips present in the endodermis prevent apoplastic transport into the root stele (Yamaji and Ma 2007). Cellular localization and expression pattern of the *OsLsi2* gene is same as that of the *OsLsi1* gene with the only difference that the *Lsi2* transport protein is located at the proximal side of both exo and endodermal cells. To prevent Si deposition in the xylem, Si must be transported out from the xylem (xylem unloading), and the unloading of Si from the xylem into xylem parenchyma cells is mostly facilitated by *OsLsi6*, an influx transporter. Therefore, *Lsi6* helps in the transport of Si out from the shoots to prevent deposition of Si in rice shoots (Yamaji et al. 2008). *Lsi6* is expressed in root tips, leaf sheaths, and blades, and is localized on the adaxial side of xylem parenchyma cells in the leaf sheaths and leaf blades in rice (Yamaji et al. 2008). Furthermore, an increase in Si deposition in the silicified epidermal cells of leaf blades and sheaths and increase excretion of Si in guttation fluid was reported in rice on knockout of *Lsi6* (Ma et al. 2011). In rice, Si uptake by the roots to the panicle is mediated by inter-vascular transfer of Si between two different vascular bundles. In the rice plant, efflux Si-transporter (*Lsi3*) is expressed in the first node indicating that it is responsible for reloading Si to diffuse into the vascular bundles (Yamaji et al. 2011). A similar type of mechanism has been observed in other plants such as barley and maize (Mitani et al. 2009a, b). Subsequently, several homologs of Si-transporter AQPs and *OsLsi2* have been identified in several monocots, dicots and primitive plant species (Table 1).

### Differences in monocot and dicot silicon uptake mechanism

Monocots such as rice can accumulate Si up to 10% of the plant mass while most of the dicots accumulate very less. The high accumulation in rice can be attributed to efficient Si-transporters as well as specialized silica cells. Dicots do not have silica-cells, and also several dicot families are known to have lost the Si-transporter AQPs (Deshmukh et al. 2015). In dicots, the first gene encoding an influx Si-transporter was identified as Pumpkin *Lsi1* (*CmLsi1*) (Mitani et al. 2011). More than half of the Si, taken up by the roots is translocated to the shoots in cucumber making it an intermediate Si accumulator crop (Nikolic et al. 2007). Si transportation in dicots involves concentration-independent (passive) and metabolically active process which is inhibited by low temperature and metabolic inhibitors (Liang et al. 2005a, b). The *CmLsi1* transporter is localized in all root

**Table 1** Silicon (Si) transporters identified from various crop plants [this table includes the transporters reviewed in Zargar et al. (2010), and other transporters identified after 2010]

S. no.	Type of transporter	Transporters	Crop	References
1	Influx (NIP/III)	OsLsi1	Rice	Ma et al. (2006)
2		OsLsi6	Rice	Yamaji et al. (2008), Yamaji and Ma (2009)
3		ZmLsi1	Maize	Mitani et al. (2009)
4		ZmLsi6	Maize	Mitani et al. (2009)
5		HvLsi1	Barley	Chiba et al. (2009)
6		HvLsi6	Barley	Yamaji et al. (2012)
7		CmLsi1	Pumpkin	Mitani et al. (2011)
8		TaLsi1	Wheat	Montpetit et al. (2012)
9		CSiT-1	Cucumber	Wang et al. (2014)
10	Efflux	GmNIP2-1 GmNIP2-2	Soybean	Deshmukh et al. (2013)
11		EaNIP4, EaNIP5	Horsetail	Grégoire et al. (2012)
12		OsLsi2	Rice	Ma et al. (2006)
13		ZmLsi2	Maize	Mitani et al. (2009a, b)
14		HvLsi2	Barley	Mitani et al. (2009a, b)
15		CmLsi2-1	Pumpkin	Mitani-Ueno et al. (2011)
16		CmLsi2-2	Pumpkin	Mitani-Ueno et al. (2011)
17		GmNIP2-2	Soybean	Deshmukh et al. (2013)
18		CSiT-2	Cucumber	Wang et al. (2014)
19		EaLsi2	Horsetail	Vivancos et al. (2016)

cells and does not show polar localization as observed in rice (Ma et al. 2006; Chiba et al. 2009; Mitani et al. 2009). The difference in the localization of the transporters present in roots accounts for the anatomical difference of rice root and other species including cucumber (Chiba et al. 2009; Mitani et al. 2009; Mitani et al. 2011b). The *CmLsi2-1* and *CmLsi2-2* (Si efflux transporters) have been isolated from two pumpkin cultivars used for the bloom or bloomless cucumber rootstocks (Mitani et al. 2011a). These transporters show an efflux transport activity for Si and are expressed in both roots and shoots (Mitani et al. 2011b). Little information is available on Si transport in dicots except for cucumber (Lux et al. 2003). Similarly, *GmNIP2-1* and *GmNIP2-2* (putative influx Si-transporter genes) belonging to NIP2 subfamily of AQPs have been identified, characterized and cloned from soybean (Deshmukh et al. 2013). There is a need to study the mechanism of Si transport in dicot species, as very less information is available on the mechanism of Si transport in dicots compared to monocots. The difference in the mechanism of Si uptake in monocot and dicot species makes the monocot species more tolerant against frost stress and certain metabolic inhibitors as the later involves concentration independent process for Si uptake. Thus, having the complete knowledge of the difference between two uptake mechanisms might be useful in generating genetically modified species with improved Si uptake and assimilation properties.

Availability of the well annotated genome sequences for over 100 plant species have provided the opportunity

to identify Si-transporters and correlated it with the Si-uptake capability. In above context, the extensive research by Deshmukh et al. (2015) with 25 plant genomes and 25 transcriptomes have highlighted the loss of Si-transporter AQPs from all the Brassicaceae members. These findings well corroborated with the very low Si observed in Brassicaceae members, such as *Arabidopsis*. Recently, the loss of Si-transporter AQPs and inability of Si-uptake have been reported with *Arabidopsis lyrata*, *Capsella grandiflora*, *C. rubella*, *Eutrema salsugineum*, *B. oleracea*, *B.rapa*, *B.napus* (Canola), and Flax (Shivaraj et al. 2017; Sonah et al. 2017). Another notable example is the Solanaceae family which was found to be poor accumulators besides having homologs of Si-transporter AQPs. The poor accumulation of Si by Solanaceae such as tomato and potato have been associated with altered spacing between the two conserved NPA motifs (Deshmukh et al. 2015). There is no report for loss of Si-transporter AQPs and the poor accumulators in monocot such as Poales. These reports suggest that the Si-uptake is primarily regulated by Si-transporter AQPs, which might be responsible for the variations among species.

## Role of silicon in biotic and abiotic stress tolerance

Silicon, previously considered as a non-essential element for the plant in early nineteenth century, has been confirmed to have a greater impact on overall plant growth and

development. There is no doubt that most of the plants can complete their life cycle without the requirement of Si but it is also true that the presence of Si in soil or media provides tolerance to plants against various biotic and abiotic stresses. In the last 20 years, numerous researches have been carried out in different crops such as rice, wheat, maize, tomato, and soybean which concluded that the presence of Si helps in reducing the biotic and abiotic pressures (Kim et al. 2014a, b; Shi et al. 2014; Yin et al. 2014; Sahebi et al. 2015; Xie et al. 2015). Recently, the perception about the membrane transport of Si and its mitigatory role in biotic stress has gained much attention (Van Bockhaven et al. 2013; Ma and Yamaji 2015; Exley 2015; Liang et al. 2015). However, there is limited knowledge regarding the mechanism(s) underlying the role of Si in abiotic stress resistance (Liang et al. 2015). In the following section, an insight into the role of Si in providing resistance to various biotic and abiotic stresses is provided.

### Biotic stress

Silicon is known to provide protection against several fungal as well as bacterial pathogens. Broadly, two mechanisms for the Si-enhanced resistance to diseases and pests have been proposed. One is that the Si is being deposited beneath the leaf cuticle or on the tissue surface as a physical barrier, and mechanically inhibits the fungal or insect pest penetration, thereby reducing infections (Samuels et al. 1991). The silicified epidermal cell walls of rice plants were closely associated with the reduced blast severity in susceptible and partially resistant cultivars (Kim et al. 2002). Si treatment may also increase the prevalence of papillae which could have increased pathogen resistance against *B. graminis* f.sp. *tritici* (Belanger et al. 2003). It was demonstrated that Si-treated rice plants infected by the sheath blight pathogen *Rhizoctoniasolani* had much more silica cells and papillae (Zhang et al. 2006). Si-supplementation in rice was found to suppress the sheath blight, leaf and neck blast, leaf scald, grain discoloration, bacterial leaf blight and stem rot infection (Datnoff and Rodrigues 2005). Si treatment suppresses anthracnose disease of tomato (Somapala et al. 2016) and sweet pepper (Jayawardana et al. 2014), increases the firmness and cuticle thickness of fruits. In the mango plant, accumulation of absorbed Si in the epidermal tissue forms a physical barrier preventing the entry of *P. syringae* pv. *Syringae* (Gutierrez-Barranquero et al. 2012). Furthermore, energy-dispersive X-ray (EDX) and X-ray mapping has revealed that Si deposition at the internode and root band is likely the reason for enhanced resistance of silicon-treated sugarcane to penetration and feeding by African sugarcane borer (*Eldana saccharina*) (Keeping et al. 2009). Higher Si content in sugarcane plant can inhibit shoot borer attack by increasing the hardness of cane (Rao 1967) and reduce

nematode infection in cucumber plants (Silva et al. 2010). Furthermore, Si has been observed to suppress root rot and powdery mildew in cucumber and wheat, leaf spot in Bermuda grass (*Cynodon dactylon*), rust in cowpea and ring spot in sugarcane (Fawe et al. 2001; Belanger et al. 2003). Sorghum grown in Si-added nutrient solution was observed to reduce severity of anthracnose (*Colletotrichum sublineolum*) (Resende et al. 2013). In coffee, promising results have been reported for rust (*Hemileia vastatrix*), leaf spot (*Cercospora coffeicola*), and phoma/ascochyta leaf spot (*Phomatarda*) (Pozza et al. 2004; Botelho et al. 2005; Reis et al. 2008; Carre-Missio et al. 2012, 2014). Other crops such as bean, strawberry, soybean, tomato and rose also showed promising results in reducing disease intensity with Si application. The reduction in disease intensity is not limited to fungal diseases, but studies have reported the Si efficacy in controlling bacterial wilt (*Ralstonia solanacearum*) of tomato (Ghareeb et al. 2011).

The second mechanism is that Si functions as a signal to induce the production of natural defense compounds including the elevated production of lignin, phenolic compounds and phytoalexins (Epstein 1999; Ma and Yamaji 2006). One of the pioneering studies by Fawe et al. (1998) reported increased level of the flavonoid phytoalexin in cucumber plants infected by powdery mildew with the Si-supplementation (*Podosphaera xanthii*). In the rice plant, increased production of momilactones A and B (diterpenoid phytoalexins) following Si treatment induces resistance to blast disease (Rodrigues et al. 2004). Si produces a broad, quick response in the plant following the pathogenic attack by releasing natural defense compounds to deter the development of the pathogen (Fauteux et al. 2005). Si application significantly enhanced the activities of pathogenesis-related proteins (PRPs) such as catalase (CAT), peroxidase (POD), polyphenol oxidase (PPO), and  $\beta$ -1,3-glucanase of asparagus plants inoculated with *Phomopsis asparagi*, and leads to the suppression of *Phomopsis* stem blight development (Lu et al. 2008). Various studies conducted on many crops viz., wheat (Yang et al. 2003), cucumber (Liang et al. 2005) and rice (Cai et al. 2008) have also revealed that Si treatment reduces disease severity by increasing the activities of protective enzymes such as POD, PPO and phenylalanine ammonia-lyase (PAL) in their leaves. Higher levels of PPO and ascorbate peroxidase (APX) in melon plants supplied with silicon decreased the severity of bacterial blotch caused by *A. citrulli* (Conceição et al. 2014). Si application also enhanced the activities of  $\beta$ -1,3-glucanase, exochitinase and endochitinase in rice plants leading to decreased intensity of *X. oryzae* pv. *Oryza* (Xue et al. 2010). In sweet pepper, calcium silicate can enhance concentrations of total protein, CAT, APX and chitinase which ultimately decrease the severity of *R. solanacearum* (Alveset et al. 2015). Supply of potassium silicate in pea seedlings increases chitinase

and  $\beta$ -1,3-glucanase activity against fungal pathogen *Mycosphaerella pinodes* causing blight disease (Dann and Muir 2002).

Numerous studies have demonstrated that a higher Si content in the soil and growth medium can help show better resistance against the infection of pests. Decreased feeding, growth longevity, fecundity and population growth of white backed plant hopper (*Sogatella frucifera*) have been observed with Si-supplementation (Salim and Saxena 1992). Moreover, foliar application of Si as calcium silicate to crop species viz., wheat, cotton, sugarcane and cucumber increased the mortality of white fly nymphs which lead to significant yield loss in these crops plants (Correa et al. 2005). Swain and Prasad (1988) found that the roots of rice plants containing high Si content resist the infection of root-knot nematodes. Si nutrition can also reduce the attack of green leaf hopper, plant hopper and stem maggot on rice plants (Malhotra et al. 2016). Furthermore, a low preference for the silicified tissues by the leaf eating caterpillars has been observed (Malhotra et al. 2016). Si-transporters from high accumulator plants could be transferred to plants lacking Si-transporters via different techniques to provide protection against diseases. Recently in *Arabidopsis*, it has been suggested that Si can provide protection to plants against disease via salicylic acid (SA)-independent pathway. Thus, it was recommended to better understand the SA-independent plant defense mechanism so that new or improved crops can be designed to cope up with changing the environment (Vivancos et al. 2016).

### Abiotic stress tolerance

Due to abiotic stresses, crop losses of more than 50% occur worldwide (Wang et al. 2003; Allahmoradi et al. 2011). Physiological processes such as photosynthesis, respiration, translocation, ion uptake, transpiration rate, stomatal behavior and conductance, seed germination, mineral nutrition and water relation are affected by abiotic stresses such as drought (Saud et al. 2014), salinity (Hayat et al. 2010) and heavy metal (Singh et al. 2015). Improvement in the physiological processes, plant growth, and development under various stresses with Si supplementation is a well-documented fact.

### Drought

Si application during drought stress provides tolerance to plant via different mechanisms. Application of Si under drought stress might up regulates aquaporin gene (PIP; Plasma membrane Intrinsic Protein) and mitigates ROS-induced aquaporin activity inhibition in plants. Under drought stress, Si supply affected the osmo-regulation by increasing the accumulation of soluble sugars and/or amino acids in the xylem sap which increases osmotic driving force

or by activating the  $K^+$  translocation to xylem sap by via SKOR (Stelar  $K^+$  Outward Rectifier) gene. Si application can improve the root hydraulic conductance by modifying the root growth and increase root/shoot ratio along with elevating aquaporin activity and osmotic driving force. Higher root hydraulic conductance results in increasing the uptake and transport of water which helps to maintain a higher photosynthetic rate and improve plant resistance to water deficiency (Luyckx et al. 2017; Chen et al. 2018). Si application can also reduce drought stress via increasing uptake of mineral nutrients by plants, altering gas exchange attributes in plants (Rizwan et al. 2015). Under drought stress, exogenous application of Si has improved seed germination, biochemical processes and protects the seedling from oxidative stress by enhancing antioxidant defense. In the maize plant, calcium silicate application in the soil increases seed germination under drought stress (Zargar and Agnihotri 2013). Silicon application increases the photosynthetic rate, leaf and root water and osmotic potential, water use efficiency (WUE), while decreases transpiration rate, membrane permeability under water-deficit conditions in different crop species viz., Kentucky bluegrass (*Poa pratensis* L.) (Saud et al. 2014), maize (Amin et al. 2014), wheat (Gong and Chen 2012; Maghsoudi et al. 2016), rice plants (Agarie et al. 1998; Ming et al. 2012), tomato (Silva et al. 2012; Shi et al. 2014), melon (Neocleous 2015), oil palm (Putra and Purwanto 2015) and Fennel (Asgharipour and Mosapour 2016), white lupin plants (Abdalla 2011a, b). However, in some plants such as soybean, rice, and pepper (*Capsicum annum* L.) Si supply increases both transpiration rate and net photosynthetic rate under drought stress (Rizwan et al. 2015). One of the major effects of drought stress is the disturbed uptake of essential nutrients by plants (Emam et al. 2014). In this regard, Si application in soil has been reported to increase the uptake of macronutrients (P, K, Ca and Mg) and micronutrients (Fe, Cu and Mn) in crop under water deficit stress (Gunes et al. 2008). An increase in level of K and total P in rice straw of Si-treated plants compared to control under drought conditions has been reported (Emam et al. 2014). The regulation of gas exchange attributes of plants by Si under drought stress has also been revealed in many studies (Gao et al. 2006; Zhang et al. 2013; Putra and Purwanto 2015). Si supply has been widely reported to decrease oxidative damage through enhancing the antioxidant enzyme (SOD, APX, CAT and POD) activities under drought stress in wheat plants (Tale Ahmad and Haddad 2011), sunflower (Gunes et al. 2008), tomato (Shi et al. 2014), and chickpea (Gunes et al. 2007). Si pretreatment was demonstrated to up-regulated the expression of both ring domain containing protein *OsRDCP1* gene and drought-specific genes, *OsCMO* coding rice choline monooxygenase and dehydrin *OsRAB16b*, in drought-stressed rice plants as compared to control (Khattab et al. 2014).

## Salinity

Si utilizes different mechanisms to reduce salt stress in plants. The key mechanisms involved in Si-mediated tolerance to salt stress are a reduction in ion toxicity and maintenance of plant water balance, increase in mineral uptake and assimilation, regulation of biosynthesis of compatible solutes and phytohormones, reduction in oxidative stress, modification of gas exchange attributes, and modification of gene expression. Reduction in  $\text{Na}^+$  uptake and accumulation by plants is one of the most important mechanisms of plant resistance to salt stress. Si supply has been widely reported to decrease  $\text{Na}^+$  uptake by plants under salt stress and increased  $\text{K}^+/\text{Na}^+$  ratio (Ali et al. 2009; Gurmani et al. 2013; Chen et al. 2014; Garg and Bhandari 2015). The salt stress leads to severe nutritional imbalances in plants (Gupta and Huang 2014) reported that Si application increased Ca and Mg contents in roots and leaf of tomato under salt stress (Li et al. 2015) and increases K, P, Ca and Mg in Egyptian clover (Abdalla 2011). Si supply also increased photosynthetic rate, stomatal conductance, transpiration rate, water use efficiency and number and size of stomata, leaf water status, root hydraulic conductance in numerous crops such as cucumber (Amirossadat et al. 2012), faba bean (Kardoni et al. 2013), sorghum leaves (Yin et al. 2013), wheat (Chen et al. 2014; Bybordi 2014), rice (Mahdih et al. 2015), tomato seedlings (Li et al. 2015), okra (Abbas et al. 2015) sweet pepper (Manivannan et al. 2016) and maize (Rohanipoor et al. 2013; Xie et al. 2015). Si application reduces the oxidative damage by increasing antioxidant enzyme activities (SOD, CAT and POD, GSH and APX), by maintaining the optimal membrane fluidity, plasma membrane  $\text{H}^+$ -ATPase and reduced ROS generation in many plant species under saline conditions (Alaghabary et al. 2005; Liang et al. 2007; Wang et al. 2011; Kim et al. 2014b; Li et al. 2015; Muneer and Jeong 2015). Si application can also enhance salt tolerance in plants by adjusting the levels of solutes such as proline, glycine betaine and total free amino acids in both shoots and roots of okra (Abbas et al. 2015) and phytohormones such as gibberellin (GA) level and decreased ABA content in salt stress soybean plant (Lee et al. 2010). Si up-regulated the AQP gene expression as well as increased the water uptake in salt stressed cucumber plants (Zhu et al. 2015). In addition, Si application was observed to activated the genes related to salt stress responses (*leDREB-1*, *leDREB-2* and *leDREB-3*), Si transport (*leLsi-1*, *leLsi-2* and *leLsi-3*), and antioxidants (*leAPX*, *leSOD* and *leCAT*), in salt-stressed tomato responsible for salt tolerance (Muneer and Jeong 2015).

## Heavy metal

Si-mediated metal detoxification mechanisms have been extensively studied in many plant species which includes immobilization of toxic metal in soil/growth media, co-precipitation of metals with Si, like co-precipitation of Si with Cd in the stem of rice lower the heavy metal concentration in leaves (Gu et al. 2011), stimulation of enzymatic and non-enzymatic antioxidants, chelation, compartmentation of metals into metabolically inactive parts such as Si decreased Cd accumulation in rice shoots by compartmentalization of Cd in the root cell walls (Zhang et al. 2008), modification of gene expression and structural alterations in different parts of plants (Jia-Wen et al. 2013). Si application can immobilize toxic metals in the soil either by increasing soil pH or changing metal speciation in soil solution through the formation of silicate complexes (Adrees et al. 2015). The role of Si in mitigating Al and Mn toxicity has been widely reported in many crop species viz., cowpea, cucumber, soybean, beans, barley, maize, rice, tomato, pumpkin and sorghum (Sahebi et al. 2015). Si supply reduces lipid peroxidation (LPO) intensity whereas increases enzymatic (superoxide dismutase (SOD), APX, and glutathione reductase) and non-enzymatic (ascorbate and glutathione) antioxidants activities in cucumber (Shi et al. 2005; Maksimovic et al. 2012), cowpea (Iwasaki et al. 2002) under Mn Stress, alleviated oxidative stress caused by arsenic (As) by reducing the As accumulation and enhancing the antioxidant system in Triguna (rice cultivar) (Tripathi et al. 2013). Si treatment increased germination percentage (GP), germination rate (GR) and relative water content (RWC) of faba bean plants as compared to Si-untreated plants under Cd and Pb stresses (Abu-Muriefah 2015) and decreases absorption of metal ions and reduces the transformation of toxic metals between the roots and shoots in case of rice seedlings that are grown under Cd stress (Shi et al. 2005). Si application was demonstrated to significantly up-regulate the expression of genes responsible for Si transport (*OsLSi1* and *OsLSi2*), and down-regulated the expression of genes encoding heavy metal transporters (*OsHMA2* and *OsHMA3*) in rice plants (Kim et al. 2014a, b). Si was also revealed to increase epidermis, xylem diameter mesophyll and the transverse area of collenchymas and mid vein under Cd and Zn stress (da Cunha and do Nascimento 2009). It has been observed that Si treatments accelerated casparian bands, suberin lamellae and root vascular tissues development in maize under Cd stress (Vaculík et al. 2012; Lukacova et al. 2013). Si application increases SPAD (Soil-Plant Analyses Development) value, net photosynthetic rate, water use efficiency, stomatal conductance, transpiration rate and chlorophyll fluorescence efficiency in barley under Cr (chromium) toxicity (Ali et al. 2013), in maize plant under Zn stress (Paula et al. 2015), in sorghum, increases root hydraulic conductance by regulating

the aquaporin activity under K deficiency (Chen et al. 2016). Silicon application enhances gas exchange characteristics in barley under Cr stress (Ali et al. 2013), in peanut under Al (aluminum) stress (Shen et al. 2014), in cotton under Pb (lead) stress (Bharwana et al. 2013) and in rice under Zn stress (Song et al. 2014). Si application in hydroponic solution increased the uptake and translocation of micronutrients (Zn and Mn) and macronutrients (Ca, Mg, P and K) by wheat plants under Cr, Cu (copper) and Cd (cadmium) stresses (Rizwan et al. 2012; Tripathi et al. 2015; Keller et al. 2015). Furthermore, Si application significantly suppressed Zn uptake and accumulation in the roots and leaves of maize and cotton (Bokor et al. 2014; Anwaar et al. 2014).

Si application also plays a protective role against the UV-B radiation by enhancing the growth, photosynthesis and antioxidant parameters in soybean seedlings (Shen et al. 2010). Si increases tolerance of wheat seedlings against UV stress by enhancing the level of antioxidant compounds (Yao et al. 2011). Malcovska et al. (2014) reported that the oxidative status of Si-treated maize plants was only slightly affected compared to non Si-treated plants under UV radiation stress. Detailed studies of Si-mediated abiotic stress tolerance in plants are given in Table 2.

## Role of silicon as nano-silicon particles in alleviating stresses

Under a variety of stress conditions, plants generate natural mineralized nano-materials for proper growth and development (Wang et al. 2001). With the advancement in science, the priming of seeds with nano-particles has revolutionized the agricultural field. Nano-particles have unique physicochemical properties which attract scientist worldwide (Monica and Cremonini 2009). Seeds coated with silicon can help in providing tolerance to different stresses in the plant (Hameed et al. 2013). Absorption of nano silicon dioxide (nSiO<sub>2</sub>) in the maize seed resulted in a significant increase in organic compounds such as proteins, chlorophyll and phenols and plant dry weight (Suriyaprabha et al. 2012). The nSiO<sub>2</sub> has a great impact on the seed germination rate in tomato as it helps in increasing percent seed germination, mean germination time, seed germination index, seed vigor index, seedling fresh weight and dry weight (Siddiqui and Al-Whaibi 2014). Addition of nSiO<sub>2</sub> in the nutrient media can improve the seed germination and seedling early growth of lentil plant under salinity stress (Sabaghnia and Janmohammadi 2014). In basil (*Ocimum basilicum*), nSiO<sub>2</sub> alleviated the effects of salinity stress and increased leaf dry and fresh weights, chlorophyll content and proline content (Kalteh et al. 2014). The application of nSiO<sub>2</sub> on *Vicia faba* can improve germination characters when exposed to salinity stress. Thus, it can be concluded that nSiO<sub>2</sub> application

in *Vicia faba* can increase the relative water content, plant height, fresh and dry weights under salinity stress conditions (Abdul Qados and Moftah 2015). Nano-silicon can also be used to alleviate seed germination and plant growth inhibition due to the salt stress and improves photosynthetic quantum in tomato (Almutairi 2016). On application of nano-silicon in tomato under salt stress, four salt stress genes, *AREB*, *TAS14*, *NCED3* and *CRK1* showed upregulation in their expression whereas six genes, *RBOH1*, *APX2*, *MAPK2*, *ERF5*, *MAPK3* and *DDF2* showed down regulation (Almutairi 2016). Nano particles (nSiO<sub>2</sub> and nMo) are commonly used as engineered oxide nano particles. Nano particles have both beneficial and toxic effect on plants. Effect of nSiO<sub>2</sub> and nMo particles was studied on rice germination (Adhikari et al. 2013). Uptake of both nano-particles was observed in the rice seedlings. Nano-Mo particle caused the arrest of root growth and elongation in rice whereas nSiO<sub>2</sub> had no toxic effect on rice. However, nSiO<sub>2</sub> enhanced the root length and volume, dry matter weight of shoot and root of rice (Adhikari et al. 2013). Application of specific nano-particles on plants directly, might have both positive and negative effects on the plant growth and development. Potassium silicate solitary in combination with salicylic acid can provide tolerance to plants against salinity stress (Hussein and Abou-Baker 2014). Direct and indirect role of nSiO<sub>2</sub> in ensuring better plant growth and productivity under different stresses makes this nanoparticle an alternative for harmful fertilizers for sustainable agricultural practices.

## New insights into silicon research: omics to unravel different stress mechanism

The dynamic role of Si in biotic and abiotic stress can be better understood with the transcriptomics and proteomic studies. At present, there is no direct and convincing evidence to explain precise molecular mechanism involved in Si-derived stress tolerance. Very few studies involving transcriptomics and proteomics approaches have been conducted to study the effect of Si on plants under different stress conditions. Most of the transcriptomics and proteomics studies were carried out in last few years. From transcriptomics, Si has been revealed to up-regulate the aquaporin gene expression as well as increase the water uptake in salt stressed cucumber plants (Zhu et al. 2015). Similarly, Si has also been reported to up-regulate the expression of several *SbPIP* aquaporin genes in salt-stressed sorghum. In addition, Si application was observed to activate the genes related to salt stress responses (*leDREB-1*, *leDREB-2* and *leDREB-3*), Si transport (*leLsi-1*, *leLsi-2* and *leLsi-3*), and antioxidants (*leAPX*, *leSOD* and *leCAT*), in salt-stressed tomato responsible for salt tolerance (Muneer and Jeong 2015). Si application in the rice plant can provide resistance against blast fungus (Liu



**Table 2** Role as well as the mechanisms used by Si in combating different biotic and abiotic stresses in crop plants

S. no.	Biotic/abiotic stress	Crop	Mechanisms	References
<b>A. Disease</b>				
1	Powdery mildew	Black gram	Increased expression of defense-related proteins	Parthasarathy and Jaiganesh (2016)
2	Bacterial wilt	Tomato	Increased activities of defense-related enzymes viz., peroxidase, phenylalanine ammonia lyase	Kurabachew et al. (2013)
3	Bacterial wilt	Sweet pepper	Increased the concentrations of total protein, catalase, ascorbate peroxidase, and chitinase	Alves et al. (2015)
4	Leaf blast	Rice	Increased activities of chitinase, $\beta$ -1,3 glucanase, peroxidase and phenylalanine ammonia-lyase	Souza et al. (2015)
5	Anthracoze	Tomato	Increased thickness of cuticle and fruit firmness	Somapala et al. (2016)
6	Anthracoze	Sweet pepper	Increases the firmness and cuticle thickness of fruits	Jayawardana et al. (2014)
<b>B. Insect pest</b>				
7	Rice leaf folder	Rice	Reduced food quality and food conversion efficiencies	Han et al. (2015)
8	Brown plant hopper	Rice	Reduction in honeydew extraction	He et al. (2015)
9	Leaf miner	Tomato	Detachment of the midgut epithelium from the basal membrane, which leads to the reduction of digestive capacity in insects	dos Santos et al. (2015)
10	Fall armyworm	Rice	Affects feeding preference as well as <i>S. frugiperda</i> larval survival	Nascimento et al. (2014)
11	Sugarcane borer	Rice	Reduced feeding injury, and increased exposure to adverse environmental conditions and natural enemies arising from reduced boring success	Sidhu et al. (2013)
12	<i>Diatraeasaccharalis</i>	Sugarcane	Promotes cuticle thickening and the accumulation of crystals on the leaf stomata	Vilela et al. (2014)
13	Stalk borer	Sugarcane	Reduced percent stalks bored and stalk length bored	Keeping et al. (2013)
14	<i>Euschistus</i>	Soybean	Increased non-preference and antibiosis resistances	de Souza et al. (2016)
<b>C. Heavy metal</b>				
15	Cu	Wheat	Cu form complex with organic acids and reduced the Cu translocation to shoots	Keller et al. (2015)
16	Cr	Barley	Increased plant height, number of tillers, root length and leaf size of barley plants	Ali et al. (2013)
17	Pb	Cotton	Increased the activities of antioxidant enzymes and preventing membrane oxidative damage of plant tissue	Bharwana et al. (2013)
18	Cd	Rapeseed	Mediated extensive development of suberin lamellae in endoderm closer to the root tips	Vatehova et al. (2012)
<b>Abiotic stress</b>				
19	Drought	Pistachio	Enhanced photochemical efficiency and photosynthetic gas exchange; activation of the antioxidant defence capacity	Habibi and Hajiboland (2013)
20		Rice	Enhanced expression of transcription factors, <i>DREB2A</i> , <i>NAC5</i> , as well as ring domain containing <i>OsRDCP1</i> gene and some drought specific genes, such as <i>OsCMO</i> coding rice choline monoxygenase and dehydrin <i>OsRAB16b</i>	Khattab et al. (2014)
21		Wheat	Increased RWC and water potential; increased net photosynthetic rate, stomatal conductance and leaf transpiration rate	Gong and Chen (2012)
22		Kentucky bluegrass	Improving plant water relations and morpho-physiological functions	Saud et al. (2014)
23		Sorghum	Increased RWC, transpiration rate, and improved various physiological processes	Yin et al. (2014)

**Table 2** (continued)

S. no.	Biotic/abiotic stress	Crop	Mechanisms	References
24	Salinity	Okra	Decreased the Na <sup>+</sup> and Cl <sup>-</sup> in the shoots and roots; increased RWC; increased antioxidant enzyme activities	Abbas et al. (2015)
25		<i>Spartina densiflora</i>	Reduced sodium uptake; increased net photosynthetic rate and water use efficiency (WUE)	Mateos-Naranjo et al. (2013)
26		Rice	Reduced the sodium accumulation, electrolytic leakage and lipid peroxidation; influenced the phytohormonal responses	Kim et al. (2014a)
27		Rice	Suppression of Na <sup>+</sup> accumulation in shoots; reduced Na <sup>+</sup> concentrations in the leaf blades and sheaths, increased net assimilation rate and stomatal conductance	Gurmani et al. (2013)
28		Canola	Reduced toxic ions (Na <sup>+</sup> and Cl <sup>-</sup> ) accumulation, increased antioxidant enzyme activity; reduction in hydrogen peroxide and lipid peroxidation	Farshidi et al. (2012)
29		Wheat	Decreased Na <sup>+</sup> and increased K <sup>+</sup> concentrations in shoots; maintained membrane permeability; improved plant water contents in shoots	Tahir et al. (2012)
30		Lettuce	Modulation of oxidative stress	Milne et al. (2012)
31		Sorghum	Increased polyamines and decreased ethylene	Yin et al. (2015)
32		Tomato	Increased expression of genes related to salt stress responses ( <i>leDREB-1</i> , <i>leDREB-2</i> and <i>leDREB-3</i> ), Si transport ( <i>leLsi-1</i> , <i>leLsi-2</i> and <i>leLsi-3</i> ), and antioxidants ( <i>leAPX</i> , <i>leSOD</i> and <i>leCAT</i> )	Muneer and Jeong (2015)

et al. 2014). In 2014, Liu and co-workers used proteomic approach viz., two-dimensional gel electrophoresis (2-DE) and liquid chromatography–mass spectrometry (LC-MS/MS) to unravel the role of Si in providing resistance to the rice plant against rice blast fungus. Si application to blast fungus inoculated rice plants results in alteration of proteins involved in energy/metabolism, photosynthesis, redox homeostasis, cellular processes and pathogen response (Liu et al. 2014). Over-expression of the *Lsi1* gene could trigger a cold stress response in the rice plant. Azeem et al. (2016) used quantitative proteomic approach (tandem mass tag) to study the *Lsi1* gene regulation in rice under cold stress. The cold-responsive proteins identified were involved in various processes such as photosynthesis, metabolism, signal transduction, redox homeostasis, cell wall organization, N-assimilation, protein processing and secondary metabolism (Azeem et al. 2016). Similarly, Si-mediated detoxification of Cd metal in suspension cells of rice was investigated using a combination of isobaric tags for relative and absolute quantification (iTRAQ), fluorescent staining, and inductively coupled plasma mass spectrometry (ICP-MS). Under metal stress, Si application maintains the cell in the normal physiological state thus improving protein use efficiency of the cell (Ma et al. 2016). Under short-term Cd stress, there is a reduction in the expression of glycosidase, cell surface non-specific lipid-transfer proteins (nsLTPs) whereas long-term Cd stress showed lower expression of glutathione

S-transferases (GST) (Ma et al. 2016). The expression level of Si transport responsive genes (*OsLSi1* and *OsLSi2*) under heavy metal stress showed up-regulation of mRNA expression on the application of Si in rice (Kim et al. 2014b). Si application may modify root morphology to modulate heavy metal stress in the rice plant (Kim et al. 2014b). Si under salinity stress alleviates chloroplast and their metabolism damage in tomato plant (Muneer et al. 2014). Si supplementation under salinity stress can make tomato plant salt tolerant by improving photosynthetic metabolism and chloroplast proteome expression (Muneer et al. 2014).

## Conclusion

Si—a multi-talented element has a much more advantageous role in combating both biotic and abiotic stresses than previously thought and understood. With the latest available literature it can be concluded that Si could be considered as a regular fertilizer particularly for high accumulator species like most of the cereals and monocots. In addition, recent findings have also highlighted the beneficial effects of Si in some of the dicot plant species. However, to increase applicability and broaden the coverage of plant species that can pursue benefits derived from Si, better understanding of underlying molecular mechanisms is critical. Presently, several models and mechanisms have been proposed to

explain how Si provides increased protection to plants under stressed conditions. But none of the proposed mechanisms describes the exact pathways or biochemical reactions where Si plays a key role. Thus, there is a need to utilize advance approach such as omics to unravel these pathways. Despite all these unanswered questions, present knowledge allows us to explore the Si-derived benefits either by supplementation or by developing novel cultivars with better Si uptake. Genetic modification of root traits of dicot would be helpful in developing dicots with better uptake and higher accumulation of Si. The improved Si-derived benefits in plants will be helpful to develop a more sustainable cropping system in the future.

## Compliance with ethical standards

**Conflict of interest** Authors declare that there is no conflict of interest.

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