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REVIEW ARTICLE

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

Sajad Majeed Zargar[1] · **Reetika Mahajan**[2] · **Javaid A. Bhat**[2] · **Muslima Nazir**[1] · **Rupesh Deshmukh**[3]

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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_2), 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 [$Si(OH)_4$ or H_4SiO_4]. 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_2) 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

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✉ Sajad Majeed Zargar
smzargar@gmail.com

✉ Rupesh Deshmukh
rupesh0deshmukh@gmail.com

[1] Division of Plant Biotechnology, Sher-e-Kashmir University of Agricultural Sciences and Technology of Kashmir, Shalimar, Srinagar, J&K 190025, India

[2] School of Biotechnology, Sher-e-Kashmir University of Agricultural Sciences and Technology of Jammu, Chatha, Jammu, J&K 180009, India

[3] 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; Henriet 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), Fabaceace (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 (NIPIIIs)	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		GmNIP2-1 GmNIP2-2	Soybean	Deshmukh et al. (2013)
11		EaNIP4, EaNIP5	Horsetail	Grégoire et al. (2012)
12	Efflux	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 phytoalexinin 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 β-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* (Conceiçao et al. 2014). Si application also enhanced the activities of β-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 al. 2015). Supply of potassium silicate in pea seedlings increases chitinase and β-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 Rectifer) gene. Si application can improves 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 annuum* 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 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 Na^+ uptake by plants under salt stress and increased K^+/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 (Mahdieh 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 H^+-ATPase and reduced ROS generation in many plant species under saline conditions (Al-aghabary 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 ($nSiO_2$) 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 $nSiO_2$ 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 $nSiO_2$ 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*), $nSiO_2$ 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 $nSiO_2$ on *Vicia faba* can improve germination characters when exposed to salinity stress. Thus, it can be concluded that $nSiO_2$ 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 ($nSiO_2$ and nMo) are commonly used as engineered oxide nano particles. Nano particles have both beneficial and toxic effect on plants. Effect of $nSiO_2$ 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 $nSiO_2$ had no toxic effect on rice. However, $nSiO_2$ enhanced the root length and volume, dry matter weight of shoot and root of rice (Adhikari et al. 2013). Application of specific nanoparticles 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 $nSiO_2$ 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
A. Disease				
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, β-1,3 glucanase, peroxidase and phenylalanine ammonia-lyase	Souza et al. (2015)
5	Anthracnose	Tomato	Increased thickness of cuticle and fruit firmness	Somapala et al. (2016)
6	Anthracnose	Sweet pepper	Increases the firmness and cuticle thickness of fruits	Jayawardana et al. (2014)
B. Insect pest				
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 *S. frugiperda* 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	*Diatraeasaccharalis*	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	*Euschistusheros*	Soybean	Increased non-preference and antibiosis resistances	de Souza et al. (2016)
C. Heavy metal				
15	Cu	Wheat	Cu form complex with organic acids and 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)
Abiotic stress				
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, *DREB2A*, *NAC5*, as well as ring domain containing *OsRDCP1* gene and some drought specific genes, such as *OsCMO* coding rice choline monooxygenase and dehydrin*OsRAB16b*	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^+ and Cl^- in the shoots and roots; increased RWC; increased antioxidant enzyme activities	Abbas et al. (2015)
25		*Spartina densiflora*	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^+ accumulation in shoots; reduced Na^+ concentrations in the leaf blades and sheaths, increased net assimilation rate and stomatal conductance	Gurmani et al. (2013)
28		Canola	Reduced toxic ions (Na^+ and Cl^-) accumulation, increased antioxidant enzyme activity; reduction in hydrogen peroxide and lipid peroxidation	Farshidi et al. (2012)
29		Wheat	Decreased Na^+ and increased K^+ 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 (*leDREB-1, leDREB-2* and *leDREB-3*), Si transport (*leLsi-1, leLsi-2* and *leLsi-3*), and antioxidants (*leAPX, leSOD* and *leCAT*)	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 spectroscopy (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.

References

Abbas T, Balal RM, Shahid MA, Pervez MA, Ayyub CM, Aqueel MA, Javaid MM (2015) Silicon-induced alleviation of NaCl toxicity in okra (*Abelmoschus esculentus*) is associated with enhanced photosynthesis, osmoprotectants and antioxidant metabolism. Acta Physiol Plant 37:1–15

Abdalla MM (2011a) Beneficial effects of diatomite on growth, the biochemical contents and polymorphic DNA in *Lupinus albus* plants grown under water stress. Agric Biol J N Am 2:207–220

Abdalla MM (2011b) Impact of diatomite nutrition on two *Trifolium alexandrinum* cultivars differing in salinity tolerance. Int J Plant Physiol Biochem 3:233–246

Abdul Qados AMS, Moftah AE (2015) Influence of silicon and nano-silicon on germination growth and yield of faba bean (*Vicia faba* L.) under salt stress conditions. Am J Soc Hortic Sci 5(6):509–524

Abu-Muriefah SS (2015) Effects of Silicon on Faba Bean (*Vicia faba* L.) plants grown under heavy metal stress conditions. Afr J Agric Sci Technol (AJAST) 3(5):255–268

Adhikari T, Kundu S, Rao AS (2013) Impact of SiO_2 and Mo nano particles on seed germination of rice (*Oryza Sativa* L.). Int J Agric Food Sci Technol 4(8):809–816

Adrees M, Ali S, Rizwan M et al (2015) Mechanisms of silicon-mediated alleviation of heavy metal toxicity in plants: a review. Ecotoxicol Environ Saf 119:186–197

Agarie S, Hanaoka N, Ueno O, Miyazaki A, Kubota F, Agata W, Kaufman PB (1998) Effects of silicon on tolerance to water deficit and heat stress in rice plants (*Oryza sativa* L.), monitored by electrolyte leakage. Plant Prod Sci 1(2):96–103

Al-aghabary K, Zhu Z, Shi Q (2005) Influence of silicon supply on chlorophyll content, chlorophyll fluorescence, and antioxidative enzyme activities in tomato plants under salt stress. J Plant Nutr 27:2101–2115

Ali A, Basra SM, Ahmad R, Wahid A (2009) Optimizing silicon application to improve salinity tolerance in wheat. Soil Environ 2:136–144

Ali S, Farooq MA, Yasmeen T, Hussain S, Arif MS, Abbas F et al (2013) The influence of silicon on barley growth, photosynthesis and ultra-structure under chromium stress. Ecotoxicol Environ Saf 89:66–72

Allahmoradi P, Ghobadi M, Taherabadi S, Taherabadi S (2011) Physiological aspects of Mung bean (*Vigna radiata* L.) in response to drought stress. In: International conference on food engineering and biotechnology, IPCBEE, vol 9, pp 272–275

Almutairi ZM (2016) Effect of nano-silicon application on the expression of salt tolerance genes in germinating tomato (*Solanum lycopersicum* L.) seedlings under salt stress. POJ 9(1):106–114

Alves AO, Santos MMB, Souza LJN, Souza EB, Mariano RLR (2015) Use of silicon for reducing the severity of bacterial wilt of sweet pepper. J Plant Pathol 97(3):419-429

Amin M, Ahmad R, Basra SM, Murtaza G (2014) Silicon induced improvement in morpho-physiological traits of maize (*Zea mays* L.) under water deficit. Pak J Agric Sci 51:187–196

Amirossadat Z, Ghehsareh AM, Mojiri A (2012) Impact of silicon on decreasing of salinity stress in greenhouse cucumber (*Cucumis sativus* L.) in soilless culture. J Biol Environ Sci 6(17):171–174

Anwaar SA, Ali S, Ali S, Ishaque W, Farid M, Farooq MA, Najeeb U, Abbas F, Sharif M (2014) Silicon (Si) alleviates cotton (*Gossypium hirsutum* L.) from zinc (Zn) toxicity stress by limiting Zn uptake and oxidative damage. Environ Sci Pollut Res. https://doi.org/10.1007/s11356-014-3938-9

Arnon DI, Stout PR (1939) The essentiality of certain elements in minute quantity for plants, with special reference to copper. Plant Physiol 14:371–375. https://doi.org/10.1104/pp.14.2.371

Asgharipour MR, Mosapour H (2016) A foliar application silicon enhances drought tolerance in fennel. J Anim Plant Sci 26(4):1056–1062

Azeem S, Li Z, Zheng H, Lin W, Arafat Y, Zhang Z, Lin X, Lin W (2016) Quantitative proteomics study on Lsi1 in regulation of rice (*Oryza sativa* L.) cold resistance. Plant Growth Regul 78(3):307–323

Belanger RR, Benhamou N, Menzies JG (2003) Cytological evidence of an active role of silicon in wheat resistance to powdery mildew (*Blumeria graminis* f. sptritici). Phytopathology 93:402–412

Bharwana SA, Ali S, Farooq MA, Iqbal N, Abbas F, Ahmad MSA (2013) Alleviation of lead toxicity by silicon is related to elevated photosynthesis, antioxidant enzymes suppressed lead uptake and oxidative stress in cotton. J Bioremediat Biodegrad 4:1–11

Bokor B, Bokorova S, Ondos S, Svubova R, Lukacova Z, Hyblova M, Szemes T, Lux A (2014) Ionome and expression level of Si transporter genes (Lsi1, Lsi2, and Lsi6) affected by Zn and Si interaction in maize. Environ Sci Pollut Res. https://doi.org/10.1007/s11356-014-3876-6

Botelho DMS, Pozza EA, Pozza AAA, Carvalho JG (2005) Effect of silicon doses and sources on the intensity of the brown eye spot of coffee seedlings. Fitopatologia Brasileira 30:582–588

Bradacova K, Weber NF, Morad-Talab N, Asim M, Imran M, Weinmann M, Neumann G (2016) Micronutrients (Zn/Mn), seaweed extracts, and plant growth-promoting bacteria as cold-stress protectants in maize. Chem Biol Technol Agric 3::19

Brenchley WE, Maskell EJ (1927) The inter-relation between silicon and other elements in plant nutrition. Ann Appl Biol 14:45–82

Broadley M, Brown P, Cakmak I, Ma JF, Rengel Z, Zhao F (2011) Beneficial elements. In: Marschner P (ed) Marschner's mineral nutrition of higher plants, 3rd edn. Elsevier, Amsterdam, pp 257–261

Bybordi A (2014) Interactive effects of silicon and potassium nitrate in improving salt tolerance of wheat. Int J Agric 13:1889–1899

Cai K, Gao D, Chen J, Luo S (2008) Probing the mechanisms of silicon-mediated pathogen resistance. Plant Signal Behav 4(1):1–3

Carre-Missio V, Rodrigues FA, Schurt DA, Rezende DC, Moreira WR, Korndorfer GH, Zambolim L (2012) Componentes epidemiologicos da ferrugem do cafeeiro afetadospela aplicaçao foliar de silicato de potássio. Trop Plant Pathol 37:50–56

Carre-Missio V, Rodrigues FA, Schur DA, Resende RS, Souza NFA, Rezende DC, Moreira WR, Zambolim L (2014) Effect of foliar-applied potassium silicate on coffee leaf infection by *Hemileia vastatrix*. Ann Appl Biol 164:396–403

Chen D, Yin L, Deng X, Wang S (2014) Silicon increases salt tolerance by influencing the two-phase growth response to salinity in wheat (*Triticum aestivum* L.). Acta Physiologiae Plantarum 36(9):2531–2535

Chen D, Cao B, Wang S, Liu P, Deng X, Yin L, Zhang S (2016) Silicon moderated the K deficiency by improving the plant-water status in sorghum. Sci Rep 6:22882

Chen D, Wang S, Yin L, Deng X (2018) How does silicon mediate plant water uptake and loss under water deficiency? Front Plant Sci 9:281. https://doi.org/10.3389/fpls.2018.00281

Chiba Y, Mitani N, Yamaji N, Ma JF (2009) HvLsi1 is a silicon influx transporter in barley. Plant J 57:810–818

Conceiçao CS, Felix KCS, Mariano RL, Medeiros EV, Souza EB (2014) Combined effect of yeast and silicon on the control of bacterial fruit blotch in melon. Sci Hortic 174:164–170

Cooke J, Leishman MR (2011) Is plant ecology more siliceous than we realise? Trends Plant Sci 16:61–68. https://doi.org/10.1016/j.tplants.2010.10.003

Cornelis JT, Delvauz B, Georg RB, Lucas Y, Ranger J, Opfergelt S (2011) Tracing the origin of dissolved silicon transferred from various soil-plant systems towards rivers: a review. Biogeosciences 8:89–112

Correa RS, Moraes JC, Auad AM, Carvalho GA (2005) Silicon and acibenzolar-*S*-methyl as resistance inducers in cucumber, against the whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) biotype B. Neotrop Entomol 34(3):429–433

da Cunha KPV, do Nascimento CWA (2009) Silicon effects on metal tolerance and structural changes in maize (*Zea mays* L.) grown on a cadmium and zinc enriched soil. Water Air Soil Pollut 197:323–330

Dann EK, Muir S (2002) Peas grown in media with elevated plant-available silicon levels have higher activities of chitinase and β-1, 3-glucanase, are less susceptible to a fungal leaf spot pathogen and accumulate more foliar silicon. Australas Plant Pathol 31(1):9–13

Datnoff LE, Rodrigues FA (2005) The role of silicon in suppressing rice diseases. Am Phytopathol Soc. https://doi.org/10.1094/APSnetFeature-2005-0205

Datnoff LE, Deren CW, Snyder GH (1997) Silicon fertilization for disease management of rice in Florida. Crop Prot 16:525–531

de Camargo MS, Amorim L, Júnior ARG (2013) Silicon fertilization decreases brown rust incidence in sugarcane. Crop Prot 53:72–79. https://doi.org/10.1016/j.cropro.2013.06.006

de Souza PV, Machado BR, Zanuncio JC, Araújo MS, Alves GCS, de Jesus FG (2016) Cultivation of resistant soybean varieties and application of silicon (Si) on biology of '*Euschistus heros*' (Hemiptera: Pentatomidae). Aust J Crop Sci 10(10):1404

Deshmukh RK, Vivancos J, Guérin V, Sonah H, Labbé C, Belzile F, Bélanger RR (2013) Identification and functional characterization of silicon transporters in soybean using comparative genomics of major intrinsic proteins in *Arabidopsis* and rice. Plant Mol Biol 83:303–315

Deshmukh RK, Vivancos J, Ramakrishnan G, Guérin V, Carpentier G, Sonah H et al (2015) A precise spacing between the NPA domains of aquaporins is essential for silicon permeability in plants. Plant J 83:489–500. https://doi.org/10.1111/tpj.12904

Ding TP, Ma GR, Shui MX, Wan DF, Li RH (2005) Silicon isotope study on rice plants from the Zhejiang province, China. Chem Geol 218:41–50

dos Santos MC, Junqueira AR, de Sá VM, Zanúncio JC, Serrão JE (2015) Effect of silicon on the morphology of the midgut and mandible of tomato leafminer *Tuta absoluta* (Lepidoptera: Gelechiidae) larvae. ISJ 12:158–165

Emam MM, Khattab HE, Helal NM, Deraz AE (2014) Effect of selenium and silicon on yield quality of rice plant grown under drought stress. Aust J Crop Sci 8(4):596

Epstein E (1999) Silicon. Annu Rev Plant Biol 50(1):641–664

Epstein E (2009) Silicon: its manifold roles in plants. Ann Appl Biol 155:155–160. https://doi.org/10.1111/j.1744-7348.2009.00343.x

Exley C (2015) A possible mechanism of biological silicification in plants. Front Plant Sci 6:853. https://doi.org/10.3389/fpls.2015.00853

Farshidi M, Abdolzadeh A, Sadeghipour HR (2012) Silicon nutrition alleviates physiological disorders imposed by salinity in hydroponically grown canola (*Brassica napus* L.) plants. Acta Physiologiae Plantarum 34(5):1779–1788

Fauteux F, Rémus-Borel W, Menzies JG, Bélanger RR (2005) Silicon and plant disease resistance against pathogenic fungi. FEMS Microbiol Lett 249(1):1–6

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

Fawe A, Menzies JG, Chérif M, Bélanger RR (2001) Silicon and disease resistance in dicotyledons. Stud Plant Sci 8:159–169

Gao X, Zou C, Wang L, Zhang F (2006) Silicon decreases transpiration rate and conductance from stomata of maize plants. J Plant Nutr 29(9):1637–1647

Garg N, Bhandari P (2015) Silicon nutrition and mycorrhizal inoculations improve growth, nutrient status, K^+ /Na^+ ratio and yield of *Cicer arietinum* L. genotypes under salinity stress. Plant Growth Regul. https://doi.org/10.1007/s10725-015-0099-x

Gérard F, François M, Ranger J (2002) Processes controlling silica concentration in leaching and capillary soil solutions of an acidic brown forest soil (Rhône, France). Geoderma 107:197–226

Ghareeb H, Bozso Z, Ott PG, Repenning C, Stahl F, Wydra K (2011) Transcriptome of silicon-induced resistance against *Ralstonia solanacearum* in the silicon non-accumulator tomato implicates priming effect. Physiol Mol Plant Pathol 75(3):83–89

Gong HJ, Chen KM (2012) The regulatory role of silicon on water relations, photosynthetic gas exchange, and carboxylation activities of wheat leaves in field drought conditions. Acta Physiol Plant 34:1589–1594

Grégoire C, Rémus-Borel W, Vivancos J, Labbé C, Belzile F, Bélanger RR (2012) Discovery of a multigene family of aquaporin silicon transporters in the primitive plant *Equisetum arvense*. Plant J 72:320–330

Gu HH, Qiu H, Tian T, Zhan SS, Chaney RL, Wang SZ et al (2011) Mitigation effects of silicon rich amendments on heavy metal accumulation in rice (*Oryza sativa* L.) planted on multi-metal contaminated acidic soil. Chemosphere 83:1234–1240

Gunes A, Pilbeam DJ, Inal A, Bagci EG, Coban S (2007) Influence of silicon on antioxidant mechanisms and lipid peroxidation in chickpea (*Cicer arietinum* L.) cultivars under drought stress. J Plant Interact 2:105–113

Gunes A, Pilbeam DJ, Inal A, Coban S (2008) Influence of silicon on sunflower cultivars under drought stress, I: growth, antioxidant mechanisms, and lipid peroxidation. Commun Soil Sci Plant Anal 39(13–14):1885–1903

Guntzer F, Keller C, Poulton PR, McGrath SP, Meunier JD (2012) Long term removal of wheat straw decreases soil amorphous silica at Broadbalk, Rothamsted. Plant Soil 352:173–184

Gupta B, Huang B (2014) Mechanism of salinity tolerance in plants: physiological, biochemical, and molecular characterization. Int J Genom. https://doi.org/10.1155/2014/701596

Gurmani AR, Bano A, Najeeb U, Zhang J, Khan SU, Flowers TJ (2013) Exogenous abscisic acid (ABA) and silicon (Si) promote salinity tolerance by reducing sodium (Na^+) transport and bypass flow in rice (*Oryza sativa indica*). Aust J Crop Sci 7:1123–1130

Gutierrez-Barranquero JA, Arrebola E, Bonilla N, Sarmiento D, Cazorla FM, de Vicente A (2012) Environmentally friendly treatment alternatives to Bordeaux mixture for controlling bacterial apical necrosis (BAN) of mango. Plant Pathol 61(4):665–676

Habibi G, Hajiboland R (2013) Alleviation of drought stress by silicon supplementation in pistachio (*Pistacia vera* L.) plants. Folia Hortic 25(1):21–29

Hameed A, Sheikh MA, Jamil A, Basra SMA (2013) Seed priming with sodium silicate enhances seed germination and seedling growth in wheat (*Triticum aestivum* L.) under water deficit stress induced by polyethylene glycol. Pak J Life Soc Sci 11:19–24

Han Y, Li P, Gong S, Yang L, Wen L, Hou M (2015) Defense responses in rice induced by silicon amendment against infestation by the leaf folder *Cnaphalocrocis medinalis*. PLoS One 11(4):e0153918

Hayat R, Ali S, Amara U, Khalid R, Ahmed I (2010) Soil beneficial bacteria and their role in plant growth promotion: a review. Ann Microbiol 60:579–598

He W, Yang M, Li Z, Qiu J, Liu F, Qu X, Qiu Y, Li R (2015) High levels of silicon provided as a nutrient in hydroponic culture enhances rice plant resistance to brown planthopper. Crop Prot 67:20–25

Heaney PJ, Prewitt CT, Gibbs GV (eds) (1994) Silica: physical behavior, geochemistry and materials applications. In: Reviews in mineralogy, vol 29. Mineralogical Society of America

Henriet C, Bodarwe L, Dorel M, Draye X, Delvaux B (2008) Leaf silicon content in banana (*Musa* spp.) reveals the weathering stage of volcanic ash soils in Guadeloupe. Plant Soil 313:71–82

Hodson M, White P, Mead A, Broadley M (2005) Phylogenetic variation in the silicon composition of plants. Ann Bot 96:1027–1046

Hussein MM, Abou-Baker NH (2014) Growth and mineral status of Moringa plants as affected by silicate and salicylic acid under salt stress. Int J Plant Soil Sci 3(2):163–177

Iwasaki K, Maier P, Fecht M, Horst WJ (2002) Leaf apoplastic silicon enhances manganese tolerance of cow-pea (*Vigna unguiculata*). J Plant Physiol 159(2):167–173

Jayawardana HARK, Weerahewa HLD, Saparamadu MDJS (2014) Effect of root or foliar application of soluble silicon on plant growth, fruit quality and anthracnose development of capsicum. Trop Agric Res 26(1):74–81

Jia-Wen WU, Yu SHI, Yong-Xing ZHU, Yi-Chao WANG, Hai-Jun GONG (2013) Mechanisms of enhanced heavy metal tolerance in plants by silicon: a review. Pedosphere 23(6):815–825

Jones LHP, Handreck KA (1967) Silica in soils, plants, and animals. Adv Agron 19:107–149

Kalteh M, Alipour ZT, Ashraf S, Aliabadi MM, Nosratabadi AF (2014) Effect of silica nanoparticles on basil (*Ocimum basilicum*) under salinity stress. J Chem Health Risk 4(3):49–55

Kardoni F, Mosavi SJS, Parande S, Torbaghan ME (2013) Effect of salinity stress and silicon application on yield and component yield of faba bean (*Vicia faba*). Int J Agric Crop Sci 6(12):814

Keeping MG, Kvedaras OL, Bruton AG (2009) Epidermal silicon in sugarcane: cultivar differences and role in resistance to sugarcane borer *Eldana saccharina*. Environ Exp Bot 66(1):54–60

Keeping MG, Meyer JH, Sewpersad C (2013) Soil silicon amendments increase resistance of sugarcane to stalk borer *Eldana saccharina* Walker (Lepidoptera: Pyralidae) under field conditions. Plant Soil 363(1–2):297–318

Keller C, Rizwan M, Davidian JC, Pokrovsky OS, Bovet N, Chaurand P, Meunier JD (2015) Effect of silicon on wheat seedlings (*Triticum turgidum* L.) grown in hydroponics and exposed to 0 to 30 µM Cu. Planta 241:847–860

Khattab HI, Emam MA, Emam MM, Helal NM, Mohamed MR (2014) Effect of selenium and silicon on transcription factors NAC5 and DREB2A involved in drought-responsive gene expression in rice. Biologia Plantarum 58(2):265–273

Kim SG, Kim KW, Park EW, Choi D (2002) Silicon-induced cell wall fortification of rice leaves: a possible cellular mechanism of enhanced host resistance to blast. Phytopathology 92:1095–1103

Kim YH, Khan AL, Waqas M, Shim JK, Kim DH, Lee KY, Lee IJ (2014a) Silicon application to rice root zone influenced the phytohormonal and antioxidant responses under salinity stress. J Plant Growth Regul 33:137–149

Kim YH, Khan AL, Kim DH, Lee SY, Kim KM, Waqas M et al (2014b) Silicon mitigates heavy metal stress by regulating P-type heavy metal ATPases, *Oryza sativa* low silicon genes, and endogenous phytohormones. BMC Plant Biol 14:13. https://doi.org/10.1186/1471-2229-14-13

Knight CTG, Kinrade SD (2001) A primer on the aqueous chemistry of silicon. In: Datnoff LE, Snyder GH, Korndörfer GH (eds) Silicon in agriculture, studies in plant science, vol 8. Elsevier, Amsterdam, pp 57–84

Kurabachew H, Stahl F, Wydra K (2013) Global gene expression of rhizobacteria-silicon mediated induced systemic resistance in tomato (*Solanum lycopersicum*) against *Ralstonia solanacearum*. Physiol Mol Plant Pathol 84:44–52

Lee SK, Sohn EY, Hamayun M, Yoon JY, Lee IJ (2010) Effect of silicon on growth and salinity stress of soybean plant grown under hydroponic system. Agrofor Syst 80:333–340

Li H, Zhu Y, Hu Y, Han W, Gong H (2015) Beneficial effects of silicon in alleviating salinity stress of tomato seedlings grown under sand culture. Acta Physiol Plant 37(4):1–9

Liang YC, Si J, Römheld V (2005a) Silicon uptake and transport is an active process in *Cucumis sativus*. N Phytol 167:797–804

Liang YC, Sun WC, Si J, Romheld V (2005b) Effects of foliar-and root-applied silicon on the enhancement of induced resistance to powdery mildew in *Cucumis sativus*. Plant Pathol 54(5):678–685

Liang Y, Sun W, Zhu Y-G, Christie P (2007) Mechanisms of silicon mediated alleviation of abiotic stresses in higher plants: a review. Environ Pollut 147:422–428. https://doi.org/10.1016/j.envpol.2006.06.008

Liang Y, Nikolic M, Bélanger R, Gong H, Song A (2015) Silicon in agriculture: from theory to practice. Springer, Dordrecht

Liu M, Cai K, Chen Y, Luo S, Zhang Z, Lin W (2014) Proteomic analysis of silicon mediated resistance to *Magnaporthe oryzae* in rice (*Oryza sativa* L.). Eur J Plant Pathol 139(3):579–592

Lu G, Jian W, Zhang J, Zhou Y, Cao J (2008) Suppressive effect of silicon nutrient on *Phomopsis* stem blight development in asparagus. Hort Sci 43(3):811–817

Lukacova Z, Svubova R, Kohanova J, Lux A (2013) Silicon mitigates the Cd toxicity in maize in relation to cadmium translocation, cell distribution, antioxidant enzymes stimulation and enhanced endodermal apoplasmic barrier development. Plant Growth Regul 70:89–103

Lux A, Luxova M, Abe J, Tanimoto E, Taiichiro H, Shinobu I (2003) The dynamics of silicon deposition in the sorghum root endodermis. N Phythol 158:437–441

Luyckx M, Hausman J-F, Lutts S, Guerriero G (2017) Silicon and plants: current knowledge and technological perspectives. Front Plant Sci 8:411. https://doi.org/10.3389/fpls.2017.0041

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

Ma JF, Takahashi E (2002) Soil, fertilizer, and plant silicon research in Japan. Elsevier, Amsterdam

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

Ma JF, Yamaji N (2015) A cooperative system of silicon transport in plants. Trends Plant Sci 20:435–442. https://doi.org/10.1016/j.tplants.2015.04.007

Ma JF, Miyake Y, Takahashi E (2001) Silicon as a beneficial element for crop plants. In: Datnoff LE, Snyder GH, Korndorfer GH (eds) Silicon in agriculture. Elsevier, Amsterdam, pp 17–39

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

Ma JF, Yamaji N, Mitani M, Tamai K, Konishi S, Fujiwara T, Katsuhara M, Yano M (2007) An efflux transporter of silicon in rice. Nature 448:209–212

Ma JF, Yamaji N, Mitani-Ueno N (2011) Transport of silicon from roots to panicles in plants. Jpn Acad Ser B 87:377–385

Ma J, Sheng H, Li X, Wang L (2016) iTRAQ-based proteomic analysis reveals the mechanisms of silicon-mediated cadmium tolerance in rice (*Oryza sativa*) cells. Plant Physiol Biochem. https://doi.org/10.1016/j.plaphy.2016.03.024

Maghsoudi K, Emam Y, Ashraf M (2016) Foliar application of silicon at different growth stages alters growth and yield of selected wheat cultivars. J Plant Nutr 39(8):1194–1203

Mahdieh M, Habibollahi N, Amirjani MR, Abnosi MH, Ghorbanpour M (2015) Exogenous silicon nutrition ameliorates salt-induced stress by improving growth and efficiency of PSII in *Oryza sativa* L. cultivars. J Soil Sci Plant Nutr 15(4):1050–1060

Maksimovic JD, Mojovic M, Maksimovic V, Romheld V, Nikolic M (2012) Silicon ameliorates manganese toxicity in cucumber by decreasing hydroxyl radical accumulation in the leaf apoplast. J Exp Bot 63:2411–2420

Malcovska SM, Ducaiova Z, Maslanakova I, Backor M (2014) Effect of silicon on growth, photosynthesis, oxidative status and phenolic compounds of maize (*Zea mays* L.) grown in cadmium excess. Water Air Soil Pollut 225(8):2056

Malhotra CH, Kapoor R, Ganjewala D (2016) Alleviation of abiotic and biotic stresses in plants by silicon supplementation. Scientia 13(2):59–73

Manivannan A, Soundararajan P, Muneer S, Ko CH, Jeong BR (2016) Silicon mitigates salinity stress by regulating the physiology, antioxidant enzyme activities, and protein expression in *Capsicum annuum* 'Bugwang'. Bio Med Res Int. https://doi.org/10.1155/2016/3076357

Marxen A, Klotzbucher T, Jahn R, Kaiser K, Nguyen VS, Schmidt A, Schadler M, Vetterlein D (2015) Interaction between silicon cycling and straw decomposition in a silicon deficient rice production system. Plant Soil. https://doi.org/10.1007/s11104-015-2645-8

Mateos-Naranjo E, Andrades-Moreno L, Davy AJ (2013) Silicon alleviates deleterious effects of high salinity on the halophytic grass *Spartina densiflora*. Plant Physiol Biochem 63:115–121

Maxim LD, Niebo R, La Rosa S, Johnston B, Allison K, McConnell EE (2008) Product stewardship in wollastonite production. Inhal Toxicol 20:1199–1214

Milne CJ, Laubscher CP, Ndakidemi PA, Marnewick JL, Rautenbach F (2012) Salinity induced changes in oxidative stress and antioxidant status as affected by applications of silicon in lettuce (*Lactuca sativa*). Int J Agric Biol 14(5):763–768

Ming DF, Pei ZF, Naeem MS, Gong HJ, Zhou WJ (2012) Silicon alleviates PEG-induced water-deficit stress in upland rice seedlings by enhancing osmotic adjustment. J Agron Crop Sci 198:14–26

Mitani N, Chiba Y, Yamaji N, Ma JF (2009a) Identification and characterization of maize and barley Lsi-2-like silicon efflux transporters reveals a distinct silicon uptake system from that in rice. Plant Cell 21:2133–2142

Mitani N, Yamaji N, Ma JF (2009b) Identification of maize silicon influx transporters. Plant Cell Physiol 50:5–12

Mitani N, Yamaji N, Ago Y, Iwasaki K, Ma JF (2011) Isolation and functional characterisation of silicon transporter in two Pumpkin cultivars contrasting in silicon accumulation. Plant J 66:231–240

Mitani-Ueno N, Yamaji N, Ma JF (2011) Silicon efflux transporters isolated from two pumpkin cultivars contrasting in Si uptake. Plant Signal Behav 6:991–994

Miyake Y, Takahashi E (1982a) Effect of silicon on the growth of solution-cultured cucumber plants, Part 17. Comparative studies on silica nutrition in plants. Jpn J Soil Sci Plant Nutr 53:23–29

Miyake Y, Takahashi E (1982b) Effect of silicon on the growth of solution-cultured cucumber plants, Part 16. Comparative studies on silica nutrition in plants. Jpn J Soil Sci Plant Nutr 53:15–22

Monica RC, Cremonini R (2009) Nanoparticles and higher plants. Caryologia 62:161–165

Montpetit J, Vivancos J, Mitani-Ueno N, Yamaji N, Rémus-Borel W, Belzile F, Ma JF, Bélanger RR (2012) Cloning, functional characterization and heterologous expression of TaLsi1, a wheat silicon transporter gene. Plant Mol Biol 79:35–46

Muneer S, Jeong BR (2015) Proteomic analysis of salt-stress responsive proteins in roots of tomato (*Lycopersicon esculentum* L.) plants towards silicon efficiency. Plant Growth Regul. https://doi.org/10.1007/s10725-015-0045-y

Muneer S, Park YG, Manivannan A, Soundararajan P, Jeong BR (2014) Physiological and proteomic analysis in chloroplasts of *Solanum lycopersicum* L. under silicon efficiency and salinity stress. Int J Mol Sci 15:21803–21824. https://doi.org/10.3390/ijms151221803

Nascimento AM, Assis FA, Moraes JC, Sakomura R (2014) Nãopreferencia a Spodopterafrugiperda (Lepidoptera: Noctuidae) induzi daemarrozpelaaplicaçao de silício. Braz J Agric Sci Revista Brasileira de Ciencias Agrarias 9(2):215–218.

Neocleous D (2015) Grafting and silicon improve photosynthesis and nitrate absorption in melon (*Cucumis melo* L.) plants. J Agric Sci Technol 17:1815–1824

Nikolic M, Nikolic N, Liang Y, Kirkby EA, Romheld V (2007) Germanium-68 as an adequate tracer for silicon transport in plants. Characterization of silicon uptake in different crop species. Plant Physiol 143:495–503

Norton LD, Hall GE, Smeck NE, Bigham JM (1984) Fraginap bonding in a late-Wisconsian loss-derived soil in East-Central Ohio. Soil Sci Soc Am J 48:1360

Parthasarathy S, Jaiganesh V (2016) Plant activator and silicon nutrient mediated resistance against powdery mildew of Black gram (*Vigna mungo* L. Hepper). Glob J Res Anal 4(6):48–49

Paula LS, Silva BC, Pinho WCS, Barbosa MAM, Guedes Lobato EMS, Batista BL, Barbosa F Jr, Lobato AKS (2015) Silicon (Si) ameliorates the gas exchange and reduces negative impacts on photosynthetic pigments in maize plants under zinc (Zn) toxicity. Aust J Crop Sci 9:901–908

Pereira HS, Korndorfer GH, Moura WF, Correa GF (2003) Extractors of available silicon in slags and fertilizers. Revista Brasileira de Cienciado Solo 27:265–274

Pozza AAA, Alves E, Pozza EA, Carvalho JG, Montanari M, Guimaraes PTG, Santos DM (2004) Effect of silicon on the control of brown eye spot in three coffee cultivars. Fitopatologia Brasileira 29:185–188

Putra ETS, Purwanto BH (2015) Physiological responses of oil palm seedlings to the drought stress using boron and silicon applications. J Agron 14(2):49

Rao SDV (1967) Hardness of sugarcane varieties in relation to shoot borer infestation. Andhra Agric J 14:99–105

Raven JA (2001) Silicon transport at the cell and tissue level. In: Datnoff LE, Snyder GH, Korndorfer GH (eds) Silicon in agriculture. Elsevier, Amsterdam, pp 41–55

Raven JA (2003) Cycling silicon–the role of accumulation in plants. New Phytol 158:419–421

Reis THP, Figueiredo FC, Guimaraes PTG, Botrel PP, Rodrigues CR (2008) Efeito da associaçaosilícioliquidosoluvel com fungicida no controlefitossanitário do cafeeiro. Coffee Sci 3:76–80

Resende RS, Rodrigues F, Costa RV, Silva DD (2013) Silicon and fungicide effects on anthracnose in moderately resistant and susceptible sorghum lines. J Phytopathol 161(1):11–17

Richmond KE, Sussman M (2003) Got silicon? The non-essential beneficial plant nutrient. Curr Opin Plant Biol 6:268–272

Rizwan M, Meunier JD, Miche H, Keller C (2012) Effect of silicon on reducing cadmium toxicity in durum wheat (*Triticum turgidum* L. cv. Claudio W.) grown in a soil with aged contamination. J Hazard Mater 209–210:326–334

Rizwan M, Ali S, Ibrahim M, Farid M, Adrees M, Bharwana SA et al (2015) Mechanisms of silicon-mediated alleviation of drought and salt stress in plants: a review. Environ Sci Pollut Res 22:15416–15431. https://doi.org/10.1007/s11356-015-5305-x

Rodrigues FA, McNally DJ, Datnoff LE, Jones JB, Labbé C, Benhamou N, Menzies JG, Bélanger RR (2004) Silicon enhances the accumulation of diterpenoid phytoalexins in rice: a potential mechanism for blast resistance. Phytopathology 94:177–183

Rohanipoor A, Norouzi M, Moezzi A, Hassibi P (2013) Effect of silicon on some physiological properties of maize (*Zea mays*) under salt stress. J Biol Environ Sci 7:71–79

Sabaghnia N, Janmohammadi M (2014) Graphic analysis of nanosilicon by salinity stress interaction on germination properties of lentil using the biplot method. Agr For 60(3):29–40

Sachs JV (1860) Vegetations versuchemitausschluss des bodensüber die nährstoffe und sonstigenernährungsbedingungen von mais, bohnen, und anderenpflanzen. Landw Versuchsst 2:219–268

Sahebi M, Hanafi MM, Siti Nor Akmar A, Rafii MY, Azizi P, Tengoua FF, NurulMayzaitulAzwa J, Shabanimofrad M (2015) Importance of silicon and mechanisms of biosilica formation in plants. BioMed Res Int. https://doi.org/10.1155/2015/396010

Salim M, Saxena RC (1992) Iron, silica, and aluminum stresses and varietal resistance in rice: effects on white backed plant hopper. Crop Sci 32:212–219

Samuels AL, Glass ADM, Ehret DL, Menzies JG (1991) Mobility and deposition of silicon in cucumber plants. Plant Cell Environ 14(5):485–492

Saud S, Li X, Chen Y, Zhang L, Fahad S, Hussain S, Chen Y (2014) Silicon application increases drought tolerance of Kentucky bluegrass by improving plant water relations and morphophysiological functions. Sci World J. https://doi.org/10.1155/2014/368694

Shen X, Zhou Y, Duan L, Li Z, Eneji AE, Li J (2010) Silicon effects on photosynthesis and antioxidant parameters of soybean seedlings under drought and ultraviolet-B radiation. J Plant Physiol 167:1248–1252

Shen X, Xiao X, Dong Z, Chen Y (2014) Silicon effects on antioxidative enzymes and lipid peroxidation in leaves and roots of peanut under aluminum stress. Acta Physiol Plant 36:3063–3069

Shi X, Zhang C, Wang H, Zhang F (2005) Effect of Si on the distribution of Cd in rice seedlings. Plant Soil 272(1):53–60

Shi Y, Zhang Y, Yao H, Wu J, Sun H, Gong H (2014) Silicon improves seed germination and alleviates oxidative stress of bud seedlings in tomato under water deficit stress. Plant Physiol Biochem 78:27–36

Shivaraj S, Deshmukh RK, Rai R, Bélanger R, Agrawal PK, Dash PK (2017) Genome-wide identification, characterization, and expression profile of aquaporin gene family in flax (*Linum usitatissimum*). Sci Rep 7:46137. https://doi.org/10.1038/srep46137

Siddiqui MH, Al-Whaibi MH (2014) Role of nano-SiO_2 in germination of tomato (*Lycopersicum esculentum* seeds Mill.). Saudi J Biol Sci 21(1):13–17

Sidhu JK, Stout MJ, Blouin DC, Datnoff LE (2013) Effect of silicon soil amendment on performance of sugarcane borer, *Diatraea saccharalis* (Lepidoptera: Crambidae) on rice. Bull Entomol Res 103(06):656–664

Silva RV, Oliveria RDL, Nascimento KJT, Rodrigues FA (2010) Biochemical responses of coffee resistance against *Meloidogyne exigua* mediated by silicon. Plant Pathol 59:586–593

Silva ON, Lobato AKS, Ávila FW et al (2012) Silicon-induced increase in chlorophyll is modulated by the leaf water potential in two water-deficient tomato cultivars. Plant Soil Environ 58:481–486

Singh S, Parihar P, Singh R, Singh VP, Prasad SM (2015) Heavy metal tolerance in plants: role of transcriptomics, proteomics, metabolomics, and ionomics. Front Plant Sci 6:1143

Somapala K, Weerahewa D, Thrikawala S (2016) Silicon rich rice hull amended soil enhances anthracnose resistance in tomato. Proc Food Sci 6:190–193

Sonah H, Deshmukh R, Labbé C, Belanger R (2017) Analysis of aquaporins in Brassicaceae species reveals high-level of conservation and dynamic role against biotic and abiotic stress in canola. Sci Rep. https://doi.org/10.1038/s41598-017-02877-9

Song A, Li P, Fan F, Li Z, Liang Y (2014) The effect of silicon on photosynthesis and expression of its relevant genes in rice (*Oryza sativa* L.) under high-zinc stress. PLoS One 9(11):e113782

Souza ACA, Sousa TP, Cortes MVB, Rodrigues F, Silva GB, Filippi MCC (2015) Enzyme-induced defense response in the suppression of rice leaf blast (*Magnaporthe oryzae*) by silicon fertilization and bioagents. Int J Res Stud Biosci 3:22–32

Suriyaprabha R, Karunakaran G, Yuvakkumar R, Rajendran V, Kannan N (2012) Silica nanoparticles for increased silica availability in maize (*Zea mays* L.) seeds under hydroponic conditions. Curr Nano sci 8(6):902–908

Swain BN, Prasad JS (1988) Influence of silica content in the roots of rice varieties on the resistance to root-knot nematodes. Indian J Nematol 18:360–361

Tahir MA, Aziz T, Farooq M, Sarwar G (2012) Silicon-induced changes in growth, ionic composition, water relations, chlorophyll contents and membrane permeability in two salt-stressed wheat genotypes. Archi Agron Soil Sci 58(3):247–256

Takahashi E, Ma JF, Miyake Y (1990) The possibility of silicon as an essential element for higher plants. Comments Agric Food Chem 2:99–122

Tale Ahmad S, Haddad R (2011) Study of silicon effects on antioxidant enzyme activities and osmotic adjustment of wheat under drought stress. Czech J Genet Plant Breed 47(1):17–27

Tripathi P, Tripathi RD, Singh RP, Dwivedi S, Goutam D, Shri M, Trivedi PK, Chakrabarty D (2013) Silicon mediates arsenic tolerance in rice (*Oryza sativa* L.) through lowering of arsenic uptake and improved antioxidant defense system. Ecol Eng 52:96–103

Tripathi DK, Singh VP, Prasad SM, Chauhan DK, Dubey NK, Rai AK (2015) Silicon-mediated alleviation of Cr (VI) toxicity in wheat seedlings as evidenced by chlorophyll florescence, laser induced breakdown spectroscopy and anatomical changes. Ecotoxicol Environ Saf 113:133–144

Tubana BS, Heckman JR (2015) Silicon in soils and plants. In Rodrigue FA, Datnoff LE (eds), Silicon and plant diseases. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-22930-0$42

Vaculík M, Landberg T, Greger M, Luxová M, Stoláriková M, Lux A (2012) Silicon modifies root anatomy, and uptake and subcellular distribution of cadmium in young maize plants. Ann Bot 110:433–443

Van Bockhaven J, De Vleesschauwer D, Hofte M (2013) Towards establishing broad spectrum disease resistance in plants: silicon leads the way. J Exp Bot 64:1281–1293. https://doi.org/10.1093/jxb/ers329

Vanderschuren H, Boycheva S, Li KT, Szydlowski N, Gruissem W, Fitzpatrick TB (2013) Strategies for vitamin B6 biofortification of plants: a dual role as a micronutrient and a stress protectant. Front Plant Sci 4:143

Vasanthi N, Saleena LM, Raj SA (2012a) Silicon in day today life. World Appl Sci J 17:1425–1440

Vasanthi N, Chandrasekeran D, Raj SA (2012b) Phytosil as an alternative carrier to talc for biocontrol agents. In: Proc. Natl. Symp.

Recent Adv. Bioinoculatns Techn. Agricultural College & Research Institute, Madurai

Vatehova Z, Kollarova K, Zelko I, Richterova-Kucerova D, Bujdos M, Liskova D (2012) Interaction of silicon and cadmium in *Brassica juncea* and *Brassica napus*. Biologia 67(3):498–504

Vilela M, Moraes JC, Alves E, Santos-Cividanes TM, Santos FA (2014) Induced resistance to Diatraeasaccharalis (Lepidoptera: Crambidae) via silicon application in sugarcane. Revista Colombiana de Entomología 40(1):44–48

Virta RL (2004) Wollastonite—U.S. geological survey. Miner Yearb 82:1–3

Vivancos J, Deshmukh R, Grégoire C, Rémus-Borel W, Belzile F, Bélanger RR (2016) Identification and characterization of silicon efflux transporters in horsetail (*Equisetum arvense*). J Plant Physiol 200:82–89

Wang LJ, Guo ZM, Li TJ, Li M (2001) The nano structure SiO_2 in the plants. Chin Sci Bull 46:625–631

Wang W, Vinocur B, Altman A (2003) Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. Planta 218(1):1–14

Wang X, Wei Z, Liu D, Zhao G (2011) Effects of NaCl and silicon on activities of antioxidative enzymes in roots, shoots and leaves of alfalfa. Afr J Biotechnol 10:545–549

Wang HS, Yu C, Fan P-P, Bao B-F, Li T, Zhu Z-J (2014) Identification of two cucumber putative silicon transporter genes in *Cucumis sativus*. J Plant Growth Regul 34(2):332–338

White AF, Brantley SL (eds) (1995) Chemical weathering rates of silicate minerals. In: Reviews in mineralogy, vol 31, Mineralogical Society of America

Williams LA, Crerar DA (1985) Silica diagenesis. II. General mechanisms. J Sediment Petrol 55:312–321

Xie Z, Song R, Shao H, Song F, Xu H, Lu Y (2015) Silicon improves maize photosynthesis in saline-alkaline soils. Sci World J 2015:245072

Xue GF, Sun WC, Song AL, Li ZJ, Fan FL, Liang YC (2010) Influence of silicon on rice growth, resistance to bacterial blight and activity of pathogenesis-related proteins. China Agric Sci 43(4):690–697

Yamaji N, Ma JF (2007) Spatial distribution and temporal variation of the rice silicon transporter Lsi1. Plant Physiol 143:1306–1313

Yamaji N, Ma JF (2009) Silicon transporter Lsi6 at the node is responsible for inter-vascular transfer of silicon in rice. Plant Cell 21:2878–2883

Yamaji N, Ma JF (2011) Further characterization of a rice Si efflux transporter, Lsi2. Soil Sci Plant Nutr 57:259–564

Yamaji N, Mitatni N, Ma JF (2008) A transporter regulating silicon distribution in rice shoots. Plant Cell 20:1381–1389

Yamaji N, Mitani-Ueno N, Ma JF (2011) Transporters involved in preferential distribution of Si to the panicles at the node in rice. In: Proceedings, the 5th international conference on silicon in agriculture; September 13–18, Beijing, China, p 210

Yamaji N, Chiba Y, Mitani-Ueno N, Ma JF (2012) Functional characterization of a silicon transporter gene implicated in silicon distribution in barley. Plant Physiol 160:1491–1497

Yang YF, Liang YC, Lou YS, Sun WC (2003) Influences of silicon on peroxidase, superoxide dismutase activity and lignin content in leaves of wheat (*Tritium aestivum* L.) and its relation to resistance to powdery mildew. Scientia Agricultura Sinica 7:013

Yao X, Chu J, Cai K, Liu L, Shi J, Geng W (2011) Silicon improves the tolerance of wheat seedlings to ultraviolet-B stress. Biol Trace Elem Res 143(1):507–517

Ye M, Song Y, Long J, Wang R, Baerson SR, Pan Z et al (2013) Priming of jasmonate-mediated antiherbivore defense responses in rice by silicon. Proc Natl Acad Sci USA 110:E3631–E3639 https://doi.org/10.1073/pnas.1305848110

Yin L, Wang S, Li J, Tanaka K, Oka M (2013) Application of silicon improves salt tolerance through ameliorating osmotic and ionic stresses in the seedling of Sorghum bicolor. Acta Physiologiae Plantarum 35(11):3099–3107

Yin L, Wang S, Liu P, Wang W, Cao D, Deng X, Zhang S (2014) Silicon mediated changes in polyamine and 1-aminocyclopropane-1-carboxylic acid are involved in silicon-induced drought resistance in *Sorghum bicolor* L. Plant Physiol Biochem 80:268–277

Yin L, Wang S, Tanaka K, Fujihara S, Itai A, Den X, Zhang S (2015) Silicon-mediated changes in polyamines participate in silicon-induced salt tolerance in *Sorghum bicolor* L. Plant Cell Environ. https://doi.org/10.1111/pce.12521

Zargar SM, Agnihotri A (2013) Impact of silicon on various agromorphological and physiological parameters in maize and revealing its role in enhancing water stress tolerance. Emir J Food Agric 25:138–141

Zargar SM, Nazir M, Agrawal GK, Kim D, Rakwal R (2010) Silicon in plant tolerance against environmental stressors: towards crop improvement using omics approaches. Curr Proteomics 7:135–143

Zargar SM, Macha MA, Nazir M, Agrawal GK, Rakwal R (2012) Silicon: a multitalented micronutrient in OMICS perspective—an update. Curr Proteomics 9:245–254

Zhang GL, Dai QG, Zhang HC (2006) Silicon application enhances resistance to sheath blight (*Rhizoctonia solani*) in rice. J Plant Physiol Mol Biol 32(5):600–606

Zhang C, Wang L, Nie Q, Zhang W, Zhang F (2008) Long-term effects of exogenous silicon on cadmium translocation and toxicity in rice (*Oryza sativa* L.). Environ Exp Bot 62:300–307

Zhang SR, Li SY, Ding X, Li F, Liu C, Liao X et al (2013) Silicon mediated the detoxification of Cr on pakchoi (*Brassica chinensis* L.) in Cr-contaminated soil. Int J Food Agric Environ 11:814–819

Zhu YX, Xu XB, Hu YH, Han WH, Yin JL, Li HL, Gong HJ (2015) Silicon improves salt tolerance by increasing root water uptake in *Cucumis sativus* L. Plant Cell Rep. https://doi.org/10.1007/s00299-015-1814-9