Silicon and Plant Responses Under Adverse Environmental Conditions

Pankaj S. Mundada, Suchita V. Jadhav, Supriya S. Salunkhe, Swati T. Gurme, Suraj D. Umdale, Rajkumar B. Barmukh, Tukaram D. Nikam, and Mahendra L. Ahire

1 Introduction

Food security is the most important fundamental need of society. The wide-ranging increase in environmental damage and the pressure of ever-increasing human population have adversely affected global food production (Etesami and Jeong 2018). The world population today is estimated to be about 7 billion and projected to reach between 7.5 to 10.5 billion by 2050 (Godfray et al. 2010). Such an enormous rise in the population would demand higher agricultural productivity per unit area from already degraded lands. Moreover, climate change has aggravated the occurrence and intensities of various biotic and abiotic stresses (Etesami and Jeong 2018). Such

P. S. Mundada
Department of Botany, Savitribai Phule Pune University, Pune, Maharashtra, India

Department of Biotechnology, Yashavantrao Chavan Institute of Science (Autonomous), Satara, Maharashtra, India

S. V. Jadhav · S. S. Salunkhe · S. T. Gurme
Department of Biotechnology, Yashavantrao Chavan Institute of Science (Autonomous), Satara, Maharashtra, India

S. D. Umdale
Department of Botany, Jaysingpur College (Affiliated to Shivaji University), Jaysingpur, Maharashtra, India

R. B. Barmukh
Post Graduate Research Centre, Department of Botany, Modern College of Arts, Science and Commerce (Autonomous), Shivajinagar, Pune, Maharashtra, India

T. D. Nikam
Department of Botany, Savitribai Phule Pune University, Pune, Maharashtra, India

M. L. Ahire (✉)
Department of Botany, Yashavantrao Chavan Institute of Science (Autonomous), Satara, Maharashtra, India

© The Author(s), under exclusive license to Springer Nature Switzerland AG 2021
A. Husen (ed.), *Plant Performance Under Environmental Stress*,
https://doi.org/10.1007/978-3-030-78521-5_14

conditions would compel farmers to cultivate marginal lands and poor soils (Glick 2014).

Stress affects the growth and development of the plants, thereby leading to more significant losses in agricultural productivity. However, plants have adopted numerous mechanisms to tolerate stress and survive stress-induced conditions. Healthy plants are capable of combating stress, and plant nutrients are vital to maintaining healthy plant growth. The microelements or micronutrients are known to give stress tolerance to plants (Vanderschuren et al. 2013; Bradáčová et al. 2016). Though the roles of several macro- and micronutrients in plants have been well documented, few of the nutrient elements have remained neglected. This chapter focuses on the role of silicon, one of the neglected plant nutrients, and its role in plants suffering from adverse environmental conditions.

2 Adverse Environmental Conditions

2.1 Biotic Stress

Throughout their life, plants get exposed to a multitude of stresses that modify plant growth and development. Organisms like fungi, bacteria, mycoplasma, insets, nematodes, weeds, and parasitic plants induce biotic stress. The viruses and viroids, though nonliving, also contribute to the biotic stress. These agents affect the plant growth and development by depriving nutrients leading to reduced plant vigor and death of plants in extreme cases (Das and Rakshit 2016). The severity of biotic stress depends on the environmental factors, cropping systems, types of crops, cultivars, and resistance levels of plants. Hot and humid conditions and poor crop management practices are the two leading causes of biotic stresses (Pantazi et al. 2020). Early recognition of biotic stress is the key to control it via integrated pest management and the use of pesticides.

Plants do not have an adaptive immune system like vertebrates. They can neither adapt to new diseases nor memorize the previous infections. However, plants have developed several mechanisms to combat biotic stresses. They rely on various physical and chemical barriers that confer strength and rigidity to survive under biological stress.

2.2 Abiotic Stress

The nonliving factors imposing adverse effects on healthy growth and development of the plants are called abiotic stresses. These include drought, salinity, heavy metals, too low or too high temperatures, and other environmental extremes. These factors can reduce the crop yield by 51–82% (Bray et al. 2000). Plants combat these stresses at various levels like morphological, physiological, biochemical, and molecular levels (Husen 2010; Getnet et al. 2015; Embiale et al. 2016; Husen et al. 2016, 2018, 2019; Hussein et al. 2017; Siddiqi and Husen 2017, 2019; Zeng et al. 2020; Kar and Öztürk 2020). Over the past few decades, advances in plant physiology, genetics, and molecular biology have greatly upgraded our understanding in terms of crops respond to stress conditions. These responses depend not only on their duration and severity but on the age and the developmental stage of the plant as well (He et al. 2018).

3 Is Silicon Essential to Plants?

Silicon (Si) is the eighth-most abundant element in the universe. In earth's crust, its abundance ranks only second to oxygen. The lithosphere contains about 27.7% silicon (Epstein 1999). It rarely occurs in its pure form, and more than 90% of the Si in the earth's crust exists as silicates (Mitra 2015).

Biological systems also contain significant amounts of silicon, as amorphous silica ($SiO_2 \cdot nH_2O$), and its soluble form, silicic acid ($Si(OH)_4$). The first indication of in vivo formation of organosilicates, their distribution, and physiological importance was discovered in a diatom *Navicula pelliculosa* (Kinrade et al. 2002). Plants also contain significant amounts of Si that can range from 0.1 to 10% on the dry weight basis (Epstein 1994; Ma and Takahashi 2002; Hodson et al. 2005; Ma et al. 2006). Differences in the levels of silicon in different plants could be due to the differential ability of roots to absorb Si (Takahashi et al. 1990). Despite its high amounts in plants, Si is looked upon as a quasi-essential element since most of the plant species can live their entire life in the absence of silicon (Arnon and Stout 1939). Nonavailability of Si-free environment due to its contamination in purified water, chemicals, and dust might be the reasons for considering Si as nonessential for higher plants (Liang et al. 2015). Therefore, adhering to the definition of essentiality proposed by Epstein and Bloom (2005), Si is a quasi-essential element in plants.

Interestingly, there are several reports on the positive roles of Si in the plant growth (Eneji et al. 2008; Soundararajan et al. 2014; Zhang et al. 2015), yield (Epstein 1999), structural toughness (Epstein 1994), nutrient management (Tripathi et al. 2012), and absorption of light (Li et al. 2004). Its role in accelerating the tolerance to biotic and abiotic stresses in plants has also been explained (Ma 2004; Cookson et al. 2007; Liang et al. 2007; Muneer et al. 2014; Soundararajan et al. 2014). How Si alleviates biotic and abiotic stresses has become a booming topic of interest. In the past 15 years, several researchers have reported and reviewed the positive effects of Si under biotic and abiotic stresses (Fig. 1a, b). However, studies on Si in conjunction with abiotic stress were significantly more than those with biotic stress (Fig. 1b). This chapter summarizes how plants use silicon and respond to Si availability during adverse environmental conditions.

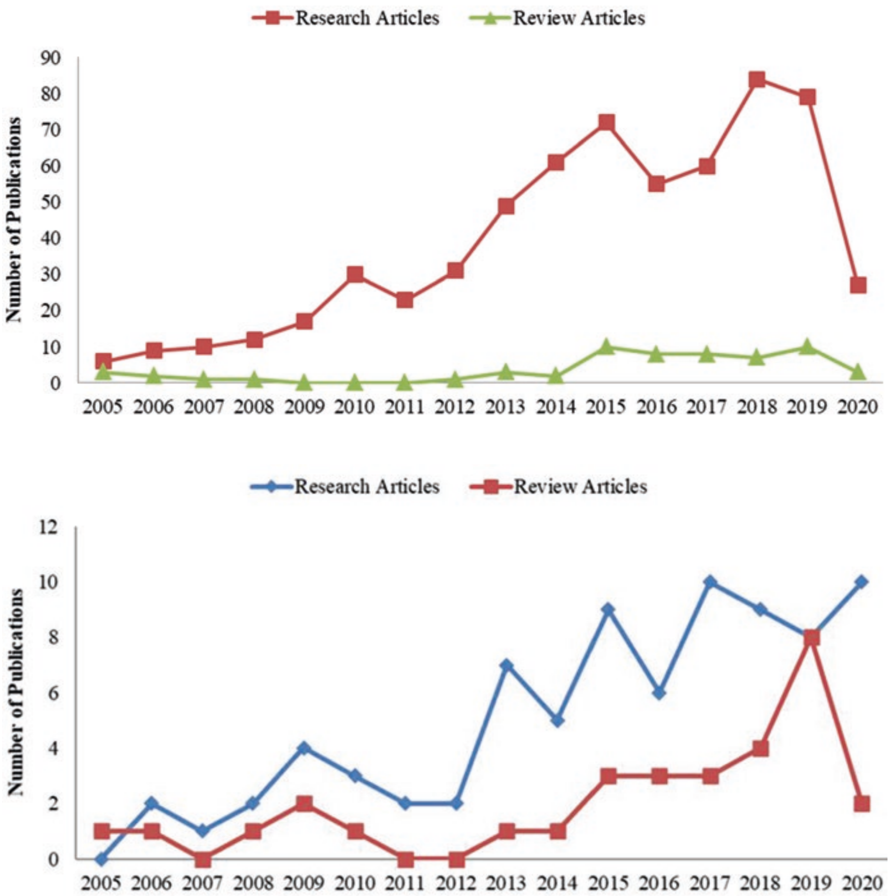

Fig. 1 (**a**) Silicon-related publications in the plant sciences from 2005 to 2020 (Till June) (Based on PubMed search with the keywords “silicon” and “abiotic stress”). (**b**) Silicon-related publications in the plant sciences from 2005 to 2020 (Till June) (based on PubMed search with the keywords “silicon” and “biotic stress”)

4 Uptake of Si in Plants Under Adverse Environmental Conditions

In plants, roots take up more than 90% of Si and translocate it to shoots (Ma and Takahashi 2002). Roots absorb Si in the form of silicic acid at pH < 9 (Takahashi and Hino 1978; Raven 2001; Ma and Takahashi 2002). The concentration of silicic acid in soil solutions usually ranges between 0.1 and 0.6 mM (Epstein 1994), and in some cases, up to 0.8 mM (Sommers and Lindsay 1979). The soil pH modulates the solubility of silicates, and with the increasing pH, solubility decreases. However, most of the crops are cultivated in soils with pH well below the alkaline mark of pH 9.0.

Studies in rice have shown that roots take up Si from the rhizosphere by some kind of transporter, which transports it radially from the root cortical cells to the xylem (Tamai and Ma 2003). Once absorbed, Si is transported to the shoot as silicic acid. In different plants like rice, cucumber, and tomato, the concentration of silicic acid in the root cell symplast was higher than that in the external solution. Rice has shown a significantly higher concentration of Si than observed in cucumber and tomato (Mitani et al. 2005). This difference in the ability to take up Si is attributed to the different modes of transport in these plants. Moreover, the xylem loading of Si in rice occurs through a transporter. In contrast, in cucumber and tomato, it occurs by passive diffusion.

Plants differ in their ability to take up and distribute Si. The highest levels of Si uptake are reported in bryophytes and lycopods and *Equisetum* among the pteridophytes. However, ferns and gymnosperms tend to accumulate Si in lesser quantities (Takahashi et al. 1990). Two of the angiosperm families, viz., Cyperaceae and Poaceae, are known to accumulate Si at higher concentrations (Hodson et al. 2005). Depending upon their ability to accumulate Si, plants are categorized into three classes: Si accumulators (e.g., rice, wheat, millet, and sugarcane) since they absorb large quantities of Si; Si non-accumulators (e.g., Snapdragon); and Si excluders (e.g., soybean) (Van der Vorm 1980; Marschner 1995).

So far, only a few genes have been identified that are involved in the uptake of Si in plants. The first of those genes is *Lsi1* that was reported in rice (Ma et al. 2006). The *Lsi1* gene is expressed mainly in roots, and its encoded protein has Si transporter activity. The *Lsi1*-encoded protein is located on the distal sides on plasma membranes in both the layers of exodermis and endodermis. Bioinformatics tools have revealed that the *Lsi1* belongs to a subfamily of aquaporin Nod26-like major intrinsic proteins (NIP). Chiba et al. (2009) have reported the *HvLsi1* gene in barley for the influx of Si from roots. The presence of *ZmLsi1* and *ZmLsi6* transporter from maize was reported by Mitani et al. (2009). Bokor et al. (2017) have studied the expression of *ZmLsi1*, *ZmLsi2,* and *ZmLsi6* genes and their effects on Si uptake and ionome content in maize (Bokor et al. 2017).

5 Transport of Si in Plants

Si absorbed by the root cells must be transported to other plant organs. Therefore, Si must be taken out of the root cells first. In marine organisms, the influx and efflux of Si are mediated by the same protein (Hildebrand et al. 1998). In rice, however, the efflux is mediated by a transporter *Lsi2* (Ma et al. 2006), and *Lsi6* mediates the influx of silicic acid from xylem to xylem parenchyma cells, thus influencing the distribution of Si in rice roots (Yamaji et al. 2008).

Plants are capable of synthesizing Si-rich molecules of various sizes. The accumulated Si provides rigidity and roughness to the plant cell walls (Epstein and Bloom 2005) and also offers other beneficial effects (Van Soest 2006). The passive transport of Si driven by transpiration also leads to its deposition on the cell wall.

Researchers have used several biophysical tools like scanning electron microscopy (SEM) coupled with X-ray microanalysis, laser ablation (LA), X-Ray fluorescence spectrometry, and X-ray absorption near edge structure (XANES) to study the distribution of Si in plants (Rufo et al. 2014; Bokor et al. 2017). Si is mostly deposited in the epidermal cells of leaves, stems, and hulls where double layers of silica-cuticle or silica-cellulose containing hydrated polymers of amorphous silica are formed on their surface (Fauteux et al. 2005; Wiese et al. 2007; Deshmukh et al. 2017).

6 Role of Si in Plants Under Adverse Environmental Conditions

It is speculated that the global climate changes will trigger more frequent incidences of biotic and abiotic stresses leading to severe agricultural losses. The abiotic stresses reduce the global agricultural yield by as much as 70% (Acquaah 2012). How to fulfill the ever-increasing food demand under such circumstances will be a real challenge. The application of Si in soils deteriorated due to abiotic stresses has been beneficial for crop productivity. A summary of the beneficial and or positive effects of Si in plants exposed to various biotic and abiotic stresses is presented in Table 1.

6.1 Si and Plant Growth

Seed germination plays a significant role during seedling establishment. Drought adversely affects seed germination leading to agriculture losses (Hubbard et al. 2012; Shi et al. 2014). However, there are few reports on the effects of Si on seed germination under drought stress (Hameed et al. 2014; Shi et al. 2014). Priming of wheat seeds with sodium silicate was beneficial in enhancing the rate of seed germination under drought stress (Hameed et al. 2014). Similar observations were reported in tomato (Siddiqui and Al-Whaibi 2014), and maize (Zargar and Agnihotri 2013) seeds germinated under drought stress.

All the essential nutrients are required in adequate amounts for the healthy growth and development of plants. The process of absorption of these nutrients from the surrounding is disturbed under various stresses (Gunes et al. 2007a; Chen et al. 2011; Khattab et al. 2014). The deposition of Si in the endodermal layer of root cells helps in the selective uptake of nutrients, and such deposition reduces the accumulation of toxic ions in different plant parts (Yeo et al. 1999). The soil application of Si has enhanced the uptake of macronutrients (P, K, Ca, and Mg) and micronutrients (Fe, Cu, and Mn) in sunflower (Gunes et al. 2008a). The application of Si to the rice plants subjected to drought stress showed an increase in the uptake of

Table 1 Summary of the beneficial effects of silicon in different plants under adverse environmental conditions

Crop	Stress	Effect of Si	Reference
Abelmoschus esculentus (Okra)	NaCl	Enhanced photosynthesis, osmoprotectants, and antioxidant metabolism	Abbas et al. (2015)
Aloe vera (Aloe)	NaCl	Growth, quality, and ionic homeostasis	Xu et al. (2015)
Arachis hypogaea (Pea nut)	Aluminum toxicity	Antioxidative enzymes and lipid peroxidation	Shen et al. (2014)
Brachypodium distachyon (stiff brome)	Antiherbivore	Jasmonic acid (JA) signaling pathway	Hall et al. (2019)
Brassica napus (Canola)	NaCl	Alleviates physiological disorders	Farshidi et al. (2012)
Capsicum annuum (Capsicum)	NaCl	Regulating the physiology, antioxidant enzyme activities, and protein expression	Manivannan et al. (2016)
Chloris gayana (Rhodes grass), *Phleum pretense* (Timothy grass), *Sorghum sudanense* (Sudan grass) and *Festuca arundinacea* (Tall fescue).	Drought	Growth and nutrient use	Eneji et al. (2008)
Cucumis sativus (Cucumber)	Drought	Physiological and biochemical mechanisms	Ma et al. (2004)
	NaCl	Antioxidant enzymes activity in leaves	Zhu et al. (2004)
	Manganese toxicity	Hydroxyl radical accumulation in the leaf apoplast	Maksimović et al. (2012)
	Iron deficiency	Mobilization of iron in the root apoplast	Pavlovic et al. (2013)
	NaCl	Lipid peroxidation and antioxidant response	Khoshgoftarmanesh et al. (2014)
	NaCl	Increasing root water uptake	Zhu et al. (2015)
	NaCl	Act as an elicitor to precondition	Zhu et al. (2019)
Dianthus caryophyllus (Carnation)	NaCl	Antioxidant enzyme activities	Soundararajan et al. (2015)
	Hyperhydricity in *in-vitro* cultures	Recovery of hyperhydric shoots by stabilizing the physiology and protein expression	Soundararajan et al. (2017)

(continued)

Table 1 continued

Crop	Stress	Effect of Si	Reference
Eleusine coracana (Finger millet)	Pink stem borer (*Sesamia inferens Walker*)	Defense hormone regulation	Jadhao et al. (2020)
(Grasslands)	High-Salinity	Biomass accumulation	Liu et al. (2020)
Gossypium hirsutum (Cotton)	Copper	Physiological and biochemical mechanisms	Ali et al. (2016)
Glycine max (Soybean)	*Helicoverpa punctigera* (Lepidoptera: Noctuidae)	Relative growth rates (RGR)	Johnson et al. (2020)
Helianthus annuus (Sunflower)	Drought	Growth, Antioxidant mechanisms, and Lipid peroxidation	Gunes et al. (2008b)
	Drought	Essential and Nonessential element uptake	Gunes et al. (2008a)
	Brackish water stress	Growth and yield improvement	Hussain et al. (2018)
Hordeum vulgare (Barley)	NaCl	Increases antioxidant enzyme activity and reduces lipid peroxidation in roots	Liang et al. (2003)
	NaCl	H^{+}-ATPase activity, phospholipids, and fluidity of the plasma membrane in leaves	Liang et al. (2005)
Mangifera indica (Mango)	Drought	Growth and mineral uptake	Aal and Oraby (2013)
Medicago sativa (Alfalfa)	NaCl	Ion distribution in the roots, shoots, and leaves	Wang and Han (2007)
Nicotiana rustica L. (Tobacco)	Salinity	Mitigation of cell death in cultured tobacco	Liang et al. (2015)
	Drought	Growth, antioxidant mechanisms, osmolytes accumulation	Hajiboland et al. (2017)
	Cuscuta europaea (Dodder)	Protein profile and antioxidant enzymes activities (POX, CAT, and SOD)	Lukacova et al. (2019)

(continued)

Table 1 continued

Crop	Stress	Effect of Si	Reference
Oryza sativa (Rice)	Drought & Heat Stress	Electrolyte leakage	Agarie et al. (1998)
	Drought	Plant water status, photosynthesis, and mineral nutrient absorption	Chen et al. (2011)
	Salinity	Decreased chloride transport	Shi et al. (2013)
	Salinity	Phytohormonal and antioxidant responses	Kim et al. (2014)
	Heavy metal stress	Regulation of P-type heavy metal ATPases, *Oryza sativa* low silicon genes, and endogenous phytohormones	Kim et al. (2015)
	cadmium toxicity	Cd-responsive transcription factor (TF) genes	Farooq et al. (2016)
	Arsenic (As)	Mineral nutrient uptake and biochemical responses through modulation of *Lsi1*, *Lsi2*, *Lsi6* and nutrient transporter genes	Khan and Gupta (2018)
	Low temperature	Plant growth and yield	Jang et al. (2018)
	Salinity	Multivariate analysis of antioxidants and osmolytes	Lekklar et al. (2019)
	Cadmium	Improving oxidative stress	Chen et al. (2019a)
	NaCl	Alters organic acid production and enzymatic activity of the TCA cycle	Das et al. (2019)
	Ultraviolet-B radiation	Antioxidant capacity, osmolytes	Fang et al. (2019)
	Cadmium and Lead	Physiological and biochemical responses (ROS Production)	Wang et al. (2020)
	Cadmium	Induction of phytochelatin and ROS scavengers	Bari et al. (2020)
Phaseolus vulgaris (Bean)	Salinity	Photosynthesis, water relations, and nutrient uptake	Zuccarini (2008)
Phaseolus vulgaris and *Vigna unguiculata* (Beans)	Salinity	Growth, physiological parameters, and mineral nutrition	Murillo-Amador et al. (2007)
Phoenix dactylifera (Date palm)	Salinity and Cadmium stress	Improvements in plant growth, physiology, and modulation of stress-related hormonal crosstalk	Khan et al. (2020a)

(continued)

Table 1 continued

Crop	Stress	Effect of Si	Reference
Pisum sativum (Pea)	Salinity	Antioxidant enzyme activity	Shahid et al. (2015)
	Boron (B) toxicity	Antioxidant defense systems	Oliveira et al. (2020)
Portulaca oleracea (Purslane)	Salinity	Root characteristics, growth, water status, proline content, and ion accumulation	Kafi and Rahimi (2011)
Raphanus sativus L. (Radish)	Ammonium toxicity	Increased photosynthesis, greater instantaneous water-use efficiency, and higher total dry biomass	Olivera Viciedo et al. (2020)
Spartina densiflora (Cordgrass)	Salinity	Physiological parameters and mineral composition	Mateos-Naranjo et al. (2013)
Spinacia oleracea (Spinach) and *Solanum lycopersicum* (Tomato)	Salinity	Some physiological and enzymatic parameters symptomatic for oxidative stress	Gunes et al. (2007a)
Spinacia oleracea (Spinach)	Boron toxicity and salinity	Oxidative damage and antioxidant activity	Eraslan et al. (2008)
Saccharum officinarum (Sugarcane)	Salinity	Improve yield and juice quality	Ashraf et al. (2009)
	Salinity	Decreased Na^+ concentration and increased K^+	Ashraf et al. (2010a)
	Salinity	Morphology and mineral content	Ashraf et al. (2010b)

(continued)

Table 1 continued

Crop	Stress	Effect of Si	Reference
Solanum lycopersicum (Tomato)	Salinity	Chlorophyll content, chlorophyll fluorescence, and antioxidative enzyme activities	Al-aghabary et al. (2004)
	Salinity	Growth, ion content, and water relation	Romero-Aranda et al. (2006)
	Cadmium toxicity	Mineral nutrient concentrations	López-Millán et al. (2009)
	Salinity	Physiological parameters	Haghighi and Pessarakli (2013)
	Drought	Seed germination and alleviates oxidative stress	Shi et al. (2014)
	Salinity	Physiological and proteomic analysis in chloroplasts	Muneer et al. (2014)
	Salinity	Proteomic analysis of salt-stress responsive proteins in roots	Muneer and Jeong (2015)
	Salinity	Gas exchange, ion accumulation, root hydraulic conductance, antioxidant defense	Li et al. (2015)
	Drought	Root Hydraulic Conductance	Shi et al. (2016)
	high-pH stress	Modification of the endogenous Na^+ and K^+ contents, regulating oxidative damage and key genes and modulating endogenous hormone levels	Khan et al. (2019)
	Bacterial Wilt	Contents of salicylic acid (SA), ethylene (ET), and jasmonic acid (JA) and the activity of defense-related enzymes	Jiang et al. (2019)
	Thermo tolerance	Activation of the antioxidant system, heat shock proteins, and endogenous phytohormones	Khan et al. (2020b)

(continued)

Table 1 continued

Crop	Stress	Effect of Si	Reference
Sorghum bicolor (Sorghum)	Drought	Silicon deposition	Lux et al. (2002)
	Drought	Drought tolerance mechanism	Ahmed et al. (2011)
	Salinity	Ameliorating osmotic and ionic stresses	Yin et al. (2013)
	Drought	Increase in root hydraulic conductance	Liu et al. (2014)
	Drought	Changes in polyamine and 1-aminocyclopropane-1-carboxylic acid	Yin et al. (2014)
	Drought	Growth and level of antioxidant enzymes	Ahmed and Fayyaz-ul-Hassan (2014)
	Salinity	Enhanced root hydraulic conductance by aquaporin regulation	Liu et al. (2015)
	Salt stress	Modifying the antioxidative defense mechanism	Calero Hurtado et al. (2020)
Sorghum bicolor (Sorghum) and *Helianthus annuus* (Sunflower)	Sodium toxicity	Improving nutritional efficiency	Calero Hurtado et al. (2019)
	salt stress	Modifying the antioxidative defense mechanism	Calero Hurtado et al. (2020)

(continued)

Table 1 continued

Crop	Stress	Effect of Si	Reference
Triticum aestivum (Wheat)	Copper	Growth	Nowakowski and Nowakowska (1997)
	Drought	Growth	Gong et al. (2003)
	Drought	Alleviation of oxidative damage	Gong et al. (2005)
	Powdery mildew	Induction of antifungal compounds	Rémus-Borel et al. (2005)
	Freezing stress	Morphology and antioxidant enzymes	Liang et al. (2008)
	Drought	Oxidative stress at different developmental stages	Gong et al. (2008)
	Salinity	Morphophysiology and Osmolyte	Tuna et al. (2008)
	Powdery mildew	Absorption of aqueous inorganic and organic silicon compounds and their effect on growth	Côté-Beaulieu et al. (2009)
	Drought	Antioxidant defense and Osmotic adjustment	Pei et al. (2010)
	Drought	Antioxidant enzyme activities and osmotic adjustment	Ahmad and Haddad (2011)
	Drought	Regulation of water relations, photosynthetic gas exchange, and carboxylation activities of wheat leaves	Gong and Chen (2012)
	Salinity	Morphophysiology and Osmolyte	Chen et al. (2014)
	Salinity	Germination, grain yield, foliar application, photosynthesis, proline, relative water content	Ahmad (2014)
	Copper	Micro and macro elements content	Keller et al. (2015)
	Drought	Transcriptional regulation of multiple antioxidant defense pathways	Ma et al. (2016)
	Drought	Tolerance by seed priming with silicon	Ahmed et al. (2016)
	Salinity	Morphology and osmolyte accumulation	Sienkiewicz-Cholewa et al. (2018)
	NaCl	Improved the growth and physiological performance	Javaid et al. (2019)
	Cadmium	Enhanced the leaf gas exchange attributes and chlorophyll a and b concentrations and antioxidant enzymes	Ali et al. (2019)
	Cadmium	Improved the plant growth indicators and photosynthesis	Khan et al. (2020c)

(continued)

Table 1 continued

Crop	Stress	Effect of Si	Reference
Trifolium repens (White Clover)	Salinity	Selective transport capacity for K^+ over Na^+	Guo et al. (2013)
Vitis vinifera (Grapevine)	Boron toxic, salinity	Antioxidant and stomatal response	Soylemezoglu et al. (2009)
Zea mays (Maize)	Drought	Plant growth and mineral nutrition composition	Kaya et al. (2006)
	Drought and oxygen deficiency	Antioxidant enzyme activities and osmotic adjustment	Sayed and Gadallah (2014)
	Salinity	Antioxidant enzyme activity and ammonia assimilation	Kochanová et al. (2014)
	Alkalinity	Physiological and biochemical responses	Latef and Tran (2016)
	Drought	Regulates morphophysiological growth and oxidative metabolism	Parveen et al. (2019)
Zingiber officinale (Ginger)	Lead toxicity	Morphology indexes, antioxidant enzyme activities	Chen et al. (2019b)

potassium and phosphorus (Khattab et al. 2014). An increased levels of phosphorus (Gong and Chen 2012), and potassium and calcium (Kaya et al. 2006) were observed in wheat under drought stress. In other grasses such as *Chloris gayana*, *Sorghum sudanense*, *Festuca arundinacea,* and *Phleum pratense*, the levels of N, P, and K were increased upon the application of Si under drought stress (Eneji et al. 2008).

6.2 Effect of Si on Structure and Physiology of Plants

Si plays two critical roles under adverse environmental conditions: physical and mechanical protection due to its deposition in the epidermal layer, and triggering a biochemical response to metabolic changes. Numerous researchers have reported the deposition of Si in the form of phytoliths in plant tissues (Katz 2015). Evidence of cross-linking of Si in cell walls with hemicellulose is also reported (He et al. 2015; Luyckx et al. 2017). Si accumulates in the epidermal layer of leaves in the form of silica bodies. This deposition of Si in various forms improves mechanical properties and may act as a physical barrier (Massey et al. 2007). Such Si deposition might also increase roughness and tensile strength of leaves, causing reduced palatability and digestibility in herbivores (Massey and Hartley 2009; Hartley et al. 2015; Frew et al. 2016).

The supplementation of Si has proven beneficial to reduce the transpirational loss of water from leaves (Gong et al. 2003). It also enhanced the UV tolerance that resulted in reduced membrane damage (Goto et al. 2003; Shen et al. 2010). Stomatal conductance in relation to turgidity in guard cells is also reduced due to the deposition of Si in leaves (Zhu and Gong 2014). Under drought stress, plants can absorb water from the soil due to Si-induced root elongation and upregulation of aquaporin genes in roots (Hattori et al. 2005; Liu et al. 2015). The supply of Si reduces the translocation of toxic ions such as Na^+, Cl^-, and heavy metals from root to shoot (Savvas and Ntatsi 2015). Si-containing materials alter the rhizospheric pH and limit the bioavailability of heavy metals (Wu et al. 2013). In contrast, soluble silicates produce metasilicic acid (H_2SiO_3), which is gelatinous and retains heavy metals (Gu et al. 2011).

6.3 Role of Si in Plant Defense Under Adverse Environmental Conditions

Supplementation of Si fertilizers enhances the defense mechanisms of plants against pathogens such as viruses, bacteria, fungi, and other organisms like nematodes, arthropods, vertebrates, and herbivores (Griffin et al. 2015; Reynolds et al. 2016). Si mitigates the biotic stress in plants by either acting as a physical barrier in the epidermal layer or by alleviating resistance to pathogens. The distribution of silica in the leaf tissues can contribute more to the defense against herbivorous insects than other animals (O'Reagain and Mentis 1989). Likewise, the deposition of phytoliths throughout the leaf epidermis acts as a barrier against leaf-chewing insects than the phloem-feeding insects (Massey et al. 2006).

The application of Si improves the plant's ability to restrict the spread of pathogens. For example, enhanced resistance to *Eldana saccharina* in sugarcane was examined by Keeping et al. (2009). Si application has also reduced the rates of infections by pathogenic fungi such as *Rhizoctonia solani* and *Bipolaris oryzae* (Ning et al. 2014; Schurt et al. 2014; Zhang et al. 2014). In the Si-supplemented wheat plants, the invasion by *Pyricularia oryzae* and *Bipolaris sorokiniana* was restricted within the leaf epidermis (Domiciano et al. 2013).

6.4 Effect of Si on the Plant Biochemical Responses Under Adverse Environments

At the biochemical level, Si contributes to the defense mechanisms by increasing the levels of diverse secondary metabolites like phenolics, flavonoids, momilactones, and phytoalexins (Cherif et al. 1994; Rémus-Borel et al. 2005; Debona et al. 2017). It also enhances the activities of defense enzymes like chitinase, lipoxygenase, peroxidase, phenylalanine ammonia-lyase, and polyphenol oxidase (Rahman et al. 2014). Signaling of key phytohormones like salicylic acid, jasmonic acid, and ethylene that are active during stress is also influenced by the Si treatments (Glazebrook 2005; Wu and Baldwin 2010; Liang et al. 2015). Si also interferes with the insect's life cycle by lowering the phenology, thereby making it more prone to predation (James 2003; Connick 2011). Elevated malondialdehyde (MDA) contents reflect membrane damage caused due to lipid peroxidation (Zhu et al. 2004). The MDA levels were reduced upon supplementation of Si in barley (Liang et al. 2003), grapevine (Soylemezoglu et al. 2009), and maize (Moussa 2006). Additionally, Si also influences the levels of osmolytes and plant growth regulators (Adrees et al. 2015; Ali et al. 2015; Noman et al. 2015; Jabeen et al. 2016).

7 Si and Osmolytes

Osmolytes are organic solutes that maintain the cellular potential for a healthy metabolism. They do not interfere with the normal metabolism of the plants (Zhang et al. 2004) but protect the cellular enzymes and cell membranes from the detrimental effects of high ion concentrations due to stress (Bohnert and Shen 1999; Ashraf and Foolad 2007). Thus, osmolytes act as osmoprotectants and include low molecular weight solutes like glycine betaine (GB), proline, polyols, alanine betaine, and simple sugars like trehalose and sucrose (Sharma et al. 2019). These solutes help the host to sustain severe osmotic stress (Singh et al. 2015) by maintaining the osmotic balance between the cytosol and surrounding medium of the cell. Osmolytes are also known to inhibit the production of ROS, thereby protecting the plants from oxidative damage. Plants produce osmolytes mainly under adverse environmental conditions, especially abiotic stress. Accumulation of osmolytes indicates the plant's adaptation to stress.

Si seems to modulate the levels of osmolytes in stressed plants. Application of Si reduced the proline levels in stressed plants of spinach and tomato (Gunes et al. 2007b), wheat (Tuna et al. 2008), sorghum (Yin et al. 2013), soybean (Lee et al. 2010), and grapevine (Soylemezoglu et al. 2009). The levels of glycine betaine, proline, and total soluble sugars were elevated after foliar application of Si in the tolerant as well as sensitive okra genotypes exposed to salt stress. However, the effect was more pronounced in sensitive genotypes (Abbas et al. 2015). A similar trend was also reported in capsicum (Pereira 2013), tobacco (Pereira 2013), and maize (Sayed and Gadallah 2014). Exposure of Si has enhanced the plant tolerance to drought stress via osmolytes modification in many crops (Crusciol et al. 2009), such as the augmented proline content in drought-stressed condition for wheat (Gong et al. 2005; Kaya et al. 2006) and pepper plants (Pereira 2013).

8 Si and Phytohormones

Phytohormones induce the vital responses needed for the healthy growth and development of plants. Apart from their regulatory functions, they also coordinate signal transduction pathways under biotic and abiotic stress (Wolters and Jürgens 2009). Si application regulates the levels of phytohormones to enhance plant tolerance to stress (Kim et al. 2014). However, the level of ethylene declined after the application of Si under salinity stress in sorghum (Yin et al. 2016). In soybean, the level of GA was elevated, and that of abscisic acid (ABA) declined in the presence of Si (Lee et al. 2010). Similarly, the level of jasmonates (JA) was reduced, and that of salicylic acid (SA) increased in the presence of Si (Hamayun et al. 2010). Si induced the thermo-tolerance in potato by regulating the endogenous level of SA and ABA. The Si-mediated tolerance to brown spot disease in rice depends on immune hormones SA and JA as well as fungal ethylene (Van Bockhaven et al. 2015). Likewise, Si priming of seeds gave tolerance to powdery mildew in *A. thaliana* (Vivancos et al. 2015).

9 Si and Antioxidant Enzymes

All kinds of stress culminate in oxidative stress caused by reactive oxygen species (ROS) such as superoxide ($O2^{\bullet -}$) radicals, hydrogen peroxide (H_2O_2), and hydroxyl ($OH^{\bullet}$) radicals (Imlay 2003). Plants have evolved many protective mechanisms against ROS. These mechanisms include the production of antioxidants and antioxidative enzymes, for instance, catalases (CAT), superoxide dismutases (SOD), peroxidases (POD), and glutathione reductases (GR) (Ahire et al. 2012). Among various antioxidative enzymes, SOD, CAT, and POD make up the first line of defense in scavenging ROS. SOD converts superoxide radicals to H_2O_2, which is noxious to the nucleic acids, proteins, and chloroplast, and is dealt with by CAT and POD (Shen et al. 2010).

Si modulates the plant antioxidant defense system to prevent oxidative damage in the stressed plants (Kim et al. 2017). Several reports have described the Si-induced upregulation of antioxidative enzymes such as CAT, GR, SOD, guaiacol peroxidase (GPX), and ascorbate peroxidase (APX) (Shen et al. 2010; Soundararajan et al. 2014; Zhu and Gong 2014; Etesami and Jeong 2018), and peroxidase mediated host defense responses as well (Torres et al. 2006). Supplementation of Si had increased the level of POD in rice and cucumber plants challenged with *Bipolaris oryzae* and *Podosphaera xantii* (Dallagnol et al. 2011).

10 Si and Nutrient Uptake

The availability and uptake of nutrients in sufficient amounts is a prerequisite for healthy plant growth and architecture. Plant nutrients are primarily divided into two groups: macronutrients and micronutrients, based on the amount in which the plants require them. Any change in the optimum levels of any of these nutrients leads to abnormalities in plants (Shrivastav et al. 2020).

The application of Si is known to influence the uptake of macronutrients like N, P, and K in plants. Such an application elevated the level of N in cowpea (Mali 2008), wheat (Mali and Aery 2008), and rice (Singh et al. 2006; Detmann et al. 2012). The use of Si fertilizers increases the availability of P (Ma 2004; Singh et al. 2006) and influences the uptake of K (Kaya et al. 2006). In soybean, the application of Si was shown to improve the growth of plants and enhance the uptake of K (Miao et al. 2010). Si also mediates enhanced uptake of Ca and Mg (Kaya et al. 2006; Mali and Aery 2008). Moreover, the presence of Si not only reduces the uptake of heavy metals like Al and Cd (Ma and Takahashi 2002; Ma et al. 2004) but also mitigates the deficiency of micronutrients like Fe, Mn, Cu, Zn, and B in plants (Pavlovic et al. 2013; Hernandez-Apaolaza 2014).

11 Conclusions

Adverse environmental conditions adversely affect plant growth, development, and yield. Si plays a vital role in the alleviation of stress caused by various harsh environments. It influences multifunctional traits such as growth, morphology, the activity of antioxidant enzymes, accumulation of osmolytes, photosynthesis, and nutrient uptake in plants. The ability to take up Si under different environmental conditions varies from species to species. Moreover, the effects and their magnitudes caused due to Si supplementation vary from species to species and the prevalent conditions. Substantial evidence exists that underline the beneficial role of Si in plants under abiotic stress, but how Si manipulates the mechanisms of alleviation is still much of a mystery.

Acknowledgments Financial assistance by the University Grants Commission, New Delhi, and Department of Science and Technology (DST), Government of India and DST-PURSE are gratefully acknowledged. Authors are also grateful to Yashavantrao Chavan Institute of Science, Satara for financial support under DBT-STAR college scheme. Financial assistance to the faculty under self-funded project is acknowledged and also for providing facilities.

References

Aal AMKA, Oraby MMM (2013) Using silicon for increasing the tolerance mango cv. Ewaise transplants to drought. World Rural Obs 5:36–40

Abbas T, Balal RM, Shahid MA, Pervez MA, Chaudhary MA, 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 37:6

Acquaah G (2012) Principles of plant genetics and breeding, 2nd edn. Wiley-Blackwell

Adrees M, Ali S, Rizwan M, Zia-ur-Rahman M, Ibrahim M, Abbas F, Farid M, Qayyum MF, Irshad MK (2015) Mechanisms of silicon-mediated alleviation of heavy metal toxicity in plants: A review. Ecotox Environ Safe 119:186–197

Agarie S, Uchida H, Agata W, Kubota F, Kaufman PB (1998) Effects of silicon on transpiration and leaf conductance in rice plants (*Oryza sativa* L.). Plant Prod Sci 1:89–95

Ahire ML, Lokhande VH, Kavi Kishor PB, Nikam TD (2012) Brinjal (*Solanum melongena* Linn.) varieties accumulate both Na^+ and K^+ under low NaCl stress, but excludes Na^+ and accumulate K + under high salt levels. Asian Australas J Plant Sci Biotechnol 6:1–6

Ahmad B (2014) Interactive effects of silicon and potassium nitrate in improving salt tolerance of wheat. J Integr Agric 13:1889–1899

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

Ahmed M, Fayyaz-ul-Hassan AM (2014) Amelioration of drought in sorghum (*Sorghum bicolor* L.) by silicon. Commun Soil Sci Plant Anal 45:470–486

Ahmed M, Fayyaz-ul-Hassen QU, Aqeel Aslam M (2011) Silicon application and drought tolerance mechanism of sorghum. African J Agric Res 6:594–607

Ahmed M, Qadeer U, Ahmed ZI, Hassan FU (2016) Improvement of wheat (*Triticum aestivum*) drought tolerance by seed priming with silicon. Arch Agron Soil Sci 62:299–315

Al-aghabary K, Zhu Z, Shi Q (2004) Influence of silicon supply on chlorophyll content, chlorophyll fluorescence, and antioxidative enzyme activities in tomato plants under salt stress. J Plant Nutr. https://doi.org/10.1081/LPLA-200034641

Ali S, Chaudhary A, Rizwan M, Anwar HT, Adrees M, Farid M, Irshad MK, Hayat T, Anjum SA (2015) Alleviation of chromium toxicity by glycine betaine is related to elevated antioxidant enzymes and suppressed chromium uptake and oxidative stress in wheat (*Triticum aestivum* L.). Environ Sci Pollut Res 22:10669–10678

Ali S, Rizwan M, Ullah N, Bharwna SA, Waseem M, Farooq MA, Abbasi GH, Farid M (2016) Physiological and biochemical mechanisms of silicon-induced copper stress tolerance in cotton (*Gossypium hirsutum* L.). Acta Physiol Plant 38:262

Ali S, Rizwan M, Hussain A, Zia ur Rehman M, Ali B, Yousaf B, Wijaya L, Alyemeni MN, Ahmad P (2019) Silicon nanoparticles enhanced the growth and reduced the cadmium accumulation in grains of wheat (*Triticum aestivum* L.). Plant Physiol Biochem 140:1–8

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

Ashraf M, Foolad MR (2007) Roles of glycine betaine and proline in improving plant abiotic stress resistance. Environ Exp Bot 59:206–216

Ashraf M, Rahmatullah AR, Afzal M, Tahir MA, Kanwal S, Maqsood MA (2009) Potassium and silicon improve yield and juice quality in sugarcane (*Saccharum officinarum* L.) under salt stress. J Agron Crop Sci 195:284–291

Ashraf M, Rahmatullah AM, Ahmed R, Mujeeb F, Sarwar A, Ali L (2010a) Alleviation of detrimental effects of NaCl by silicon nutrition in salt-sensitive and salt-tolerant genotypes of sugarcane (*Saccharum officinarum* L.). Plant Soil 326:381–391

Ashraf M, Rahmatullah AR, Bhatti AS, Afzal M, Sarwar A, Maqsood MA, Kanwal S (2010b) Amelioration of salt stress in sugarcane (*Saccharum officinarum* L.) by supplying potassium and silicon in hydroponics. Pedosphere 20:153–162

Bari MA, Prity SA, Das U, Akhter MS, Sajib SA, Reza MA, Kabir AH (2020) Silicon induces phytochelatin and ROS scavengers facilitating cadmium detoxification in rice. Plant Biol 22:472–479

Bohnert HJ, Shen B (1999) Transformation and compatible solutes. Sci Hortic 78:237–260

Bokor B, Ondoš S, Vaculík M, Bokorová S, Weidinger M, Lichtscheidl I, Turňa J, Lux A (2017) Expression of genes for Si uptake, accumulation, and correlation of Si with other elements in ionome of maize kernel. Front Plant Sci 8:1063

Bradáčová 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

Bray EA, Bailey-Serres J, Weretilnyk E (2000) Responses to abiotic stresses. American Society of Plant Physiologists, Rockville, MD

Calero Hurtado A, Chiconato DA, de Mello Prado R, da Silveira Sousa Junior G, Felisberto G (2019) Silicon attenuates sodium toxicity by improving nutritional efficiency in sorghum and sunflower plants. Plant Physiol Biochem 142:224–233

Calero Hurtado A, Chiconato DA, de MelloPrado R, da Silveira Sousa Junior G, Gratão PL, Felisberto G, Viciedo DO, Mathias dos Santos DM (2020) Different methods of silicon application attenuate salt stress in sorghum and sunflower by modifying the antioxidative defense mechanism. Ecotoxicol Environ Saf 203:110964

Chen W, Yao X, Cai K, Chen J (2011) Silicon alleviates drought stress of rice plants by improving plant water status, photosynthesis and mineral nutrient absorption. Biol Trace Elem Res 142:67–76

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 Physiol Plant 36:2531–2535

Chen D, Chen D, Xue R, Long J, Lin X, Lin Y, Jia L, Zeng R, Song Y (2019a) Effects of boron, silicon and their interactions on cadmium accumulation and toxicity in rice plants. J Hazard Mater 367:447–455

Chen Z, Xu J, Xu Y, Wang K, Cao B, Xu K (2019b) Alleviating effects of silicate, selenium, and microorganism fertilization on lead toxicity in ginger (*Zingiber officinale* Roscoe). Plant Physiol Biochem 145:153–163

Cherif M, Menzies JG, Ehret DL, Bogdanoff C, Bélanger RR (1994) Yield of cucumber infected with *Pythium aphanidermatum* when grown with soluble silicon. HortScience 29:896–897

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

Connick VJ (2011) The impact of silicon fertilisation on the chemical ecology of grapevine, *Vitis vinifera* constitutive and induced chemical defenses against arthropod pests and their natural enemies. MS Thesis, Faculty of Science, School of Agriculture and Wine Sciences, Charles Sturt University

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

Côté-Beaulieu C, Chain F, Menzies JG, Kinarde SD, Bélanger RR (2009) Absorption of aqueous inorganic and organic silicon compounds by wheat and their effect on growth and powdery mildew control. Environ Exp Bot 65:155–161

Crusciol CAC, Pulz AL, Lemos LB, Soratto RP, Lima GPP (2009) Effects of silicon and drought stress on tuber yield and leaf biochemical characteristics in potato. Crop Sci 49:949–954

Dallagnol LJ, Rodrigues FA, Damatta FM, Mielli MVB, Pereira SC (2011) Deficiency in silicon uptake affects cytological, physiological, and biochemical events in the rice — *Bipolaris oryzae* interaction. Phytopathology 101:92–104

Das IK, Rakshit S (2016) Millets, their importance, and production constraints. In: Das IK, Padmaja PG (eds) Biotic stress resistance in millets. Academic Press, Amsterdam, pp 3–19

Das P, Manna I, Sil P, Bandopadhyay M, Biswas AK (2019) Exogenous silicon alters organic acid production and enzymatic activity of TCA cycle in two NaCl stressed indica rice cultivars. Plant Physiol Biochem 136:76–91
Debona D, Rodrigues FA, Datnoff LE (2017) Silicon's role in abiotic and biotic plant stresses. Annu Rev Phytopathol 55:85–107
Deshmukh RK, Ma JF, Bélanger RR (2017) Role of silicon in plants. Front Plant Sci 8:1–3
Detmann KC, Araújo WL, Martins SCV, Sanglard LMVP, Reis JV, Detmann E, Rodrigues FÁ, Nunes-Nesi A, Fernie AR, DaMatta FM (2012) Silicon nutrition increases grain yield, which, in turn, exerts a feed-forward stimulation of photosynthetic rates via enhanced mesophyll conductance and alters primary metabolism in rice. New Phytol 196:752–762
Domiciano GP, Rodrigues FA, Guerra AMN, Vale FXR (2013) Infection process of *Bipolaris sorokiniana* on wheat leaves is affected by silicon. Trop Plant Pathol 38:258–263
Embiale A, Hussein A, Husen A, Sahile S, Mohammed K (2016) Differential sensitivity of *Pisum sativum* L. cultivars to water-deficit stress: changes in growth, water status, chlorophyll fluorescence and gas exchange attributes. J Agron 15:45–57
Eneji AE, Inanaga S, Muranaka S, Li J, Hattori T, An P, Tsuji W (2008) Growth and nutrient use in four grasses under drought stress as mediated by silicon fertilizers. J Plant Nutr 31:355–365
Epstein E (1994) The anomaly of silicon in plant biology. Proc Natl Acad Sci U S A 91:11–17
Epstein E (1999) Silicon. Annu Rev Plant Physiol Plant Mol Biol 50:641–664
Epstein E, Bloom AJ (2005) Mineral nutrition of plants: principles and perspectives, 2nd edn. Sinauer Assoc. Inc., Sunderland, UK
Eraslan F, Inal A, Pilbeam DJ, Gunes A (2008) Interactive effects of salicylic acid and silicon on oxidative damage and antioxidant activity in spinach (*Spinacia oleracea* L. cv. Matador) grown under boron toxicity and salinity. Plant Growth Regul 55:207–219
Etesami H, Jeong BR (2018) Silicon (Si): review and future prospects on the action mechanisms in alleviating biotic and abiotic stresses in plants. Ecotoxicol Environ Saf 147:881–896
Fang C, Li L, Zhang P, Wang D, Yang L, Reza BM, Lin W (2019) *Lsi1* modulates the antioxidant capacity of rice and protects against ultraviolet-B radiation. Plant Sci 278:96–106
Farooq MA, Detterbeck A, Clemens S, Dietz KJ (2016) Silicon-induced reversibility of cadmium toxicity in rice. J Exp Bot 67:3573–3585
Farshidi M, Abdolzadeh A, Sadeghipour HR (2012) Silicon nutrition alleviates physiological disorders imposed by salinity in hydroponically grown canola (*Brassica napus* L.) plants. Acta Physiol Plant 34:1779–1788
Fauteux F, Rémus-Borel W, Menzies JG, Bélanger RR (2005) Silicon and plant disease resistance against pathogenic fungi. FEMS Microbiol Lett 249:1–6
Frew A, Powell JR, Sallam N, Allsopp PG, Johnson SN (2016) Trade-offs between silicon and phenolic defenses may explain enhanced performance of root herbivores on phenolic-rich plants. J Chem Ecol 42:768–771
Getnet Z, Husen A, Fetene M, Yemata G (2015) Growth, water status, physiological, biochemical and yield response of stay green sorghum {*Sorghum bicolor* (L.) Moench} varieties — a field trial under drought-prone area in Amhara regional state, Ethiopia. J Agron 14:188–202
Glazebrook J (2005) Contrasting mechanisms of defense against biotrophic and necrotrophic pathogens. Annu Rev Phytopathol 43:205–227
Glick BR (2014) Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiol Res 169:30–39
Godfray HCJ, Beddington JR, Crute IR, Haddad L, Lawrence D, Muir JF, Pretty J, Robinson S, Thomos SM, Toulmin C (2010) Food security: the challenge of feeding 9 billion people. Science 327:812–818
Gong H, Chen K (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
Gong HJ, Chen KM, Chen GC, Wang SM, Zhang CL (2003) Effects of silicon on growth of wheat under drought. J Plant Nutr 26:1055–1063

Gong H, Zhu X, Chen K, Wang S, Zhang C (2005) Silicon alleviates oxidative damage of wheat plants in pots under drought. Plant Sci 169:313–321

Gong HJ, Chen KM, Zhao ZG, ChenGC ZWJ (2008) Effects of silicon on defense of wheat against oxidative stress under drought at different developmental stages. Biol Plant 52:592–596

Goto M, Ehara H, Karita S, Takabe K, Ogawa N, Yamada Y, Ogawa S, Yahaya MS, Morita O (2003) Protective effect of silicon on phenolic biosynthesis and ultraviolet spectral stress in rice crop. Plant Sci 164:349–356

Griffin M, Hogan B, Schmidt O (2015) Silicon reduces slug feeding on wheat seedlings. J Pest Sci 2004 88:17–24

Gu HH, Qiu H, Tian T, Zhan SS, Deng THB, Chaney RL, Wang SZ, Tang YT, Morel JL, Qiu RL (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, Inal A, Bagci EG, Coban S, Pilbeam DJ (2007a) silicon mediates changes to some physiological and enzymatic parameters symptomatic for oxidative stress in spinach (*Spinacia oleracea* L.) grown under B toxicity. Sci Hortic 113:113–119

Gunes A, Inal A, Bagci EG, Pilbeam DJ (2007b) Silicon-mediated changes of some physiological and enzymatic parameters symptomatic for oxidative stress in spinach and tomato grown in sodic-B toxic soil. Plant Soil 290:103–114

Gunes A, Kadioglu YK, Pilbeam DJ, Inal A, Coban S, Aksu A (2008a) Influence of silicon on sunflower cultivars under drought stress, II: Essential and nonessential element uptake determined by polarized energy dispersive X-ray fluorescence. Commun Soil Sci Plant Anal 39:1904–1927

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

Guo Q, Meng L, Mao P, Tian X (2013) Role of silicon in alleviating salt-induced toxicity in white clover. Bull Environ Contam Toxicol 91:213–216

Haghighi M, Pessarakli M (2013) Influence of silicon and nano-silicon on salinity tolerance of cherry tomatoes (*Solanum lycopersicum* L.) at early growth stage. Sci Hortic 161:111–117

Hajiboland R, Cheraghvareh L, Poschenrieder C (2017) Improvement of drought tolerance in Tobacco (*Nicotiana rustica* L.) plants by silicon. J Plant Nutr 40:1661–1676

Hall CR, Waterman JM, Vandegeer RK, Hartley SE, Johnson SN (2019) The role of silicon in antiherbivore phytohormonal signalling. Front Plant Sci 10:1–7

Hamayun M, Khan SA, Shinwari ZK, Khan AL, Ahmad N, Lee IJ (2010) Effect of polyethylene glycol induced drought stress on physio-hormonal attributes of soybean. Pakistan J Bot 42:977–986

Hameed A, Sheikh MA, Hameed A, Farooq T, Basra SMA, Jamil A (2014) Chitosan seed priming improves seed germination and seedling growth in wheat (*Triticum aestivum* L.) under osmotic stress induced by polyethylene glycol. Philipp Agric Sci 97:294–299

Hartley SE, Fitt RN, McLarnon EL, Wade RN (2015) Defending the leaf surface: Intra- and interspecific differences in silicon deposition in grasses in response to damage and silicon supply. Front Plant Sci 6:1–8

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

He C, Ma J, Wang L (2015) A hemicellulose-bound form of silicon with potential to improve the mechanical properties and regeneration of the cell wall of rice. New Phytol 206:1051–1062

He M, He CQ, Ding NZ (2018) Abiotic stresses: General defenses of land plants and chances for engineering multistress tolerance. Front Plant Sci 9:1771

Hernandez-Apaolaza L (2014) Can silicon partially alleviate micronutrient deficiency in plants? A review. Planta 240:447–458

Hildebrand M, Dahlin K, Volcani BE (1998) Characterization of a silicon transporter gene family in *Cylindrotheca fusiformis*: sequences, expression analysis, and identification of homologs in other diatoms. Mol Gen Genet 260:480–486

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

Hubbard M, Germida J, Vujanovic V (2012) Fungal endophytes improve wheat seed germination under heat and drought stress. Botany 90:137–149

Husen A (2010) Growth characteristics, physiological and metabolic responses of teak (*Tectona grandis* Linn. f.) clones differing in rejuvenation capacity subjected to drought stress. Silva Gene 59:124–136

Husen A, Iqbal M, Aref IM (2016) IAA-induced alteration in growth and photosynthesis of pea (*Pisum sativum* L.) plants grown under salt stress. J Environ Biol 37:421–429

Husen A, Iqbal M, Sohrab SS, Ansari MKA (2018) Salicylic acid alleviates salinity-caused damage to foliar functions, plant growth and antioxidant system in Ethiopian mustard (*Brassica carinata.* A. Br). Agri Food Sec 7:44

Husen A, Iqbal M, Khanum N, Aref IM, Sohrab SS, Meshresa G (2019) Modulation of salt-stress tolerance of niger (*Guizotia abyssinica*), an oilseed plant, by application of salicylic acid. J Environ Biol 40:94–104

Hussain SA, Farooq MA, Akhtar J, Saqib ZA (2018) Silicon-mediated growth and yield improvement of sunflower (*Helianthus annus* L.) subjected to brackish water stress. Acta Physiol Plant 40:180

Hussein M, Embiale A, Husen A, Aref IM, Iqbal M (2017) Salinity-induced modulation of plant growth and photosynthetic parameters in faba bean (*Vicia faba*) cultivars. Pakistan J Bot 49:867–877

Imlay JA (2003) Pathways of oxidative damage. Annu Rev Microbiol 57:395–418

Jabeen N, Abbas Z, Iqbal M, Rizwan M, Jabbar A, Farid M, Ali S, Ibrahim M, Abbas F (2016) Glycinebetaine mediates chromium tolerance in mung bean through lowering of Cr uptake and improved antioxidant system. Arch Agron Soil Sci 62:648–662

Jadhao KR, Bansal A, Rout GR (2020) Silicon amendment induces synergistic plant defense mechanism against pink stem borer (*Sesamia inferens* Walker.) in finger millet (*Eleusine coracana* Gaertn.). Sci Rep 10:1–15

James DG (2003) Field evaluation of herbivore-induced plant volatiles as attractants for beneficial insects: methyl salicylate and the green lacewing, *Chrysopa nigricornis*. J Chem Ecol 29:1601–1609

Jang SW, Kim Y, Khan AL, Na CI, Lee IJ (2018) Exogenous short-term silicon application regulates macro-nutrients, endogenous phytohormones, and protein expression in *Oryza sativa* L. BMC Plant Biol 18:1–12

Javaid T, Farooq MA, Akhtar J, Saqib ZA, Anwar ul-Haq M (2019) Silicon nutrition improves growth of salt-stressed wheat by modulating flows and partitioning of Na^+, Cl^- and mineral ions. Plant Physiol Biochem 141:291–299

Jiang N, Fan X, Lin W, Wang G, Cai K (2019) Transcriptome analysis reveals new insights into the bacterial wilt resistance mechanism mediated by silicon in tomato. Int J Mol Sci 20:1–21

Johnson SN, Rowe RC, Hall CR (2020) Silicon is an inducible and effective herbivore defence against *Helicoverpa punctigera* (Lepidoptera: Noctuidae) in soybean. Bull Entomol Res 110:417–422

Kafi M, Rahimi Z (2011) Effect of salinity and silicon on root characteristics, growth, water status, proline content and ion accumulation of purslane (*Portulaca oleracea* L.). Soil Sci Plant Nutr 57:341–347

Kar M, Öztürk Ş (2020) Analysis of *Phaseolus vulgaris* gene expression related to oxidative stress response under short-term cadmium stress and relationship to cellular H_2O_2. Biologia 75:1009–1016

Katz O (2015) Silica phytoliths in angiosperms: phylogeny and early evolutionary history. New Phytol 208:642–646

Kaya C, Tuna L, Higgs D (2006) Effect of silicon on plant growth and mineral nutrition of maize grown under water-stress conditions. J Plant Nutr 29:1469–1480

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 66:54–60

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

Khan E, Gupta M (2018) Arsenic-silicon priming of rice (*Oryza sativa* L.) seeds influence mineral nutrient uptake and biochemical responses through modulation of *Lsi-1*, *Lsi-2*, *Lsi-6* and nutrient transporter genes. Sci Rep 8:1–16

Khan A, Kamran M, Imran M, Al-Harrasi A, Al-Rawahi A, Al-Amri I, Lee IJ, Khan AL (2019) Silicon and salicylic acid confer high-pH stress tolerance in tomato seedlings. Sci Rep 9:1–16

Khan A, Bilal S, Khan AL, Imran M, Al-Harrasi A, Al-Rawahi A, Lee IJ (2020a) Silicon-mediated alleviation of combined salinity and cadmium stress in date palm (*Phoenix dactylifera* L.) by regulating physio-hormonal alteration. Ecotoxicol Environ Saf 188:109885

Khan A, Khan AL, Imran M, Asaf S, Kim YH, Bilal S, Numan M, Al-Harrasi A, Al-Rawahi A, Lee IJ (2020b) Silicon-induced thermotolerance in *Solanum lycopersicum* L. via activation of antioxidant system, heat shock proteins, and endogenous phytohormones. BMC Plant Biol 20:1–18

Khan ZS, Rizwan M, Hafeez M, Ali S, Adrees M, Qayyum MF, Khalid F, Zia ur Rehman M, Sarwar MA (2020c) Effects of silicon nanoparticles on growth and physiology of wheat in cadmium contaminated soil under different soil moisture levels. Environ Sci Pollut Res 27:4958–4968

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. Biol Plant 58:265–273

Khoshgoftarmanesh AH, Khodarahmi S, Haghighi M (2014) Effect of silicon nutrition on lipid peroxidation and antioxidant response of cucumber plants exposed to salinity stress. Arch Agron Soil Sci 60:639–653

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

Kim MY, Lee SH, Jang GY, Park HJ, Li M, Kim S, Lee YR, Noh YH, Lee J, Jeon HS (2015) Effects of high hydrostatic pressure treatment on the enhancement of functional components of germinated rough rice (*Oryza sativa* L.). Food Chem 166:86–92

Kim YH, Khan AL, Waqas M, Lee IJ (2017) Silicon regulates antioxidant activities of crop plants under abiotic-induced oxidative stress: a review. Front Plant Sci 8:510

Kinrade SD, Gillson AME, Knight CTG (2002) Silicon-29 NMR evidence of a transient hexavalent silicon complex in the diatom *Navicula pelliculosa*. J Chem Soc Dalt Trans 3:307–309

Kochanová Z, Jašková K, Sedláková B, Luxová M (2014) Silicon improves salinity tolerance and affects ammonia assimilation in maize roots. Biol 69:1164–1171

Latef AA, Tran LSP (2016) Impacts of priming with silicon on the growth and tolerance of maize plants to alkaline stress. Front Plant Sci 7:1–10

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

Lekklar C, Chadchawan S, Boon-Long P, Pfeiffer W, Chaidee A (2019) Salt stress in rice: multivariate analysis separates four components of beneficial silicon action. Protoplasma 256:331–347

Li Q, Ma C, Li H, Xiao Y, Liu X (2004) Effects of soil available silicon on growth, development and physiological functions of soybean. Chinese J Appl Ecol 15:73–76

Li H, Zhu Y, Hu Y, Han W, Gongn H (2015) Beneficial effects of silicon in alleviating salinity stress of tomato seedlings grown under sand culture. Acta Physiol Plant 37:71

Liang Y, Chen Q, Liu Q, Zhang W, Ding R (2003) Exogenous silicon (Si) increases antioxidant enzyme activity and reduces lipid peroxidation in roots of salt-stressed barley (*Hordeum vulgare* L.). J Plant Physiol 160:1157–1164

Liang Y, Zhang W, Chen Q, Ding R (2005) Effects of silicon on H^+-ATPase and H^+-PPase activity, fatty acid composition and fluidity of tonoplast vesicles from roots of salt-stressed barley (*Hordeum vulgare* L.). Environ Exp Bot 53:29–37

Liang Y, Sun W, Zhu YG, Christie P (2007) Mechanisms of silicon-mediated alleviation of abiotic stresses in higher plants: a review. Environ Pollut 147:422–428

Liang Y, Zhu J, Li Z, Chu G, Ding Y, Zhang J, Sun W (2008) Role of silicon in enhancing resistance to freezing stress in two contrasting winter wheat cultivars. Environ Exp Bot 64:286–294

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

Liu P, Yin L, Deng X, Wang S, Tanaka K, Zhang S (2014) Aquaporin-mediated increase in root hydraulic conductance is involved in silicon-induced improved root water uptake under osmotic stress in *sorghum bicolor* L. J Exp Bot 65:4747–4756

Liu P, Yin L, Wang S, Zhang M, Deng X, Zhnag S, Tanaka K (2015) Enhanced root hydraulic conductance by aquaporin regulation accounts for silicon alleviated salt-induced osmotic stress in *sorghum bicolor* L. Environ Exp Bot 111:42–51

Liu L, Song Z, Yu C, Yu G, Ellam RM, Liu H, Singh BP, Wang H (2020) Silicon effects on biomass carbon and phytolith-occluded carbon in grasslands under high-salinity conditions. Front Plant Sci 11:657

López-Millán AF, Sagardoy R, Solanas M, Abadía A, Abadía J (2009) Cadmium toxicity in tomato (*Lycopersicon esculentum*) plants grown in hydroponics. Environ Exp Bot 65:376–385

Lukacova Z, Svubova R, Janikovicova S, Volajova Z, Lux A (2019) Tobacco plants (*Nicotiana benthamiana*) were influenced by silicon and were not infected by dodder (*Cuscuta europaea*). Plant Physiol Biochem 139:179–190

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

Luyckx M, Hausman JF, Lutts S, Guerriero G (2017) Impact of silicon in plant biomass production: focus on bast fibres, hypotheses, and perspectives. Plan Theory 6:1–12

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 CC, Li QF, Gao YB, Xin TR (2004) Effects of silicon application on drought resistance of cucumber plants. Soil Sci Plant Nutr 50:623–632

Ma JF, Kazunori T, 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 D, Sun D, Wang C, Qin H, Ding H, Li Y, Guo T (2016) Silicon application alleviates drought stress in wheat through transcriptional regulation of multiple antioxidant defense pathways. J Plant Growth Regul 35:1–10

Maksimović JD, Mojović M, Maksimović V, Römheld 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

Mali M (2008) Silicon effects on nodule growth, dry-matter production, and mineral nutrition of cowpea (*Vigna unguiculata*). J Plant Nutr Soil Sci 171:835–840

Mali M, Aery NC (2008) Influence of silicon on growth, relative water contents and uptake of silicon, calcium and potassium in wheat grown in nutrient solution. J Plant Nutr 31:1867–1876

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". Biomed Res Int 2016:3076357

Marschner H (1995) Beneficial mineral elements. In: Marschner H (ed) Mineral nutrition of higher plants. Academic Press, San Diego, pp 405–435

Massey FP, Hartley SE (2009) Physical defences wear you down: progressive and irreversible impacts of silica on insect herbivores. J Anim Ecol 78:281–291

Massey FP, Ennos AR, Hartley SE (2006) Silica in grasses as a defence against insect herbivores: contrasting effects on folivores and a phloem feeder. J Anim Ecol 75:595–603

Massey FP, Ennos AR, Hartley SE (2007) Grasses and the resource availability hypothesis: the importance of silica-based defences. J Ecol 95:414–424

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

Miao BH, Han XG, Zhang WH (2010) The ameliorative effect of silicon on soybean seedlings grown in potassium-deficient medium. Ann Bot 105:967–973

Mitani N, Jian FM, Iwashita T (2005) Identification of the silicon form in xylem sap of rice (*Oryza sativa* L.). Plant Cell Physiol 46:279–283

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

Mitra GN (2015) Regulation of nutrient uptake by plants: a biochemical and molecular approach. Springer, New Delhi, pp 181–187

Moussa H (2006) Influence of exogenous application of silicon on physiological response of salt-stressed maize (*Zea mays* L.). Int J Agric Biol 8:293–297

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 77:133–146

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

Murillo-Amador B, Yamada S, Yamaguchi T, Rueda-Puente E, Ávila-Serrano N, García-Hernández JL, López-Aguilar R, Troyo-Diéguez E, Nieto-Garibay A (2007) Influence of calcium silicate on growth, physiological parameters and mineral nutrition in two legume species under salt stress. J Agron Crop Sci 193:413–421

Ning D, Song A, Fan F, Li Z, Liang Y (2014) Effects of slag-based silicon fertilizer on rice growth and brown-spot resistance. PLoS One 9:1–9

Noman A, Ali S, Naheed F, Ali Q, Farid M, Rizwan M, Irshad MK (2015) Foliar application of ascorbate enhances the physiological and biochemical attributes of maize (*Zea mays* L.) cultivars under drought stress. Arch Agron Soil Sci 61:1659–1672

Nowakowski W, Nowakowska J (1997) Silicon and copper interaction in the growth of spring wheat seedlings. Biol Plant 39:463–466

O'Reagain PJ, Mentis MT (1989) Leaf silicification in grasses: a review. J Grassl Soc South Africa 6:37–43

Oliveira KR, Souza Junior JP, Bennett SJ, Checchioa MV, de Cássia AR, Felisberto G, de Mello PR, Gratão PL (2020) Exogenous silicon and salicylic acid applications improve tolerance to boron toxicity in field pea cultivars by intensifying antioxidant defence systems. Ecotoxicol Environ Saf 201:110778

Olivera Viciedo D, de Mello PR, Lizcano Toledo R, Aguilar DS, Santos LCND, Hurtado AC, Calzada KP, Aguilar CB (2020) Physiological role of silicon in radish seedlings under ammonium toxicity. J Sci Food Agric. https://doi.org/10.1002/jsfa.10587

Pantazi XE, Moshou D, Bochtis D (2020) Utilization of multisensors and data fusion in precision agriculture. In: Intelligent data mining and fusion systems in agriculture. Academic Press, USA, pp 103–173

Parveen A, Liu W, Hussain S, Asghar J, Perveen S, Xiong Y (2019) Silicon priming regulates morpho-physiological growth and oxidative metabolism in maize under drought stress. Plan Theory 8:431

Pavlovic J, Samardzic J, Maksimović V, Timotijevic G, Stevic N, Laursen KH, Hansen TH, Husted S, Schjoerring JK, Liang Y, Nikolic M (2013) Silicon alleviates iron deficiency in cucumber by promoting mobilization of iron in the root apoplast. New Phytol 198:1096–1107

Pei ZF, Ming DF, Liu D, Wan GL, Geng XX, Gong HJ, Zhou WJ (2010) Silicon improves the tolerance to water-deficit stress induced by polyethylene glycol in wheat (*Triticum aestivum* L.) seedlings. J Plant Growth Regul 29:106–115

Pereira TS, da Silva Lobato AK, Tan DKY, da Costa DV, Uchôa EB, Ferreira RDN, Pereira EDS, Ávila FW, Marques DJ, Guedes EMS (2013) Positive interference of silicon on water relations, nitrogen metabolism, and osmotic adjustment in two pepper (*Capsicum annuum*) cultivars under water deficit. Aust J Crop Sci 7:1064–1071

Rahman H, Jagadeeshselvam N, Valarmathi R, Sachin B, Sasikala R, Senthil N, Sudhakar D, Robin S, Muthurajan R (2014) Transcriptome analysis of salinity responsiveness in contrasting genotypes of finger millet (*Eleusine coracana* L.) through RNA-sequencing. Plant Mol Biol 85:485–503

Raven JA (2001) Chapter 3: Silicon transport at the cell and tissue level. Stud Plant Sci 8:41–55

Rémus-Borel W, Menzies JG, Bélanger RR (2005) Silicon induces antifungal compounds in powdery mildew-infected wheat. Physiol Mol Plant Pathol 66:108–115

Reynolds OL, Padula MP, Zeng R, Gurr GM (2016) Silicon: potential to promote direct and indirect effects on plant defense against arthropod pests in agriculture. Front Plant Sci 7:744

Romero-Aranda MR, Jurado O, Cuartero J (2006) Silicon alleviates the deleterious salt effect on tomato plant growth by improving plant water status. J Plant Physiol 163:847–855

Rufo L, Franco A, de la Fuente V (2014) Silicon in *Imperata cylindrica* (L.) P. Beauv: Content, distribution, and ultrastructure. Protoplasma 251:921–930

Savvas D, Ntatsi G (2015) Biostimulant activity of silicon in horticulture. Sci Hortic 196:66–81

Sayed SA, Gadallah MAA (2014) Effects of silicon on *Zea mays* plants exposed to water and oxygen deficiency. Russ J Plant Physiol 61:460–466

Schurt DA, Cruz MFA, Nascimento KJT, Filippi MCC, Rodrigues FA (2014) Silicon potentiates the activities of defense enzymes in the leaf sheaths of rice plants infected by *Rhizoctonia solani*. Trop Plant Pathol 39:457–463

Shahid MA, Balal RM, Pervez MA, Abbas T, Aqeel MA, Javaid MM, Garcia-Sanchez F (2015) Foliar spray of phyto-extracts supplemented with silicon: an efficacious strategy to alleviate the salinity-induced deleterious effects in pea (*Pisum sativum* L.). Turk J Bot 39:408–419

Sharma A, Shahzad B, Kumar V, Kohli SK, Sidhu GPS, Bali AS, Handa N, Kapoor D, Bhardwaj R, Zheng B (2019) Phytohormones regulate accumulation of osmolytes under abiotic stress. Biomol Ther 9:285

Shen X, Zhou Y, Duan L, Li Z, Egrinya Eneji A, 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 Y, Wang Y, Flowers TJ, Gong H (2013) Silicon decreases chloride transport in rice (*Oryza sativa* L.) in saline conditions. J Plant Physiol 170:847–853

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

Shi Y, Zhang Y, Han W, Feng R, Hu Y, Guo J, Gong H (2016) Silicon enhances water stress tolerance by improving root hydraulic conductance in *Solanum lycopersicum* L. Front Plant Sci 7:1–15

Shrivastav P, Prasad M, Singh TB, Yadav A, Goyal D, Ali A, Dantu PK (2020) Role of nutrients in plant growth and development. In: Naeem M, Ansari AA, Gill SS (eds) Contaminants in agriculture. Springer, Cham, pp 43–59

Siddiqi KS, Husen A (2017) Plant response to strigolactones: current developments and emerging trends. Appl Soil Ecol 120:247–253

Siddiqi KS, Husen A (2019) Plant response to jasmonates: current developments and their role in changing environment. Bull Natl Res Cent 43:153

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

Sienkiewicz-Cholewa U, Sumisławska J, Sacała E, Dziągwa-Becker M, Kieloch R (2018) Influence of silicon on spring wheat seedlings under salt stress. Acta Physiol Plant 40:54

Singh K, Singh R, Singh JP, Singh Y, Singh KK (2006) Effect of level and time of silicon application on growth, yield and its uptake by rice (*Oryza sativa*). Indian J Agric Sci 76:410–413

Singh M, Kumar J, Singh S, Singh VP, Prasad SM (2015) Roles of osmoprotectants in improving salinity and drought tolerance in plants: a review. Rev Environ Sci Biotechnol 14:407–426
Sommers LE, Lindsay WL (1979) Effect of pH and redox on predicted heavy metal-chelate equilibria in soils. Soil Sci Soc Am J 43:39–47
Soundararajan P, Sivanesan I, Jana S, Jeong BR (2014) Influence of silicon supplementation on the growth and tolerance to high temperature in *Salvia splendens*. Hortic Environ Biotechnol 55:271–279
Soundararajan P, Manivannan A, Park YG, Muneer S, Jeong BR (2015) Silicon alleviates salt stress by modulating antioxidant enzyme activities in *Dianthus caryophyllus* 'Tula'. Hortic Environ Biotechnol 56:233–239
Soundararajan P, Manivannan A, Cho YS, Jeong BR (2017) Exogenous supplementation of silicon improved the recovery of hyperhydric shoots in *Dianthus caryophyllus* L. by stabilizing the physiology and protein expression. Front Plant Sci 8:738
Soylemezoglu G, Demir K, Inal A, Gunes A (2009) Effect of silicon on antioxidant and stomatal response of two grapevine (*Vitis vinifera* L.) rootstocks grown in boron toxic, saline and boron toxic-saline soil. Sci Hortic 123:240–246
Takahashi E, Hino K (1978) Effect of different Si forms on silicic acid uptake. J Sci Soil Manure, Japan 33:453–455
Takahashi E, Ma JF, Miyake Y (1990) The possibility of silicon as an essential element for higher plants. Comments Agric Food Chem 2:99–102
Tamai K, Ma JF (2003) The apoplast and its significance for plant mineral nutrition. New Phytol:431–436
Torres MA, Jones JDG, Dangl JL (2006) Reactive oxygen species signaling in response to pathogens. Plant Physiol 141:373–378
Tripathi DK, Singh VP, Kumar D, Chauhan DK (2012) Impact of exogenous silicon addition on chromium uptake, growth, mineral elements, oxidative stress, antioxidant capacity, and leaf and root structures in rice seedlings exposed to hexavalent chromium. Acta Physiol Plant 34:279–289
Tuna AL, Kaya C, Higgs D, Murillo-Amador B, Aydemir S, Girgin AR (2008) Silicon improves salinity tolerance in wheat plants. Environ Exp Bot 62:10–16
Van Bockhaven J, Spíchal L, Novák O, Strnad M, Asano T, Kikuchi S, Höfte M, De Vleesschauwer D (2015) Silicon induces resistance to the brown spot fungus *Cochliobolus miyabeanus* by preventing the pathogen from hijacking the rice ethylene pathway. New Phytol 206:761–773
Van der Vorm PDJ (1980) Uptake of Si by five plant species, as influenced by variations in Si-supply. Plant Soil 56:153–156
Van Soest PJ (2006) Rice straw, the role of silica and treatments to improve quality. Anim Feed Sci Technol 130:137–171
Vanderschuren H, Boycheva S, Li K-T, 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
Vivancos J, Labbé C, Menzies JG, Bélanger RR (2015) Silicon-mediated resistance of Arabidopsis against powdery mildew involves mechanisms other than the salicylic acid (SA)-dependent defence pathway. Mol Plant Pathol 16:572–582
Wang XS, Han JG (2007) Effects of NaCl and silicon on ion distribution in the roots, shoots and leaves of two alfalfa cultivars with different salt tolerance. Soil Sci Plant Nutr 53:278–285
Wang C, Rong H, Zhang X, Shi W, Hong X, Liu W, Cao T, Yu X, Yu Q (2020) Effects and mechanisms of foliar application of silicon and selenium composite sols on diminishing cadmium and lead translocation and affiliated physiological and biochemical responses in hybrid rice (*Oryza sativa* L.) exposed to cadmium and lead. Chemosphere 251:126347
Wiese H, Nikolic M, Römheld V (2007) Silicon in plant nutrition. In: Sattelmacher HWJ (ed) The apoplast of higher plants: compartment of storage, transport and reactions. Springer, Dordrecht, pp 33–47

Wolters H, Jürgens G (2009) Survival of the flexible: hormonal growth control and adaptation in plant development. Nat Rev Genet 10:305–317
Wu J, Baldwin IT (2010) New insights into plant responses to the attack from insect herbivores. Annu Rev Genet 44:1–24
Wu D, Shen Q, Cai S, Chen ZH, Dai F, Zhang G (2013) Ionomic responses and correlations between elements and metabolites under salt stress in wild and cultivated barley. Plant Cell Physiol 54:1976–1988
Xu CX, Ma YP, Liu YL (2015) Effects of silicon (Si) on growth, quality and ionic homeostasis of aloe under salt stress. South Afr J Bot 98:26–36
Yamaji N, Mitatni N, Ma JF (2008) A transporter regulating silicon distribution in rice shoots. Plant Cell 20:1381–1389
Yeo AR, Flowers SA, Rao G, Welfare K, Senanayake N, Flowers TJ (1999) Silicon reduces sodium uptake in rice (*Oryza sativa* L.) in saline conditions and this is accounted for by a reduction in the transpirational bypass flow. Plant Cell Environ 22:559–565
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 Physiol Plant 35:3099–3107
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 S, Zhang S (2016) Silicon-mediated changes in polyamines participate in silicon-induced salt tolerance in *sorghum bicolor* L. Plant Cell Environ 39:245–258
Zargar SM, Agnihotri A (2013) Impact of silicon on various agro-morphological and physiological parameters in maize and revealing its role in enhancing water stress tolerance. Emirates J Food Agric 25:138–141
Zeng J, Wu C, Wang C, Liao F, Mo J, Ding Z, Tie W, Yan Y, Hu W (2020) Genomic analyses of heat stress transcription factors (HSFs) in simulated drought stress response and storage root deterioration after harvest in cassava. Mol Biol Rep 47:5997–6007
Zhang F, Yang YL, He WL, Zhao X, Zhang LX (2004) Effects of salinity on growth and compatible solutes of callus induced from *Populus euphratica*. In Vitro Cell Dev Biol Plant 40:491–494
Zhang W, Han Z, Guo Q, Liu Y, Zheng Y, Wu F, Jin W (2014) Identification of maize long noncoding RNAs responsive to drought stress. PLoS One 9:e98958
Zhang XH, Zhou D, Cui JJ, Ma HL, Lang DY, Wu XL, Wang ZS, Qiu HY, Li M (2015) Effect of silicon on seed germination and the physiological characteristics of *Glycyrrhiza uralensis* under different levels of salinity. J Hortic Sci Biotechnol 90:439–443
Zhu Y, Gong H (2014) Beneficial effects of silicon on salt and drought tolerance in plants. Agron Sustain Dev 34:455–472
Zhu Z, Wei G, Li J, Qian Q, Yu J (2004) Silicon alleviates salt stress and increases antioxidant enzymes activity in leaves of salt-stressed cucumber (*Cucumis sativus* L.). Plant Sci 167:527–533
Zhu YX, Bin XX, 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 34:1629–1646
Zhu Y, Yin J, Liang Y, Liu J, JIa J, Huo H, Wu Z, Yang R, Gong H (2019) Transcriptomic dynamics provide an insight into the mechanism for silicon-mediated alleviation of salt stress in cucumber plants. Ecotoxicol Environ Saf 174:245–254
Zuccarini P (2008) Effects of silicon on photosynthesis, water relations and nutrient uptake of *Phaseolus vulgaris* under NaCl stress. Biol Plant 52:157–160