



# Silicon: A Plant Nutritional “Non-Entity” for Mitigating Abiotic Stresses

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## Abstract

In the present era, the progression of plant development in the environment is adversely affected by increasing incidences of abiotic and biotic stresses. These stressors singly or in combination negatively pose pressure on plants. As a result, the plants display a wide range of morphological, physiological, biochemical, metabolic, molecular as well as epigenetic responses that help them in averting stress-triggered alterations. In addition to “Omics,” plant breeding, functional genomics, transgenic technology, and genome editing approaches, better mineral nutrition coupled with soil-health amendments is still considered as the key management practice. Use of Silicon (Si), the second most predominant and quasi-essential element, has been recommended in the recent past. Si not only promotes growth and development of plants, it also works as “anti-stress agent.” Si mitigates this alleviating effect mainly by ROS detoxification, immobilization, and compartmentation of toxic metal ions, modification in water and nutrients

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uptake, alteration in gene expression and phytohormone biosynthesis, maintenance of osmotic potential and gaseous exchange, and formation of Si–cuticle double layer. Moreover, being non-corrosive and non-pollutive, Si-supplementation has proven to be the most economic as well as eco-friendly method. The present chapter is an attempt to primarily address the involvement of Si in minimizing the negative effects of abiotic stresses.

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**Keywords**

Abiotic stress · Silicon · Drought · Salinity · Nanoparticles

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## 2.1 Introduction

The term “stress” signifies a set of conditions that deviate plant growth, development, and other characteristics adversely from its “normal state” (Lal et al. 2018; Mehta et al. 2019a). Plants encounter these stresses during their entire life cycle initiating from germination and seedling stage to the post-harvest stage (Singh et al. 2018; Sharma et al. 2020). All these growth-limiting “stresses” can be categorized into two major categories, namely abiotic and biotic stresses (Singh et al. 2019; Mehta et al. 2019b; Ramegowda et al. 2020). Abiotic stress conditions arise due to fluctuation in plant’s physical environment (naturally occurring inanimate factors) like rain, drought, floods, salinity, metal/metalloid toxicity, nutrient paucity, dwindling seasonal patterns, and temperature shifts (Lal et al. 2018; Mohammadi et al. 2020). On the other hand, the latter one is a consequence of living disturbances, such as fungi, bacteria, virus, nematodes, rodents, oomycetes, etc., that negatively affect the plant’s well-being (Rahman et al. 2019; Ali et al. 2020).

The most frightening fact is that the frequency and incidences of these stresses have increased in the last 50 years (Xu 2016; Surówka et al. 2020). It is actually because of amalgamated effects of growing human population and anthropogenic activities (Cripps 2016; Mahmoud and Gan 2018; Tamburino et al. 2020). These activities include over-exploitation of resources, deforestation, desertification, pollution, and global warming (Mahmoud and Gan 2018; Mona et al. 2019; Baldos et al. 2019). All these factors either individually or in combination have affected the total food productivity negatively and the whole scenario of food production will turn worse in the near future (Kamanga and Mndala 2019; Rafique et al. 2020). There is a huge gap between food productivity, demand, and supply (Grafton et al. 2015; Müller et al. 2020). Therefore, the most serious challenge at present is to refine the scientific research as well as administrative strategies, so as to feed the every-minute increasing population in future (Conceição et al. 2016; Martin-Shields and Stojetz 2019; Tyagi 2020). Additionally, the focus must be given on enhancing the already declined soil fertility as the soil provides habitat, nutrients, and beneficial microbes, which is required for proper growth and development of plants (Shahid et al. 2019).

In order to resolve the issue on food security in a best possible manner, it is highly important to understand the responses as well as adjustments that occur during averting stress-triggered alterations (Pecinka and Mittelsten Scheid 2012; Goswami et al. 2020). As an effort, various groups of researchers are keenly focusing on understanding the mechanism through various newly developed tools and techniques (Anamika et al. 2019; Shahbazy et al. 2020). These efforts have resulted in generating knowledge regarding the “changes and adjustments” and their associated mechanisms up to an extent (Gilliham et al. 2017; Vakilian 2020). Furthermore, many crossbred and transgenic plants have also been developed in the last 15 years (Hasanuzzamam et al. 2018; Dixit et al. 2020). However, time, efforts, and environment suitability are primary factors that are considered majorly. Hence, there is a need to look for reliable environment-friendly methods for sustainable agriculture (Kawalekar 2013; Ahirwar et al. 2020).

In this context, one of the most reliable practices has been to supply adequate mineral nutrition coupled with maintenance of sound soil-health (Pandey et al. 2015; Fresno et al. 2018; Lu et al. 2020). This method assures both environmental and economic benefits and crop plants can be supplemented with required components directly in the form of fertilizers and its effect can be observed at morphology, physiology, biochemistry, and metabolome levels (Ma 2004; Marschner 2012; Liang et al. 2015; Mu et al. 2020). Till date, few elements have been studied for promoting a range of tolerance mechanisms for alleviating various stresses in several important agricultural and horticultural crops (Kaur et al. 2016; Chauhan et al. 2017; Salgado et al. 2020). One such studied element is Si, a “multi-talented” quasi-essential element that has been established as a stimulant to trigger growth and development in stressed plants at an optimal concentration (Malhotra and Kapoor 2019; Ahanger et al. 2020; Singh et al. 2020). This is because the Si is being directly supplemented by the small and marginal farmers in their fields since 1840s in the form of non-corrosive, non-pollutive, regular fertilizer for economic as well as ecological benefits (von Liebig 1843). Now, due to its positive effects, the status of Si has shifted from “beneficial but non-essential” to “quasi-essential” by the International Plant Nutrition Institute (IPNI) (<http://www.ipni.net/>). Furthermore, in 2013, the Association of American Plant Food Control Officials (AAPFCO) also officially announced Si as a plant “beneficial substance” ([http://www.ipni.net/publication/bettercrops.nsf/0/26A7E8FDB7F2FBBF85257C28007A07BB/\\$FILE/BC%202013-4%20p14.pdf](http://www.ipni.net/publication/bettercrops.nsf/0/26A7E8FDB7F2FBBF85257C28007A07BB/$FILE/BC%202013-4%20p14.pdf)). Besides, the beneficial effects of Si for imparting stress tolerance is also well documented in the form of Si nanoparticles and Si priming (Abdel Latef and Tran 2016; Rastogi et al. 2019; Parveen et al. 2019; Siddiqui et al. 2020). This chapter focuses on highlighting the significance of Si as a growth regulator and anti-stress agent.

## 2.2 Silicon: Occurrence and Sources

In accordance with multiple sources, the soils inherit their element composition primarily from parent rocks that were subjected to geochemical as well as pedochemical weathering processes primarily. As per the data evaluated, silicon is the second most abundant element in the earth's crust in terms of quantity after oxygen, i.e. 27.7%. (Mitra 2015; Malhotra and Kapoor 2019). In the earth's crust, Si has been deposited in the form of quartz ( $\text{SiO}_2$ ), sand, and sandstone (Rédei 2008; Malhotra and Kapoor 2019). Within the soil, it comprises even up to 70% of soil mass in the form of monosilicic acid, polysilicic acid as well as complexes with organic and inorganic compounds such as aluminum oxides and hydroxides (Rao and Susmitha 2017). Out of all, the most important form is plant-available form, i.e. silicic acid ( $\text{H}_4\text{SiO}_4$ ), a non-charged plant-available molecule that considerably ranges between 10 ppm to over 100 ppm (Epstein 2009; Liang et al. 2015; Zargar et al. 2019). During the crop use, the polysilicic acid, and inorganic and organic complexes act as important sinks/sources that replenish the monosilicic acid (Rao and Susmitha 2017). In soil solution, the concentration of Si is equivalent even up to many macroelements such as potassium (K), calcium (Ca), and phosphorus (P) (Epstein 1994; Malhotra and Kapoor 2019). Silicon solubility in the soil is affected by a variety of factors, which include irrigation water, the particle size of the silicon fertilizer employed, critical soil characteristics (moisture, temperature, and pH), presence of organic complexes concentration of iron (Fe), phosphate (P), and aluminum (Al) ions as well as dissolution reactions occurring (Gérard et al. 2002; Tavakkoli et al. 2011; Rao and Susmitha 2017; Zargar et al. 2019). As per one report, the range of silicon present in the soil around the globe lies within 50–400 g silicon/kg of soil (Matichenkov and Calvert 2002; Haynes 2019). The silicon present within soil improves water absorption capacity, soil physical and chemical properties as well as maintain other nutrients in plant-available form by creating silica bridges (Rao and Susmitha 2017; Malhotra and Kapoor 2019; Zargar et al. 2019). Compared to the soil, silicon comprises 0.0001% and 0.026% in terms of quantity in oceans and humans, respectively (<http://www.elementalmatter.info/element-silicon.htm>).

On the other hand, the availability of Si in plants is low but ranges from 0.1 to 10% of dry weight (Hodson et al. 2005; Balakhnina and Borkowska 2013; Malhotra and Kapoor 2019). In here, the most important fact to be noted is that concentration of Si ranges distinctly within and among plant species which depend directly on the capability of the roots to uptake Si (Hodson et al. 2005; Ma and Yamaji 2006; Malhotra and Kapoor 2019). Plants have been categorized into three major classes such as accumulators, intermediate, and excluders based on the Si accumulation in their tissues (Mitani and Ma 2005; Marschner 2012; Luyckx et al. 2017). The best examples of accumulators are members of Equisetales, Cyperales, and Poales (especially rice, sugarcane, and maize) with a value of more than 1 for silicon/calcium ratio. On the contrary, tomato and soybean are examples of Si excluders that show the value of <0.5 for silicon/calcium. However, nettle and snapdragon are examples of the intermediate type (Mitani and Ma 2005; Luyckx et al. 2017;

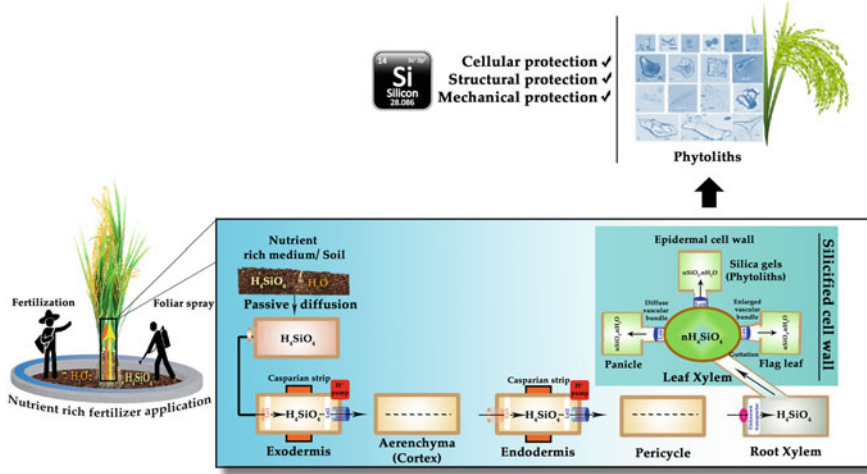
Malhotra and Kapoor 2019). Within angiosperms, the monocots tend to accumulate more silicon in their aerial parts due to the presence of silicon transporters (Henriet et al. 2006; Malhotra and Kapoor 2019). For a long time, it is a noted fact that the silicon levels in the soil is enhanced by fertilization. The agricultural wastes such as silicate slag, bagasse furnace ash, lignite fly ash, and rice straw are considered as rich silicon sources that are being employed mostly. The other sources of silicon employed these days include wollastonite, calcium silicate, potassium silicate, garnet, silica gel, diopside, calcium silicate hydrate, etc. (Kalra et al. 2003; Daniel Maxim et al. 2008; Malhotra and Kapoor 2019; Zargar et al. 2019).

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### 2.3 Silicon: Uptake, Transportation, and Accumulation

The majority of the investigations regarding silicon uptake and transportation has been focused more on monocots; however, the speed for enhancing knowledge regarding dicots has also increased in the last 5 years. As per literature, Si is absorbed by lateral roots actively in the form of neutral, monomeric monosilicic acid,  $\text{Si}(\text{OH})_4$ , whose concentration ranges between 0.1–0.6 mM (Knight and Kinrade 2001; Rao and Susmitha 2017). The ability of monosilicic acid to cross the plasma membrane of lateral root depends highly on the physiological pH and water (Raven 2001). The vehicle for its uptake and distribution is a simple molecule, i.e. water; however, both molecules vary in size (Exley et al. 2020). Therefore, the pace of both water uptake and Si adsorption has been classified into three possible situations, namely (1) active (Si-uptake > water uptake), (2) passive (where Si-uptake = water uptake), and lastly (3) rejective (Si-uptake < water uptake) in higher plants (Cornelis et al. 2011; Zargar et al. 2019). Ostensibly, upon the entry with water via the symplastic route, silicic acid encounters a myriad of different enumerable water channels that control the movement of silicic acid further. For example, in rice, a high silicon accumulating plant, the silicon transportation is highly governed by majorly three low silicon rice genes, i.e. *OsLSi1*, *OsLSi2*, and *OsLSi6* (Ma et al. 2006, 2007; Yamaji and Ma 2009; Dhakate et al. 2019). Among these genes, *LSi1* (influx transport activity) and *LSi2* (efflux transport activity) have been shown to be involved in silicon transport from root cells to the apoplast (Ma and Yamaji 2008; Rao and Susmitha 2017) (Fig. 2.1).

*OsLSi1* gene belonging to the NIP-III (nodulin26-like intrinsic proteins) subfamily of aquaporin is primarily found to be constitutively located in the basal zones of roots. Within this, the *OsLSi1* gene is found to be localized exactly on the plasma membrane of the distal side of both exodermis and endodermis cells where casparian stripes are located (Yamaji and Ma 2007; Ma and Yamaji 2008; Dhakate et al. 2019). On the other hand, expression patterns and cellular localization studies have revealed that the *OsLSi2* gene (efflux Si-transporter) is localized on the proximal side of the same cells (Yamaji and Ma 2009; Yamaji and Ma 2011; Dhakate et al. 2019). This rice *OsLSi2* gene is found to be responsible for reloading and diffusing Si into the vascular bundles (Yamaji and Ma 2011; Ma and Yamaji 2015). After reaching the apoplast, monosilicic acid in xylem sap needs to be unloaded so as to prevent the Si



**Fig. 2.1** Diagrammatic representation of silicon uptake, transportation, and accumulation

deposition within xylem. In this regard, *OsLSi6* gene plays role in transferring Si from the large vascular bundles to the panicles (Yamaji and Ma 2009; Feng et al. 2011; Rao and Susmitha 2017). The knock-out and localization studies revealed that the *OsLSi6* gets localized on the adaxial side of xylem parenchyma cells in the leaf sheaths as well as leaf blades (Feng et al. 2011; Ma and Yamaji 2015). Therefore, it is important to keep a note that both apoplastic and symplastic route operates for silicic acid (Exley et al. 2020). In addition to the rice, homologs of Si-transporters have also been observed in other plant species. The list includes barley (Mitani et al. 2009a, b; Chiba et al. 2009), maize (Mitani et al. 2009a, b), crookneck pumpkin (Mitani et al. 2011), wheat (Montpetit et al. 2012), soybean (Deshmukh et al. 2013), field horsetail (Vivancos et al. 2016), cucumber (Sun et al. 2017, 2018), tobacco (Zellner et al. 2019), poinsettia (Hu et al. 2020), and tomato (Sun et al. 2020). The possible reason for the identification of Si-transporters lies in the ability to mine the well-annotated plant genome sequences available for more than 100 species.

Upon successful transport, the silicon gets deposited under the cuticle and in intercellular spaces or vascular bundles (Heckman 2013). Beneath the cuticle, the silicon gets deposited as a cuticle–silicon double layer (silicic acid) (Rao and Susmitha 2017; Rao et al. 2017). Furthermore, with the age, the concentration of monosilicic acid increases which results in polymerization to form silica gel ( $\text{SiO}_2 \cdot n\text{H}_2\text{O}$ ) through a non-enzymatic reaction (Mitani and Jian 2005; Zargar et al. 2019). In addition, amorphous silica particles polymerize in plant cells to form phytoliths without incurring any energy as soon as its concentration exceeds a critical mark of 2 mM. These phytoliths are found as silica cells in vascular bundles and silica bodies in bulliform cells, and fusoid cells (Rao and Susmitha 2017; Nawaz et al. 2019).

## 2.4 Silicon and Abiotic Stresses

As per the literature, the important roles attributed to Si in plants include elevation in growth, crop yield, and quality, photosynthesis, nitrogen (N<sub>2</sub>) fixation as well as protection against abiotic and biotic stresses (Balakhnina and Borkowska 2013; Steiner et al. 2018; Malhotra and Kapoor 2019; Zargar et al. 2019; Ahanger et al. 2020; Singh et al. 2020). Interestingly, the abiotic stresses are the first and foremost reason that besets the annual productivity rate. Abiotic stresses include salinity, extreme temperature, UV-B radiation, heavy metal/metalloid toxicity, mechanical injury, nutrient deficit, nutrient toxicity, and drought (Sharma et al. 2020). All these stresses result in oxidative, osmotic as well as an ionic inconvenience in plants that ultimately culminate into reactive oxygen species (ROS) accumulation, altered metabolic and physiological processes (Sharma et al. 2020). This ultimately results in hampered growth and net productivity which affect the farmer fields, farmer pockets, and overall economy (Sharma et al. 2020).

A plethora of lab-scale, greenhouse-level, and field experiments have been conducted that endorses the numerous benefits of silicon on the plants growing under adverse conditions (Soundararajan et al. 2014; Manivannan et al. 2016; Luyckx et al. 2017; Liu et al. 2019; Malhotra and Kapoor 2019; Zargar et al. 2019; Ahanger et al. 2020). It has also been deduced that it is not single but an amalgamation of key mechanisms that alleviate stresses which include: (1) attunement of antioxidant systems and osmolytes for harmful ROS detoxification, (2) immobilization or complex formation/co-precipitation or compartmentation of noxious metal ions and enhanced uptake of nutrients, (3) modifying water as well as nutrients uptake processes, (4) regulating expression of various genes, phytohormone biosynthesis, maintenance of osmotic potential, photosynthetic apparatus, and gaseous exchange, and (5) formation of Si–cuticle double layer (Tripathi et al. 2016; Etesami and Jeong 2018; Etesami and Jeong 2020; Souri et al. 2020) (Fig. 2.2).

### 2.4.1 Drought

Drought imposes a grave threat to plant population on earth as the morphological as well as physiological functions of a plant get affected (Kusaka et al. 2005; Shao et al. 2008). Drought stress can be injurious to physiological and metabolic events such as turf quality, growth rate, root/shoot ratio, leaf carbon/nitrogen content, photosynthesis, transpiration, and stomatal conductance (Saud et al. 2014). Application of Si ameliorates stressful drought conditions by elevating photosynthesis, total leaf water content, chlorophyll content, and turf rate by 44%, 33%, 42%, and 44%, respectively (Saud et al. 2014). It often results in disrupted water supply via the xylem, which consequently results in lost turgor pressure and reduced stomatal closure (Taiz and Zeiger 2006). It also convulses the photosynthetic framework via its association with UV or visible rays (Garcia-Plazaola and Becerril 2000). The effectiveness of Si in combating drought stress has been noted in many plants; for example, exogenous



**Fig. 2.2** Key mechanisms involved in the ameliorative effect of silicon on plants facing various abiotic stresses

supply of Si regulate, leaf structure, water potential, erectness, and structure of xylem vessels (Gong et al. 2005; Hattori et al. 2005a, b).

An interesting study was carried out to comprehend the differences between drought-tolerant and drought-sensitive tomato lines in response to exogenous application of Si. Elevation in amino acid biosynthesis is noted in drought-tolerant tomato lines due to Si-induced increase in sulfur (S) and ammonia ( $\text{NH}_4^+$ ) levels. Whereas in drought-sensitive tomato lines, the application of Si results in accumulation of gamma-aminobutyric acid (GABA) proline and, which is key to the maintenance of cellular ionic redox equilibrium (Ali et al. 2018). *Brassica napus* faces extreme oxidative stress. Silicon application provides defense against antioxidant enzymes such as glyoxalase, ascorbate-glutathione, proline, and so on (Hasanuzzamam et al. 2018).

The deposition of exogenously supplemented Si on leaf epidermis helps to generate a higher water potential under scarce conditions (Lux et al. 2003). Similarly, suberin-containing endodermis also accumulates Si in drought-stressed cereal cultivars. In Si-treated plants, the water uptake is higher and faster from the rhizosphere to roots (Hattori et al. 2003, 2005a, b). Si strengthens plant's tolerance against water stress by elevating root silicification, lignification, and suberization (Guerrero et al. 2016). During water scarcity, Si forms a complex with hemicellulose (He et al. 2013; Ma et al. 2015). Si also enhances Casparian strip development leading to an increase in the level of suberization in roots of rice plants (Fleck et al. 2015).



Moreover, Si-supplementation also enhances transpirational bypassing of toxic ions from symplast streamflow (Coskun et al. 2016). This theory allows to propose that the movement of  $\text{Na}^+$  and  $\text{Cl}^-$  is limited in rice plants by suberized exodermis and endodermis of roots, thereby bypassing the step of xylem loading via symplast (Coskun et al. 2016). Much like in salinity stress, foliar supplementation of Si brings about an increase in the expression of different aquaporins (AQPs) located in the membranes of root cells.

### 2.4.2 Salinity Stress

About 20% of global crop production is affected by salinity stress (Hussain et al. 2018). Under salt stress, rice plants display an interesting deviation in the apoplastic movement of noxious  $\text{Na}^+$  and  $\text{Cl}^-$ , on exposure to Si (Shi et al. 2013). Si-mediated amelioration of salt stress has been studied and deciphered at various biochemical and physiological levels. Starting from its impact on roots, the primary site of ion uptake to serial tissue like leaves wherein salt stress has a drastic effect on several proteins and enzymes related to photosynthesis and stomatal opening (Liu et al. 2019; Gogna and Bhatla 2019, 2020). Silicon protects photosynthetic machinery of plants under stress due to persisting soil salinity by preventing pigment degradation and regulation of several photosystems and chloroplast-related proteins (Muneer et al. 2014; Soundararajan et al. 2017). Exogenous application of Si modulates enzymatic antioxidant machinery constituting enzymes like catalase, superoxide dismutase, and guaiacol/ascorbate peroxidase (Zhu et al. 2004; Manivannan et al. 2015). The primary action undertaken by a stressed plant to overcome salinity is the restriction of  $\text{Na}^+/\text{Cl}^-$  uptake via roots (Liu et al. 2019; Gogna et al. 2020). Exogenously supplied Si not only limits the uptake of toxic ions by plant roots but also regulates several other essential biochemical aspects like photosynthesis, maintenance of redox equilibrium, and effective distribution of nutrients to the plant (Liu et al. 2019). Similar to  $\text{Ca}^{2+}$ , the application of Si not only restricts excess uptake of  $\text{Na}^+$  but also mediates accumulation of  $\text{K}^+$ , thereby impacting tolerance against salinity. This study has been extensively carried out across sugarcane, aloe, zinnia, and rose (Ashraf et al. 2010; Manivannan et al. 2015; Garg and Bhandari 2016; Soundararajan et al. 2018). The foremost role of Si in alleviating salt stress is its possible interaction with noxious ions responsible for oxidative stress and disrupted ionic homeostasis.  $\text{K}^+$  is the most essential element necessary for plant growth, development, and yield. However, uptake of  $\text{Na}^+$  under salt stress often results in  $\text{K}^+$  deficiency (Liebersbach et al. 2004). Thus, the addition of Si not only negates the competition between  $\text{Na}^+$  and  $\text{K}^+$  but also alleviates  $\text{K}^+$  distribution in salt-stressed wheat and blueberry (Tuna et al. 2008).

Plant root aquaporins are involved in the facilitation of water and mineral nutrition transportation (Liu et al. 2019). NIP family of AQPs has been found to play a significant role in the uptake and transport of Si and other metalloids (Wu and Beitz 2007). Studies pertaining to rice plants have revealed that efflux and influx of Si are carried out via the NIP family of AQPs (Ma et al. 2006). Apart from NIPs,

PIPs (plasma membrane intrinsic proteins) also regulate Si levels in the cell under abiotic stress conditions in roots of Sorghum plants (Liu et al. 2014, 2015). Salinity stress often disrupts the hydraulic conductance of roots. Recent studies on sorghum reveal that hydraulic conductance can be restored by exogenous application of Si (Liu et al. 2014, 2015). Morphologically, Si application revived suppressed lateral root growth and enhances the mechanical strength of the primary root (Liu et al. 2019).

Some other major consequences of salinity stress include reduction in photosynthetic efficiency, diminished stomatal conductance and level of transpiration, and lastly, damaged photosynthetic apparatus (photosystem I and II) (Hetherington and Woodward 2003; Gupta and Huang 2014; Yang et al. 2015). Recent studies in wide varieties of plants such as sorghum, maize, tomato, tobacco, and pumpkin have shown that application of Si not only improves stomatal conductance in plants but also elevates the capacity of leaves to fix CO<sub>2</sub> (Parveen and Ashraf 2010; Nabati et al. 2013; Hajiboland and Cheraghvareh 2014; Hu et al. 2014; Li et al. 2015). Stomatal malfunction under salt stress conditions leads to a loss in levels of reduced CO<sub>2</sub> and disrupts the process of gaseous exchange. Thus, exogenously applied Si repairs stomatal conductance (Hetherington and Woodward 2003; Abbas et al. 2015; Parveen and Ashraf 2010). Similarly, in salt-stressed leaves of *Capsicum annuum*, stomata remained open when supplemented with exogenous Si (Manivannan et al. 2016). Recent reports also show that salinity is deleterious to photosystem I and II of tomato plants. PS I and II can be revived by foliar application of Si (Mateos-Naranjo et al. 2015). Similarly, Si application also improves pigment quality and efficiency in PS II of C4 grass, *Spartina densiflora* under salt stress (Gorbe and Calatayd 2012; Ouakroum et al. 2015; Mateos-Naranjo et al. 2015). Si exhibits the same mitigating effects as 24-Epibrassinolide on *Brassica juncea* under salt stress (Siddiqui et al. 2018). Si (Na<sub>2</sub>SiO<sub>3</sub>) has also been noted to carry out biofortification and reduce water loss in salt-tolerant and -sensitive cultivars of rice. The impact of Si application has been found to vary with varying sensitivities of salt (Das et al. 2018).

### 2.4.3 Heavy Metal Stress

Silicon has the ability to restrict and ameliorate heavy metal toxicity by several mechanisms. It increases the rate of chelation in cells via stimulation of plant root exudates which play a role in limiting uptake of heavy metals (Adrees et al. 2015). It can quench the free heavy metallic ions from its apoplastic region which results in reduced translocation (Adrees et al. 2015). Biosilicification is another silicon-mediated tolerance mechanism wherein silicic acid undergoes polymerization in the apoplast and a barrier of amorphous Si is formed which prevents penetration of toxic heavy metals such as aluminum (Al), manganese (Mn), cadmium (Cd), zinc (Zn), arsenic (As), and sodium (Na) into symplast or water transportation stream (Ma et al. 2015; Exley 2015; Guerriero et al. 2016). Another mechanism of counteracting heavy metals is via lignification. Lignified cell walls are good metal binders and therefore prevent metal movement from roots to plant aerial tissue

(Ma and Yamaji 2006; Ye et al. 2012). Silicon holds the unique ability to form complexes with metal ions in the cell wall and eventually, forming a precipitate of metal ions as co-factors (Pontigo et al. 2017). Silicon can react to form silicates and oxides with heavy metals (Exley 2015) keeping the toxicants out of any plant metabolic process (Exley 2015). Application of silicon to the soil is beneficial since it balances the disrupted soil and immobilizes heavy metals like Cd making them unavailable to plants (Wu et al. 2013).

#### 2.4.3.1 Cd Toxicity

Presence of Cd in soil inhibits root growth of rice plants. The toxicity can be identified by the appearance of black spots in the cortex and pericycle of roots (Kim et al. 2014). In wheat and maize crops, it affects seed germination, nutrient content, and lowers shoot and root length. (Ma et al. 2015). In barley, photosynthetic apparatus, pigments, and lipids are affected by Cd-induced toxicity (Hodson et al. 2005). Heavy metal stress studies have revealed that silicon has the ability to decrease cadmium uptake and further limits its translocation to plant aerial tissue like shoots. Cd and Mn are often precipitated on the epidermis of the shoot or leaf blade by forming amorphous silica (Ma et al. 2015). Cd is often compartmentalized in root cell walls by Si, leading to its lowered accumulation in shoots of rice (Bhat et al. 2019). In maize plants, Cd forms colloidal silicon embedded in the cell walls to prevent its uptake or transport to the aerial parts (Bhat et al. 2019). Similarly, the application of Si to *Poa annua* seedlings imparts tolerance to cadmium toxicity (Zama et al. 2018).

#### 2.4.3.2 As Toxicity

Arsenic toxicity is majorly seen in rice and spinach plants. In rice plants, it is overcome by competition with other heavy metal ions at the point of entry/site of uptake in roots. Dry biomass of leaves is regulated positively upon the application of Si to spinach plants. A subsequent increase in levels of glutaredoxin (GRX) is also noted (Dubey et al. 2018). Si-biochars are components composed by coupling bamboo with Si. The element has been used to reduce bioaccumulation of arsenic in spinach leaves by ~38% (Li et al. 2017) (Table 2.1).

#### 2.4.3.3 Al Toxicity

Recent studies have revealed that silicon has the ability to regulate malic and formic acid formation in plants. The formation of these cellular byproducts is helpful in regulating uptake of aluminum (Pontigo et al. 2017). Phenolic compounds of maize have also been investigated in relation to their ability to reduce Al-uptake (Adrees et al. 2015). Si often complexes with Al to form Si–Al or aluminum silicate localized in the plant cell wall, primarily in epidermis and hypodermis. Complex formation makes toxic Al unavailable to the plants (Horst et al. 2010; Liu et al. 2013). Another mechanism to combat Al toxicity is to form hydroaluminosilicates in root apoplast, thereby, reducing mobility of noxious Al (Rogalla and Romheld 2002).

**Table 2.1** Si-mediated mitigation of major abiotic stress responses in different plants

Stress	Plant species	Effect of stress	Effect of Silicon supplementation	References
Salinity	<i>Sorghum bicolor</i>	Inhibits uptake of noxious ions, photosynthesis as well as stomata opening	Modulation of catalase, peroxidase, SOD; restricts ion uptake via roots	Soundararajan et al. (2017), Liu et al. (2019)
Drought	<i>Brassica napus</i> , <i>Solanum lycopersicum</i>	Oxidative stress, Decreased photosynthesis	Accumulation of proline, GABA and ascorbate-glutathione cycle members	Ali et al. (2018), Hasanuzzamam et al. (2018)
Heavy metals	<i>Zea mays</i> , <i>Oryza sativa</i> , <i>Spinacia oleracea</i> , <i>Bambusa vulgaris</i>	Reduced toxic ion uptake and accumulation	Lignification, suberization	Li et al. (2017), Dubey et al. (2018), Bhat et al. (2019)
Cold stress	<i>Hordeum vulgare</i>	Loss of membrane integrity	Accumulation of soluble carbohydrates and other osmolytes	Joudmand and Hajibolan (2019)

## 2.4.4 Thermal Stress

Thermal stress is often caused by extreme fluctuations in temperature such as heat, chilling, and freezing stress. High temperature or heat stress causes the burning of aerial plant tissues (mostly, leaves), scorched twigs, senescence, and discoloration of leaves (Fahad et al. 2017). A rise in temperature can cause a loss in germination vigor of seeds and therefore poor growth and yield. They may also lead to reduced flower and seed-set in sorghum and several cereal crops (Fahad et al. 2017). Similar observations have also been made in maize and sugarcane. Heat stress leads to reduction in oil, protein, and starch contents of oilseed crops. Several physiological and biochemical processes are damaged on exposure to heat stress leading to water scarcity, reduction in leaf tissue, reduced root conductance, and increased transpiration (Huang et al. 2012). It also impacts nutrient metabolism in plants. Nitrate reductase activity is drastically reduced under temperature stress (Klimenko et al. 2006). As observed in drought and salt stress, heat stress also visibly affects photosynthesis and associated apparatus. Low CO<sub>2</sub> availability, stomatal closure, reduced moisture, and changes in photosynthetic pigments are noted under heat stress (Fahad et al. 2017). Heat stress also impairs photosystem II along with the regeneration capacity of RuBP (Wise et al. 2004).

Foliar application of Si is an effective method for protecting rice and grapevine plants growing in chilling and freezing growth conditions, respectively (Habibi 2015; Azeem et al. 2016). Temperature and salinity stress modulate catalase activity in wheat and *Salvia*, which is effectively countered by the application of exogenous

silicon (Liang et al. 2003). Electrolyte leakage is an important indicator of thermal stress in plants. Si-supplementation causes reduced electrolyte leakage due to high temperature (Ma et al. 2015). Thus, Si may have a role in generating thermal stability in cell membranes although further investigations need to be carried out to decipher the mechanisms and pathways involved.

In congruence with heat stress, chilling temperature conditions limit the growth and development of plants drastically, by diminishing root proliferation and early plant growth (Moradtalab et al. 2018). Cold stress and tolerance studies have been extensively studied using maize as a model plant. Chilling stress results in chlorosis, necrosis of leaf tissue, and inhibits root and shoot extension growth (Imran et al. 2013). These morphological deviations are often accompanied by physiological stress responses such as elevated production of ROS (Pei et al. 2010). Mechanisms involved in mitigating chilling stress still remain unexplored. Recent studies reveal that cold stress amelioration is often carried out by Zn, Mn, and Si, commonly known as the “cold stress protectants” (Bradáčová et al. 2016). Si helps to translocate micronutrients of seed reserved to seedlings under cold stress (Moradtalab et al. 2018). Silicon has the ability to prevent leaching due to cold stress by maintaining Zn/Mn reserves in the seed, which also act as cold stress suppressants. The most significant role of Si in mitigating cold stress is the restoration of root growth in maize plants. A similar role of Si under cold stress has been noted in soybean plants as well (Pascual et al. 2016).

Recent studies have shed some light on the existence of the ICE–CBF–COR pathway, which plays a key role in imparting cold stress acclimatization (Ritonga and Chen 2020). Activation of C-binding repeats (CBF) via cold induction by the inducer CBF-expression (ICE) results in the activation of cold responsive genes. Activation and regulation of the ICE–CBF–COR pathway result in the expression of several downstream genes, necessary for imparting tolerance against cold and chilling environmental conditions (Ritonga and Chen 2020). Low-temperature stress can often be categorized into chilling stress ( $<20^{\circ}\text{C}$ ) and freezing stress ( $<0^{\circ}\text{C}$ ) (Mickelbart et al. 2015; Guo et al. 2017; Liu and Zhou 2018; Shi et al. 2018). Crops such as tomato, soybean, cotton, corn, rice, and potato are intolerant to cold environmental conditions (both chilling and freezing stress). However, plants like oats, barley, rye, and wheat show good adaptability to cold stress (Zhang et al. 2011, 2017). Under low-temperature stress conditions, ICE mediated regulation of Gibberellic acid (GA) level is essential for cold tolerance. Plants facing cold stress have to maintain the stability of cell membranes and structural integrity for survival (Chen et al. 2018). Exposure to freezing conditions can often lead to the formation of ice nucleators and crystals in plant cell apoplast which ultimately results in dehydration, electrolyte leakage, and membrane disintegration (Puhakainen 2004). Under extreme situations, these ice crystals can puncture the cell leading to plants death (Demidchik et al. 2014; Sun et al. 2019). The most commonly observed mechanism for studying cold temperature tolerance is the accumulation of cryoprotective polypeptides, sugars, and osmolytes (Khan et al. 2015).

Furthermore, application of silicon to leaves of barley under cold (chilling as well as freezing stress) leads to an increase in levels of antioxidant enzymes, soluble

carbohydrates, and osmolytes, especially in leaf apoplast (Joudmand and Hajibolan 2019) (Table 2.1). Being the first site to be exposed to the cues of low temperature, overwintering plants often accumulate anti-freeze amino acids and compatible sugars in their apoplast (Liang et al. 2015).

#### 2.4.5 Nutrition Stress

Since a long time, there is a common observation that tremendous use of nitrogen fertilizers is being practiced by farmers for the multiple benefits, however, this also results in adverse effects such as enhanced lodging coupled with susceptibility to both pests and diseases (Ma 2004; Thomidis et al. 2016; Khan et al. 2018; Hosseini et al. 2015). There are many reports in which silicon has been used to minimize this offside issues as the silicate crystals provide mechanical strength as well as hinder insect feeding and inhibit penetration of fungal germ tube on the plant surface (Elsherbiny and Taher 2018; Singh et al. 2020). Besides, there are many reports which endorse the enhanced uptake and assimilation of an important nutrient, i.e. nitrogen in the presence of silicon (Pati et al. 2016; Malav Jugal and Ramani 2017; Patil et al. 2018; Haddad et al. 2018; Laíné Haddad et al. 2019; Gou et al. 2020; Raj et al. 2020). In addition, the use of silicon has also resulted in improved nodulation, better N<sub>2</sub> fixation, increased N use efficiency, and stimulated amino acid remobilization (Detmann et al. 2012; Steiner et al. 2018; Kurdali et al. 2019; Mohanty et al. 2020). Furthermore, excessive concentration of nitrogen is also toxic as it negatively affects plant and the quality of their products (Nielsen et al. 2008; Hilbert et al. 2015; Abrol et al. 2017). Si also mitigates excessive nitrogen stress (Singh et al. 2006; Liang et al. 2015; Campos et al. 2016; Barreto et al. 2016, 2017; Vicedo et al. 2019, 2020).

Next to nitrogen, phosphorus is another essential mineral element required for plant vigor in higher amount but the contrasting point is low availability of plant-available phosphorus in soil (Achary et al. 2017; Chu et al. 2020). In this regard, the application of soluble silicon fertilizers has resulted in an increased amount of bioavailable phosphorus as well as water-soluble phosphorus concentration (Owino-Gerroh and Gascho 2005; Singh et al. 2006; Liang et al. 2015; Tripathi et al. 2016; Agostinho et al. 2017; Zia et al. 2017; Kostic et al. 2017; Rezakhani et al. 2019; Zhang et al. 2019; Liao et al. 2020). The mechanism operating for how the silicon influence phosphorus uptake in plants was solved before the onset of the twenty-first century (Etesami and Jeong 2018, 2020).

In addition, potassium is also one of the major macronutrients that play important role in plant's growth, development, and metabolism as well as even range up to 2–10% of the dry mass (Cruz et al. 2019; Etesami and Jeong 2020). Silicon application has been also reported to alleviate the K-deficiency stress in stressed plants by modifying K-availability in both plants as well as soil (Mali and Aery 2008; Miao et al. 2010; Chen et al. 2016; Cuong et al. 2017). Sulfur-deficient barley crops were alleviated by supplementation of Si which helps regulate the action of ABA metabolism-related genes (Maillard et al. 2018). Additionally, application of

silicon has been also found to support the plant in nutrient deficiency stress conditions as well as toxicity; for example, calcium (Mali and Aery 2008; Etesami and Jeong 2018; Dong et al. 2018; do Nascimento et al. 2020), magnesium (Hosseini et al. 2019; do Nascimento et al. 2020), boron (Savić and Marjanović-Jeromela 2013; Liu et al. 2017; Metwally et al. 2018; Pereira de Souza Junior et al. 2019; Oliveira et al. 2020), iron (You-Qiang et al. 2012; Pavlovic et al. 2013; Bitvutskii et al. 2014; Patil et al. 2018; do Nascimento et al. 2020; dos Santos et al. 2020), manganese (Dragišić Maksimović et al. 2007; Patil et al. 2018; de Oliveira et al. 2019; do Nascimento et al. 2020), zinc (Gu et al. 2012; Bitvutskii et al. 2014; Hernandez-Apaolaza 2014; Pascual et al. 2016; do Nascimento et al. 2020; Raj et al. 2020), copper (Frantz et al. 2011; Patil et al. 2018; Raj et al. 2020; El-Beltagi et al. 2020), and sulfur (Maillard et al. 2018; Réthoré et al. 2020). The interaction of silicon with the above-mentioned nutrient elements has not been explored extensively and further investigation in this direction is highly recommended.

#### 2.4.6 UV-B Radiation Stress

Apart from the above-mentioned stresses, UV-B stress is considered as harmful stress for both plants and animals including humans (Jordan 2002; Yin and Ulm 2017; Chakraborty et al. 2017). The reason lies in its ability to influence biochemistry, physiology, and genetic changes in plants (Jordan 2002; Tripathi et al. 2017; Etesami and Jeong 2018; Azarafshan et al. 2020). The exogenous application of silicon to the plants has also resulted in alleviating the effects of UV-B stress on many plants (Fang et al. 2011; Yao et al. 2011; Schaller et al. 2013; Tripathi et al. 2017). All these studies together in combination have revealed that the exogenous application of silicon results in the formation of a cuticle–Si double layer, which acts as a glass layer and reduces the further transmission of UV radiation from the epidermis (Gatto et al. 1998; Currie and Perry 2007; Etesami and Jeong 2018). In addition, the silicon application induces resistance in plants by modifying ROS consumption (Shen et al. 2010), levels of UV absorbing compounds (Liang et al. 2015), and antioxidative enzyme activities (Fang et al. 2019).

#### 2.4.7 Wounding Stress

One of the interesting stresses among the variety of non-biological stresses is wounding stress that results in physical injury in the plants (Malhotra and Kapoor 2019). This arises actually from strong winds or water and due to the attack by herbivores (insects, birds, and nematodes) (Malhotra and Kapoor 2019; Singh et al. 2020; Souri et al. 2020). Primarily, these physical injuries increase the vulnerability to pathogenic attack by creating openings in plant organs as well as initiate oxidative stress at the secondary level that ultimately leads to death in serious cases via cell apoptosis (Malhotra and Kapoor 2019). In order to cope-up with wounding stress, the silicon treatment results in modulation in the levels of antioxidant enzymes (such

as phenylalanine ammonia-lyase, peroxidase, polyphenol oxidase, and catalase), malondialdehyde, hormones, and changes in gene expression pattern (Kim et al. 2011, 2014, 2016; Hajiboland et al. 2017; Hall et al. 2019).

#### 2.4.8 High pH Stress

Over the last century, due to the continuous anthropogenic activities and farming, there has been a paradigm shift in the pH of soil which either results in acidic or alkaline conditions (Wang et al. 2017; Shen et al. 2019). This pH changes in the pH of soil affect not only the plant roots but their functionality too. As a result of it, many modifications are induced frequently in the root and shoot physiology due to change in the pH of the xylem sap. Even in this regard, exogenous application of silicon has also resulted in alleviating the effects of pH stress on many plants (Abdel Latef and Tran 2016; Wang et al. 2017; Liu et al. 2018; Khan et al. 2019; Ju et al. 2020) (Table 2.2).

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### 2.5 Necessity of Silicon in Agriculture

With increasing incidences and severity of climate change, the challenges to the crop production will also increase in a long way to the future (Mahmoud and Gan 2018; Tamburino et al. 2020). This will be truly reflected in the form of more and more cases of diseases, pest attack, salinity, and drought conditions (Bashyal 2018; Rathee and Dalal 2018; Balamurugan et al. 2019; Shiru et al. 2020). Moreover, the intensified cum successive cropping has resulted in the elimination of basic cations from the soil (Jaiyeoba 2003; Xiao et al. 2013; Hao et al. 2019; Macedo et al. 2020). In addition, the continuous fertilization by the farmers necessitates the liming programs for maintenance of yields (Tubana et al. 2016; Hao et al. 2019; Xu et al. 2020). In this case, the high liming potential of silicon sources like silicate slags serves as a good agronomic option to correct soil pH (Tubana et al. 2016; Keeping et al. 2017; Etesami and Jeong 2018; Haynes 2019). In addition, many silicon and fertilizers act as a low-cost, good source of some important nutrients in plants such as  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  as well as fertilization enhance uptake of N, P, and K (Tubana et al. 2016; Zhao et al. 2020). Furthermore, various silicon sources that are being employed are actually low-cost byproducts from industries (Chanchal Malhotra et al. 2016). Even in few cases, many farmers have used straws of wheat and rice straw along with other small grain crops as a potential Si source (Marxen et al. 2016; Seleiman et al. 2019). Additionally, there are many reports on a foliar spray of Si containing solution (Haynes et al. 2013; Rodrigues et al. 2015; Oliveira et al. 2019). In the recent past, many liquids as well as granulated forms of Si fertilizers have been also generated due to the advances in the field of nanotechnology (Tubana et al. 2016; Rastogi et al. 2019; Siddiqui et al. 2020). These nano-size scale high-bioavailability fertilizers easily penetrate and create a thick-silicate layer on the surfaces of leaves (Chanchal Malhotra et al. 2016; Siddiqui et al. 2020). All these



**Table 2.2** Highlights of silicon-mediated mitigation of minor abiotic stress conditions

Stress	Experimental study	Plant species	Silicon application	Effect of silicon application	References
Wounding	Effect of silicon on mitigation of wounding stress	<i>O. sativa</i>	0.5 and 2 mM Na <sub>2</sub> SiO <sub>3</sub>	Improved leaf chlorophyll content and reduced oxidative stress	Kim et al. (2016)
	Effect of silicon on local and systemic response to mechanical stress in tobacco	<i>Nicotiana rustica</i>	1 mM Na <sub>2</sub> SiO <sub>3</sub>	Decreased production of peroxidases, polyphenol oxidase and augmented lignin accumulation in local response	Hajiboland et al. (2017)
UV-B	Effect of silicon on alleviating UV-B radiation damage	<i>Glycine max</i>	1.7 mM K <sub>2</sub> SiO <sub>3</sub>	Reduced accumulation of cyclobutane pyrimidine dimers (CPDs), increased production of UV-B absorbing compounds, increased photolyase gene expression	Chen et al. (2016)
	Role of silicon nanoparticles on alleviating UV-B stress	<i>Triticum aestivum</i>	10 µM SiNPs	Reduced oxidative stress, enhanced antioxidant production, increased nitric oxide production, overall SiNP appear to be better than Si	Tripathi et al. (2017)
Nutrient	Role of silicon in decreasing iron deficiency responses in soybean plants	<i>G. max</i>	1 mM Na <sub>2</sub> SiO <sub>3</sub>	Improved biomass and iron concentration, improved photosynthesis	Muneer and Jeong (2015)
	Effect of silicon on potassium deficiency in sorghum	<i>S. bicolor</i>	1 mM H <sub>2</sub> SiO <sub>3</sub>	Improved potassium concentration in xylem sap and improved growth and water status	Chen et al. (2016)
	Role of silicon in phosphorus uptake under low P conditions	<i>T. aestivum</i>	Na <sub>2</sub> SiO <sub>3</sub> (400 mg Si kg <sup>-1</sup> dry soil)	Improved P uptake and increased expression of Pi transporter genes	Kostic et al. (2017)
	Role of silicon in nitrogen uptake under low N conditions	<i>B. napus</i>	1.7 mM Na <sub>2</sub> SiO <sub>3</sub>	Improved uptake of N and increase expression of nitrate transporter gene	Haddad et al. (2018)
	Effect of silicon on plants growing under phosphorus deficiency conditions	<i>S. lycopersicum</i>	1.5 mM K <sub>2</sub> SiO <sub>3</sub>	Increased photosynthesis, biomass, reduced ROS and malondialdehyde levels and enhanced uptake of most essential elements	Zhang et al. (2019)
	Effect of silicon on rice plants growing under sulphur deficiency	<i>O. sativa</i>		Lower accumulation of stress phytohormones, enhanced growth and	Réthoré et al. (2020)

(continued)

Table 2.2 (continued)

Stress	Experimental study	Plant species	Silicon application	Effect of silicon application	References
pH			1 mM Monosilicic acid [Si(OH) <sub>4</sub> ]	balanced source to sink metabolic homeostasis	
	Effect of silicon on tolerance to alkaline stress	<i>Z. mays</i>	1.5 mM Na <sub>2</sub> SiO <sub>3</sub>	Improved growth of stressed plants, enhanced relative water content and photosynthetic pigments	Abdel Latef and Tran (2016)
	Effect of silicon on mitigating pH stress	<i>Festuca arundinacea</i>	0, 2, 8 mM Na <sub>2</sub> SiO <sub>3</sub>	Under acid stress, low Si concentration is effective in alleviating pH stress and under alkali stress it was opposite	Wang et al. (2017)
	Effect of silicon priming on high alkaline stress tolerance	<i>Medicago sativa</i>	0.075–3.75 mM Na <sub>2</sub> SiO <sub>3</sub>	Increased biomass as well as chlorophyll content and reduced oxidative stress	Liu et al. (2018)
	Effect of silicon and salicylic acid on high pH tolerance in tomato	<i>S. lycopersicum</i>	1 mM Na <sub>2</sub> SiO <sub>3</sub>	Plants displayed high chlorophyll content, reduced accumulation of ROS and high relative water content	Khan et al. (2019)
Effect of silicon on rice plants under acid rain stress	<i>O. sativa</i>	0, 1, 2 and 4 mM Na <sub>2</sub> SiO <sub>3</sub>	Improved plant growth, chloroplast structure and photosynthesis	Ju et al. (2020)	

factors establish the importance of a common agronomic practice worldwide, i.e. silicon fertilization. Therefore, owing to the above-described points along with the benefits of silicon in alleviating both non-biological stresses, it is a point to admit that silicon is a plant nutritional “non-entity” for mitigating plethora of abiotic stresses.

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## 2.6 Future Prospects

According to the current status of Si-research, it has been deciphered that there are multiple unaddressed questions related to many avenues which can be explored in a long way to the future, including

1. Detailed deduction of the complete “omics network” that operates during both non-biological and biological stresses in presence of silicon,
2. Deducing the effect of silicon amendments on plants exposed to combinatorial stresses,
3. Deducing the transport mechanisms that work during foliar uptake of Si in leaves,
4. Determining the effect of silicon fertilizers on the plant “whole microbiome” as well as plant–microbe interactions,
5. Effect of Si on non-accumulator plant species for enhancing stress resistance,
6. Understanding the detailed effects of Si on root anatomy around the whole plant kingdom,
7. Evaluating the economic feasibility of various Si sources,
8. Complete chemical analysis of the products made from slag,
9. Developing a prediction model that correlates the Si-mediated recovery with carbon accumulated and amino acid metabolism during stresses,
10. Evaluating the complete potential of SiNPs for alleviating abiotic stresses in farmer fields on large scale, and
11. Quantification of the content of monosilicic acid and polysilicic acid as well as grain size to develop an optimized system that works well for every crop that is being cultivated by humans.

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