Review

Silicon (Si): Review and future prospects on the action mechanisms in alleviating biotic and abiotic stresses in plants

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ABSTRACT

In the era present, due to increasing incidences of a large number of different biotic and abiotic stresses all over the world, the growth of plants (principal crops) may be restrained by these stresses. In addition to beneficial microorganisms, use of silicon (Si)-fertilizer is known as an ecologically compatible and environmentally friendly technique to stimulate plant growth, alleviate various biotic and abiotic stresses in plants, and enhance the plant resistance to multiple stresses, because Si is not harmful, corrosive, and polluting to plants when presents in excess. Here, we reviewed the action mechanisms by which Si alleviates abiotic and biotic stresses in plants. The use of Si (mostly as industrial slags and rice straw) is predicted to become a sustainable strategy and an emerging trend in agriculture to enhance crop growth and alleviate abiotic and biotic stresses in the not too distant future. In this review article, the future research needs on the use of Si under the conditions of abiotic and biotic stresses are also highlighted.

1. Introduction

Food security is one of the fundamental needs that can never be ignored by any society. The extensive increases in both environmental damage due to unsuitable agricultural practices, and human population pressure have the unlucky consequence that global food production may soon become inadequate to feed all of the world's people. The world's populace, therefore (approximately seven billion), is envisaged to surge to roughly 10 billion in the subsequent 50 years (Glick, 2014). The ever increasing pressure put on agricultural land by burgeoning human populations has resulted in land degradation, a cultivation shift to more marginal areas and soil types, and heavier requirements for agricultural productivity per unit area (Glick, 2014). Climate change has similarly exacerbated the incidence and gravity of sundry abiotic stresses (i.e., drought and elevated temperatures), with considerable harvest reductions reported in major cereal species such as wheat, maize, rice, and barley (Carmen and Roberto, 2011). In many parts of the world, precipitation has become less predictable, more intense, and, due to increasing temperatures, subjected to higher evapotranspiration (Jewell et al., 2010). Higher yields are also only sustainable with higher nutrient use, and the heavy demand for fertilizers has caused rising production costs for farmers worldwide. On the other hand, it is known one of the most important constraints to agricultural production in

world is abiotic stress conditions prevailing in the environment (Meena et al., 2017). Various environmental stresses caused by complex environmental conditions have affected the production and cultivation of agricultural crops (Meena et al., 2017).

Soil salinization is decreasing annually by about 1–2% of the areas suitable for agriculture, which is higher in arid and semiarid regions (Rasool et al., 2013). Drought accounts for about 30% of the world's land area. Drought stress has many common features with salinity stress, which is more destructive to agricultural production than salt stress (Bodner et al., 2015). In present era, heavy metal pollution is rapidly increasing which presents many environmental problems. The heavy metal toxicity to various environmental habitats is a major concern for environmentalists due to their prolonged toxic effects in the environment (Etesami, 2017). Nutritional imbalance hampers the growth, development, and yield of plant (Paul and Lade, 2014). Pathogenic microorganisms affecting plant health are a major and chronic threat to agricultural production and ecosystem stability worldwide (Compant et al., 2005). These abiotic and biotic stresses might increase in the near future even because of global climate change. The costs associated with abiotic and biotic stresses are potentially enormous and the effects of these stresses may impact heavily on agriculture, biodiversity and the environment. Worldwide, it has been estimated that approximately 70% of yield reduction is the direct result of abiotic

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stresses (Acquaah, 2007). Hence, the urgency of feeding the world's growing population while combating various environmental stresses has given plant and soil productivity research a vital importance. In addition to the use of soil beneficial microorganisms (Etesami and Beattie, 2017), previous research suggests that the use of silicon (Si) in agricultural is a sustainable strategy for the alleviation of biotic and abiotic stresses in various plants (Adrees et al., 2015; Balakhnina et al., 2012; Cooke and Leishman, 2011; Guntzer et al., 2012; Hernandez-Apaolaza, 2014; Meena et al., 2014a; Rizwan et al., 2015; Van Bockhaven et al., 2013; Wang et al., 2017).

Si constitutes a major portion of the soil in the form of silicate or aluminum silicates. Next to oxygen, Si is the most copious element in the Earth's crust. Si is present as silicic acid (or Si[OH]4) at concentrations between 0.1 and 2.0 mM (pH < 9) (Epstein, 1994). It is present in the soil solution in the form of monomeric or monosilicic acid (H_4SiO_4) and is readily absorbed into the root system. Si concentration varies greatly in a plant's aboveground parts, ranging from 0.1% to 10.0% of dry weight (Liang et al., 2007). The content of Si in plants is equivalent to or more than the major nutrients N, P, and K, which are supplied through fertilizers (Meena et al., 2014a). Although it is not considered essential nutrient for plants, Si is classified by many authors as beneficial or useful as it might have an important role in metabolic or physiological and/or structural activity, and improved plant survival of higher plants exposed to different abiotic and abiotic stresses (Liang et al., 2015d).

One of the main reasons for not being the essentiality of Si for higher plants is that a Si-free environment cannot be created currently due to technical problems as Si contamination from purified water, chemicals and dust cannot be avoided (Liang et al., 2015d). In general, it may be expected that the essentiality for Si will be finally recognized in higher plants according to the newly established definition of essentiality proposed by Epstein and Bloom (2005). Although the soil abounds with Si, much of this element cannot be taken in wholly by plants (Zhu and Gong, 2014). Moreover, Si is noncorrosive and pollution-free, and therefore, Si-fertilizer is a high-quality fertilizer for developing ecologically green agriculture. Effect of Si on crop growth, yield and quality has been well documented (Liang et al., 2015a). Si has been testified to foster progression and biomass, yield, and quality of a broad range of crops including monocotyledonous crops, some dicotyledonous crops, and some vegetable and fruit crops, which actively take up and accumulate high amounts of Si in their organs (Liang et al., 2015d).

The reaction of plants to biotic and abiotic stresses at biochemical, physiological and molecular levels is very similar to when Si is absorbed by the roots and transmitted to the shoots, which indicates the active role of the element in one or more plant defense signaling paths (Debona et al., 2017). By increasing biotic and abiotic stress resistance, adjusting pH, and acquiring macro- and micronutrients contained in the Si-fertilizers, Si has increased the plant growth and yield. In general, the beneficial effects of Si in stressed plants are more visible than non-stressed plants (Cooke and Leishman, 2016). Since one of the key challenges for plant growth is biotic and abiotic stresses which limit crop yields, the aim of this review was to summarize the action mechanisms through which Si could enhance plant resistance to biotic and abiotic stresses including salinity, drought, heavy metal toxicity, nutritional imbalance, and diseases. This paper shows that Si has significant and noticeable effects on alleviating all of the biotic and abiotic stresses in plants (Fig. 1). According to new findings on the positive effects of Si on stress tolerance in higher plants, the potential mechanisms are described below.

2. Mode of action of Si in alleviating salinity and drought stress in plants

2.1. Increase in plant root system

Since both water and nutrients are absorbed from the root of plant, drought and salinity can have a negative effect on plant growth through reduced root growth (Gupta and Huang, 2014). An increase in the root's surface area provides additional exposed sites for the absorption of diffusible ions (Barber, 1995). It has been reported that Si improves not only root growth (morphological traits such as diameter, area, volume, root dry bulk, and total and main root lengths) but also the shoot biomass of salt-stressed plants as well (Kim et al., 2014; Lee et al., 2010). The former has positive effects on water acquisition (increased WUEi) and nutrient uptake, while alleviating the stress effects of salinity in plant (Liang et al., 2007). Increases in root growth caused by Si supplement have also been reported in some studies under drought conditions (Ahmed et al., 2011; Hameed et al., 2013). The effect of Si stimulation on growth of roots may be due to increased root elongation caused by an increase in cell wall extensibility in the growth region, as observed in sorghum (Hattori et al., 2003).

In the study performed by Wang et al. (2015), the root/shoot ratio in Si-treated plants was increased, suggesting that Si-mediated modifications of root morphology may also account for the increased water uptake ability of Si-treated plants. In certain studies, Si application enhanced water uptake; although Si did not trigger root progress under drought stress (Sonobe et al., 2010). This contributes to the stimulation of nutrient absorption. The augmented water uptake during the addition of Si in a drought condition is the result of improved root hydraulic conductance (Hattori et al., 2008a) and root activity (Chen et al., 2011). Despite the above findings, further study is still required to clarify the details of the relationship between the impact of Si on root morphology and Si-enhanced tolerance to salt and drought simultaneously.

2.2. Regulation of biosynthesis of compatible solutes

Under stressful conditions such as salinity and drought, compatible solutes or osmolytes increase in plants mainly proline (Gzik, 1996; Pei et al., 2010), glycine betaine (Mansour, 1998), polyols (Parida and Das, 2005), etc. The above mentioned compounds may alleviate the limiting effect of increasing the high ion concentrations on the activity of enzymes by stabilizing proteins and their complexes, as well as membranes under environmental stresses (Zhu and Gong, 2014).

There are many reports that Si application can also increase plant tolerance to salinity and drought stress by modifying the levels of solutes such as proline (Lee et al., 2010; Yin et al., 2013), glycine betaine (Torabi et al., 2015), carbohydrates (Ming et al., 2012), polyols, antioxidant compounds like total phenolics (Hashemi et al., 2010), total soluble sugars, and total free amino acids (Hajiboland et al., 2016; Sonobe et al., 2010), which minimize the osmotic shock created by NaCl stress due to ion toxicity (Na^+ and Cl^-). Compatible solutes may also function as oxygen radical scavengers (Abbas et al., 2015). The improvement in osmotic adjustment potential in terms of increase in osmolytes by Si (Pereira et al., 2013) could be highly associated with high photosynthetic activity and better growth under saline conditions. There is little information about the relationship between Si and metabolism of compatible solutes and water transfer in plants, which needs further research in the future (Zhu and Gong, 2014). For future perspectives, it will also be worthwhile to investigate how Si regulates the metabolism of the osmolytes under water and salt stress at physiological, biochemical, and molecular levels.

2.3. Regulation of biosynthesis of phytohormones and polyamines

Phytohormones are known to play vital roles in the ability of plants

TREATMENT   MECHANISMS   STRESS ALLEVIATED

Silicon fertilizer

Increased plant root system
Regulation of biosynthesis of phytohormones
Ion homeostasis in plants
Osmolyte accumulation in plants
Induced plant synthesis of antioxidative enzymes
Improvement of water relations
Induction of stress resistance genes
Reduced heavy metal toxicity
Reduced uptake of heavy metals by plants
Improvement in the uptake of nutrient elements
Immobilization (precipitation) of toxic metals
Formation of physical barriers
Formation of chemical barriers
Induced oxidizing capacity of roots
Stimulated production of root exudates
Enhancement in gas exchange attributes
Structural alterations in plants
Change in distribution of nutrients in plant
Change in soil properties (*e.g.*, pH, etc.)
Increased growth and biomass of plants

Salinity

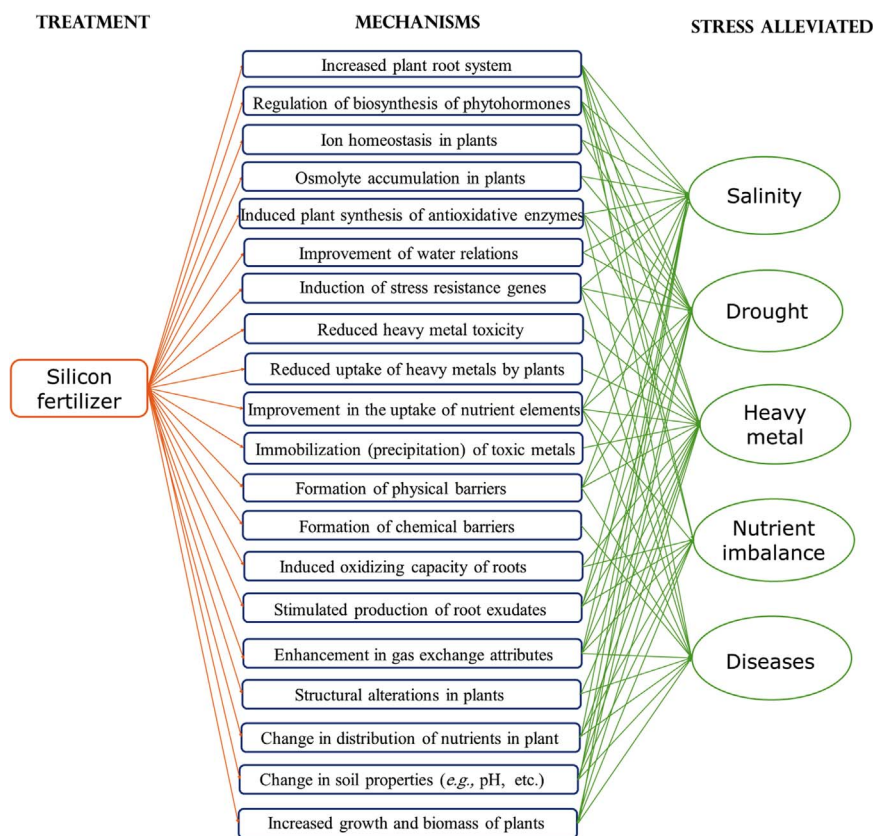Drought

Heavy metal

Nutrient imbalance

Diseases

Fig. 1. The multiple action mechanisms of Si in alleviating all of the biotic and abiotic stresses in plants. For details, see the text and these references - Adrees et al., 2015; Chanchal Malhotra et al., 2016; Cooke and Leishman, 2016; Coskun et al., 2016; Hernandez-Apaolaza, 2014; Imtiaz et al., 2016; Kim et al., 2017; Liang et al., 2007; Luyckx et al., 2017; Meena et al., 2014; Pozza et al., 2015; Rizwan et al., 2015; Wang et al., 2017; Zhang et al., 2017; Zhu and Gong, 2014.

to acclimatize to varying environments by different mechanisms (Fahad et al., 2015). These hormones, as studies generally indicate, serve to reinforce a plant's capability to hold up against salt stresses (Fahad et al., 2015; Iqbal et al., 2014). It has also been known that Si application may enhance the plant tolerance to drought and salinity stress by adjusting the levels of phytohormones (Kim et al., 2014; Yin et al., 2016). Yin et al. (2016) reported that Si application decreased ethylene in sorghum under salt stress. Exogenously applied gibberellin (GA) can also alleviate the inhibitory effect of NaCl on plant growth (Chakrabarti and Mukherji, 2003). Lee et al. (2010) reported that addition of Si to salt-stressed soybean enhanced the levels of endogenous GA, whereas it reduced the level of abscisic acid (ABA) and proline. ABA is involved in altering salt stress-induced gene expression and helps plants survive under stress conditions (Wang et al., 2001). Hamayun et al. (2010) found that Si treatment diminished jasmonates (JA) levels while increasing the levels of salicylic acid (SA) in soybean plant shoots. Pei et al. (2010) also uncovered that adding Si marginally increased ABA concentration in water-stressed wheat's leaves.

It has been reported that Si is involved in regulating polyamines (PAs) (LIU and XU, 2007). PAs participate in the defense reaction of plants against abiotic stresses such as salinity (Gupta et al., 2013). Growth promotion, cell division, DNA replication, and cell differentiation are some of the plant's processes that PAs are involved in regulating them (Martin-Tanguy, 2001). It is known that accumulation of PAs, especially spermidine and spermine, may help to tolerate salinity (Zhu and Gong, 2014). Si plays an important role in the production and accumulation of PAs such as putrescine, spermidine, and spermine, thereby helping to increase the plant's resistance to salinity (Wang et al., 2015; Yin et al., 2016). PAs production may function in this way via regulating K^+ and Na^+ transport, improving antioxidant ability and modifying osmotic potential (Alcázar et al., 2011). The results of the patch-clamp analysis of the epidermal and cortical protoplasts of salinity-stressed barley root showed that PAs blocked inward and outward Na^+ and K^+ currents through non-selective cationic channels, thereby

preventing intracellular accumulation of Na^+ ion concentrations (Zhao et al., 2007); nevertheless, it is important to note that there is currently no *in planta* evidence of non-selective cation channels-mediated fluxes (Coskun et al., 2013). Yin et al. (2014) have reported that Si treatment improved sorghum's drought tolerance by altering the synthesis of polyamine and 1-aminocyclopropane-1-carboxylic acid (ACC). Microarray research on the influences of Si in rice infested with *Magnaporthe oryzae* exhibited Si generating ethylene signaling pathway (Brunings et al., 2009; De Vleesschauwer et al., 2006). Fauteux et al. (2005) proposed that Si interacts with several key elements in plant stress signaling structures, thereby causing resistance. To further understanding of the possible role of Si in the metabolism of polyamines, deeper analysis is required. More research is also needed to clarify the relationship between these changes and to tolerate salinity stress and potential involvement of Si in signaling (Zhu and Gong, 2014). In general, research that is related to Si's repercussions on growth hormones under drought and salinity stress conditions is limited. Study of how to adjust the levels and initial adaptive responses of phytohormones and secondary metabolites by Si can be an interesting research field in the future (Zhu and Gong, 2014).

2.4. Increase in mineral nutrient uptake and assimilation

Salt stress leads to excessive nutritional deficiency among plants (Gupta and Huang, 2014). Water deficit also limits nutrient uptake through roots and subsequent transport to shoots, thereby reducing nutrient availability and metabolism (Farooq et al., 2009). All plants require adequate amount of essential plant nutrients for normal growth and development. Si may play an important role in balancing the uptake, transport, and distribution of minerals in drought and salinity stressed plants (Rizwan et al., 2015; Zhu and Gong, 2014). A report stated that Si treatment expanded the accretion of nutrients such as Mg (Gunes et al., 2008; Xu et al., 2015), N (Detmann et al., 2012; Hellal et al., 2012), K (Abdalla, 2011; Chen et al., 2016), P (Emam et al., 2014;

Farshidi et al., 2012), Ca (Kaya et al., 2006; Mateos-Naranjo et al., 2013), Fe (Farshidi et al., 2012; Pavlovic et al., 2013), Zn (Pascual et al., 2016), Mn (Wang and Han, 2007), and Cu (Gunes et al., 2008) in plant under drought and salt stress.

Some researchers attributed the increased absorption of some nutrients, such as Ca^{2+} and K^+, to Si-mediated decrease in plasma membrane permeability and Si-induced increase in plasma membrane H^+-ATP activity (Kaya et al., 2006; Liang, 1999). Since nutrients are mostly absorbed from root, it seems that the increase in root surface area and length can provide more exposed sites for uptake of diffusible ions (Barber, 1995). It is known that Si can increase the uptake of nutrients by increasing root activity (Chen et al., 2011), enhancing water uptake (Sonobe et al., 2010), and improving hydraulic conductance of roots (Hattori et al., 2008a). The aforementioned research shows how Si could alleviate salt and drought stress among plants by not only interfering with Na^+ absorption, but by influencing the absorption, translocation, and eventual allocation of certain nutrient elements among plants (via balancing nutrient uptake) (Rizwan et al., 2015; Zhu and Gong, 2014).

It is not also known that the absorption of which nutrient element by plant is most affected by Si under salinity conditions. Identifying this issue will help to better manage saline soils (in terms of fertility). More research is also needed to identify the factors influencing the effect of Si on the absorption of nutrients (Zhu and Gong, 2014), to study Si-induced root changes on the speciation and dynamics of nutrient elements in rhizosphere, and to determine whether Si-induced root changes affect the special form of the nutritional elements or all forms of an element in rhizosphere.

2.5. Reduction in ion toxicity

Increased concentration of soluble salts, such as NaCl, leads to an increase in the concentration of Na^+ and Cl^- ions in soil solution and subsequently in plant. The high absorption of Na^+ by the plant prevents the absorption of K^+ and Ca^{2+} ions. High levels of Na^+ in the plant damage the plant cells, disrupt cellular metabolism, and result in the production of reactive oxygen species (ROS), and eventually decrease the growth of the plant (Mahajan and Tuteja, 2005). Under such conditions, the plants increase their resistance to salinity stress by reducing the entry of Na^+ ion from the external solution into cytosol and increasing the efflux of this ion from cytosol to vacuoles, which lead to reducing cytosolic Na^+ pools (Munns and Tester, 2008) and thereby prevent leaf metabolic disorders, ion imbalances, and the desiccation of leaf tissue via osmotic stress (Kronzucker et al., 2013a, 2013b). In addition, homeostatic maintenance of intracellular K^+ pools is effective in maintaining the proper role of cell under salt stress (Kronzucker et al., 2013a, 2013b).

Si can also help increase plant resistance to salt stress by reducing the absorption of Na^+ ions (via the Na^+-H^+ exchangers HvSOS1 and HvNHX1 in the plasma membrane and tonoplast, respectively) and increasing K^+ ion absorption (via K^+-H^+ symporters such as HvHAK1) (Rizwan et al., 2015; Zhu and Gong, 2014). For example, under salinity stress, a decrease in Na^+ absorption and transfer and an increase in K^+ uptake in plants of alfalfa (*Medicago sativa* L.) (Wang and Han, 2007), bean (*Vicia faba* L.) (Shahzad et al., 2013), wheat (*Triticum aestivum* L.) (Tuna et al., 2008), and sorghum (*Sorghum bicolor* L.) (Yin et al., 2013) treated with Si were observed compared to untreated plants. Si also increases Na^+ efflux and K^+ influx by activating root plasma membrane H^+-ATPase, and tonoplast H^+-ATPase, and H^+-PPase in salt-stressed plants (Liang, 1999; Liang et al., 2005b). Increased activity of these enzymes may affect the structure, integrity and functions of plasma membranes by influencing the stress-dependent peroxidation of membrane lipids (Liang et al., 2005b, 2006). The Na^+/H^+ antiporter plays an important role in maintaining a low Na^+ concentration by removing Na^+ from the cytosol or compartmentalizing it in vacuoles (Yue et al., 2012), helping maintain osmotic homeostasis (Blumwald,

2000; Zhu, 2001). Despite showing recent physiological evidence of Na^+-H^+ antiport activity (Hamam et al., 2016) and *in planta* K^+ fluxes (Coskun et al., 2014), more research is still needed on measurements of Na^+ fluxes in root tips (Coskun et al., 2016). It is also unknown whether Si regulates the transport activity or expression of the Na^+/H^+ antiporter under salinity stress conditions that requires more research (Zhu and Gong, 2014).

It has been known that the polymerization of Si within the apoplast (biosilicification in plants) leads to the formation of an amorphous silica barrier (Exley, 2015), which can reduce membrane permeability, improve structure and stability of root cells, and hinder the penetration of Na^+ ion into the symplast and/or transpiration stream (Guerriero et al., 2016). Si, by stimulating the transcription of the genes involved in the synthesis of lignin and suberin, the constituents of forming barriers to apoplastic Na^+ transport in roots (Fleck et al., 2010), prevents the transfer of Na^+ into the root of plants. The formation of these obstacles is correlated with higher resistance to salt in plants (Krishnamurthy et al., 2011a, 2011b). For example, Si deposition has been proposed in the endodermis to restrict the transport of Na^+ in the "transpirational bypass" route from root to stem in rice (Gong et al., 2006). It has recently been confirmed that Si in rice, a species with a high capacity for Si uptake and accumulation, prevents the absorption and transfer of Na^+ to the plant's organs through the formation of a mechanical barrier. However, it should not be assumed that the effect of this physical barrier on other plants also works in the same way, especially in plants with lower capacities for Si uptake and accumulation (Wang et al., 2015). It has been reported that the Si applied to leaves as foliar spray could have translocated to the roots, where it could strengthen the membranes of root cells by depositing around the cell walls and changing their permeability to various toxic ions such as Na^+ and Cl^- (Abbas et al., 2015). Gong et al. (2006) observed that Si is deposited on the exodermis and endodermis of rice roots, which dramatically decreases apoplastic transport (the so-called transpirational bypass flow) and therefore Na^+ accumulation. For example, Faiyue et al. (2010) suggested that the lateral root may play a role in bypass flow because it lacks an exodermis, whereas Si can enhance exodermal development in rice. Therefore, in rice, both Si-enhanced exodermal development and Si deposition on the exodermis contribute to decreased loading of salt ions into the xylem of roots, resulting in decreased salt ion accumulation in shoots (Fleck et al., 2010).

Lately, Yin et al. (2016) reported that Si reduced the absorption and accumulation of Na^+ by modifying some of the important metabolic processes associated with the regulation of ion chancel. These authors also reported that PAs metabolism plays a role in this regulation. PAs regulate homeostasis of ions in plants under salt stress conditions. These compounds were found to block plasma membranes K^+ and non-selective cation channels, which assisted in the retention of intracellular K^+ and the reduction of Na^+ influx, thus ameliorating the detrimental effects of salt stress on plant ionic homeostasis (Velarde-Buendía et al., 2012; Yin et al., 2016). In the study performed by Wang et al. (2015), under salt stress, Si induced PAs accumulation and the K/Na homeostasis was alleviated. Regarding the confirmation of the role of PAs in regulating ion homeostasis and thus in enhancing plan tolerance to salinity stress (Yin et al., 2016), more investigation will be necessary to determine whether the same mechanism exists in plants under other environmental stresses.

Si may also improve cell-wall Na^+ bounding and thereby decrease potential Na^+ toxicity (Saqib et al., 2008). For example, Si prevented the transfer of Na^+ ion to the aerial parts of salt-sensitive and -tolerant wheat plants by increasing the binding of Na^+ to the cell wall of wheat roots (Saqib et al., 2008). However, there is little evidence of direct Na^+ complexation by Si, which may establish this potentially important salt tolerance mechanism (Coskun et al., 2016). From the above studies, it can be safely concluded that Si mediated selective transport capacity for K^+ over Na^+ and resultantly increasing K^+/Na^+ ratio might be one of the main mechanisms improving plant growth and yield under salt

stress (Rizwan et al., 2015; Zhu and Gong, 2014). Overall, mechanisms of Si-mediated alleviation of salt stress in plants are poorly understood at the molecular and genetic levels; more genetic experiments (including molecular recognition, signal transduction, and gene expression) are required to determine relationships between Si and salt stress to study the expression level of genes related to transport, deposition, and translocation of Na^+ and Si in different plant species (Rizwan et al., 2015). The results of the research may help us to better understand the physiological and biochemical functions of Si.

2.6. Regulation of the activities of various antioxidant enzymes

One of the immediate responses of plants exposed to salinity and drought stresses is the production of ROS (*e.g.,* singlet oxygen, superoxide anion, hydrogen peroxide, and hydroxyl radicals). The production and accumulation of ROS in the plants result in severe destruction of the cell structure, organelles, and roles (damage to the plasma membrane and endomembrane systems). Developed a complex antioxidant system to maintain homeostasis through enzymatic antioxidants (*e.g.,* superoxide dismutase, SOD; peroxidase, POD; catalase, CAT; and ascorbate peroxidase, APX; dehydroascorbate reductase, DAR; guaiacol peroxidase, GPOD; and glutathione reductase, GR) and non-enzymatic ones (carotenoids, non-protein amino acids, phenolic compounds tocopherols, ascorbate, and glutathione, GSH) is one of the strategies of the plants to alleviate and repair the damage caused by ROS (Kim et al., 2017). The plants grown under salt stress suffer from water shortages, resulting in the overproduction of ROS in the plants (Liang, 1999).

By modulating the plant antioxidant defense systems, Si can also alleviate oxidative damage in plants under salinity and drought stress (Kim et al., 2017). Following the treatment of salinity and drought-stressed plants with Si, an increase in the activity of key enzymes SOD, POD, CAT, APX, and GR as well as GSH concentration was observed (Kim et al., 2017; Zhu and Gong, 2014). Si has been reported to prevent the damage of membrane caused by the formation of malondialdehyde (MDA) (involvement in lipid peroxidation of membranes) (Zhu et al., 2004) by regulating antioxidant defense in plants (Zhu and Gong, 2014). For example, Si has also been shown to decrease the concentration of MDA, the end-product of lipid peroxidation, in salt-stressed barley (Liang et al., 2003), maize (Moussa, 2006), and grapevine rootstock (Soylemezoglu et al., 2009), and thus may help to maintain membrane integrity and decrease membrane permeability (Liang et al., 2015d). Khoshgoftarmanesh et al. (2014) showed that the concentration of MDA was positively correlated with Na^+ absorption in salt-stressed cucumber, but had a negative correlation with Ca^{2+} and K^+ absorption in the Si-treated cucumber plant. However, how Si mediates this response is unclear. Under drought stress, Si effect on antioxidant enzymes in plants varies not only among plant species but also at different growth stages of the same plant (Gong et al., 2008).

Overall, based on the above studies and available findings (Kim et al., 2017; Zhu and Gong, 2014), it can be concluded that Si can alleviate the oxidative damage in plants by modulating antioxidant defense systems (both enzymatic constituents and non-enzymatic ones).

Despite the above findings, the interactions between the plant antioxidant enzyme system and Si remain poorly understood, and a deeper analysis at the transcriptomic level is necessary to understand the mechanisms responsible for the Si-mediated regulation of stress responses (Kim et al., 2017). Further studies are also needed to explain how Si starts these responses (Zhu and Gong, 2014). In addition, many of these results are obtained from hydroponics experiments, and thus, further trials under field conditions are required.

2.7. Maintenance of plant water balance

In plants under drought and salt stress, the amount and absorption of water by the plant decreases. High concentrations of salt in soil solution result in increased osmotic stress, which limits water absorption by the plant and in turn affects leaf water content, stomatal conductance, leaf growth (acceleration of leaf senescence and leaf death) and photosynthesis (decrease in chlorophyll concentrations) and ultimately results in a reduction in plant growth (Munns and Tester, 2008). Primary stress that occurs in plant in saline soil is osmotic stress that has an immediate effect on plant growth (Horie et al., 2011). Plants have a specific strategy to maintain water balance when stressed (Horie et al., 2011). Osmotic adjustment helps plants to retain water despite low water potential, and thus to alleviate osmotic stress (Osakabe et al., 2014). There are reports that show that Si can improve water status and WUE in many plant species (Wang et al., 2015; Zhu et al., 2015), alleviating salt-induced osmotic stress (Chen et al., 2014). Furthermore, several studies have reported that plants treated with Si maintain a higher stomatal conductance and transpiration rate, stomatal conductance, leaf water content, and root and whole-plant hydraulic conductance (Liu et al., 2015; Yin et al., 2013).

In plants, the limiting factor for water transfer is mainly in roots (Rubio-Asensio et al., 2014). The hydraulic conductivity of root indicates the water absorption capacity and depends mainly on the root anatomy, root permeability, and the driving force (Sutka et al., 2011). One of the primary reactions of the plants to osmotic stress is the reduction of root hydraulic conductivity (Boursiac et al., 2005). It has been reported that Si reduces salt-induced osmotic stress by increasing root hydraulic conductivity (Liu et al., 2015; Wang et al., 2015). In a study, Zhu et al. (2015) found that Si can improve salt tolerance of cucumber plants through enhancing the root water uptake ability. The amount and activity of water channels, known as acupoinins, in cell membranes play an important role in regulating water absorption, especially under stress conditions (Liu et al., 2014). Si is involved in increasing root hydraulic conductance through increased expression of plasma-membrane intrinsic protein (PIP) aquaporins, which may in part contribute to the increase in water uptake (Liu et al., 2015; Zhu et al., 2015) and reduce oxidative stress and membrane damage (Shi et al., 2016). In studies, Liu et al. (2014), Liu et al. (2015), and Wang et al. (2015) observed that Si increased the root hydraulic conductance under salt stress. These authors attributed this effect to Si-mediated transcription up-regulation of some aquaporin genes (increased the aquaporin expressions). The produced aquaporins, in turn, lead to increased root hydraulic conductivity, absorption of water, and the entry of Si into the cells (Rios et al., 2017). Although the mechanisms by which Si nutrition affects aquaporin expression and activity have yet to be resolved (Coskun et al., 2016), determining whether other mechanisms are also involved will also require further study.

Oxidative stress causes plasma membrane injury and affects the activity of aquaporins (negative regulation of the activities of plasma membrane aquaporins) (Liu et al., 2015) and subsequently root hydraulic conductance. Benabdellah et al. (2009) observed that high concentrations of exogenous H_2O_2 affected the root hydraulic conductance, and the changes of hydraulic conductance were inversely matched with the changes of membrane electrolyte leakage and ROS level. It has been found that Si can increase water stress tolerance of Si-treated plants by decreasing oxidative damage of membrane and subsequently increasing root hydraulic conductance (increased the root water uptake ability) (Liu et al., 2015; Shi et al., 2016). It is not clear how oxidative damage exactly affects the root hydraulic conductance. It is reasonable to assume that oxidative damage causes a malfunction of the plasma membrane and therefore may affect the performance of plasma membrane aquaporins, which play an important role in root water absorption, especially under water pressure (Liu et al., 2014; Vandeleur et al., 2009).

It has been shown that H_2O_2 plays a role in the formation of suberin lamellae (Razem and Bernards, 2002). Suberin forms a hydrophobic barrier in endodermis and exodermis of roots (Enstone et al., 2002). In the study of Shi et al. (2016), Si developed less suberin lamellae in the roots of water stressed tomato, and therefore resulted in higher water

permeability. Fleck et al. (2010) also observed that Si enhanced suberization and lignification in the roots of rice. However, whether Si enhances suberization in the roots of other plants remains unclear. The effects of Si and H_2O_2 on the formation of suberin lamellae also need to be investigated under water stress conditions. Further studies are needed to explore, how Si triggers the antioxidant defense in various plants under water stress.

In addition to the mentioned mechanisms (effect on hydraulic conductance and water transport by modulating aquaporin expression/activity and expression of salinity resistant genes), Si can affect the transfer of water and facilitate the absorption of root water by adjusting the osmotic potential of cells through the accumulation of osmolites (Lee et al., 2010; Ming et al., 2012; Sonobe et al., 2010), increasing root hydraulic conductivity. The referenced authors suggested that this osmotic regulation can be a consequence of soluble sugars and amino acids including glutamic acid and alanine. Under stress conditions, the Si-mediated accumulation of compatible acids (such as proline) may reduce the osmotic potential of the cell and thus form an osmotic gradient (an increase in osmotic driving force in plant). Sonobe et al. (2010) expressed that Si's inclusion in the culture solution could improve water absorption by root under water-deficit stress through active accumulation of soluble sugars and amino acids. However, in the study of Wang et al. (2015), leaf and root osmotic potentials were not decreased by Si. This result demonstrates that osmotic adjustment cannot be the only mechanism by which Si helps to maintain water balance in plants.

Leaf water status is determined using water absorption and transport, as well as transpirational loss (Shi et al., 2016). The change in the rate of transpiration is another mechanism by which plants can regulate water balance (Wang et al., 2015). Under the conditions of osmotic stress, the closure of the stomata is an immediate reaction of the plant, which leads to a reduction in the water loss (Cornic, 2000). The increase in leaf water content and water capacity in the presence of Si under drought stress state might be caused by the leaves' thickness in comparison to the control plant that did not receive Si treatment (Gong et al., 2003). Moreover, the rise in leaf water potential can be the result of Si's deposition in leaves (the creation of Si cuticle double layer on a leaf's epidermal tissue), decreasing transpiration from their surface since water molecules may not readily escape from the surface because of Si treatment (Ahmed et al., 2014; Lux et al., 2002). Gao et al. (2006) observed that Si application enhanced WUEi in drought-stressed maize by reducing leaf transpiration rate through stomata and water flow ratio in xylem vessels which indicated that Si influences stomatal movement in plants (Gong and Chen, 2012; Kurdali and Al-Chammaa, 2013). The authors suggested that Si's deposition on the root cell wall might influence the wetting features of xylem vessels, as well as water or solute transport. A similar phenomenon was also observed in rice (Ming et al., 2012). However in some cases, it is reported that although the transpiration rate of plants has not decreased, the plant water status is better in Si-added plants. For example, in corn, Si supplementation does not affect the leaf cuticular-transpiration, but significantly decreases the stomatal transpiration (Gao et al., 2006). Recently studies indicate that Si-mediated increase in drought tolerance may be associated not only with leaf transpiration but also with root-water absorption (Shi et al., 2016). Based on the results of recent studies (Katz, 2014; Liu et al., 2015; Shi et al., 2016), it can be concluded that the Si effect is not proportional to its accumulation in the plant, and the low Si accumulation does not mean its low function. In addition, reducing the transpirational loss of water is not a global mechanism for Si-mediated improvement of water status in plants (Shi et al., 2016). It has been reported that the effect of Si on plant transpiration may be related to plant species and environmental conditions (Shi et al., 2016), so that in some plants, after the addition of Si, transpiration is increased (Chen et al., 2011), in some others, transpiration is reduced (Gao et al., 2006), and in others, no change in transpiration is observed (Hattori et al., 2008b). Such variations suggest that there are different strategies

among species, because they balance the amount of water absorption and the amount of water loss in the leaf surface. The main mechanisms behind these strategies and the responses to Si need to be further explored and analyzed (Coskun et al., 2016).

During a salt-stressed condition, the diminution of relative water content (RWC) of leaf is also a wide-ranging reaction among plants, implying that they are experiencing osmotic stress (Fahad et al., 2015). It was found that the treatment of Si enhanced RWC of leaf among such treated plants (Esmaeili et al., 2015; Zhu et al., 2015). By improving water storage in foliage, Si can diminish the salt toxicity to plants (Romero-Aranda et al., 2006). Greater water content contributes to salt dilution, resulting to a decline in salt toxicity and improvement in plant growth (Romero-Aranda et al., 2006; Tuna et al., 2008). The hydrophilic nature of Si (SiO_2-nH_2O deposition, known as phytoliths, in cells walls and cell lumens of all plant tissues may to some extent contribute to water restoration in salt-stressed plants (Romero-Aranda et al., 2006). This is interesting to be found that whether a Si layer exerts a proportionately greater effect in enhancing resistance in water stressed Si treated plants than in unstressed Si-treated plants. Previous researchers have shown that Si may also affect cell wall properties of xylem vessels (Diogo and Wydra, 2007). Si-induced changes in the characteristics of the cell wall of xylem vessels can regulate water transport and thus affect plant water relations. It has been reported that improved structural stability due to the binding of Si with cell-wall hemicellulose can be beneficial in conditions of water shortage for the plant (Ma et al., 2015).

The above studies clearly show that Si application can improve plant water balance under salinity and drought induced osmotic stress conditions. However, more detailed studies are still needed to discover the Si-mediated mechanisms of osmotic regulation in plants, especially at the molecular and genetic levels. Although much work has been done to find out the Si-mediated salinity and drought tolerance mechanisms, most of the previous research has been conducted on Si-accumulating plant species (Zhu and Gong, 2014). Investigating the role of Si in low Si-accumulating plants will help clarify the biochemical role of Si and understand the exact mechanisms for Si-mediated drought tolerance in plants other than its physical role (e.g., by Si deposition) in Si-accumulating plants (Shi et al., 2016). As noted by Katz (2014), the effect of Si is not proportional to its accumulation in plants, and the low Si concentration does not mean its low function in the plants. Furthermore, little information is available about this possible relationship between Si-mediated changes in root hydraulic conductance and H_2O_2 accumulation under water stress (Shi et al., 2016). The study of this relationship in less Si-accumulating plants can also be interesting. Due to the complexity of the relationship between Si addition and transpiration in drought stressed plants, more comprehensive studies are needed to clarify the regulatory role of Si on the metabolism of water throughout the plant and on root water uptake in the future.

Aside from the research aspects mentioned above, these studies were performed with potted seedlings or polyethylene glycol-stressed seedlings, in which the experimental duration was relatively short. However, little work has been done in the field, which requires more studies. Because the responses of the plant to gradual water stresses, such as field conditions, is different from these responses to short-term water stresses in greenhouse conditions (Zhu et al., 2005). Supplementary experiments are also needed to investigate how exogenous Si is involved in regulating water movement in all plants under salinity and drought stress conditions simultaneously (Zhu and Gong, 2014).

2.8. Modification of gas exchange attributes

Photosynthetic gas exchange characteristics in plants are highly sensitive to salt stress (Gupta and Huang, 2014). However, the exogenous treatment of Si was found to advance the gas exchange features in many plant types subject to salt stress (Liu et al., 2015; Rizwan et al., 2015) and drought stress (Gong and Chen, 2012; Rizwan et al., 2015).

For example, in the study of Xie et al. (2015), Si enhanced maize tolerance to salinity stress under filed conditions by increasing photosynthetic rate, stomatal conductance, and intercellular CO_2 concentrations and decreasing transpiration rate. Stomata regulate the plant's water level by controlling transpiration rate, especially under drought stress (Rizwan et al., 2015). Following the treatment of plants with Si under drought conditions, a decrease in leaf transpiration rate and an increase in the photosynthetic rate, stomatal conductance (Abdalla, 2011; Chen et al., 2011), higher water uptake (Hattori et al., 2005), and WUEi (Gao et al., 2006) of the plants were observed. The above studies show that Si can increase photosynthesis, nutrients uptake, and ultimately plant growth and biomass under drought and salinity conditions through increasing gas exchange and decreasing Na^+ uptake by decreasing transpiration and other mechanism might be involved in Si-mediated reduction in Na^+ uptake by plants. Comprehensive studies are required to examine other mechanisms of Si-mediated regulation of gas exchange characteristics under drought and salinity stress in the future. As an example, there is little information on the role of Si in diurnal changes in gas exchange characteristics of plants (Rizwan et al., 2015).

2.9. Regulation of lignin biosynthesis

Si is involved in regulating of lignin biosynthesis (LIU and XU, 2007; Zhu and Gong, 2014). Salinity increases the activities of certain ROS-scavenging enzymes related to greater lignin biosynthesis, which in turn hinders plant growth (Ortega et al., 2006). Hashemi et al. (2010) discovered that added Si diminished canola's lignin content. Si's capacity to decrease tissue lignification may lead to the extensibility of cell walls, leading to plant development under stress environments (Dragišić Maksimović et al., 2007; Hattori et al., 2003). That Si in a plant helps to synthesize lignin (*e.g.,* deposition of lignin in sclerenchyma cells of rice) (Fleck et al., 2010) and in another plant prevents lignin synthesis (*e.g.,* decreases the lignin content in canola) (Hashemi et al., 2010) is related to the ability of these plants to absorb and accumulate Si, which requires further study in the future. In addition, further investigations are needed to clarify the relationship among these changes (Si-mediated increase or decrease of lignin synthesis in stressed plants), stress tolerance, and the possible involvement of Si in signaling.

3. Mode of action of Si in alleviating heavy metal toxicity stress in plants

3.1. Diminution in plants' metal absorption

One of the major effects of Si on the reduction of metal toxicity is reducing the metal uptake and transport in plants. In previous studies, reduced uptake and translocation of metals and subsequently increased tolerance to toxic metals in Si-treated plant species have been reported by many researchers (Anwaar et al., 2015; Keller et al., 2015; Tripathi et al., 2015). The polymerization of H_4SiO_4 inside apoplast (biosilicification in plants) has been known to result in the formation of an amorphous silica barrier (Exley, 2015), which can hinder the penetration of potential toxicants such as Al, Mn, Cd, and Zn into the symplast and/or transpiration stream (Guerriero et al., 2016).

This decrease in metal uptake in the presence of Si can be explained in many ways. For example, Si may trigger the production of root exudates which can chelate metals and reduce their absorption by roots (Kidd et al., 2001). In addition, this reduction in metal uptake can also be explained by the fact that Si reduced the apoplasmic transport of metals by decreasing free metal concentration in the apoplasm (Iwasaki et al., 2002; Rogalla and Römheld, 2002). Furthermore, the physical limitation formed by the deposition of Si in the endoderm region may reduce the cell wall's porosity in the inner root tissues, thus decreasing the metal concentration in the xylem (da Cunha and do Nascimento,

2009; Keller et al., 2015). Similarly, Si decreased apoplasmic transport of metals through the enhanced adsorption of metals on the cell walls (Liang et al., 2007; Ye et al., 2012). Si accumulation in the roots endodermis may reduce the mobility of heavy metals (da Cunha and do Nascimento, 2009; Keller et al., 2015). A diminution in metal absorption via plants is moderately linked to the development of apoplasmic obstacles and the maturation of vascular tissues in the root (Greger et al., 2011; Vaculík et al., 2012). According to the studies listed above, it can be concluded that Si reduces the toxicity of heavy metals in plants by reducing the metal absorption and blocking the transfer of metals in plants.

3.2. Enhancement in gas exchange facets and photosynthetic pigments

Positive effects of Si on chlorophyll biosynthesis and photosynthetic machinery under metal toxicity have been widely reported (Adrees et al., 2015; Imtiaz et al., 2016). It was found that Si application increased the contents of chlorophyll a, chlorophyll b, and carotenoid in leaves and enhanced the activities of gas exchange features (net photosynthetic quotient, stomatal conductance, transpiration ratio, and WUEi) under conditions of heavy metal stress (Farooq et al., 2013; Hussain et al., 2015; Rizwan et al., 2012; Tripathi et al., 2015).

3.3. Changes in plant growth, biomass, and mineral nutrient supply

Mineral nutrients are the major constituents of the plant structural component and provide mechanical, biochemical, and physical strengths to the plants. Mineral nutrients are also essential in the development of plants, with heavy metals being able to intervene with the absorption and movement of crucial nutrients, thereby disturbing minerals' nutritive composition. Si can decrease metal toxicity among plants by intermingling with other elements. Si serves a chief role in the uptake of nutrients by plants under metal stress. Si plays an important role in the absorption of nutrients by plants under metal stress. Si application increased the content and accumulation of micronutrients (*e.g.,* Zn, Fe and Mn), and macronutrients (*e.g.,* Ca, Mg, P and K) by plants under metal stress (Adrees et al., 2015; Keller et al., 2015; Mehrabanjoubani et al., 2015; Tripathi et al., 2015). Feng et al. (2010) observed that Si supply diminished the limiting effects of metals on the enzymes in plants' nitrogen metabolism. This covers nitrogen reductase (NR), glutamine synthetase (GS), glutamate synthase (GOGAT), and glutamate dehydrogenase (GDH). Si, by increasing the growth and biomass of plants and boosting the xylem sap under metal stress, may decrease metal toxicity by a dilution effect (the same uptake, but larger biomass) (Adrees et al., 2015; Gu et al., 2012).

3.4. Immobilization of toxic metal in the growth media

Si application can immobilize toxic metals in soil by increasing soil pH and changing metal speciation in soil (Adrees et al., 2015). The Si-influenced mitigation of metal toxicity in plants might be the result of an external plant effect based on decreasing the availability of phytotoxic metals in the culture media (da Cunha and do Nascimento, 2009; Naeem et al., 2015). It has been shown that Si application in soil affects the soil properties which in turn controls heavy metals availability to plants (Liang et al., 2007; Rizwan et al., 2012). Si can also change the speciation of metals in soil solution by the formation of silicate complexes, the formation of Si polyphenol complexes, and the formation of insoluble metal silicates in soil (Gu et al., 2012; Liang et al., 2007; Shim et al., 2014). A.-m. Zhang et al. (2013) reported that addition of Si markedly decreased the proportion of exchangeable heavy metals in metals-contaminated soil by increasing the proportion of precipitation-bound and organic matter bound metals fraction, thus reducing metals availability in the soil.

3.5. Expanding the antioxidant defense structure

Oxidative stress may occur in plants when they are exposed to heavy metal stress (Kim et al., 2017). On the other hand, by lowering the production of ROS and by enhancing antioxidant enzymes' activities (*e.g.,* SOD, POD, CAT, and APX), Si application may reduce oxidative stress in plants (Adrees et al., 2015; Anwaar et al., 2015; Kim et al., 2017). Above literatures showed that Si application could notably increase plant defense system by reducing oxidative damage and altering the activities of antioxidant enzymes up to a certain level of metal stress.

3.6. Plant compartmentalization

Several studies have observed the compartmentation of metals in shoots and roots of plants to understand Si detoxification mechanisms in plants (Adrees et al., 2015; Imtiaz et al., 2016). It was found that Si enhanced metal concentrations in plant roots in comparison to shoots (Keller et al., 2015; Naeem et al., 2015; Rizwan et al., 2012; Ye et al., 2012). Sequestration of heavy metals in metabolically less active cell compartments such as the cell walls might be an important mechanism for Si-mediated heavy metal tolerance in plants (Dragišić Maksimović et al., 2012; Liu et al., 2009; Ye et al., 2012). Doncheva et al. (2009) stated that a surplus of Cu that is sequestrated in non-photosynthetically and active leaf epidermal cells could be a Mn tolerance system in maize. Thus, Si localization in the root endodermis might function as an obstacle to inhibit the penetration of metals into cells. Taken together, effects of Si on metal compartmentation in the leaves and roots might be the crucial mechanism in metal uptake and detoxification in plants.

3.7. Si's co-precipitation with heavy metals

The co-precipitation of Si with metals in plants might be a mechanism which reduced metal toxicity in plants (Adrees et al., 2015). Many studies reported Si and metal co-precipitation in leaves and roots of many plant species (Gu et al., 2012; Oliva et al., 2011; You-Qiang et al., 2012). Previous studies also showed Si and metal complex formation in the roots (da Cunha and do Nascimento, 2009; Ma et al., 2015).

3.8. Chelation process

The mechanisms by which Si mitigates heavy metal stress in plants might be related to the chelation of flavonoid-phenolics or organic acids with metals (Collin et al., 2014; Wang et al., 2004). Furthermore, Si addition increased citrate, malate, and aconitate concentration in roots of plant (influencing root exudates) (Adrees et al., 2015; Fan et al., 2016). Authors mentioned that Cu could shape a complex with organic acids and decrease heavy metal translocation to shoots (Collin et al., 2014; Keller et al., 2015). Such studies showed that the Si-facilitated release of chelates might be a mechanism which could decrease the toxic impacts of metals in plants up to a certain extent. However, further studies are needed to highlight the role of Si-mediated chelation of metals in Si-accumulating and non-accumulating plants.

3.9. Physical alterations in plants

Si supply increased length of leaves, leaf area, number of leaves per plant, total root length, total root surface area, root volume and number of root tips, and length of primary seminal root under heavy metal stress (Anwaar et al., 2015; Bokor et al., 2014; Farooq et al., 2013; Keller et al., 2015). It has also been found in some reports that Si treatments accelerate the generation of suberin lamellae and Casparian bands, along with the development of root vascular tissues and lignification. Si increased the shaping of the tertiary endodermal cell walls, if compared with metal treatments alone. The enhanced improvement of endodermal apoplasmic obstructions with the addition of Si in plant was also exhibited (Lukačová et al., 2013; Tripathi et al., 2015; Vaculík et al., 2012). There is evidence that Si ameliorates the ultra-structural disorders caused by metal stress in many plant species (Ali et al., 2013). Si is then of importance in protecting photosynthetic machinery from being impaired under metal stress. Si protected the chloroplast ultrastructure from disorganization due to stress effected by Cd, Cr, and/or Zn in plants such as rice, cucumber, maize, and barley (Feng et al., 2010; Song et al., 2014). Added Si decreased the permeability of plasma membrane of leaf cells of barley and maize under excess Zn (Kaya et al., 2009; Liang et al., 1996).

As a conclusion, Si treatment under metal stresses protected the plant configuration, which might be due to compartmentalization, co-precipitation, and/or chelation of heavy metals in different plant parts, leading to decreased concentrations of free metal ions while generating increased plant growth and biomass (Abbasi et al., 2015; Imtiaz et al., 2016).

It is noteworthy that the generalization of Si-mediated alleviation of metal toxicity should be made with caution, because the mechanisms used by Si to reduce the stress of heavy metals in plant depend on plant species, genotypes, metal elements, growth conditions, duration of the stress imposed, etc. (Adrees et al., 2015). For future perspectives, it will be worthwhile to investigate the mechanisms of Si mediated alleviation of heavy metal stress at the molecular and genetic levels (*e.g.,* to study expression level of genes related to transport, deposition, and translocation of metals and Si in different plant species), although there are some reports about Si application in activating the genes of heavy metal-stressed plants responsible for heavy metal tolerance (Bokor et al., 2014; Khandekar and Leisner, 2011; Ma et al., 2015). In most research, the effect of Si on alleviating heavy metal stress has been studied only on a heavy metal, under hydroponic conditions and in a short term (Adrees et al., 2015), which can lead to an overestimation of metal absorption and translocation. Therefore, it is necessary to study the effect Si under natural conditions in the presence of a set of heavy metals and in a long term, because the ability of silicates to sequester heavy metals over time is likely to decrease.

4. Mode of action of Si in alleviating nutritional imbalance stress in plants

4.1. Macronutrients (N, P, K, Ca, and Mg)

The application of Si-fertilizers significantly increased the concentration of N in plants. Thus, the yield response to Si may be related to an improved uptake of this nutrient (Huang et al., 1997). Better uptake of N and Ca by cowpea and wheat, along with improved nodulation and evidently enhanced N_2 fixation in cowpea were observed as the plants were fertilized with extending doses of sodium metasilicate (50–800 mg Si kg^{-1}) (Mali, 2008; Mali and Aery, 2008). Detmann et al. (2012) verified that Si augmented N use efficiency and transformed primary metabolism by stimulating amino acid remobilization. Si has also been said to alleviate stress from excessive N (Liang et al., 2015b). It has been reported that a decrease of erectness in rice leaves following excess of N application can be alleviated if Si was applied to the nutrient formula (Singh et al., 2006).

It is well-known that P availability increases following Si-fertilization in various graminaceous species (Ma, 2004; Singh et al., 2006). The role of Si in P absorption in plants was one of the primary effects of Si ever evaluated (Eneji et al., 2008). The outcome of Si under P deficiency could be the result of an *in planta* mechanism, indicating an enhanced utilization of P, probably via an increase in phosphorylation (Cheong and Chan, 1973) or a decline in the absorption of unnecessary Fe and Mn (Ma and Takahashi, 1990; Ma, 2004). In addition, the beneficial effects of Si on P availability have been ascribed to a competitive sportive interaction and exchange of these two elements

(Smyth and Sanchez, 1980) such as an enhancement of soil P availability by increasing soil pH (Owino-Gerroh and Gascho, 2005), decrease of metal uptake (*e.g.*, Mn, Fe, Al and Cd), interactions with cationic metals such as Fe and Mn (MA and Takahashi, 1990), and increase of water-soluble P concentration (Eneji et al., 2008) which indirectly improve P utilization by plants (Liang et al., 2005a; MA and Takahashi, 1990). Sorption of P is the major cause of P deficiency in acidic soils. Phosphate ions ($H_2PO_4^-$) are specifically adsorbed onto hydrated Fe and/or Al oxides by replacing OH groups from the coordination sphere of the metals. The chemical competition between the anions $H_2PO_4^-$ and silicate ($H_3SiO_4^-$) for the sorption sites has been demonstrated in soils resulting in displacement of Si by P, and vice versa (Smyth and Sanchez, 1980). Furthermore, Si has been found to alleviate excess stress of P (Liang et al., 2015b). When P was applied in excess amounts, Si restricted P uptake and the appearance of chlorosis, apparently through lowering the rate of transpiration (Ma et al., 2001; Singh et al., 2006).

The application of Si can influence the availability of K in the soil and nutrient contents in plants (Chen et al., 2016; Kaya et al., 2006). In a study, Miao et al. (2010) ascertained that the application of Si- to K-deficient soybean (*Glycine max*) plants improved both internal K status and plant growth. Si similarly assuaged K-deficiency-induced membrane lipid peroxidation and oxidative stress by activating antioxidant enzymes. In a report by Mali and Aery (2008), K uptake in hydroponics and in soil increased even at depleted Si dilutions upon the establishment of H^+-ATPase. Recently Chen et al. (2016) showed that Si moderated K's deficiency by improving the plant-water status.

The application of Si increased the levels of Ca and Mg in soil and plant (C.H. Huang et al., 2011; H.-R. Huang et al., 2011; Kaya et al., 2006; Mali and Aery, 2008). The improved absorption of Ca may be ascribed to a diminution in plasma membrane penetrability and an increase in the movement of plasma membrane H^+-ATPase due to the addition of Si (Kaya et al., 2006; Liang, 1999).

4.2. Micronutrients (Fe, Mn, Cu, Zn, and B)

Several studies on the effect of Si on micronutrient deficiency are found in the literature (Bityutskii et al., 2014; Gonzalo et al., 2013; Hernandez-Apaolaza, 2014; Pavlovic et al., 2013). It has been reported that the addition of Si to the nutrient solution is able to mitigate Fe deficiency-caused chlorosis in plants (Bityutskii et al., 2010; Gonzalo et al., 2013; Pavlovic et al., 2013). A propositioned hypothesis denotes that Si addition increases the oxidation ability of rice roots, as well as Fe oxidations to insoluble ferric compounds (You-Qiang et al., 2012), forming the Fe plaque. Although oxide-bound ions in soils are repeatedly and relatively inaccessible to plants, the root–plaque–bound ions may become available for plant uptake, rendering the metal soluble yet again in the proximate environs of the root, if the plant exudes phytosiderophores that chelate the metal or dissolve the iron oxide (Zhang et al., 1998). You-Qiang et al. (2012) also concluded that Si increased Fe transport from the root to the shoot. A study showed that the increase in expression of Si transporters after Si addition might impact Fe uptake and translocation, improving Fe nutrition under deficiency conditions (You-Qiang et al., 2012). High accumulation of Fe in the roots was observed when plants were treated with Si (Bityutskii et al., 2014; Gonzalo et al., 2013; Pavlovic et al., 2013), which is attributed to a high amount of Fe in the root apoplastic pools (Pavlovic et al., 2013) or to its precipitation at root surfaces. Another hypothesis is that Si probably contributes to maintaining balances in other micronutrients, such as Fe/Mn ratio (Pich et al., 1994), which is also beneficial in enhancing chlorophyll synthesis, providing a possible explanation for the stimulation in growth of Fe-deficient plants supplied with Si (Bityutskii et al., 2014; Gonzalo et al., 2013; Pavlovic et al., 2013). Application of Si also facilitated mobility and xylem translocation of Fe toward the shoot, along with tissue accumulation of Fe-mobilizing compounds such as citrate (in xylem sap, root, and shoot

tissues) or catechins (in the roots) (Bityutskii et al., 2014; Pavlovic et al., 2013). Therefore, another proposed mechanism involves the enhancement of citrate in plants treated with Si. Citrate is one of the molecules that joins Fe on its transport through the xylem (Rellán-Álvarez et al., 2010). The increase of citrate concentration in leaf and root tissues, and in the xylem sap of Si-treated plants, especially the first day after Fe elimination from the nutrient solution (Bityutskii et al., 2014; Pavlovic et al., 2013), should engender long-distance transport and Fe utilization in leaves. Other hypotheses have been tested in cucumber, as the Si influences the Fe chelate reductase and the expression profile of the strategy of I-related units FRO2, IRT1, and HA1 (Pavlovic et al., 2013). In general, Si influence on Fe deficiency is mainly as a consequence of the development of Fe distribution in the plant. Storage of Fe in the root (apoplastic or plaque) pools seems to be favored by Si addition, and its remobilization figures to be a chief facet among the advantageous effects of Si on Fe insufficiency. In addition, based on new findings, the alleviating effect of Si appears to be more indirect by affecting the activation of Fe-deficiency-associated genes responsible for the enhanced root acquisition and tissue mobilization of Fe (Pavlovic et al., 2013).

Under Fe toxicity conditions, it is apparent that Si stimulates the oxidizing ability of the roots, changing ferrous iron into ferric iron and inhibiting a significant absorption of iron while obstructing its toxic feature (Ma and Takahashi, 2002). A report advised Si taking the role of facilitating Fe absorption from acidic soils through the discharge of OH^- by the roots when enhanced with Si (Wallace, 1992). Fe toxicity has been effectively alleviated in rice after Si addition (Ma, 2004; You-Qiang et al., 2012), mainly by an increase in the Fe precipitation in the growth media or at root surfaces (iron plaque). The Si addition probably increased pH and may lead to Fe precipitation. The Fe and Si could also co-precipitate, as Fe(III)-silicates, or Si may precipitate as negatively charged silica particles (Currie and Perry, 2007), in which the positively charged Fe may be bound with the consequent Fe depletion from the solution.

Mn and Si interaction in some plants (Horst and Marschner, 1978; Ji et al., 1992; Li et al., 1999) has been evaluated. Si furthers the enhancement of the oxidizing capacity of rice roots, lending a higher Mn-oxidation quotient in the rhizosphere and elevating the external precipitation of foliage (Okuda and Takahashi, 1962). As mentioned previously for Fe, such deposits could be expended under Mn deficiency and could ameliorate Mn deficiency. Si helped a homogeneous distribution of Mn in the leaf, instead of focusing on necrotic sites. A lower amount of Mn in the apoplast of cowpea was obtained when Si was added to the medium. This could be expounded through the metal adsorption on cell walls interceded by the Si deposits (Horst et al., 1999). Soluble Si in the apoplast may affect the Mn-oxidation state, promoting its precipitation (Iwasaki et al., 2002). Dragišić Maksimović et al. (2007) concluded that Si contributes indirectly to a decrease in OH^- in the leaf apoplast upon lowering the free apoplastic Mn^{2+}, thus regulating the Fenton reaction and protecting plants against Mn toxicity.

Si also affects plant Zn nutrition under deficiency stress conditions (Bityutskii et al., 2014; Li et al., 1999). The Zn solubility in the rhizosphere is controlled through growth medium acidification and excretion of low molecular weight chelating agents by the roots (Sinclair and Krämer, 2012). There are several evidences that Zn distribution in plant is altered by the Si supplement in hydroponic and soil investigations (Bityutskii et al., 2014; Gu et al., 2011, 2012), with both elements presenting an analogous site in plants (Gu et al., 2012). Si addition contributed to the root cell wall strength, delaying the Zn^{2+} transport to the shoots (Currie and Perry, 2007; Gong et al., 2006; Huang et al., 2009; Peleg et al., 2010). Si and Zn were mainly sited in the vicinity of the root endodermis (Gu et al., 2011), precipitated as Zn silicates, which may in some measure inhibit Zn xylem loading and transport (da Cunha and do Nascimento, 2009). This precipitate incurred a slow degradation to SiO_2, with Zn accumulated in vacuoles in an indefinite

shape (Neumann and zur Nieden, 2001). Silicate precipitation on the plant cell wall (Currie and Perry, 2007) increased the Zn^{2+}-binding sites, which may enhance Zn^{2+} adsorption on the silicate deposits (Wang et al., 2000). Such points toward a detoxifying behavior, avoiding the metal transport to more sensitive organs inside the plant (da Cunha and do Nascimento, 2009; Shi et al., 2005). Root Zn deposits could be used under Zn-deficient settings through the triggering of the Zn-deficiency mechanism. The enrichment of citrate in plants treated with Si has been described under Fe deficiency (Bityutskii et al., 2014; Pavlovic et al., 2013); this citrate could also play a chief role on Zn allocation in plants. As for Fe and Mn, the Zn pools in the roots could be more mobile under deficient conditions when Si was supplemented to the plant, supporting a better distribution of it, which may assist in ameliorating the Zn deficiency symptoms. As Si and Zn accumulations were also uncovered in leaves, the remobilization of the nutrient via phloem could return higher seed and fruit Zn content, which implies a more efficient use of the available Zn, especially under Zn shortage (Bityutskii et al., 2014; Hernandez-Apaolaza, 2014).

There are a few studies that reviewed the Si–Cu interaction in plants (Frantz et al., 2011; Ji et al., 1992; Khandekar and Leisner, 2011; Li et al., 2008). In *Arabidopsis thaliana*, Cu toxicity indicators including leave chlorosis and reduction of the shoot and root biomass were diminished by Si addition to the nutrient solution (Khandekar and Leisner, 2011; Li et al., 2008). Similar discoveries were discerned for wheat (Nowakowski and Nowakowska, 1997) where the Si shaped the distribution or bioavailability of Cu within leaves under Cu stress (Li et al., 2008). The formation of Si deposits on the cell wall increased the Cu-binding sites and avoided the impact of such high Cu doses on plant cells. This was proposed to explain this fact, similar to those proposed for other micronutrient toxicity (Frantz et al., 2011; Liang et al., 2007). Elevated levels of molecules that bind Cu, as a strategy to decreasing its toxic effect, were conserved or even augmented when Si was put in. More than one response, therefore, ought to be started to tolerate Cu toxicity (Khandekar and Leisner, 2011). Authors proposed that Si assists in generating additional apoplastic Cu-binding sites, sequestering the metal and thereby decreasing its toxic impacts (Hernandez-Apaolaza, 2014; Samuels et al., 1991). Si also promotes Cu-binding sites in the apoplast or cell wall and its incidence on some oxidative mechanisms induced by Cu deficiency (Samuels et al., 1991).

As regards the rest of the micronutrients, metal root deposits similar to those of Fe were reported in the literature under toxicity. Liang and Shen (1994) established in their report that under circumstances of sufficient or excessive boron (B) concentrations, Si supply steered a diminution in B uptake, whereas under states of B deficiency, Si supply helped B uptake in oilseed rape. Amendment of Si to high B soil effectively mitigated B toxicity in spinach, wheat, and barley by decreasing root-to-shoot translocation of B and also by preventing ROS membrane damages due to the modulation of the activities of antioxidative enzymes (Inal et al., 2009; Karabal et al., 2003).

Although the beneficial role of Si in alleviation of abiotic stress is well established, little is known of the relevance of Si nutrition under micro and macroelements deficiency and its underlying mechanisms are poorly understood. Detailed studies about roots will contribute to explain the Si role on metal accumulation at non-toxic concentrations and the possibilities of the accumulated metal to be transported to the shoot or not. In addition, the effect of Si addition on the accompanying metal molecules (for example, citrate) that are involved in long-distance transport in plants also needs attention (Hernandez-Apaolaza, 2014).

5. Si and alleviating other abiotic stresses

Since drought is occasionally associated with high temperatures (Epstein, 1994; Halford, 2011), Si treatment may be a substitute to mitigating the damages brought about by drought and heat stresses. In a study (Agarie et al., 1998), it was observed that electrolyte leakage

caused by high temperature in the leaves of plants treated with Si was less than those that grown without Si. These researchers attributed this effect to the involvement of Si in the thermal stability of lipids in cell membranes; although the actual mechanism of this effect is not well understood, which needs further study. There are reports that indicate the role of Si in alleviating the flooding stress in plants. The root of plants such as rice has a conductive tissue called aerenchyma, which transports oxygen from the photosynthesis process through the tissue to the root and thus resists oxygen deficiency under flood conditions (Kotula et al., 2009a, 2009b). The root of these plants has large amounts of suberin and lignin in the outer part that prevents radial oxygen from loss by forming a strong barrier (Pavlovic et al., 2013). Si through an effect on root anatomy, such as the development of casparian bands in the exodermis and endodermis, and on genes associated with the synthesis of lignin and suberin, increases the plant's resistance to flooding stress conditions (Fleck et al., 2010). On the other hand, since Fe and Mn toxicity occurs under flooding conditions, Si can, by increasing oxidation power of submerged roots, lead to the oxidation of Mn^{2+} and Fe^{2+} ions and their precipitation on the root surface and, consequently, the absorption of these ions is decreased by the plant (Okuda and Takahashi, 1961). Despite the mechanism mentioned, the precise role of Si in in alleviating flooding stress is still unknown.

It is well-known that Si can decrease stress caused by UV-B radiation in different plants (Fang et al., 2011; Yao et al., 2011). Stress of UV-B is one of the most important abiotic stresses, which could influence all aspect of the physiology and biochemistry of stressed plants. Si, through the deposition in the space immediately beneath the cuticle layer in leaves, leads to the formation of a cuticle–Si double layer in leaf blades (Currie and Perry, 2007). This Si-double layer acts like a glass layer and reduces the further transmission of UV radiation from the epidermis (Gatto et al., 1998). In addition, Si can reduce UV-B radiation stress through oxidation by enhancing antioxidative enzyme activities and thereby contributing to higher ROS consumption (Shen et al., 2010). In general, the mechanisms of Si-mediated alleviation of damage caused by enhanced UV-B stress remain unclear. For example, it is not yet known whether the protective role of Si is related to the ability of the plant to increase the formation of the double layer of Si in response to the UV-B, or only to a side effect of species-specific variations of Si stored in the plants. In addition, Si's role in the metabolic response to UV radiation stress, such as biosynthesis of low molecular weight UV absorbing compounds (*e.g.*, phenolic acid and flavonoids), is still unclear (Liang et al., 2015b). Since the increased UV-B radiation greatly affects the growth and yield of crop plants, studies on the effects of Si on UV-B-stressed plants to protect crop plants will be interesting and effective (Tripathi et al., 2014).

Si can increase the rice resistance to lodging through depositing silica in rice and increasing the thickness of the culm wall and the size of the vascular bundle (Ma et al., 2001). In addition, by neutralizing the negative effects of increased N supply on stalk stability and on lodging susceptibility of rice and wheat, Si can prevent lodging in these plants (Liang et al., 2015b).

Si is thought to lead to the detoxification of Al in plants through the formation of hydroxyaluminum silicate (Hodson and Evans, 1995). In a study (Kidd et al., 2001), the reason for increasing the resistance of maize to Al toxicity was attributed to higher exudation of Al chelating catechin and quercetin, as well as malic acid in Si-treated maize plants. Habibi (2015) showed that foliar-applied Si could effectively alleviate adverse effects of freezing on grapevine plants via maintaining membrane integrity and alleviating photoinhibition during recovery.

6. Mode of action of Si in alleviating disease stress in plants

6.1. Formation of physical barriers

The formation of physical barriers is one of the mechanisms to control diseases in plants (Guerriero et al., 2016; Kim et al., 2002; Liang

et al., 2015c). The precipitation of amorphous silica in plants acts as a mechanical barrier (Fauteux et al., 2005). The postulation of a potential physical obstruction formation depends on the type of Si deposition in foliage, particularly in the cell wall. In its incline movement via apoplast, commencing from the roots to the leaves, Si polymerization transpires in the extracellular spaces, building up on the walls of leaves' and xylem vessels' epidermal cells (Fawe et al., 2001; Kim et al., 2002). Indeed, over the years, it had been generally accepted that polymerized Si in the plant cell wall and apoplast prevents pathogen penetration (Fleck et al., 2010). The tomato resistance to *Fusarium* crown and root rot caused by *Fusarium oxysporum f.* sp *radicis-lycopersici* (C.H. Huang et al., 2011), the oil palm resistance to basal stem rot caused by *Ganoderma boninense* (Najihah et al., 2015), the coffee resistance to leaf rust caused by *Hemileia vastatrix* (Carré-Missio et al., 2014), and the belle pepper resistance to *Phytophthora* blight caused by *Phytophthora capsici* (French-Monar et al., 2010) are some examples that Si through the physical mechanisms has increased plant resistance to these diseases. In general, our knowledge regarding the mechanism of Si accumulation and its deposition in plant tissues is slightly known. Recent studies have reported that Si biochemical mechanisms compared to physical mechanisms play a more important role in increasing plant resistance to disease stress (Ratnayake et al., 2016; Song et al., 2016), which require further study in the future.

6.2. Formation of biochemical barriers

Based on previous reports (Wang et al., 2017), Si-mediated resistance of plants to disease involves not only mechanical but also biochemical defense reactions in Si- amended plants.

Studies attribute another effect of Si on the disease decline to the establishment of chemical impediments such as (i) enhanced performance of enzymes related to resistance (Fortunato et al., 2012) such as chitinases (Cruz et al., 2013), β-1,3-glucanases (Tatagiba et al., 2014), peroxidase (Mburu et al., 2016), polyphenol oxidases (PPO), phenylalanine ammonia lyase (PAL), involved in the synthesis of plant secondary antimicrobial substances, (G. Zhang et al., 2013), uperoxide dismutase, ascorbate peroxidase, glutathione reductase, catalase, lipoxygenase, and glucanase (Waewthongrak et al., 2015). Since the cell wall of fungi consists of the carbohydrates chitin and β-1,3-glucan, Si-induced chitinases and β-1,3-glucanases enzymes can hydrolyze these compounds to oligosaccharides and, as a result, the plant's defense responses is elicited (Keen and Yoshikawa, 1983). In the study performed by Cruz et al. (2013), an increase in chitinases activity occurred early in the onset of Asian soybean rust symptoms for the plants treated with Si. Peroxidase (POX) plays a role in the host defense response through the production of antimicrobial quantities of H_2O_2, in cell wall lignification or cross-linking with the cell wall proteins (Torres et al., 2006). This enzyme is also linked to the polymerization of phenolics that increases tissue lignification (Vidhyasekaran, 1988). An increase in the amount of POX transcripts in rice plants susceptible to *Pyricularia grisea* and supplied with Si was reported by Datnoff et al. (2007). Rice and cucumber plants supplied with Si and inoculated with *Bipolaris oryzae* and *Podosphaera xantii*, respectively, showed an increase in the activities of POX and chitinases (Dallagnol et al., 2011). The role of PPO in disease resistance is to oxidize phenolic compounds to quinines, which are often more toxic to plant pathogens than the original phenols. PPO also plays a significant role in lignin biosynthesis (Song et al., 2016).

In a study (Silva et al., 2010), resistance to disease in Si-treated plants increased compared to untreated plants. The researchers attributed this effect to increasing the activity of PAL caused by Si. Increase in this enzyme, in turn, leads to an accumulation of total soluble phenolic and lignin-thioglycolic acid derivatives in the leaves of plants, which are linked to low disease incidence; (ii) increased expression of genes related with plant defense mechanisms against pests and disorders, the genes encoding proline-rich protein (PRP1) (Kauss et al., 2003; Rodrigues et al., 2005), and the genes that encode chief enzymes

in the production of phenylpropanoids (*e.g.,* phenylalanine ammonia lyase, cinnamyl alcohol dehydrogenase, and chalcone synthase) (Shetty et al., 2012); (iii) augmented production of phenolic compounds (Tatagiba et al., 2014), callose, or methylaconitate (phytoalexins) and lignin (Fauteux et al., 2005); (iv) increased concentrations of antimicrobial flavonoids, polyphenol, and anthocyanin (Pozza et al., 2015; Resende et al., 2013); and (v) regulated systemic signals, such as salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) (Van Bockhaven et al., 2015). It has been known that SA (active against biotrophic and hemibiotrophic pathogens), JA, and ET (involved against necrotrophic pathogens) are involvement in plant immunity networks and regulate plant defense responses (Devadas et al., 2002; Pieterse et al., 2012).

Some of the examples of Si-enhanced biochemical resistance include the soybean resistance to target spot caused by *Corynespora cassiicola* (by inducing chitinases, β-1–3-glucanases, PAL, POX, and PPO) (Fortunato et al., 2015), the perennial ryegrass resistance to gray leaf spot caused by *Magnaporthe oryzae* (by defense-related antimicrobial phenols or lignin-associated polyphenolic compounds) (Rahman et al., 2015), the wheat resistance to blast caused by *Pyricularia grisea* (by accumulation of phenolic and lignin or ligninthioglycolic acid derivatives) (Filha et al., 2011), the *Arabidopsis* resistance to powdery mildew caused by *Erysiphe cichoracearum* (by the biosynthesis of SA, JA, and ET in leaves) (Fauteux et al., 2006), and the tomato resistance to *Ralstonia solanacearum* (by upregulating the expression of genes involved in defense and stress responses) (Ghareeb et al., 2011).

Although there are many studies that show that Si has been able to increase the plant's resistance to diseases through physical, biochemical and molecular mechanisms (Wang et al., 2017), there is still not much information about the mechanisms which by Si regulates plant– microbe interactions such as plant signaling transduction and transcriptome regulation of defense-related pathways which are necessary to further study in the future. In addition, compared to numerous reports on Si-enhanced resistance to fungal diseases, there is little information on Si and bacterial disease interactions in plants (Song et al., 2016), which needs further study.

6.3. Effect on plant mineral nutrition

It is known that plants with balanced nutrition are more resistant to diseases. As mentioned above, Si can increase the amount of essential nutrients for plant (Section 2.4.) (Pozza et al., 2015). The silicate anion works on soils as a competitive anion for the uptake sites, raising the availability of sulfate, nitrate, and phosphate in soil with elevated ability to retain these anions (Pozza et al., 2015). As an example, the P desorbed from the reactive surfaces of the soil components becomes available in the soil solution and can be incorporated into plants, thus going into metabolic pathways to reinforce the resistance of plants against diseases upon forming defense walls with the given nutrients.

As mentioned above, Si is the element which is able to enhance resistance to multiple stresses. When present excessively, Si does not pose any harm to plants (Epstein, 1994) since Si is noncorrosive and pollution-free. Si fertilizers are, therefore, high-quality fertilizers that can be used for cultivating an ecologically sound agronomy (Zhu and Gong, 2014). From an economic perspective, Si fertilizers are also relatively affordable, assuming 10–20% of the cost of other fertilizers (Feng, 2000). It is then vital to utilize Si fertilizers (both organic sources such as biochar, rice hull ash, and livestock manure composts, and inorganic ones such as wollastonite, silica gel, si-rich slag, silicic acid, sodium silicate, potassium silicate, calcium silicate, calcium silicate slag, amorphus silica, etc.) in areas lacking in silicon in order for them to experience both its economic and ecological profits. The application of Si may be one of the available pathways to improve crop growth and its production in arid or semi-arid areas (Meena et al., 2014a).

7. Conclusions and future prospects

A thorough review of available literature showed that Si could stimulate plant growth and alleviate various biotic and abiotic stresses in plants. It seems that the use of Si in agriculture will be a sustainable strategy for the alleviation of biotic and abiotic stresses in the future. In addition, the utilization of Si may result in the promotion of plant health and may play a significant role in low-input sustainable agriculture for both food and nonfood crops.

Based on the knowledge generated up to now, we suggest several future avenues of research approaches: (i) although the current understanding of how this overlooked element affects plants against pathogen infections, pest attacks, and abiotic stresses has advanced, the exact mechanism(s) by which it modulates plant physiology through the potentiation of host defense mechanisms still needs further investigation at the genomic, metabolomic, and proteomic levels (Debona et al., 2017). Further studies are required to explore the effect of Si on microbial gene expression and plant biochemistry; (ii) comparative studies of interactions between Si and plant, now lacking, would shed light on the mechanisms governing biotic and abiotic stresses; (iii) the most important aspect for further studies on Si in plant biology should be focused on making full use of the role of Si in conferring tolerance in plants against abiotic stresses, and thus their roles in environmental remediation; (iv) there is not any information on the metabolically active roles of Si in plants under abiotic and biotic stress conditions, particularly on the molecular aspects of plants and Si-mediated nutrient; (v) the role of Si in alleviating biotic as well as abiotic stresses is known. However, the potential of Si- nanoparticle (SiNP) in regulating abiotic stress and associated mechanisms have not yet been explored (Tripathi et al., 2017), which needs further study; (vi) there is a need of applied research to know the optimum Si concentration and suitable time and methods of Si application on the crop plants specially when plant is under abiotic and biotic stress conditions (Chanchal Malhotra et al., 2016); (vii) Above studies showed that Si was applied under a stress separately and in short-term but plants are exposed to multiple stress simultaneously in nature. Hence, since most of the environmental stresses such as salinity, drought, heavy metal toxicity, etc. are present at the same time in agricultural fields, the study of Si effect on increasing resistance to various stresses is suggested simultaneously; (viii) most studies have focused on the effect of Si on the Si-accumulating plants. It is suggested that this research be also carried out on less Si-accumulating plants to determine whether the mechanisms determined to alleviate stress in Si-accumulating plants can also work in plants that do not accumulate this element?; (ix) although different types of Si transporters for Si uptake have been identified from several plant species, the transporter or channel protein responsible for Si loading remains unknown. Moreover, the Si transporters identified so far are mostly from monocots. Therefore, more work is needed to compare and clarify the process of Si absorption and transport (including Si xylem loading) in different plant species/cultivars that exhibit different Si accumulation (*e.g.,* monocots versus dicots) (Zhu and Gong, 2014); (x) further study is required to clarify the details of the relationship between the impact of Si on root anatomy (such as the development of casparian bands and suberization, and lignification) and Si enhanced tolerance to environmental stresses. At the subcellular level, most Si-related research has concentrated on the cell wall. It would be interesting to investigate the distribution of Si in the cell nucleus and organelles, which may help explain the biological roles of Si in enhancing plant tolerance to environmental stress; (xi) studies related to the effects of biogenic silica and its nanoparticles on proteomics would be interesting, and results may further contribute to the understanding of mechanisms of Si-mediated impact on stressed as well as non-stressed crop plants. Since Si recycling and its effects on proteomics and genetic engineering are still lacking, it would also be interesting to investigate these aspects (Tripathi et al., 2014); and (xii) it is needed to study the compound use of Si and silica solubilizing bacteria to alleviate different abiotic and biotic stresses and compare their effects on plant as separately and dually. The underlying mechanisms of Si regulated plant–microbe interactions have not been identified so far in higher plants.

In general, developing more detailed fundamental knowledge about the interactions between plant and Si would facilitate a better understanding of alleviating abiotic and biotic stresses and perhaps would allow better predictions regarding the plant response. We anticipated that there would be a growing interest to study the mechanisms of Si-mediated stress tolerance in plants in near future. Taken together, well-designed, large-scale and long-term field trials are required to evaluate the feasibility of Si application in alleviating abiotic and biotic stresses and economic feasibility of different Si sources should also be investigated.

Acknowledgment

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