Efficient Exploration of Silicon Derived Benefits to Combat Biotic and Abiotic Stresses in Fruit Crops

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Abstract

Silicon (Si) is the most abundant element after oxygen on the earth crust surface. It plays essential role in crop production by stimulating the growth and development. Very substantial efforts have been performed to better explore Si derived benefits for horticulture crops. In the present review, molecular and physiological mechanisms explaining the observed beneficial effects plant derive from the Si supplementations, more particularly in horticultural species have been discussed. In general, horticulture crops need extensive management and higher crop protection measures compared to agronomical crops. Therefore, integrated approaches including Si supplementations will help to improve plant resilience under biotic and abiotic stresses. Application of Si to plants promotes cell walls strength and provides additional support through increased mechanical and biochemical support. Horticultural crop production is frequently subjected to the naturally occurring different biotic and abiotic stresses that can substantially reduce the absorption and translation of essential elements and ultimately decrease the crop yield. Fruit and vegetable production in Drought, salinity, high and low temperature, toxic metals and pest infection prone areas is the key to meet the world minimum nutrients demand. Here, molecular mechanism involved in the Si uptake by root and subsequent transport to areal tissues is also illustrated. However, Si uptake mechanism at molecular level poorly studied in horticulture crops. Here we described the role of Si and its transporters in mitigating abiotic stress condition in horticultural plants.

Introduction

Food security is one of the fundamental needs in present world that can never be ignored by society and police maker. The extensive increase in both human population and environmental damage due to unsustainable agriculture practices have the unlucky consequence to feed the world's population (Glick 2014). Climate change has similarly worsened the incidence and gravity of sundry abiotic stress with considerable reduction in economic yield in major cereals (Carmen and Roberto 2011). To increase the crop productivity, crops demand for fertilizer has caused rising production costs for farmers worldwide. So use of excess fertilizer in farming considered as one of the most important constraints to agriculture production in world. Various stresses instigated by complex environmental conditions have affected the production and cultivation of crops (Meena et al. 2017). Drought accounts for about 30% of the total worlds cultivable land area. Water stress has many similar features with salinity stress, but it is considered as more destructive to agricultural as compared to salt stress (Bodner et al. 2015). Now heavy metal pollution is rapidly increasing with modernization in farming system. It has major concern for ecosystem due to their prolonged toxic effect with long half-life in the environment (Etesami 2018). Nutritional imbalance by abiotic stresses may hampers the normal physiological activities of plants (Paul and Lade 2014). In future, environmental stresses may increase with climate change. The cost associated with these stresses may impact heavily on agriculture, biodiversity and the environment (Acquaah 2007). Hence now feeding the worlds growing population with shrinking cultivable land area along with environmental stresses has given vital importance in research (Etesami and Bettie 2017).

Previous soil and plant researchers suggests that use of beneficial soil microorganisms and silicon (Si) in agriculture is a sustainable strategy for alleviation of various biotic and abiotic stresses in plants (Rizwan et al. 2015; Wang et al. 2017). Earth crust comprises over 28% silicon (Si) and it is one of the most abundant element after oxygen (Spripanyakorn et al. 2009). Besides omnipresence, most of the soil types world-wide are deficient in plant available form of Si. Plant roots uptake it in the form of water-soluble silicic acid (H_4SiO_4) and follow the ascent of sap route to reach transpiration site via passive and active transport mechanism (Raven 2001). Earliest agronomist not considered Si as an essential element as N, P and K for plant growth because of non-availability of positive evidence to show Si involvement in any metabolic activities of plants (Datnoff et al. 2007). Plants are grouped into three categories based on Si uptake: low (rejecters), intermediate and high accumulators. Wide range of variation starting from less than 0.1 to as much as 10% of plant dry weight was observed in different plant species. Major Si accumulators in the plant kingdom are monocots (Ma and Takahashi 2002) whereas, dicots such as tomatoes and canola contain less than 0.1% Si in their biomass while some aquatic species have Si content over 5% (Deshmukh et al. 2015). Silica is taxonomically diverse biomineral (Knoll and Kotrc 2015) and its presence was recorded in almost all eukaryotes. Rhizarians, stramen opiles, opisthokonts, amoebae, animals, and land plants utilize silica for the formation of protective cell coverings, collagen, vertebrate bones, copepod mouthparts and other rigid structures (Henstock et al. 2015). It is necessary for coccolithophore calcification (biomineralization) processes (Durak et al. 2016).

Horticulture crops, especially fruit and vegetables, acquire a key role in the food industry because of their higher demand for human consumption. They play an important role in commerce, employment and industrialization. On the other hand they are very vulnerable to the wide range of biotic and abiotic stresses, to overcome these hassles, they requires an optimum supply of balanced micro and macro nutrients. To meet the nutrition's demand under stress condition, Si commonly recommended in package of practices as per the plant need. Si can alleviate high temperature stress (Ashraf et al. 2010), reduce the heavy metal toxicity and protect from UB-radiation (Shen et al. 2009). Recently omics based were applied in different crops to gain a genomic level perception of the mechanisms by which SI application aids horticulture crops under unfavorable environmental circumstances. The role of Si on plant health under stress analyzed under open field, protected, hydroponics and tissue culture conditions. Still, presently there are limited number of study reports are present in horticulture crops to demonstrate there are advantages of Si and its transporters resent in plants under hoarse environmental condition. Therefore, we have framed our review focusing on the role of Si application and its transporters present in horticulture plants.

Importance Of Silicon In Horticulture Crops

Several studies reported that Si as a most essential element for horticulture crops, as it can promote photosynthesis by increased chlorophyll content, regulate fruit absorption of major and minor nutrients and prevent fruit cracking, early defoliation, pest infection and other physiological disorders and control the respiration, fruit firmness and enhance resilience to horticulture crops and improved storage and transportation (Chen et al. 2016). Silicon supplemented plants produce firm fruits which resist external

infection with increased fruit storage life by depositing Si beneath the cuticle layer of fruit (Kim et al. 2002), and consequently suppress the fruit transpiration and respiration rate (Vogler and Ernst 1999). By morphological and biochemical modification, Si minimize the negative impact of various biotic and abiotic stresses in plants without compromising final crop yield.

Most of the studies shows that Si has positive effect on yield and stress management components in agronomical crop. Same result observed even in numerous studies conducted on horticulture crops also. Foliar application of silicic acid at a dose of 2 or 4 cm³ dm⁻³ doubled or tripled the yield (kumari et al. 2020) by increasing in the number of pods by approx. 14 % and seed weight per plant by 21% in relation to the control (Kalandyk et al. 2017). Whereas in potato, high Si in tuber skin delays the skin maturation. Compared to control, Si treated plants produce tubers with greater skin cell area, suberin biosynthetic genes were upregulated and skin cell wall enriched with oxidized aromatic moieties along with improved lignification and suberization (Vulavala et al. 2016). In study conducted in Poland on strawberry, it was observed that Si at concentration of 0.1% significantly improves the yield by increasing dry matter content in fruits and firmness (Mikiciuk et al. 2009). Fertilization of lettuce with Si at a dose of 2.0-2.7 dm³ ha⁻¹ on 20th DAP increased its leaf yield, relative water content, number of leaves per plant and postharvest firmness (Kleiber et al. 2015). In the experiment conducted in Poland, 0.2% Alkaline K + Si (0.51% Si) composite spray on seed lettuce resulted in a significant increase in the test weight and germination percentage (Janas and Borkowski 2009).

Effect of fertilization with marne calcite using Herbagreen mineral fertilized was examined in Bulgaria in years 2011-12 to know the effect of Herbagreen (as a source of Si) on seed production of melons. They found significant result with a fertilizer dose of 0.04% at an interval of 14 days for three times had a positive response for seed production by improving fruits per plant without dropping seed quality (Velkov et al. 2014). In study conducted in India on onion, the higher yield were obtained with treatment 200kg ha⁻¹ Si in the form of ash from bagasse (Nazirkar et al. 2017). Foliar application of calcium silicate in combination with peat substrate increased the onion seedling weight up-to 37% in studies conducted in Poland (Gorecki et al. 2009). then investigation conducted in north-eastern China in the year 2005-06, in which Si was directly applied to the rhizosphere of cucumber and observed 13.7% increase in average (Liang et al. 2015). The increase in cucumber yield was associated with the increase in fruit number rather than weight (Jarosz et al. 2013).

Where as in fruits crops like baanana is very efficient in accumulation of Si, with foliar concentration may reach up to 2% of dry weight so, it considered as Si accumulator (Henriet et al. 2006) and it contains opaline phytoliths mainly in vascular bundles (Prychid et al. 2004). Silicon improves water transmission, nutritional status, physical status, fruit yield and maturity, and resistance against biotic leaf chlorophyll content, metabolism and abiotic stresses (Ibrahim and Al-Wasfy 2014). When silicate fertilizer applied for the grapevine, it significantly improved the TSS, fruit firmness, total soluble acids to titrable acids ratio, berry size, berry weight, berry size, and cluster weight but the negative impact also observed on fruit respiration intensity, decay incidence and weight loss (Zang et al. 2007). When passion fruits seedlings were treated with calcium silicate increased the final dry matter of shoot and fruit with enlarged stem

diameter (Prado and Natale 2005). After the application of Si at 0.05-0.1% in zaghloul date palms increased total chlorophyll content, leaf area, bunch weight, and final yield (El-Kareem et al. 2014). In a study of post-harvest application of potassium silicate as a Si, supplier enhanced the fruit quality and reduced the ethylene evolution with increasing catalyze enzymatic activities in avocado fruit crops (Kaluwa et al. 2010). Several fruit crops are treated with different concentrations and formulation to know both positive and negative effects on fruit quality parameters, including final economic yield.

Molecular mechanism involved in Si uptake and Transport

Plants have numerous transporter protein biomolecules which facilitate the uptake and accumulation of different metal ions and other mineral nutrition's from soil via aquaglyceroporins, ATP binding (ABC) cassette transporter, phosphate and nitrogen transporters (Bouain et al. 2014). These transporters helps to regulate the accumulation of unwanted elements beyond toxic level, as they play prominent role among all the crop plants.

Silicon transporters initially identified in diatoms and extended family of Si transporters reported in some non-silicified living organisms. Based on the phylogenetic study of *SITs* and *Lsi2*, they developed parallel by environmental selective pressure. *SIT* structure evolved multiple times via duplication and fusion of 5-transmembrane-domain *SIT-Ls*. Later researchers identified the *Lsi2* family similar to primary Si transporters, and they broadly distributed in siliceous and non-siliceous eukaryotes. These transporters involved in bio-silicification. NPA motifs present in the aquaporins regulate the exclusion of H⁺ and various isoforms of nodulin26-like intrinsic proteins (*NIPs*) control the movement of water, boric acid, metabolites, and Si through different transporters (Wu and Beitz 2007). Identification of two *Lsi* Si transporters genes using rice mutants by Ma et al (2007) are the milestone for new research works on importance of Si and its transporters and impact of Si on aquaporins. *Lsi1* (OsNIP2;1) is the first Si transport protein identified in rice plant (Ma et al. 2006) which is bidirectional transporter although its activity depends on the plant species but it mainly act as a Si influx transporter. Whereas *Lsi2* is an active Si effluxer which enable the flux of Si across the vascular system. The *Lis2* proteins are H⁺ antiporters and similar to arsenic transporters (ArsB) of prokaryotes (Ma et al. 2007). Structurally *Lsi1* has six transmembrane domains and two half helix harboring highly conserved Asn-Pro-Ala (NPA) motifs. The NIP's transports neutral solutes like glycerol, lactic acid, ammonia, boric acid, arsenite, selenite, silicic acid, and water also (Mitani et al. 2009 and Zhao et al. 2010). All *Lsi1* present in plant species belongs to the NIP III group, which has a aromatic arginine (ar/R) selectivity filter (SF) comprising Gly (G), Ser (S), Gly (G), and Arg (R) popularly known as GSGR SF. Although *Lsi1* acts as a bidirectional passive channel (Mitani et al. 2011).

Tomato plants, uptake of Si in the roots is mediated by *Lsi1* (influx transporter) and *Lsi2* (efflux transporter). Sun H (2019) isolated and functionally characterized a *SILsi1* expression in tomato, *SILsi1* seems to be constitutively expressed in the root system but tomato plants accumulates very low Si (Deshmukh et al. 2015) as compared to cucumber (Mitani and Ma 2005). As the *SILsi1* expression increased, the Ge (an analogue of Si) level increased but there is no significant variation observed in Si

concentration in the root cells sap (Sun H 2019). Deshmukh et al (2015) proposed that, a precise distance of 108 amino acids required between the asparagine-proline-alanine (NPA) must require for Si permeability, while *SILsi1* present in tomato plants has 109 amino acids between NPA domains. In potato, *Lsi1* has expressivity at both roots and leaves, and its expression increased at slower rate after Si supply; while expression of *Lsi2* decreased in tuber flush (Vulavala et al. 2016). Whereas in cucumber, the *Lsi2* elevated expression observed in root system after 6 h of Si treatment (Sun et al. 2018).

Based on the past experiments, the expression of Si transport genes depends on the plant species, external stimulants and treatment periods although the exact mechanism in number of horticulture crops be remain to be investigated in future.

Importance Of Silicon Under Stress Condition

In recent years, the effect of Si on plants growth and involvement in biotic (blast, rust, downy mildew, powdery mildew, leaf spot, canker, leafhoppers, stem borer) and abiotic (metal toxicity, nutrient imbalance, lodging, drought, radiation, temperature, freezing, and wind) stress mitigating activities observed in a wide range of plant species (Ma et al. 2008). The concentration of Si varies within the genotypes belongs to the same species and even it can vary based on environmental conditions and other external stress conditions (Currie and Perry 2007). Silicon mostly deposited below the cuticle and epidermal layer of leaf and in the vascular system to strengthen cell wall and helps plants fend off biotic and abiotic stress (Debona et al. 2017; Etesami and Jeong 2018). It also gives better strength to control the transpiration rate and thus a greater resistance to both internal and external stress conditions (Kim et al. 2002). Silicon is known to participate in many cellular activities which can enhance the plant resilience under stress condition such as, it improves the acclimatization potential of the plants by cell wall lignin and hemicellulose deposition (Camargo et al. 2007), tolerance to UV stress and increased production of chlorophyll a and b (Yao et al. 2010).

Even increased phytohormones activity were observed in stressed plants after Si application to acclimatize to varying environmental condition (Kim et al., 2014). Number of studies reported that, Si decreases endogenous ethylene (Yin et al., 2016) and JA (Hamayun et al. (2010) concentration and enhance the GA and SA level, whereas it reduces the ABA and proline level and helps plants to survive under stress condition (Wang et al. 2001). Liu and Xu (2007) identified the role of Si regulating polyamines (Pas) activities. PAs involved in different defense reactions of plants against numerous stress factors (Gupta et al. 2014) by increased s putrescine, spermidine, and spermine accumulation (Wang et al. 2015b). Increased production of PAs may improve the antioxidant ability and modifying osmotic potential in stressed plant cells (Alcázar et al. 2011) and block inward and outward Na⁺ and K⁺ currents through non-selective cationic channels thereby control the Na⁺ concentration in intercellular space (Zhao et al. 2007).

Under stress condition, Si alleviate oxidative damage in plants by increasing the activity of key enzymes APX, CAT, SOD, POD, GR and GSH concentration (Kim et al. 2017) and prevent the membrane damage

causes by the formation of malondialdehyde (MDA) (Zhu and Gong 2014). When Si applied to the plants rhizosphere zone, it increases the soil pH that ultimately enhances the soil phosphorus availability (Owino-Gerroh and Gascho, 2005; Eneji et al. 2008) and interact with iron and manganese metal ions (Ma and Takahashi 1990), and decreased metal uptake (Al, Cd, Fe, and Mn) to diminution the heavy metal stress on plants (Liang et al. 2005). Water and mineral uptake and transportation mainly controlled by the aquaporins present in the cell membrane (Maurel et al. 2015) and these aquaporins comes under membrane intrinsic proteins (MIP) family and further classified into nodulin26-like intrinsic proteins (NIP), plasma membrane intrinsic proteins (PIP), uncharacterized intrinsic proteins (XIP), tonoplast intrinsic proteins (TIP), small basic intrinsic proteins (SIP), and hybrid intrinsic proteins (HIP) based on the phylogenetic distribution, subcellular localization, substrate selection, length of the sequence, and function (Bienert and Chaumont et al. 2011). Apart from water uptake, these aquaporins involved in the mineral transportation. Numerous previous studies demonstrated the role of aquaporins in the regulation of solute transports such as ammonia, hydrogen peroxide, silica acid and lactic acid (Wu and Beitz 2007). The substrate selectivity of an aquaporins is primarily depends on the NPA motifs for the exclusion of H⁺ and a filter consisting of an aromatic/arginine region in the pore area (Ma et al. 2006). As compared to other NIP subfamily isoforms, *NIP1* is highly permeable to water, whereas *NIP2* helps transportation of metalloids and Si, and *NIP3* regulate boric acid transportation (Wu and Beitz 2007). Absorption of Si from the soil by the plant depends on the *Lsi1* and *Lsi2* gene expression level, cellular localization, and polarity in the plant cell. *Lsi1* activity extensively observed in roots, within a root, the *Lsi1* expression is very low in root tip region and in root hairs and downregulated by ABA and dehydration stress (Ma and Yamaji 2007). Whereas *Lsi2* localized on distal and proximal sides of the epidermis (Maa et al. 2007). Therefore, *Lsi1* help to transport Si into the exodermis cells and later it released into the apoplast of a spoke-like structure across the aerenchyma by *Lsi2*.

Fauteux et al. (2005) unveils that Si interact with several key components at different levels in plant signaling structures, thereby causing resistance in plants. Despite the above findings, still very less is known about Si transporters in horticulture crops. All findings concentrated only on confirmation of presence of *Lsi1* and *Lsi2* in horticulture crops. Except tomato, cucumber, strawberry and apple, very limited amount of works were done to identify special Si transporters present in horticulture crops. The list of different Si transporters identified in horticulture crops are studied by the abovementioned researchers, are listed in Table 1. Further study is still required to identify the Si transporters present in horticulture crops and recognize the role of these transporters on root morphology and Si- enhanced tolerance to biotic and abiotic stresses simultaneously (Table 2).

Role of silicon in water stress condition

Drought is one of the key sources of environmental stress which severely affects the plant growth and development at any stage from germination to physiological maturity (Bodner et al. 2015). Water deficit during plant growth period adversely affects the normal physiological activities like photosynthesis, essential nutrient transport and production of excessive reactive oxygen species (ROS) leads to cell membrane damage (Reddy et al. 2005) and finally restrict biomass production (Noman et al. 2015).

Higher plants have some strategies to minimize the drought effect through osmotic change (Osakabe et al. 2014) by soluble sugars and amino acids such as alanine and glutamic acid (Sonobe et al. 2010), increasing root volume (Hong-Bo et al. 2008), reduction in leaf area and CO₂ assimilation by limiting stomata opening (Santos et al. 2006), increased chlorophyll a and b content (Pei et al. 2010) and accumulate ABA in different organs of the cell to minimize the water loss.

Always free proline accumulates in the cytosol of a cell during stress condition to protect the protein and cell structural integrity by osmotic regulation as calcium during stress condition (kaya et al. 2006). K⁺ maintains the homeostasis in a cell under water stress condition and Si enhances the accumulation of K⁺ in the cell by stimulating H⁺ATPase activity (Liag 1999) but negatively regulates the Na uptake (Tuna et al. 2008). Silicon application during drought condition improves the seed germination in tomato (Hameed et al. 2013) and biological yield in maize (Zargar and Agnihotri 2013), wheat (Ahmed et al. 2015), sorghum (Ahmed et al. 2011b), rice (Nolla et al. 2012), soybean (Hamayun et al. 2010). Some researchers reported that Si application minimizes the effect of drought without compromising the yield (Ali et al. 2013b). It increases the amylose, phenolic components, total carbohydrates, phytin during drought conditions in growing plants (Emam et al. 2014).

Root system helps plant to absorb essential nutrients and water from soil, but under water stress conditions, reduced root growth and physiological activities observed (Gupta and Huang 2014). An increased root surface area is required to improve the water uptake ability to minimize the impact of these water stress conditions (Barber 1995); although Si did not trigger root progress under drought condition (Sonobe et al. 2010). It has been reported that Si improve the root system in all dimension and enhances the shoot biomass of stressed plants (Hameed et al. 2013).

Beside the prominent role of K transporters in modifying drought stress in higher plants, Si has also shown to minimize the water stress responses in many crop plants (Ma et al. 2015). Numerous studies have reported enhanced drought tolerance in horticultural plants with Si supplementation. For instance, foliar application of Si increased Chlorophyll a and b ratio in chestnut (*Castanea spp*) leaves (Zhang et al. 2013). Similarly, Si application enhanced the transpiration rate and photosynthetic rate in soybean (Shen et al. 2010b) and pepper (Pereira et al. 2013) under drought conditions. It substantially increases water potential in treated plant leaves (Ali et al. 2013). For example, Si application increased water content in cucumber (Ma et al. 2004b), chickpea (Fawaz et al. 2013) and sunflower (Gunes et al. 2008b) and *Poa pratensis* L. (Amin et al. 2014). Si uptake significantly increased in tomato (Marodin et al. 2014), citrus (Matichenkov et al. 1999), forage grass (De Melo 2010) and cucumber (Adatia 1986) plants when Si applied externally.

In tomato plants, Si accumulate much less as compared to the monocotyledons such as rice and wheat (Nikolic et al. 2007). Muneer and Jeong (2015) analyzed the root proteomics in tomato plants under salt stress condition and found that, around, 17% stress responsive proteins, 11% to plant hormones, 11% to cellular biosynthesis, and transcriptional regulation, RNA binding, and secondary metabolisms related proteins were seen upregulated when Si applied to these stressed plants (Chakrabarti and Mukherji

2003). Zhang (2018) reveals that Si treated plants shows increased water stress tolerance by enhancing root hydraulic conductivity with decreased oxidative damage in root cells. Whereas, Si improves the photosynthesis and antioxidant parameters under drought stress in soybean (Hamayun et al. 2010) and tomato (Ullah et al. 2016) seedlings by improving root hydraulic conductance and water uptake (Cao et al. 2017). In another study by Soudararajan et al. (2017) reveals that Si improves the carbon fixing cycle such as Calvin cycle, tricarboxylic cycle (TCA) cycle, and pentose phosphate cycle in salt stressed *Rosa hybrid* 'Rock fire' and ensure photo-protection and physiological development. Increased expression of β -glucosidases, β -galactosidases, and glucose-1-phosphate adenylyltransferase large subunit, acetyl-CoA carboxylase, and Glycerol-3-phosphate dehydrogenase (GPDH) (NAD^+), observed after Si treatment and this leads to improvement in starch and sucrose metabolism, fatty acid biosynthesis and maintain the NADH yield.

During water limiting condition, increase in water absorption coincided with the increase in plasma membrane intrinsic protein (PIP) aquaporins expression (Liu et al. 2015). Silicon transport also mediated by cell aquaporins, especially members of the Nod26-like major intrinsic protein III subgroup, but they shows varying responses to Si application in different crops. For example, down regulated in soybean (Deshmukh et al. 2013) upregulated in cucumber after Si application (Ma and Yamaji 2015). Si enhances the shaker-like potassium channels (SKOR) activities and increases the potassium translocation into the xylem which result in increased hydraulic conductivity. It upregulate the expression of *OsRDGP1*, *OsRAB16b*, *OsCMO* (Khattab et al. 2014) and *SbPIP* (Liu et al. 2014) genes in drought stressed plants. The homolog of both *OsLsi1* and *OsLsi2* downregulated upon Si supply (Ma et al. 2006) in response to drought stress (Yamaji and Ma 2007). In barley, the expression of *HvLsi1* gene was unaffected by external Si application (Chiba et al. 2009), while *HvLsi2* expression was downregulated (Mitani et al. 2009). *HvZEP1*, plastid related pathway gene expression strongly increased with increasing Si concentration under stress condition, while expression of *HvNCED1* and *HvNCED2* increased in dose-dependent manner (Kim et al. 2013). Several studies shows that Si directly or indirectly involve in physiological and biochemical activities during water stress condition. However, the mechanism of Si-mediated water stress tolerance in horticulture crops still need to be explored

Role of silicon in salt stress condition

Salinity stress also known as osmotic stress and ionic stress and it is one of the major constraint for agriculture including horticulture crops under surface irrigation system, thereby instigating damage and inhibition of crop growth and development. So now a days, salinity was considered as a one of major threat to worldwide crop production. Salt affected land increasing drastically with an increase in intensified cropping systems. Nearly 7% of the earth land and 20% of the cultivable land under salinity stress condition (Hu and Schmidhalter 2002). Unscientific irrigation practices, excess fertilizer use, low precipitation, industrial pollution and high soil water evaporation are the various reasons that can be associated with the emergence of salinity-affected land (Ouhibi et al. 2014). When EC level at root zone exceeds the 4 dS m^{-1} at 25°C with exchangeable sodium of 15%, the land is said to be saline affected land and considered as unfit for farming especially for horticulture crops (Munns et al. 2005). The

presence of high salinity by deposition of excess salt around the root zone of soil causes osmotic, oxidative, and ionic stress on growing plants. Thus, breeding strategy to develop salinity tolerant horticulture crops are major challenge so as to surpass the reducing quality food production at surplus quantity. Where drainage system is not proper, salinity stress occurs due to excess accumulation of Na^+ and Cl^- ions in turn affecting the K^+/Na^+ ratio (Golldack et al. 2011). During salinity stress, the reduction in leaf area, stomatal conductance, chlorophyll content and function, stomatal conductance, decreased photosystem II efficiency (Netondo 2004). Along with osmotic stress and other nutrients deficiencies lead to the increased production of ROS (Hong et al. 2000).

Several attempts are made for effective salinity management, such as by changing farming system, introducing salt tolerant crops so as to include perennials in rotation with annual crops, in mixed farming (intercropping, alley cropping, etc.), or precision plantings (Munns 2002), . But the implementation is restricted by numerous factors such as non-availability of salt tolerant cultivars, good quality irrigation water, and cost. Other than agronomic methods, salt-tolerant varieties development through transgenic method, application of growth promoting hormones and using the micro irrigation techniques are the alternatives are present to minimize the salinity impact on total world production. Nevertheless little information present in public domain regarding the mineral status and plant dynamics towards tolerance to salinity stress (Manchanda et al. 2008). Therefore, a major challenge present in front of researchers to develop efficient, affordable, and easily adaptable mechanism to counter the salinity stress on plants.

The importance of Si under salt stress conditions studied in aloe (Garg and Bhandari, 2016), sugarcane (Blumwald 2000), roses (Soundararajan 2017), and zinnia (Manivannan et al. 2015) at the anatomical, physiological, biochemical and molecular level. Si minimizes the certain level of salt stress in plants by maintaining the normal photosynthesis rate, detoxification of radicles produced during metabolic activities, and proper nutrient management. Silicon reduces the Ca^{2+} ion concentration intracellular level by reducing the influx and increasing the efflux of Ca^{2+} to minimize the salt stress on plant cells (Rios et al. 2017). Na^+ enters the plant through a non-selective cation channels and Si manages the Na^+/K^+ channels by selective ion uptake and it minimizes the Na^+ influx but elevates the K^+ accumulation in the root system (Blumwald 2000).

Si mediated alleviation of salinity stress is associated with, decrease in electrolyte leakage and significant increase in activities of antioxidants (Zhu et al. 2004). Likewise, the increase in activity of catalase (CAT), superoxide dismutase (SOD), was reported in bitter melon and spinach under salinity (Eraslan et al. 2008; Wang et al. 2010). The relationship between amount of different antioxidants in different plant tissues and plant growth under salinity stress condition has been studied for cucumber (Khoshgoftarmanesh et al. 2014) tomato (Yeo et al. 1999) and soybean (Shen et al. 2010a). However, these studies were concentrated on morphological and physiological responses of plants against salinity and very little have been shed on the proteome response under Si supplementation. Plants response to salt stress through a proteome approach has been studied on canola (Bandeagha et al. 2011), soybean (Sobhanian et al. 2010), peanut (Jain et al. 2006), tomato (Chen et al. 2009), potato (Aghaei et al. 2008) and cucumber (Du et al. 2010).

Si improves the photosynthesis rate (20%), water use efficiency (17%), turgor pressure (42%) and the ratio of plant dry matter to drought ratio (16%) in tomato (Romero-Aranda et al. 2006). Similar result found in sweet pepper (Tantawy et al. 2015) and squash (Siddiqui et al. 2014) in mitigating salinity induced hazardous effect. It has also been concluded that application of Si combination with *Melia azadirchta* phytoextract can effectively alleviate salinity stress in pea (Tantawy et al. 2015).

Plant transporters play a vital role in regulating mineral uptake and deposition in different tissues from growth medium. PIP regulate the water conductance under salinity stress condition (Liu et al. 2015) and is responsible for Si influx into the root system even under moderate salinity stress condition (Ma et al. 2006). Salt stress responsive (*LeDREB-1*, *LeDREB-2* and *LeDREB-3*), antioxidants (*LeAPX*, *LeSOD* and *LeCAT*) and Si transport (*leLsi-1*, *leLsi-2* and *leLsi-3*) genes are activated after application of Si as a fertilizer to tomato plants (Muneer and Jeong 2015).

The mechanism of Si mediated salinity tolerance in horticulture crops is still not fully understand at physiological level. Some researchers assumes that Si alleviate salt- induced osmotic stress by enhancing root water uptake and upregulation of aquaporin specific gene expression (Zhu et al. 2015), increasing the activity of antioxidant enzymes (Manivannan et al. 2016) and polyamines (Yin et al. 2019).

Silicon In Micronutrient Homeostasis And Heavy Metal Stress.

Farming lands are started polluting by industrial waste, heavy metals, chemical inorganic fertilizer and pesticides. That leads to convert fertile land into barren land. Most of the pollutants contains heavy metals and they are non-biodegradable (Alharbi et al. 2018; Burakova et al. 2018). Metal toxicity has a greater negative impact and relevance not only to plant kingdom but also they affects the surrounding ecosystem, in which plant forms a major integral component (Liang et al. 2007). Heavy metals affects the normal physiological activities by binding with protein sulphhydryl groups, distressing the other metal transporters activities, and disturbing cellular homeostasis (Hossain et al. 2012).

Whereas some heavy metals like Zn, Cu, and Ni are essential micronutrients and they serve as cofactor in various enzymatic activities when they are present in trace. Interestingly, plants are natural non-selective bio-accumulators and they uptake heavy metals with other nutrition's (Ozturk et al. 2017). While Cd and Ld are supplied to the plants through pesticides as ingredients but they do not have any beneficial role. But they become more toxic when applied in excess amount with pesticides (Ali et al., 2017b). Heavy metal stress fuels superoxide radicals (O_2^-), hydroxyl radical ($\cdot OH$), hydrogen peroxide (H_2O_2) and singlet oxygen (1O_2) like ROS production, which have strong harmful influence on photosynthesis, respiration, plasma membrane and fatty acids integrity (Stohs and Bagchi 1995). Plants have enzymatic antioxidants to protect the plant cell by ROS. Ascopate peroxide (APX), catalase (CAT), peroxidase (POD), superoxide dismutase (SOD), ascorbate peroxidase (APX) and glutathione reductase (GR), as well as non-enzymatic constituents such as ascorbic acid (AsA), carotenoid (Car) and glutathione (GSH) are more prominent antioxidants which regulates the ROS level in plant cell (Tiryakioglu et al. 2006). The rate of

heavy metal absorption, transportation and accumulation in various organs varies from species to species. Excess accumulation of heavy metals may shows toxic symptoms like stunted growth, chlorosis, root browning, decline and death (Ozturk et al. 2015).

At cellular level, heavy metals severely damages the intra- and inter- DNA and protein molecules cross linkage, DNA bases deletion, modification, rearrangements, strand breakage and depurination. Heavy metals produces promutagenic adduct 8-OxoG (7,8-dihydro8-oxoguanine) that miss pairs with adenine and leads to transversion of C to T (Cunningham 1997; Kasprzak 1995). Cation diffusion facilitator (CDF) and macrophage protein family (Nramp) family play important role in homeostasis but also draw stratagem for heavy metal tolerance (Williams et al. 2000). ZIP gene family transporters transport Cd, Fe, Mn and Zn, so regulation of ZIP genes expression may control the accumulation of these metals (Guerinot 2000). Usually, A ZIP family proteins has eight transmembrane domains and all domains has C and N terminus and they are exposed to apoplast. *ZIP1* and *ZIP3* expression mainly found in roots and their activities reach maximum level when plants under Zn stress condition (Manara 2012). *NRAMP* metals transporters present in plasma membrane and tonoplast membrane regulates Cd and Fe transportation (Thomine et al. 2000). The Cu transporters (CTR) also located in the cell membrane and they express when plants need Cu (Puig and Thiele 2002). The smooth metal transporters like HMAs and CPx-type ATPase act as efflux pumps as they remove excess metal ions deposited in cells and same time they involved in uploading Cd and Zn in xylem from the surrounding tissues. Overexpression of *AtHMA4* increases Cd and Zn stress tolerance in plants (Verret et al. 2004). Another family of transporters MATE involved in multidrug and poisonous compounds transportation from the cell (Schaaf et al. 2004).

In an attempt to detoxify the cells, metal ions are transported into the vacuoles present in the cells. Where they are stored as complex compounds in neutral activities condition. The tonoplasts present in the cell contains number of highly specific transporters which regulate the metals transportation. While, ABC family transporters chelate and sequestering the excess heavy metals present in the cells and then transport to vacuoles (Ortiz et al. 1995). CDF and MTP transport family transport heavy metals to endoplasmic reticulum or apoplast and also they act as sensors for metals present (Maser et al. 2001). MHX and CAX members of CaCA family are involved in homeostasis of metals. They antiport the Mg^{2+} and Zn^{2+}/H^{+} from xylem cells and also involved in Cadmium transport (Manara 2012). Other than these transport family proteins, various other biomolecules and structural component present in the cells regulate the homeostasis of heavy metals.

In vitro study of Si-mediated metal, precipitation provides the sufficient information, in which Si decrease the availability of toxic metals to plants (Fu et al. 2012) by precipitation (Liang et al. 2007). In some circumstances, Si reduces the bioavailability of metals to plants (Liang et al. 2005). In some circumstances, Si induces use of stored immobilized metals as a source of plant nutrients when deficiency condition occurred by Si induced reversible processes (Garcia-Mina et al. 2013). When comes to soil, Si increases the pH of the rhizosphere region of the plants by forming silicate precipitates that decrease the heavy metal phyto-availability (Cocker et al. 1998). Higher Si accumulators like rice, external Si application increases plant growth even under multi metal contaminated acidic soil (Gu et al. 2011).

Exogenous Si reduces the lipid peroxidation and fatty acid desaturation in plants and improves the plant physiological activities under heavy metal stress (Nagajyoti et al. 2010). Most widely accepted Si mediated heavy metal detoxification mechanism are metal immobilization in soil before absorption from plant roots and stimulation of enzymatic and non-enzymatic antioxidants, co-precipitation of metals, metal ion chelation, and compartmentation. The possible mechanism for reducing heavy metals can be explained that Si strongly form complexes with cell wall molecules and alter the structural integrity which leads to the blockage of the apoplastic transport and directly or indirectly restricts the entry of these heavy metals (Meharg and Meharg 2015). It was widely accepted that, Si has beneficial to plant growth and development by mitigating multifarious biotic and abiotic stresses including heavy metal stress (figure 1.). Below, we discussed in detail about the mechanism of Si-induced mitigation of heavy metal toxicity in plants.

Arsenic (As)

Arsenic (As) being considered as non-essential element and it may cause severe damage to soil health, plant growth and reproduction and ultimately affect human health after consumption of contaminated plant produce (Zhao et al. 2010). Due to excess accumulation of As in soil reduces the plants nutrient absorption ability which resulting in impaired plant physiological activities (Sanglard et al. 2016). K being analogous to As and compete for some carriers present in the plasma lemma by providing same ionic strength. This result in reduction in As influx (Hasanuzzaman et al. 2015). As is a semi-metallic element and form the organic and inorganic arsenicals by reacting with other elements. In these, inorganic As compounds are more lethal to plants as compared to the others. Inorganic As species largely occurs in arsenite $\text{Fe}(\text{As}^{\text{III}})$ in a reduced form and arsenate (As^{V}) an oxidized form (Finnegan et al. 2012). Nodulin 26-like intrinsic protein (NIP) is a major entry point for arsenite, whereas arsenate is taken by plants roots from rhizosphere via phosphate transporters (Wu et al. 2011). It is well known that As accumulation leads to oxidative stress by generating reactive oxygen species (ROS). To combat oxidative stress, plants produces enzymatic and non-enzymatic biomolecules. However, response of all the detoxification machineries influenced by As bio-availability, toxicity and mobility and presence of other ligands (Violante et al. 2010).

Silicon has potential to abate As toxicity and improves photosynthesis, carbohydrate accumulation. In some tomato cultivars, Si application significantly increases seed germination with inhibiting As accumulation in plants (Marmioli et al. 2014). Under As stress condition, various transporters helps the movement of Si from root epidermis into root steel, and then shoot via xylem sap. Furthermore, study conducted on *Lsi1* and *Lsi2* transporter genes under arsenite treatment reveals that these Si transporters effectively serve as major entry path for arsenite transport. Upregulation of *OsLsi1*, *OsLsi2* and *OsLsi6* recorded in As (III) + Si as compared to As (III) alone treated plants, indicating that the concentration of *OsLsi* family genes expression might not be sufficient to accrue As in the presence of Si (Sanglard et al. 2016). Increased activity of GPX and GST observed under As stress due to activation of GSH-dependent peroxide scavenging mechanism, which helps in the reduction of oxidative damage, and

prevent membrane damage with the help of Si. Till now Si- dependent amelioration of As toxicity from germination not studied in horticulture crops in detail.

Aluminum (Al)

Aluminum toxicity is the one of the limiting factor for crop growth in acidic soil (Von Uexkull and Mutert, 1995). Al normally form insoluble oxides and complex aluminosilicates (AS) at pH value higher than 5.0, whereas at lower pH (acidic condition) Al is solubilized to the monomeric form (Al^{+3}) which becomes available to plants, thereby affecting a wide range of physiological processes with a consequent reduction in plant growth (Singh et al. 2017). Al^{+3} affects the cell wall functions (Horst et al. 2010), nutrient homeostasis (Delhaize and Ryan, 1995), plasma membrane properties (Yamamoto et al. 2001) and signal transduction pathways (Goodwin and Sutter 2009). To cope with the deleterious effects of Al, plants adopted Al exclusion and /or internal tolerance mechanisms (Poschenrieder et al. 2008). Several membrane transporter genes are involved in regulating efflux of organic acid anions, including membrane of the ALMT aluminum-activated malate and MATE families (Ryan et al. 2011).

Si has been used in horticulture crops especially in vegetable crops to alleviate the Al toxic effect by forming hydroxylaluminium silicate (Hodson and Evans 1995). For the first time in horticulture crops, Baylis et al. (1994) showed the alleviation of Al toxicity by Si recorded in soybean crops. Later similar result was observed in barley (Hammond et al. 1995), wheat (Zsoldos et al. 2003), rice (Singh et al. 2011), and some coniferous crops (Hodson and Sangster 1999). Cocker et al. (1998a) suggested that Si can regulate the Al toxicity by three ways: (i) by increasing the pH of the solution, (ii) reduce the Al availability to plants by forming complexes of hydroxylaluminosilicates (HAS) in the external solution and (iii) improves the Al detoxification mechanism in the plants. Bityutskii et al. (2017) proved that, Si down regulate the Al toxicity under acidic conditions in cucumber. Recently Dorneles et al. (2019) highlighted that Si remove the physiological damage caused by Al in the root system in potato via elevating activity of antioxidant enzymes. When maize seeds treated with Si just before sowing leads to higher exudation of Al chelating catechin and quercetin as well as malic acid observed (Kidd et al. 2001). It has been reported that Al availability to plants in the presence of Si can be minimized by forming hydroxylaluminosilicate (HAS) like Al-Si complexes at root zone (Hodson et al. 1994).

Nickel (Ni)

In recent years, Nickel (Ni) also considered as an essential element at a low concentration for normal physiological activities of the plant (Eskew et al. 1984). But when concentration crossed $0.05-5 \mu g g^{-1}$ dry weight by plants (Rizwan et al. 2017), it may become severely toxic to plants and reduce the normal growth and yield (Matraszek and Hawrylak-Nowak, 2010). It act as cofactor for several enzymes which are involved in glyoxalases, hydrogenase, methyl-CoM reductase, urease, superoxide dismutase and peptide deformylases. It also has crucial rule in hydrogen metabolism, ureolysis, methane biogenesis and acidogenesis as well as regulate the stress tolerance by maintain cellular redox potential (Vatansever et al. 2017). Fluctuation of net photosynthetic rate, stomatal conductance, carbon dioxide concentration, and

transpiration rate in plant under high Ni content is due to the interference in normal stomatal activities (Chen et al. 2009; Yusuf et al. 2011). The increase of Ni to toxic levels is due to excess fertilizer application, sewage incineration, smelting, mining and burning of fossil fuel and other electronic compounds (Aziz et al. 2015; Rizwan et al. 2018). Available form of Ni compounds could be transported by Fe^{2+} , Mg^{2+} , Cu^{2+} and Zn^{2+} transporters by forming chelates such as citric acid, histidine and nicotianamine. Even proteins such as metallothionein, metallochaperones and permeases involved in Ni transportation (Vatansever et al. 2017). Plants grown in soil contain excess Ni produces symptoms like necrosis, chlorosis, and nutrients deficiency (Yadav 2010). Ni at high concentration stimulate the excess production of ROS (Turan et al. 2018) and cytotoxic α,β -dicarbonyl aldehyde compounds called 'methylglyoxals' (MG) (Kaur et al. 2014), disturb the normal activities of photosynthesis reaction centers (P680 for PSII, and P700 for PSI) and reduces the electron transport (Sirhindi et al. 2016). An increase in uptake of Ni leads to reduced root and shoot growth, decrease in K, Ca, and Mg content in different tissues of plants. Elsayed F. Abd Allah (2019) reveals that excess accumulation of Ni in mustard plants significantly reduces plant growth (34.46%), total chlorophyll content (57.63%), LRWC (24.34%), and enhances the H_2O_2 (3.23 fold), MDA (2.07 fold) and methylglyoxal (MG by 3.23%) content in plant cells.

One of the suitable premium approaches is the use of Si in alleviation of Ni induced stress. Several researchers suggest that Si reduces the endogenous Ni level in plants by creating reducing environment. When Ni stressed mustard plants were treated with Si at 10^{-5} concentration, drastically ameliorated the negative effect of Ni in plants. Si improves the dry matter content in tomato plants even by Si-Ni precipitation in root zone (Ashraf et al. 2013). Foliar application of Si reduces the electrolyte leakage and proline contents in periwinkle (*Catharanthus roseus* L.) with restoring normal growth process and enhanced the alkaloid content (Indrees et al. 2013). Si plays a prominent role in ROS metabolism and MG detoxification under Ni stress by activating numerous defence systems mainly, AsA-GSH cycle in plants. Increased phenols and flavonoids production and accumulation was observed to protect plants from oxidative damage as marked by decreased MDA content has been reported in Brassica spp, tomato (Marmiroli et al. 2017) and gladiolus (Zaheer et al. 2017).

Lead (Pb):

Among the listed soil contains heavy metals, lead (Pb) is one of the most toxic pollutants of the environment and it has lethal effects on both plants and animal health (Ashraf et al., 2015). The toxicity effect of Pb depends on the amount of Pb uptake by plant and soil type (Reddy et al. 2005). Once entered into the plant cells, Pb changes hormonal activities, cell membrane integrity, inhibiting sulfhydryl group containing enzymes activity and reduce the water and mineral content in the cells. At physiological level, it adversely affect the photosynthesis pathways, blocks the chlorophyll and carotenoid like essential pigments, inhibit Calvin cycle and electron transport chain and also downregulate stomatal movement (Sharma and Dubey 2005). It was observed that Pb accumulate large amount in roots followed by petiole and leaf tissues (Malar et al. 2014).

Application of Si in Pb contaminated soil markedly reduced the uptake and translocation of Pb, electrolyte leakage, limited hydrogen peroxide (H₂O₂) and malondialdehyde (MDA) content and increased biomass yield with the lowest amount of Pb contamination in seed (Bharwana et al. 2013). Shi et al. (2005) reported that Si minimize the Cd toxicity by reducing Cd absorption from soil. Similarly, Shim et al. (2014) have recorded the externally applied Si immobile the excess soil Pb by forming Pb-silicate in the soil.

Cadmium (Cd)

In agriculture, Cd content of soil is limited to 100mg/kg, if concentration crossed this limit, than the field is declared as unfit for farming (Salt et al. 1995). Cd toxicity results in chlorosis, retardation of plant growth and development, modification of enzyme activities, accumulation of excess ROS and protein denaturation (Shi et al. 2010). Even it inhibit or modify the Fe⁺³ reductase activity, that leads to Fe⁺² deficiency. Cd also interferes with the uptake of macro and micro nutrients mainly, Ca, P, K and Mg and reduces the absorption and translocation of nitrate by inhibiting nitrate reductase. In higher plants, excess Cd level can effectively inhibit photosynthesis by downregulating carotenoids function (Prasad 1995). At cellular level, it has potential to cause nucleolus damage leading to chromosome fragmentation and aberration, reduces the respiration by decomposition of mitochondria, affects the electron transport chain by interfering with redox reactions and it replace the Ca in calmodulin which is involved in cell signaling (Rivetta et al. 1997). In *Brassica napus*, even low concentration of Cd (5 µM) reduced the plant growth, photosynthesis and transpiration by closing stomatal activities (Barylá et al. 2001). Similar negative result was obtained in the root structure of Cd treated rice plant. However, application of Si greatly minimized the Cd side effects and improved the plant biomass and chlorophyll content in rice plants (Yoon-Ha Kim et al. 2014). Normally Cd deposit slowly in endodermis and epidermis of the root by absorption whereas Si deposition in endodermis act as a physical barrier for the apoplastic bypass flow across the roots and limit the Cd transportation. Si increases the cell wall extensibility, enhanced water use efficiency, light use efficiency, carboxylation of ribulose-1, 5 bisphosphate carboxylase oxygenase (RuBisCO) (Chika and Alfredo 2011), and stimulate the antioxidant activity (Gangrong et al. 2010). As well as upsurge the activities of CAT, APX and SOD, but reduces the concentration of MDA and H₂O₂ in pakchoi (Song et al. 2009b).

To clarify the roles of Si in mitigating Cd toxicity, Nwugo and Huerta (2011) analyzed leaf proteome and they found 60 proteins were responsible to minimize the Cd toxicity in plants when grown in Cd contaminated soil, among them over 50 proteins associated with photosynthesis, regulation of protein synthesis system, redox homeostasis, and pathogen response were differentially regulated by Si with up-regulation of a class III peroxidase activities. Previously studies in *Arabidopsis thaliana* confirmed that, HMAs (*AtHMA1*, *AtHMA2*, *AtHMA3*, and *AtHMA4*) detoxify the Zn present in the chloroplast organs and regulate the Cd accumulation in various cell organelles especially in vacuoles and plasma membrane. Various researchers assessed the *OsHMA2* and *OsHMA3* genes expression in response to Cd stress in rice plants, and they found that the expression of *OsHMA2* at 1-DAT was significantly increased with Si treatment (Courbot et al. 2007).

Addition of Si in rhizosphere zone contaminated by Cd, enhances the shoot and root biomass by 43-90% and 38-50% respectively. A similar detoxification mechanism has also been observed in peanut (*Arachis hypogaea* L.) (Shi et al. 2010), cucumber (*Cucumis sativus* L.) (Feng et al. 2010), pakchoi (*Brassica chinensis* L.) (Song et al. 2009a) and strawberry (*Fragaria x ananassa*) (Treder and Cieslinski 2005). In general, Si improves the tolerance to Cd stress. In Cd stressed cucumber plants, exogenous Si alleviate blade necrosis, prevent chloroplast swelling, protect thylakoids and increase pigment contents (Feng et al. 2010). Song et al. (2009) also confirmed the role of Si in increasing concentration of GSH, AsA and non-protein thiols (NPT). The mechanism of Si-promoted plant growth under Cd stress at molecular level is still unclear in horticulture crops, while several research work shows the positive role against Cd toxicity in several cereal crops. So, Si is recommended in horticulture crops also.

Mercury (Hg)

Mercury doesn't involve in any plant biochemical and physiological activities and it has no beneficial effect at all (Hameed et al. 2017). Hg exist in many forms in soil such as methyl-Hg, HgS and Hg²⁺ with ionic form. It can persist in soil for longer period by forming carbonate, hydroxide sulfide and phosphate chelates. Anaerobic bacterium present in the soil convert precipitated Hg into methylated form (Tangahu et al. 2011). From there, it get absorbed by plant roots with water and bind to water channel proteins and impede water movement. Later in plants, Hg affect the chloroplast and mitochondrial activities by creating oxidative stress along with membrane degradation and biomolecules oxidation occurs (Nagajyoti et al. 2010). It blocks cellular functions and normal plant growth and development (Malar et al. 2015). There is very diminutive information is available in regards to role of Hg in plants and how plants defend from Hg toxicity.

Chromium (Cr)

Industrial and sewage water are the major source of Cr, which causes serious contamination in soil, groundwater and sedimentation (Shanker et al. 2005). In recent years global emission of chromium (Cr) has significantly increased with industrialization (Kabata-Pendias and Mukherjee 2007). The most toxic form of Cr for a living being is Cr⁺⁴ because it can easily enter cytoplasm with no restriction from the cell membrane and affect the metabolic processes (Singh et al., 2013). Cr directly affects the photosynthesis processes by degrading photosynthesis pigments and anthocyanin (Boonyapookana et al. 2002), water balance and nitrogen metabolism in a cell with a drastic reduction in seed germination percentage (Singh et al., 2013). Cr depresses the activity of amylases during seed germination and hence sugar availability to developing seedlings from embryo is restricted. It also affect the various enzymatic activities which are involved in the carbon fixation, electron transport, etc. (Yadav 2010). Cr increases metabolite production especially, glutathione and ascorbic acid which deleteriously affect the plant growth (Shanker et al. 2003).

From laser-induced breakdown spectroscopy (LIBS) and inductively coupled plasma atomic emission spectroscopy (ICAP-AES) study, the accumulation of Cr in plant tissue reduced after Si application and improves the nutrients (K, Ca, Mg and Na) uptake. Silicon application under chromium stress condition

improves the transpiration rate and chlorophyll fluorescence efficiency and retreating leaves and root structure, swelled chloroplast, damaged thylakoid membrane, increased in plastoglobuli, damaged vacuole and disruption of the nucleus (Shafaqat et al. 2013).

Ding et al. (2013) have shown that the Si markedly decrease the exchangeable Cr content in soil by accelerating the precipitation of organic matter bound Cr fraction. The Si treated plants shows the increased plant growth and development even under Cr-stressed conditions. Hosain et al. (2002) hypothesized that exogenous application of Si cell wall extensibility. The possible mechanism for the reticence of Cr absorption in growing seedling by Si are mainly involved in the two aspects: (i) lignin deposition in cell wall and induces Cr bind to cell wall, that reduce the transportation of Cr from roots to shoot (Shi et al. 2005a; Kaya et al. 2009), (ii) the Si-Cr complex formation (Hodson and Sangster 1993). Other than these, there are several methods present in plants which reduces the Cr uptake and transportation (Nwugo and Huerta 2008). Thus it may be conclude that exogenous application of Si successfully ameliorates Cr- induced toxicity. Although the exact physiological mechanism associated with the Si in regulation of Cr toxicity have not been established in horticulture crops.

Iron (Fe):

Iron (Fe) plays a crucial role in plant metabolism (Ricachenevsky et al. 2010; Vigani et al. 2013). When excess Fe accumulation occurs in the plants, increased the production of ROS via Fenton and Haber-Weiss reaction (Onaga et al. 2016), which ultimately damage the plants by degrading cell wall components (Pereira et al. 2013), increase nutritional disorders (Muller et al. 2015) and iron plaques formation in roots to immobile Fe ions (Pinto et al. 2016). Excess Fe accumulation disturb the carbon metabolism by inhibit the ATP and NADPH synthesis by lowering the efficiency of Calvin-Benson cycle (Siedlecka et al. 1997). Fe deficiency causes major stress as compared to access Fe in plants. Fe deficiency symptoms are common in calcareous soil, as the soil pH reaches 7.5-8.5 because of high bicarbonate accumulation (Romheld and Marschner 1986). Deficiency symptoms like interveinal leaf yellowing, necrosis appeared during plant growth period and ultimately reduces quality and yield. Plants developed a different anatomical and physiological strategy to minimize the Fe deficiency under high soil pH such as, increased Fe reduction power by the help of Fe (III) - chelate reductase enzyme along with an increase in Fe (II) transporters biosynthesis especially in non-graminaceous crops and phenolic compounds released from the roots to rhizosphere zone for acidification to increase the availability of Fe for a certain level (Hindt and Gueriot 2012). Same as other stress conditions, accumulation of metabolites such as glucose, fructose and organic acids observed under high Fe accumulation in plants. Which may modify cell redox balance or non-cyclic functioning of the mitochondrial tricarboxylic acid cycle (Igamberdiev and Eprintsev 2016).

Fe uptake and translation increased with the addition of Si into the soil (Fu et al. 2012). At pH7, all forms of Si like solid silica, crystalline, and amorphous dissolve completely in the water at a different rate based on the surface area and phase of solute. The equilibrium concentration of monomeric silicic acid (H_4SiO_4 or $\text{Si}(\text{OH})_4$) at neutral pH is less than 2mM. If the pH of the solution increased, silicic acid forms the

polyconditionized colloidal particles (Birchall 1990). You-Qiang et al. (2012) observed that Si increase the transportation of Fe from roots to shoot by increasing Si transporters expression. Increased Fe level observed in root system after Si treatment to Fe deficient plants (Bityutskii et al. 2014), which attributed to increase in Fe level in the apoplastic pool of roots (Pavlovic et al. 2013) or it can precipitate at root external (Fu et al. 2012). Si improve the chlorophyll synthesis and stimulate the plant growth when planted in Fe deficient soil by improving Fe mobility (Pavlovic et al. 2013) and metabolism (Bityutskii et al. 2014). In some situations, Si per se did not affect the net assimilation rate in Fe toxicity affected plant (Detmann et al. 2012). In various research, the downregulation of leaf conductance in response to excess Fe was reversed by Si application. Si enhance the roots oxidizing ability and inhibit the significant amount of iron absorption by converting iron into ferric ion under Fe toxic condition (Ma and Takahashi 2002). But exact effect of Fe toxicity at genetic level remain unclear in horticulture crops, although the effect of Fe in various crops have been reported (Sanglard et al. 2014).

Zinc (Zn)

Zinc (Zn) is one of the essential element for plants for its normal physiological activities. It involved in various plant physiological events including auxin, carbohydrate and protein metabolism and participate in several enzymatic activities as cofactor chiefly in pollen formation (Aziz et al. 2016). Same as iron, Zn availability is limited by calcareous soil and this condition becomes more complex as the alkalinity of the soil increases (Marschner 1995). However it requires in vary lower amount and sometime, excess accumulation may cause impede plant growth even complete senescence may occurs. Plants shows Zn deficiency as concentration goes below 15-20 mg per kg of plant dry mass. When Zn concentration crosses the plant threshold limits, it produces visible symptoms like phosphorous deficiency (Lee et al. 1996; Nagajyoti et al. 2010), photosynthesis inhibition, low floral fertility with flower and fruit drop (Marschner 1995). Lower Cu/Zn superoxide dismutase (Cu-Zn-SOD) activity during Zn toxicity may downregulate the ATPs synthesis with increased production of ROS resulting. These symptoms are reversible after normalizing Zn concentration in plants. Whereas Zn toxicity effects may become permanent if stress persists. Such as, by replacing Mg^{2+} ions in RUBISCO (ribulose-1,5-bisphosphate-carboxylase/oxygenase), ultimately inhibit the carbon fixation which leds to plant death (Todeschini et al. 2011). Cell vacuoles act as Zn storehouse and they controls the level of Zn content by immobilization and detoxify the cell. Based on the organic acid concentration in different parts of the plant, Vacuoles of Shoot tissue considered as the storehouse of metals in the form of organic acid complexes (Sinclair and Kramer 2012).

Several experiments were conducted to know the exact impact of Si application on Zn distribution in plants (Gu et al. 2012; Bityutskii et al. 2017). After Si application, the deposition of cell wall bond Zn increased in roots, stem, and leaves at the seedling stage (Gu et al. 2012). Even in dicotyledonous *Minuartia Verna* plant, Zn silicates were detected in the leaf epidermal cell wall, which explains its Zn tolerance after application of Si (Neumann et al. 1997). Citrate level in plant increased when plants are treated with Si under Fe deficiency condition (Bityutskii et al. 2014), same phenomenon could occurs during Zn distribution in the plant. When Si applied under the absence of Zn to cucumber seedlings.

Copper (Cu)

Copper (Cu) is an essential element and which can play various key biochemical activities including photosynthesis, carbon assimilation and ATP synthesis. Cu is an important constituent of cytochrome and plastocyanins and cytochrome oxidase, both of which are vital components of both respiration and photosynthetic systems (Yadav 2010). In rhizosphere region, 1-20% of Cu present in an available form and remaining bond to organic matter. It is considered as nearly immobile in plants, so initially, fresh leaves and reproductive parts show Cu deficiency symptoms. At the physiological level, symptoms of Cu deficiency include reduced respiration, impaired photosynthetic electron transport, and stunted growth symptoms that appeared after Cu deficiency (Marschner 1995). Neelima and Reddy (2002) studied the effect of Cu on *Solanum melongena* seeds and found that, excess Cu can adversely affect the germination and seedling establishment.

There are fewer studies conducted to know the Si–Cu interaction in plants (Frantz et al. 2011). Cu toxicity causes chlorosis on leaves and root biomass reduction in *Arabidopsis thaliana* (Khandekar and Leisner 2011) and *Triticum aestivum* (Nowakowski and Nowakowska 1997), after application of Si, these Cu toxic symptoms were diminished by Cu binding with deposited Si on cell wall (Rogalla and Römhild 2002) but the level of Cu content was not significantly changed in leaf even after external application of Si (Li et al. 2008).

Manganese (Mn)

At low concentration, Mn is essential for normal enzymatic activities. Plant species like peach, wheat and soybean are very susceptible to Mn deficiency whereas maize and rye are much less vulnerable (Reuter et al. 1988). Significantly yield reduction observed mainly in winter crops when Mn availability is below the critical level. Mn deficiency symptoms like decreased dry matter accumulation, decline in photosynthesis and chlorophyll content were normally observed in plants when grown in Mn deficient soil. (Papadakis et al. 2007). In dicotyledonous, interveinal chlorosis of younger leaves observed whereas, in cereals, a gray speck are major common symptoms. Observed in plants when grown in sandy and calcareous soils.

Positive interaction observed in-between Manganese and Si in rice (Okuda and Takahashi 1962), barley (Horiguchi and Morita 1987), trichomes base (Iwasaki and Matsumura 1999), cowpea (Iwasaki et al. 2002) cucumber and bean (Shi et al. 2005a), and pumpkin (Iwasaki and Matsumura 1999). Exogenous Si application improves the root oxidation capacity in root rhizosphere region and also precipitate the Mn outside the plant roots. These deposited Mn oxides are used when plants feel deficiency for Mn. In pumpkin, When cucumber plants are treated with Si presented that almost 90% of Mn bond to the cell wall, in which Mn distributed in symplast and apoplast in equal quantity (Rogalla and Römhild 2002). However, the effect of Si in plants grown under Mn toxic conditions has been scarcely studied. For that reason, further studies should be done in depth to know the exact mechanism involved in plummeting Mn toxicity in plants by exogenous Si application.

Si And Falleivating Other Abiotic Stresses

Since drought, flood, high temperature and wind are the occasionally occurs during crop cultivation. Application of Si in available form at proper dose to plants mitigate some amount of reversible damage caused by these stresses. It was observed that electrolyte leakage was drastically reduces by plants when treated with Si. Number of researchers attributed the role of thermal stability of lipids in cell membranes, although the actual correct physiological mechanism of Si is not well understand.

UV radiation:

Over time, depletion in ozone has led to the increase in solar UV-B light without filtering with deleterious and inevitable effects on plants. High incidence of UV-B irradiation on plants may can cause irreversible damage to the plants by disturbing anatomic and physiological activities which leads to depletion plant height and leaf area which ultimately affect the photosynthesis and biomass accumulation (Zancan et al. 2008).

It is well known that Si has positive role in downregulating stress caused by UV-B radiation in different plants. Si can create physiological barrier for UV radiation and reduces the further transmission of UV radiation from the epidermal layer by excess cuticle deposition (Gatto et al. 1998). In addition, Si stimulate the production of ROS under UV light stress condition to trigger the defence mechanism (Shen et al. 2010a). They have observed that exogenous application of Si protect the soybean seedlings from UV-B stress and even it can lowers the phenolic substances production in plants, which induced by UV-B light (Yao et al. 2011). It plays as supportive role in minimizing internal injuries such as avoiding dwindling in the thickness of both palisade and spongy mesophyll layers under UV-B stress. UV-B stress increases the cellular leakage, whereas Si treated plants maintain the cell integrity even under severs UV-b stress condition. Further overproduction of proline in wheat seedling lowered by the addition of Si suggesting significant role of Si in marinating proline level against UV-B stress (Shen et al. 2010a; Yao et al. 2011). Till now, it is not clear about the role of Si to increase the formation of the double layer of Si in response to UV-B and metabolic response at genetic and physiological level (Liang et al. 2019b).

The reactive oxygen species (ROS) and oxidative stress

In natural, plant produces ROS during photosynthesis and respiration processes to maintain the cell homeostasis (Wu et al. 2017). In some conditions, the ROS production rate sharply increases (Jalmi et al. 2018; Schippers et al. 2016). ROS is an exited oxygen or nascent oxygen (1O_2) (Blokhina 2003), which produced from chloroplast (Dietz et al. 2016), mitochondria (Huang et al. 2016) and peroxisomes (Sandalio and Romero-Puetas 2015). ROS have a dual role depending on level of reactivity, site of production and potential to cross cell membrane (Miller et al. 2010). Excess ROS accumulation disturbs the normal physiological activities of several cellular components by oxidizing or modifying their structural and bio-chemical integrity (Mittler et al. 2004). Even it can cause DNA damage and incorrect timing of PCD (Xie et al. 2014). At low concentration, ROS positively regulate various processes including cellular proliferation and differentiation, (Tsukagoshi et al. 2010; Zafra et al. 2010), activating

biochemical defence mechanism, programmed cell death and stomatal behavior in response to biotic and abiotic stresses. Among all ROS, H₂O₂ is considered as an important redox molecule with remarkable stability in cell with half-life of 10⁻³s (Mittler 2017). Active OH ions are produced when the O–O double bond in H₂O₂ cleaves occurs. They react with almost every biomolecules present in the cell. OH can oxidize the cell wall polysaccharides, resulting in cell wall losing (Karkonen and Kuchitsu 2015), and it can damage nucleic acids by breaking hydrogen bonds present between two sister strands (Hiramoto et al. 1996). In healthy plants, several ROS scavengers such as, catalase (CAT), ascorbate peroxidase (APX), glutathione peroxidase (GPX) and mainly superoxide dismutase (SOD) are present to regulate the ROS production and metabolism (Mittler 2017).

Plant has enzymatic and non-enzymatic antioxidants mechanism which directly (catalase and peroxidase) or indirectly (ascorbate and glutathione) regulates the ROS level in plant cells (Sharma et al. 2012). Si-induced reduction in ROS level in plants is the crucial effect of exogenous Si against various biotic and abiotic stresses which has been demonstrated by several researchers (Hasanuzzaman et al. 2017). During oxidative stress, Si stimulates glutathione (GSH) synthesis which may play important role in MG detoxification process by regulating sulfur transport system (Noctor et al. 2002). In rapeseed, exogenous Si prevents the production of ROS by enhanced antioxidant systems (Khoshgoftarmanesh et al. 2014). Ascorbate, which is one of most effective primary antioxidant is disproportionate to DHA and monodehydroascorbate (MDHA) while scavenging ROS. These DHA and MDHAR enzymes activities regenerates AsA through the AsA-GSH cycle (Hasanuzzaman et al. 2017). Another compound, Glutathione, is a water soluble low molecular tripeptide γ -glutamyl cysteinyl glycine (γ -Glu-Cys-Gly). Which reduces the oxidative stress in plants by scavenging ROS of various forms indirectly (Foyer and Noctor, 2005). Whereas, exogenous Si also increases the GSH content (Farooq et al. 2016) by improving activities of APX, MDHAR and GR with enhanced level of AsA and GSJ with diminishing oxidative stress (Jiao-jing et al. 2009).

Among all phenolic compounds, carotenoids present in vegetables and fruits crops in high amount (Racchi 2013). Carotenes includes the carbon and hydrogen atoms whereas, Xanthophylls of carotenoids contains oxygenated form of carotenes. The most important role of α -tocopherol is that regulate or eliminate the oxidative atoms or molecules, which are generated in the thylakoid membrane; thus, it can prevents lipid peroxidation (Kataria 2017). Si application under oxidative stress condition increases the activities of carotenoids along with SOD, GPX, APX, GR, and CAT actions (Liang et al. 2003).

High pH stress

High pH or Alkalinity is the major problem for plant growth and development (Adil Khan et al. 2019). According to Jin et al. (2006), up to 831×10^6 ha world land is affected by saline. Out of which, nearly 434×10^6 ha is severely affected by saline-alkalinity, which causing severe reduction in world agriculture production and productivity. Under medium to high alkaline condition, high rhizosphere pH significantly affect the essential nutrients availability from by converting them into non-available form. High pH enhances the ROS level and hence plants need to produce antioxidants to neutralize the side effect of

ROS (Peng et al. 2008). High pH stress activates many signal messengers such as, calcium, jasmonic acid (JA), salicylic acid (SA) and ethylene (Klessig and Malamy 1994). Out of which, SA effectively regulate the ROS production with the help of SOD (Molina et al. 2002). Si been implicated similar benefits on plant growth and development as SA during high pH stress conditions. Exogenous application of Si improves the chlorophyll content but reduces the MDA contents in the plants (Adil Khan et al. 2019; Abdel Latef and Tran LSP 2016). APX, CAT, POD, and PPO contents in cells even under alkaline stress condition improved after Si application (Gill and Tuteja 2010). Eraslan et al (2008), suggested that Si treated plants grown in saline soils shows higher defense against various biotic and abiotic stresses as compared to control. Further to avoid excess production of ROS due to high pH stress, plant roots absorb several minerals including K⁺ and Na⁺, they are more dangerous to plants growth. Hence the maintenance of minerals concentration below the toxic level is essential for normal physiological functions. Exogenous application of Si increases the K⁺ level and improves the tolerance of the tomato plants under alkaline conditions (Adil Khan et al 2019). ABA is a critical plant hormone, with an important role regulating various stresses in plants (Yoshida et al. 2019). Usually ABA concentration in plants increases with salinity (Lee et al. 2016), resulting in reduction respiration, transpiration and other metabolic activities. Kim et al. (2016) found lower ABA concentration in Si treated plants as compared to control and also Si improves the growth attributes by improving tolerance against high pH stress.

To further explore the molecular mechanism behind the improved plant growth in response to Si application under alkaline conditions. Kim et al. (2014) has explained the role of *Lsi* genes, *Lsi1* upregulated under alkaline soil condition, suggesting improved uptake of nutrients and water and reduces the harmful effects of ions present in the soil. This is might due to accumulation of Si in various plant parts especially in root system (Adil Khan et al., 2019). Kim et al. (2016) also explained the role of *Lsi1* and *Lsi2* expression to improve the tolerance in plants against heavy metal and high pH stresses. But till today, the actual role of Si in pH stress regulation still remain unclear.

Role of silicon in plant symbiotic and pathogenic relationships.

Si has a major role in disease management through creating a mechanical barrier against pathogen and activation of defense-related pathways such as ethylene, jasmonic acid and reactive oxygen pathways upon infection (Cai et al. 2009; Ghareb et al. 2011). It does not affect any physiological and morphological activities when Si content in plants and in soil below the toxic level (Henriet et al. 2006). However, as early as 1965, some researchers argued that toughness of plant tissue after Si treatment does not resist the penetration of pathogens but Kim et al. (2002) explained that deposition of polymerized Si at penetration site provide the extra resistance against pathogen penetration (Cherif et al. 1992). The spread of powdery mildew stopped within a short period of Si treatment observed in different crops (Samuels et al. 1991) by enhancing activities of chitinase, polyphenol oxidase, phytoalexins, peroxidase and increased the phenolic compound deposition (Cherif et al. 1994). Si treated plants shows an increased branching of rhamnogalacturonan-I to strengthen the vessels pit membrane and parenchyma walls and making less easily degradable from digestive enzymes released from the infective agents by upregulating defense genes and an increase in inhibitory chemicals like phenol (Cai et al.

2009). During *Blumeria graminis* infection, Si stimulate the papilla formation, increased callose production, and glycosylated phenolics in cucumber (Fauteux et al. 2005). It stimulates the accumulation of diterpenoid phytoalexins under the pressure of *M. grisea* infection in rice crops (Datnoffs, 2004) however exact interaction of Si with the biochemical defense system still unclear. As the accumulation of Si in plant tissues increases, the plant defense system becomes stronger against herbivorous insects and other pests (Massey et al. 2007). High Si contains in leaves are less digestible to insects even it can harm the insect mandibles during chewing and macerating, thus decrease the insect's fitness (Massey and Hartley 2009).

When Silicon applied in different formulation with an optimum concentration in fruit crops like apple, mango, citrus, banana, orange and other fruit crops, decreased the level of diseases incidence and economic losses by fungal pathogens (Helaly et al. 2017), bacterial (Cazorla et al. 2006), insect pests (Vieira et al. 2016) and physiological disorders (Edgerton et al. 1976). Compared with those in agronomic crops, the effects of applying silicate fertilizers to horticulture crops have been In several studies have shown that Si may substantially increase tolerance against different biotic stresses in tomato (Heine et al., 2006), sunflower (Kamenidou et al. 2008), rice (Cai et al., 2008), and wheat (Ling et al., 2008). The silicified epidermal layer and increased in prevalence in papillae after Si treatment reduces the Panama disease infection in banana (Jones 2014), Root rot in Avacado (Bekker et al., 2006), Fungal leaf spot in pea (Dann and Muir, 2002), root rot and powdery mildew in cucumber, rust in cowpea, ringspot in sugarcane, leaf spot in Bermuda grass (Fawe et al. 2001; Belanger et al. 2003), Sigatoka and black rot in banana (Kablan et al. 2012), nematode infection in cucumber (Silva et al. 2010), *P. syringae* pv. *Syringae* infection in mango by increased cuticle thickness (Gutierrez-Barranquero et al. 2012), *Ralstonia solanacearum* in tomato (Kurabachew and Wydra 2014) rust, leaf spot and ascochyta leaf spot in coffee (Pozza et al. 2004) anthracnose in sorghum (Carre-Missio et al. 2014), tomato (Somapala et al. 2016) and sweet pepper (Jayawardana et al. 2015), bacterial wilt in tomato (Ghareeb et al. 2011). Deposition of Si at the root band and internode in sugarcane enhanced the resistance against African sugarcane borer (*Eldana saccharina*) (Keeping et al. 2009) and Shoot borer (Rao 1967).

The second mechanism of Si that protects plants against pathogens is increased production of defensive biochemical like lignin, phenolic compounds, and phytoalexins like secondary metabolites (Ma and Yamaji 2006). Some studies reported that flavonoid concentration increased in cucumber plants when powdery mildew infected (Fawe et al. 1998). Biosynthesis of momilactones A and B increased in blast infected rice plants after Si treatment (Rodrigues et al. 2004). Increased activities of peroxidase (POD), Catalase (CAT), polyphenol oxidase (PPO) and β -1,3-glucanase observed to suppress the Phomopsis stem blight development in asparagus (Lu et al. 2008) and for bacterial blotch in rice after application of Si to the soil. Calcium silicate can enhance the production and deposition of total protein, CAT, APX, and chitinase to minimize the *R. Solanacearum* severity (Alves et al. 2015). Si foliar application drastically reduces the hoppers, nymph, mites, leaf-eating caterpillars infection by thickening epidermal layer and activation of salicylic acid (SA)- independent plant defense mechanism (Malhotra et al. 2016; Vivancos et al. 2016) and it also enhanced the β -1,3-glucanase activity, when exposed to *Mycosphaerella pinodes* in pea plant (Brunings et al. 2009).

Conclusion

Si treated plants shows increased environmental stress tolerance as compared to other micronutrients. Si improves the plant growth and development even under stress condition by improving photosynthesis, metabolism, and solute transportation. In this review, we intended to clarify the mechanism of Si and its transporters role in alleviation of different stresses in horticulture crops. Silicon has much more role in both biotic and abiotic stress conditions in agriculture as well as in horticulture crops. It can be used as a universal agent to minimize the effects of known and unknown factors. Based on the previous works, now Si considered an essential element and it also applied to horticultural crops along with the main fertilizer complexes. It has a positive effect on seed imbibition, germination, vegetative and reproductive stage of the plant. Nowadays, the salt-affected area increasing at a drastic rate leads to shrinking in cultivable land but the use of Si under this condition, some amount of salt effect can be minimized. Recent studies summarized the importance of Si in the horticultural crop at the anatomical and physiological levels. Several models including Si as the main elements are recommended to protect the plants under uncommon stress conditions. Now need to utilize advanced approaches like omics to know the complete phenomenon in deep. No need to genetically modify the plants for specific characteristics like resistance against the pathogen, metal toxicity, and other environmental condition. Most of the problems are solved some level by standardization of Si application or mutating Si transporters through CRISPR/Cas9 technology to enhance their activity and minimize the negative impact of biotic and abiotic stresses.

Declarations

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Tables

Table 1. List of crop specific Si transporters identified in different crops.

S. No	Horticulture crops	Si transporter genes
1	Soybean	<i>GmNIP2-1</i> and <i>GmNIP2-2</i>
2	Potato	<i>StLsi1</i>
3	Horsetail	<i>EaLsi2-1</i> and <i>EaLsi2-2</i>
4	Tomato	<i>SILsi1</i>
5	cucumbe	<i>CmLsi1</i>
6	strawberry	<i>FvNIP2-1</i>

Table 2. Role and mechanisms of Si in combating different abiotic stresses in horticulture crops.

Table 2. Role and mechanisms of Si in combating different stresses in fruit crops.			
S.No.		Effect of Silicon application	References
		Fruit crops	
1	Apple	Enhanced the fruit quality and growth	(Cai and Quian 1995)
		Formation of silicide layer in fruit wall to increase resistance against pathogen	(Wang et al. 2016)
		Low polygalacturonase content and increased storage life with low pectin degradation	(Wang et al. 2016)
		It increase the manganese level in aierial part and cause the internal bark necrosis (IBN) by manganese toxicity	(Gao et al. 2006; Su et al. 2011)
		Control apple blue mold disease caused by <i>Uncinullanector burrill</i>	(Etebarian et al. 2013; Farahani et al. 2012; Ebrahimi et al. 2012)
		Control the <i>M. fructiola</i> infection	(Yang et al. 2010)
		Enhanced the biological efficacy of antagonist <i>C. laurentii</i>	(Yu and Zheng, 2006)
		Decreased ethylene, LOX activity, MDA content, DI, softening & respiration rates, TSS & activated the SOD, POD, CAT&APX enzymes	(Mo et al. 2008)
2	Banana	Increased TSS, self life, pulp peel ratio, acidity and reducing sugar content	(Hanumanthaiah et al. 2015)
		Increased epidermal, mesophyll and palisade paranchyma thickness	(Magno Queiroz Luz et al. 2012)
		Increased photosynthesis rate	(Magno Queiroz Luz et al. 2012)
		Increased macro (N,P,K,Ca and Mg) and micro (Zn and Cu) level in plant leaves	(Asmar et al. 2011)
		Increased cho a and b, and totoal chlorophyll contenet	(Putra et al. 2010)
		Reduced root necrosis caused by <i>Cylindrocladium spathiphylli</i>	(Risede, 2008; Vermeire et al. 2011)
		Reduced the intensity of fusarium wilt caused by <i>Fusarium oxysporum</i> f sp. <i>Cubense</i>	(Fortunato et al. 2012a, b; Kidane and Laing, 2008)
		Decreased the incidence of black sigatoka disease caused by <i>Mycosperell fijiensis</i>	(Kablan et al. 2012)
		Decrease in fruit softening, pulp/peel ratio, reducing sugar content, invertase activity & respiration rate, inhibition of cellulase, PG, xylanase, CAT & POX activity	(Srivastava and Dwivedi 2000)
3	Sapota	Improved in number of shoots, total chlorophyll content, number of flowers and less mummified fruit production	(Lalithya et al. 2013)
		Increased fruit weight, self life, shape and	(Lalithya et al.

		economic yield	2014)
4	Mango	Quadrative increase in fruit diameter	(Costa et al. 2015)
		Improved fruit quality and yield	(More et al. 2015)
		Improved the leaf of IAA, GA and CK content in plants	(Helaly et al. 2017)
		Decreased the ABA level	
		Reduced the antioxidant enzymes of POX, CA and SOD	
		Reduced disease severity of <i>Colletotricum gloeosporoides</i>	(Umana-Rojas, 2009)
5	Pomogranate	Reduced fruit cracking	(El-Rhman 2010)
		Increased yield parameters valves	
		Reduced sunburn damage	(Yazici and Kaynak 2008)
		Increased premium quality fruits with minimum number of unmarketable fruits	(Melgarejo et al. 2004)
		Inhibition of PAL activity, retention of vitamin C content reduction of CI & EL	(Sayyari et al. 2009)
6	Guava	Increased in N contenet in plants and amino acid remobilization	(Huang et al. 1997; Ji et al. 1992; Li et al. 1997)
7	Grape	Increased fruit yield and berry shape	(Zang et al. 2017)
		Increased TSS/TA ratio and fruit firmness	
		Decreased respiratory and decay ncidence	(Kader et al., 1992; Kim et al. 2002; Asghari et al. 2009)
		Reduced powdery mildew (<i>Uncinulla nector</i>) colonies	(Bowen et al. 1992)
8	Marsh grape fruit	Increase shoot and root dry matter content	(Matichenkov et al. 2001)
9	Passion fruit	Increased diameter and stem thickness	(Prado and Natale et al. 2005)
10	Zaghoul date palm	Improved chlorophyll content and quality parameters	(Kl-Kareem et al. 2010)
11	Citrus	Increased plant growth and fruit yield	(Matichenkov et al. 2000)
		Improve plant health status	(Matichenkov et al. 2001)
		Increased root mass	
		Reduced brownspot disease caused by <i>Alternaria alternata</i>	(Asanzi et al. 2015)
		Controlled green mould disease caused by <i>Penicillium digitatum</i>	(Liu et al. 2010; Abraham et al. 2010; Moscoso Ramiraz and Palou et al. 2014)
12	Avacado	Supress respiration, reduced ethylene production and increased catylaze activities	(Kaluwa et al. 2010)
		Decreased severity and incidence of anthracnose caused by <i>Colletotrichum</i>	(Anderson et al. 2005)

		<i>gloesporioides</i>	
		Decreased severity of anthracnose in stored fruits	(Boss et al. 2011)
		Reduced root necrosis caused by <i>Calonectctria ilicicola</i>	(Dann and Le 2017)
		Controlled root rot caused by <i>Phytophthora cinnamomi</i>	(Bekker et al. 2007)
		Increased fruit quality by accumulation of phenolics in mesocarp	(Tesfay et al. 2011)
13	Lemon	Increased the resistance against <i>P. digitanium</i>	(Mkhize et al. 2012)
14	Strawberry	Reduced powdery mildew caused by <i>Podosphaera xanthii</i>	(Lepolu torlon et al. 2016)
		Marketability retention, decrease in ethylene production & fungal decay	(Babalar et al. 2007)
		Decay, Ripening& weight loss reduction	(Shafiee, Taghavi and Babalar 2010)
15	Oilpalm	Suppressed basal stem rot (<i>Ganoderma boninense</i>)	(Nijihah et al. 2015)
16	Coffee	controlled the leaf rust development caused by <i>Hemilela vastatrix</i>	(Carre-Missio et al. 2014)
17	Cherry	Decreased fruit decay which caused by <i>Pencillium expansum</i> and <i>Monilina fructicola</i>	(Qin and Tain, 2005)
18	Jujube fruit	Control the apple blue mold disease caused by <i>Pencillium expansum</i> and Controlled the <i>A. alternata</i> infection	(Tian et al. 2005)
19	Kiwi fruit	Inhibition of ACS, ACO & LOX activity, suppression of ethylene & superoxide free radical production, increase in total SA content,	(Zang et al. 2003)
		Inhibition of ethylene production, ripening & decay control	(Aghdam et al. 2008, 2009)
		Inhibit the cellwall and membrane degrading enzymes (PG, LOX,PME)	(Srivastava and Dwivedi, 2000; Zang et al. 2003)
20	Peach	Increase in firmness, APX, GR activity, AsA/DHAsA & GSH/GSSG ratios, decrease in CI, DI	(Wang et al. 2006)
		induction of HSP101 & HSP73 genes	
21	Sweet cherry	Increase in b-1, 3-glucanase, PAL & POD activity,	(Yao and Tian 2005)
		Decay control, increase in CAT, GPX, b-1, 3-glucanase& chitinase	(Xu and Tian 2008; Babalar et al. 2007)
22	Orange	Acceleration of H2O2 accumulation,	(Hung et al. 2007)
23	Watermelon	Increase in GPX, APX, CAT, SOD & GR activity, induction of resistance to CI	(Jing-Hua and Zhang 2008)
24	Loquat	Inhibition of PAL, CAT & POD decrease in superoxide free radical production & CI	(Cao, Zeng and Jiang 2006)
25	Pear	Induction of resistance to diseases, increase in POD, PAL, GR, Chitinase & b-1,	(Cai et al. 2006)

		3-glucanase, decrease in CAT & APX	
26	Chestnut	Delayed discoloration and decay maintained edible quality, activity of PPO, POD & PAL	(Peng and Jiang 2006; Asghari et al. 2007)
DI: decay index, GR: glutathione reductase, GSSG: oxidized glutathione, GSH: reduced glutathione, DHAR: dehydroascorbate reductase, AsA: ascorbate, DHAsA: dehydroascorbate, MDA: Malondialdehyde, hydrogen peroxide (H ₂ O ₂), total soluble phenolics (TSP) and lignin-thioglycolic acid (LTGA) derivatives and greater activities of PLAs: phenylalanine ammonialyases, PPOs: polyphenoloxidases, POXs: peroxidises, GLUs: b-1,3- glucanases and CHIs: chitinases.			

Figures

Figure 1

Role of silicon in plants

Figure 2

Silicon mediated heavy metal stress regulation in fruit crops by modifying different morphological, biochemical and molecular events (the downside arrow indicates downregulation and upside arrow indicates increased activities).