

Effects of silicon in plants with particular reference to horticultural crops - Review article

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Summary: Silicon (Si) has long been considered as non-essential element for plant's growth and production. Numerous efforts are being made for the discovery of its beneficial effects with large scale studies laying foundation for new findings and hypotheses. Therefore, Si has been suggested to be a quasi-essential element due to its positive effects against biotic and abiotic stresses alike. Though Si is the second most abundant element in the soil profile, its availability to plants is limited to the form of monosilicic acid only. Besides, plants' ability to take-up Si and use it in their physiological processes also depends on the available transporters associated with it. Thus, the present review covers uptake and transport of silicon in plants as well as Si mediated physiological processes, including mechanisms underlying induced tolerance against biotic and abiotic stresses with a particular emphasis on horticultural species.

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Introduction

The main constraints for agricultural production include abiotic (Meena et al., 2017) and biotic stresses (Compant et al., 2005), which limit cultivation, quality and yield of crops.

Si plays a major role in several plants' life cycle, with one of these roles to improve plant growth and yield especially in stress conditions. Some of the most important functions of Si include promoting plant photosynthesis by exposing leaves to light, increasing resistance to disease and pathogens, and regulating metal toxicities as well as salinity and drought stresses. Others include protection against extreme temperatures, coping with insufficient mineral composition and detrimental enzyme activities etc., (Ma, 2004; Zhu & Gong, 2014; Adrees et al., 2015). Generally, it has been shown to have an important role in proper physiological activity, structure formation and improved plant survival in several plant species upon exposure to various biotic and abiotic stresses (Liang et al., 2015). Plant growth is dependent upon the availability of essential elements in the soil, while further minerals may be beneficial or toxic (Bienert et al., 2008). Elements categorized into the toxic group unconsciously affect plant growth, contrary to essential elements that are critical for all plants in various growth conditions. Beneficial elements are vital for some plant species in certain growth conditions. The beneficial effects of Si have been well documented in different plant species. Even though the essentiality of Si has always been a debate, regardless of its beneficial use and consideration by many authors as well as studies conducted on numerous plants. Nevertheless, Si is not only having positive effects on plants themselves but also

benefits human health through food products derived from Si exposed plants by offering greater bone strength and improved nervous and immune system (Farooq & Dietz, 2015).

The forms of Si and its occurrence

Silicon is a nonmetallic chemical element in the carbon family, which rarely exists in its pure form. The oxidized form of Si is called silicium dioxide and silicates are common in Earth's crust and particularly important component of Earth's mantle. It is found practically in all rocks, sand, clays and other soil types. Its compound also occurs in all kinds of natural waters, in the atmosphere as siliceous dust, in many plants as well as in the skeleton, tissues and body fluids of some animals.

Earth surface is covered with 27.7% of silicon, being next abundant to oxygen (46.6%) (Mitra, 2015). Generally, 50 – 400 g of Si are contained per kg of soil. There are several types of Si forms available, including quartz and crystalline combined silicates, secondary or clay and Si-rich minerals, as well as amorphous silica that is present in most soils (Orlov, 1985). They constitute a major portion of the soil in the form of aluminum or other silicates, which account for 90% of the earth's crust by mass. Generally, all Si forms are sparingly soluble and biogeochemically inert. Principal soluble forms of silicon in soil are monosilicic and polysilicic acid (Mica, 1986).

Monosilicic acid occurs in weakly adsorbed state in the soil (Matichenkov, 1990; Matichenkov et al., 1997) and has a low

capacity for migration down the soil profile (Khalid & Silva, 1980). It can interact with aluminum, iron, manganese and heavy metals to form slightly soluble silicates (Horiguchi, 1988; Lumsdon & Farmer, 1995). Unlike monosilicic acid, polysilicic acid acts as an adsorbent. It is an integral component of the soil solution and mainly affects soil physical properties and it is important for the formation of soil structure (Matychenkov et al., 1995).

According to tissue analysis studies conducted in a wide variety of plants, Si concentration ranged from 1 to 100 g kg⁻¹ of dry weight (Faroq & Dietz, 2015). These values of silicon present in plants are equivalent to macrolelements such as phosphorous, nitrogen and calcium. Among plants, rice (*Oryza sativa*) 150–300 kg ha⁻¹, and wheat (*Triticum* spp.) 50–150 kg ha⁻¹ absorbed the largest amount of Si (Datnoff et al., 2001) in the field. Moreover, dicotyledonous plants including cucumber (*Cucumis sativus*) (Liang et al., 2005; Nikolic et al., 2007) absorb Si actively (Liang et al., 2006). Nonetheless, some plants like tomato (*Solanum lycopersicum*), bean (*Phaseolus vulgaris*) and several others absorb Si passively from soil solution (Mitani & Ma, 2005; Liang et al., 2005, 2006; Nikolic et al., 2007).

Silicon uptake and accumulation in plants

Incorporation of Si by plants depends on the uptake ability and permits potential beneficial effects (Takahashi et al., 1990; Ma, 2004). Thus, plants are classified into three groups based on their variable capacity to accumulate silicon under average field conditions. These include high accumulators (>5%), intermediate accumulators (1%), and low accumulators (<0.1% of their dry weight basis), such as rice, cucumber and tomato respectively (Deshmukh & Bélanger, 2016). Monocot plants tend to accumulate higher tissue concentrations of Si than dicots (up to 10%) (Table 1).

Plant roots absorb Si in the form of monosilicic acid (H₄SiO₄) at concentrations of 0.1 – 2.0 mM. Monosilicic acid crosses plasma membranes only at a certain pH range (Epstein, 1994; Raven, 2001; Ma & Yamaji, 2006). Due to significant differences among plant species, three possible types of Si uptake mechanisms have been proposed by Takahashi et al. (1990). Plants having higher Si uptake levels than would be expected by water transport are classified as active, plants with similar Si and water uptake rates are classified as passive, whereas those with lower Si uptake than water are referred as rejective types. High accumulators are expected to show active Si uptake from available resources.

Remarkably, molecular studies have found a large group of genes and respective proteins in diverse species that are responsible for Si absorption and transport. These Si transporters allow Si translocation from soil solution into the root and further into the shoot. (Ma & Yamaji, 2015). Si transporters are specific transmembrane proteins that mediate the uptake mechanism (Marron et al., 2016).

The very first Si transporter was identified in rice. This discovery suggested that a specific system for an active Si transport existed. Identification and cloning of the *Lsi1* (*Low silicon 1*) transporter gene occurred by studying a rice mutant (Ma et al., 2004). This transporter gene localized on chromosome 2, and its protein product belonged to the aquaporin subfamily (Gomes et al., 2009) of the NIP3 (Nod 26-like major intrinsic protein 3) major protein family. These proteins facilitate transmembrane movements of small molecules. Presumably LSI1, when present in the plasma membrane of exo- and

endodermis, promotes Si uptake into the root stele. Without this transporter uptake is prevented by the presence of Casparian strip. *Lsi1* is expressed predominantly in the main and lateral roots but not in root hairs, which is consistent with a previous study showing no participation of root hairs in the Si uptake process (Ma et al., 2001). Thus, LSI1 is proven to be a major influx transporter of Si into rice root cells.

Further studies identified LSI2 as another Si transporter, which is potentially accountable for active loading Si from the exo- and endodermis to the cortex and stele respectively in rice (Ma et al., 2007, 2011). LSI2 is located on the plasma membrane of exo- and endodermal cells at the proximal side and builds up in the mature root zone. Its localization is consistent with its role as being an efflux transporter for silicic acid. Another influx transporter LSI6, was found expressed in the parenchyma cells of the leaves. Presumably, this transporter moves Si across vascular bundles in shoot.

Homologous genes to these transporters of rice have also been found in other monocots and in dicot plants, such as soybean (*Glycine max*) (Deshmukh et al., 2013), pumpkin (*Cucurbita moschata*) (Mitani et al., 2011) and cucumber (*Cucumis sativus*) (Wang et al., 2014; Sun et al., 2017, 2018).

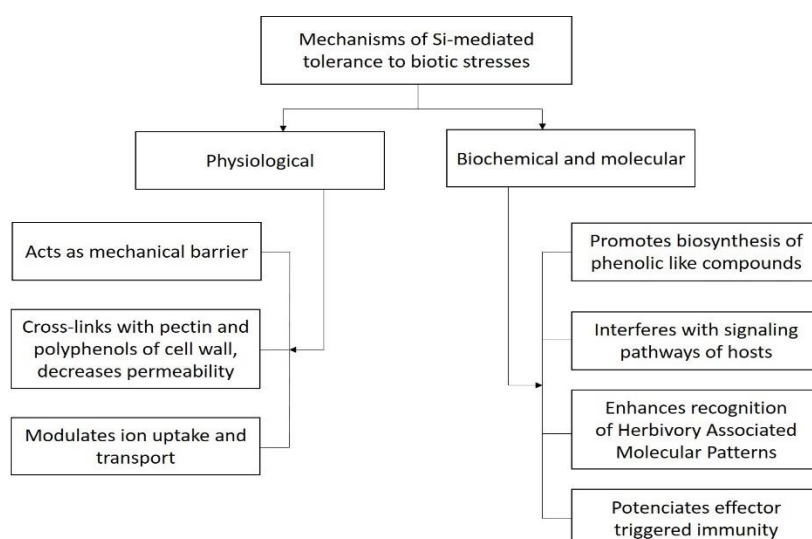
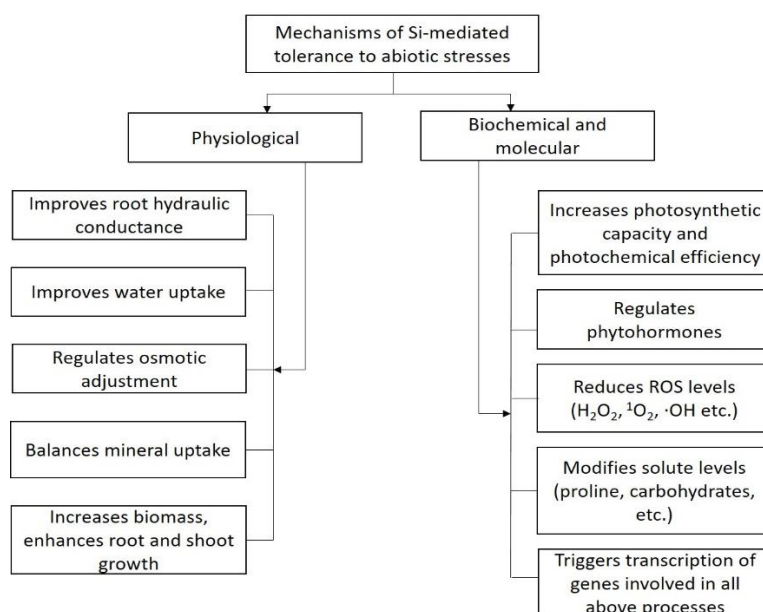
Effects of silicon in biotic stress situations

Biotic stress is caused by pathogens, insect pests and other living organisms. Plants have developed defense mechanisms to overcome these biotic stresses. Si increased resistance of plants against biotic stresses as has been documented by various studies. Many scientists laid a foundation for hypotheses regarding different defense mechanisms (Figure 1). The first hypothesis rooted from work of Wagner (1940), who suggested that Si acted as a mechanical barrier when deposited on the tissue surface, which prevented the penetration of pathogens into different host plants. Another hypothesis was that plants prevented the propagation of pathogens by accumulating phenolic like material when Si is applied (Samuels et al., 1991; Chérif et al., 1992). This hypothesis has been further analyzed and supported by Fawe et al. (1998) with the interaction of Si treated cucumber and powdery mildew infection.

Interestingly, field and experimental data suggest that Si triggered benefit in biotic stress is limited to biotrophic (e.g. powdery mildew) and hemi-biotrophic (e.g. rice blast) pathogens. In recent years the importance of effector proteins has been highlighted especially in case of biotrophic and hemi-biotrophic host–pathogen interactions. According to Giraldo & Valent (2013), effectors can modify host cell ultrastructure, metabolism and function by interfering with relevant signaling pathways. Fungal effectors are released into the apoplast and translocated into the cytoplasm through extrahaustorial matrix and the cell membrane (Bozkurt et al., 2012). This makes the apoplast a likely interaction site for effectors and plant targets (Wang & Wang, 2018). In plants, SiO₂ deposition also located in apoplast, more specifically at the interface of the plasma membrane and the cell wall (Bauer et al., 2011; Zhang et al., 2013). Number of studies support the evidence that Si interferes with effectors or receptors in order to contribute to plant resistance (Ghanmi et al., 2004; Rasoolizadeh et al., 2018). Therefore, Si fertilizations are considered as a better alternative to fungicides and supported by numerous studies for controlling powdery mildew in variety of horticultural crops such as cucumber, zucchini (Vercelli et al., 2017), melon (Dallagnol et al., 2012), strawberry (Liu et al., 2020) and tomato (Garibaldi et al., 2011).

Table 1. Si concentration and Si transporters identified in some important crops

Plant name	Species	Mean Si concentration in shoots (g kg ⁻¹ DW)	Si transporters described
Rice	<i>Oryza sativa</i>	41.67	<i>OsLsi1, OsLsi2, OsLsi3, OsLsi6</i>
Horse tail	<i>Equisetum arvense</i>	39.92	<i>EaLsi2-1, EaLsi2-2, EaNIP3;1, EaNIP3;1</i>
Cucumber	<i>Cucumis sativus</i>	19.66	<i>CsLsi1, CsLsi2, CSIT1, CSIT2</i>
Sunflower	<i>Helianthus annuus</i> L	18.76	-
Tomato	<i>Solanum lycopersicum</i>	15.45	-
Soybean	<i>Glycine max</i>	13.99	<i>GmNIP2-1, GmNIP2-2</i>
Common bean	<i>Phaseolus vulgaris</i>	9.49	-
Watermelon	<i>Citrullus lanatus</i>	8.37	-
Maize	<i>Zea mays</i> subsp.	8.27	<i>ZmLsi1, ZmLsi2, ZmLsi6</i>
Wax gourd	<i>Benincasa hispida</i> L	3.22	-
Onion	<i>Allium cepa</i>	0.62	-
Horseradish	<i>Armoracia rusticana</i>	0.58	-
Potatoes	<i>Solanum tuberosum</i>	0.4	<i>StLsi1</i>
Pepper	<i>Capsicum annuum</i>	0.03	-

**Figure 1.** Mechanisms of Si mediated tolerance to biotic stress**Figure 2.** Mechanisms of Si mediated tolerance to abiotic stresses

Evidently, these are also true with plant–insect (particularly piercing–sucking type) interactions, which involves herbivory associated molecular pattern and effector triggered immunity that mediates plant defense mechanism (Vercelli et al., 2017). Si deposited within the apoplastic space interferes with insects having piercing and sucking type feeding, which showed reduced probing time. The Si affected extracellular matrix prevented insects from impeding the plant defense response by trapping insect effectors within or by preventing recognition of the plant as a suitable host (Hogenhout & Bos, 2011). To this date, there are number of reports on Si mediated resistance against such type of insects including silverleaf whitefly on soybean (Ferreira et al., 2011) and Asian citrus psyllid on lime (Ramírez-Godoy et al., 2018).

Effects of silicon in abiotic stresses

Abiotic stresses cover a wide range of adverse environmental conditions such as high or low temperature, drought, salinity, ultraviolet radiation and metal toxicity (Epstein, 1999; Ma & Takahashi, 2002; Ma, 2004). In order to increase food quality and quantity plants need to mobilize different strategies to overcome the losses due to these adverse conditions.

With respect to salinity and drought stress, Si was shown to improve root growth (Kim et al., 2013) and increased water uptake due to improved hydraulic conductance (Wang et al., 2015) and root activity (Chen et al., 2011), which in turn increased root/shoot ratio in Si treated plants (Wang et al., 2015). Further metabolic changes involved modification of solute levels, as was reported for proline (Lee et al., 2010), carbohydrates (Ming et al., 2012), glycine betaine (Torabi et al., 2015), total phenolics (Shi et al., 2014), total soluble sugars and total amino acids (Crusciol et al., 2009). These adjustments may minimize the osmotic shock created by salt and drought exposures. Moreover, Si supply can interfere with hormonal regulatory circuits under diverse stresses (Kim et al., 2013) by decreasing JA (Kim et al., 2013) and enhancing the concentration of endogenous GA (Lee et al., 2010) and salicylic acid (Hamayun et al., 2010). In a noteworthy example, upregulated cytokinin level was associated with silicon treatment in tomato (Barreto et al., 2021) and cucumber (Zhu et al., 2020). In terms of the oxidative component of stresses Si plays an important role by improving antioxidant ability (Gunes et al., 2007) and regulates the production of polyamines, like putrescine, spermidine and spermine (Liu & Xu, 2007; Wang et al., 2015). Our own recent research elucidated that Si could downregulate pro-oxidant systems in plants as well. Lipoxigenases were found downregulated in Si treated cucumber shoot tissues along with an overall decrease in oxidative stress level (Bat-Erdene et al., 2021). Based on the coordinated attenuation of all lipoxigenases' expression, it was assumed that this regulation may be at least partly responsible for the observed antioxidant effect of silicon, potentially also contributing to the growth promoting effect observed. Under salt stress Si decreased MDA concentration, which is an end product of lipid peroxidation in lemon (Mditshwa et al., 2013) and in grapevine rootstock (Soylemezoglu et al., 2009). Moreover, MDA concentration was positively correlated with Na^+ absorption in salt stressed cucumber and negative correlation with Ca^{2+} and K^+ absorption in the Si treated cucumber (Khoshgoftarmanesh et al., 2014).

Under drought condition, excess Si is deposited under the cuticle forming a second layer which decreases water loss via peristomal transpiration in shoots (Ma et al., 2001; Ma, 2004). In

roots Si accumulates around exodermis and endodermis cells, at sites where Si transporters are located. Si deposits at these positions were postulated to block apoplastic bypass route of solutes containing toxic ions. Due to this inhibition less Na^+ , Cl^- and Cd^{2+} enter via Casparian strip breaks or underdevelopments, resulting decreased bypass in sap flow. The discrimination against the problematic ions can be more strict at membrane transport, these ions will be less likely to accumulate in sensitive tissues of the shoot to a toxic level (Shi et al., 2005; Zuccarini, 2008; Savvas et al., 2009; Flam-Shepherd et al., 2018). Si also stimulates to the formation of the Casparian strip by promoting suberin and lignin biosynthesis, which further protects plants against toxicants through the bypass apoplastic route (Fleck et al., 2015).

Like most environmental stresses, ultraviolet radiation also induces reactive oxygen species production in plants (Shen et al., 2010; Rybus-Zajac & Kubiś, 2010; Beckmann et al., 2012). According to Li et al. (2008) Si is shown to increase plant tolerance to UV-B radiation, which has adverse effects on plant growth. Shen et al. (2010) reported that Si application significantly reduced the membrane damage caused by combination of drought and UV-B radiation in soybean seedlings.

Extreme temperatures also frequently limit plant growth, development and reproduction. When plants are subjected to high or low temperature, cell membrane permeability increases. Under these conditions increased ROS generation is common, including more intense lipid peroxidation, which results from imbalance between production and scavenging (Jaleel et al., 2009). Hu et al., (2020) reported that Si supply during high temperature (40 °C) stress kept stomata open in poinsettia plants. In the same study enhanced resistance to cold stress was reported, which was explained through increased epicuticular wax deposition when the plants were exposed to chilling (4 °C) temperatures.

In the apoplast, H_4SiO_4 polymerization results in an amorphous silica barrier (Exley, 2015), which can limit intercellular penetration of toxicants like Al, Cd, Mn and Zn and their uptake into the symplast (Guerriero et al., 2016). Apoplastic uptake of metal ions may also be reduced by Si depositions along with a decrease in free metal mobility (Iwasaki et al., 2002; Rogalla & Römheld, 2002). This effect can be accelerated by enhanced adsorption of metals in the cell wall of root tissues (Liang et al., 2006; Ye et al., 2012). Transport of metals can also be restricted through the endodermis as a result of Si accumulation. Porosity of cell wall in the inner root tissues may also be reduced, thus decreasing metal concentration in the xylem sap. (Keller et al., 2015). Limited transfer of metals through endodermal cells and decreased ionic mobility in root tissues are the main mechanisms of reducing adverse effects of metal toxicity stress by Si (Etesami & Jeong, 2018). In other studies, however, effects of silicon on the uptake of micronutrients were found variable in tomato, depending on the genotype and mineral concentration (Kleiber et al., 2015). Effects are probably dependent on the transport process of the minerals, including compartmentalization. Whereas, in cucumber Si supply greatly decreased the phenolic compounds and lipid peroxidation caused by excess Mn (Shi et al., 2005; Maksimović et al., 2007). Different results may also stem from the use of unrelated species, growth and treatment conditions. Interestingly, even in stress free conditions, Si treatments have shown to improve growth and appearance of various horticultural plants, which also resulted in greater yield (Fleck et al., 2011; Toresano-Sánchez et al., 2012; Fleck et al., 2015; Bat-Erdene et al., 2021)

Table 2. Literature summary on effects of Si in biotic stress

Stress type	Common name of disease/insect	Pathogenic fungal/insect species	Host plant & species	Si concentration	Si effects and symptoms on host plant	References
Disease	Powdery mildew	<i>Blumeria graminis</i>	Barley (<i>Hordeum vulgare</i> L.) Oat (<i>Avena sativa</i>)	K-silicate	Mechanical barrier + resistance	Wagner, 1940
		<i>Erysiphe cichoracearu</i>	Cucumber (<i>Cucumis sativus</i>)	20mg Ca-silicate 15 gm Na-silicate	+ resistance Prolonged incubation	Ghanmi et al., 2004
			<i>Arabidopsis thaliana</i>	100 ppm K-silicate	Production of fungitoxic substances	
		<i>Sphaerothecafuliginea</i>	Cucumber (<i>Cucumis sativus</i> L.)	1.7 mM (100 ppm) K-silicate	- fungal growth - hyphal length + Flavonoid phytoalexins	Samuels et al., 1991 Fawe et al., 1998
			Zucchini (<i>Cucurbita pepo</i> L.)	0.1 mM 1 mM	- expansion of powdery mildew	Savvas et al., 2009
		<i>Podosphaera xanthii</i>		100 ppm	+ chlorophyll content - disease incident - disease severity	Vercelli et al., 2017
			<i>Podosphaera aphanis</i>	Melon (<i>Cucumis melo</i>)	2 mM K-silicate	- disease severity - disease progress rate - conidial production - infection efficiency - colony area
		<i>Podosphaera aphanis</i>		Strawberry (<i>Fragaria</i> L.)	0.003 mg/ml	+ plant resilience - disease severity - infection rate - AUDPC
		<i>Oidium neolycopersici</i>	Tomato (<i>Solanum lycopersicum</i>)	100 mg/L	- disease incidence - disease severity	Garibaldi et al., 2011
		Black leg of seedlings	<i>Pythium ultimum</i>	Cucumber (<i>Cucumis sativus</i> L.)	1.7 mM K-silicate	- wilting - root decay - senescence
Soybean root rot	<i>Phytophthora sojae</i>	Soybean (<i>Glycine max</i> L.)	1.7 mM	Apoplast interaction - release of effectors	Wang & Wang, 2018 Rasoolizadeh et al., 2018	
Two-spotted spider mite	<i>Tetranychus urticae</i>	Strawberry (<i>Fragaria</i> L.)	0.003 mg/ml	- AUPPC - number of insects per leaf	Liu et al., 2020	
Insect	Asian citrus psyllid	<i>Diaphorina citri</i>	Persian lime (<i>Citrus latifolia</i>)	2 ml/L K-silicate	- eggs + plant resistance	Ramírez-Godoy et al., 2018
	Silverleaf whitefly	<i>Bemisia tabaci</i>	Soybean (<i>Glycine max</i> L.)	250 ml of a 1% silicic acid	- phenolic compounds + nitrogen production + resistance - insect population	Ferreira et al., 2011

+ stands for increased, improved or enhanced

- stands for decreased, alleviated or mitigated

Abbreviations: AUDPC-Area Under the Disease Progress Curve; AUPPC- area under the pathogen progress curve.

Table 3. Literature summary on effects of Si in abiotic stresses

Stress	Species	Si concentration applied	Effects of Si	References
Salinity	Rice (<i>Oryza sativa</i>)	0.5 mM	+ ABA tissue concentration	Kim et al., 2013
		1.0 mM	- JA	
		2.0 mM	+ SA biosynthesis	
		3mM	+ Shoot growth	Flam-Shepherd et al., 2018
Cucumber (<i>Cucumis sativus</i>)	0.83 mM	- Apoplastic transport of Na ⁺ - bypass flow		
		+ root hydraulic conductance	Wang et al., 2015	
		+ K ⁺ + Na ⁺		
		1 μM	- Lipid peroxidation	Khoshgoftarmansh et al., 2014

			+ CAT activity + APX activity + GPX activity	
	Zucchini (<i>Cucurbita pepo</i> L.)	0.1 mM 1 mM	+ photosynthesis - Na ⁺	Savvas et al., 2009
	Common bean (<i>Phaseolus vulgaris</i> L.)	1.5 mM	+ K ⁺ concentration + Relative water content (RWC) - Na ⁺ - Cl ⁻	Zuccarini, 2008
	Chinese apple (<i>Zizyphus jujuba</i>)	-	+ net photosynthetic rate (P _N) + spermine/spermidine ratio + putrescine	Liu & Xu, 2007
	Soybean (<i>Glycine max</i> L.)	2.5 mM	+ plant height + FW & DW + chlorophyll contents + Gibberellins - ABA - proline.	Lee et al., 2010
		100 mg L 200 mg L	+ GA + SA - JA	Hamayun et al., 2010
	Borage (<i>Borago officinalis</i> L.)	0.5 mM 1 mM 1.5 mM 2 mM 2.5 mM	+ FW & DW - Glycine betaine - proline	Torabi et al., 2015
	Canola (<i>Brassica napus</i> L.)	2 mM	- lipid peroxidation + chlorophyll contents + CAT activity + POD activity - lignification	Hashemi et al., 2010
	Soybean (<i>Glycine max</i> L.)	2.5 mM	+ plant height + DW & FW + chlorophyll content + GA - NaCl - ABA - proline	Lee et al., 2010
Drought	Potato (<i>Solanum tuberosum</i> L.)	284.4 mg dm ⁻³	- total sugar - soluble proteins - stalk lodging + mean tuber weight + tuber yield	Crusciol et al., 2009
	Rice (<i>Oryza sativa</i>)	52.64 mg/kg	+ photosynthetic rate (Pr) + transpiration rate (Tr) + basal quantum yield F_v/F_0 + Maximum quantum efficiency of PSII photochemistry F_v/F_m	Chen et al., 2011
		2.5 mM	+ water potential (W _w) + osmotic potential (W _p) + OA + photosynthesis + WUE	Ming et al., 2012
	Tomato (<i>Solanum lycopersicum</i> L.)	0.5 mM 2.5 mM	+ Seed germination + SOD activity + CAT activity - O ₂ ^{-•} (singlet oxygen) - H ₂ O ₂ - total phenol concentration + Root Hydraulic Conductance	Shi et al., 2014 Shi et al., 2016
Ammonium toxicity	Tomato (<i>Solanum lycopersicum</i>)	1.28 mM	- NH ₄ ⁺ + <i>trans</i> - zeatin (<i>tZ</i>) content	Barreto et al., 2021
Boron toxic + salinity	Spinach (<i>Spinacia</i> L.)	2.5 mM	- Na ⁺ content - Cl ⁻ content	Gunes et al., 2007
	Tomato (<i>Solanum lycopersicum</i>)	5 mM	- B accumulation + LOX activity + AA	
	Grapevine rootstock (<i>Vitis vinifera</i> L.)	4 mM	+ SOD activity + CAT activity + APX + Shoot DW - Na ⁺ concentration - MDA - H ₂ O ₂	Soylemezoglu et al., 2009
UV-B radiation	Rice (<i>Oryza sativa</i>)	200 mg/L	Lsi1 gene regulation	Fang et al., 2011

UV-B + drought	Soybean (<i>Glycine max</i> L.)	1.7 mM	+ relative leaf water content + Anthocyanin level + phenol level + photosynthesis	Shen et al., 2010
Temperature stress	Tomato (<i>Solanum lycopersicum</i>)	75 mg/L	+ stomatal closure + epicuticular wax + photosynthetic rate - MDA + hydrogen sulfide + APX activity	Hu et al., 2020
	Lemon (Citrus L.)	50 mg/L 150 mg/L 250 mg/L	- MDA + total antioxidants - total phenolics	Mditshwa et al., 2013
Mn toxicity	Tomato (<i>Solanum lycopersicum</i>)	0.3 mg dm ³	+ Microelement level + photosynthesis	Kleiber et al., 2015
	Cucumber (<i>Cucumis sativus</i>)	0.5 μM	+ biomass production	Maksimović et al., 2007
		50 μM	- phenolic compounds	
		100 μM	No symptoms of Mn toxicity	
		1 mM	+ SOD activity + APX activity + DHAR activity + GR activity + Ascorbate concentration + GSH concentration - lipid peroxidation	Shi et al., 2005
K ⁺ deficiency	Maize (<i>Zea mays</i> L.)	2 mM	Nutritional Physiological Growth variables	dos Santos Sarah et al., 2021
No stress condition	Rice (<i>Oryza sativa</i>)			
	Maize (<i>Zea mays</i>)	1.78 mM 1.07 mM	Casparian band formation + phenol complex	Fleck et al., 2015
	Onion (<i>Allium cepa</i>)			
	Cucumber (<i>Cucumis sativus</i>)	1.67 mM	+ Shoot growth - MDA - H ₂ O ₂ - LOX	Bat-Erdene et al., 2021
	Cherry tomato (<i>Lycopersicon esculentum</i> var. <i>cerasiforme</i>)	250 mL/ha	+ fruit + yield	Toresano-Sánchez et al., 2012

+ stands for increased, improved or enhanced

- stands for decreased, alleviated or mitigated

Abbreviations: AA-antioxidant activity; ABA- Abscisic acid; APX-Ascorbate peroxidase; CAT-catalase; FW-fresh weight, DR-dry weight; DHAR- dehydroascorbate reductase; GA-gibberellins; GR- Glutathione reductase; GSH-glutathione; JA-Jasmonic acid; LOX-lipoxygenase; MDA-Malondialdehyde; POD-peroxidase; SA-salicylic acid; SOD-superoxide dismutase; WUE-water use efficiency.

Conclusion

In recent years a growing number of transporters have been identified that mediate Si uptake and transport in plants and various molecular studies have been conducted on their expression and activities. However, it is still a great challenge ahead to dig deeper into their regulation as well as to fully understand their function. Hence, transcriptional regulation of Si transporter genes and transmembrane Si transport needs further investigations. Apparently, only limited characterization of Si transporters is available at present in a few plant species, including horticultural crops. Clearly more research is needed for a deeper understanding of the physiological significance of Si transporters in different plants. This will facilitate breeding programs for exploiting most potential benefits of Si accumulation in crops.

As for the molecular mechanisms to explain the diverse effects silicon can exert in plants a unifying concept has been put forward. The “apoplastic obstruction hypothesis” postulates that most, if not all, effects of extra silicon supplementation are attributable to extracellular accumulation of Si depositions and derive from disturbed physiological events there with diverse downstream consequences (Coskun et al., 2019). In view of

most above examples and that of our own results we agree with this conclusion.

In practical application, Si fertilizers have been spreading in cultivation of horticultural crops for improved performance and protection against adverse environmental effects. Their larger scale application requires precise information about Si effects in specific genotypes, media and treatment regimes. To meet this demand more laboratory and field trials are required in order to ensure high quality products and safe harvest in crop production.

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