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Potential Role of Silicon in Plants Against Biotic and Abiotic Stresses

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Abstract
In climate change scenarios, biotic and abiotic stresses are among the serious environmental strains that limit agricultural productivity worldwide. Silicon (Si) compounds are now getting much attention in agriculture as a result of explorations into their beneficial effects on plant growth, and development under adverse environments. This review seeks to understand the roles of transport pathways, the up- and down-regulation of biochemical responses, and transporter genes in Si's effects. Exogenous application of Si enhances plant antioxidant defenses and decreases oxidative stress by limiting production of reactive oxygen species (ROS). Biofortification is one of the best techniques to reduce biotic and abiotic stresses by enhancing a plant's capacity to accumulate Si. Identifying the novel genes involved in Si transport and modulating their expression level through genetic engineering is one option being considered to prevent biotic and abiotic damage to crop, and to reduce the applications of toxic pesticides, herbicides, and fungicides.

Keywords Abiotic stress · Biotic stress · Biofortification · Reactive oxygen species · Biochemical responses · Antioxidant defence

1 Introduction

Silicon (Si) was first used in agriculture in China more than 2000 years ago. The emperor of that time ordered that manure and rice straw must be incorporated and used as fertilizer to increase crop yield. Today, several studies have reported that rice tissues contain Si ranging from 1 to 10 dag/kg. This could be considered as the first evidence of indirect Si application in agriculture as fertilizer to enhance the yield. Later in 1971, a Japanese plant chemist evaluated the potential of Si in reducing the effect of blast disease in rice and his results got the attention of scientists worldwide to discover more about this element. In 1939, for the first time, the role of Si in stimulating plant growth and development under biotic stresses in dicot plant species was reported. As a result of research from the 1980s until today, silicon's potential to decrease the intensity of many biotic and abiotic stresses is now known for a large number of plant species [1].

Climate change in recent years has become a serious threat to agricultural productivity by bringing biotic and abiotic stresses with greater force [2–4]. Biotic and abiotic stresses are widespread throughout the world and adversely affect crop productivity by reducing 70% average yield in all major staple crops. Plants come up with strategies to escape from stresses and induce such mechanisms at molecular and physiological levels that fit well in the changing environment [5–7]. Plants are capable of sensing external stimuli and inducing metabolic instability to activate an array of defense mechanisms to alleviate biotic and abiotic stress [8–11]. Several external stimuli can activate the plant defense mechanism under stressful conditions but the current focus is on Si in mitigating biotic and abiotic stresses and its interaction with other stimulus factors.

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Si is the 8th most common naturally occurring element. It is the second most abundant element after oxygen in rocks and soil [12]. Si is a non-essential element involves in the growth and development of plants [13]. Crops like rice, barley, wheat or silicifiers (plants that can accumulate Si at high concentration to benefit themselves by building silicified architectures under certain conditions like drought stress or fungal infection), such as horsetail perform better during Si supplementation and suffer under adverse climatic conditions if Si deficiency occurs.[14, 15]. Si is available to the plants in the form of silicic acid, $Si(OH)_4$, through aquaporin channels, NIPs (Nod26-like intrinsic proteins) [16]. The permeability of wheat to silicic acid is determined by a specific amino acid arrangement in the conserved asparagine–proline–alanine (NPA) domains of aquaporins [17]. Plants are categorized into excluders, intermediate, and accumulator types depending upon the ability of Si accumulation [18]. Accumulators (plant species that have capability of accumulating Si at concentration ≥ 1 g-kg^{-1} in their tissues) include wheat, Equisetales, cyperales and rice. They can accumulate Si up to 10% of dry shoot weight, which is why these crops are known as high silicifiers [19]. Tomato is considered as Si excluder (plant species that can accumulate Si < 1 g-kg^{-1} in their tissues), whereas common nettle (*Urtica dioica*) is an example of an intermediate (plant species that can accumulate moderate level of Si in their tissues) [20]. A list of plant species classified into the three Si accumulation categories is shown in Table 1.

Table 1 Classification of plants according to their silicon accumulation capacity

Excluders $\leq$0.5% Si	Intermediates 0.5–1.5% Si	Accumulators $>$1.5% Si	References
Grape	Squash	Wheat	[21–23]
Sunflower	Soybean	Lentil	[24–27]
Petunia	Marigold	Rice	[27–29]
Begonia	Pumpkin	Horsetail	[30–32]
Snapdragon	Rose	Moss	[33–35]
Tomato	Chrysanthemum	Fern	[36–38]
Geranium	Cucumber	Conifers	[39–41]
Pansy	Zinnia	Sugarcane	[42, 43]
Gerbera daisy	New Guinea impatiens	Spinach	[44–46]

Addition of silicic acid to growth media results in greater resistance to biotic stresses and increased plant vigour [18, 47]. Plant tissue culture is a vital method for culturing plant cells, tissues, and even complete plants under controlled environmental and nutritional conditions [48]. Plant growth media is composed of both organic and inorganic nutrients essential for plant growth and development. The type and concentration of nutrient is determined according to the particular species of plants [49, 50]. Care must be taken to include only desirable nutrients in the culture media because some compounds may have adverse effects on plant growth. For example, application of an unsuitable nutrient composition might result in physiological disorders in plants like shoot tip necrosis and hyperhydricity. Upward curling of leaves is caused by inappropriate concentrations of inorganic nutrients in the culture medium [51]. Several reports are found that exogenous Si application in media improved the growth and yield of plants under biotic as well as abiotic stress [52–55]. Exogenous application of suitable amounts of Si in culture media, showed significant improvements on plant growth such as healthy roots and shoots and greater plant vigour [48]. It has also been reported that application of Si to plants under salinity stress resulted in better development of promising traits. Silicon added up to 3.6 mM in culture media resulted in an increase in both fresh and dry weight of shoots and roots and also in the number of leaves per shoot. Raising the Si concentration up to 7.2 mM increased root length [48, 56]. Adding Si at a concentration of 3.6 mM also resulted in maximum production of chlorophyll; however, concentrations greater than this might adversely affect the chlorophyll level [48, 57].

To optimize food production in terms of quality and quantity, different plants need to be exposed to specific nutrient blends to enhance resistance to various adverse environmental effects. Through genome editing technologies like CRISPR/Cas9 and TALEN, modification in plant genome can be done to develop tolerance against adverse environmental effects; but these technologies are expensive and labour-intensive [58, 59]. Toxic elements suppress plant growth and development whereas contrarily essential elements have been proven vital for plant growth and development even under adverse conditions [60]. Scientists have conducted many experiments to measure the effects of Si on plant growth and concluded that Si improves plant performance throughout the lifecycle [61]. For example, an investigation showed that Si controlled the fungal disease (cucumber powdery mildew) by accumulating in leaf and root tissues to make a silica layer over epidermal cells. It was concluded that macro-elements have the ability to produce inactive glycosylates or phytoalexins, which are activated by Si to cause fungal cell death [62]. It was also reported that Si reduced membrane damage and enhanced tolerance to stress in tomato (*Solanum lycopersicum*) and spinach (*Spinacia oleracea*) [44, 63]. In wheat (*Triticum aestivum*), Si promoted resistance to powdery mildew and oxidative damage under drought stress [64, 65]. In this review we will present and discuss in detail, the current knowledge about Si's role in plant defence against abiotic and biotic stress.

2 Silicon Concentration and Biofortification

Sorghum (*Sorghum bicolor* L.) is an important cereal crop that is considered as an intermediate Si accumulator with Si at 2–3% dry weight (DW) in the tissues [66]. Plants, with < 0.1% Si by dry weight are excluders, those with 1% are intermediate and plants that can accumulate up to 5% Si are accumulators. Monocot species such as wheat, rice, and maize are accumulators [22], while most of the dicots are unable to accumulate much Si in their tissues and therefore, considered as excluders. Notable exceptions exist in members of the *Cucurbitaceae*, *Urticaceae*, and *Asteraceae* as they were found to improve with Si feeding [67–69].

Seven hundred and thirty-five plant species were subjected to analyse the concentration of Si in their shoots under 125 different studies. Silicon absorbance by these plant species has been controversial due to the comparison of comprehensive databases and accessibility of the species to Si. Their classification was completely based on phenotypic data that was obtained under diverse conditions. For example, some of the data were collected from field observations, where concentrations of Si in soil varied greatly. Typical Si concentrations in soil range from 0.1 to 0.6 mM, which is why it is difficult to assess the exact exposure of a plant to Si [22]. An experiment was conducted to determine plant responses to Si under various conditions such as hydroponic, tissue culture, liquid medium, and in the field. Plants were exposed to different Si concentrations in different medias (open field, growth media and water) and it was concluded that high Si concentration was observed under natural field conditions [70, 71]. Si concentration in shoots is highly variable among species, ranging from 0.1% to 10.0% DW [72, 73]. This variation in Si accumulation resulted due to differences in the ability of roots to uptake Si, but the molecular mechanism behind Si accumulation in plant tissues still remains unknown [74, 75].

Among plant species, there is a genotypic variation in Si levels in shoots, but this variation is not as large as that among the species overall. For example, when 400 cultivars of *Hordeum vulgare* (barley) were tested for Si concentration, the results showed variations in Si concentration from 1.24 to 3.80 mg g^{-1} [76]. *Oryza sativa* L. ssp. *Japonica* (rice variety) can accumulate higher Si levels than *Oryza sativa* L. ssp. *Indica* [77]. An experiment was conducted, where different varieties of rice were grown in solutions containing 100 mg L^{-1} SiO_2 and results revealed that the Si concentration among the rice varieties was highly variable, ranging from 117 to 171 mg g^{-1}. When the same varieties were grown in the field, Si levels ranged from 41 to 60 mg g^{-1} [78]. In *Saccharum officinarum* (sugarcane) shoots, Si ranged from 6.4 to 10.2 mg g^{-1} [54]. Another study on two rice varieties Nipponbare and Kasalath revealed that Si uptake increase with the increase in external application of Si. The maximum concentration of Si in root DW was about 3.0 and 2.1 mg g^{-1}, in both varieties respectively [79].

Si concentration in plants needs to be increased to moderate levels to enable plants to survive easily under stressful conditions easily. Different techniques have already been introduced for enhancing macro and micronutrients concentration in plant tissues. These techniques include meganucleases or homing endonucleases, ZFNz, TALENs, CRISPR-Cas9 and biofortification. The above-mentioned genome editing techniques (except biofortification) are known for regulating gene expressions, gene knock-in and knock-out but the problem lies with their off-target efficiencies, high application cost and most importantly the ethical concerns. Therefore, biofortification remains the only suitable option for improving crops in terms of nutrients. Biofortification is a process of delivering micro or essential nutrients to plants that are important for plant growth and development in a cost effective and feasible means. Two basic approaches are being adopted for biofortification: first, increase macro or micro-nutrients and second, reduce anti-nutritional factors like oxalates and phytates (compounds capable of reducing the bioavailability of nutrients) [80]. Both approaches can be accomplished via various mechanisms such as agronomic practices, genetic engineering and traditional plant breeding [81] carried out an experiment to enhance Si concentration in chicory and land cress plants to improve quality and production of leafy vegetables through biofortification. They used two different sources of Si (sodium silicate and potassium silicate) with four different concentrations: 0, 0.84, 1.68 and 2.52 g L^{-1}. Foliar application of Si enhanced Si accumulation in leaves and reduced leaves water loss during storage. They recommended 2.52 g L^{-1} as the most suitable dose from both sources. Si biofortification also stimulates concentration of some beneficial hormones such as Ascorbate (strong antioxidant and act as stress coping hormone in plants) [82]. Several studies have reported that Si supplementation increases the concentration of ascorbate within plants but the mechanism linking the increase in Si supplementation with the increase in ascorbate concentration is still unknown. Besides, the Si biofortification strategies in strawberries not only enhances the Si accumulation in leaves, roots and fruit but also increases the total flavonols content to enhace the nutritious profile of strwa berry without affecting the taste [83]. Moreover, Si biofortification also induces resistance to several biological pathogens by interacting with various plant stress-signaling compounds. Direct application of Si as fertilizer (especially in rice) promotes Si biofortification through accumulation in edible grains and other vegetative parts and increases contents of essential amino acids such as Leu, Ile, Thr, Pro, Arg, Tyr, Ala, Ser, Glu and Asp [84]. Development of Si biofortified crop varieties through plant breeding or other practies can help in avoiding the use of toxic incesticides, fungicides and other chemicals to portect plant from diseases. Moreover, Si biofortification can also reduce post-harvest losses, improve crop quality and extend storage duration.

3 Influx and Efflux Silicon Transporters in Monocot and Dicot Species

Si transporters are identified in nearly every form of life. Diatoms were the first organisms in which Si transporters were reported [85]. Before 2006, researchers had failed to identify Si transporters in plants via sequence homology. In 2006, Si influx transporter was identified in rice that had a rear property of being permeable to silicic acid [86]. The transporter identified (Lsi1) and other Si transporters belong to the NIP protein subfamily (nodulin-26-like intrinsic protein) of aquaporin. Aquaporins are membrane proteins involve in transportation of water and small solutes, including silicic acid, ammonia, boric acid and glycerol through cell membranes. They are part of the major intrinsic protein (MIP) family, which is present in all organisms [87]. Aquaporins comprised of six transmembrane domains arranged in tetramers within the cell membrane [88–91]. The selectivity of NIPs (Nod26-like intrinsic proteins) for a particular solute is linked to two regions that create the pores in the central channel: two highly conserved NPA motifs and four-amino acid residues forming aromatic/arginine (Ar/R) selectivity filter [22]. This selectivity of NIPs (Nod26-like intrinsic proteins) is for all Si influx transporters such as Lsi1, Lsi6 but not for Si efflux transporter as they belong to putative anions transportation. Scientists used the sequence of rice Si transporter to search for homologues in other plants and today many Si influx transporters have been found in *Hordeum vulgare* (barley) [92, 93], *Cucurbita* (pumpkin) [94], *Zea mays* (maize) [95], *Triticum aestivum* (wheat) [96] and *Equisetum arvense* (horsetail) [31].

Efflux Si transporters have also been reported in the roots of rice, wheat, barley and finger millet [97–100]. Existing Si efflux transporters are involved in transport of Si into xylem [22]. Lsi2 is a Si efflux transporter and is structurally different from the Si influx transporter Lsi1.. Lsi2 is a transmembrane protein comprised of 9–12 domains similar to the anion transporter family, which has not been well characterized. Unlike the passive aquaporins, Lsi2 is considered an active transporter because the Si efflux is driven by a proton gradient [101, 102]. In higher plants, only a small number of Si efflux transporters are reported from pumpkin, wheat, rice, maize, *Eleusine coracana* and *Arabidopsis thaliana* [103]. In the case of rice, the Lsi1 influx transporter is situated on the plasma membrane towards distal side of the endodermis and exodermis cells. The Lsi2 efflux transporter is situated on the proximal side of those cells that are involved in transport of silicic acid out of the cell [28]. The transport of silicic acid through Lsi1 is a passive process, while the efflux of silicic acid through Lsi2 is carried out by ATP utilization and H + pump [22].

The total number of Si transporters currently identified are sequence homologues of rice Lsi1 which were isolated and characterized in rice (Lsi6) [104], maize (*Zea Mays*; ZmLsi1, ZmLsi6) [105], wheat (*Triticum aestivum*;TaLsi1) [106], barley (*Hordeum vulagre*;HvLsi1, HvLsi6) [107], soybean (*Glycine max*; GmLsi) [108], cucumber (CSiT-1, CSiT-2) [109], and pumpkin (*Cucurbita moschata*; CmLsi1) [94]. All these transporters belong to the subfamily of NIP (Nod26-like intrinsic proteins) aquaporin-like proteins. All of the Lsi1 silicon transporters from different plant species have been associated with the NIP III group (Nod26-like intrinsic proteins), and are characterized by having a specific selective filter region composed of glycine (G), serine (S) and glycine-arginine (R) [34]. The small residues of NIPs III (Nod26-like intrinsic proteins) assemble to form a larger constriction compared to other NIPs (Nod26-like intrinsic proteins) groups. The Lsi1 passive channel is bidirectional, but functions as an influx transporter through cooperation with Lsi2. A new additional Si transport protein has been discovered in *Equisetum arvense* (horsetail), which belongs to another NIPs (Nod26-like intrinsic proteins) aquaporin subfamily [110]. Horsetail is a major Si reservoir in the plant kingdom [111]. Silicic acid can also be transported through EaNIP3s, which have a different selectivity filter composed of threonine (T), alanine (A) and arginine (R) [112].

The function of Lsi2 (efflux transporter) is to transport Si out of plant cells. Lsi2 was first reported in *Oryza sativa* (rice) [78] and later homologous sequences were found in pumpkin (CmLsi2) [113], maize (ZmLsi2) and barley (HvLsi2) [105, 114]. Efflux transporters have no similarity with influx transporters in the Si channel, but do show some similarities with the arsenite efflux transporter, arylsulfatase B (ArsB). ArsB was first reported in archaea and bacteria. Lsi2 transports Si by consumption of ATP to create a proton gradient through the plasma membrane [115]. Both influx and efflux transporters have different patterns of expression depending on plant species. Influx transporters are mostly expressed within roots of wheat, maize, barley and rice, whereas the other homologs, including CSiT1, CSiT2, CmLsi1, GmNIP2-1, GmNIP2-2, ZmLsi6, OsLsi6, and HvLsi6 are expressed in both roots and shoots [116, 117]. The expression of Lsi1 genes by Si is regulated in various ways. The levels of GmNIP2-1 and GmNIP2-2 in soybean and OsLsi1 and OsLsi6 in rice are down-regulated by silicic acid. CSiT1 and CSiT2 in *Cucumis sativus* (cucumber) show circadian rhythm [118], but in *Oryza sativa*, Lsi1 expression does not have a strong circadian influence [119]. In roots, the expression level of Lsi1 genes among plant species varies greatly. Lsi1 is highly expressed in mature roots of barley and rice, [120, 121], whereas its homolog, Lsi6, is only found in the root tips of rice and barley [122].

4 Silicon Uptake, Distribution and Accumulation Channel in Plants

Si influx or efflux transporters are localized to specific areas in different tissues of wheat. These transporters are involved in a series of steps leading to Si accumulation in wheat from uptake via roots, distribution throughout the plant, and xylem loading. Lsi1 expressed at a higher rate in roots while Lsi2 expressed at a low level in roots [123–125]. Lsi1 and Lsi2 are present in the same cells, and their distinct polarities suggest that Lsi1 and Lsi2 cooperation is needed for uptake of Si. The plant roots composed of two Casparian strips at the endodermis and exodermis, which stop apoplastic.

Movement of Si, solutes and water across the cell layers [127]. As the roots mature, many of the cortical cells in the exodermis and endodermis are remodelled and aerenchyma formation takes place, while the leftover cell wall pieces and remaining cells together make thin, spoke-like connection in the apoplast. Thus, Lsi1 imports Si first to the exodermal symplast on the distal side, which is then exported to apoplastic connections by Lsi2. Si is further introduced into the endodermal symplast through Lsi1 present on the distal side of the endodermis and then transferred through Lsi2 on the proximal side of the endodermis to steles [128]. Lsi1 and Lsi2 have similar expression profiles; therefore, knockout of either gene can lead to a reduction in Si concentration in roots (Fig. 1).

Lsi1 and Lsi2 are present on separate layers in maize and barley. Si taken from soil through ZmLsi1 and Hvlsi1 transporters is deposited in different cells including cortical, hypodermal, and epidermal types. The symplastic pathway is involved in transportation of Si to the endodermis, and release it in stele through Zmlsi2 and HvLsi2 located on endodermis in maize and barley, respectively [129]. All these variations in the Si transport pathways from soil to xylem among wheat, rice, maize and barley are due to differences in root structure. To accumulate Si at high concentration in aerenchyma cells through roots in wheat and rice both set of transporters are necessary [130]. Roots of maize do not have functional aerenchyma. Under non-stressed conditions, only a single casparian strip develops in the root endodermis of barley and maize. According to a study using a mathematical model, the presence of both efflux and influx transporters at both the epidermis and endodermis constituted the best combination for significant uptake of Si via roots in rice [127].

After root absorption, Si is transferred to shoots by xylem through transpiration volume flow. In rice, 90% of the Si accumulated in roots, was transported to the shoots [79].

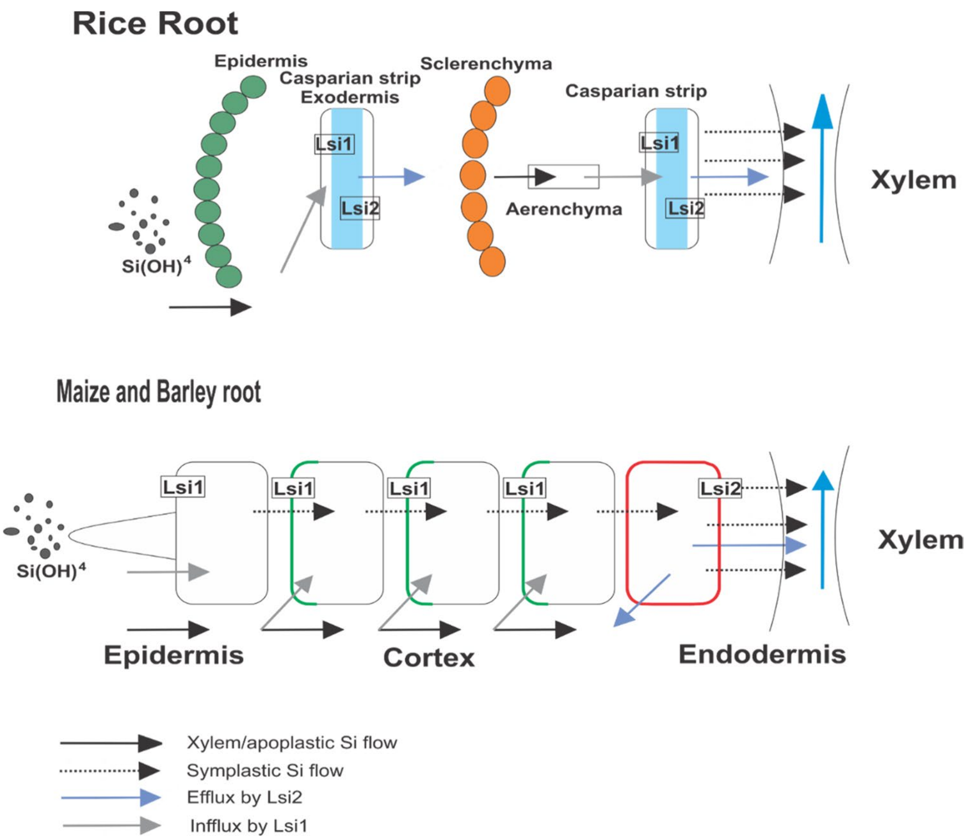

Fig. 1 A channel of silicon transport in plants. Arrows in different colors indicating the transportation processes conciliate by Si transporters, symplastic and apoplastic flow. The contribution of each process is indicated by the thickness of the arrows. Low Si 1 and 2 (Lsi1 and Lsi 2), which are located at the proximal and distal sides of both endodermis and exodermis, cooperate to mediate Si uptake in rice roots. Lsi1 and Lsi2 are also responsible for Si uptake in maize and barley roots but they are located at different cell layers. Lsi6 in leaves releases Si from the xylem sap, but it is unknown which transporters allow Si to be deposited at particular cells. Lsi6, which is located at the xylem transfer cells, also releases Si from the xylem enlarged vascular bundles in nodes [126]

The Si has been found in many forms such as silicic acid, Si $(OH)_4$in xylem. Many studies have claimed that Lsi6 is located in parenchymatous cells of the xylem at the adaxial sides of leaf blades and sheaths. It involves in unloading the xylem and transports Si out of the xylem in wheat, barley, maize and rice [131, 132]. It has been found that loss of Lsi6 in rice resulted in augmentation of Si in guttation drops, and involves in alteration of Si distribution in leaves [133]. Then Si finally accumulates in the husk during the reproductive stage. The Si accumulation at high concentration in the husk is vital to improve grain fertility since it reduces water loss and averts pathogenic infections [134]. Si concentration in the grains of wheat and rice is low compared to other parts of the plant, because Si distribution through transpiration to grains is limited. Apparently, there is no stomata on the outer surface of the husk, and secondly the grain surface area is less than the expanded leaves [135]. Recently, a study has shown that minerals taken up through roots are not transported to grains directly but are redirected to nodes, especially in graminaceous plants [135]. Diffuse and enlarged vascular bundles are the two main types found at nodes. Lsi6 is located on xylem transfer cells with polarity facing toward the xylem vessel [65, 136, 137]. Thus, Lsi6 transports Si from enlarged vascular bundles of roots to the diffuse vascular bundles of panicles. Lsi6 knockout results in the reduction of Si concentration in panicles and improves Si concentration in flag leaves. HvLsi2 is also reported in barley nodes located in the parenchymatous cell layer, next to transfer cells where it has a different polarity from HvLsi6. Si reloading in xylem of diffuse vascular bundles might be performed by Hvlsi2 for greater Si accumulation in the husk [138]. Thus, a collaborated system of transport in nodes is needed for distribution of Si.

5 Silicon Regulates Candidate Genes to Combat Stresses

Among various Si-mediated stress mechanisms, the primary strategy used by Si to combat stress is the enrichment of photosynthetic compounds in stressed plants. Although, several studies have reported the adventitious effects of Si on photosynthesis, only few have examined the molecular mechanisms behind the regulation of gene expression by Si, especially in rice. [139] demonstrated the transcriptional regulation of genes associated with photosynthesis under Si supplementation and zinc stress. Si supplementation enhanced the transcriptional level of *PsbY* gene (*PsbY* gene proteins are associated with photosystem II) and on the other hand high concentration of zinc down-regulated the expression of *PsbY*. PsbY is a low molecular mass subunit of oxygen evolving complex of photosystem-II with manganese binding polypeptide consisting L-arginine metabolizing enzyme activity. Moreover, an increase in the *PsbY* expression due to Si supplementation could increase the electron transfer rate, and water oxidation might improve photosystem-II efficiency and also activate the manganese binding capacity [139]. Similarly, Si supplementation increases the abundance of *PsaH* that encodes essential polypeptide subunits in the photosystem-I dimer. It is reported that knockout of PsaH resulted in damage to LCH-II complex which further delayed the energy transition between Photosystem-II and Phototsystem-I [140]. A high concentration of zinc down-regulates the expression *PetC* gene that codes for cytochrome bf complex Rieske Fe-S center binding polypeptides. This complex has the responsibility of ensuring the proper functioning of cytochrome. Si supplementation up-regulated the *PetC* expression under zinc stress which maintained the structural integrity of chloroplast [139]. Additionally, Si mediation also up-regulated the expression of another gene named as *PetH* in the same way as *PetC*. PetH encodes ferredoxin $NADP^+$ oxido-reductase enzyme which is responsible for NADPH synthesis through electron transport chain of photosynthesis. PetH also maintained the concentration of glutathione when reduce under stresses. Thus, the up-regulation of these genes by Si under stress conditions indicates the importance of Si in maintaining the electron transport chain [141]. Besides, Si supplementation also up-regulate the expression of light harvesting complex genes (Os09g26810 and Os03g57120).

Generally, housekeeping genes are expressed constitutively all the time in each cell. They are acquired for cellular maintenance to regulate ubiquitous and basic cellular functions. [142] reported that Si supplementation up-regulated the expression of housekeeping genes (Os03g0226400, Os12g0227400, Os01g0898500) in rice under blast disease. Si in excluders such as tomato can also up-regulate housekeeping genes like phosphoglycerate kinase (*PGK*), alpha-tubulin (*TUB*) and actin (*ACT*) to induce resistance against *Ralstonia solanacearum* [143]. Transcription factors (TFs) are considered the first line of defense against stress-inducing genes by down-regulation the expression of these genes. Generally, TFs facilitated by specific cis-elements called regulons that are located in the promoter region of target genes, A plant's genome is composed of a large number of regulons that are responsible for responding to stresses. For instance, dehydration responsive element binding proteins (*DREB2*) activated by drought and temperature stress [144]. Si supplementation in rice up-regulates TFs responsible for *OS-RING*, *NAC5* and *DREB2A* domain containing dehydrin *OsRAB16b*, *OsCMO* and *OsRDCP1* proteins [145]. *OsDREB* in rice triggers stress responsive genes expression that confers tolerance to osmotic stress in an abscisic acid (ABA)-independent manner. Moreover, *OsDREB2A* elevated levels in rice confirm resistance to drought. *OsNAC5* up-regulation in rice stimulates tolerance to stresses trough enhancing expression of stress induces genes such as *LEA3*. Furthermore, *OsRAB16b* with LEA genes that are expressed in response to abiotic stresses in both reproductive and somatic tissues. Si supplementation in sorghum increased the water uptake by enhancing the activities of aquaporin proteins by up-regulating SbPIP2:6, SbPIP2:2 and SbPIP1:6 genes in roots [146]. Furthermore, up-regulation of genes associated with aquaporins channel proteins in roots can enhance the speed of water uptake under drought stress and dilutes excessive Na^+ ions under salinity stress. The extensive study by [147] elucidated the positive regulation of genes by Si under *Magnaporthe grisea* infection related to the defense mechanism such as β-1, 3-glucanases, chitinases, peroxidase (POX), pathogenesis-related protein (PR1), phenylalanine-ammonia lyase (PAL) and chalcone synthase (CHS). In the above mentioned genes, PAL contributes to the synthesis of secondary metabolites with potential chemical defense properties through the phenyl-propanoid pathway and CHS is the rate-limiting enzyme in the flavonoid biosynthesis pathway. Some of the reported genes up and down regulated by Si to combat stresses are listed in Table 2 below.

6 The Significance of Silicon in Plants

Si deposition in plant tissues is often associated with stress resistance mechanisms and improve resilience under stress conditions. A number of scientific reports have indicated the

Table 2 List of genes up and down regulated by Silicon in defense to biotic and abiotic stresses

Biotic and Abiotic stress	Studied plant	Gene identifier	Si-impact on gene	Functional annotation	References
Heat	Wheat	*PsbD*	Up-regulated	Photosystem-II D2 protein	[148]
Heat	Wheat	*PsbB*	Up-regulated	Photosystem-II CP47 reaction center protein	[148]
Heat	Wheat	*PsbH*	Up-regulated	Photosystem-II reaction center protein H	[148]
Drought	Tomato	*Psb28*	Up-regulated	Photosystem-II reaction center Psb28 protein	[149]
Drought	Tomato	*PsbW*	Up-regulated	Photosystem-II oxygen evolving enhancer protein 3	[149]
Drought	Tomato	*PsbQ*	Up-regulated	Photosystem-II reaction center PsbW protein	[149]
Drought	Tomato	*PsbP*	Up-regulated	Photosystem-II oxygen evolving complex protein	[149]
Drought	Tomato	*PetF*	Up-regulated	Ferredoxin $NADH^+$	[149]
Drought	Tomato	*PetE*	Up-regulated	Plastocyanin	[149]
Low light stress	Soybean	*PAL*	Up-regulated	Control phenylpropanoid product biosynthesis	[108]
Low light stress	Soybean	*CAD*	Up-regulated	Reduction of cinnamaldehydes into cinnamayl alcohols	[108]
Low light stress	Soybean	*POD*	Up-regulated	Oxidative stress reductant antioxidant	[108]
Salinity stress	Sorghum	*Sb04g021790*	Up-regulated	N-Carbamoyl putrescine amidohydrolase	[66]
Salinity stress	Sorghum	*Sb10g002070*	Up-regulated	Arginine decarboxylase	[66]
Salinity stress	Sorghum	*Sb06g021540*	Up-regulated	S-Adenosyl-Metdecarboxylase	[66]
Salinity stress	Sorghum	*Sb04g025720*	Up-regulated	S-Adenosyl-Met-decarboxylase	[66]
Salinity stress	Sorghum	*Sb02g025110*	Up-regulated	S-Adenosyl-L-methionine decarboxylase	[66]
Bacterial Wit	Tomato	*X99147*	Up-regulated	Arabinogalactan protein	[150]
Bacterial Wit	Tomato	*M83314*	Up-regulated	Phenylalanine ammonia lyase	[150]
Bacterial Wit	Tomato	*X94943*	Up-regulated	Peroxidase	[150]
Bacterial Wit	Tomato	*AF494201*	Up-regulated	Tomato stress responsive factor	[150]
Blast disease	Rice	*Os03g0405500*	Up-regulated	PDI-like protein	[151]
Blast disease	Rice	*Os05g0495600*	Up-regulated	P-type ATPase	[151]
Blast disease	Rice	*Os02g0584800*	Up-regulated	Detoxification protein	[151]
Blast disease	Rice	*Os01g0713200*	Up-regulated	β-1,3-Glucanase precursor	[151]
Blast disease	Rice	*Os03g0803500*	Up-regulated	2OG-Fe(II) oxygenase-domain contains gene	[151]
Salinity stress	Sorghum	*Sb01g009450*	Down-regulated	1-Aminocyclopropane-1-carboxylic acid synthase	[66]
Blast disease	Rice	*Os01g0627800*	Down-regulated	Cytochrome P450 mono-oxygenase	[151]
Blast disease	Rice	*Os01g0770200*	Down-regulated	Tyrosine decarboxylase-1	[151]
Blast disease	Rice	*Os10g0154700*	Down-regulated	Cyclophilin Dicy-2	[151]
Blast disease	Rice	*Os09g0110300*	Down-regulated	Putative cyclase family protein	[151]
Blast disease	Rice	*Os10g0191300*	Down-regulated	Type 1 pathogenesis-related proteins	[151]
Blast disease	Rice	*Os03g0266300*	Down-regulated	Heat shock protein Hsp20	[151]

beneficial effects of Si in higher plant, yet Si has not been considered as an significantl element for plants. Since these scientific reports have become strong evidence of Si's significance for plants, Si-based fertilizers are being worldwide today. Besides, some of the research institutes, centers, and agencies such as the International Plant Nutrition Institute (www.ipni.net/topic/silicon-si) are promoting Si applications in agriculture sectors. Anyhow, the optimum requirement of Si by any particular specie is not yet well defined and similarly, the effect of different doses or amounts in different tissues on plant physiology is poorly understood. Additionally, excess application of any beneficial element or nutrient can become toxic for plants and result in physiological disorders such as necrosis of the shoot tip and hyperhydricity [152]. The amount of Si accumulation in plant tissues and it's significance on plant physiology depends on the concentration of Si or silicic acid in the soil [153]. The concentration of Si greatly varies within plant species. For example, Plants like wheat (*Triticum spp.*), rice (*Oryza sativa*) and sugarcane (*Saccharum officinarum*) absorb Si in large amounts: 50–150, 150–300, and 300–700 kg ha^{-1} respectively [154–156]. Normally, graminaceous plants take up Si in more abundant concentrations than other plant species. For instance, wheat and rice are very good Si accumulators that absorb silicon in active progression [157, 158]. Moreover, several studies have reported the significance of Si even in excluders like Arabidopsis, canola and tomato when applied exogenously. However, yet researchers have not paid as much attention to the significance of Si in excluder species as they should due to the Si-derived benefits associated with accumulators. Once the significance of any element on plant physiology is evaluated through phenotypic data, the next step should be to locate the site of accumulation of that particular element in plants. Si deposition and accumulation have been extensively studied in various plant species. The site of silicification includes intracellular shoots and roots, partially or wholly filled cell lumens, the cell wall and specialized silica cells. Silicification mostly occurs in vascular tissues, epidermis, storage tissue, fiber and sclerenchyma. Moreover, the pattren of Si deposition, the amount and it's role drastically vary among tissue types [128]. Below we have discussed in detail the significance of Si in different aspects of plants with examples.

6.1 Silicon for Plant Growth and Development

Si plays a vital role in plant growth and development and helps plants cope with both biotic and abiotic stress conditions. [128, 159, 160]. For example, salinity stress known to reduce the germination percentage of *Lathyrus odoratus* upto 70% but seed priming with Si before sowing significantly reduces the negative effect of salinity in shoots. Moreover, Si nano-particals application at seedling stage enhance water uptake, promote seedling and root growth [161]. [162] evaluated the effect of Si in upland rice along with plant growth-promoting microorganisms (PGPMs) *Trichoderma asperellum, Burkholderia pyrrocinia, Pseudomonas fluorensces*. The main theme of their study was to figure out the most PGPM type and most appropriate Si dose for rice to gain maximum vegetative growth. They concluded that Si combined application with *Trichoderma asperellum* promoted a 35% and 65% increase in shoot and root lengths, enhanced root dry matter biomass by 54% and suppressed the severity of rice blast by 99% as comapre to control conditions. Roots play an important role in plant performance throughout the life cycle including biotic and abiotic stresses. For instance, under drought stress plants need to meet their water requirements for survival and therefore, plants with greater root length can easily escape from stress when compared to shallow-rooted crops. However, plants (both shallow and deep-rooted) have evolved their root lengths according to the changing environment after taking several decades. [153] gave a detailed review of Si effects on different root traits such as root length in different crops including wheat, rice, barley, soybean, etc. using a high throughput imaging technique. Advances in high throughput techniques have made possible the studies of those traits which can not be measured or studied manually or with traditional phenotypic techniques. Besides, manually recorded data is always prone to errors and can not be as accurate as of data recorded through high-throughput phenotyping. High throughput phenotyping technique can allow the study of plant growth and development and physiological changes throughout the life cycle. Si supplementation improves plant water potential at pre-flowering stage, increases chlorophyll a, b and carotenoids contents, reduces heavy metals uptake, enhances plant height, and improves the overall growth of plants [163]. [164]reported that Si application in soybean enhanced nitrogen uptake from 6 to 34%, Si from 7 to 47%, nodulation from 25 to 46%, root length from 16 to 33% and shoot dry weight from 6 to 23% when compared to control (no application of Si) plants. A possible role of Si in improving plant growth is attributed to the alteration in cellular and biochemical mechanisms as well as enhanced membrane integrity and antioxidant defense system under various abiotic stresses conditions. Antioxidant enzymes enhance the growth and morphological characteristics of wheat and other several plants. The activities of certain antioxidant enzymes in diverse crops were elevated by treatment with Si [48]. Si supplementation included 2ip and IAA improved regeneration of adventitious roots while increasing activity of the antioxidant enzymes, SOD, CAT, and APX [165, 166].

6.2 Advantageous Effects of Silicon in Plants under Abiotic Stress

Several studies indicate, Si has the capability to overcome both chemical stress such as metal toxicity, nutrient imbalance, and salinity, and physical stress, including freezing, UV, high temperature, and loading (Fig. 3). Salinity is a major problem in semi dry and dry areas as it results in a large reduction in yield; it can be overcome, however, through the application of sufficient exogenous Si [167]. For example, in tissues of cucumber, Si indirectly reduced oxidative damage by regulating the activities of superoxide dismutase (SOD), glutathione reductase (GR), ascorbate peroxidase, guaiacol peroxidase, and dehydroascorbate reductase [167–169]. Silicon application to tomatoes under stress conditions reduced oxidative damage to leave by enhancing SOD and catalase (CAT) activities. Application of Si can increase protein content in leaves, enhance activity of ascorbate peroxidase, and reduce H_2O_2 malondialdehyde levels [154, 170–174].

In various crops including wheat, Si positive effects have been demonstrated over abiotic stresses. Application of Si to wheat under drought stress significantly helped to reduce stress by up-regulating GR, CAT, and SOD. During drought, Si enhances the uptake of water in wheat and other plants via regulation of aquaporin channels [175]. In higher plants the application of Si can protect against toxicity of heavy metals, increase yield to satisfactory levels, and improve overall plant health. Silicon has the ability to eliminate manganese (Mn) toxicity either by detoxification of Mn or through reduction of soluble apoplastic Mn content in cell walls [176, 177]. It was reported in cucumbers, sorghum and wheat that Si decreased Mn toxicity by enhancing enzymatic and non-enzymatic antioxidant activities and reducing peroxidase effects on membrane lipids [177–179]. The effects of Si on various plant species under abiotic stress (salinity, drought, heavy metal, etc.) are shown in Table 3 below.

6.3 Effects of Silicon on Salinity Stress

Yield reduction in wheat from salinity stress is a serious problem. Salinity stress is a major threat in semidry and fully dry areas of Pakistan and other part of the world, where wheat has been grown for decades, such as Balochistan, Punjab, and India. However, the oxidative damage caused by salinity stress can be remedied through exogenous application of Si at sufficient concentrations [202–205], for example to sweet peppers, cucumbers and tomatoes [116, 186, 206] (Fig. 2).

Si enhances protein content in leaves and reduces the concentration of malondialdehyde, ascorbate peroxidase, and hydrogen peroxide. The positive effects of Si on salinity stress have already been confirmed in wheat, cucumber, maize, rice, and tomato[116, 186, 206–209].

It has been reported that when rice plants were kept under both control and salinity stress conditions, Si application along with NaCl resulted in a better performance of rice under salinity stress compared to control. Tolerance against NaCl in wheat could be enhanced significantly by application of a nutrient solution containing a high concentration of Si [210]. Si has the capacity to enhance the soluble protein content in leaves and increase plant efficiency to recover the soluble proteins that were lost under salinity stress [211, 212].

6.4 Effects of Silicon Under Heavy Metals Stress

Stress of metals, such as cadmium (Cd), manganese (Mn), and chromium (Cr) results in stunted growth, poor development, and most importantly, makes monocot and dicot crop species susceptible to insect attack and reduces the final yield (Fig. 3). The Si application of stimulated heavy metal transport, prevented crops from being damaged and reduced the malondialdehyde (MDA) content [175, 213–216]. Heavy metal accumulation in wheat reduced antioxidant enzyme activity and promotes production of ROS. Silicon nanoparticle (SiNP) application along with chromium (Cr) in plants increased antioxidant enzyme activity and photosynthetic pigments [217].

6.5 Effects of Silicon Under Drought Stress

Photosynthetic pigments are significantly influenced by drought stress, which causes an imbalance between antioxidant enzymes and the production of ROS, thus reducing overall crop production [218–220]. Crop treatment with Si applications reduced the concentration of flavonoids, glutathione, and lipid peroxidation while enhancing ascorbate content [221]. Supplementation with Si and polyethylene glycol (PEG) on tomatoes led to induction of drought stress and produced tolerance through enhancing CAT and SOD activities and promoting high water uptake [222].

6.6 Effects of Silicon on Ultraviolet Irradiation

Ultraviolet radiation (UV) has adverse effects on crop growth, vigour, and protein, amino acid, sugar, and chlorophyll contents, with chlorophyll contents being primarily affected. Si application under such conditions induces resistance to UV stress through biochemical and physiological processes [21, 175, 223]. Application of Si to tropical plants under UV stress enhanced SOD and POD activity and also increases MDA and anthocyanin contents [174, 224]. Si nanoparticle application improved the overall growth of crops at the seedling stage against UV stress [225].

6.7 Advantageous Effects of Silicon in Plants Under Biotic Stress

Few plants have the ability to develop well in the absence of Si, and in some cases like rice and the silicifier, horsetail, Si deficiency results in high susceptibility to fungal attack [226–228]. Si has been proven to reduce rice susceptibility to sheath blight disease (Fig. 3) [154] by the formation

Table 3 Effects of silicon on plant growth and development under various abiotic stresses

Plants Species	Stress	Silicon Supplementation	Beneficial Effects	References
Triticum aestivum	50, 75 and 100% of drought stress	Silicon applied with concentration of 50 and 150 mg kg^{-1}	Enhanced yield, spike weight, height and biomass Also enhanced uptake and high Si accumulation in plant tissues	[180]
Triticum aestivum	Drought stress (100%, 60%, and 40% F.C.)	Foliar application of silicon	Significantly improved membrane stability index (MSI), Chl stability index (CSI), carotenoids, Chl contents and carbon dioxide (CO_2) concentration	[181]
Zea mays L	Heavy metal stress (100 µM nickel)	Exogenous application of silicon	Si application improved Chl contents, RWC, antioxidant enzymes activities and reduced oxidative stress	[182]
Fragaria × ananassa	Effect of Si at vegetative, flowering and fruiting stages in greenhouse	Exogenous application of silicon	Improvement was seen both in qualitative and quantitative parameters	[183]
Glycine max	under normal light and shade conditions	Foliar application of silicon	Si application decreased CO_2 concentration and improved transpiration rate, stomatal conductance, and photosynthetic rate under light and shade	[184]
Solanum lycopersicum	Drought stress under greenhouse conditions	Foliar application of silicon at concentrations of 0, 1.0, 2.0, 3.0, and 4.0 g L^{-1}	Water deficit inhibited plant growth and Si application increased biochemical activities along with transpiration rate and stomatal conductance	[185]
Capsicum annuum	Salinity stress (1500 and 3000 ppm sodium chloride)	Foliar application of silicon	Si application under salinity stress enhanced fruit yield, antioxidant enzyme activity, photosynthesis and water status	[186]
Glycine max L	Light stress	Foliar application of silicon	Si application improved plant growth and development by regulation of genes involved in lignin biosynthesis	[108]
Polianthes tuberosa L	Salinity stress (control, 50 and 100 mM NaCl)	Foliar application of silicon with concentration of (control, 50, 100 and 150 mg L^{-1})	POD, SOD, APX, GR and CAT activities were improved with Si application along with photosynthesis under salinity stress	[187]
Coriandrum sativum L	Lead toxicity stress (0, 500, 1000, and 1500 mg/kg of soil)	Application of silicon nanoparticles (SiNPs) (0 and 1.5 mM)	Foliar application of 1.5 mM SiNPs reduced malondialdehyde accumulation and enhanced SOD, POD and CAT activities	[188]
Zea mays	Salinity stress (150 mM NaCl)	Si $(OH)_4$ applied at concentrations of 2.8, 2.0, 1.6, 0.8 and 0.4 mM	Healthier plant growth Enhanced transpiration, net carbon dioxide assimilation and concentration of carbon dioxide in leaves substomatal	[189]
Vitis vinifera	Salinity stress (20 mM NaCl)	$Na_2Si_3O_7$ applied at concentration of 4 mM	Enhanced activity of APX Decreased content of H_2O_2 and MDA. Decrease stomatal resistance	[190]
Spartina densiflora	Salinity stress (NaCl at 680 and 171 mM	(Na_2SiO_3) applied at concentration of 500 µM	Decreased NaCl concentration in tissues and enhanced rate of photosynthesis, increased water utilization efficiency and healthier growth	[191]

Table 3 (continued)

Plants Species	Stress	Silicon Supplementation	Beneficial Effects	References
Saccharum officinarum	Salinity stress (NaCl applied at concentration of 100 mM)	Ca_2SiO_4 applied at concentration of 2 mM	Decreased NaCl level in tissues Enhanced Ca^{2+} and uptake of K^+. Improved root and shoot dry matter. Enhanced activities of antioxidant enzymes	[192]
Brassica napus	Salinity stress (NaCl applied at concentration of 300 mM)	K_2SiO_3 applied at concentrations of 4 and 2 mM	Enhanced chlorophyll content, improve NR and APX activities, and enhanced photosynthesis, leaf fresh weight, seed yield and leaf area	[193]
Sorghum Bicolor	Drought stress by withholding irrigation	Silicon at a concentration of 200 mg L^{-1}	Enhanced net rate of photosynthesis and reduced ratio from root to shoot by boosting root growth	[194]
Glycine max	Drought stress (0.5 MPa)	Na_2SiO_3 at a concentration of 1.70 mM	Decline in electrolyte leakage and lipid peroxidation Enhanced chlorophyll content and rate of photosynthesis. Increased water holding capacity and growth	[195]
Citrus limon	Cold stress (28 days freezing at 0.5 °C)	K_2SiO_3 at concentrations of 250, 150 and 50 mg L^{-1}	Enhanced concentration of flavonoids and phenolic compounds. Reduced chilling injury and increased fruit quality	[196]
Cucumis sativus	Chilling at 15–8 °C	K_2SiO_3 at concentrations of 0.1 to 1 mM	Improved APX, GR, SOD, GSH, GPX, and MDHAR activities and enhanced AsA content	[197]
Triticum aestivum	Freezing at -5 °C	K_2SiO_3 at concentration of 0.1 to 1 mM	Enhanced quantity of water in leaves and increase antioxidant enzyme activities. Decreased content of MDA and H_2O_2	[198]
Brassica chinensis	Heavy metal stress (0.5 and 5 mg Cd L^{-1})	K_2SiO_3 at a concentration of 1.5 mM	Enhanced activities of CAT, SOD, APX and reduced concentration of H_2O_2 and MDA Reduced Cd uptake and transport from root to shoot	[199]
Oryza sativa	Heavy metal stress (100 µM $K_2Cr_2O_7$)	Na_2SiO_3 at concentrations of 2.5 and 1.25 mM	Reduced Cr uptake and transport. Enhanced concentrationof total soluble proteins, biomass, and seedling height	[200]
Vitis vinifera	Heavy metal stress (H_3BO_3 at concentration of 20 mg kg^{-1})	Na $_2Si_3O_7$ at concentration of 4 mM	Decreased concentration of boric acid in tissues, improved APX and CAT activities,and decreasd MDA and H_2O_2 content,	[190]
Zea mays	Heavy metal stress ($MnSO_4$ at concentrations of 500 and 200 µM	Si $(OH)_4$ at concentration of 1 mM	Detoxified Mn and prevented chloroplast damage	[201]
Glycine max	Ultraviolet radiation at wavelengths of 290–320 nm	Silicon applied at concentration of 1.70 mM	Increased ratio of root to shoot length and biomass Reduced H_2O_2 content and increased photosynthesis	[195]
Cucumis sativus	Heavy metal stress ($CdCl_2$ at 100 µM	Na_2SiO_3 at concentration of 1 mM	Increased intracellular CO_2 concentration, pigment content, and water utilization efficiency	[175]

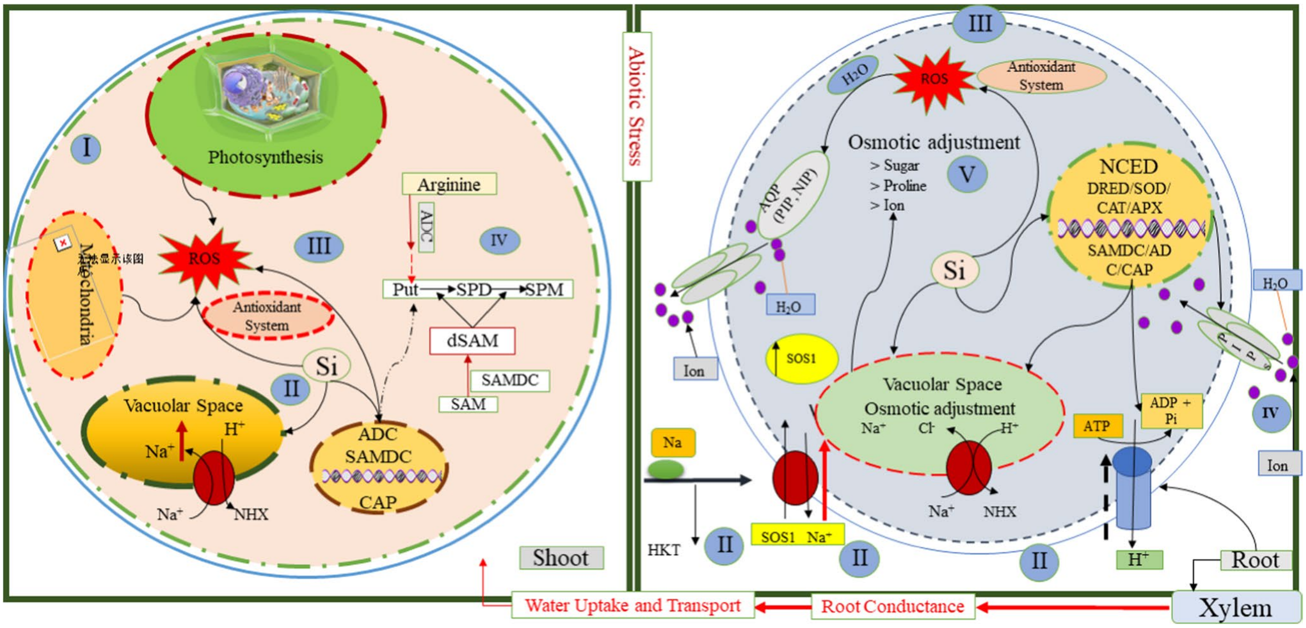

Fig. 2 The pictorial representation of silicon impact on plants under salinity stress. Alleviation of silicon salt stress involves six main strategies: First, Si can increases the photosynthetic activity, increase carbon dioxide utilization rate, increase PS-II activity in reaction center and promote pores opening. Second, Si regulates homeostasis of ions by mediating Na+uptake, compartmentalization, transport and associated genes expressions (e.g. HKT and NHX). Third, Si possesses potential of regulation enzymatic and non-enzymatic concentration/activities of antioxidants and endogenous polyamine accumulation in order to reduce the oxidative stress induced by salt stress. Fourth and fifth, Si improves hydraulic conductance of roots by regulating activities of aquaporin proteins and increasing osmo-regulatory capacities that contributes in an increase in water-uptake and transportation. Sixth, Si might mediate homeostasis of ions and reduces oxidative stress by regulating polyamine metabolism. Single solid red line along bar at the end: process of mediating. Red arrows show up (increase) and down (decrease)

of a silica gel-like structure of silicon dioxide (SiO_2) in the cuticle layer of the rice plants that prevents fungus penetration into the cells, another defensive mechanism of Si against fungal diseases [229, 230]. Si treatment reduced the effects of sheath blight by boosting the crop's defence mechanism against pathogenesis, enhancing the components of phenolic compounds and raising the activities of *β-1*,3-glucanases, polyphenol oxidase, phenylalanine ammonialyase and peroxidase[231]. The destruction from leaf blast and neck in rice could be reduced by application of Si, depending on the Si dose and severity of the disease [232, 233]. Powdery mildew is one of the well-known fungal diseases of plants caused by *Sphaerotheca fuliginea*, that can be prevented by Si treatment [234, 235]. Enhancing the Si concentration in shoots of cucumber reduced the chances of powdery mildew occurrence[154]. It has also been found that Si helped plants to withstand against insect attack such as leaf spider, leaf hoppers, mites, and brown hoppers. Resistance to these insects also depends on the Si concentration within the plant [236].

6.8 Effects of Silicon Against Insect and Other Pests

Insects are some of the most highly diverse living creatures on earth. They are found in every corner of the planet and are composed of more than one million species [237]. They have the ability to adapt to any kind of natural climatic conditions; therefore, they are found in greater number than any other living animals. They play an important role in the surrounding environment and also have shown importance for human beings. About 0.5% of the insect species are pests, and a few of them can be a threat to plants and human beings [238]. Application of Si induces tolerance in plants against insect and pest attack. Several studies have shown that Si supplementation stimulates defence mechanism of plant by developing tolerance against disease caused by insects and pest, such as *Sogatella furcifera, Nilaparvata lugens,* and *Cicadella viridis* [239] (Table 4). *Magnaporthe grisea* is a fungi that attack rice and wheat, form lesions on upper side of leaves, and treatment with Si prevents lesion formation [240, 241]. Si develops resistance in wheat against *Sesamia inferens* and *Scirpophaga incertulas* [55, 239–241].

7 Effects of Silicon Against Fungi and Fungal Diseases

Fungal pathogens are one of the key constraints on production of high-quality crops for human consumption and livestock. Fungicides are chemicals that are produced on large

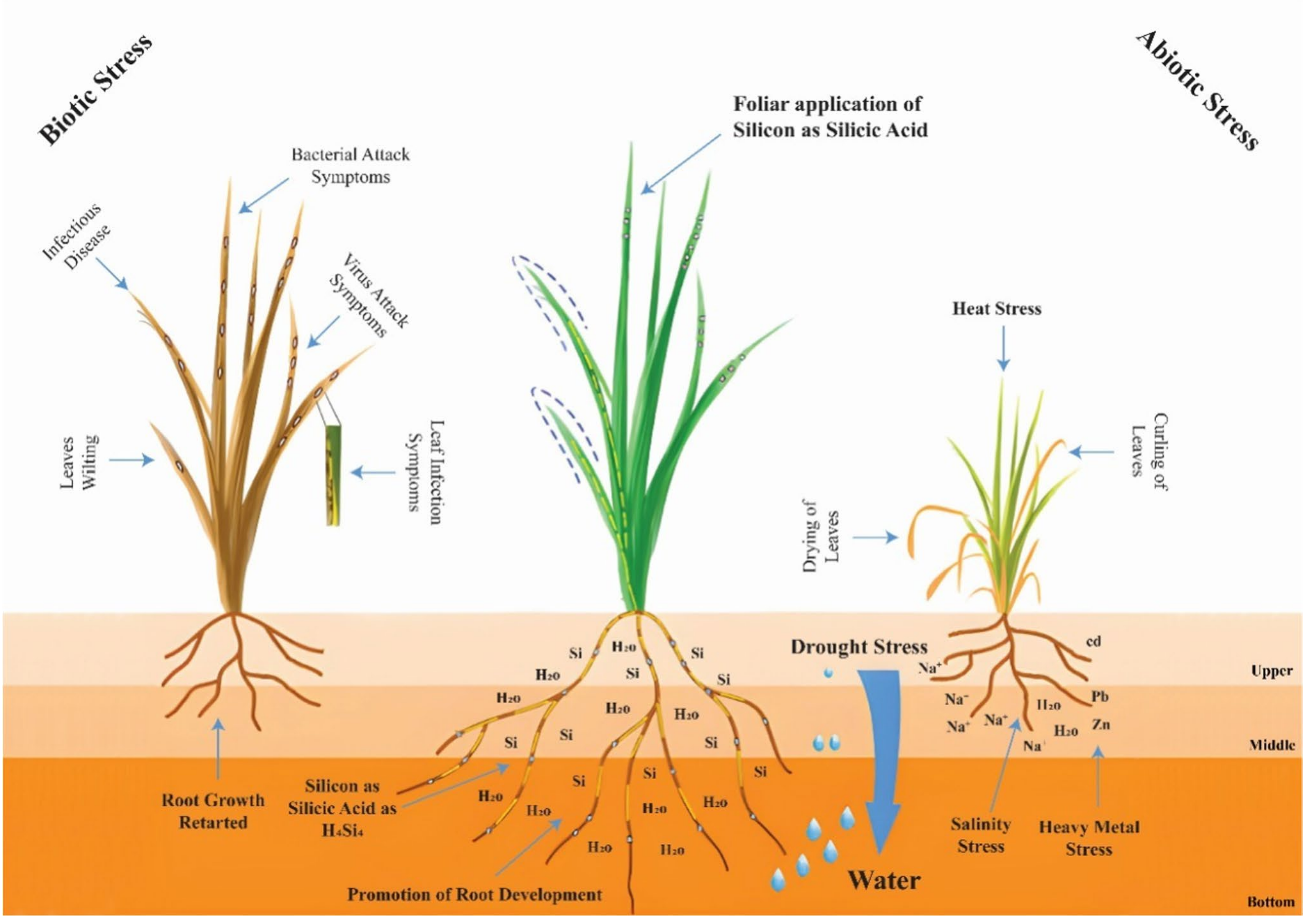

Fig. 3 Role of silicon against biotic and abiotic stresses. Si application either as foliar or fertilizer under biotic stress reduces the severity of disease and helps plants to escape from stress and maintain overall plant growth. Si under abiotic stress reduces the uptake of heavy metals and increases the uptake of water to escape from drought, heat and salinity stresses. Silicon promotes root growth and development and induces salicylic acid (SA) signaling to recognize pathogenic attacks and develop local resistance in infected regions of plants

scale from chemical industries to control diseases caused by fungi. Over use of these chemicals on a large scale affects human health and harms the environment. With the passage of time different strains of fungi have developed resistance against these chemicals, therefore use of Si against fungi is an effective alternative with no side effects on humans or the environment [242]. Si deposition in epidermal tissues of wheat developed a physical barrier against insertion of fungal pathogens into specific tissues. Moreover, Si helps in thickening the cellulose membrane, produces a dense silica layer, and increases the density of the silicified cells present in the epidermis of leaves. Exogenous application of Si in the field is effective in controlling fungal pathogens under natural conditions. Therefore, Si could be included as a defensive component in plans for disease management to substantially decrease losses in yield [243]. Plant height, leaf area, number of tillers, size of panicle, seed yield, and biomass can be increased under field conditions by Si supplementation, and significant levels of tolerance can be developed against fungi [244]. Foliar application of Si against powdery mildew is far more effective than any of the other chemical. Foliar application of Si has the same effects on surface of leaves as uptake via roots from soil or other medium [245].

8 Silicon Against Bacteria and Bacterial Diseases

Si has the ability to develop systemic acquired resistance (SAR) similar to that of commercially available products, like acibenzolar-S-methyl (ASM) and benzothiadiazole (BTH) [246]. Bacterial wilt is a well-known disease of tomatoes caused by bacteria. Research was conducted to evaluate the effect of Si against this bacterial disease in the field. Results showed that exogenous application of Si was highly effective in control of this disease [63]. A few years ago, it was reported that plants that were treated with Si had increased enzymatic activities of defence mechanisms

Table 4 Role of silicon against insects and pests on different plant species

Plant species	Insect or pest	Infestation ↓≈
Triticum. Aestivum L	*Sitobion avenae*	↓
Triticum. Aestivum L	*Schizaphis graminum*	↓
Triticum. Aestivum L	*Aphidius colemani*	≈
Triticum. Aestivum L	*Chrysoperla externa*	≈
Triticum. Aestivum L	*Schizaphis graminum*	↓
Triticum. Aestivum L	*Schizaphis graminum*	↓
Triticum. Aestivum L	*Mayetiola destructor*	↓
O. sativa L	*Chilozacconius*	↓
O. sativa L	*Nilaparvata lugens*	↓
O. sativa L	*Chilo suppressalis*	↓
O. sativa L	*Cnaphalocrocis medinalis*	↓
Z. mays	*Busseolafusca*	↓
Grass spp.	*Spodoptera exempta*	↓
C. sativus	*Tetranychus urticae*	↓
M. truncatula	*Spodoptera exigua*	↓

↑ incr ↓ reduction in insect population, ≈ non-significant effect on insect population

like phenylalanine ammonia-lyase (PAL) and peroxidase (POX). An increase in the activity of these enzymes ultimately helped monocot and dicot plant species develop tolerance against bacterial attack especially on leaves [247]. Si stimulated the expression of those genes, which were involved in plant defences against bacteria, fungi, and viruses [248]. The seedling stage of cereal plants is always considered as critical because at this stage wheat is exposed to many microorganisms. Bacterial attack at this stage results in huge losses of grain yield and total biomass production of wheat. At seedling stage, application of calcium silicate has been found as safeguard for wheat against bacterial leaf streak [249]. Application of calcium silicate at a concentration of 1.14 g/kg against bacterial leaf streak (BLS) was highly effective in cereal crops [250]. Bacterial rice blight is a serious disease of rice responsible for about 60% loss of rice yield. The causal organism of this disease is *Xanthomonas oryzae*. Application of Si in high concentration to rice reduces bacterial rice blight up to 75% during the growing season [70, 251].

9 Concluding Remarks and Future Directions

In this review, we have discussed the importance of Si, its transport from roots to shoots, the associated biochemical changes and regulations of the transport genes in monocot and dicot plant species under biotic and abiotic stresses. Biofortification strategies can help in increasing the intake of Si in order to overcome deficiencies in plants in a cost-effective way. Exogenous applications or applications in the growth media have found to have significant effects on plant fitness, vigour, growth, and development under abiotic and biotic stresses. Si concentration in soil varies from region to region and country to country. For good performance of plants in stressed environments, Si is required in high concentration. ROS are generated during stress, possess highly active species like singlet oxygen and hydrogen peroxide, which by perturb the normal biochemical and physiological processes of plants. Si application increases the production of antioxidant enzymes like POD, SOD, and CAT, and thus reduces oxidative stress. Further research is still required to determine the optimal moderate concentration of Si, which is advantageous for improving plant growth and performance, specifically to avoid Si toxicity. Identification of novel genes or gene families and up- or down-regulation of genes associated with Si accumulation at moderate concentration in plants through genetic engineering might help in the reduction of environmental pollution caused by toxic chemicals applied on plants under biotic stress. Marker assist breeding (MAB) or marker assist selection (MAS) might help in the identification of novel genes and the genetic diversity among different plant species for Si uptake and accumulation through use of DNA markers such as SSR, RFLP, and RAPD.

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Data Availability NA.

Declarations

Competing Interests The authors declare no competing interests.

Ethics Approval The authors declare that there was no Ethics problem.

Consent to Participate The authors declare their consent to participate.

Consent for Publication The authors declare their consent to publication.

Research Involvement with Human Participants/ or Animals The research does not involve human and animal participants.

Informed Consent I have read and I understand the provided information and have granted permission to ask the questions. I understand my participation in the research and liable to produce the given information at any stage.

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