

Review

Advances in Understanding Silicon Transporters and the Benefits to Silicon-Associated Disease Resistance in Plants

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Abstract: Silicon (Si) is the second most abundant element after oxygen in the earth's crust and soil. It is available for plant growth and development, and it is considered as quasi-essential for plant growth. The uptake and transport of Si is mediated by Si transporters. With the study of the molecular mechanism of Si uptake and transport in higher plants, different proteins and coding genes with different characteristics have been identified in numerous plants. Therefore, the accumulation, uptake and transport mechanisms of Si in various plants appear to be quite different. Many studies have reported that Si is beneficial for plant survival when challenged by disease, and it can also enhance plant resistance to pathogens, even at low Si accumulation levels. In this review, we discuss the distribution of Si in plants, as well as Si uptake, transport and accumulation, with a focus on recent advances in the study of Si transporters in different plants and the beneficial roles of Si in disease resistance. Finally, the application prospects are reviewed, leading to an exploration of the benefits of Si uptake for plant resistance against pathogens.

Keywords: Silicon; transporter; disease stress; disease resistance



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1. Introduction

In recent years, plant disease incidence has been rising gradually with changes in climate, cultivation habits, crop varieties of crops and some human-made factors. During growth and development, plants may will be affected by a variety of diseases, with the degree of damage gradually increasing. Difficulties in disease prevention and control are increasing instead of decreasing, which seriously threatens food security and farmers' ability to increase both yield and income [1,2]. At the beginning of the 21st century, rice stripe leaf blight broke out in a large area of involving Jiangsu and Henan provinces [3], having a great negative impact that resulted in heavy losses to local rice growers. In southwestern Europe, a region known for its grape cultivation, a disease caused by phytoplasma called *Flavescence doree* is widespread and is a major cause of annual economic losses [4]. Potato virus disease generally reduces potato production by 20–50%, and more than 80% in severe cases, resulting in smaller tubers [5]. During the tomato planting process, late blight, early blight, gray mold and leaf mold occur frequently, which intensifies the use of chemical pesticides and seriously hinders development of "green" agriculture and rural areas [6].

Silicon (Si) is the second most abundant element in the earth's crust. Due to its role in promoting plant growth and development, it has received extensive attention from researchers. It acts as a beneficial element and increasing Si fertilizer applications improve fruit quality. In addition, it enhances plant photosynthetic potentials [7]. Studies have shown that Si can effectively alleviate abiotic stresses [8], including drought [9],

radiation [10], salinity [11] and heavy metal-induced toxicity [12]. In addition, Si can effectively enhance the resistance levels of different plants to pests and pathogens [13]. Thus, Si plays very important roles in ameliorating plant resistance to biotic and abiotic stresses.

A large number of data showed that Si improves plant resistance to a variety of diseases, such as blast [14] and sheath blight [15] in rice, powdery mildew in wheat and other crops [16,17], as well as tomato bacterial wilt [18]; Si is taken up by roots in the form of orthosilicic acid $[\text{Si}(\text{OH})_4]$, an uncharged monomeric molecule, when the solution pH is less than 9. Three types of Si uptake in higher plants have been proposed: active, passive and rejective. However, the silica content varies greatly among different plant species. The Si content in the leaf sheaths of rice can reach 20%; those of graminaceous plants, such as barley and wheat, can reach approximately 2–4%, but the Si contents in most legumes and other dicotyledons are less than 1%.

Ma et al. [19] found and cloned the first Si transporter gene *Lsi1* in rice and proved that the *Lsi1* gene functions to transport silicic acid into root cells. The Si content in rice is significantly reduced after the *Lsi1* gene is deleted, and the yield and disease resistance of rice are also significantly reduced. In recent years, homologous genes have been found in barley [20], maize [21], pumpkin [22], horsetail [23], wheat [24], soybean [25], cucumber [26] and tomato [27]. The discovery of Si transporter genes provided direct molecular evidence for studying Si functions, which provide molecular basis for Si transport and uptake, and this enhances our understanding of the molecular mechanism responsible for disease resistance in plants. In this review, research progress on Si, Si transporters and their beneficial roles in disease resistance are summarized, and existing issues in the field are discussed to provide effective directions and methods for using Si to increase disease resistance in plants.

2. Distribution of Si in Plants

All plants contain Si in their bodies, but its accumulation varies widely among species. Generally speaking, the Si content in a monocotyledonous plant is significantly higher than that in a dicotyledonous plant [28]. On the basis of the different Si content in plants, plants are divided into three types: high, such as horsetail and rice, containing 10–15% Si, intermediate, such as sugarcane, containing 1–3% Si, and low, such as tomato and pea, containing less than 0.5% Si [12]. In addition, the types of Si accumulation by plants can also be divided into three types: active, passive and rejective, on the basis of the Si/Ca ratio. An Si/Ca ratio greater than 1 indicates active uptake, ratios of 0.5–1 indicate passive uptake, and ratios less than 0.5 suggest exclusion [29].

However, the Si concentrations in different parts of the same plant also show large differences. The Si distribution types in the same plant are as follows: (1) low-Si plants with approximately the same Si content as the root system or a slightly higher root system content, such as tomato and cabbage; (2) middle-Si plants in which the Si content in shoots is much lower than that in roots, such as crimson clover, which has a root level that is approximately eight times that in shoots; (3) high-Si plants in which Si mainly accumulates in shoots, such as rice and oats [30].

Most of the Si in plants is distributed in the apoplast; consequently, Si in rice mainly accumulates in the cell wall, cell lumen and intercellular space or between the epidermal cells and the stratum corneum. The Si deposits in the epidermal cells of rice leaves forms a cuticle–Si double layer. In a leaf sheath, Si is deposited in the cell walls of the epidermis and parenchyma. In stems, it is mainly distributed in the cell walls of epidermal cells, vascular bundles, sclerenchyma and parenchyma. In inflorescence and rice husks, it is mainly deposited in the space between the cuticle and epidermal cells and in vascular bundles. The Si distribution in the roots is relatively uniform, but mainly concentrated in maturation zone, with less Si being deposited in the elongation zone [31].

3. Uptake, Translocation and Accumulation of Si in Plants

The uptake of Si from the soil depends mainly on the plant species and the chemical form of the Si in the soil. The only form of Si that can be absorbed by plants is monosilicic acid (chemical formula: $\text{Si}(\text{OH})_4$). Mitani et al. [32] reported that Si uptake in rice, cucumber and tomato is from soil to root, from root to cortical cells and then to xylem vessels. However, the Si concentration in the symplast is higher than that in the soil. Additionally, Si accumulation in rice is three to five times higher than in cucumber or tomato. The uptake and transportation of Si differ among various plants. In addition, it has been reported that the radial transport of Si is mediated by a type of transporter with a K_m value of 0.15 mM in all species. However, the different V_{\max} values have the following order: rice > cucumber > tomato. It has been reported that the uptake of Si in rice is an energy-dependent process that works even at low temperatures or even in the presence of metabolic inhibitors [32]. The Si concentration in the xylem sap of rice is much higher than those in cucumber and tomato. Furthermore, the xylem loading of Si is mediated by a transporter in rice, whereas in cucumber and tomato Si xylem loading occurs by diffusion. Thus, the Si transporter in rice shoots is the most decisive factor affecting its high-level accumulation. However, the lower levels of Si accumulations in cucumber and tomato may be due to lower densities of Si transporters to take up Si from external solutions and the lack of, or defective, xylem loading transport. Gong et al. [27] suggested that the low Si accumulation in tomato results from the low efficiency of Si export from the endodermis, resulting in extremely low root-to-shoot translocation of Si and subsequent low accumulation in the shoots. In the xylem loading process, after taking up Si from the external solution, it is transported to the xylem. At present, the specific mechanism of xylem loading of Si remains unclear [33]. It has been suggested that Si is transferred to the shoot through the xylem, and when the silicic acid concentration exceeds 2 mM, the silicic acid polymerizes to form silica gel ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$). Whereas the Si concentration in xylem sap is usually greater than 5.0 mM, it remains unclear how high concentrations of silicic acid remain unpolymerized in xylem sap. There are no silicate complexes in rice xylem sap that may prevent Si polymerization in xylem tissues [32,34].

Ma et al. [31] reported that, after Si was transferred from the root, silica in the form of hydrated polymers was deposited in the cell walls of stems, leaves and fruit shells. In the shoot, silicic acid is further concentrated and polymerized by transpiration. As the concentration of silicic acid increases, it is eventually converted to silica gel. The distribution and accumulation of Si in the shoots depends on the transpiration rate, and their deposition occurs below 0.1 mm of the cuticle layer, forming a cuticle-Si double layer. Silica-motor cells and silica cells are two forms of silicified cells present in rice leaves, and they form different shapes after accumulating in specific cells [35].

In addition to being applied to the soil, Si is also applied to the foliage. Different types of Si-containing compounds are used as foliar sprays, such as silicates, stabilized silicic acid and Si nanoparticles (Si-NPs) [36]. Positive effects of foliar Si applications have been observed in accumulating and non-accumulating Si plant species [37–40]. Despite the observed benefits of foliar applications, the mechanisms of Si uptake and transport in leaf cells are not well understood. Further research is needed to study the Si transport mechanism in the shoots at the molecular level.

4. Si Transporters

Exley et al. [41] reported that silicic acid is co-transported by aquaporins. Aquaporins belong to the major intrinsic protein family and help transport various types of substrates, such as Si, boron, urea, carbon dioxide and hydrogen peroxide [42]. Plant aquaporins are categorized into seven subfamilies. Their specificity is governed by four amino acid residues (aromatic/arginine selectivity filters) located at specific positions. Jadhao et al. [43] indicated that the Si transporters Lsi1 and Lsi6 belong to the nod26-like major intrinsic protein (NIP2) subfamily. Moreover, they are all influx transporters of Si. The aromatic/arginine (ar/arg) region and proton repulsion are major factors in the selective

transport of molecules, and they play key roles as primary filters of the pores. Plant silicon transporters, such as OsLsi1, AtLsi1 and ZmLsi1, absorb and accumulate Si in different parts of plants (Table 1).

Table 1. Si content and Si transporters in various plants with different Si uptake types.

Si Accumulation	Species	Si Content (%d.w.)	Si Transporter	Reference
High	Horsetail	10% [44]	EaLsi2-1; EaLsi2-2	[23,45]
	Rice	10% [35]	OsLsi1; OsLsi2; OsLsi3; OsLsi6	[19,46–48]
	Maize	4–7.5% [49]	ZmLsi1; ZmLsi2; ZmLsi6	[50]
	Barely	2–4% [49]	HvLsi1; HvLsi2; HvLsi6	[20,51]
Intermediate	Cucumber	2–4% [49]	CmLsi1; CmLsi2	[26,52]
Low	Tomato	<0.2% [49]	SlLsi1; SlLsi2	[27]
	Potato	<0.5% [53]	StLsi1; StLsi2	[54]
	Soybean	<0.5% [55]	GmNIP2-1; GmNIP2-2	[25]

4.1. Influx and Efflux of Si Transporters in Rice

Rice requires a large amount of Si to improve its growth, development and yield; consequently, the first Si-influx transporter was identified from rice. Ma et al. [35] found that a mutant Si transporter (*Lsi1*) was defective in Si uptake in rice, and further isolated mutant seeds from a Germanium (Ge)-containing environment. Ma et al. [19] used map-based cloning to clone *OsLsi1* on the second chromosome of rice. It consists of four introns and five exons, and the cDNA content is 1409 bp, containing 298 aa. On the basis of a BLAST search and CLUSTALW analysis, it is speculated that *Lsi1* belongs to the NIP subfamily. It has been predicted that the *Lsi1* amino acid sequence contained six transmembrane regions conserved in typical aquaporins and two Asn-Pro-Ala motifs.

Ma et al. [19] conducted a series of experiments on transgenic rice and concluded that the *Lsi1* promoter region tagged with GFP is located in the lateral and main roots of plants, but they do not exist in root hairs. This result indicates that only the roots are involved in the uptake of Si. A subcellular localization of *Lsi1* revealed that cells expressing *Lsi1*-GFP fusion only displayed GFP signals on the plasma membrane. Therefore, *Lsi1* is localized in the distal regions of the endodermis and exodermis of the root [56]. In addition, abscisic acid and dehydration stresses inhibit and down-regulate the expression of *Lsi1*. Injections of *Xenopus laevis* oocytes showed that *Lsi1* is a bidirectional transporter of silicic acid [21]; however, it only exhibits the function of Si uptake into rice roots [56]. *OsLsi1* is an import transporter of Si in rice roots, primarily responsible for Si transport from external solutions into root cells. The expression of the Si transporter was found to follow a diurnal pattern in the maturation zones of root tips. This typically results in the fluctuating expression of the *Lsi1* transporter of Si in many monocots, with *Lsi1* expression being highest from 12 PM to 12 AM and then declining from 4 AM to 8 AM. Moreover, *Lsi1* shows differential expression at each growth stage. Studies have shown that approximately 60% of Si is taken up by transporters at the beginning of the rice reproductive period. The depletion of Si at this time leads to a reduction in the number of grains; conversely, high yields require more Si. By comparing the transgenic material with the wild type, it has also been confirmed that the *OsLsi1* transporter plays a key role in the uptake of Si in rice, increasing the uptake and accumulation of Si, thereby enhancing the activity of antioxidant enzymes and improving the morphological traits of rice [57].

After cloning the *Lsi1* transporter gene, an export transporter gene *Lsi2*, located on chromosome 3, was cloned. The gene contains one intron and two exons, and its full-length cDNA is 1416 bp, encoding 472 aa [46]. Based on a BLAST search and CLUSTALW analysis, *OsLsi2* is a putative anion transporter, and it is not similar to the Si-influx transporter *OsLsi1*. The subcellular localization of *Lsi2* confirmed that it is also expressed on the

plasma membrane. *Lsi2* also localizes on exodermal and endodermal cells; however, unlike *Lsi1*, *Lsi2* is located proximally. This gene's activity is opposite to the uptake activity of *Lsi1* in *X. laevis* oocytes, as shown by heterologous expression experiments. This indicates that *OsLsi2* cannot transport Si from an external solution into cells, and the transporter *OsLsi2* only has the function of Si export, with the Si exporting activity being silicon is inversely proportional to the acidity of the medium. The addition of three protonophores, 2,4-dinitrophenol, carbonylcyanide 3-chlorophenylhydrazone and carbonylcyanide *p*-(trifluoromethoxy) phenylhydrazone and a low temperature treatment significantly reduced the Si export activity, which differed from *OsLsi1* (Figure 1). Therefore, it has been concluded that *OsLsi2*-mediated Si transport is an active transport process driven by a proton gradient [46]. Due to the different localization and transport properties of *OsLsi1* and *OsLsi2* in rice root cells, deletion of any of these genes results in a dramatic decrease in the rice uptake of Si [50]. It has been speculated that the two proteins have a synergistic effect on Si absorption in rice. The identification of this Si transporter revealed a unique mechanism of nutrient transport in plants: an influx transporter on one side of the cell and an efflux transporter on the other to ensure efficient nutrient transport across cells.

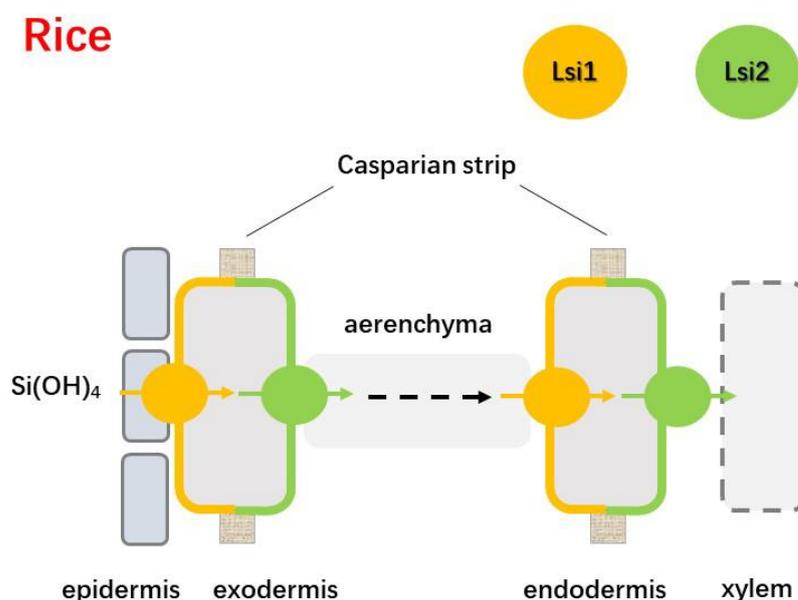


Figure 1. Schematic model of the Si transport system in rice.

In recent years, homology-based studies of the rice genome found that *Lsi6* and *Lsi1* have a close homologous relationship. However, after verifying the expression of *Lsi6* in different tissues, in contrast with *Lsi1* and *Lsi2*, *Lsi6* is expressed in leaf sheaths, leaves and root tips. A knockout of *Lsi6* affected the distribution of Si in the shoots. Moreover, a knockout of *Lsi6* did not affect the uptake of Si by the roots, but resulted in the accelerated excretion of Si in the spit fluid. These results suggest that *OsLsi6* is a transporter involved in the transport of Si out of the xylem and in the distribution of Si in leaves.

Yamaji et al. [47] showed that *OsLsi3* also has a Si export transport activity. In addition, we expressed *Lsi3* in the *lsi2* rice mutant under the control of the *Lsi2* promoter. In the above two independent transgenic lines, the introduction of *Lsi3* significantly increased the Si uptake. Unlike *Lsi2* and *Lsi6*, *Lsi3* shows no polar distribution, and *OsLsi3* localizes apolarly in the parenchyma between enlarged and diffuse vascular bundles. Similar to that of *Lsi6*, knockouts of *Lsi2* and *Lsi3* reduced Si distributions in panicles but increased Si in flag leaves. Among them, the Si content in the panicle decreased the most after knocking out *Lsi6*.

The high Si accumulation in rice is mainly related to the Si transport gene expression pattern and its root structure. The polar localizations of *Lsi1* and *Lsi2* on the same cell and the double-layer structure of the Casparian are important factors in the active Si uptake

system [58]. In fact, the absence of Casparian strips in the endodermis significantly reduces Si uptake [59]. The expressions of *OsLsi1* and *OsLsi6* in rice roots were down-regulated after a Si application in the external environment. In diatoms (high-Si accumulating model plants), the gene *SIT*, encoding the Si transporter, is also down-regulated after exogenous Si application. This is an important signaling process for diatoms to perceive the Si concentration in the external environment. Studies have shown that another necessary condition for high-Si accumulation in rice is the down-regulation of Si transport genes in response to exogenous Si applications [60]. Therefore, it is very likely that a diatom-like mechanism exists in rice.

4.2. Brief Introduction of Si Transporters in Some Other Plants

4.2.1. Barley and Maize

Various plants accumulate Si, which helps improve resistance against all sorts of abiotic and biotic stresses. The Si-influx and efflux transporters HvLsi1 [20], HvLsi2 [51] and HvLsi6 [51] are found in barley. Bombardment of rice epidermal cells with *HvLsi1*-GFP complexes demonstrated that HvLsi1 is localized to the plasma membrane. HvLsi1 is a Si import transporter involved in the radial transport of Si through the epidermis and cortex of basal region of seminal roots [20]. Moreover, HvLsi2 localizes at the parenchyma cell layer adjacent to the transfer cells (Figure 2). The Si translocated via the enlarged vascular bundles is unloaded to the transfer cells by HvLsi6, then Si is reloaded into the diffuse vascular bundles connecting the upper part of the plant by HvLsi2.

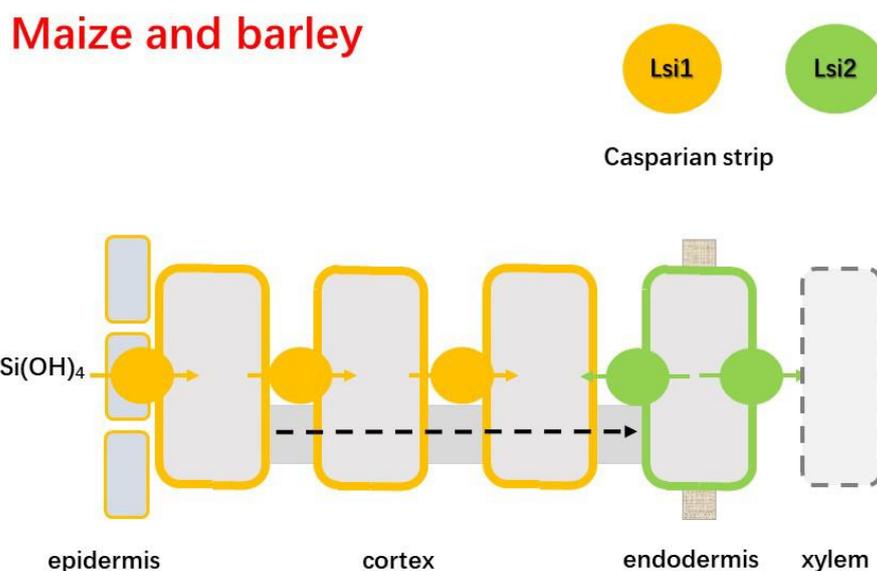


Figure 2. Schematic model of the Si transport system in both maize and barley.

The high accumulation of Si also occurs in maize and is responsible for these three transporter genes, *ZmLsi1*, *ZmLsi2* and *ZmLsi6* [50]. *ZmLsi1* is expressed in roots, whereas *ZmLsi6* is expressed in leaves and leaf sheaths. In contrast to rice influx transporters, their expressions are thought to be unaffected by the exogenous supply of Si (Figure 2).

The Lsi1 and Lsi2 proteins of maize and barley reveal that their Si uptake systems are different from that of rice. This difference is due to the different localization patterns of Si-influx and -efflux transporters on different cells. HvLsi2/*ZmLsi2* only localizes to endothelial cells at the base of radicle and lateral roots, and it has not been found to have a polarity distribution similar to that of *OsLsi2* [21,50].

4.2.2. Cucumber

Similar to maize and barley, the Lsi1 and Lsi2 transporters of cucumber are found in every cell of the root with non-polar localization on the cell membrane [26]. A single

amino acid change in the *Lsi1* transporter of cucumber, and its improper localization results in reduced Si uptake. However, the expression of *Lsi1* occurs in the endodermis and exodermis with a polar distribution, *Lsi2* are in endodermal cells (Figure 3) [52]. Studies have shown that the two Si transporters in cucumber have distinct circadian expression patterns in leaves and roots.

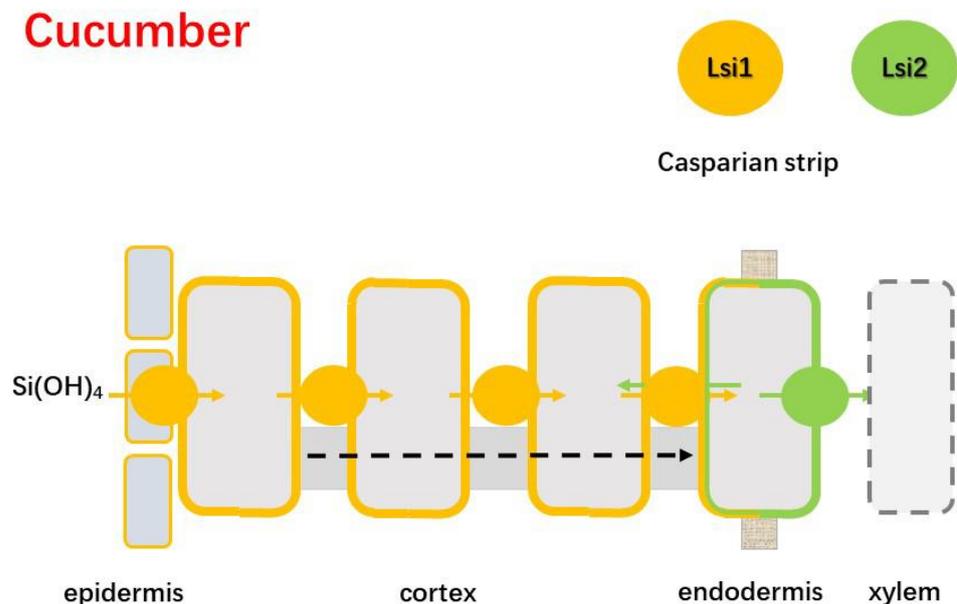


Figure 3. Schematic model of the Si transport system in cucumber.

4.2.3. Tomato

Using the whole-genome sequence of tomato, a NIP subfamily gene was identified and isolated. This gene is highly homologous to the reported rice *OsLsi1* amino acid sequence, so it was named *SILsi1* [28]. The full-length *SILsi1* gene is 1109 bp, with an ORF of 852 bp, encoding a 284-aa protein. The amino acid sequence of *SILsi1* is predicted to contain six transmembrane regions and two Asn-Pro-Ala motifs. *SILsi1* exhibits Si transport activity in both the rice *lsi1* mutant and *X. laevis* oocytes. The expression of *SILsi1* in the roots is constitutive. Using immunostaining, *SILsi1* was located on the plasma membrane of the root tip and basal region and showed no polar distribution. In addition, the overexpression of *SILsi1* in tomato increased the Si concentrations in the root and root cell sap but had no effect on the Si concentration in the shoot, suggesting that *SILsi1* is a functional Si import transporter. However, after expressing the cucumber functional gene *CsLsi2* in tomato, the uptake of Si in tomato was significantly increased, resulting in increased Si accumulation in leaves and enhanced leaf tolerance to water shortage and high temperature. The findings suggest that the low Si accumulation in tomato is attributable to the lack of a functional Si efflux transporter *Lsi2* for active uptake of Si, despite the functionality of *SILsi1* (Figure 4) [27].

4.2.4. Horsetail

Horsetail, as a pteridophytic plant, has extremely high Si accumulation ability and is a very important model plant, but it has been neglected in Si research [45]. Two putative Si-efflux transporter genes, *EaLsi2-1* and *EaLsi2-2*, have been identified using the sequenced horsetail transcriptome. The sequences of these genes have very low similarity to their homologues in higher plants. The localization of *EaLsi2-1* to the plasma membrane has been verified by subcellular localization. It was confirmed that *EaLsi2-1* is an effective Si-efflux transporter by heterologous expression experiments in which it was injected into *X. laevis* oocytes [23].

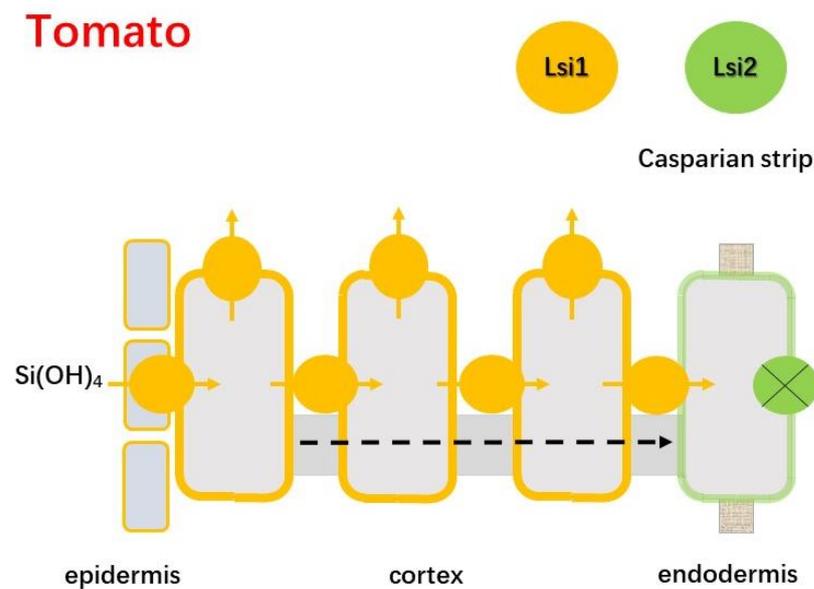


Figure 4. Schematic model of the Si transport system in tomato.

4.2.5. Potato

Vulavala et al. [54] isolated the transporter *StLsi1* that has a conserved amino acid domain for Si transport. It has been verified by Rt-PCR that *StLsi1* is only expressed in roots and leaves, and the signal amount increases after Si fertilizer applications. However, *StLsi2* is expressed in all cells, but the expression did not increase after Si applications. The expression of *StLsi1* in roots and leaves increased two-fold after Si applications and increased approximately five-fold in leaves after an interaction between Si and drought. Despite the up-regulation of *StLsi1* expression, the low accumulation of Si in potato roots and leaves may result from its low transport activity.

4.2.6. Soybean

Deshmukh et al. [25] cloned two putative Si transporter genes, *GmNIP2-1* and *GmNIP2-2*, from soybean. Both are expressed in roots and shoots and decrease as Si increases. When the protein encoded by *GmNIP2-2* is expressed in *Xenopus* oocytes, it functions in Si transport, thereby confirming the genetic ability of soybean to absorb Si. Using genome-wide analysis of major intrinsic proteins, we identified two influx transporters in soybean and confirmed their irreplaceable roles in the Si uptake of this species. Studies have also shown that Si-influx and efflux transporters act synergistically to regulate the accumulation of Si in soybean.

5. Silicon Accumulation Improves Plant Disease Resistance

As early as 2007, a study showed that the susceptibility of the rice silicon uptake-deficient mutant *lsi1* to rice blast was significantly higher than that of wild-type rice [61]. Ma et al. also reported that the brown spot indices of mutant *lsi1* and wild-type rice were significantly reduced by 88% and 53%, respectively, in the presence of Si. Additionally, it has been shown that the functional Si transporter *Lsi1* is beneficial to the increase in the Si concentration in rice husks, which improves its resistance to brown spot disease [62]. However, the resistance mechanism is not completely clear and also has been the subject of debate. On the basis of domestic and foreign research (Table 2), its possible potential mechanisms include two aspects: physical and biochemical barriers.

Table 2. Studies showing the beneficial role of Si in alleviating disease-associated stress.

Types of Disease	Plant	Disease Response of Si Deposition	Pathway	References
Fungal pathogen	Tomato	Improve resistance to anthracnose	Physical and Biochemical Barriers	[63]
		Improve resistance to root rot	Physical Barriers	[64]
		Improve resistance to early blight	Biochemical Barriers	[65]
	Pumpkin	Improve resistance to powdery mildew	Physical Barriers	[16]
	Oil palms	Improve resistance to powdery mildew	Physical Barriers	[66]
	Coffee	Improve resistance to leaf rust	Physical Barriers	[67]
	Pepper	Improve resistance to Phytophthora blight	Physical Barriers	[68]
	Sorghum	Improve resistance to leaf spot	Physical Barriers	[69]
	Rice	Improve resistance to brown spot	Physical Barriers	[62]
		Improve resistance to leaf Scald	Physical Barriers	[15]
		Improve resistance to rice blast	Physical Barriers	[14,70]
		Improve resistance to sheath blight	Physical and Biochemical Barriers	[71]
	Wheat	Improve resistance to leaf blast	Physical Barriers	[72]
		Improve resistance to tan spot and fusarium head blight	Physical Barriers	[73]
Bacterial pathogen	Beans	Improve resistance to Phytophthora blight	Biochemical Barriers	[74]
		Improve resistance to frog-eye leaf spot	Biochemical Barriers	[75]
		Improve resistance to anthracnose	Biochemical Barriers	[76]
	Perennial Ryegrass	Improve resistance to leaf spot	Biochemical Barriers	[77]
	Bitter melon	Improve resistance to powdery mildew	Biochemical Barriers	[78]
	Maize	Improve resistance to leaf spot	Physical and Biochemical Barriers	[79]
	Cotton	Improve resistance to <i>Fusarium oxysporum</i>	Physical and Biochemical Barriers	[80]
	Rose	Improve resistance to powdery mildew	Physical and Biochemical Barriers	[81]
	Potato	Improve resistance to late blight	Biochemical Barriers	[82]
	Tomato	Improve resistance to bacterial wilt	Biochemical Barriers	[18,83,84]
	Melon	Improve resistance to bacterial fruit blotch	Physical Barriers	[85]
	Banana	Improve resistance to black sigatoka	Physical Barriers	[86]
	Beans	Improve resistance to leaf spot	Physical Barriers	[40]

5.1. Formation of Physical Barriers as Influenced by Si

The formation of physical barriers is one of the mechanisms by which plants control diseases. Precipitation of amorphous silica in plants is a mechanical barrier [87,88]. The hypothesis of potential physical barrier formation depends on the type of Si depositions in the leaves, especially in the cell walls. In fact, it was widely believed for many years that polymeric Si in plant cell walls and apoplast can prevent the penetration of pathogens [69]. SIs are mainly deposited in the epidermal cells of leaves and leaf sheaths, forming silicified cells and a cuticle–Si double-layer structure, which can enhance the mechanical strength and stability of the host plant cell wall, thereby delaying and resisting the invasion and expansion of pathogens. Studies on the resistance of tomato to root rot disease caused by *Fusarium* [64], of oil palm to stem rot [60], of coffee to leaf rust [67], of pepper to *Phytophthora capsici* [68], are all examples of Si increasing plant disease resistance using physical mechanisms.

5.2. Formation of Biochemical Barriers as Influenced by Si

Recent studies have shown that the biochemical mechanisms of Si play more important roles in improving plant disease resistance than the physical mechanisms [78]. The main

way to resist the invasion of pathogenic bacteria through physiological and biochemical defense mechanisms is to increase the activity of plant leaf protective enzymes, such as peroxidase, polyphenol oxidase and phenylalanine ammonia-lyase, and induce the host to synthesize secondary metabolic antimicrobial compounds, such as phenolic metabolic products, phytoalexins and pathogenesis-related proteins. Thus, Si activates the plant's inductive defense system and enhance the resistance to pathogenic bacteria.

The biochemical mechanisms of Si mainly include three aspects. One is to enhance the activity of protective enzymes related to plant disease resistance, such as peroxidase (POD), phenylalanine ammonia-lyase (PAL) and polyphenol oxidase (PPO), as well as enhance membrane integrity and stability, thereby maintaining plant cell membrane permeability [89]. Protective enzymes are not only involved in the metabolism of phenolic substances, but also in the synthesis and accumulation of secondary metabolic antimicrobial compounds such as lignin which are regarded as regulators of the entire metabolic pathway. In particular, the two main components of fungal cell wall chitin and β -1,3-glucan are degraded by chitinase (CHT) and β -1,3-glucanase, respectively. Some reports have shown that the activities of CHT, POD and PPO in leaves of cucumbers inoculated with *Podosphaera xanthii* are enhanced after Si applications [90]. In addition, Si applications in peas can also reduce the incidence of leaf blight by enhancing the activities of CHT and β -1,3-glucanase [76]. Increased resistance to brown spot in rice treated with Si fertilizers is also associated with enhanced CHT and POD activities [91]. These findings indicate that the accumulation of Si can enhance the activities of plant leaf protective enzymes and that changes in secondary metabolic antimicrobial compounds play substantial roles in plant disease resistance.

The second aspect is to increase resistance by inducing secondary metabolites. Briefly, Si can improve the host's resistance to disease by inducing the production of secondary antimicrobial compounds such as phytochemicals, lignin, phenolic substances and pathogen-related proteins. Among secondary metabolites, Si-mediated regulation of phenolics has been extensively studied. Studies have shown that phenolic compounds such as hydroxycinnamate and flavonoids act as ROS scavengers, preventing the accumulation of ROS by activating antioxidant enzymes, such as guaiacol peroxidases [92]. Several studies have also shown that the beneficial effects of Si on plant disease resistance can be attributed to the induction of phenolic compounds. For example, Shetty et al. [93] showed that exogenous application of Si stimulates the accumulation of phenolic compounds in rose to enhance its resistance to powdery mildew. Similarly, Si enhances rice resistance to bacterial leaf blight by stimulating the accumulation of soluble phenols and lignin in rice leaves and the activities of PPO and PAL [94]. Si enhances chestnut resistance to chestnut blight by increasing the synthesis of phenolic compounds in leaf tissues [95]. Fawe et al. [96] first extracted a phytoalexin (3, 5, 3c, 4c-tetrahydroxy-7-O-methoxy flavone) from powdery mildew-infected cucumber leaves treated with Si. It is believed that Si participates in the antibacterial activities of the invaded host, causing the plant to produce some small molecular metabolites (such as flavonols). In contrast to salicylic acid or jasmonic acid-induced plant resistance, soluble Si acts as a regulator of plant resistance induction, allowing plants to defend against pathogen attack faster or more effectively. The Si accumulation plays a preventive role but does not directly affect plant metabolism. The rice treated with Si after inoculation produce large amounts of phenolic substances and phytochemicals, thereby enhancing the resistance of rice to rice blast [97]. Moreover, plant terpenoid metabolites play important roles in adaptation to adverse environments, such as those with biotic and abiotic stresses [98]. A study has shown the accumulation of diterpene phytoalexins in rice as a potential mechanism against rice blast [99]. Finally, nitrogen-containing metabolites are an important class of secondary compounds in plant defense, especially in mitigating oxidative damage. When pathogens infect plants, plant tissues accumulate large amounts of polyamines, which limit the growth and reproduction of plant pathogens [100].

The third is the molecular mechanisms, Si and Si transporters induce gene expression associated with plant defense mechanisms, interact with disease-resistant signal molecules,

such as salicylic acid, jasmonic acid and ethylene for signal transduction [101]. Studies have found that Si applications can induce the transcription of PR-1 and peroxidase genes closely related to disease resistance, thereby enhancing the resistance of tomato to early blight [65]. Furthermore, Si can resist *Ralstonia solanacearum* by inducing the expression of the tomato transcription factor *WRKY1* and the disease-resistance response protein ferritin and trehalose phosphatase genes [102]. In addition, *Arabidopsis* overexpressing the wheat Si-influx transporter gene *TaLsi1* showed enhanced resistance to powdery mildew.

5.3. Application of Si in Plant Diseases

The role of Si in enhancing plant resistance to various disease stresses has been confirmed, indicating that Si can be used as a conventional fertilizer in most plants. The solid and liquid form of Si fertilizer enhances plant resistance to various pathogens. Liquid potassium silicate or sodium silicate can be applied to soil irrigation or foliar application, while solid calcium silicate fertilizers are integrated into the soil. In a field study, 15 kg of Si fertilizer per 100 m² significantly reduced the average incidence of fusarium wilt [103]. Application of calcium silicate at a rate of 5 metric tons ha⁻¹ reduced the incidence and severity of ryegrass rice blast by 39.5% and 47.3%, respectively [77]. The application of Si in the substrate and foliar spraying of Si reduce the severity of bacterial spots and the area under the disease curve in melon [104]. A 2mM concentration potassium silicate foliar spray applied to common bean plants decreased anthracnose disease severity by 34% [105]. In field trials, the application of solid Si fertilizer, Si foliar fertilizer, and both significantly reduce the incidence and disease index of *Sclerotinia sclerotiorum* rot, with no negative effects on major agronomic traits and seed quality [106]. Soluble Si could be a useful tool in integrated management against fusarium head blight pathogens by reducing the disease development on wheat [107]. The external application of Si can effectively reduce the disease index and incidence of sugarcane disease caused by *Xanthomonas albilineans* [108]. The application of slag-based fertilizer to Si-deficient paddy soil is necessary for improving both rice productivity and brown spot resistance [109].

6. Future Perspectives

Diseases caused by pathogens such as fungi or bacteria threaten plant growth and development, especially during the production of horticultural crops. In agricultural production, chemical measures such as pesticide spraying are mainly adopted for disease prevention and control. With the improvement in living standards, the safety of agricultural products has attracted more attention from consumers. It is now urgent to adopt safe, efficient and “green” methods to control various disease-related stresses and improve crop yields and quality. Although Si is the second most abundant element in the earth’s crust, it is not defined as an essential element for plants. However, its roles in regulating plant responses to various diseases and stresses have been demonstrated. The external application of Si helps to reduce the spraying of pesticides and has broad application prospects in the “green” and environmentally friendly management of agriculture. Therefore, understanding the transport of Si from soil into plant cells and the accumulation of Si in plants is essential. In plants, Si transport is an active process, regulated by the specific Si transporters, *Lsi1*, *Lsi2* and *Lsi6* which play roles in different parts of the plant. Thus, it is necessary to further study Si transporters in other plants to promote the effective transport of Si. Despite numerous reports on the beneficial roles of Si in enhancing plant resistance to pathogens, it was mainly analyzed from the aspects of physical barrier, physiology and biochemistry, whereas the potential mechanisms related to Si remain largely unclear. In future research, transcriptome, proteome and metabonomics techniques should be used to carry out systematic and comprehensive analyses, in order to clarify the exact pathways of Si and its transporters, to understand their regulation and influence on the transcriptional pathways, as well as the changes of induced metabolites. This will help provide a basis for a “green”, safe and effective method to regulate against crop adversity.

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