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REVIEW

Silicon acquisition and accumulation in plant and its significance for agriculture

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Abstract

Although silicon (Si) is ubiquitous in soil and plant, evidence is still lacking that Si is essential for higher plants. However, it has been well documented that Si is beneficial for healthy growth of many plant species. Si can promote plant mechanical strength, light interception, as well as resistance to various forms of abiotic and biotic stress, thus improving both yield and quality. Indeed, application of Si fertilizer is a rather common agricultural practice in many countries and regions. As the beneficial effects provided by Si are closely correlated with Si accumulation level in plant, elucidating the possible mechanisms of Si uptake and transport in plants is extremely important to utilize the Si-induced beneficial effects in plants. Recently, rapid progress has been made in unveiling molecular mechanisms of Si uptake and transport in plants. Based on the cooperation of Si influx channels and efflux transporters, a model to decipher Si uptake, transport and distribution system in higher plants has been developed, which involves uptake and radial transport in root, xylem and inter-vascular transport and xylem unloading and deposition in leaf. In this paper, we overviewed the updated knowledge concerning Si uptake, transport and accumulation and its significance for the major crops of agricultural importance and highlighted the further research needs as well.

Keywords: silicon, uptake, transport, Si-based fertilizer, agriculture

1. Introduction

Silicon (Si), an essential element for animals and human beings, is a broadly recognized beneficial but not essential element for higher plants (Epstein 1994; Liang *et al.* 2015). Although the essentiality of Si for plant has not been proven yet, beneficial effects of Si in promoting plant growth, especially for plants under stressful conditions, have been verified in both laboratory experiments and field trials. Silicon could ameliorate detrimental effects of many abiotic (e.g., heavy metals, nutrient deficiency and imbalance, salt, drought, extreme temperatures, UV-B radiation) and biotic (e.g., insect pests and pathogen diseases) stresses, thereby stimulating plant growth (Ma 2004; Liang *et al.* 2007; Guntzer *et al.* 2012; Van Bockhaven *et al.* 2013; Hernandez-Apaolaza 2014; Zhu and Gong 2014; Adrees *et al.* 2015; Pontigo *et al.* 2015; Coskun *et al.* 2016; Wang *et al.* 2017).

As a long-time overlooked nutrient element in plant, Si is receiving more and more attention due to its importance and beneficial effects in plant physiology and agriculture. Obviously, plants with different Si accumulation abilities will benefit from external Si supply in varying degrees. Researches show that the beneficial impacts are actively associated with Si accumulation rates in plants which significantly differ between and within plant species (Epstein 1999; Hodson et al. 2005). In recent molecular studies on Si uptake and transport, a large group of proteins and genes with distinct characters have been found to be responsible for Si transport from soil solution into root and from root to shoot in varying plant species (Ma and Yamaji 2015). And the species and tissues which have different levels of Si accumulation can be, at least partially, explained by the differences in existence, density and localization of the complex Si transport protein system.

Si has also been proven to be an "agronomically essential" element which could improve the yields and qualities of a large group of crops (Mayland et al. 1991; Savant et al. 1999; Alvarez and Datnoff 2001; Vulavala et al. 2016). Application of Si fertilizers to croplands, especially those with low-available Si, is a rather common and routine agricultural practice in many countries (like China, Japan, Korea, Brazil, USA, etc.) for high productivity and sustainable production (Ayres 1966; Ma and Takahashi 2002; Liang et al. 2015). Recent researches also focus on the use of Si in different agricultural systems with distinct aims like biofuel plant production, animal-feeding plants yield and livestock nutrition, etc. (Agbagla-Dohnani et al. 2003; Van Soest 2006; Zhang et al. 2015; Smith et al. 2016). In this review, we provide an updated overview of Si uptake, transport, distribution and accumulation systems in plants and the roles of Si in agricultural practices.

2. Si in soil and plant

Si is a tetravalent metalloid and the second most abundant element both on the surface of the Earth and in soil, comprising approximately 28% of the Earth's crust (Epstein 1994). Nevertheless, most Si exists in soil in the form of insoluble crystalline aluminosilicates, which are not directly available for plants (Richmond and Sussman 2003; Liang et al. 2015). Monosilicic acid, the soluble form of Si in soil solution, which could be taken up by plant root, occurs as an uncharged monomeric molecule (H_4SiO_4) at pH values ranging from 2 to 9 (Knight and Kinrade 2001). The concentration of plant-available monosilicic acid ranges from 0.1 to 0.6 mmol L^{-1} in soil solution, which is, for instance, hundred times higher than plant-available phosphorus (Tisdale et al. 1993; Epstein 1994, 1999; Gunnarsson and Arnorsson 2000). The relative higher concentration of

monosilicic acid in soil solution is still much less than that in saturated solution (about 2 mmol L^{-1}). The concentration of available Si is dominated by soil parent materials and factors that could affect Si adsorption-desorption process in soil such as pH, water status, temperature, and accompanied ions. The significant difference of available Si between soil types indicates that specific soil types could be Si deficient. For instance, highly-weathered acid soils in tropical and subtropical areas are proven to be Si-depleted in the early time (Ayres 1966; Cheong and Halais 1970). However, the measured plant-available SiO_2 content in calcareous paddy soils can be as high as 250–380 mg kg^{-1}. Research results demonstrate that calcareous soil is also Si-deficient because part of plant-unavailable Si bound to carbonate can be extracted by the acetate buffer solution (Liang et al. 1994).

Silicon has been found in the tissues of virtually all terrestrial plant species with its concentration in shoot varying between 0.1 and 10% on a dry weight basis (Epstein 1999; Richmond and Sussman 2003; Ma et al. 2011; Liang et al. 2015). In higher plants (Angiospermae), only few taxa show high (>4% Si; Cyperaceae, Poaceae and Balsaminaceae) to moderate (2–4% Si; Cucurbitales, Urticalesand Commelinaceae) accumulation of Si, whereas most species accumulate Si at a relatively low level (Ma and Takahashi 2002; Hodson et al. 2005). Yet, a genotypic variation of Si concentration in shoot has been found both within and among plant species, although the former variation is usually much lower (Deren 2001; Ma et al. 2003; Broadley et al. 2011). Phylogenetic studies show that the difference in existence, density, localization of proteins related to Si transport would be responsible for the distinct capacities of Si accumulation in plant kingdom.

Despite its ubiquity and abundance in both soil and plant, Si has not been fully accepted as an essential element for higher plants according to the criteria of essentiality of element established by Arnon and Stout (1939) except certain species like horsetail (Lewin and Reimann 1969). So far convincing evidence that could prove the necessity of Si for completion of the whole life cycle of rice is still lacking due to the extreme difficulty in growing plants with Si contamination excluded thoroughly. However, when grown under Si-deficient conditions, lowland rice (Oryza sativa) showed necrosis on mature leaves and wilting of plants, followed by inhibited vegetative growth and grain yield decline (Lewin and Reimann 1969). Rice mutants defective in Si uptake (discussed in next chapter) also showed growth limitation compared to wild type when grown in same condition (Ma et al. 2006, 2007). In contrast, no direct evidence has been found that excessive Si has detrimental effects on plant growth and development up to now. Epstein (1994) suggested that Si could be "quasi-essential" for rice and many other crops.

Plant is a major component of Si geochemical cycle in soil with multiple roles like biosilicification and silicate weathering (Cooke and Leishman 2011; Trembath-Reichert et al. 2015). A research in Hawaiian Island shows the amount of silicon in stream from litter biosilica is much higher than that from mineral-water interaction (Derry et al. 2005). However, different terrestrial ecosystems like forest and grassland have distinct Si cycle models (Watteau and Villemin 2001; Conley 2002). It should be stressed that silica harvest in agricultural systems could alter Si flow and cycle, and its ecology impact on global Si cycle needs further research (Vandevenne et al. 2012). More and more studies also focus on phytolith-occluded carbon in plants including rice, bamboo, and grass, etc. and its related ecology effects (Parr et al. 2010; Song et al. 2012, 2013).

3. Si uptake, transport, distribution and accumulation systems in plant

Plants take up Si in the form of undissociated molecule of orthosilicic acid (H_4SiO_4), which is the sole molecular species likely to cross plant root plasma membrane at physiological pH ranges (Epstein 1994; Raven 2003). Due to the significant difference in plant ability to accumulate Si, the mechanisms of Si uptake by root obviously differ among plant species. Takahashi et al. (1990) proposed three possible uptake types of Si for higher plants in relation to water uptake: active (faster/higher than water uptake), passive (similar speed to water uptake), and rejective (slower/lower than water uptake). Plants with an active Si uptake system would cause significant Si depletion thus reducing Si concentration in the nutrient solution; whereas for plants taking up Si passively, Si concentration in the solution would remain unchanged. In contrast, plants with a rejective type of Si uptake tend to increase Si concentration in the external medium (Fig. 1-A). Passive transport by diffusion and/or by facilitated diffusion via proteinaceous channels is a concentration-dependent component of Si uptake, which is present in all plant species regardless of their abilities to accumulate Si (Raven 2003). Active uptake, a concentration-independent component of Si transport, has been identified in various Si-accumulating plant species including both high and intermediate accumulators.

It has been reported that most monocots, such as rice (Takahashi et al. 1990; Tamai and Ma 2003), wheat (Triticum aestivum) (Jarvis 1987; Rains et al. 2006), ryegrass (Lolium perenne) (Jarvis 1987; Nanayakkara et al. 2008), barley (Hordeum vulgare) (Nikolic et al. 2007), maize (Zea mays) (Liang et al. 2006) and banana (Musa spp) (Henriet et al. 2006) as well as some cyperaceous plants, take up Si actively. On the contrary, most dicots take up Si passively (Takahashi et al. 1990), whereas some dicots such as

cucumber (Cucumis sativus) (Liang et al. 2005a; Nikolic et al. 2007), sunflower (Helianthus annuus L.) and wax gourd (Benincasa hispida L.) (Liang et al. 2006) take up Si actively. On the other hand, some dicots such as tomato (Lycopersicon esculentum) and faba bean (Vicia faba) are found to exclude Si from their roots (Takahashi et al. 1990; Liang et al. 2005a; Nikolic et al. 2007). In fact, active and passive components of Si uptake machinery coexist in the roots of high and intermediate Si accumulators, with their relative contribution being dependent upon plant species and external Si concentration (Liang et al. 2006) (Fig. 1-A).

It has also been shown that the active uptake of silicic acid is an energy-dependent process and plant species differing in Si accumulation level have a silimar K_m value of 0.15 mmol L^{-1} while the V_{max} is significantly different, suggesting the involvement of specific Si transporters. Phylogenetic researches show distinct transport system between higher plants and diatom, a typical Si accumulator, because no homologue of diatom Si transporters (SIT) was found in higher plants (Hildebrand et al. 1997; Tamai and Ma 2003; Mitani et al. 2005; Ma and Yamaji 2006). Since the first gene encoding Si transport protein in higher plants, OsLsi1, was identified in rice, two groups of proteins mediating Si transport have been found in higher plants including Si channel (e.g., OsLsi1, OsLsi6) and Si efflux transporters (e.g., OsLsi2, OsLsi3) (Ma et al. 2006; Ma and Yamaji 2006, 2015). A model of Si uptake, transport and distribution system in higher plants which could be subdivided into three parts (uptake and radial transport in root; xylem and inter-vascular transport; xylem unloading and deposition in leaf) is roughly established based on the cooperation of influx and efflux transport proteins.

3.1. Si uptake and radial transport in root

Rice Lsi1 (OsLsi1) is the first gene identified in higher plants responsible for Si influx from external solution into root cells using a rice mutant (lsi1, low silicon 1) defective in active Si uptake (Ma et al. 2002, 2006). After OsLsi1, rice Lsi2 (OsLsi2), the first gene encoding Si efflux transporter, was also cloned using a novel rice mutant (lsi2, low silicon 2) defective in Si uptake (Ma et al. 2007). Besides in rice, Lsi1 and Lsi2 have also been identified in barley (HvLsi1, HvLsi2) (Chiba et al. 2009; Mitani et al. 2009a), maize (ZmLsi1, ZmLsi2) (Mitani et al. 2009a, b), wheat (TaLsi1) (Montpetit et al. 2012), pumpkin (Cucurbita moschata, CmLsi1) (Mitani et al. 2011), soybean (Glycine max, GmNIP2-1, GmNIP2-2) (Deshmukh et al. 2013), cucumber (CSiT1, CSiT2, CsLsi1) (Wang H S et al. 2015; Sun et al. 2017) and horsetail (EaNIP3-1, EaNIP3-3, EaNIP3-4, EaLsi2-1, EaLsi2-2) (Gregoire et al. 2012; Vivancos et al. 2016).

OsLsi1 and its homologues encoding Si influx channels
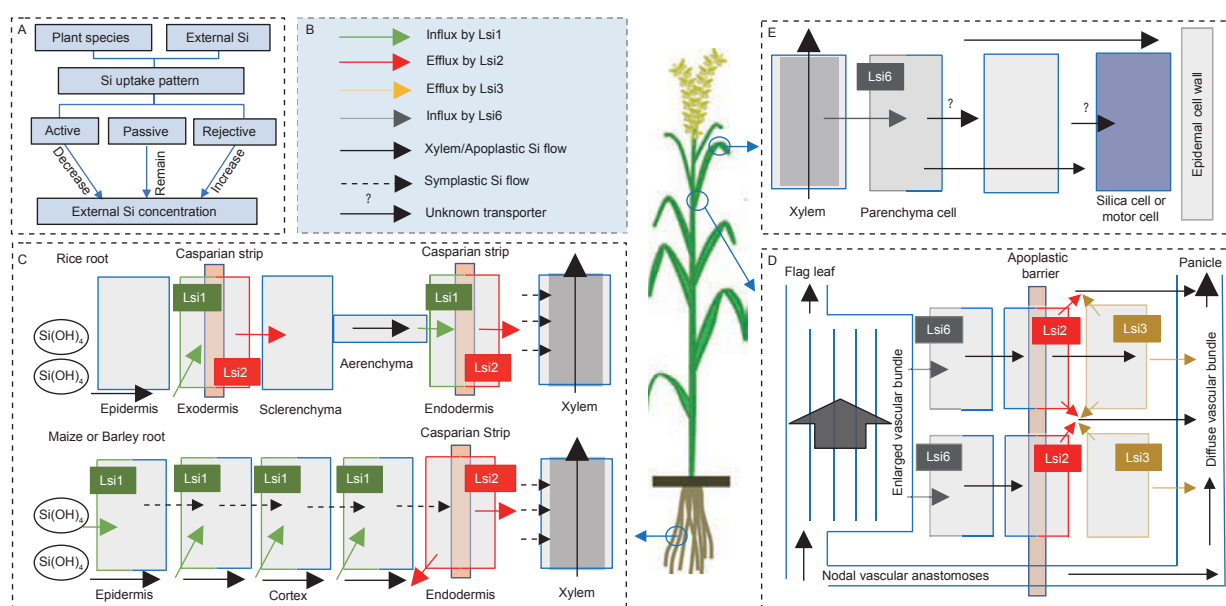
Fig. 1 A schematic model of silicon (Si) transport in plants modified from Ma and Yamaji (2015) and Yamaji et al. (2015). A, three types of Si uptake. B, arrows with different colors or symbols showing different Si flow in C–E. C, two possible Si uptake and radical transport pathways in root. D, possible Si transport and distribution model in node. E, possible Si unloading and deposition pathway in leaf.

all belong to the noduline-26 major intrinsic protein (NIP), a subfamily of plant aquaporin (AQP) which has six well-conserved transmembrane domains. NIP could facilitate transmembrane transport of water and/or some small uncharged molecules like glycerol, ammonia, boron acid etc. (Bienert et al. 2011). The selectivity of AQP is determined by two conserved motifs and an aromatic/arginine (ar/R) selectivity filter comprising four amino acid residues (Quigley et al. 2002; Tajkhorshid et al. 2002; Tornroth-Horsefield et al. 2006). All Lsi1s except that of horsetail belong to NIP3 and show distinctive ar/R selectivity filter (Gly (G), Ser (S), Gly (G), Arg (R), GSGR) (Wu and Beitz 2007; Ma et al. 2008; Ma and Yamaji 2008; Mitani et al. 2011). However, Lsi1 in horsetail has a STAR ar/R filter and shows more sequence homology to NIP2 (Gregoire et al. 2012). GSGR and STAR are the only two filters found yet that could form constriction pores allowing silicic acid to permeate. It should be stressed that Lsi1 in horsetail has a higher permeability of Si than that of OsLsi1, which could be dependent on the difference between two ar/R filters. Besides well-conserved ar/R filter, all Lsi1s have two conserved Asn-Pro-Ala (NPA) motifs (Ma and Yamaji 2015) and phylogenetic research results show that a precise space of 108 amino acids between the two NPA motifs is also essential for Si permeability in all Lsi1s known yet (Deshmukh et al. 2015).

OsLsi2 and its homologues are predicted to encode active efflux Si transporters, Lsi2. Lsi2 protein, which is predicted to have 11 transmembrane domains, belongs to a putative anion-channel transporter family with no similarity to Lsi1 and is responsible for Si transport out of the root cells (Yamaji and Ma 2011). Lsi2 activity is inhibited by low temperature, protonophores (e.g., DNP, CCCP and FCCP), and higher external pH values (Ma et al. 2007). In consideration of the activity inhibition mentioned above, Lsi2 seems to be an active efflux transporter which can transport silicic acid against the concentration gradient. Yet, a $H^+/Si(OH)_4$ symport and involvement of H^+-ATPase in energizing this secondary active transport seem to be most likely (Ma et al. 2011).

Although all Lsi1s show high identities among plant species, and so do Lsi2 transporters, Lsi1s and Lsi2s in different plant species have distinct localizations which, in turn, affect Si uptake and radial transport in root. OsLsi1 and OsLsi2 are localized to the plasma membrane of both exodermis and endodermis, where the Casparian strips would impede Si apoplastic transport. Both transporters show polar localization, with OsLsi1 localized at the distal side of both exodermal and endodermal cells and OsLsi2 at the proximal side (Yamaji and Ma 2006, 2007, 2011). However, influx and efflux transporters in barley and maize (HvLsi1/ZmLsi1 and HvLsi2/ZmLsi2) are localized in different cells. HvLsi1/ZmLsi1 is polarly localized to epidermal, hypodermal and cortical cells at the distal side, while HvLsi2/ZmLsi2 is localized exclusively on the endodermis without polarities (Chiba et al. 2009; Mitani et al. 2009a, b). These differences of localizations result in

two differential pathways of Si transport from the external solution to the xylem vessels in barley/maize and rice (Ma *et al*. 2011; Ma and Yamaji 2015). In rice, Si is taken up from the external solution by OsLsi1 at the distal side and released into the apoplast of aerenchyma by OsLsi2 at the proximal side of exodermal cells, and Si is then transported into the stele by both OsLsi1 and OsLsi2 through the endodermal cell layer (Fig. 1-C). In barley and maize roots, Si can be taken up from external solution by HvLsi1/ZmLsi1 localized at the distal side of epidermal and cortical cells and then transported symplastically to the endodermis and then released by Si efflux transporter (HvLsi2/ZmLsi2) followed by transport to the stele apoplastically (Fig. 1-C).

3.2. Si distribution and accumulation in plants

Although xylem transport of Si is driven by transpiration stream, some tissues with low transpiration rates can accumulate Si at extremely high level (e.g., rice husk). The imparity between transpiration rate and Si accumulation level in specific tissue implicates the existence of metabolism-controlled distribution of root absorbed Si. Recent researches show that the node, where the vascular systems are highly developed, is the key position regulating Si distribution at the reproduction stage (Ma *et al*. 2011; Yamaji *et al*. 2015). At the first node below the panicles, there are two different vascular bundles: enlarged vascular bundle (EVB) and diffuse vascular bundle (DVB). Large and small vascular bundles come from the lower nodes and connect to the flag leaf (both enlarged at the node region). DVBs are parallel to and surround EVBs and connect to the panicle. Therefore, the inter-vascular transfer of Si across the parenchyma cell bridge (PVB) between two kinds of vascular bundle is required in regulating distribution of Si to panicle and flag leaf (Ma *et al*. 2011).

Yamaji *et al*. (2015) showed that three transporters (Lsi2, Lsi3, and Lsi6), located at the node, are involved in the inter-vascular transfer in rice. Lsi2 is polarly localized to the bundle sheath cell (BSC) layer around the EVBs, which is next to the xylem transfer cell (XTC) layer where Lsi6 is localized, while Lsi3 is located in the parenchyma tissues between EVBs and DVBs without polarity. Knockout of each of *OsLsi6*, *OsLsi2* and *OsLsi3* decreased Si accumulation in the panicle, but increased Si accumulation in the flag leaf (Yamaji and Ma 2009) and knockout of *OsLsi6* resulted in the largest decline of Si in panicle (Yamaji *et al*. 2015). In rice nodes, there are two different ways of inter-vascular transfer of Si between DVB and EVB. First, Si could be transported through nodal vascular anastomoses (NVAs) from EVB to DVB, which is independent from Si transporters. The amount of Si transported by NVA is so low that cannot afford the high accumulation of Si in husk. Another possible way is Si transporter-mediated PVB transport. Based on the experiments with mutants and in silico simulation results, a possible model involving three Si transporters is found to be responsible for Si distribution in node. Lsi6 appears to be a transporter involved in transfer of silicic acid from the EVBs coming from the roots to the XTCs and then moved symplastically across the BSCs through Lsi2. Before being reloaded to the DVBs connected to the panicles, Lsi3 could transport Si across parenchyma cell layers (Yamaji *et al*. 2015). Once across the apoplastic barrier in BSCs, Si could also be transported apoplastically with a fusion of efflux flow mediated by Lsi2 and Lsi3 from PVB cells (Fig. 1-D).

In barley, HvLsi6 and HvLsi2 are found at the parenchyma cells adjacent to the transfer cells, suggesting that both transporters are involved in the inter-vascular movement of Si at the nodes in barley. In addition, HvLsi6 is also found to be localized in the outer parenchyma cells surrounding phloem besides xylem parenchyma cells. In conclusion, Si can be translocated through the EVBs and unloaded to the transfer cells by HvLsi6, followed by HvLsi2 to reload Si to the DVBs and panicles (Yamaji *et al*. 2012).

3.3. Si xylem unloading and deposition in leaves

Once transported *via* Lsi1 and Lsi2 into the stele, Si is then translocated to the shoot by transpiration stream through the xylem. More than 90% of Si taken up by root is translocated to shoot (Ma and Takahashi 2002), albeit some amount of Si can be deposited in the cell wall of root and xylem vessels (Balasta *et al*. 1989), which may prevent the vessels from compression when the transpiration rates are high (Raven 1983). The concentration of Si in the xylem sap of Si-accumulating plant species can be several-fold higher than the critical concentration for polymerization of silicic acid *in vitro*, however such extremely high concentrations are present transiently with no tendency towards polymerization. And xylem Si concentration shows high correlation with the ability of Si accumulation in different plant species (Mitani *et al*. 2005; Mitani and Ma 2005).

Finally, before being deposited on the epidermis cell walls as well as the specific shoot cells, Si must be transported out of the xylem *via* specific Lsi6 transporter (Fig. 1-E). This protein is responsible for the transport of silicic acid from the xylem into xylem parenchyma cells (xylem unloading), thereby influencing subsequent Si distribution and deposition within shoots. The gene encoding for the Lsi6 transporter has been characterized in rice (*OsLsi6*) (Yamaji *et al*. 2008), barley (*HvLsi6*) (Yamaji *et al*. 2012), and maize (*ZmLsi6*) (Mitani *et al*. 2009a). OsLsi6 is an influx Si transporter and a homologue of OsLsi1 (Yamaji *et al*. 2008). Like *OsLsi6*, *ZmLsi6* and *HvLsi6* also express in both roots and shoots and show polar localization in the xylem parenchyma cells

that are adjacent to the vessels in both leaf sheaths and leaf blades (Mitani *et al*. 2009b; Yamaji *et al*. 2012).

After being translocated to the shoots as discussed above, silicic acid is further concentrated through loss of water derived from the transpiration process and then polymerized to amorphous silica ($(SiO_2)_n\times nH_2O$; known in minerals as opal) with no need of energy at the concentrations exceeding 2 mmol L^{-1} (Mitani *et al*. 2005; Ma and Yamaji 2006). Amorphous silica seems to be virtually the only form of Si accumulated mainly on the cell wall of leaves, stems, and hulls (Prychid *et al*. 2003; Ma and Yamaji 2006). To a lower extent it can also be deposited on the cell wall of root endodermis cells (Lux *et al*. 2003) and tubers (Chandler-Ezell *et al*. 2006). In the leaf epidermis cell wall, a hydrated amorphous polymer (opal) can form silica-cuticle double layers, and can be deposited in specific silicified cells as well (Ma and Takahashi 2002; Prychid *et al*. 2003). In the leaves of Si-accumulating species such as rice, wheat and bamboo, phytoliths are found in specific cells so-called silica cells located on vascular bundles and/or present as silica bodies in bulliform cells, fusoid cells or prickle hairs (Guntzer *et al*. 2010). Proportions and locations of phytoliths vary with not only the species, but also the age of a plant (Sangster *et al*. 2001).

3.4. Mechanisms of high accumulation of Si in rice

As the beneficial effects of Si in plants show active correlations with Si accumulation levels in plants, it is extremely important to investigate into the mechanisms of Si uptake, distribution and accumulation in plants in order to introduce the beneficial effects of Si to plants with moderate and low ability to accumulate Si. As a typical Si accumulator and model plant in Si research, rice could accumulate Si in shoot at a high level relative to many other plants. Recent researches showed the high accumulation of Si in rice was related to Si transporters and casparian strips (Sakurai *et al*. 2015).

As a key player in controlling Si uptake, distribution and accumulation in plants, genes encoding Si transporters show species-specific expression pattern in response to external Si. When Si is supplied in medium solution, the expression of *OsLsi1* and *OsLsi6* are down-regulated while *HvLsi1*/*ZmLsi1* and *HvLsi6*/*ZmLsi6* remain unchanged. At the same time, the expression of *Lsi2* in all three types of plants is down-regulated. These expression differences induced by external Si between plant species may determine the Si accumulation abilities of different species as recent research shows it is necessary in rice to down-regulate *OsLsi1* and *OsLsi2* expression for high Si accumulation in the shoot (Mitani-Ueno *et al*. 2016; Sakurai *et al*. 2017). The expression pattern of *OsLsi1* has some similarity to that of *SIT* in diatom in which the down-regulated expression of

Si transporter genes is considered to play a role in sensing Si concentration in external solution (Thamatrakoln and Hildebrand 2008; Shrestha and Hildebrand 2015). Also, Si transport related genes show spatial expression patterns. *OsLsi1* and *OsLsi2* are constitutively expressed in the roots and much higher in the mature root zones (>10 mm) than in the root tips (Ma *et al*. 2007; Yamaji and Ma 2007). This difference is attributed to the anatomical difference between root tips and mature roots where casparian strips are formed. Homologs of rice *OsLsi1* and *OsLsi2* in barley (*HvLsi1*, *HvLsi2*) and maize (*ZmLsi1*, *ZmLsi2*) also show similar expression patterns (Mitani *et al*. 2009a, b; Montpetit *et al*. 2010, 2012).

Because of the special trait of rice root, two layers of casparian strip in both exodermis and endodermis play an important role in improving shoot Si accumulation probably by preventing Si leaking and facilitating root-to-shoot Si transport (Sakurai *et al*. 2015). And in silico simulation modeling research shows that the localization pattern of Si transporters in wild-type rice is the most efficient one in Si uptake and transport. However, a transgenic experiment to introduce pumpkin *CmLsi1* (no polar localization) into rice root shows polar localization of *CmLsi1* similar to the pattern of *OsLsi1* when expressed under *OsLsi1* promoter. In conclusion, differences in transporter allocations, related genes expression patterns and plant root anatomic traits seem to be responsible for distinct Si accumulation abilities in plant kingdom. Besides genes expression, the regulators of transporter activity are equally important in regulating Si transport in plants. Recently, non-specific phospholipase C1 (NPC1) was found to change Si concentration in node and distribution to flag leaf through regulating phosphorous acid metabolism which could, in turn, affect Lsi6 transport activity (Cao *et al*. 2016).

4. Si in agricultural production

As discussed above, soil available Si concentration differs significantly with soil types which can be one of the major factors limiting crop production in certain regions. Crops with large Si demand, such as rice and sugarcane, would show significant growth limitation and yield decline when grow in low-Si soils. To remedy the Si deficiency and promote crop production, several Si sources have been taken as Si fertilizer including slag-based silicate, soluble potassium or sodium silicates, slow-releasing potassium silicate manufactured from feldspar etc. (Liang *et al*. 2015). It has been well-documented that Si-based fertilizers can enhance the growth, yield and quality of a wide range of crops that are of agricultural and horticultural importance (Savant *et al*. 1997, 1999; Wang *et al*. 2001; Guntzer *et al*. 2012). The crops exhibiting positive responses to Si fertilization include

typical cereal crops such as rice and wheat, as well as sugarcane, however, some of these crops proven to respond positively to Si addition are even not Si accumulators (e.g., tomato, see Liang *et al*. 2015).

Large-scale field application of Si fertilizers can be traced back to the 1950s in Japan and the 1960s in South Korea, which contributed significantly to high and sustainable rice production and stable food supply (Park 2001; Ma and Takahashi 2002). Si fertilization is also a rather common agricultural practice in Southeast Asia including China, Thailand, the Philippine, Ceylon, Vietnam, Sri Lanka and India, as well as in South, North and Central America (Datnoff *et al*. 1992; Liang *et al*. 1994, 2015; Savant *et al*. 1997; Alvarez and Datnoff 2001; Korndorfer and Lepsch 2001). In a review article by Wang *et al*. (2001), field application of Si fertilizer increased rice yield by up to 4-fold in 16 provinces of China from 1979 to 1999 with averaged yield increment of 10%. The results from fifty field experiments conducted in northeast China show that addition of slag-based Si fertilizer increased rice yield by 3.5 to 28.5% in paddy soils derived from meadow soil, black soil, chernozem and bleaching soil which differ greatly in soil properties and availability of Si (Liang *et al*. 2015).

Sugarcane is another typical Si-accumulating plant species that is highly Si-responsive. It is documented that the aboveground parts of 12-month aged sugarcane contained 379 kg ha^{-1} of Si, compared to 362 kg ha^{-1} of K and 140 kg ha^{-1} of N (Samuels 1969). Because of the large demand of Si, Si deficiency symptoms are frequently observed in the field condition, for example, soil available Si concentration of less than 110 mg SiO$_2$ kg^{-1} could result in Si-deficiency symptoms in sugarcane such as twisted leaves and leaf freckling (Wang *et al*. 2001). Si deficiency is one of the major edaphic factors limiting yield and quality of sugarcane grown on highly weathered tropical soils (typical Si-deficient soils) including Oxisols, Ultisols, Entisols and Histosols (Savant *et al*. 1999; Meyer and Keeping 2001). The efficacy of Si fertilizers on yield increment in sugarcane has been proven in many field trials including Hawaii, Mauritius, Puerto Rico and Florida (Ayres 1966; Fox *et al*. 1967; Samuels 1969; Anderson 1991). The sugarcane yield increment due to field application of silicate slag ranged from 10 to 50% on the Si deficient soils in Asia like China, Indonesia, Malaysia and Pakistan (Liang *et al*. 2015). The field experiments conducted in South America, Australia, and South Africa also show that Si fertilizers are effective in increasing sugarcane yield (Savant *et al*. 1999; Alvarez and Datnoff 2001; Berthelsen *et al*. 2001; Meyer and Keeping 2001; Wang *et al*. 2001; Ashraf *et al*. 2009). In consideration of the beneficial effects of Si in plants under stressful conditions, the positive yield responses to Si fertilization are even more significant in sugarcane grown under various forms of abiotic and biotic stress. It should be stressed that such yield responses under stressful conditions are genotype-dependent. For example, Si addition increased sugarcane yield by 59 and 28% compared with no Si addition controls in salt-sensitive and salt-tolerant genotypes, respectively (Ashraf *et al*. 2009).

Wheat is also one of the upland crops that have a positive yield response to Si fertilizer (Wang *et al*. 2001). Based on field experiments conducted in northern China, Zhu and Chen (1963) reported that furnace slag application increased wheat yield by 6–12%. The field trials across China show that wheat yield responded to silicate slag actively with the yield increment ranging from 5 to 12% (Liang *et al*. 1994; Wang *et al*. 2001). The results of a consecutive four-year field trial indicate that wheat yield increased by 4.1–9.3% on a calcareous paddy soil amended with Si fertilizer although the content of "plant-available" Si extracted with 1.0 mol L^{-1} acetate buffer was around 250–380 mg SiO$_2$ kg^{-1} (Liang *et al*. 1994).

Besides crops mentioned above, many other plant species of agricultural and horticultural importance including barley, maize, millet (*Pennisetum glaucum*), sorghum, cotton (*Gossypium hirsutum*), tomato, potato (*Solanum tuberosum*), and cherry tomato (*Lycopersicon esculentum*) etc., can benefit from Si fertilizers in terms of better plant growth and higher yield (Korndorfer *et al*. 2001; Korndorfer and Lepsch 2001; Wang *et al*. 2001; Stamatakis *et al*. 2003; Toresano-Sanchez *et al*. 2012; Chagas *et al*. 2016; Vulavala *et al*. 2016). As reported by Liang *et al*. (2015), field trials with slag-based silicate fertilizer across China show positive responses in cucumber, tomato, maize, soybean and peanut (*Arachis hypogaea*) with significant economic advantage (Table 1). It is reported by Liu *et al*. (2011) that long-term field application of the slow-released potassium silicate manufactured from feldspar significantly increased the yield of 20 crops including wheat, maize, potato (*Solanum tuberosum*), peanut, radish (*Raphanus sativus*), soybean (*Glycine max*), green bean, sugar beet (*Beta vulgaris*), tomato, cabbage (*Brassica* spp.), chili pepper (*Capsicum annuum*), pumpkin, peach (*Prunus persica*), grapevine, banana, citrus (*Citrus* spp.), longan (*Dimocarpus longan*), tea (*Camellia sinensis*), ginseng (*Panax* spp.) and papaya (*Carica papaya*) (Table 2).

Si fertilization has also been proven effective in improving quality of crops like rice, sugarcane, vegetables and fruits. It is reported that Si fertilizer increased brown rice rate, milled rice rate and head rice rate as well as fatty acid content, but decreased chalky grain rate and chalkiness compared with Si-untreated controls (Zhang *et al*. 2007; Shang *et al*. 2009). Apart from higher sugar recovery rate in Si-treated sugarcane genotypes, Si addition also resulted in improved quality parameters of

Table 1 The effect on field application of blast furnace slag-based silicate fertilizer on crop yield and benefit/cost ratio during 2005–2006 in northeastern China (Liang *et al*. 2015)

Crops tested	Yield increase (%)	Average yield increases (%)	Benefit/Cost ratio	Number of trials
Rice	3.5–28.5	10.3**	4.4	50
Maize	5.6–10.4	7.7*	3.1	44
Cucumber	9.35–25.6	13.7**	42.9	40
Tomato	8.7–15.9	12.0**	35.7	35
Soybean	7.5–13.6	11.0**	1.7	32

* and ** indicate significantly different at *P*<0.05 and *P*<0.01, respectively, compared with Si-untreated controls.

Table 2 Effects of slow-released potassium silicate on 20 crops yield in 26 provinces of China (Liu *et al*. 2011)

Crops tested	Yield increase (%)	Crops tested	Yield increase (%)
Wheat	13.8	Chili pepper	8.4
Maize	7.3	Pumpkin	11.7
Potato	12.3	Peach	18.1
Peanut	6.7	Banana	4.8
Radish	11.2	Citrus	12.3
Soybean	5.1	Longan	10.7
Green bean	6.0	Tea	11.0
Sugar beet	4.7	Ginseng	3.2
Tomato	8.8	Papaya	9.7
Cabbage	15.2	Grapevine	6.5

sugarcane juice like Brix (% soluble solids in juice) and Pol (% sucrose in juice) (Ashraf *et al*. 2009). In tomato grown in hydroponic solution, total soluble solids and vitamin C content in tomato fruits were improved by supplemental Si (Stamatakis *et al*. 2003). And Si fertilization with silicic acid increased tissue consistency and durability of fruits during post-harvest in strawberry (*Fragaria*×*ananassa* Duch.) (Babini *et al*. 2012). In addition, improved floricultural quality traits were observed in gerbera (*Gerbera*×hybrida) (Savvas *et al*. 2002; Kamenidou *et al*. 2010) and zinnia (*Zinnia elegans*) (Kamenidou *et al*. 2009) grown in greenhouse condition with supplementation of Si.

Multiple forms of Si-based fertilizers have been manufactured from chemical products, natural minerals and by-products of metallurgic wastes (Liang *et al*. 2015). Although these different Si-based fertilizers are, in general, effective in promoting crop performance, their efficacy and economic costs differ from each other. Slag-based Si fertilizers including blast furnace slags, silicomanganese slags, carbon-steel slags, and phosphorus slags, etc. are cost-effective (Liang *et al*. 2015), but when used as fertilizers or additives, these by-products raise potential environmental risks due to their potential accumulation of heavy metals contained in such raw materials. Slow-releasing silicate fertilizers commercially available are manufactured from different sources of environmentally friendly minerals such as fused magnesium phosphate, slow-releasing potassium silicate fertilizer, and fused potassium magnesium silicate etc. Sodium silicate and potassium silicate are the only two forms of water-soluble silicate which can be used as soluble silicate fertilizer. These soluble silicate fertilizers are often taken as foliar sprays in consideration of their high cost for soil application. Although whether foliar-applied Si can be absorbed or not is still under debate (Liang *et al*. 2015), the beneficial effects of foliar sprays on crop performance have been reported in many crop species (Liang *et al*. 2005b; Wang S *et al*. 2015; Park *et al*. 2018).

The crop yield response of Si fertilization depends largely upon the availability and supply capability of Si in soil, which is mainly impacted by available Si content in Si fertilizers, soil pH, organic matter content, mineral fertilizer application rates and other edaphic or environmental factors (Liang *et al*. 1994; Savant *et al*. 1997; Park 2001; Wang *et al*. 2001). Up to now, Si-based fertilizers have been widely used in agricultural production across the world and positive yield and quality responses have been proven across a wide range of crops. However, it should be stressed that the yield and quality improvement by Si fertilizer is attributed to not only beneficial Si effects on growth promotion, but also some other comprehensive effects caused by pH adjustment, texture regulation, acquisition of macro- and micro-nutrients from the Si-based fertilizers (e.g., slag-based Si fertilizer and potash feldspar or potash-rich minerals). It is still unknown how much crop yield and/or quality improvement comes from Si itself in crops amended with Si-based fertilizers, which needs quantifying in the further research. Another question to be addressed is the residual effect of slag-based Si fertilizers. As Datnoff *et al*. (1997) reported, the residual effect of slag-based Si fertilizers made yearly applications not needed, and the subsequent application rates could be considerably reduced. Applications of slag-based silicate fertilizers to a rice-sugarcane rotation system of southern Florida not only significantly increased rice yield but also enhanced the growth and yield of sugarcane that was grown immediately after rice harvest (Alvarez and Datnoff 2001). In addition, crop yield responses to Si fertilizers are more distinct under various forms of abiotic and biotic stress compared with normal condition. Recent research also highlights the role Si plays in human health (Farooq and Dietz 2015).

5. Conclusion and perspective

Although, a model of Si uptake, transport, distribution and accumulation depending on the cooperation of multiple transporters has been established roughly, the molecular mechanisms of Si transporter genes transcription regulation, regulators of Si transporter activity, structural basis of Si transmembrane transport and mechanisms of polar localization are still poorly understood. And Si transporters have been identified only in a few plant species, more research work is still needed to characterize Si transporters in many other plants. These factors would be the foundation of genetic engineering to improve Si accumulation level and subsequently generate broad beneficial effects in plants.

Si-based fertilizers are proven to be the compensation to conventional fertilizers and effective in promoting crop yield and quality with significant economic advantages, however, large-scale application of Si fertilizers to the major field crops still has a long way to go. More field trials should be performed to investigate the optimum addition rate suiting for different soils and crops. In addition, more efforts should be made on research and development of cheaper and more effective Si-based fertilizers. In addition, the ecological issues of Si in both natural and agricultural ecosystems deserve more attention.

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