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Si Uptake and Transport in Higher Plants

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Mini Review

Silicon (Si) is the second most abundant element in the earth crust and is valued for its innumerable beneficial properties required for the growth and development of the plant specially under stressed environmental conditions [1]. Despite of this fact, it is not considered as an essential element for majority of the plants; as it was believed that most plants can complete their normal life cycle without supplementation of silicon to the soil [2]. However, more recently it has been observed that continuous application of NPK and other chemical fertilizers have depleted the normal Si availability in the soil. The beneficial effects such as in protecting and stabilizing the plant structure, salt and drought tolerance, diseases resistance, yield and development of the plant imposed by the element have made plant physiologist to realize the importance of adding additional silicon fertilizers to the soil [3,4]. Now a days, Si fertilizers are regularly added to rice and sugarcane crops to enhance crop yields [2]. However, the availability of Si towards the plant is another interesting point to study as the uptake and translocation mechanism is greatly dependent on the uptake ability of the plant root system [5].

Silica is mainly taken up by the plants as silicic acid [Si $(OH)_4$], an uncharged monomeric molecule [6]. Following its uptake by the roots, it is further transported to shoots via xylem wherein; it gets chemically mineralized to form silica gel (SiO_2. nH_2O) due to higher transpiration rates [7]. This mineralized silica aggregates i.e. phytoliths which resemble Si nanoparticles (SiNP) provides protection and strength to the plant structure [8]. This further bring in resurgence of interest in studying the underlying mechanism of uptake and translocation of silicon into the plants. Different parameters play different parts in the uptake and accumulation process. Some of these are highlighted in this review.

Role of Si transporters in uptake process

Based on diverse absorption ability of the roots, different plants have different Si accumulation levels and are categorized as high, low and intermediate accumulators. For instance, higher plants of family Gramineae and Cyperacea show high Si accumulation and plants belonging to family Cucurbitales, Urticales, and Commelinaceae show intermediate Si accumulation, while many other plant families like Asteraceae and Fabaceae shows low Si accumulation [8,9]. The difference in the Si uptake system is attributed to the participation of different parts of the root structure. A root system consists of primary roots, lateral roots and root hairs. Different experiments were conducted to study the effects of different root parts in Si uptake process. Ma [10] conducted experiment on two different rice mutants one defective in the formation of root hairs (RH2) and the other in the formation of lateral roots (RM109). From the experiments, it was concluded that plants that lacked lateral roots (RM109) resulted in reduced Si uptake while in the RH2 type plants there was no significant effect on the uptake process. Thus, it was very clear that lateral roots are the major components of the root systems wherein a specific transport system is present which aids in the Si uptake [11]. Therefore, based upon physiological studies; it was revealed that a specific transport system consisting of Si transporters exists across the membranes which help mediates the entire uptake process [6,12]. This transport system consisted of various channel proteins of NIP major protein family and aquaporins subfamily [13]. An efficient transport system helps plant to benefit from the useful effects of Si.

The very first report in higher plants was from rice wherein two different genes Lsi1 and Lsi2 were identified [2]. The influx transporter Lsi1, absorbs Si from the soil solution and transports across the exodermis while Lsi2, the efflux transporter helps transporting Si from endodermal cells into the xylem parenchyma, surrounding the xylem translocation vessel. There from, either Lsi 6 in the case of Si accumulators or a passive transport in non-accumulators will facilitate the transport into the xylem vessel and thereafter the Si translocation to the shoots [14]. Structural localization of different Si transporters help facilitates the influx and efflux across the different plant parts.

Homologs of rice transporters Lsi1 and Lsi2 have further been identified and characterized in number of other plants including barley (*Hordeum vulgare*), maize (*Zea mays*), pumpkin (*Cucurbita moschata*), horsetail (*Equisetum arvense*), Cucumber (*Cucumis sativus*), Wheat (*Triticum aestivum*), Soy bean (*Glycine max*) and Potato (*Solanum tuberosum*) (Table 1).

Table 1: Presence of influx and efflux transporters in different plants.

Plants	Si Influx Transporters	Si Efflux Transporters	Reference
Wheat	*TaLsi1*	----	Montpetit [15]
Barley	*HvLsi1*	*HvLsi2*	Chiba [16]
Maize	*ZmLsi1; ZmLsi6*	*Zmlsi2*	Mitani [17]
Pumpkin	*CmLsi1(B+); Cmlsi1(B-)*	----	Mitani [4]
Cucumber	*CsLsi1*	*CsLsi2*	Sun [18,19]
Potato	*StLsi1*	----	Vulavala [20]
Soybean	*GmNIP2-1*	*GmNIP2-2*	Deshmukh [21]
Horsetail	*EaNIP3;1; EaNIP3;4*	*EaLsi2-1; EaLsi2-2*	Vivancos [22], Gregoire [23]

Role of metabolic inhibitors on Si uptake

It has been observed that plants such as rice, wheat, barley, ryegrass and some belonging to cyperaceous family have an active intake of Si while some dicots such as melon, strawberry and soybean take up Si passively [10,24,25]. Plants having active uptake process have much higher intake of Si, which is not affected by the transpiration but is influenced by the presence of various inhibitors such as NaCN, NaF, H_2S, 2,4-DNP (2,4-dinitrophenol), iodo-acetate, 2, 4-D (2,4-dichlorophenoxyacetic acid), $HgCl_2$ [26,27]. The very first report to study the effect of metabolic inhibitors was by Okuda and Takahashi [24] in rice roots and shoots. The experiments clearly showed that excised roots were strongly inhibited by metabolic inhibitors such as NaF and 2,4-D. On the other hand, shoots were not affected thereby showing that in shoots passive transport of Si occurs which is along the transpiration stream while in roots active process using ATP is involved. Commonly studied metabolic inhibitors influencing Si uptake studies are listed in Table 2.

Table 2: Commonly used metabolic inhibitors.

Metabolic Inhibitors
2, 4-D (2,4-dichlorophenoxyacetic acid)
2,4-dinitrophenol (2,4-DNP)
Sodium phosphate (Na_3PO_4)
Mercuric chloride ($HgCl_2$)
Malonic acid ($C_3H_4O_4$)
NaCN, NaF

Liang [28] studied inhibitory effect of three metabolic inhibitors (NaF, NaCN and 2,4-DNP) on Si uptake in four different plant species and found that the effects were much enhanced in *Oryza sativa* and *Zea mays* as compared to *Helianthus annuus* and *Benincase hispida*. In another study by Zhang [29] effect of four different inhibitors including $HgCl_2$, 2,4-dinitrophenol (2,4-DNP), malonic acid ($C_3H_4O_4$), and sodium phosphate (Na_3PO_4) were studied in the Si uptake in association with their effects on ATPase activity and ATP concentration in rice.

Other factors affecting Si uptake

The other factors contributing towards the uptake of Si includes transpiration, nutrient salts, temperature, and light. In different sets of experiments conducted on rice to study the transpiration rates it was observed that Si concentration is higher in aerial parts where the transpiration rates are higher [30]. Similarly, light also stimulated the uptake effect of Si as prolonged exposure of rice plants to light enhanced the Si content as compared to short exposures [30]. In Cucumber, it was found that low temperature exposure strongly inhibited the Si uptake process [31]. Deficiency of nitrogen and phosphorous in rice plants increased silicon uptake suggesting that different nutrient salts have varied influences on the uptake process [32]. Similar results were obtained in another experiment on *Oryza sativa* L. cv. Akebono, where uptake of Si in shoots was reduced when the concentration of phosphorous was increased [33]. Effect of temperature on Si uptake was studied in four different plants including *Oryza sativa, Zea mays, Helianthus annuus* and *Benincase hispida*. It was observed that low temperatures significantly suppressed the Si uptake levels independent of higher external Si concentrations [28].

Even though Si exerts numerous useful effects on the plant's growth and development; most plants are deprived of these benefits from Si due to the lack of an efficient transport mechanism. Therefore, it is of utmost importance to study the various parameters influencing the uptake and translocation process to get a better insight of the transport system of silica. In the present review, we tried to pin point some of the most important factors influencing silicon uptake in higher plants which could become the blocks for future research experiments.

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