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Silicon uptake, transportation and accumulation in Rice

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Abstract
Silicon (Si) is the important nutrient for sustainable production of rice. Rice is a typical silicon accumulating plant and it benefits from silicon nutrition. In the soil, silicon is present as monosilicic acid and polysilicic acid as well as complexes with organic and inorganic compounds such as aluminium oxides and hydroxides. Silicon is absorbed by plant roots as monosilicic acid. Silicon transportation in rice is governed by three genes *i.e.* LSi1, LSi2 and LSi6. Among these, LSi1 and LSi2 are responsible for transport of silicon from root cells to the apoplast, whereas LSi6 is involved in transfer of Si from the large vascular bundles to the panicles. When the concentration of monosilicic acid exceeds, it gets polymerized to form silica gel ($SiO_2.nH_2O$). Silicon is deposited beneath the cuticle as cuticle-silicon double layer in the form of silicic acid. Amorphous silica particles that precipitate in plant cells are called Phytoliths or Plant opal. Phytoliths can be assembled without any energy by polymerization of silicic acid, when its concentration exceeds 2 mM. Phytoliths are found in specific cells called silica cells located on vascular bundles and/or are present as silica bodies in bulliform cells, fusoid cells or prickle hairs in rice. The silica accumulation of plant is higher during the reproductive period.

Keywords: silicon, low silica genes, phytoliths, rice, silicic acid

Introduction
Silicon is the second most abundant element in the earth's crust. The average concentration of Si in the lithosphere is about 28 per cent and in soils normally ranges between 23-35 per cent. It is a principal soil component lost during weathering and the conversions of silicon to secondary minerals are most important mechanisms of soil formation. It is well known that silicon is present in primary silicate minerals, secondary aluminosilicates and various forms of $Si0_2$. The amount of silicon present in soils varies with the type of soils, climatic conditions, geological materials, nature of rocks and minerals forming soils etc. However, sandy soils contain more than 40 per cent silicon as compared to 9 per cent silicon in highly weathered tropical soils. Si is a tetravalent Si^{+4} element, which is not found in free-state. In soil solutions, the prevailing form is monosilicic acid $Si(OH)_4$, which is in equilibrium with quartz (SiO_2) and the concentrations in the soil solution is usually ranging from 14 to 20 mg l^{-1} Si. All soil-grown plants contain Si. However, the Si concentration of plant shoots varies greatly among plant species, ranging from 0.1 to 10% Si on a dry weight basis. It has been estimated that in excess of 200 million tons of silicon are removed annually from arable soils globally when crops are harvested (Matichenkov *et al.*, 2002) [8].
Silicon is not considered as an essential element, but is a beneficial element for crop growth, especially for Poaceae crops. Silicon has been officially designated as a “beneficial substance” by the Association of American Plant Food Control Officials and plant-available Si may now be listed on fertilizer labels. Silicon plays a crucial role in amino acid and protein metabolism. Silica strengthens the plant, protects the plant against disease, insect, and fungi, increases crop production and quality, stimulates active immune systems of plants, increases plant nutrition, increase plant salt resistance and neutralizes heavy metal toxicity in acid soils. Numerous laboratory, greenhouse, and field experiments have shown benefits of application of silicon fertilizer for rice, corn, wheat, barley, and sugar cane. Silicon fertilizer has a double effect on the soil-plant system. First, improved plant-silicon nutrition reinforces plant-protective properties against diseases, insect attack, and unfavorable climatic conditions. Second, soil treatment with bio-geochemically active silicon substances optimizes soil fertility through improved water, physical and chemical soil properties and maintenance of nutrients in plant-available forms. Plants vary widely in their capacity to take up silicon. In accumulating plants, silicon uptake largely exceeds water uptake and in silicon non-accumulating plants silicon uptake is similar to or less than water uptake. In soil, silicon is not a much mobile element to plants. Therefore, a continued supply of this element would be required particularly for the healthy and productive development of plant during all growth stages.

Rice is a high silicon accumulating plant and the plant is benefited from Si nutrition. Rice crop can uptake Silicon in the range of 230-470 kg ha^{-1}. Si is a beneficial element for plant growth and is agronomically essential for improving and sustaining rice productivity. Besides rice yield increase, Si has many fold advantages of increased nutrient availability (N, P, K, Ca, Mg, S, Zn), decreases nutrient toxicity (Fe, Mn, P, Al) and minimizing biotic and abiotic stress in plants. Hence, the application of Si to soil or plant is practically useful in laterite derived paddy soils, not only to increase yield but also to alleviate the iron toxicity problems. Si increases the mechanical strength of the culm, thus reducing crop lodging (Savant *et al*., 1997) [10].

Silicon in Soils

In the soil solution or liquid phase, Si is present as Monosilicic acid and Polysilicic acid as well as complexes with organic and inorganic compounds such as aluminium oxides and hydroxides. While it is the PAS (plant available silicon) that is taken up by the plants and has a direct influence on crop growth, the polysilicic acid, and inorganic and organic complexes are important sources/sinks that replenish the monosilicic acid following crop use. The solubility of silicon in the soil is affected by a number of dynamic processes occurring in the soil including the particle size of the silicon fertilizer, the soil pH, organic complexes, presence of Aluminium, iron and phosphate ions, temperature, exchangeable/dissolution reactions and soil moisture. Silicon can be added via irrigation water and fertilization (Berthelsen *et al*., 2003) [1]. Si improves physical, chemical and biological properties of soil.

Silicon Uptake and Transport in Rice

In soil solution, silicon is mainly present as monosilicic acid, with concentrations generally within the range of 0.1-0.6 mM. Monosilicic acid is the predominant form of Si absorbed by roots by active uptake. Silicon uptake is performed by lateral roots, but not root hairs. (Ma *et al*., 2001) [4].

Table 1: Silicon uptake by various crops

CROP	Plant available Si (kg/ha)	Major nutrients (kg/ha)		
		N	P	K
Rice	230-470	34	22	67
Sugarcane	500-700	90	17	202
Cereals	100-300	-	-	-
Potato	50-70	-	-	-

(Ma *et al*., 2002)

Silica transportation in rice is mainly due to the presence of three low silica genes (LSi) *i.e*., LSi1, LSi2, and LSi6 (Yamaji *et al*., 2009) [13]. LSi1 is a low silicon rice gene that belongs to aquaporin family, controlling the silicon accumulation in rice. LSi1 is primarily located in the basal zones of roots rather than at root tips. This gene is constitutively depressed in roots. LSi1 was localized on the plasma membrane of the distal side of both exodermis and endodermis cell where Casparian stripes are located. LSi2 is localized on the proximal side of the same cells. LSi1 shows influx transport activity for Si, while LSi2 shows efflux transport activity. LSi1 and LSi2 were responsible for transport of silica from root cells to the apoplast. (Ma *et. al.*, 2008). Si in xylem sap is present in the form of monosilic acid and is unloaded by LSi6, a homolog of LSi1 in rice. LSi6 is a transporter involved in intravascular transfer *i.e.* transfer of silicon from the large vascular bundles to the panicles. Knockout of LSi6 decreased silicon in panicles and increased silicon in flag leaves, showing its physiological role in silicon distribution in the plant (Ma *et al.*, 2011) [7].

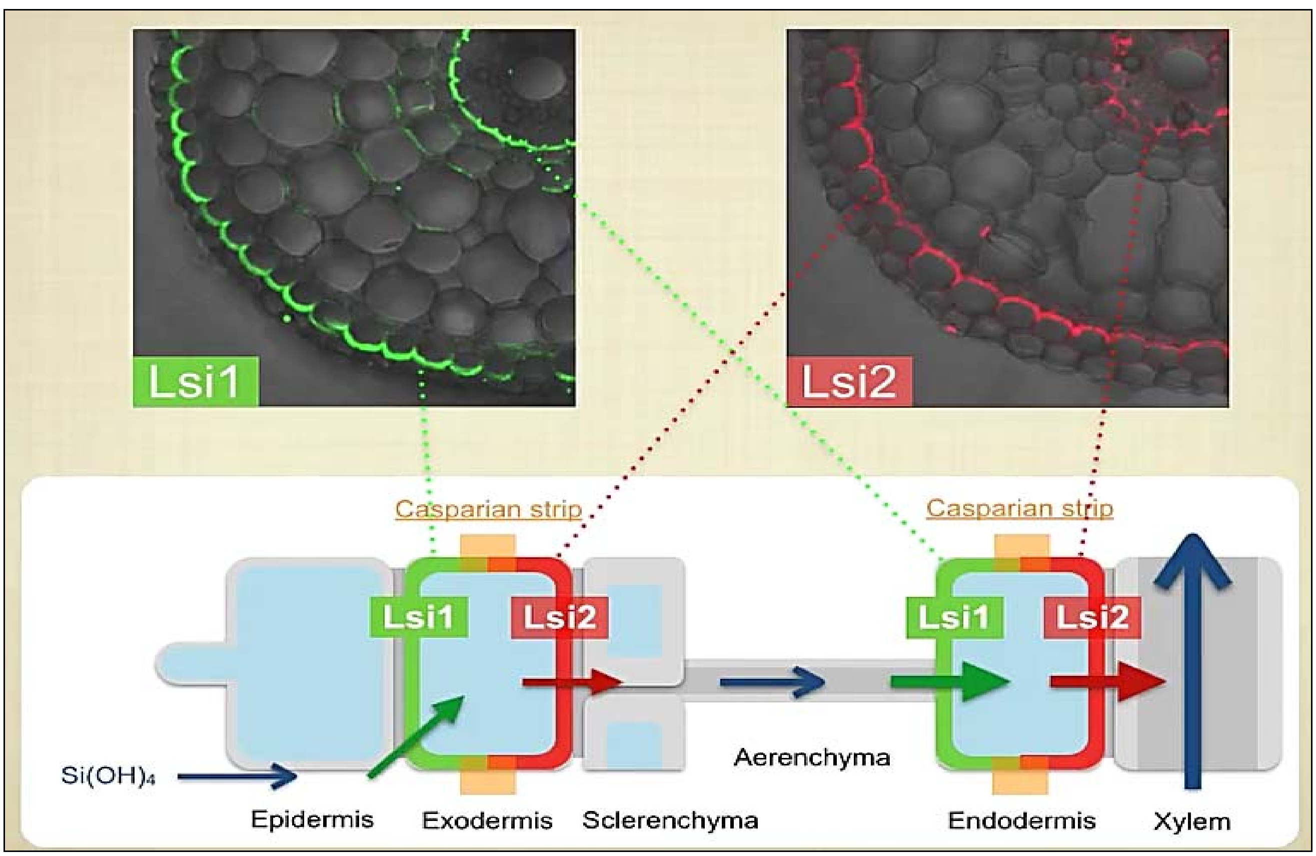

Fig 1: LSi1 and LSi2 genes in the rice root

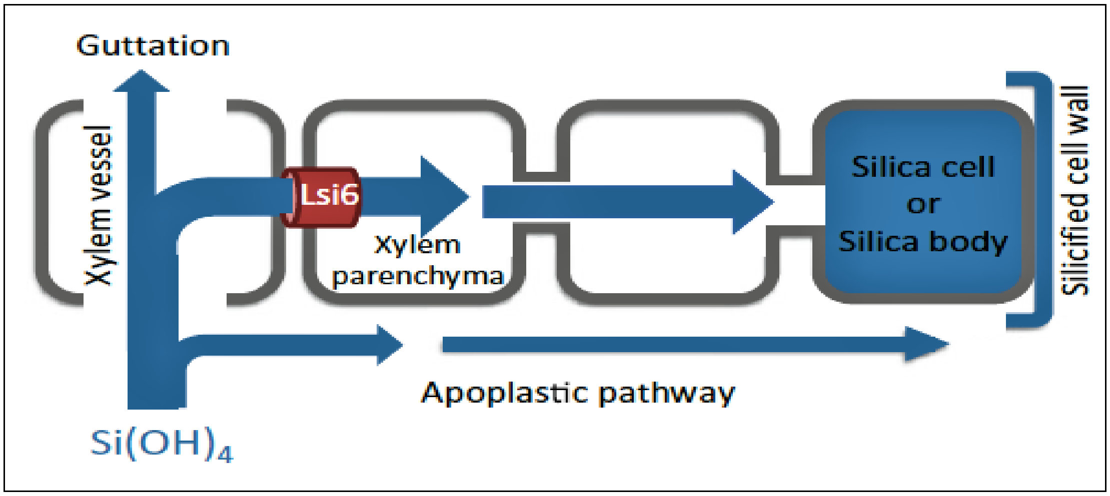

Fig 2: Transfer of silicon from root to shoot by LSi6 gene

Silicon Accumulation and Deposition

Silicon is translocated from the roots as silicic acid through the xylem until it deposits under the cuticle and in intercellular spaces (Heckman, 2013) [3]. Silicon is absorbed by the plant as monosilicic acid, the absorbed water is lost through transpiration and the silicon stays in the plant tissue when silicon concentration increases in the plant, monosilicic acid polymerize into silica gel through a non-enzymatic reaction (Mitani *et al.*, 2005) [9]. The chemical nature of polymerized silicon has been identified as Silica gel. Of the polymerized silica within the plant, 87-89% exists as a very slightly soluble form in hulls, leaf blades, and leaf sheaths. In these tissues, silica tends to be deposited as a 2.5 µ thick layer in the space immediately beneath the thin cuticle layer forming a Cuticle-Silicon double layer. The location and the mechanical strength of this Cuticle Si double layer help to maintain erect leaves, minimize transpiration and protects the rice plant from fungal diseases and insect pests (Savant *et al.*, 1997) [10]. Sangster *et al*. (2001) [11] studied that after 8-10 days of silica gel formation, silicon was almost exclusively found in a solid form in the aerial parts.

Amorphous silica is therefore virtually the only form of silicon in plants. Amorphous silica particles that precipitate in plant cells are called Phytoliths or Plant opal. Phytoliths can be assembled without any energy by polymerization of silicic acid when its concentration exceeds 2 mM. Proportions and locations of phytoliths vary with the species, but also with the age of the plant. In the leaves, silicon at first preferentially deposited in the abaxial epidermis, and then in both epidermis as the leaf grows. Among those tissues, phytoliths are found in specific cells called silica cells located on vascular bundles and/or are present as silica bodies in bulliform cells, fusoid cells or prickle hairs in rice.

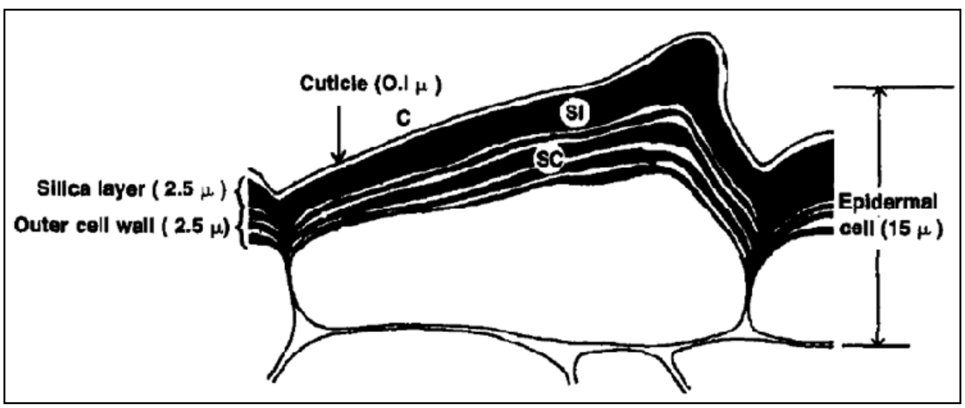

Fig 3: Cuticle Si Double layer in rice leaf blade

The reported critical limit for optimum growth and yield of rice is 5% Si in rice straw. The silica content of the leaf blades, culm, and the whole plant increased with the progress of growth and was low during the vegetative period and high after flowering. Silicon content in culms, leaves, and sheaths were 8.8-10.2, 16.8-22, 14.4-20.6 per cent respectively. Silicon content of leaves increased with supplied silicon and was closely correlated with the silica bodies per unit leaf area in the epidermal system (Singh *et al.*, 2005) [12]. Rice accumulates 4-20 % silicon in straw and almost every part of rice contains this element which is not at all added exogenously as fertilizer as done with N, P and K, the trinity of nutrients. In rice leaf blades 90 per cent or more of silicic acid exists as silica gel (Polysilicic acid) and 0.5 per cent as low molecular weight silicic acids (orthosilicic acid). The Silica content of rice straw at harvest ranged from 4.8 to 13.5 per cent in the dry season and from 4.3 to 10.3 per cent in the wet season (Devanur, 2015) [12].

Conclusion

Silicon shows beneficial effects on growth and production of rice by alleviating abiotic and biotic stresses including pests, diseases, lodging, heavy metal toxicity, salt stress, drought stress and nutrient imbalance. Two kinds of transporters such as influx transporters (LSi1 and LSi2) and efflux transporters (LSi6) are identified in rice which is involved in active uptake of silicon. LSi1 was localized on the distal side of both exodermis and endodermis of the root, whereas LSi2 is localized on the proximal side of the same cells. This alternative arrangement of LSi1 and LSi2 genes on exodermis and endodermis is responsible for the active uptake of silicon making the rice plant, highly silicon accumulating species. Knockout of LSi6 gene in rice resulted in less and uneven distribution of silicon in aerial parts of rice, thereby showing its importance in the transport of silicon from root to shoot. Scientists presume that there is scope for identification of more silicon transporters in rice, which will help to understand the mechanisms of Si uptake, translocation, and distribution.

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