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The mystery of silica and its role in stress tolerance

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INTRODUCTION

Silicon (Si) is a metalloid belonging to carbon group with atomic number 14, and its importance for the plant is being paid attention from the recent times. Studies on element limitation stress under experimental conditions was made possible during the period of 1860 by the initiation of utilizing the technique of hydroponic culturing of plants, which made possible to study elemental stress on plant and later, recognition of silicon as an important mineral for plants was started during the early 1900s based on the observation of its role in increasing the disease resistance in field conditions (Epstein, 2005). Silicon uptake by plant system was nearly equal or marginally greater than the essential nutrients such as N and P in crops like sugarcane and rice (Savant et al., 1999), which was demonstrating the inevitable role of Si in the plant system. Despite of its abundant nature in soil, Si is not freely available in soil but it is found be combined with other elements in the form of oxides / silicates. Although Si is found in all the plants, wide variation in Si concentration exists from 0.1% to 10% of above ground dry weight (Epstein, 1999; Ma and Takahashi, 2002). Most of the algae belonging to marine or fresh water environment were found to be using Si in formation of protective silica structures.

The distinct beneficial effects of silicon fertilization include heavy metal toxicity such as Aluminium, cadmium drought, salinity, mineral deficiencies, UV stress and also several biotic stresses in plants (Table 1). In animal kingdom, the regurgitating animals were found to be benefitted when moderate silicon grasses were fed as the element might contribute for release of cell components due to physical amorphous nature of silicon bodies. The abrasiveness caused by silica results in internal new tissue generation akin to the loss of cells on external surface due to constant abrasion. Several of the slag based calcium, potassium based silicate fertilizers (Table 2) are being extensively used in many of the Asian, African and North and South American countries particularly for rice and sugarcane. It was interesting to note that, application of silicon fertilizers in the rice irrigated and aerobic rice fields resulted in reduced methanogenesis and GHG emissions by 9%. The reasons attributed were changes in soil redox potentials aided with nitrification inhibition.

Unlike other elements, studying silicon and its role in plants is difficult due to its 1) difficulties in solubilisation 2) detection in the biological systems in active forms as it is not directly involved in any biochemical reactions thus, the essentiality criteria laid out are not been meted out and 3) limited genetic studies conducted for its variation across the plant species. However, detection of silica in its amorphorus form in ash is much easier and the large amounts of its presence in species like rice, horse tails and others has left the scope to imagination of the investigators. The advent of the modern tools of detection particularly in the plant physiology and molecular biology led to identification of the transporters, genes helped not only to identify the presence of this element in various plant species but also the spatial and temporal accumulation across the biological samples. Interest rose over the past decade chemical processes as well as microbial associations rendering the solubilisation of silica have been advanced making the way forward about the role of silica in plant biology. The polymeric insoluble silica present in soils needs to be solubilised and released into the soil solution in the form of monosilicic acid which is the bioavailable form of silicon absorbed by plants. A silicate solubilizing bacterium was isolated from rhizopshere soil of rice and characterized for plant growth promoting traits. The isolate demonstrated silicate solubilizing potential by releasing soluble silicon from various insoluble inorganic silicate sources and silicates of biological origin (Plates 1 & 2). Incubation of magnesium tri silicate and diatomaceous earth with the isolate was found to release at the end of seven

Table 1. Content of silicon in various products.

Food crops	Si content (mg/100g)	Others	Si content (mg/100g)
Cereals and Grains	7.8	Milk & products	0.31
Breads	1.5	Tap water	0.37
Biscuits	1.11	Mineral water	0.55
Raw & canned fruits	1.3	Tea	0.38
Vegetables	1.79	Carbonated drinks	1.4
Legumes	1.46	Beer	1.92
Nuts & Seeds	0.8	Wines	1.35

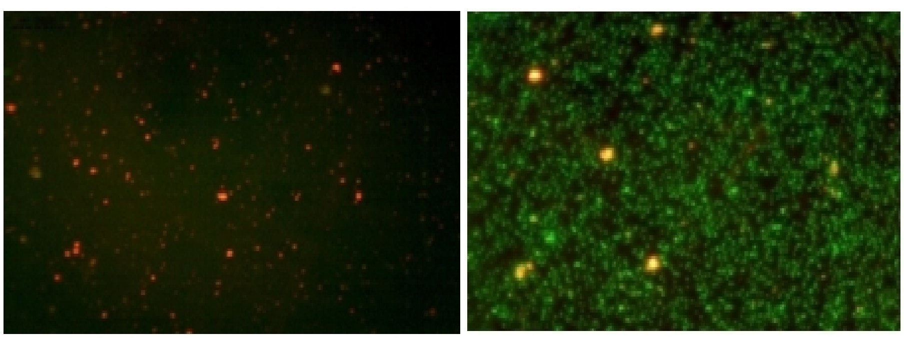
(Source: Powell, 6th Int Conf. Silicon, Sweden)

days, 3.0 and 0.14 µg silicon/ µg cell respectively. The isolate produced plant growth promoting phytohormones, also solubilised insoluble P, K and Zn and was found to secrete iron chelating siderophore and protease enzyme with biocontrol potential.

The published literature and evidences accumulated in recent past, emphasizing that, silica indeed plays a role in providing biotic as well as abiotic stress tolerances in various plants and listed Tables 3 and 4. Genetic diversity has been revealed with identification of transporters and the process of transport similar to other elements i.e, through mass flow, active and passive absorption, in the root cortical cells and its accumulation on the plant leaf surfaces, rice husk and other parts of the organ in amorphous

Table 2. Silica content in inorganic silicates and silica containing materials of biological origin

S.No	Name	Percentage of silica
Inorganic silica containing compounds		
1	Magnesium tri silicate	> 45
2	Kaolin	> 46.5
3	Potassium alumina silicate	> 45.57
4	Calcium alumina silicate	> 44
5	Quartz	>99.24
6	Fullers earth ((Hydrated Al. Silicate)	> 64.1
7	Bentonite (Hydrated Al. Silicate)	> 68
Silica containing materials of biological origin		
8	Diatomaceous earth	> 90
9	Siliceous earth	> 90
10	Husk	> 90
11	Straw	> 74.67



A B

Fig. 1. Epifluorescent images of acridine orange stained magnesium trisilicate in a) uninoculated medium and b) inoculated medium

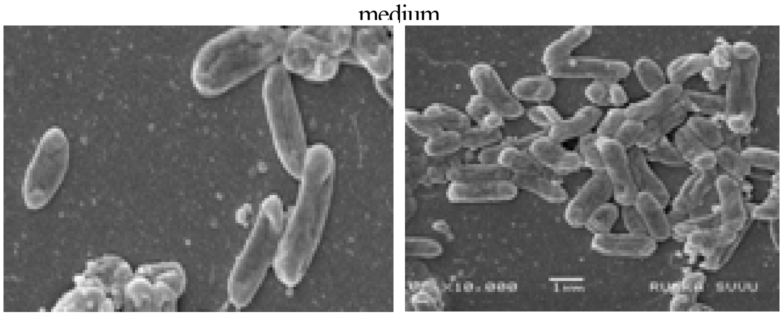


Fig. 2. Morphology of the isolate was examined using Scanning electron microscope

Table 3. Silicon and abiotic stress tolerance

S.No	Name of the Crop	Type of stress	Form of silica applied	Remark	Reference
1	Rice	Drought stress/aerobic stress	Potassium silicate/Silicon solubilizers	Si application increased drought tolerance by enhancement of photosynthetic rate, photochemical efficiency, mineral nutrient absorption.	Chen et al., 2011Sujatha et al 2011
2	Rice	Nitrogen	Sodium silicae	Increasing nitrogen concentration has reduced Si uptake.No effect on SPAD, photosynthesis, conductance, transpiration	Allahyar 2012
3	Rice	-	OryMaxSL and SiliysolMS (commercial)	Increased rice yields, internode diameter, internode wall thickness	Nhan et al., 2012
4	Rice	-	Soluble silicic acid	Spary of soluble silicic acid increased yields up 4 ml L^{-1}, Yields were decreased at 8 ml L^{-1} concentration.	Prakash et al., 2011
5	Rice	Aluminium Stress		Si application protected rice seedlings against Al toxicity by maintaining optimum levels of Mg and Zn levels.	Sing et al., 2011
6	Rice	Cd toxicity	Potassium silicate	Si increased plant growth and reduced Cd accumulation in shoots.	Zhang 2007
7	Borago officinalis L	NaCl Stress	Sodium silicae	Pretreatment with Si can alleviate salt stress. Pretreatment has reduced lipid peroxidation, aldehyde and carbohydrate content of root	Enteshari 2011
8	Lettuce	Organic and Conventional Fertilizers	Horn Silica	Silicon sprays increased Lettuce dry matter yield and crude protein content in fresh leaves in both the treatments	Bacchus 2010
9	Sorghum	Water stress	Silicon dioxide solution	Sililcon increased water uptake, stomatal conductance and increased water supply to leaves	Sonobe et al., 2009
10	Sorghum	Water stress	Silicon dioxide solution	The reduction in dry weight was alleviated by Si application along with increased root water uptake	Sonobe 2011
11	Sorghum	Water stress	Sodium silicate (Hydraulic stress)	Si application improved water uptake and mitigated hydraulic sress.	Hattori et al., 2008
12	Bean	Manganese Toxicity (High Manganese concentration)	Aerosil	Up to 1000ppm of Mn concentration, a molar ratio of 6 si/Mn was able prevent manganese toxicity. But above 1000ppm of manganese, there was no positive effect of Si/Mn molar ratio on growth depression.	Horst and Marschner, 1978
13	Tomato	-	Monosilicic acid	Silicon application increased fruit number per plant and fruit yield kg m^{-2}	Toresano-Sanchez et al., 2012
14	Tomato	Salt stress	Sodium silicate	Si increased salt tolerance by mitigating oxidative dame. Si also increased chlorophyll content, PSII efficiency.	Aghabary et al., 2004
15	Tomato	Salt stress		Si increased plant dry weight, total plant leaf area, leaf turgor potential, leaf photosynthetic rate. Si also improved water storage in plant tissues.	Aranda et al., 2005
16	Cucumber	Drought stress	Potassium sililcate	Silicon application increased biomass, photosynthesis and water holding capacity. Positive correlation observed between Si application and physiological characters, indicating Si application increased drought tolerance.	Ma et al., 2004
17	Cucumber	Osmotic Stress	Hydroponics/Silicon	Si application resulted in lesser growth reduction, increased photosynthetic rate. Si application	Hattori et al., 2008
18	Cucumber	Drought Stress	Potassium sililcate	Silicon application increased drought tolerance by increasing water holding capacity, Biomass, Photosynthesis	Ma et al., 2004
19	Barley	Aluminium toxicity	Silicic acid		Liang et al., 2001
20	Wheat	Drought stress	Sodium silicate	Application of Si increased leaf weight ratio, leaf thickness. Maintained higher RWC and water potential.	Gong et al., 2003
21	Wheat	Drought	Potassium sililcate	Silicon increased drought tolerance by decreasing electrolyte leakage under drought stress	Karmollachaab et al., 2013

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22	Wheat	-	Sodium meta silicate	Yield, Relative water content, Ca, K levels increased upto 25 to 200ppm Si concentration, further increasing Si concentration decreased above parameters	Mali and Aery 2008
23	Wheat	-	Silicic acid	Increased plant growth and yield up to 0.5% silicic acid application, increasing silicic acid concentration to 0.75% decreased plant yield and growth	Abro et la., 2009
24	Grass sps.	Drought stress	Silica gel, $CaSiO_3$, K_2SiO_3	Si Increased biomass yield, Strong associations between Si uptake with N and P	Eneji et al., 2008
25	Rye	Water stress	Potassium silicate	Increased dry weight, photosynthesis, stomatal conductance, water use efficiency, leaf water potential	Hattori et al., 2009
26	Maize	Salt stress	Potassium silicate	Si mitigated salt stress by increasing Shoot, root, stem length, leaf area, chlorophyll content and RWC	Rohanipoor et al 2013
27	Maize	Zinc stress	Sodium silicate	Si gives tolerance to Zn stress by reducing Zn concentration and increased Fe concentration of leaves.	Kaya et al., 2009
28	Maize	Water stress	Sodium silicate	Silicon application increased waterstress tolerance, Increased calcium uptake, total dry matter, Chlorophyll content, Relitive dry matter.	Kaya et al., 2006

The basic required conditions for its solubility, availability and the forms are determined particularly soil PH, acid- base reactions that favour the formation and release of insoluble forms to soluble forms and the microbial systems associated with its release along with the chemical reactions that might happen in root zone. Once soluble forms of silica in the monomeric forms are available comes the role of transporters. Indeed transporters identified on the root surface using Lsil mutants, candidate genes in Kasalath (Ma et al., 2004) are identified, later the mutations and the positional replacements of amino acid in 132 region was shown to influence the silica uptake in rice plants. Plants accumulated monosilicilic acid in root zone will move forward into the shoots. It is proposed that, phosphorus co-transported into the shoots which might result in sturdy stems and healthy plants. The monosilicilic acid thus, would be released to the cell wall and cellulose regions slowly modifying into the amorphous form on the surfaces preventing the entry of fungal pathogens, there by aided biotic stress tolerance.

Plant species contain approximately 72 aquaporins and are divided into 5 major groups which contain selectivity for substrates including silicon. One such aquaporin with selectivity filter has been identified (NIP) and spacing of a specific length between 2 domains was necessary for selectivity. Based on this study species possessing NIP-III proteins with a GSGR selectivity filter is essential and distance of 108 AA between the NPA domains is required which determine Si accumulation.

Based on the three year field studies, using 5 each of hybrids and varieties, with and without silicon fertilizer application multi-location trials were also conducted resulting in increased panicles per sq.m, TDM at harvest by 11-4% over control. Also, Silicon treatments significantly ($P<0.05$) affected the grain yield by 9% of rice genotypes. Incidence of major diseases like Blast and BLB and important pests like stem borer and leaf folder reduced. Reduction in pest and disease incidence associated with yield enhancement in rice with a B: C ratio of 1.16-1.5 in different seasons in rice has been reported (Padmakumari et al., 2018). This reduction in pest incidence has been attributed to the insect mandibles wear associated with silicon accumulation in the tissues of stem as a result pest attack is avoided in rice. Apart

Table 4. Silicon and biotic stress tolerance

S.No	Name of the Crop	Organism	Form of silica applied	Remark	Reference
1	Coffee	Meloidogyne exigua	Wollastonite	Si increased root resistance of M.exigua by decreasing the pathogens reproductive capacity	Silva et al., 2010
2	Cucumber	Podosphaera xanthii	potassiummetasilicate	Si increased defence infection by forming physical barrier on leaf surface and osmotic.	Liang et al., 2005
3	Cucumber	Pythium sps.	Potassium silicate	Si induced plant defence reactions by increasing ??glucosidase activity and fungitoxic aglycones in roots	Cherif et al., 1994
4	Cucumber, Muskmelon, Zucchini squash	Powdery mildew	Potassium silicate	Si concentration of ???17.0 mM Si has resulted in fewer mildew colonies compared to control.	Menzies et al 1992
5	Wheat	Blumeria graminis f. sp. tritici	exogenously supplied nutrient solution or calcium silicate slag	Si mediates active localized cell defences against B. graminis f. sp. tritici attack by papilla formation, production of callose, and release of electron-dense osmiophilic material identified by cytochemical labeling as glycosilated phenolics.	Bélanger et al 2002
6	Wheat	Powdery mildew	potassium silicate	Si application reduced disease severity	Guével et al., 2007
7	Rice	*Brown spot*	potassium silicate *(Bipolaris oryzae)*	Reduced Si concentration in plant tissues assfected its resistance to brown spot, suggesting requirement of minimum concentration of Silicon for resistance. Si application lowered lipid peroxidation and electrolyte leakage and increased total soluble phenolics	Dallagnol et al., 2008, 2010
8	Rice	BLAST (Pyricularia oryzae)	potassium silicate	Application of Si has reduced blast ratings and increased rice yield. The order of resistance was $CaSiO_3$>Potassium silicate>Husk ash>Straw ash>Straw.	Muriithi et al.,
9	Rice	sheath blight (*Rhizoctoniasolani* Kühn)	$CaSiO_3$	Si application increased plant dry weights and Si application is a promising method to control sheath blight	Rodrigues et al., 2002
10	Rice	Blast	Wollastonite (CaSiO3)	Application of Si reduced blast better than edifenphos	Seebold 2003
11	Rice	Blast and Leaf Scald	calcium metasilicate	Si application reduced leaf and neck blast severity from 26% and 53% to 15%. Leaf Scald and grain discoloration was reduced from 42% to 6% and 4.2 to 1%.	Victoria et al., 2001
12	Rice	Sheath Blight		Increasing Si concentration from 0 to 1.92 g pot_1 reduced the number of sheath blight lesions, severity of disease. Overall Si reduced inhibited sheath blight and further progression.	Rodrigues et al., 2003
13	Rice	YSB	Imidazole/rice husk ash	Si increase reduced YSB	Voleti et al., 2006 Padmakumari et al., 2018 (MS in press)
14	Rice	Blast	Si solubilizers	Regardless of origin levels of cultivar, silicon was an important component in the mechanism of resistance to blast.	Canizalez et al., 1991/ Ranganathan et al., 2004/ 2011 a and b

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15	Rice	Blast	Potassium silicate	Potassium silicate pulverization on laves decreased disease incidence	Buck et al., 2008
16	Rice	Magnaporthe grisea	Silica gel	Si uptake protected the rice plants from the damage caused by pathogen infection	Nakata et al., 2007/Voleti et al., 2011a
17	Soybean	Rust	Wollastonite ($CaSiO_3$) / potassium silicate (K_2SiO_3)	Green hose experiments demonstrated that application Si delayed disease onset by 3 days	Lemes 2010
18	Banana	Root Fuungi (Cylindrocladium)	monosilicic acid	Si application reduced root necrosis by 50% and also alleviated growth reduction caused by pathogen	Vermeire et al 2011
19	Perennial Ryegrass Turf	Grey leaf spot	Wollastonite / calcium silicate slag	Increase in tissue silicon concentration decreased disease incidence.	Nanayakkara and Uddin 2007
20	Sorghum	Anthracnose	Wollastonite	Increase in leaf Si content and disease resistance in	Renata et al., 2009

from sturdy stems, favouring leaf angle exposure to radiation, mitigating the radiation load, reduced Na uptake and its redistribution within the cell organs under saline conditions are a few beneficial effects of silicon fertilization. Abundance Silicon solubilising bacteria (SSB) presence further aided by rice stubbles and or application of fly ash have not only resulted in the biotic abiotic stress tolerance but also improved yields of crops.

In summary, methods of detecting silicon, its universal presence in biological systems despite variation in degree of its accumulation in monocotyledonous and dicotyledonous plant species do not occur as mere coincidence. The association, genetic diversity, identification of candidate genes associated with transporters, and the silicon uptake driven physiological process are energy driven. The simplest mechanism of silicon solubilisation in soils by microbiological organisms, novel mechanisms of release by simple amino acids have been ascertained and also the abrasive phenomenon and its accumulation on leaf surfaces resulting in biotic and abiotic stress tolerance evident as revealed in the recent studies. However, that, Though silicon accumulation apparently associated with tolerance of not only biological but also abiological stress syndromes, but its mechanism of action is still a mystery which needs to be unravelled.

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