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Research Review Articles

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Silicon application mitigates abiotic stresses in rice: A review

DINESH JINGER*[1], MOIRANGTHEM THOITHOI DEVI[2], SHIVA DHAR[3], ANCHAL DASS[3], V K SHARMA[4], VIJAYA KUMAR S[5], EKTA JOSHI[6], HANUMAN SINGH JATAV[7] and NEELAM SINGH[8]

ICAR-Indian Institute of Soil and Water Conservation, Research Centre, Vasad, Anand, Gujarat 388 306, India

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ABSTRACT

Rice (*Oryza sativa* L.) is the paramount staple crop, providing food to more than 50% people globally. Although, India has attained the apex position in producing rice after China, however, its productivity is still below the world's average productivity due to several physical abiotic and chemical stress. Silicon (Si) is a multipurpose element that acts as a panacea for multiple stresses. Rice is a heavy accumulator (200–300 kg Si/ha) of Si. Addition of Si prevents movement of heavy metals and salts through cell wall (apoplastic) eventually decreasing their uptake, particularly when rice face iron (Fe) and manganese (Mn) toxicity and increase the rice yield by 20.5–72.7%. Studies have revealed that application of Si mitigates arsenic (As) stress in rice by diminishing its uptake and improving the antioxidants activities. Foliar application of Si increases rice production by 30% under As and cadmium (Cd) contamination conditions. Besides, Si reduces transpiration in rice crop by 30% and also eliminates the effect of heat stress (42.5°C). Further, application of Si in rice has been shown to increase culm strength, integrity and stability of vascular bundle thus, preventing crop against lodging. These review results clearly reveal the importance of Si in imparting abiotic stress tolerance and need for its application in rice crop.

Key words: Abiotic stresses, Mitigation, Rice, Silicon

Rice (*Oryza sativa* L.) is the most important staple food crop of more than 3.4 billion people worldwide (Khush 2004) and in India it is grown over an area of 43.9 mha with total production of 110 million tonnes (Jinger *et al.* 2018a) and productivity of 2505 kg/ha which is still below the world's average yield (FAOSTAT 2017). To ensure food and nutritional security of rice, the country ought to add 3 mt grain production every year by raising rice yield levels substantially (Dass *et al.* 2017a; b). There had been bumper productions of rice during green revolution (Chauhan and Mahajan 2013). However, today, various physical abiotic (crop lodging, water-deficit, low- and high-temperature, etc.) and chemical stresses (salinity, heavy metal injury, etc.) are the major constraints in rice production. Moreover, declining water table, climate change, imbalanced use of fertilizers and lack of tolerant rice cultivars to biotic and abiotic stresses, also impose serious limitations to rice production (Vijayakumar *et al.* 2019a). Si is a beneficial element for rice crop and its application is imperative for rice production to minimize the yield gap (Ma and Yamaji 2006, Jinger *et al.* 2017). Rice has a tremendous capacity to absorb Si for growth and production. Inadequate uptake of Si reduces rice yield and quality as well (Jinger *et al.* 2018). Fig 1 shows several stresses attacking crops may be alleviated by Si (Richmond and Sussman 2003, Ma and Yamaji 2006). These advantages stem from the deposition of Si in cell walls of hulls, canopies, shoots and roots. Accumulation of Si in the roots minimizes the uptake and translocation of harmful heavy metals and salts, imparts toughness and integrity to plant cell walls and reduces transpiration thereby making the plant resistant to lodging, temperature and water stresses. Its antioxidant defence abilities minimizes water and salt stresses (Gong *et al.* 2005). Besides, Si application in soil influences the absorption, translocation and uptake of almost all micro and macro nutrients (Epstein 1999). Si application reduces nutrient losses like leaching of

*Corresponding author: dinesh.jinger@icar.gov.in; dineshjinger28@gmail.com

[1]Scientist, ICAR-Indian Institute of Soil and Water Conservation, Research Centre, Vasad, Anand 388 306; [2]Scientist, ICAR-Research complex for NEH Region, Umiam, Meghalaya 793 103; [3]Principal Scientist, Division of Agronomy, [4]Principal Scientist, Division of SSAC, ICAR-Indian Agricultural Research Institute, New Delhi 110 012; [5]Scientist, ICAR-National Rice Research Institute, Cuttack, Odisha 753 006; [6]Scientist, Rajmata Vijyaraje Scindia Krishi Vishva Vidhyalaya, College of Agriculture, Gwalior 474 002; [7]Assistant Professor, Division of SSAC, S K N Agriculture University, Jobner, Rajasthan ; [8]Ph D Scholar, Rajmata Vijyaraje Scindia Krishi Vishva Vidhyalaya, College of Agriculture, Gwalior 474 002.

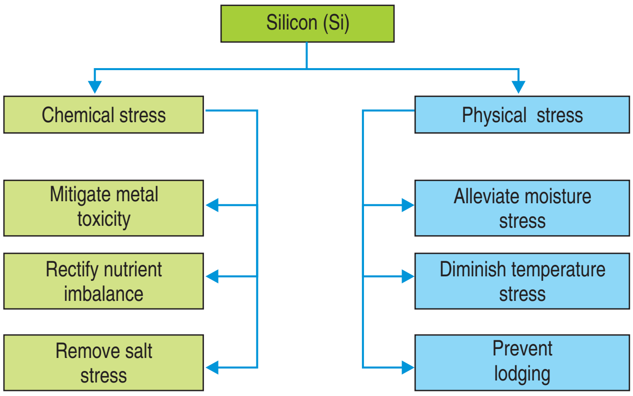

Fig 1 Abiotic stresses mitigated by silicon.

phosphate, nitrate and potash to a great extent (Matichenkov and Bocharnikova 2010).

Si in mitigating drought stress

Drought diminishes rate of growth and development and reduces yield of several crops (Showemimo and Olarewaju 2007). Si acts as an anti-transpirant which reduces water stress by supressing the transpirational process. Si application reduces transpiration rate up to 30% in rice (Ma *et al.* 2001a); the impact of Si on rice growth was more peculiar under water-stressed condition (Ma *et al.* 2001a). Rate of photosynthesis increases during drought stress (Trenholm *et al.* 2004) due to low transpiration caused by Si accumulation in leaves (Kamenidou *et al.* 2009). Si imparts drought resistance in crops plants by retaining water, CO_2 fixation efficiency, and uprightness of canopy and anatomy of water transporting tissues (Hattori *et al.* 2005). The difference between the performance of plants grown under Si-deficient and Si-sufficient condition was up to 30% (Lewin and Reimann 1969). Japanese researchers reported up to 30% reduction in transpiration loss due to application of Si. Si minimizes water loss by maintaining the optimum transpiration rate of the plant (Freitas *et al.* 2011). In plants the transpiration is conducted by the stomata present in leaves and cuticle present in shoot (Kerbauy 2004). Rice crop treated with Si showed improvement in transpiration rates by reducing water uptake (Marschner 1995, Takahashi 1996). Maximum Si is accumulated at epidermal cell walls on both adaxial (upper) and abaxial (lower) surfaces of the leaves after evaporation (Hodson and Sangster 1989). It has been reported that grain yield showed linear relationship with Si application rates at 60% FC. Thickness of silica gel layer is correlated with the cellulose in epidermal cell walls and it decides the water balance in plant as thickened layer reduces water loss through transpiration (Cheong *et al.* 1972). According to Agarie *et al.* (1998), increasing levels of Si in rice leaves reduces the electrolyte leakage from the leaf tissues as concentration of Si in leaves is correlated with level of polysaccharides in the cell wall. This finding suggests that Si in rice leaves plays a vital role in water relations of cells, like mechanical properties and water permeability. Si application significantly influences the size and number of matured grains in rice and barley (Ma and Takahashi 2002) which could be due to the eradication of water stress by Si. Si-containing spikelets lost only 7% water as compared to Si-deficient spikelets where loss was 20% higher during both milking and maturity phases (Ma *et al.* 2001a). For proper growth of panicles, a congenial water balance within the hull is essential for ripening and maturity. Si Application reduces the water loss from panicles up to 30% either at milking or maturity phases (Ma and Takahashi 1990). Si treatment improves chlorophyll and relative water content of rice to a great extent (Biglary *et al.* 2011).

Si and temperature stress

Si application can mitigate heat stress in rice plants by enabling the plant resistant to heat stress. Water loss caused by high temperature (> 42.5°C) was less conspicuous from the leaves of Si treated rice (Agarie *et al.* 1998) which indicates role of Si in maintaining the thermal stability of lipids in cell membranes. Rice is sensitive to not only high

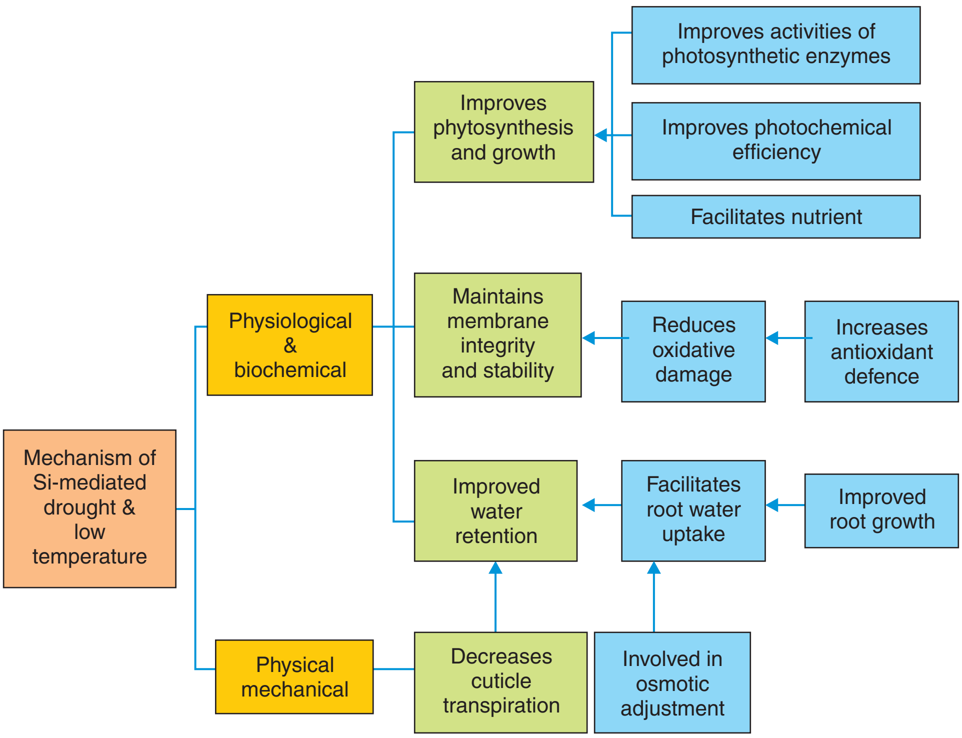

Fig 2 Mechanisms of Si-mediated drought and freezing tolerance in plants.

temperatures, but also to low temperature stress like frost. Organo-silicon compounds protect the rice plants from frost and only 0–5% rice plants succumb to frost injury. Active forms of Si protect crop plants from short-term frost (Loginov *et al.* 2011). Thus, Si can impart the resistance to temperature stress in crop plants due to physiological, biochemical and physical phenomenon illustrated in Fig 2.

Si, nitrogen (N) and lodging

Application of heavy doses of N-fertilizers for obtaining maximum grain yields reduces plant's tolerance to pest and diseases attack besides causing lodging and mutual shading. Lodging is a serious constraint for the cultivation of rice, especially in modern cultivars as it reduces yield and quality of produce leading to negative impact like hindrance in harvesting operation (Fallah 2012). Application of Si significantly increases the strength of rice stalk by nullifying the negative impacts of higher dose of N on stability of stalk and susceptibility to lodging (Balasta *et al.* 1989).

Si protects the rice crop from the negative impacts of lodging by increasing the culm rigidity and structure of the vascular bundles (Ma *et al.* 2001). Perpendicular orientation of leaves greatly influences the light interception by the plants. The erectness of rice leaves is either decreased or changed by heavy doses of N, whereas Si application increases erectness of leaves thus, enhancing plants ability to withstand the ill-effects of heavy dose of N on light interception and penetration (Marschner 1995).

Si and deficiency of phosphorus (P)

The promising results of Si under P deficiency have been detected in various crop plants like rice and barley. As reported by Ma and Takahashi (1990a), Si application significantly improves the dry biomass of rice at low amount of P as compared to medium level of P. Neither the P-fixation capability of P-deficient soil was influenced by silicic acid application (Ma and Takahashi 1990b) nor P-fixed in soil was desorbed by it which means it doesn't affect uptake and translocation of P at low level in both soil and solution culture (Ma and Takahashi 1991). However, Si improves P translocation to the rice panicles (Nagaoka 1998). Besides, it remarkably reduces Fe and Mn uptake by the plants leading to greater proportion of P/N and P/Fe (Ma and Takahashi 1990a). Hence, Si application increases availability and utilization of P (Ma *et al.* 2001) due to increased accessibility of P through reduction in the luxury uptake of Fe and Mn. The findings elaborate the beneficial effects of Si on the growth and development of crop plants under P-deficit situation.

Si and excess of P

Over abundance of P rarely occurs in natural soils. However, it was reported where P had been applied indiscriminately or in solution culture where a huge concentration of P is applied. Indiscriminate application of P leads to chlorophyll loss or death of plant cell in plant leaves by reducing accessibility to essential micro-nutrients like Fe and Zn. Si can lessen this injury by reducing the immoderate uptake of P. The formation of apoplastic hurdle due to Si deposition on inner cells of roots (Lux *et al.* 1999; 2003) decreases the internal P content. Si induces reduction in P uptake in many non-Si- accumulating plants also (tomato, soybean, strawberry and cucumber (Ma *et al.* 2001a). The absorption, uptake and translocation of various essential nutrients are influenced by Si in nutrient culture (Epstein 1994). It improves the uptake of Zn, especially when the P is present in ample amount (Marschner *et al.* 1990). The application of amalgamation of active Si and P fertilisers can improve the phosphorus use efficiency by 40–60% (Matichenkov *et al.* 1997). Ghanbari-Malidarreh *et al.* (2011) revealed that various levels of P and Si significantly influenced the grain yield of rice by 23 % as compared to control besides increasing spikelets/panicle, straw and biological yields.

Si and potassium (K)

Addition of Si to K-deficit soybean increases growth and yield attributes, internal K status and mitigates the membrane lipid peroxidation and oxidative stress aggravated by K-deficiency by modulating antioxidant enzymes. Under K-deficient condition, it not only enhances K uptake in paddy but also removes K deficiency (Miao *et al.* 2010). Under salt stress condition, Si may not improve the K content in rice (Yin *et al.* 2013). The presence of anions in fertilizers affects the Si-K Interaction (Jones and Handreck 1967). For instance, Sulphate-based K-fertilizers enhance uptake and deposition of Si to a greater deal than the chloride-based K-fertilizers.

Si and heavy metal toxicity

Silicon enhances the plants resistance to toxic metals which may stimulate the antioxidant systems, mitigate the inhibition to photosynthesis and complexation of heavy metals with Si (Epstein and Bloom 2005, Liang *et al.* 2007). The accumulation of Si in the roots system decreases uptake and transport of toxic metals and salts from roots to the shoot system (Ma and Yamaji 2006). Application of Si improves plants tolerance to metals toxicity like aluminium (Al) (Ma 2004, Liang *et al.* 2001), boron (B) (Gunes *et al.* 2007), Cd (Inal *et al.* 2009), manganese (Mn) (Nwugol and Huerta 2008) and zinc (Zn) (Kaya *et al.* 2009). The Fe toxicity is a serious malady in rice, which leads to "bronzing" (brown leaves). The availability of optimum available Si at the root surface nullifies the lethal levels of Fe and Mn (Perry and Keeling-Tucker 1998) thereby, hampering the luxury consumption and mitigating Fe toxicity in rice (Okuda and Takahashi 1962). Li *et al.* (2011) reported that excess of Fe and Mn condition improves the rice yield by 21–73%. The deficiency of Si enhances the uptake of Mn causing deleterious effects in rice, barley, rye and ryegrass which can be corrected by applying Si-based fertilisers.

Si decreases the uptake of Mn by enhancing roots Mn oxidizing capacity and its redistribution (Okuda and Takahashi 1962, El-Jaoual and Cox 1998) and nullifies its toxicity by improving Mn fraction bound in cell wall (Rogalla and Romheld 2002). Tripathi *et al.* (2013) reported that application of Si removes oxidative stress caused by As in *Triguna* (rice variety) by decreasing its accumulation and improving the antioxidant system. The antioxidant defence power was improved due to foliar application of Si on rice grown under As or Cd stress (Liu *et al.* 2011). Application of Si removes the ill effects of Zn and Cd and increases the DMA and rice yields significantly and simultaneously reduces Cd and Zn concentration in rice. In addition, accumulation of heavy metals is significantly reduced in grain and root system.

The root attributes decreased by Cd and Zn stress in a hydroponic experiment were significantly improved by Si application (Wen and Cai 2011). Application of Si nullifies the lethal effects of Cd/Cu during various stress conditions. The decreased heavy metals uptake in roots modulated the signalling of phyto-hormones imparts responses to stress and host defence, such as ABA, JA and salicylic acid (SA) (Kim *et al.* 2014). Reduction in lipid peroxidation and fatty acid desaturation in rice plant was also found. In fact, Si is the only nutrient which has the capability to increase resistance to multiple stresses because it binds the metals and arrests their concentration to lethal levels at localized sites. Si and heavy metal complexes in root cell walls prevent translocation of metals in non-Si accumulating crops. In saturated condition, it improves volume of air filled spaces in roots and shoots helping in oxygen translocation into the roots, oxidizing Fe and Mn into their less pernicious form (Ma and Takahashi 1990).

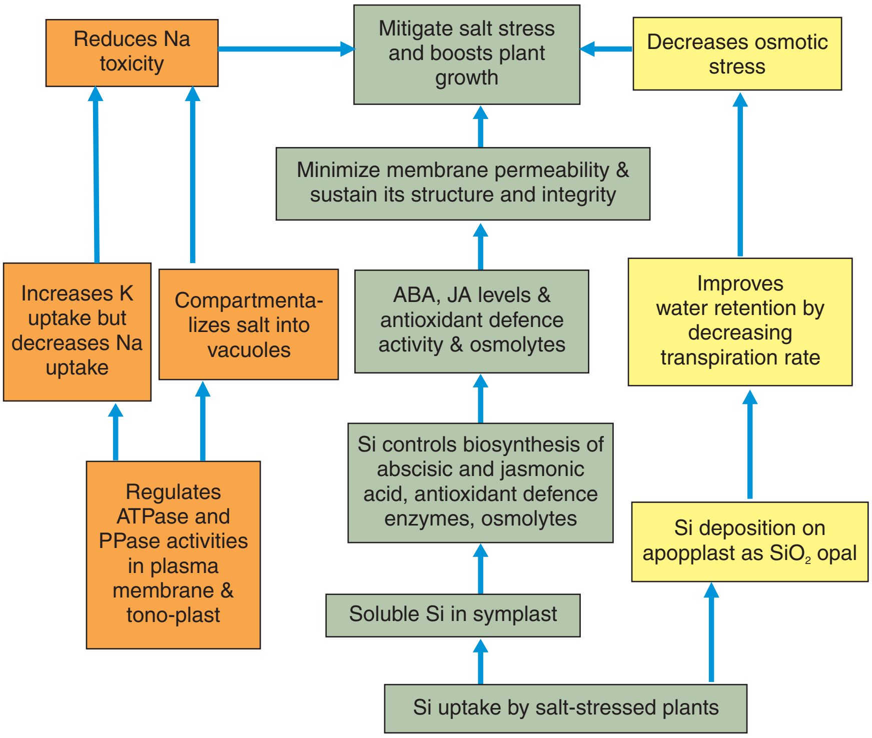

Fig 3 A modus operandi of Si to alleviate the salt stress in plants.

Si and salinity

Ionic phyto-toxicity is one of the systems responsible for salt toxicity in plants leading to accumulation of plethora of salt ions (Na^+ and Cl^-) in the plants (Liang and Ding 2002). The ability of Si to nullify the negative impacts of NaCl on plant growth and development are well elaborated. The advantageous impacts of Si under salt condition have been reported in rice (Liang *et al.* 2007). Application of Si reduces Na uptake through decreased transpiration, eventually impairing growth, development and PS actuated by salt stress (Yeo *et al.* 1999). An equal distribution of both Na and Cl ions due to Si in the whole root system, ultimately increases the salt tolerance ability of the plants (Liang and Ding 2002). According to Saqib *et al.* (2008), Si has potential to alleviate the salinity stress through improvement in Na exclusion and reduction in lipid membrane peroxidation. Application of Si enhances both shoot and root growth under salinity stress condition which ultimately imparts beneficial effect on the whole plant system (Yoshida 1965) leading to

Table 1 Mitigation of physical abiotic stress in crops by Si application

Physical abiotic stress	Reduction in stress (%)	Yield increase (%)	Crops	References
Lodging	66–90	10–34	Wheat	Jinger *et al.* (2018)
			Rice	Matoh *et al.* (1986)
			Rice	Liang *et al.* (1999)
			Rice	Wang *et al.* (2001)
Drought	31–40	25–30	Augustine grass	Brecht *et al.* (2004)
			Tomato	Romero-Aranda *et al.* (2006)
High temperature	42–45	40-50	Rice	Idris *et al.* (1975)
Freezing	88–94	24–38	Cucumber	Marschner *et al.* (1990)
			Rice	Loginove *et al.* (2011)
Radiation, UV	–	–	Soybean	Shen *et al.* (2010)

Table 2 Mitigation of chemical abiotic stress in crops by Si application

Chemical abiotic stress	Reduction in stress (%)	Yield increase (%)	Crops	References
Salinity	50–60	40–50	Rice	Matoh *et al.* (1986)
			Canola	Hashemi *et al.* (2010)
Mn	20–30	20–70	Wheat	Ahmad *et al.* (1992)
			Maize	Parveen and Ashraf (2010)
			Rice	Li *et al.* (2011)
As	28–30	24–33	Rice	Li *et al.* (1989)
				Liu *et al.* (2011)
Fe	20–30	25–72	Sugarcane	Fox *et al.* (1967)
			Rice	Li *et al.* (2011)
Cd	30–40	25–40	Rice	Nwugo and Huerta (2008)
			Brassica	Liu *et al.* (2009)
Zn	32–38	59–80	Maize	Cunha *et al.* (2008)
Al	55	30–40	Wheat	Zsoldos *et al.* (2003)

increase in total DMA due to increased net CO_2 assimilation (NCA) rates (Savvas *et al.* 2009). Gas exchange in PS is extremely sensitive to salt deposition on the leaves (Yeo *et al.* 1985). Application of Si reduced the Na^+ content in leaves, however, NCA rate was increased significantly (Yin *et al.* 2013). A modus operandi of Si to alleviate the salt stress in plants is depicted through Fig 3.

Si and aluminium (Al) toxicity

Toxicity of Al is a serious constraint for the cultivation of rice, particularly in acid soils (Foy *et al.* 1978). Various processes for mitigation of Al toxicity by Si application has been reported in rice and other crops; encompassing co-deposition Si of with Al in the plant, activity in the protoplasm, impact on enzymatic activity (Cocker *et al.* 1998). Application of Si in maize crop significantly mitigates Al induced root elongation problem (Ma *et al.* 1997) and decreases toxic concentration of Al. It has also been reported that Si mitigates Al toxicity in crop plants by reducing the Al uptake and translocation by the plants and findings recommend that Si minimizes Al toxicity in rice (Singh *et al.* 2011). Some of the physical and chemical abiotic stresses mitigated by Si application are given in Table 1 and 2.

Conclusion

Rice has a high ability to absorb, accumulate and deposit Si among different parts of the plant. The factors limiting higher productivity of rice include a set of abiotic factors. Application of Si in rice crop could be a good alternative in this regard. Application of Si not only improves productivity but also mitigates all types of stresses in rice. Although, it is not considered as necessary component for the growth of rice crop, but it improves leaf angle and erectness thus reduces self-shading and lodging. Application of Si increases photosynthetic rate, number of spikelets, spikelet fertility, and reduces transpiration rate under water stress condition, resulting in higher productivity. Most of these effects are due to Si deposition on different plant parts like leaves, stems and hulls. Thus, it can be concluded that Si may be a boon for sustainable rice production particularly under constraint conditions.

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