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Review

Silicon, the silver bullet for mitigating biotic and abiotic stress, and improving grain quality, in rice?

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ABSTRACT

Adequate silicon fertilization greatly boosts rice yield and mitigates biotic and abiotic stress, and improves grain quality through lowering the content of cadmium and inorganic arsenic. This review on silicon dynamics in rice considers recent advances in our understanding of the role of silicon in rice, and the challenges of maintaining adequate silicon fertility within rice paddy systems. Silicon is increasingly considered as an element required for optimal plant performance, particularly in rice. Plants can survive with very low silicon under laboratory/glasshouse conditions, but this is highly artificial and, thus, silicon can be considered as essential for proper plant function in its environment. Silicon is incorporated into structural components of rice cell walls were it increases cell and tissue rigidity in the plant. Structural silicon provides physical protection to plants against microbial infection and insect attack as well as reducing the quality of the tissue to the predating organisms. The abiotic benefits are due to silicon's effect on overall organ strength. This helps protect against lodging, drought stress, high temperature (through efficient maintenance of transpiration), and photosynthesis by protecting against high UV. Furthermore, silicon also protects the plant from saline stress and against a range of toxic metal stresses (arsenic, cadmium, chromium, copper, nickel and zinc). Added to this, silicon application decreases grain concentrations of various human carcinogens, in particular arsenic, antimony and cadmium. As rice is efficient at stripping bioavailable silicon from the soil, recycling of silicon rich rice straw biomass or addition of inorganic silicon fertilizer, primarily obtained from iron and steel slag, needs careful management. Silicon in the soil may be lost if the silicon-cycle, traditionally achieved *via* composting of rice straw and returning it to the land, is being broken. As composting of rice straw and incorporation of composted or non-composted straw back to land are resource intensive activities, these activities are declining due to population shifts from the countryside to cities. Processes that accelerate rice straw composting, therefore, need to be identified to aid more efficient use of this resource. In addition, rice genetics may help address declining available silicon in paddy soils: for example by selecting for characteristics during breeding that lead to an increased ability of roots to access recalcitrant silicon sources from soil and/or *via* selection for traits that aid the maintenance of a high silicon status in shoots. Recent advances in understanding the genetic regulation of silicon uptake and transport by rice plants will aid these goals.

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1. Introduction

Rice can be considered as a silicon accumulator and can have shoot silicon concentrations above 10% of shoot dry weight (Yamamoto et al., 2012), with typical ranges from low to high being 1.7 to >3.4% (Korndorfer et al., 2001). Other members of the Poaceae share this characteristic (Epstein, 1999; Kido et al., 2015; Ma and Takahashi, 2002; Van Bockhaven et al., 2013), but silicon in rice is the most studied because of the economic importance of rice. Rice has specific mechanisms for assimilating silicon from soil as soluble silicic acid, and for unloading silicic acid into the xylem, through the aquaglyceroporins lsi1 and lsi2 (*i.e.* Ma et al., 2006; Ma et al., 2006). Grasses, in general, seem to utilize silicon in their tissue for defense against biotic and abiotic stresses such as herbivory, leaf microbial pathogen resistance, lodging, salinity, high light intensity, toxic metal stress and drought tolerance (Goto et al., 2003; Kim et al., 2014; Khattab et al., 2014; Ma and Takahashi, 2002; Van Bockhaven et al., 2013). Plants fertilized with silicon, tend to have higher yields than non-fertilized plants. In fact, silicon fertilization has been shown to increase the number of grains per panicle by *circa.* 25–100% (Ma and Takahashi, 2002; Ma and Takahashi, 2002a). This can be attributed to the fact that silicon fertilization leads to better structural support and enhanced biomass and, consequently, higher yield bearing capacity, as well as increased resistance against various biotic and abiotic stresses that would otherwise cause yield decline.

Evidence, to date, suggests that silicon does not seem to be directly involved in regulation of cell functions besides its direct role in plant structural components and cell wall chemistry. Furthermore, silicon appears to interact with defense associated signaling pathways and silicon status seems to regulate a range of physiological activities (Ye et al., 2013; Van Bockhaven et al., 2013). Silicon appears to be fundamental to regulating grain nutrition by playing an important role with respect to assimilation of the problematic toxins arsenic, antimony and cadmium in rice (Liu et al., 2014b; Li et al., 2009).

This review aims to give an overview of the current state of knowledge of silicon in rice considering: soil-plant biogeochemistry; plants genetics involved in silicon accumulation, transport and deposition in tissues; the role of silicon in maintaining yield by counteracting biotic and abiotic stress; and how silicon impacts on grain quality. The review, furthermore, provides an overview of topics that require further investigation as it appears that silicon nutrition of paddy soils is declining.

2. Silicon soil-plant biogeochemical cycle

2.1. Silicon soil chemistry

Total silicon is high in soils as it is the second most abundant element in the earth's crust (Sommer et al., 2006). Soils contain >50% SiO_2 (Ma and Takahashi, 2002), predominantly in the form of silicates (aluminum, calcium, iron *etc.*), quartz, biogenic SiO_2 (phytoliths and diatoms) and silica gel (polymerized silicic acid). Soil silicon concentrations range between 1 and 45% dependent on soil type (Sommer et al., 2006), and soil mineral composition is

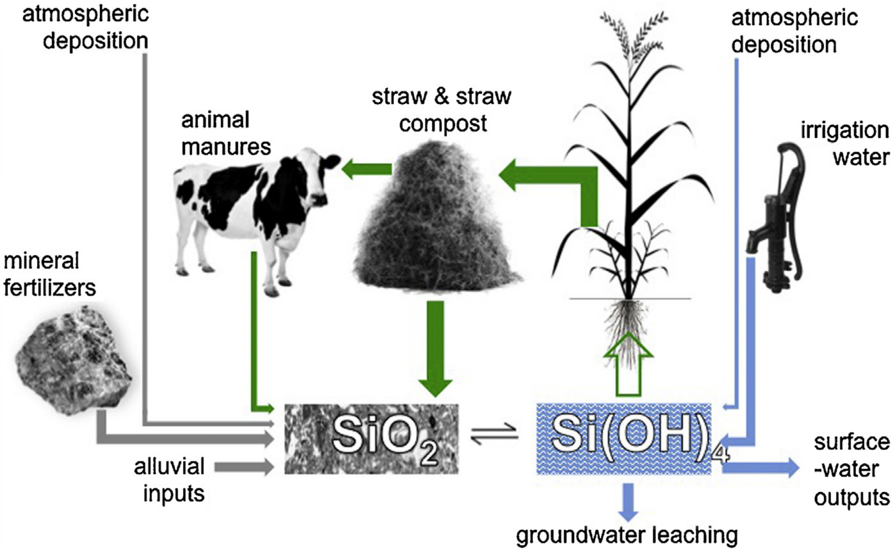

Fig. 1. The paddy soil system silicon cycle.