

Cadmium Stress in Rice: Influence of Silicon

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Abstract

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Rice plants grown in Cd-contaminated soils are facing concerns of human health and food safety. To reduce the uptake of Cd by rice plants from the soil, several strategies have been adopted for management of Cd-contaminated soil. Silicon (Si) is an element that is agronomically essential for rice growth. To minimize the negative effect of Cd, application of Si fertilizers has been used as one of strategies to reduce Cd accumulation in and toxicity of rice plants. In this review, we briefly discuss the mechanisms of Si-reduced Cd levels in rice plants.

Key words: Cadmium stress, Silicon, Rice.

INTRODUCTION

Cadmium (Cd) is a heavy metal that is toxic to humans and plants. This metal enters the environment mainly from industrial process, application of phosphate fertilizers and sewage sludges. In Taiwan, inappropriate disposal of industrial waste has given rise to the widespread Cd contamination in rice paddy by irrigated water. Due to the unregulated dismantling of electronic and electric waste (E-waste), some agricultural soils in southeast China have become severely contaminated with high levels of Cd (Fu *et al.* 2008). Thus, the disposal of E-waste is also becoming a serious environmental problem. Cd can be readily taken up by rice roots and translocated to shoot and then to grains (Song *et al.* 2015). Cd enters into the food chain through rice consumption and causes toxicities to humans (Aziz *et al.* 2015). It has been estimated that rice consumers ingest about half or more of their daily Cd intake from rice (Iwao 1977). Thus, rice plants grown in Cd-contaminated soils are facing problems

of human health and food safety.

To reduce the uptake of Cd by rice plants from the soil, several strategies have been adopted for management of Cd-contaminated soil (Rizwan *et al.* 2016). One of which is the application of silicone (Si) fertilizers. Si is an element that is capable of enhancing multiple (biotic and abiotic) stresses (Ma 2004; Liang *et al.* 2007; Wu *et al.* 2013; Meharg & Meharg 2015; Lin *et al.* 2017). Various studies have shown that Si is able to enhance the heavy metal (including Cd) stress tolerance (Ma 2004; Liang *et al.* 2007; Wu *et al.* 2013; Lin *et al.* 2017). In this review, we discuss the possible mechanisms of Si-mediated alleviation of Cd damage in rice plants.

SILICON IS BENEFICIAL FOR PLANT GROWTH

Silicon is the second most abundant element in soil and readily absorbed by plants. For this reason, plants contain an appreciable amount of Si, ranging from 0.1% to 15% dry

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weight (Epstein 1994; Ma & Yamaji 2006; Farooq & Dietz 2015). Monocot plants such as rice, maize, wheat and barley are considered as Si-accumulating plants because of their very high contents of Si (10–15%). In contrast, most dicot plants accumulate less than 0.5% Si in dry weight (Farooq & Dietz 2015). The amount of Si that is able to be accumulated in rice plants is several-fold more than macronutrients such as nitrogen, phosphorus, and potassium (Yamaji *et al.* 2015). Si is known to be required for normal cell growth and imparts structural benefits to diatoms (Farooq & Dietz 2015). Up to now, Si is still not considered as an essential element. However, several pieces of evidence support the conclusion that Si is beneficial for plant growth and development, and regarded Si as an element that is “quasi-essential” (Epstein 1999). In a subsequent review article, Epstein (2009) considered Si as an inorganic secondary nutrient, which is analogous to organic secondary metabolite. For rice growth, Si has been considered as an essential element agronomically in 1976 (Lian 1976). Si is routinely applied to rice in Asian countries such as Japan and Korea to enhance high and sustainable crop yield.

SILICON UPTAKE AND TRANSPORT IN RICE PLANTS

Weathering of silicate-containing minerals is the major source of Si for plants. The mineral breakdown releases soluble silicic acid (H_4SiO_4) into the soil solution (Malhotra *et al.* 2016). H_4SiO_4 in the soil solution is then taken up by plant roots as an uncharged monomeric molecule below pH 9 (Takahashi & Hino 1978). He *et al.* (2013, 2015) used suspended rice single cells to investigate the localization of Si and demonstrated that Si is present in cell wall as a hemicellulose-bound form of Si.

Basically, passive and active are two mechanisms of Si uptake by higher plants (Ma *et al.* 2004; Mitani & Ma 2005). Passive uptake of Si takes place along transpiration stream.

Most dicots absorb Si passively. Active Si uptake usually occurs in rice plants. However, Liang *et al.* (2006) reported that both active and passive mechanisms are operating in rice plants. Ma *et al.* (2002) isolated the first known rice mutant that is defective in active Si uptake. Using this mutant, they cloned the *low silicon rice 1 (Lsi1)* gene (Ma *et al.* 2006), which encodes a membrane protein similar to water channel proteins (aquaporins). Suppression of *Lsi1* expression resulted in reduced silicon uptake. *Lsi1* functions as an influx transporter in rice plants. In a subsequent paper, Ma *et al.* (2007) reported the identification of *low silicon rice 2 (Lsi2)*. The protein encoded by this gene is localized, like *Lsi1*, on the plasma membrane. In contrast to *Lsi1*, *Lsi2* functions as a silicon efflux transporter. Based on the results of mathematical modeling study, Ma & Yamaji (2015) concluded that the cooperation of *Lsi1* and *Lsi2* in rice permits effective transcellular transport of the Si in rice.

Rice plants show genotypic difference in Si accumulation. *Japonica* rice varieties usually have a higher Si concentration than *indica* rice varieties (Deren *et al.* 1992). Ma *et al.* (2007) compared the difference between the *japonica* variety and the *indica* variety in Si uptake. They found that the difference in the Si accumulation results from the difference in abundance of in *Lsi1* and *Lsi2* transporter in rice roots. After transmembrane transport via *Lsi1* and *Lsi2* into the stele, Si is translocated to the shoot by transpiration flow through the xylem (Mitani *et al.* 2005). *Lsi6* is now known as a transporter responsible for the transport of Si out of the xylem (xylem unloading) and subsequently affects the distribution of Si in rice shoots (Yamaji *et al.* 2008).

SILICON REDUCES CADMIUM TOXICITY OF RICE PLANTS

Okuda & Takahashi (1962) demonstrated that Mn toxicity in rice plants was alleviated by exogenous addition of Si. The discovery

that Si-alleviated Mn toxicity in turn led to the finding that this role of Si can also be applied to other metal ions, such as Cd. Wang *et al.* (2000) were the first to report that application of Si significantly prevents the uptake of Cd into rice cells. In a pot experiment, Ping *et al.* (2008) found that addition of calcium silicate, a Si fertilizer, enhances the yield and decreases the Cd content in straw and grain of rice plants grown in a soil that was contaminated with Cd. Fly ash and steel slag, Si-rich amendments, are low cost industrial by-products. The results from a pot experiment by Gu *et al.* (2011) clearly showed that the application of fly ash and steel slag decreases the phytoavailability of Cd and further suppressed Cd uptake by rice. Recently, Ji *et al.* (2017) investigated the effect of different types of Si-rich soil amendments (slag, ground slag, and diatomaceous earth) and fertilizers on the distribution of soluble and insoluble forms of Cd in the rice plants grown on long-term cultivated paddy soil contaminated with Cd in China. They demonstrated that the Si-rich materials increase rice biomass and reduce the total leaf Cd. Si fertilizers used in the application were mainly applied into soil directly. Liu *et al.* (2009) conducted an experiment to investigate the effect of foliar application of two types of impurity-free SiO₂ solution on Cd toxicity in rice. They found that the total accumulation of Cd in rice grains decreased with the foliar application of Si solution. Similarly, Wang *et al.* (2015) also reported foliar application with nano-Si alleviated Cd toxicity in rice seedlings.

Nwugo & Huerta (2008) investigated the effect of Si nutrition on low-level Cd toxicity symptoms in rice seedlings. Their results showed that low-level Cd treatment generally inhibited growth. Application of Si significantly reduced root- and leaf-Cd content and alleviated low-level Cd-induced inhibition of growth. Most nutrient studies on the interaction between Si and Cd are short term. Zhang *et al.* (2008) conducted a long-term experiment, in which rice was grown for 105 d and harvest-

ed at four different growth stages to measure biomass accumulation and Cd uptake and distribution in shoots and roots. The results from their experiments concluded that Si enhances plant growth and decreases Cd accumulation in shoots. Despite evidence of the role of Si in the mitigation of Cd toxicity in rice plants at the whole-plant level (Shi *et al.* 2005; Tripathi *et al.* 2012; Srivastava *et al.* 2015), involvement of Si in inhibiting Cd uptake at the single-cell level of rice has been reported (Liu *et al.* 2013; Ma *et al.* 2015).

MECHANISMS OF SILICON-INHIBITED CADMIUM UPTAKE IN RICE PLANTS

It is now clear that the effect of Si application on reducing Cd toxicity of rice plants is related to the reduction on Cd uptake. Si could decrease Cd uptake in rice through mechanisms occurring at both soil and plant levels.

The interaction between Si and Cd occurs in the soil is an indirect effect (Ji *et al.* 2017). It has been shown that soil pH is a predominant factor which limits Cd uptake (Takjima & Katsumi 1973; Ping *et al.* 2008). Application of Si-rich substances was reported to increase the soil pH (Takijima & Katsumi 1973; Ping *et al.* 2008; Gu *et al.* 2011; Ji *et al.* 2017). These results suggest that increase in pH may lead the reduction of Cd bioavailability in the soil.

Liu *et al.* (2009) reported that foliar application of Si reduced Cd concentration in rice grains, suggesting that Si alleviates Cd accumulation in rice grains may be related to the Cd sequestration in shoot cell walls. Using rice single cells, Ma *et al.* (2015) demonstrated that the interaction of Si with Cd occurs in the cell walls via a [Si-hemicelluloses] Cd co-complexation. Gu *et al.* (2011) also found that Cd translocation from stem to leaf of rice was dramatically inhibited by adding Si-rich amendments. They found that the increase of Si concentration may form complex with Cd in stem.

Shi *et al.* (2005) investigated the effect of Si on the distribution of Cd in rice seedlings and proposed that Si partially physically blocks the apoplast bypass flow across the rice roots, and restrains the apoplastic transport of Cd. More recently, Ma *et al.* (2016) reported that Si-modified cell walls inhibited Cd uptake under short-term Cd stress, whereas the compartmentation of Cd into vacuoles under long-term Cd stress is the possible mechanism reducing Cd uptake.

In Cd-treated rice plants, about 50 proteins were significantly regulated by the presence of Si (Nwugo & Huerta 2008), suggesting that Si-enhanced Cd tolerance of rice might be associated with the synthesis of relevant proteins. The natural resistance-associated macrophage proteins (Nramps) are metal-ion transporters (Nevo & Nelson 2006). OsNramp5 is known to mediate Cd transport in rice plants (Sasaki *et al.* 2012). *Low cadmium (LCD)* is a gene related to Cd accumulation (Shimo *et al.* 2011). The heavy metal ATPases (HMAs), also known as the P_{1B}-ATPases, are localized mainly in vacuole of rice roots. Based on the available data, it appears that, when treated with Si, the expression of *OsLsi1* and *OsLsi2*, genes responsible for Si transport (Ma *et al.* 2006, 2007), is highly up-regulated in rice, resulting in down-regulated *OsLCD*, *OsNRamp5*, *OsHMA2*, and *OsHMA3* under Cd stress (Kim *et al.* 2014; Lin *et al.* 2017).

CONCLUSIONS AND PERSPECTIVES

Rice plants grown in Cd-contaminated soils are facing problems of human health and food safety. In this review, we clearly show that application of Si-rich substances is able to mitigate the Cd stress of rice plants. Si nutrition and management in rice have received great attention in Japan. Compared with *japonica* rice, research information concerning Si nutrition in *indica* rice is less adequate. The reports on Si nutrition of rice suggest that high Si rice is better adapted to Cd stress. It is now

well established that the difference in the Si accumulation results from the difference in abundance of *Lsi1* and *Lsi2* transporters in rice roots. Screening and genetic analysis of rice germplasm for high Si content will be the aid in the acceleration of breeding of rice that is higher in Si status.

Rice is a known Si accumulator. Due to continuous culture of high-yielding rice cultivars with intensive cultivation practices, especially if farmers are not replacing the Si removed by rice plants, the soil used in growing rice plants may contain an inadequate supply of Si. The challenge of how to effectively sustain Si levels in the soil appears to be of prime importance in future research.

In Taiwan, stress physiology of Cd has been extensively studied using 'Taichung Native 1', an *indica* cultivar in our laboratory. Unfortunately, the importance of Si-rich substances in mitigating Cd stress has been overlooked and poorly understood. Based on the present discussion, we strongly suggest that future work here in Taiwan to be focused on large-scale and long-term well-designed-field trials. Such results are certainly helpful for obtaining information regarding the feasibility of Si application for mitigation of Cd stress in rice plants.

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水稻鎘逆境：矽元素的影響

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摘要

高景輝。2018。水稻鎘逆境：矽元素的影響。台灣農業研究 67(1):1-8。

水稻生長於鎘污染土壤，會面臨人體健康及食品安全問題，很多策略可用來管理鎘污染土壤。在農藝上，矽是水稻生長所需重要元素。為降低鎘負面影響，矽肥可用來降低鎘之累積與水稻毒害。本文旨在探討矽肥降低鎘吸收可能機制。

關鍵詞：鎘逆境、矽元素、水稻。

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