



Review

Cadmium in rice: Transport mechanisms, influencing factors, and minimizing measures[☆]

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ABSTRACT

Cadmium (Cd) accumulation in rice and its subsequent transfer to food chain is a major environmental issue worldwide. Understanding of Cd transport processes and its management aiming to reduce Cd uptake and accumulation in rice may help to improve rice growth and grain quality. Moreover, a thorough understanding of the factors influencing Cd accumulation will be helpful to derive efficient strategies to minimize Cd in rice. In this article, we reviewed Cd transport mechanisms in rice, the factors affecting Cd uptake (including physicochemical characters of soil and ecophysiological features of rice) and discussed efficient measures to immobilize Cd in soil and reduce Cd uptake by rice (including agronomic practices, bioremediation and molecular biology techniques). These findings will contribute to ensuring food safety, and reducing Cd risk on human beings.

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1. Introduction

Among all hazardous heavy metals, cadmium (Cd) possesses higher mobility and toxicity to living organisms (He et al., 2015; Song et al., 2015). Approximately 2.35×10^{12} m² of arable land worldwide were contaminated by heavy metals (Bermudez et al., 2012). In China, about 2.786×10^9 m² of agricultural soils were polluted with Cd (Liu et al., 2015a). Moreover, Cd is easily transferred from soil to plants with a high bioconcentration factor [for example, the soil-to-grain bioconcentration factors of 20 rice cultivars ranging from 0.300 to 1.112 (Song et al., 2015)], influencing the soil properties (pH, organic matter, etc.) and the physiological features of plants (shoot and root biomass, leaf size, evaporation rate, etc.) (Liu et al., 2015a). Cadmium accumulated in grains can

enter the food chain and thus menace human well-being (Xie et al., 2015; Xue et al., 2014; Aziz et al., 2015). Due to daily ingestion of rice grain, Cd exposure in the general Japanese population can be as high as 3–4 mg kg⁻¹ body weight every week (Tsukahara et al., 2003).

The “Itai-Itai disease” happened in Japan during the 1950s that resulted from the prolonged intake of Cd-contaminated rice has aroused worldwide concern (Huang et al., 2009). Rice (*Oryza sativa* L.) is a major staple cereal crop, feeding most of the population in the world (Liu et al., 2014). At present, Cd pollution in soil severely threatens the rice quality (Hu et al., 2009), and Cd-contaminated rice becomes the main Cd exposure to humans posing health risk. As a result, it is needed to develop effective techniques to lower Cd accumulation in rice. Previous studies on strategies to minimize Cd in rice mainly concentrated on agronomic practices e.g., soil amendments (Guo et al., 2006), fertilizer management (Yan et al., 2015), water management (Honma et al., 2016), and tillage management (Yu et al., 2014)], bioremediation [e.g., phytoremediation (Liu et al., 2011) and microbial remediation (Dixit et al., 2015)]. In recent years, more and more investigations on the uptake and transport pathways of Cd in rice have been conducted, which provide detailed information on Cd transport mechanisms

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(Uraguchi et al., 2009; Yoneyama et al., 2010; Uraguchi and Fujiwara, 2013). This better understanding of Cd transport in rice and the fast development of molecular biology, resulting in transgenic rice (Takahashi et al., 2014) and rice mutants (Ishikawa et al., 2012), used in minimizing Cd uptake and accumulation. This review aims to provide a comprehensive summary of updated research achievements in this field. Firstly, the primary pathways of Cd uptake by rice were reviewed. Secondly, the influence factors of Cd uptake and transport in rice, including physicochemical characters of soil and ecophysiological features of rice, were systematically elucidated. Finally, measures pertaining to reduce Cd in rice were discussed in detail.

2. Uptake and transport pathway of Cd in rice

There are four major processes that mediate Cd transport from roots to shoots and subsequently, grains (Fig. 1): (i) uptake by roots (route a), (ii) xylem-loading-mediated translocation to shoots (route b₁-b₂), (iii) redirection of transport through intervacular transfer at nodes (route c), and (iv) remobilization from leaf blades via phloem (route d₂) and finally transportation into grains (route d₁) (Uraguchi and Fujiwara 2012, 2013). After root absorption, Cd is transferred to shoots by xylem in a short time. The xylem-mediated Cd translocation from roots to shoots as the main decisive factor for shoot Cd accumulation has been confirmed in a number of plants including rice (Uraguchi and Fujiwara, 2012). OsHMA2 and OsHMA3 were reported to take effect in this process (Sasaki et al., 2014; Satoh-Nagasawa et al., 2012, 2013; Takahashi et al., 2012). OsHMA3 plays a critical role in Cd compartmentation into vacuoles in root cells; while OsHMA2 is involved in the delivery of Cd to developing tissues (Miyadate et al., 2011; Takahashi et al. 2012). After transfer from xylem to phloem at nodes, Cd is favorably transported to the upper nodes and eventually into the panicle instead of into leaves (Uraguchi et al., 2011). Several studies noted that further accumulation of Cd into grains is mediated by phloem (Tanaka et al., 2007; Wu et al., 2015b).

Two possible pathways are involved for root-to-grain transport during grain maturation: (i) Cd is directly transported to the developing grains via xylem; (ii) Cd is transported to the

transpiring parts, e.g., rachis, culms, flag leaves and the outer parts of panicles, followed by rapidly remobilized to grains through phloem (Rodda et al., 2011). These two pathways have been confirmed by Uraguchi et al. (2009) and Yoneyama et al. (2010). It should be noted that nodes are the central organ for xylem-to-phloem transfer, which play a vital role in Cd translocation from soil to grains at the grain-filling stage (Fujimaki et al., 2010). Uraguchi et al. (2011, 2014) have identified OsLCT1 as a Cd transporter that expressed at the nodes for transporting Cd into grains. They also observed prominent OsLCT1 expression in leaf blades and nodes during the reproductive stage in rice (Uraguchi et al., 2011).

For plants, root cell wall is directly in contact with heavy metals dissolved in the soil solution, and is the outermost layer of protection for protoplast from Cd toxicity (Fu et al., 2011; Hall, 2002). Cadmium ions move into the root via the rhizodermis cell walls, from soil solution towards vascular cylinder (Redjala et al., 2011). Two parallel pathways are involved for transporting Cd via the root cortex towards the shoot (Fig. 2): (i) active transport from cell to cell in the symplast, namely selective transport across membranes, and (ii) passive transport by diffusion and convection through the apoplast, i.e. cell walls and intercellular spaces (Zhao et al., 2010). Cadmium compartment in root cell wall is one of the approaches to suppress Cd uptake by plants (Qiu et al., 2011). Root cell walls can provide some functional groups to join Cd ions together and restrain their movement across the cytomembrane, which is one of the detoxification mechanisms of heavy metals in plants (Qiu et al., 2011). In addition, vacuoles can also act as the subdominant site of Cd binding, which can further reduce the amount of Cd interfering with the organelle (Wang et al., 2008). Being a non-essential element, Cd can actively enter into plant cells by uptake mechanisms for essential elements, such as Zn, Ca and Fe (Lu et al., 2009). For example, Cd is believed to share an entry route with Fe and Mn (Ishimaru et al., 2012; Sasaki et al., 2012).

As a member of the Natural Resistance-Associated Macrophage Protein (NRAMP), OsNRAMP5 is responsible for the transport of Fe, Mn and Cd from the external solution to root cells in rice (Ishimaru et al., 2012; Sasaki et al., 2012). Although knockout of OsNRAMP5 resulted in a decrease of Cd uptake and accumulation in grains, it also caused reduction in growth and yield due to Mn deficiency (Sasaki et al., 2012). Another NRAMP gene, OsNRAMP1, is localized to the plasma membrane, which was suggested to participate in cellular Cd uptake (Takahashi et al., 2011b). Takahashi et al. (2011a) also found that OsNRAMP1 expression in roots was increased in the presence of 1 μM Cd under Fe deficiency, resulting in increased uptake of Cd in rice. The same goes for OsIRT1 and OsIRT2. Yeast mutants expressing OsIRT1 and OsIRT2 became more sensitive to Cd, and were probably related to Cd absorption in rice (Nakanishi et al., 2006). Therefore, manipulation of the transporters of

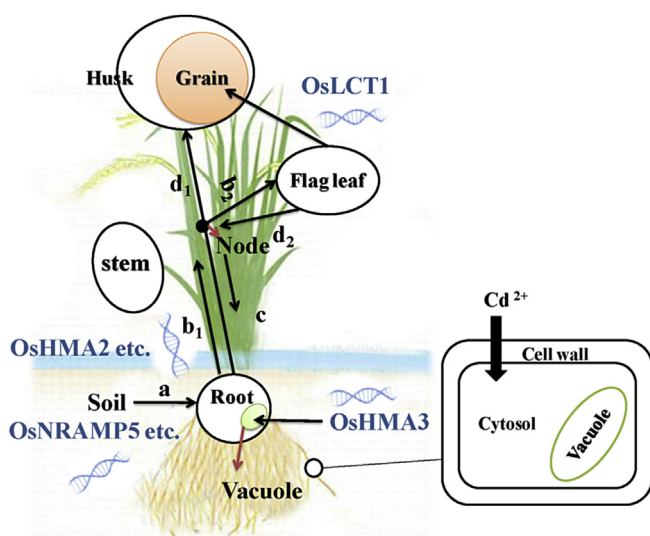


Fig. 1. A schematic of Cd transport from soil to grains (route a: uptake by roots; route b₁-b₂: xylem-loading-mediated translocation to shoots; route c: redirection of transport through intervacular transfer at nodes; route d₁: transportation into grains; route d₂: remobilization from leaf blades via phloem) (Uraguchi and Fujiwara, 2013).

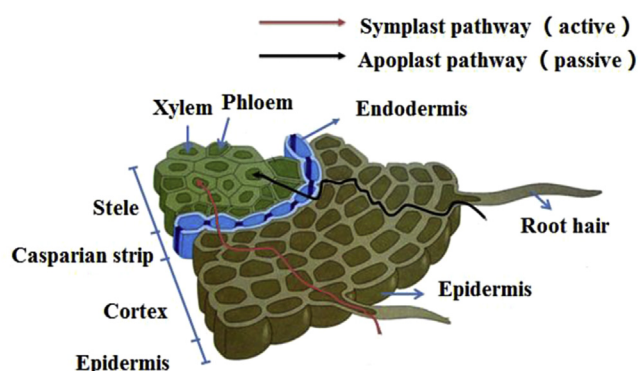


Fig. 2. Pathways for Cd transport from roots toward shoots.

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