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Rice breaks ground for cadmium-free cereals

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It is important to reduce the risk of long-term cadmium (Cd) exposure through ingestion. Cd in plant-derived foods (especially rice grain in Japan) is a major source of human Cd intake. In rice, Cd uptake and xylem loading in roots, remobilization from leaf blades and intervascular transfer in nodes to redirect Cd transport are crucial for grain Cd accumulation. Different metal transporters mediate these processes with cell-type specific expressions. In this review, we summarize and discuss the recent rapid advance in molecular understanding of Cd transport in rice. The achievements and perspectives in developing 'low-Cd rice' by the use of various alleles of Cd transporter genes are also discussed.

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Introduction

Cadmium (Cd) is a useful material in industry but a non-essential and toxic heavy metal for organisms. Plant-derived foods (especially cereals) are the major source of the Cd exposure in general populations [1,2]. The biological half-life of Cd in the human body is estimated to be up to 30 years and thus the internal Cd level increases cumulatively by daily Cd exposure. A number of recent epidemiological studies suggest a risk of chronic adverse effects from ingesting staple foods with lower Cd contamination in general populations [3]. The infamous and terrible case of Cd toxicity was 'itai-itai disease' in the middle of the 20th century. Itai-itai (meaning 'ouch-ouch' in Japanese) disease was caused by the daily ingestion of Cd-contaminated rice produced around the Jinzu River basin in Toyama Prefecture of Japan. The patients suffered severe pain, bone fractures, osteomalacia and renal dysfunction [4,5].

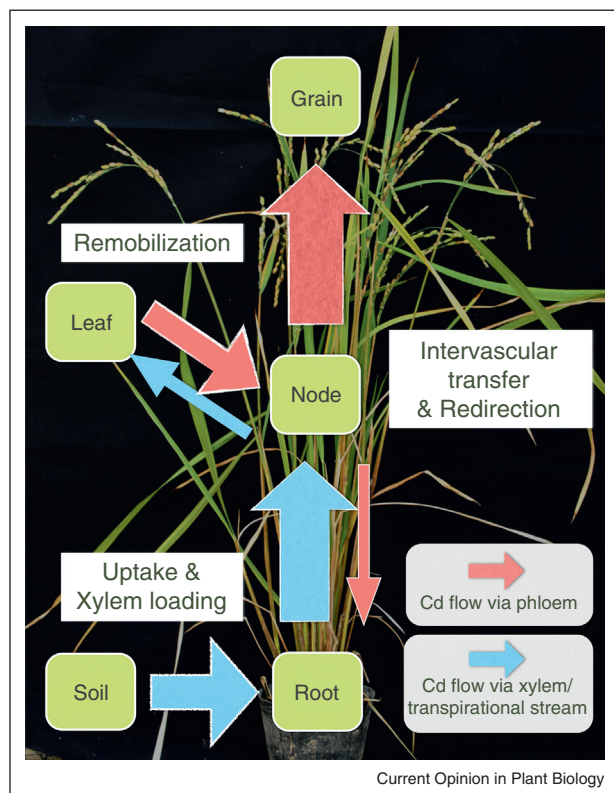
Reducing Cd contents in edible parts of crops is one promising option for decreasing risks to human health [6].

Plant roots absorb Cd in soil solution via transport pathways for mineral nutrients. Thus, molecular understanding of Cd and nutrient transport in plants will enable the developing of low-Cd-crops [6]. In rice (*Oryza sativa* L.), the model plant of cereals, several transporters involved in Cd accumulation have been identified within recent years [7]. In this review, we discuss the Cd transport mechanisms from soil to rice grains toward establishing 'low-Cd rice' (other reviews are suggested for the history of Cd toxicity [8], Cd contamination in Japanese paddy fields and various remediation techniques [9] and general knowledge of Cd and other metal transporters [7,10,11]).

Physiology of Cd transport from soil to grains

The key Cd transport processes from soil to rice grains are first, root uptake and xylem loading (root-to-shoot translocation), second, redirection of transport through intervascular transfer at nodes and third, remobilization from leaf blades via phloem (Figure 1). Xylem-mediated Cd transport from roots to shoots rather than root Cd uptake is suggested as the principal process for determining shoot (and eventually grain) Cd levels [12]. After Cd is transported from roots to shoots, phloem transport mediates Cd deposition into grains and governs grain Cd levels [13,14]. These suggest that Cd is transferred from xylem to phloem in shoots before being transported into grains. In a culm of rice, there are a number of nodes. Nodes control nutrient transport and distribution through a complex of vascular bundles which connect roots, leaves and upper nodes (the uppermost node is connected to a panicle). Fujimaki *et al.* [15^{*}] demonstrated using a positron-based live imaging technique called PETIS (Positron Emitting Tracer Imaging System) that a node is the tissue controlling Cd distribution from roots into upper nodes and a panicle. This study gives a clue that Cd is transferred from xylem to phloem in nodes. Recently, intervascular Cd transfer in nodes was also suggested by other imaging techniques [16,17]. Remobilization from leaf blades contributes nearly half of Cd deposition into grains, probably via phloem transport [18,19]. Remobilized Cd from leaf blades is also redirected at a node to an upper-node (a panicle) and somewhat to roots (Uraguchi *et al.*, unpublished data). In summary, Cd is absorbed by roots and translocated into shoots through xylem and then accumulated in leaves and stems. During grain maturation, most Cd transported through xylem is transferred to phloem at nodes and this results in preferential Cd transport into upper nodes and finally into grains rather than into leaf blades. In leaf blades, the stored Cd is remobilized through phloem and transported into grains after redirection at nodes (Figure 1).

Figure 1



Simplified schematic of Cd transport from soil to grain. Root cells absorb Cd from soil solution and Cd is transported into the xylem. Transpiration-driven xylem flow mediates root-to-shoot Cd translocation through all growth stages and delivery of Cd into leaves during vegetative stages. During reproductive stages, Cd translocated from roots is preferentially distributed into a panicle through phloem rather than into leaves as a result of xylem-to-phloem transfer in nodes. Leaf blades function as a source of Cd during grain ripening, and remobilization of Cd from leaf blades contributes to nearly half of grain Cd accumulation. The majority of remobilized Cd from leaves through phloem is also redirected at nodes toward upper nodes and a panicle. A portion of Cd is likely to be transported into lower nodes and roots through phloem.

Root uptake and xylem loading

In rice roots, Casparian strips exist in the exodermis and endodermis (Figure 2). These Casparian strips block apoplastic transport of solutes into the inner root. Expression of influx transporters at the distal side of these cells is essential for efficient transport of minerals toward xylem [20]. An iron (Fe) transporter OsIRT1 (iron regulated transporter1) is responsible for Fe²⁺ intake in the exodermis and endodermis [21]. OsIRT1 shows Cd uptake activity in yeast cells and OsIRT1 is potentially involved in Cd influx at the exodermis and the endodermis during transition of paddy soils from anaerobic (Fe-deficient) to aerobic conditions [22]. However, there is no genetic evidence for the involvement of OsIRT1 in Cd intake. Recently, Ishimaru *et al.* [23] reported that *OsNramp5* (natural resistance-associated macrophage protein 5) is

responsible for manganese (Mn) and probably Cd transport in roots. Their hypothesis is based on results from the promoter-GUS analysis and the phenotypes of the *OsNramp5* RNAi lines and overexpressing lines. This study indicated the importance of *OsNramp5* in root Cd uptake; however, the detailed mechanism of root Cd uptake through *OsNramp5* remained unclear. A later study by Sasaki *et al.* [24^{••}] clearly demonstrated the polar localization of *OsNramp5* and its role in root metal uptake. *OsNramp5* is expressed on the distal (outer) side of plasma membrane of the exodermis and endodermis, and Mn and Cd contents in shoot and grains are drastically reduced in the knock-out mutant as well as in the knock-down plants. Ishikawa *et al.* [25^{••}] identified a few independent 'extremely low-Cd mutants' from the ion-beam irradiated mutant population and *OsNramp5* is the causal gene for their 'extremely low Cd accumulation'. The huge reduction in Cd and Mn uptake and their grain contents by disruption of *OsNramp5* shown in both studies demonstrates that *OsNramp5* is the major transporter for Mn and Cd transport into the inner root (Figure 2a). Although *OsNramp1*, another members of rice *Nramp* genes, and *OsIRT1* have also been expected to play some roles in root Cd uptake [21,22,26], their contributions are probably negligible compared to that of *OsNramp5*. The expression of *OsNramp1* in roots is much lower than *OsNramp5* [25^{••}] and the Fe-deficient treatment, which enhanced *OsIRT1* and *OsNramp1* expression, did not increase root Cd uptake in the *nramp5* mutant [24^{••}].

Another unique finding of root Cd transporters in rice is that of OsHMA3 (heavy metal ATPase 3). There is a large variation in Cd accumulation among rice cultivars, and some specific *indica* cultivars like 'Anjana Dhan' show much higher Cd accumulation in shoot and grains than standard *indica* and *japonica* rice [12]. The quantitative trait locus (QTL) and molecular analyses of different cultivars reached the same conclusion — that in *japonica* rice, OsHMA3 functions in vacuolar sequestration of Cd in root cells and this finally reduces Cd in the xylem (Figure 2a) [27[•],28,29[•]]. However, the high-Cd *indica* cultivars have the non-functional allele of *OsHMA3*. This mutated OsHMA3 fails to isolate Cd to vacuoles and eventually increases the Cd concentration in xylem and shoots (Figure 2c). This crucial role of OsHMA3 in determining root-to-shoot Cd translocation efficiency is further confirmed by comparing Cd uptake and translocation between the *japonica* cultivars and high-Cd cultivars by the PETIS technique [30]. The initial Cd uptake into roots does not differ between the lines, but Cd is rather stalled in the *japonica* roots. In contrast, Cd is rapidly transported from roots to shoots in the high-Cd cultivars.

Cd absorbed from soils is finally transported into the stele after passing the endodermis and Casparian strip with help from *OsNramp5* (Figure 2a). In the stele, OsHMA2, an efflux-type metal transporter on the plasma membrane

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