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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.



## 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 × $10^{12}$ $m^2$ of arable land worldwide were contaminated by heavy metals (Bermudez et al., 2012). In China, about 2.786 × $10^9$ $m^2$ 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 $b_1$-$b_2$), (iii) redirection of transport through intervascular transfer at nodes (route c), and (iv) remobilization from leaf blades via phloem (route $d_2$) and finally transportation into grains (route $d_1$) (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

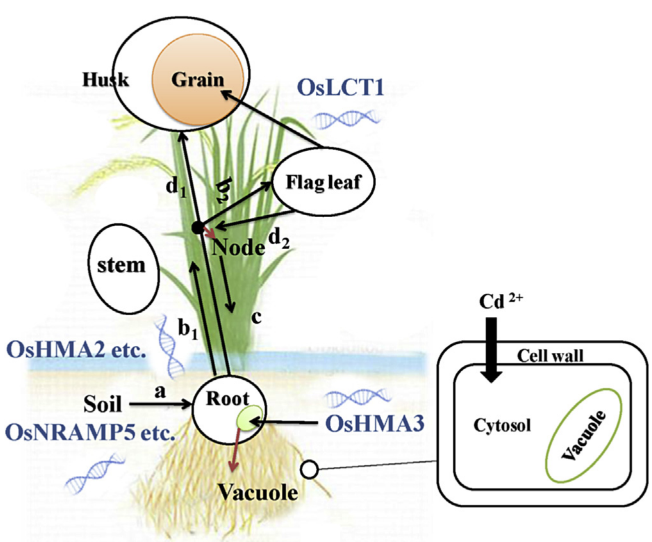


**Fig. 1.** A schematic of Cd transport from soil to grains (route **a**: uptake by roots; route **$b_1$-$b_2$**: xylem-loading-mediated translocation to shoots; route **c**: redirection of transport through intervascular transfer at nodes; route **$d_1$**: transportation into grains; route **$d_2$**: remobilization from leaf blades via phloem) (Uraguchi and Fujiwara, 2013).

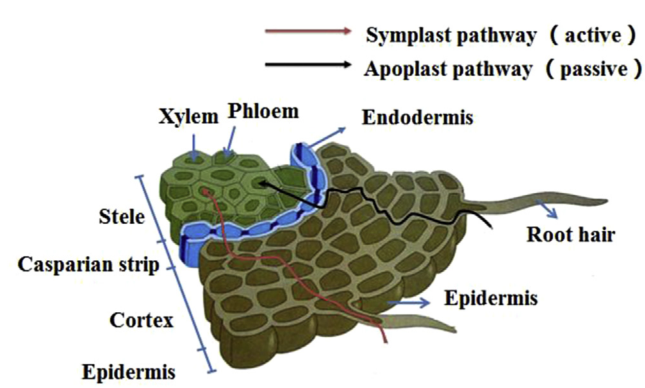


**Fig. 2.** Pathways for Cd transport from roots toward shoots.

essential elements may influence the uptake and distribution of both the essential elements and Cd, and eventually affect plant growth and Cd accumulation in rice grains.

Following the development of molecular technology, more and more studies focused on Cd transport in rice. The detailed pathways and responsible genes for Cd transport have been systematically described by previous review papers (Uraguchi and Fujiwara, 2012, 2013; Sebastian and Prasad, 2013). To explore which process determines Cd concentrations in grains, a large experiments set in terms of various rice cultivars and soils with different Cd contamination degree is needed. Investigating the relationship of Cd concentrations in xylem sap and phloem sap with that in grains is also helpful. Further research of unknown transporters or other molecules is still needed to provide molecular understanding of Cd transport and tolerance of rice.

## 3. Factors affecting Cd uptake and transport

Not all of the Cd exist in soil is available for plant uptake. The bioavailable Cd is referred to soil Cd that is available to plants, and is the major concern related to its uptake and accumulation in plants (Sarwar et al., 2010). Mechanisms assisting in the acquisition of phosphorus contribute to the increase of bioavailability of certain micronutrients. Both the acidification of rhizosphere and exudation of carboxylates are considered potential targets for enhancing metal accumulation. Alternative approaches to increase carboxylate secretion include the engineering of phosphoenolpyruvate carboxylase, pyruvate dikinase or ATP-citrate lyase expression. The same applies for the proposed modulation of plasma membrane $H^+$-ATPase activity to support rhizosphere acidification (Palmgren, 2001). Regulated local increases in metal availability would also help to circumvent problems associated with applying chelators such as EDTA to the soil (Clemens et al., 2002). The bioavailable Cd in rice mainly depends on physicochemical characters of the soil and ecophysiological features of the rice. Physicochemical properties that affect Cd bioavailability include soil redox potential, soil pH, organic matter content, and essential trace element status in the soil. These elements can influence the solubility of Cd, and further impact the Cd uptake by rice. In addition, these factors can be controlled and incorporated into a variety of field management measures that can be applied for reducing Cd in rice (Sebastian and Prasad, 2013).

### 3.1. Redox potential of the soil

The changes of soil redox potential (Eh) that closely related to water management in rice fields essentially determine Cd solubility (Pan et al., 2016; Honma et al., 2016). During flooding of paddy soils, soil microbes respire by utilizing oxidized soil components, including $NO_3^-$, $SO_4^{2-}$, Mn(III/VI) and Fe(III) species that present in oxide phases, as well as the dissimilation products of organic matter. These species receive electrons during the reduction reactions, which generates $NO_2^-$, $S^{2-}$, $Mn^{2+}$, $Fe^{2+}$, and low molecular weight organic acids, accompanied by a decrease of the redox potential (de Livera et al., 2011). Consequently, Cd solubility will be decreased due to the enhanced adsorption of Cd on Fe and/or Mn oxyhydroxides and also precipitation of CdS (Sun et al., 2007). Oppositely, during drainage period, the paddy soil is in an oxidative condition with increased Eh. Cadmium will form water-soluble cadmium sulfate ($CdSO_4$), leading to a higher solubility and uptake of Cd by rice (Sebastian and Prasad, 2013). Therefore, water management can be utilized as a strategy to control Cd uptake by rice since it can affect the redox potential of soil (Arao et al., 2009). This method will be discussed in Section 4.

### 3.2. Soil pH

Among the soil characters that affect Cd absorption of plants, soil pH is considered to be the crucial factor, since pH can significantly impact solubility and speciation distribution of Cd in soil solution (Zeng et al., 2011; Sarwar et al., 2010). Substantial studies noted soil pH is negatively correlated with the availability of heavy metals in plants (Kirkham, 2006; Zeng et al., 2011). Actually, the soil pH can be affected by the soil redox status, which can possibly be controlled by water management (Honma et al., 2016). After soil flooding, the soil pH will increase to near neutral, which is attributed to proton consumption under reducing conditions and the buffer effect via the $H_2CO_3$-$HCO_3^-$ reaction due to the emission of $CO_2$ (Sun et al., 2007; Hindersmann and Mansfeldt, 2014; Pan et al., 2016). At low soil pH, the solubility of Cd in solid phases, such as carbonates, hydroxides and phosphates, will be increased (Reddy and Patrick, 1977). At higher soil pH, Cd is likely to form $Cd(OH)^+$ by hydrolysis, which resulted in the enhancement of Cd adsorption affinity to soil. Therefore, the mobility of Cd will be decreased, leading to lower Cd accumulation in rice (Sun et al., 2007). Thus, soil acidification must be avoided to prevent the release of bioavailable Cd in soil (Sebastian and Prasad, 2013).

### 3.3. Organic matter in soil

Organic matter content has a vital role in deducing the mobility and availability of Cd in soil. On one hand, it reduces the bioavailable Cd in soil through adsorption or forming stable complexes with humic substances (Halim et al., 2014). This influence of organic matter is in favor of decreasing Cd accumulation in rice, and has been verified by Xu et al. (2010), who found a remarkable reduction of Cd levels in grains, straws and roots of rice in the existence of organic acids and ethylenediamine tetraacetic acid (EDTA). Under most soil conditions, organic acids exist as negative anions, and therefore react vigorously with Cd ions and immobilize Cd in soil, hence decrease the bioavailability of Cd to rice. On the other hand, organic matter also supplies organic chemicals to the soil solution that can act as chelates and enhance Cd availability to rice (Zeng et al., 2011; Halim et al., 2014). A study on spatial variation of heavy metals in soil and rice in Nanxun, China conducted by Zhao et al. (2015) revealed that high organic matter in soil would enhance the accumulation and availability of Cd in rice. These contrary results may be due to different experimental conditions for example, vary in environmental conditions and in rice cultivars chosen. Therefore, it is hard to acquire consistent conclusions.

### 3.4. Plant nutrients

The essential plant nutrients are classified into two categories: macronutrients, which include nitrogen (N), phosphorus (P), and potassium (K); and micronutrients, which include copper (Cu), iron (Fe), manganese (Mn) and zinc (Zn) (Sarwar et al., 2010). Different element supplies will affect gene expression, enzyme activities, subcellular distribution and chemical forms of Cd, and could have contrary effects on Cd accumulation in rice. For example, according to hydroponic experiments conducted by Yang et al. (2016) recently, it was showed that although $NO_3^-$ is often used to promote rice yields, excessive $NO_3^-$ supply did not promote rice growth significantly and resulted in increased OsIRT1 expression as well as Fe and Cd uptake. These results implied that fertilizers should be utilized correctly to avoid Cd entry into rice. Moreover, supplements of Fe (40 μM) and Mn (2 μM) resulted in more biomass and lower Cd accumulation in rice under Cd exposure of 5 and 25 μM (Sebastian and Prasad, 2015). Similarly, Zhang et al. (2014) recorded that Cd content in rice roots generally declined with increasing S concentration from 0 to 720 mg $L^{-1}$. Silicon (Si), another important mineral element for plants, which is not considered to be essential, has numerous positive impacts on plant growth (Epstein, 1994). Shi et al. (2005) has found Si might obstruct the apoplast bypass flow through the roots, and suppress the apoplastic transport of Cd and thus decreased rice shoot Cd by 33%. Nutrient uptake by rice is controlled by multiple factors, the interaction of different nutrients must be taken into consideration to minimize Cd in rice.

### 3.5. Rice cultivars

The uptake and translocation of Cd in rice may differ significantly amongst different cultivars (Arao and Ae, 2003; Ishikawa et al., 2005; Uraguchi et al., 2009; Xu et al., 2010). For instance, the effects of rice genotype on Cd uptake were investigated by Ye et al. (2012), and they observed that Cd accumulation in indica polished grain were higher than that in hybrid and japonica grain. A significant difference in Cd levels of rice grains among 20 rice cultivars in the same Cd treatment (0.3 mg $kg^{-1}$ or 0.6 mg $kg^{-1}$) in soil was observed by Song et al. (2015), who also derived Cd toxicity thresholds (0.507 mg $kg^{-1}$). A possible explanation is that these differences are associated with the root acidifications, root organic acid and oxidation abilities secretions (Ye et al., 2012), but there is still a lack of direct evidence. To further elucidate the detoxification mechanisms in different rice cultivars, a hydroponics experiment was conducted by Wang et al. (2015) with low and high grain-Cd-accumulating cultivars. The former was more tolerant to Cd toxicity, and the physiological mechanisms were summarized as follows: (i) low grain-Cd-accumulating cultivar had a stronger capacity in restraining Cd transport to soluble or organelle fractions due to the crucial role of cell wall to bind more Cd than high grain-Cd-accumulating cultivar; and (ii) low grain-Cd-accumulating cultivar owned a higher transportation rate in stem and higher Cd outflow in the roots, which resulted in less injury to roots and ultimately lower Cd accumulation in grains (Zhang et al., 2009a; Wang et al., 2015).

In addition, there are a series of studies to find out quantitative trait loci (QTL) (Ishikawa et al., 2005, 2010; Ueno et al., 2009a) or genes (Zhao et al., 2015; Ueno et al., 2010) related to rice cultivars and the control of Cd concentration in rice grains. Ueno et al. (2009b) detected a major QTL for Cd accumulation on chromosome 7 in a population obtained from two different rice cultivars: Nipponbare (low Cd-accumulating) and Anjana Dhan (high Cd-accumulating). This QTL explained 85.6% of the phenotypic variation in Cd concentration. The responsive gene of this QTL has been identified as OsHMA3, which was isolated from a mapping population derived from a cross between the two cultivars by Ueno et al. (2010). Furthermore, this gene relates to other high-Cd-accumulating cultivars, Jarjan and Cho-ko-koku (Ueno et al., 2011; Miyadate et al., 2011). Developing DNA markers to help marker-assisted selection of cultivars carrying mutant OsNRAMP5 and establishing “low-Cd Koshihikari” is a feasible practical strategy (Ishikawa et al., 2012).

### 3.6. Radial oxygen loss (ROL) and Fe plaque formation

Radial oxygen loss (ROL) is an adaptive trait for rice growing in flooded soil (namely, anaerobic conditions) (Cheng et al., 2014). In anaerobic conditions, aerenchyma is developed on rice roots to transfer oxygen from the aerial parts to the roots (Wang et al., 2013). The aerenchyma can emit additional oxygen to the rhizosphere with approximately 30–40% of the oxygen being lost into the soil. This process is defined as ROL (Armstrong, 1980; Wang et al., 2011). The released oxygen from roots by ROL reacts with reduced soluble $Fe^{2+}$ and form a smooth regular reddish precipitate or irregular plaque coating on root surfaces, known as iron (Fe) plaque (Cheng et al., 2014). The formation of Fe plaque on root surfaces is extensively observed in rice, and ROL from roots is regarded as one of the most significant physiological factors influencing Fe plaque formation (Wang et al., 2011). A positive correlation between the rates of ROL and Fe plaque formation was verified by Cheng et al. (2014). However, the mechanisms underlying Fe plaque formation are extremely intricate. Besides ROL, other biotic (iron-oxidizing microbes and root exudates) and abiotic ($Fe^{2+}$ availability, soil feature and moisture) factors may also affect the formation of Fe plaque, which requires further studies (Cheng et al., 2014).

Owing to the high binding ability of functional groups on Fe hydroxides, Fe plaque can sequester Cd on root surface by adsorption and/or co-precipitation, influencing Cd bioavailability in the rhizosphere and may alter the absorption and accumulation of Cd by rice (Wang et al., 2013). Several studies revealed a negative correlation between the rates of ROL or Fe plaque formation and grain Cd concentrations in rice (Wang et al., 2011, 2013; Cheng et al., 2014; Liu et al., 2008). Additionally, the rates of ROL and Fe plaque formation vary not only among rice cultivars, but also among different growth periods in the same cultivar (Wang et al., 2011, 2013; Cheng et al., 2014; Zhou et al., 2014). For example, in a rhizobag experiment conducted by Cheng et al. (2014), a large differences was observed in the rates of ROL (1.55–6.88 mmol $O_2$ $kg^{-1}$ root d.w. $h^{-1}$) and Fe plaque formation (Fe: 6.12–48.2 g $kg^{-1}$; Mn: 0.13–1.09 g $kg^{-1}$) among 25 rice cultivars. The dynamic variations of ROL and Fe plaque formation and the temporal changes in the accumulation and translocation of Cd at four growth stages of two rice cultivars (Huaxinzhan and Tianyou 116) were investigated by Wang et al. (2013). They observed that ROL and Fe plaque increased remarkably from tillering to ear emergence stages and then declined at grain-filling stage. At the ear emergence stage, more Fe plaque was formed on the roots of rice with higher ROL, which could sequester large amounts of Cd onto root surfaces or in the rhizosphere, and consequently, less Cd being transferred to the shoots. Therefore, the ear emergence stage is crucial to restrict the uptake and translocation of Cd in rice when grown in Cd-contaminated soil.

## 4. Minimizing Cd in rice

To prevent Cd exposure to human, effective measures should be taken to immobilize or reduce Cd in soil, and eventually reduce Cd uptake into rice. These measures can be classified as follows (Fig. 3): (i) agronomic practices [including soil amendments (Guo et al., 2006; Madejón et al., 2006), fertilizer management (Yan et al., 2015), water management (Hu et al., 2015; Honma et al., 2016), and tillage management (Yu et al., 2014), etc.]; (ii) bioremediation [including phytoremediation (He et al., 2015; Liu et al., 2011), microbial remediation (Dixit et al., 2015), etc.]; (iii) molecular biology technologies [including transgenic rice (Takahashi et al., 2014) and rice mutants (Ishikawa et al., 2012)].

### 4.1. Agronomic practices

The *in situ* immobilization of Cd in polluted soil is considered as one of the most effective techniques to lower the concentration of bioavailable Cd in rice. Agronomic practices, which mainly include the use of soil amendment (Guo et al., 2006; Madejón et al., 2006), fertilizer (Yan et al., 2015), water (Hu et al., 2015; Honma et al., 2016) and tillage management (Yu et al., 2014), can be potential strategies to improve the physicochemical characters of soil and immobilize Cd in polluted soils. Besides, many physical and chemical approaches such as excavation, transport, soil dressing

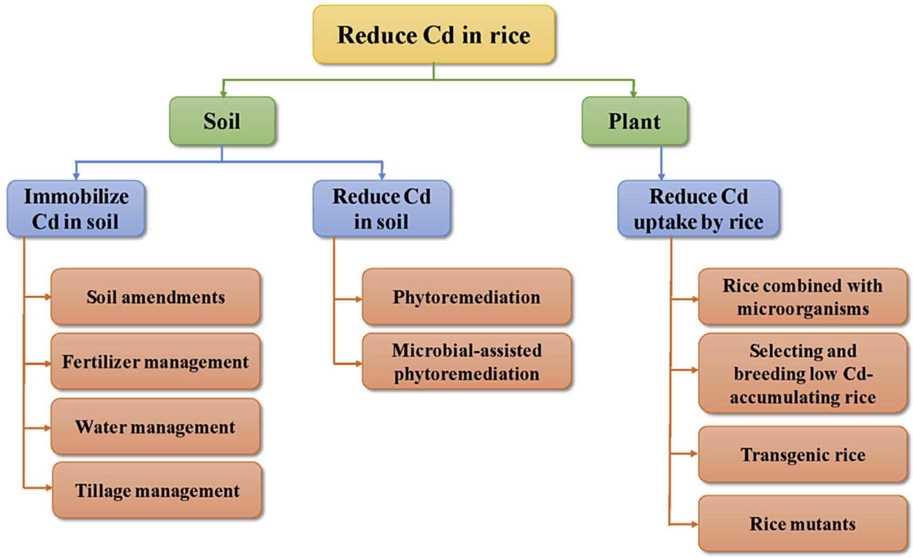


**Fig. 3.** A brief summary of measures for reducing Cd in rice.

etc. (Barrutia et al., 2010; Bolan et al., 2013; Dermont et al., 2008; Suthar et al., 2014), have also been confirmed to improve the physicochemical properties of soil. However, these physical and chemical methods are extremely expensive, labor intensive and prone to cause secondary pollution, and should be only used in serious contaminated areas.

The principal mechanisms of Cd immobilization by soil amendments are adsorption, precipitation, cation exchange, and surface complexation (Guo et al., 2006; Madejón et al., 2006; Shaheen and Rinklebe, 2015). The selection of a suitable soil amendment depends on their local acquisition and financial implications (Mahar et al., 2015). Recent efforts have been paid to searching for new, practical, and cost effective improvements. By assessing the effects of various emerging and low-cost improvements on the immobilization of Cd in a contaminated soil, Shaheen and Rinklebe (2015) found that cement bypass kiln dust, lime stone and sugar beet factory significantly decreased the Cd solubility in soil due to their high content of calcium, total calcium carbonates and high alkalinity. Rinklebe et al. (2016) further used biochar to immobilize Cd in highly contaminated floodplain soils and observed that Cd concentrations were considerable lower with the addition of biochar, which demonstrated that biochar is also a promising amendment to immobilize Cd in soil. The biochar contained shell limestone (carbonate) leading to a higher pH, which can induce Cd precipitation, reduce Cd solubility, and promote Cd sorption by enhancing the net negative charge of variably charged soil constituents (Karami et al., 2011).

Fertilizers can alter soil characteristics, such as surface charge, soil pH and soil available phosphate, or can react with Cd directly in soils, leading to conversion of the mobile Cd into more stable forms (Yan et al., 2015). This effect of fertilizer management on Cd immobilization was evidenced by Yan et al. (2015), who evaluated the Cd immobilization efficiency by using four phosphate fertilizers, including potassium phosphate monobasic (MPP), diammonium phosphate (DAP), calcium phosphate tribasic (TCP) and calcium superphosphateon (SSP). These fertilizers could supply available phosphate and cause a decrease in bioavailable Cd in soil. Such treatments have the advantage in increasing soil pH, which will lead to sorption of Cd in soil, except formation of Cd-carbonate precipitates and complexes. Similar results were noted by Ahn et al. (2015), who selected two phosphate-based agents [natural phosphate fertilizer (PF) and mono-potassium phosphate (MKP)] and red mud (RM) as stabilizers, and evaluated the stabilization efficiency of Cd, Pb, and Zn in mine tailings by single and combined stabilizers of these agents. Given the conversion efficiency from the plant-available species to the non-plant-available species, the mixed stabilizer of MKP/RM was the most effective for plant growth as well as stabilizing Cd, Pb, and Zn in the mine tailings. However, some elements contained in fertilizers, like $NO_3^-$ can neither promote rice growth significantly, nor elevate Cd accumulation in rice (Yang et al., 2016). Therefore, fertilizers should be supplied precisely to balance the rice growth and grain Cd concentration.

As stated in Section 3, water management can change the redox potential and pH of soil, and subsequently affect Cd solubility in soil and availability to rice and thus manipulate its accumulation in rice (Li et al., 2015b; Honma et al., 2016). Common finding from pot and field experiments showed that flooding prior to and after heading was successful in reducing Cd concentration, whereas aerobic treatment increased Cd concentration in rice (Hu et al., 2015; Arao et al., 2009). Heading stage is a crucial period in reducing Cd uptake by rice. After soil flooding at this stage, the increased soil pH will enhance the mobility of Cd in soil, and lessen Cd in grains (Sun et al., 2007). The Ministry of Agriculture, Forestry, and Fisheries of Japan have turned these findings into practice by encouraging farmers to keep paddy fields flooded prior to and after heading in order to decrease Cd accumulation of rice in areas with Cd contamination. This is due to the fact that $Cd^{2+}$ is turned to CdS under the flooded condition (Iimura and Ito, 1978), whereas CdS is changed to $Cd^{2+}$ under drained condition (Ito and Iimura, 1976). Overall, water management would be a practical and cheap strategy to lower Cd accumulation in rice.

Intercropping and rotation systems and tillage management (reduced-tillage, conventional tillage etc.) can reduce Cd uptake by rice via improving the physical, chemical and biological properties of soil (Liu et al., 2016; Rehman et al., 2015; Ogbazghi et al., 2015; Yu et al., 2014; Gao et al., 2010). For example, Yu et al. (2014) revealed that rotating crops with a high Cd-accumulating oilseed rape could reduce the Cd contents of rice. Gao et al. (2010) also reported that compared to conventional tillage, reduced-tillage management decreased grain Cd concentrations and accumulation in wheat. It may due to the fact that higher soil organic matter in reduced-tillage soils, caused by residue from previous crops, can enhance the adsorption and complexation of Cd. Moreover, the reduced-tillage management may decrease microbial activity and the Cd released from residue (Gao et al., 2010).

Overall, the information related to the effects of agricultural management practices on Cd phytoavailability is important in order to select the suitable management that optimizes crop yield and lower Cd concentration in rice grains.

### 4.2. Bioremediation

Bioremediation is an eco-friendly and sustainable process for eliminating heavy metals of the environment. This technique makes use of microorganisms, green plants or enzymes to treat the contaminated sites so as to regain their healthy conditions (Gaur et al., 2014). Bioremediation usually refers to phytoremediation and microbial remediation or their combination.

Phytoremediation refers to the application of certain metal-accumulating plants to lower the concentrations of contaminants or alleviate the toxic effects in the environments (Salt et al., 1995; Ali et al., 2013; Luo et al., 2016). The installation and maintenance cost of phytoremediation is relatively low compared to other remediation techniques. Among various phytoremediation techniques, phytoextraction is the primary and most efficient phytoremediation approach for the removal of metalloids and heavy metals from polluted soils, sediments or water (Ali et al., 2013; Liu et al., 2011). Plants that are tolerant to Cd stress and can absorb high concentrations of Cd from soil are often used in this technique (He et al., 2015). Some of these plants, such as *Arabidopsis halleri* (Ueno et al., 2008), *Solanum nigrum* (Wei et al., 2013), and *Noccaea caerulescens* (Seregin et al., 2015), etc., are defined as Cd-hyperaccumulators which generate relatively less shoot biomass but gather Cd to a greater extent (Ali et al., 2013). In addition, other non-hyperaccumulators can also be candidate plant species to absorb high amount of Cd. For example, Li et al. (2015a) provided a new prospect for remediation of Cd-contaminated soil by the use of moso bamboo with deep root system and large biomass. By conducting hydroponics experiments, it was stated that Cd concentrations in leaves, stems and roots of moso bamboo can reach the maximum concentration (25.6, 129.8 and 377 mg $kg^{-1}$, respectively) at the highest Cd level (400 μM), although the growth was significantly inhibited. Moreover, it is noteworthy that some rice cultivars, such as Indica-type rice cultivars, are able to absorb high levels of Cd (up to 15.9 mg $kg^{-1}$ dw in shoots and 3.9 mg $kg^{-1}$ d.w. in grains) (Arao and Ae, 2003), and therefore can also be used for reducing soil Cd contents (Murakami et al., 2007). Phytoextraction with the Indica rice (Chokoukoku) grown for 2 years removed 883 g Cd $ha^{-1}$, and eventually decreased the grain Cd contents in later grown Japonica food rice by 47% without lower yield (Murakami et al., 2009). It is applicable to use high Cd-accumulating cultivars for the remediation of paddy fields contaminated with Cd, on condition that mindful awareness should be given to the disposal of Cd-accumulated plants.

As soil microorganisms can influence plant growth as well as the mobility of nutrients, metals, and contaminants in soil, increasing attention has been focused on the interaction between the plant and the soil microbial community (Dixit et al., 2015). Understanding the complexed interaction between metal-accumulating plants and their rhizosphere microbes is a critical move for best performance of phytoremediation (Muehe et al., 2015). For example, plant growth-promoting rhizobacteria (PGPR) are a group of useful rhizosphere bacteria that is able to increase the plant tolerance against heavy metal toxicity and promote plant development. Liu et al. (2015b) isolated nine strains of Cd-tolerant PGPR from the roots of Cd-accumulating plants, and found that the Cd hyperaccumulator – *S. plumbizincicola* inoculated with strains *Rhodococcus erythropolis* NSX2 and *Cedecea davisae* LCR1 showed better growth and higher Cd accumulation in shoots (0.59 and 0.57 mg $pot^{-1}$ for inoculated with NSX2 and LCR1, respectively, compared with control of 0.50 mg $pot^{-1}$). In addition, using rhizospheric microbes for example, arbuscular mycorrhizal fungi (AMF) in phyto/bioremediation of heavy metal contaminated soils has gained more awareness lately. Arbuscular mycorrhizal fungi are key soil microbes which form symbiotic correlated with majority of plant species. They can enhance plant development by increasing water and nutrient absorption and enhance plant tolerance under various stresses, like heavy metal, drought, and salinity stress (Guo et al., 2013; Shahabivand et al., 2012). The use of AMF can reduce heavy metal absorption by rice. It has been reported that rice inoculated with *Funneliformis mosseae* reduced the Cu concentrations in shoots and roots significantly (Zhang et al., 2009b). Similarly, rice inoculated with single or combined AMF decreased As uptake in rice and enhanced grain yield at the same time (Chan et al., 2013; Wu et al., 2015a). On the other hand, Li et al. (2011, 2013, 2016a) conducted a series of experiments of AMF/rice combination, and revealed that AMF inoculation gave rise to either positive, neutral or negative impacts on grain As concentration, grain yield and grain phosphorous uptake, depending on rice cultivars, AMF species and ROL, which suggested the functional diversity in AMF symbiosis when As is absorbed and transported by rice. An earlier study by Zhang et al. (2005) suggested that inoculation with AMF could enhance rice growth and lessen the potential toxicity to shoots developed by the combination of Cu, Zn, Pb, and Cd. Our previous study also demonstrated that AMF could reduce Cd uptake by rice grown in Cd solutions, through altering subcellular distribution and chemical forms of Cd in rice (Li et al., 2016b). Based on the current knowledge, it would be worthwhile screening suitable microorganisms that can combine with rice and reduce Cd uptake by rice. However, before the application of microorganisms in paddy field, field studies are needed to investigate the effects of exogenous microorganisms on indigenous microorganisms, and monitor rice growth since rice is susceptible to the attach of various microbial pathogens.

### 4.3. Molecular biology technologies

Selecting and breeding low grain-Cd-accumulating cultivars can be a safe method to directly reduce Cd accumulation in rice grains, and further decrease Cd dietary exposure to human. For high Cd-accumulating cultivars, transgenic technology or rice mutants may provide alternatives to reduce Cd in rice. Gene identification and characterization are fundamental steps for understanding the molecular mechanisms of Cd accumulation and tolerance for producing low Cd-accumulation transgenic rice (Sun et al., 2015). Identification of key transporter genes responsible for grain Cd accumulation acts as a guide to lowering rice Cd contents through regulating transporters' expression. As mentioned in Section 2, various genes are responsible for Cd translocation in rice, and their expression will affect Cd accumulation to different extent. For example, Takahashi et al. (2014) found knockdown of OsNRAMP5 can reduce Cd uptake by rice. Management of Cd transporters by transgenic technique has been successfully applied to decrease Cd accumulation in rice or promote phytoremediation efficiency of Cd-polluted soil (Ueno et al., 2010; Uraguchi et al., 2011).

However, commercial transgenic rice is not commonly accepted by the general public and prohibited in many countries. This prompted Ishikawa et al. (2012) to produce three non-transgenic rice mutants by carbon ion-beam irradiation, which were more liable to be accepted by public. When grown in Cd-contaminated paddy fields, there was almost undetectable Cd in *japonica* rice cultivar. Moreover, the mutants did not induce serious harmful impacts on plant or grain or straw yield, grain morphology, or eating quality, indicating that they can be directly applied in breeding programs. The molecular mechanisms underlying natural variation between *japonica* and *indica* should be examined further. Another possible strategy is marker-assisted breeding, which can develop rice cultivars from the mutants with the assistance of molecular markers that trace the genetic makeup of rice (Collard and Mackill, 2008). For instance, identification of a QTL from a low-Cd-accumulating cultivar, then introducing the low-Cd QTL into a high-Cd cultivar may be a feasible method (Uraguchi and Fujiwara, 2012). The related genetic engineering by developing Cd excluder rice was described in a review paper by Sebastian and Prasad (2013). Overall, the transgenic or non-transgenic rice (mutants) can provide some potential methods for decreasing Cd levels in rice and reducing Cd exposure via the food chain.

## 5. Conclusions and perspectives

Cadmium exposure could cause a series of adverse effect on organisms and human beings. Therefore, understanding the mechanisms of Cd translocation and the factors affecting Cd accumulation in rice is important to come up with efficient strategies to reduce Cd in rice. Substantial advancement has been made in understanding Cd uptake and translocation mechanisms in the past few years, and a few Cd transporter families have been identified in rice. To achieve an in-depth understanding of Cd transport mechanisms in rice, it is essential to identify unknown transporters or other molecules based on molecular biology technologies. Meanwhile, the progress of understanding and technology in rice related to Cd transport can be applied to other cereals.

Physicochemical characters of the soil and ecophysiological features of rice contribute an important role in the bioavailable Cd of rice. The effects of these factors have been extensively investigated. Flooding paddy soils before and after heading, selecting practical bioremediation methods according to local conditions, screening the suitable microorganisms, and breeding rice cultivars with a low Cd content in grains are all feasible methods. Further research is needed in the field to confirm extensive application of these technologies, and evaluate the residual influences of a variety of amendments on reducing Cd uptake by rice under different environmental conditions.

In conclusion, given the significance of reducing Cd risk on human and ensuring food safety, future research should focus on the following: (i) identifying unknown transporters which are related to Cd transport or tolerance in rice; (ii) screening microorganisms that can combine with rice and reduce Cd uptake by rice; (iii) exploring more non-transgenic rice that accumulate lower Cd and can be accepted by the general public; and (iv) selecting low grain-Cd-accumulating cultivars with high yields through genetic engineering.

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