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Salinity and Heavy Metal Stress

REVIEW ARTICLE

Recent progress in understanding cadmium toxicity and tolerance in rice

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Abstract

Heavy metal bioaccumulation in the soil, water and atmosphere may be seriously hazardous to both human and animals with the contamination of food supply chain. Cadmium is a toxic heavy metal with no defined biological function. It is provided to environment mostly through effluent from sewage sludge, mining, burning, industries and fertilization with phosphate. Cadmium uptake and accumulation in rice (*Oryza sativa* L.) results in negative effect on plant growth. It inhibits physiological activities, such as photosynthesis, respiration, mineral nutrition, and cell elongation, leading to low yield and poor growth. Cadmium damages the photosynthesis system by lowering chlorophyll content and preventing stomata opening. The discrepancy in genotype, cellular distribution, and binding forms of cadmium has a significant role in rice tolerance and cadmium accumulation. Current progress on heavy metals and their interaction with important elements has widely increased our understanding of toxicity in the plants. In this review, the important aspects of cadmium uptake and effects in rice growth, yield, and yield components elucidated.

Key words: Bioavailability, Cadmium, Rice, Uptake

Introduction

Heavy metals are regarded as stable environmental contaminants, and trace metals that are at least five times denser than water. These toxic metals are occasionally traversing the food chain to humans. They have also toxic impacts on the environment and life in aquatic system too. Once released into the environment through the air, food, drinking water, or human made chemicals and products, heavy metals are taken into the body by inhalation, ingestion, and skin absorption. They have no activity in the body and body cannot metabolize them (Es'haghi et al., 2011). These metals consist of mercury, nickel, lead, arsenic, cadmium, aluminum, platinum and copper. Cadmium (Cd), a divalent cation, is a nonessential metal for plant growth with long biological half-life in the range of 10-30 years (Ellis et al., 1985). Rice (*Oryza sativa* L.) grains are well known as a major source of human Cd intake and therefore, contamination of paddy soils by Cd and accumulation of Cd in rice are the important issues. Cadmium may induce human renal tubular dysfunction, severe bone damage, and carcinogenic effects (Wang et al., 2003; Jin et al., 2004; Chaney et al., 2005). Papers focusing on the effect of rice harvested from Cd polluted area on human health are overwhelming (Ishihara et al., 2001; Wang et al., 2003; Jin et al., 2004; Chaney et al., 2005; Davis et al., 2006). However, comprehensive review on the effect of Cd on rice yield and quality has not been conducted. In this paper, we review recent advances in understanding the effect of Cd in rice from seedling to maturity.

Cadmium

Cadmium is one of the most mobile elements among all the toxic heavy metals with large solubility in water (Pinto et al., 2004), which quickly absorb and compound into plant tissues and transfer to aerial organs where it can cumulate to high levels in contrast with lead and mercury (Singh and McLaughlin, 1999). Cadmium is a toxic metal due to its interaction with important metals such as Fe and Zn, thus, interference with the many biochemical activities that are controlled by metallic enzymes (Wright and Welbourn, 1994). The elevated level of reactive oxygen species created by Cd is connected with its toxicity also (Brennan and Schiestl, 1996). Cadmium in soils is known to originate from geogenic (natural) and

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anthropogenic (industrial) sources (Garrett, 2000; McLaughlin and Singh, 1999). Cadmium normally finds in high amount in zinc and lead ores and in phosphate fertilizers (Garrett, 2000; McLaughlin and Singh, 1999). Agricultural usages of phosphate fertilizers, sewage sludge and industrial applications of Cd have been known as a main reason of common distribution of the metal at trace levels into the general environment and human foodstuffs. Other factors causing Cd dispersal are increased natural emission and bioaccumulation occurring in certain plants, mammals and filter feeder organisms containing crustaceans and mollusks (Satarug et al., 2003). Non-polluted soil solutions have Cd concentrations ranging from 0.04 to 0.32 µM (Wagner, 1993). Soil solutions which have a Cd concentration differing from 0.32 to about 1 µM can be considered as polluted to moderate level (Sanitá di Toppi and Gabreilli, 1999).

The toxic results of Cd on plant systems are studied by different researchers (Prasad, 1995; Das et al., 1997; Kirkham, 2006). The most typical symptom of Cd toxicity in plants is stunting and chlorosis (Das et al., 1997). Chlorosis (chlorophyll loss) occurrence by the excess level of Cd appears to be due to a direct or an indirect interaction of Cd with foliar Fe content. Cadmium directly or indirectly prevents physiological activities, such as photosynthesis, respiration, cell proliferation (by the low mitotic index) (Rosas et al., 1984), plant water relationship, nitrogen metabolism and mineral nutrition, leading to poor growth and low biomass (Sanitá di Toppi and Gabrielli, 1999). It also causes membrane damage, inactivation of enzymes, and decrease of the water stress tolerance of plants (Prasad, 1995). The prevention of photosynthesis has been accounted for either an indirect function of Cd on plant water relations, stomatal conductance and CO_2 accessibility (Baryla et al., 2001; Costa et al., 1994), or to a more direct effect on chlorophyll biosynthesis, chloroplast organization, electron transport, and activity of Calvin Benson Bassham cycle enzymes (Vassilev et al., 1995; Horváth et al., 1996; Chugh and Sawhney, 1999).

Cadmium in rice field

Rice is the most important foodstuff of almost half of the world’s population, where its production constitutes over 90% of the global production. Rice consumption has been increasing over the traditional rice-grown areas for the last decades, especially in Europe (Abdullah et al., 2005). It turned into model plant among monocots for biological research owing to its remarkable economic, nutritional importance and small genome size (Fasahat et al., 2012; Fasahat et al., 2013). In general, the uptake of heavy metal by plant grown in heavy metal-polluted areas is correlated directly with the heavy metal accumulation in paddy land (Monni et al., 2001). Thus, there is an increasing concern about the present status of heavy metal contamination in rice grains. Rice has also been known as one of the main sources of Cd uptakes for some Asian population, where people rely mainly on this kind of cereal for energy of everyday life (Clemens et al., 2013). It is also found that people, primarily those who take rice as staple food for everyday energy, are necessarily subjected to considerable proportion of Cd by rice; rice cropped even from non-polluted areas may have Cd. The consumption of rice with increased Cd concentrations has been demonstrated to be responsible for Itai-Itai disease which occurred in Japan after World War II (Nordberg, 2004). Cadmium concentrations in agricultural soils are usually lower than 1 mg kg-1. Although due to long-term usage of phosphate fertilizers and sewage sludge, higher records have been identified in many agricultural soils (Adriano, 2001). The standard level of Cd for rice has been suggested as being from 0.2 to 0.4 mg kg-1 the weight of polished rice (Ishikawa, 2005).

From the time Cd enters rice plant it can accumulate and diffuse in various organs or cell organelles (He et al., 2008; Yu et al., 2006). The usual symptoms of Cd toxicity of rice plants comprise growth inhibition, progressive chlorosis in certain leaves and leaf sheaths, wilted leaves, and browned root systems, especially in the root tips (Das et al., 1997; Chugh and Sawhney, 1999). Brown pigment is likely to be a deposit of different metal-sulfide complexes (Howden et al., 1995). The well evidenced Cd toxicity in rice plants is the implement of oxidative stress and the production of lipid peroxidation (Shah et al., 2001). Moreover, Cd influences the uptake, transport and use of necessary elements in plants, such as Fe, Zn, Mn and Cu (Rehman Shah et al., 2010). Cadmium has also negative impact on light harvesting centre and photosystem II, as well as chlorophyll metabolism in rice leaves (Pagliano et al., 2006).

Cadmium uptake

Cadmium uptake and dispersion inside the plant depends on soil type, pH, the presence of competing ions, and species (Issa et al., 1995; Wu et al., 2006). Among the soil factors controlling Cd availability, organic matter and pH are two main factors (Barančiková et al., 2004). There is a negative correlation between soil pH and Cd uptake by plants (Tudoreanu and Phillips, 2004). Several studies indicated that Cd uptake by plants closely depends upon Cd bioavailability rather than on the total metal content (Kalis et al., 2007). It is well known that the accumulation of Cd in paddy rice grain occurs during grain filling (Simmons et al., 2003, 2008) which coincides with pre-harvest drainage of the flooded paddy (Iimura, 1981; Arao and Ae, 2003; Inahara et al., 2007). In order to optimize yields and facilitate harvesting, paddy fields are drained usually 2 weeks before plant maturity which accompanies grain filling phase. Because of drainage, the paddy soil system changes from an anoxic condition with a near neutral pH to a toxic condition, with either an increased or decreased pH as influenced by the precedent pH before flooding (Chaney et al., 1996; Gao et al., 2002; Simmons et al., 2008). Within this time, Cd becomes more available to plants as compared with Fe and Zn (Chaney et al., 1996; Kikuchi et al., 2007). This can be owing to higher Cd:Fe and Cd:Zn ratios in the soil solution, and as a result less competition from Fe and Zn with Cd at the root surface for uptake by rice plants (Smolders et al., 1997). Studies such as that, conducted by Das et al. (1997) have shown that the highest grain Cd concentrations occurred at a soil pH of about 6. However, Hinesly et al. (1984) reported lowered uptake of heavy metals by plants with the increase of soil pH. The various results from large number of studies can be ascribed to the variations in the Cd concentrations applied, the kind of medium used, and the age of the plant when it was exposed to Cd treatments (He et al., 2008). In a pot study (Cui et al., 2008), four white and five dark color rice grain cultivars were subjected to three Cd concentrations (0, 5 and 10 mg kg-1) in soil to investigate the Cd uptake difference. Since the color of the grains didn't affect results, they suggested that Cd uptake depends on the genotypes but not the color of grains (Cui et al., 2004).

Cadmium accumulation in rice

It is clearly shown that Cd in plants accumulates in shoots and roots but mainly increases in roots (He et al., 2008; Rascio et al., 2008; Du et al., 2009) indicating that a higher amount of Cd take up by plant remains in the roots (Cui et al., 2008; Rascio et al., 2008; Chao et al., 2011; Paul et al., 2011; Chang et al., 2012). Root Cd may represent for more than 80% of the total Cd in plants (Cui et al., 2004; Liu et al., 2007). Cd proportion decreases in the following order: roots > leave > grains or seeds (Wagner, 1993; He et al., 2008; Pereira et al., 2011). In a study conducted in China, it was observed that nearly 0.73% of the total Cd taken in by six rice cultivars was translocated to the grain in which embryo showed five times more average Cd concentration than that in chaff and polished rice (Liu et al., 2007). Most of the heavy metal is kept outside the cells in the apoplastic environment by roots. This system is used as a part of defense strategy against metal abundance by many plants, which depend on Cd binding to anionic groups of cell walls (Ernst et al., 1992). However, it is not considered as a general system; for example, in maize roots, Cd cumulates in both cell wall and soluble fraction of the cells, whilst in pea roots it cumulates largely in the soluble fraction (Lozano-Rodriguez et al., 1997). Furthermore, just an insignificant reposition of Cd occurs in cell walls of Silene vulgaris roots (Verkleij et al., 1990). The cells which transfer Cd from roots to the shoots are positioned in the vascular bundles of vascular plants (Prasad, 1995). The conductance of Cd from roots to the shoots occurs via xylem, driven by transpiration from the leaves (Figure 1, Uraguchi et al., 2009). In consequent studies, measurement of ^{109}Cd dispensation ratios between rice grain and legumes illustrated that in the panicle neck, phloem is the main Cd transport path into the grains (Tanaka et al., 2007).

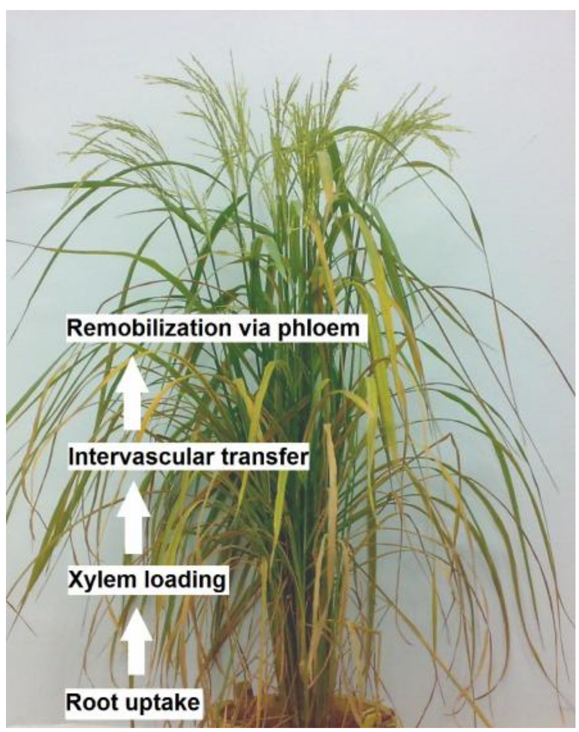

Figure 1. Schematic illustration of Cd transport in rice based on Uraguchi and Fujiwara (2012).

Table 1. QTL analysis of cadmium concentration in rice.

Population/type	Parents	Marker interval	Marker	Reference
Chromosome 3				
Koshihikari/ Kasalath (CSSLs)	*japonica/indica*	S1513 and R663	RFLP	Ishikawa et al. (2005b)
Chromosome 4				
Kasalath/Nipponbare (BILs)	*indica/japonica*	RM515-G235 RM93-C513	RFLP and SSR	Kashiwagi et al. (2009)
Chromosome 6				
Koshihikari/ Kasalath (CSSLs)	*japonica/indica*	R2171-R2549	RFLP	Ishikawa et al. (2005b)
JX17/ ZYQ8 (DH)	*japonica/indica*	CT115-CT506 CT380B-G294	RFLP and SSR	Xue et al. (2009)
Chromosome 7				
Cho-Ko-Koku/ Akita 63 (F2)	*indica/japonica*	RM6776-RM5436	SSR	Tezuka et al. (2010)
JX17/ ZYQ8 (DH)	*japonica/indica*	RG528-RG769	RFLP and SSR	Xue et al. (2009)
Chromosome 8				
Koshihikari/ Kasalath (CSSLs)	*japonica/indica*	C390-C1121	RFLP	Ishikawa et al. (2005b)
Chromosome 11				
Kasalath/Nipponbare (BILs)	*indica/japonica*	C189-C50	RFLP and SSR	Kashiwagi et al. (2009)

CSSLs: chromosome segment substitution lines, BILs: backcross inbred lines; DH: doubled haploid lines; F_2: population; RFLP: restriction fragment length polymorphism, SSR: simple sequence repeat.

Significant differences in the uptake and translocation of Cd among cultivars in rice have been reported (Arao and Ae, 2001, 2003; Arao and Ishikawa, 2006; Cui et al., 2008; Ishikawa et al., 2005a; Pereira et al., 2011; Wu et al., 2006). The variability in the capacity of plants to accumulate heavy metals has been related to variations in their root morphology (Hemphill, 1972; Schierup and Larsen, 1981). The latter reported that a plant possesses multiple thin roots would accumulate more metals than one with few thick roots.

Identification of quantitative trait loci for cadmium accumulation

Identification of quantitative trait loci for Cd concentration on chromosomes 3, 6 and 8 in brown rice was first reported by Ishikawa et al. (2005b) using chromosome segment substitution lines (CSSLs) derived from cultivars Koshihikari and Kasalath (Table 1). After Ishikawa et al. (2005b) report, several studies conducted QTL analyses to detect the responsible transporter gene for these processes (Ueno et al., 2009; Ishikawa et al., 2010; Tezuka et al., 2010). Kashiwagi et al. (2009) located three QTLs for Cd concentration in the upper plant parts of rice on chromosome 4 (two QTLs) and chromosome 11 (one QTL) using backcross inbred lines derived from a cross between Kasalath/Nipponbare. By using a similar approach with the JX17/ZYQ8 double haploid population, Xue et al. (2009) identified two QTLs for root Cd concentration on chromosome 6 and one QTL for shoot Cd concentration on chromosome 7 (Table 1).

In study by Tezuka et al. (2010), a single recessive gene increasing Cd translocation detected on qCdT7 of Cd hyperaccumulator *indica* rice variety Cho-Ko-Koku. They also found that the higher rate of Cd accumulation in Cho-ko-koku plants was owing to the higher rate of Cd translocation rather than higher uptake of the metal. The gene (*OsHMA3*) responsible for this QTL was also identified, isolated and characterized from the Anjana Dhan/Nipponbare population (Ueno et al., 2010). *OsHMA3* gene is localized at the tonoplast of all root cells and encodes a transporter belonging to the P_{1B}-type ATPase family, which is responsible for the Cd sequestration in the vacuoles of root cells in rice (Ueno et al., 2010). The gene expresses in low Cd accumulating cultivar, whilst that from the high Cd accumulating cultivar is not functional (Ueno et al., 2010). The loss of function of *OsHMA3* in rice cultivar Anjana Dhan owing to an amino acid mutation at position 80 results in high root to shoot translocation of Cd. As above mentioned, rice Cd uptake is greatly influenced by different soil properties and symbiosis of other heavy metals. Hence, candidate QTLs for Cd accumulation should be identified and evaluated in different soil environments to corroborate their stability across environmental conditions (Abe et al., 2011).

In hyperaccumulator plants, heavy metal concentrations are higher in the shoots than the roots contrary to non-accumulator species, which concentrate metals in their roots (Kirkham, 2006). The tolerance of vascular plants to heavy metals does not generally involve a restricted uptake of these elements by the roots. This suggests that tolerant plants with a high ability of collecting heavy metal ions in their root tissues have to renew the most active parts of their below-ground biomass more frequently than non-tolerant plants in normal soils (Das et al., 1997). This is likely acceded by trapping of these metals with metal-binding proteins. Peroxidase induction is a common reaction of higher plants to uptake of toxic levels of metals (Van Assche and Clijsters, 1990). Cd resulted in peroxidase activity in roots and leaves of *Oryza sativa*, with roots showing 10-20 fold higher activity than leaves (Reddy and Prasad, 1992).

Morphological and physiological responses of rice to cadmium

Plant life cycle begins with seed germination. Perturbation or inhibition of seed germination may be one of the various Cd influences on adventure of plant growth and segregation (He et al., 2008). Cadmium binds the sulphydryl groups of proteins and then denaturizes it through changing the hydrogen-sulfur bond, which leads to the delay of plants normal growth and development (Aina et al., 2007). It has been demonstrated that the effect of Cd on rice germination relies on its concentration and varies widely with genotypes. Wu et al. (2006) showed that seed germination relatively stimulated under low Cd concentration (0.01-1.5 µM Cd), while sharply decreased under higher Cd concentration (2.0 µM). Cadmium stress could considerably cause growth reduction (Chao et al., 2011) and inhibit root, shoot, plumule and radicle growth (He et al., 2008; Liu et al., 2007; Rascio et al., 2008). Increasing Cd concentration decreased the root dry matter (Hsu and Kao, 2005; Wu et al., 2006) with 20% reduction in 100 mg kg-1 Cd concentration treatment (Kukier and Chaney, 2002). The decrease of root growth caused by Cd is directly correlated with proline accumulation in roots. It is known that growth is an energy demanded process and as a result, proline level increase caused by Cd is most probably performing as a way to save energy through preventing root growth (Chen and Kao 1995). However, in study by Rascio et al. (2008), rice cultivar seed germination was not influenced by different concentrations of Cd tested at 50, 100 and 250 µM of $Cd(NO_3)_2$.

While the Cd reaches the rice leaves, it causes serious damage. Leaf growth inhibits and blade thickness decreases owing to the lower enlargement of mesophyll cells (Rascio et al., 2008). Furthermore, leaf conductance severely drops and comes to be insensitive to light (Rascio et al., 2008), implying that stomatal activity impairs (Perfus-Barbeoch et al., 2002). In plants exposed to Cd, the reduction in leaf area was not only because of reduced cell size, but also owing to the reduced intercellular space (Prasad, 1995). Whilst Cd induces a lowered cell enlargement in leaf tissues, it causes cell enlargement in tissues of the root apical region (Rascio et al., 2008). Cadmium may influence several steps of the photosynthesis activity (Pagliano et al., 2006). Decreased chlorophyll content were observed in Cd treated leaves (Hsu and Kao, 2003a; Wu et al., 2006; Chang et al., 2012), whose chloroplasts illustrated a lower number of thylakoids which resulted in the decrease of photosynthesis rate due to the drop of both CO_2 assimilation (because of the increase in leaf resistance) and O_2 emission (Rascio et al., 2008). It has to be noted that a reduction in photosynthesis rate may also occur by a compromised mineral nutrition, and it is evidenced that Cd largely influences uptake and accumulation of significant microelements (Hernández et al., 1996; Ramos et al., 2002). Cadmium can deter the uptake of manganese (Hernández et al., 1998), which is essential in the H_2O photolysis by photosystem II. Cadmium can also interact with manganese at the donor side of the photosystem, hence impeding the photosynthetic electron flow (Pagliano et al., 2006).

The most general symptom of Cd toxicity in plants is chlorosis of the leaves (Das et al., 1997). Chlorosis caused from excess Cd is nearly similar to that from Fe deficiency (Chang et al., 2012). Rice seedlings exposed to $CdCl_2$ at high (0.5-1.5 mM) and low (10-50 µM) concentrations show chlorosis (Hsu and Kao, 2003b; Hsu and Kao, 2005) with longer period (more than 6 days) needed to show chlorosis for rice seedlings treated with low concentrations of $CdCl_2$ (Hsu and Kao, 2003a). While plants accumulate higher amounts of Cd in roots and shoots, stronger chlorosis occurs together with leaf necrosis (Kukier and Chaney, 2002).

Previous studies (Wu et al., 2006; Du et al., 2009; Paul et al., 2011) showed that plant height significantly reduced by high Cd level. Plant height decrease by 64.7% was recorded in soil contaminated by Cd at concentrations ranging from 20 to 40 mg kg^{-1} (Quynh et al., 2002). In another study using pot-culture method, the effects of Cd (0-1.5 mg kg^{-1} dry soil weight) and other heavy metals such as Cu (0-100 mg kg^{-1} dry soil weight), Pb (0-300 mg kg^{-1} dry soil weight), As (0-30 mg kg^{-1} dry soil weight) and Zn (0-200 mg kg^{-1} dry soil weight) were studied on variety 616 of rice. The average height of mature rice decreased in the sequence, Cu > Zn > As > Pb > Cd compared with the control. In other words, single Zn, As, Pb or Cd treatment may prevent the growth of rice plants, but single Cu treatment can promote the growth of rice plants under the condition of the tested concentration (Zhou et al., 2003).

In a pot experiment, Huang et al. (2008) showed negative effects of Cd (with a concentration of 150 mg kg^{-1} according to the dry soil weight) on rice grain yield by 6.2-8.9% reduction for Cd-tolerant genotypes and 38.3-47.1% for the Cd-susceptible ones compared with their respective controls (no Cd addition) which was consistent with other studies (Zhou et al., 2003; Hsu and Kao, 2005; Pereira et al., 2011). They identified grain yield reduction as a consequence of the reduction in panicles and spikelets per panicle which leads to a decrease in matter production. Quynh et al. (2002) reported 80% decline in the number of tillers and the rice yield under Cd contamination. With increasing Cd concentration in soil, yield, length and weight of stems of both glutinous and nonglutinous rice significantly decreased (Muramoto, 1990). However, in another study by Yu et al. (2006), under a high (75.69-77.55 mg kg^{-1}) and a low (1.75-1.85 mg kg^{-1}) Cd treatments, yield was increased in some paddy rice cultivars and decreased in others in response to increased soil Cd, implying that farmers cannot rely on yield reduction as an index of toxicity of the grains. Cadmium content in rice grain was negatively correlated with the weight of grains (Ishikuro and Yamada, 1997).

Alternative countermeasures against Cd contamination of field crops

Different measures are applying for minimizing the absorption of Cd by agricultural crops including:

(a) Addition of different amendments (Kirkham, 2006) such as phosphorous (Brown et al., 2004), muck (Zhang et al., 2004), silicon (Shi et al., 2005), zinc (Oliver et al., 1994; Choudhary et al., 1995), chloride (Makino et al., 2006) and industrial by-products to soil (Illera et al., 2004), i.e., Silicon reduced the toxicity of Cd in rice seedlings grew hydroponically under toxic levels of Cd in growth chamber and relatively conquered the decrease in growth because of Cd (Shi et al., 2005).

(b) Soil dressing: an efficient soil improvement method which impedes agricultural products from contamination by Cd. Briefly, it entails covering the contaminated soil with a 20-40 cm uncontaminated soil. The disadvantages of this method are that the unit cost of soil dressing is high and the materials are difficult to produce (Arao et al., 2010).

(c) Water management (paddy field): when a paddy field is submerged, the redox potential leads to the reduction of sulfate ions to sulfide ions which may form complexes with Cd ions. Therefore, immobilization of sulfide ions as insoluble salts reduces the amount of Cd release into the water (Cattani et al., 2008).

(d) Breeding and selection of low Cd concentration rice cultivars: from variety to variety, Cd absorption potential of paddy rice varies. Different attempts have been done to generate new low Cd absorption varieties through hybridization of African and Japanese varieties and also as it discussed before by identifying the QTLs linked to the Cd concentration in brown rice (Arao et al., 2010).

(e) Phytoextraction: it is used to improve the soil quality by growing the hyper accumulator plants which absorb high amounts of Cd from soil. By utilizing the functions of plants such as sorghum, kenaf (which are considered to be able to absorb high quantities of Cd) Cd can be absorbed and therefore removed from Cd contaminated agricultural land (Krämer, 2005; McGrath et al., 2006; Pilon-Smits, 2005).

Conclusion

Understanding of Cd effect in rice yield and yield components have been largely advanced. There is a large discrepancy among the rice cultivars in the absorption of Cd and some interaction is found in absorption and translocation between Cd and Cu, Fe and Zn. Breeding programs are in progress to produce low-Cd cultivars of rice. An improved knowledge in this area will help to further clarify the molecular mechanisms that lie beyond rice Cd tolerance.

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