J. Plant Biol. (2019) 62:239-253
DOI 10.1007/s12374-019-0112-4

REVIEW ARTICLE

Understanding Heavy Metal Stress in a Rice Crop: Toxicity, Tolerance Mechanisms, and Amelioration Strategies

Namira Arif[1], Nilesh C. Sharma[2], Vaishali Yadav[1], Naleeni Ramawat[3], Nawal Kishore Dubey[4], Durgesh Kumar Tripathi[3,*], Devendra Kumar Chauhan[1,*] and Shivendra Sahi[5]

[1]D D Pant Interdisciplinary Research Laboratory, Department of Botany, University of Allahabad, Allahabad, India
[2]Department of Biology, Western Kentucky University, Bowling Green, KY 42101, USA
[3]Amity Institute of Organic Agriculture, Amity University Uttar Pradesh, I 2 Block, 5th Floor, AUUP Campus Sector-125, Noida-201313
[4]Centre of Advanced Study in Botany, Banaras Hindu University, Varanasi, India
[5]Department of Biological Sciences, University of the Sciences in Philadelphia (USP), Philadelphia, Pennsylvania, USA

Received: February 20, 2019 / Accepted: March 25, 2019

Abstract Heavy metal (HMs) pollution is regarded as one of the major concerns for soil and water, causing varieties of toxic and stress effects on plants and ecosystems. It has become one of the important limiting factors to crop productivity and quality. Due to an ever-increasing population growth and food demands, this situation has further worsened. Rice, a leading staple food crop that feeds more than 50% populations of the world, is constantly affected by abiotic stressors including HMs. In most of the countries, a major source of HM intake by humans is the rice grain produced through the paddy soils contaminated with HMs such as As, Al, Cu, Cr, Cd, Pb, Hg, Mn, Se, and Zn. Thus, gradual agglomeration of HMs in rice grains and their subsequent transfer to the food chain is a major menace to agriculture and human health. In recent years, several studies examined the impact of HMs toxicity on rice at multiple levels: molecular, biochemical, physiological, cellular and tissue, and demonstrated a correlation between HMs toxicity and the decreasing trend in rice productivity. Therefore, it is necessary to understand the interaction of HMs with rice crop spanning from the cell to whole plant level and devise appropriate effective means to alleviate these stress responses. This review focuses on tracing the pathways involved in stress responses and stress tolerance mechanisms displayed by different varieties of rice. However, it is essential to uncover the mechanisms related to stress responses in rice for designing improved investigations to develop novel varieties with high attributes. Therefore, this communication summarizes various defense strategies induced against HM stress and includes the function of metabolites (metabolomics), trace elements (ionomics), transcription factors (transcriptomics), and various stress-inducible proteins (proteomics) including the role of plant hormones.

Keywords: Heavy metals, Ionomics, Metabolomics, metallophytes, Proteomics, Rice, Transcriptomics

Introduction

Notable abiotic environmental constraints, involved in adversely affecting crop productivity worldwide, can be identified as drought, salinity, metal toxicities, extremes of temperature (Ashraf et al. 2007), increased irradiance, UV light exposure, low nutrient availability and high air pollutants (Lin et al. 2000). Among these environmental factors, heavy metals (HMs) are among most exposed environmental contaminants. They enter into the environment through different sources (Tripathi et al. 2014). One of the HM sources, fly ash adds huge amount of trace elements such as; Copper (Cu), Zinc (Zn), Manganese (Mn), and molybdenum (Mo) and toxic elements such as; vanadium (V), arsenic (As), boron (B), aluminum (Al), cadmium (Cd), lead (Pb), mercury (Hg) and Chromium (Cr) (Gupta et al. 2002). Any HM excess affects the paddy crops but some of the highly bio-hazardous metals like As, Cd, Pb and Hg can cause metal toxicity on multiple scales (Arif et al. 2016a). Their acquisition and accumulation in plants cause a series of physiological instability, like reduced growth, increased senescence, deformed photosynthetic apparatus (Hu et al. 2016), and inactivation of biomolecules

---

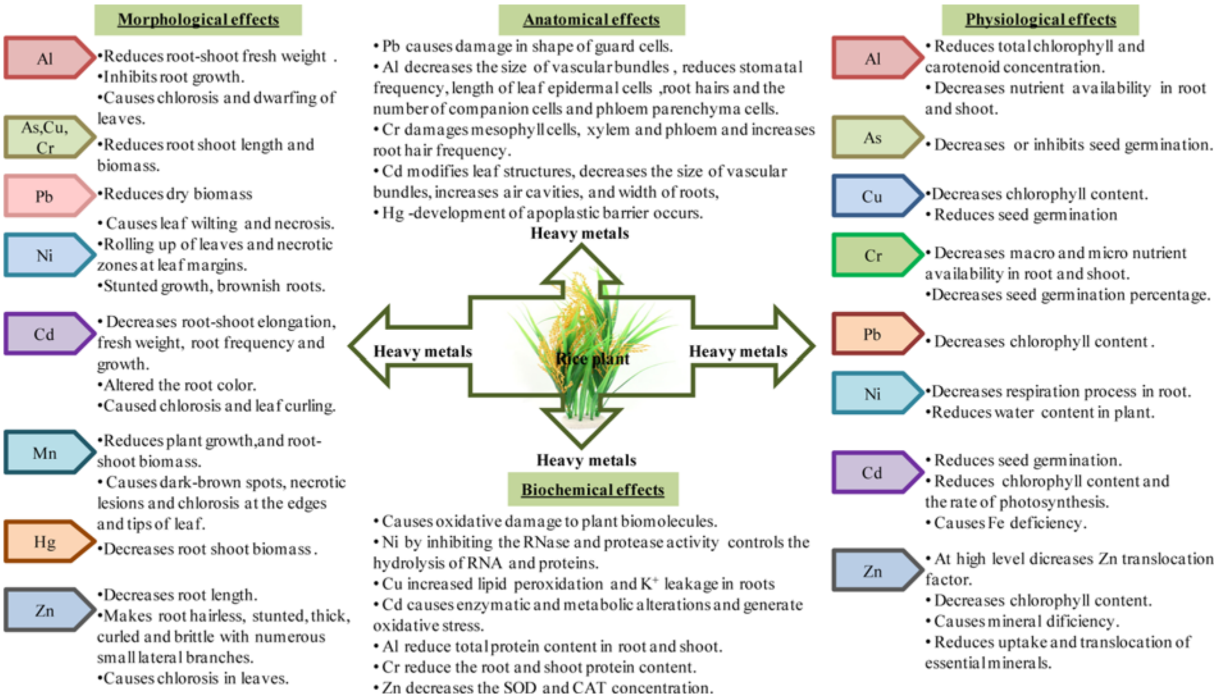
*Corresponding author; Durgesh Kumar Tripathi; Devendra Kumar Chauhan
Tel : +919453088595; +918081022287
E-mail : dktripathiau@gmail.com; dkchauhanau@yahoo.com

(Beyersmann et al. 2008). It also triggers water loss-related cell dehydration which become harmful to enzymes, organelles, and membranes (Duan et al. 2012). The autoxidation of redox-active HMs and the generation of Reactive Oxygen Species by the Fenton reaction cause cellular damage.

Worldwide, people rely largely on rice for the energy of everyday life (Fangmin et al. 2006). Rice cultivation is reliant on water, although water contaminated with toxic HMs such as As, Cd, Pb and Hg are carcinogenic to humans and typically hazardous elements to all forms of life (Jallad 2015). They have the ability to alter reactions that helps in producing ROS, $OH^{\cdot}$ and H_2O_2 in living cells. However, highly reactive radicals react with H_2O to generate the $OH^{\cdot}$, which can damage cell biomolecules, like DNA, amino acid, lipids and carbohydrate (Wysocki et al. 2010; Sharma et al. 2011; Hu et al. 2016). In response to these stresses, or to regulate metal homeostasis, plants have evolved multiple survival strategies (Liang et al. 2013) and they utilize a number of physiological and molecular mechanisms to minimize possible damage (Mahajan et al. 2005). These include regulating expression profiling of different genes, inducing upregulation and down regulation of genes, proteins or enzymes, or modulating the amount of metals to exclude non-essential forms through regulating their uptake, accumulation, compartmentation, chelation and sequestration as well as extrusion (Sharma et al. 2008). In view of complex interactions that exist between HMs and plant adaptations, this review article is a modest attempt to summarize the numerous studies focused on the stress effects of HMs, particularly the hazardous metals (As, Cd, Hg and Pb) and plant adaptations developed as a result of modulations of metabolomic, ionomic, transcriptomic, and proteomic shifts in plants.

Effects of Heavy Metal Stress on Morphological, Physiological and Anatomical Traits of Rice

Presence of copious amount of HMs adversely affects the accumulation and transportation of essential elements in plants that ultimately leads to differential alterations in morphological parameters (Seneviratne et al. 2017) including changes in the leaf area, shoot length and root length (Pant et al. 2014), eventually caused by shifts in the physiological milieu attributed to plant growth performance (Doni et al. 2014). These alterations also include numerous anatomical modifications in plants, for instance, dissolution and reduction of parenchymatous cells, mesophyll cells, and decrease in the number of xylem vessels as well as in the diameter of root stem and leaf (Batool et al. 2015). Apart from the tissue damage caused, changes in anatomical structures may also be attributed to an adaptive strategy in the form of apoplastic barrier (Lux et al. 2011) to prevent the HM infiltration and toxicity. Investigations show significant changes in metabolic pathways of photosynthesis, respiration, gaseous exchange and nutrient absorption, thus causing decrease in plant growth under HM exposures (Sharma et al. 2005; Gomes et al. 2011) (Fig. 1). HM exposure also interferes with the function of photosynthetic apparatus such as leaf tissue, cytosolic enzymes, chloroplast membranes, photosynthetic pigments: chiefly PS II and PS I, and cause disturbances in the photosynthetic carbon reduction cycle and xanthophyll cycle (Rai et al. 2016). One of the most devastating metalloids, Arsenic (As) was reported to cause stress in rice seedlings by reducing the root length, and shoot length (Shri et al. 2009, Upadhyay et al. 2016) thus decreasing the plant height and root growth (Abedin et al. 2002) (Fig. 1). Reduction in growth of plant occurs by manipulation in the rate of cell elongation. So far, several studies have demonstrated that HMs reduce the rate of photosynthesis (Rahman et al. 2007; Dias et al. 2013; Jin et al. 2015). As suggested in one study, arsenic exposure to rice seedling causes significant reduction in the germination percentage, root-shoot elongation and also in plant biomass (Shri et al. 2009). Moreover, As (III) and Hg together damage the root and cause significant lipid peroxidation. Observations also indicate the mutual competition between As and Hg, as such As impeded Hg uptake at a low concentration (0.5 mg L^{-1}) and increased it at a high concentration (2.5 mg L^{-1}) while Hg (1.25 mg L^{-1}) impeded As uptake and translocation in rice seedling (Ren et al. 2014). Arsenic affects cells of rice crop by causing breakage to the root epidermal cells and aerenchymatous cortex (Choudhury et al. 2011). Study conducted by Deng et al. (2010) demonstrated clearly how As caused structural changes in root anatomy by reducing the diameter of adventitious roots, and by forming the arenchyma and densely packed suberized epidermal cell wall that acted as a barrier. In an interesting study, toxic concentrations of As and Hg were implicated in cellular damages such as, degradation of plasma membranes, organellar structures, decreased number of endoplasmic reticulum tubules and mitochondria as well (Ren et al. 2014). Study on brown rice treated with As and Cd revealed that arsenic concentration had diminished from bottom to the top of brown rice whereas, Cd increased in the first node. Different nodes marked the significant difference between As and Cd in their accumulation and barrier capacities (Feng et al. 2017). Verma et al. (2003) demonstrated that reduction in root length in rice seedlings occurs due to Cd toxicity. Cd also significantly suppressed the seed germination (Mahmood et al. 2007; Eshagberi 2012). Dias et al. (2013) illustrates that photosynthetic apparatus does not display any change at a low concentration of Cd, whereas, excess of Cd reduces the photosynthetic rate (Parmar et al. 2013), obstructs the synthesis of chlorophyll molecule by causing interference with d-aminolevulinic acid dehydratase. Additionally, Cd was also found to be involved in dysfunction of photosynthetic process by causing damage to chloroplast structure and thylakoids stacking (Wang et al. 2014). Safarzadeh et al. (2013) based on a comparative study on seven rice cultivars, suggested that accumulation of Cd reduces the uptake as well as translocation of essential minerals like Fe, Zn, Cu, and Mn. This metal initiated chlorophyll loss, suppressed growth and causeda reduction in Fe translocation leading to the symptomatic deficiency of Fe (Parmar et al. 2013; Silva et al. 2014), and lower potassium (K) content in leaves of rice seedling (Liu et al. 2012). Li et al. (2014) working with four genotype of rice (maintainer lines Yixiang B and E2B, restorer lines R892 and Mianhui725), observed that new roots had developed in the cortex region in all genotypes and the diameter and frequency of roots differed significantly under low Cd concentrations. As well as, stress symptoms manifested as broken epidermis, damaged cortex and appearance of more black spots in both restorer lines than both maintainer lines at high Cd concentrations. Another study by Tripathi et al. (2012b) indicated that excess Cd was a cause of anatomical modifications in leaf structures where vascular bundles constricted in size, mesophyll cells displayed chlorosis, the air cavities became larger and much prominent, and the stomatal frequency decreased in comparison to the control (Fig. 1). Additionally, roots were observed to have expanded as an adaptive strategy against Cd stress in order to make it easily accumulated and mostly sequestered into the vacuoles. Rice seeds, treated with 100 µM Cd, generated oxidative stress, significantly slowed down the root-shoot elongation and also repressed the root-shoot fresh weight (Liu et al. 2013). Moreover, another toxic element, Hg, was found to cause a significant reduction in root-shoot biomass in a hydroponic set up with rice plants (Wang et al. 2014), as roots have the strongest potential for enrichment with HMs (Singh et al. 2013; Jin et al. 2015) (Fig. 1). Moreover, the Hg accumulations in four cultivars of rice (cvs. NF, WFY, ZX and ZD) caused changes in root anatomy: two (NF and WFY) out of four cultivars developed stronger apoplastic barriers on the radial and tangential wall of the endodermal cells in the form of lipophilic thin suberin lamellae, while, other two (ZX and ZD) cultivars did not develop the lipophilic casparian bands into the radial and transverse endodermal cell walls. These apoplastic barriers like suberin lamellae and casparian bands restrict metal acquisition and their transport into the xylem (Lux et al. 2011; Wang et al. 2014). Another hazardous metal Pb when accumulates in rice crop, decreases the dry biomass (Zeng et al. 2007) (Fig. 1). Srivastava et al. (2014) worked on the interactive effects of Cd and Pb in rice seedlings and observed that Pb caused more damage in guard cell's shape in leaf stomata than Cd. Moreover, Zeng et al. (2007) reported that Pb at a higher concentration (500-900 mg/kg) gradually decreased the chlorophyll content in rice. Both Cd and Pb, at a toxic level, lead to dysfunction of stomata by causing ultra-structural damage in guard cells of stomata (Srivastava et al. 2014). When it comes to water and nutrient availability to the plant, various studies have tackled



Morphological effects

Al
- Reduces root-shoot fresh weight .
- Inhibits root growth.
- Causes chlorosis and dwarfing of leaves.

As,Cu, Cr
- Reduces root shoot length and biomass.

Pb
- Reduces dry biomass

Ni
- Causes leaf wilting and necrosis.
- Rolling up of leaves and necrotic zones at leaf margins.
- Stunted growth, brownish roots.

Cd
- Decreases root-shoot elongation, fresh weight, root frequency and growth.
- Altered the root color.
- Caused chlorosis and leaf curling.

Mn
- Reduces plant growth,and root-shoot biomass.
- Causes dark-brown spots, necrotic lesions and chlorosis at the edges and tips of leaf.

Hg
- Decreases root shoot biomass .

Zn
- Decreases root length.
- Makes root hairless, stunted, thick, curled and brittle with numerous small lateral branches.
- Causes chlorosis in leaves.

Anatomical effects

- Pb causes damage in shape of guard cells.
- Al decreases the size of vascular bundles , reduces stomatal frequency, length of leaf epidermal cells ,root hairs and the number of companion cells and phloem parenchyma cells.
- Cr damages mesophyll cells, xylem and phloem and increases root hair frequency.
- Cd modifies leaf structures, decreases the size of vascular bundles, increases air cavities, and width of roots,
- Hg -development of apoplastic barrier occurs.

Biochemical effects

- Causes oxidative damage to plant biomolecules.
- Ni by inhibiting the RNase and protease activity controls the hydrolysis of RNA and proteins.
- Cu increased lipid peroxidation and K^+ leakage in roots
- Cd causes enzymatic and metabolic alterations and generate oxidative stress.
- Al reduce total protein content in root and shoot.
- Cr reduce the root and shoot protein content.
- Zn decreases the SOD and CAT concentration.

Physiological effects

Al
- Reduces total chlorophyll and carotenoid concentration.
- Decreases nutrient availability in root and shoot.

As
- Decreases or inhibits seed germination.

Cu
- Decreases chlorophyll content.
- Reduces seed germination

Cr
- Decreases macro and micro nutrient availability in root and shoot.
- Decreases seed germination percentage.

Pb
- Decreases chlorophyll content .

Ni
- Decreases respiration process in root.
- Reduces water content in plant.

Cd
- Reduces seed germination.
- Reduces chlorophyll content and the rate of photosynthesis.
- Causes Fe deficiency.

Zn
- At high level dicreases Zn translocation factor.
- Decreases chlorophyll content.
- Causes mineral dificiency.
- Reduces uptake and translocation of essential minerals.

Fig. 1. Heavy metal interaction with rice plant causes alterations in morphological, physiological, anatomical and biochemical characteristics.

this problem. The availability of a high concentration of HMs in soil disturbs the osmotic potential and nutrient acquisition in plants. Water absorption in plants is primarily governed by the primary root, root hairs, vascular and the leaves tissues, which are disturbed at the cellular levels by HMs, ultimately affecting the water and nutrient movement in plants (Rucińska-Sobkowiak 2016).

Effects of Heavy Metal Stress on Biochemical and Molecular Traits of Rice

Excess of HMs present in the soil may trigger a wide array of biochemical and molecular reactions in plant roots and shoots (Dubey et al. 2002; Maheshwari et al. 2007; Fig. 1). They affect the key metabolizing enzyme activities that may lead to modifications in biomolecules quantity and quality, and cause alterations in metabolisms of carbohydrate, protein and nucleic acids (Sharma et al. 2005). Plants generate the ROS including superoxide radicals, hydroxyl radicals, and hydrogen peroxides via different metabolic pathways in response to HM stress, which inhibits vital cellular processes at assorted levels of metabolism (Sytar et al. 2013) and causes oxidative damage on plant biomolecules, for instance, lipid, amino acids, DNA and RNA (Kanazawa et al. 2000). The toxic metalloid Arsenic exposures: 100 mM As(III) and 500 mM As(V)- to the rice plant were demonstrated to enhance MDA content in root and shoot signifying oxidative stress, as lipid peroxidation (Shri et al. 2009) consecutively altered the membrane permeability with an increased ion leakage (Mishra et al. 2011; Kumar et al. 2014). According to the report by Ma et al. (2006a) arsenic enters into the xylem of rice in the presence of gene encoding silicon/ arsenite effulxer protein Lsi2. When As gets rendered to the plant, it down-regulates the genes entailing cellular changes like morphogenesis, growth and cell division (Sharma 2012). It was apparent through the work of Norton et al. (2008) that a long term arsenic exposure to rice plants leads to mass down regulation of gene expressions; expression of expansion genes (Os01g14660 and Os04g46650), tubulin genes (Os03g45920 and Os03g56810), actin genes (Os01g64630) and microtubule genes (Os03g13460 and Os09g27700) were significantly affected (Table 1). Cd, reportedly, causes enzymatic and metabolic modification in plants (Parmar et al. 2013). The activities of superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and dehydroascorbate reductase (DHAR) increase with an increase in Cd exposure to the rice varieties (Iqbal et al. 2010). Moreover, Cd treatment to the rice seedlings induced the ROS accumulation by increasing the level of malondialdehyde (MDA) and H_2O_2 (hydrogen peroxide) thus inhibited the antioxidant capacity in both roots and shoots. Plant root produces varieties of organic acids and other exudates that chelate soil Cd, preventing its entry into the roots (Schwab et al. 2005; Dong et al. 2007). Lee et al. (2013) demonstrated that Cd-stressed rice plants undergo apoptosis due to oxidative stress coupled with over expression of glutamine synthetase (GS) gene. Investigations focused on understanding the rice Cd stress illustrates that Cd treatment significantly induce OsIRT1 (Iron-regulated transporter 1) transcript in roots of rice seedlings (Chang et al. 2012) because of the iron deficiency led by Cd (Ishimaru et al. 2006). According to the study of Moons (2003a,b) PEG (polyethylene glycol) and the HMs like Cd (20 μM), Zn (30 μM), Co and Ni distinctly induced osgstu4,osgstu3 and also the ospdr9 (pleiotropic drug resistance protein) in the roots of rice seedling. Pb induced-toxicity in rice seedling led to an increase in GSH (glutathione)/GSSG (glutathione disulphide) ratio and the total GSH pool (Sytar et al. 2013). More often, HMs induce various stress responses in cell molecules such as degradation of cell membranes, proteins and nucleic acid (Ou et al. 2012). Pb toxicity causes the imbalance in the synthesis of carbohydrates, and also affects the nitrogen metabolism by affecting the protein content of plant cells (Chatterjee et al. 2004). Huang et al. (2008) reported that an increase in ROS production with supplementation of Pb ions occurs and that affects root cell viability, accelerating the cell death in rice seedling. More interestingly, the treatment of HMs: Cu^{2+} (1000 μm), Cd^{2+} (100 μm), Cr^{3+} (1000 μm) and Hg^{2+}(50 μm) to the rice (ssp. *japonica*, cv. Matsumae) seedlings caused modifications in specific DNA methylation patterns, which are responsible for the toxic environment and considered as most stable epigenetic markers (Wada et al. 2004). Moreover, their findings suggest that the cytosine methylation patterns of both transposable elements and protein-coding genes could be altered in rice under HM stress. Generally, in response to abiotic stress, HMs induce the synthesis of such proteins that are related to stress, and also activate signaling molecules, for example, heat-shock-protein (HSPs) in rice, which is a class-I low molecular weight signaling molecules (Tseng et al. 1993).

Tolerance Mechanisms and Management of Crop Under Heavy Metal Stress

The viability of rice plant is negatively affected by the presence of toxic HMs via ever-increasing applications of chemical fertilizers in the field (Jamil et al. 2011). As plants accumulate and translocate HMs to different plant parts including grains, there is a need to reduce their transfer to food chain making the rice agriculture more sustainable. In response to an increasing HMs exposure, many species have developed defense strategies against the metal–induced toxicities. For example, plants exhibit defense mechanisms through "avoidance" and "tolerance" in response to HM exposure (DalCorso et al. 2010). Under "Avoidance", plantshave evolved potential to prevent HMs entry into cells (Lang et al. 2011; Choppala et al. 2014). Less uptake of HMs into the root cells would obviously be considered as the tolerance mechanism of plants (Choppala et al. 2014; Gao et al. 2016). The following section depicts the various defensive strategies adopted by rice plants against varieties of toxic effects caused by HMs.

Antioxidative Mechanism

Abiotic stresses including HMs are known to accelerate the production and accumulation of ROS (Kao 2014). The generation of ROS is the outcome of aerobic reactions and plants have developed significant mechanisms to mitigate the toxic impacts of these radicals in the cell under normal situations. Plants subjected to stress situation display a disturbed cell homeostasis with an increased production of ROS which, in turn, invokes the antioxidative mechanisms in order to reduce the effect of excess ROS (Mittler et al. 2004; Arif et al. 2016b; Fig. 2). These defense mechanisms, though dependent on the concerning metal and plant species, generally involve major antioxidants such as ascorbate-glutathione cycle, and other antioxidant enzymes like Catalase, peroxidase (POD), and superoxide dismutase (Fig. 2). In rice seedling, under Arsenic (III) and (V) toxicity, SOD, APX and GR (glutathione reductase) content increased in root and shoot with increasing concentration of arsenic (Shri et al. 2009). Rice seedlings exposed to 100 µM Cd had demonstrated a dramatic increase in MDA and H_2O_2 while the levels of SOD, GPX (guaiacol peroxidase) and APX had decreased (He et al. 2014). Moreover, Srivastava et al. (2014) demonstrated that rice seedlings with Cd (150 µM) and Pb (600 µM) application had resulted in the production of ROS ($O_2^{\cdot -}$ and H_2O_2) which, in turn, induced antioxidant enzymes such as SOD and GPX (Fig. 2; Table 1). The toxic Pb treatment (1000 µM) to the growing rice seedling induced lipid peroxidation and elevated the levels of SOD, guaiacol peroxidase, ascorbate peroxidase and GR enzymes, which indicate an essential antioxidant activity to reduce the accumulation of lead in plant.

Defensive Metabolites & Metabolomics

As a rigorous osmotic stress causes severe damage of cellular components, therefore, cellular machinery produces a range of metabolites to avoid damages. Such metabolites include amino acids, quaternary and other amines such as glycine-betaine and polyamines and a several types of sugars as well as sugar alcohols for instance; mannitol and trehalose (Vinocur et al. 2005). Glycine betaine (GB) and proline like major organic osmolytes concentrate in different species of plants to detoxify them from HM stress. Rice (*Oryza sativa*) naturally does not produce GB under any condition. However, the quantity of GB in rice was found in much less concentration than GB-accumulating plants, mostly under stressed environment (Ashraf et al. 2007). Several studies have demonstrated increasing accumulations of non-enzymatic antioxidants, secondary metabolites, particularly, proline in

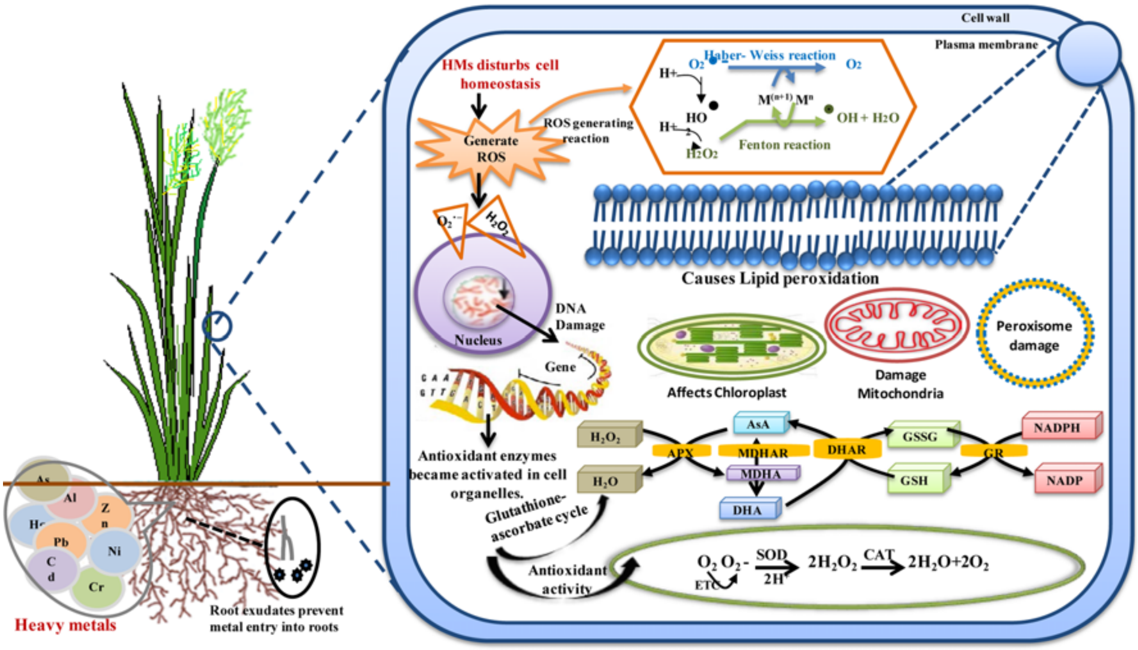


Fig. 2. Heavy metal-induced ROS generation and toxicity invoking antioxidant pathway in rice cells.

Table 1. Effect of different heavy metals on the protein and gene expressions of various rice varieties

Heavy metal	Concentrations	Rice varieties	Changes in protein expression	Reference
As	100 µM	*Oryza sativa* L.	Negatively regulate the RuBisCO and chloroplast 9 kDa ribonucleo proteins	Ahsan et al. 2010
As	100 µM	*Oryza sativa* L.	The increased expression of S-adenosylmethionine synthetase, GSTs, cysteine synthase, GST-tau, and tyrosine-specific protein phosphatase proteins	Ahsan et al. 2008
As	25 µM AsIII 250 µM AsV	Indica cultivar, IR64 (*Oryza sativa* L.)	Increased expression of glutaredoxin (Os01g26912) in the AsIII-treated shoot. AsV induced expression of one of the cytochrome P450 genes (Os01g43740) in rice root	Chakrabarty et al. 2009
AsV	13.3 µM	Rice Azucena (*japonica*) and Bala (*indica*)	Down regulated the phosphate: H^+ symporter gene OsPT2 (03g05640) and two aquaporin genes (Os05g14240 and Os12g10280)	Norton et al. 2008
Cd	0.2 mM	*Oryza sativa* L. cv. Zhonghua No. 11	Transcription of MAPK is inhibited	Zhao et al. 2013
Cd	100 µM	*Oryza sativa* Dongjin	Cd reduces the concentration of the OEE2 protein and increase 11 and 23 kDa photosynthetic proteins, RuBisCO activase precursor fragment, OsPR5, and OsPR10 proteins	Lee et al. 2010
Cd	10 µM	*Oryza sativa* ssp. Japonica cv Zhonghua11	Aquaporins are reprssed in plasma memebrane due to Cd toxicity. auxin transport protein REH1, two auxin (IAA) efflux carrier proteins, and one gibberellins (GA) response modulator were all down-regulated after Cd treatment	Yang et al. 2016
Cd	1.0 mM	*Oryza sativa* L.cv. DongJin	Methionine synthase and phosphoglucomutase (PGM) decreased	Kim and Lee 2009
Cd	100 µM	Rice (*Oryza sativa* L. cv. TN67)	Induces the alteration in gene involved in unfolded protein binding and sulfate assimilation	Lin et al. 2013
Cd, Hg	250 µM	*Oryza sativa* L. cv. Nipponbare	Heavy metals cause damage in photosynthetic apparatus by degrading the RuBisCO LSU	Hajduch et al. 2001

rice plant in response to increased HM concentrations. Detoxification of rice plant from arsenic stress is possible by the mechanism of binding of metalloid with phytochelatins (PCs), a HM binding peptide. In an acidic condition, the vacuole-sequestered As-PC complex decreases the level of free As concentration in cytoplasm (Zhao et al. 2009; Liu et al. 2010; Sharma 2012). Duan et al. (2011) also enumerated that PCs complexation of arsenite decreases As movement from rice leaves to the seed, and the manipulation of PC synthesis helps in diminishing the As content of rice grains. Similarly, Batista et al. (2014) also illustrated that plants adopt a strategy, under high level of As, to induce various As-PC complexes, to prevent As mobility between soil and different parts of the plant. A Cd chelator, phytochelatins (PC) has been implicated in reducing cadmium toxicity (Yadav et al. 2010). The amino acid such as phytopsiderophores, present in root exudates, form more suitable complex with Cd in order to regulate the uptake of HMs in rice plant (Xu at al. 2005). Yang et al. (2000) accounted that the secretion of oxalate compounds from the root of Pb intoxicated rice seedling checks the uptake and accumulation of Pb ions.

Defensive Ions & Ionomics

Ionomics is basically considered as the study of the mineral nutrients and beneficial metals present in the organism's cells as well as analysis of cellular inorganic components (Salt et al. 2008; Yadav et al. 2016). It also signifies the investigation about the interactions between mineral elements (Lyubenova et al. 2013; Chu et al. 2015) and analyzes the uptake and accumulation of mineral nutrients and HM contamination in plants particularly by the high elemental analysis (Salt 2004; Feng et al. 2017). Numerous studies on silicon (Si) proved efficacy of Si in the mitigation of HM stress as well as the improvement in rice crop with altered characteristics (Singh et al. 2011). Adding up Si can reduce total arsenic and inorganic arsenic content from root and shoot, significantly enhance biomass of straw and DMA content in rice genotypes [lower radial oxygen loss (ROL) genotype and high ROL genotype], however, arsenic content decreases more in lower ROL genotype than in higher ROL genotype (Wu et al. 2015). Phosphate has the capacity to reverse the damage and severe stress caused by As; application of phosphate along with As increases root-shoot growth and metabolism of rice seedling (Choudhury et al. 2011). It is well known how As(V), after dominant As species occurring in aerobic soil competes with phosphate (Pi) in plant uptake as they both share some of the common transporters located in the plasma membrane. The oxyanion As(V) is structurally analogous to that of Pi (Li et al. 2015). In a recent study, Kumar et al. (2016) revealed that SeVI is involved partly in reversing the stressed phenotype and minimizing AsIII accumulation and toxicity, at the same time, improving nutrition quality in rice (Table 1). Although, interestingly, Si in Silica gel was reported to decrease the amount of As in all parts of rice plant (Fleck et al. 2013). It occurs because of the sharing of same influx transporter Lsi1 (Low silicon rice1) by Si and As (Guo et al. 2009; Adrees et al. 2015). Application of Mn oxide-modified biochar in the arsenic contaminated soil decreases the level of arsenic in rice (brown rice) by oxidizing arsenite As(III), to arsenate As(V), thus increasing the total plant biomass and positively effects amino acids (Yu et al. 2017). Treatment of iron materials can significantly reduce accumulation of total arsenic from rice plant (Matsumoto et al. 2016). Meharg et al (2015) studied the role of silicon in reducing the toxic effects of Cd, inorganic arsenic and antimony. Ma et al. (2016b) had shown that Si dampens the glycosidase expression, cell surface non-specific lipid-transfer proteins, and many other proteins activated in stress condition (Table 2). However, in case of high Cd exposure in cytoplasm, Si accumulating cells provoke the distribution of Cd into vacuoles, causing diminished expression of GST (glutathione S-transferase). According to She et al. (2005) Si and Cd accumulate in endodermis of rice root and reduce inner cell wall porosity, resulting into co-precipitation of Si along the cadmium. Tripathi et al. (2012b) used Si amendment in the rice seedlings suffering from various alterations and damage caused by the high dose of Cd (Table 1). In their investigation, Si reduced ROS and metal accumulation, increased the level of antioxidative enzymes and added to the total length and surface area of rice root. Moreover, Si, along with Cd, minimized the deformities in mesophyll cells, and conduction bundle of rice (Tripathi et al. 2012a) (Table 1). Whereas, Chang et al. (2012) reported a significant reduction in Cd accumulations and toxicity in rice seedlings upon exogenous application of Fe-citrate (Table 2). It was reported by Wang et al. (2013) that rice under Cd stress improved its tolerance by increasing the mineral element uptake, for instance, Fe accumulation increases to resist plant from Cd stress (Table 1). Moreover, Wang et al. (2014) demonstrated the role of Selenium in reducing Hg uptake and accumulation in rhizospheric region and in the root structures (Table 2). It is also evidenced that

Table 2. Different management practices for alleviation of heavy metal toxicity in rice varieties

Metals	Rice varieties	Management methods	Concentration used	Effects on rice plant	References
As	*Oryza sativa* L. cultivar Zhonghan 221	Arbuscular mycorrhizal fungi (AMF)	Twenty-seven g of AMF inoculums per pot	Enhanced total phosphorus uptake and reduced total As uptake in different rice parts. Increased rice grain biomass	Chan et al. 2013
AsIII	*Oryza sativa* L. var. Sarju-52	Selenate VI	25 µM	Reduced As uptake and accumulation in root and shoot of rice seedlings and enriches the quality of rice grain. Induced the levels of non-protein thiols, glutathione and phytochelatins and modulated the activity of enzymes of thiol metabolism. Increased the level of essential amino acids.	Kumar et al. 2016
Cd	*Oryza sativa* L. cv. N07-63	Hydrogen peroxide (H_2O_2)	100 µM H_2O_2	Reduced metal toxicity and translocation. Induced enzyme activities for SOD, CAT, GPX, and APX, elevated contents of GSH and AsA.	Hu et al. 2009
Cd	Rice (*Oryza sativa* L.) variety MSE-9	Nitric oxide (NO)	100 µM of SNP (NO donor)	Regulated the stress metabolism, alleviated oxidative stress.	Panda et al. 2011
Cd	*Oryza sativa* (Y Liangyou 1928)	Titanium oxide Nanoparticles (TiO_2 NPs)	1000 mg/L	Alleviated Cd induced toxicity by reducing its uptake and translocation in rice roots and leaves. Significantly enhanced net photosynthetic rate and chlorophyll content.	Ji et al. 2017
Cd	*Oryza sativa* L.	Rapeseed cake (RSC)	3.00 g kg^{-1}	Decreased the heavy metal accumulation and its concentrations in soil solution and rice thus reduces the bioavailability of heavy metal to rice crop. Alleviated heavy metal toxicity by immobilizing metals in soil.	Yin et al. 2016
Cd	*Oryza sativa* L. cv. Taichung Native 1	Fe-citrate	30.6 µM	Diminished concentration and toxicity of Cd in rice seedlings.	Chang et al. 2012
Cd	*O. sativa* L. cv Zhonghua 11	Silicon	1 mM	Regulated different proteins under Cd stress and down-regulated most of proteins. Maintained cell in normal physiological conditions. Inhibited Cd uptake by modifying cell walls and reduced several stress related proteins. Caused a lower expression of glutathione S-transferases.	Ma et al. 2016b
Cd, Pb	*Oryza sativa* L.	Biochars	5% biochar by weight	Decreased heavy metal content in rice shoot and also decreased the pore water concentrations of Cd and Zn.	Zheng et al. 2012
Hg	*Oryza sativa* var. *japonica*, 'Zixiang' ('ZX') and *indica*, 'Nanfeng'('NF'),	Selenium	5µg g^{-1}	Reduced total content of water soluble Hg and MeHg in rhizosphere soil. Increased the brown rice yield and selenium content of rice. Caused development of apoplastic barriers in root endodermis to reduce Hg uptake by roots.	Wang et al 2014

selenium (Se) speciation (selenite and selenate) is more effective in reducing accumulation of inorganic Hg in the rice, here also, the rhizospheric region act significantly in detoxification than the above ground part (Tang et al. 2017). In addition, Si applications in rice plants lead to the reduction in Pb bioavailability by increasing Se accumulation.

Transcriptomics

Transcriptomics analysis is an essential part of investigation exploring the transporters involved in different pathways and traits, thus providing a map for the movement of HMs within plant parts. HMs: As and Cd are highly prone to accumulate in rice and, at the same time, are acutely toxic. Chakrabarty et al. (2009) performed the comparative transcriptomic analysis of As effects in rice and examined the genome-wide expression with regard to As [arsenate (AsV) and arsenite (AsIII)] (Table 1). Investigators in this study reported that AsV stress caused more up-regulation or down-regulation of an additional set of genes than AsIII, and also, that AsV induced the expression of cytochrome P450 (Os01g43740) in the root of *oryza sativa* whereas AsIII specifically induced the expression of glutaredoxin (Os01g26912) in shoot**.** As also evidenced by Sasaki et al. (2014) several genes have already been identified or cloned, which unlock a chance for the rice yield improvement (Rebouillat et al. 2008; Uga et al. 2013; Wu et al. 2014). Hu et al. (2016) studied the over expression of OsLEA4 gene (Late embryogenesis abundant protein) in improving the tolerance of transgenic rice (*Oryza sativa* L.) under high levels of abiotic stress. Although expression of OsLEA4 gene occurs during each developmental stage of rice, over expression of this gene enhanced the resistance of transgenic rice to HM stress compared to wild rice variety. When Cd enters into the cytosol, there is a directional pathway mediating the sequestration of Cd within the vacuole by the transporter OsHMA3 (Takahashi et al. 2012), which further reduces Cd mobilization in the cytosol and its transportation from root to shoot (Choppala et al. 2014; Shahid et al. 2016). Knock-out of Cd transporter OsNramp5 decreases the Cd accumulation (Slamet-Loedin et al. 2015). Consecutively, Slamet-Loedin et al. (2015) suggested that down-regulation of OsNRAMP5 is a special mechanism to reduce Cd accumulation in roots. Auxin transporter OsAUX1 is reported to take part in Cd tolerance in rice (Yu et al. 2015). In plants, Mitogen-activated protein kinase (MAPK) cascades have specific functions in response to hormones, cell division and development, as well as in stress conditions (Tena et al. 2001; Jonak et al. 2002; Gao et al. 2008). Cd was also reported to induce the OsMAPKs gene activation in rice (Yeh et al. 2007; Gao et al. 2008). The mechanism working under Si application to the plants for the removal of metal induced stress, involves the modification in gene expressions under Cd stress. Si is reported to activate the genes OsHMA3 and OsLsi in rice that further participate in neutralizing toxicity (Kim et al. 2014). Another study suggests that, to resist Cd, the presence of Si in plants up-regulates the expression of Lsi1 gene, while down-regulates the natural resistance-associated macrophage protein5 (Nramp5) gene, associated with Cd transportation (Ma et al. 2015). Recently, Dubey et al. (2014), analyzed the genome-wide alteration in transcriptome of rice (IR-64 cultivar) root in response to different concentrations of arsenate (V), Cd, chromium (VI) and Pb in hydroponic condition and revealed that, from the total 51279 genes in the case of As(V), 282 genes were significantly up-regulated and 604 genes were down- regulated. Whereas, under Cd supplementation, 707 genes were up-regulated and 831genes were down-regulated significantly. Pb significantly affected the expression of 896 genes of which 392 genes were up-regulated and 504 were down-regulated. Study further illustrates that transcriptional factors that were over/under expressed related to the WRKY family of transcription factors [Cd and Cr (VI)), MYB family, As(V) and Cr(VI)], RING-H2 finger protein, RING finger, CHY zinc finger domain-containing protein and bZIP transcription factors. It is evident that a large number of stress-related genes are transcriptionally modulated as their up and down-regulations, while dealing with specific HM toxicity in rice, some notable players among them being glutathione S-transferase dehydrin, sulphite oxidase, L-ascorbate peroxidase (APX), L-ascorbate oxidase and germin-like proteins (Dubey et al. 2014).These data clearly indicate the phytotoxicity of Cd in rice plants. However, Lin et al. (2013) differentiated between Cu and Cd actions in rice root by identifying related genes and pathways (Table 1). Their study revealed that Cu and Cd exposures regulated transcription of 1450 and 1172 genes, respectively, among which 882 genes were responsive under Cu stress. whereas 604 unique genes to Cd. Cu was found in altering the genes roled in vesicle trafficking transport and fatty acid metabolism as well as in cellular component biogenesis, whereas Cd-regulated the genes responsive to unfolded protein binding and sulfate assimilation. Hg induces severe stress in rice plant through the generation of ROS; the transcriptome analysis of Hg-exposed roots and nodes cells reveals that the expression of OsTCTP in the cytosol and nucleus helps to tolerate the Hg stress by down-regulating the ROS reactions (Wang et al. 2015).

Proteomics

Study of proteomics helps in unraveling the mechanistic pathways involved in HM stress and detoxification strategies. A large number of proteins play major roles in plant growth and tolerance to environmental stress. Through the artificial alterations of those proteins, it has become possible to produce high yielding crops (Komatsu 2008). Zhao et al. (2013) documented that mitogen-activated protein kinase (MAPK) regulates the growth of rice root, and also modifies the cycle-related gene expression through auxin signaling variations under Cd exposure (Table 1). The first study of rice proteome revealed that Cd causes damage in photosynthetic apparatus by degrading the RuBisCO LSU (Hajduch et al. 2001), it reduces the concentration of the OEE2 protein and further, increases the photosynthesis 11 and 23 kDa proteins, like, RuBisCO activase precursor fragment, OsPR5, and OsPR10 proteins (Lee et al. 2010; Table 1). In response to stress generated by Cd exposure in rice seeds, homeostasis mechanism displays the involvement of regulatory, stress and detoxification related proteins (Singh et al. 2013). Another investigation illustrated accumulations of regulatory proteins, as well as receptor-like protein kinase (RLK), DnaK-type molecular chaperone BiP, pentatricopeptide repeat (PPR) containing-like proteins, putative retro-element, and Ulp1 protease-like proteins and stress and detoxification-related proteins, such as putative disulfide isomerase, myosin heavy chain-like protein, putative aldose reductase glyoxalase I, and peroxiredoxin in Cd (0.8 mM) stressed rice seedlings. Nitric Oxide (NO)has been shown recently to be beneficial for the rice against Cd stress as it was demonstrated to effect dynamic changes in rice plasma membrane proteins (Yang et al. 2016). They identified sixty-six differentially expressed proteins involved in the modulation of plasma membrane proteins, of which, many function as transporters, ATPases, kinases, metabolic enzymes, phosphatases, and phospholipases (Table 2). Increased expression of a several heat shock proteins shows that it has a very significant role against Cd toxicity in rice (Dubey et al. 2014). Nwugo and Huerta, (2010) recognized 60 protein spots that were differentially expressed because of Cd supplemented with Si. Under toxicity of both forms of Hg (inorganic and organic) rice root protein analysis points to 29 differentially expressed proteins that are known to be work in oxidative defense system, sulfur and glutathione (GSH) metabolism, sugar and energy metabolism, necrosis and apoptopsis, as well as in pathogen resistance. Further results also exhibited that 15-25 kDa proteins were found bounded to Hg in rice roots resulting into irreversible damage of root growth under Hg stress (Li et al. 2016). Pb ions were observed to increase the Ca accumulation and activatethe MAP kinase protein that is known to act like a transducer into intracellular responses in rice seedlings (Huang et al. 2008).

Role of Hormones

Various reports have established the potential of plant hormones in recovering crop under conditions of environmental stress. Recent studies have suggested that phytohormones such as auxins, cytokines, ethylene, and gibberellins, and some stress hormones, including brassinosteroids, jasmonates, and strigolactones, are probable metabolic engineering targets that hold promise for crops tolerant to abiotic stress (Wani et al. 2016). Asgher et al. (2015) reviewed the role of major plant growth regulators (PGRs) in regulation of plant growth under HM (Cd) stress conditions (Piotrowska-Niczyporuk et al. 2012). Brassinosteroids (BRs), a steroidal hormone, act in developmental events related to plants and in stress tolerance (Choudhary et al. 2012; Fariduddin et al. 2014). BRs display a high action even at a very low concentration (0.1 nM). Another stress hormone salicylic acid (SA) has beneficial role in alleviating oxidative damage caused by Cd. Therefore, the treatment of salicylic acid increases antioxidant activities by inducing H_2O_2 signaling in root of rice (Guo et al. 2007). However, Jasmonic acid, as signaling molecules, causes defense responses; induces development and secondary metabolism (Agrawal et al. 2003). Similar ameliorative effect of Jasmonic acid was also found in rice against Cu (Mostofa et al. 2013) and As (Singh et al. 2015) by enhancing the capacity of antioxidative and glyoxalase systems and also by regulating mineral translocation. Plant growth regulator, auxin has functional ability to regulate growth and development, and act as a stress manager. Pandey et al. (2015) convincingly demonstrated the synergistic beneficial roles of selenium and auxin for the As stressed rice seedlings by inducing an improvement in growth parameters, chlorophyll content, protein content and lipid peroxidation significantly.

Ameliorative Strategies

Plants have developed multiple ways to ameliorate the stress effects caused by toxic HM by self-regulating mechanisms, however, a number of research efforts have indicated the efficacy of exogenous treatment in reducing stress even under extreme conditions. Exogenous application of special signaling molecules like nitric oxide (NO) (Panda et al. 2011; Zhang et al. 2012) and hydrogen peroxide (H_2O_2) has been used for the mitigation of Cd stress in rice seedlings (Wu et al. 2015b; Table 2). Hsu et al. (2007) postulated that treating the rice seedlings with H_2O_2 (hydrogen peroxide) against non-heat shock stress elevates the level of APX content to defend the rice seedling from Cd induced toxicity. Furthermore, Sodium nitroprusside (SNP) used as an exogenous NO donor acts as a ubiquitous signal molecule and ameliorates the inhibitory effect of Cd on seed germination and growth by avoiding the Cd accumulation (He et al. 2014) restoring membrane integrity and recovering the H_2O_2 and $O_2{\bullet}^-$ levels (Singh et al. 2014).The same beneficial effect of NO was reported for rice seed germination under Al toxicity (Marciano et al. 2010). Other methods have also been standardized for maintaining the balanced metal content in rice production. The use of nanoparticles (NPs) in alleviating HM stress is seen as a new trend of research that holds promise for sustainable agriculture. Ji et al. (2017) observed that TiO_2 (Titanium dioxide) nanoparticles have the potential to successfully detoxify rice seedlings from the stress caused by Cd (Table 2). As transgenic crops expressing various desirable characteristics have begun to dominate the post green revolution in agriculture, an important question to answer is how these modified crops will respond to the soil contaminated with HMs. Haiyan et al. (2009) examined the variations in the accumulation pattern of some HMs, particularly Cd and Pb in Bt (*Bacillus thuringiensis*) transgenic rice and reported a significant increase in the accumulations of Cd followed by Pb, compared to other HMs in Bt crops. They further suggested that growing Bt transgenic rice in Cd-polluted area might be unsafe. In another study, upregulation of nicotianamine synthase and ferritin gene through the CaMV 35S increases the concentration of essential nutrients such asFe and Zn and Mn in rice (Sebastian et al. 2015). A notable management practice involves the technique of organic amendment applications. In a recent study, among the applications of rapeseed cake (RSC), organic carbon material (OCM) and pig manure (PM), RSC was demonstrated to effectively reduce the Cd concentrations in brown rice and, at the same time, increase the rice grain yield by increasing dissolved organic carbon and dissolved organic nitrogen in the soil solution of rice crop (Yin et al. 2016; Table 2). Similarly Zhou et al. (2015) also reported about the amendment of combustion products of organic material, Biocharhas proven to cause a significant reduction in the metal accumulations in rice grains (Zheng et al. 2015). Several studies provide the evidence about the beneficiary role of biochar in reducing metal (Cd and Pb) accumulations in soil, thereby reducing their availability to the rice (Zheng et al. 2012; Table 2). Similarly, in Cd and Pb contaminated rice paddy field, biochar potentially increased the rice gain production by alleviating metal stress and carbon emission from metal polluted rice field (Zhang et al. 2015). However, these management practices are less feasible because of high maintenance costs and time investment. Alternatively, arbuscular mycorrhizal fungi (AMF) have shown some promise in reducing accumulations of HMs such as As in rice (Chan et al. 2013). Li et al. (2016) also demonstrated the significant role of AMF in reducing the Cd concentrations from rice root cell wall as well as shoot by transforming Cd into inactive form, thus increasing the rice tolerance to Cd. Water management is another promising method for minimizing the bioavailability of toxic HMs to the rice plant. Biochar is beneficial in reducing methylmercury (MeHg) in rice grains by immobilizing MeHg in soil and bio-dilution of MeHg in grains; it also enhances the biomass of grain (Shu et al. 2016).

Conclusion and Future Prospect

Cultivation of rice demands fertile soil and a plenty of water, but unfortunately, the excessive application of chemical fertilizers and pesticides to the paddy fields has already generated a huge burden on soil and water quality with substantial accumulations of toxic metals (Cd, As, Pb or Hg). Research shows that these agents can not only affect crop yield and grain quality but also human health in dramatic ways because of mass consumption of rice. Above account amply indicates how HMs can build up stress in plants, modify the cellular process and affect plant genome or gene expressions. This article also discusses, in some detail, how plants have developed smart strategies to minimize stress effects of metal accumulations in tissues and organs. These defensive mechanisms operate at multiple levels: morpho-anatomical-physiological levels at one hand, and at other hand, at the level of gene regulation, genetic and epigenetic modifications of the genome. Besides, to increase the yield and quality of rice grains, a number of HM stress mitigation methods have been suggested in different studies, for example, the exogenous supplementation of beneficial ions, stress hormones, special signaling molecules, nanoparticles, organic amendments, fungal treatments, and water management in the contaminated soils. All these mitigation measures require a thorough scrutiny under field conditions. As cultivation of transgenic crops is on rise, it is also important to monitor the concentration of these toxic metals in grains harvested from transgenic cultivars. The issue of HM accumulations by transgenic crops is not yet settled, as reports are conflicting. A number of studies indicate significant accumulations while some point to no concerns, for instance, in rice, upregulation of nicotianamine synthase and ferritin using CaMV 35S increases the concentration of Fe and Zn and Mn. Whereas, biofortified *indica* rice grains, enriched with Fe and Zn, demonstrated no significant accumulation of Cd from Cd-contaminated soils. Endosperm, which is the major part of the transition elements reserve in the seed grain, shows site-specific expression of heavy metal chelating compounds and transporters that are the open areas of genetic manipulation for control against toxic metals. Sound stress remediation strategies should be explored at all levels, from agronomic practices, soil management to genetic manipulation, for the safe production of this staple food crop.

Acknowledgements

Authors are thankful to the University Grants Commission, New Delhi for financial support.

Author's Contributions

NA and DKT designed the manuscript; NA,VY, NS and DKT wrote the manuscript. NS, SS, DKC, NKD and SVS critically evaluated the manuscript.

References

Arif N, Yadav V, Singh S, Singh S, Ahmad P, Mishra RK, Sharma S, Tripathi DK, Dubey NK, Chauhan DK (2016a) Influence of high and low levels of plant-beneficial heavy metal ions on plant growth and development. Front Environ Sci 4:69

Arif N, Yadav V, Singh S, Kushwaha BK, Singh S, Tripathi DK, Vishwakarma K, Sharma S, Dubey NK, Chauhan DK (2016b) Assessment of antioxidant potential of plants in response to heavy metals. In Plant responses to xenobiotics 97-125. Springer, Singapore

Abedin MJ, Cotter-Howells J, Meharg AA (2002) Arsenic uptake and accumulation in rice (*Oryza sativa* L.) irrigated with contaminated water. Plant Soil 240:311–319

Adrees M, Ali S, Rizwan M, Zia-ur-Rehman M, Ibrahim M, Abbas F, Irshad MK (2015) Mechanisms of silicon-mediated alleviation of heavy metal toxicity in plants: a review. Ecotoxico Environ Saf 119:186-197

Agrawal GK, Jwa NS, Shibato J, Han O, Iwahashi H, Rakwal R (2003). Diverse environmental cues transiently regulate OsOPR1 of the "octadecanoid pathway" revealing its importance in rice defense/stress and development. Biochem Biophys Res Commun 310:1073–1082

Ahsan N, Lee DG, Alam I, Kim PJ, Lee JJ, Ahn YO, Renaut J (2008) Comparative proteomic study of arsenic-induced differentially expressed proteins in rice roots reveals glutathione plays a central role during. As Stress Proteomics 8:3561–3576

Ahsan N, Lee DG, Kim KH, Alam I, Lee SH, Lee KW, Lee BH (2010) Analysis of arsenic stress-induced differentially expressed proteins in rice leaves by two-dimensional gel electrophoresis coupled with mass spectrometry. Chemosphere 78:224–231

Ahsan N, Lee SH, Lee DG, Lee H, Lee SW, Bahk JD, Lee BH (2007) Physiological and protein profiles alternation of germinating rice seedlings exposed to acute cadmium toxicity. C R Biols 330:735–746

Asadi M, Saadatmand S, Khavari-Nejad RA, Ghasem-Nejad M, Fotokian MH (2002) Effect of Zinc (Zn) on some physiological characteristics of rice seedling. Ind J Fund Appl Life Sci 2:89–96

Asgher M, Khan MIR, Anjum NA, Khan NA (2015) Minimising toxicity of cadmium in plants—role of plant growth regulators. Protoplasma 252:99–413

Ashraf M, Foolad M (2007) Roles of glycine betaine and proline in improving plant abiotic stress resistance. Environ Exp Bot 59:206–216

Batool R, Hameed M, Ashraf M, Ahmad MSA, Fatima S (2015) Physio-Anatomical Responses of Plants to Heavy Metals. In Phytoremediation for Green Energy. Springer Netherlands 79–96

Beyersmann D, Hartwig A (2008) Carcinogenic metal compounds: recent insight into molecular and cellular mechanisms. Arch Toxicol 82:493

Chakrabarty D, Trivedi PK, Misra P, Tiwari M, Shri M, Shukla D, Tripathi RD (2009) Comparative transcriptome analysis of arsenate and arsenite stresses in rice seedlings. Chemosphere 74:688–702

Chan WF, Li H, Wu FY, Wu SC, Wong MH (2013) Arsenic uptake in upland rice inoculated with a combination or single arbuscular mycorrhizal fungi. J Hazard Mater 262:1116–1122

Chang YC, Chao YY, Kao CH (2012) The role of iron in stress response to cadmium in rice seedlings. Crop Environ Bio 8:175–183

Chatterjee C, Dube BK, Sinha P, Srivastava P (2004) Detrimental effects of lead phytotoxicity on growth, yield, and metabolism of rice. Commun Soil Sci Plant Anal 35:255–265

Choppala G, Saifullah Bolan N, Bibi S, Iqbal M, Rengel Z, Ok YS (2014) Cellular mechanisms in higher plants governing tolerance to cadmium toxicity. Cr Rev Plant Sci 33:374–391

Choudhary SP, Yu JQ, Yamaguchi-Shinozaki K, Shinozaki K, Tran LSP (2012) Benefits of brassinosteroid crosstalk. Trends Plant Sci 17:594–605

Choudhury B, Chowdhury S, Biswas AK (2011) Regulation of growth and metabolism in rice (*Oryza sativa* L.) by arsenic and its possible reversal by phosphate. J Plant Interact 6:15–24

Chu Q, Watanabe T, Sha Z, Osaki M, Shinano T (2015) Interactions between Cs, Sr, and other nutrients and trace element accumulation in *Amaranthus* shoot in response to variety effect. J Agric Food Chem 63:2355–2363

DalCorso G, Farinati S, Furini A (2010) Regulatory networks of cadmium stress in plants. Plant Plant Signal Behave 5:663–667

Deng D, Wu SC, Wu FY, Deng H, Wong MH (2010) Effects of root anatomy and Fe plaque on arsenic uptake by rice seedlings grown in solution culture. Environ Pollut 158:2589–2595

Dias MC, Monteiro C, Moutinho-Pereira J, Correia C, Gonçalves B, Santos C (2013) Cadmium toxicity affects photosynthesis and plant growth at different levels. Acta Physiol Plant 35:1281–1289

Dong J, Mao WH, Zhang GP, Wu FB, Cai Y (2007) Root excretion and plant tolerance to cadmium toxicity-a review. Plant Soil Envirn 53:193

Doni F, Isahak A, Zain CRCM, Yusoff WMW (2014) Physiological and growth response of rice plants (*Oryza sativa* L.) to Trichoderma spp. inoculants. AMB Express 4:45

Duan GL, Hu Y, Liu WJ, Kneer R, Zhao FJ, Zhu YG (2011) Evidence for a role of phytochelatins in regulating arsenic accumulation in rice grain. Environ Expe Botany 71:416–421

Duan J, Cai W (2012) OsLEA3-2, an abiotic stress induced gene of rice plays a key role in salt and drought tolerance. PLoS One 7:e45117

Dubey RS, Pessarakli M (2002) Physiological mechanisms of nitrogen absorption and assimilation in plants under stressful conditions. Handbook of Plant and Crop Physiology 605–625

Dubey S, Shri M, Misra P, Lakhwani D, Bag SK, Asif MH, Chakrabarty D (2014) Heavy metals induce oxidative stress and genome-wide modulation in transcriptome of rice root. Funct Integr Genomic 14:401–417

Eshagberi GO (2012) Toxic Effects of Heavy Metals on Crop Plants. Multidisciplinary J Empir Res 10

Fangmin C, Ningchun Z, Haiming X, Yi L, Wenfang Z, Zhiwei Z, Mingxue C (2006) Cadmium and lead contamination in japonica rice grains and its variation among the different locations in southeast China. Sci Total Environ 359:156–166

Fariduddin Q, Yusuf M, Ahmad I, Ahmad A (2014) Brassinosteroids and their role in response of plants to abiotic stresses. Biol Plantarum 58:9–17

Feng X, Han L, Chao D, Liu Y, Zhang Y, Wang R, Huang B (2017) Ionomic and transcriptomic analysis provides new insight into the distribution and transport of cadmium and arsenic in rice. J Hazard 331:246–256

Fleck AT, Mattusch J, Schenk MK (2013) Silicon decreases the arsenic level in rice grain by limiting arsenite transport. J Plant Nutr Soil Sc 176:785–794

Gao JP, Chao DY, Lin HX (2008) Toward understanding molecular mechanisms of abiotic stress responses in rice. Rice 1:36–51

Gao L, Chang J, Chen R, Li H, Lu H, Tao L, Xiong J (2016) Comparison on cellular mechanisms of iron and cadmium accumulation in rice: prospects for cultivating Fe-rich but Cd-free rice. Rice 9:39

Gomes MP, Marques TCLLD, e Melo S, Nogueira MDOG, Castro EMD, Soares ÂM (2011) Ecophysiological and anatomical changes due to uptake and accumulation of heavy metal in *Brachiaria decumbens*. Sci Agric 68:566–573

Guerinot ML, Yi Y (1994) Iron: nutritious, noxious, and not readily available. Plant Physiol 104:815

Guo B, Liang YC, Zhu YG, Zhao FJ (2007) Role of salicylic acid in alleviating oxidative damage in rice roots (*Oryza sativa*) subjected to cadmium stress. Environ Pollut147:743–749

Guo W, Zhang J, Teng M, Wang LH (2009) Arsenic uptake is suppressed in a rice mutant defective in silicon uptake. J Plant Nutr Soil Sc 172:867–874

Gupta DK, Rai UN, Tripathi RD, Inouhe M (2002) Impacts of fly-ash on soil and plant responses. J Plant Res 115:401–409

Haiyan WANG, Huang J, Qingfu YE, Dianxing WU, Ziyuan CHEN (2009) Modified accumulation of selected heavy metals in Bt transgenic rice. J Environ Sci 21:1607–1612

Hajduch M, Rakwal R, Agrawal GK, Yonekura M, Pretova A (2001) High-resolution two-dimensional electrophoresis separation of proteins from metal-stressed rice (*Oryza sativa* L.) leaves: Drastic reductions/fragmentation of ribulose-1, 5-bisphosphate carboxylase/oxygenase and induction of stress-related proteins. Electrophoresis 22:2824–2831

He J, Ren Y, Chen X, Chen H (2014) Protective roles of nitric oxide on seed germination and seedling growth of rice (*Oryza sativa* L.) under cadmium stress. Ecotox and Environ Safe 108:114–119

He J, Ren Y, Chen X, Chen H (2014) Protective roles of nitric oxide on seed germination and seedling growth of rice (*Oryza sativa* L.) under cadmium stress. Ecotoxicol Environ Safe 108:114–119

Hsu YT, Kao CH (2007) Heat shock-mediated H_2O_2 accumulation and protection against Cd toxicity in rice seedlings. Plant Soil 300:137–147

Hu P, Ouyang Y, Wu L, Shen L, Luo Y, Christie P (2015) Effects of water management on arsenic and cadmium speciation and accumulation in an upland rice cultivar. Ecotox and Environ Safe 27:225–231

Hu T, Zhu S, Tan L, Qi W, He S, Wang G (2016) Overexpression of OsLEA4 enhances drought, high salt and heavy metal stress tolerance in transgenic rice (*Oryza sativa* L.). Environ Exp Bot 123:68–77

Hu Y, Ge Y, Zhang C, Ju T, Cheng W (2009) Cadmium toxicity and translocation in rice seedlings are reduced by hydrogen peroxide pretreatment. Plant Growth Regul 59:51

Iqbal N, Masood A, Nazar R, Syeed S, Khan NA (2010) Photosynthesis, growth and antioxidant metabolism in mustard (*Brassica juncea* L.) cultivars differing in cadmium tolerance. Agr Sci China 9:519–527

Ishimaru Y, Suzuki M, Tsukamoto T, Suzuki K, Nakazono M, Kobayashi T, Nakanishi H (2006) Rice plants take up iron as an Fe^{3+}-phytosiderophore and as Fe^{2+}. Plant J 45:335–346

Jallad KN (2015) Heavy metal exposure from ingesting rice and its related potential hazardous health risks to humans. Environ Sci Pollut Res 22:15449–15458

Jamil, H, Theng LP, Jusoh K, Razali AM, Ali FB, Ismail BS (2011) Speciation of heavy metals in paddy soils from selected areas in Kedah and Penang, Malaysia. Afr J Biotechnol 10:13505–13513

Ji Y, Zhou, Y, Ma C, Feng Y, Hao Y, Rui Y, Xing B (2017) Jointed toxicity of TiO_2 NPs and Cd to rice seedlings: NPs alleviated Cd toxicity and Cd promoted NPs uptake. Plant Physiol Biochem 110:82–93

Jin M, Liu X, Wu L, Liu M (2015) An improved assimilation method with stress factors incorporated in the WOFOST model for the efficient assessment of heavy metal stress levels in rice. Int J Appl Earth Obs 41:118–129

Jonak C, Ökrész L, Bögre L, Hirt H (2002) Complexity, cross talk and integration of plant MAP kinase signalling. Curr Opin Plant Biol 5:415–424

Kanazawa S, Sano S, Koshiba T,Ushimaru T (2000) Changes in antioxidative enzymes in cucumber cotyledons during natural senescence: comparison with those during dark-induced senescence. Physiol Plantarum 109:211–216

Kao CH (2014) Cadmium Stress in Rice Plants: Influence of Essential Elements

Khush GS (2005) What it will take to feed 5.0 billion rice consumers in 2030. Plant Mol Boil 59:1–6

Kim YH, Khan AL, Kim DH, Lee SY, Kim KM, Waqas M, Lee IJ (2014) Silicon mitigates heavy metal stress by regulating P-type heavy metal ATPases, *Oryza sativa* Low silicon genes, and endogenous phytohormones. BMC Plant Boil 14:13

Kim YK, Lee MY (2009) Proteomic analysis of differentially expressed proteins of rice in response to cadmium. J Korean Soc Appl Bi52:428–436

Komatsu S (2008) Research on the rice proteome: the contribution of proteomics technology in the creation of abiotic stress-tolerant plants. Rice1:154–165

Kumar A, Dixit G, Singh AP, Dwivedi S, Srivastava S, Mishra K, Tripathi RD (2016) Selenate mitigates arsenite toxicity in rice (*Oryza sativa* L.) by reducing arsenic uptake and ameliorates amino acid content and thiol metabolism. Ecotox Environ Safe 133:350–359

Kumar A, Dixit G, Singh AP, Dwivedi S, Srivastava S, Mishra K, Tripathi RD (2016) Selenate mitigates arsenite toxicity in rice (*Oryza sativa* L.) by reducing arsenic uptake and ameliorates amino acid content and thiol metabolism. Ecotox Environ Safe 133:350–359

Kumar A., Singh RP, Singh PK, Awasthi S, Chakrabarty D, Trivedi PK, Tripathi RD (2014) Selenium ameliorates arsenic induced oxidative stress through modulation of antioxidant enzymes and thiols in rice (*Oryza sativa* L.). Ecotoxicology 23:1153–1163

Lang I, Wernitznig S (2011) Sequestration at the cell wall and plasma membrane facilitates zinc tolerance in the moss *Pohlia drummondii*. Environ Exp Bot 74:186–193

Lee HJ, Abdula SE, Jang DW, Park SH, Yoon UH, Jung YJ, Cho YG (2013) Overexpression of the glutamine synthetase gene modulates oxidative stress response in rice after exposure to cadmium stress. Plant Cell Rep 32:1521–1529

Lee K, Bae DW, Kim SH, Han HJ, Liu X, Park HC, Chung WS (2010) Comparative proteomic analysis of the short-term responses of rice roots and leaves to cadmium. J Plant Physiol1 67:161–168

Lemos Batista B, Nigar M, Mestrot A, Alves Rocha B, Barbosa Junior F, Price AH, Feldmann J (2014) Identification and quantification of phytochelatins in roots of rice to long-term exposure: evidence of individual role on arsenic accumulation and translocation. J Exp Bot 65:1467–1479

Li B, Quan-Wang C, Liu H, Li HX, Yang J, Song WP, Zeng M (2014) Effects of Cd^{2+} ions on root anatomical structure of four rice genotypes. J Env Biol 35:751

Li H, Luo N, Zhang LJ, Zhao HM, Li YW, Cai QY, Mo CH (2016) Do arbuscular mycorrhizal fungi affect cadmium uptake kinetics, subcellular distribution and chemical forms in rice?. Total Environ 571:1183–1190

Li N, Wang J, Song WY (2015) Arsenic uptake and translocation in plants. Plant Cell Physiol 57:4–13

Li X, Bu N, Li Y, Ma L, Xin S, Zhang L (2012) Growth, photosynthesis and antioxidant responses of endophyte infected and non-infected rice under lead stress conditions. J Hazard Mater 213:55–61

Li Y, Zhao J, Li YF, Xu X, Zhang B, Liu Y, Chai Z (2016) Comparative metalloproteomic approaches for the investigation proteins involved in the toxicity of inorganic and organic forms of mercury in rice (*Oryza sativa* L.) roots. Metallomics 8:663–671

Liang J, Zhou M, Zhou X, Jin Y, Xu M, Lin J (2013) JcLEA, a novel LEA-like protein from Jatropha curcas, confers a high level of tolerance to dehydration and salinity in *Arabidopsis* thaliana. PLoS One 8:e83056

Lin CC, Kao CH (2000) Effect of NaCl stress on H_2O_2 metabolism in rice leaves. Plant Growth Regul 30:151–155

Lin CY, Trinh NN, Fu SF, Hsiung YC, Chia LC, Lin CW, Huang HJ (2013) Comparison of early transcriptome responses to copper and cadmium in rice roots. Plant Mol Boil 81:507–522

Liu CH, Huang WD, Kao CH (2012) The decline in potassium concentration is associated with cadmium toxicity of rice seedlings. Acta Physiol Plant 34:495–502

Liu J, Leng X, Wang M, Zhu Z, Dai Q (2011) Iron plaque formation on roots of different rice cultivars and the relation with lead uptake. Ecotoxicol Environ Saf 74:1304–1309

Liu J, Ma J, He C, Li X, Zhang W, Xu F, Wang L (2013) Inhibition of cadmium ion uptake in rice (*Oryza sativa*) cells by a wall-bound form of silicon. New Phytol 200:691–699

Liu WJ, Wood BA, Raab A, McGrath SP, Zhao FJ, Feldmann J (2010) Complexation of arsenite with phytochelatins reduces arsenite efflux and translocation from roots to shoots in *Arabidopsis*. Plant Physiol 152:2211–2221

Lux A, Martinka M, Vaculík M, White PJ (2011) Root responses to cadmium in the rhizosphere: a review. J Exp Bot 62:21–37

Lyubenova L, Pongrac P, Vogel-Mikuš K, Mezek GK, Vavpetič P, Grlj N,Schröder P (2013) The fate of arsenic, cadmium and lead in *Typha latifolia*: a case study on the applicability of micro-PIXE in plant ionomics. J Hazard Mater 248:371–378

Ma J, Cai H, He C, Zhang W, Wang L (2015) A hemicellulose-bound form of silicon inhibits cadmium ion uptake in rice (*Oryza sativa*) cells. New Phytolt 206:1063–1074

Ma J, Lv C, Xu M, Chen G, Lv C, Gao Z (2016a) Photosynthesis performance, antioxidant enzymes, and ultrastructural analyses of rice seedlings under chromium stress. Environ Sci Pollut R 23:1768–1778

Ma J, Sheng H, Li X, Wang L (2016b) iTRAQ-based proteomic analysis reveals the mechanisms of silicon-mediated cadmium tolerance in rice (*Oryza sativa*) cells. Plant Physiol Biochem 104:71–80

Ma JF, Tamai K, Yamaji N, Mitani N, Konishi S, Katsuhara M, Yano M (2006) A silicon transporter in rice. Nature 440:688–691

Mahajan S, Tuteja N (2005) Cold, salinity and drought stresses: an overview. Arch Biochem Biophys 444:139–158

Maheshwari R, Dubey RS (2007) Nickel toxicity inhibits ribonuclease and protease activities in rice seedlings: protective effects of proline. Plant Growth Regul 51:231–243

Mahmood T, Islam KR, Muhammad S (2007) Toxic effects of heavy metals on early growth and tolerance of cereal crops. Pak J Bot 39:451

Makino A (2011) Photosynthesis, grain yield, and nitrogen utilization in rice and wheat. Plant Physiol 155:125–129

Matsumoto S, Kasuga J, Makino T, Arao T (2016) Evaluation of the effects of application of iron materials on the accumulation and speciation of arsenic in rice grain grown on uncontaminated soil with relatively high levels of arsenic. Environ Exper Bot 125:42–51

Meharg C, Meharg AA (2015) Silicon, the silver bullet for mitigating biotic and abiotic stress, and improving grain quality, in rice?. Environ Exp Bot 120:8–17

Mishra S, Jha AB, Dubey RS (2011) Arsenite treatment induces oxidative stress, upregulates antioxidant system, and causes phytochelatin synthesis in rice seedlings. Protoplasma 248:565–577

Mittler R, Vanderauwera S, Gollery M, Van Breusegem F (2004) Reactive oxygen gene network of plants. Trends Plant Sci 9:490–498

Moons A (2003a) Osgstu3 and osgtu4, encoding tau class glutathione S-transferases, are heavy metal-and hypoxic stress-induced and differentially salt stress-responsive in rice roots. FEBS Letters 553:427–432

Moons A (2003b) Ospdr9, which encodes a PDR-type ABC transporter, is induced by heavy metals, hypoxic stress and redox perturbations in rice roots 1. FEBS Letters 553:370–376

Msilini N, Zaghdoudi M, Govindachary S, Lachaâl M, Ouerghi Z, Carpentier R (2011) Inhibition of photosynthetic oxygen evolution and electron transfer from the quinone acceptor QA− to QB by iron deficiency. Photosynth Res 107:247–256

Norton GJ, Lou-Hing DE, Meharg AA, Price AH (2008) Rice–arsenate interactions in hydroponics: whole genome transcriptional analysis. J Exp Bot 59:2267–2276

Nwugo CC, Huerta AJ (2010) The effect of silicon on the leaf proteome of rice (*Oryza sativa* L.) plants under cadmium-stress. J Proteome Res 10:518–528

Ou X, Zhang Y, Xu C, Lin X, Zang Q, Zhuang T, Liu B (2012) Transgenerational inheritance of modified DNA methylation patterns and enhanced tolerance induced by heavy metal stress in rice (*Oryza sativa* L.). PloS One 7:e41143

Panda P, Nath S, Chanu TT, Sharma GD, Panda SK (2011) Cadmium stress-induced oxidative stress and role of nitric oxide in rice (*Oryza sativa* L.). Acta Physiol Plant 33:1737–1747

Pandey C, Gupta M (2015) Selenium and auxin mitigates arsenic stress in rice (*Oryza sativa* L.) by combining the role of stress indicators, modulators and genotoxicity assay. J Hazard Mat 287:384-391

Pant PP, Tripathi AK (2014) Impact of Heavy Metals on Morphological And Biochemical Parameters of *Shorea Robusta* Plant. Ekol 33:116–126

Parmar P, Kumari N, Sharma V (2013) Structural and functional alterations in photosynthetic apparatus of plants under cadmium stress. Botanical Studies 54:1

Peres da Rocha Oliveiros Marciano D, Toledo Ramos F, Neiva Alvim M, Ronaldo Magalhaes J, Giovanni Costa França M (2010) Nitric oxide reduces the stress effects of aluminum on the process of germination and early root growth of rice. J Plant Nutr Soil Sci 173:885–891

Pinto SDS, Souza AED, Oliva MA, Pereira EG (2016) Oxidative damage and photosynthetic impairment in tropical rice cultivars upon exposure to excess iron. Sci Agric 73:217–226

Piotrowska-Niczyporuk A, Bajguz A, Zambrzycka E, Godlewska-Żyłkiewicz B (2012) Phytohormones as regulators of heavy metal biosorption and toxicity in green alga *Chlorella vulgaris* (*Chlorophyceae*). Plant Physiol Biochem 52:52–65

Rahman MA, Hasegawa H, Rahman MM, Islam MN, Miah MM, Tasmen A (2007) Effect of arsenic on photosynthesis, growth and yield of five widely cultivated rice (*Oryza sativa* L.) varieties in Bangladesh. Chemosphere 67:1072–1079

Rai R, Agrawal M, Agrawal SB (2016) Impact of heavy metals on physiological processes of plants: with special reference to photosynthetic system. In Plant Responses to Xenobiotics. Springer, Singapore 127–140

Rebouillat J, Dievart A, Verdeil JL, Escoute J, Giese G, Breitler JC,Périn C (2008) Molecular genetics of rice root development. Rice 2:15–34

Ren JH, Sun HJ, Wang SF, Luo J, Ma LQ (2014) Interactive effects of mercury and arsenic on their uptake, speciation and toxicity in rice seedling. Chemosphere 117:737–744

Rizwan M, Ali S, Adrees M, Rizvi H, Zia-ur-Rehman M, Hannan F, Ok YS (2016) Cadmium stress in rice: toxic effects, tolerance mechanisms, and management: a critical review. Environ Sci Pollut R 1–21

Roychoudhury A, Basu S, Sengupta DN (2012) Antioxidants and stress-related metabolites in the seedlings of two indica rice varieties exposed to cadmium chloride toxicity. Acta Physiol Plant 34:835–847

Rucińska-Sobkowiak R (2016) Water relations in plants subjected to heavy metal stresses. Acta Physiol Plant 38:257

Safarzadeh S, Ronaghi A, Karimian N (2013) Effect of cadmium toxicity on micronutrient concentration, uptake and partitioning in seven rice cultivars. Arch Acker Pfl Boden 59:231–245

Salt DE, Baxter I, Lahner B (2008) Ionomics and the study of the plant ionome. Annu Rev Plant Biol 59:709–733

Sasaki A, Yamaji N, Ma JF (2014) Overexpression of OsHMA3 enhances Cd tolerance and expression of Zn transporter genes in rice. J Exp Bot 65:6013–6021

Schwab AP, He Y, Banks MK (2005) The influence of organic ligands on the retention of lead in soil. Chemosphere 61:856–866

Sebastian A, Prasad MNV (2015) Trace element management in rice. Agronomy 5:374–404

Seneviratne M, Rajakaruna N, Rizwan M, Madawala HMSP, Ok YS, Vithanage M (2017) Heavy metal-induced oxidative stress on seed germination and seedling development: a critical review. Environ Geochem Health 1–19

Shahid M, Dumat C, Khalid S, Niazi NK, Antunes PM (2016) Cadmium Bioavailability, Uptake, Toxicity and Detoxification in Soil-Plant System

Sharma I (2012) Arsenic induced oxidative stress in plants. Biologia 67:447–453

Sharma P, Dubey RS (2005) Modulation of nitrate reductase activity in rice seedlings under aluminium toxicity and water stress: role of osmolytes as enzyme protectant. J Plant Physiol 162:854–864

Sharma RK, Agrawal M (2005) Biological effects of heavy metals: an overview. J Environ Biol 26:301–313

Sharma SK, Goloubinoff P, Christen P (2008) Heavy metal ions are potent inhibitors of protein folding. Biochem Bioph Res Co 372:341–345

Sharma SK, Goloubinoff P, Christen P (2011) Non-native Proteins as Newly-Identified Targets of Heavy Metals and Metalloids. In Cellular Effects of Heavy Metals. Springer Netherlands 263–274

Shi X, Zhang C, Wang H, Zhang F, (2005) Effect of Si on the distribution of Cd in rice seedlings. Plant Soil 272:53–60

Shri M, Kumar S, Chakrabarty D, Trivedi PK, Mallick S, Misra P, Tuli R (2009) Effect of arsenic on growth, oxidative stress, and antioxidant system in rice seedlings. Ecotoxicol Environ Saf 72:1102–1110

Shu R, Wang Y, Zhong H (2016) Biochar amendment reduced methylmercury accumulation in rice plants. J Hazard Mater 313:1–8

Silva MLDS, Vitti GC, Trevizam AR (2014) Heavy metal toxicity in rice and soybean plants cultivated in contaminated soil. Revista Ceres 61:248–254

Singh P, Shah K (2014) Evidences for reduced metal-uptake and membrane injury upon application of nitric oxide donor in cadmium stressed rice seedlings. Plant Physiol Biochem 83:180–184

Singh VP, Tripathi DK, Kumar D, Chauhan DK (2011) Influence of exogenous silicon addition on aluminium tolerance in rice seedlings. Biol Trace Elem Res 144:1260–1274

Singh R, Jwa NS (2013) Understanding the responses of rice to environmental stress using proteomics. J Proteome Res 12:4652–4669

Slamet-Loedin IH, Johnson-Beebout SE, Impa S, Tsakirpaloglou N 2015 Enriching rice with Zn and Fe while minimizing Cd risk. Front Plant Sci 6:121

Srivastava RK, Pandey P, Rajpoot R, Rani A, Dubey RS (2014) Cadmium and lead interactive effects on oxidative stress and antioxidative responses in rice seedlings. Protoplasma 251:1047–1065

Sytar O, Kumar A, Latowski , Kuczynska P, Strzałka K, Prasad MNV (2013) Heavy metal-induced oxidative damage, defense reactions, and detoxification mechanisms in plants. Acta Physiol Plant 35:985–999

Takahashi R, Ishimaru Y, Shimo H, Ogo Y, Senoura T, Nishizawa NK (2012) The OsHMA2 transporter is involved in root-to-shoot translocation of Zn and Cd in rice. Plant Cell Environ 35:1948–1957

Tang W, Dang F, Evans D, Zhong H, Xiao L (2017) Understanding reduced inorganic mercury accumulation in rice following selenium application: Selenium application routes, speciation and doses. Chemosphere 169:369–376

Tena G, Asai T, Chiu WL, Sheen J (2001) Plant mitogen-activated protein kinase signaling cascades. Curr Opin Plant Biol 4:392–400

Trijatmiko KR, Dueñas C, Tsakirpaloglou N, Torrizo L, Arines FM, Adeva C, Rey J (2016) Biofortified indica rice attains iron and zinc nutrition dietary targets in the field. Scientific Reports 6:19792

Tripathi DK, Singh VP, Kumar D, Chauhan DK (2012a) Impact of exogenous silicon addition on chromium uptake, growth, mineral elements, oxidative stress, antioxidant capacity, and leaf and root structures in rice seedlings exposed to hexavalent chromium. Acta Physiol Plant 34:279–289

Tripathi DK, Singh VP, Kumar D, Chauhan DK (2012b) Rice seedlings under cadmium stress: effect of silicon on growth, cadmium uptake, oxidative stress, antioxidant capacity and root and leaf structures. Chem Ecol 28:281–291

Tripathi DK, Singh VP, Chauhan DK, Prasad SM, Dubey NK (2014) Role of macronutrients in plant growth and acclimation: recent advances and future prospective. InImprovement of Crops in the Era of Climatic Changes 197–216. Springer, New York, NY

Tseng TS, Tzeng SS, Yeh KW, Yeh CH, Chang FC, Chen YM, Lin CY (1993) The heat-shock response in rice seedlings: isolation and expression of cDNAs that encode class I low-molecular-weight heat-shock proteins. Plant Cell Physiol 341:65–168

Ueno D, Koyama E, Kono I, Ando T, Yano M, Ma JF (2009) Identification of a novel major quantitative trait locus controlling distribution of Cd between roots and shoots in rice. Plant Cell Physiol 50:2223–2233

Uga Y, Sugimoto K, Ogawa S, Rane J, Ishitani M, Hara N, Inoue H (2013) Control of root system architecture by DEEPER ROOTING 1 increases rice yield under drought conditions. Nat Genet 45:1097–1102

Upadhyay AK, Singh NK, Singh R, Rai UN (2016) Amelioration of arsenic toxicity in rice: Comparative effect of inoculation of *Chlorella vulgaris* and *Nannochloropsis* sp. on growth, biochemical changes and arsenic uptake. Ecotoxicol. Environ Saf 124:68–73

Verma S, Dubey RS, (2003) Lead toxicity induces lipid peroxidation and alters the activities of antioxidant enzymes in growing rice plants. Plant Sci 164:645–655

Vinocur B, Altman A (2005) Recent advances in engineering plant tolerance to abiotic stress: achievements and limitations. Curr Opin Biotech 16:123–132

Wada Y, Miyamoto K, Kusano T, Sano H (2004) Association between up-regulation of stress-responsive genes and hypomethylation of genomic DNA in tobacco plants. Mol Genet Genomics 271:658–666

Wang J, Fang Z, Cheng W, Yan X, Tsang PE, Zhao D (2016) Higher concentrations of nanoscale zero-valent iron (nZVI) in soil induced rice chlorosis due to inhibited active iron transportation. Environ Pollut 210:338–345

Wang X, Tam NFY, Fu S, Ametkhan A, Ouyang Y, Ye Z (2014) Selenium addition alters mercury uptake, bioavailability in the rhizosphere and root anatomy of rice (*Oryza sativa*). Ann Bot 114:271–278

Wang X, Yao H, Wong MH, Ye Z (2013) Dynamic changes in radial oxygen loss and iron plaque formation and their effects on Cd and As accumulation in rice (*Oryza sativa* L.). Environ Geochem Hlth 35:779–788

Wang Y, Jiang X, Li K, Wu M, Zhang R, Zhang L, Chen G (2014) Photosynthetic responses of *Oryza sativa* L. seedlings to cadmium stress: physiological, biochemical and ultrastructural analyses. Biometals 27:389–401

Wang ZQ, Li GZ, Gong QQ, Li GX, Zheng SJ (2015) OsTCTP, encoding a translationally controlled tumor protein, plays an important role in mercury tolerance in rice. BMC Plant Boil 15:123

Wani SH, Kumar V, Shriram V, Sah SK (2016) Phytohormones and their metabolic engineering for abiotic stress tolerance in crop plants. The Crop Journal 4:162–176

Wu C, Zou Q, Xue S, Mo J, Pan W, Lou L, Wong MH (2015) Effects of silicon (Si) on arsenic (As) accumulation and speciation in rice (*Oryza sativa* L.) genotypes with different radial oxygen loss (ROL). Chemosphere 138:447–453

Wu W, Cheng S (2014) Root genetic research, an opportunity and challenge to rice improvement. Field Crop Res 165:111–124

Wu Z, Zhang C, Yan J, Yue Q, Ge Y (2015) Effects of sulfur supply and hydrogen peroxide pretreatment on the responses by rice under cadmium stress. Plant Growth Regul 77:299–306

Wysocki R, Tamás MJ (2010) How *Saccharomyces cerevisiae* copes with toxic metals and metalloids. FEMS Microbiol Rev 34:925–951

Xu J, Yang L, Wang Y, Wang Z (2005) Advances in the study uptake and accumulation of heavy metal in rice ({\sl *Oryza sativa*}) and its mechanisms. Chinese Bulletin of Botany 22:614–622

Yadav SK (2010) Heavy metals toxicity in plants: an overview on the role of glutathione and phytochelatins in heavy metal stress tolerance of plants. S Afr J Bot 76:167–179

Yadavalli V, Neelam S, Rao AS, Reddy AR, Subramanyam R (2012) Differential degradation of photosystem I subunits under iron deficiency in rice. J Plant Physiol 169:753–759

Yang L, Ji J, Harris-Shultz KR, Wang H, Wang H, Abd-Allah EF, Hu X (2016) The dynamic changes of the plasma membrane proteins and the protective roles of nitric oxide in rice subjected to heavy metal cadmium stress. Front Plant Sci 7:190

Yang YY, Jung JY, Song WY, Suh HS, Lee Y (2000) Identification of rice varieties with high tolerance or sensitivity to lead and characterization of the mechanism of tolerance. Plant Physiol 124:1019–1026

Yeh CM, Chien PS, Huang HJ (2007) Distinct signalling pathways for induction of MAP kinase activities by cadmium and copper in rice roots. J Exp Bot 58:659–671

Yin B, Zhou L, Yin B, Chen L (2016) Effects of organic amendments on rice (*Oryza sativa* L.) growth and uptake of heavy metals in contaminated soil. J Soil Sediment 16:537–546

Yu C, Sun C, Shen C, Wang S, Liu F, Liu Y, Geisler M (2015) The auxin transporter, OsAUX1, is involved in primary root and root hair elongation and in Cd stress responses in rice (*Oryza sativa* L.). Plant J 83:818–830

Yu Z, Qiu W, Wang F, Lei M, Wang D, Song Z (2017) Effects of manganese oxide-modified biochar composites on arsenic speciation and accumulation in an indica rice (*Oryza sativa* L.) cultivar. Chemosphere 168:341–349

Yadav V, Arif N, Singh S, Srivastava PK, Sharma S, Tripathi DK, Dubey N, Chauhan DK (2016) Exogenous mineral regulation under heavy metal stress: advances and prospects. Biochem Pharmacol 5:2167–0501

Zeng LS, Liao M, Chen C, Huang CY (2007) Effects of lead contamination on soil enzymatic activities, microbial biomass, and rice physiological indices in soil–lead–rice (*Oryza sativa* L.) system. Ecotox Environ Safe 67:67–74

Zhang A, Bian R, Li L, Wang X, Zhao Y, Hussain Q, Pan G (2015) Enhanced rice production but greatly reduced carbon emission following biochar amendment in a metal-polluted rice paddy. Environ Sci Pollut Res 22:18977–18986

Zhang L, Chen Z, Zhu C (2012) Endogenous nitric oxide mediates alleviation of cadmium toxicity induced by calcium in rice seedlings. J Environ Sci 24:940–948

Zhao FJ, Ma JF, Meharg AA, McGrath SP (2009) Arsenic uptake and metabolism in plants. New Phytol 181:777–794

Zhao FY, Hu F, Zhang SY, Wang K, Zhang CR, Liu T (2013) MAPKs regulate root growth by influencing auxin signaling and cell cycle-related gene expression in cadmium-stressed rice. Environ Sci Pollut 20:5449–5460

Zheng R, Chen Z, Cai C, Tie B, Liu X, Reid BJ, Baltrėnaitė E (2015) Mitigating heavy metal accumulation into rice (*Oryza sativa* L.) using biochar amendment-a field experiment in Hunan, China. Environ Sci Pollut R 22:11097–11108

Zheng RL, Cai C, Liang JH, Huang Q, Chen Z, Huang YZ, Sun GX (2012) The effects of biochars from rice residue on the formation of iron plaque and the accumulation of Cd, Zn, Pb, As in rice (*Oryza sativa* L.) seedlings. Chemosphere 89:856–862

Zhou L, Wu L, Li Z, Yang B, Yin B, Luo Y, Christie P (2015) Influence of rapeseed cake on heavy metal uptake by a subsequent rice crop after phytoextraction using sedum plumbizincicola. Int J Phytoremediat 17:76–84