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Mercury toxicity, molecular response and tolerance in higher plants

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Abstract Mercury (Hg) contamination in soils has become a great concern as a result of its natural release and anthropogenic activities. This review presents broad aspects of our recent understanding of mercury contamination and toxicology in plants including source of Hg contamination, toxicology, tolerant regulation in plants, and minimization strategy. We first introduced the sources of mercury contamination in soils. Mercury exists in different forms, but ionic mercury (Hg^{2+}) is the predominant form in soils and readily absorbed by plants. The second issue to be discussed is the uptake, transport, and localization of Hg^{2+} in plants. Mercury accumulated in plants evokes severe phytotoxicity and impairs numerous metabolic processes including nutrient uptake, water status, and photosynthesis. The mechanisms of mercury-induced toxicology, molecular response and gene networks for regulating plant tolerance will be reviewed. In the case of Hg recent much progress has been made in profiling of transcriptome and more importantly, uncovering a group of small RNAs that potentially mediates plant tolerance to Hg. Several newly discovered signaling molecules such as nitric oxide and carbon monoxide have now been described as regulators of plant tolerance to Hg. A recently emerged strategy, namely selection and breeding of plant cultivars to minimize Hg (or other metals) accumulation will be discussed in the last part of the review.

Keywords Mercury · Plants · Toxicology · Tolerance · Small RNA · Gene expression · Molecular response

Introduction

Mercury contamination has become a global environment problem because millions of tons of mercury have been released to ecosystems due to anthropogenic activities. Since 1500, approximate one million tons of metallic mercury has been extracted from cinnabar and other ores (Hylander and Meili 2003). It has been estimated that, in 2000, the average mercury level in global arable lands was 39 kg km^{-2} (Han et al. 2002). Before 1900, mercury was released from the following sources, (1) it was applied as an amalgamation agent to extract silver and gold (e.g. the discovery of gold in California in 1847 that initiated the famous gold rushes in North America resulted in the widespread use of Hg in gold amalgamation); and (2) red mercury mines were explored for producing

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cinnabar and pigment (Hylander and Meili 2003). In the 20th century, due to the industrialization (e.g. chlor-alkali industry and coal burning), global mercury release increases remarkably (Sznopek and Goonan 2000; Kolker et al. 2006). In China, coal-fired power plants, metal smelters and other industries contribute approximately a quarter of the world annual total Hg emissions to the atmosphere (Larssen 2010; Wu et al. 2006). The atmospheric Hg, which undergoes oxidation reactions and deposits to the ground, increases the abundance of Hg in soils and waters (Lindberg et al. 2007). Additionally, considerable amounts of mercury introduced into agricultural soils in the forms of mercury-containing compounds such as fertilizers, pesticides, lime, manures, and soil amendments contribute a great deal to mercury contamination (Han et al. 2002). Mercury in soil exists in many forms, including the elemental (Hg^0), ionic (Hg^{2+}), methyl (MeHg), hydroxide ($Hg(OH)_2$), and sulfide (HgS) forms, but Hg^{2+} is a predominant and bioavailable form for plants (Heaton et al. 2005; Han et al. 2006). Recent study has indicated that Hg-contaminated wastewater discharged from a factory, located at Yangtze River Delta region of China, led to considerable accumulation of Hg in both soils and crops (Huang et al. 2011). Therefore, it is of great importance to investigate toxicological process and adaptive mechanisms to minimize Hg accumulation in crops.

Uptake, transport, and localization of Hg in plants

Hg is readily taken up by plant roots and dominantly accumulated in roots. Usually, some of Hg remained in roots can be translocated to the above-ground and detected in leaves, flowers and other development tissues (Sierra et al. 2009). In white lupin, there is a short and long-term transport system for Hg uptake and translocation (Esteban et al. 2008), suggesting there are transport systems for Hg influx to plant cells. Hg import into root cells is possibly through Fe, Cu, or Zn transporters/channels (Patra and Sharma 2000; Esteban et al. 2008). These transport systems usually have broad substrates (Clemens 2006). Hg uptake by plants is also affected by other factors in soils. For instance, the presence of arsenate significantly promoted the accumulation of Hg^{2+} in the root of rice (Du et al. 2005). This may be the result that the absorption of arsenate increased the negative charge on root surface, and thereby enhanced the adsorption of Hg on the root surface.

Most of accumulated Hg in plants remains in roots, and only a small proportion can be translocated to shoots (Wang 2004). For Hg trapped in roots, approximate 80 % of it is bound to cell wall (Wang and Greger 2004). This may be possibly because (1): Hg ion is easy to interact with anionic compounds (e.g. carbonate, sulfate, and phosphate) and form insoluble precipitates, which limit symplastic mobility of Hg^{2+} and (2) Hg ion bound to root cell walls has high cationic exchange capacity (Chen et al. 2009b). For long distance transport of Hg from roots to shoots, xylem-uploading process is indispensible. Some metal transport is active, whereas others are positive. Cd translocation is an active process in hyperaccumulating ecotype *Sedum alfredii*, where the symplastic pathway contributes greatly to Cd uptake, xylem loading, and translocation from roots to shoots (Lu et al. 2009).

In addition to Hg uptake from roots, the aerial part of plants, particularly leaf is another important way for accumulation of Hg (Ericksen and Gustin 2004; Ericksen et al. 2003; Millhollen et al. 2006a; Fay and Gustin 2007), due to the industrial emission of Hg to the air and microorganism-mediated Hg emission from soils (Lindberg et al. 2007). In a field study, the above ground tissues of maize and wheat were exposed to an open top chamber filled with Hg-contaminated air for an entire growing season; Hg concentrations in foliages were closely correlated to the air but not related to the soil Hg concentrations, indicating that the air Hg was the major source of Hg accumulated in crop foliages (Niu et al. 2011). Linear correlations ($R^2 = 0.64$–0.98) between foliar Hg concentrations and air Hg concentrations have been established in ryegrass and leafy vegetables (De Temmerman et al. 2007; De Temmerman et al. 2009). It is shown that the high concentrations of Hg in bottom leaves of *Rudbeckia hirta* were attributed to the Hg emission from soils (Millhollen et al. 2006a, b). Hg exchange between foliar and surrounding air is a dynamic process. The net deposition rates of Hg on leaves increased with the atmospheric Hg concentrations (Ericksen and Gustin 2004). The mechanisms of how Hg enters into leaves remains elusive, but stomata may be responsible for the uptake of atmosphere Hg by leaves through gas exchange.

Hg-induced oxidative stress is the best representative feature of Hg phytotoxicity

Hg-induced growth stunt has been demonstrated extensively in wheat (Ge et al. 2009), maize (Rellán-Álvarez et al. 2006), tomato (Cho and Park 2000), cucumber (Cargnelutti et al. 2006), alfalfa (Zhou et al. 2007; Zhou et al. 2008b), Indian mustard (Shiyab et al. 2009a), fern (Chen et al. 2009a), and other plants (Israr et al. 2006; Gao et al. 2010; Costa et al. 2011). The growth inhibitory effect of Hg on plants has been directly linked to the unltrastructural damage. Analysis with scanning electron microscopy (SEM) shows that plant exposure to Hg resulted in loss of cell shape, decrease in intercellular spaces, and vascular abnormality in leaves of Boston fern (*Nephrolepis exaltata*) and Indian mustard (*Brassica juncea*) (Chen et al. 2009a; Shiyab et al. 2009a). Hg treatment also reduced the amount of chlorophyll and resulted in breakdown of thylakoid. Furthermore, Hg stress inhibited the activity of NADPH: protochlorophyllide oxidoreductase (POR), which is responsible for the biosynthesis of chlorophyll (Lenti et al. 2002).

Hg stress significantly induced the generation of reactive oxygen species (ROS) (Meng et al. 2011). Superoxide anion radical ($O_2^{\bullet -}$) and hydrogen peroxide (H_2O_2) are the two important ROS species in plants under abiotic stress (Gill and Tuteja 2010), both of which could be visually detected in vivo by using nitro blue tetrazolium (NBT) and 3,3-diaminobenzidine (DAB), respectively (Zhou et al. 2008b). Hg induced the accumulation of $O_2^{\bullet -}$and H_2O_2 in the leaves of alfalfa (*Medicago sativa*) in a dose-dependent manner. Under abiotic stress, $O_2^{\bullet -}$ is the early-responding ROS species. Generation of $O_2^{\bullet -}$ may trigger the formation of more active ROS like $HO^{\bullet}$, $^1O_2$, and H_2O_2, each of which may cause peroxidation to macromolecules such as proteins and lipids (Gill and Tuteja 2010). Hg-induced generation of ROS is closely linked to oxidative damage as expressed as lipid peroxidation and loss of membrane integrity (Zhou et al. 2007; Meng et al. 2011). The sensitive histochemical-based detection of Hg-triggered accumulation of ROS and oxidative injury can be used as biomarkers to indicate the toxicity in plants. In addition to Indian mustard and *M. sativa*, there are many other plant species that have been reported to response to Hg stress and display oxidative injury (Ali et al. 2000; Cargnelutti et al. 2006; Chen et al. 2009a; Cho and Park 2000; Israr et al. 2006; Ortega-Villasante et al. 2007; Rellán-Álvarez et al. 2006; Zhou et al. 2007; Zhou et al. 2008b; Shiyab et al. 2009b; Wang et al. 2009). However, the mechanisms of how Hg evokes oxidative responses are not fully understood.

Molecular response to Hg

Genome-wide transcriptome analysis has become a powerful tool to identify a set of genes that are specifically regulated by heavy metals (Becher et al. 2004; Weber et al. 2004; Herbette et al. 2006; van de Mortel et al. 2008; Gorfer et al. 2009; Yamaguchi et al. 2010; Ding et al. 2011). Using suppression subtractive hybridization (SSH), six genes (*PsSAMT*, *PsI2′H*, *PsNDA*, *PsAPSR*, *PsPOD*, *PsHMIP6B*) were identified and strongly regulated by Hg in roots of pea (*Pisum sativum*) (Sävenstrand and Strid 2004). These genes, along with their transcripts are involved in salicylic acid (SA) biological defense system, biosynthetic pathway of isoflavonoids, antioxidant reactions, sulphur metabolism, and cell wall rigidity. Heidenreich et al. (2001) profiled the transcriptome of *Arabidopsis thaliana* exposed to Hg^{2+} and found Hg-induced genes encoding proteins involved in chlorophyll synthesis, cell wall metabolism, P450-mediated biosynthesis of secondary metabolites. Notably, some genes induced by Hg are also induced by other heavy metals (Yamaguchi et al. 2010). Two full-length cDNAs coding for a putative metallothionein type 2 protein (*SdMT2*) and an auxin responsive protein (*SdARP*) were identified from heavy metal hyperaccumulator *Sesbania drummondii* under Hg exposure; the up-regulated expression of *SdARP* may contribute to the survival of *Sesbania* plants with Hg, whereas *SdMT2* is likely to be involved in alleviation of Hg toxicity (Venkatachalam et al. 2009). In addition, several other genes responsible for Hg tolerance or accumulation have been identified (Rugh et al. 1998; Hsieh et al. 2009; Ruiz et al. 2011; Shen et al. 2011; Wei et al. 2011).

Regulation of gene expression can be also achieved at post-transcriptional and translational levels. Recently, the post-transcriptional regulation of genes by a group of microRNAs (miRNAs) represents a newly discovered mechanism for plant development and response to environmental stresses (Jones-Rhoades et al. 2006; Phillips et al. 2007). miRNAs are processed from single-stranded RNA precursors capable of forming imperfectly complementary hairpin structures by the RNase III enzyme DICER-LIKE1 (DCL1) or DCL4. They are known to base-pair their target mRNAs to repress their translation or induce their degradation in organisms (Bartel 2004; Li and Mao 2007). A set of miRNAs in response to Hg stress was first identified from *M. truncatula* (Zhou et al. 2008a) and *B. napus* (Xie et al. 2007) using bioinformatic prediction and RT-PCR. With the development of the high-throughput sequencing technology, more novel miRNAs in response to heavy metals have been discovered. More recently, a deep sequencing approach developed by Solexa (Illumina Inc.) has been adopted to investigate global expression and complexity of miRNAs and their targets from *M. truncatula* under Hg (Zhou et al. 2012a) and Cd (Zhou et al. 2012b) exposure. Two small RNA libraries and two degradome libraries were constructed from Hg-treated and Hg-free seedlings of *M. truncatula*, respectively. For miRNAs, each library generated 18.5–18.6 million short sequences, resulting in 10.2–10.8 million clean reads. From this study, at least 52 novel miRNAs with ~21 nucleotides were identified from the *M. truncatula* genome. Statistical analysis on transcript abundance of the new candidate miRNAs revealed that most of them were differentially regulated by the heavy metal mercury Hg, with 12 miRNAs being specifically induced by Hg exposure. Additionally, they identified 201 individual miRNAs representing 63 known *M. truncatula* miRNA families, including 12 new conserved and one non-conserved miRNAs that have not been described before.

In addition, 130 targets for 58 known (37 conserved and 21 non-conserved) miRNA families and 37 targets for 18 new *M. truncatula*-specific candidate miRNA families were identified by high-throughput degradome sequencing (Zhou et al. 2012a). Most of miRNAs target genes coding for tolerance proteins or enzymes. For instance, miR2681 targets several transcripts coding TIR-NBS-LRR disease resistance proteins. A salt tolerance protein (TC114805) was identified as the target of miR2708. Notably, miR2687 targets a gene coding xyloglucan endotransglucosylase/hydrolase (XTH), which is recognized as a cell wall-modifying enzyme, participates in cell wall development and confers plant tolerance to abiotic stresses. These results indicate that Hg is able to alter significantly genes expression in Hg-treated plants and the Hg-induced gene regulatory frameworks will contribute a great deal to our understanding of the molecular mechanism for plant tolerance to Hg stress.

A group of signaling molecules are involved in plant response to Hg stress

Nitric oxide

Recently, several signaling molecules such as nitric oxide (NO) have been demonstrated to involve the regulation of Hg-induced oxidative stress and plant tolerance to Hg. While production of H_2O_2, one of the typical species of oxidants, is triggered by heavy metals in plants, NO is shown to depress the generation of H_2O_2 and alleviate phytotoxicity by enhancing antioxidative capability (Wang and Yang 2005). Both NO and H_2O_2 may act as important signaling components in plants response to heavy metal stress (Hsu and Kao 2004; Mazid et al. 2011). Exogenous application of sodium nitroprusside (SNP), an NO donor, was shown to reduce H_2O_2 accumulation in tomato seedlings and ameliorate heavy metals-induced toxicity by modulating activities of the antioxidant enzymes superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APX) (Wang et al., 2010). Pre-treatment with SNP stimulated root elongation of *Cassia tora* L. under aluminum (Al) stress by inhibiting the activity of lipoxygenase (LOX) that catalyzes the peroxidation of unsaturated fatty acids to produce ROS, thus reducing Al-induced oxidative injury; the protective effect of SNP on Al toxicity could be reversed by administrating NO scavenger cPTIO [2-(4-carboxy-2-phenyl)-4,4,5,5-tetramethylinidazoline-1-oxyl-3-oxide], suggesting that SNP-released NO is able to protect *Cassia tora* from Al toxicity (Wang and Yang 2005). In wheat, treatment with SNP reduced H_2O_2 accumulation and attenuated Cd^{2+}-induced root stunt (Singh et al. 2008) and Cu^{2+}-induced block seed germination (Hu et al. 2007). Singh et al. (2009) has demonstrated that exogenous NO provided resistance of rice to As-toxicity and As-induced oxidative stress by reducing ROS accumulation.

Heavy metals can regulate the generation of endogenous NO (Bartha et al. 2005), which is closely associated with the intrinsically physiological process in plants. Zhang et al. (2008) reported that endogenous

NO generated was positively associated with the proline level in Cu-treated algae. Pre-treatment with SNP was able to stimulate the activity of Δ-pyroline-5-carboxylate synthetase (P5CS), the key enzyme of proline biosynthesis and up-regulate the expression of *P5CS* in Cu-stressed algae. But the effect could be blocked by cPTIO, suggesting that NO is playing a role in proline metabolism under heavy metal stress.

In plants, nitrate reductase (NR) and nitric oxide synthase (NOS) have been proposed as two enzymatic systems responsible for NO production, and the activity of NOS had been detected, but the *NOS* gene has not been identified from plants (Gas et al. 2009; Neill et al. 2008). De Michele et al. (2009) reported that NOS-dependent NO production was actually required and acted upstream of H_2O_2 for Cd-induced programmed cell death (PCD) in *Arabidopsis*. Similarly, PCD induced by NOS-dependent NO production in root tips exposed to excess Zn is favorable for *Solanum nigrum* seedlings response to long-term Zn toxicity by modulating root system architecture and subsequent adaptation to Zn stress (Xu et al. 2010). Nutritional disturbance by endogenous NO affects remarkably the heavy metal-induced toxicity in plants. NOS-dependent NO production contributes to Cd toxicity by favoring Cd^{2+} versus Ca^{2+} uptake and initiating a cellular pathway resembling those activated upon iron deprivation in *A. thaliana* (Besson-Bard et al. 2009). However, the depression of NO production was also observed in plant cells under heavy metal stress. The reduced endogenous NO concentrations resulting from inhibition of NOS activity could underpin Al-induced arrest of root elongation in *Hibiscus moscheutos* (Tian et al. 2007). Xiong et al. (2009b) demonstrated that Cd decreased crown root number by inhibiting NOS activity, but not NR activity, and thus redued endogenous NO content in rice seedlings. Treatment with Ca^{2+} prevented the depression of NOS-dependent NO production in leaves of Cd-treated pea (*Pisum sativum*), suggesting that Cd-induced decrease in NO levels resulted from Ca^{2+} deprivation. Further investigation suggested that H_2O_2 accumulation due to the decrease in Ca^{2+} concentration induced the biosynthesis of ethylene (ET) and activated the ET-mediated defensive signaling cassette (Rodríguez-Serrano et al. 2009). Furthermore, NO is involved in alleviation of heavy metals-induced toxicity by directly regulating accumulation and translocation of heavy metals in plants. Application of SNP was able to protect *B. napus* from nickel (Ni) stress by reducing considerably root-to-shoot translocation of Ni (Kazemi et al. 2010). The inhibitory effect of NO on heavy metal accumulation in plants may be closely related to the modification of cell wall, because exogenous application of NO increased pectin and hemicelluloses content in cell wall and thus partially trapped Cd in rice roots and resulted in the decrease in Cd accumulation in soluble fraction of rice leaves and roots (Xiong et al. 2009a). However, how NO is signaling the molecular process remains elusive.

Salicylic acid

Hg-induced generation of H_2O_2 has been proposed as an event of oxidative stress (Cho and Park 2000; Zhou et al. 2007, 2008b). Eexcess H_2O_2 may be toxic to plants (Gill and Tuteja 2010). However, a moderate level of H_2O_2 generated can be considered as signals activating various genes for oxidative or antioxidative responses to external environmental changes (Miller et al., 2008). Recent studies have shown that salicylic acid (SA) as a well known signaling molecule is involved in both local defense reactions and induction of systemic resistance to pathogen attack, in which SA interacts with H_2O_2 to co-regulate resistant mechanisms (Vlot et al. 2009). Interestingly, SA and H_2O_2 have a cross-talk that is involved in the regulation of plant tolerance to heavy metals (Metwally et al. 2003; Choudhury and Panda 2004; Freeman et al. 2005; Guo et al. 2007). In alfalfa, SA depressed the generation of H_2O_2 in Hg-treated roots by balancing H_2O_2 generator (NADH oxidase) and H_2O_2 scavengers (antioxidant defense systems, e.g. enzymatic and no-enzymatic components) (Zhou et al. 2009). The increased formation of H_2O_2 due to stimulated activity of NADH oxidase is required for lignification of cell wall (Mittler 2002). This may decreases cell wall extensibility and hampers the uptake of toxic metals (Xue et al. 2008). Al-induced exudation of organic acids from roots has been proposed as a mechanism for Al tolerance in plants. Al exposure induced increase in endogenous free-SA and conjugated SA in soybean (*Glycine max*) roots. Exogenous application of SA significantly enhanced citrate secretion from Al-treated roots of *Glycine max* and treatment with paclobutrazol, an inhibitor of SA biosynthesis, decreased the Al-induced enhancement of endogenous free SA and citrate exudation (Liu et al. 2012). In *Cassia tora*, increased citrate efflux due to the SA treatment was associated with decreased inhibition of root growth and Al content in root tips (Yang et al. 2003). These data indicate that heavy metals can induce endogenous SA under the stress, and increased SA abundance in turn regulates plant tolerance to the heavy metals.

Carbon monoxide

Carbon monoxide (CO) is a gaseous molecule generated in organisms from prokaryotes to mammals and serves as an essential intrinsic signaling component regulating a variety of physiological processes (Boczkowski et al. 2006; Naito 2008). Recent studies show that CO plays a pivotal role in the regulation of root branching (Guo et al. 2009, 2008), iron deficiency (Kong et al. 2010), and copper toxicity (Zheng et al. 2011). More interestingly, CO can serve as an antioxidant against Hg-induced oxidative stress (Meng et al. 2011). CO is mainly produced by heme oxygenase (HO, EC 1.14.99.3), which is highly conserved within plant species. Four *HO* genes (*HO-1*, *HO-2*, *HO-3*, *HO-4*) from *Arabidopsis* have been identified (Davis et al. 2001; Terry et al. 2002; Emborg et al. 2006; Gisk et al. 2010). Among them, *HO-1* is well investigated. Expression of *HO-1* was significantly up-regulated in green alga (*Chlamydomonas reinhardtii*) under Hg stress (Elbaz et al. 2010). Also, exposure of Hg remarkably stimulated the expression of *HO-1* in the roots of *B. juncea* (Indian mustard) and *B. napus* in a time- and dose-dependent manner (Meng et al. 2011; Shen et al. 2011). More importantly, transgenic *B. napus* and *C. reinhardtii* over-expressing HO-1 produced more intracellular CO, and as a consequence conferred the tolerance of plants to Hg toxicity by decreasing ROS and Hg accumulation and increasing biomass (Shen et al. 2011; Wei et al. 2011).

Minimization of Hg accumulation

Phytoremediation refers to the direct use of living plants for in situ removal of contaminated soils without disturbance of soil itself (USEPA 1999). It has gained considerable attention over the last decades, because it is a cost-effective "green revolution" in the field of innovative clean-up technologies. Despite the development of diverse remediation techniques (including phytoremediation) that are currently applied to reducing risks to human health, there are still limitations for these approaches used on a large scale. Recently, an alternative way has been proposed to limit heavy metals entering the food chain without treating soils. This concept concerns the technique to minimize heavy metal accumulation in organisms. Based on the criteria, the genetically selected and modified plants should be those with the capability of increasing accumulation of desirable trace elements and decreasing potentially harmful trace elements (e.g. toxic heavy metals) (Grant et al. 2008, Liu et al. 2009, 2010). This approach emphasizes very low accumulation of toxic metals in growth tissues, particularly in crop edible parts (e.g. seed and fruit) when crops are grown in heavy metal-contaminated soils.

Uptake, translocation, and accumulation of heavy metals in plants are mainly controlled by genetic traits (Grennan 2009; Verbruggen et al. 2009). The variation of Cd concentrations in grains partially depends on the ability of plants to control movement of Cd to seeds (Tanaka et al. 2007). Genetic differences occurred in translocation of Cd from shoots to grains (Arao and Ishikawa 2006). Wide variations in the concentration of Cd among cultivars have been demonstrated in many species (Grant et al. 2008). Recently, 43 cultivars of paddy rice (including 20 normal and 23 hybrid cultivars) were reported for their abilities to accumulate Cd in grains; Cd accumulation in rice grain is genotype-dependent, suggesting that selection of low-Cd cultivars is possible (Yu et al. 2006). The low-Cd trait also has been best presented in Chinese cabbage, of which three cultivars (Lvxing 70, New-Beijing 3, and Fengyuanxin 3) were identified as candidates to be used in moderate Cd-contaminated soils (Liu et al. 2009, 2010). The first commercially successful low-Cd cultivar of durum wheat (Strongfield) was released in 2004 and is now sown on >25 % of the durum area in Canada (Clarke et al. 2006). This confirms the feasibility of selection and breeding of plant cultivars with low accumulation of heavy metals. In order to breed low metal-containing cultivars precisely, it is necessary to learn the inheritance of genetic characters of the cultivars from variant genotypes, and to develop a breeding strategy to combine low-heavy metal traits with high yields, disease resistance and other quality traits in modern cultivars (Grant et al. 2008).

With the development of molecular biotechnology in crop breeding, gene manipulation is considered as a powerful tool to improve the efficiency of selecting and breeding low metal-containing cultivars. Identification of functional genes to minimize toxic metal accumulation is possible. Recent studies have shown that plant heme oxygenases-1 (HO-1) plays an important role in regulating plant growth and response to environmental stresses (Shekhawat and Verma 2010). We recently demonstrated that transgenic rapeseeds (*B. napus*) overexpressing *HO-1* display significantly lower Hg concentrations in seedlings compared to the untransformed plants under Hg exposure (Shen et al. 2011). Also, transgenic green algae (*C. reinhardtii*) overexpressing *HO-1* show remarkable increase in the cell number over the wild type but accumulated less Hg (Wei et al. 2011). These studies provide a new example for molecular modification designed for plants that do not accumulate or accumulate less toxic trace metals growing on heavy metal-contaminated soils.

Conclusions

Due to its emission into environments, the toxic mercury has become globally environmental problems. Hg accumulated by crops not only exerts detrimental effects on crops, but also threatens to human health through food chains. Overload of Hg into crops disrupts many biological processes. Thus, it is very important to dissect toxicological and adaptive response to the toxic heavy metal. Hg-induced phytotoxicity is mediated by several important signaling molecules such as NO, SA, and CO. Furthermore, genome-wide transcriptome analysis contributes greatly to our understanding of Hg-induced gene expression and its regulatory networks in plants at transcriptional and post-transcriptional levels. This approach provides numerous genes that can be potentially used for studying regulatory mechanisms leading to heavy metal accumulation in plants. Gene manipulation and molecular breeding of plant cultivars to minimize Hg accumulation seems to be a prospective substitute to reduce the risk of Hg entering the human food chain.

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