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REVIEW ARTICLE

Mechanisms underlying mercury detoxification in soil–plant systems after selenium application: a review

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Abstract

Feasible countermeasures to mitigate mercury (Hg) accumulation and its deleterious effects on crops are urgently needed worldwide. Selenium (Se) fertilizer application is a cost-effective strategy to reduce Hg concentrations, promote agro-environmental sustainability and food safety, and decrease the public health risk posed by Hg-contaminated soils and its accumulation in food crops. This holistic review focuses on the processes and detoxification mechanisms of Hg in whole soil–plant systems after Se application. The reduction of Hg bioavailability in soil, the formation of inert HgSe or/and HgSe-containing proteinaceous complexes in the rhizosphere and/or roots, and the reduction of plant root uptake and translocation of Hg in plant after Se application are systemically discussed. In addition, the positive responses in plant physiological and biochemical processes to Se application under Hg stress are presented to show the possible mechanisms for protecting the plant. However, application of high levels Se showed synergistic toxic effect with Hg and inhibited plant growth. The effectiveness of Se application methods, rates, and species on Hg detoxification is compared. This review provides a good approach for plant production in Hg-contaminated areas to meet food security demands and reduce the public health risk.

Keywords Selenium (Se) · Detoxification · Mercury (Hg) · Bioavailability · Physiological · Soil–plant

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Highlights
- Se application reduced Hg soil bioavailability via transformation to immobile species.
- Se application in soil led to formation HgSe complexes in rhizosphere and/or roots.
- Se application prevented to root uptake and translocation of Hg to aerial parts.
- Se application positively affected physiological and biochemical processes of plants.
- Se doses only significantly given the narrow range between deficiency and toxicity.

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Introduction

Mercury (Hg) is the most dangerous heavy metal (HM) because of its high toxicity to living organisms even at low concentrations. It is ranked third among the 87 hazardous substances by Agency for Toxic Substances and Disease Registry (ATSDR 2017) and has become a public concern since the recognition of Minamata disease in 1956 (Gallego et al. 2012; Ren et al. 2014). The global amount of Hg mass accumulated in soils was assumed to be in the range of 250–1000 Gg (Obrist et al. 2018). The world distribution of known sites contaminated with Hg from active and previous Hg gold and silver mining and processing, non-ferrous metal smelters, chlor-alkali plants, and factories that used or may have used Hg as a catalyst to produce acetaldehyde, polyvinylchloride, and vinyl acetate (Chen et al. 2012a) is presented in Fig. 1 (Map by Kocman et al. 2013). Mercury enters agricultural soils through anthropogenic activities, such as smelting, metalliferous mining, coal burning, pesticide, fertilizer, sludge application, and sewage irrigation (Saunders et al. 2010; Meunier et al. 2011).

Mercury ions are easily taken up by plant roots and rapidly transported to edible plant parts (Ren et al. 2014). The accumulation of Hg in plants can result in disorders in biochemical and physiological processes (Patra and Sharma 2000; Benavides et al. 2005), such as blocking essential functional groups in biomolecules, displacing essential metal ions from biomolecules in photosynthetic pigments, reducing photosynthetic rates, and negatively affecting plant nutrient uptake and homeostasis, which lead to the inhibition of root and shoot growth and yield production (Wang and Greger 2004; Patra et al. 2004). After accumulating in plants, Hg is readily biomagnified in the food chain and can threaten human health and the ecological environment (Templeton and Liu 2010; Han et al. 2015). Therefore, feasible countermeasures for the remediation of Hg-contaminated farmlands are urgently necessary to reduce toxic Hg concentrations, promote agro-environmental sustainability and food safety, and reduce the public health risk posed by Hg-contaminated soils.

Over the past several decades, techniques such as soil washing (Makino et al. 2008), low-temperature thermal desorption (Qiu et al. 2014), and phytoremediation (Belimov et al. 2005) have been applied to the treatment of Hg-polluted soils. Although soil washing can remove soluble and exchangeable Hg from heavily polluted soils, it can also remove essential soil elements (Wang et al. 2020). The high costs and soil disturbance associated with soil washing also need to be considered, as well as the costs of thermal treatment and its effects on soil properties. Phytoremediation, an inexpensive and facile approach for soil remediation, involves the selection of capable plant species to degrade, extract, contain, or sequester a soil contaminant through physical, chemical,

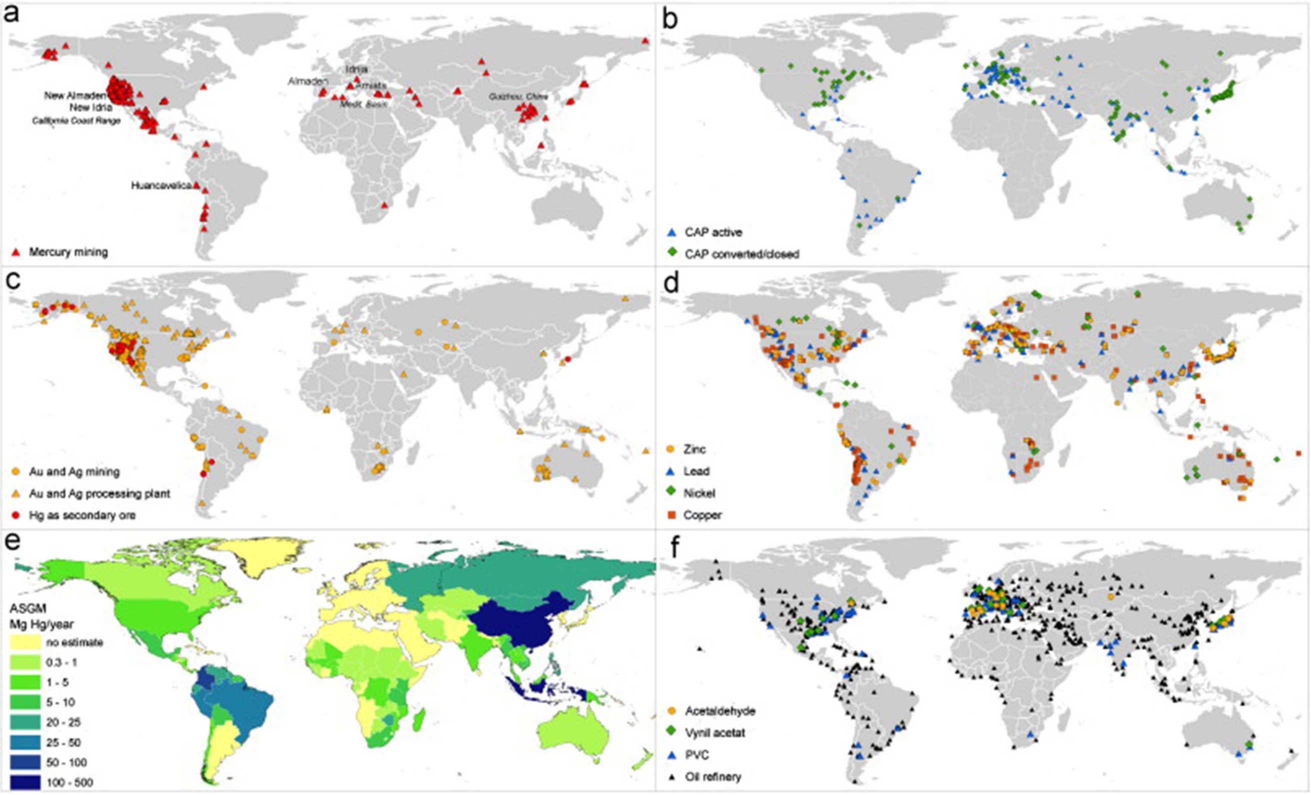

Fig. 1 Global distribution of contaminated sites with Hg: primary Hg mining (**a**), chlor-alkali plants (**b**), large-scale precious metal mining (**c**), non-ferrous metals processing (**d**), artisanal and small-scale gold mining (**e**), and other industrial sites (**f**) (Map by Kocman et al. 2013).

and biological processes (Burd et al. 2000). However, this method can result in plant death from exposure to high contaminant concentration. Therefore, identifying other approaches that can maintain a plant species, while reducing plant Hg accumulation is highly desired.

Selenium (Se) is an essential micronutrient for humans and animals; it is predominantly obtained by consumption of cereals, vegetables, meat, and fish (Rayman 2000). Recently, the application of Se fertilizers to reduce Hg has gained considerable attention as a cost-effective strategy for mitigating Hg accumulation and the deleterious effects of Hg on plants (Feng et al. 2013b; Wang et al. 2016a). Many previous studies found that the application of exogenous Se could reduce the accumulation of Hg in plants cultivated in flooded soils (Zhang et al. 2012; Wan et al. 2016), unflooded soils (Shanker et al. 1995; Tran et al. 2018a), or in hydroponic systems (Mounicou et al. 2006; Lin et al. 2012). In addition, some studies also confirmed that Se application could alleviate Hg-induced oxidative stress by regulating the metabolism of reactive oxygen species (ROS), such as superoxide anions (O_2^-), hydroxyl radicals (OH^-), and hydrogen peroxides (H_2O_2). Moreover, the resultant processes may scavenge excess oxygen free radicals, decrease lipid peroxidation (LPO), enhance the activity of antioxidant enzymes, and prevent the inhibition of photosynthesis (Pandey and Gupta 2015; Wu et al. 2016). Therefore, Se application at appropriate dosages could stimulate plant growth and counteract the diverse environmental stresses caused by Hg contamination (Kumar et al. 2012; Malik et al. 2012).

This review explored available information on the mechanisms underlying Hg detoxification in soil–plant systems through the application of exogenous Se. The transformation of Hg speciation and bioavailability in soils, the uptake from the soil and translocation, the transformation of Hg within plants, and the physiological and biochemical responses of the plant after Se application are discussed to confirm the possible mechanisms (Fig. 2). In addition, the effects of Se species, rates, and application methods under Hg stress are also discussed.

Reduction of Hg bioavailability in soil after Se application

The protective effect of Se against Hg toxicity was first noted by Pařízek and Oštádalová (1967) over 50 years ago in rats; most of the early studies were in mammals. Later, there were many studies that demonstrated that Se application could reduce the toxicity of many heavy metals, including Hg, Cd, and Pb, through reduction of HMs accumulation by plants (Mukherjee and Sharma 1988; Shanker et al. 1996a; Thangavel et al. 1999). The protective effect involved the binding of Se to Hg, thereby acting as a “tonic” that sequestered Hg in a form that no longer harmed important biomolecules. To understand how Se protects against Hg toxicity, it is necessary to understand the interaction processes between Hg and Se in the soil.

Immobilization of Hg in soil after Se application

The speciation of Hg and Se in soil

The speciation of Hg in soil The most common forms of Hg in soils include elemental Hg (Hg^0), mercuric mercury (Hg^{2+}), mercuric sulfide (HgS), and methyl Hg (CH_3Hg^+) (Clarkson and Magos 2006; Yang et al. 2008). Hg^{2+} is the dominant and highly soluble Hg species under the highly oxidizing conditions of unflooded soils (Fernandez-Martinez et al. 2015). Mercury is reduced in the soil environment, as follows:

$Hg^0 \leftrightarrows Hg_2^{2+} \leftrightarrows Hg^{2+} \leftrightarrows (CH_3)Hg \leftrightarrows (CH_3)_2Hg$ (Shanker et al. 1996b; McNear et al. 2012)

Bacterial *merB* (organomercurial lyase) facilitates the protonolysis of organic-Hg to Hg^{2+}, whereas bacterial *merA* (mercuric ion reductase) transforms Hg^{2+} to Hg^0 (Ruiz and Daniell 2009).

Mercuric chloride and mercuric hydroxide are likely to be reduced to Hg^0 as follows:

$Hg^{2+} + Cl_2$ and $Hg^{2+} + [OH]_2$ into Hg^0) (Shanker et al. 1996b; McNear et al. 2012)

The speciation of Se in soil Selenium exists in different forms in the soil, including selenate (SeO_4^{2-}), selenite (SeO_3^{2-}), elemental Se (Se^0), and selenide (Se^{2-}) (Zhang et al. 2014). Se^0 and Se^{2-} have poor mobility (Tolu et al. 2011). SeO_3^{2-} and SeO_4^{2-} are both highly available for plant uptake, whereas SeO_3^{2-} is less available than SeO_4^{2-} due to its strong adsorption onto soil particles (Nakamaru and Altansuvd 2014). Long periods of overlying water cause low pH values and anoxic conditions in flooded paddy soil (Rothenberg and Feng 2012). Under anoxic conditions, SeO_4^{2-} can be reduced to SeO_3^{2-} and then rapidly transformed into Se^0 and even to Se^{2-} or organic Se by sulfate-reducing bacteria (SRB) as follows:

$SeO_4^{2-} \rightarrow SeO_3^{2-} \rightarrow Se^0 \rightarrow Se^{2-}$ (Yang et al. 2008; Li et al. 2014a)

Immobilization processes of Hg in soil

Immobilization of Hg in soil via HgS complex formation The anoxic conditions or highly oxidizing conditions of rhizospheres enhance microbial activity, decrease pH, and promote the release of carbon-rich root exudates that can facilitate the formation of sulfides (S^{2-}) (Jia et al. 2015). In addition, Hg^{2+} ion is a class B metal ion with a strong affinity for ligands with soft donor atoms (Rayner-Canham and Overton 2010). At typical concentrations in soil, Hg^{2+} tends to form stable complexes with OH^-, Cl^-, and S containing functional groups of

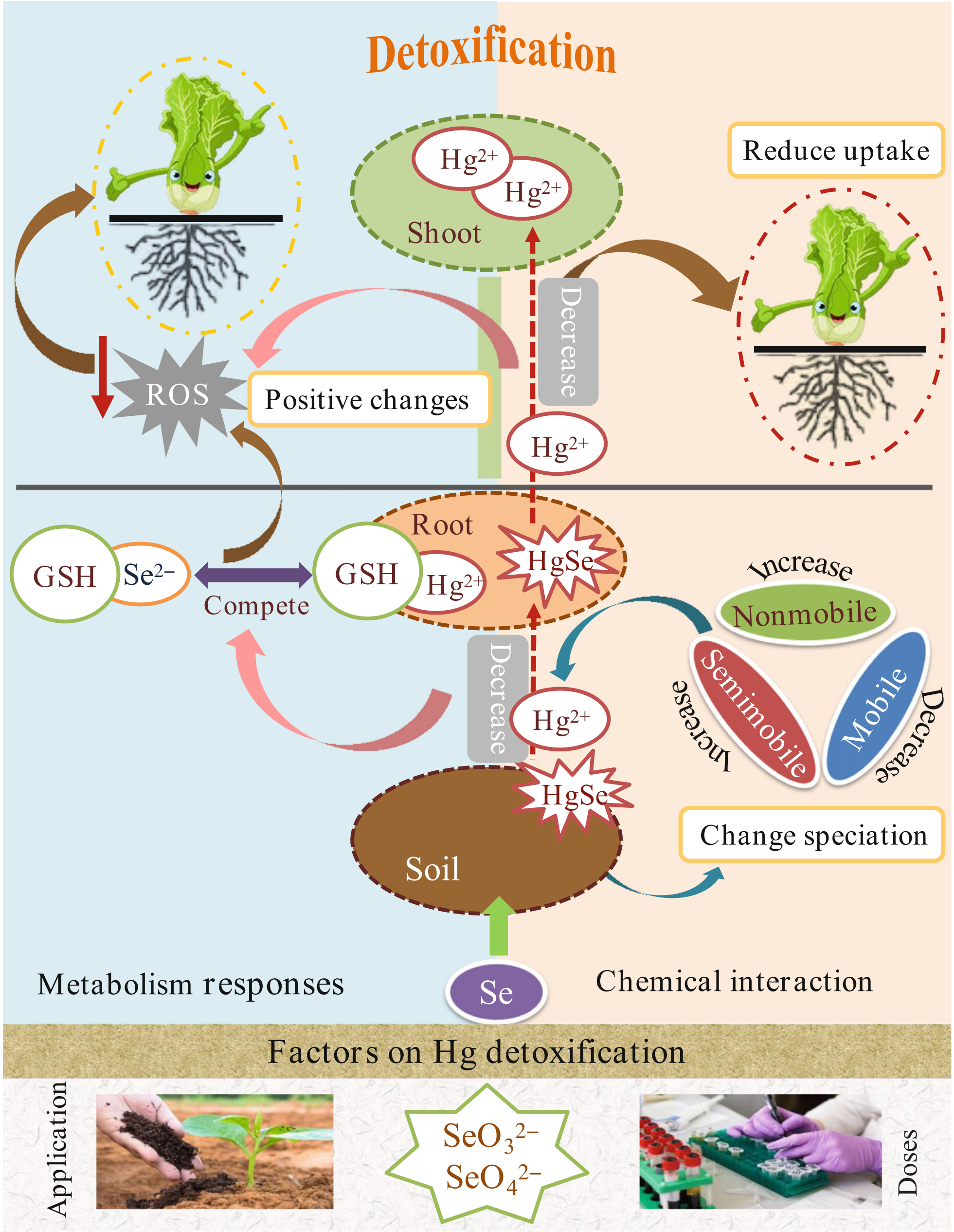

Fig. 2 Mechanisms underlying Hg detoxification in soil–plant systems after Se application

organic ligands (Powell et al. 2004). In addition, Barnett et al. (1997) postulated that Hg can form HgS upon binding with –SH groups of organic matter that exists at a higher redox potential than S^{2-}. The affinity of Hg^{2+} for S^{2-} results in the formation of mercuric sulfide precipitation (HgS) low solubility complex, as follows:

$Hg^{2+} + S^{2-} \rightarrow HgS$ (Boszke et al. 2006; Jonsson et al. 2012)

Immobilization of Hg in soil via inert HgSe complex formation

Selenium often occurs as an isomorphous substituent of sulfur (S) in sulfide crystal lattices. In addition, S and Se have the same atomic structure, the same charge (S^{2-} and Se^{2-}), and similar atomic radii and ionic radii (S: 0.184 nm, Se: 0.191 nm); thus, Se can easily be incorporated into the crystalline lattices of S (Zhang 2014b). Therefore, S^{2-} can be replaced by Se^{2-} to form inert mercuric selenide (HgSe) precipitates or an isomorphous series of HgS–HgSe (in cinnabar ore), because the binding affinity of Se^{2-} with Hg (log$K$ 10^{45}) is one million times greater than that of S with Hg (log$K$ 10^{39}) (Syversen and Kaur 2012; Zhang et al. 2014). Moreover, the solubility product constants of HgSe precipitates (K_{sp}~10^{-58}–10^{-65}) are drastically lower than those of HgS precipitates (K_{sp} ~10^{-52}) (Björnberg et al. 1988). When Se and Hg coexist in soil under appropriate conditions, Hg can first thermodynamically react with Se to form an inert, highly stable HgSe precipitate.

Se may thermodynamically react with Hg^{2+}/Hg^0 to form an insoluble HgSe complex in the rhizosphere (Yang et al. 2008; McNear et al. 2012), as presented in the following chemical equations:

$$Hg^0 + Se^0 \rightarrow HgSe$$
$$\text{and/or } Hg^{2+} + Se^{2-} \rightarrow HgSe$$

Immobilization of Hg in soil via organo-HgSe complex processes Besides inert HgSe complex, organic HgSe complexes are also found in soil. When paddy soil is supplemented with Se, Se may displace S in the R-SH, R-SSH, and R-SS-R groups to form more stable chemicals, such as R-SeH, R-SeSeH, and R-SeSe-R (Khan and Wang 2009). Simultaneously, Hg binds to non-R-SH, R-SSH, and R-SS-R and may be released and readsorbed by strong Se functional groups (Laurier et al. 2003; Shoham-Frider et al. 2007), thereby forming strong complexes with Se-organic ligands, which are more inert and stable and less available to microbes and plants. Xu et al. (2019) further suggested that HgSe in soil may contain HgSe, CH_3HgSe^-, and $(CH_3Hg)_2Se$, as well as HgSeR, RSHgSeR, CH_3Hg-SeR, and CH_3Hg-SeSR, which play dominant roles in soil Hg levels. However, this finding needs to be verified further.

Promotion of Hg immobilization in soil

Wang et al. (2016b) demonstrated that Se^{2-} can react with Hg^{2+} under anoxic and suboxic conditions and form HgSe complexes, despite sulfate input in paddy soil. They also found by transmission electron microscopy and energy-dispersive X-ray spectroscopy that the molar ratios of Hg:Se and Hg:S were 1 in nanoparticles. However, another study showed that Hg L_{III}-edge synchrotron radiation X-ray absorption near-edge structure (XANES) spectrum exhibited that the typical spectral feature was HgSe instead of α-HgS (Wang et al. 2016a). Furthermore, Zhang et al. (2012) found that Se contents were positively correlated ($P < 0.01$) with Hg contents in flooded soil due to the formation of HgSe complexes in the rhizosphere. Other studies reported that application of SeO_3^{2-}- or SeO_4^{2-}- to dryland soil promoted the formation of HgSe precipitate in the rhizospheres of radish (*Raphanus sativus* L.) (Shanker et al. 1996b), tomato (*Solanum lycopersicum* L.) (Shanker et al. 1996a), or pak choi (*Brassica rapa* L. var. *chinensis*) (Tran et al. 2018a). In addition, HgSe compounds may react further with dissolved organic matter in the rhizosphere to form high molecular weight HgSe complexes (Plant et al. 2003; Chiasson-Gould et al. 2014).

Transformation of Hg into immobile Hg speciation in soil after Se application

The formation of sufficiently stable insoluble HgSe bonds in soils after Se application may limit the amount of bioavailable Hg^{2+} in the soil rhizosphere through the transformation of Hg species.

The fractions of Hg in soil

Mercury exist in different speciations in soil, and Hg fractions were arranged following the sequential mobile levels with toxicity decreasing in that order, such as mobile fractions, semi-mobile fractions, and non-mobile fractions (Han et al. 2003; Fernandez-Martinez et al. 2005). The mobile Hg fraction (water-soluble and exchangeable Hg) represents less than 2% of total soil Hg, but this fraction contains the most available Hg, including oxidized inorganic (Hg^{2+}-mercuric and Hg_2^{2+}-mercurous) and oxidized organic (CH_3Hg^+-methyl mercury and $C_2H_5Hg^+$-ethyl mercury) (Boening 2000; Li et al. 2009). The semi-mobile fractions force Hg to strongly bind to sites in natural organic matter, iron and manganese oxides, humic acid, fulvic acid, and amino acids, thereby forming thermodynamically stable complexes (Han and Banin 2000; Zhong and Wang 2009). The non-mobile fractions, which include the combination of Hg^0, HgS, and HgSe, have lower bioavailability because of their very low solubility, thereby leading to less toxicity (Boszke et al. 2002; Covelli et al. 2009).

Transformation of Hg into less mobile fractions in soil

Chemical and biological reactions can change Hg speciation and binding to different chemical species in the soil addition of Se, which in turn changes the solubility and bioavailability of Hg-bound chemicals (Reis et al. 2010; Xu et al. 2017). The results of our recent study on pak choi under dryland cultivation conditions demonstrated that the application of SeO_3^{2-} and SeO_4^{2-} in soil with concentration from 0.5 to 2.5 mg/kg reduced Hg bioavailability and plant uptake (with reduce Hg 10.7–77.7% in root and 5.8–59.2% in shoot) by enhancing Hg binding in soils via changes in soil Hg fractions (Tran et al. 2018a). This transformation was accompanied by a large increase in the proportions of residual Hg fractions (as HgSe) and a dramatic reduction in the proportions of water-soluble Hg fraction (Tran et al. 2018a), as shown in Fig. 3.

Under flooded soil conditions, Wang et al. (2014) reported that SeO_3^{2-} application at low dose (1 μg/g) and high dose (5 μg/g) reduced Hg concentrations in water-soluble fractions, thereby reducing Hg bioavailability. Tang et al. (2017) also indicated that Hg^{2+} levels in soil solution are significantly reduced ($P > 0.05$) during rice (*Oryza sativa* L.) growth with soil SeO_3^{2-} and SeO_4^{2-} application 3.0 and 6.0 mg/kg^{-1}. Xu

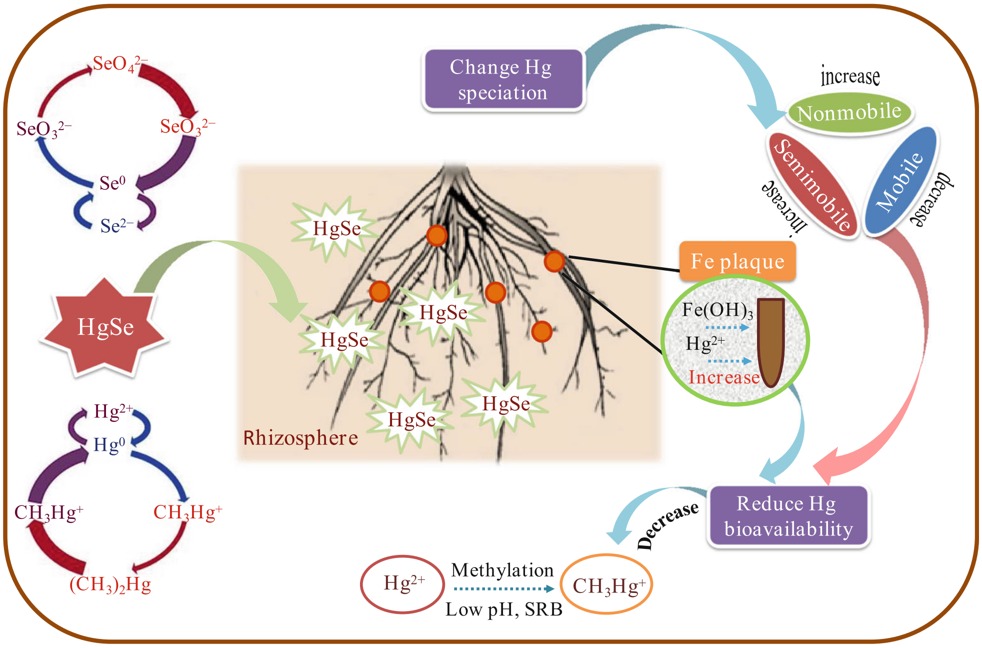

Fig. 3 Reducing Hg bioavailability in soil-plant systems

et al. (2019) demonstrated that the water-soluble fraction and human stomach acid soluble fraction were reduced with addition Se concentrations of 20–500 mg/kg under anoxic conditions, because HSe^- and Se^{2-} can react with bioavailable Hg in these mobile fractions to form a stable and insoluble Hg-Se complex in the rhizosphere or on the root surface of rice plants. Moreover, Se may displace S in the ReSH, R-SSH, and R-SS-R groups to form more stable chemical forms, such as ReSeH, R-SeSeH, and R-SeSe-R. As a result, humic acid fractions are converted into strong-complexed fractions (Xu et al. 2019). Humic acid fraction is composed of Hg bound to the non-RSH functional groups in humic acid, which can be readily released. The strong-complexed fraction includes elemental Hg, Hg bound up to organo-sulfurs, Hg-Ag amalgams, and Fe/Mn oxides (Shoham-Frider et al. 2007), as shown in Fig. 3.

The water-soluble Hg fraction is the most mobile and bioavailable fraction and can be easily transported by natural processes and absorbed by plants (Issaro et al. 2009). The reduced bioavailability of Hg in soils after Se application is reflected by the increase in I_R value (reduced partition index), which is used to describe the relative binding strength and fractional redistribution of Hg in soils (Tran et al. 2018a).

Prevention of methyl Hg production in soil after Se application

Despite numerous studies on the interaction between Hg^{2+} and Se in soil, the mechanisms by which CH_3Hg^+ interacts with Se are not well understood. Selenium can serve as a mediator to prevent CH_3Hg^+ production through the formation of Hg–Se complexes, thereby decreasing the amount of available Hg^{2+} to methylating bacteria.

Methyl Hg processes in soil

Under reducing conditions that occur in many permanently or periodically flooded soils, Hg may be biogeochemically transformed into organo-Hg forms, of which CH_3Hg^+ is the most prevalent form (Boszke et al. 2006; Kerin et al. 2006; Frohne et al. 2012). CH_3Hg^+ is also the most toxic Hg species because of its high mobility and bioavailability (Boening 2000; Li et al. 2009). The most mobile Hg fractions are the most susceptible to Hg methylation, whereas the direct conversion of insoluble HgS species to CH_3Hg^+ in anaerobic soils is insignificant (Boszke et al. 2002; Covelli et al. 2009; Gray et al. 2015). The potential mechanism for Hg^{2+} uptake by methylating microorganisms is the energy-dependent uptake of Hg^{2+} by active transport (Zhang et al. 2010; Thomas et al. 2018). SRB is considered the primary methylator of Hg^{2+}, whereas Fe-reducing bacteria also methylate Hg (Rothenberg et al. 2014; Wang et al. 2016a).

Prevention of methyl Hg processes in soil

Limiting the amount of bioavailable Hg^{2+} decreased or at least considerably prevented the production CH_3Hg^+ in the soil rhizosphere. Wang et al. (2014) reported that SeO_3^{2-} application restricts the amount of bioavailable Hg^{2+} in paddy soils by decreasing microbial CH_3Hg^+ production (reduce 13–44% CH_3Hg^+ concentration in soil), which is primarily mediated by SRB (Yang et al. 2008; Truong et al. 2014), and suppresses Hg methylation, and reduces CH_3Hg^+ concentrations in soil

(Wang et al. 2014; Zhang 2014a). Wang et al. (2016a) suggested that CH_3Hg^+–Se antagonism in soil results in reduction of soil CH_3Hg^+ levels under anoxic or suboxic conditions (CH_3Hg^+ levels reduced 10–87% in low-Se soil with addition Se concentrations of 0.5–6.0 mg/kg; and CH_3Hg^+ levels decreased 13–46% in high-Se soil with addition Se concentrations of 0.5–2.0 mg/kg). In addition, CH_3Hg^+–Se antagonism may be predominantly governed by microbial processes, specifically by strains of SRB. Soil CH_3Hg^+ concentrations were consistently lower after Se treatments under anoxic and suboxic conditions independent of sulfate input (Wang et al. 2016b), as shown in Fig. 3.

In addition, Se may also directly affect the microbes that regulate Hg methylation. Hg and Se co-exposure reportedly decreases the growth of SRB in comparison with Hg exposure alone (Truong et al. 2013). Selenium addition also enhanced the demethylation and evaporation of CH_3Hg^+ (Khan and Wang 2010; Dang et al. 2019), leading to the reduction in soil CH_3Hg^+ production.

Reduction of Hg availability on the interface of soil–plant root after Se application

Besides decreases of Hg bioavailability in soil after Se application, decline of Hg availability on the interface of soil–plant root also was identified by directly tracking inert HgSe or/and HgSe-containing proteinaceous complexes in the roots. These complexes reduced Hg accumulation in plants by inhibiting Hg uptake and transport. In addition, the restriction of Hg access into the root of plants, due to the promotion of the formation of Fe plaques outside plant roots after Se application, may also be important for reducing the accumulation of Hg in roots and shoots.

Reduction of Hg availability by formation of insoluble HgSe precipitate in root

Formation of insoluble HgSe precipitate in root

Formation of inert insoluble HgSe precipitate The formation of HgSe insoluble complexes within plants cannot be completely ruled out, although HgSe insoluble precipitate likely dominates in the soil. Hypothetical pathways for Hg uptake in plants involve cellular entry through ionic channels and competition with the closest chemical relatives of essential metals for Hg^{2+} transporters (Blazka and Shaikh 1992; Clemens 2006). Hg^{2+} and CH_3Hg^+ are the principal chemical forms of Hg taken up by roots from the soil (Clemens 2013), and Hg^{2+} accumulates in roots (Meng et al. 2014; Zhao et al. 2014). Selenium is primarily taken up from the soil by plants as SeO_4^{2-} or SeO_3^{2-} (Zhu et al. 2009). After absorption by the plant root, SeO_4^{2-} is reduced to SeO_3^{2-}, reacts with glutathione (GSH), and is reduced to Se^{2-} in the rhizosphere (Zhu et al. 2009; Han et al. 2015).

The combination of Se^{2-} with Hg^{2+} forms the HgSe complexes in roots, as follows:

$Hg^0 + Se^0 \rightarrow HgSe$

and/or $Hg^{2+} + Se^{2-} \rightarrow HgSe$, which may drastically increase the accumulation of Hg in roots (Zhang et al. 2012; Li et al. 2015).

Under flooded soil conditions, over 90% of Hg was restricted to rice roots after SeO_3^{2-} application of 0.01–0.5 μg/mL in Hg-contaminated soil, and 27.8% of Hg was present as the HgSe complex (Li et al. 2015). Zhao et al. (2013) analyzed the speciation of Hg (with Hg L_3-edge XANES) in garlic (*Allium sativum* L.) tissues under hydroponic solution conditions, and they concluded that the direct binding of Se and Hg as HgSe only occurs in roots (<10%) and bulbs (<1%). Zhang et al. (2012) reported that the molar ratio of Hg:Se in the roots was approximately 1:1, which was not found in the aerial shoots. Zhao et al. (2014) suggested that rice exposure to both Se and Hg may lead to the formation of a HgSe complex in rice roots that is easily absorbed, as indicated by the significant correlation between Se and Hg in rice roots. Synchrotron radiation X-ray fluorescence (SRXRF) technique revealed that Se and Hg is concentrated in the epidermis and pericycle of rice roots (Zhao et al. 2014), as shown in Fig. 4.

However, Zhou et al. (2013) demonstrated that Hg concentration in rice shoots decreased by approximately 50%, whereas the transfer coefficient of Hg from roots to shoots did not drastically change after SeO_3^{2-} amendment of 14.6–100 g/L. These results indicated that an insoluble HgSe complex formed in the rhizosphere and not in the root. Therefore, the presence of insoluble HgSe and/or proteinaceous complexes in plant roots is still unknown and requires further study.

Formation of Se- and Hg-containing proteinaceous complex

In addition to the inert insoluble HgSe precipitate in the roots, a high molecular weight Se- and Hg-containing proteinaceous complex also forms in the root extract of plants under hydroponic conditions (Afton and Caruso 2009; McNear et al. 2012).

When taken up by plant cells, Hg^{2+} exhibits high affinity and can react intensely with the sulfhydryl (–SH) groups of proteins in the root cell walls (Carrasco-Gil et al. 2011; Azevedo and Rodriguez 2012). SeO_3^{2-} could replace S in essential S metabolites (Cys and Met) by physicochemical similarity and be converted quickly to SeCys and SeMet (Aborode et al. 2016; Bluemlein et al. 2009). Then, SeCys and SeMet can be incorporated into selenoenzymes and selenoproteins by replacing Cys and Met (Montesbayon et al. 2002; Navarro-Alarcon and Cabrera-Vique 2008).

In biological systems, selenols can readily replace thiols in amino acids because of the chemical resemblance of selenols to thiols, thereby leading to the complexation of Hg^{2+} and

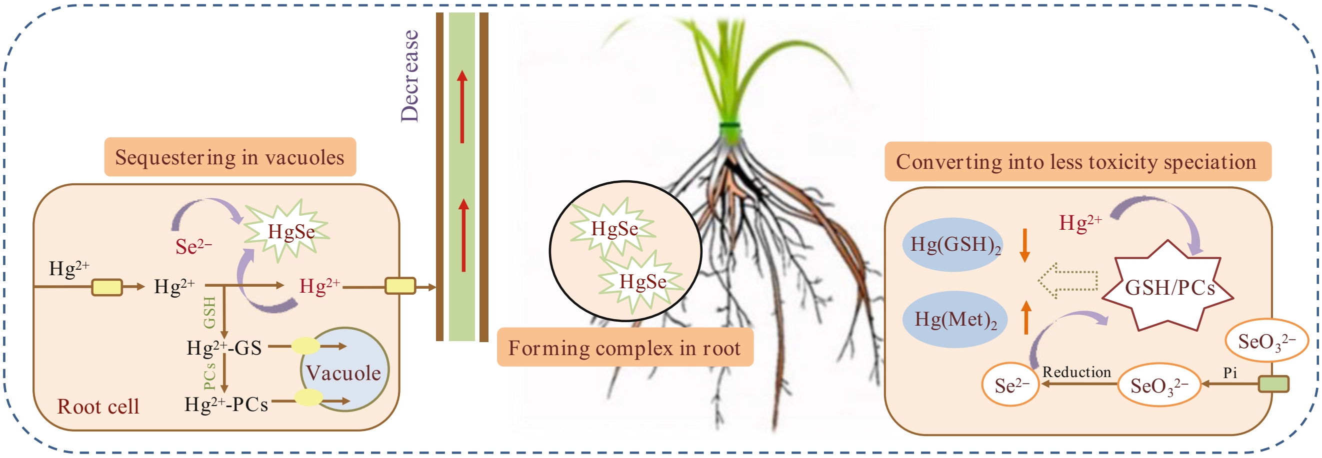

Fig. 4 Reducing Hg accumulation and toxicity within plant

CH_3Hg^+ with selenol-containing biomolecules. Compared with thiols, binding between Hg and selenols was stronger. Therefore, Hg^{2+} and CH_3Hg^+ complexes with selenols were more stable than their thiol analogs, thereby showing Hg–Se antagonism, resulting in the effective reduction of Hg^{2+} and CH_3Hg^+ in plant with the addition of Se into the soil (Wang et al. 2014; Zhang et al. 2012).

Size exclusion chromatography and proteolysis revealed that water-soluble Hg was localized in the roots in association with Se in the form of a high molecular weight entity, which was difficult to be translocated and metabolized. Yathavakilla and Caruso (2007) found that water-soluble Hg associated with Se and formed a high molecular weight (>600 kDa) proteinaceous complex in the roots of soybean (*Glycine max* L.) grown in soil containing both Hg and Se. Mounicou et al. (2006) found a high molecular weight (>70 kDa) compound containing Se and Hg in the root extract of Indian mustard (*Brassica juncea* L. Czern.) grown in hydroponics. This compound was associated with either a polysaccharide or a protein (Mounicou et al. 2006). Afton and Caruso (2009) identified a possible Se–Hg association in a plant-root protein in green onion (*Allium fistulosum* L.) grown in perlite media by applying size exclusion and capillary-reversed phase chromatography coupled with inductively coupled plasma mass spectrometry (ICPMS). McNear et al. (2012) used capillary-reversed phase chromatography coupled with ICPMS, μ-XANES, and micro-synchrotron X-ray fluorescence and found that Hg may bind to –SH groups of the cell wall or plasma membrane proteins in green onion roots and may react with reduced Se^{2-} to form a HgSe–BSS complex. However, Se^{2-} reacted with an abundant amount of free Hg^{2+} to form a solid HgSe precipitate outside the root in the perlite media. HgSe–BSS comprised a Hg^{2+} and Se^{2-} core to which GSH was appended via a Se–S or Hg–S bond (McNear et al. 2012). Compared with Hg-containing proteins with small molecular weights, the formation of Hg-Se-containing proteins with high molecular weights can more effectively inhibit the translocation of CH_3Hg^+ to the aboveground parts of rice plants (Fig. 4).

Wang et al. (2016a) also proposed that a CH_3Hg^+–Se interaction can exist within rice roots through the formation of CH_3Hg^+–Se complexes, when CH_3Hg^+ distribution in roots was enhanced under the SeO_3^{2-} and SeO_4^{2-} fertilization. They concluded that CH_3Hg^+–Se antagonism within plants was likely sufficient to induce such a reduction (Wang et al. 2016a).

Reduction of Hg uptake by plant root by formation of insoluble HgSe precipitate

The reduction in the Hg bioavailability in the rhizosphere can drastically inhibit Hg^{2+} uptake from soil by roots. Tang et al. (2017) reported that Hg^{2+} concentrations in rice roots decreased by 22–48% after 3.0 and 6.0 mg/kg SeO_3^{2-} and SeO_4^{2-} application to flooded soil. Zhao et al. (2014) also speculated that Se (after SeO_3^{2-} application of 1 and 5 mg/kg) inhibits Hg^{2+} uptake through a substantial decrease of Hg^{2+} concentrations in rice tissues. Previous pot experiments found that SeO_3^{2-} and SeO_4^{2-} application of 0.5–6.0 μg/mL decreased root Hg concentrations by approximately 90% in tomato (Shanker et al. 1996a) and > 90% in radish (Shanker et al. 1996b) and by approximately 80% in pak choi with SeO_3^{2-} and SeO_4^{2-} application of 0.5–2.5 mg/kg under dryland cultivation conditions (Tran et al. 2018a). Under hydroponic conditions, the formation of insoluble HgSe complexes in the rhizosphere resulted in the reduction of root Hg accumulation. Hg^{2+} accumulation in rice roots decreased by 10.3–53.0% at Hg concentration of 100 μg/L with SeO_3^{2-} application of 14.6–100 g/L (Zhou et al. 2013) or at high Hg exposure (1 and 10 mg/L) with SeO_3^{2-} application of 1.0–10 mg/L (Zhao et al. 2014).

Reduction of Hg availability to root by promotion of the formation of Fe plaques after Se application

The reduction in Hg bioavailability in the rhizosphere under flooded conditions can also be explained by another hypothesis; the promotion of Fe plaques on root surfaces after Se application may sequester Hg through adsorption and/or coprecipitation.

Formation of Fe plaques on root surfaces

Iron plaque is a layer of crystalline or amorphous Fe (hydr)oxides formed through the reaction of oxygen and soluble reductive Fe^{2+} (Fu et al. 2018). Flooded soils present a strongly reducing environment, in which SO_4^{2-}, Fe^{3+}, and Mn^{4+} can be reduced to S^{2-}, Fe^{2+}, and Mn^{2+} by S^{2-}, thereby promoting the formation of Fe plaques on root surfaces (Murase and Kimura 1997). Previous studies showed that wetland plants with more soluble reductive Fe^{2+} in the medium can readily form thicker Fe plaques (Cheng et al. 2014), and Fe plaque formation can contribute to less metal accumulation in the roots of plants (Wang et al. 2011; Sebastian and Prasad 2016). Iron plaques on root surfaces can sequester Hg through adsorption and/or coprecipitation and reduce the amount of bioavailable Hg in the rhizosphere.

Reduction of Hg uptake by plant root via promotion of the formation of Fe plaques

The addition of Se enhanced the development of Fe plaque of root, which hindered both Hg^{2+} and CH_3Hg^+ uptake (Li et al. 2014b; Zhou et al. 2014). Specifically, Se^{2-} exhibited enhanced reducing ability and increased Fe^{2+} and Mn^{2+} concentrations in the soil solution by reducing high-valence Fe and Mn in the soil (Huang et al. 2019). These changes dramatically enhanced the Fe content of Fe plaque on root surfaces and likely blocked the entry of Hg^{2+} into root tissues because Hg enters root cells under the mediation of essential element transporters (Zhou et al. 2017). In addition, Fe oxide and Fe plaques on roots had a high affinity for SeO_3^{2-}, thereby reducing the probability of contact between Fe bacteria and $Fe(OH)_3$ (Zhou and Shi 2007). This phenomenon possibly further blocked the dissolution of $Fe(OH)_3$ in Fe plaques to Fe^{2+} by the action of Fe bacteria (Qu et al. 2003) and increased root surface areas (Ding et al. 2014). Therefore, Se addition can promote amount of Fe plaque on the root surface, thereby acting as a natural barrier that blocked Hg uptake in plant root. For example, the adsorption capacity of Hg on Fe plaque of rice roots surface increased by 1.42 times with Se application, which markedly restricted the translocation of Hg from root to the shoot under hydroponics condition (Zhou and Li 2019), as shown in Fig. 3.

Reduction of Hg translocation within plant after Se application

The reduction of Hg translocation from root to aerial part of plant after Se application was due to the conversion of labile Hg species to insoluble HgSe and/or proteinaceous complexes in the rhizosphere and/or roots. These complexes reduced Hg^{2+} bioavailability in soil, suppressed Hg methylation in the rhizosphere, and decreased Hg accumulation by the plant root and shoot. However, insoluble HgSe and/or proteinaceous complexes were not detected in stem and leaf extracts. The reduction in Hg bioavailability in aerial part of plant after Se application can also be explained by transformation of Hg into less toxicity speciation and sequestration of Hg in the vacuoles of root cell.

Restrict HgSe and/or proteinaceous complexes in roots of plant

A high molecular weight Se- and Hg-containing proteinaceous complex was not detected in stem and leaf extracts. Mounicou et al. (2006) and Afton and Caruso (2009) suggested that the interaction between Hg and Se is primarily restricted to plant roots. The interaction of root-bound Hg and Se resulted in the production of a putative high molecular weight proteinaceous complex that was not metabolized or translocated to plant shoots, leaves, or fruits (Mounicou et al. 2006; Afton and Caruso 2009). In line with this finding, Zhang et al. (2012) reported a 1:1 molar ratio of Hg:Se in rice roots with none bound in the aerial shoots, indicating that a HgSe insoluble complex formed in the roots (Zhang et al. 2012). Tang et al. (2017) also found that Hg uptake was reduced only after soil SeO_3^{2-} and SeO_4^{2-} application but not after foliar application (Table 1).

Reduction Hg translocation within plant by insoluble HgSe and/or proteinaceous complexes in the root

The conversion of labile Hg species to insoluble HgSe and/or proteinaceous complexes in the root may act as an effective barrier for the translocation of Hg from the root to the aboveground tissues. Under hydroponic conditions, the reduction of Hg accumulation in plant stems and leaves after SeO_3^{2-} application of 1−5 mg/L (Mounicou et al. 2006) or in plant leaves after SeO_3^{2-} application of 30 mg/L (Afton and Caruso 2009) resulted in the formation of HgSe complex, which was unavailable to plants because of its high stability. The upward translocation of Hg through the root vessel to the leaf tip may be obstructed after SeO_3^{2-} and SeO_4^{2-} application by using μ-SRXRF, thereby resulting in the absence of Hg^{2+} in garlic leaves (Zhao et al. 2013) or in rice stalks and leaves (Zhao et al. 2014).

Table 1 The synthesis of detoxification mechanisms of Se on Hg via chemical interaction

Medium treated	Plant species	Se species are set	Se concentration can reduce Hg	Soil and plant tissues, in which Hg concentration is reduced	Reduction of Hg concentration	Hg species is reduced	Precipitation location	References
Soil and sand	Tomato (*Lycopersicon esculentum*)	SeO_3^{2-}	0.5–6.0 μg mL^{-1}	Root Fruit	13–86% 14–88%	Hg	In rhizosphere (*hypothesis*)	Shanker et al. (1996a)
		SeO_4^{2-}		Root Fruit	19–83% 22–82%			
Soil and sand	Radish (*Raphanus sativus*)	SeO_3^{2-}	0.5–6.0 μg mL^{-1}	Root Shoot	18–92% 21–69%	Hg	In rhizosphere (*hypothesis*)	Shanker et al. (1996b)
		SeO_4^{2-}		Root Shoot	34–92% 17–77%			
Unflooded soil	Pak choi (*Brassica chinensis*)	SeO_3^{2-}	0.5, 1.0 and 2.5 mg kg^{-1}	Root Shoot	10.7–77.7% 5.8–59.2%	Hg	In rhizosphere (*hypothesis*)	Tran et al. (2018a)
		SeO_4^{2-}		Root	5.9–41.4%			
Unflooded soil 50:50 mix of soil and ProMix	Soybean (*Glycine max*)	SeO_3^{2-}	60 mM	NA	NA	Hg	In root	Yathavakilla and Caruso (2007)
Flooded soil	Rice (*Oryza sativa* L.)	NA	NA	Root, stem, leaf, husk, and grain Stem, leaf, husk, and grain	NA	Hg^{2+} CH_3Hg^+	In rhizospheres and/or roots	Zhang et al. (2012)
Flooded soil	Rice (*Oryza sativa* L.)	SeO_3^{2-}	0.01, 0.1, 0.5 μg mL^{-1}	Grain	NA	Hg	In root	Li et al. (2015)
Flooded soil	Rice (*Oryza sativa* L.)	SeO_3^{2-} and SeO_4^{2-}	0.5, 3.0 and 6.0 mg kg^{-1} (low-Se soil) Soil fertilization	Soil Root Straw Brown rice White rice	10–87% 3–44% 3–44% 7–73% 8–72%	CH_3Hg^+	In rhizosphere	Wang et al. (2016a)
			0.5, 1.0 and 2.0 mg kg^{-1} (high-Se soil) Soil fertilization	Soil Root Brown rice White rice	13–46% 0.2–55% 3–38% 5–21%			
			30 and 80 g ha^{-1} (low-Se soil) Foliar fertilization	No difference				
Flooded soil	Rice (*Oryza sativa* L.)	SeO_3^{2-} and SeO_4^{2-}	3 mg kg^{-1}	Soil	23–86%	CH_3Hg^+	In rhizosphere	Wang et al. (2016b)
Flooded soil	Rice (*Oryza sativa* L.)	SeO_3^{2-} and SeO_4^{2-}	Foliar application 30 and 80 g ha^{-1}	No difference				Tang et al. (2017)
			Soil application 3.0 and 6.0 mg kg^{-1}	Soil Root Straw Brown rice White rice	data not shown 22–48% 30–58% 35–74% 44–74%	Hg^{2+}	In rhizosphere (*hypothesis*)	
Flooded soil	Rice (*Oryza sativa* L.)	SeO_3^{2-}	1 and 5 mg kg^{-1}	Root, stalk and , leaf Root	NA Somewhat	Hg^{2+} CH_3Hg^+	In root (*hypothesis*)	Zhao et al. (2014)
			1, 5 and 10 mg L^{-1}	Root, stalk and leaf	NA	Hg		

Table 1 (continued)

Medium treated	Plant species	Se species are set	Se concentration can reduce Hg	Soil and plant tissues, in which Hg concentration is reduced	Reduction of Hg concentration	Hg species is reduced	Precipitation location	References
Hydroponic condition			(1 and 10 Hg mg L^{-1})				In root circumference environment (*hypothesis*)	
Hydroponic condition	Rice (*Oryza sativa* L.)	SeO_3^{2-}	10 µM	Root Shoot	22% 29%	THg	NA	Wang et al. (2014)
Flooded soil			5 µg g^{-1}	Brown rice	47% 55%	THg CH_3Hg^+		
			1 and 5 µg g^{-1}	Soil	13–44%	CH_3Hg^+		
Hydroponic condition	Indian mustard (*Brassica juncea*)	SeO_3^{2-}	1, 3, and 5 mg L^{-1}	Stem and leaf	NA	Hg	In root	Mounicou et al. (2006)
Perlite media	Green onion (*Allium fistulosum*)	SeO_3^{2-}	30 mg L^{-1}	Root Leaf	12.2% NA	Hg	In root	Afton and Caruso (2009)
Perlite media	Green onion (*Allium fistulosum*)	SeO_3^{2-}	30 mg L^{-1}	NA	NA	Hg	In root	McNear et al. (2012)
Hydroponic condition	Garlic (*Allium sativum*)	SeO_3^{2-} and SeO_4^{2-}	>1 mg L^{-1} (> 1 Hg mg L^{-1})	Root and leaf	NA	Hg	In root and bulb	Zhao et al. (2013)
Hydroponic conditions	Rice (*Oryza sativa* L.)	SeO_3^{2-}	14.6–100 g L^{-1} (100 Hg µg L^{-1})	Root Shoot	10.3–53.0% 12.2–48.8%	Hg^{2+}	In root circumference environment (*hypothesis*)	Zhou et al. (2013)

In addition, the reduction of Hg uptake in the soil–root systems may also be the cause of the inhibition of Hg translocation to the aerial parts of the plant. Zhou et al. (2013) found that Hg concentration in rice shoots decreased by approximately 50% after SeO_3^{2-} application of 14.6–100 g/L in hydroponics, whereas the translocation factor (TFs) of Hg from the roots to shoots did not drastically change. Zhang et al. (2012) found a consistent reduction in the translocation of Hg^{2+} to aerial shoots of rice (i.e., stem, leaf, husk, and grain) with increasing Se levels under flooded soil conditions. They also found that Se concentrations in soil had significant negative correlations with the TFs of Hg^{2+} in different aerial shoots (Zhang et al. 2012). Tang et al. (2017) also reported that the concentrations of Hg^{2+} in straw and brown rice tissues were reduced by 15–58% and 26–74% by soil-applied SeO_3^{2-} and SeO_4^{2-} of 3.0 and 6.0 mg/kg, respectively. Rice grains exhibited the lowest Hg accumulation (decreased by 30%) when 0.5 μg SeO_3^{2-} mL^{-1} was applied (Li et al. 2015). Similar results were also reported in another research; Hg levels were reduced by 90% in tomato (Shanker et al. 1996a), 90% in radish (Shanker et al. 1996b), and 60% in pak choi (Tran et al. 2018a) after SeO_3^{2-} was applied to upland soil (Table 1).

However, increasing shoot Hg concentration was observed under SeO_4^{2-} and Hg co-exposure; shoot Hg concentration was threefold greater at the highest Se and Hg co-exposure treatment levels in our previous study (Tran et al. 2018a). The relatively high shoot Hg accumulation in plants may be due to the presence of Hg^0 in the soil (Kocman et al. 2004), which may have volatilized from the soil and condensed on the leaf surface or enter inner leaf tissues through stomata openings (Patra and Sharma 2000; Martínez-Trinidad et al. 2013).

Reduction of Hg translocation within plant by transformation of Hg into less toxic speciation

Mercury phytotoxicity can be mitigated by changes in the localization patterns and speciation of Hg in plant tissues treated with exogenous Se; Hg species are transformed into low-toxicity species through the reduction of the Hg–protein complex. Zhao et al. (2013) suggested that the percentage of high-toxicity Hg–S binding species, i.e., $Hg(GSH)_2$, decreased, whereas that of low-toxicity Hg–S binding species, i.e., $Hg(Met)_2$, increased in garlic tissues treated with SeO_3^{2-} and SeO_4^{2-}. Selenium can compete with Hg in binding with –SH groups, such as the thiol groups of Cys in membrane proteins (Feng et al. 2013a). A SeO_3^{2-} can enter the root and be quickly converted into organic forms or other biomolecules (de Souza et al. 1998; Zhu et al. 2009). As a result, Hg phytotoxicity was reduced, because GSH is a tripeptide that comprises glutamic acid, Cys, and glycine; these substances protect cells from oxidative stress by binding with oxidizing agents (Patty et al. 2009), as shown in Fig. 4.

Reduction of Hg translocation within plant by sequestration of Hg in the vacuoles of root cell

Huang et al. (2017) proposed another hypothesis for the reduction in HM translocation to the aboveground tissues of plants, as follows: Se decreases HM transport from the roots to the shoots by changing HM speciation and distribution in the root. Selenium application increased GSH and phytochelatin (PC) synthesis in plant tissues through the transformation of SeO_3^{2-} into organic Se (SeCys or SeMet) (Han et al. 2015; Abd-Allah et al. 2016). After the chelation of Hg^{2+} and GSH and PC in the cytoplasm of root cells, Hg–PCs or Hg–GS complexes were sequestered in vacuoles via the mediation of ATP-binding cassette (ABC) transporters (Park et al. 2012; Sharma et al. 2016). Thus, the increase of GSH and PC concentrations after Se application led to the reduction in Hg mobility in the root (Park et al. 2012; Sharma et al. 2016). Moreover, Krupp et al. (2009) identified Hg^{2+}-PC, but no CH_3Hg^+ PC complexed in the rice roots, suggesting that the binding to PCs may inhibit the translocation of Hg^{2+} from rice roots to stems, but not CH_3Hg^+ (Fig. 4).

In addition, the amendment of Se can enhance the development of apoplastic barriers in the root endodermis and exodermis, which can mediate the uptake of Hg through the apoplastic pathway or reduce the activity of membrane transporters and thereby reduce the uptake of Hg by roots (Meyer et al. 2009; Wang et al. 2014). Selenium addition also decreased the absorption of Hg into root cells through the symplastic pathway, because Se induced a lower activity of membrane transporters (Wang et al. 2014). The recent study also demonstrated that the main detoxification mechanism for plants in Hg-contaminated soil is the sequestration of Hg into inactive compartments, such as the epidermis, the vacuole, and the cuticle (Geng et al. 2019).

Reduction of oxidative stress induced by Hg in plants after Se application

The possible mechanisms of Hg phytotoxicity can be induced by change of the permeability of the cell membrane, Hg's high affinity to react with the –SH groups, Hg's affinity to react with phosphate groups and active groups of ADP or ATP, the replacement of essential ions metalloproteins, and Hg's ability to disrupt functions involving critical or nonprotected proteins (Patra and Sharma 2000; Patra et al. 2004). Mercury inhibits the activity of plasma membrane–localized aquaporins, which are water channel proteins that enhance water permeation, thereby causing a physical obstruction to the water flow and reducing plant water uptake and transpiration rate (Sas-Nowosielska et al. 2008; Clemens 2013). The substitution of the central atom of chlorophyll (Chl) and magnesium (Mg) by Hg in vivo prevents photosynthetic light harvesting in the

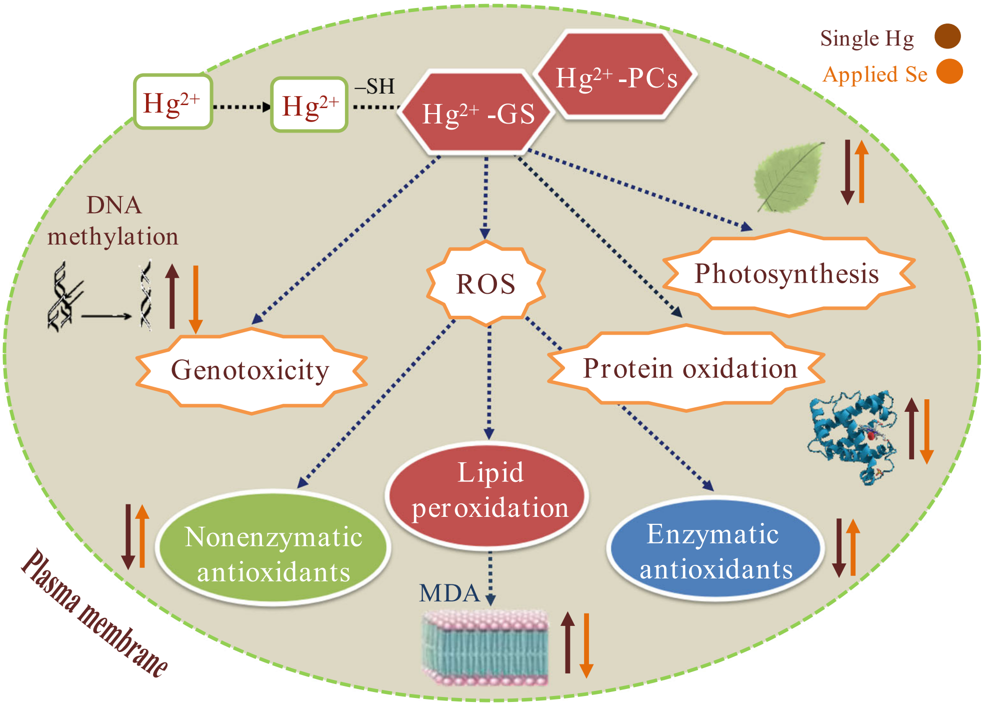

Fig. 5 Positive changes to physiological metabolism

affected Chl molecules, resulting in a breakdown of photosynthesis (Patra et al. 2004; Tangahu et al. 2011). The strong interaction with –SH groups disrupts the stability of the group, resulting in the overproduction of ROS and free radicals (Patra et al. 2004; Clemens 2013), triggering oxidative stress (Shiyab et al. 2009), modifying nucleic acids, oxidizing proteins, and inducing LPO (Cho and Park 2000; Moreno-Jimenez et al. 2009). These interactions influence the antioxidant defense system (Israr and Sahi 2006) by interfering with the modulation of the nonenzymatic antioxidants and the enzymatic antioxidants (Sparks 2005; Ortega-Villasante et al. 2005; Israr et al. 2006). Both organic and inorganic Hg accumulation in

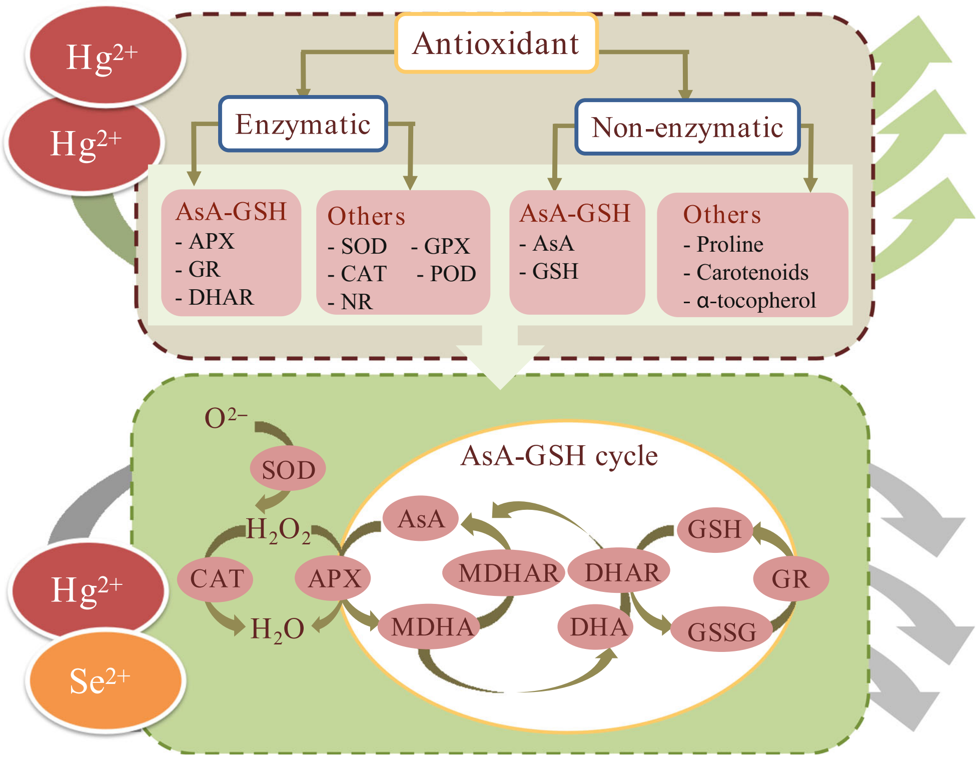

Fig. 6 The effect to antioxidant defense system of plant by Se application

root may block the entry or binding of ions, such as potassium, magnesium, and manganese, ion carriers, thereby reducing the uptake and transport of some mineral nutrients and inducing nutrient deficiency (Boening 2000). Mercury can bind with DNA, thus causing damage to chromosomes and inducing genotoxicity (Sharma et al. 1990; Cenkci et al. 2009).

The application of appropriate levels of Se significantly balances ROS production by increasing the activity of enzymatic and nonenzymatic antioxidant systems, reducing the amount of lipid peroxidation products, and increasing the concentrations of photosynthetic pigments and essential elements and the level of DNA methylation. However, Se application in excess concentration is toxic to plants and may trigger oxidative stress and reduce crop yields (Hartikainen 2005; Kolbert et al. 2016) (Fig. 5).

Balance ROS production after Se application

The stability of –SH groups is disrupted through their strong interactions with Hg (Patra et al. 2004; Clemens 2013). The disruption of –SH group stability results in ROS and free radical overproduction, which triggers oxidative stress (Shiyab et al. 2009). Accordingly, Hg stress interferes with the modulation of nonenzymatic antioxidants, such as GSH, PCs, ascorbic acid (AsA), proline, carotenoids (Cars), and α-tocopherol, and enzymatic antioxidants, such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), peroxidase (POD), glutathione peroxidase (GSH-Px), and nitrate reductase (NR) (Sparks 2005; Ortega-Villasante et al. 2005; Israr et al. 2006). Moreover Hg stress induces LPO (Cho and Park 2000; Moreno-Jimenez et al. 2009), as shown in Fig. 6.

Scavenging ROS species overproduction

The enhanced production of ROS is the precursor of oxidative stress and cell damage (Shahid et al. 2014a; Shahid et al. 2014b; Natasha et al. 2018), and O_2^- and H_2O_2 are the two most important ROS species in plants under metal stress (Shahid et al. 2013). In plants, O^{2-} can first be catalyzed to H_2O_2 by SOD with remarkably high reaction rates and then is further degraded into H_2O by CAT and APX. APX utilizes ascorbate as a specific electron donor to reduce H_2O_2 to H_2O. A high H_2O_2 content exerts toxic effects on plants by inducing electrolyte leakage, plasmolysis, and membrane damage (Singh et al. 2018). Mercury exposure can induce reactive oxygen species production and lead to oxidative damage to biological macromolecules.

The ameliorative effects of Se on metal-induced oxidative stress responses may be partly attributed to the improvement of ROS scavenging capability and the change in membrane physicochemical characteristics, such as O_2^- and H_2O_2. Under hydroponic conditions, the pretreating rice with SeO_3^{2-} decreased metal-induced growth inhibition, recovered root cell viability, and dramatically depressed O_2^- and H_2O_2 accumulation in rice tissues (Lin et al. 2012). Huang et al. (2019) also showed that the addition of SeO_3^{2-} greatly reduced H_2O_2 concentrations in rice tissues (roots and shoots) under two different water management regimes, i.e., flooded and unflooded.

Increasing enzymatic antioxidants

The Hg-induced generation of ROS triggers the activation of components of the antioxidative defense system of plants. Plants contain various types of enzymatic antioxidants to respond to oxidative stress, such as SOD, APX, CAT, GR, GSH-Px, POD, and NR. SOD can protect plant cells from harmful peroxidation reactions (Zhao et al. 2019) and is the first line of intercellular defense against ROS because it catalyzes O_2^-. CAT and APX are involved in H_2O_2 detoxification and its conversion to nonphytotoxic H_2O and O_2 (Alscher et al. 2002; Dinakar et al. 2008). GSH-Px plays an important role in maintaining the cellular antioxidant to pro-oxidant ratio by scavenging H_2O_2 with the help of GSH (Feng et al. 2013a). NR catalyzes the first step in nitrate assimilation and enhances nutrient metabolism (Beauvais-Flück et al. 2018). GR is crucial for maintaining optimal GSH levels, which is required for the synthesis of PCs, for the function of the GSH–AsA cycle, and as a reductant in numerous biochemical reactions (Pawlik-Skowronska et al. 2007).

The formation of Hg–Se precipitates may equilibrate ROS production and scavenging by restricting Hg^{2+} to the roots (Liu et al. 2015; Wang et al. 2015), thereby limiting the association between Hg^{2+} and –SH groups and enhancing shoot GSH translocation (Patra and Sharma 2000). Therefore, Se supplementation can improve the efficiency of antioxidant defense systems and protect the plant against oxidative stress under Hg contamination. The dramatic increase in the activities of antioxidant enzymes, such as SOD, CAT, POD, and GSH-Px in pak choi shoots (Tran et al. 2018b) or NR and POD in common bean leaves (*Phaseolus vulgaris* L.) (Shrivastava et al. 2016), was observed after SeO_3^{2-} application. Moreover, Se markedly increased the efficiency of the GSH–AsA cycle, which is involved in modulating the concentrations of GSH and AsA and the activities of GR and DHAR in Chinese cabbage (*Brassica rapa* subsp. *pekinensis*) tissues (Wu et al. 2016). Huang et al. (2019) also suggested that SeO_3^{2-} application increased SOD, CAT, APX, GSH-Px, and GR activities in rice grown in flooded and unflooded soil (Fig. 6).

Increasing nonenzymatic antioxidants

Glutathione and phytochelatin Glutathione (GSH) is one of the most important antioxidants in plants that efficiently plays a role in counteracting the adverse effects of heavy metals (Gratao et al. 2005; Asgher et al. 2017). Under metal stress conditions, GSH is converted to a GSSG, disulfide bridge; the increase of the ratio of GSH/GSSG is an indicator of oxidative stress (Jozefczak et al. 2012; Hernandez et al. 2015). The balance between GSH and GSSG is a central component in maintaining the redox state of the cell (Sharma et al. 2012). GSH functions as an indicator of oxidative stress and can react directly with ROS. This reaction promotes the regeneration of AsA, which also plays a crucial role in protecting cells against oxidative stress in plants (Aravind and Prasad 2005). PCs are the oligomers of GSH, produced by the enzyme PC synthase. PCs are a group of novel heavy metal-binding polypeptides (Cobbett 2000) that act as chelators and are important for heavy metal detoxification in plants. They belong to a family of cysteine-rich polypeptides that are produced in plants under Hg stress (Yadav 2010).

The SeO_3^{2-} ion is reduced to Se^{2-} by GSH and subsequently chelated by PC (Cui et al. 2008; Bluemlein et al. 2009). The formation of the intermolecular Se–S bond between Se–cysteinyl-serine and GSH indicates that Se^{2-} can bind to –SH groups present in GSH and PCs and reduce the number of free –SH groups necessary for Hg detoxification. Limiting the association between Hg^{2+} and –SH groups and enhancing shoot GSH translocation (Patra and Sharma 2000) results in direct chelation of PCs with Hg ions to reduce toxicity through the synthesis of metal-binding peptides of GSH (Mishra et al. 2006; Jozefczak et al. 2012). This response may directly degrade ROS-like OH^- and reduce the translocation of Hg in the plants. The reactions are as follows (Bluemlein et al. 2009):

$4GSH + SeO_3^{2-} + 2H+ \rightarrow GSSG + GS\text{–}Se\text{–}GS + 3H_2O,$

$GS\text{–}Se\text{–}GS + 2H^+ \rightarrow 2GSH + Se\text{–}PC_2$

In addition, GSH content drastically increases the synthesis of several important substances, such as GSH-Px, which protects cells by reducing and counterbalancing intracellular peroxide levels (Han et al. 2015). Under hydroponic conditions, Han et al. (2015) found that increasing SeO_3^{2-} levels enhanced the GSH and AsA contents in leaves of flue-cured tobacco (*Nicotiana tabacum* L.). The addition of SeO_4^{2-} increased GSH concentrations in Chinese brake fern (*Pteris vittata* L.) fronds, and this effect intensified with prolonged exposure period to Se (Srivastava et al. 2009) (Fig. 6).

Ascorbic acid Ascorbic acid (AsA) is an important antioxidant that maintains the GSH pool in a plant system and acts as a substrate in the AsA–GSH cycle. AO and APX can catalyze the oxidation of AsA to dehydroascorbate (DHA) (Ohkawa et al. 1989). The hydrolyzed DHA is recycled to AsA, and the reaction is catalyzed by dehydroascorbate reductase (DHAR), which also involves the conversion of GSSG to GSH (Hossain et al. 2010; Yin et al. 2010), thereby regulating the redox state of the cell (Chen and Gallie 2004). GR and DHAR play important roles in keeping the metabolic balance between GSH and AsA contents in the GSH-AsA cycle (Sharma and Dietz 2009).

The response of AsA to Hg accumulation in plants has been observed in many plants in different studies. Cui et al. (2014) demonstrated that alfalfa (*Medicago sativa* L.) exposed to Hg-induced oxidative stress enhanced concentrations of AsA to mitigate the oxidative stress and reestablish the redox homeostasis. Kováčik et al. (2017) studied the effect of AsA on the Hg-induced oxidative damage in green algae (*Coccomyxa subellipsoidea*). Singh et al. (2018) treated rice plants treated with 10 μM SeO_4^{2-} and increased the AsA content by 14.7% compared to those not treated with Se (Fig. 6).

Proline Proline is an antioxidant amino acid used in protein biosynthesis. Proline tends to accumulate in the cytosol of the plants under metal stress (Matysik et al. 2002; Aslam et al. 2017). Proline can scavenge free oxygen radicals (Alia et al. 2001) by promoting GSH synthesis in plant cells (Pavlikova et al. 2007). Thus, proline is considered a ROS scavenger under Hg stress conditions. In addition, an increased level of proline in plants enhances the production of glutamate kinase and may increase the glutamic acid level due to the synthesis of GSH and PCs in the plant cell (Pavlikova et al. 2007). This process leads to further chelation with metals and reduces metal toxicity by vacuolar sequestration (Chandrakar et al. 2016).

Thus, exogenous applied SeO_3^{2-} reduced proline accumulation in pak choi shoots through GSH regulation under Hg stress (Tran et al. 2018b). Moreover, high proline accumulation is an important adaptive mechanism for plants under HM stress, because proline acts as an osmolyte and reduces osmotic potential (Pandey and Gupta 2015). The supplementation of SeO_3^{2-} through seed priming reduced the total phenolic content of rice seedlings (Moulick et al. 2016). Phenolics have a well-known protective role in plants, and the synthesis and accumulation of proline in plant tissues increases under various biotic and abiotic stresses (Khaliq et al. 2015), as shown in Fig. 6.

Carotenoids Carotenoids (Cars) are plant pigments that function as nonenzymatic antioxidants (Strzalka et al. 2003). Cars play an important role in the protection of chlorophyll pigments under stress conditions. Carotenoids are produced in response to metal stresses (Hale et al. 2001) and increase the antioxidant response of plants to protect regular physiological status against biotic or abiotic stresses (Neill et al. 2002). The role of Cars during Hg stress seems to be limited since their content decreased with increasing Hg concentration (Baek et al. 2012). However, an increase in Car concentrations is reflective of the beneficial effect of Se supplementation on HM stress in cucumber (*Cucumis sativus* L.) (Hawrylak-Nowak et al. 2014) or tomato (Alyemeni et al. 2018), indicating that Se plays a protective role in Chl and ROS elimination (Han et al. 2012) (Fig. 6).

α-Tocopherol Tocopherol nonenzymatic antioxidants are also known as vitamin E. Naturally, there are four types of tocopherols (α, β, γ, and δ-tocopherol), which differ in the position of their methyl group (Li et al. 2012). α-Tocopherol is the main form of tocopherol in the green organs of plants (Munné-Bosch and Alegre 2002). It is a membrane-associated nonenzymatic antioxidant that helps in the scavenging of single oxygen and lipid peroxidases (Stahl and Sies 2003). Narang et al. (2008) determined the antioxidant response of α-tocopherols to Hg-induced oxidative stress. The concentration of α-tocopherol increased after 10 days of SeO_3^{2-} treatment in broccoli leaves (*Brassica oleracea* L. var. *italica*) of metal-enriched plants (Pedrero et al. 2008) (Fig. 6).

Decreasing lipid peroxidation

Free radicals and H_2O_2 are widely reported to cause damage to the lipid bilayer, which mostly results in lipid peroxidation (LPO) (Shahid et al. 2017; Abbas et al. 2018). Malondialdehyde (MDA) is an index of LPO that rapidly increases when membrane lipids are damaged under ROS overproduction (Mishra et al. 2011; Sharma et al. 2012). The production of MDA to protect lipid membranes against Hg stress has been well documented (Alfanie et al. 2015; Cabrita et al. 2019). Lipid peroxidation and loss of membrane integrity increased linearly with increasing accumulation of Hg in the leaf tissues of Hg-stressed plants (Ansari et al. 2009; Chen and Yang 2012; Cui et al. 2014).

The ameliorative effects of Se on Hg-induced oxidative stress responses may be partly attributed to the improvement of the scavenging capability of ROS, the decrease in LPO, and the change in membrane physicochemical characteristics, such as O_2^-, H_2O_2, and MDA levels. Tran et al. (2018b) demonstrated that MDA content decreased in pak choi shoots after SeO_3^{2-} application in unflooded soil (Fig. 5).

Increase in photosynthetic pigment content after Se application

Photosynthesis is a key metabolic process of autotrophs that is sensitive to toxic metals. In plants during photosynthesis, Hg ions may substitute for other essential metal ions and thereby disturb the photosynthetic electron transport chain (Patra et al. 2004; Azevedo and Rodriguez 2012). The substitution of Mg as the central atom of Chl with Hg in vivo prevents photosynthetic light collection in affected Chl molecules and results in the breakdown of photosynthesis (Patra et al. 2004; Tangahu et al. 2011).

Restricting Hg uptake and translocation within plants through Se application may prevent Hg^{2+} from replacing metal ions (Mg^{2+}), which ultimately balances the photosynthetic electron transport chain and increases photosynthesis rates. Thus, Se helps maintain the integrity of membrane systems in chloroplasts (Vinit-Dunand et al. 2002; Patra et al. 2004; Azevedo and Rodriguez 2012). The SPAD values (represent for Chl content) increased in pak choi leaves after SeO_3^{2-} application in unflooded soil because of the amelioration of Chl deficiency under Hg stress (Tran et al. 2018b). Similarly, Mozafariyan et al. (2014) showed that Chl *a* and Chl *b* concentrations significantly increased in Cd-exposed peppers (*Capsicum annuum* L.) after SeO_3^{2-} application (Fig. 5).

Reduction of genotoxic effects after Se application

Mercury is considered genotoxin. Most of the DNA damage caused by Hg stems from ROS formation or by its interaction with the proteins associated with DNA replication systems (Kültz 2005; Angelé-Martínez et al. 2017). These ROS have the potential to interact and damage the purine and pyrimidine bases of the DNA strand, which may lead to strand breakage (Fracasso et al. 2002; Sallmyr et al. 2008). The dramatic change in genomic template stability values suggested that the presence of SeO_4^{2-} effectively reduced the toxic effect of HMs on the DNA of rice seedlings grown in solution (Pandey and Gupta 2015). Specifically, the reduction in genomic template stability indicated that DNA repair and replication were effective in the presence of low levels of DNA alteration (Pandey and Gupta 2015). Selenium addition induced methylenetetrahydrofolate reductase, which was repressed in rice roots subjected to Se and CH_3Hg^+ co-exposure, suggesting that Se supplementation alleviated the effect on DNA damage and DNA synthesis induced by Hg treatment (Li et al. 2018).

Moreover, the accumulation of free radicals produced from methylation stress and the direct attack of DNA cytosine by methyl radicals increased DNA methylation level in leaves (Parra et al. 2001). Selenium supplementation to hydroponically grown plant under HM stress protected ramie tissues from abnormal methylation by reducing the level of DNA methylation (Wang et al. 2014). The protective role of Se against changes in DNA methylation patterns may be attributed to the removal of ROS and/or the elimination of HMs from enzymes (Fig. 5).

Reduction of the toxicity of Hg to plant proteins after Se application

The cellular toxicity of Hg^{2+} ions is considered to be associated with its binding with –SH groups in functional proteins because Hg^{2+} ions have high affinity for S ligands (Chen et al. 2012b). Hg^{2+} or CH_3Hg^+ exposure can form Hg-binding proteins (15–25 kDa) in rice roots (Li et al. 2016). Similar to other heavy metals, Hg interacts with plant proteins (Sheng Zhou et al. 2009; Krishna Sahu et al. 2012). The ability of Hg to change cell membrane permeability with its high affinity for –

SH groups, replace essential ion metalloproteins, and disrupt functions involving critical or unprotected proteins, phosphate groups, and active ADP or ATP groups can cause protein precipitation (Patra and Sharma 2000; Patra et al. 2004). The abundance of 49 proteins changed significantly in the roots of Hg-stressed knotgrass (*Paspalum distichum* L.); 32 proteins were up-regulated, and 17 were down-regulated (Ding et al. 2019).

The reduced disturbance of functional proteins in roots with Se treatment is an important mechanism for the protective effects of Se against Hg. Selenium can regulate the expression of proteins associated with stress response, sulfur and GSH metabolism, DNA replication and the cell cycle, and energy and carbohydrates, suggesting that these proteins participate in the protective effects of Se on Hg toxicity (Li et al. 2018). Considering the thermodynamically higher stability of Hgsenols than Hg-thiols, the formation of Hg-Se complexes in rice roots can prevent the binding of Hg to functional proteins (Feng et al. 2013a). High molecular weight proteinaceous complexes in the rhizosphere are formed under Se addition (Mounicou et al. 2006; Yathavakilla and Caruso 2007) (Fig. 5).

Sun et al. (2016) applied two-dimensional gel electrophoresis (2-DE) coupled with mass spectrometry to perform proteomic analysis and found that the expression of 21 of the 26 identified HM-associated proteins in cucumber tissues increased after the addition of SeO_3^{2-}. Selenium can also effectively influence ATPase synthesis by maintaining membrane lipid integrity, modulating pH and Ca^{2+} homeostasis, and competing with HMs for entrance to root cells via ion channels. Thus, the addition of SeO_3^{2-} sharply alleviates HM toxicity in rice tissues by increasing root H^+-ATPase and Ca^{2+}-ATPase activities (Lin et al. 2012). Li et al. (2018) also found that Se addition induced the formation of additional Hg-containing proteins in the range of 55–70 kDa (high molecular weight) but decreased the Hg content of functional proteins of 15–25 kDa (small molecular weight), and protected the proteins and enzymes from Hg destruction (Fig. 5).

Toxic effects of Se application with excess concentration to plants

Selenium doses need to be specifically monitored given the narrow range between deficiency and toxicity in plants. Others have applied high levels Se and showed synergistic toxic effect with Hg and inhibited plant growth as a pro-oxidant (Han et al. 2013; Zhao et al. 2013; Feng et al. 2013a).

Under hydroponic conditions, the study of Han et al. (2015) reported that the addition of Se (5 mg/L) decreased concentration of HM but decreased the fresh weights of leaves and roots in flue-cured tobacco and increased the MDA content (Han et al. 2015). In the roots of faba bean (*Vicia faba* L.) exposed to 50 μM Pb, the addition of a higher level of Se (6 μM) greatly enhanced the O_2^- level and decreased the cell viability and total –SH content (Mroczek-Zdyrska and Wójcik 2011). High doses of Se (>2 mg/L) exerted toxic effects on growth of spinach (*Spinacia oleracea* L.) plants because of its interaction with different nutrients (Saffaryazdi et al. 2012). In ryegrass (*Lolium perenne* L.), 1 mg/kg SeO_4^{2-} added to soil was believed to be marginally toxic (Hartikainen et al. 2000), which is similar to the Se level considered to be toxic to paddy rice in a hydroponic system (0.8 mg/L SeO_3^{2-}) (Feng et al. 2013a). Under unflooded soil conditions, a significant growth improvement of pak choi was only found at low Se treatment (1.0 mg/kg) because of the synergistic toxic effect of Se with Hg when applied at a high Se rate (2.5 mg/kg) in our previous study (Tran et al. 2018b). In addition, excess Se (≥11.1 mg/kg) also inhibited the growth of flue-cured tobacco (Han et al. 2013).

When Se was added in soil at an excessive rate, inorganic Se strongly transformed into organic species led some vital substances (for example GSH) might not satisfy the metabolism demands, caused GSH deficient (Han et al. 2015). An imbalance in the levels of GSH by excessive Se gives rise to ROS production because GSH are not sufficient to quench ROS and result in a ROS burst. Thus, oxidative stress appeared and plant growth was inhibited (Hartikainen et al. 2000; de la Luz Mora et al. 2008; Feng et al. 2013a). In addition, the toxicity of Se is thought to be due to its chemical similarity to S, leading to the non-specific replacement of S by Se in proteins and other S compounds (Cheng et al. 2016). The photosynthetic performance may be decreased by Se replacing S amino acids in photosynthetic proteins (Freeman et al. 2010). Specifically, higher exogenous Se levels caused an inhibition in the chlorophyll contents in lettuce (*Lactuca sativa* L.) (Abbas 2013; Abbas 2012; Chen et al. 2005; Xue et al. 2001). Besides, high Se concentrations may also be incorporated as SeCys and SeMet into selenoenzymes and selenoproteins, which replace Cys and Met and induce Se toxicity in plants (Montesbayon et al. 2002; Navarro-Alarcon and Cabrera-Vique 2008). Moreover, Hawrylak-Nowak (2008) suggested that reduction in maize (*Zea mays* L.) plant biomass at higher Se concentration might have been a result due to the accumulation of phosphorus in the shoot tissues.

Effects of different Se application approaches on Hg detoxification

Selenium application has been demonstrated to reduce the accumulation of Hg in plants. However, its mechanism is clarified by exploring the potential effects of Se species (SeO_3^{2-} and SeO_4^{2-}), Se doses, and Se application methods (soil or foliar application) on Hg^{2+}–Se and CH_3Hg^+–Se antagonistic interactions in soil–plant systems (Fig. 2).

Se species

Earlier studies have investigated Se accumulation in plants by treating plant growth media or soil with SeO_3^{2-} and SeO_4^{2-}, which are the main Se species taken up by plants (Ellis and Salt 2003). Both forms of Se can limit the absorption and bioaccumulation of Hg in plants (Hu et al. 2014; Tang et al. 2017; Huang et al. 2018). The Se species SeO_3^{2-} and SeO_4^{2-} were equally effective in reducing the Hg content in radish and tomato plants cultivated in upland soil (Shanker et al. 1996b; Shanker et al. 1996a) and in reducing Hg accumulation in garlic in hydroponic culture (Zhao et al. 2013). Moreover, SeO_3^{2-} and SeO_4^{2-} were equally effective in reducing the CH_3Hg^+ concentrations of high-Se and low-Se paddy soils (Wang et al. 2016a) or inhibiting sulfate-mediated CH_3Hg^+ production regardless of sulfate input (Wang et al. 2016b). Tang et al. (2017) demonstrated that the inhibitory effects of Se application on Hg^{2+} bioaccumulation in rice depended on Se doses rather than on the Se species (SeO_3^{2-} and SeO_4^{2-}), given that SeO_4^{2-} is rapidly transformed to SeO_3^{2-} under flooded conditions (Wang et al. 2016a; Wang et al. 2016b; Tang et al. 2017). The conversion of SeO_3^{2-} and SeO_4^{2-} to other Se species (e.g., Se^0 and Se^{2-}) under anoxic conditions (Martin et al. 2011; Li et al. 2014a; Wang et al. 2016a) may account for the similar abilities of SeO_3^{2-} and SeO_4^{2-} to reduce CH_3Hg^+ concentrations.

Our recent study demonstrated that SeO_3^{2-} application can reduce the concentrations of Hg in pak choi roots more than SeO_4^{2-} for upland soil (Tran et al. 2018a). Selenite treatments significantly decreased the proportion of Hg in pak choi shoots, whereas Hg accumulation notably increased in shoots of pak choi when treated with SeO_4^{2-}. These different phenomena can be ascribed to the differences in Hg tolerance among various plant species and different experimental conditions. Thus, these results helped identify the Se species that can be useful for Se amendment in future studies.

In addition, Se may have different effects on the accumulation and translocation of Hg species (Hg^{2+} and CH_3Hg^+) in plant tissues. The inhibitory effect of Se on Hg^{2+} uptake rather than the direct effect of Se on CH_3Hg^+ substantially decreased Hg^{2+} concentrations and negligibly decreased root CH_3Hg^+ concentrations in rice tissues (Zhao et al. 2014). These results were consistent with those obtained by Zhang et al. (2012), who suggested that increasing soil Se concentrations can inhibit the absorption of Hg^{2+} in rice roots but not that of CH_3Hg^+. Soil Se levels were negatively correlated with the TFs of Hg^{2+} that mediate Hg uptake from the soil to the root, which were positively correlated with the TFs of CH_3Hg^+ (Zhang et al. 2012).

Se doses

Selenium dose is more important than Se speciation in controlling Hg accumulation in plant. The results of our study showed that the SeO_3^{2-} or SeO_4^{2-} application can inhibit the absorption and bioaccumulation of Hg in pak choi grown in dryland soil. Notably, this inhibition may only significantly occur when SeO_3^{2-} or SeO_4^{2-} application rate is at an appropriate level (2.5 mg/kg) (Tran et al. 2018a). Under flooded conditions, Hg^{2+} levels of rice root decreased significantly by 36 to 48% under 6.0 mg/kg SeO_3^{2-} or SeO_4^{2-} treatment, respectively, which was higher compared with the decrease of ~22% for 3.0 mg/kg SeO_3^{2-} or SeO_4^{2-} (Tang et al. 2017). Feng et al. (2009) also found that the inhibition and stimulation effects of SeO_3^{2-} on the essential elements depended on the Se dosage applied. Low SeO_3^{2-} dosages significantly decreased essential element contents in Chinese brake fern, whereas high dosages enhanced the uptake of essential elements (Feng et al. 2009). Zhao et al. (2013) also found that a high amount of SeO_3^{2-} or SeO_4^{2-} (100 mg/L) treatment significantly increased Hg concentrations in the roots of garlic. In addition, high concentrations of SeO_3^{2-} or SeO_4^{2-} also inhibited garlic growth due to the phytotoxicity induced by Se. High Se application (Se > 5 μg/mL) did not reduce Hg accumulation in rice plants (Li et al. 2019).

In addition, Se also showed a dose-dependent effect on the formation of Fe plaques; only low doses of Se (≤ 1.0 mg/kg) promoted Fe plaque formation (Chang et al. 2013). Thus, the mechanisms underlying Hg detoxification in soil–plant systems after Se application resulted in the reduction of the accumulation of Hg in plants and improvement of the growth of plants. Li et al. (2015) demonstrated that the treatment with the appropriate level of Se (0.5 μg/mL in this study) is an efficient way to reduce Hg accumulation in rice and increase rice yield and quality.

Se application methods

The Hg–Se interactions were found in the rhizosphere (i.e., soil or rice root) instead of in the aboveground tissues (Wang et al. 2016a; Tang et al. 2017), which is probably be the reason for the reduced Hg bioaccumulation following Se application. Therefore, the two Se applications (to soil and leaves) differed distinctly in terms of their effects on Hg accumulation in plants. Soil Se application significantly reduced Hg accumulation in most cases, whereas foliar Se application had insignificant effects (Wang et al. 2016a). Specifically, the accumulation of CH_3Hg^+ in rice grains was largely inhibited (7–73%) after soil SeO_3^{2-} and SeO_4^{2-} application of 0.5–6.0 mg/kg, whereas no significant changes were found after foliar application (30 and 80 g/ha). Similarly, Tang et al. (2017) reported that Hg^{2+} concentrations in rice roots decreased after soil SeO_3^{2-} and SeO_4^{2-} application but not after foliar application, indicating that soil application could evidently reduce tissue Hg^{2+} concentrations by 0–48% in root, 15–58% in straw, and 26–74% in brown rice, although both applications resulted in comparable Se accumulation in aboveground tissues. In addition, foliar application of Se also has no effect on Hg accumulation in grape berries (*Vitis vinifera* L.), while the heavy metal content of Pb, Cr, Cd, As and Ni in grape berries was reduced under Se fertilizer treatments reduced compared to the control (Zhu et al. 2017).

Conclusion and future perspectives

The applications of Se at the appropriate rate can serve as potential strategy for Hg detoxification in soil and plant tissues and can reduce the public health risk. This review showed that the mechanisms for Hg detoxification by Se application included the following:

(1) Selenium application reduced the bioavailability of Hg in soil through the transformation of Hg into an immobile speciation and suppression of Hg methylation.
(2) Selenium application led the formation of inert HgSe or/and HgSe-containing proteinaceous complexes in the rhizosphere and/or roots results in immobilization of Hg on the interface of soil–plant root.
(3) Prevention of plant root uptake and translocation of Hg by increasing Fe plaques on root surfaces and sequestering Hg into the vacuoles of root cells.
(4) Reduction of plant oxidative stress under Hg stress by activating antioxidant systems, increasing photosynthetic pigment concentrations, decreasing lipid peroxidation products, alleviating the effect on DNA damage, and reducing protein participation.
(5) However, application of high rate Se showed synergistic toxic effect with Hg and inhibit the plant growth.

Besides the Hg bioavailability and the changes of Hg speciation in soil, Hg uptake, and transport within plants, more research is needed on the mechanisms associated with the detoxification of Hg by application of Se better. In addition, application methods need to be studied to understand the following:

(1) Selenium bioavailability and speciation transformation in soil and the combined capacity of Se and Hg to form stable HgSe complexes need to be clarified.
(2) The changes in Se speciation in plants must also be clarified given their effects on competitive adsorption or chelation between Se and Hg.
(3) Selenium absorption and transport within plants and the physiological and biochemical mechanisms underlying these processes need to be examined.

Author contribution Thi Anh Thu Tran synthesized document for the section "Reduction of Hg bioavailability in soil" and wrote the whole manuscript; Quang Toan Dinh synthesized document for the section "Reduction of Hg availability on the interface of soil–plant root"; Fei Zhou and Hui Zhai synthesized document for the section "Reduction of Hg uptake and translocation within plant"; Mingyue Xue and Zekun Du synthesized document for the section "Reduction of oxidative stress induced by Hg in plants"; Gary S Bañuelos revised and commented on the manuscript; Dongli Liang developed article ideas, revised, and commented on the manuscript.

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