Environmental and Experimental Botany 87 (2013) 58–68

Contents lists available at SciVerse ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Review

The roles of selenium in protecting plants against abiotic stresses

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ARTICLE INFO

Article history:
Received 1 May 2012
Received in revised form 14 August 2012
Accepted 11 September 2012

Keywords:
Abiotic stress
Antioxidants
Metalloids
Metals
Plants
Selenium

ABSTRACT

Selenium (Se), an essential element for animals and humans, has also been found to be beneficial to plants. In some countries around the world, such as China and Egypt, Se deficiency in the diet is a common problem. To counteract this problem, Se compounds have been used to increase the Se content in the edible parts of crops, through foliar sprays or base application of fertilizers. Se has also been shown to counteract various abiotic stresses induced in plants by cold, drought, high light, water, salinity and heavy metals (metalloids) (HMs), but the associated mechanisms are rather complicated and still remain to be fully elucidated. In this paper, we have focused on reviewing the effects of Se on HM-induced stress in plants, with an emphasis on the potential roles of Se compounds (e.g., selenite and selenate) in conferring tolerance against abiotic stresses. Numerous studies have implicated Se in the following mechanisms: the regulation of reactive oxygen species (ROS) and antioxidants, the inhibition of uptake and translocation of HM, changes in the speciation of HM and finally, rebuilding of the cell membrane and chloroplast structures and recovery of the photosynthetic system. In addition, two other mechanisms may be involved along with the established ones described above. Firstly, it may affect by regulating the uptake and redistribution of elements essential in the antioxidative systems or in maintaining the ion balance and structural integrity of the cell. Secondly, it may interfere with electron transport by affecting the assembly of the photosynthesis complexes. Future relevant studies should be increasingly focused on the changes in the cellular distribution of HM, the formation of Se–HM complexes, the substitution of S by the incorporation of Se into Se-Fe clusters and the relationships between Se, Fe, S and lipid peroxidation.

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http://dx.doi.org/10.1016/j.envexpbot.2012.09.002

1. Introduction

Selenium (Se) had long been considered as a toxic element until it was found also to be essential in 1957 (Schwarz and Foltz, 1957). Since then, the role of Se in mitigating environmental stress has been extensively investigated in animals and humans and, to a lesser extent, in plants. Selenium deficiency has been found to directly damage human health, and more than 40 types of diseases have been found to be associated with Se deficiency, such as Keshan disease, Kashin–Beck disease, cancer, cardiovascular disease, liver disease and cataracts (Tapiero et al., 2003; Cox and Bastiaans, 2007). In some areas of the world, e.g., in China, Egypt and Thailand (Tapiero et al., 2003), the inherent Se concentration in the soil is quite low, causing a Se deficiency in the human diet. In China, Se deficiencies, in some cases severe, have been reported in approximately 72% of counties, where the average daily intake of Se by adults is only 26–32 μg (Chen et al., 2002), far less than the recommended daily Se intake of 50–200 μg (Gailer, 2009).

On the other hand, heavy metal (metalloid) (HM) contamination has become a growing concern because of intensive anthropogenic activities over the last century. HMs have been widely documented to damage plants upon uptake, causing the following effects: (1) agents such as cadmium (Cd) (Kumar et al., 2012), arsenic (As) (Malik et al., 2012), lead (Pb) (Mroczek-Zdyrska and Wójcik, 2011), aluminum (Al) (Cartes et al., 2010) and antimony (Sb) (Feng et al., 2011) can induce oxidative stress; (2) HMs such as Cd (Filek et al., 2009), Pb, copper (Cu) zinc (Zn) (Fargašová et al., 2006) and As (Malik et al., 2012) inhibit photosynthesis and decrease the chlorophyll contents; (3) HMs such as Cd destroy the cell membrane integrity (Filek et al., 2009); and (4) agents such as Cd (Zembala et al., 2010), As (Cao et al., 2004) and Sb (Shtangeeva et al., 2011) inhibit the uptake of certain essential elements. Increased levels of HMs in crops have caused severe health risks in local residents, particularly in the population in developing countries such as China.

A current technology to apply Se fertilizer as a foliar spray or base fertilizer has been used to increase the Se content in the edible portion of crops (Broadley et al., 2010; Pezzarossa et al., 2012) and often to simultaneously counteract the injuries generated by different environmental stresses. For example, in a field experiment, He et al. (2004) found that the addition of selenite to lettuce (*Lactuca sativa* L.) plants subjected to Pb and Cd significantly decreased the accumulation of these heavy metals and at the same time enhanced the uptake of certain essential elements, including Se. However, when using this technology, the question is often raised: What is the optimal Se dosage? Se often exerts a dual effect on plant growth. At low doses, it can stimulate the growth of plants and counteract many types of environmental stresses, including HM, whereas at high dosages, it can also act as a pro-oxidant and cause damage to plants. In ryegrass (*Lolium perenne*), 1 mg kg^{-1} Se (H_2SeO_4) added to soil (Hartikainen et al., 2000) was believed to be marginally toxic, which is similar to the level we observed to be toxic to paddy-rice in a hydroponic system (0.8 mg L^{-1} Se (Na_2SeO_3), our unpublished data). Pezzarossa et al. (2012) also observed that 1 mg L^{-1} Se supplied with a foliar or fruit spray significantly increased the levels of Se in peaches and pears and simultaneously delayed the reduction in flesh firmness and fruit ripening, thus positively impacting the storage quality of fruits. However, Se levels up to 5 mg L^{-1} have been found to have beneficial effects on some Se-tolerant or Se-accumulating plants, such as red seaweed (*Gracilaria dura*) (Kumar et al., 2012), *Pteris vittata* L. (Feng and Wei, 2012) and *Spirulina platensis* (Belokobylsky et al., 2004). Currently, the Se doses routinely used in studies under hydroponic conditions to counteract environmental stress are often less than 1 mg L^{-1} (both for Se^{6+} and Se^{4+}) (Table 1).

Recently, Se has been found to counteract the detrimental effects of diverse environmental stressors, such as HM (Kumar et al., 2012), drought (Hasanuzzaman and Fujita, 2011), UV-B (Yao et al., 2010a,b), salt (Hasanuzzaman et al., 2011), water (Wang, 2011), senescence (Hartikainen et al., 2000), cold (Chu et al., 2010), high temperature (Djanaguiraman et al., 2010), and desiccation (Pukacka et al., 2011). The possible mechanisms of the Se-enhanced resistance and/or tolerance of plants to environmental stresses have not been fully clarified. In fact, the ability of Se to counteract various environmental stresses can be ascribed to several different mechanisms. In this paper, we attempt to summarize the current knowledge as well as gaps in knowledge, regarding the roles of Se in conferring tolerance in plants against abiotic stresses, especially HM stress.

2. Se regulates the production and quenching of reactive oxygen species (ROS)

Many stresses can result in the accumulation of ROS in plants, including cold, drought, high light, excess of water, salinity and HM. The enhanced production of ROS can pose a threat to plants, but ROS are also believed to act as signals for the activation of the stress-response and defense pathways (Mittler, 2002). ROS mainly include superoxide anion ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), hydroxylic free radical ($OH^\bullet$), singlet oxygen ($^1O_2$), methyl radical ($CH_3^\bullet$) and lipid peroxidation free radicals ($LOO^\bullet$, $ROO^\bullet$). After its generation, $O_2^{\bullet-}$ induces a series of electron transfer processes in plants, such as the spontaneous or enzyme-assisted (superoxide dismutase (SOD)) dismutation to H_2O_2 and a reaction with Fe^{3+} (or Cu^{2+}) to generate Fe^{2+} (or Cu^+), which will then react with H_2O_2 to generate hydroxyl radical ($OH^\bullet$) (which is highly active and affects the cell membrane) (Fig. 1).

Generally, two types of antioxidants are triggered in plants to balance the elevated ROS levels. One type is the low molecular weight substances, such as glutathione (GSH), ascorbate (AsA) and tocopherol, and the other type is the enzymes, such as, SOD, peroxidase (POD), catalase (CAT), ascorbate peroxidase (APX), glutathione peroxidase (GSH-Px), guaiacol peroxidase (GPOX) and glutathione reductase (GR) (Thompson et al., 1987; Lu, 1999; Hartikainen et al., 2000; Meharg and Hartley-Whitaker, 2002; Cao et al., 2004; Asada, 2006). These antioxidants can react with ROS directly or indirectly via enzyme catalysis (Fig. 1).

2.1. Optimal dosages of Se reduce the levels of ROS

Either directly or indirectly via the regulation of antioxidants, Se can control the production and quenching of ROS. The regulation of ROS levels by Se may be a key mechanism for counteracting

Table 1
Summary of effects of different species and dosage Se on the uptake, toxicity and detoxification of heavy metals (semimetals/metalloids) in plants.

Stresses	Speciation of heavy metals (metalloids)	Dosages of heavy metals/metalloids	Se speciation	Se dosages	Plants	Experimental details	Different effects of Se in heavy metal stressed plants, and the associated potential mechanisms	References
As	As(V)	1–20 μM	Se(IV)	5 μM	*Thunbergia alata*	Hydroponic culture	Enhances As toxicity because of enhanced As uptake and the competition between Se and As for PCs	Bluemlein et al. (2009)
	As(V)	0–5 mg L^{-1}	Se(IV)	0–5 mg L^{-1}	*Pteris vittata* L.	Hydroponic culture	Decreases As uptake and its translocation from root to aboveground	Feng et al. (2009a,b)
	As(V)	0, 0.05, 0.1 mg L^{-1}	Se(VI)	0, 0.05, 0.1 mg L^{-1}	Alfalfa [*Medicago sativa* L., Germain WL 512]	Hydroponic culture	Decreases As uptake	Khattak et al. (1991)
	–	0, 2.5, 5, 10 μM	–	0, 2.5, 5 μM	*Phaseolus aureus* Roxb.	Hydroponic culture	Decreases As uptake and lipid peroxidation; enhances levels of antioxidants, chlorophyll, MTs, thiols and GST; increases cellular viability, and rebuilds membranes	Malik et al. (2012)
	As(V)	0, 150, 300 μM	Se(VI)	0, 5, 10 μM	*Pteris vittata* L.	Hydroponic culture	Although enhances As concentration, Se induces more production of thiols and GSH to counterbalance the negative effects of increased As and inhibits lipid peroxidation	Srivastava et al. (2009)
Cd	Cd(II)	10, 20, 50 mg L^{-1}	Se(IV)	2, 5 mg L^{-1}	Garlic (Allium s ativum)	Hydroponic culture	Decreases Cd uptake and stimulates growth of root and seedlings	Sun et al. (2010)
	Cd(II)	600 μM	Se(VI)	2 μM	Rape (*Brassica napus* L., Polish genotype cv. Bojan) and wheat (*Triticum aestivum*, Polish genotype cv. Kamila and a Finnish genotype cv. Manu)	Hydroponic culture	Promotes growth, reduces lipid peroxidation, enhances membrane stability, and counterbalances the Cd-induced changes in nutrients	Zembala et al. (2010)
	Cd(II)	2 mg L^{-1}	Se(VI)and Se(IV)	0.5–6 mg L^{-1}	Kidney bean (*Phaseolus mungo*)	Pot culture	Decreases Cd uptake and selenite has more effective in decreasing Cd uptake than selenate	Shanker et al. (1995)
	Cd(II)	–	Se(VI)and Se(IV)	–	Maize (Zea mays)	Pot culture	Decreases Cd uptake	Shanker et al. (1996b)
	Cd(II)	1 mg L^{-1}	Se(IV)	1 mg L^{-1}	Broccoli (*B. oleracea*)	Hydroponic culture	Decreases Cd uptake in fruit and leaves, but enhances it in roots	Pedrero et al. (2008)
	Cd(II)	0.4 mM	Se(IV)	50 μM	Red seaweed *Gracilaria dura*	Hydroponic culture	Decreases Cd uptake, MDA, ROS, levels and increases the levels of chlorophyll, carotenoids, NP—SH, GSH, PCs DHA and AsA	Kumar et al. (2012)
	Cd(II)	400, 600 μM	Se(VI)	2 μM	winter rape (*Brassica nap.* L. var. Górczański)	Murashige-Skoog media	Stimulates growth, decreases Cd uptake, MDA, H_2O_2 contents and diminishes the induced-increases in SOD, CAT and APX activity	Filek et al. (2008)
	Cd(II)	400 μM	Se(VI)	2 μM	Rape seedlings	Murashige-Skoog media	Increases chloroplast size, monogalactosyl-diacylglycerol and phospholipid contents, fatty acid saturation; rebuilds ultrastructure; decreases digalactosyl-diacylglycerol content	Filek et al. (2010)

Table 1 (*Continued*)

Stresses	Speciation of heavy metals (metalloids)	Dosages of heavy metals/metalloids	Se speciation	Se dosages	Plants	Experimental details	Different effects of Se in heavy metal stressed plants, and the associated potential mechanisms	References
Cd, Zn, Cu, Pb	–	Cu: $3\,\mathrm{mg\,L^{-1}}$; Cd: $6\,\mathrm{mg\,L^{-1}}$; Zn: $15\,\mathrm{mg\,L^{-1}}$; Pb: $100\,\mathrm{mg\,L^{-1}}$	Se(IV)	$3\,\mathrm{mg\,L^{-1}}$	Mustard seedlings (*Sinapis alba* L.)	Hydroponic culture	Decreases their uptake and/or translocation	Fargašová et al. (2006)
Cd, Pb	–	Cd: $1\,\mathrm{mg\,kg^{-1}}$; Pb: $10\,\mathrm{mg\,kg^{-1}}$	Se(IV)	$1\,\mathrm{mg\,kg^{-1}}$	Chinese cabbage (*Brassica rapa*) and lettuce (*Lactuca sativa* L.)	Pot culture and farmland experiment	Decreases their uptake	He et al. (2004)
Cr	Cr(III)and Cr(VI)	–	Se(VI) and Se(IV)	–	Spinach (*Spinacea oleracea*)	Sand and soil culture	Decreases Cr uptake	Srivastava et al. (1998)
	Cr(III)	$3\,\mathrm{mg\,L^{-1}}$	Se(IV)	$5\,\mathrm{mg\,L^{-1}}$	*Spirulina platensis*	Hydroponic culture	Decreases Cr uptake	Belokobylsky et al. (2004)
Sb	Sb(III)	$5\,\mathrm{mg\,L^{-1}}$	Se(IV)	$0–5\,\mathrm{mg\,L^{-1}}$	Hybridrice (*Oryza sativa* L.,cv. Weiyou402)	Hydroponic culture	Decreases Sb uptake and MDA content	Feng et al. (2011)
Hg	Hg(II)	$2, 5\,\mathrm{mg\,L^{-1}}$	Se(VI) and Se(IV)	–	Tomato (*Lycopersicum esculentum*)	Sand and soil culture	Decreases Hg uptake	Shanker et al. (1996a)
	Hg(II)	$2, 5\,\mathrm{mg\,L^{-1}}$	Se(VI) and Se(IV)	$0.5–6\,\mathrm{mg\,L^{-1}}$	Radish plants (*Raphanus sativus*)	Pot culture	Decreases Hg uptake and possibly forms HgSe insoluble complex in soil	Shanker et al. (1996c)
	Hg(II)	45 μM	Se(IV)	60 mM	*Glycine max* (soybean)	Soil and a 50:50 mix of soil and ProMix	Forms a high molecular weight entity containing Se and Hg in plants	Yathavakilla and Caruso (2007)
Al	Al(III)	0.2 mM	Se(IV)	0–10 μM	Ryegrass (*Lolium perenne* L. cv. Nui)	Hydroponic culture	Enhances Al uptake, accompanying with enhanced antioxidative capacity; however, above 2 μM Se will induce stresses	Cartes et al. (2010)
Pb	Pb(II)	50 μM	Se(IV)	1.5, 6 μM	*Vicia faba* L. *minor* cv. Nadwiślański	Hydroponic culture	Has limited effects on Pb uptake and translocation	Mroczek-Zdyrska and Wójcik (2011)

– Indicates the relevant information cannot be obtained.

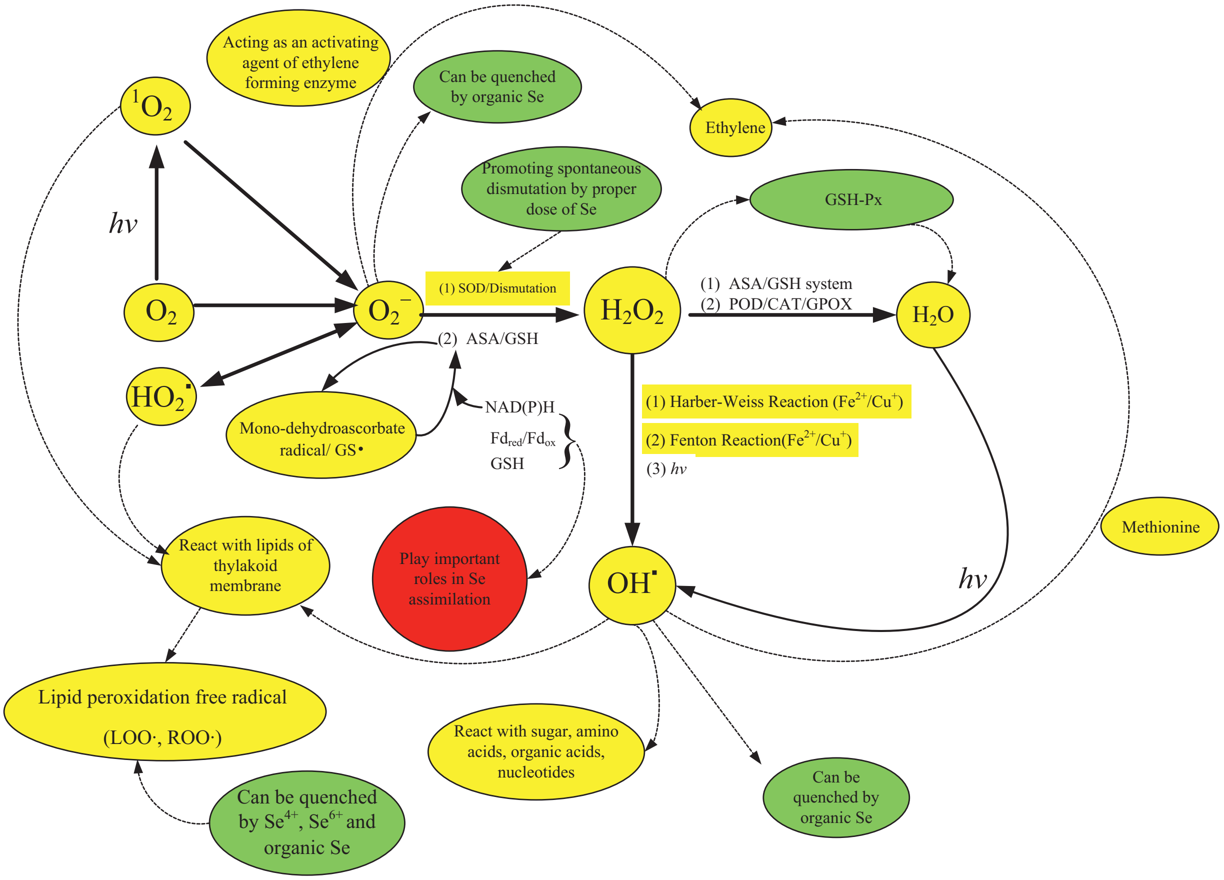

Fig. 1. Overview of the mechanisms responsible for the production and quenching of reactive oxidative species (ROS) after selenium (Se) addition to stressed plants. Selenium can regulate the ROS levels in stressed plants through three pathways: (1) by stimulating the spontaneous dismutation of $O_2^{\bullet -}$ into H_2O_2; (2) by a direct reaction between Se-containing compounds and ROS; and (3) by the regulation of antioxidative enzymes. Another possible mechanism is that Se may affect the assembly of photosynthetic complexes to regulate the levels of ROS.

environmental stress in plants. Under normal conditions, the production of ROS in plant cells is maintained at low levels, i.e., less than 240 μM s^{-1} $O_2^{\bullet -}$ and 0.5 μM H_2O_2 in chloroplasts. However, under stress conditions, the corresponding levels increase to 240–720 μM s^{-1} $O_2^{\bullet -}$ and 5–15 μM H_2O_2 (Mittler, 2002). The minor addition of Se to the growth substrates can reduce the excess ROS generation, especially that of $O_2^{\bullet -}$ and/or H_2O_2, in plants subjected to diverse environmental stresses. Cartes et al. (2010) observed that selenite alleviated Al-induced oxidative stress in ryegrass roots mainly by enhancing the spontaneous dismutation of $O_2^{\bullet -}$ to H_2O_2. Mroczek-Zdyrska and Wójcik (2011) found that a low dosage of Se (1.5 μM Na_2SeO_3) decreased the $O_2^{\bullet -}$ levels in the roots of *Vicia faba* L. exposed to Pb. In Cd-stressed marine red alga, 50 μM Se (Na_2SeO_3) was observed to efficiently ameliorate the Cd toxicity by decreasing the accumulation of ROS ($O_2^{\bullet -}$ and H_2O_2) (Kumar et al., 2012). In an experiment using rape (*Brassica napus*) seedlings exposed to 400 or 600 μM Cd, the addition of 2 μM Se (Na_2SeO_4) was found to decrease the H_2O_2 accumulation in the shoots and roots of the plant (Filek et al., 2008). Decreases in the ROS levels upon Se addition in plants subjected to other stresses have also been observed, such as in grain sorghum (*Sorghum bicolor* (L.) Moench) exposed to high temperature ($O_2^{\bullet -}$ and H_2O_2) (Na_2SeO_4; Djanaguiraman et al., 2010), wheat (*Triticum aestivum* L., cv. Han NO.7086) seedlings under UV-B radiation stress ($O_2^{\bullet -}$) (Na_2SeO_3; Yao et al., 2010a,b, 2011) and cold stress ($O_2^{\bullet -}$) (Na_2SeO_3; Chu et al., 2010), rapeseed seedlings under salt and drought stress (H_2O_2) (Na_2SeO_4; Hasanuzzaman et al., 2011; Hasanuzzaman and Fujita, 2011), *Trifolium repens* L. under water stress (H_2O_2) (Na_2SeO_4; Wang, 2011) and mungbean (*Phaseolus aureus* Roxb.) under As stress (H_2O_2) (Malik et al., 2012).

Three possible mechanisms have been proposed for the decrease in $O_2^{\bullet -}$ levels when the appropriate doses of Se were added, including the spontaneous dismutation of $O_2^{\bullet -}$ into H_2O_2 (without catalysis by the SOD enzyme) (Hartikainen et al., 2000; Cartes et al., 2010), the direct quenching of $O_2^{\bullet -}$ and $OH^{\bullet}$ by Se compounds (Xue et al., 1993; illustrated in Fig. 1), and the regulation of antioxidative enzymes.

However, in their *in vitro* experiment Xue et al. (1993) found that Se compounds failed to directly scavenge H_2O_2 but could eliminate free radical-mediated lipid peroxidation. In accordance with the above findings, other researchers have found that low doses of Se had limited effects on the reduction of H_2O_2 levels in non-stressed rape seedlings (Filek et al., 2008) and marine red algae (Kumar et al., 2012). Interestingly, when stresses were present in these studies, the H_2O_2 levels were greatly diminished by the proper doses of Se, possibly due to the reactivation of antioxidants by Se, especially of H_2O_2-quenchers (e.g., GSH-Px).

2.2. Excess Se triggers the accumulation of ROS

Reports have shown that excess Se gives rise to the robust accumulation of ROS in plants, although the actual role of Se in plants has not yet been resolved (Tamaoki et al., 2008; Freeman et al., 2010; Mroczek-Zdyrska and Wójcik, 2011). We have proposed that the increased production of ROS at high Se levels may be partially related to an imbalance in the levels of GSH, thiols

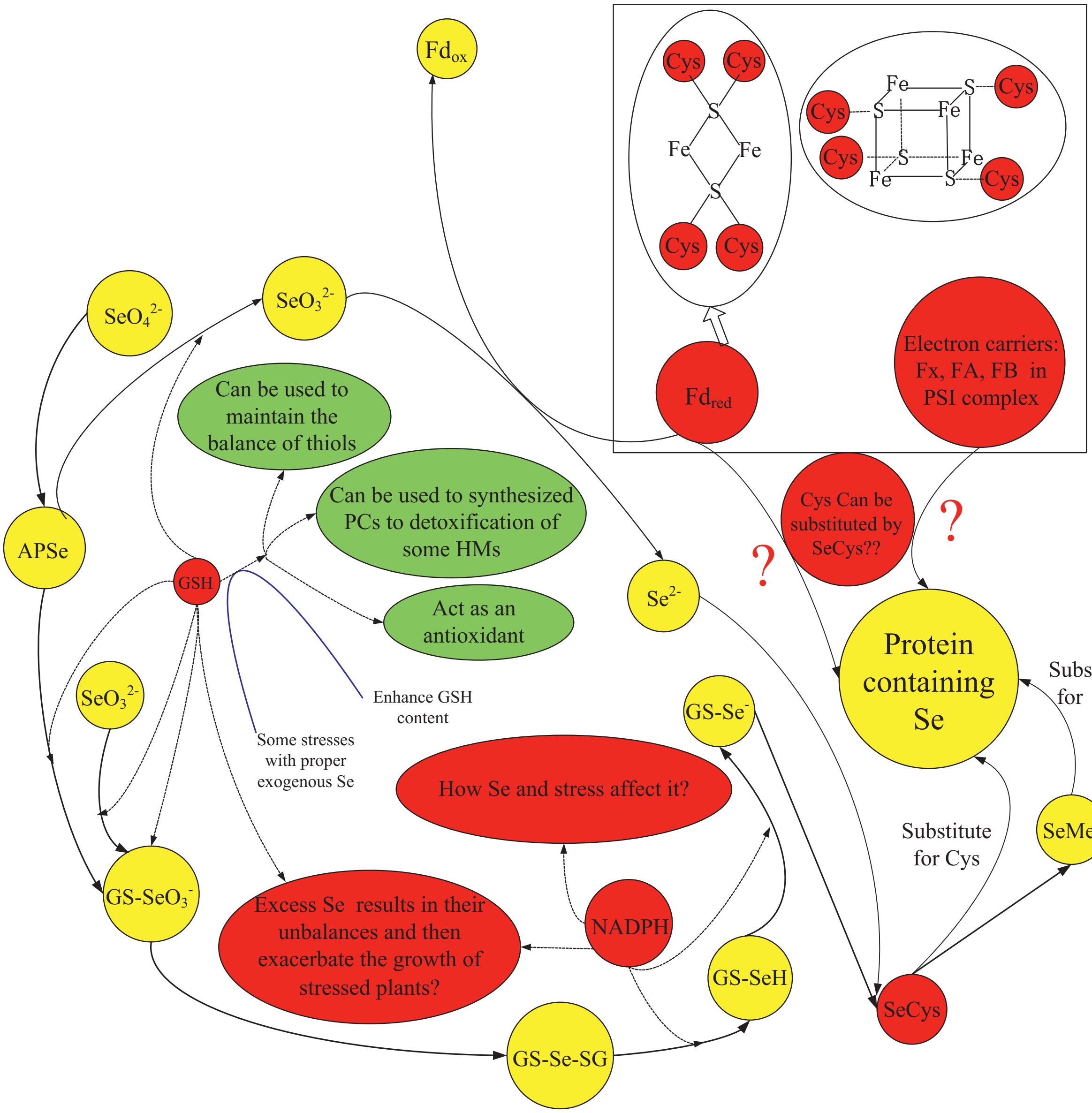

Fig. 2. The major Se assimilation pathways in plants. Commonly, plants will convert Se into Se-Met and Se-Cys and ultimately incorporate them into proteins in place of S, thereby causing Se toxicity. During this process, the levels of GSH, S, Fd_S and NADPH play vital roles, possibly determining the switch between the beneficial and toxic effects of Se in plants.

(—SH), ferredoxins (Fd_{red}) and/or NADPH, which can play vital roles in the assimilation of Se (Fig. 2). If these substances are not sufficient to simultaneously meet the needs of Se-assimilation and ROS quenching, the addition of Se may lead to a ROS burst and the inhibition of plant growth. For example, in the roots of *Vicia faba* L. plants exposed to 50 μM Pb, the addition of 1.5 μM Se is found to enhance the cell viability and total —SH content (Mroczek-Zdyrska and Wójcik, 2011), whereas a higher level of Se, 6 μM, to greatly enhance the $O_2^{\bullet-}$ level and decreased the cell viability and total —SH content (Mroczek-Zdyrska and Wójcik, 2011).

The responses of ROS to excess Se may be species dependent. Paciolla et al. (2011) observed that the leaf discs of *Senecio scandens* L. treated with selenite manifested significantly elevated H_2O_2 level, whereas in the presence of the same Se dose in the form of selenate, no such elevation was observed. These differences in the ROS response to different Se species may be ascribed to the rate-limiting step of reduction from selenate to selenite in plants. Plants (*Brassica oleracea* var. *botrytis* L., *Brassica juncea* L., *Beta vulgaris* L. and *Oryza sativa* L.) exposed to selenate have been reported to take up and transfer Se to the aboveground parts, and the Se species remained as selenate. However, when exposed to selenite, the Se was mainly accumulated in the roots and transformed into L-selenomethionine (SeMet) and SeMet-like species in the plants (Zayed et al., 1998). A large reducing potential is required for the transformation of selenite into SeMet-like species, consequently disturbing the quenching of ROS (Fig. 2).

2.3. *The responses of antioxidants on reducing ROS*

2.3.1. *GSH-Px enzyme*

The addition of Se to stressed plants can influence the activities or levels of antioxidants and thus regulate the ROS levels. In plants, GSH-Px is a powerful scavenger of H_2O_2 and lipid hydroperoxides, with the help of GSH. GSH-Px is believed to be a key enzyme, which can be widely and robustly activated by Se in various plants exposed to diverse environmental stresses. In the absence of Se, the external H_2O_2 in *Chlamydomonas* cells is found to be quenched by the APX and CAT enzymes; however, in the presence of Se, H_2O_2 is primarily scavenged by GSH-Px instead of APX and CAT (Takeda et al., 1997). Hartikainen et al. (2000) reported a dramatic increase in the activity of GSH-Px in both young and older ryegrass seedlings treated with different levels of Se. The activation of the GSH-Px enzyme is also observed in many Se-treated plants subjected to diverse stresses, e.g., in rape seedlings under Cd stress (Filek et al., 2008), salt-stress (Hasanuzzaman et al., 2011) and drought stress (Hasanuzzaman and Fujita, 2011), in Cd-stressed marine red algae (Kumar et al., 2012), in Pb-stressed *Vicia faba* L. roots (Mroczek-Zdyrska and Wójcik, 2011), in senescing lettuce (Xue et al., 2001) and soybean (Djanaguiraman et al., 2005), in desiccation-stressed silver maple (*Acer saccharinum* L.) seeds (Pukacka et al., 2011), and in high-temperature-stressed grain sorghum (Djanaguiraman et al., 2010). The increase in the activity of the GSH-Px enzyme in response to the presence of Se suggests a unique role for this enzyme in counteracting oxidative stress in plants.

2.3.2. SOD enzyme

The response of the SOD enzyme (which quenches $O_2{}^{\bullet-}$ to produce H_2O_2) is found to be complicated when plants are stressed under various adverse environmental conditions in the presence of Se. Comparing the results of the relevant studies reported in the literatures, we believe that three main factors may control the SOD activity in plants exposed to Se.

The first factor is the level of stress. At low stress levels, the antioxidative capacity in a plant should be sufficient to support the normal growth of the plant. The ROS production and quenching can thus be well controlled by antioxidants, such as GSH-Px, resulting in the spontaneous reduction of $O_2{}^{\bullet-}$ and a reduced requirement for SOD (Hartikainen et al., 2000). However, under a severe stress, high levels of ROS ($O_2{}^{\bullet-}$) will be produced, and SOD activity is required. For example, with the addition of Se, Hartikainen et al. (2000) observed decreased SOD activity in younger, but increased SOD activity in older (senescence stress) ryegrass. Similar results were observed by Xue et al. (2001) in lettuce plants. Several authors have also observed enhanced SOD activity after Se addition in many stressed plants, such as in Al-stressed ryegrass (Cartes et al., 2010), light-stressed potato (*Solanum tuberosum* L.) (Seppänen et al., 2003), Se-stressed *Pteris vittata* L. (Feng and Wei, 2012), senescing soybean (Djanaguiraman et al., 2005), UV-B-stressed wheat seedlings (Yao et al., 2010a,b), water-deficient *Trifolium repens* L. (Wang, 2011), Cd-stressed marine red algae (Kumar et al., 2012), As-stressed mungbean (Malik et al., 2012) and high-temperature-stressed grain sorghum (Djanaguiraman et al., 2010).

The second factor affecting SOD activity in Se-exposed plants is the dose of the Se supplementation. For example, Cartes et al. (2010) observed that when ryegrass was subjected to 0.2 mM Al, the addition of 2 μM Se (selenite) significantly decreased, but 10 μM Se increased, the SOD activity. The enhancement in SOD activity might suggest the excess production of $O_2{}^{\bullet-}$ due to the toxicity of Se. Our previous results have also shown that SOD activity was inhibited at relatively low Se levels ($\leq 2\,mg\,L^{-1}$) but enhanced at a high level of Se ($\geq 5\,mg\,L^{-1}$) in the Se accumulator *Pteris vittata* L. (Feng and Wei, 2012).

The final factor involves variations in the concentrations of SOD cofactors, such as iron (Fe), manganese (Mn), Cu and Zn (discussed below). For example, in light-stressed potato plants, chloroplast CuZn-SOD transcript was found to decrease with the addition of $0.3\,mg\ Se\ L^{-1}$ (H_2SeO_3), whereas no significant changes in mitochondrial Mn-SOD transcript levels were observed (Seppänen et al., 2003).

2.3.3. Other antioxidants

In addition to GSH-Px and SOD, other antioxidants can also function when Se is used to diminish the damage of environmental stress to plants, such as the enzymes CAT, POD, GR, GPX and APX, as well as some low molecular substances such as AsA and tocopherol. These antioxidants are largely responsible for scavenging H_2O_2. APX is believed to function as a signaling substance for the fine modulation of ROS, whereas CAT (mainly localized in peroxisomes) might be responsible for the removal of excess ROS (Mittler, 2002). In stressed plants, Se was observed to significantly reactivate these two enzymes, particularly CAT (Yao et al., 2009a,b; Djanaguiraman et al., 2010; Yao et al., 2010a,b; Hasanuzzaman et al., 2011; Yao et al., 2011; Malik et al., 2012). Thus, it is reasonable to speculate that the increased activities of these enzymes may indicate excess ROS (H_2O_2) in these studies.

H_2O_2 and $O_2{}^{\bullet-}$ are relatively stable and less toxic compared with the other ROS, and their major threat lie in their ability to produce highly reactive $OH^{\bullet}$ via the metal-dependent Haber–Weiss or Fenton reactions (Fig. 1). $OH^{\bullet}$ is the most powerful oxidizing species and can react non-specifically with any biological molecule (Mittler, 2002). However, no information about the changes in $OH^{\bullet}$ levels upon Se supplementation in stressed plants has been available up to now. It is critical to maintain steady-state levels of H_2O_2 and $O_2{}^{\bullet-}$ to avoid the over production of $OH^{\bullet}$. To achieve this goal, maintaining the balance between SOD and APX or CAT activities in plants is crucial. If ROS levels are largely increased by excess Se and/or high stress levels (as described), the overproduction of SOD, CAT and APX is required to maintain the balance of H_2O_2 and $O_2{}^{\bullet-}$.

In addition, maintaining a high reducing power of AsA and GSH is essential to quench excess ROS in plants (Mittler, 2002). To this end, high levels of GR, monodehydroascorbate reductase (MDAR), dehydroascorbate reductase (DHAR) and NADPH are required (Mittler, 2002). Because Se can increase the GSH content to synthesize organic-Se (Fig. 2, see below), high levels of AsA, GR, MDAR, DHAR and NADPH are thus expected. This conclusion is supported by the results of Hasanuzzaman and Fujita (2011), who found that when rapeseed seedlings were exposed to drought stress, Se-pretreated seedlings exhibited increased AsA levels and significantly enhanced APX, DHAR, MDAR, GR, GPX and CAT activity compared to drought-stressed plants without Se. The increased activation/levels of APX, GSH, CAT and GR were also observed in the Se accumulator *Pteris vittata* L. after excess Se addition (Feng and Wei, 2012).

2.4. The vital roles of S, GSH and other sulfhydryl compounds

It is well established that GSH may directly react with Se to form Se-containing cysteine (SeCys) and methionine (SeMet) and ultimately synthesize Se-containing proteins (Terry et al., 2000; Fig. 2). ROS is produced during the selenite reduction processes by sulfhydryl groups, such as GSH (Kramer and Ames, 1988). In non-accumulating plants, the substitution of Se for S to form Se-containing proteins is considered a major mechanism of Se toxicity (Terry et al., 2000). Generally, sulfate exerts antagonistic effects on selenate uptake in plants because of the competition between selenate and sulfate for the sulfate transporters in the plasma membranes. Thus in practice, sulfate can reduce the toxicity of excess Se. Occasionally, the S concentration in plants can be enhanced by increasing the Se levels (Zhang et al., 2007; Tamaoki et al., 2008; Freeman et al., 2010).

Therefore, if Se is added to stressed plants, more S is expected to be required to synthesize more GSH or non-protein-thiols to meet the needs of Se-assimilation and ROS quenching. The results of many studies indirectly support this postulation. For example, Kumar et al. (2012) observed that in marine red algae treated with 400 μM Cd, the addition of 50 μM Na_2SeO_3 significantly enhanced the levels of GSH, non-protein-thiols and phytochelatin (PCs). Similarly, Hasanuzzaman et al. (2011) and Hasanuzzaman and Fujita (2011) reported that the GSH content was also enhanced by Se both in salt-stressed and drought-stressed rapeseed seedlings. In As-stressed mungbean, the concentrations of GSH, metallothioneins

(MTs) and thiols (—SH) and the activity of glutathione-s-transferase (GST) were found to be enhanced by Se (Malik et al., 2012). In Pb-stressed *Vicia faba* L., 1.5 μM and 6 μM Se markedly enhanced the total —SH content (Mroczek-Zdyrska and Wójcik, 2011). However, the inhibition of S uptake by the addition of Se has also been observed in some circumstance. For example, Zembala et al. (2010) found that in the absence of environmental stress, the addition of Se (2 μM Na_2SeO_4) enhanced the uptake of S in rape seedlings, but in the presence of Cd, increasing Se levels decreased the concentrations of both S and Cd dramatically. Bluemlein et al. (2009) suggested that the competition between As and Se for PCs as binding partner (see reaction (2)) might drastically decrease the ability of *Thunbergia alata* to detoxify cellular arsenite. They also claimed that if the levels of free —SH and PCs were insufficient, the addition of Se would enhance, rather than diminish, the arsenate toxicity in *Thunbergia alata*. Therefore, it can be concluded that the restoration of the damage to plants by Se might be significantly associated with S and its derivative (such as GSH, MTs, —SH and PCs):

$$4GSH + SeO_3{}^{2-} + 2H^+ \rightarrow GSSG + GS\text{–}Se\text{–}GS + 3H_2O(\text{seeFig.1}) \quad (1)$$

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

Furthermore, in *in vitro* trials, H_2O_2 was reported to be predominantly produced at low —SH concentrations, whereas $O_2{}^{\bullet -}$ was mainly produced at high —SH concentrations (Kramer and Ames, 1988). Accordingly, the Se-induced increases in —SH levels in the studies of Kumar et al. (2012), Hasanuzzaman et al. (2011) and Malik et al. (2012) were well in line with the burst of $O_2{}^{\bullet -}$ at high Se levels. We hypothesize that high levels of Se enhance the production of —SH, resulting in a burst of $O_2{}^{\bullet -}$, which may thus activate SOD and other antioxidative enzymes to restore the balance of $O_2{}^{\bullet -}$.

The resistance mechanism of Se in *Arabidopsis* was found to be associated with enhanced S uptake and reduction (Tamaoki et al., 2008). Moreover, GSH and other sulfhydryl compounds might also play important roles in Se tolerance mechanisms. Freeman et al. (2010) claimed that in *Stanleya pinnata* (*Brassicaceae*), the Se tolerance mechanisms were highly connected to the increased levels of AsA, GSH, total S and non-protein —SH. In three Se-stressed genotypes of wheat seedlings, more GSH was synthesized than in non-Se-stressed plants (Łabanowska et al., 2012). Therefore, if stressed plants lose their ability to maintain balanced levels of agents including GSH, total S and non-protein —SH, the addition of excess Se can aggravate the damage caused by other sources of environmental stress.

2.5. *Possible roles of Se in the assembly of iron–sulfur clusters*

In chloroplasts, Fe-S clusters are required to maintain the normal operation of the cytochrome B/F complex, photosystem I, and ferredoxin, and thus, affect electron transport in the thylakoids (Raven et al., 1999). It is possible that the substitution of Se for S may occur under conditions of supplementation with either optimal or excess Se. The Se, which will insert into the Fe–S clusters (Fig. 2), may be an important factor influencing the electron transfer chain, the emergence and quenching of ROS and the responses of antioxidants in stressed plants. To date, indirect evidence from *in vivo* experiments, but not direct evidence, has led to this hypothesis (Fig. 2, for example: Fd_{red}, F_X, F_A, F_B electron carriers in the PSI complex). To prevent the incorporation of Se into proteins to reduce the Se toxicity, Se could be volatilized as dimethyl(di)selenide or accumulated as non-protein seleno-amino acids or elemental Se (Se^0) (which is insoluble, has relatively low toxicity and is expected to block elemental S (S^0) to assemble Fe–S clusters) (Garifullina et al., 2003). Se^0 can be formed by a selenite reduction reaction or through the cleavage of SeCys by SeCys lyase (SL) activity. If SL is overexpressed in plants, Se^0, and not selenoproteins, might be expected to accumulate, consequently enhancing the tolerance of plants to Se. However, when mouse SL is overexpressed in *Brassica juncea* (Indian mustard), enhanced Se accumulation was observed in both the cytosol and chloroplast, but the tolerance to Se was not enhanced in the chloroplast (Garifullina et al., 2003). The lack of augmented tolerance to Se suggested that the generated Se^0 may participate in other physiochemical reactions in chloroplasts. The chloroplasts, rather than the cytosol, are the site of Fe–S cluster formation (Garifullina et al., 2003). Therefore, based on above results, the following two speculations are reasonable: (1) Se^0 can feasibly compete with S^0 and disrupt the formation or function of Fe-S clusters in chloroplasts and (2) simultaneously, the non-specific incorporation of SeCys into proteins can also be inhibited by the enhanced mouse SL activity because the cytosol is an important site of SeCys cleavage into Se^0.

The above hypotheses are well supported by the results of Pilon et al. (2003), whose study involved two transgenic models, one overexpressing the gene for SL in the chloroplast (chloroplastic-SL transgenics) and the other in the cytosol (cytosolic-SL plants). They demonstrated that the cytosolic-SL plants showed enhanced tolerance to Se, but the chloroplastic-SL transgenics displayed decreased Se tolerance, indicating an overproduction of toxic Se^0 in the chloroplasts. Regulatory mechanisms in the chloroplast might exist to modulate CpNifS (a chloroplastic protein that has both Cys desulfurase and SL activity), but not mouse SL, activity toward both Cys and SeCys, resulting in the protection against the incorporation of Se into both proteins and Fe-Se clusters (Van Hoewyk et al., 2005).

3. Se restores cellular structure and function

3.1. *Restoration of cell membrane structure and cell integrity*

The decreases in $O_2{}^{\bullet -}$ and H_2O_2 levels upon Se addition suggest a disturbance of the ROS reaction chain, which diminishes the damages to the lipids of the plant cell membranes. Optimal Se supplementation has been shown to inhibit the accumulation of malondialdehyde (MDA, an indicator of the extent of lipid peroxidation) in many stressed plants, such as Cd-stressed rape seedlings (Zembala et al., 2010), Sb-stressed paddy rice (Feng et al., 2011), Cd-stressed broccoli (*Brassica oleracea*) (Pedrero et al., 2008) and red seaweed (Kumar et al., 2012), Pb-stressed *Vicia faba* L. (Mroczek-Zdyrska and Wójcik, 2011), Al-stressed ryegrass (Cartes et al., 2010), As-stressed mungbean (Malik et al., 2012), senescence-stressed ryegrass (Hartikainen et al., 2000; Xue et al., 2001), salt- and drought-stressed rapeseed seedlings (Hasanuzzaman et al., 2011; Hasanuzzaman and Fujita, 2011), senescence-stressed soybean (Djanaguiraman et al., 2005), high-temperature-stressed sorghum (Djanaguiraman et al., 2010) and salt-stressed cucumber (*Cucumis sativus* L.) cv. Polan F1 seedlings (Hawrylak-Nowak, 2009).

In Cd-treated rape seedlings, Filek et al. (2010) found that Cd caused the degradation of internal chloroplast membranes. However the addition of 2 μM Se allowed the rebuilding of the chloroplast ultrastructure, reorganization of the structure of the thylakoids and stroma, and increase in the chloroplast size, fatty acid unsaturation and fluidity of the cell membrane. In their previous study, Filek et al. (2009) also observed that in Cd-stressed wheat, Se could regulate the degree of galactolipid unsaturation and thus reconstruct the lipid and fatty acid composition of the plastid envelope membranes. Therefore, Filek et al. (2009) hypothesized that the detoxification of Cd by Se might be associated with as the following two mechanisms: (1) the addition of Se could reactivate membrane enzymes and restore the transport of metabolites important for chloroplast function and (2) Se could compete with Cd for specific binding sites, such as the thiol groups of cysteine, in envelope membrane proteins. The improvement of cell membrane integrity in response to Se may reduce the electrolyte leakage in plants exposed to environmental stresses caused by the herbicide paraquat (Seppänen et al., 2003), desiccation (Pukacka et al., 2011), As (Malik et al., 2012), and Cd (Zembala et al., 2010).

3.2. Recovery of the photosynthesis functions

When plants are subjected to environmental stress, their chloroplasts are damaged, leading to disrupted photosynthesis. However, the addition of appropriate levels of Se can somewhat reduce the damage to the chloroplasts and increase the chlorophyll contents (Filek et al., 2009; Hawrylak-Nowak, 2009; Chu et al., 2010; Wang, 2011; Yao et al., 2011; Malik et al., 2012).

Through proteomic analysis, Wang et al. (2012) revealed that in rice (*Oryza sativa* L.) seedlings, low doses of Se enhanced photosynthesis. In addition, in sorghum, Se application significantly increased the photosynthetic rate, stomatal conductance and transpiration rate (Djanaguiraman et al., 2010). The restoration of photosynthesis in stressed plants after Se application may be closely related to the decreased ROS levels, reactivation of antioxidants, restored structure of the damaged chloroplasts and enhanced production of other vital metabolites (such as GSH and —SH-like substances).

However, excess Se may aggravate the damage to the photosynthesis system in plants. Higher levels of Se can damage photosynthesis apparatus, inhibit photosynthesis, and result in the overproduction of starch (Vítová et al., 2011; Wang et al., 2012). Excess Se was found to decrease the light energy absorbed by the antenna system (ABS/CS), the stream of excitation energy (TRo/CS), the transport of electrons through PSII (ETo/CS), the efficiency of energy transport from the antennas to reaction centers (φ_{p0}), the outside these centers (ψ_0), the quantum yield of electron transport in PSII (φ_{E0}) and the density of active centers of photochemical reactions in PSII (RC/CS) and to impair the O_2 evolving center (OEC) in three genotypes of wheat (Łabanowska et al., 2012).

4. Other mechanisms for counteracting HM toxicity

4.1. Direct inhibition of the uptake and translocation of HM

Reports have shown that proper doses of Se can protect plants against the damage caused by HMs, including As, mercury (Hg), Pb, Cd, Zn, Cu, chromium (Cr) and Sb (Khattak et al., 1991; Shanker et al., 1995; Shanker et al., 1996a,b,c; Srivastava et al., 1998; Ebbs and Weinstein, 2001; Belokobylsky et al., 2004; He et al., 2004; Belzile et al., 2006; Fargašová et al., 2006; Yathavakilla and Caruso, 2007; Filek et al., 2008; Pedrero et al., 2008; Feng et al., 2009a; Sun et al., 2010; Zembala et al., 2010; Feng et al., 2011; Kumar et al., 2012; Malik et al., 2012). The relevant HM detoxification mechanisms by Se might be connected to the inhibition of uptake and translocation of HMs from the roots to aboveground and/or the speciation transformation to nontoxic species. The different effects of Se on HM toxicity in stressed plants and the potential associated mechanisms are illustrated in Table 1.

It is interesting to note that in some cases, Se addition can stimulate the accumulation of HM, such as As in *Thunbergia alata* (Bluemlein et al., 2009), Al in ryegrass (Cartes et al., 2010), Cd and Cu in the roots of *Sinapis alba* L. seedlings (Fargašová et al., 2006) and Cd and Cu in wheat (*Triticum aestivum* L. cv. Sunny) and pea (*Pisum sativum* L. cv. Fenomen) (Landberg and Greger, 1994), which might be attributable to an improper dose of Se, abnormal S assimilation (although this was not detected in the studies), and/or the different plant species.

4.2. Regulation of the uptake and distribution of essential elements

The regulation of the uptake and redistribution of some essential elements by Se is believed to be an important mechanism to reactivate associated antioxidants, reduce the ROS levels and improve plant tolerance to stress. However, the information about the effects of Se on the uptake of essential elements in stressed plants is insufficient. The effects of Se on the uptake and assimilation of S in plants have been intensively investigated because of the similarities in the chemical properties of S and Se. In some cases, supplementation with appropriate Se levels stimulated S uptake in many plant species, as described above. So far, very few studies have been undertaken to explore the changes in additional essential element concentrations when plants are co-exposed to Se and environmental stress.

Variations in the concentrations of essential elements (e.g., Fe, Mn, Cu and Zn) in plant tissues may reflect the activities of the enzymes that use these elements as co-factors, such as SOD enzyme (Fe, Mn, Cu and Zn), POD enzyme (Fe), CAT (Fe) enzyme and enzymes involved in the chlorophyll biosynthesis pathway (Fe). In fact, 80% of leaf Fe is localized to the chloroplast, and this Fe is largely distributed in the complexes responsible for photosynthetic electron transport (Terry and Abadia, 1986). Thus, the status of the leaf Fe concentration is believed to be significantly related to plant photosynthesis. Zembala et al. (2010) observed that Cd could stimulate Zn accumulation in rape seedlings, suggesting the enhanced activity of SOD isoenzymes (CuZn-SOD). In addition, they found that 2 μM Na_2SeO_4 reduced the Fe concentrations in rape and wheat seedlings exposed to 600 μM Cd. The inverse effect on the Fe concentration is consistent with the Se-mediated restoration of chloroplast structure described in other studies using Se to detoxify Cd, as discussed above. Consequently, it can be hypothesized that the regulation of Fe levels in plants by Se may be an important mechanism behind the use of Se to reduce environmental stress.

The dual effects of Se on non-stressed plants have been established, and the regulation of Fe is likely a factor that allows Se to exert these effects. Our previous studies have found that the changes in the Fe concentration, MDA content and SOD activity in *Pteris vittata* L. were consistent; they decreased at the Se concentration of 2 mg L^{-1} but increased at the highest Se concentration of 20 mg L^{-1} (Feng et al., 2009b; Feng and Wei, 2012). We suggested that the regulation of Fe accumulation by Se in the fronds of *Pteris vittata* L. might be partially due to the dual effects of Se (Feng et al., 2009b). Similar changes in the Fe concentration in other plants have also been observed; for example, in Chinese cabbage and lettuce grown in pots, 1 mg kg^{-1} Se (a low dose of Se) significantly inhibited the uptake of Fe and Cu, but in a field test treated with 75 mg m^{-2} Se (a relatively high level of Se), the uptake of Fe by lettuce was found to be enhanced (He et al., 2004). Unfortunately, the related physiological parameters, such as the MDA content and enzyme activity, were not analyzed in these studies, which prevents us from drawing further conclusions.

4.3. Conversion of toxic HM to non-toxic Se-metal complexes

In humans and animals, Se is believed to possess a strong ability to combine with HMs, such as Cd, Hg, Ag and Tl, to form nontoxic Se-metal complexes (Shanker et al., 1996c). However, in plants, nontoxic Se-metal complexes have not yet been detected (Table 1). Yathavakilla and Caruso (2007) found that in the roots of soybean

(*Glycine max*), most of the water-soluble Hg was associated with Se in a high molecular weight entity identified by size exclusion chromatography. Belzile et al. (2006) suggested the mutual detoxification between Se and Hg in *Pseudomonas fluorescens* might be due to the formation of Se–Hg complexes; furthermore, in tomato (*Lycopersicum esculentum*) and radish (*Raphanus sativus*). Shanker et al. (1996a,b) also suggested the incorporation of Se–Hg complexes in the soil-root environment when Se was used to reduce Hg toxicity, although no direct proof was presented in this study. In *Thunbergia alata*, Bluemlein et al. (2009) found that unlike in mammalian organism, no As complexes containing seleno-peptides or mixed As–Se peptides were identified.

5. Perspectives for future studies

Over a narrow range of concentrations, the effect of Se on plants changes from beneficial to toxic, as reflected in the metabolism and growth of the plants. There is much interest in the unique role of Se in counteracting the negative effects of various abiotic stresses in plants, rather than on its essentiality. Over the past 30 years, significant progress has been made in understanding the behavior of Se in plants, including the uptake, assimilation, volatilization, toxicity and tolerance. However, the mechanisms by which Se counteracts stress are poorly understood. The most extensively investigated mechanisms for Se-mediated detoxification have involved the antioxidative stress response. In this context, the relationships among antioxidants (GSH-Px, SOD, CAT, APX and GSH), S assimilation, different Se species and the uptake and redistribution of co-factors for some of the enzymes (such as Fe, Mn, Cu and Zn) should be taken into account in future studies.

The prevention of HM toxicity via the addition of Se has been well documented in plants, animals and humans. Se is expected to reduce the toxicity of HMs mainly by inhibiting HM uptake and/or translocation. However, in some cases, the addition of Se stimulated the uptake of certain HMs in plants, such as As in *Pteris vittata* L. (Srivastava et al., 2009) and Al in ryegrass (Cartes et al., 2010), in which Se-mediated detoxification of Al and As toxicity was also observed. The authors suggested this effect was partially related to the enhanced antioxidative capability. However, the contributory cause may be the formation of compounds containing Se—HM bonds that reduce the HM toxicity. In rabbits, compounds containing As—Se and Hg—Se bonds (via GSH-driven formation) are found to be formed in the bloodstream (Gailer, 2007). However, these compounds have not yet been identified in plants, and their detection should clearly become a topic for future studies on Se in plants.

Another important area requiring more research is whether and how Se can block the formation of Fe-S clusters in the chloroplasts of plants exposed to other environmental stresses. These studies may help to shed light on the mechanisms underlying excess Se toxicity, the reduction in adverse stress by proper doses of Se, and the effects of Se on the electron transfer chain in plants.

Acknowledgements

This research was supported by the National Science Foundation of China (41103075, 40971264), the Central Public Research Institute Basic Fund for Research and Development (11-szjj-frw) and the President Funding of Chinese Academy of Agricultural Sciences (2011-frw-11).

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