

The Interactions between Selenium, Nutrients and Heavy Metals in Higher Plants under Abiotic Stresses

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SELENIUM, the beneficial or quasi-essential element to higher plants, is an essential micronutrient for animals and humans as well as lower plants. In several countries around the world, about one billion of people are Se-deficient and counteract this problem, e.g., Brazil, Thailand, China and Egypt due to the low inherent Se concentration in soils. Therefore, different Se forms have been used in different crops using foliar and soil application as well as seed priming to increase the Se content in the edible parts of these crops. Due to its physiological roles in higher plants, Se has been used in counteracting various abiotic stresses including chilling, freezing, heat, drought, salinity, UV-B and heavy metals. Concerning Se and its interactions with some nutrients like Cu, Mo, Zn and Iodine, a very few studies have been published, so further studies are needed. On the other hand, nano-Se and its roles in plant physiology under different abiotic stresses still also need further researches. Therefore, this review will focus on the physiological importance of Se and nano-Se for higher plants under abiotic stresses as well as the interaction of Se with some nutrients including Cu, Mo, Zn and Iodine and some heavy metals such as As, Sb, Cd, Cr, Hg and Pb.

Keywords : Selenium, Nano-Se, Higher plants, Abiotic stress, Heavy metals, Nutrients.

Introduction

Selenium (Se) was misidentified initially as tellurium by Klaproth and later in 1817 was discovered and named by the Swedish chemist J. Berzelius. This name was derived from the Greek goddess for Moon (Selene). The properties of Se lie between both adjacent sulfur and tellurium and it exists in different chemical forms including selenide, selenite, selenate, and elemental nano-Se etc. (Kabata-Pendias 2011; Kumar and Priyadarsini 2014). The importance of Se in human nutrition was documented in 1957

by Schwarz and Foltz (Schwarz and Foltz 1957). Later, the roles of Se in mitigating environmental stress have been extensively investigated in animals and humans but in higher plants still need more investigations (Feng *et al.* 2013a). Due to its several physiological roles in higher plants (Tamaoki *et al.* 2008; Pilon-Smits and Quinn 2010; Hasanuzzaman *et al.* 2010; Hajiboland 2012; Feng *et al.* 2013a; Pilon-Smits *et al.* 2014; El-Ramady *et al.* 2015a; Pilon-Smits 2015), Se has been used in counteracting various abiotic stresses including chilling, freezing, heat, drought, salinity, UV-B and heavy metals, but the associated mechanisms

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are rather complicated and still remain to be fully elucidated (Feng *et al.*, 2013a). In higher plants, several beneficial and/ or toxic effects of Se on physiology and biology of these plants including their metabolism and growth have been well documented (Hasanuzzaman *et al.*, 2010; El-Ramady *et al.*, 2015a). Moreover, a significant progress has been made in understanding Se behavior in higher plants including uptake, assimilation, and its metabolism (Pilon-Smits and Quinn 2010; Pilon-Smits 2015) as well as volatilization, toxicity and its tolerance (Feng *et al.* 2013a; Pilon-Smits *et al.*, 2014; Winkel *et al.* 2015). However, the mechanisms by which Se counteracts the environmental stresses are still not fully understood.

The most extensively investigated mechanisms for Se-mediated detoxification have been involved the antioxidative stress response. The relationships among enzymatic antioxidants including glutathione peroxidase (GPx), superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APx) and non-enzymatic antioxidants including glutathione (GSH), vitamin E and ascorbate as well as S-assimilation, different Se species, the uptake and redistribution of co-factors for some enzymes (*e.g.*, Cu, Fe, Mo, Mn and Zn) should be taken into account in future studies (Feng *et al.*, 2013a).

The recent review will basically cover Se physiology and biology in higher plants under different abiotic stresses. Se and its interactions with nutrients and heavy metals as well as effects of nano-Se on higher plants under these abiotic stresses will be also highlighted.

Physiological importance of Se and nano-Se for higher plants

It is well known that, abiotic stresses including nutritional deficiency, high light (UV-B), drought, high CO₂, ozone (O₃), heat, cold, chilling, freezing, salinity, flooding, soil compaction and heavy metals can have devastating or detrimental impacts on plant growth, yield and hence the agricultural production (Fig.1; Suzuki *et al.* 2014; Nakabayashi and Saito 2015; Ramegowda and Senthil-Kumar 2015). According to recent studies, the plant response to combinations of more than two stress conditions is seldom and can not be directly distinguished from the individual response of these plants to different applied stresses. Furthermore, a very high degree of

complexity in plant responses can be found and resulted from the simultaneous occurrence of different stresses (Suzuki *et al.* 2014). Concerning the combined stresses and their effects on plants, a few studies have been published including Suzuki *et al.* (2014), Nakabayashi and Saito (2015), Pandey *et al.* (2015), Ramegowda and Senthil-Kumar (2015) and Mahalingam (2015). Various aspects of Se and nano-Se roles in counteracting abiotic stresses in different plant species have been published by several authors (Table 1). These abiotic stresses include salinity, drought, high or low temperature as well as stresses resulting from high or low Se and nano-Se levels.

It has been identified 25 selenoproteins and discovered their physiological role for lower plants (bacteria and algae), animals and human metabolism, in which Se is an enzymatic cofactor (Kumar and Priyadarsini 2014). Se has been recognized as a constituent of selenoenzymes including glutathione peroxidase (GPx), thioredoxin reductases (TR), and proteins with unknown functions that are involved in maintaining the cell redox potential (Rayman 2000). Several experimental attempts have been made to recognize these selenoproteins also in higher plants but it is still open question (Mora *et al.* 2015). However, many studies have been showed that Se in higher plants improves the plant growth, increases the tolerance against biotic and abiotic stress (Pennanen *et al.* 2002) and improves other physiological parameters (Turakainen *et al.* 2006; Pilon-Smits *et al.* 2009; Mora *et al.* 2015; Handa *et al.* 2016).

Concerning the main physiological benefits of Se in higher plants, it could be summarized the following results of some published studies using the proper Se concentration (Table 1):

(1) Enhancement of plant germination, growth and dry matter accumulation (Turakainen *et al.*, 2004; Djanaguiraman *et al.*, 2005; Ramos *et al.*, 2011; Mao *et al.*, 2015; Owusu-Sekyere *et al.*, 2013; Cappa *et al.* 2014; Hawrylak-Nowak *et al.*, 2015; Jain *et al.* 2015; Li *et al.*, 2015; Longchamp *et al.*, 2015; Sasmaz *et al.*, 2015; Zhao *et al.*, 2016; Feng *et al.*, 2016; Longchamp *et al.*, 2016).

(2) Increases carbohydrate or starch accumulation in chloroplasts (Turakainen 2006; Malik *et al.*, 2011; Hashem *et al.*, 2013; Hajiboland *et al.*, 2015);

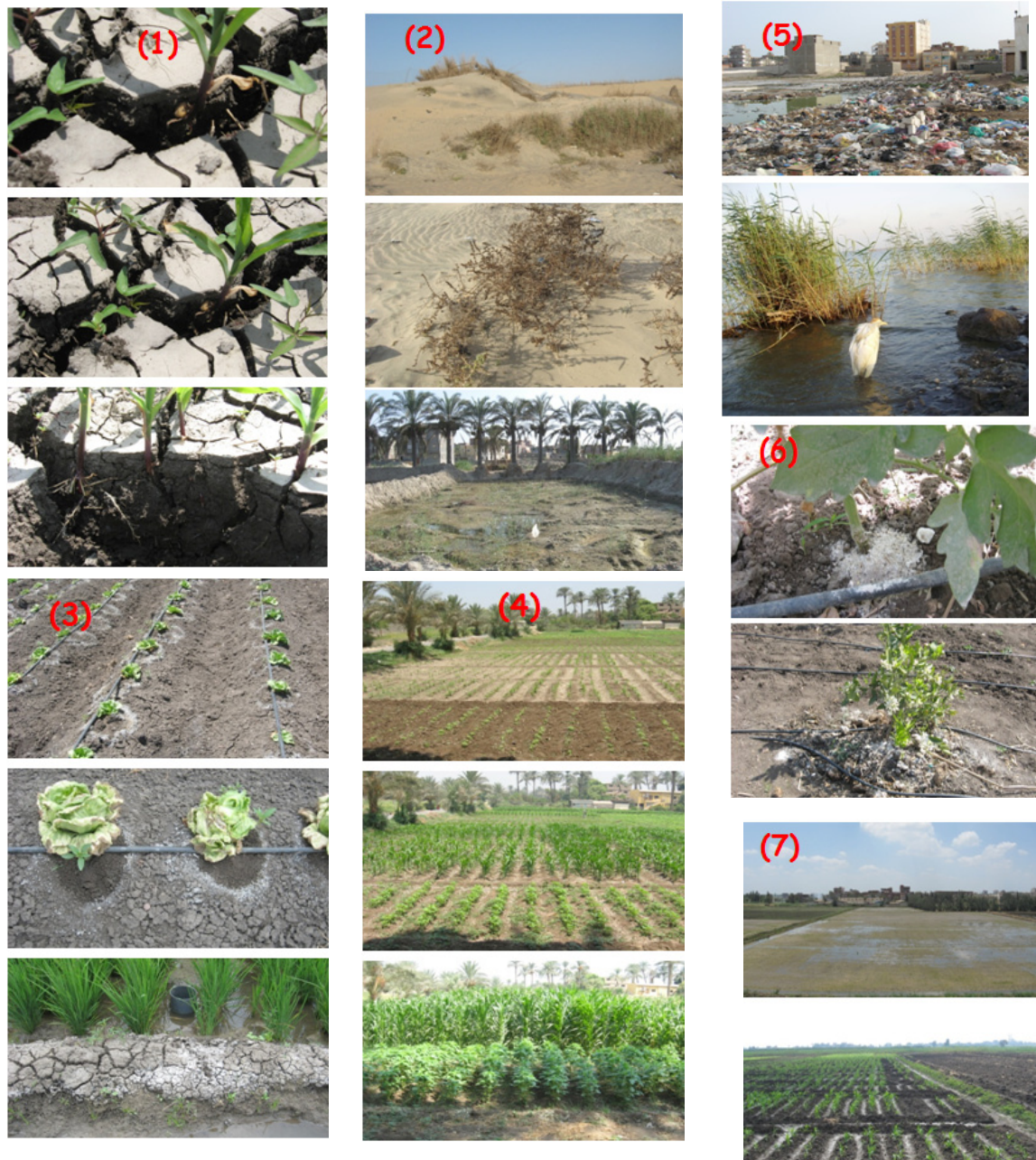


Fig. 1 : Some environmental abiotic stresses including drought under salt affected soils and temperature more than 50 °C during August 2015 (photo 1), low soil fertility or nutrient deficiency under sandy soils (photo 2), soil salinity (photo3), soil management including tillage by time (photo4), environmental pollution (photo5), over-use of fertilizers (photo 6) and flooding (photo 7) in Kafr El-Sheikh and Giza, Egypt (Photos by El-Ramady)

(3) Regulates the water status in plants (Yao *et al.*, 2009a; Soleimanzadeh 2012; Hajiboland *et al.*, 2014; Nawaz *et al.*, 2015a, b).

(4) Enhances production of stress hormones (e.g., ethylene, jasmonic acid and salicylic acid) or Se involves in both salicylic and jasmonic acid pathway of plants stress response (Oraghi Ardebili *et al.*, 2014; Iqbal *et al.* 2015b; Pilon-Smits 2015);

(5) Improves plant tolerance to oxidative stress (Cartes *et al.* 2011; Ibrahim 2014; Iqbal *et al.* 2015b; Bachiega *et al.* 2016)

(6) Activates antioxidant defense system as well as cytosolic calcium and ROS in higher plants (Yuan *et al.*, 2013a; Talukdar 2013; Diao *et al.*, 2014; Saidi *et al.*, 2014; Naz *et al.*, 2015; Feng *et al.*, 2016)

TABLE 1: A survey for main studies on various aspects of Se and nano-Se role in counteracting abiotic stresses in different plant species.

Plant species	Stressor level (Exp. medium)	Se form & dosage (exposure period)	Different effects of Se on stressed plants and associated potential mechanisms (Reference)
Salinity or salt stress			
<i>Glycine max</i> var. L17	100 mM NaCl (pot experiment)	25, 50 mg Se L ⁻¹ (7 d)	The alleviating effects of Se and/or salicylic acid (0.5 mM) had significant inducing effects on enzymatic (POD, CAT, SOD); non-enzymatic (AsA) antioxidant system (Oraghi Ardebili et al. 2014)
Lycopersicon M. esculentum M. (2 varieties)	100 mM NaCl (hydroponics)	0.05 mM Se as Na ₂ SeO ₃ (10 d)	Promotes growth, photosynthesis of tomato seedlings, enhances chloroplast antioxidant defense system: SOD, APX, GR, GPx, POD, DHAR; AsA, GSH (Diao et al. 2014)
<i>Brassica napus</i> L. var Pactole	2, 4, 6 g L ⁻¹ saline solution (pot exp.)	2.5, 5, 10 mg L ⁻¹ Se as Na ₂ SeO ₄ (15 d)	Protective effect of Se on canola subjected to salinity stress was observed in increased plant growth, yield and changes in photosynthetic pigments, proline, regulation of antioxidant enzyme activities: SOD, POD, CAT (Hashem et al. 2013)
<i>Brassica napus</i> L. cv. BINA Sharisha 3	100, 200 mM NaCl (petri plates)	25 mM Se as Na ₂ SeO ₄ (48 h)	Decreased MDA and H ₂ O ₂ levels and chlorosis, Se increased the tolerance of the plants to drought-induced oxidative damage by enhancing their antioxidant defense: SOD, GR, CAT, GPx, as well as AsA, GSH (Hasanuzzaman and Fujita 2011)
<i>Cucumis sativus</i> L.	2 g L ⁻¹ NaCl (7 d in pot exp.)	1 mg L ⁻¹ Se as Na ₂ SeO ₃ (14 d)	Increased activities of POD, CAT, SOD, APX, PAL; reduction in electrolyte leakage, MDA content (El-Shalakany et al. 2010)
<i>Cucumis sativus</i> L. cv. Polan	50 mM NaCl (14 d in hydroponics)	5, 10, 20 mM Se as Na ₂ SeO ₄ (14 d)	Improved the growth rate, photosynthetic pigments, decreased Cl ⁻ ions, enhanced antioxidative capacity: APX, MDHAR, DHAR, GR, as well as AsA, GSH (Hawrylak-Nowak 2009)
Drought or water deficit stress			
<i>Triticum aestivum</i> L. cv. Pasban-90	60 % from field capacity (FC) (pot experiment)	40 mg Se L ⁻¹ as Na ₂ SeO ₄ , foliar application	Improved uptake of some nutrients (Se, Fe and Na); increased wheat yield, osmoprotectants, antioxidant activity: CAT (11%), POX (58%), APX (27%) (Nawaz et al. 2015a)
<i>Triticum aestivum</i> L.	60 % from field capacity (FC) (lysimeter exp.)	5.1, 0.50, 0.48 mg L ⁻¹ Se as Na ₂ SeO ₄ by seed priming, fertigation and foliar spray, resp.	Enhancement in the production of osmoprotectants (proline, total soluble sugars, total soluble proteins, total free amino acids); increased activity of antioxidant enzymes (POX, CAT, APX); the foliar spray of Se was more effective than Se fertigation and Se seed treatment (Nawaz et al. 2015b)
<i>Olea europaea</i>	Deficit water regime (pot and field exp.)	300 mg L ⁻¹ Se as Na ₂ SeO ₄	Under drought stress, Se induced pollen viability and germination, strongly counteracted the reactive oxygen species accumulation (Tedeschini et al. 2015)
<i>Triticum durum</i> L.	30 % from FC (pot exp.)	10 µg L ⁻¹ Se as Na ₂ SeO ₄ (28 d)	Se application improves some physiological parameters (photosynthetic rate, accumulation of osmolytes and water use efficiency) but did not change significantly plants biomass or water relation parameters (Hajiboland et al. 2014)

<i>Triticum aestivum</i> L. cv. Giza 168	Stop irrigation 50-70 days from sowing (field and Lab exp.)	Soaking of grains in 5 and 10 mg L ⁻¹ Se as Na ₂ SeO ₄	H ₂ O ₂ and MDA contents were decreased whereas the activities of antioxidant enzymes (CAT, SOD); content of non-enzymatic antioxidants (AsA, GSH) were increased resulting in elevated membrane stability index and root viability (Ibrahim 2014)
<i>Hordeum vulgare</i> L. cv. Rihane-03	Drought for 35 days exposure (field exp.)	30 g Se ha ⁻¹ as Na ₂ SeO ₄ (10 d)	MDA, H ₂ O ₂ remained unchanged under Se supplemented water-deficit plants; an efficient scavenging following enhancement of POD, SOD, APX, CAT, GPx activities (Habibi 2013)
<i>Olea europaea</i> L. cv. Maurino	Irrigated at 25% available water (pot exp.)	Foliar spray 50 and 150 mg Se L ⁻¹ as Na ₂ SeO ₄	Increases photosynthesis and fruit yield; regulate the water status of trees, the activities of APX, CAT, GPx; reduced the content of MDA (Proietti et al. 2013)
Temperature (Heat, chilling and freezing) stress			
<i>Triticum aestivum</i> L. (2 cultivars)	Heat stress at 38 ± 2 °C (field exp.)	Foliar 2, 4 mg Se L ⁻¹ as Na ₂ SeO ₄ (at heading stage)	Increased enzymatic (CAT, APX); non-enzymatic (carotenoids, anthocyanins, AsA contents) antioxidants; decreased oxidants: H ₂ O ₂ , MDA (Iqbal et al. 2015a)
<i>Brassica napus</i> L.	Stress at 38 °C for 24 or 48 h (hydroponics)	25 µM Se as Na ₂ SeO ₄ (10 d)	Enhanced enzymatic (MDHAR, DHAR, GR, GPx, CAT, Gly I, II); nonenzymatic (proline, AsA, GSH) antioxidant components of defense subjected to heat stress; decreased oxidants: H ₂ O ₂ , methylglyoxal, MDA (Hasanuzzaman et al. 2014)
<i>Sorghum bicolor</i> L. Moench	40/30 °C for 45 days (pot exp.)	Foliar 75 mg Se L ⁻¹ as Na ₂ SeO ₄ after 63 days from sowing	Se decreased membrane damage <i>via</i> enhancing antioxidant defense (SOD, CAT, POX); increase photosynthetic rates, grain yield; decrease reactive oxygen species content under heat stress (Djanaguiraman et al. 2010)
<i>Cucumis sativus</i> L. cv. Polan F1	Chilling stress: 10°C/5°C for 24 h (hydroponics)	2.5, 5, 10, 20 µM Se (14 days)	Se (at 2.5–10 µM) modified the physiological response (Chl a,b, carotenoids) of cucumber to chilling stress, causing an increase in proline content in leaves and diminishing lipid peroxidation (MDA) in roots (Hawrylak-Nowak et al. 2010)
Selenium (Se) stress			
<i>Lemna minor</i> L.	Hydroponic system	0.5, 1, 2, 5, 10 mg Se L ⁻¹ as Na ₂ SeO ₃ (7 weeks)	Higher concentrations of Se (2, 5, 10 mg L ⁻¹) negatively affect Chl a, b, electron transport system activity; duckweed under 10 mg Se L ⁻¹ survived for 14 days and contained 6.5 mg g ⁻¹ DM; survived for 21 days contained 19.5 mg Se g ⁻¹ DM; higher than 10 mg L ⁻¹ is the toxic level for duckweed (Mechora et al. 2015)

<i>Oryza Sativa</i> L. genotype PR 118	Co-exposed with ascorbic acid (50 µM) in hydroponics	1, 2.5, 5 mg Se kg ⁻¹ as Na ₂ SeO ₄ (10 days)	Se at 5 ppm inhibits of roots and shoots by 47% 60%, Se-stressed plants supplemented with AsA showed significant up-regulation of MTs, total thiols, GST activity to reduce the toxic effects of Se (Sharma et al. 2014)
<i>Oryza sativa</i> L.	Field experiments	10, 20, 50, 100 g Se ha ⁻¹ as Na ₂ SeO ₃	50 g Se ha ⁻¹ recorded the highest grain yield; photosynthesis (Pn, Gs, Tr) or chlorophyll fluorescence parameters could be used to determine the Se status for production of Se-rich rice (Zhang et al. 2014)
<i>Brassica oleracea</i> L. var. <i>capitata</i> , cv. Pandion	65 days after emergence of plants (field ex.)	Soil (2 µg Se L ⁻¹) and foliar (20 mg L ⁻¹) as Na ₂ SeO ₄	At harvest, Se concentration was lower than 0.1 mg Se kg ⁻¹ DW (in control), while plants treated with 20 mg Se L ⁻¹ contain 5.5 mg Se kg ⁻¹ ; Se enriched cabbage could be used in human nutrition; Chl a, b, Tr, anthocyanins, photosynthetic rate did not change significantly for both Se methods (Mechora et al. 2014)
<i>Solanum lycopersicon</i> L. cv. Margoble	For 24 h and 5 days (Hydroponic and pot exp.)	5, 10, 25, 50 µM Se as well as foliar 2 mg per plant as Na ₂ SeO ₄ (20 – 40 days)	Low Se doses (5 and 10 µM) <i>via</i> roots stimulate synthesis of phenolic compounds in leaves, reduced of Mo, Fe, Mn, and Cu in roots; higher Se doses (25 and 50 µM Se) enhance leaf GSH by 3–5-fold; Se supply <i>via</i> foliar spray (up 20 mg Se plant ⁻¹) result in Se-biofortified tomato fruits, enhancing antioxidant, flavonoids (Schiavon et al. 2013)
<i>Oryza sativa</i> L. ssp. japonica	0.525, 10.5, 21 g Se ha ⁻¹ (pot and field exp.)	2, 6, 10, 20, 30, 40, 50, 60 mg L ⁻¹ as Na ₂ SeO ₃ (11 d)	Major Se species in rice include SeMet and SeCys (54 and 21% of total Se, resp.); spray with 10.5 g Se ha ⁻¹ increase Se content in grain rice from 0.03 µg g ⁻¹ to 1.54 µg g ⁻¹ without any Se symptoms toxicity; promote rice seedling growth by activating endogenous antioxidant system (Wang et al. 2013)
Nano-Se stress			
<i>Lycopersicon esculentum</i> Mill. cv. Haili	Temperature stress: 10, 25, 40 °C for 24 h (hydroponic)	2.5, 5, 8 µM Se as Na ₂ SeO ₄ & nano-Se 1, 4, 8, 12 µM (3 d)	Se and nano-Se can improve tomato shoot fresh and dry weight and diameter, root fresh and dry weight and root volume under high and/or low temperature stress; Se and nano-Se increased relative water content and root volume significantly after a short-term of high and/or low temperature stress (Haghighi et al. 2014)
<i>Arundo donax</i> L. 2 ecotypes Blossom and 20SZ	Nano-Se: 100 mg L ⁻¹ Se as <i>Lactobacillus</i> <i>casei</i> (<i>in vitro</i> exper.)	0.1, 1, 10, 50, 100 mg L ⁻¹ Se as Na ₂ SeO ₄ (8-16 d)	Both <i>Arundo</i> ecotypes could uptake and accumulate nano-Se however in lower concentration comparing to the selenate; the toxic level of selenate was 20 and 50 mg L ⁻¹ for Blossom and 20SZ accumulating 920 and 896 mg kg ⁻¹ Se in clusters resp. (Domokos-Szabolcsy et al. 2014)

(7) Delay of plant senescence (Djanaguiraman *et al.*, 2004; Pezzarossa *et al.*, 2014; Wu *et al.*, 2016b)

(8) In accumulator species protects plants from fungal infection and herbivores including aphids, caterpillars, spider mites and thrips (Hanson *et al.*, 2003, 2004; Freeman *et al.*, 2007, 2009; Quinn *et al.*, 2010; El Mehdawi and Pilon-Smits 2012; Alford *et al.*, 2012; El Mehdawi *et al.*, 2015; Pilon-Smits *et al.*, 2016).

(9) Alleviation of abiotic and biotic stresses such as UV-B radiation, low and high temperatures, and heavy metal toxicity (Hasanuzzaman *et al.*, 2010; Feng *et al.*, 2013a; Mora *et al.*, 2015) as well as plant diseases (Kumar *et al.*, 2015; Wu *et al.*, 2016a; Zhang *et al.*, 2016).

It is worth to mention that, very few studies have been conducted regarding different physiological benefits of nano-Se on higher plants (Premarathna *et al.*, 2010; Domokos-Szabolcsy *et al.*, 2012, 2014; Haghghi *et al.*, 2014). It has been reported that, nano-Se has a higher efficiency in upregulating Selenoenzymes and exhibits less toxicity than selenite (Wang *et al.*, 2007). There is still open question related to the biological effects of this form of Se in higher plants. It is also well documented that, nano-Se has a distinguished effect on rooting of different plants such as giant reed and tobacco (El-Ramady *et al.*, 2015a).

Therefore, it could be concluded that, Se and nano-Se have a great role in plant physiology. Several different physiological benefits of Se on higher plants have been documented whereas nano-Se is still in need for more and more studies.

Antioxidative effects of Se and its roles under abiotic stresses.

It is demonstrated that, different beneficial effects of Se in higher plants subjected to different stress conditions has been attributed to increased antioxidant activity (Hasanuzzaman *et al.*, 2010).

Se can promote growth and development of plants as well as increase the resistance and antioxidant capacity of higher plants under different abiotic stresses (Djanaguiraman *et al.* 2005), where it can increase plant resistance against oxidative stress caused by free oxygen radicals or ROS (Hassanuzzaman *et al.*, 2010).

Several in vitro and/ or field experiments have been shown that Se may interact with other elements such as Al, Sb, As, Cd, Pb and Hg thus this may reduce the toxicity of Heavy metals (Yasin *et al.*, 2015c). The factors driving these relationships between Se, soil characterization including SOM and pH as well as characterization of these elements are not fully clear and further studies are mandatory to elucidate the role of soil and different climate variables in driving these relationships (Winkel *et al.*, 2015; El-Ramady *et al.*, 2015d,e).

Furthermore, some plant species grown on Se-enriched media have shown enhanced resistance to certain abiotic stresses such as.

(1) Drought (Germ *et al.*, 2007; Yao *et al.*, 2009a, b; Hasanuzzaman and Fujit 2011; Bañuelos *et al.*, 2011; Sajedi *et al.*, 2011; Yao *et al.*, 2012; Habibi 2013; Proietti *et al.*, 2013; Nawaz *et al.*, 2013, 2014; Khattab *et al.*, 2014; Hajiboland *et al.* 2014; Emam *et al.*, 2014; Nawaz *et al.*, 2015a,b),

(2) Salinity (Hawrylak-Nowak 2009; Hasanuzzaman *et al.*, 2011; Bañuelos *et al.*, 2011; Hashem *et al.*, 2013; Oraghi Ardebili *et al.*, 2014; Diao *et al.*, 2014),

(3) Temperature including chilling (Chu *et al.*, 2010; Hawrylak-Nowak *et al.* 2010), low and high temperature (Akladios 2012; Hasanuzzaman *et al.*, 2014; Haghghi *et al.*, 2014; Iqbal *et al.*, 2015a)

(4) Heavy metals (Van Hoewyk 2013; Kaur *et al.*, 2014; Tedeschini *et al.*, 2015; Gu *et al.*, 2016) including Al (Cartes *et al.*, 2010; Sae-Lee *et al.*, 2012), Sb (Feng *et al.*, 2011, 2013b; Ding *et al.*, 2015; Feng *et al.*, 2016), As (Malik *et al.*, 2012; Hasanuzzaman and Fujita 2013; Kumar *et al.*, 2013, 2014, 2015; Hu *et al.*, 2014b; Han *et al.*, 2015; Pandey and Gupta 2015), Cd (Lin *et al.*, 2012; Barrientos *et al.*, 2012; Elguera *et al.*, 2013; Feng *et al.* 2013c; Ojeda *et al.*, 2013; Ding *et al.*, 2014; Wang *et al.*, 2014; Wu *et al.*, 2014; Mozafariyan *et al.*, 2014; Hawrylak-Nowak *et al.*, 2014; Hu *et al.*, 2014a; Saidi *et al.*, 2014; Liu *et al.*, 2015a; Thiruvengadam and Chung 2015; Tang *et al.*, 2015; Issam *et al.*, 2015; Iqbal *et al.*, 2015b; Bao *et al.*, 2016; Wan *et al.*, 2016), Cr (Qing *et al.*, 2015), Pb (Mroczek-Zdyrska and Wójcik 2012; Yuan *et al.*, 2013b, 2014; Hu *et al.*, 2014a), Mn (Saidi *et al.*, 2014), Hg (Zhang *et al.*, 2013; Zhao *et al.*, 2013, 2014; Wang *et al.*, 2014; Zhang *et al.*,

2014; Zhang 2014; Li *et al.*, 2015; Yin *et al.* 2016), Ni (Hawrylak *et al.*, 2007; Gajewska *et al.*, 2013),

(5) UV-B stress (Yao *et al.*, 2010a, b; Yao *et al.*, 2013; Mostafa and Hassan 2015) and

(6) Plant senescence (Djanaguiraman *et al.*, 2004, 2005; Liu *et al.*, 2011; Pezzarossa *et al.*, 2014; Wu *et al.*, 2016b).

some studies have discussed the different mechanisms of se behavior under different stresses in higher plants (e.g., feng *et al.*, 2013a; van hoewyk 2013; ahmad *et al.*, 2015; detar *et al.*, 2015). using antioxidants upregulation and its enzymes, exposure to se has been linked at optimal levels to the reduction of various ros (feng *et al.*, 2013a), inhibition of uptake and translocation of heavy metals, changing in heavy metals speciation and rebuilding of cell membrane, chloroplast structures as well as recovery of the photosynthetic system. at high levels of se, its oxyanions can be also a source of the oxidative stress (van hoewyk 2013; detar *et al.*, 2015). in relation to the role of se in preventing of heavy metals toxicity, it is involved the reduction of heavy metals toxicity by inhibiting their uptake and/or translocation (feng *et al.*, 2013a). on the other hand and under drought stress, two roles can be expected from se; decreasing the oxidative damage resulting from ros by production of the compatible solutes and improving the tolerance of plants to drought by increasing sod, gpx, cat activities protecting plants against oxidative stress (ahmad *et al.*, 2015).

Several studies have been implicated the antioxidative effects of nano-Se for animals (Zhang *et al.*, 2001; Pelyhe and Mézes 2013; Rezvanfar *et al.* 2013; Suchý *et al.*, 2014; Sarkar *et al.*, 2015) including mice (Wang *et al.*, 2007; Zhang *et al.*, 2008; Bhattacharjee *et al.*, 2014; Rastgoo and Sadeghi 2015; Abd-Allah and Hashem 2015), sheep (Xun *et al.*, 2012; Sadeghian *et al.*, 2012; Kojouri *et al.*, 2012), goat (Shi *et al.*, 2010, 2011), chicken (Cai *et al.*, 2012; Hu *et al.*, 2012; Mohapatra *et al.*, 2014; Boostani *et al.*, 2015; Radwan *et al.*, 2015; Selim *et al.*, 2015), fish (Sarkar *et al.*, 2015; Khan *et al.*, 2016), whereas a very few studies have been recorded for higher plants (Haghighi *et al.*, 2014; El-Ramady *et al.*, 2015a). Recently, the general effects of nano – particles on plants include plant growth, and its cell structure as well as both physiological and

biochemical functions have been reported (Rico *et al.*, 2015). Moreover, the role of these nano – particles in antioxidant defense system in plants includes the effects on photosystems and some plant enzymes (CAT, POD, SOD, APx, GR and DHAR) as well as some low molecular weight antioxidant thiols (e.g., GSH) and ascorbate.

Therefore, it could be concluded that, Se has a distinguished role in increasing resistance and antioxidant capacity of higher plants. It strengthens the antioxidative capacity in higher plants by preventing the reduction of tocopherol concentration and by enhancing SOD activity. After Se addition to forage plants, it may not only increase the yield of plants but also improve their nutritive quality in many ways. It could be also summarized that, Se acts as an antioxidant, inhibiting lipid peroxidation via increased levels of thiols and GSH. It could be also suggested that, Se is either an antioxidant or it activates plant protective mechanisms, thereby alleviating oxidative stress and improving heavy metals uptake in higher plants. Optimal Se supply is favorable for growth of some plants (like wheat seedlings) during drought condition. The growth and physiological responses of seedlings were different depending on the Se concentration.

The interactions between Se, nutrients and heavy metals

The remediation process of different contaminated soils with multiple pollutants or contaminants is a difficult issue and thus it is compulsory to develop and sustain novel customized strategies for this remediation (Tripathi *et al.*, 2015). Therefore, it is very important to investigate the interaction between different nutrients in the context of biofortification and phytoremediation. According to the recent studies, Se has a few studies concerning the interaction with some nutrients including Cu, Mo, Zn, and iodine with exception for S. Their different properties comparing with Se are summarized in Table 2 as well as a survey of the recent studies for this interaction in Table 3. On the other side, several publications related to Se detoxification of some toxic heavy metals including Sb, As, Cd, Cr, Pb and Hg are presented in Table 4. Therefore, different relationships between Se and its role in detoxification of these heavy metals as well as the interaction between Se and some other nutrients (S, Cu, Mo, Zn and iodine) will be highlighted in this section.

TABLE 2. Some selected physical, chemical and biological properties of selenium comparing with sulfur, copper, iodine, molybdenum and zinc in higher plants.

Properties or items (unit)	Copper (Cu)	Iodine (I)	Molybdenum (Mo)	Selenium (Se)	Sulphur (S)	Zinc (Zn)
Discoverer (year)	Sommer (1931)	B. Courtois (1811)	P. Hjelm (1781)	J. Berzelius (1817)	von Sachs, Knop (1865)	Marggraf (1746)
World mine production in 2014 (metric tons)	18,700,000	31,600	266,000	2,275	72,400,000	13,300,000
Abundance in the Earth's crust	55 mg kg ⁻¹	0.25-0.5 mg kg ⁻¹	1.2 mg kg ⁻¹	0.05 mg kg ⁻¹	0.06 – 0.1 (%)	70 mg kg ⁻¹
Abundance or usual soil content	20 mg kg ⁻¹	2.8 mg kg ⁻¹	0.5 – 5.0 mg kg ⁻¹	0.33 mg kg ⁻¹	0.01 – 0.1 (%)	63 mg kg ⁻¹
Ranking of abundance in earth crust	26	63	58	69	14	24
Most important minerals	Chalcopyrite: CuFeS ₂ , Malachite: Cu ₂ (OH) ₂ (CO ₃), Cuprite: Cu ₂ O	Lodargrite (AgI) and marshite (CuI)	Molybdenite: MoS ₂ , Molybdenite: MoO ₃	Klockmannite: CuSe, Clausthalite: PbSe, Triemannite: HgSe	Gypsum: CaSO ₄ ·2H ₂ O, Pyrite: FeS ₂ , Galena: PbS	Sphalerite: (Zn, Fe)S, Smithsonite: ZnCO ₃
Common valence states	+1 and +2	-1 (+1 to +7)	+2, +4 and +6	-2 and +2	-2, 0, +2, +4, +6	+2
Density at 20°C, g cm ⁻³	8.94	4.93	10.2	4.79	2.07	7.13
Melting point (°C)	1083	113.7	2,617	217	112.8	419.6
Functions in Plants	Constituent of superoxide dismutase (SOD)	Component of di-iodotyrosine, triiodothyronine, antioxidant system	Component of enzymes: nitrogenase and nitrate reductase	Constituent of glycane reductase and glutathione peroxidase	Component of 3 amino acids, glucosides, coenzyme A, vit. B1	Component of some enzymes: dehydrogenase, proteinase, SOD
Principal forms for plant uptake	Cupric cation (Cu ²⁺)	Iodide (I ⁻), iodate IO ⁻	Molybdate (MoO ₄ ²⁻)	Selenate (SeO ₄ ²⁻) or selenite (SeO ₃ ²⁻)	Sulphate (SO ₄ ²⁻)	Zinc (Zn ²⁺)
Essentiality for animals and plants	Essential for both	Essential: animals, beneficial: plants *	Essential for both	Essential: animals, beneficial: plants	Essential for both	Essential for both
Critical or sufficient level in plant leaf	1.0 – 5 mg kg ⁻¹ DW	0.1 mg kg ⁻¹ DW	0.1 – 1.0 mg kg ⁻¹ DW	0.1 – 2.0 mg kg ⁻¹ DW	0.1 – 0.5 % DW	15 – 30 mg kg ⁻¹ DW
Leaf toxic level, DW	15 – 30 mg kg ⁻¹	0.5 – 1.0 mg kg ⁻¹	1000 mg kg ⁻¹	5.0 – 30 mg kg ⁻¹	0.5 – 0.7 %	100 – 300 mg kg ⁻¹
Uptake by plants and its transporter(s)	Active (Cu ²⁺): Cu transporters (proteins and gene families)	Iodine uptake through roots and leaf stomata, carriers halide-specific	Active (MoO ₄ ²⁻): sulphate transporter (Sultr 5:2) and MOT1	Passive (SeO ₃ ²⁻ ; by phosphate transporter), active (SeO ₄ ²⁻ & SeMe): sulphate transporter	Active (SO ₄ ²⁻): sulphate transporter (Sultr5:2)	Active (Zn ²⁺): metal chelators (phytochelatin; metallothionein), Zn ²⁺ transporters
Movement in soil	Mass flow	Mass flow	Mass flow and diffusion	Very mobile in soil by mass flow (SeO ₄ ²⁻)	Mass flow (SO ₄ ²⁻)	Mass flow and root interception
US recommended daily allowances for human	0.9 mg	(10 ⁻²) 150 µg	45 µg	55 µg	None specified	8 – 11 mg

Source: Compiled from Mengel et al. (2001), Jones (2003), White and Broadley (2005), Jones (2005), Kabata-Pendias and Mukherjee (2007), White and Brown (2010), Kabata-Pendias (2011), Kirkby (2012), Fuge (2013), El-Ramady et al. (2014a,b), USGS (2015), Mitra (2015), Tatsuo (2015) and Kabata-Pendias and Sateke (2015).

Abbreviation: SeMe, selenomethionine

* According to Mengel et al. (2001), iodine is essential for the marine brown alga *Patellaria fasciata*

TABLE 3: A survey for main studies on various aspects of Se interaction with some nutrients including S, Cu, Mo, Zn and iodine in different plant species.

Plant species	Co-application nutrient (medium)	Se form & dosage (exposure period)	Subject or scope for the study and its results (Reference)
Selenium and iodine interaction			
<i>Lactuca sativa</i> L. cv. Melodion	Iodine: 7.88 µM I as KIO ₃ (NFT hydroponics)	Selenium: 6.33, 19 µM Se as Na ₂ SeO ₄ (interval 7 d)	A limiting factor for the development of agro-technical methods of I and Se application is poor recognition of its interaction with respect to plant growth and metabolism; foliar application of Na ₂ SeO ₄ + KIO ₃ decreased level of Ca, Mg and Fe in roots, synergistic interaction of IO ₃ ⁻ on SeO ₄ ²⁻ uptake by leaves; foliar application of I together with Se improved SeO ₄ ²⁻ uptake by leaves; transport of I and Se may occur from leaves to roots through phloem (Smolen <i>et al.</i> , 2014)
<i>Triticum aestivum</i> L. (Jordao) and <i>Triticum durum</i> Desf. (Marialva)	Iodine: 10 µM I as KI (field condition) Se added at both booting and grain filling stage	Selenium: 4, 20, 100 g Se ha ⁻¹ (or 0.2, 1, 5 mg L ⁻¹) as Na ₂ SeO ₄ and Na ₂ SeO ₃	Foliar Se fertilization of Portuguese wheat cultivars through foliar treatment at booting and grain filling stages in presence of iodine; presence of potassium iodide does not seem to affect the Se accumulation in mature grains for cultivars and stages; foliar of Se can increase Se contents in mature grains up to 15 and 40 times for Marialva and Jordao, respectively, when compared to control (Galinha <i>et al.</i> , 2013)
Microalga <i>Chlorella sorokiniana</i>	Iodine: 0.15–4 mg I mL ⁻¹ as KI and exposure for 4 h	Selenium: 0.02–0.5 mg Se mL ⁻¹ as Na ₂ SeO ₄ repeated three times	The microalga <i>Chlorella sorokiniana</i> can be used for the bio-accumulation of both Se and I in the production of functional food enriched in these elements; accumulating 1.2 mg g ⁻¹ within 24 h under exposure of iodide (0.15 mg mL ⁻¹) and Se can be accumulated up to 3 µg g ⁻¹ by the alga after 100 h of exposure to 50 µg mL ⁻¹ of selenite in the culture medium (Gómez-Jacinto <i>et al.</i> , 2012)
Selenium and sulfur interaction			
<i>Triticum aestivum</i> L.	Exper. I: 150, 300 mg S kg ⁻¹ harvested at 70 d (pot exper.) Exper. II: 0.1, 1, 2 mmol L ⁻¹ S as MgSO ₄ 7H ₂ O (hydroponics)	Exper. I: 15 mg Se kg ⁻¹ as Na ₂ SeO ₃ (7 d) Exper. II: 1 µmol L ⁻¹ Se as Na ₂ SeO ₃ and Na ₂ SeO ₄ 10H ₂ O (24 h)	Pot and hydroponic experiments were conducted at wheat seedling stage to study effects of applied S on the uptake of Se by plant; application of 150 mg kg ⁻¹ S reduced Se in wheat shoots (47 %) and roots (45%); S treatment changed soil pH (max. decrease of 0.52 units) and OM content (max. increase of 0.96 g kg ⁻¹), thereby reduced soluble Se, increased Fe/Mn oxide bound Se; the content of Se in crops can be effectively controlled by increasing S-fertilizer applications in the high Se regions (Liu <i>et al.</i> , 2015b)
Rape (<i>Brassica napus</i> L.)	Exper. I: 0.02, 0.1, 0.5, 2.0 mM as MgSO ₄ 7H ₂ O Exper. II: 0.1 mM sulphate Exper. III: 0.5, 2 mM (hydroponic)	Exper. I: 1 µM as Na ₂ SeO ₃ or Na ₂ SeO ₄ 10H ₂ O (24 h) Exper. II: 0.1, 0.5, 1, 5 10 µM SeO ₃ ²⁻ or SeO ₄ ²⁻ (2 h) Exper. III: 5 µM selenite/selenate (7 d)	Se translocation factor significantly reduced by up to 46.4 and 60.5 % with increasing selenite and selenate in solution resp., while sulphate had effect only on Se translocation in selenate treatment; Se absorption capacity of rape supplied with selenite or selenate depends on sulphate concentration; sulphate is involved in the root-to-shoot translocation of Se in <i>B. napus</i> supplied with selenate, but not selenite; correct selection of Se fertilizers depends on applied S-fertilizer, effective Se resources and the attenuation of environmental pollution arising from chemical fertilization (Liu <i>et al.</i> 2015c)
Plant species	Co-application nutrient (medium)	Se form & dosage (exposure period)	Subject or scope for the study and its results (Reference)

<i>Stanleya pinnata</i> and <i>Brassica juncea</i>	Sulfur: 0.5, 5 mM in combination with Se (hydroponics)	Selenium: 10, 20 μM as Na_2SeO_4 (3 days)	Se accumulation was ~10-fold with increasing sulfate supply in <i>B. juncea</i> , while <i>S. pinnata</i> only had a 2–3-fold difference in Se uptake between the highest (5 mM) and lowest sulfate (0 mM) treatments; Se/S ratio was generally higher in hyper-accumulator than the non-hyperaccumulator; transcript levels of <i>Sultr1.2</i> and <i>2.1</i> and <i>APSI.2</i> , and <i>4</i> were generally much higher in <i>S. pinnata</i> than <i>B. juncea</i> , and the species showed differential transcript responses to S and Se supply (Schiavon et al., 2015)
Selenium and copper interaction <i>Pakchoi (Brassica chinensis</i> L., Qinqbai 2)	Copper: 200, 400, and 800 mg kg^{-1} Cu as CuSO_4 (pot experiment)	Selenium: 2.5, 10, 20 mg Se kg^{-1} as Na_2SeO_3 (14 d)	Soil enzymes inhibited by single Cu or Se as well as Cu and Se combined pollution in different degrees: nitrate reductase > urease > CAT > alkaline phosphatase; The joint effects of Cu and Se on CAT showed synergism at low concentrations and antagonism at high concentrations; the opposite was observed for urease activity; synergism showed for nitrate reductase activity both with and without plant treatments (Hu et al., 2013)
Selenium and zinc interaction <i>Broccoli (Brassica oleracea</i> L.)	Zinc: 6.59 ppm $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ (pot experiment)	Selenium: 0.5, 1, 2, 4 mg Se L^{-1} as both Na_2SeO_4 and Na_2SeO_3 (50 d)	Se inhibited germination of broccoli at doses above 50 and 100 mg L^{-1} for selenite and selenate, resp.; Se ameliorates effect of Zn deficiency on growth of broccoli; Zn reduced toxicity of Se at high Se doses; Zn may exert a Se detoxification effect at high Se doses, while Se may exert a sparing/substitution effect for Zn under Zn deficiency; at high Se levels (up to 4 mg L^{-1}): biomass, water use, photosynthesis and gas exchange inhibited with selenite (more toxic than selenate) with high values in presence of Zn (Mao et al., 2015)
Wheat (<i>Triticum aestivum</i> cv. Reska)	Zinc: fertilizer by 1 g kg^{-1} ZnNO_3 (pot experiment)	Se sprayed: 20 mg L^{-1} Se as Na_2SeO_4 or 3 mg Se per plant and 15 mg per pot (before flowering)	Since Se is assimilated in plants via S assimilation pathway, over-expression of sulphate transporters in Zn treated plants might be the reason for more efficient Se assimilation: double biofortification with Zn and Se may be a feasible strategy to efficiently coordinate the mineral quality of wheat grain due to alteration of sulphate metabolism in the presence of Zn (Germ et al., 2013)
Selenium, sulfur and molybdenum interaction <i>Astragalus racemosus</i> , <i>A. bisulcatus</i> and <i>A. drummondii</i> , <i>A. convallarius</i>	Molybdate: 12, 24, 48 mg L^{-1} as Na_2MoO_4 (in vitro exper.)	Selenium: 1.6, 3.2 mg L^{-1} as Na_2SeO_4 (7 weeks)	Differences between Se hyperaccumulators and non-accumulators in Se, S and Mo interactions (in uptake mechanisms); sulfate transporters in hyperaccumulating <i>Astragalus</i> appear to have higher sulfate specificity over other oxyanions, compared to nonaccumulators and <i>A. racemosus</i> may have a transporter with enhanced selenate specificity relative to sulfate or molybdate (DeTar et al., 2015)
<i>Stanleya pinnata</i> , (CO and CA ecot.) <i>Brassica juncea</i> L., Czern. (Cv. PI 426314)	Sulfate: 0.5, 5 mM S as Na_2SO_4 (pot experiment)	For <i>S. pinnata</i> : 10, 20, 40, 80 $\mu\text{M Se as Na}_2\text{SeO}_4$ For <i>B. juncea</i> : 10, 20, 40 $\mu\text{M Se as Na}_2\text{SeO}_4$ (twice/ week for 5 months)	Selenate may outcompete molybdate for transport better than sulfate; interactions among Mo, S and Se happen at level of various enzymes involved in sulfate assimilation, such as ATP sulfurylase, which may act on molybdate and selenate in addition to sulfate; <i>S. pinnata</i> contains a modified sulfate transporter with a higher specificity for selenate; at high Se levels <i>B. juncea</i> had significantly more Mo in roots and mature leaves than without Se (Harris et al., 2014)
Selenium, iodine and zinc interaction <i>Zea mays</i> L., <i>Glycine max</i> L., <i>Solanum tuberosum</i> L., <i>Brassica rapa</i> L., <i>Triticum aestivum</i> L., and <i>Brassica napus</i> L.	(1) Soil applied: 0.21, 22.7 and 0.59 kg ha^{-1} for Se, Zn and I (2) Foliar applied: 0.23, 0.45, 0.68, 0.91, 1.14 kg Zn ha^{-1} as $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ (field trial)	(1) Soil applied: 0.5 $\text{kg Na}_2\text{SeO}_4 \text{ ha}^{-1}$, 0.46 $\text{kg Na}_2\text{SeO}_3 \text{ ha}^{-1}$, 100 $\text{kg ZnSO}_4 \cdot 7\text{H}_2\text{O}$ and 1 kg KIO_3 (2) Foliar applied: 4, 20, 30, 46, 60 g Se ha^{-1} as selenite	Soil application of Se, Zn, and I was not effective in increasing the concentrations of other micronutrients (B, Cu, Fe and Mn); soil-applied selenate and foliar-applied selenite were found to be effective for Se biofortification; foliar zinc sulphate is effective in biofortifying winter wheat, and soil-applied Zn is effective in increasing the Zn concentration in cabbage leaf and canola seed; soil-applied I was found to be only effective in increasing I concentration in cabbage leaf; agronomic biofortification of the crops with Se as soil-applied sodium selenate was unaffected by co-application of Zn and/or I (Mao et al., 2014)

TABLE 4: A survey for main studies on various aspects of Se interaction with some heavy metals including Sb, As, Cd, Cr, Pb and Hg in different plant species.

Plant species	Stressor level (Exp. medium)	Se form & dosage (exposure period)	Different effects of Se on stressed plants and associated potential mechanisms (Reference)
Antimony (Sb)			
<i>Oryza sativa</i> L.	1, 5, 9 mg Sb L ⁻¹ as K ₂ Sb ₂ O ₇ · 10.5 H ₂ O for 14 d (hydroponics)	0.1, 0.3, 1.5 mg Se L ⁻¹ as Na ₂ SeO ₃ (14 days)	Se (0.8 mg L ⁻¹) counteracted the negative effects of Sb on the cell membrane lipids & shoot biomass; reduced root growth parameters; SOD, APX, CAT play roles in rebalance in excess ROS resulting from exposure to Se and/or Sb (Feng et al. 2016)
<i>Oryza sativa</i> L. cv. Fengnaxian	1, 2.2, 5, 7.8, 9 mg Sb L ⁻¹ as K ₂ Sb ₂ O ₇ · 10.5 H ₂ O for 14 days (hydroponics)	0.1, 0.3, 0.8, 1.3, 1.5 mg Se L ⁻¹ as Na ₂ SeO ₃ (14 days)	Paddy rice can accumulate high concentrations of Se and Sb in its tissues (79% in root cell wall). Se can reduce Sb toxicity via regulating its subcellular distribution in which cell wall & cytosol fractions may act as vessels to sequester excess Se and Sb (Ding et al. 2015)
<i>Oryza sativa</i> L. cv. Fengnaxian	1, 2.2, 5, 7.8, 9 mg Sb L ⁻¹ as K ₂ Sb ₂ O ₇ · 10.5 H ₂ O for 14 days (hydroponics)	0.1, 0.3, 0.8, 1.3, 1.5 mg Se L ⁻¹ as Na ₂ SeO ₃ (14 days)	Se-mediated alleviation of Sb toxicity could be closely connected with the direct inhibition of Sb uptake and the uptake regulation of some essential elements, such as Ca, Cu, K, Mg and Zn. Sb higher than 7.8 mg L ⁻¹ appeared to have antagonistic effects on the uptake of these elements (Feng et al. 2015b)
<i>Oryza sativa</i> L. cv. Weiyu-402	5 mg Sb L ⁻¹ as K ₂ Sb ₂ O ₇ · 10.5 H ₂ O for 14 days (hydroponics)	0.1, 1, 5 mg Se L ⁻¹ as Na ₂ SeO ₃ (14 days)	Se (1.5 mg L ⁻¹) could alleviate Sb toxicity (5 mg L ⁻¹) in paddy rice through two effects as antagonism and antioxidant; decrease in MDA content and increase in biomass of plant (Feng et al. 2011)
Arsenic (As)			
<i>Nicotiana glauca</i> L. var. K376	1, 5 mg L ⁻¹ as Na ₂ AsO ₄ · 2H ₂ O (hydroponics)	0.1, 1, 5 mg L ⁻¹ as Na ₂ SeO ₃ (14 days)	Low Se dose (0.1 mg L ⁻¹) alleviated the toxicity of high As dose (5 mg L ⁻¹); the addition of As counteracted the toxicity of high Se dose of 5 mg L ⁻¹ (Han et al. 2015)
<i>Oryza sativa</i> L. cv. Masima research-I	5 µg ml ⁻¹ as NaH ₂ AsO ₄ (hydroponics)	0.5, 1, 2 µg ml ⁻¹ as Na ₂ SeO ₃ (7 days)	Higher antioxidant enzymes (CAT, SOD, GST, POD, GR, AO) in As ³⁺ -Se ²⁻ Pading with lower level of H ₂ O ₂ , maximum reduction of As toxicity was achieved with combined application of 1 µg Se ml ⁻¹ and 10 µg PO ₄ ³⁻ ml ⁻¹ (Kumar et al. 2015)
<i>Oryza sativa</i> L. var. PB-I	150 µM As as NaAsO ₂ (hydroponics)	20 µM Se as Na ₂ SeO ₃ (12 days)	Co-application of Se and auroin (5 µM as AA) improved growth of rice seedlings; level of stress indicators (chlorophyll, protein, MDA) and modulators (cysteine, proline) as compared the individual treatment of As (Pandey and Gupta 2015)
<i>Oryza sativa</i> L. cv. Jinhai-1	1 µM As as NaAsO ₂ · 2H ₂ O (pot. exper.)	1 µM as Na ₂ SeO ₃ and Na ₂ SeO ₄	Se supply decreases translocation of As from roots to shoots; play antagonistic role in As translocation from roots to shoots, due to As ligands such as PC ⁻ and GSH in roots, which sequester As into vacuoles of roots (Hu et al. 2014b)
<i>Oryza sativa</i> L.	25 µM As as Na ₂ HAsO ₄ (hydroponics)	5, 10, 25, 50 µM Se as Na ₂ SeO ₃ (7 days)	Se ameliorates induced oxidative stress through modulation of antioxidant enzymes (APX, CAT, GPX, thiols); modulate thiol metabolism enzymes including γ-GCS, GST and PCS (Kumar et al. 2014)
<i>Oryza sativa</i> L. cv. Prabhat	4 µg ml ⁻¹ As as NaAsO ₂ (hydroponics)	0.75, 1.5 mg ml ⁻¹ as Na ₂ SeO ₃ (7 days)	Co-application of P (5 mg ml ⁻¹) and Se (0.5 mg ml ⁻¹) provides maximum amelioration of As (4 µg ml ⁻¹) toxicity in rice seedlings; achieving a higher SOD, APX, POD activities in these previous Se, P and As doses (Kumar et al. 2013)
<i>Phaseolus aureus</i> Robt.	2.5, 5, 10 µM As (hydroponics)	2.5, 5 µM Se (10 days)	Se antagonizes toxic As on mungbean by restricting its uptake and enhancing the antioxidant (SOD, CAT, APX, GR as well as AsA, GSH), detoxification by increasing MTS, thiols, GST activity in Se-treated plants (Malik et al. 2012)

	Cadmium (Cd)	
<i>Triticum aestivum</i> cv. WH 711	200 mg Cd kg ⁻¹ as CdCl ₂ (pot exper)	2 mg Se kg ⁻¹ as Na ₂ SeO ₃ ·5H ₂ O (15 days)
<i>Brassica rapa</i> ssp. <i>rapa</i>	100 µM Cd as CdCl ₂ (tray experiments)	25 µM Se as SeO ₃ selenium dioxide (7 days)
<i>Helianthus annuus</i>	20 µM as CdCl ₂ (hydroponics)	Seeds soaking: 5, 10, 20 µM Se as Na ₂ SeO ₃ ·10H ₂ O (14h)
<i>Nicotiana tabacum</i> L.	50 µM Cd for 7 days (hydroponics)	3 µM Se (7 days)
<i>Bracharia distachya</i> L. Gand.	5 mg L ⁻¹ Cd as CdCl ₂ (hydroponics)	1 µmol L ⁻¹ as Na ₂ SeO ₃ (7 d) beside 1 mmol S L ⁻¹
<i>Cucumis sativus</i> L. cv. Polona F1	25, 50 µM Cd as CdCl ₂ , 2, 8, 10 (14 d) (hydroponics)	5, 10 µM Se as Na ₂ SeO ₃ (14 d)
<i>Oryza sativa</i> var. Shuangyou 998	1, 4, 12 mg Cd L ⁻¹ for 14 d (pot exper)	0.2, 0.8 mg Se L ⁻¹ as Na ₂ SeO ₃ (14 d)
<i>Oryza sativa</i> L. cultivar Jinhua 1	0.22, 1.03 and 98.1 mg kg ⁻¹ of Se, Cd and Pb in soil used (pots)	0.5, 1 mg Se kg ⁻¹ as Na ₂ SeO ₃ (14 d)
	Chromium (Cr)	
<i>Brassica campestris</i> L. sp. Petrossis	Chromium: 1 mg L ⁻¹ , 7 as K ₂ Cr ₂ O ₇ (hydroponics)	Selenium: 0.1 mg L ⁻¹ Se as Na ₂ SeO ₃ (30 days)
Lead (Pb) <i>Colea Blumei</i> Benth.	Lead: 1 mM Pb, 5 Pb(NO ₃) ₂ (pot and hydroponic experiments)	Selenium: 0.1, 0.5, 1, 2, 5, 5 mM Se as Na ₂ SeO ₃ (21 days)
<i>Vicia faba</i> L. minor cv. Nadebiński	Lead: 50 µM Pb as Pb(NO ₃) ₂ (hydroponics)	Selenium: 1.5, 6 µM as Na ₂ SeO ₃ (14 days)
<i>Oryza sativa</i> L.	2.36 and 0.16 mg kg ⁻¹ of Hg, Se content in soil used (field)	0.01, 0.1, 0.5, 1, 5 µg Se ml ⁻¹ as Na ₂ SeO ₃

Previous studies discussed the interaction between Se with other elements included 2 or maximum 3 of the elements mentioned above (e.g. Pickering 2016). Concerning this interaction between Se and these previous nutrients (Table 3), some publications have been issued including relationship with S (White *et al.*, 2004; Galeas *et al.*, 2007; White *et al.*, 2007; Pilon-Smits and Quinn 2010; Cabannes *et al.*, 2011; Hawrylak-Nowak 2013; Cappa *et al.* 2014; Chao *et al.*, 2014; Khan and Hell 2014; Schiavon *et al.*, 2015; Liu *et al.*, 2015b; Qin *et al.*, 2016), iodine (Zhu *et al.*, 2004; Gómez-Jacinto *et al.*, 2012; Galinha *et al.*, 2013; Smolen *et al.*, 2014), Zn (Germ *et al.*, 2013; Mao *et al.*, 2015), Cu (Landberg and Greger 1994; Hu *et al.*, 2013; Longchamp *et al.*, 2015), as well as the multiple interaction for both Se, S, Mo (Zhang *et al.*, 2012; Harris *et al.*, 2014; DeTar *et al.*, 2015), Se, Zn and iodine (Bevis 2015).

In general, Se and these nutrients have a similar trend in connection with the uptake and its transporters, the biological functions in plants (as a component of some enzymes) and antagonism behavior. For example, selenate, sulfate, molybdate and iodate are similar oxyanion forms that plants uptake from soil as well as all can make use of the same sulfate transporters (Shinmachi *et al.*, 2010; DeTar *et al.*, 2015). Increased Se levels in plants suppress the concentrations of N, P, and S, as well as several amino acids, thus high Se concentrations inhibit the absorption of metals, mainly Mn, Zn, Cu and Cd (Kabata-Pendias 2011).

Although Se and its essentiality are established for human and animals as well as lower plants, nano-Se and Se are required much more evidence for this essentiality in higher plants. The role of Se under different biotic and abiotic stresses has been recorded in case of animals and somehow higher plants, whereas nano-Se is still in needing for more researches to cover this area. The documented behavior of higher plants under Se and abiotic stresses includes the role of Se in enhancing plant defense system including enzymes (CAT, GPx, SOD, GR, DHAR, etc.) and nonenzymes (GSH, GSSG, AsA, etc.). The roles of Se in protecting photosystems from generation/ scavenging of reactive oxygen species are also well known. This role of nano-Se for higher plants needs much more studies comparing with this effect on animals. The interaction between Se and S can be found in several publications for many plants, whereas this interaction between Se and some nutrients

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including Cu, Mo, Zn and iodine is not fully clear and this issue needed to be explored.

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