

INVOLVEMENT OF SELENIUM IN PROTECTIVE MECHANISMS OF PLANTS UNDER ENVIRONMENTAL STRESS CONDITIONS – REVIEW

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In recent years there has been growing interest in selenium (Se) as an important micronutrient not only for animals and humans but also for plants. In particular, its protective effect in plants exposed to stress conditions has been suggested. In spite of many studies, the mechanism of Se action is not fully understood. In this review, possible ways of interaction of Se with stress factors leading to optimal growth and development of plants are presented. As the majority of experiments have focused on the effects of Se application under stress conditions induced by heavy metals, special attention is paid to the results obtained in such studies. Changes of physiological and biochemical properties of plant cells, with particular regard to the influence of Se on the activation of enzymatic and non-enzymatic antioxidants under this stress, are summarized. Experiments in which Se was used in some other environmental stresses (drought, UV, cold and high temperature) are also cited. On the basis of the presented literature it is suggested that a positive effect of Se depends on both its doses and on chosen plant genotypes and is mainly connected with activation of antioxidative defense in plant cells.

Key words: Selenium, environmental stresses, protective mechanisms

INTRODUCTION

Selenium, an element of the VI main group of the periodic system is rather rarely present in the environment. Usually it is chemically bonded to metals forming selenides as MexSe, where Se occurs as an anion in minerals like: crookesites (salts of Cu, Tl, Ag), clausthalite (PbSe), tiemannite (HgSe), antimonselite (Sb₂Se₃) and kullerudite (NiSe₂). With copper it can form compounds in which Se exhibits different degrees of oxidation: berzelianite (Cu₂Se), krutaite (CuSe₂), klockmannite (CuSe). Due to chemical similarity, it can partly replace sulfur in some minerals: sphalerite (Zn(S,Se)), pyrrhotite (Fe(S,Se)), mandarinoite ((Fe₂SeO₃)₃·6H₂O), chalcopyrite (CuFe(S,Se)₂) and pyrite (Fe(Se,S)₂) (Fordyce, 2005). In coal layers, besides pyrite and chalcopyrite, Se has been found in unnamed minerals containing Ni₃As₃S₃Se (Zhu et al., 2012). Another source of Se in the environment are volcano emissions. It was indicated that in the years 1976–2007, Etna eruption increased the content of this element in the surrounding areas from 0.3 to 23 kg/year (Calabrese, 2009). In the air, the most important Se form is selenium dioxide generated in processes of coal combustion. This compound can

be transformed to methyl derivatives or selenium acid and, after adsorption on dust particles, may be transferred into water and soil (Babula et al., 2008).

On a global scale, the average concentration of Se in soils was found at the level of 4 mg/kg, however, due to the geological structure of areas, its local content varies even within the same country. In Europe: Finland, Sweden, Germany, Hungary and Scotland, where Se amount in soils is about 0.05 mg/kg, are considered to be particularly poor in this element (Fordyce, 2005). In Poland, Se concentration in soils is also rather low, and is estimated on average 0.27 mg/g (Borowska, 1998; Cuvardić, 2003). On large areas of the USA, New Zealand and China there are regions of both: very low (0.02–0.1 mg/kg) and high (greater than 4.5 mg/kg) Se levels (Fordyce, 2005).

The content of Se in the soil determines accumulation of this element in plants. Se bioavailability depends on its chemical form and is affected by pH, redox potential, organic matter, competitive ions and microbiological activity of soil (Elrashidi et al., 1987; Hartikainen, 2005; Zhang et al., 2007; Hawrylak-Nowak et al., 2015). Selenate (SeO₄²⁻) is the predominant form in alkaline pH, whereas in acidic and neutral pH Se exists mainly as selenite

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(SeO_3^{2-}) (Zhu et al., 2009). Moreover, in soils under strongly reducing conditions, Se can also occur as selenide (Se^{2-}) (Cuvardić, 2003). In addition to these inorganic Se compounds, it has been demonstrated that plants may absorb Se from soil in its organic forms (Abrams et al., 1990; Zhu et al., 2009; Keskinen et al., 2010). Depending on the amount of accumulated Se ions, plants were classified as so-called "non-accumulators", which usually contain less than 25 $\mu\text{g Se/g}$ dry weight (DW), "indicators" – accumulating from 25 to 1000 $\mu\text{g Se/g DW}$ and "hyper-accumulators" having the ability to uptake even more than 1000 μg of this element in 1g of DW (Galeas et al., 2007). Despite the ascertained accumulation of Se in plants, the presence of specific membrane receptors for this element has not been recognized yet (Zheng et al., 2014). It is assumed that the uptake of selenate occurs through high-affinity sulfate transporters (Terry et al., 2000; Sors et al., 2005), whereas of selenite – by phosphate transporters (Li et al., 2008) and that the preference of the uptake pathway is dependent on the plant species (Keskinen et al., 2010). Selenate supplementation stimulates translocation of Se from the roots to the leaves (De Souza et al., 1998; Zhang et al., 2003; Mazej et al., 2008; Mehdi et al., 2013) but when selenite is present in soils, Se occurs in the root system (De Souza et al., 1998; Terry et al., 2000; Li et al., 2008). Both these Se forms are activated by ATP-sulfurylase-adenosine 5'-phosphoselenate (APSE), reduced by adenosine 5'-phosphosulfate reductase into selenite, and then non-enzymatically reduced by glutathione to selenide (Mehdi et al., 2013). In plants with lower ability to uptake Se, the next steps of this Se-transformation are connected with activation of mechanisms leading to synthesis of selenocysteine and seleniomethionine with dimethylselenide (DMSE) as the final product, contrary to plants with high ability to Se accumulation, where selenocystine is bi-methylated to dimethyl diselenide (DMDSe) (Mehdi et al., 2013).

In recent years numerous articles have been published describing Se as a protective substance counteracting various stress factors (see review Feng et al., 2013). Because the mechanism of plant resistance/tolerance to environmental stresses has not been fully clarified yet (Kacperska, 2004; Sharma et al., 2012), it is also difficult to describe precisely the mechanism of Se-defense action. Since this element is not classified as essential for normal plant metabolism, both its minimum/maximum concentrations and chemical form may be important for the protective mechanism. The proposed Se-defense mechanism assumes its effect on the detoxification of cells (Hanson et al., 2004; Babula et al., 2008). In this review the hypotheses about the protective role of Se in diminishing of cell damage caused by various stressors are summarized.

HEAVY METAL STRESS

Heavy metal pollution has become a serious problem because of its intensive growth over the last century caused by anthropogenic activities (Cabala and Teper, 2007). It is associated not only with impaired growth and development of plants but also with the increased content of metals in crops, causing severe health risks for animals and humans (Boughriet et al., 2007). Typical heavy metal stress is referred to action of such metals as: cadmium (Cd) (Santos et al., 2012; Asgher et al., 2014), lead (Pb) (Sengar et al., 2008), arsenic (As) (Sharma, 2012), mercury (Hg) (Sahu et al., 2012), aluminum (Al) (Panda et al., 2009) and antimony (Sb) (Pan et al., 2010). However, other metals, even those that are necessary for the proper plant development such as: zinc (Zn) (Baran, 2013), manganese (Mn) (Todorović et al., 2009), copper (Küpper et al., 2009) and iron (Fe) (Connolly and Guerinot, 2002) act as stressors when present at higher concentrations.

Supplementation of Se (in both selenite and selenate forms) to "hyper-accumulator" and "indicator" plant species resulted in diminishing of the effects of heavy metal stress. As it was summarized in Table 1, to induce protective action in monocotyledons (usually considered as "indicators") generally smaller doses of Se (2–15 μM) were applied, whereas for dicotyledons ("hyper-accumulators") higher levels of these substances (even to 800 μM) were needed. However, for the latter genotypes in some cases similar doses, as in the case of monocotyledons, were also used (Table 1). Defense reactions were usually described as a combination of various physiological and biochemical effects.

The visual effect associated with the addition of small amounts of Se ions to the soil was an increase in mass of plant tissues and organs, blocked during growth in heavy metal presence. The main reason for reduction of plant development is connected with disorders of the photosynthesis process. For metal-stressed plants, an increase of photosynthetic efficiency in Se presence was indicated *inter alia* by Issa and Adam (1999), Filek et al. (2010c) and Zhang et al. (2014). On the basis of measurements of photosynthesis parameters it was suggested that in such conditions Se induces stimulation of the energy flux through the transport systems in PS II. The explanation of this Se-effect is not evident. It was shown, that Se applied alone in low concentrations, did not (or only slightly) influence the chlorophyll fluorescence parameters (Valkama et al., 2003; Hawrylak-Nowak et al., 2015). Since heavy metals cause a reduction in photosynthetic capacity and disturbances of electron transport, Se-initiated restoration of these processes can occur in two ways: 1) by a direct Se action on the protein-enzymes localized in chloroplasts and/or 2) indirectly – by such modifica-

TABLE 1. Protective effects of Se dosages on different plant species in the metal stress conditions.

	Plants	Stresses heavy metal/ dosages	Se speciation/ dosages	References	
Mono-cotyledones	<i>Triticum aestivum</i>	Cd 600 - 800 μ M	Se(VI) 2 μ M	Zembala et al. 2010, Filek et al. 2009, Wrona et al. 2007	
		Ni 50 μ M	Se (IV) 15 μ M	Bernat et al. 2014	
		As 20-100 μ M	Se (VI) 10 μ M	Ghosh et al. 2013	
	<i>Zea mays</i>	Cd 8.5-21 μ M	Se (IV, VI) 2.5-35 μ M	Shanker et al. 1996b	
		Cd 50 μ M	Se (IV) 2.5 μ M	Sun et al. 2013	
	<i>Oryza sativa</i>	Cd 35.5-178 μ M	Se (IV) 1.3-12.7 μ M	Feng et al. 2013	
		Sb 14 μ M	Se (IV) 0.6 -6 μ M	Feng et al. 2011	
		Cd 50 μ M	Se(VI) 3 μ M	Lin et al. 2012	
	<i>Lolium perenne</i>	Al 0.2 mM	Se (IV) 10 μ M	Cartes et al. 2010	
	<i>Alium sativum</i>	Cd 55-273 μ M	Se (IV) 14.4 μ M	Sun et al 2010	
Di-cotyledones	<i>Brassica napus</i>	Cd 400-600 μ M	Se(VI) 2 μ M	Filek et al. 2008; Zembala et al. 2010; Filek et al. 2010a,c	
		Cd 0.5-1.0 mM	Se 50-100 μ M	Hasanuzzaman et al. 2012	
		Cd 100 μ M	Se (VI) 2 μ M	Dziubińska et al. 2010	
	<i>Brassica campestris.</i>	Cr 3.5 μ M	Se (IV) 0.6 μ M	Qing et al. 2015	
	<i>Brassica rapa</i>	Cd 100 μ M	Se (IV) 25 μ M	Thiruvengadam and Chung 2015	
	<i>Brassica oleracea</i>	Cd 5.5 μ M	Se(IV) 6 μ M	Pedrero et al. 2008	
	<i>Capsicm annuum</i>	Cd 0.5 mM	Se (IV) 3-7 μ M	Mozafariyan et al. 2014	
	<i>Bechmeria nivea.</i>	Cd 12-38 μ M	Se (VI) 2 μ M	Wang et al. 2014	
	<i>Pteris vittata L.</i>	As 15-300 μ M	Se (VI) 5-10 μ M	Srivastava et al. 2009	
	<i>Coleus blumei</i>	Pb 1 mM	Se (IV) 0.1-1 mM	Yuan et al. 2013	
	<i>Vicia faba L.</i>	Cd 1.83-183.31 μ M	Se (IV) 0.08-8 μ M	Taspinar et al. 2009	
	<i>Phaseolus mungo</i>	Cd 8.5 μ M	Se(VI, VI) 2.5-35 μ M	Shanker et al. 1995	
	<i>Phaseolus aureus</i>	As about 2.5- 10 μ M	Se about 2.5- 5 μ M	Malik et al. 2012	
	<i>Sinapis alba</i>	Cd 33 μ M, Cu 12 μ M, Zn 52 μ M; Pb 302 μ M	Se (IV) 27 μ M	Fargašová et al. 2006	
	<i>Spinacea oleracea</i>	Cr 9.2-22 μ M	Se (IV, VI) 2.5-34.7 μ M	Srivastava et al. 1998	
	<i>Lepidium sativum</i>	Cd 2.7-11 μ M	Se (IV) 2.8-11.5 μ M	Barrientos et al. 2012	
	<i>Lactuca sativa</i>	Cd about 8 μ M, Pb about 90 μ M	Se (IV) about 6 μ M	He et al. 2004	
	<i>Lycopersicum esculentum</i>	Hg 12.5 μ M	Se (IV, VI) 2.5-35 μ M	Shanker et al. 1996a	
	<i>Raphanus sativus</i>	Hg 12.5 μ M	Se (IV, VI) 2.5-35 μ M	Shanker et al. 1996c	
	<i>Glycine max</i>	Hg 45 μ M	Se (IV) 60 mM	Yathavakilla and Caruso 2007	
	<i>Vicia faba</i>	Pb 50 μ M	Se (IV) 1.5- 6 μ M	Mroczek-Zdyrska and Wójcik 2012	
	<i>Medicago sativa</i>	As 2.7-0.5 μ M	Se (VI) 0.25-0.5 μ M	Khattak et al. 1991	
	<i>Helianthus annus</i>	Cd 20 μ M	Se (VI) 5-20 μ M	Saidi et al. 2014	
	<i>Thunbergia alata</i>	As 1-20 μ M	Se (IV) 5 μ M	Bluemlein et al. 2009	
	Other organism	<i>Clorophytum comosum</i>	As 150 μ M	Se (IV, VI) 140-170 μ M	Afton et al. 2009
		<i>Scenedesmus oblioguus</i>	Cd, Zn, Mn, Ni 0.1 mM	Se (VI) 0.1 mM	Issa and Adam 1999
		<i>Pteris vittata</i>	As 2.3 -16 μ M	Se (IV) 4.2 - 29 μ M	Feng et al. 2009
As 150-300 μ M			Se (VI) 5-10 μ M	Srivastava et al. 2009	
<i>Gracillaria dura</i>		Cd 0.4 mM	Se (IV) 50 μ M	Kumar et al. 2012	
<i>Spirulina platensis</i>	Cr about 57.6 μ M	Se about 63.3 μ M	Belokobylsky et al. 2004		

tion of the membrane structure (by changes of fluidity), which promotes activation of protein-enzymes (by steric interaction). Studies of the isolated chloro-

plasts/plastids indicated that for plants treated with heavy metals at simultaneous Se presence partial remodeling of the membrane lipid composition dis-

turbed by heavy metals was observed (Filek et al., 2009, 2010a). Thus, the protective role of Se may be connected with ensuring the optimal hydrophilic/hydrophobic conditions necessary for membrane integrity and functioning of integral protein-transporters under heavy-metal stresses. Either competition of Se and metal ions for adsorption on specific sites located on the membrane surface or attaching Se to metal cations present in the environment, was suggested (Gzyl-Malcher et al., 2009). Investigations performed on model lipid membranes indicated the influence of both: Se ions alone, and in mixture with molecules (of cationic and anionic character) on structural and electric properties of monolayers (Gzyl-Malcher et al., 2009; 2011). The preference of Se ions to adsorb on specific lipid domains may be responsible for protection of membranes, against action of toxic metals. As another possibility, connection of Se anions and metal cations in the medium (soil or cytoplasm) may decrease their toxic concentration for plants.

Involvement of Se in the defense mechanisms of biomembranes (plasmalemma) was also indicated by Wrona et al. (2007). The rise of membrane permeability measured as an increase of ions' leakage, caused by Cd-stimulated damages, was partly diminished by Se application in wheat *in vitro* cells. Changes of membrane permeability is usually referred to an alteration of fatty acids' saturation, which in turn affects their fluidity. There are numerous articles devoted to both: an increase and a decrease (Hernández and Cooke, 1997; Nouairi et al., 2006; Chaffai et al., 2007) of lipid unsaturation degree under heavy metal stresses. Se-induced changes of the proportions in fatty acid content were indicated mainly as an increase of membrane unsaturation, in contrast to heavy metal stresses resulting in formation of more saturated lipid layers, under heavy metal stresses (Filek et al., 2008; 2010a).

Another possibility of Se action was also considered – through its direct effect on the activity of membrane protein-transporters. Dafré et al. (1996) and Ramos et al. (2002) suggested inhibition of photosynthesis in heavy metal presence in terms of chloroplast protein damage by irreversible binding of Me to SH-groups of enzymes and membrane proteins. Thus, Se ions can prevent such binding through the "inactivation" of metals even before their binding to protein (in the form of $\text{MeSeO}_{3(4)}$) or by formation of SeH-groups in proteins (due to chemical similarity of Se and S). This gives additional possibilities for the formation of bonds in protein transporters. The impact of Se on heavy metal modification of ion channel activities was indicated by Dziubińska et al. (2010) in studies of slow vacuolar channels in *Brassica nap.* plants.

Both suggested Se-protective actions, i.e. its influence on changes of properties of membrane

lipids and of the activities of ions channels and transporters, disrupted by adsorption of heavy metal ions, may be the important steps to restore the ionic homeostasis in plant cells. On the one hand, Se actions may reduce the accumulation of toxic metals, which was confirmed in numerous works (e.g. Afton et al., 2009; Bernat et al., 2014). A decrease in heavy metal uptake was also suggested as an important factor in maintaining proper water balance in cells, disturbed by their presence at high concentrations (Ajiboso and Adenuga, 2012). On the other hand, Se presence may influence the distribution of elements essential for plant growth and development (Filek et al., 2010c; Feng et al., 2013; Tobiasz et al., 2014).

Dysfunction of photosynthesis caused by heavy metals was considered as the main reason for the increased accumulation of reactive oxygen species (ROS) in the cells and for induction of oxidative stress. The following particles are considered as ROS: superoxide anion (O_2^-), singlet oxygen ($^1\text{O}_2$), hydroxylic free radical (OH^\cdot), hydrogen peroxide (H_2O_2). The enhanced generation of ROS may pose a threat to plants, but ROS are also regarded as signals to create stress response and defense pathways (Mittler, 2002). As an indirect indicator of oxidative stress, an increase in the concentration of antioxidants and rise in activity of antioxidant enzymes are usually determined. Among antioxidant enzymes, the activity of superoxide dismutases (SOD), catalase (CAT) and glutathione- and ascorbate-peroxidases (POX) were measured (Bartosz, 1997; Alscher et al., 2002; Seppänen et al., 2003). Regarding other antioxidants, an increase in the level of glutathione (GSH) and ascorbates (AsA) (hydrophilic substances) as well as of α -tocopherol and carotenoids (hydrophobic antioxidants) was detected (Gzyl-Malcher et al., 2010; Szarka et al., 2012). As to the Se-protective action, most of the articles are focused on changes in the level of these substances in comparison to that after heavy metal application. Since the increase in the concentration/activity of antioxidants was already described (as a defense mechanism to maintain redox balance in cells), it is difficult to interpret data obtained under both Se+metal presence. For example, Wang et al. (2014) and Qing et al. (2015) found that metal stress (Me) induced a decrease in SOD activities (due to a damage of the protein structure), whereas Se addition stimulated an increase in the activity of these enzymes. However, Ghosh et al. (2013) suggested an opposite tendency: an increase in SOD activity at Me (As) application and its decrease in Se+Me presence. The analyzed SOD activity was regarded as the sum of the effects of individual components (various Me-SOD). This causes additional difficulties in the interpretation of the specificity of Se-protection mechanism (i.e. which of Me-SOD forms is activated).

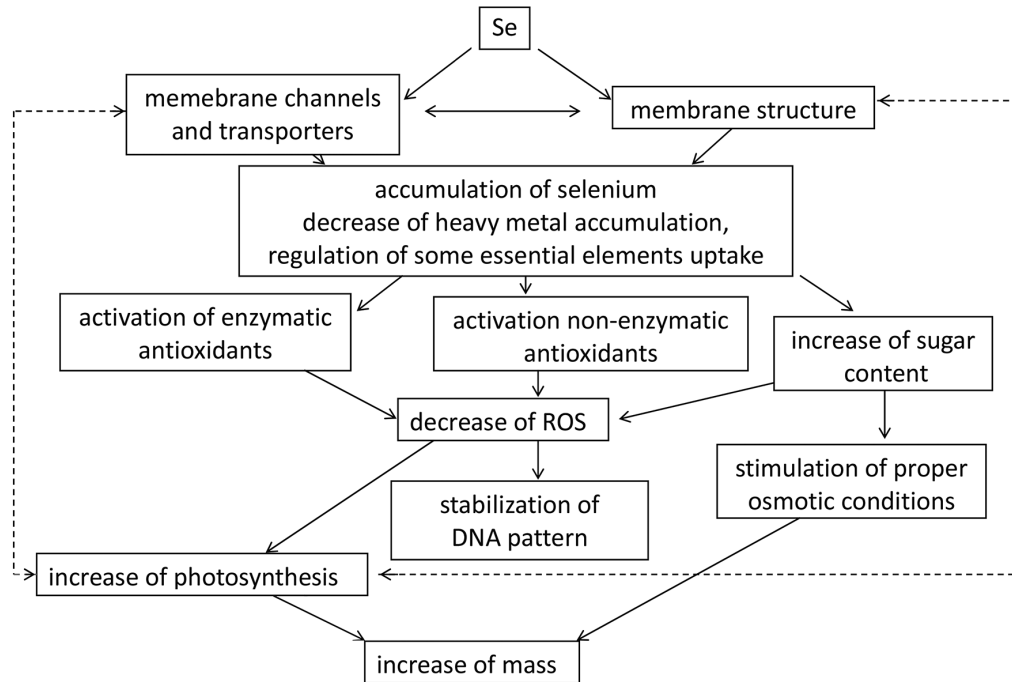


Fig. 1. Schematic summarization of selenium action on some biochemical and physiological properties of plant cells exposed to stress factors prepared on the basis of research presented in this article. Detailed description was introduced in the text. Suggested steps of the induction of biochemical reactions were marked by a solid line. Dotted line marked the direct effect of Se-modified membrane lipids (and membrane channels) on photosynthesis process.

Ambiguous results were also obtained for non-enzymatic antioxidants. For example, the content of tocopherol (localized in hydrophobic part of biomembranes and preventing lipid peroxidation), either decreased or increased in additional Se-presence. These changes in the synthesis of antioxidants in conjunction with registered reduction in the accumulation of heavy metals may indicate that the latter effect is critical for the interpretation of the mechanism of oxidative stress in both metal and Se presence (Srivastava et al., 2009; Feng et al., 2011).

Recent studies indicate the possibility of including also the so-called "organic traps" for free electrons (which are localized mainly on the carbohydrate rings) in the protective mechanism against oxidative stress (Łabanowska et al., 2012a; 2013). As the Se-stimulated rise of carbohydrate concentrations has been shown in studies of Turakainen et al. (2004) and Owusu-Sekyere et al. (2013), it is suggested that synthesis of higher amounts of sugars in the presence of Se ions can be an effective step in the "inactivation" of radicals, produced in heavy metals-initiated oxidative stress (Łabanowska et al., 2014).

Based on the observations found for animal cells, that both heavy metals (Cd) and Se influence the level of DNA methylation (Davis et al., 2000; Takiguchi et al., 2003), similar dependence was analyzed also for plants. The obtained data suggest that

Se application to plants prevents changes in the DNA methylation pattern triggered by high heavy metal concentrations (Filek et al., 2008).

In conclusion, the scheme of the protective role of Se during the heavy metals stress is presented in Fig. 1.

DROUGHT STRESS

Drought stress in plants is usually understood as a water deficit in the cells, associated with impaired osmotic conditions. It may be caused by lack of availability of water through the root system initiated by soil drought and/or salt stress. Due to the detected lowering of the groundwater levels and increasing soil salinity, which reduces availability of water for the germinating plant, this kind of stress is presently a serious problem for food production. Besides the observed remarkable reduction in plants weight, drought stress was accompanied by a significant decrease in maximal efficiency of photosynthesis in PSII and by an increase in synthesis of enzymatic and non-enzymatic antioxidants suggesting an initiation of oxidative stress in these conditions (Filek et al., 2014; Grzesiak et al., 2013).

Se application at low concentrations usually did not affect the growth parameters of plants under drought stress, in spite of the stimulation of photo-

TABLE 2. Protective effects of Se dosages on different species in drought/NaCl conditions.

	Plants	Drought/NaCl	Se speciation/ dosages	References
Mono-cotyledones	<i>Triticum aestivum</i>	drought	Se (IV) 2.8–17.3 μM	Yao et al. 2009 ab
			Se(IV) 0.57 μM	Yao et al. 2012
			Se (IV) 2.9 μM	Xiaoquin et al. 2009
			Se (VI) 4–21 μM	Ibrahim et al. 2014
			Se(IV) 0.01–0.25 μM	Kuznetsov et al. 2003
			Se (IV) 2.9–17.34 μM	Yao et a. 2009
			Se (VI) 3.7–14.7 μM	Nawaz et al. 2014
			Se 2.5 μM	Ajiboso and Adenuga 2012
Di-cotyledones	<i>Oryza sativa</i>	drought	Se (VI) 30 μM	Emam et al. 2014
	<i>Brassica napus</i>	drought	Se (VI) 79–159 μM	Zahedi et al. 2011
			Se (VI) 25 μM	Hasanuzzaman and Fujita 2011
			Se (IV) 16–21 g/ha	Pazoki et al. 2010
	<i>Cucumis melo</i>	100 mM	Se (IV) 0–16 μM	KeLing et al. 2013
	<i>Cucumis sativus</i>	50 mM	Se (VI) 5–10 μM	Hawrylak- Nowak 2009
	<i>Hordeum vulgare</i>	drought	Se (VI) 30g/ha	Habibi 2013
	<i>Olea europea</i>	drought	Se (VI) 265 μM ; 794 μM	Proietti et al. 2013
	<i>Rumex patientia</i> · <i>R. tianshanicus</i>	100 mM	Se (VI) 1–5 μM	Kong et al. 2005
	<i>Solanum tuberosum</i>	drought	Se (VI) 53 μM	Germ et al. 2007
Se (VI) 53 μM			Germ 2008	
<i>Trifolium repens</i>	drought	Se (VI) 5 μM	Wang 2011	

TABLE 3. Protective effects of Se dosages on different plant species under UV – ultraviolet radiation, LT – low temperature and HT – high temperature conditions.

	Plants	Other stresses	Se speciation/dosages	References
Mono-cotyledones	<i>Triticum aestivum</i>	UV	Se (IV) 2.9–17.3 μM	Yao et al. 2010ab
		UV	Se (IV) 5.7 μM	Yao et al 2011
		LT	Se (IV) 2.9–17.3 μM	Chu et al. 2010
		LT	Se (VI) 26 μM	Akladious 2012
	<i>Hordeum vulgare</i>	UV	Se (VI) ok. 0.6–6.6 μM	Valkama et al. 2003
	<i>Lolium perenne</i>	UV	Se (VI) ok. 0.6–6.6 μM	Xue and Hartikainen 2000
	<i>Sorghum bicolor</i>	HT	Se (VI) 400 μM	Djanaguiraman et al. 2005, 2010
		LT	Se (VI) 16–32 μM	Abbas 2012
	<i>Fagopyrum esculentum</i>	UV	Se (IV, VI) 26.5–115.5 μM	Ozbolt et al. 2008
			Se (VI) 5.3 μM	Breznik et al. 2005ab
Se (VI) 52.9 μM			Germ et al. 2006	
Di-cotyledones	<i>Cucumis sativus</i>	LT	Se (VI) 2.5–10 μM	Hawrylak-Nowak et al. 2010
	<i>Lactuca sativa</i>	UV	Se 0.01–0.05 mg/kg	Pennanen et al. 2002
	<i>Cucurbita pepo</i>	UV	Se (VI) 8 μM	Germ 2005
	<i>Lactuca sativa</i>	UV	Se (VI) ok. 0.6–6.6 μM	Xue and Hartikainen 2000
	<i>Acer saccharinum</i>	HT	Se (IV) 58 μM	Pukacka et al. 2011
	<i>Fragaria</i> × <i>ananassa</i>	UV	Se (VI) ok. 0.6–6.6 μM	Valkama et al. 2003

synthesis and/or antioxidative defence system (Tab. 2). In Se-supplemented plants growing under water-deficit conditions the higher (in comparison to plants cultured without Se addition) activities of such antioxidative enzymes as CAT and POX were

detected (Xiaoqin et al., 2009; Habibi, 2013; Proietti et al., 2013). However, Ibrahim (2014) and KeLing et al. (2013) registered also an increase in SOD activity under these conditions. Moreover, the content of non-enzymatic antioxidants (AsA and GSH)

(Ibrahim, 2014) and total carbohydrates level (Emam et al., 2014) were increased. It was concluded that Se ions can improve plant tolerance against drought-induced oxidative stress through stimulation of the plant's antioxidant system (Ibrahim, 2014). As a confirmation of the reduction of the ROS amount may serve an observation that the level of lipid peroxidation, increased due to reaction with oxygen radicals (under drought stress conditions), decreased in the presence of Se to the value close to not-stressed plants (Yundeao et al., 2012; Proietti et al., 2013). Participation of selenium ions in regulation and ensuring optimum water status in cells is considered as the main mechanism associated with the protective action under drought conditions (Proietti et al., 2013). The Se – stimulated increase in the concentrations of organic (total carbohydrate and protein) and non-organic (Ca and P ions) osmo-protectants may cause enhanced water retention in wheat tissue (Emam et al., 2014). Further research will help to better describe the mechanism of interaction of Se with drought stress.

OTHER STRESSES

Demonstration of the protective action of Se against antioxidative stress led researchers to use this element also in relation to other stressors. In Table 3 the positive effect of this ion in mitigating the effect of stresses induced by UV radiation, senescence, desiccation, high and low temperature has been presented.

It was generally indicated that addition of Se diminishes the negative influence of these stresses on biomass production in plants and fruits (Hartikainen et al., 2000; Xue et al., 2001; Turakainen et al., 2004; Breznik et al., 2005ab; Germ et al., 2005; Germ et al., 2007). It was suggested that Se applied in appropriate doses can regulate oxidative stress via activation of antioxidative enzymes (Hartikainen et al., 2000; Cartes et al., 2010) and/or by direct quenching of $O_2^{\cdot-}$ and OH^{\cdot} radicals (Xue et al., 1993). Enhanced content of anthocyanin, sugars and proline under these conditions may indicate involvement of synthesis of other non-enzymatic substances (Akladios, 2012). An increase in chlorophyll content and in activity of quantum yield of photosynthesis (in PSII system) were also indicated (Breznik et al., 2005a). Thus, it seems that basic mechanism of Se impact in plant protection against other stresses may be similar to that found in the case of heavy metal stresses.

IN CONCLUSION

On the basis of presented articles the beneficial effect of selenium application, manifested by increasing tolerance of plants to the stress factors,

mainly induced by heavy metals, was indicated. The suggested properties of Se as a substance responsible for the activation of antioxidant system in plant cells, led to extending its application in the case of action of other stresses (drought, UV, low/high temperature). As it was presented in this review, the range of Se-protective doses changed depending on the stress factor as well as on the plant genotypes. Especially, mono-cotyledons needed smaller Se-concentration, in comparison to di-cotyledons, to obtain antioxidative effects. This review can help in choosing the optimal Se concentrations for receiving the protective effects in selected plant genotypes. Moreover, the presented and summarized physiological and biochemical reactions may be used in future studies to clarify all stages of the mechanism of Se action in plant cells. In spite of spectacular action of Se ions resulting in reduction of toxic changes in plant cells, this element high concentration can induce also the stress conditions. Hartikainen and Xue (1999), Hartikainen et al. (2000), Filek et al., (2010b), and Łabanowska et al. (2012) indicated that too high Se doses were toxic to plants and caused e.g. stunting, chlorosis, a decrease in protein synthesis, blocking of micro- and macroelement transport and an increase in oxidative stress. Ebbs and Leonard (2001), Bluemlein et al. (2009) and Malik et al. (2012) reported that Se application was responsible for the increase in arsenate (As) toxicity. To obtain positive physiological effects of Se-supplementation one should recognize the possibility of accumulation of this element in the studied genotypes and probability of its interaction with other uptaken elements.

AUTHORS' CONTRIBUTIONS

AS – conception and design of manuscript; AS, MF and AK – analysis and interpretation of data, acquisition of data and drafting of manuscript. The authors declare that they have no conflicts of interest.

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