
The Essentiality of Selenium for Plants, and Their Role in Plant Physiology. A review

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ABSTRACT

Selenium (Se) is a trace element indispensable for humans, animals and some microorganisms. For plants, its essentiality has not yet been established, despite its responsibility for a number of beneficial effects in several plant species. Plants take up Se mainly as selenate and selenite, using root high-affinity membrane transporters that normally mediate the influx of sulfate and phosphate ions, respectively. Se can access the sulfur (S) assimilation pathway and incorporated into the Se-amino acids Se-cysteine (SeCys) and Se-methionine (SeMet). Studies with transgenics showed that some enzymes working in this pathway are rate limiting for Se uptake, tolerance and accumulation in plants. Selenium at high concentration is toxic for plants, both due to oxidative stress and because Se-amino acids are non-specifically incorporated into proteins, which lose their folding and function as a result. Therefore, plants have evolved different strategies to cope with Se toxicity. They usually involve the conversion of Se-amino acids into less harmful volatile compounds. Specifically, plants that do not accumulate Se at high levels produce dimethylselenide (DMSe) using SeMet as a precursor, while Se-hyperaccumulators, i.e. plants able to tolerate and accumulate significant amounts of Se in their tissues, and generate dimethyldiselenide (DMDS₂) starting from the amino acid SeCys. Selenium hyperaccumulators have additional mechanisms to prevent SeCys disincorporation into protein, like methylation of SeCys to methylselenocysteine (MeSeCys) via SeCys methyltransferase (SMT), and breaking down of SeCys into elemental Se and alanine. Hyperaccumulators also have elevated selenocysteine methyltransferase (SMT) levels, whose product is the main form accumulated, methylselenocysteine. This form is sequestered in hyperaccumulators mainly in epidermis and reproductive tissues. Transcriptomic and biochemical analyses indicate constitutively elevated levels of the hormones jasmonic acid, salicylic acid and ethylene, which may explain the constitutive up regulation of sulfate uptake and assimilation. Hyperaccumulators also have higher transcript levels of genes involved in oxidative stress resistance and defense against biotic stress, which may contribute to Se tolerance and are upregulated by the same stress/defense hormones.

Keywords: Selenium uptake, Translocation, Formation of Seleno-Amino Acids, drought stress

Introduction

Selenium (Se) is not a very abundant element; soil levels are typically below 1 ppm (mg/kg soil), but 4–100 ppm can be found in seleniferous soils. Vegetation on most soils contain less than 1 ppm Se (mg/kg plant dry weight). On seleniferous soils most plant species contain 1–10 ppm Se, but so-called Se hyperaccumulator plants (e.g. from the genera *Stanleya* and *Astragalus*) can accumulate 1000–15 000 ppm (0.1–1.5% Se), even from low external concentrations. Selenium is chemically similar to sulfur (S) and metabolized via the same mechanisms. While the stoichiometry of Se and S in plants generally reflects that of their environment, hyperaccumulators typically contain elevated Se/S ratios, suggesting they can preferentially take up Se by means of specialized transporters. The main bioavailable form of Se in soils is selenate, which can be taken up by plants via sulfate transporters and assimilated into selenocysteine (SeCys) and selenomethionine (SeMet). While Se is essential for many animals and bacteria as well as the green alga *Chlamydomonas reinhardtii*, it has not been shown to be an essential element for higher plants Fu *et al.*, (2002). The reason for Se's essentiality for some organisms is that it is a structural component of specific selenoproteins and seleno-tRNAs. Selenoproteins contain SeCys

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in their active site and often have a redox function, such as the scavenging of free radicals that cause oxidative stress and cancer. The SeCys in selenoproteins is encoded by the opal stopcodon when present in the context of a specific secondary mRNA structure (SeCys insertion sequence). In higher plants, SeCys insertion sequences have not yet been found, and plant homologues of selenoproteins (e.g. glutathione peroxidase, GPX) were found to contain

Cys instead of SeCys in their active site Lobanov *et al.*, (2007). While there is no proof of essentiality for Se in plants, there have been reports of beneficial effects of Se on plant growth. Among higher plants, the largest beneficial effects of Se on growth (up to 2.8-fold higher biomass with Se) have been observed in the Se hyperaccumulator plants, and Se has been suggested to be essential for these species Shrift (1969). Since the beneficial effect of Se on hyperaccumulator growth was much less when the plants were grown at lower phosphate levels, it has also been suggested that Se may act as an antagonist against phosphate toxicity in hyperaccumulators Broyer *et al.*, ((1969). Trace amounts of Se also stimulated growth in a variety of non-hyperaccumulator species including ryegrass, lettuce, potato, and duckweed Hartikainen (2005). The Se-supplied plants showed lower levels of lipid peroxidation and higher levels of GPX activity, and were more resistant to ultraviolet radiation. The mechanism of this apparent positive effect of Se on antioxidant capacity may be direct, owing to antioxidant activity of seleno compounds, or indirect, via Se-induced upregulation of general stress resistance mechanisms. There is mounting evidence that Se can also protect plants from biotic stresses. Supply of Se to hyperaccumulator and non-hyperaccumulator species protected the plants from a wide variety of herbivores, as well as from fungal infections Quinn *et al.* (2007) against biotic stresses may again be a combination of direct and indirect effects. Volatile Se (dimethylselenide) emitted by plants deters herbivores, and plant-accumulated Se is toxic to herbivores and pathogens. Se treatment has also been shown to up regulate plant JA and ethylene production and the production of defence related proteins and up regulation of sulfate/selenate assimilation Tamaoki *et al.* (2008). Thus, fertilization with low doses of Se may promote plant growth and increase resistance to pests and other stresses. While sulfur pathways generally metabolize Se, there is some evidence that plants have evolved Se specific enzymes that facilitate Se accumulation, perhaps to serve an ecological or physiological function. Hyperaccumulators such as two-grooved milkvetch (*Astragalus bisulcatus*), but also broccoli (*Brassica oleracea*) have a Se specific selenocysteine methyltransferase, leading to accumulation of Se as relatively non-toxic methyl-selenocysteine Lyi (2005), Sors *et al.* (2005). There is also a report of an *Arabidopsis thaliana* Se-binding protein that conferred Se tolerance when overexpressed Agalou *et al.* (2005). Since Se is essential at low levels for humans and other mammals, fertilization of crops with Se may not only benefit plant productivity but may have the additional benefit of enhancing its nutritional value White and Broadley, (2009). The window between deficiency and toxicity is relatively narrow for Se, so in case of biofortification with Se it is important to carefully monitor the Se levels in the final food products, to avoid toxicity.

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, and Ag), clausthalite (PbSe), tiemannite (Hg Se), antimonselite (Sb₂Se₃) and kullerudite (NiSe₂). With copper, it can form compounds in which Se exhibits different degrees of oxidation: berzelianite (Cu₂Se), krutaite (CuSe₂), kloekmannite (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). In coal layers, besides pyrite and chalcopyrite, Se has been found in unnamed minerals containing Ni₃As₃S₃Se (Zhu *et al.*, 2012). 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-Nowack *et al.*, 2015). Selenate SeO₄⁻² is the predominant form in alkaline pH, whereas in acidic and neutral pH Se exists mainly as selenite SeO₃⁻² (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). Fig (1)

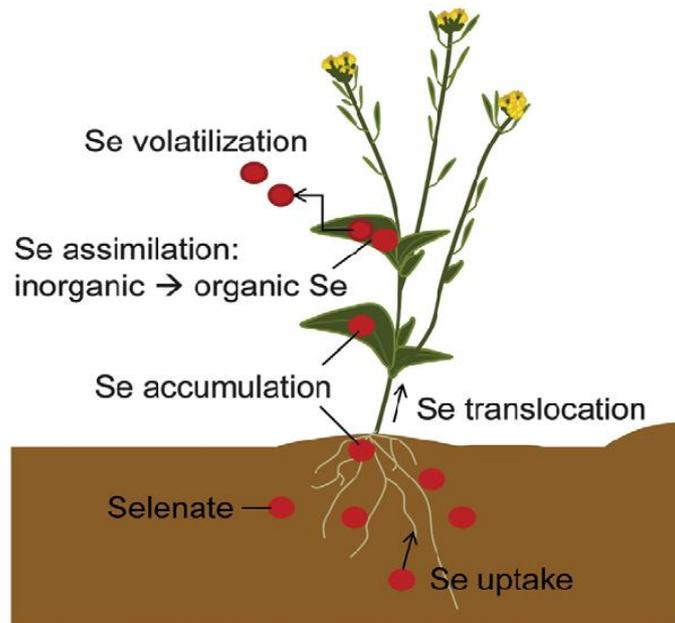


Fig. 1: Schematic diagram represent adsorption of selenium in different forms (After Keskinen *et al.*, 2010).

Depending on the amount of accumulated Se ions, plants were classified as so-called "non-accumulators", which usually contain less than $25 \mu\text{g Se.g. DW}^{-1}$, "indicators" – accumulating from 25 to $1000 \mu\text{g Se.g. DW}^{-1}$ and "hyper-accumulators" having the ability to uptake even more than 1000g of this element in 1g. DW^{-1} Galeas *et al.*, (2007).

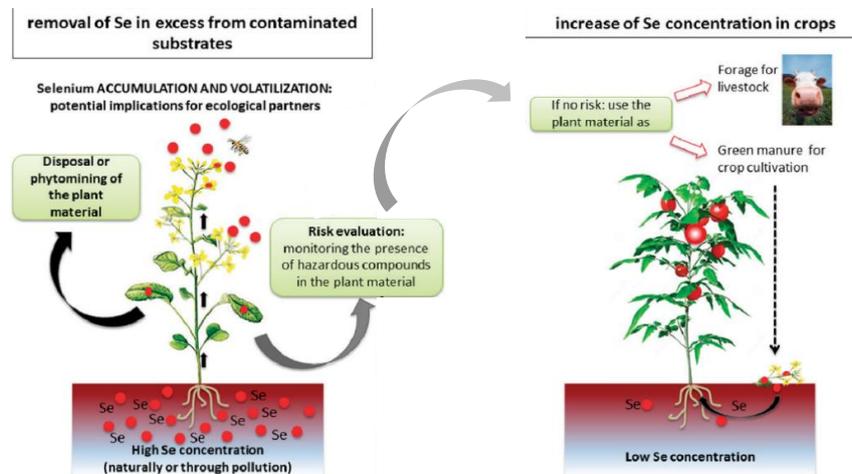


Fig. 2: Summarize selenium action on some biochemical and physiological properties of plant cells

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 (Keskenen *et al.*, 2010).

Fig. (3) Illustrate phosphate transport in plant cells. From which Cytosolic Pi homeostasis depends on Pi transporters at the plasma membrane and tonoplast. Under Pi-sufficient conditions, PHT1 proteins are localized at plasma membranes or delocalized from plasma membranes for degradation in the vacuole based on physiological demands to maintain a stable supply of Pi Meanwhile, the vacuole

utilizes tonoplast-localized transporters to collect cytosolic Pi into the vacuolar lumen. VPT1/ PHT5; 1 and OsSPX-MFS1/3 are major vacuolar influx transporters responsible for vacuolar Pi storage in Arabidopsis and rice, respectively. Under low Pi conditions, expression of PHT1 and VPEs is induced by PHR transcriptional factors, leading to an increase in PHT1 and VPEs protein abundance at the plasma membrane and tonoplast, respectively. Consequently, apoplastic Pi influx through PHT1, and vacuolar Pi efflux through VPEs, coordinately facilitate cytosolic Pi homeostasis. This vacuolar Pi transport system (After Cardona-Lopez *et al.* (2015).

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 accumulate in the root system (De Souza *et al.*, 1998; Terry *et al.*, 2000; Li *et al.*, 2008). 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 selenocysteine is bi-methylated to dimethyl diselenide (DMDS₂) Fig.(3)

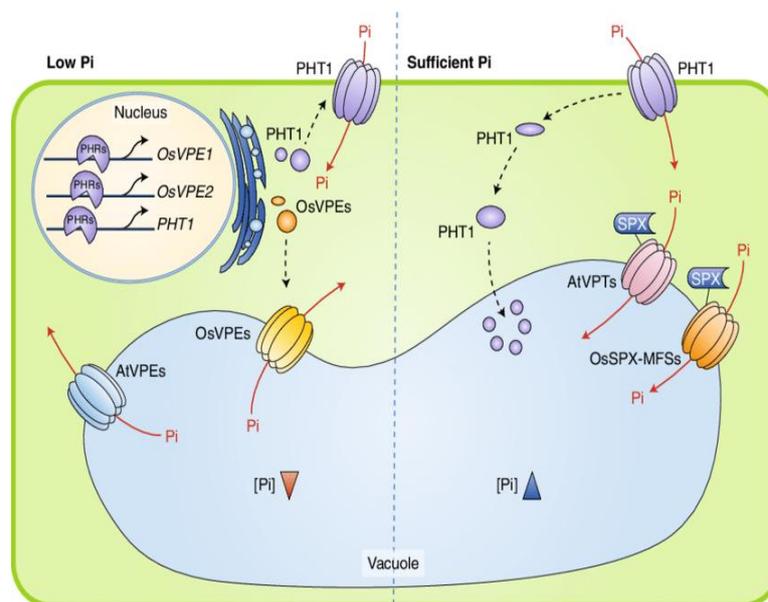


Fig. 3: Illustrate phosphate transport in plant cells (After Cardona-Lopez, X. *et al.* (2015).

(Mehdi *et al.*, 2013). Several reports have been describe Selenium as a protective substance counteracting various stress factors (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 Fig.(4) .

Although it is not classified as essential element 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) Fig. (5).

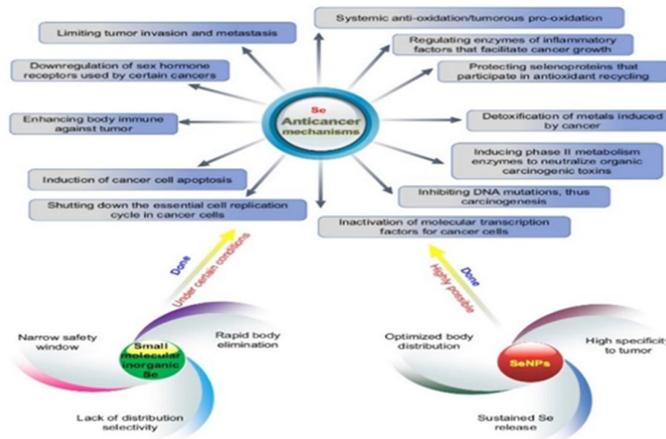


Fig. 4: Schematic diagram outlining the principal effects of selenium on the physiological system.

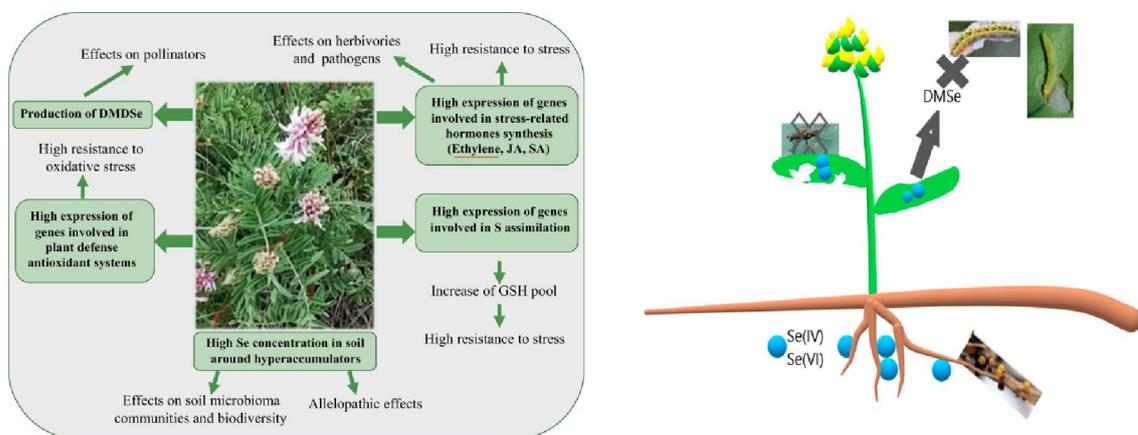


Fig. 5: Schematic diagram proposed Se-defense mechanism and its effect on detoxification of cells (After Babula *et al.*, 2008).

Uptake and Translocation of Selenium

Se can be taken up by plants in two forms, either selenate SeO_4^{2-} or selenite SeO_3^{2-} , plants can also take up organic Se compounds as well. However, White and Broadley (2009) stated that plants that take up elemental Se or metal selenide are unable to utilize these compounds. Selenate is the most common and easiest form of Se taken up by plants and is the predominant bioavailable form particularly in alkaline and well-oxidized soils; however, selenite is the main identifiable bioavailable form under anaerobic conditions (Fordyce 2012).

Due to its chemical similarities to sulfur (S), Se in the form of selenate is transported throughout the plant via the sulfate transport system, which is characterized in *Arabidopsis thaliana* selenate-resistant mutants (Shibagaki *et al.*, 2002) and can be clustered into 4 main groups.

Group 1 includes high affinity sulfate transporters, such as *SULTR1;1* and *SULTR1;2*, which are the best-characterized and primarily found in the roots (Buchner 2004). Group 2 transporters have a low affinity for sulfate, are found throughout the plant, and have a role in sulfate loading into the vascular systems, and thus in translocation. Two isoforms have been identified in *A. thaliana*, *SULTR2;1* and *SULTR2;2*, both expressed in leaves and roots. *AtSULTR2;1* localizes to the xylem parenchyma, as well as the phloem cells in leaves and pericycle cells in roots, while *AtSULTR2;2* is found in the phloem cells in roots and the bundle sheath cells in leaves (Takahashi *et al.*, 2000; Buchner 2004). Group 3 sulfate transporters are only found in leaves, and do not show responsiveness to the sulfur status of the plant (Buchner 2004). *AtSULTR3;1* localizes to the chloroplasts, and loss of this transporter greatly reduced

the sulfate uptake capacity of these organelles Cao *et al.*, (2012). Group 4 includes sulfate transporters localized in tonoplast.

Zuber *et al.*, (2010) reported that *AtSULTR4;1* and *AtSULTR4;2* in *A. thaliana*, characterized as low affinity sulfate transporters which playing a role in sulfate vacuolar efflux, and make sulfate more available for export through the vasculature. They also stated that *AtSULTR4;1* and *AtSULTR4;2* have been involved in contributing to root-shoot translocation and supply sulfate to developing seeds. SeO_4^{2-} enters roots system over high affinity sulfate transporters *SULTR1;1* and *SULTR1;2*, which are proton-sulfate symporters, several researchers Lass and Ullrich-Eberius (1984); Hawkesford *et al.*, (1993) reported that for every molecule of selenate that enters the roots, 3 protons are also taken up. The expression of *SULTR1;1* and *SULTR1;2* is controlled by the sulfur status of the plant. White *et al.*, (2007) stated that *SULTR1;1* expression is lower and control under S-deficient conditions, while *SULTR1;2* is highly expressed under both sufficient and deficient S-conditions. Barberon *et al.*, (2008), they stated that both two transporters have the capacity to mediate selenate transport from the soil into the root, but there is unequal functional redundancy between them. *Arabidopsis thaliana* *SULTR1;2* mutants displayed a higher tolerance to selenate as compared to *SULTR1;1* mutants and wild-type plants, while *SULTR1;1 - SULTR1;2* double mutants exhibited the greatest tolerance to selenate Barberon *et al.* (2008), suggesting that *SULTR1;2* is the essential carrier for selenate entry into the plant, compared to *SULTR1;1*.

SULTR1;2 shares 70% amino acid homology with other high-affinity plant sulfate transporters, and is localized in the root hairs as well as the root epidermis and cortex, and was found to complement the function of two yeast sulfate transporters located in the plasma membrane Yoshimoto (2002). White (2015) in recent research suggests that *SULTR1* homologs found in Se hyperaccumulator species may have a favorite for selenate transport over sulfate, which may explain the high Se/S ratio and Se hyperaccumulator status of these plants. *SULTR1* sequences isolated from several hyperaccumulator species in the genus *Astragalus* (Fabaceae) contain an alanine residue instead of the glycine found in *SULTR1* isoforms of non-accumulating angiosperms, which may play a role in the preferential uptake of selenate over sulfate White (2015); Cabannes *et al.*, (2011). However, high-affinity of sulfate transporters are responsible for transporting selenate into the plant, selenite is taken up through a separate pathway. Root phosphate transporters mediate uptake of selenite. Studies in perennial ryegrass (*Lolium perenne* L. cv. Evening Shade) and strawberry clover (*Trifolium fragiferum* L. cv. O'Conner) observed that uptake of selenite was gradually reduced up to 50% in response to a 10-fold increase in phosphate treatment Hopper and Parker (1999).

Li *et al.*, (2008) noticed that the kinetic parameters (K_m) of selenite influx increased in the presence of phosphate in wheat (*Triticum aestivum*) These results indicate the existence of competition for uptake between selenite and phosphate, suggesting the two molecules share a common transporter, as has been reported for yeast Lazard *et al.* (2010). Plants also have the capacity to take up organic forms of Se through amino acid permeases, which are plasma membrane-localized transporters mediating the uptake of amino acids in the cell. Two common forms of organic Se are selenocysteine (SeCys) and selenomethionine (SeMet) Fig (6).

Normally, these products are formed from inorganic pools of Se through the S assimilation pathway, but there is evidence that plants can take up organic seleno compounds directly. Studies in durum wheat (*Triticum turgidum*) and spring canola (*Brassica napus*) showed that organic forms of Se, specifically selenomethionine and selenocystine, were taken up at rates over 20-fold higher than selenate or selenite Kikkert and Berkelaar (2013). A broad specificity amino acid permease isolated from *A. thaliana* complemented proline uptake in yeast mutant strains, with the strongest competitors for proline uptake being cysteine and methionine Frommer *et al.*, (1993). It is conceivable that this amino acid transporter takes up selenocysteine and selenomethionine as well.

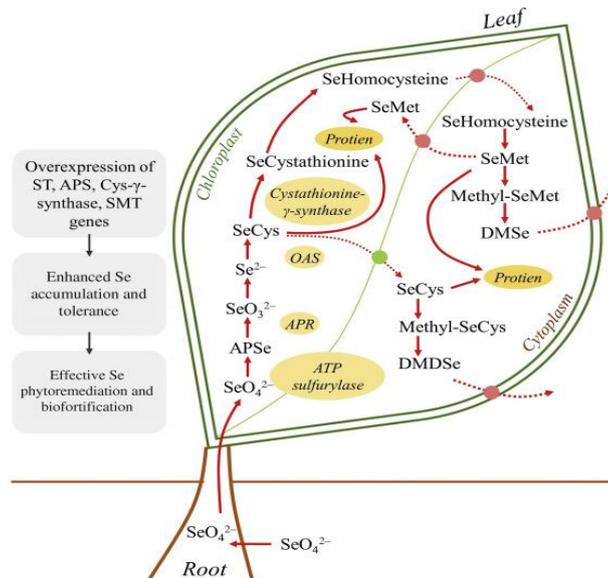


Fig. 6: Illustrate forms of organic Se selenocysteine (SeCys) and selenomethionine (SeMet) S assimilation pathway

Transformation of inorganic Selenium into Organic Forms

Steps of Selenium Assimilation

After selenium, penetrate to roots system, subsequently selenate SeO_4^{2-} needs to be converted into a biologically active form for assimilation into the plant Fig. (7). This step is carried out by the enzyme ATP sulfurylase, which couples selenate SeO_4^{2-} (or sulfate) to ATP, through forming adenosine 5'-phosphoselenate (APSe) or adenosine 5'-phosphosulfate (APS) Pilon-Smits and Le Duc (2009); Schiavon *et al.*, (2015).

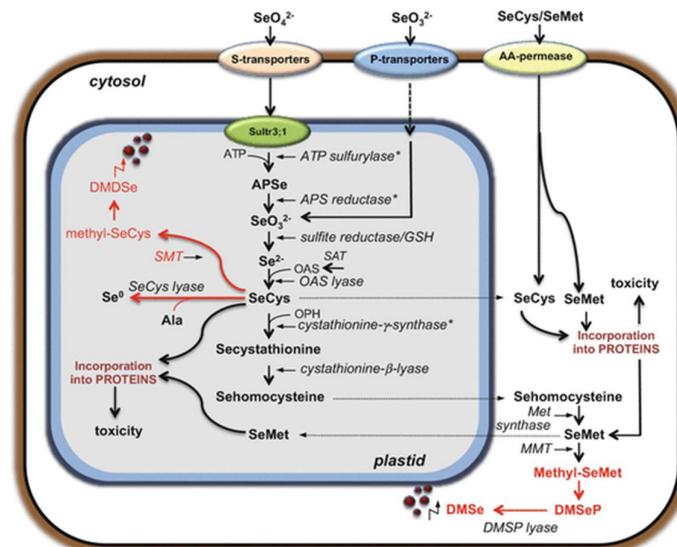


Fig. 7: Schematic diagram of Se assimilation and metabolism in plant mesophyll cells. Red text and arrows indicate Se hyperaccumulator processes. Asterisks indicate enzymes overexpressed through genetic engineering. Sultr sulfate/selenate cotransporters, APSe adenosine phosphoselenate, GSH glutathione, SAT serine acetyltransferase, OAS O-acetylserine, (Se)Cys (seleno)cysteine, OPH O-phosphohomoserine, (Se)Met (seleno)methionine, MMT methyl methionine methyltransferase, DMSeP dimethylselenopropionate, DM(D)Se dimethyl(di)selenide (volatile), SMT selenocysteine methyltransferase. (After White (2015).

This step, was create to be rate limiting in Se assimilation, Pilon-Smits and Le Duc (2009) occurs in both the cytosol and plastids White *et al.* (2007); Pilon-Smits and Le Duc (2009); Pilon-Smits (2012). First characterized during studies of S assimilation, ATP sulfurylase was depressed by a selenate concentration 1/10th that of sulfate, indicating it is responsible for the assimilation of both molecules Reuveny (1977). There have been 4 isoforms of ATP sulfurylase identified in *A. thaliana* (*APS1-4*), all localizing to the plastids of cells Anjum *et al.*, (2015), but *A. thaliana* *APS2* was found to have dual localization to both the plastids and cytosol Bohrer *et al.*, (2015). *ATP* sulfurylase has been a target for genetic engineering of plants with higher Se uptake capacity, with the aim of developing plants for use in phytoremediation. Transgenic Indian mustard (*Brassica juncea*) overexpressing *APS1* from *A. thaliana* showed increased selenate reduction, with roots and shoots containing mostly organic Se compounds as compared to wild-type plants that mostly accumulated selenate Pilon-Smits *et al.* (1999). Greenhouse experiments conducted with *B. juncea* APS transgenic grown on naturally seleniferous soils demonstrated that these plants accumulated Se up to 3-fold higher than wild type plants Huysen *et al.* (2004). Field experiments in California on Se-contaminated soil confirmed these findings, with APS transgenic accumulating 4-fold more Se than wild type plants Bañuelos *et al.* (2005). APSe is converted to selenite by the activity of APS reductase (APR). This reaction happens exclusively in the plastids. APR is an essential enzyme and is reported to be another rate-limiting step in selenate assimilation Sors *et al.*, (2005a, b). The reaction equilibrium of *ATP* sulfurylase favors the reverse direction, and so the products of this reaction need to be converted rapidly in order for assimilation to proceed Sors *et al.*, (2005a, b); Saito (2004). While native expression of APR in several *Astragalus* species was not found to correlate with Se hyperaccumulation, transgenic experiments have shown that overexpression of APR enhances selenate reduction into organic forms, thus suggesting a role for this enzyme in selenate assimilation Sors *et al.*, (2005a, b). APR's role in the Se assimilation pathway is also supported by the fact that increased activity of this enzyme contributed to increased Se flux through the plant (Sors *et al.*, 2005a,b). Apr2-1 Arabidopsis mutants showed enhanced levels of selenate, but decreased levels of selenite, implicating APR2 in converting APSe into selenite Grant *et al.*, (2011). Selenate tolerance decreased by gene alteration, that decreasing levels of glutathione, which helps to prevent the formation of damaging superoxides in the cell Grant *et al.*, (2011). The next step in the Se assimilation pathway is the reduction of selenite to selenide, for incorporation into organic molecules such as amino acids. The conversion of selenite into selenide may occur either enzymatically or non-enzymatically. Sulfite reductase (SiR) is responsible for the conversion of sulfite to sulfide during reductive sulfate assimilation (Yarmolinsky *et al.*, 2012),

Conversion also to selenide may occur non-enzymatically through an interaction between selenite and reduced glutathione (GSH) Anderson and McMahon (2001); Terry *et al.*, (2007); Pilon-Smits (2012). This conversion takes place in multiple steps, with selenite first converted to the organic molecule GSSeSG non-enzymatically, then converted to GSSeH and finally to selenide through the action of glutathione reductase (GR) using NADPH as a reductant Hsieh and Ganther (1975). In support of a GR role in Se assimilation, yeast glutathione was shown to reduce selenite to selenide Hsieh and Ganther (1975). Thus, while the reduction of selenite may be non-enzymatic, the enzyme GR. mediates the regeneration of reduced glutathione. It belongs to the oxidoreductase family of proteins, which require NADP⁺ or NAD⁺ to transfer electrons from one molecule to another Price and Stevens (1999). Glutathione reductase is responsible for converting glutathione from its oxidized state to reduced form, which is essential in numerous cellular processes such as combating oxidative stress, promoting enzyme stability, and the regulation of cell metabolism Jocelyn (1972); Williams (1976). In plants, this enzyme is active in chloroplasts and cytosol Foyer and Halliwell (1976). Several researchers reported that reduction of oxidized glutathione by GR in chloroplasts was to be coupled to photosynthetic electron transport, and may suggest that the reduction of selenite to selenide occurs in the chloroplasts as part of a light-dependent reaction Ng and Anderson (1979). Selenium toxicity in plants can be attributed to many factors, including oxidative stress, but the main cause is considered to be the mis incorporation of selenoamino acids into proteins Pilon-Smits (2012). Brown and Shrift (1982), stated that the avoidance of Selenium toxicity due to incorporating selenoamino acids into proteins is consider a key feature of Se hyperaccumulator species, and is mechanisms for their high Se tolerance.

Formation of Seleno-Amino Acids for Avoiding Selenium Toxicity

White (2015) stated that the Cysteine synthase described as enzyme complex (CS), which catalyzes the formation of Se Cys from O-acetyl serine (OAS) and selenide, is the first step carried out in the formation of selenoamino acids. Such process gradually occurs in the cells of chloroplasts, but also in the cytosol and mitochondria Ng and Anderson (1979), Wirtz *et al.*, (2001). During mass assimilation, Cys is formed by the reaction between O-acetyl serine (OAS) and hydrogen sulfide Giovanelli (1990). Selenocysteine formation is identical to this reaction, with the substitution of hydrogen selenide as a reactant. Cysteine synthase is a complex formed by the association of two enzymes, serine acetyltransferase (SAT) and OAS thiol-lyase (OAS-TL) Bogdanova and Hell (1997). SeCys can be incorporated into proteins nonspecifically, which can lead to disruption of protein function and thus Se toxicity Stadtman (1990); Neuhierl and Bock (1996); Huysen *et al.*, (2003). The prevention of non-specific incorporation of SeCys into proteins is critical in preventing Selenium toxicity. The methylation of SeCys to form methyl-SeCys (MeSeCys) is a key mechanism used by hyperaccumulator species to reduce the amount of SeCys available for incorporation into proteins Pilon-Smits and Le Duc (2009). The enzyme SeCys methyltransferase (SMT) is responsible for this conversion Neuhierl and Bock (1996).

SMT is uniform to other enzymes with similar functions, such as (*Yag D*) in *Escherichia coli*, a homocysteine methyltransferase (HMT) able to methylate both SeCys and homocysteine, and belongs to a class of methyltransferase involved in the metabolism of S-methyl methionine Neuhierl *et al.*, (1999); Sors *et al.*, (2005a, b). SMT was also found to be highly symmetrical to HMTs isolated from *A. thaliana* and *Oryza sativa* Sors *et al.*, (2005a,b), and is localized in the chloroplasts Sors *et al.* (2009). SMT also shows a preference for the methylation of SeCys over Cys by at least 3 orders of magnitude Neuhierl and Bock (1996), further solidifying its role in conferring Se tolerance to plants Neuhierl *et al.*, (1999). SMT has been identified in multiple non-accumulator and Se hyperaccumulator species of *Astragalus* but only the isoform from the hyperaccumulators had the ability to produce MeSeCys, indicating its essential role in the ability to tolerate and accumulate high levels of Se, Sors *et al.* (2009) Fig.(8)

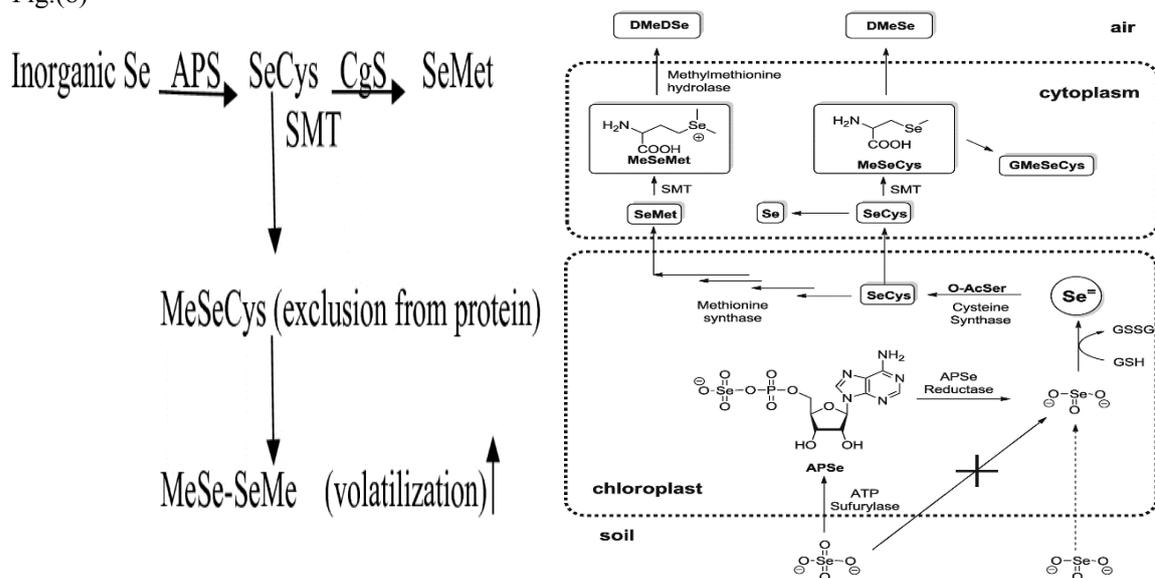


Fig. 8: Volatilization of Se involves assimilation of inorganic Se into the organic selenoamino acids selenocysteine (SeCys) and selenomethionine (SeMet). Selenomethionine can be methylated to dimethylselenide and is volatile Afer Terry *et al.* (2007).

The main form of Se found in the hyperaccumulators *A. bisulcatus* and *Stanleya pinnata* is MeSeCys, due to the high activity of the SMT enzyme Neuhierl *et al.* (1999); Birringer *et al.*, (2002); Pickering (2003); Sors *et al.*, (2005a, b); Freeman (2006, 2010); Lindblom *et al.*, (2013); Alford *et al.* (2014); White (2015), while selenate was the major Se compound found in related non-accumulator species Pilon-Smits (2012). Although SMT is found to be highly expressed specifically in hyperaccumulators

Sors *et al.*, (2009), some Se accumulator species, such as *Brassica oleracea* (Broccoli) also have an SMT enzyme, but it is expressed only in the presence of Se Lyi *et al.*, (2007); Pilon-Smits (2012). SMT has been used in transgenic studies to confer increased Se accumulation and tolerance in non-accumulating species. SMT isolated from *A. bisulcatus* induced the accumulation of MeSeCys and γ -glutamyl-MeSeCys in *A. thaliana*, and increased Se accumulation and volatilization in *B. juncea* Leduc *et al.*, (2006); Ellis *et al.*, 2004). While the production of MeSeCys is critical to Se tolerance in plants, further processing of this molecule into volatile compounds serves as another mechanism by which plants tolerate high levels of Se. The volatile compound dimethylselenide (DMSe) is formed by oxidation and methylation of MeSeCys Meija *et al.*, (2002); Sors *et al.*, (2005a, b). First, MeSeCys is converted to methylselenocysteine selenide oxide (MeSeCysSeO), whose sulfur analog methyl cysteine sulfoxide (MeCysSO) is responsible for many Brassica varieties' characteristic flavors Chin and Lindsay (1994).

This compound is then converted to another key intermediate methaneselenol (CH₃SeH) through the action of the enzyme Cys sulfoxide lyase Chin and Lindsay (1994); Griffiths *et al.* (2002); Ellis and Salt (2003). DMSe production occurs in the leaves, and has been detected in the Se hyperaccumulator *Astragalus racemosus* Evans *et al.*, (1968). Volatile Se compounds have been hypothesized to aid in defense against herbivory. This is supported by not only the fact that the production of these volatiles occurs in the leaves, but that it also occurs primarily after tissue injury Ellis and Salt (2003). The formation of SeMet occurs through the enzymatic conversion of SeCys. There are multiple steps involved in the synthesis of SeMet, which include potential targets for transgenic phytoremediation efforts. First, SeCys is converted to Se-Cystathionine by the enzyme Cystathionine- γ -synthase (CGS) Pilon-Smits (2012). CGS catalyzes the formation of Se-Cystathionine via the condensation of O-phosphohomoserine (OPH) and SeCys Huysen *et al.*, (2013); Sors *et al.*, (2005a, b). CGS was shown to be a rate-limiting enzyme in the conversion of SeCys to volatile DMSe Huysen *et al.*, (2003). Transgenic *B. juncea* overexpressing CGS had 2–3 fold higher Se volatilization rates and concurrent 20–40% lower shoot and 50–70% lower root Se levels compared to wild type plants, highlighting the value of this approach for applications in Se phytoremediation Huysen *et al.*, (2003), (2004). Se-Cystathionine is converted to Se-homocysteine through a reaction between Se-Cystathionine and water, mediated by the enzyme Cystathionine beta-lyase. This enzyme is shared in both the Se and S assimilation pathways, evidenced by the fact that Cystathionine beta-lyase isolated from both Se hyperaccumulator and non-accumulator plant species had the capacity to cleave both Se-Cystathionine and Cystathionine into Se-homocysteine and homocysteine, respectively Sors *et al.*, (2005a, b); McCluskey *et al.*, (1986). Finally, the conversion of Se-homocysteine to SeMet is catalyzed by the enzyme Met synthase. Met synthase has been isolated from plants from various angiosperm taxa, including *A. thaliana*, *Catharanthus roseus*, and *Coleus blumei* Eichel *et al.*, (1995); Petersen *et al.*, (1995); Ravel *et al.*, (1998). Using methyl-tetrahydrofolate as a carbon donor, Met synthase catalyzes the conversion of Se-homocysteine to SeMet Cossins and Chen (1997). Like SeCys, SeMet is subject to further processing steps that reduce its incorporation into proteins. The volatile Se compound DMSe is synthesized via the S volatilization pathway starting from SeMet Tagmount (2002). Enzymes involved in the S volatilization pathway and formation of dimethyl sulfide (DMS) have been discovered to be involved in the production of DMSe Terry and Zayed (1994); Tagmount (2002). The production of DMSe in plants is important not only as a defense against herbivores, but it also diverts large pools of potentially toxic SeMet to the significantly less toxic DMSe. DMSe was found to be almost 600 times less toxic than inorganic Se compounds McConnell and Portman (1952); Wilber (1980). The sulfur analog DMSP is a biologically important molecule, playing important roles in osmoprotection of plants and bacteria Mason and Blunden (1989); Hanson *et al.*, (1994); Kocsis (1998). The mechanisms by which plants accumulate, assimilate, and tolerate Se mirror aspects of the S assimilation pathway, but the roles these two elements play in the plant are very different. By better understanding the pathways of Se assimilation, new approaches to developing plants for phytoremediation and biofortification can be exploited, and mechanisms that hyperaccumulator species exploit in their uptake and assimilation of Se can be further elucidated.

Role of Selenium in Trace Metal Stress Tolerance

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 modification of the membrane structure (by changes of fluidity), which promotes activation of protein-enzymes (by steric interaction). Studies of the isolated chloroplasts/ plastids indicated that for plants treated with heavy metals at simultaneous Se presence partial remodeling of the membrane lipid composition disturbed 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. Wrona *et al.* (2007) also indicated involvement of Se in the defense mechanisms of bio membranes plasma lemma). 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 membranelipids 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 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 ($O_2^{\cdot-}$), singlet oxygen (O_2), hydroxylic free radical (OH), 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. 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). Ambiguous results were also obtained for non-enzymatic antioxidants. For example, the content of tocopherol (localized in hydrophobic part of bio membranes 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 "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).

Selenium Improves Drought Tolerance of Crop Plants

A number of adverse environmental factors often disrupts plant metabolism; therefore, it is important to conduct research towards the increasing ability of plants to survive in these unfavorable conditions. Drought is one of the main factors limiting crop yielding. About 45% of the world crop area is exposed to continuous or frequent drought stress, and over 40% of worldwide yields, especially vegetables, are obtained on artificially irrigated soils Yokota, *et al.*, (2006). High water requirements are one of the reasons for restricted cucumber cultivation. This species is extremely sensitive to a water

deficit (WD) Liu *et al.*, (2009), Fan *et al.*, (2014), which is associated with a poorly developed and shallow root system, the production of a large mass of above-ground parts, and a high water content in fruits. Low soil moisture reduces the size and quality of a cucumber *yield* Wang *et al.*, (2004) Fig.(9). Various biotic and abiotic stress factors, including a WD, induce, in plants, oxidative stress, which is one of the earliest universal responses of cells revealed by a violent increase of the intracellular level of reactive oxygen species (ROS) in form of hydrogen peroxide (H_2O_2), superoxide anions (O_2^{-}), and hydroxyl radicals (OH^{-}) Dat *et al.* (2000), Van *et al.* (2006).

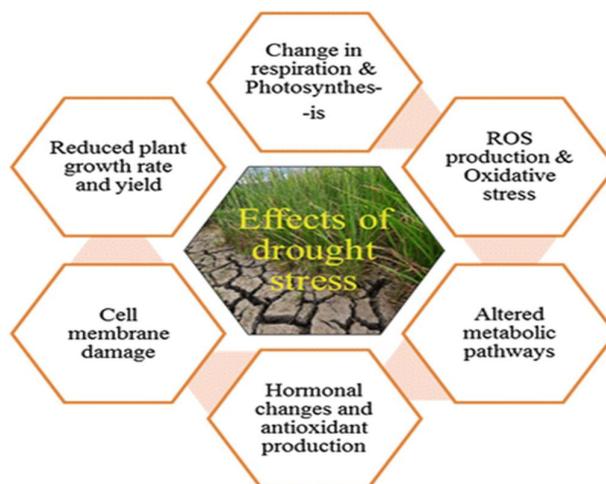


Fig. 9: Effects of water deficit stress in crop plants (Iqbal *et al.* (2017)

For the proper course of metabolic processes, it is necessary to maintain a balance between ROS generation and scavenging. Oxidative stress relies on disturbing the balance between the formation and degradation of ROS. However, when the amount of ROS exceeds the efficiency of antioxidant systems, free radical changes may occur in the cells that damage cellular components, including the oxidation of thiol groups of proteins, lipid peroxidation, and the disruption of DNA strands Fig. (10)

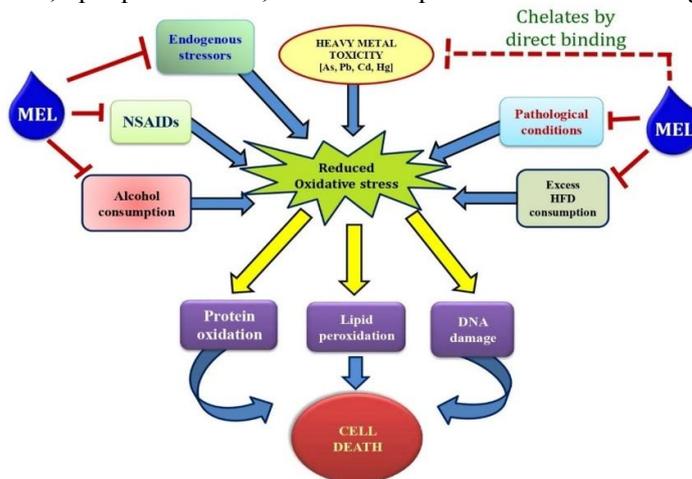


Fig. 10: Schematic diagram represent difference between ROS and antioxidant systems.

Plants have developed various defensive mechanisms that allow for ROS removal, thus, minimize, and prevent progressive damage to cellular components. The antioxidant system includes the action of small-molecule antioxidants and the induction of antioxidant enzymes. Selenium is an essential element in animal cells and the human body, but its importance for plants is still the object of research. This element, occurring in a narrow range of concentrations, may have a positive effect on plants. In higher concentrations, however, it is toxic Golubkina *et al.*, (2018), (2019).

The beneficial antioxidant activity of Se has been observed under stress conditions when increased amounts of ROS are generated. The enzymes of the antioxidant system that protect cells by eliminating ROS include catalase (CAT), superoxide dismutase (SOD), and numerous peroxidases (POXs), among which ascorbate peroxidase (APX) is included. The mechanism of the antioxidant activity of Se in plants has not yet been fully elucidated. To date, it has been shown that CAT, SOD, and POX activities are induced by Se Sieprawska *et al.*, (2015). In addition to their harmful effects, ROS have the role of mediating signal transmission in the defence and acclimatization responses of cells to stress factors Miller *et al.*, (2010), the effects of which are shown with lower concentrations of ROS. Therefore, the regulation of certain elements of the antioxidant system by Se may affect the reduction of ROS levels and, in this way, change their role from harmful to beneficial. Plant organisms are exposed to various stress factors that can interact or follow one another. The combined action of stress factors can modify response patterns. Studies on the interactions of unfavorable factors on plants have proven that there is a so-called phenomenon of cross-reactions that results in the increasing resistance or susceptibility to a stress factor because of an earlier action of another factor. Plant response depends on the intensity of stress factors, the sensitivity of species to these stress factors, the duration of exposure, and the mode of action. Protective effects are usually observed as the sequential or simultaneous actions of stress factors, especially when one of them occurs at a low, sub-lethal level Bandurska *et al.*, (2013). Numerous studies have shown that Se, by affecting the activity of the antioxidant system, can counteract the negative effects of various stress factors, including a WD Sieprawska *et al.*, (2015). However, most of these studies concern the response of the aboveground parts of the plant. In this work, the roots are the object of the research. Roots, in addition to their structural function, play a key role in the survival of plants under unfavorable conditions. The initial stress signal is, further passed to other organs of the plant, a passing that is extremely important for inducing a specific response, i.e., tolerance or susceptibility to a given stress factor Selote *et al.*, (2010).

Conclusion

Selenium (Se) is both essential at low levels and toxic at higher levels to most organisms. Plant Se accumulation therefore may affect interactions with ecological partners positively or negatively. Environmental stresses can cause over-accumulation of ROS and induction of oxidative stress in plant cells. It seems that the basic mechanisms involved in the beneficial effects of Se on plants grown under abiotic stress conditions are associated with the ability of this element to modulate the antioxidative machinery and, in consequence, increase their tolerance to oxidative stress induced by these factors. However, it seems that this is not the only mechanism, as different additional effects can be observed after exogenous application of Se, which largely depend on the nature of the stress factor. Suggesting that the beneficial effect of exogenous Se application on plants exposed to environmental stresses is a multifaceted network, covering several complex physiological, biochemical, and molecular interactions. The ecological implications of plant Se accumulation are especially intriguing for Se hyperaccumulator species, which have evolved the capacity to take up Se to extraordinarily high levels, around 1% of dry weight. Insight into ecological implications of plant Se accumulation sheds light on evolutionary pressures that led to Se hyperaccumulation, and the importance of plant Se (hyper) accumulation for Se cycling. In addition, better understanding of the ecological impacts of Se in plants can help manage seleniferous habitats and optimize crop Se biofortification and the use of plants in phytoremediation to clean up Se polluted areas.

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