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Review

Selenium and agricultural crops

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Higher plants have different capacities to accumulate and tolerate selenium, referred to as accumulative and non-accumulative plants. Selenium-accumulators plants may contain hundreds of times more selenium than non-accumulators even when grown in the same soil, or can also grow in soils with low and medium selenium reserves; while selenium non-accumulator plants present low accumulation and tolerance to high selenium levels in the culture medium. Several studies have demonstrated the protective role of selenium in relation to oxidative stress in plants. Depending on the dose used, Se can activate certain enzymes such as superoxide dismutase, glutathione reductase and glutathione peroxidase. These enzymes are activated in the presence of Se, reducing the rate of lipid peroxidation and formation of hydrogen peroxide in plant tissue cells, which results in reduced senescence. Symptoms of selenium toxicity include reduced growth, chlorosis of leaves and pink coloration of the roots, yellowing of leaves and black spots. Studies provide evidence on a beneficial role of Se in plants and for environmental phytoremediation. However more research is needed to consolidate the beneficial effects of Se in plants.

Key words: Selenium, accumulating plants, metabolism, functions plant, toxicity.

INTRODUCTION

Selenium (Se) is an essential mineral micronutrient for the health of humans, animals, archaea and some other microorganisms (El-Ramady et al., 2016), occurring naturally in almost every part of the earth (Feng et al., 2013). Selenium was considered a toxic element until being recognized as an essential element for animals in 1957 (Schwarz and Foltz, 1957).

Regarding the role of Se in plants, several studies have shown that at low concentrations this element has beneficial effects on growth and stress tolerance by increasing its antioxidant capacity (Pilon et al., 2003).

Some studies have demonstrated the benefits of adding small amounts of Se, including increased tuber yields and greater concentration of starch in young potato leaves (Turakainen et al., 2004). This response was associated with inhibition of lipid peroxidation vi the increase in GSH- Px (Xue and Hartikainen, 2000).

However, at high concentrations Se is toxic to plants due to its incorporation in molecules which contain S (Pilon et al., 2003).

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The amount of available Se in soil determines the amount of Se in foods from plants that are grown in the soil. Awareness that ingestion of plants with desirable, non-toxic levels of Se is the first step for input of Se into the food chain may explain why biofortification with this element has received great attention (Mora et al., 2015).

However, when using this technology the question is often raised: What is the ideal dosage of Se? Selenium often has a dual effect on plant growth. At low doses it may stimulate plant growth and neutralize various types of environmental stresses, including those of heavy metals, whereas at higher dosages it can also act as a pro-oxidant and cause damage to plants (Feng et al., 2013).

In this context, this literature review aims to report on the functions, benefits and toxicity of selenium in agricultural crops.

SELENIUM ACCUMULATING AND NON-ACCUMULATING PLANTS

Higher plants have different capacities to accumulate and tolerate Se, therefore they are classified as accumulating and non-accumulating plants. Non-accumulating Se plants can be indicative of selenium-rich soils (White et al., 2004) and some plant species are classified as selenium hyperaccumulators, where the genus *Astragalus* is one of the largest hyperaccumulators, groups of this element (Terry et al., 2000).

Selenium hyperaccumulators, plants are divided into two groups, the first being primary selenium accumulators, which are able to accumulate 100 to 10000 mg selenium per kg^{-1} dry matter. This group includes the species *Astragalus, Machaeranthera, Haplopappus* and *Stanleya*. These species grow in selenium-contaminated soils with selenium contents greater than 5 mg kg^{-1} soil (Gupta and Gupta, 2000) and are responsible for selenosis in grazing animals. These selenium accumulating plants may contain hundreds of times more selenium than non-accumulating plants growing in the same soil (Kopsell and Kopsell, 2007).

Secondary selenium-accumulators can grow in soils with low and medium selenium reserves and can adsorb 25 to 100 mg selenium kg^{-1} of dry matter. This group includes different genera, such as *Aster, Astragalus, Atriplex, Brassica, Castilleja, Comandra, Grindelija, Machaeranthera* and others (Kopsell and Kopsell, 2007). Furthermore, these plants are tolerant to soil salinization (Terry et al., 2000).

According to White et al. (2004), selenium non-accumulating plants present low accumulation and tolerance to high levels of selenium in the culture medium, which usually contains less than 25 mg kg^{-1} of selenium in the dry mass. This group includes most crops such as cereals, potatoes, herbs, fruits and many natural plant species growing in the same soil as cultivated plants (Kopsell and Kopsell, 2007).

In non-accumulating plants, selenium is mainly found in the form of proteins; however, accumulating plants have the ability to synthesize it at non-protein amino acids, which prevents toxicity (Bergmann, 1982).

FUNCTIONS OF SELENIUM IN PLANTS

Selenium is involved in the metabolism of transfer RNA, as a radical 5-methylamino-7-seleno uridine, which acts in protein synthesis from the incorporation of amino acid analogs containing S, and via this radical becomes part of proteins. Selenocysteine ($CH_2SeHCHNH_2COOH$) is considered the 21^{st} amino acid in terms of protein synthesis mediated by ribosomes (Stadman, 1990).

When a large selenoprotein was discovered in mung bean seedlings (*Vigna radiata* L.) supplemented with 2 mg L^{-1} selenite, the function of Se in the mitochondrial membrane was discovered (Easwari and Lalitha, 1994). Another role of Se in plants was indicated by the discovery that a cysteine desulfurase (NIF) as a protein may be engaged in selenoprotein synthesis in chloroplasts (Pilon Smits et al., 2010), which together with the mitochondria are subject to high levels of oxidative stress.

Several studies have demonstrated the protective role of Se in relation to oxidative stress in plants, wherein the presence of this element increases glutathione peroxidase activity (GSH-PX) and decreases the activity of lipid peroxidation (Hartikainen and Xue, 1997; Cartes et al., 2005; Djanaguiraman et al., 2005).

Studies have shown that the addition of low concentrations of Se decreased the oxidative stress caused by ultraviolet radiation in lettuce and ryegrass (Hartikainen and Xue, 1999) and strawberry (Valkama et al., 2003). Suitable levels of Se were sufficient to increase the antioxidant capacity and delay senescence in leaves of lettuce, rye and soybean (Hartikainen and Xue, 1999; Xue et al., 2001; Xue and Hartikainen, 2000; Pennanen et al., 2002; Djanaguiraman et al., 2005; Hartikainen, 2005).

In potatoes, Xue et al. (2001) and Pennanen et al. (2002) showed that the addition of Se in the culture had an effect on the mesophyll of leaves, affecting the integrity of the cell membranes (Kong et al., 2005).
Accordingly, soybean plants when sprayed with sodium selenate at a concentration of 50 mg L^{-1} after 78 days of planting in tests on the ability of the culture to retard senescence related to oxidative stress, showed that plants can incorporate selenium in their physiological reactions so that it can act as an antioxidant agent, preventing degradation of chlorophyll (Djanaguiraman et al., 2004). This process occurs in many other plants by association of increased enzymatic activity of superoxide dismutase (SOD) and GSH-PX (Djanaguiraman et al., 2005).

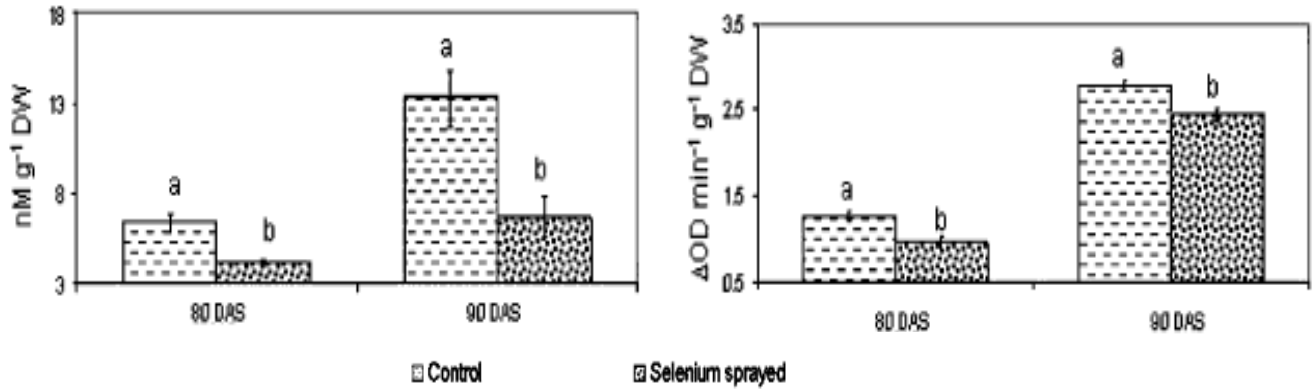

Figure 1. Effect of Se spray on stability of the cell membrane in soybeans at 80 and 90 days after sowing (DAS) (Djanaguiraman et al., 2005).

It was observed that Se promoted growth and acted as antioxidant for inhibition of lipid peroxidation and the percentage of injury to the cell membrane. These enzyme contents were positively correlated with the selenium content.

Work performed by Djanaguiraman et al. (2005) when studying selenium as a protective antioxidant in soybeans during senescence of the culture in India, noted that in plants control the content of superoxide and hydrogen peroxide was higher at 80 and 90 days after planting compared to treatment with Se (Figure 1). This result can be explained by the presence of two selenoproteins, GSH- Px and thioredoxin reductase induced by Se acting to protect the cells against oxidative stress.

Regarding the activity of SOD and GSH-Px, there is increased activity of these enzymes in treatments with the application of Se (Figure 2). Although the SOD did not present in its composition, Se may have altered the transcription levels of SOD thereby altering gene expression (Noctor and Foyer, 1998).

The reduction of the SOD activity in control plants may be due to increased superoxide and hydrogen peroxide, which destroy the SOD enzyme. It is possible that there is elimination of superoxide and hydrogen peroxide by increasing the activity of GSH-Px. The reason could be that GSH-Px, which is present throughout the cell and substrate, has a higher affinity in the presence of glutathione as a reductant (Noctor and Foyer, 1998).

The antioxidative action of Se also can be confirmed in the studies performed by Ríos et al. (2008), who observed the form of selenium accumulation in lettuce plants and the time of leaf antioxidative capacity. After different rates of selenite and sodium selenate were applied (5, 10, 20, 40, 60, 80 and 120 μ mol L^{-1}); the results showed that the least toxic form for this culture was selenate which induce the same production time for a larger amount of biomass, increased accumulation of selenium and a larger quantity of antioxidant compounds compared to selenite.

The treatment of 40 μmol L^{-1} was best suited for the lettuce plants, where the antioxidant capacity and selenium accumulation increased without decreasing the biomass, and making these plants appear healthier in comparison with the control plants.

Some studies have demonstrated benefits of adding small amounts of Se, including increased tuber yield and greater concentration of starch in young potato leaves (Turakainen et al., 2004). This response was associated with inhibition of lipid peroxidation through increase of GSH- Px (Xue and Hartikainen, 2000).

Lyons et al. (2009) studied increasing selenium on seed production in Brassica in Australia, and found that the pollen of plants control showed an average 14% non-viable grains compared to an average of 2% non-viable grains in treated plants. However electron microscopy revealed no apparent morphological differences in pollen grains of the treatments.

They observed that plants treated with Se presented higher total respiratory activity in leaves and flowers (Figure 3), which may have contributed to higher seed production. This response of the fertilized plants with Se is primarily due to an increase in capacity via the cytochrome, mediated by cytochrome oxidase (COX) (Lyons et al., 2009).

Immunoblot analysis of protein extracts from flowers of the control and treated plants with Se showed an increase in the relative amount of the protein COX II in flowers to which Se was applied (Figure 4). This observation indicates an increase in the amount of COX complex (Lyons et al., 2009).

An increase in the total respiratory activity of leaves and flowers of the treatment to which Se was applied compared to the control suggests that mitochondrial activity in plants treated with Se is greater. This may be due to protection of the mitochondria in plants treated with Se against damage caused by reactive oxygen species (ROS), for an up-regulation of the cellular antioxidant defense system. The increase observed in

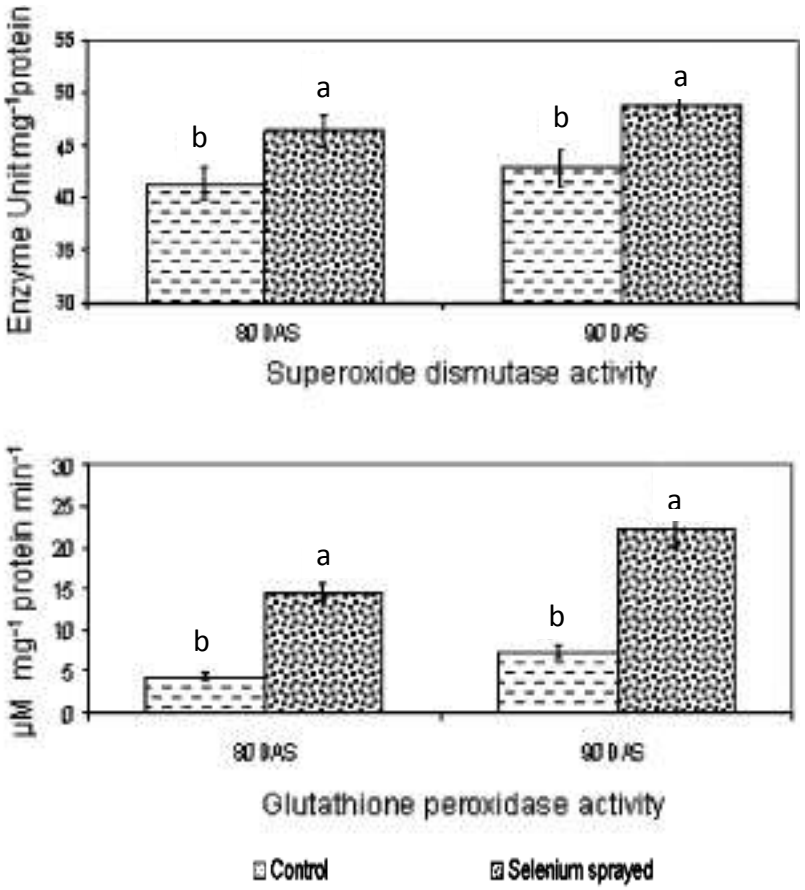

Figure 2. The effect of Se spraying on superoxide dismutase and glutathione peroxidase in the soybean crop at 80 and 90 DAS (Djanaguiraman et al., 2005).

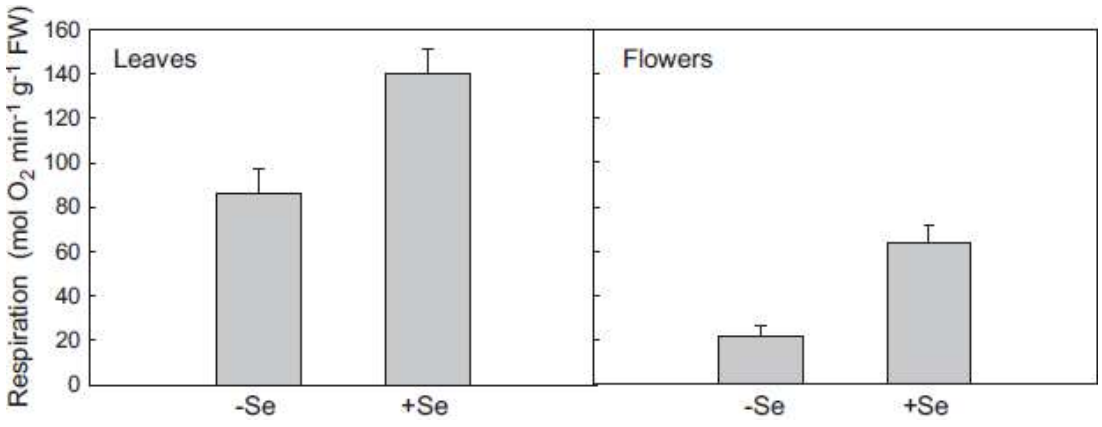

Figure 3. Respiration rate in Brassica leaves and flowers grown in nutrient solutions with or without sodium selenite (Lyons et al., 2009).

respiration is not likely to be a partial response to oxidative stress, since the Se concentrations were below toxic levels (Lyons et al., 2009).

Regarding the germination of seeds, 92% germination was observed for seeds from plants treated with Se in relation to the control treatment which showed 81% (Lyons et al., 2009).

This study therefore provides further evidence on the

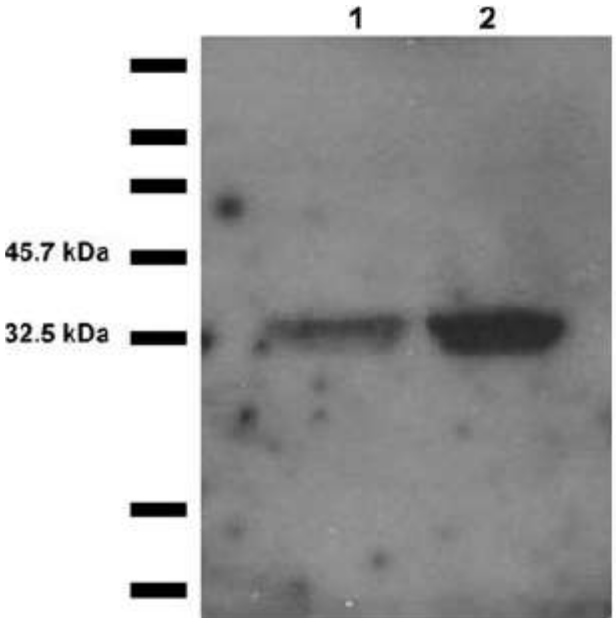

Figure 4. Immunoblot analysis of protein extracts COX from flower tissues treated with Se and untreated plants. Track 1 is the control plant while track 2 is the plant treated with Se (Lyons et al., 2009).

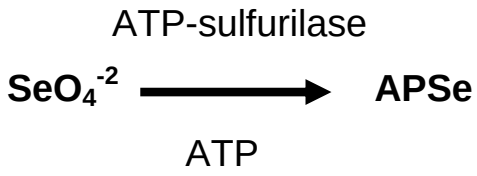

Figure 5. Reaction controlled by the ATP-sulfurylase enzyme, which activates the SeO_4^{-2} in adenosine phospho-selenate (APSe), similar to active sulfate (APS).

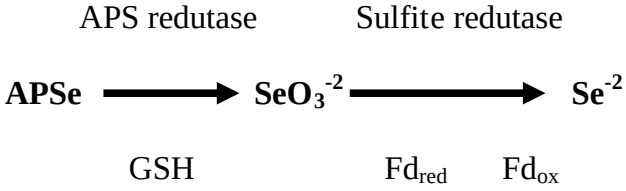

Figure 6. Selenium (Se^{-2}), receiving electrons supplied by ferredoxin, mediated by action of the enzyme sulfite reductase.

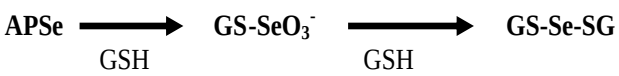

Figure 7. Selenite reduced via GSH into seleno-diglutathione (GS-Se-SG).

beneficial role of Se in plants. However more research is needed to consolidate the beneficial effect of Se in plants.

PARTICIPATION IN PLANT METABOLISM

Selenium is mainly absorbed in the oxidized form, selenate (SeO_4^{-2}) and, similar to sulfur, must be reduced to the selenium ion (Se^{2-}) either enzymatically or non-enzymatically for subsequent incorporation into organic compounds such as amino acids and proteins. Thus, these reactions have been studied in non Se accumulating plants (> 25 mg Se kg^{-1} DM) when grown in soils with high concentrations of this element (Terry et al., 2000).

In Se reduction via the enzymatic route, when allocated in the leaves by xylem, it enters the chloroplasts to be metabolized. Even in the sulfate reduction process (Prado, 2008), the first reaction is controlled by the ATP-sulfurylase enzyme, which activates the SeO_4^{-2} in adenosine phospho-selenate (APSe), similar to active sulfate (APS) (Figure 5).

The produced active selenate is reduced to selenite (SeO_3^{-2}) using reduced glutathione (GSH reducer) and the enzyme APS reductase, as in the reduction of sulfate to sulfite (Bick and Leustek, 1998). Thus, the selenite formed is reduced again to form the ion selenium (Se^{-2}), receiving electrons supplied by ferredoxin, mediated by action of the enzyme sulfite reductase (Figure 6).

Reduction through a non-enzymatic enzyme, or selenium reduced by ATP-sulfurylase the APSe

In 1977 Gregory and collaborators demonstrated the non-enzymatic reduction of this active selenium by reaction with GSH ($GS\text{-}SeO_3^-$) in bacteria of the genus *Saccharomyces*. Thus, the conjugate selenite is reduced again via GSH into seleno-diglutathione (GS-Se-SG) (Figure 7):

Finally, GS-Se-SG is reduced to selenol (GS-SEH) and the combined selenium ion ($GS\text{-}Se^-$) with the reducing power of NADPH and the GSH reductase enzyme.

However, for incorporation of the Se absorbed in amino acids, and subsequently in proteins, non-specific enzymes are needed that act on previous products ($GS\text{-}Se^-$ and Se^{-2}). Thus, selenium-cysteine (Cys-If) and selenium-methionine (Se-Met) are synthesized by cysteine synthase (Cys synthase) and methionine synthase (Met synthase), respectively (Figure 8).

Brown and Shrift (1981) found high contents of Se in proteins of non-accumulating species when subjected to sodium selenate. The authors attributed the results obtained in these plants to the rapid incorporation of the element in proteins. However, in tolerant species their lower Se contents could be caused by the synthesis of

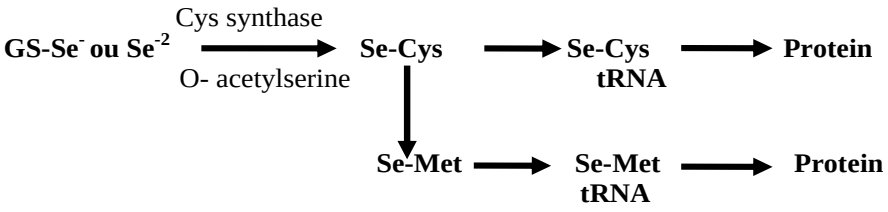

Figure 8. Selenium-cysteine (Cys-If) and selenium-methionine (Se-Met) synthesized by cysteine synthase (Cys synthase) and methionine synthase (Met synthase).

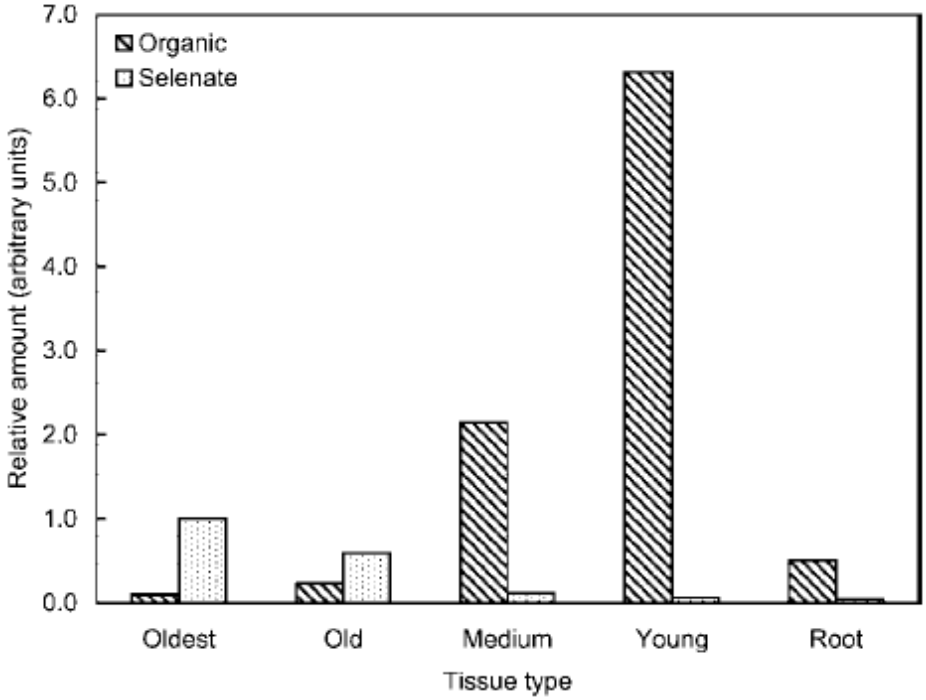

Figure 9. Relative quantities of Se in tissues of *A. bisulcatus* (Pickering et al., 2003).

other Se non-protein amino acids such as Se-metil-SeCys (MeSeCys).

Thus, the capture of Se and the formation of these metabolites reduces the integration of Se-Cys and Ser-Met in proteins. Accordingly, Pickering et al. (2003) observed larger contents of organic Se (MeSeCys) in different plant tissues of the tolerant species, *Astragalus bisulcatus* (Figure 9).

The beneficial effect of Se on environmental phytoremediation is observed when passing through a volatilization process in the cytosol of plant cells, being converted to the gas dimethyl selenide (DMSE), whose toxicity is much smaller than that of the ion Se^{-2}, and is also the primary volatile compound of Se in non-accumulating plants (Lewis et al., 1974). These authors observed the primary metabolic pathway for the production of DMSE in brassicas leaves, where the source was methyl selenomethionine (methyl-SeMet), which is produced by breakdown of the Se-Met amino acid and the action of the enzyme methyltransferase methionine (MMT), which is possibly the same enzyme responsible for the production of S-methylmethionine (SMM) in the metabolic pathway of sulfur (Sors et al., 2005). Finally, the methyl-SeMet is converted to the DMSe gas by the enzyme DMS hydrolase (Figure 10):
Another route is by carboxylation of methyl-SeMet and production of an intermediate product called dimethylsulfoniopropionate (DMSeP), which is then transformed to DMSe by the DMSP-lyase enzyme. Thus, Souza et al. (2000) compared the percentage of volatilization of Se absorbed in *Brassica juncea* L. When submitted to different sources of Se, and showed the greatest results when using DMSeP. This makes the volatilization process more efficient, thus demonstrating the existence of this alternative pathway in the volatilization of Se (Table 1).

In the case of accumulating plants it was observed that the incorporation of selenate in SeCys occurs in a

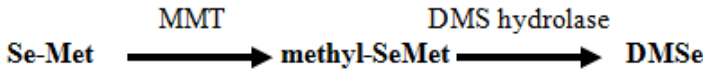

Figure 10. Methyl-SeMet converted to the DMSe gas by the enzyme DMS hydrolase.

Table 1. Absorption and volatilization percentage of Se by *B. juncea* subjected to various Se sources (adapted from Souza et al., 2000).

Source of Se	Total absorption (µg Se)	% volatilized (From being absorbed)
Selenate	382 ± 151	1.8
Selenite	157 ± 61	6.3
Se-Met	529 ± 114	21.5
DMSeP	953 ± 375	59.6

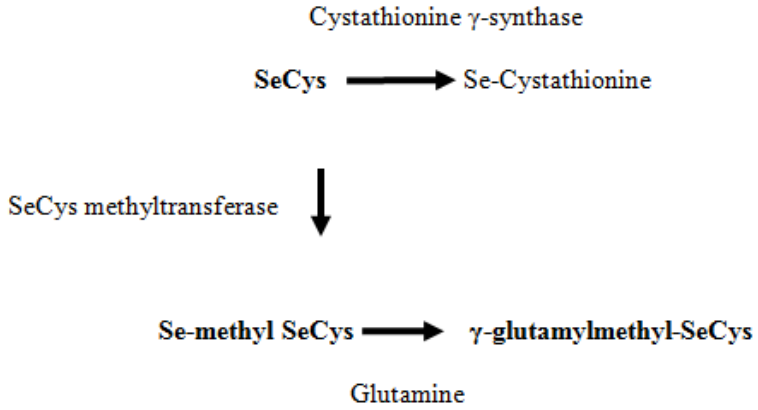

Figure 11. γ-glutamylmethyl-SeCys formed by the combination of the Se-methyl SeCys with glutamine in the peptides.

manner similar to non-accumulating plants, as previously mentioned. However, there are plants capable of volatilizing Se from a compound called di-methyl di-selenide (DMDSe), the main volatile compound of Se hyperaccumulator plants (Terry et al., 2000).

The SeCys is substituted by the action of the SeCys methyltransferase enzyme to form methylselenocysteine (Se-methyl SeCys), the first compound (non-protein amino acid selenium) that could be accumulated in plants and that could explain their higher tolerances to stress conditions (Pilon-smits and Quinn, 2010). Moreover, some plants have the ability to convert SeCys in non-protein compounds, to Se-cystathionine to be accumulated. Finally, the third compound to be accumulated by hyperaccumulators plants is γ-glutamylmethyl-SeCys formed by the combination of the Se-methyl SeCys with glutamine in the peptides; however the enzyme that catalyzes this reaction is still not well understood (Figure 11).

Finally, there is evidence which suggests the oxidation of Se-methyl SeCys for formation of MeSeCysSeO and subsequent methylation by the enzyme Cys-sulfoxide lyase and the consequent formation of the volatile compound DMDSe (Sors et al., 2005).

TOXICITY

At high concentrations, Se is toxic to plants due to its incorporation in the molecules which contains S and especially the indiscriminate substitution of cysteine for selenocysteine (Pilon et al., 2003). In this sense the non-specific integration of selenoamino acids, selenocysteine and selenomethionine in proteins are considered the largest contributor of Se toxicity in plants (Brown and Shrift, 1981).

High Se levels depress growth, protein synthesis and nucleic acid synthesis (Terry et al., 2000). High Se levels can damage the photosynthetic apparatus inhibiting photosynthesis, and result in excessive starch production (Vitová et al, 2011; Wang et al., 2012).

Symptoms of selenium toxicity are reduced growth, chlorosis of the leaves and pinkish coloration of the roots (Bergmann, 1982; Neal, 1990), yellowing of leaves and

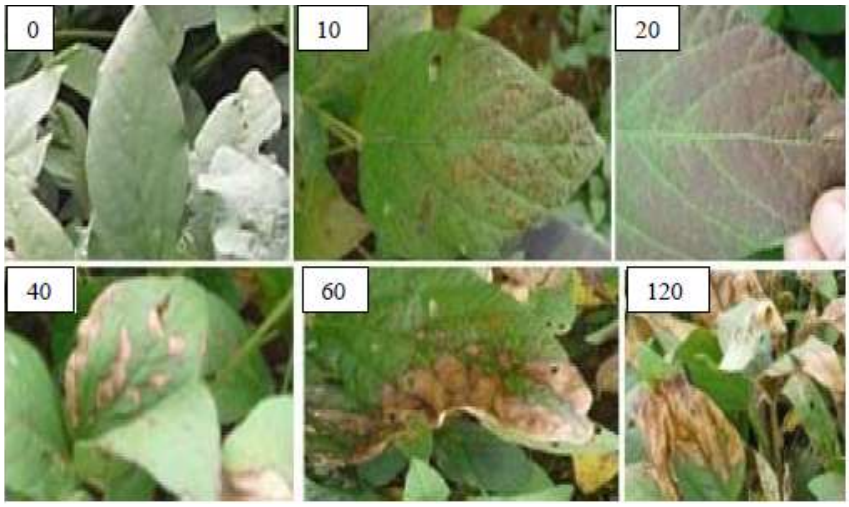

Figure 12. Increasing phytotoxic effect on soybean plants with increasing doses of sodium selenite applied to the leaves (Martinez, 2013).

black spots (Jacobs, 1989; Wu, 1994).

It is common that leaves present Se concentrations in regions of growth and in seed may reach 1500 ppm. However, there is variation in the ability of plants to absorb Se, presented in descending order: Crucifer, forage grasses, legumes and cereals, which is associated with a distinct metabolic capacity to divert Se, preventing its participation in protein synthesis (Brown and Shrift, 1981) for detoxification, linking it to non-protein amino acids (Correia, 1986).

According to Brown and Shrift (2008), the toxicity of selenate and selenite to most plants can be attributed to the combination of three factors. Firstly, selenate and selenite are readily absorbed from the soil by the roots and translocated to other plant parts. Secondly, metabolic reactions convert these anions in organic forms of selenium; and thirdly, organic selenium metabolites act as analogous essential sulfur compounds and interfere with cellular biochemical reactions.

The selenite is rapidly converted to organic forms which are incorporated into proteins in place of S, causing toxicity (Hopper and Parker, 1999). Sharrer and Schropp reported that 1.3 ppm of selenium and 25 ppm of sulfur in a soil solution is toxic to wheat, Barley and oats.

The absence of phytotoxicity symptoms has been reported in the USA, but experimental evidence has shown a negative correlation between the increase in selenium in the soil and growth (dry weight, root length and shoot height). In alfalfa, a decrease in yield was observed when Se extraction exceeded 500 mg kg^{-1} in the soil.

In China, phytotoxicity caused by high Se concentrations in the soil promoted pink discoloration of corn embryos, where the pink color is attributed to the presence of elemental selenium. Yang et al. (1983) observed that levels of 2 and 1.25 mg kg^{-1} of selenium are harmful to the growth and yield of wheat and pea, respectively.

With respect to food crops, the present relatively low tolerance to selenium toxicity and most crops have the potential to accumulate the element in amounts which are toxic to animals and humans. In general, tubers contain selenium concentrations higher than other organs and leaves often contain higher concentrations than the tuber.

In this context Yang et al. (1983) observed in seleniferous soils of China that selenium concentrations in plants (0.3 to 81.4 mg kg^{-1}) were higher in cereal crops (0.3 to 28.5 mg kg^{-1} rice and maize). The turnip showed high Se content with an average of 457 compared to an average of 12 mg kg^{-1} in tubers.

In moderate to low selenium content environments, alfalfa accumulated more Se in relation to other forage crops, which may be due to greater rooting causing more alkaline conditions, thus more selenium is available at greater depths. However, in general the species grown in soils high Se levesl present little difference in selenium content (Jacobs, 1989), by an exception was reported in New Zealand.

According to Marschner (1995) and Lyons et al. (2004), different plant species vary widely in both selenium accumulation capacity and in the ability to tolerate high concentrations of this element in the soil solution. These results corroborated with those of other studies in literature, which show that tobacco and soybean plants are sensitive to selenium and may be affected by this element (Lyons et al., 2004; Martin and Trelease, 1938).

In this context, Martinez (2013) evaluated the effects of foliar fertilization with sodium selenite in biofortification of the soybean culture cv BRS Favorita RR in the municipality of Itutinga-MG under field conditions. A phytotoxic effect was observed in all foliar application levels (0, 10, 20, 40, 60 and 120 g ha^{-1} Se) (Figure 12).

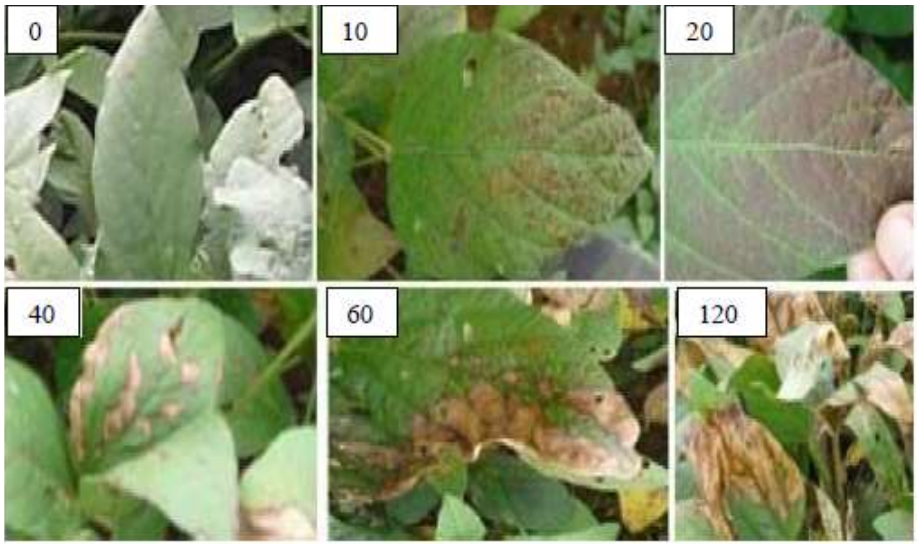

Figure 12. Increasing phytotoxic effect on soybean plants with increasing doses of sodium selenite applied to the leaves (Martinez, 2013).

CONCLUSION

Several studies on the growth of companies have beneficial effects on plant growth and stress tolerance by increasing their antioxidant capacity. However in high concentrations, the Se is toxic to plants. Thus, this literature review was developed based on studies of Se in plants, mainly for its role in metabolism, functions, benefits and toxicity in agricultural crops. This information may contribute to a better understanding of the role of Se in plants and to encourage future research in this area of study.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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