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Selenium in Higher Plants: Physiological Role, Antioxidant Metabolism and Abiotic Stress Tolerance

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Abstract: It is now well established that virtually all abiotic and biotic stresses induce or involve oxidative stress to some degree and the ability of plants to control oxidant levels is highly correlated with stress tolerance. Recently, the role of Selenium (Se) as an antioxidant has generated a wide interest in it. In trace amounts, Se is an essential micronutrient and has important benefits for animal and human nutrition although it has not been confirmed to be an essential micronutrient in higher plants. Selenium has been shown to exert a positive effect on crop growth and stress tolerance at low concentrations. However, the specific physiological mechanisms that underlie the positive effects of Se in plants have not been clearly elucidated. There is a wealth of evidence that low concentrations of Se enhance the growth of plants and improve antioxidative capacity of plants either by acting as antioxidant directly or by increasing the activities of antioxidant enzymes and bring out the tolerance under stressful condition. In contrast at high concentrations, Se acts as a pro-oxidant and leads to drastic reduction in yield. In this study we reviewed available literature regarding the possible regulatory role of Se in the various physiological processes of plants as well as its protective role under abiotic stress condition.

Key words: Selenium, reactive oxygen species, trace element, abiotic stress, antioxidant defense, plant metabolism

INTRODUCTION

Selenium (Se) is a non-metal, whose Greek name (*Selene*) means moon. Selenium was first discovered by J.J. Berzelius in 1817. He found a residual slime forming during the oxidation of sulfur (dioxide) from copper pyrites. Se, similar to sulfur (S) as regards its chemical properties, has been demonstrated as trace element in human and animal based on its presence in antioxidant defense systems which is needed for the maintenance of animal and human health (Schwartz and Foltz, 1957; Flohe *et al.*, 1973; Rotruck *et al.*, 1973) and in

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hormonal balance (Arthur *et al.*, 1990; Pallud *et al.*, 1997). During last two decades the physiological role of Se in plants has been explored by researchers. In plants Se can be found both in inorganic and organic Se forms, including selenoamino acids and methylated compounds. Current interest in Se is focused on the health benefits of high-Se plants as a source of cancer preventative Se compounds (Finley *et al.*, 2000, 2001) and the metabolism of Se in plant species that accumulate Se and are able to remediate Se-polluted soils and prevent Se from entering into the food chain (Berken *et al.*, 2002). However, there is evidence that Se might be an essential micronutrient for accumulator plants species (Terry *et al.*, 2000; Sors *et al.*, 2005). Moreover, it has been shown that Se is required for an optimal growth of the unicellular green alga. In contrast, Se non-accumulator plants, including most species of crops, do not appear to require Se for their growth and in general, these plants have a low tolerance to this element (Terry *et al.*, 2000). The essentiality of Se to higher plants, however, is still under debate. Although it is harmful for plants in high concentrations, it can exert beneficial effects at low concentrations (Germ *et al.*, 2007a).

Although Se is not yet confirmed to be required by higher plants (Terry *et al.*, 2000), several studies demonstrate that at low concentrations it may exert diverse beneficial effects, including growth-promoting activities (Hartikainen and Xue, 1999; Terry *et al.*, 2000; Xue *et al.*, 2001; Turakainen *et al.*, 2004; Djanaguiraman *et al.*, 2005). Moreover, some plant species grown in Se-enriched media have shown enhanced resistance to certain abiotic stresses, e.g. drought (Kuznetsov *et al.*, 2003; Germ *et al.*, 2007b; Yao *et al.*, 2009), salinity (Kong *et al.*, 2005; Djanaguiraman *et al.*, 2005; Hawrylak-Nowak, 2009), chilling (Chu *et al.*, 2010; Hawrylak-Nowak *et al.*, 2010), heavy metals (Fargašová *et al.*, 2006; Hawrylak *et al.*, 2007; Pedrero *et al.*, 2008; Filek *et al.*, 2008; Srivastava *et al.*, 2009; Cartes *et al.*, 2010) and UV-irradiation (Valkama *et al.*, 2003; Hartikainen and Xue, 1999; Yao *et al.*, 2010a, b) stresses. Se exerts beneficial effects on growth and stress tolerance of plants by enhancing their antioxidative capacity (Hartikainen and Xue, 1999; Xue and Hartikainen, 2000; Xue *et al.*, 2001; Djanaguiraman *et al.*, 2005; Kong *et al.*, 2005; Ríos *et al.*, 2009). Se increases plant resistance against oxidative stress caused by free oxygen radicals. However, agricultural crop plants are sensitive to high Se concentrations which vary among plant species (Hartikainen *et al.*, 2000, 2001; Rani *et al.*, 2005; Lyons *et al.*, 2005).

Nevertheless, the specific physiological and molecular mechanisms that underlie the beneficial effects of Se in plants have not been fully explained yet. In this review, we discuss the progress in understanding the possible role of Se in plant growth and its involvement in the antioxidant metabolism towards abiotic stress tolerance in plants.

SELENIUM IN SOIL ENVIRONMENT

In the soil, Se may be present in four different oxidation states: selenate (+6), selenite (+4), elemental Se (0) and as inorganic and organic selenide (-2). The chemical form, the soil redox potential, pH and clay content determine the bioavailability of Se in the soil (Gissel-Nielsen, 1971; Mikkelsen *et al.*, 1989; McNeal and Balistrieri, 1989). The predominant Se inorganic forms in cultivated soils are selenate and selenite. Selenate is more soluble and available for plants under oxidized and alkaline soil conditions (Masscheleyn *et al.*, 1990; Mayland, 1994). Selenite is less available to plants than selenate because it is adsorbed more strongly by iron oxide surfaces and soil clays (Ylaranta, 1983a, 1985; Mikkelsen *et al.*, 1989).

Selenium content of most soils varies between 0.1 and 2.0 mg kg^{-1} depending on geographical area (Mayland, 1994; Dhillon and Dhillon, 2003). The Se concentration of soil

depends on the composition of bedrock from which the soil component derives and the geochemical processes that produce the soil. In clay soils, Se content was generally higher than one coarse mineral soils. The mean Se content in clay soils was 0.29 mg kg^{-1} and in coarse mineral soils 0.17 mg kg^{-1}. The highest Se concentration (0.46 mg kg^{-1}) was measured from organic soils (Koljonen, 1975; Sippola, 1979; Ylaranta, 1983b).

The plant-availability of Se in soil is largely depend on the predominant Se species and the soil factors controlling their behavior, such as the quantity of the sorption components (Al and Fe oxides), pH and redox status. Furthermore, the presence of anions (sulfate, phosphate, organic anions, etc.) competing for the same sorption surfaces contributes to the retention of Se (Elrashidi *et al.*, 1987; Neal, 1995; Fordyce, 2005; Hartikainen, 2005).

SELENIUM UPTAKE AND METABOLISM IN PLANTS

Plants play a unique role in recycling and delivering Se from the soil to the food chain. The concentration of Se in agricultural products and fodder depends on the content of Se in the soil and its bioavailability (Sippola, 1979; Koivistoinen, 1980; Ylaranta, 1983a, 1985). Availability of Se is restricted in soils and its content is relatively low as a result of reduced weathering status and acidity (Koljonen, 1975; Sippola, 1979; Yläranta, 1983b). Plant roots take up Se from soil water in either the selenate or the selenite ionic forms. In higher plants metabolism of Se is closely related to that of sulfur due to their chemical similarity. Quantities in the soil solution are governed by the solubility of adsorbed forms and by the biological transformation of organic forms (Fig. 1).
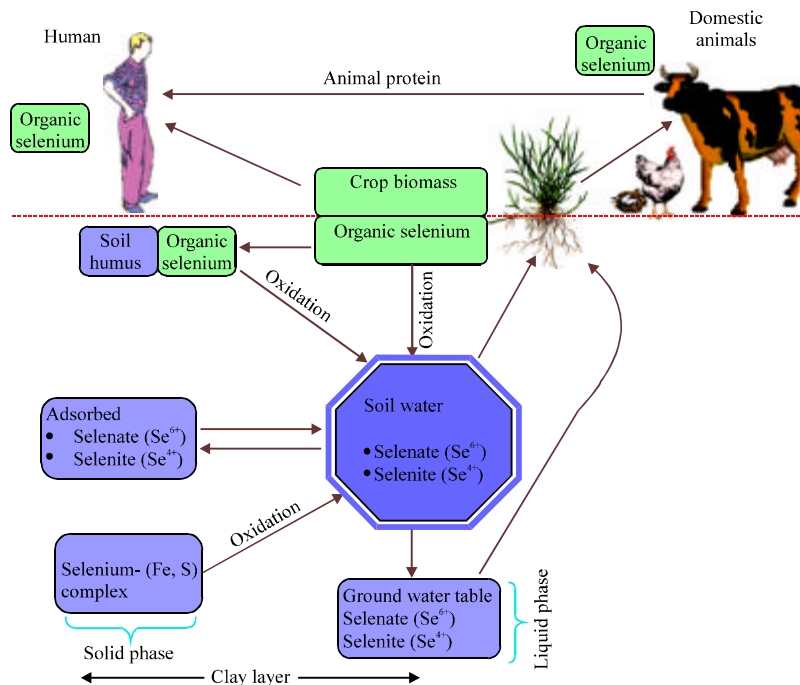

Fig. 1: Selenium in the Soil-Plant-Water consumer system. Plant roots take up selenate or selenite forms of Se from the soil water. The Se concentration in the soil solution depends on the solubility of the forms of Se present and the biological transformation of organic forms (Burau, 1985)

Higher plants have different capacities to accumulate and tolerate Se. They are classified into non-accumulators, indicators and accumulators (Rosenfeld and Beath, 1964; Terry *et al.*, 2000; Dhillon and Dhillon, 2003; White *et al.*, 2004). Approximately 25 genera of plants are classed as Se accumulators (Burau, 1985) which includes garlic (*Allium sativum* L.), onion (*Allium cepa* L.), broccoli (*Brassica oleracea* L.) and wild leek (*Allium tricoccum* L.) (Neuhriel *et al.*, 1999; Whanger, 2002). Some particular plant species are termed Se hyperaccumulators. The largest group of hyperaccumulators belongs to the genus *Astragalus* and *Stanleya* (Rosenfeld and Beath, 1964; Neuhriel *et al.*, 1999; Terry *et al.*, 2000). The Se hyperaccumulators are placed into two groups: the primary Se accumulators are able to accumulate thousands of milligrams of Se kg^{-1} (>4000 mg kg^{-1}) and the secondary accumulators hundreds of milligrams Se kg^{-1}. Brassicaceae species including Indian mustard (*Brassica juncea* L.), broccoli (*Brassica oleracea botrytis* L.) and canola (*Brassica napus* sp. *oleifera* L.) have been classified as primary accumulators. Plant species with a high capacity to accumulate and tolerate Se could be used in the phytoremediation of Se-contaminated sites (Terry *et al.*, 2000; Berken *et al.*, 2002). However, most cultivated crop plants have a low tolerance to high Se levels. Generally, they contain less than 25 µg Se g^{-1} DW and are considered to be non-accumulators. Potato is classified as a Se non-accumulator (White *et al.*, 2004). Although non-accumulators are sensitive to high Se concentration, they can tolerate as well as accumulate even high concentrations of Se without growth reduction when grown in Se-enriched soils (Rani *et al.*, 2005). The critical Se concentration in plant tissues, which decreased the yield in Indian mustard was 105 µg g^{-1} DW, in maize (*Zea mays* L.) 77 µg g^{-1} DW, in rice (*Oryza sativa* L.) 42 µg g^{-1} DW and in wheat 19 µg g^{-1} DW, a levels attained by Se addition as selenite of 5 µg g^{-1} soil for Indian mustard and maize, 4 µg g^{-1} soil for wheat and 10 µg g^{-1} soil for rice (Rani *et al.*, 2005).

Se uptake and metabolism also differ due to the plant species, growth stage and the plant organs. Broccoli (*Brassica oleracea* var. *italica*) is known for its ability to accumulate high levels of Se, with the majority of the selenoamino acids in the form of Se-Met (SeMeSeCys) (Lyi *et al.*, 2005). Increased Se fertilization results in Se concentration in potato (Munshi and Mondy, 1992; Poggi *et al.*, 2000; Turakainen *et al.*, 2004). The majority of plants accumulate more Se in shoot and leaf than in root tissues, but there are exceptions (Zayed *et al.*, 1998). Turakainen (2007) observed that the Se concentrations in the upper leaves, roots, stolons and tubers of potato increased with increasing Se supplementation. The highest Se concentration was reached in young upper leaves, roots and stolons, indicated that added selenate was efficiently utilized and taken up at an early stage. During the growing period the Se concentration declined in the aerial parts, roots and stolons of potato plants whereas an intensive accumulation took place in immature and mature tubers (Turakainen *et al.*, 2006; Turakainen, 2007). Se accumulation was also affected by the methods of application. In tea plants, foliar application with selenate significantly increased Se content in the leaves (Hu *et al.*, 2003). The results of Smrkolj *et al.* (2006) showed that the Se content of pea seeds obtained from untreated and once and twice foliarly-treated plants was directly proportional to the number of sprayings.

From several studies it is clear that Se is taken up from the soil by plants primarily as selenate (SeO$_4^{2-}$) or selenite (SeO$_3^{2-}$) (Ellis and Salt, 2003). Lyons *et al.* (2005) suggested that for higher toxicity of selenite compared to selenate is due to the faster incorporation of selenite than selenate. In addition, the uptake of selenate into roots and its distribution in plants is much faster than that of selenite (Arvy, 1993; De Souza *et al.*, 1998; Pilon-Smits *et al.*, 1998; Cartes *et al.*, 2005). De Souza *et al.* (1998) reported that total Se accumulation in a plant was about 10-fold higher from selenate compared to selenite.
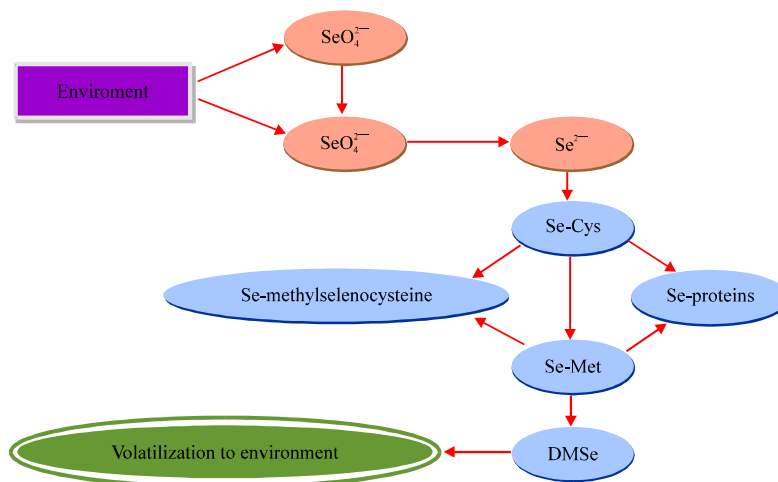
Fig. 2: Overview of the main steps of Se metabolism in plants (Dumont *et al.*, 2006). (Cys-Cysteine, Met- Methionine, DMSe- Dimethylselenide)

Kahakachchi *et al.* (2004) stated that actively growing tissues usually contain the largest amounts of Se. The metabolism of Se in plants postulated by Dumont *et al.* (2006) is shown in Fig. 2.

ROLE OF SELENIUM IN PLANT GROWTH AND PHYSIOLOGY

Se has not yet been classified as an essential element for plants, although its role has been considered to be beneficial for plants that are is capable of accumulating large amounts of the element (Shanker, 2006). The role of Se in plant depends mainly on its concentration. According to Hamilton (2004), Se has three levels of biological activity: (1) trace concentrations are required for normal growth and development; (2) moderate concentrations can be stored to maintain homeostatic functions and (3) elevated concentrations can result in toxic effects. Studies on ryegrass (*Lolium perenne*) and lettuce (*Lactuca sativa*) showed that, although Se is harmful for the plants at high concentrations >10 and 1.0 mg kg^{-1}, respectively (reduction of biomass), it can exert beneficial effects at low concentrations, namely 0.1 mg kg^{-1} soil (Hartikainen *et al.*, 2000; Xue *et al.*, 2001).

Most probably the first positive effect of Se on plant growth was reported by Singh *et al.* (1980), who showed that the application of 0.5 mg kg^{-1} Se as selenite stimulated growth and dry matter yield of Indian mustard (*Brassica juncea* L.). More recently, it was revealed that Se, applied at low concentrations, enhanced growth and antioxidative capacity of both mono- and dicotyledonous plants. The growth-promoting response to Se was demonstrated in lettuce and ryegrass (*Lolium perenne* L.) (Hartikainen *et al.*, 1997; Hartikainen and Xue, 1999) and in soybean (*Glycine max* L.) (Djanaguiraman *et al.*, 2005). Se can also delay senescence and promote the growth of aging seedlings (Hartikainen and Xue, 1999; Xue *et al.*, 2001).

Se has also demonstrated its effect on germination. Carvalho *et al.* (2003) reported that at higher supplementation level than 29 mg kg^{-1} soil, Se inhibited the growth and germination of tomato, lettuce and radish (*Raphanus sativus* L.) seeds. In contrast, priming of seeds with

selenite promoted germination of bitter gourd (*Momordica charantia* L.) seeds at sub-optimal temperatures (Chen and Sung, 2001). The positive effect on germination was linked to antioxidative activity.

Foliar application, performed manually only on plants, is the most appropriate way to add Se, since contamination of the soil is minimal. Foliar application to barley at 10 and 20 g Se ha^{-1}, as sodium selenate, increased the Se contents of barley grain and straw and red clover forage (MacLeod *et al.*, 1998). A stimulatory effect of foliar application of Se on growth has been reported for ryegrass (Hartikainen *et al.*, 2000), lettuce (Xue *et al.*, 2001), potato (Turakainen *et al.*, 2004) and green tea leaves (Hu *et al.*, 2003). Se affected plant growth promotion might be the result of increased starch accumulation in chloroplasts (Pennanen *et al.*, 2002) and that protected cell content (Xue *et al.*, 2001).

Simojoki (2003) reported that small Se addition that increased Se contents in lettuce shoots up to 1-5 mg kg^{-1} dry matter (DM) tend to enhance plant growth. But the yields drop drastically at Se contents above 20 mg kg^{-1} DM. Se fertilization changes root morphology and the effects are diverse in different parts of the root system. Moderate Se additions decrease the specific length and specific surface area of basal and lateral roots, whereas large additions increase the specific volume of roots (Simojoki, 2003). In potato plant, Se increased carbohydrate accumulation in the young upper leaves and in stolons, roots and tubers at maturity. However, it could not be explained by increased production of photoassimilates as net photosynthesis did not differ among Se treatments. The Se treated plants produced higher tuber yields than control plants and at the highest Se concentration (0.3 mg kg^{-1}) lower numbers of larger tubers were harvested. Increased yield of Se treated plants suggested that Se may enhance the allocation of photoassimilates for tuber growth, acting as a strong sink for both Se and for carbohydrates. It was also observed that Se improves the processing and storage quality of potato tubers (Turakainen *et al.*, 2004; Turakainen, 2007). The positive impact of Se on the yield of potato plants could be related to its antioxidative effect in delaying senescence. Se at a concentration of 1.5 mg L^{-1} increased yield in pumpkins (*Cucurbita pepo*) (Germ *et al.*, 2005). Some possible roles of Se studied by different researchers are presented in Table 1.

Table 1: Role of Se on plant growth and physiology

Se mediated effects	Observed plant species	Reference
Stimulate growth and dry matter accumulation	Indian mustard	Singh *et al.* (1980)
Beneficial effect on the growth	Alfalfa, subterranean clover	Broyer *et al.* (1966)
	Lettuce	Pennanen *et al.* (2002)
	Green tea	Hu *et al.* (2003)
Enhanced growth and antioxidative capacity	Lettuce, ryegrass	Hartikainen *et al.* (1997), Hartikainen and Xue (1999)
	Soybean	Djanaguiraman *et al.* (2005)
Increase growth and quality of tuber	Potato	Turakainen (2007)
Promote shoot and root growth	Ryegrass	Cartes *et al.* (2010)
Nitrogen assimilation	Barley	Aslam *et al.* (1990)
Increase respiratory potential	*Eruca sativa*	Germ and Osvald (2005)
Induced starch accumulation in chloroplasts	Lettuce	Pennanen *et al.* (2002)
Increased the shoot dry matter production	Soybean	Djanaguiraman *et al.* (2005)
Promote germination	Bitter gourd	Chen and Sung (2001)
Increase the antioxidative capacity of senescing plants and delay senescence	Lettuce, ryegrass	Xue *et al.* (2001)
Regulate the water status of plants	Wheat	Kuznetsov *et al.* (2003)
Delay the death of plants subjected to severe UV-stress	Lettuce	Pennanen *et al.* (2002)
Promote growth of plant subjected to short UV-B episodes	Lettuce	Hartikainen and Xue (1999)

Table 1: Continued

Se mediated effects	Observed plant species	Reference
Alleviated the oxidative stress caused by UV-irradiation	Lettuce, ryegrass	Hartikainen and Xue (1999), Hartikainen *et al.* (2000)
	Strawberry	Valkama *et al.* (2003)
	Soybean	Djanaguiraman *et al.* (2005)
Improve the recovery of plant from light and chilling stress	Potato	Seppänen *et al.* (2003)
Enhance salt tolerance	Sorrel	Kong *et al.* (2005)
	Cucumber	Hawrylak-Nowak (2009)
Improve the utilization of short-wavelength light by plants	Lettuce	Hartikainen and Xue (1999)
Enhance chilling tolerance	Cucumber	Hawrylak-Nowak *et al.* (2010)
	Wheat	Chu *et al.* (2010)
Protect against the oxidative stress	Ryegrass, lettuce, soybean	Xue and Hartikainen (2000), Djanaguiraman *et al.* (2005), Cartes *et al.* (2005)
Minimize the toxic effect and oxidative stress cause by heavy metal stress	Rice	Qi *et al.* (2004), Peng *et al.* (2002)
	Rapeseed	Filek *et al.* (2008)
	Ryegrass	Cartes *et al.* (2010)

ANTIOXIDATIVE ROLE OF SELENIUM

Oxidative stress describes a condition when the generation of reactive oxygen species (ROS) in a system exceeds the system's ability to neutralize and eliminate them (Sies, 1985, 1986; Sies and Cadenas, 1985). The imbalance can resulted from a lack of antioxidant capacity caused by disturbance in production, distribution, or by an overabundance of ROS from endogenous sources or environmental stressors. If not regulated properly, excess ROS can damage cellular lipids, proteins or DNA, thus inhibiting signal transduction pathways, and, in general, normal cellular function.

Recent researches have demonstrated that Se not only able to promote growth and development of plants but also increase resistance and antioxidant capacity of plants subjected to various stresses (Hartikainen and Xue, 1999; Djanaguiraman *et al.*, 2005; Peng *et al.*, 2002). The beneficial effect of Se in plants subjected to stress conditions has in most cases been attributed to increased antioxidant activity. Research works conducted by Xue *et al.* (2001) and afterwards by Djanaguiraman *et al.* (2005) showed the effect of Se application in the form of selenate on senescence in lettuce and soy, confirming that the decline in antioxidant enzyme activity was milder in plants treated with this element, which offsets oxidative damage by boosting growth in plants treated with Se.

However, Ríos *et al.* (2009) showed the effect of different application rates (5, 10, 20, 40, 60, 80 and 120 µM) of selenite or selenate on the production and detoxification of H_2O_2 in lettuce plant in non-stressed condition. The results indicate that the selenate form of Se is less toxic than selenite. On the contrary, the application of selenite triggered a higher foliar concentration of H_2O_2 and a higher induction of lipid peroxidation (MDA content and LOX activity) in comparison to that observed after the selenate application. Also, the plants treated with selenate induced higher increases in enzymes that detoxify H_2O_2, especially ascorbate peroxidase (APX) and glutathione peroxidase (GPX), as well as an increase in the foliar concentration of antioxidant compounds such as ascorbate (AsA) and glutathione (GSH). These data indicate that an application of selenate at low rates can be used to promote the induction in plants of the antioxidant system, thereby improving stress resistance.

Nowak *et al.* (2004) showed a significant change in the activities of oxidoreductase enzymes in response to added Se in wheat plants. The nature of the changes can not be clearly determined, however, they were found to depend on both the concentration of Se and

the enzyme. However, the greenhouse experiment revealed an increase in activity of both catalase (CAT) and peroxidase (POD) in plants, treated with Se at 0.05 mM kg^{-1}, whereas these activities were respectively, reduced and increased at 0.15 mM kg^{-1}. The highest concentration (0.45 mM kg^{-1}) caused a reduction in both enzyme activities. Comparing these results to those of other authors, it can be generalized that the lowest Se concentration positively affected the antioxidant defense in wheat plants, but higher concentrations provoked stress responses. Hence, higher concentrations can be regarded as a prooxidant. Nowak *et al.* (2004) also reported that, a significant increase in nitrate reductase activity was observed in the later development stages of wheat plants grown on Se treated soil, probably due to incorporation of selenocysteine to one of the active sites, where NAD(P)H is bound. Enzymes with selenocysteine in the active site acquire a greater, more powerful redox potential towards their substrates, because selenocysteine has a greater nucleophilic power and a lower pK than cysteine (Eshdat *et al.*, 1997; Campbell, 2001).

Se acted as an antioxidant, inhibiting lipid peroxidation in ryegrass (*Lolium perenne*) in the concentrations 0.1 and 1.0 mg Se kg^{-1} (Hartikainen *et al.*, 2000). In the senescing plants, the addition of Se strengthens the antioxidative capacity by preventing the reduction of tocopherol concentration and by enhancing superoxide dismutase (SOD) activity (Xue *et al.*, 2001). Several studies have shown that a protective role of Se against the oxidative stress in higher plants coincided with enhanced GPX activity and decreased lipid peroxidation (Xue and Hartikainen, 2000; Djanaguiraman *et al.*, 2005; Cartes *et al.*, 2005). Senescence processes are partly delayed due to enhanced antioxidation, which is associated with an increase of GPX activity (Hartikainen *et al.*, 2000). The positive relationship between the Se concentration and GPX activity suggests the presence of Se-dependent GPX (Hartikainen *et al.*, 2000). Cartes *et al.* (2005) demonstrated that selenite was more efficient than selenate as an inductor of GPX activity in ryegrass plants. Takeda *et al.* (1997) demonstrated that in algae, H_2O_2 was eliminated primarily by the enzyme APX in the absence of Se; however, when this trace element was applied, the H_2O_2 was detoxified mainly by GPX. However, apart from GPX, other enzymes such as SOD form an integral part in oxidative metabolism and function to transform the radical superoxide into H_2O_2 (Gratao *et al.*, 2005). In this respect, Kong *et al.* (2005), in sorrel plants under saline stress found stronger SOD activity. In addition, Se affected the activity of CAT and glutathione *S*-transferase (GST) (Xue and Hartikainen, 2000). In potato, moreover, Xue *et al.* (2001) and Pennanen *et al.* (2002) showed that Se retarded the decline of tocopherols, especially the more biologically active form, α-tocopherol. Sreekala *et al.* (1999) observed that mitochondrial SOD activity exhibited a progressive enhancement with Se supplementation, 3-fold at 0.5 ppm, 4-fold at 0.75 ppm and 7-fold at 1.0 ppm. The increase was seen with respect to both total and specific activities. Soluble SOD decreased by 60% in the Se at 0.5 ppm, but an increase of 70% was elicited at 0.75 ppm with no further enhancement at 1.0 ppm. Sreekala *et al.* (1999) also observed that levels of mitochondrial CAT activity remained unaffected in the Se group (0.5 ppm) with respect to both total and specific activities. In the Se groups (0.75 and 1.0 ppm), both total and specific activities registered 60% and 70% decreases, respectively. The response of mitochondrial APX to Se exposure was similar to that of CAT activity (Sreekala *et al.*, 1999) with a decrease in both total and specific activities up to 50-70% with Se supplementation at 0.5 ppm and no further changes in the Se groups (0.75 and 1.0 ppm).

ROLE OF SELENIUM IN ABIOTIC STRESS TOLERANCE

In short, the effect of Se in promoting antioxidant activity has been reported basically in plants subjected to any type of stress, while the possible action of this trace element

(different application rates as well as forms selenate versus selenite) in the oxidative metabolism of non-stressed plants has hardly been documented. In fact, exogenous application of Se acted differently under different abiotic stress in plants as studied by many researchers.

Salinity

The production of ROS is the important cause of damage to plants when subjected to salt stress, thus leading to the growth suppression (Dionisio-Sese and Tobita, 1998; Zhu, 2001; Hasanuzzaman *et al.*, 2009; Nahar and Hasanuzzaman, 2009; Hossain and Fujita, 2010). Research results obtained by different researchers showed the ability of Se to protect plants from salt stress-induced damages when applied at low concentration. Kong *et al.* (2005) reported that at low concentrations (1-5 µM), Se tended to stimulate the growth, the activities of SOD and POD enzymes, as well as the accumulation of water-soluble sugar in leaves of sorrel seedlings. However, at higher concentrations (10-30 µM), Se exerted diminished beneficial effects on growth and enzyme activities. Results revealed that SOD and POD activities of salt-stressed seedlings increased when exposed to concentrations ranging 1-5 µM Se. At concentrations between 10 and 30 µM, there were adverse effects on both enzymes compared with that at 5 µM Se. In cucumber leaves, Se treatments at 5 and 10 µM significantly improved the growth rate and increased the photosynthetic pigments and proline contents when subjected to salt stress (Hawrylak-Nowak, 2009). Additionally, Se enhanced the salt tolerance of seedlings by protecting the cell membrane against lipid peroxidation. Se subdued MDA formation also in experiments performed by Djanaguiraman *et al.* (2005). Recently, in our laboratory we observed that Se-treated salt-stressed seedlings showed higher tolerance compared to the seedling treated with salt alone which was supported by the lower level of MDA and H_2O_2 content and higher enzymatic activities as well as non-enzymatic antioxidant viz. AsA and GSH. Khedr *et al.* (2003) reported that proline induces the expression of salt-stress-responsive proteins and improves the salt-tolerance in the desert plant *Pancratium maritimum*. Increase of proline content in Se-treated soybean plants has also been reported by Djanaguiraman *et al.* (2005). However, the mechanisms and the reasons for proline accumulation in Se-supplied plants have not been fully investigated.

The interaction of Se with soil salinity has also been studied by Terry *et al.* (2000). It is hardly surprising that sulfate salinity drastically inhibits plant uptake of selenate (Mikkelsen *et al.*, 1988; Wu and Huang, 1991; Zayed *et al.*, 1998). Not all plant species are affected to the same extent of sulfate salinity. In Se-accumulators, selenate is taken up preferentially over sulfate. Chloride salinity had much less effect on selenate uptake than sulfate salinity (Wu and Huang, 1991). Generally, there is a small decrease in shoot accumulation of Se with increasing salt levels (Banuelos *et al.*, 1996).

Drought

Drought is a multi-dimensional stress, which causes various physiological and biochemical changes on plants (Dhanda *et al.*, 2000; Wang *et al.*, 2003; Verhagen *et al.*, 2004; Hossain *et al.*, 2009). One of the earliest responses of plants to drought is the accumulation of active oxygen species such as O_2^-, $\cdot OH$, H_2O_2 and $^1O_2$ (Mittler, 2002; Shigeoka *et al.*, 2002; Apel and Hirt, 2004). Plants protect cell systems from the cytotoxic effects of these active radicals using enzymes such as SOD, APX, glutathione reductase (GR), CAT and non-enzymatic antioxidants: GSH, AsA and carotenoid (Car) (Foyer *et al.*, 1997; Foyer and Noctor, 2000). However, there are few reports on the protective role of exogenous Se on drought stress in plant.

In common buckwheat, Tadina *et al.* (2007) observed that in water deficit plants the stomatal conductance (gs) was significantly lower, while Se-supplemented water-deficit plants had significantly higher gs. A significantly higher actual photochemical efficiency of PSII was obtained in Se- and water-deficit plants, which was possibly due to improvement of plant water management during treatment. A significant interaction was also observed between the effects of water deficit and Se on respiratory potential.

Recently, Yao *et al.* (2009) suggested that optimal Se supply is favorable for growth of wheat seedlings during drought condition. The growth and physiological responses of seedlings were different, depending on the Se concentration. Use of higher (3.0 mg Se kg^{-1}) and lower amount used (0.5 mg Se kg^{-1}) did not significantly affect on biomass accumulation. Treatments with 1.0 and 2.0 mg Se kg^{-1} promoted biomass accumulation of wheat seedlings. Treatments at 1.0, 2.0 and 3.0 mg Se kg^{-1} significantly increased root activity, proline content, POD and CAT activities, Car content, chlorophyll content and reduced MDA content of wheat seedlings. Lower Se treatment did not significantly effect on chlorophyll content and MDA content, although it also increased some antioxidant index (proline and Car content, POD and CAT activities) in wheat seedlings. However, Xiaoqin *et al.* (2009) observed that extra Se supply did not effect on the activities of CAT and POD, while the combination of drought and Se significantly increased activities of POD and CAT, but the increase did not counteract the lipid peroxidation.

Chilling

Many crops often encounter cold stress in growing periods, which brings greater loss to agricultural production. It has already been established that Se increases resistance and antioxidant capacity of plants, whereas there has been little effort to understand the role of Se in plants under cold stress. In a recent study on wheat plant, Chu *et al.* (2010) reported the protective role of Se under cold stress. They observed that Se treatments with 1.0 mg kg^{-1} significantly reduced MDA content and the rate of O_2^- production in wheat seedlings grown under cold stress, which indicated that suitable Se treatment reduced membrane lipid peroxidation and oxidative stress in seedlings subjected to stressful condition. Additionally, compared with the control, Se treatments significantly increased contents of anthocyanins, flavonoids and phenolic compounds of seedlings subjected to cold stress (Chu *et al.*, 2010) which have the ability to scavenge free radicals and inhibit membrane lipid peroxidation of seedlings. The effects of different Se treatments on POD and CAT activities in seedlings exposed to cold stress were also reported by Chu *et al.* (2010). They showed a significant increase in activities of POD and CAT in Se treated wheat seedlings under cold stress. The increases in antioxidant enzymes' activities and contents of antioxidant compounds probably decreased the toxicity of ROS (Chu *et al.*, 2010). The results of the study indicated that Se could provide an ecological adaptation for young seedlings subjected to stress conditions by the increase in antioxidant levels and enzymes' activities.

In another recent study, Hawrylak-Nowak *et al.* (2010) reported that under short-term chilling, the contents of chlorophylls and carotenoids showed no significant change after Se supplementation. Hawrylak-Nowak *et al.* (2010) also observed that, compared with the control, the Se-treated plants showed an increase of proline content in leaves, once after chilling and again after 7 days of re-warming. After stress, the MDA content in the root of plants decreased directly when it was treated with 2.5-10 μM Se. This was in comparable with the plants grown without Se, whereas MDA level increased in roots and leaves of plants exposed to 20 μM Se. Seven days later, the MDA level in the root of plants grown in the

presence of Se was still lower than those of plants not treated with Se and generally witnessed no significant change in leaves. Nevertheless, Se at concentrations of 2.5-10 µM modified the physiological response of cucumber to short-term chilling stress, causing an increase in proline content in leaves and diminishing lipid peroxidation in roots, the resistance of plants to low temperature was not clearly enhanced (Hawrylak-Nowak *et al.*, 2010).

Heavy Metals and Al

Although many heavy metals in trace amounts are essential for various metabolic processes in organisms, they create physiological stress leading to generation of free radicals when in high concentration (Hossain *et al.*, 2010). Last few years several researches have been conducted on the role of Se on heavy metal stress tolerance in plants. Results obtained by Vorobets (2006) suggest that the size of GSH pool shows a marked alteration in response to a combined lead and Se treatment. Vorobets (2006) concluded that during heavy metal stress Se might prevent its toxic effect in plants. It has been suggested that the protective effects of Se are due to the formation of non toxic Se-metal complexes (Whanger, 1992; Vorobets and Mykiyevich, 2000). Pedrero *et al.* (2008) observed that the proportion of α-tocopherol was similar in the control plants and in those supplied with Se separately or in combination with cadmium (Cd). However, the percentage of α-tocopherol concentration increased to the level found in control and Se-enriched plants when Se was added simultaneously with Cd. It has been reported that an increase of α-tocopherol favors the stress tolerance of plants as it favors the scavenging of singlet oxygen species in chloroplasts (Munné-Bosch and Alegre, 2002; Munné-Bosch, 2005). Therefore, the increase of α-tocopherol in plants exposed to Se and Cd simultaneously, in comparison to those grown only in Cd, shows evidence that Se assists the plants in the adaptation.

Srivastava *et al.* (2009) observed that Se acted as an antioxidant, inhibiting lipid peroxidation (reduced by 26-42%) via increased levels of thiols and GSH (increased by 24%). The results suggest that Se is either an antioxidant or it activates plant protective mechanisms, thereby alleviating oxidative stress and improving arsenic uptake in *Pteris vittata*. The added Se significantly inhibited lipid peroxidation in the fronds. Compared to the controls, addition of 5 and 10 µM Se reduced the TBARS (thiobarbituric acid reactive substances) concentrations in the fronds by 26-42 and 27-35%, respectively. There were no significant differences in TBARS between two application rates of Se (5 and 10 µM) or two exposure times (5 and 10 day). Recently, a beneficial effect of Se on heavy metal toxicity has been reported. Pedrero *et al.* (2008) studied the response of broccoli submitted to Cd toxicity together with the application of Se. This study reported that Se application diminished the MDA content and decreased the translocation of Cd towards the shoot, thereby reducing oxidative stress provoked by this heavy metal. Pedrero *et al.* (2008) showed that, when plants were exposed simultaneously to Se and cd, the MDA level noticeably decreased to the level found in the control. In the plants supplied only with Se, the level of MDA was the lowest. These findings can be attributed to the antioxidative effect of Se reported in previous studies (Hartikainen *et al.*, 2000; Djanaguiraman *et al.*, 2005).

Under heavy metal stress, there are some possible mechanisms by which Se confers tolerance to stress. Filek *et al.* (2008) observed a protective role of Se ions on the Cd stress in the changes in growth and fresh weight of rape seedlings followed by considering two possible mechanisms: (1) removal of Cd from metabolically active cellular sites and (2) reduction of oxygen radicals. However, their results suggest that the Se effect is linked mainly to a reduction of oxygen radicals that are produced in the presence of Cd.

Non-enzymatic deactivation of oxygen radicals by Se can also be enhanced at the low (2 µM) Se concentration. In that study, Se-induced production of antioxidants was high enough to ameliorate the toxicity of Cd at concentration levels of 400-600 µM. In contrast, compared with Cd concentration, Se concentration seemed to be too low to remove Cd from proteins, especially at higher concentration levels. Very recently, Sun *et al.* (2010) observed the detoxification action of Se on garlic growth under Cd stress. They also considered the mechanisms for the protective role of Se ions on the Cd stress which were: (1) removal of Cd from metabolically active cellular sites, (2) induction of Se to harm the Cd induced free oxygen radical and (3) the regulation of Se to phytochelatin activity. The three actions mitigated the effects of Cd on garlic. In our laboratory, we observed the pre-treatment of mustard seedling with exogenous Se showed better performance in response to enzymatic and non-enzymatic antioxidant when subjected to short-term Cd stress.

Cartes *et al.* (2010) first suggested that at low concentration Se alleviated the Al-induced oxidative stress by means of two mechanisms: (1) the improvement of the spontaneous dismutation of superoxide free radicals to H_2O_2, as previously hypothesised by (Hartikainen *et al.*, 2000) and (2) through the activation of POD enzyme, an H_2O_2 scavenger, in response to the increased disproportion of O_2^- which possibly occurred by effect of the applied Se. Cartes *et al.* (2010) observed that Al enhanced lipid peroxidation and activated the POD, APX and SOD enzymes in the roots of ryegrass. Interestingly, Se application up to 2 µM improved root growth and steadily decreased TBARS accumulation in plants treated with 0 and 0.2 mM Al. However, above 2 µM, Se induced stress in plants grown with or without Al. Significant changes in antioxidant enzymes activities were also found as a result of the added Se. At low Se addition levels POD was activated, whereas APX activity decreased irrespective of added Al. Furthermore, Se supplied up to 2 µM greatly decreased root SOD activity in Al-stressed plants. Qi *et al.* (2004) and Peng *et al.* (2002) reported that Se enhanced resistance to oxidizing ability and reduced membrane lipid peroxidation of rice roots under ferrous stress.

UV-Radiation

Depletion of the stratospheric ozone layer in the atmosphere is known to result in an increase in ultraviolet-B (UV-B) radiation at the earth's surface (Madronich *et al.*, 1998). Enhanced UV-B radiation alter transpiration and photosynthesis (Gaberšèik *et al.*, 2002a), respiration potential (Gaberšèik *et al.*, 2002b) and growth, development and morphology of plants (Gao *et al.*, 2003; Flint *et al.*, 2003). Several reports indicated the protective role of Se against UV-B radiation.

In their recent report, Yao *et al.* (2010a) reported that appropriate amount of Se could significantly enhance the antioxidant ability and reduce membrane lipid peroxidation in aboveground parts of wheat seedlings exposed to enhanced UV-B radiation. In addition, Yao *et al.* (2010b) demonstrated that Se treatments significantly reduced the rate of O_2^- production and MDA content in roots of wheat seedlings grown under enhanced UV-B radiation. The results were similar with the previous study on aboveground parts of wheat seedlings (Yao *et al.*, 2010a). This indicated that Se treatments could reduce active oxygen content and oxidative stress in aboveground and belowground parts of wheat seedlings subjected to stressful condition. Se supply alleviated the damage of enhanced UV-B on wheat seedlings to some extent. Previously, Xue and Hartikainen (2000) observed that Se reduced the lipid peroxidation irrespective of light conditions, even though in the second assay the antioxidative effect was relatively more pronounced in the plants subjected to the short wave length light.

Although UV irradiation generally diminished the activities of enzymes other than GPX, in combination with Se it increased CAT in lettuce and rye grass, SOD in the lettuce and GST in ryegrass. This suggests that Se may increase the antioxidative capacity of plants by multiple systems that act alone or synergistically and are likely different at different growing stages. For instance, the antioxidative capacity of ryegrass against UV was strengthened by simultaneous increase in CAT, GST and GPX. Se treatments also induced an increase in activities of POD and SOD of wheat roots (Yao *et al.*, 2010b). Similarly, an increase in antioxidant enzymes' activities of aboveground parts in seedlings subjected to stress condition has also been reported earlier (Xue *et al.*, 2001; Kong *et al.*, 2005; Yao *et al.*, 2010a), indicating that optimal Se could provide an ecological adaptation for aboveground and belowground parts of seedlings by enhanced contents of antioxidant compounds and activities of antioxidant enzymes under stress conditions. It is noteworthy that APX did not increase in order to resist UV-induced oxidative stress and always responded negatively to exogenous Se, although it shares a common substrate H_2O_2 with GPX and CAT (Xue and Hartikainen, 2000). Analysis of SOD and APX expression carried out by Willekens *et al.* (1994) in ozone sensitive tobacco revealed that the induction of cytosolic copper/zinc, SOD and cAPX under ozone stress occurs only with the onset of visible damage. The results show that the synergistic effect of UV and Se added at non-toxic levels on plant growth is at least partly associated with the antioxidative role of Se through increased activity of GPX. The contribution of CAT and GST to the synergistic growth-promoting effect can be concluded from their analogous behavior; under normal light they responded indifferently or even negatively to Se but increased under UV-light (Xue and Hartikainen, 2000). In addition, the slight toxicity-alleviating effect of UV at the high Se addition level seemed to be associated with antioxidative enzymes: the high-energy light increased CAT in ryegrass and SOD in lettuce.

NEGATIVE EFFECT SELENIUM IN PLANTS AND ENVIRONMENT

Despite the widespread occurrence of Se deficiency globally, Se toxicity (selenosis) is a problem in some areas. Some soils and mineral deposits are naturally Se rich and exploitation of these seleniferous soils or fossil fuels can lead to toxic accumulation of Se in the environment. Se contamination of sediments, soils and drainage water particularly occurs in arid seleniferous areas with intensive crop irrigation (Ohlendorf *et al.*, 1986).

Spallholz and Hoffman (2002) suggested three major Se toxicity mechanisms: (1) generation of superoxide radicals, (2) substitution of Se for sulfur (S) in proteins and (3) inhibition of methylation. Uptake of high concentration of Se by plant's root may exhibit symptoms of injury including stunting of growth, chlorosis, withering and drying of leaves, decreased protein synthesis and premature death of the plant (Trelease and Beath, 1949; Mengel and Kirkby, 1987). There are striking differences between the Se-accumulating plants and the non-accumulators in the maximum amount of Se they can absorb without showing symptoms of toxicity. In nonaccumulators, the threshold Se concentration in shoot tissue resulting in a 10% reduction in yield varied from 2 mg Se kg^{-1} in rice to 330 mg Se kg^{-1} in white clover (Mikkelsen *et al.*, 1989). Se accumulators, on the other hand, may contain Se concentrations in excess of 4000 mg Se kg^{-1} without exhibiting any negative effects on growth (Shrift, 1969). The threshold Se concentration may also vary with plant age and with sulfate supply. For example, Rosenfeld and Beath (1964) observed that in the nonaccumulators, wheat and corn, younger plants were more susceptible and growth inhibition was greater than in mature plants. Tolerance to Se toxicity may increase with

increasing sulfate supply so that threshold Se concentrations may not be the same at different sulfate concentrations in the root environment (Mikkelsen *et al.*, 1989). In non-accumulators, the threshold toxicity concentration is also dependent on the form of Se accumulated. Selenate and selenite are the major forms that are toxic to plants because both are readily absorbed by the plant and assimilated to organic Se compounds. Some studies indicate that selenite is more toxic than selenate.

Kápolna *et al.* (2009) observed that when carrot plants are exposed to high concentrations of Se in their root medium or exposed to excessive Se concentrations in foliar sprays, they may show symptoms of damage like stunting of growth, chlorosis, withering and necrosis of leaves (Trelease and Beath, 1949). Such phenomena, like chlorotic and necrotic leaves were observed in this study when Se(+4) was applied on the leaves at 100 µg Se mL^{-1}, whereas no symptoms developed when the leaves were sprayed with the 10 µg Se mL^{-1} concentration. On the other hand, Se did not cause any visible damage to the leaves at 10 and at the 100 µg Se mL^{-1} concentrations. This indicated that the upper practical Se concentration for Se (+6) had been reached at 100 µg Se mL^{-1}. Oxidative stress in ryegrass (*Lolium perenne*) was found with the addition of Se at 10 mg kg^{-1} or more, which resulted in drastic loss of yield. The toxicity of Se can be attributed to its pro-oxidative effects, as well as to metabolic disturbance (Hartikainen *et al.*, 2000). Pro-oxidative effect of Se possibly increased the demand for counteracting antioxidative capacity. The accumulation of harmful lipid peroxide radicals (LOO) could be counteracted by increasing the concentration of α-tocopherol scavenging them to LOOH which, in turn, were transformed to less toxic LOH through increased GPX activity. The activity of SOD increased to counteract a possible abnormal accumulation of anion radicals (O$_2^-$). A higher Se dosage (1.0 mg kg^{-1} soil) was toxic to lettuce and reduced the yield of young plants. Breznik *et al.* (2004) indicated a slightly negative effect of Se on primary branching and on seed production in buckwheat.

Most recently, Aggarwal *et al.* (2010) reported that at 4 and 6 ppm Se levels, the growth of Bean (*Phaseolus vulgaris* L.) seedlings was inhibited appreciably, which was associated with increase in stress injury measured as damage to membranes and decrease in cellular respiration, chlorophyll and leaf water content. The oxidative injury as elevation of lipid peroxidation was larger compared to H$_2$O$_2$ accompanied by reduced levels of enzymatic (SOD, CAT, APX and GR) and non-enzymatic (AsA and GSH) antioxidants. Proline content was significantly higher at 1 and 2 ppm Se but diminished considerably at 4 and 6 ppm levels concomitant with the reduced growth. However, exogenous application of proline (50 µM) resulted in substantiation of its endogenous levels that antagonised the toxic effects of Se by improving the growth of seedlings.

CONCLUSION

The moon goddess 'Selene' appears to have conferred not only her name, but also her nature on this micronutrient. The facts of Se is intriguing, enigmatic and challenging (even capricious) for researchers. Although, a number of report indicated the protective role of Se under abiotic stress condition, to date the research works conducted on the physiological role of Se under stressful condition is scarce. The studies reported in this issue increase our knowledge of Se in soil and plant and also raise further questions for researchers to try to answer. Controversy exists over the question of whether Se is an essential plant micronutrient. On a cautionary note, the appropriate concentration of exogenous Se is still a matter of intensive research. Complete elucidation of the role of Se as well as detailed protective mechanisms would be helpful for developing stress tolerance in plants.

REFERENCES

Aggarwal, M., S. Sharma, N. Kaur, D. Pathania and K. Bhandhari *et al.*, 2010. Exogenous proline application reduces phytotoxic effects of selenium by minimising oxidative stress and improves growth in bean (*Phaseolus vulgaris* L.) seedlings. Biol. Trace Elem. Res., 10.1007/s12011-010-8699-9

Apel, K. and H. Hirt, 2004. Reactive oxygen species: Metabolism, oxidative stress and signal transduction. Ann. Rev. Plant Biol., 55: 373-399.

Arthur, J.R., F. Nicol and G.J. Beckett, 1990. Hepatic iodothyronine 5-deiodinase. The role of selenium. Biochem. J., 272: 537-540.

Arvy, M.P., 1993. Selenate and selenite uptake and translocation in bean plants (*Phaseolus vulgaris*). J. Exp. Bot., 44: 1083-1087.

Aslam, M., K.B. Harbit and R.C. Huffaker, 1990. Comparative effects of selenite and selenate on nitrate assimilation in barley seeding. Plant Cell. Environ., 13: 773-782.

Banuelos, G.S., A.Zayed, N. Terry, L. Wu and S. Akohoue, 1996. Accumulation of selenium by different plant species grown under increasing sodium and calcium chloride salinity. Plant Soil, 183: 49-59.

Berken, A., M.M. Mullholland, D.L. LeDuc and N. Terry, 2002. Genetic engineering of plants to enhance selenium phytoremediation. Crit. Rev. Plant Sci., 21: 567-582.

Breznik, B., M.Germ, A. Gaberšèik and I. Kreft, 2004. The combined effects of elevated UV-B radiation and selenium on Tartary buckwheat (*Fagopyrum tataricum*) habitus. Fagopyrum, 21: 49-64.

Broyer, T.C., D.C. Lee and C.J. Asher, 1966. Selenium nutrition of green plants. Effect of selenite supply on growth and selenium content of alfalfa and subterranean clover. Plant Physiol., 41: 1425-1428.

Burau, R.G., 1985. Environmental chemistry of selenium. Calif. Agric., 39: 16-18.

Campbell, W.H., 2001. Structure and function of eucaryotic NAD(P)H: Nitrate reductase. Cell Mol. Life Sci., 58: 194-204.

Cartes, P., L. Gianfera and M.L. Mora, 2005. Uptake of selenium and its antioxidative activity in ryegrass when applied a selenate and selenite forms. Plant Soil, 276: 359-367.

Cartes, P., A.A. Jara, L. Pinilla, A. Rosas and M.L. Mora, 2010. Selenium improves the antioxidant ability against aluminium-induced oxidative stress in ryegrass roots. Ann. Appl. Biol., 156: 297-307.

Carvalho, K.M., M.T. Gallardo-Williams, R.F. Benson and D.F. Martin, 2003. Effects of selenium supplementation on four agricultural crops. J. Agric. Food Chem., 51: 704-709.

Chen, C.C. and J.M. Sung, 2001. Priming bitter gourd seeds with selenium solution enhances germinability and antioxidative responses under sub-optimal temperature. Physiol. Plant., 111: 9-16.

Chu, J., X. Yao and Z. Zhang, 2010. Responses of wheat seedlings to exogenous selenium supply under cold stress. Biol. Trace Elem. Res., 136: 355-363.

De Souza, M.P., E.A.H. Pilon-Smits, C.M. Lytle, S. Hwang and J. Tai *et al.*, 1998. Rate-limiting steps in selenium assimilation and volatilization by Indian mustard. Plant Physiol., 117: 1487-1494.

Dhanda, S.S., G.S. Sethi and R.K. Behl, 2000. Indices of drought tolerance in wheat genotyopes at early stages of plant growth.Indices of drought tolerance in wheat genotyopes at early stages of plant growth. J. Agron. Crop Sci., 190: 6-12.

Dhillon, K.S. and S.K. Dhillon, 2003. Distribution and management of seleniferous soils. Adv. Agron., 79: 119-185.

Dionisio-Sese, M.L. and S. Tobita, 1998. Antioxidant responses of rice seedlings to salinity stress. Plant Sci., 135: 1-9.

Djanaguiraman, M., D.D. Devi, A.K. Shanker, A., Sheeba and U. Bangarusamy, 2005. Selenium-an antioxidative protectant in soybean during senescence. Plant Soil., 272: 77-86.

Dumont, E, F. Vanhaecke and R. Cornelis, 2006. Selenium speciation from food source to metabolites: A critical review. Anal. Bioanal. Chem., 385: 1304-1323.

Ellis, D.R. and D.E. Salt, 2003. Plants, selenium and human health. Curr. Opin. Plant Biol., 6: 273-279.

Elrashidi, M.A., D.C. Adriano, S.M. Workman and W.L. Lindsay, 1987. Chemical-equilibria of selenium in soils - a theoretical development. Soil Sci., 144: 141-152.

Eshdat, Y., D. Holland, Z. Faltin and G. Ben-Hayyim, 1997. Plant glutathione peroxidases. Physiol. Plant., 100: 234-240.

Fargašová, A., J. Pastierová and K. Svetková, 2006. Effect of Se-metal pair combinations (Cd, Zn, Cu, Pb) on photosynthetic pigments production and metal accumulation in *Sinapis alba* L. seedlings. Plant Soil Environ., 52: 8-15.

Filek, M., R. Keskinen, H. Hartikainen, I. Szarejko, A. Janiak, Z. Miszalski and A. Golda, 2008. The protective role of selenium in rape seedlings subjected to cadmium stress. J. Plant Physiol., 165: 833-844.

Finley, J.W., C.D. Davis and Y. Feng, 2000. Selenium from high-selenium broccoli is protective against colon cancer in rats. J. Nutr., 130: 2384-2389.

Finley, J.W., C. Ip, D.J. Lisk, C.D. Davis, K.J. Hintze and P.D. Whanger, 2001. Cancer-protective properties of high-selenium broccoli. J. Agric. Food Chem., 49: 2679-2683.

Flint, S.D., R.J. Ryel and M.M. Caldwell, 2003. Ecosystem UV-B experiments in terrestrial communities: A review of recent findings and methodologies. Agr. Forest Meteorol., 120: 177-189.

Flohe, L., W.A. Günzler and H.H. Schock, 1973. Glutathione peroxidase: A selenoenzyme. FEBS Lett., 32: 132-134.

Fordyce, F., 2005. Selenium deficiency and toxicity in the environment. In: Essentials of Medical Geology, Selinus, O., B. Alloway, J. Centeno, R. Finkelman, R. Fuge, U. Lindh and P Smedley (Eds.), Elsevier, pp: 373-415.

Foyer, C.H., H. Lopez-Delgado, J.F. Dat and I.M. Scot, 1997. Hydrogen peroxide and glutathione-associated mechanism of acclamatory stress tolerance and signaling. Physiol. Plant., 100: 241-254.

Foyer, C.H. and G. Noctor, 2000. Oxygen processing in photosynthesis: Regulation and signaling. New Phytol., 146: 359-388.

Gaberšèik, A., M. Voncina, T. Trošt, M. Germ and L.O. Björn, 2002a. Growth and production of buckwheat (*Fagopyrum esculentum*) treated with reduced, ambient and enhanced UV-B radiation. J. Photoch. Photobiol. B., 66: 30-36.

Gaberšèik, A., M. Germ, A. Škof, D. Drma and T. Trošt., 2002b. UV-B radiation screen and respiratory potential in two aquatic primary producers: *Scenedesmus quadricauda* and *Ceratophyllum demersum*. Verh. Int. Verein Limnol., 27: 91-96.

Gao, W., Y.F. Zheng, J.R. Slusser and G.M. Heisler, 2003. Impact of enhanced ultraviolet-B irradiance on cotton growth, development, yield and qualities under field conditions. Agr. Forest Meteorol., 120: 241-248.

Germ, M. and J. Osvald, 2005. Selenium treatment affected respiratory potential in *Eruca sativa*. Acta Agric. Slov., 85: 329-335.

Germ, M., I. Kreft and J. Osvald, 2005. Influence of UV-B exclusion and selenium treatment on photochemical efficiency of photosystem II, yield and respiratory potential in pumpkins (*Cucurbita pepo* L.). Plant Physiol. Biochem., 43: 445-448.

Germ, M., V. Stibilj, J. Osvald and I. Kreft, 2007a. Effect of selenium foliar application on chicory (*Cichorium intybus* L.). J. Agric. Food Chem., 55: 795-798.

Germ, M., V. Stibilj and I. Kreft, 2007b. Metabolic importance of selenium for plants. Eur. J. Plant Sci. Biotechnol., 1: 91-97.

Gissel-Nielsen, G., 1971. Influence of pH and texture of the soil on plant uptake of added selenium. J. Agric. Food Chem., 19: 1165-1167.

Gratao, P.L., A. Polle, P.J. Lea and R.A. Azevedo, 2005. Making the life of heavy metal-stressed plants a little easier. Funct. Plant Biol., 32: 481-494.

Hamilton, S.J., 2004. Review of selenium toxicity in the aquatic food chain. Sci. Total Environ., 326: 1-31.

Hartikainen, H., P. Ekholm, V. Piironen, T. Xue, T. Koivu and M. Yli-Halla, 1997. Quality of the ryegrass and lettuce yields as affected by selenium fertilization. Agric. Food Sci. Finland, 6: 381-387.

Hartikainen, H. and T. Xue, 1999. The promotive effect of selenium on plant growth as triggered by ultraviolet irradiation. J. Environ. Qual., 28: 1372-1375.

Hartikainen, H., T. Xue and V. Piironen, 2000. Selenium as an antioxidant and pro-oxidant in ryegrass. Plant Soil, 225: 193-200.

Hartikainen, H., L. Pietola and A. Simojoki, 2001. Quantification of fine roots responses to selenium toxicity. Agric. Food Sci. Finland, 11: 53-58.

Hartikainen, H., 2005. Biogeochemistry of selenium and its impact on food chain quality and human health. J. Trace Elem. Med. Biol., 18: 309-318.

Hasanuzzaman, M., M. Fujita, M.N. Islam, K.U. Ahamed and K. Nahar, 2009. Performance of four irrigated rice varieties under different levels of salinity stress. Int. J. Integrative Biol., 6: 85-90.

Hawrylak, B., R. Matraszek and M. Szymańska, 2007. Reaction of lettuce (*Lactuca sativa* L.) to selenium in nutrient solution contaminated with nickel. Veg. Crops Res. Bull., 67: 63-70.

Hawrylak-Nowak, B., 2009. Beneficial effects of exogenous selenium in cucumber seedlings subjected to salt stress. Biol. Trace Elem. Res., 132: 259-269.

Hawrylak-Nowak, B., R. Matraszek and M. Szymańska, 2010. Selenium modifies the effect of short-term chilling stress on cucumber plants. Biol. Trace Elem. Res., 10.1007/s12011-010-8613-5

Hossain, M.A. and M. Fujita, 2009. Exogenous glycinebetaine and proline modulate antioxidant defense and methylglyoxal detoxification systems and reduce drought-induced damage in mung bean seedlings (*Vigna radiata* L.). Proceedings of the 3rd International Conference on Integrated Approaches to Improve Crop Production Under Drought-Prone Environments, Oct. 11-16, Shanghai, China, pp: 138-138.

Hossain, M.A. and M. Fujita, 2010. Evidence for a role of exogenous glycinebetaine and proline in antioxidant defense and methylglyoxal detoxification systems in mung bean seedlings under salt stress. Physiol. Mol. Biol. Plants, 16: 19-29.

Hossain, M.A., M. Hasanuzzaman and M. Fujita, 2010. Up-regulation of antioxidant and glyoxalase systems by exogenous glycinebetaine and proline in mung bean confer tolerance to cadmium stress. Physiol. Mol. Biol. Plant., (in press).

Hu, Q.H., J. Xu and G.X. Pang, 2003. Effect of selenium on the yield and quality of green tea leaves harvested in early spring. J. Agric. Food Chem., 51: 3379-3381.

Kahakachchi, C., H.T. Boakye, P.C. Uden and J.F. Tyson, 2004. Chromatographic speciation of anionic and neutral selenium compounds in Se-accumulating *Brassica juncea* (Indian mustard) and in selenized yeast. J. Chromatogr. A., 1054: 303-312.

Khedr, A.A., M.A. Abbas, A.A. Abdel Wahid, W.P. Quick and G.M. Abogadallah, 2003. Proline induces the expression of salt-stress-responsive proteins and may improve the adaptation of *Pancratium maritimum* L. to salt-stress. J. Exp. Bot., 54: 2553-2562.

Koivistoinen, P., 1980. Mineral element composition of Finnish foods: N, K, Ca, Mg, P, S, Fe, Cu, Mn, Zn, Mo, Ni, Cr, F, Se, Rb, Al, B, Br, Hg, As, Cd, Pb and ash. Acta Agric. Scand., 22: 170-170.

Koljonen, T., 1975. The behaviour of selenium in finnish soils. Ann. Agric. Fenn., 14: 240-247.

Kong, L., M. Wang and D. Bi, 2005. Selenium modulates the activities of antioxidant enzymes, osmotic homeostasis and promotes the growth of sorrel seedlings under salt stress. Plant Growth Regul., 45: 155-163.

Kuznetsov, V.V., V.P. Kholodova, V.V. Kuznetsov and B.A. Yagodin, 2003. Selenium regulates the water status of plants exposed to drought. Dokl. Biol. Sci., 390: 266-268.

Kápolna, E., P.R. Hillestrøm, K.H. Laursen, S. Husted and E.H. Larsen, 2009. Effect of foliar application of selenium on its uptake and speciation in carrot. Food Chem., 115: 1357-1363.

Lyi, S.M., L.I. Heller, M. Rutzke, R.M. Welch, L.V. Kochian and L. Li, 2005. Molecular and biochemical characterization of the selenocysteine Se-methyltransferase gene and Se-methylselenocysteine synthesis in broccoli. Plant Physiol., 138: 409-420.

Lyons, G.H., J.C.R. Stangoulis and R.D. Graham, 2005. Tolerance of wheat (*Triticum aestivum* L.) to high soil and solution selenium levels. Plant Soil, 270: 179-188.

MacLeod, J.A., U.C. Gupta, P. Milburn and J.B. Sanderson, 1998. Selenium concentration in plant material, drainage and surface water as influenced by Se applied to barley foliage in a barley red clover potato rotation. Can. J. Soil Sci., 78: 685-688.

Madronich, S., R.L. McKenzie, L.O. Björn and M.M. Caldwell, 1998. Changes in biologically active UV radiation reaching the earths surface. J. Photochem. Photobiol. B. Biol., 46: 5-19.

Masscheleyn, P.H., R.D. Delaunne and H.P. Jr. William, 1990. Transformations of selenium as affected by sediment oxidation-reduction potential and pH. Environ. Sci. Technol., 24: 91-96.

Mayland, H.F., 1994. Selenium in Plant and Animal Nutrition. In: Selenium in the Environment, Frankenberger, Jr. W.T. and S. Benson (Eds.). Marcel Dekker, Inc., NY, USA, pp: 29-45.

McNeal, J.M. and L.S. Balistrieri, 1989. Geochemistry and Occurrence of Selenium: An Overview. In: Selenium in Agriculture and the Environment, Jacobs, L.W. (Ed). American Society of Agronomy and Soil Science Society of America, Madison, WI, pp: 2-13.

Mengel, K. and E.A. Kirkby, 1987. Principles of Plant Nutrition. International Potash Institute, Bern, pp: 687.

Mikkelsen, R.L., A.L. Page and G.H. Haghnia, 1988. Effect of salinity and its composition on the accumulation of selenium by alfalfa. Plant Soil, 107: 63-67.

Mikkelsen, R.L., G.H. Haghnia and A.L. Page, 1989. Factors Affecting Selenium Accumulation by Crop Plants. In: Selenium in Agriculture and the Environment, Jacobs, L.W. (Ed.). American Society of Agronomy and Soil Science Society of America, Madison, WI, pp: 65-93.

Mittler, R., 2002. Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci., 7: 405-410.

Munné-Bosch, S. and L. Alegre, 2002. The functions of tocopherols and tocotrienols in plants. Crit. Rev. Plant Sci., 21: 31-57.

Munné-Bosch, S., 2005. The role of a-tocopherol in plant stress tolerance. J. Plant Physiol., 162: 743-748.

Munshi, C.B. and N.I. Mondy, 1992. Glycoalkaloid and nitrate content of potatoes as affected by method of selenium application. Biol. Trace Elem. Res., 33: 121-127.

Nahar, K. and M. Hasanuzzaman, 2009. Germination, growth, nodulation and yield performance of three mungbean varieties under different levels of salinity stress. Green Farming, 2: 825-829.

Neal, R.H., 1995. Selenium. In: Heavy Metals in Soils, Alloway, B.J. (Ed.). Blackie Academic and Professional, London, pp: 260-283.

Neuhriel, B., M., Thanbichler, F. Lottspeich and A. Bock, 1999. A family of S-ethylmethioninedependent thiol/selenol methyltransferases. Role in selenium tolerance and evolutionary relation. J. Biol. Chem., 274: 5407-5414.

Nowak, J., K. Kaklewski and M. Ligocki, 2004. Influence of selenium on oxidoreductive enzymes activity in soil and in plants. Soil Biol. Biochem., 36: 1553-1558.

Ohlendorf, H.M., R.W. Lowe, P.R. Kelly and T.E. Harvey, 1986. Selenium and heavy-metals in San-Francisco bay diving ducks. J. Wildl. Manage., 50: 64-70.

Pallud, S., M.A. Ramauge, J.M. Gavaet, W. Croteau, M. Pierre, F. Courtin and D.L. Germain, 1997. Expression of type II iodythyronine deiondinase in cultured rat astrocytes is selenium-dependent. J. Biol. Chem., 272: 18104-18110.

Pedrero, Z., Y. Madrid, H. Hartikainen and C. Cámara, 2008. Protective effect of selenium in broccoli (*Brassica oleracea*) plants subjected to cadmium exposure. J. Agric. Food Chem., 56: 266-271.

Peng, X.L., Y.Y. Liu and S.G. Luo, 2002. Effects of selenium on lipid peroxidation and oxidizing ability of rice roots under ferrous stress. J. Northeast Agric. Univ., 19: 9-15.

Pennanen, A., T. Xue and H. Hartikainen, 2002. Protective role of selenium in plant subjected to severe UV irradiation stress. J. Appl. Bot., 76: 66-76.

Pilon-Smits, E.A.H., M.P. de Souza, C.M. Lytle, C. Shang, T. Lugo and N. Terry, 1998. Short communication. Selenium volatilization and assimilation by hybrid poplar (*Populus tremula* alba). J. Exp. Bot., 49: 1889-1892.

Poggi, V., A. Arcioni, P. Filippini and P.G. Pifferi, 2000. Foliar application of selenite and selenate to potato (*Solanum tuberosum*): Effect of a ligand agent on selenium content of tubers. J. Agric. Food Chem., 48: 4749-4751.

Qi, X., Y.Y. Liu and T.X. Song, 2004. Effects of selenium on root oxidizing ability and yield of rice under ferrous stress. J. Northeast Agric. Univ., 11: 19-22.

Rani, N., K.S. Dhillon and S.K. Dhillon, 2005. Critical levels of selenium in different crops grown in an alkaline silty loam soil treated with selenite-Se. Plant Soil, 277: 367-374.

Rosenfeld, I. and O.A. Beath, 1964. Selenium. Geobotany, Biochemistry, Toxicity and Nutrition. Academic Press, New York, USA, pp: 411.

Rotruck, I.T., A.L. Pope, H.E. Ganther, A.B. Swanson, D.G. Hafeman and W.G. Hoekstra, 1973. Selenium: Biochemical role as a component of glutathione peroxidase. Science, 179: 588-590.

Ríos, J.J., B. Blasco, L.M. Cervilla, M.A. Rosales, E. Sanchez-Rodriguez, L. Romero and J.M. Ruiz, 2009.. Production and detoxification of H_2O_2 in lettuce plants exposed to selenium. Ann. Appl. Biol., 154: 107-116.

Schwartz, K. and C.M. Foltz, 1957. Selenium as an integral part of factor 3 against dietary necrotic liver degradation. J. Amer. Chem. Soc., 79: 3292-3293.

Seppänen, M., M. Turakainen and H. Hartikainen, 2003. Selenium effects on oxidative stress in potato. Plant Sci., 165: 311-319.

Shanker, A.K., 2006. Countering UV-B stress in plants: Does selenium have a role? Plant Soil, 282: 21-26.

Shigeoka, S., T. Ishikawa, M. Tamoi, Y. Miyagawa, T. Takeda, Y. Yabuta and K. Yoshimura, 2002. Regulation and functions of ascorbate peroxidase isoenzymes. J. Exp. Bot., 53: 1305-1319.

Shrift, A., 1969. Aspects of selenium metabolism in higher plants. Ann. Rev. Plant Physiol., 20: 475-494.

Sies, H., 1985. Oxidative Stress: Introductory Remarks. In: Oxidative Stress, Sies, H. (Ed.), Academic Press, San Diego, New York, London, pp:1-8.

Sies, H. and E. Cadenas, 1985. Oxidative stress: Damage to intact cells and organs. Philos Trans. R. Soc. Lond. B Biol. Sci., 311: 617-631.

Sies, H., 1986. Biochemistry of oxidative stress. Angew. Chem. Int. Edn. Eng., 25: 1058-1071.

Simojoki, A., 2003. Allocation of added selenium in lettuce and its impact on root. Agric. Food Sci. Finland, 12: 155-164.

Singh, M., H. Singh and D.K. Bhandari, 1980. Interaction of selenium and sulphur on the growth and chemical composition of raya. Soil Sci., 129: 238-244.

Sippola, J., 1979. Selenium content of soils and timothy (*Phleum pratense* L.) in Finland. Ann. Agric. Fenn., 18: 182-187.

Smrkolj, P., M. Germ, I. Kreft and V. Stibilj, 2006. Respiratory potential and Se compounds in pea (*Pisum sativum* L.) plants grown from Se-enriched seeds. J. Exp. Bot., 57: 3595-3600.

Sors, T.G., D.R. Ellis and D.E. Salt, 2005. Selenium uptake, translocation, assimilation and metabolic fate in plants. Photosynth. Res., 86: 373-389.

Spallholz, J. and D. Hoffman, 2002. Selenium toxicity: Cause and effects in aquatic birds. Aquat. Toxicol., 57: 27-37.

Sreekala, M., T.R. Santosh and K. Lalith, 1999. Oxidative stress during selenium deficiency in seedlings of *Trigonella foenum-graecum* and mitigation by mimosine. Part I. hydroperoxide metabolism. Biol. Trace Elem. Res., 70: 193-207.

Srivastava, M., L.Q. Maa, B. Rathinasabapathib and P. Srivastava, 2009. Effects of selenium on arsenic uptake in arsenic hyperaccumulator *Pteris vittata* L. Bioresour. Technol., 100: 1115-1121.

Sun, H.W., J. Ha, S.X. Liang and W.J. Kang, 2010. Protective role of selenium on garlic growth under cadmium stress. Commun. Soil Sci. Plant Anal., 41: 1195-1204.

Tadina, N., M. Germ, I. Kreft, B. Breznik and A. Gaberšèik, 2007. Effects of water deficit and selenium on common buckwheat (*Fagopyrum esculentum* Moench.) plants. Photosynthetica, 45: 472-476.

Takeda, T., Ishikawa T. and S. Shigeoka, 1997. Metabolism of hydrogen peroxide by scavenging system in *Chlamydomonas reinhardtii*. Physiol. Plant., 99: 49-55.

Terry, N., A.M. Zayed, M.P. de Souza and A.S. Tarun, 2000. Selenium in higher plants. Annu. Rev. Plant Physiol. Plant Mol. Biol., 51: 401-432.

Trelease, S.F. and O.A. Beath, 1949. Selenium: Its Geological Occurrence and its Biological Effects in Relation to Botany, Chemistry, Agriculture, Nutrition and Medicine. Trelease and Beath, New York, pp: 292.

Turakainen, M., H. Hartikainen and M.M. Seppänen, 2004. Effects of selenium treatments on potato (*Solanum tuberosum* L.) growth and concentrations of soluble sugars and starch. J. Agric. Food Chem., 52: 5378-5382.

Turakainen, M., H. Hartikainen, P. Ekholm and M. Seppänen, 2006. Distribution of selenium in different biochemical fractions and raw darkening degree of potato (*Solanum tuberosum* L.) tubers supplemented with selenate. J. Agric. Food Chem., 54: 8617-8622.

Turakainen, M., 2007. Selenium and its Effects on Growth, Yield and Tuber Quality in Potato. University of Helsinki, Helsinki. ISBN: 9521034661, pp: 50.

Valkama, E., M. Kivimäenpää, H. Hartikainen and A. Wulff, 2003. The combined effects of enhanced UV-B radiation and selenium on growth, chlorophyll fluorescence and ultrastructure in strawberry (*Fragaria ananassa*) and barley (*Hordeum vulgare*) treated in the field. Agric. For. Meteorol., 120: 267-278.

Verhagen, J., M. Put, F. Zaal and H. van Keulen, 2004. Climate change and drought risks for agriculture. Environ. Poll., 39: 49-59.

Vorobets, N. and I. Mykiyevich, 2000. Single and combined effects of lead and selenium on sunflower seedlings. Sci. Works. Hortic. Veg. Growing, 19: 390-390.

Vorobets, N., 2006. Glutatione peroxidase activity in sunflower shoots exposed to lead and selenium. Ann. Univ. Mariae Curie - SK Lodowska Lublin, 19: 151-154.

Wang, W., B. Vinocur and A. Altman, 2003. Plant responses to drought, salinity and extreme temperatures: Towards genetic engineering for stress tolerance. Planta, 218: 1-14.

Whanger, P.D., 1992. Selenium in the treatment of heavy metal poisoning and chemical carcinogenesis. J. Trace Elem. Electrol. Health Dis., 6: 209-221.

Whanger, P.D., 2002. Selenocompounds in plants and animals and their biological significance. J. Am. College Nutr., 21: 223-232.

White, P.J., H.C. Bowen, P. Parmaguru, M. Fritz and W.P. Spracklen *et al.*, 2004. Interactions between selenium and sulphur nutrition in *Astragalus thaliana*. J. Exp. Bot., 55: 1927-1937.

Willekens, H., W. Van Camp, M. Van Montagu, D. Inze, C. Langbartels and H.J. Sandermann, 1994. Ozone, sulfur dioxide and ultraviolet B have similar effects on mRNA accumulation of antioxidant genes in *Nicotiana plumbaginigolia* L. Plant Physiol., 106: 1007-1014.

Wu, L. and Z.Z. Huang, 1991. Chloride and sulfate salinity effects on selenium accumulation by tall fescue. Crop Sci., 31: 114-118.

Xiaoqin, Y., C. Jianzhou and W. Guangyin, 2009. Effects of drought stress and selenium supply on growth and physiological characteristics of wheat seedlings. Acta Physiol. Plant., 31: 1031-1036.

Xue, T. and H. Hartikainen, 2000. Association of antioxidative enzymes with synergistic effect of selenium and UV irradiation in enhancing plant growth. Agric. Food Sci. Finland, 9: 177-186.

Xue, T., H. Hartikainen and V. Piironen, 2001. Antioxidative and growth-promoting effect of selenium in senescing lettuce. Plant Soil, 27: 55-61.

Yao, X., J. Chu and G. Wang, 2009. Effects of selenium on wheat seedlings under drought stress. Biol. Trace Elem. Res., 130: 283-290.

Yao, X.Q., J.Z. Chu and C.J. Ba, 2010a. Antioxidant responses of wheat seedlings to exogenous selenium supply under enhanced ultraviolet-B. Biol. Trace Elem. Res., 136: 96-105.

Yao, X., J. Chu and C. Ba, 2010b. Responses of wheat roots to exogenous selenium supply under enhanced ultraviolet-B. Biol. Trace Elem. Res., 10.1007/s12011-009-8580-x

Yläranta, T., 1983a. Sorption of selenite and selenate added in the soil. Ann. Agric. Fenn., 22: 29-39.

Yläranta, T., 1983b. Selenium in finnish agricultural soils. Ann. Agric. Fenn., 22: 122-136.

Yläranta, T., 1985. Increasing the selenium content of cereals and grass crops in Finland. Academic Dissertation, Agricultural Research Centre, Institute of Soil Science, Jokioinen. Yliopistopaino, Helsinki, pp:72.

Zayed, A.M., C.M. Lytle and N. Terry, 1998. Accumulation and volatilization of different chemical species of selenium by plants. Planta, 206: 284-289.

Zhu, J.K., 2001. Plant salt tolerance. Trends Plant Sci., 6: 66-71.