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Metabolic Importance of Selenium for Plants

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ABSTRACT

Selenium (Se) is a trace element that is both an essential nutrient for humans and animals and an environmental toxicant; the boundary between the two roles is narrow and depends on its chemical form, concentration, and other environmentally influenced variables. Se is important in the metabolism of cyanobacteria and some plants, being involved in their antioxidative processes. 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. It can increase the tolerance of plants to UV-induced oxidative stress, delay senescence, and promote the growth of ageing seedlings. Recently it has been shown that Se is able to regulate the water status of plants under conditions of drought. It is widely distributed on the Earth's surface and available for plants in at least small traces. Cultivation of plants enriched with Se could be an effective way of producing Se-rich foodstuffs which can be beneficial to health. Se is also a major contaminant in the effluents from some oil refineries, power plants, and in mine drainage water. Se has become the primary element of concern in much environmental contamination because of its bioaccumulation in food webs. Bioaccumulation of Se is leading to toxic impact and changes in communities. However, it is possible to remove it from soils and Se-contaminated agricultural drainage water using plants in a phytoremediation process.

Keywords: essentiality, nutrition, phytoremediation

Abbreviations: DMDSe, dimethyldiselenide; **DMSe**, Dimethylselenide; **ETS**, electron transport system; **GPx**, glutathione peroxidase; **PSII**, photosystem II; **SeCys**, selenocysteine; **SeMet**, selenomethionine; **SeMeSeCys**, Selenomethylselenocysteine; **SOD**, superoxide dismutase; **TBARS**, thiobarbituric acid reactive substances

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INTRODUCTION

Selenium (Se) is one of the most widely distributed elements of the Earth's crust. Much of it occurs associated with sulphide minerals. The presence or absence of Se in any soil depends on the composition of the ground material and on leaching or other processes subsequent to soil formation that have added Se (Shamberger 1981). Soil Se level in Central Europe is less than 1.0 mg Se kg^{-1} (Kadrabova *et al*. 1997; Klapec *et al*. 1998; Pfannhauser *et al*. 2000; Kreft *et al*. 2002; Smrkolj *et al*. 2005; Sager 2006; Germ *et al*. 2007), in Finland 0.04 to 0.7 mg Se kg^{-1} (Hartikainen and Xue 1999; Xue *et al*. 2001), and in Norway cca 0.25 mg Se kg^{-1} (Øgaard *et al*. 2006).

Se is an essential microelement for animals, humans, and microorganisms (Rotruck *et al*. 1973). It has three levels of biological activity (Hamilton 2004): (i) trace concentrations are required for normal growth and development; (ii) moderate concentrations can be stored to maintain homeostatic functions; and (iii) elevated concentrations can result in toxic effects. Se is important in antioxidation in humans and may play a role in antioxidative mechanisms in plants (Ekelund and Danilov 2001). Se added at appropriate levels (0.1 mg kg^{-1}) can also delay senescence and promote the growth of ageing seedlings in lettuce (*Lactuca sativa*) (Xue *et al*. 2001). Large additions are toxic and may induce pro-oxidative reactions. In areas where soils are low in bioavailable Se, its deficiency can occur, constituting health risks for humans and animals. Although higher plants have been supposed not to require Se, in Finland (with low-Se soils) the supplementation of fertilizers with sodium selenate affects positively the whole food chain from soil to plants, animals and humans, including the amount of plant yields (Hartikainen 2005). Although Se is an essential trace nutrient important to humans and most other animals as an antioxidant, it is toxic at high concentrations due to incorporation of Se in place of sulphur in amino acids, with subsequent alteration of protein three-dimensional structure and impairment of enzymatic function (Amweg *et al*. 2003).

The widespread occurrence of Se in surface waters results from a variety of natural and anthropogenic sources. Se accumulation in soils and waters is associated with agricultural irrigation, geochemical processes, mining, and a variety of other industrial sources is a major environmental

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problem (Shardendu *et al.* 2003). Industrial and agricultural activity has by relocation of ores, industrial wastes, exposure of geological strata to weather conditions, impact of plants, including the release of H^+ ions from plant roots and changeable pH hastened the release of Se from geological sources and made it available to fish and wildlife in aquatic and terrestrial ecosystems around the globe. Agricultural drain water, sewage sludge, fly ash from coal-fired power plants, oil refineries, and mining of phosphates and metal ores are all sources of Se contamination of the aquatic environment (de Souza *et al.* 2002; Lemly 2002). Se is also a major contaminant arising from the natural weathering and irrigation-induced leaching of Se-containing rocks and soils. Some plant species for example *Morinda reticulata* and *Neptunia amplexicaulis* growing on seleniferous soils are Se-tolerant and accumulate very high concentrations of Se (Se accumulators). They accumulate and tolerate up to 4000 mg Se kg^{-1} dry matter. However most plants are Se non-accumulators (contain less than 25 mg Se kg^{-1} dry matter) and are sensitive to Se (Terry *et al.* 2000; Ellis and Salt 2003; Tinggi 2003). Terrestrial plants can remove Se from the soil (Kahakachchi *et al.* 2004) and macrophytes also can assimilate Se present in Se-contaminated agricultural drainage water (Lin *et al.* 2002). Selenate, the analog of sulfate, was shown to be transported by sulfate permease and then reduced via ATP sulfurylase, the enzyme that activates sulfate (Pilon-Smits *et al.* 1999). In addition to accumulating Se into the biomass, primary producers are able to remove Se from sites by volatilizing Se via the production of volatile Se compounds. Se volatilization is useful for the phytoremediation of contaminated soil and water as inorganic Se is converted to the gas dimethylselenide (DMSe), which is approximately 600 times less toxic in comparison to inorganic Se (de Souza *et al.* 2002). In the acid rain areas the availability of Se for plants is lower due to lower soil and water pH (Gerhardsson *et al.* 1994). The use of plants and microorganisms to volatilize Se constitutes an environmentally sound technology (Pilon-Smits *et al.* 1999).

ESSENTIALITY OF Se FOR HUMAN AND ANIMAL NUTRITION

Deficiency of Se in various animal species results in Se-responsive diseases such as muscular dystrophy, exudative diathesis and hepatosis dietetica (Shamberger 1981). In contrast, Se plays a role in the prevention of atherosclerosis, certain specific cancers, arthritis, and altered immunological functions (Shamberger 1981). Where more Se occurs in the environment, human death rates from cancer are lower (Shamberger 1981). Human mortality from heart disease is also lower in high Se areas. In China, a large clinical trial showed that Se prevents congestive heart failure in children from severely Se deficient areas (Shamberger 1981).

The essentiality of Se for animals was discovered in 1957, leading to the question as to which form of Se is biologically active. An important turning point was in 1973, when glutathione peroxidase (GPx) was identified as a selenoenzyme (Rotruck *et al.* 1973; Behne and Kyriakopoulos 2001).

Cultivation of plants enriched with Se could be an effective way of producing Se-rich foodstuffs, with benefits to health (Ip and Lisk 1994; Lyons *et al.* 2005). Environmental toxicity of Se in animals and humans is rare. In horses and cattle ingestion of plants containing over 5 but usually less than 50 mg kg^{-1} caused chronic poisoning. In humans there have been a number of cases reported Se poisoning as a result of accidental ingestion of selenic acid (30 g L^{-1}) (Tinggi 2003). The beneficial effects of Se are dependent on the chemical form, selenomethionine (SeMet, $H_3N^+CH(COO^-)CH_2CH_2SeCH_3$) being the most readily assimilated form (Patrick 2004). Duffield-Lillico *et al.* (2003) reported that supplementation of the human diet with selenium yeast, containing SeMet as the main chemical form, significantly reduced the occurrence of prostate cancer. However, Peters *et al.* (2007) reported that greater prediagnostic serum Se concentrations were not associated with prostate cancer risk, although greater concentrations were associated with reduced prostate cancer risk in men who reported a high intake of vitamin E, in multivitamin users, and in smokers.

Even though currently used techniques enable the detection of a large number of Se species, their physicochemical identification is not complete. The sparsity of such information caused the European Parliament to establish a "positive list" (Directive 2002/46EC) of dietary supplements, which states that the only authorized forms of Se are selenite, selenate and sodium hydrogen selenite; any other chemical form of Se was prohibited as of 1st August 2005.

THE EFFECT OF Se ON PLANTS

The content of Se in plants can be increased in different ways; by addition of Se to soil, soaking seeds in Se solution before sowing, hydroponic and aeroponic cultivation in a nutrient solution containing Se, and foliar application of plants with Se solution. Uptake and accumulation of Se by plants is determined by the chemical form and concentration, by soil factors such as pH, salinity and $CaCO_3$ content, the identity and concentration of competing ions, and by the ability of the plant to absorb and metabolize Se (Kabata Pendias 2001; Wu 2004). Se sorption is highest at lower pH values, with Se(IV) sorption decreasing at pH values above 6, whereas Se(VI) decreased over the entire pH range (2.5-10). Se sorption increases with increasing Ca^{2+} concentrations while SO_4^{2-} suppresses sorption well above enhancements by Ca^{2+} (Hyun *et al.* 2006). There is a complex interaction of factors influencing Se sorption by plants. Selenium uptake and accumulation by plants may be affected by the concentration of major anions (e.g. SO_4^{2-}, Cl^-) often present in saline drainage waters. Root transport of SO_4^{2-} and SeO_4^{2-} by many crop plants is mediated by a common cell membrane carrier and the anions compete for the binding sites on this carrier. As a result of this antagonism, Se uptake is inhibited to a greater extent by external SO_4^{2-} than by Cl^- (Grieve *et al.* 2001).

Se has not been classified as an essential element for plants, although its role has been considered to be beneficial in plants capable of accumulating large amounts of the element (Shanker 2006). It acted as an antioxidant, inhbiting lipid peroxidation in ryegrass (*Lolium perenne*) in concentrations 0.1 and 1.0 mg Se kg^{-1} (Hartikainen *et al.* 2000). Se increased yield under ambient radiation conditions in pumpkins (*Cucurbita pepo*) at a concentration 1.5 mg L^{-1} (Germ *et al.* 2005). Studies on ryegrass (*Lolium perenne*) and lettuce (*Lactuca sativa*) show that, although Se is harmful for plants at high concentrations >10 mg kg^{-1} 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). It has been shown to promote the growth of plants subjected to UV-induced oxidative stress (Xue and Hartikainen 2000); the UV intensity at the top of the pots was 0.177 UV-B and 0.077 UV-A mW cm^{-2}, plant were illuminated for one or three minutes daily (Xue and Hartikainen 2000). Se can also delay senescence and promote the growth of ageing seedlings (Hartikainen and Xue 1999; Xue *et al.* 2001). 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). Senescence processes are partly delayed due to enhanced antioxidation, which is associated with an increase of glutathione peroxidase (GPx) activity (Hartikainen *et al.* 2000). In ryegrass (*Lolium perenne*) up to Se addition of 1.0 mg kg^{-1}, the decreased lipid peroxidation (decreased TBARS-thiobarbituric acid reactive substances) is connected with Se-induced increase in GPx activity. The positive relationship between the Se concentration and GPx activity suggests the presence of Se-dependent GPx (Hartikainen *et al.* 2000).

It is known that some of plants accumulate high concentrations of Se, becoming toxic for animals fed with these plants (Tinggi 2003). It was reported by Auger *et al.* (2004) that garlic (*Allium sativum*) cultivated on naturally seleniferous soils contained 7 ppm Se. The "alkali disease" is a chronic poisoning of horses and cattle from ingestion of plants containing over 5 but usually less than 50 mg kg^{-1} Se. The "blind staggers" is also a chronic poisoning in animals which often associated with feeding on plant species that can naturally accumulate Se up to 1000 mg kg^{-1} (Tinggi 2003).

Oxidative stress in ryegrass (*Lolium perenne*) was found with the addition of Se at ≥10 mg kg^{-1}, 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. In the senescing plants, it diminished the dry weight yield but not the fresh weight yield (Xue *et al.* 2001).

Breznik *et al.* (2005) studied the combined effects of elevated UV-B radiation and addition of Se on common and tartary buckwheat. The effective quantum yield of PSII was reduced due to UV-B radiation in both buckwheat species and was mitigated by the addition of Se. Se treatment also mitigated the stunting effect of UV-B radiation and lowering of biomass in common buckwheat plants. The results from a similar experiment (Breznik *et al.* 2004) indicated a slightly negative effect of Se on primary branching and on seed production in tartary buckwheat.

The response of pumpkins (*Cucurbita pepo*) to foliar spraying of Se at concentration 1.5 mg L^{-1} and ambient UV-B radiation was studied (Germ *et al.* 2005). A stimulatory effect on the yield of pumpkin fruits was observed that is consistent with similar observations made on ryegrass (Hartikainen *et al.* 2000), lettuce (Xue *et al.* 2001), and potato (Turakainen *et al.* 2004). The increase in yield in pumpkins was much higher in plants that were exposed to UV-B-excluded solar radiation together with Se spray than those that received either treatment independently. Pennanen *et al.* (2002) investigated whether Se (0.01 and 0.05 mg kg^{-1} soil) enhances growth of plants subjected to severe UV stress (UV-B and a small amount of UV-C) in lettuce (*Lactuca sativa*). Young plants grown without UV used Se to build up energy reserves. These reserves resulted in the increase in shoot yields. Under severe UV stress, lipid peroxidation markedly increased, and the protecting role of Se via enhanced antioxidative capacity became apparent. Se was able to promote the growth of UV-stressed plants, presumably through protection of chloroplast enzymes. Ekelund and Danilov (2001) observed that Se played a key role in the protective mechanisms in *Euglena gracilis* during UV irradiation. Photodamage of photosynthesis is due to oxidative damage. One of the protective mechanisms could be to strengthen the antioxidative capacity of plants and algae. Ekelund and Danilov (2001) investigated the role of Se in "light-enhanced dark respiration" (LEDR) and photosynthesis in the flagellate *Euglena gracilis*, after exposure to UV-radiation (UV-A, 320-400 nm, of 1.02 W m^{-2} plus UV-B, 280-320 nm, of 0.73 W m^{-2}). Se was added into the growth medium at different concentrations of selenite (10^{-7}, 10^{-8}, 10^{-9} and 10^{-10} M, $Na_2SeO_3{\cdot}5H_2O$). *E. gracilis* were subjected to six different light pulses with a photon fluence rate of 59, 163, 600, 1180, 2080 and 3340 µmol m^{-2} s^{-1} and periods of darkness between the light pulses. Photosynthetic saturation occurred at irradiances higher than 600 µmol m^{-2} s^{-1} and at the highest irradiance the photosynthetic rate decreased due to photoinhibition. After 40 min exposure to UV-radiation, photosynthetic rate and LEDR as functions of photon fluence rate were reduced. Neither in control (no UV-radiation) nor when measured immediately after exposure to UV-radiation Se had no stimulating effects on photosynthesis and LEDR. However, after UV-treatment and 24 h of recovery the presence of Se led to an increase in photosynthesis and LEDR at higher irradiances. The results indicate that Se might play a role in the repair mechanisms in *E. gracilis* after UV treatments.

The addition of Se did not ameliorate the harmful effects of UV-B on strawberry (*Fragaria* × *ananassa*) in greenhouse experiments, but the lower level of added Se (0.1 mg kg^{-1}) increased leaf growth (Heijari *et al.* 2006). Valkama *et al.* (2003) provided evidence that a high Se concentration in soil (1 mg kg^{-1}) had no ameliorative effect but increased the sensitivity of strawberry to enhanced UV-B radiation in the field. Although barley leaves accumulated higher Se concentrations than strawberry there were no apparent changes in their growth, biomass or chlorophyll fluorescence due to Se effect, either alone or in combination with UV-B.

Studies by Pennanen *et al.* (2002) indicated that plant growth promoted by Se is the result of increased starch accumulation in chloroplasts. It was shown that Se also has positive effects on potato carbohydrate accumulation (Turakainen *et al.* 2004). At the highest Se addition (0.3 mg Se kg^{-1}), the highest soluble sugar concentration was observed in the upper leaves 4 weeks after planting (from cca 75 to cca 90 mg g^{-1} DW) and in the roots (from cca 25 to cca 50 mg g^{-1} DW) and stolons (from cca 150 to cca 175 mg g^{-1} DW) at maturity. The positive effects of Se on the recovery of potato from photooxidative and paraquat-generated oxidative stress point to mechanisms that, although unknown, protect chloroplasts during stress (Seppänen *et al.* 2003). It was shown that Se has the ability to regulate the water status of plants under conditions of drought (Kuznetsov *et al.* 2003) and that the protective effect of Se under drought stress conditions was achieved by increasing the water uptake capacity of the root system (Kuznetsov *et al.* 2003).

The addition of Se induced a higher respiratory potential, measured by electron transport system (ETS) activity, in young Se enriched plants of *Pisum sativum* (Smrkolj *et al.* 2006a), and young chicory (*Cichorium intybus*) plants (Germ *et al.* 2007). The respiratory potential of *Eruca sativa* significantly increased in plants grown from Se-treated seeds (Germ and Osvald 2005). Possible explanations are: (i) a higher ETS activity reflects increased GPx activity in mitochondria. It was shown (Xue and Hartikainen 2000; Hartikainen *et al.* 2000; Xue *et al.* 2001; Cartes *et al.* 2005) that Se exposure increased GPx activity in ryegrass and lettuce; (ii) plants need energy to repair damage caused by Se. The latter is consistent with the fact that Se can mimic sulphur, forming Se analogues of S compounds, for example replacing S in amino acids (methionine and cysteine). The conformation of proteins containing seleno amino acids could be perturbed, and their catalytic activity thereby disturbed (Brown and Shrift 1982).

Turakainen *et al.* (2006) studied the raw darkening of potato tubers supplemented with selenate. At low levels, Se improved the processing quality of potato tubers by diminishing and retarding their raw darkening.

Se COMPOUNDS IN Se-ENRICHED PLANTS

Most cereal crops and fodder plants are reported to be relatively weakly able to absorb Se, even when grown on soils with higher Se content (Nowak *et al.* 2004). Se is taken up from the soil by plants primarily as selenate (SeO_4^{2-}) or selenite (SeO_3^{2-}) (Ellis and Salt 2003). Kahakachchi *et al.* (2004) stated that actively growing tissues usually contain the largest amounts of Se. The majority of plants accumulate more Se in shoot and leaf than in root tissues, but there are exceptions (Zayed *et al.* 1998). Dumont *et al.* (2006) described the metabolization of Se in plants, which is presented in **Fig. 1**.

Se uptake (as selenate) by spinach plants (*Spinacia ole-*

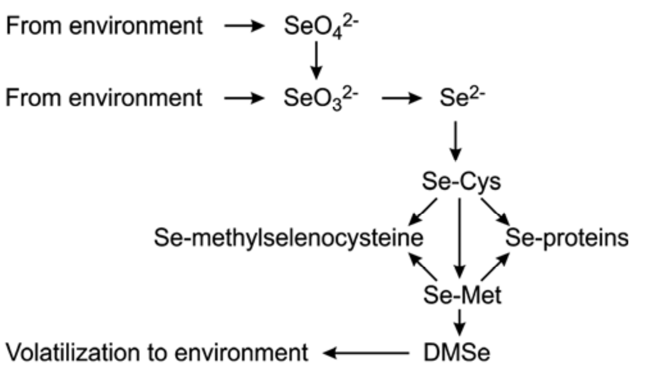

Fig. 1 Schematic representation of the main steps of Se-metabolism in plants (adapted from Dumont *et al.* 2006).

racea) was studied under controlled conditions using solution culture. Spinach readily accumulated Se in the edible parts, the leaves. Values of the distribution coefficient for Se between leaves and roots ranged from 4.51 to 8.59. These results suggest the feasibility of supplementing plant growth substrates with Se to improve human nutrition where Se is deficient in the diet (Zhu *et al.* 2004).

Besides the total content of Se, the chemical form in which Se is present is also very important, since the different forms exhibit differences in bioavailability and toxicity (Mazej *et al.* 2006). 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 Semethylselenocysteine (SeMeSeCys) (Lyi *et al.* 2005). Increased Se fertilization results in Se concentration in potato (Munshi *et al.* 1992; Poggi *et al.* 2000; Turakainen *et al.* 2004). In tea plants, foliar application with selenate significantly increased Se content in the leaves (Hu *et al.* 2003). The results of Smrkolj *et al.* (2006a) 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. After hydrolysis, SeMet was the only Se compound found in supernatants by anion and cation exchange chromatography. SeMet has been found to be the major Se species in other plant seeds enriched with Se in different ways. In buckwheat and pumpkin seeds grown from plants that were foliarly-treated with selenate solution, SeMet was the main Se species, comprising 93 and 81% of the total Se content, respectively (Smrkolj *et al.* 2005, 2006a, 2006b). Stadlober *et al.* (2001) cultivated different cereals in soil to which selenate was added and in wheat, barley and rye, between 70 and 83% of the Se was found in the form of SeMet.

Sugihara *et al.* (2004) germinated soybean and kidney bean, both leguminous plants, in selenite solution and harvested the resulting sprouts. The Se content was 8 to 10 µg g^{-1} of wet weight, and the major part of Se was in the form of SeMeSeCys, with only a minor proportion in the form of SeMet and one unidentified Se species.

Se concentration in shoots has been shown to increase with the application of both selenite and selenate in ryegrass (Cartes *et al.* 2005). However, the highest shoot Se concentrations were obtained in selenate-treated plants.

Turakainen *et al.* (2006) reported that Se fertilization can improve the nutritive value of potato by increasing the level of organic Se compounds in tubers. Se-enriched pea seeds are a potential source of dietary Se, on account of their ability to accumulate Se, mainly as SeMet, is known to be very favourable for human consumption (Smrkolj *et al.* 2006a). Se fertilization may improve the nutritive value of potato by increasing the amount of organic Se compounds in tubers (Turakainen *et al.* 2006). Total concentration and forms of Se in leaves of some cultivated plants exposed to Se is presented in **Table 1**.

TOXICITY OF Se AT THE ECOSYSTEM LEVEL

The toxicity of Se to animals varies with the amount and chemical form of Se ingested, with the duration and continuity of intake, and with the type and nature of the diet, especially its protein and sulphate content (Shamberger 1981).

Se, a metalloid, is toxic to aquatic life in relatively low concentrations (US EPA 1987). Se contamination in aquatic ecosystems has been linked to adverse ecological effects in several field settings (Skorupa 1998) that include reproductive and developmental impairment of aquatic birds and fish (Sappington 2002).

The environmental and biological factors that affect the biogeochemical cycling of Se in the environment have a profound influence on its subsequent availability and toxicity to organisms (Amweg *et al.* 2003). These factors are: (i) Se occurs in several different oxidation states in the aquatic environment that include oxidized forms of Se, selenates (Se^{+6}) and selenites (Se^{+4}), elemental selenium (Se^{0}) and the reduced form of Se, selenides (Se^{-2}). Elemental selenium (Se^{0}), the primary form found in sediments, has little toxicological significance for most organisms. Selenate (Se^{6+}) and selenite (Se^{4+}) are both water soluble inorganic species, found typically in aerobic water sources. Selenite is more bio-available and approximately 5-10 times more toxic for organisms than selenate (Lemly *et al.* 1993). Organic Se, bound in organic compounds such as Se amino acids, is the most bio-available form, and is taken up by algae 1000 times more readily than inorganic forms (Amweg *et al.* 2003). (ii) Se can undergo biotransformations between inorganic and organic forms as a result of biotic and abiotic processes, which are not well characterized. (iii) Se has also been shown to bioaccumulate in aquatic food webs, to the extent that dietary exposure to Se becomes a critical exposure pathway for top predatory aquatic and aquatic-dependent organisms. Since traditional laboratory chronic toxicity tests rarely include realistic exposures to the diet, they are less relevant for directly assessing the toxicity of Se in natural settings (Sappington 2002). As far as Se ecotoxicology is concerned, a critical point is that chronic toxicity resulting from dietary Se uptake and food chain transfer constitutes a

Table 1 Total concentration and forms of Se in leaves of cultivated plants exposed to Se (adapted from Mazej *et al*. 2006).

Plant	**Se addition**	**TotalSe^{a} (µg g^{-1})**	**Se species (%)^{b}**					**References**
			SeMet	**$SeCys_2$**	**SeMeSeCys**	**SeO_4^{2-}**	**SeO_3^{2-}**	
Cichory (*Cichorium intybus*)	Na_2SeO_4 (7 mgl^{-1}) 5 days	88	4	<DL	<DL	72	0.2	Mazej *et al*. 2006
	Na_2SeO_4 (7 mgl^{-1}) 10 days	131	4	<DL	<DL	73	0.3	
	Na_2SeO_4 (7 mgl^{-1}) 41 days	480	8	<DL	0.7	63	0.2	
Lupine (*Lupinus albus*)	Na_2SeO_4 (1 mgl^{-1}) 14 days	631	-	-	-	95	-	Ximénez-Embún *et al.* 2004
	Na_2SeO_3 (1 mgl^{-1}) 41 days	50	-	20	-	-	3	
Sunflower (*Helianthus annuus*)	Na_2SeO_4 (1 mgl^{-1}) 14 days	73	20	-	-	35	-	
	Na_2SeO_3 (1 mgl^{-1}) 14 days	12	15	-	-	-	3	
Onion (*Allium cepa*)	Na_2SeO_4 (5 mgl^{-1}) 8 days	601	0.2	0.1	2	Majority	-	Wróbel *et al*. 2006
	Na_2SeO_3 (5 mgl^{-1}) 8 days	154	0.3	0.5	4	-	-	
Lettuce (*Lactuca sativa*)	Na_2SeO_3 (10 mgl^{-1}) 7 days	27^{e}	3	-	90	-	7	
	Na_2SeO_3 (10 mgl^{-1}) 8 days	32^{e}	-	-	94	-	2	

(-) not detected, ^{a} µg Se g^{-1} dry weight, ^{b} % Se species relative to total Se in sample, ^{c} species detected but not quantified, ^{e} µg Se g^{-1} wet weight.

far greater problem than acute toxicity associated with direct water exposure. In addition, extensive biotransformations and food chain transfer make it difficult to predict Se risk based on waterborne Se concentrations alone (Fan *et al*. 2002).

It was reported that Belews Lake, North Carolina, was contaminated by Se in wastewater released from a coal-fired electric generating facility between 1974 and 1985. Se accumulated in aquatic food chains, and caused severe reproductive failure and teratogenic deformities in fish (Lemly 2002). Beginning in 1986, the electric utility company changed its ash disposal practices and Se-laden wastewater no longer entered the lake. Hazard ratings indicate that a high hazard existed prior to 1986 and that a moderate hazard is still present, primarily due to Se in the sediment-detrital food pathway. Concentrations of Se in sediments have fallen by about 65-75%, but remain sufficiently elevated (1-4 $\mu g\ g^{-1}$) to contaminate benthic food organisms for fish and aquatic birds. At the ecosystem level, recovery has been slow. Toxic effects are still evident 10 years after Se input was stopped. The sediment-associated Se will probably continue to be a significant hazard to fish and aquatic birds for years (Lemly 2002).

Once Se contamination begins, a cascade of bioaccumulation events is set into motion which makes meaningful intervention nearly impossible. However, this cascade of events need not happen if adequate foresight and planning are exercised. Early evaluation and action are important. Prudent risk management, based on environmentally sound hazard assessment and water quality goals, can prevent biological impacts (Lemly 2004).

Se and sulphur are nutrients with very similar chemical properties and their uptake and assimilation proceed through common pathways (Eapen and D'Souza 2005). That is also the reason for the widely studied effect of sulphate in relation to Se uptake and toxicity in aquatic organisms as a function of water hardness, temperature, pH and other parameters (Sappington 2002).

Antagonistic effects of sulphate on uptake and acute toxicity of selenate by algae and aquatic macrophytes have been reported (Sappington 2002). The macrophyte species *Ruppia maritima* takes up two orders of magnitude more selenate under low sulphate conditions than under high sulphate conditions, indicating a sulphate/selenate antagonism (Bailey *et al*. 1995). High background sulphate strongly reduces Se accumulation, suggesting that the potential for phytoremediation is greatest in saline areas having low to moderate sulphate levels (Vickerman *et al*. 2002). Exposure to concentrations greater than 100 mg kg^{-1} had an inhibitory effect on the growth of four macrophytes (Carvalho and Martin 2001).

PHYTOREMEDIATION

Phytoremediation as a plant-based technology involving the use of plants, in conjunction with their associated microbial activity, has already been used successfully to extract, accumulate, and volatilize Se (Pilon-Smits *et al*. 1999). In addition to accumulating Se into the biomass, the aquatic producers are the main drivers for the volatilization of Se via the production of methylated selenides including dimethylselenide (DMSe) and dimethyldiselenide (DMDSe) (Fan *et al*. 2002). Once the plants have successfully accumulated and stored Se in their tissues, the plant tissues must be harvested, removed from the contaminated site, and disposed of safely. The presence of Se in plants resulting from its removal from soil has a certain advantage; Se is, in certain low concentrations, an essential trace element for adequate nutrition and health in mammals. One safe disposal method would involve using the Se-enriched plant material as forage for animals with low Se feed levels. Canola plants used for field phytoremediation of Se may be harvested and fed safely, but without the seeds, to lambs and cows to help meet normal Se intake requirements (Bañuelos and Mayland 2000). The Se concentration in beef is directly related to the Se-concentration of the crops which are fed to animals. Pork and beef can also accumulate large amounts of Se when the animals are fed a Se-rich diet (Dumont *et al*. 2006). Another possibility would be to use the Se-enriched plant material as an organic Se fertilizer added to forage crops. Finally, if the Se-enriched plant material also contains toxic elements, such as mercury and arsenic, at levels that exceed the safe limits for animal consumption, the plant tissue could be used as fuel to generate electricity (Carvalho and Martin 2001). In the similar way, it is possible to use extracted canola oil in the mixture with diesel fuel for the production of both biofuel for diesel engines, and using the seed by-products after oil extraction for animal feed supplement. Canola oil (*Brassica napus*), as well as oils from such oil plants, e.g., sunflower (*Helianthus annuus*), safflower (*Carthamus tinctorus*), soybean (*Glycine max*), cotton (*Gossypium hirsutum*), and peanut (*Arachis hypogaea*) are possible potential alternative fuel materials for diesel engines. This could be well an suitable fuel with chemical and physical characteristics close to those of commercial diesel fuel (Bañuelos 2006). Se can also be removed by phytovolatilization (Carvalho and Martin 2001). The idea of using plants for this is very attractive because the Se is completely removed from the local ecosystem by being released to the atmosphere in relatively non-toxic volatile forms. The main product of phytovolatilization is DMSe (dimethylselenide) (Dumont *et al*. 2006). Several plant species are Se accumulators which can take up large amounts of Se (>1,000 mg Se kg^{-1}). High concentrations of accumulated Se are not toxic to plants, because only a small amount is protein-bound (Dumont *et al*. 2006).

The ability of terrestrial plants to remove Se from the soils has been well documented (Kahakachchi *et al*. 2004); however, macrophytes also can assimilate Se present in contaminated agricultural drainage water (Lin *et al*. 2002). At Se concentrations of 100 mg kg^{-1} or less, fairly good to excellent removal of Se from the water has been achieved (65 to 100%), by four species of macrophytes (Carvalho and Martin 2001). The macroalga, muskgrass (*Chara canescens*), plays an important role in the removal of Se from agricultural drainage water (Lin *et al*. 2002), as has also been shown for *Phragmites australis* (Shardendu *et al*. 2003) and *Potamogeton crispus* (Wu and Guo 2002). Uptake of SeMet is the most rapidly taken up compound in all trophic levels (Simmons and Wallschlager 2005). Selenite is taken up faster and in greater amounts than selenate by macrophytes (Hamilton 2004).

Although hyperaccumulators are efficient Se extractors, their phytoremediation potential is often limited by their slow growth rate and low biomass production. More effective Se phytoremediation has been achieved using fast-growing plant species with only moderate Se accumulation abilities, such as Indian mustard (*Brassica juncea*) (LeDuc *et al*. 2006) because of its fast growing cycle and high biomass (Kahakachchi *et al*. 2004).

The biological process of Se volatilization in drainage sediment has been studied (Bañuelos *et al*. 2005). Wild-type *Brassica* plants volatilized more Se than the other perennial plants, and the addition of organic amendments has been shown to contribute to a greater volatilization of Se by genetically engineered *Brassica* plants. The mean rate of Se volatilization by 14 wetland species after the equilibration period was 400 μg Se $m^{-2}d^{-1}$; however, authors claimed that the rate of Se volatilization continued to increase over the entire research period eventually reaching 500 μg Se $m^{-2}d^{-1}$ (Ye *et al*. 2003).

The essentiality of Se to plants remains unclear, even though there is some evidence for its positive effect on many plant processes. On the other hand, Se is toxic to plants and other biota when it is present at high concentrations. Further research is needed to establish the essentiality of Se for higher plants. Bioaccumulation of Se can create toxicity problems for wildlife. Se can be effectively removed from the soil and water by phytoextraction and volatilization.

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