

Review Article**Selenium in the Soil-Plant Environment: A Review**Uttam Saha¹, Abioye Fayiga^{2, *}, Leticia Sonon¹¹Agricultural and Environmental Services Laboratories, University of Georgia Cooperative Extension, Athens, Georgia, USA²Freelancer, Ibadan, Nigeria**Email address:**

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Abstract: Selenium (Se) exhibits a “double-edged” behavior in animal and human nutrition. It is a micronutrient required in low concentrations by animals and humans, but toxic at high concentrations. Selenium deficiency has been associated with cancer and other health problems. Selenium requirements are commonly met through soils and plants such as wheat, rice, vegetables and maize in many countries. Selenium concentration in the soil generally ranges from 0.01-2.0 mg kg⁻¹ but seleniferous soils usually contain more than 5 mg kg⁻¹. Seleniferous soils have been reported in Ireland, China, India and USA. Weathering of parent rocks and atmospheric deposition of volcanic plumes are natural processes increasing Se levels in the environment. Anthropogenic sources of Se include irrigation, fertilizer use, sewage sludge and farmyard manure applications, coal combustion and crude oil processing, mining, smelting and waste incineration. Mobility of Se in the soil-plant system largely depends on its speciation and bioavailability in soil which is controlled by pH and redox potential. Plant uptake of Se varies with plant species and Se bioavailability in the soil. The uptake, translocation, transformation, metabolism, and functions of Se within the plant are further discussed in the paper. The release of Se in soils and subsequent uptake by plants has implications for meeting Se requirements in animals and humans.

Keywords: Selenium, Speciation, Metabolism, Transformations, Antioxidative Activity, Plant Uptake

1. Introduction

Selenium (Se) is a metalloid which plays important roles in plants, animals and human growth and development. It's an essential micronutrient for animals and humans but not yet established as an essential nutrient for plants. It has been estimated that approximately 3 billion people are Se deficient which makes them susceptible to health problems such as Keshan disease, Kashin-Beck disease and cancer [1, 2]. The deficiency of Se has also been associated with occurrence of diseases such as HIV/AIDS in sub Saharan Africa [3]. Selenium deficiency has been reported in countries such as Canada, China, Scotland, Japan, Finland, New Zealand, Spain, and USA [2, 4-7]. A daily Se requirement of 55µg is recommended for adults by the National Academy of Science in the United States [8]. Daily intake of Se must not be greater than 400 µg in humans because Se can be toxic at high

concentrations [9].

The Se requirements for animal and human nutrition can be met by ensuring adequate Se in crops frequently consumed in diet. Increasing the Se content of food crops such as wheat, cereals and vegetables could increase the Se intake of whole populations [10]. Selenium status of populations is dependent on the Se content of soils and food crops produced thereon [11]. Selenium concentrations in the soil largely determines its concentration in food and the Se levels in human populations [12]. The low Se intake by the Brazilian population was linked with the consumption of foods with low Se concentrations which is also a result of low Se concentrations of most Brazilian agricultural soils [13-14]. Low Se levels in about 67% of agricultural soils of China are responsible for a wide-spread Se deficiency in the Chinese population [15-16]. A study in Algeria showed that the concentration of Se in wheat was a reflection of Se levels in regional soils [17]. Low Se concentrations in wheat in Belgium were also associated with

low Se levels of Belgian soils [18]. Fertilization of the low Se soils of Finland increased plant yields and Se levels in the whole food chain from soil to plants, animals and humans [2].

Selenium is one of the few trace elements whose presence and introduction into the food chain is desirable and acceptable, howbeit, at low concentrations. This may be because the numerous positive effects of Se in plants could be far outweighed by its adverse effects at high concentration. Selenium levels are in increasing trend in the environment due to different natural and anthropogenic activities. However, the actual environmental impact of Se depends on its concentration and speciation. The speciation of Se is also greatly influenced by factors such as redox potential and pH which controls its mobility in the soil [19]. Selenium is transformed from one chemical form to another within the plant-soil environment [20]. The transformations of Se within the plant explain its metabolism and mechanisms for coping with high concentrations. The speciation, bioavailability, metabolism, biotransformation and functions of Se in the plant-soil environment have implications for animal and human health. There are numerous review papers on Se but most are focused on human and animal nutrition without detailed information about plant and soil processes involved in meeting nutritional requirement of Se in animal and human. This paper presents an up-to-date review of the available literature on Se in the soil-plant environment. It discusses the sources of Se in the environment; speciation, mobility and bioavailability of Se in the soil; uptake, translocation, metabolism and transformation of Se in plant.

2. Sources of Selenium in the Environment

2.1. Natural Sources

2.1.1. Parent Rocks

Weathering of parent rocks is one of the fundamental processes involved in soil formation. Parent rocks are composed of various trace elements, most of which exist as ores and are released into the soil by physical and chemical weathering. Trace element concentrations in the soil have been found to be related to the parent material [21]. For example, a past study has shown that the average contents of Se in soil profile increased with the Se contents in parent material [22]. Selenium concentrations in the soil vary with type of parent material from which it is formed. Jurassic siltstones and sandstones are generally low in Se, whereas high concentrations occur in areas underlain by Permian carbonaceous strata [23]. Igneous rocks usually have low concentrations of Se while Se concentrations of metamorphic and sedimentary rocks are variable [24]. Selenium tends to be lower in intrusive igneous rocks due to its volatile nature but abundant in extrusive rocks such as basalt and ash [25]. High concentrations of Se are present in clay rich sedimentary rocks such as mudstones and shales because of the affinity of Se for clay minerals [26-27].

It has been reported that soils overlying black shales and

slates have Se concentration twice that from nearby limestone and phyllites in Korea [28]. A small amount of Se is incorporated into the lattice of pyrite (Iron sulfide, FeS₂) by isomorphous substitution in carbonaceous siliceous rocks and carbonaceous shales (stone coal). The weathering of Se sulfides results in the formation of native Se. There are three types of native Se in these rocks based on their origin; first type occurs in carbonaceous-siliceous rocks and the tiny Se crystals formed during tectonic activity; the second is the Se found in the weathered carbonaceous siliceous rocks and highly carbonaceous mudstones; and the third, crystalline Se within the near-surface of abandoned stone coal spoils, which was derived from natural combustion of stone coal [29].

2.1.2. Volcanic Activity

Volcanoes are a major source of inorganic Se because they emit high amounts of Se into the atmosphere [30]. It has been estimated that about 400-1200 tons of Se are released into the atmosphere by volcanic activity every year [31]. Tens of kilograms of Se are volatilized daily in the magmatic plumbing system by a single volcano [32]. Based on high temperature thermodynamic models, volcanic plumes probably consists of H₂Se, elemental Se and SeO₂ which are transformed to selenite and selenate by oxidation and cooling processes (Figure 1) in the atmosphere [30, 33].

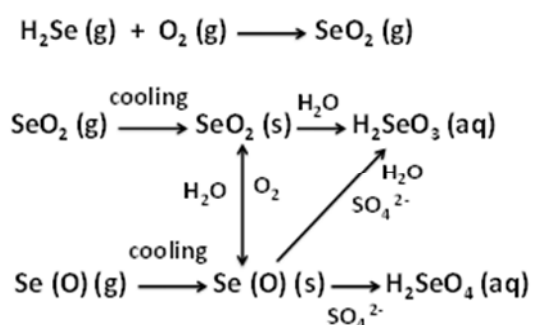


Figure 1. Selenium reactions in volcanic plumes.

A large amount (1.6-4.4 t/a) of Se in volcanic plumes is deposited locally in nearby areas [34]. Deposition of Se from volcanic emissions in local soils is responsible for high Se concentrations reported in soils around volcanoes [35]. For example, high Se concentrations (6-15 mg/kg) occur in Hawaii soils around volcanoes, though the world average is 0.4 mg/kg [36]. These volcanic soils have variable colloidal surfaces, high anion fixing power, and low mobility of Se due to the presence of iron and aluminum oxides [36-37]. However, the mobility of Se may increase in volcanic soils after acid rainfall which may occur due to the interaction between volcanic gases and water vapor in atmosphere [38]. A past study showed that acid rain mobilized Se within volcanic soils which could lead to leaching of Se to aquifers [39]. The presence of other anions such as sulfate in acid rain can increase mobility of Se due to competition for adsorption on exchange sites in the soil since both S and Se are chemical analogs of each other and both are members of group VI on the periodic table with similar chemical properties [40].

2.2. Anthropogenic Sources

2.2.1. Agriculture

Agricultural activities that increase Se loading in the soil include irrigation, phosphate fertilizers, application of sewage sludge and farmyard manure (Figure 2). There are two ways irrigation may impact Se levels in the environment; first, by increasing dissolution of Se from underlying minerals rich in Se and secondly, by increasing Se loadings when soil is irrigated with Se rich water. It has been shown that irrigation of agricultural lands overlying Se rich rocks mobilizes Se which leads to high Se concentrations in subsurface drainage especially in semiarid regions [41-42]. Selenium is readily mobilized to groundwater and surface water by rainwater or irrigation of selenium rich soils and bedrock [43-44]. Dissolved nitrate has been found to inhibit reduction of Se in groundwater which leads to high concentrations of Se in groundwater [44-45]. Se enriched water is sometimes used for irrigation of farmlands which could lead to Se enrichment of soils. Irrigation of agricultural lands with Se enriched groundwater has led to enrichment of topsoils with Se in Northwest India [46-47].

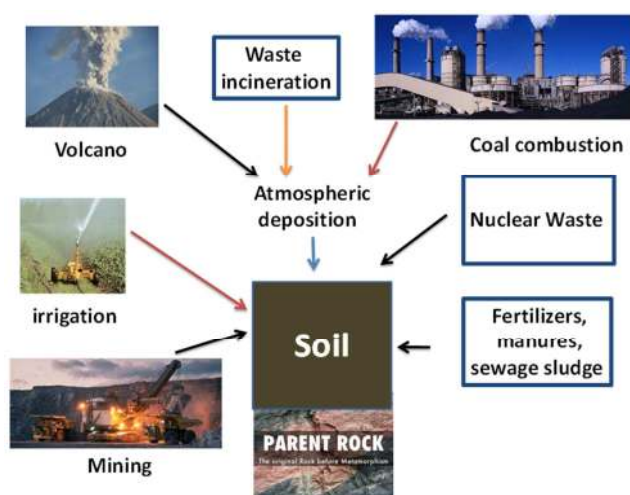


Figure 2. Some Sources of Selenium in the Environment.

Long term application of organic and inorganic fertilizers can also lead to an increase of Se in agricultural soils [48]. A recent study has reported that Se content of various inorganic fertilizers sold in Germany ranges from 0.81 to 7.3 mg kg⁻¹, while P fertilizers and phosphate rock contain 4.4 to 12.2 mg kg⁻¹ [49]. A past study has also reported that application of phosphate fertilizers increased plant available Se in soils from 0.14 to 0.57 mg kg⁻¹ and total Se in soils from 1.6 to 3.33 mg kg⁻¹ [50]. Selenium in finished P fertilizers probably originates from their raw materials, phosphate rocks, since Se concentrations ranging between 2 and 9 mg kg⁻¹ have been reported for phosphate rocks deposits from around the world [51]. Thus, long-term application of P fertilizers may lead to Se enrichment in the soil.

Application of sewage sludge as fertilizer may also have implications on soil Se since sewage sludge has higher concentrations of Se than compost and commercial fertilizers

[52]. Even though Se concentrations in sewage are relatively low compared with other trace elements or heavy metals, it has the potential to increase Se concentrations in soil and crop when used as organic fertilizer. In a greenhouse study, application of commercially processed sludge and incinerated sludge ash increased total Se content in soil [53]. In another study, sludge addition to a previously untreated garden soil increased the total Se concentration 2.5 times after the initial application and 3 times after the second year of application [52]. Total soil Se increased ten times after 8 to 10 yrs of composted Los Angeles sewage sludge applications to land [54]. Recently, the suitability of sewage sludge for cultivation of sugar beet and wheat was tested. Even though, sewage sludge increased Se concentrations in the soil, it was still within acceptable limits. However, Se concentrations in the sugar beets and wheat grown in sewage sludge were above standard limits [55].

Animal manure contains high concentrations of Se because Se is often added as supplements in animal feeds to meet requirements. Hence, application of animal manure may increase Se levels in the soil. [56] reported that application of farmyard manure (cattle manure) increased the Se concentrations of soils and plant uptake of Se in spring barley plants. Cattle manure has also been shown to reduce adsorption of Se in the soil thereby increasing its mobility and availability in the soil [57]. This was attributed to the presence of low molecular weight organic acids in the manure which can compete with Se oxyanions for sorption sites in the soil.

2.2.2. Industrial Processes

Some industrial processes and waste may contribute to increased Se concentrations in the environment. Industrial activities such as fossil fuel combustion, mining, smelting, industrial waste disposal and nuclear fuel processing may increase Se levels in the environment. Fossil fuel is defined as a natural fuel formed in the geological past from the remains of living organisms and includes petroleum, coal and natural gas. Crude oil produced from geological formations containing seleniferous marine shale often contain high levels of selenium which ends up being concentrated into the wastewater during the refining process [58-60].

[61] measured Se in crude oil and wastewater at different stages of the refining process. According to them, the first step of the refining process called desalting releases Se in low concentrations from crude oil. The second step of the refining process, atmospheric distillation, favors the formation and partition of elemental Se within suspended matter and sediments which act as a sink for selenium. During the third and fourth steps, hydrotreatment and catalytic cracking, high concentrations of Se are released into the process stream waters. The last step, sour water treatment showed that the processed oil still contained elevated concentrations of Se. Selenium concentrations range from 0.02 to 2 mg kg⁻¹ Se in crude oil from Germany [62]. However, coal contains more Se (3 mg kg⁻¹ Se) than petroleum (0.2 mg kg⁻¹ Se) in the US [63].

Fossil fuel combustion emits large amounts of Se into the atmosphere because fossil fuel such as coal and crude oil

contains significant amounts of Se [26]. For example, when coal undergoes combustion, Se is transported over long distances because it's preferentially partitioned to the submicron-sized particles [26]. The combustion of coal to produce electricity resulted in an enrichment of Se by as much as 1250 times [64]. Rainwater further exacerbates the release of Se into the environment as it percolates through storage piles of coal [64]. The processing of coal also produces a coal ash slurry stream that can pick up over 1000 ug SeL⁻¹ within 15 min [65]. Thus, the waste generated from the coal industry has very high concentrations of Se.

Industrial waste may also be a source of Se in the environment. Selenium is a component of many electronics and computer accessories such as capacitors, printer/toner products and photocopiers [66]. Selenium is also used in the manufacture of ceramics, glass, photoelectric cells, pigments, rectifiers, semiconductors, and steel as well as used in photography, pharmaceutical production, and rubber vulcanizing [67]. The disposal of waste from these products in landfills and waste incinerators may increase the levels of Se in the environment. Leachates containing high concentrations of Se may be generated at landfills where these products are discarded [64].

Selenium-79 (⁷⁹Se₃₄) is a radioisotope of Se present in spent nuclear fuel and the wastes resulting from reprocessing this fuel. Hence, the radioactive selenium isotope ⁷⁹Se can be a component of radioactive waste produced in nuclear power plants which can pollute the environment. The accidental release of ⁷⁹Se in the environment from power plants or nuclear waste repositories, can lead to transfer of ⁷⁹Se into soils, plants and food chain [68].

The processing of metal ores containing Se also releases Se into the environment. Smelting of copper, nickel and zinc ores volatilizes Se into the atmosphere which settles as atmospheric deposition on soil, plant and water bodies [69]. Elevated concentrations of Se (up to 200 mgkg⁻¹) were reported in soils around a nickel refinery at Clydach in the

Lower Swansea Valley, UK [70]. The soil pollution with Se in these areas was attributed to industrial pollution that occurred 80 yrs ago.

3. Selenium in Soil

3.1. Speciation, Transformation and Mobility of Selenium in Soils

3.1.1. Speciation of Selenium

Selenium can exist in different organic and inorganic forms with different oxidation numbers such as -2, 0, +4, +6 (Table 1). Elemental Se (0) is relatively inert and present as the solid phase or in colloidal forms. Selenite (IV) is present as SeO₃²⁻ while selenate (VI) is present as SeO₄²⁻ in the aqueous phase. Selenide (Se (-II)) occurs in minerals under reducing conditions or in organic and biochemical compounds [71]. Elemental Se (0) is formed either through biotic or abiotic reduction of selenate or selenite [72-74]. The mobility of Se in the soil depends on its speciation and chemical form [19]. Under oxic conditions, selenate and selenite are more mobile while under anoxic conditions, elemental Se and selenide are thermodynamically stable [75-76]. Selenite is more strongly adsorbed than selenate in soils and sediments while selenate is highly soluble and mobile under highly oxic conditions [75, 77-78]. Though, Se usually exists in the inorganic forms in the soil, Se in Dutch agricultural soils and grasslands was predominantly in the organic forms accounting for 78 and 87% of total Se [79]. It has also been shown that Se in agricultural soils was mainly associated to soil organic carbon [80]. It can either exist as selenopyrite or as Se fixed to organic matter in unweathered shale [81]. The predominance of organic Se in the soil may be due to the fact that the oxidation of selenopyrite is faster than oxidation of organic matter which results into higher proportion of organic matter bound to Se as shales weather into soils [44, 82-83].

Table 1. Speciation of Selenium.

Name	Chemical formulae	Oxidation number	Where found	Eh range
Elemental selenium	Se	0	Abundant in acidic, low redox soils	< -200 mV
Selenide	Se ²⁻	-2	Abundant in acidic, low redox soils	< -200 mV
Selenite	SeO ₃ ²⁻	+4	Predominant in acidic, medium redox soils	0 to 200 mV
Selenate	SeO ₄ ²⁻	+6	Predominant in alkaline, high redox soils	500 mV

Eh-redox potential

3.1.2 Effect of Soil PH and Redox Potential

The chemical forms of Se present in soils and sediments are dependent on the oxidation-reduction potential (Eh) and pH of the soil [26]. In alkaline soils, selenate predominates over selenite while in acidic soils, selenite supersedes selenate [84]. The adsorption of selenate and selenite on solid phases in the soil decreases with increasing soil pH [85]. This may be due to the fact there are more positive surface charges in acidic soils to adsorb the negatively charged Se oxyanions compared to alkaline soils with predominantly negative surface charges. However, elemental Se, selenides and selenium sulphide salts

are abundant in reducing, acidic and organic rich environments [86]. Redox reactions are important chemical processes which determine the mobility and transformation of Se in the environment. At high redox potential, selenate (+6) is the dominant species in solution (pe + pH > 15.0); selenite (+4) species are predominant in the medium redox range (pe + pH < 15.0 and >7.5) while selenide (-2) is the major species at low redox (pe + pH < 7.5) [87]. A past study showed that selenate (+6) was the predominant soluble Se species under oxidized condition (Eh = 500 mV), selenite (+4) was predominant for the Eh range from 0 to 200 mV, while elemental Se and metal selenides were predominant under more reduced conditions

(Eh <-200 mV) [88]. Under wetland conditions Se(VI) can be reduced to Se(IV) which is also reduced to elemental Se(0). Formation of elemental Se (0) or metal selenide (-2) at low redox potential reduces Se solubility. Under oxidized and moderately reducing conditions, Se solubility and mobility is controlled by adsorption than by precipitation and dissolution reactions [89]. Selenium is more mobile under oxidizing conditions than under reducing conditions because of the formation of insoluble and immobile elemental Se and selenide under reducing conditions [90]. On the contrary, a recent study has shown that mobilization of Se was high under low Eh in deltaic soils [91]. This was attributed to remobilization of immobilized Se under reducing conditions.

3.1.3. Microbial Transformations in Waters, Sediments and Soils

Selenium can be transformed biologically via reduction, oxidation, methylation, and demethylation reactions mediated by microorganisms such as bacteria and fungi [19, 92-93]. Microorganisms can reduce selenate and selenite to elemental Se directly or by changing pH and redox potential (Eh) [76, 94]. It has been reported that microbial activities increased Se retention in the soil thereby decreasing Se mobility in the soil [76]. This may be due to microbial reduction of selenate and selenite in the soil to elemental Se or selenide which are less mobile than other Se species. The transformation of selenite and selenate to elemental Se can occur in both aerobic and anaerobic environments [19]. Bacteria can make use of both selenite and selenate as terminal electron acceptors during respiration under anaerobic conditions. The reduction of selenite to insoluble elemental Se by the Proteobacteria, *Anaeromyxobacter dehalogenans*, is seen as a detoxification mechanism since selenite is more plant available than elemental Se [95]. Inorganic and organic forms of Se can also be transformed into volatile methylated organic compounds by bacteria, fungi and roots [96]. Example of volatile methylated Se compounds include dimethyl selenide, dimethyl diselenide, dimethylselenone, and methane selenol [97]. However, dimethyl selenide is the main compound produced by microbial and plant respiration [98]. *Pseudomonas aeruginosa*, isolated from the rhizosphere of crop plants growing in seleniferous soils in India, was able to reduce 53 and 21% of sodium selenite and selenate to elemental selenium, and volatilize 4.7 and 5.1%, respectively within 72-hour duration [99].

3.2. Total Selenium and Plant Bioavailable Selenium in Soils

Selenium is an essential micronutrient for animals and humans that is primarily supplied via forages and food crops. Selenium in forages and food crops is dependent on Se content of the soil in areas where there is no other supplementation [84]. The normal range for total Se in the soil is 0.01-2 mg kg⁻¹ but in order to meet the requirements for human nutrition, soils have been classified (Table 2) as deficient (<0.125 mg kg⁻¹), marginal (0.125-0.175 mg kg⁻¹), moderate to high (0.175-3 mg kg⁻¹) and excessive (>3mg kg⁻¹) based on total Se

in soil [100-101]. Soils with a high concentration of Se (seleniferous soils) contain more than 5 mg kg⁻¹ and have been associated with animal poisoning [102]. Seleniferous soils have been reported in Ireland [103], USA [26], China [104], and India [105]. Bioavailable Se provides a more accurate estimate of plant available Se and ecotoxicology of Se [106]. In soils with low Se concentrations (<2 mg kg⁻¹), the relationship between total and bioavailable selenium was roughly linear whereas in soils with total Se more than 2 mg kg⁻¹, there was no relationship between total and bioavailable selenium [27]. Water soluble Se is a better indicator of Se deficiency or toxicity than total Se in the soil [107]. Total concentrations do not give an adequate representation of environmental impact of Se because of its partitioning on solid phases within the soil.

Sequential extractions with different solvents are used to separate operationally defined fractions of Se in the soil. A past study has shown that Fe- and Mn oxide-bound Se was the dominant fraction in upland soil, while organic matter-bound Se was dominant in paddy soil in seleniferous soils of China cultivated with maize plants [108]. This may be due to lower decomposition of organic matter in the paddy soil. The study further showed that Se uptake in maize plants were significantly correlated with organic matter bound Se in upland soil, but not with Fe/Mn oxide-bound Se. This suggests that organic matter bound Se is more plant available than the oxide bound fraction. Past studies have also reported a relationship between Se and organic matter in the soil [109-110]. Other adsorbents of Se in the soil include clay, iron and aluminum oxides and manganese oxides. [111] showed that Se availability in two silt loam soils was higher than in the silty clay soil and the Se distribution in soil was controlled by soil properties, such as pH, oxide, clay, and calcium carbonate (CaCO₃) contents.

Table 2. Soil Classification for Human Se Requirements.

Se Concentration (mg kg ⁻¹)	Classification	Reference
<0.125	Deficient	Tan et al., 1989
0.125-0.175	Marginal	Tan et al., 1989
0.175-3	Moderate - High	Tan et al., 1989
>3	Excessive	Tan et al., 1989
>5	Seleniferous	Oldfield, 1999

Several studies have reported more plant uptake of Se with addition of selenate than selenite in the soil [112-113]. Selenate is more bioavailable in the soil than selenite because selenite is more strongly adsorbed on soil colloidal surfaces than selenate. The strong adsorption of selenite is attributed to the formation of inner sphere surface complexes while selenate is adsorbed via weak electrostatic forces [85, 114]. It has been reported that phytosiderophores (in root exudates), which are highly effective iron chelating agents, can desorb selenite from ferrihydrite (iron mineral) [115]. The availability of Se in the soil also depends on soil management and soil properties. In a recent study, uncultivated soils had higher adsorption of Se while cultivated soils had higher Se mobility/availability probably due to the presence of competing anions such as phosphates applied into the soil as fertilizers [116]. It has been reported that the addition

of phosphate may lead to desorption of adsorbed Se in the soil [117].

4. Selenium in Plants

4.1. Plant Uptake of Selenium

Plants can be classified into three main groups based on the Se concentrations in their tissues; non accumulators, accumulators and hyperaccumulators. Non Se accumulating plants rarely contain greater than 50 mg kg⁻¹ Se and often have less than 5 mg kg⁻¹Se in their tissues [26]. Accumulators can be further divided into two groups; primary and secondary accumulators. Primary Se accumulators grow well on soils with high available Se concentrations and contain up to 1000 mg kg⁻¹Se [26, 118]. Secondary Se accumulators are plant species such as *Atriplex*, *Castilleja*, *Grindelia*, and *Gutierrezia*, which do not contain more than 50 to 100 mg Se kg⁻¹ [26]. Se hyperaccumulators contain between 1000-15000 mg kg⁻¹Se and examples include *Astragalus bisulcatus* and *Stanleya pinnata* [119-120].

Hyperaccumulating plants are commonly used for removal of contaminants from contaminated soils, sediments and water in a process referred to as 'phytoremediation'. Three different types of phytoremediation technologies have been used for Se; phytoextraction, phytovolatilization and rhizofiltration. In phytoextraction, Se is removed by plants from contaminated soils while in phytovolatilization, Se is converted to gaseous forms which are consequently removed from the soil plant system while rhizofiltration utilizes plant roots to remove Se

from contaminated water. Plants such as Indian mustard (*Brassica juncea* Czern. L.) and canola (*Brassica napus* cv. *Westar*) have been used for the phytoextraction of contaminated soils in on farm trials. Canola removed nearly all extractable selenium from farm plots after 90 days while Indian mustard reduced the total soil Se content by almost 50% at a depth of up to 75 cm after 3 years [121-122]. Plants with high rates of Se volatilization includes rice and hybrid poplars which can be used in phytovolatilization [123-124]. Several aquatic plants have been used for the rhizofiltration of Se from wastewater in constructed wetland soils [125].

Examples of non Se accumulators are grains and grasses, even though, grasses have higher concentrations of selenium than leguminous plants [26, 126]. The maximum concentration of Se in vegetables such as turnips, peas, beans, carrots, tomatoes, beets, potatoes and cucumbers is 6000 mg kg⁻¹, even when they are grown on soil with high Se concentrations [118]. The concentration of Se in fruits is generally low while they are high in Brazil nuts [12]. Se uptake in rice plants (*Oryza sativa*) is relatively lower than in maize (*Zea mays*), wheat (*Triticum aestivum*), and rapeseed (*Brassica napus*) [127]. This was attributed to the dominance of selenite in anaerobic conditions under which rice is grown. Selenite has low translocation and uptake in plants. Table 3 shows Se uptake in non Se accumulators and hyperaccumulators. Wheat and Indian mustard accumulated Se when grown in seleniferous soils with high bioavailable Se in the soil [128].

Table 3. Selenium uptake in some plants.

Name of plant	Se in plant (mg kg ⁻¹)			Se in soil (mg kg ⁻¹)	Reference
	Roots	Leaves	Seed/grain		
Tobacco	16.7-58.6	2.6-37.3	NA	2.2-22.2	Han et al., 2013
Maize	0.31-12.3	0.16-36.1	0.05-14.5	4.11-33.1	Wang et al., 2012
Rice	NA	0.48-1.95	1.38-3.33	0.13-2.85	Sharma et al., 2014
Cabbage	NA	0.04-0.2	NA	0.21-4.08	Huang et al., 2009
Lettuce	NA	1.59-3.95	NA	NA	Wakim et al., 2010
Onion	NA	1.29	NA	NA	Wakim et al., 2010
Chickpeas	NA	NA	0.79	NA	Wakim et al., 2010
Wheat	196	387	NA	13.1	Eiche et al., 2015
Indian mustard	186	931	NA	6.8	Eiche et al., 2015
Hyperaccumulators					
<i>Astragalus bisulcatus</i>	NA	NA	5750	NA	Freeman et al., 2012
<i>Astragalus bisulcatus</i>	65	436	NA	NA	Alford et al., 2012
<i>Astragalus praelongus</i>	1281	2925	NA	NA	Alford et al., 2012
<i>Stanleya pinnata</i>	NA	NA	1329	NA	Freeman et al., 2012

NA-not available

Plant uptake of Se can be reduced or enhanced by soil chemical, biological or physical properties. In a field experiment in the UK, irrigation increased wheat grain yield but soil compaction and irrigation reduced plant uptake and grain Se concentrations [129]. The presence of competing ions can also affect Se uptake in plants. For example, addition of arsenic stimulated Se uptake at low levels of Se (<2.5 mg L⁻¹) and suppressed Se uptake at high levels of Se (>2.5 mg L⁻¹) in roots of Chinese brake fern (*Pteris vittata*). Addition of Se suppressed arsenic uptake in the same plant (*Pteris vittata*)

indicating an antagonistic relationship between As and Se [130].

Arbuscular mycorrhizal (AM) colonization reduced plant uptake of selenium in ryegrass but had no effect on the distribution and translocation of selenium [131]. This is not in agreement with an earlier study that reported a 10-fold increase in Se uptake in garlic due to AM colonization [132]. This inconsistency may be due to differences in the form of Se supplied to the plant. [133] showed that the effect of AM inoculation on plant uptake of Se depends on the chemical

form of Se applied to the soil. In their study, when Se (IV) was added to the soil, AM inoculation reduced Se concentration in both maize roots and shoots, but when Se (VI) was added, AM inoculation enhanced Se concentration in shoots but did not affect Se concentration in roots.

4.2. Transport Within Plants

Due to similarities, selenate and sulfate anions both compete for plant uptake and are both probably taken up via a sulfate transporter in the root plasma membrane while selenite uptake occurs via phosphate transporters [134-135]. Previously, it was believed that selenite absorption by plant roots occurs via passive transport while absorption of selenate and organic forms of Se occurs via active transport [134-135]. However, recent studies have shown that selenite transport can also occur via active transport [137-138].

Selenium is transported to the leaves first before accumulation in the seed or fruits in Se accumulator plants while in non Se accumulators, Se accumulation in the roots is the same as that of the seeds or grains [139]. However, Se concentration in seeds of the Se hyperaccumulator, *Astragalus bisulcatus*, was much higher (Table 3) than the roots and leaves while the seeds had a higher concentration than the roots in *Stanley pinnata* [140]. A recent study has shown that the Se contents in roots and stems of soybeans were higher than those in the fruits during the whole soybean growing period [141]. This agrees with the findings of a past study on 17 vegetables which reported that Se concentrations of edible parts were lower than non edible parts [142].

[143] explained that selenite is transported by symplastic mechanism whereas selenate is transported by the apoplastic mechanism in onions. Selenite absorbed into the cytoplasm through the apoplastic mechanism is transformed into selenide, whereas selenate movement involves an inert transport via the microcapillaries in the root peripheral tissues toward the other parts without the infiltration of selenium compounds inside the cell and without being transformed into other chemical forms. This may explain why selenate is more easily transported than other forms of Se within the plant system [144]. Selenite usually accumulates in the plant roots because it is not easily translocated within the plant and is converted easily into organic forms. Past studies have reported lower Se concentrations in leaves of onion and broccoli plants exposed to selenite compared with selenate [145-146]. A recent study has also reported that addition of selenate to the soil increased rice grain Se concentrations more than selenite [14].

4.3. Selenium Biotransformation in the Soil-Plant Environment

There are evidences for the transformation of Se in plants after exposure to Se either in soil or hydroponic studies. In a recent study, alfalfa, lentil and soybean were grown in hydroponic solutions with selenate and selenite for three weeks. Results showed that even though, selenate was the main form of Se in the plants after harvest, there were also significant concentrations of selenomethionine (SeMet) with

low concentrations of selenocysteine (SeCys) in the shoots and roots of the plants. This indicates a transformation of the supplied inorganic Se forms to organic Se forms in the plants with a larger proportion converted to SeMet. The concentration of SeMet was three times higher than selenite in lentil plants though soybean plants had the highest SeMet concentrations [20]. Selenocysteine can be further transformed into other organic species such as SeMet, methylselenocysteine (SeMeCys), and methylselenomethionine (MeSeMet) [147].



The conversion of SeCys to other organic species is thought to be a detoxification mechanism because it prevents the incorporation of Se into proteins [148]. High concentrations of the methylated organic Se species, SeMeCys, were present in the young leaves of the Se hyperaccumulator, *Astragalus bisulcatus*, suggesting that this might be a detoxification mechanism in the hyperaccumulator [149].

Similar results were obtained from a study on wheat and mustard plants growing on seleniferous soils. Although inorganic forms of Se was the dominant fraction in the soil, only organic Se species (SeMet) were detected in wheat grains suggesting a complete transformation of the inorganic species to organic species in the grains. Methylated species of Se (DMeSe, SeMeCys) were present in all plant parts, except in the leaves of wheat. The study also showed that mustard has the ability to methylate Se to SeMeCys or DMeSe [128]. The conversion of Se to organic forms by both wheat and mustard plants may be a detoxification mechanism for adapting to the seleniferous soil on which they were growing. The SeMet and SeMeCys can be further converted into volatile selenide species (Figure 3.) (dimethylselenide (DMeSe) or dimethyldiselenide (DMeDSe)) in plants [150]. The only process that removes Se from the whole soil-plant system is volatilization [128]. Hence, the transformation of non-volatile Se into volatile Se may be a detoxification process for seleniferous soils and Se hyperaccumulators [151].

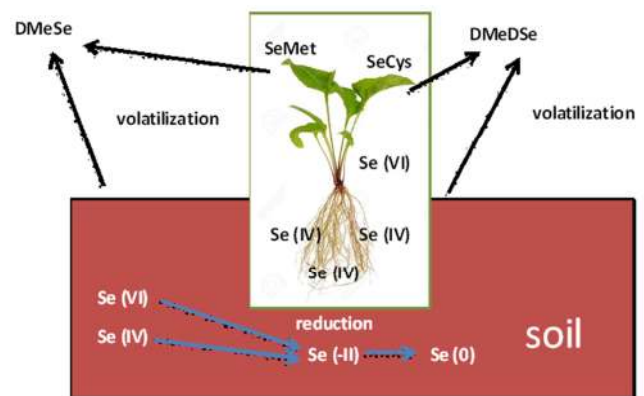


Figure 3. Transformations of Selenium in the Soil Plant Environment. [SeMet- selenomethionine; SeCys- selenocysteine; DMeSe- dimethylselenide; DMeDSe- dimethyldiselenide].

4.4. Selenium Metabolism in Plants

Selenate is more available in the soil for plant uptake because it is weakly adsorbed to the solid phase by electrostatic attraction. Most plants take up selenate unintentionally because of its similarity to sulfate and then metabolize it via the sulfur (S) assimilation pathway in the chloroplast [139]. Selenate is first activated by ATP sulfurylase-adenosine 5'-phosphosélénate (APSE) and then reduced by adenosine 5'-phosphosulfate reductase into selenite [118] which is also reduced to selenide (II), in a process involving reduced glutathione [152].

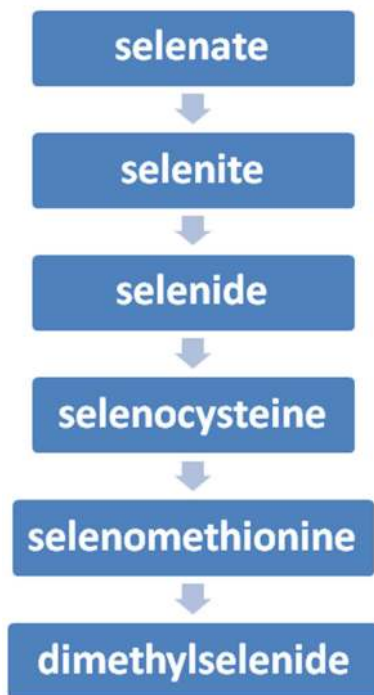


Figure 4a. Metabolism of selenium in non accumulators.

Metabolic processes and end products of Se metabolism depend on the accumulating capacity of the plant [118]. In non Se accumulating plants, five steps lead to the formation of dimethylselenide (DMSE) while in Se accumulating plants, the end product is dimethyl diselenide (DMDSe) [153-154]. The five steps of Se metabolism in non Se accumulating plants (Figure 4a) are first, reduction of selenate to selenite; second, reduction of selenite to selenide; third, conversion of selenide to selenocysteine; fourth, conversion of selenocysteine to selenomethionine; fifth, conversion of selenomethionine to dimethylselenide [153]. The transformation of selenite into selenide and into volatile species such as dimethylselenide in plants is probably a detoxification mechanism for the toxic Se species [143].

In Se accumulating plants, there are four steps (Figure 4b) involved in the metabolism of Se; first, reduction of selenate to selenite; second, reduction of selenite to selenide; third, conversion of selenide to selenocysteine, fourth, selenocysteine is bi-methylated to form dimethyl diselenide (DMDSe) [153-154]. The volatilization of dimethyl diselenide

occurs in the Se hyperaccumulator *Asparagus racemosus* and might be a detoxification pathway in the plant [135]. Much of the Se in non-accumulating species is found in the form of protein bound SeMet while in the Se accumulator plants, Se is mostly found in non-protein forms like Se-methylselenocysteine [26]. The exclusion of Se from protein in Se accumulators may be a detoxification mechanism because Se incorporation into proteins could result in alteration of the protein structure, inactivation of the protein, and eventual poisoning of the plant [155-156]. A past study reported that Se was converted to SeMet in cereals [157]. More than a decade later, it was reported that SeMet can be further metabolised to Se-adenosyl-SeMet, which is also converted to Se-methylselenocysteine and c-glutamyl-Se-methylselenocysteine [143]. Recently, it was shown that inorganic Se (mixture of selenite and selenate) was converted to selenoaminoacids, such as SeCys and SeMet in alfalfa, soy and lentil plants grown in hydroponic medium [20].

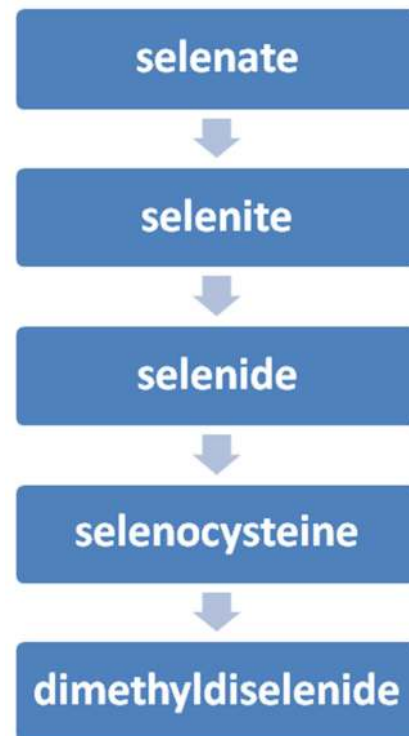


Figure 4b. Metabolism of selenium in accumulators.

5. The Functions of Selenium in Plants

5.1. Anti-oxidative and Pro-oxidative Effects

Plants produce reactive oxygen species (ROS) and free radicals under both biotic and abiotic stress. Reactive oxygen species (ROS) includes superoxide anion, singlet oxygen, hydroxyl free radical and hydrogen peroxide [158]. One major source of ROS in plants is the generation of oxygen in the chloroplast during photosynthesis. Mitochondria and peroxisomes are other sources of ROS in plants. When the production of ROS exceeds the ability of the plants to

eliminate them, plants undergo oxidative stress; excess ROS can damage cellular lipids, proteins or DNA, inhibit signal transduction pathways, and disturb normal cellular function [159]. Selenium has been shown to increase tolerance of plants against oxidative stress by decreasing lipid peroxidation and increasing the activity of anti-oxidative enzymes when applied in small concentrations [160-161].

Plants possess both enzymatic and non-enzymatic antioxidant defense system which is able to protect plant cells from oxidative damage by quenching ROS. Enzymatic anti-oxidative enzymes include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione peroxidase (GPX), guaiacol peroxidase (GOPX) and glutathione-S-transferase (GST). Non-enzymatic antioxidants include ascorbic acid, glutathione, (GSH), phenolic compounds, alkaloids, non-protein amino acids and a-tocopherols [162]. SOD removes the superoxide radicals by catalyzing its dismutation while other enzymatic antioxidants such as CAT and APX are involved in the removal of hydrogen peroxide. Ascorbic acid scavenges the superoxide radicals while GSH is a potential scavenger of singlet oxygen, hydroxyl radicals and hydrogen peroxide. Proline is a scavenger of singlet oxygen and hydroxyl radicals while carotenoids and tocopherols are involved with scavenging of singlet oxygen [162].

Conversely, high concentrations of Se can also lead to oxidative stress in plants in which case Se acts as a pro-oxidant [163]. [164] suggested that this may be due to an imbalance in the levels of GSH, thiols, ferredoxins and NADPH which control assimilation of Se at high concentrations. They explained that if these substances are not present in sufficient amounts to assimilate high concentrations of Se, it could lead to oxidative stress.

However, selenite-induced high levels of hydrogen peroxide has been observed in the leaf discs of *Senecio scandens* L which did not happen with selenate when applied at the same dosage [165]. This implies that the pro-oxidative effects of Se may be dependent on its chemical form or speciation. Three mechanisms have been proposed for the toxic effects of Se in plants; first, generation of superoxide radicals, secondly, substitution of Se for S in proteins and thirdly, inhibition of methylation [166].

5.2. Reducing Adverse Effects of Environmental Stresses

Exposure of plants to environmental stressors like drought, cold, flooding, salinity, and heavy metals leads to the production of reactive oxygen species (ROS) which are harmful to plant cells [164]. Selenium plays a protective and regulatory role in ensuring that the plant is able to quench the free radicals and harmful species induced by these environmental stressors. This is important as plants are subjected to extreme climatic events such as droughts and flooding as well as extreme temperatures due to global

warming and resulting climate change.

Droughts have a devastating effect on crop production while extreme temperatures have also been shown to reduce crop yield [167]. The positive effect of Se on plants exposed to drought stress has been widely reported in literature. The addition of 1.0, 2.0, and 3.0 mg Se kg⁻¹ significantly increased root activity, proline content, peroxidase, and catalase activities, carotenoids content, chlorophyll content, and reduced malondialdehyde (MDA) content of wheat seedlings exposed to drought stress [168]. In another study with wheat under drought stress, foliar application of Se significantly lowered osmotic potential resulting in increased turgor, enhanced transpiration rate, improved accumulation of total soluble sugars and free amino acids, and increased antioxidant activity which increased the grain yield by 24% [169]. Selenium also induced pollen germination in olive trees under drought stress [170].

Plants growing in temperate and tropical environments are exposed to cold and heat stress respectively. Selenium has been shown to alleviate stress in wheat seedlings exposed to cold stress by increasing antioxidant enzyme activity which reduced the production of free radicals, reduced lipid peroxidation, and increased chlorophyll content [171]. When sorghum was grown under high-temperature stress, application of Se reduced membrane damage by increasing antioxidant defense which resulted in higher grain yield [172]. This may be due to the ability of Se to repair damage caused by UV radiation which increased photosynthetic efficiency [173-174]. Selenium was also able to alleviate damage caused by UV-B to wheat seedlings by increasing antioxidant enzyme activity [175]. Increasing anti-oxidant enzyme activities leads to elimination of harmful ROS induced by UV radiation.

High heat may lead to salinity in dry areas which may inhibit plant growth by reducing the ability of plants to absorb water due to the osmotic potential. This is a serious problem in arid and semi-arid regions of the world. Salinity inhibits biochemical processes such as photosynthesis in plants which affects plant growth and development [176]. The exposure of salt-stressed rapeseed seedlings to Se led to a reduction in the levels of hydrogen peroxide (H₂O₂) and MDA (lipid peroxidation) [177]. Similarly, application of Se at 1, 2.5, 5 mg kg⁻¹ alleviated damage in salt-stressed mungbeans resulting in enhanced pod number and seed yield per plant. Application of Se at 1 mg kg⁻¹ improved their productive function of mungbeans as indicated by pollen germination, viability and tube growth; increased activity of anti-oxidative enzymes such as CAT, APX, GR and GPX; and increased sucrose concentration [178].

The adverse effects of heavy metals and metalloids on plant growth are well documented in literature [179-181]. Selenium has been reported to reduce metal or metalloid stress through its antioxidative activities. It has been shown that Se can alleviate the toxic effects of As in mungbean plants and rice seedlings by reducing arsenic uptake and increasing antioxidant activity [182-183]. The addition of Se to medium reversed a Cd-induced decrease in fresh biomass yield of rape seedlings and prevented changes in the DNA methylation

pattern [184]. Selenium alleviated Al-induced oxidative stress in ryegrass roots through the enhancement of the spontaneous dismutation of superoxide radicals. However, above 2 μM , Se induced stress in plants grown with or without Al [185]. Two mechanisms proposed for the alleviation of heavy metal stress by Se are the competition of Se and metal ions for adsorption on specific sites located on the membrane surface and attachment of Se anions to metal cations present in the soil or plant tissues [186]. [158] explained that Se probably alleviates heavy metal stress by direct and indirect action on protein-enzymes localized in chloroplasts, promoting the functioning of protein transporters and ensuring optimal conditions necessary for membrane integrity.

5.3. Growth Promoting Effect

The first study that showed the growth promoting effect of Se was demonstrated when Indian mustard was exposed to 0.5 mg kg^{-1} selenite [187]. Since then some other studies have reported that Se facilitated the growth of lettuce, pumpkin, ryegrass and soybeans [188-191]. In potato plants, application of Se increased tuber yields than control plants; Se also increased carbohydrate accumulation, processing and storage quality of potato tubers [192-193]. In another study, foliar and soil application of Se increased the yield of common buckwheat in China [16]. Similarly, the application of Se increased grain yield of rice probably by increasing the photosynthesis rate, the intercellular CO_2 concentration, and the transpiration efficiency [15]. Selenium was able to rebuild the structure of chloroplast, thylakoids, and stroma in cadmium-treated rape seedlings [194]. There was also an increase in chloroplast size, fatty acid unsaturation, and fluidity of the cell membrane in cadmium-treated rape seedlings after the addition of low concentration of Se [194]. This indicates that the growth promoting effect of Se may be dependent on solution concentrations. The addition of low concentration of Se increased Se concentrations in lettuce shoots up to 1.5 mg kg^{-1} but yields dropped when exposed to high concentrations [195].

5.4. Senescence Delay

Senescence, the process of aging in plants, can be either stress induced or developmental. Senescence is the final stage of leaf development which occurs in response to internal and external signals [196]. Leaf senescence plays important roles in plant development by recycling nutrients to vigorously growing organs [197-198]. The concentrations of 58 elements including major, minor and rare earth elements increased during the course of beech leaf senescence and decomposition in a Swedish beech forest [199]. The role of Se in plant senescence is very clear from numerous studies conducted on several crops. The effect of Se on lettuce senescence was studied in pot experiments at different Se concentrations [160]. At low Se concentrations, Se reduced senescence-induced lipid peroxidation and enhanced the growth of senescent lettuce by 14%. Total tocopherols (vitamin E) decreased during senescence, but Se counteracted their decrease and

improved the nutritive value of lettuce. Selenium increased the activity of GPX and SOD activity in young and senescing plants [160]. Similar results were obtained with soybeans where Se delayed senescence by increasing activities of SOD and GPX [190].

In faba bean plants, Se ameliorated adverse effects of induced senescence by increasing the activity of antioxidant enzymes (CAT and peroxidase) which increased other biochemical parameters such as chlorophyll content, total protein, free amino acids, and photosynthetic efficiency [200]. Flowering was delayed for 10 d in rice plants growing in seleniferous soils in India probably because of the high concentration of Se [127]. Selenium also delayed senescence in garlic seedlings by alleviating the peroxide stress and increasing activities of GPX and CAT [201]. An addition of Se at 1 mg L^{-1} delayed the onset of fruit ripening in tomato plants grown in hydroponics [202]. This implies that Se can be used to increase the shelf life of tomato plants and reduce post-harvest losses. Recently, Se delayed leaf senescence induced by N deficiency, leaf detachment and plant development in oilseed rape plants. Se increased total carbohydrate and protein pools which decreased with leaf age; increased nonphotochemical quenching that was declining in old leaves; maintained the green color of Se-treated detached leaves while untreated leaves became chlorotic and necrotic [203].

5.5. Reduced Herbivory

Plants employ several tactics for defending against herbivory, ranging from physical structures to chemical defenses that are produced within the plant [204]. One of the potential benefits of selenium accumulation in Se hyperaccumulators is the protection of plants from a wide variety of herbivores, including vertebrates and invertebrates based on both deterrence and toxicity [205-206]. Selenium protected Se-hyperaccumulating plants from herbivory by arthropods and arthropod species than comparable non-hyperaccumulators growing in the same seleniferous habitat [207]. Selenium also protected two Se-hyperaccumulator species, *Astragalus bisulcatus* and *S. pinnata*, from cell-disrupting herbivores such as western flower thrips and two-spotted spider mites [119]. Even Se-rich neighbors of hyperaccumulators experienced less herbivory and caused higher grasshopper Se accumulation and mortality [208]. Herbivory by birds and aphids was reduced on Se-treated radish plants, indicating a potential reproductive advantage for the plant [209].

6. Research Gaps

A lot of work has been done on effect of redox and pH on Se mobility in the soil but more work is needed to explain factors that may contribute to high Se mobility in reducing environments. This is necessary because a recent study has reported high mobility of Se under reducing conditions which is contrary to results of past studies on Se. There are conflicting reports on effects of microbial activities on Se mobility in the soil. More work is needed to clarify the

interactions of redox, pH and microbial activities in the soil. Field trials based on microbial reduction and volatilization of Se can be applied in bioremediation of Se contaminated soils to further validate this pathway as a detoxification mechanism. Research is needed to reduce the toxicity of seleniferous soils where its currently found to reduce adverse effects on animal and human health. Few countries have done a nationwide research on Se status of its population to determine deficiency or sufficiency. More research is needed especially in developing countries to ensure that countries deficient in Se are supplemented like the case of Finland. This is important because of the effect of Se on public health. A database of Se status of soils, food crops, animals, and human population in all nations can be organized by the World Health Organization (WHO). Numerous scientists have investigated the antioxidative activities of Se but very few have studied the prooxidative effects of Se. More research is needed in this area to elucidate the triggers, pathway and mechanism involved.

7. Conclusion

It is essential to understand Se chemistry in soils and plants because Se deficiency in animals and humans has been associated with low concentrations in soils and plants. Some important sources of Se in the soil-plant environment include parent material, volcanic activity, agriculture and industrial processes. However, the mobility of Se in the soil-plant environment depends on its speciation which is greatly influenced by pH and redox potential. Transformations of Se can be both biotic and abiotic during reactions such as reduction, methylation, and demethylation in the soil-plant environment. Even though the metabolism of Se in plants depends on the amount of Se in plant tissues, the end products are two different organic volatile Se species. Conversion of inorganic Se species to organic volatile Se species is a detoxification mechanism which removes Se completely from the soil-plant environment. Although Se is not an essential element for plants, it plays several important roles such as increasing activities of antioxidants, alleviating external stresses, promoting growth, delaying senescence and provides defense against herbivores.

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