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Approaches for Amelioration of Selenium Deficiencies/toxicities in Crop Plants

***G.S. Sanghera*[1*]*, Prabhjot S. Sanghera*[2] *and Rajan Bhatt*[3]**
[1]*Principal Scientist (PBG), PAU, Regional Research Station, Kapurthala, 144601, (Punjab), India.*
[2] *Research Scholar, PAU, College of Agriculture, Ludhiana, 144004, (Punjab), India.*
[3]*Senior Scientist (Soils), PAU, Regional Research Station, Kapurthala, 144601, (Punjab), India.*

(Corresponding author: G.S. Sanghera)*
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ABSTRACT: Selenium (Se) is a widely dispersed trace element that has both positive and harmful effects on people, animals, and plants. The structure of the parental material and the activities that follow soil formation affect the availability of Se in the soil. The amount of Se in the environment is influenced by human activities. Despite the fact that plants are the primary source of selenium in animal and human diets, the significance of selenium in plants is still controversial. Under both ideal and unfavourable climatic conditions, a low Se concentration can be helpful to plant growth, development, and ecophysiology. However, excess Se on the contrary, has harmful consequences, especially in Se sensitive plants, since it alters protein structure and function and causes oxidative/nitrosative stress, which affects numerous metabolic processes. Se hyper accumulators, on the other hand, absorb and tolerate extremely high levels of Se and might be utilized to remediate, i.e., remove, transfer, stabilise, and/or detoxify Se-contaminants in the soil and groundwater. As a result, Se-hyperaccumulators have the potential to play a pivotal role in addressing the global problem of Se insufficiency and toxicity. Knowledge of Se absorption and metabolism, however, is required for successful phytoremediation to remove this element. Furthermore, for successful phytoremediation of a Se-contaminated region, selecting the most efficient Se-accumulating species is critical. The focus of this review is on Se toxicity in plants and the environment, as well as phytoremediation.

Keywords: Selenium, phytoremedation, toxicity, metabolism, oxidative stress.

INTRODUCTION

Selenium (Se) is a trace element found in almost all organisms. It is documented to be both advantageous and poisonous, with the line between these two dual impacts being very thin and varying between plant species. Se at low doses protects the plants from a variety of abiotic stresses such as cold, drought, desiccation, and mental stress. The physicochemical characteristics of Se and sulfur (S) are very close, which results in non-specific binding of Se rather than S. These substitutions can disrupt the cell metabolism and alter the protein structures, causing toxicity (Bodnar *et al.* 2012). It is rarely found in elemental form in nature and is only present in a few minerals. The speciation of Se is controlled by physical, chemical, and biological factors, with the pH and redox state of the environment playing a major role (Peng *et al.* 2017; Chauhan *et al.* 2019). Because of the variability of physiological and biochemical nature, the absorption and metabolism of Se vary substantially in different soil and plant systems (Sobolev *et al.*, 2020; Trippe *et al.* 2020; Wrobel *et al.* 2020). Selenium is a byproduct of metallurgical engineering and is a prominent pollutant in the environment (Mehdi *et al.* 2013; Kumar and Prasad 2020). A breakthrough in selenium (Se) research (Schwartz and Foltz 1957) by demonstrating that adding Se to fodder reduced muscular degeneration and hepatic cirrhosis in rats (Rayman and Hoffmann 2000). Later Reeves *et al.* 2009 suggested that a lack of Se in the human diet is the primary cause of development retardation, poor bone metabolism, and thyroid function problems. For example, certain parts of the world, Italy, Egypt, Turkey, and Nepal, are Se-inadequate, while some are Se-toxic as a result of natural and anthropogenic processes (Zhu *et al.* 2009, Etteieb *et al.* 2020). Humans and animals are thus harmed by both Se insufficiency and Se toxicity (Kumar and Prasad 2020). The World Health Organization (WHO) recommends a Se intake of 50–55 g per day in the human diet (WHO 2009, Malagoli *et al.* 2015, Wu *et al.* 2015). In humans, Se deficiency occurs when dietary intake is less than 40 g per day, while chronic poisoning occurs when intake surpasses 400 g per day (Winkel *et al.* 2012). It is required in cattle at a level of 0.05–0.10 mg kg1 dry forage, however, the hazardous amount in animal feed is 2–5 mg kg1 dry forage (Wu *et al.* 2015). Crops are one of the key sources of Se for most species, hence Se-rich crops could help to prevent Se deficiency

(Schiavon *et al.* 2017; Ye *et al.* 2020). Its supplementation at a modest dose can help plants cope with a variety of abiotic challenges by enhancing growth and development (Hasanuzzaman *et al.* 2020). The uptake and translocation of heavy metals/metalloids were limited when Se was applied to plant roots. Selenium toxicity, also known as selenosis, can manifest itself in two ways: the formation of seleno-proteins and the induction of oxidative stress. In Arabidopsis, for example, a Se concentration of 2 mg kg-^{1} dry weight (DW) is hazardous and causes a 10% loss in biomass without causing apparent symptoms (Kabata-Pendias, 2010). Organic-rich soils on the lowest concentration of Se that resulted in a substantial reduction in cucumber (Cucumis sativus) biomass was 20µ M for SeO_3^{2-} and 80 µM for SeO_4^{2-}(22). SeO_3^{2-} (50 or 100 M) also inhibited vegetative growth and hampered reproductive development. It has also been discovered to interact with other harmful metals and metalloids, speeding up the toxic effects. Many plants efficiently absorb Se, and phytoremediation techniques such as phytoextraction, phytovolatilization, and rhizofiltration could be used to remove Se from contaminated areas (Feng *et al*. 2013, Ponton *et al*. 2020). Brassica napus and *Brassica juncea*, for example, have been employed for Se phytoextraction because of their high levels of accumulation (Banuelos *et al.* 1997). In the case of Se volatilization, to volatilize the Se from the contaminated environment, *Astragalus bisulcatus* (Se hyper accumulator) was used (Yasin *et al.* 2015). Among many plant species, *B. oleracea* and *A. bisulcatus* have the highest Se volatilization, followed by *Medicago sativa* and *Solanum lycopersicum*. Using genetically altered plants to remove metals has made tremendous progress in recent decades (Ozyigit *et al.* 2020). Although there has been a lot of interest in Se's dual role in plants, the detailed mechanism of Se toxicity and its treatment has yet to be established. In this article, attempt has been made to explore recent developments associated in Se toxicity/deficiency in crop plants in relation to environment in light of contemporary research and experimental findings to suggest mitigation strategies with the prospects for Se phytoremediation processes.

Understanding the pathway of Selenium. Se was first considered a hazardous element after its discovery by Swedish chemist J.J. Berzelius in 1817. Meanwhile, it has been discovered in all four compartments of the Earth, namely the atmosphere, hydrosphere, geosphere, and biosphere, and is the 67th most abundant element on the planet (Charya 2017). Industrial operations (pharmaceuticals manufacture, ceramics factories, glass industry) are the most common anthropogenic sources of Se. Physical (soil and sediment sorption effects), chemical (pH, redox potential, organic matter content, and competitive ions) and biological (bacterial strain reduction, alkylation, dealkylation, and oxidation of Se) mechanisms determined Se biogeochemistry (reactivity, mobility, and bioavailability) in nature and are responsible for its elemental speciation(Peng *et al.* 2017; Chauhan *et al*. 2019). Biological mechanism like catalysis induced by microorganisms regulating Se speciation is a crucial biological process that influences Se mobility and bioavailability (Vriens *et al.* 2014, Nancharaiah *et al.* 2015). The key transformation mechanisms for the speciation of Se are assimilatory and dissimilatory reduction, alkylation, dealkylation, and oxidation. Bioremediation often involves microbial reduction of SeO_4^{2-} and SeO_3^{2-} to Se. SeO might then be further lowered to Se/Se2, which is stable under decreasing conditions. These Se/Se2 may, however, react with metals (zinc, Zn, and cadmium, Cd), creating very insoluble metal-Se/Se^{2-} and decreasing Se availability (Mal *et al.* 2016). Selenium occurs in different environmental compartments in different forms (Fig. 1). Se levels in soils range from m 0.1 to 0.7 mg kg^{-1} globally, with clay soils containing 0.8–2 mg kg^{-1}. The amount of Se in the soil is determined by its texture, organic matter content, and rainfall (El-Ramady *et al.* 2015). Clay soils, for example, contain significantly more Se than coarse soils (Hartikainen *et al.* 2005). In highland areas like Finland, Scotland, and Sweden, volcanic soils and igneous rocks have extremely low Se content. Sedimentary rocks, on the other hand, are high in Se and tend to be mobile in arid-climate rocks, where it can affect animals.

Sediments, soil wastes, and sub-soils containing selenium reach groundwater. Furthermore, excessive use of Se-enriched fertilizers raises Se levels in groundwater in Western European nations such as Belgium and France (0.12 g L^{-1} and 2.4–40 g L^{-1}, respectively), as well as some Se-enriched west areas of Punjab, India (341 g L^{-1}) (Mehdi *et al.* 2013; Winkel *et al.* 2012). It is also released into the atmosphere as a result of human actions (such as the burning of papers, tyres, and fossil fuels) and natural processes (such as wildfires and soil erosion). Selenious acid is generated when SeO_2 is converted to a gas (H_2SeO_3). Se levels in the atmosphere range from 1 to 10 ng m3 and are far lower than those found in water and soil (Mehdi *et al*. 2013).

Toxic Effects of Selenium on Plant Growth and Development

The toxicity of selenium is determined by the plant's species, age, and the amount of selenium available (Table 1). Se toxicity affects young plants significantly more than adult plants, and SeO_3^{2-} is more phytotoxic than SeO_4^{2-}. Only known case of SeO_4^{2-} toxicity in Font colour to black *Chlamydomonas reinhardtii*.

Effects on Physiological Processes. Selenium deficiency in plants has a deleterious impact on various physiological and biochemical processes. One of the most serious side effects is a decrease in chlorophyll biosynthesis, which leads to chlorosis.

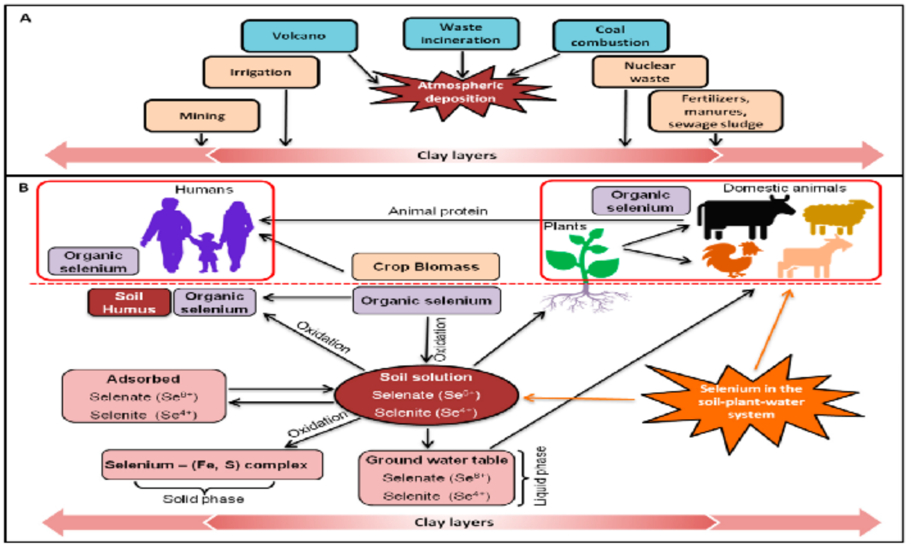

Fig. 1. Occurrence of selenium in different environmental compartments and its different forms.

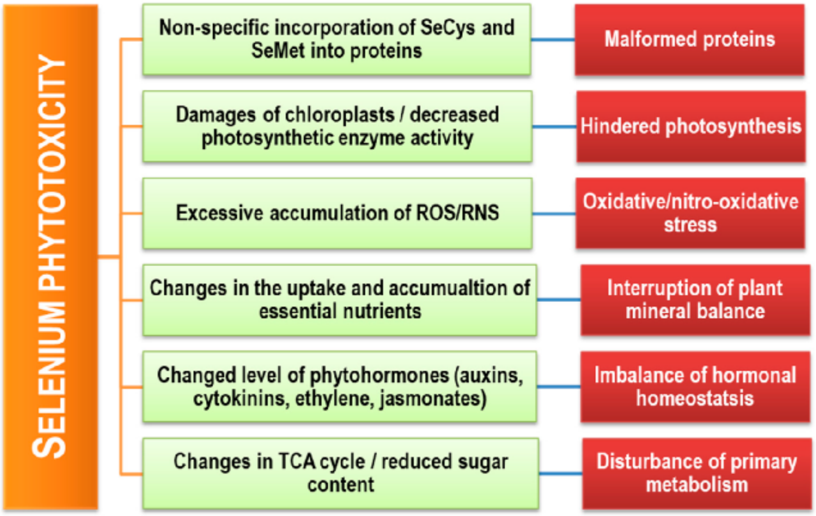

Fig. 2. A schematic representation of the causes and consequences of Se toxicity in plants.

Saffaryazdi *et al.* (2012) demonstrated that SeO32– >1 mg L1 in the nutritional solution lowered chlorophyll content in spinach, which could be connected to lipid peroxidation mediated by lipoxygenase (LOX), changes in antioxidant enzyme activity, and/or negatively impacted synthesis and activity of porphobilinogen synthetase. In *Chlamydomonas reinhardtii*, both SeO_3^{2-} and SeO_4^{2-} (4.5 0.2 M) exhibited various toxic symptoms, including ultrastructural damage to appressed regions of the chloroplast, which disrupted the photosynthetic electron chain, inhibited photosynthetic electron transport, and slowed photosynthesis (Geoffroy *et al.* 2007). PSII and PSI system activity were lower in wheat subjected to 100 µM SeO_4^{2-} (Labanowska *et al.* 2012). *Stanleya albescens* was also subjected to the free amino acid selenocystathionine, as well as SeCys and SeO_4^{2-} (20 M), and displayed reduced growth, necrosis and chlorosis, as well as the photosynthetic problem (Freeman *et al.* 2010). Phytotoxic Seismic induced growth retardation could be the result of mineral dietary imbalances. Se impacts various biochemical events and physiological processes by changing mineral nutrient intake, accumulation, and transport (growth, photosynthesis, respiration, gas exchange, water uptake, phloem unloading, and activation of protease inhibitor genes). Furthermore, Se has the potential to minimise or increase the toxicity of necessary or harmful elements by reducing or worsening the stress caused by these elements. In SeO_4^{2-} treated *Brassica oleracea* L., Kopsell *et al.* (2000) found decreased foliar concentrations of B, Fe, and P, as well as increased S and K.P and Ca content in maize treated with SeO_3^{2-} (5–100 M) rose, whereas K content dropped

(Hawrylak-Nowak-III et,al 2008). SeO_4^{2-} treated tall fescue and white clover, on the other hand, showed Ca bioconcentration and an opposing P reduction (Wu *et al*. 1992). Furthermore, upon Se exposure, a synergic effect of Se and Fe was discovered, with Fe concentration increasing in tandem with the expanding tissue Se concentration. In a separate investigation utilising lettuce, greater shoot Se concentrations were found, but lower macronutrient accumulation, N, P, K, Ca, Mg, and S in lettuce leaves, as well as growth reduction symptoms.

Table 1: Toxic effects of selenium in different plant species.

Plant Species	Se Form and Dosage	Detrimental Effect on Growth and Physiology	Reference
Raphanus sativus, Helianthus annuus, Medicago sativa	SeO_3^{2-}, 5 or 10 mg Se L^{-1}	Growth inhibition.	(Moreno *et al.* 2018)
Pisum sativum	SeO_3^{2-}; 50 or 100 µM	Altered vegetative and reproductive development. Shoot and root length and FW decreased. chlorophyll a, chlorophyll b, chlorophyll a/b, total chlorophyll, total carotenoids content decreased.	(Lehotai, *et al.* 2016)
Cucumis sativus	SeO_4^{2-}; 80 µM SeO_3^{2-}; 20 µM	Decreased shoot root growth, biomass and leaf area. Impaired nutrient content. Reduced photosynthetic pigments accumulation and chlorophyll fluorescence. Increased lipid peroxidation.	(Hawrylak-Nowak 2015)
Oryza sativa	SeO_3^{2-}; 100 g Se ha^{-1}	Increased Se content in root and shoot. Reduced photosynthesis and transpiration rate, and intercellular (CO_2). PSII quantum yield is impaired and diminished potential photosynthetic capacity. Reduced grain yield.	(Zhang *et al.* 2014)
Triticum aestivum	SeO_4^{2-}; 100 µM	Reduction of PSII and PSI activities.	(Labanowska *et al.* 2012)
Spinacia oleracea	SeO_3^{2-}; 6 mg L^{-1}	Increased Se accumulation. Declined growth parameters, e.g., shoot and root length, and FW and DW. Increased Na and Ca content, but decreased K content.	(Saffaryazdi *et al.* 2012)
Brassica juncea	SeO_4^{2-}; 80 µM	Augmented Se and S concentration in different floral parts. Increased floral Se accumulation and impaired pollen germination.	(Quinn *et al.* 2011)
Hordeum vulgare	SeO_4^{2-}; 2, 4, 8, or 16 ppm	Decreased plant height. Reduced chlorophyll concentrations.	(Akbulut *et al.* 2010)
Zea mays	SeO_3^{2-}; 50 and 100 µmol L^{-1}	Decreased DW accumulation. The root tolerance index severely decreased.	(Hawrylak-Nowak (2008)
Z. mays	SeO_4^{2-} or Selenomethionine ($C_5H_{11}NO_2Se$); 100 µM	High Se accumulation in root and shoot. Reduction in root and shoot FW. Altered anthocyanin level. Reduced chlorophyll level.	(Hawrylak-Nowak lI 2008)

Fw: fresh weight, DW: dry weight

In a separate investigation utilizing lettuce, greater shoot Se concentrations were found, but lower macronutrient accumulation, N, P, K, Ca, Mg, and S in lettuce leaves, as well as growth reduction symptoms (Matraszek *et al.* 2009). In comparison to mesocotyls of maize exposed to selenite, treated or untreated with auxin (IAA), exhibited lower Mg content in the leaves and roots. Moreover, Se supplementation increased the shoot Fe content (Pazurkiewicz-Kocot 2008). Besides, in wheat shoots, SeO_4^{2-} elevated Cd bioaccumulation up to 50%, while Cd bioaccumulation increased up to 300% in pea roots by SeO_3^{2-} supply (Landberg *et al.* 1994). The usage of SeO_4^{2-} (50 mg Se L1) and iodide (100 mg L1) together reduced nitrate accumulation, increased flavonoid biosynthesis, increased B and Al accumulation, and decreased Sr and Cd bioconcentrations in *Brassica juncea* (Golubkina *et al.* 2018). It was found that SeO_3^{2-} (2–10 µM) in the rooting medium inhibited root elongation in wheat, which is further enhanced by $CaCl_2$, $MgCl_2$, $SrCl_2$

supplementation, along with pH reduction (Kinraide 2003). Moreover, these compounds raised the plasma membrane activity, enhancing Se uptake by roots (Bailey *et al.* 1995). Since high-affinity SeO$_4^{2-}$ transporters transport SeO$_4^{2-}$ across the cell membrane, there is strong evidence that SeO$_4^{2-}$ directly competes with SeO$_4^{2-}$ for absorption by plants, whereas PO$_4^{2-}$ transporters are involved in SeO$_3^{2-}$ transport (Li *et al.* 2008). As a result, applying SeO$_3^{2-}$ to lettuce shoots raised their foliar S concentration. SeO$_3^{2-}$ is easily converted into organic Se in roots after uptake, whereas SeO$_4^{2-}$ is swiftly translocated and either metabolised or stored in plastids via the S metabolic pathway (Schiavon *et al.* 2017; Gupta *et al.* 2017; White 2016). Same mechanism assimilates both SeO$_4^{2-}$ and SeO$_3^{2-}$ as their S analogues, resulting in Se inclusion in nearly all S metabolites. As a result, Se non-accumulators have more Se in their proteins than Se-accumulators (Hasanuzzaman *et al.* 2020). Small but significant alterations in the biological characteristics of Se-substituted proteins emerge from physicochemical differences between Se and S. Although the Se-Se link is longer and weaker than the S–S bond, it is more labile and modifies tertiary protein structure, resulting in enzyme catalytic failure. SeCys is more reactive than Cys due to its greater nucleophilicity, and replacing Cys with SeCys causes Se-Se bridges to form instead of S-S bridges, changing redox potential and enzyme kinetics. (Hondal *et al.* 2013). Various mechanisms have been proposed to explain Se-exacerbated oxidative stress and its detrimental consequences in plant cells.

Excessive Se causes overproduction of reactive oxygen species by inhibiting the antioxidant defense mechanism (ROS). Excess Se can produce reactive oxygen species (ROS) when it reacts directly with a variety of metabolites. Furthermore, in hazardous Se concentrations, altered chloroplast and mitochondrial processes cause an excess of ROS. Secondary nitrooxidative stress caused by selenium is caused by nitric oxide. Under Se exposure, increased lipoxygenase (LOX) activity produces peroxide radicals (LOO•) and inhibits the glyoxalase system, resulting in methylglyoxal (MG) toxicity and oxidative stress in different plants (Table 2). Selenium poisoning causes reactive and misshapen selenoproteins (SeCys/SeMet) to develop, altering the redox potential and distorting the kinetics of chloroplastic and mitochondrial enzymes (Sabbagh *et al*. 2012).

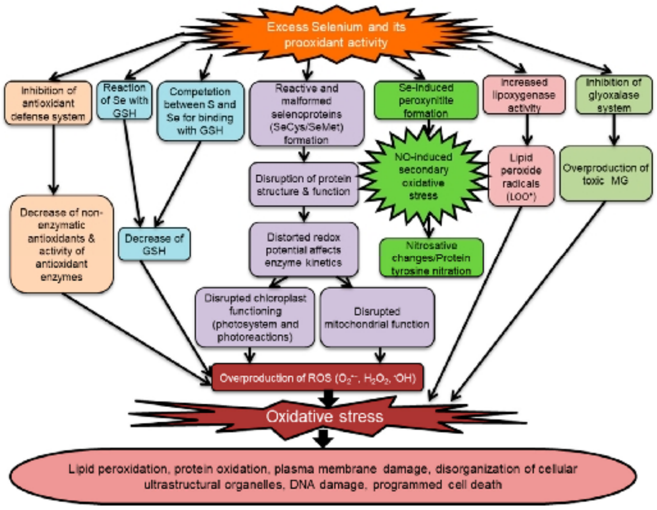

Fig. 3. Selenium-induced oxidative stress and consequent damage to the plant cell.

It also disrupted the ultrastructure and function of chloroplasts (photosystems and photoreactions) and mitochondrial activity, leading to ROS overproduction. The alternative oxidase pathway is activated by selenite-induced increased mitochondrial O^{2-} generation and decreased aconitase activity (Balk *et al.* 2011). In-plant cells, both SeO$_4^{2-}$ and SeO$_3^{2-}$ cause an excess of reactive oxygen species (ROS) and oxidative stress. According to studies, SeO$_3^{2-}$ interacts with GSH in vitro to generate O^{2-} (Spallholz 1994). Se acts as a prooxidant at high concentration. (Hartikainen *et al.* 2000) found an enhanced SOD activity and increased tocopherol content in ryegrass due to excess Se (>10 mg kg^{-1}), which indicated the prooxidative activity of Se. Excessive accumulation of toxic LOO was also observed by them, which α-tocopherol scavenged to produce LOOH, and subsequently converted to less toxic LOH by enhanced GPX activity. Approaches Amelioration of Selenium Toxicity. Se is among the most important sort of contaminant in the environment and plant system. To mitigate its toxicity several mechanisms/methods are taken into consideration. Some important approaches/strategies are suggestive and can be put into practice are described below in subsequent sections.

Phytoremediation for curing Se Toxicity. It often known as green biotechnology, is a process that uses a range of plant species to remove hazardous chemicals from a contaminated environment. Toxic components can also be readily removed by harvesting or volatilizing plants into less dangerous volatile forms. This is known to be more ecologically friendly and cost-effective than other methods. It has no effect on soil fertility, unlike some other technical enhancements. (Zhu *et al.* 2009; Schiavon *et al.* 2017). Almost all plants readily absorb Se, and this phenomenon, might be used to remove Se from polluted regions as well as for other purposes.

Table 2: Different form and concentration of Se-induced physiological (oxidative) stress in plants.

Plant Species	Form and Concentration of Se	Indicators of Oxidative Stress and Changes in Antioxidant Enzymes Activities under Se Exposure	References
Pisum sativum	SeO_3^{2-}; 50 or 100 µM	Increased H_2O_2 concentration in leaves and roots. Increased content of thiobarbituric acid reactive substances (TBARS). Altered GSH content, APX and CAT activities. Increased nitric oxide level in shoot and root. Nitric oxide- instilled nitrooxidative stress by increasing peroxynitrite formation, as well as tyrosine nitration.	(Lehotai *et al.* 2016)
Brassica rapa	SeO_3^{2-}; 0.03–0.46 mM	Increased endogenous total ROS, $O_2^{\bullet-}$, and enhanced lipid peroxidation. Loss of plasma membrane integrity in the roots.	(Chen *et al.* 2014)
Triticum aestivum	SeO_4^{2-}; 100 µM	Altered carbohydrates (soluble and starch) level. AsA and GSH contents were modified. Suppressed activities of SOD, APX, and GR. Higher generation of ROS. Augmented lipid peroxidation. Repressed PSII and PSI system activities. Modified redox status connected with Mn(II)/Mn(III), and semiquinone/quinone ratios.	(Łabanowska *et al.* 2012)
Vicia faba	SeO_4^{2-}; 6 µM	Elevated lipid peroxidation and total -SH (T-SH) content. Increased GPX activity. Decreased guaiacol peroxidase (GPOX) activity. Increased O2•− production in the roots. Cell membrane injury and reduced cell viability.	(Mroczek-Zdyrska *et al.* 2012)
Hordeum vulgare	SeO_4^{2-}; 4, 8 and 16 ppm	Increased membrane lipid peroxidation. Higher proline accumulation. Stimulated CAT, APX, GR, and glutathione-S-transferase (GST) activities.	(Akbult *et al.* 2010)

Table 3: List of selected plant species used for Se phytoremediation.

Plant Species	Family	References
Brassica oleracea var. *capitata*, *B. oleracea* var. *italica*, *B. oleracea* var. *botrytis*, *B. juncea*, *B. napus*, *Stanleya pinnata*	Brassicaceae	(Banuelos *et al.* 1997, 2000, 2015, Parker *et al.* 2003, Esringü *et al.* 2012)
Gaillardia aristata and *Calendula officinalis*	Asteraceae	(Barceló *et al.* 2011, Dhillon *et al.* 2017, Liu *et al.* 2018)
Astragalus bisulcatus	Fabaceae	(Bañuelos *et al.* 2015, Beath *et al.* 1939)
Arundo donax, *Triticum aestivum*, and *Oryza sativa*	Poaceae	(Yasin *et al.* 2015, Terry *et al.* 2000)
Eichchornia crassipes	Pontederiaceae	Carey *et al.* 2012)
Populus spp.	Salicaceae	(Pal *et al.* 2010)
Lemnoideae spp.	Lemnaceae	(Bañuelos *et al.* 1999, Zayed *et al.* 1998)
Hippuris vulgaris L.	Plantaginaceae	(Landesmam *et al.* 2010)
Typha latifolia	Typhaceae	(Carvalho *et al.* 2000)
Ipomoea purpurea	Convolvulaceae	(Jeke *et al.* 2015)
Azolla caroliniana	Salviniaceae	(Sabogal *et al.* 2007)
Pteris vittata	Pteridaceae	(Pilon-Smits *et al.* 1999 a)
Juncus xiphioides	Juncaceae	(Feng *et al.* 2012)
Bolboschoenus maritimus	Cyperaceae	(Feng *et al.* 2012)
Chara spp.	Characeae	(Pilon-Smits *et al.* 1999 b, Lin *et al.* 2002)
Corchorus capsularis	Malvaceae	(Dhillon *et al.* 2009)
Eucalyptus globulus	Myrtaceae	(Dhillon *et al.* 2008)

Plant species differ in their Se absorption and accumulation, as well as their production of volatile Se-compounds to prevent Se toxicity (Schiavon *et al.* 2017, White *et al.* 2007). Plants are classified into three types based on their ability to absorb, use, and accumulate Se (Se hyperaccumulators (accumulate ≥ 1000g Se g^{-1} DW), secondary Se accumulators (accumulate 100–1000g Se kg^{-1} DW), and non-accumulators (contain <100g Se g^{-1} DW). Selenium Hyperaccumulation. In 1930, a group of researchers led by Orville Beath discovered seleniferous hyperaccumulation and characterised indicator plant species growing on seleniferous soils. Se hyperaccumulators were found in 6 plant families, 14 genera, and 45 taxa (White, 2016). The Fabaceae family, *Astragalus* genus has been shown to contain 25 Se hyperaccumulating taxa. Others are from the Asteraceae) (genera *Oonopsis*, *Xylorhiza, and Symphyotrichum*) and Brassicaceae (species *Stanleya pinnata* and *S. bipinnata*) (El Mehdawi *et al.* 2015). Hyperaccumulators express more SO_4^{2-} transporters than secondary accumulators and non-accumulators, which explains why their tissues have higher Se levels. Additionally, hyperaccumulators' over expression of SO_4^{2-} transporters enables them to absorb and translocate Se to aboveground plant organs (Cabannes *et al.* 2011). Hyperaccumulators have a few distinguishing features that enable them flourish in Se-rich soils. These organisms can convert inorganic Se into non-protein organic Se, lowering the risk of oxidative stress (Van Hoewyk 2013). They can also prevent *Se-Cys* from being incorporated into proteins by converting it to Se0 through selenocysteine lyase activity (Van Hoewyk *et al.* 2005). To avoid Se poisoning, Se hyperaccumulators may sequester organic Se. In hyperaccumulator species, Se is considered to have a role in upregulating antioxidant defence, where enzymatic and non-enzymatic antioxidants, as well as phytohormones including *jasmonic acid* (JA), *salicylic acid* (SA), and *ethylene* (ET), play key roles in Se tolerance (Freeman *et al.* 2010, Hasanuzzaman *et al.* 2012, Malik *et al*. 2012). The processes of Se hyperaccumulation interest Se researchers. Hyperaccumulators may have developed independently in different taxonomic groupings, genera, and species under similar ecological and physiological selection mechanisms (Bañuelos *et al.* 2000, 2015; El Mehdawi *et al*. 2015, Van Hoewyk *et al.* 2005).

Phytoextraction. Phytoextraction entails harvesting plants for the removal of metals/metalloids from contaminated soil; this method is cost-effective and environmentally acceptable, but it is inefficient owing to the poor phytoavailability of metals in soils and the sluggish removal of metals/metalloids (Bañuelos *et al.* 2000, 2009; Bhargava *et al.* 2012). Se-hyperaccumulators comprise a wide range of plants that flourish in Se-contaminated soils, but their growth is limited, and their low biomass output leads to inadequate Se removal (Chaney 1983). Because of their great potential for accumulation, several Brassica crops including rapeseed and mustard have been discovered as phytoextractors of Se from contaminated areas. Chelating compounds such as EDDS, DTPA, and *ethylenediaminetetraacetic acid* (EDTA) are being investigated as a possible weapon to improve the availability of metal/metalloids for improving phytoextraction efficiency. On the other hand, Chelator-assisted phytoextraction may cause water pollution by increasing hazardous ion mobilisation and subsequent leaching (Robinson *et al.* 2003; Wu *et al.* 2007). The absorption and phytoaccumulation of Se may be affected by changes in soil physicochemical characteristics such as pH, organic carbon and chelators (Vamerali *et al.* 2014). Banuelos *et al.* (2000) found that Brassica plants took around 50% of the Se from the soil, whereas barley removed approximately 20%. Furthermore, (Johnsson, 1991) states that increasing organic amendments in the plough layer by 1.4 to 39% reduced Se levels in wheat seeds from 1350 to 150 g/kg. Later, (Dhillon *et al.* 2010) reported that the addition of chicken manure and sugarcane press might reduce the uptake of Se by 44–97%. As a result, phytoextraction attempts for diverse Se-contaminated soils should focus on the use of Se-enriched plant biomass that is not assisted by chelation.

Phytovolatilization. A hazardous form of Se may be converted by plants into less toxic molecules, such as volatile organic seleno-compounds. Phytovolatilization is the process by which plants absorb contaminants from the soil and release them in a volatile form (Limmer *et al.* 2016). Direct phytovolatilization is defined as the release of volatile organic components from stems and leaves, whereas indirect phytovolatilization is defined as the increase in volatile contaminant flow from contaminated soils caused by root activity (Limmer *et al.* 2016).

Beath *et al.* (1939) first reported Se volatilization by Se-hyperaccumulator (*A. bisulcatus*). Cabbage and *A. bisulcatus* are the plants that volatilize the most Se, followed by alfalfa and tomato (Duckart *et al*. 1992). Plants of the Brassicaceae family (cabbage and broccoli) have better volatilization capacity, according to Bañuelos *et al*. (2007); Terry and Zayed (1994). Se-hyperaccumulators' phytoremediation potential is limited by their sluggish development and low biomass output (Bañuelos *et al.* 2015). As a result, the combined impact of phytovolatilization and phytoextraction can enhance the effectiveness of phytoremediation by two to three times. Plant type, Se form, microbial group configuration, type of macrophytes, temperature, the presence of other elements in the growth media, microorganisms in the rhizosphere, and many other physiochemical parameters all influence selenium volatilization efficiency (Salhani *et al.* 2003, Terry and Zayed 1994; Lin *et al.* 2010). Higher temperature promotes selenium volatilization and boost plant metabolic processes (Salhani *et al.* 2003; Lin *et al.* 2010). As a result, field studies are still needed to investigate the impact of these variables on phytovolatilization efficiency.

Rhizofiltration. It is a phytoremediation technology that uses a plant's root system to absorb pollutants, mostly toxic metals, from the rhizosphere's surrounding solution, groundwater, surface water, and wastewater (Krishna *et al*. 2012). Short-term studies in aqueous solutions were used to investigate the suitability of several aquatic plants for Se rhizofiltration, including *Myriophyllum brasiliense*, *Potamogeton crispus*, *Juncus xiphioides*, *Typha latifolia*, *Ruppia maritima*, *Scirpus robustus*, and *Hydrilla verticillate* (Krishna *et al*. 2012; Ornes *et al.* 1991; Miranda *et al*. 2014; Nattrass *et al.*, 2019).

Cattail (*Typha angustifolia*) growing in wetlands was shown to remove 89 per cent and 46 per cent of Se applied as SeO_3^{2-} and SeO_4^{2-}, respectively (Salhani *et al.* 2003), whereas musk grass removed 70–75 per cent of added Se from the aquatic environment (Carey *et al.* 2012; Pal *et al.* 2010). Duckweed (*Lemna minor*), which is renowned for its inherent ability to collect selenium, eliminated 55–99 per cent of the supplied selenium (Miranda *et al.* 2014; Carvalho *et al.* 2001). Due to its abundance in wetlands, soft rush (*Juncus effusus* L.) can be used for Se rhizofiltration instead of cattail. Miranda *et al.* (2014) showed that the biomass of many aquatic plants has significant biofuel potential.

Biotechnological Approaches for Se Phytoremediation. Genetic Engineering for Se Phytoremediation is a modern technology utilized in Phyto-technologies and to increase plant abiotic stress tolerance (phytoremediation and biofortification). Recent advancements in omics methods have made it possible to effectively phyto-remediate Se by molecularly altering plants (Visioli *et al.* 2015). The principle is to change the gene expression in non-accumulators or secondary accumulators to target multiple pathways and processes for phytoremediation, or to transfer the traits into a slow-growing hyperaccumulator (Barceló *et al.* 2011). List of some candidate genes for the targeted Se-phytoremediation are depicted herewith (Table 4).

Table 4: Transgenic plants and the candidate genes for the targeted Se-phytoremediation.

Transgenic Species	Gene Transferred	Effects	Reference
Brassica juncea	Cystathionine-γ-synthase (CgS)	Increased Se volatilization	(Huysen *et al*. 2004)
A. thaliana	Selenocysteine lyase (SL)	Enhanced Se accumulation	(PilonM *et al.* 2003)
B. juncea	SL	Enhanced Se accumulation	(Garifullina *et al*. 2003)
A. thaliana	Selenocysteine methyltransferase (SMT)	Enhanced Se accumulation and volatilization	(LeDuc *et al*. 2004)
B. juncea	SMT	Enhanced Se accumulation and tolerance	(Ellis *et al.* 2004)
B. juncea	APS	Three-fold increased Se accumulation in leaves	(Bañuelos *et al.* 2005)
B. juncea	γ Glutamyl-cysteine synthetase (ECS)	Improved Se accumulation	(Bañuelos *et al.* 2005)
B. juncea	APS×SMT	Increased Se accumulation under both SeO42− and SeO32− exposure	(Bañuelos *et al.* 2007)
B. juncea	SL×SMT	Enhanced Se accumulation	(Bañuelos *et al.* 2007)

SeO_4^{2-} is reduced to SeO_3^{2-} by ATP sulfurylase (APS) after entering the root cell, which is the first step in assimilation of SeO_4^{2-} to organic Se. As a result, an attempt to overexpress APS from A was made. *B. thaliana* , *B. juncea*. As a result, the transgenic plants accumulated two to three times more Se than the unmodified plants, but the transformation did not affect the Se volatilization rate. The cystathionine-synthase (*CgS*) enzyme is responsible for converting *Se-Cys* to *Se-Met*, which is then transformed to volatile *DMe-Se* in the Se metabolism pathway. Plants, as previously stated, may absorb Se-amino acids and integrate them into proteins, resulting in Se toxicity. The enzyme selenocysteine methyltransferase (SMT) converts *Se-Cys* to *MeSe-Cys* to prevent *Se-Cys* from being incorporated into proteins. Taking this into account, an attempt to overexpress the SMT gene in *A. bisulcatus* , in both *B. juncea*, *A. thaliana* resulted in upregulation of Se accumulation and tolerance, as well as enhanced Se-volatilization, were observed in thaliana (LeDuc *et al.* 2004; Ellis *et al.* 2004). However, when exposed to SeO_3^{2-} rather than SeO_4^{2-}, these plants were more effective in Se volatilization. Therefore, an attempt to overexpress two enzymes (APS and SMT) showed approximately nine-fold higher Se-accumulation. The majority of the Se was *in MeSe-Cys* form and 8-fold higher than wild plants (LeDuc *et al.* 2006).

CONCLUSION

The causes of Se phytotoxicity, methods of Se-induced cell damage, and Se biogeochemistry and phytoremediation aspects were all reviewed in this study. Due to oxidative stress, altered and malformed protein structure, disrupted enzymatic function, interrupted biosynthesis and metabolism of carbohydrates, proteins, and other metabolites, distorted chloroplast, and mitochondrial ultrastructure and functioning, a high amount of Se has several negative and harmful effects on the plant. These negative impacts have a significant impact on plant growth, development, and overall yield. The adequacy and toxicity of selenium are separated by a narrow margin. As a result, both Se deficiency and toxicity are common worldwide, overlapping with soils that are poor and high in Se, respectively. Although several recent publications have revealed both good and negative impacts of Se, other elements of Se biological activity remain unknown, such as the essentiality of Se for plants and the selection of plants that develop better when exposed to Se. Furthermore, the effective Se concentrations that cause a favorable or negative influence on plant growth, development, and ecophysiology must be established. Furthermore, the processes that cause these impacts should be disclosed. It's also crucial to clarify the link between Se and S biogeochemistry and how it influences Se and S uptake in natural settings. Additionally, for effective phytoremediation of Se-polluted regions, plant tolerance to Se, remediation capacity, and Se detoxification systems must be improved. To lower the concentration of Se in contaminated soils, promising plant species for phytoremediation, phytoextraction, phytovolatilization, or rhizofiltration should be discovered. Furthermore, certain intriguing properties of Se hyperaccumulators must still be uncovered. For example, why and how these unique plant species differ in their ability to absorb and accumulate Se, the processes by which plants cause Se hyperaccumulation, the benefits and drawbacks of Se accumulation in plants, and so on. Notably, the creation of genetically altered transgenic Brassica plants has a high potential for removing Se at a faster pace, which will likely aid in the rapid remediation of Se from the contaminated environment.

To learn more about Se tolerance and toxicity, researchers should analyze the results of different genomic, biochemical, and genetic engineering investigations, as well as the overexpression of critical Se and S accumulation pathways. Furthermore, cutting-edge omics approaches, primarily transcriptomics, metabolomics, and proteomics, can aid in identifying the key genes, metabolites, proteins, and regulators encoding actual seleno-compound transporters into and within hyperaccumulator plants, as well as the metabolic pathways involved in Se translocation. Following that, overexpression of essential genes would aid in the development of Se hyperaccumulators with high biomass output for more efficient Se contaminated area restoration. Furthermore, the modified Se-associated metabolic pathways can offer new insights into current information and contribute in the discovery of Se translocation mechanisms for future research.

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