

Review Article

Selenium species transforming along soil–plant continuum and their beneficial roles for horticultural crops

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Abstract

Selenium (Se) acquirement from daily diet can help reduce the risk of many diseases. The edible parts of crop plants are the main source of dietary Se, while the Se content in crops is determined by Se bioavailability in soil. We summarize recent research on the biogeochemical cycle of Se driven by specific microorganisms and emphasize the oxidizing process in the Se cycle. Moreover, we discuss how plant root exudates and rhizosphere microorganisms affect soil Se availability. Finally, we cover beneficial microorganisms, including endophytes, that promote crop quality and improve crop tolerance to environmental stresses. Se availability to plants depends on the balance between adsorption and desorption, reduction, methylation and oxidation, which are determined by interactions among soil properties, microbial communities and plants. Reduction and methylation processes governed by bacteria or fungi lead to declined Se availability, while Se oxidation regulated by Se-oxidizing microorganisms increases Se availability to plants. Despite a much lower rate of Se oxidation compared to reduction and methylation, the potential roles of microbial communities in increasing Se bioavailability are probably largely underestimated. Enhancing Se oxidation and Se desorption are crucial for the promotion of Se bioavailability and uptake, particularly in Se-deficient soils. Beneficial roles of Se are reported in terms of improved crop growth and quality, and enhanced protection against fungal diseases and abiotic stress through improved photosynthetic traits, increased sugar and amino acid contents, and promoted defense systems. Understanding Se transformation along the plant–soil continuum is crucial for agricultural production and even for human health.

Introduction

Selenium (Se) is a naturally occurring trace element with a significant importance for human health. Crucial functions of different selenoproteins detected in human bodies have clearly demonstrated the fundamental role of Se for life [1]. The selenoproteins involved in a series of enzyme systems, such as glutathione peroxidase and thioredoxin reductase, show functions as anti-cancer agents, in the inhibition of HIV development and in other related immune system disorders [2]. The distribution of Se is uneven on the surface of the Earth, leading to both Se-deficient and seleniferous regions [3, 4]. Their concentration in most soils ranges from 0.01 to 2.0 mg kg⁻¹ with an average Se content of 0.4 mg kg⁻¹ [5]. An estimated 15% of the global population is Se-deficient, i.e. having a lower daily Se intake than 26–34 µg per day [6]. However, a high bioaccumulation of selenium (>400 µg per day) can also be toxic to humans [5, 7]. Therefore, both Se deficiency and toxicity are emerging issues that attract the attention of researchers worldwide.

For instance, volcanic eruptions and anthropogenic sources generate atmospheric Se (Fig. 1) [8]. Se in the atmosphere, and in marine and terrestrial ecosystems can be transported and transformed into different forms via diverse pathways [8]. Different Se forms are then affected by soil properties, transformed by microorganisms and taken up by plants (Fig. 1). Several studies have considered the crucial roles of microorganisms in influencing the biogeochemical cycle of Se (reduction, methylation, or oxidation), which alter Se speciation and contents [9–11]. However, the results of most studies have utilized culture-based approaches, and individual microorganisms involved in Se species transformation in Se cycling processes have been identified. Information concerning interactions/connections among or within functional guilds (reduction, methylation, and oxidation) is still lacking. Nowadays, the crucial role of plants in driving soil nutrient cycles has received much attention in forest, grassland, and agricultural ecosystems [12, 13]. Because Se is critical to crop plants, understanding the migration and transformation of Se in the plant–soil continuum and plant

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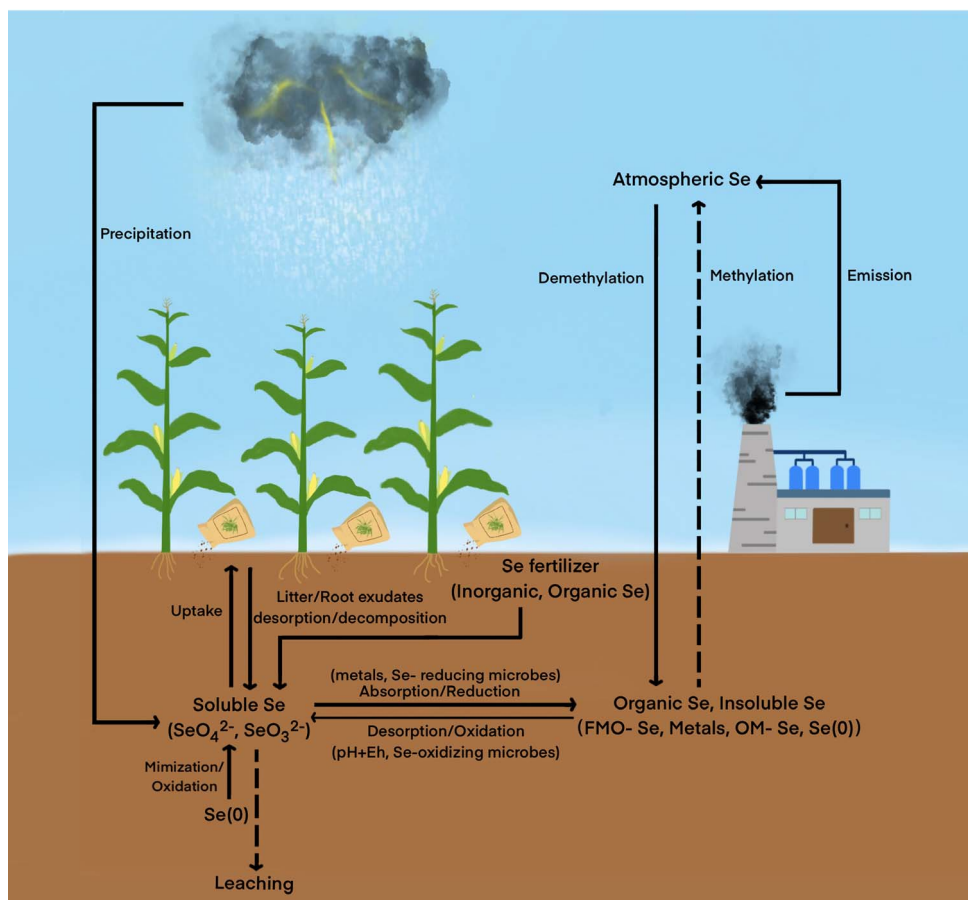


Figure 1. A framework of the selenium (Se) cycle. The Se availability depends on Se oxyanion (SeO_4^{2-} and SeO_3^{2-}) contents in soil, but is determined by adsorption and desorption, reduction, methylation, and oxidation. Soil organic matter, pH, and other properties mainly affect adsorption and desorption, while reduction, methylation, and oxidation processes are mainly driven by microbial communities. Crops can affect Se availability through root exudates and species-specific microbial communities. FMO-Se: Se absorbed by soil metals like Fe and Mn. OM-Se: Se absorbed by soil organic matter.

uptake of Se, as affected by microorganisms, is of particular importance (Fig. 1).

In this review, the effects of soil properties, microorganisms, and plants on Se species and cycle are discussed. It is important to know the underlying mechanisms that affect the contents of selenate, selenite, and some organic Se species, particularly in Se-deficiency areas, as they are the available forms for absorption by crop plants. In addition, more studies are focusing on the beneficial roles of Se in terms of improving plant growth and crop quality, and enhancing protection against fungal diseases or abiotic stresses. Therefore, how Se affects plant growth, quality, and defense is also discussed.

Selenium species and fractions in soil

Selenate (SeO_4^{2-}), selenite (SeO_3^{2-}), elemental Se (Se^0), and selenide (Se^{2-}) are four oxidation states of Se in soil. Selenate and selenite can be acquired by plants due to their high solubility in soil. The inorganic Se (SeO_4^{2-} , SeO_3^{2-} and Se^0) is the main form distributed in soil, but organic forms, such as selenomethionine (SeMet), selenocysteine (SeCys), and methylselenocysteine are also present [14]. Se fractions are separated into soluble Se, exchangeable Se, Fe-Mn oxide-bound Se, organic matter-bound Se, and residual Se [15]. Changes among different valent states affect Se fractions due to their differences in migration mobility and binding intensity, further affecting Se bioavailability in soil.

Soluble Se fractions in soil include soluble organic Se and Se oxyanions (SeO_4^{2-} and SeO_3^{2-}) [16]. Some Se species can be bound by metal ion oxides like iron, manganese, and organic matter in soil to form Fe-Mn oxide-bound Se and organic-bound Se [17, 18]. The bound Se fractions are suggested as potential Se pools at a given moment, because these fractions can be released [16]. Most Se in soil is not available for plants [15, 19, 20]. The distribution pattern of Se fractions is at a dynamic equilibrium state [21], which is regulated by sorption/desorption, precipitation/dissolution, and oxidation/reduction processes. The strength of these transformation processes is controlled by soil properties, such as soil moisture, pH, redox conditions, organic matter, and microbial functions.

Inorganic Se(VI) and Se(IV) are the main Se fractions that determine the bioavailable Se content in soil. Selenate is more soluble and available to plants, whereas selenite is efficiently absorbed by different soil constituents, especially clay and metal-oxides, thus being less soluble in soil. The transformation between Se(VI) and Se(IV) largely depends on soil pH and redox potential (Eh). Se(VI) is the dominant Se form in well-aerated alkaline soils but it is readily converted to selenite along decreasing pH in neutral and acid soils [22]. The increased pH facilitates desorption of Se from metals and increases the availability of soil Se [23]. However, the contents of insoluble Se(0) and Se(-II) (Se^{2-}) increase under reduced conditions (for example $\text{Eh} < -200$ mV), resulting in low Se bioavailability [22, 24]. In general, acid soils release less

selenium than alkaline ones, because selenite is easily fixed by metals like iron hydroxides. In alkaline soils, selenite is oxidized and it forms selenate [16, 25].

Different sorptive behaviors of SeO_4^{2-} and SeO_3^{2-} adsorbed onto geocolloidal phases of soil are due to their different mechanisms, including inner- and outer-sphere complexation [26, 27]. Outer-sphere adsorption formed by weak electrostatic forces (via hydration shell) between SeO_4^{2-} and the functional groups of soil sorbent phases (like metals) is usually reversible [16, 26]. Inner-sphere complexes formed by covalent bonding between the ions and functional groups (directly via the Se atom) result in stronger sorption [16, 27]. As mentioned above, soil metals, such as iron and aluminum, are other crucial factors that affect Se fractions, because of their extensive chelating ability in different soil pH and Eh conditions [16, 28].

Soil clay and organic matter contents are also key factors in regulating Se transformation in soils [25, 29]. Selenium oxyanions can be adsorbed by positively charged clay minerals [17]. Twidwell (2011) [30] reported a stronger Se(IV) adsorption by clay compared to Se(VI) because of differences in inner- and outer-sphere. Previous studies have reported that even over half of the total soil Se is bound with and/or incorporated into organic matters [18, 31]. Other soil conditions like moisture and oxygen are also important factors in determining Se fractions by affecting metals, Eh, pH, dissolved organic matter, and microbial activity [31]. Decreasing soil Eh but increasing dissolved organic carbon under water-saturated conditions result in the reduction of Se(VI) into low valences like Se(IV), Se(0), or Se(-II) [32]. It is obvious that the Se forms in soil are largely dependent on soil pH, organic matter, Eh, and texture. These factors in combination or alone could affect reactions like sorption/desorption, precipitation/dissolution, and oxidation/reduction processes, and determine the fate and behavior of Se in soil.

Selenium biochemical cycle driven by microorganisms

The composition and structure of soil microbial communities affect the availability of multiple nutrients by determining their cycling processes. Since the first discovery of selenite demand for the growth of *Escherichia coli*, there has been a growing interest in the biochemical role of Se in microbes [33]. Wang et al. (2022) [19] reviewed that in the presence of metals, such as Pb, Zn, Cd, Cu, Ag, and Bi, soil microorganisms can reduce Se (IV) to corresponding nanostructured metal selenides. As mentioned above, some specific bacterial and fungal species in soil are obligated to transform Se among different valent states and, thus, affect its bioavailability by reduction/oxidation and methylation/demethylation during the biogeochemical cycle of Se.

Selenium reduction and methylation processes

The reduction and methylation processes by environmental microorganisms are well studied due to recent interest to remove Se toxicity in selenium contaminated environments or high selenium soils [34]. Many bacteria have been successfully isolated and proved to transform Se oxyanions to insoluble and less bioavailable Se(0) and Se(-II) through assimilatory and/or dissimilatory reduction pathways [9, 35]. Different studies have demonstrated that the reduction processes occur either in the periplasmic space (intracellularly) or extracellularly [36, 37]. The functioning of a series of reductases, such as nitrate reductases, respiratory selenate reductases and fumarate reductases, are well characterized in different Se-reducing bacteria [19, 38].

Selenate and selenite are first transported into bacterial cells and then they go through assimilatory reduction to selenocysteine or selenomethionine, which can be incorporated into proteins during bacterial growth. The dissimilatory Se-reducing bacteria can obtain metabolic energy by reducing SeO_3^{2-} and SeO_4^{2-} to selenium nanoparticles (Se^0), and they are considered to remove Se oxyanions more efficiently than assimilatory Se-reducing bacterial species [39, 40]. Several excellent reviews have discussed the mechanisms of Se reduction [19, 38–40]. For example, Eswayah et al. (2016) [39] and Wang et al. (2022) [19] reviewed the reduction of different Se species through diverse microbes, including bacteria and archaea, in different environments. Several new bacterial isolates, such as *Chitinophaga* sp. and *Comamonas testosteroni*, from paddy soil can transform selenite to elemental Se nanoparticles with different reducing rates under aerobic conditions [35]. Bacteria *Bacillus selenitireducens* and *Thiobacillus ferrooxidans* can generate selenide by reducing Se(0) [41, 42]. Some bacteria, such as *T. ferrooxidans* and *Desulfovibrio desulfuricans* subsp. *aestuarii*, are capable of reducing both sulphur and selenium [41, 43].

The effects of fungal species on Se behavior have recently been explored [44]. Six aerobic fungi *Pyrenochaeta* sp., *Plectosphaerella cucumerina*, *Paraconiothyrium sporulosum*, *Acremonium strictum*, *Stagonospora* sp., and *Alternaria alternata* have showed their ability to reduce Se oxyanions to selenium nanoparticles or volatile selenium compounds [9]. However, the Se reduction processes of *P. sporulosum* and *Stagonospora* sp. were simultaneously accompanied by the biomineralization process of mycogenic Mn(II) oxidation to Mn oxides [45]. Liang et al. (2019) [46] also reported that four fungal species (*Aureobasidium pullulans*, *Mortierella humilis*, *Trichoderma harzianum*, and *Phoma glomerata*) were able to reduce SeO_3^{2-} and SeO_4^{2-} to Se nanoparticles, and *P. glomerata* could precipitate elemental Se intracellularly and extracellularly when grown with selenite [47]. However, molecular mechanisms of these Se-reducing fungi need further research.

Different studies have confirmed that microorganisms govern the Se methylation process by transforming SeO_3^{2-} and SeO_4^{2-} to volatile compounds, such as dimethyl selenide and dimethyl diselenide [10, 39]. Thus, these microbes converting Se forms play an important role in Se cycling and may provide an efficient detoxification mechanism for selenium contaminated soil. The predominant Se-methylating bacteria and fungi are well summarized by Eswayah et al. (2016) [39]. The six fungal species mentioned in Rosenfeld et al. (2017) [10] are able to remove at least 15–20% of the supplied Se via volatilization.

Selenium-oxidizing bacteria

Compared to the well-studied reduction and methylation processes, microbial Se oxidation has received less attention. To our knowledge, there are no studies conducted to assess the oxidation of Se(-II) and Se(0) in anoxic environments. Wells and Stolz (2020) [40] have suggested that having the expensive Na_2Se or highly toxic H_2Se as a source of Se(-II) was one principal obstacle. Some early studies have demonstrated that certain microbes are capable of aerobic oxidation of Se(0) and SeO_3^{2-} [48, 49], and the oxidation is determined by the type of microbes [50]. However, the oxidation of Se(0) to SeO_3^{2-} and SeO_4^{2-} occurs at relatively low rates [40, 50]. In contrast, the Se reducing rates are much more rapid [40]. For example, approximately 51% of China has Se-deficient soil [51]. Organic or inorganic forms of Se fertilizers are now widely applied in agriculture to enhance plants' Se content [32, 52], whereas a maximum of 10% of inorganic Se fertilizers can be acquired by plants [52]. The bioavailability of Se dramatically

declines through adsorption with organic matters and metals, and through reduction and methylation processes as reviewed above. Therefore, the potential roles of soil microorganisms in increasing the bioavailability of Se but reducing the environmental risk of inorganic Se fertilizers are important.

For both the control and optimization of Se oxidation, there is an increasing interest in understanding the underlying microbiological processes, including the biochemical fundamentals of the oxidation reactions. The Se-oxidizing bacteria have been reported to increase soil SeO_3^{2-} and SeO_4^{2-} contents although at low rates [49, 53, 54]. For instance, the heterotrophic bacterium *Bacillus megaterium* was discovered to oxidize elemental Se to selenite [49]. Then, heterotrophic and autotrophic oxidation of Se(0) yielding both SeO_3^{2-} and SeO_4^{2-} were found, which suggested that diverse soil microbes probably have a Se oxidation ability. A recent study clearly demonstrated that four strains of bacteria (*Dyella* spp. LX-1 and LX-66, and *Rhodanobacter* spp. LX-99 and LX-100) isolated from seleniferous soil can oxidize Se(0) to Se(IV) and dramatically increase water-soluble Se and exchangeable Se fractions in soil [53]. More importantly, the authors firstly found the oxidation of organic Se (selenomethionine and selenocystine) to Se(IV) with a higher oxidation efficiency at pH 8.56 than at pH 5.25 [53].

We have discussed that high soil pH oxidizes selenite to form selenate and also facilitates the desorption of Se from metals and increases Se availability in soil. High pH may enhance functions of these Se-oxidizing bacteria [54]. Several Se-oxidizing bacteria can also be found: the major oxidation product of Se(0) by *Thiobacillus* ASN-1 and *Leptothrix* MnB1 is Se(VI) rather than Se(IV) [55] (Dowdle and Oremland 1998), while the bacterial strain *Agrobacterium* sp. T3F4 mainly oxidizes Se(0) to Se(IV) [54]. These different Se oxidation products by diverse bacteria isolated from soil suggest the presence of complex processes of selenium species, for which the enzymes and pathways have not yet been reported. In addition, selenium is always bound with other metals, and chemical changes caused by bacteria may also induce Se transformations. For example, in the metabolic oxidation process of copper selenide by *T. ferrooxidans*, Se(-II) is transformed to Se(0) [48].

To date, all studies investigating Se-oxidation have used culture-based methods with aerobic bacterial species. Biological cycling of different nutrients are driven and determined by cooperation of different functional microbial groups. Although the oxidation rate of a bacteria-oxidizing strain is much lower than the reduction rate, the cooperation among diverse oxidizing species and other microorganisms probably has a great effect on the Se oxidation.

Selenium availability promoted by fungi

Arbuscular mycorrhizal fungi (AMF) form symbiotic relationships with the majority of plant species and enhance the nutrient acquisition and transport of hosts. The added selenite and selenate fertilizers are easily absorbed or reduced as mentioned above. However, Li et al. (2020) [56] firstly found that the incubation of two AMF species, *Funneliformis mosseae* and *Glomus versiforme*, increased the concentration of available Se forms and facilitated Se uptake by crops. Another important result of Li et al. (2020) [56] is that the two AMF species also significantly increased Se bioavailability in soil without Se addition. While Se reduction is primarily physically associated with the fungal hyphae [9], information regarding the increasing selenite or selenate transformation to Se(0) is lacking. No studies have reported oxidative reactions of Se by fungi. However, AM fungi release diverse hyphae compounds to recruit a diversity of microbes in the hyphosphere,

thus affecting nutrient cycling [57,58]. It is supposed that Se-oxidizing bacterial species may be recruited by AM fungi, which would increase the soil Se bioavailability. The inoculation of *F. mosseae* and *G. versiforme* were found to increase the relative abundance of Firmicutes, which led to a high content of available Se [59]. The successfully isolated Se-oxidizing *Bacillus* species belong to Firmicutes. However, the effects of environmental conditions, such as temperature, pH and water, on the activities of Se-oxidizing microorganisms have not been explored.

Besides AM fungi, diverse fungal species are expected to increase Se bioavailability. An application of Se-enriched organic plant material has been recommended as substitutes for inorganic Se to solve environmental problems [52]. Selenate and selenite species in soil are the most common forms used by crops and they are easily transformed to organic forms, such as selenomethionine, selenocystine, and methy-selenocystein [60]. How are these organic Se species released from plant materials to soil and then transformed or oxidized to soluble Se forms? Up to now, no studies have explored the specific mechanisms involved. Basidiomycota contains large numbers of fungal species that decompose organic plant material [61,62], suggesting that the Se cycle is related with the carbon cycle in soil.

Quinn et al. (2011) [63] conducted a litter decomposition experiment between Se hyperaccumulator plants (*Astragalus bisulcatus*) and non-accumulator species (*Astragalus drummondii* and *Medicago sativa*) in a seleniferous habitat. They found that high-Se litter supported more microbes and arthropods decomposed faster when compared to low-Se litter. Some studies have confirmed that the Se cycle processes are affected by cycles of nitrogen, carbon, sulfur, and other elements [19, 45]. Se concentration in rice grain was found to be positively connected with increasing soil nitrogen [64,65], while Li et al. (2015) [66] has also reported that Se content in horticulture crop and vegetable is influenced by soil nitrate. The application of nanoselenium (Se^0) to soil enhanced SeO_4^{2-} and selenocystine contents, and interestingly also increased soil ammonium content [56].

Many known nitrogen cycling bacterial strains are capable to reduce Se oxyanions; for example, the well documented nitrogen denitrification bacterium *Azospirillum brasilense* can reduce selenite [67]. *A. brasilense* also synthesizes extracellular selenium-sulfur nanoparticles in selenite medium under aerobic conditions [39], which implied a close and complex linkage of the Se cycle with nitrogen and sulfur cycles in soil microbial communities. The observations imply that the selenite reduction probably competes with nitrogen denitrification in *A. brasilense*. The application of phosphorus contributes to Se release from soil particles [68,69], suggesting a potential connection between phosphorus and Se cycling. While the oxidation rate by single Se-oxidizing microorganisms is quite low, the combined impacts of diverse microorganisms may be strong. Thus, the microbial communities rather than functions or activities of individual organisms are important for Se transformation in natural environments. The Se-oxidizing abilities and rates of soil microbial communities have probably been largely underestimated.

Selenium availability in the plant-soil continuum

Understanding how plant species affect soil nutrient cycling is an important theme in different terrestrial ecosystems. Plants can directly influence the nutrient cycling via uptake, use and loss of soil nutrients [70–72]. For example, resource-acquisitive plant species with higher carbon fixation and soil nitrogen uptake

induce a stronger acceleration of nitrogen cycling than resource-conservative species (slow growth) [71]. More importantly, a substantial amount of photosynthesis-derived compounds, including carbohydrates, amino acids and organic acids, show their great power in affecting soil nutrients through their influence on soil properties and recruitment of diverse microbial communities. For example, phosphatases released by roots can provide an additional source of phosphorus by hydrolyzing organic P-containing compounds [73]. The increasing P content has been shown to enhance soil Se availability [69].

The microbial community of the rhizosphere is largely determined by different plant species through sensing and responding to root-derived signals [74]. It is becoming increasingly clear that plants can control nutrient transformation mediated by diverse soil microbes in and near the rhizosphere by releasing root exudates [74–76]. An early study found a higher Se availability to rice seedlings, including soluble Se and exchangeable Se, in rhizosphere soil than in bulk soil [77], which demonstrated a potential role of plants in controlling Se transformation. As for Se transformation in soil, Oram et al. (2011) [78] have confirmed that a higher Se(VI) concentration was present in the rhizosphere of *Symphyotrichum eatonii* than in bulk soil, and an enhanced Se bioavailability via oxidation of reduced Se within the rhizosphere occurred.

Plants have a large impact on the physical and chemical behavior of soil due to root exudates and decomposition [79,80]. Girkin et al. (2018) [79] showed that low molecular weight organic acids (acetate, formate, and oxalate organic acids) can significantly increase soil pH, whereas sugars (glucose, sucrose, and fructose) decrease pH. They also found that soil redox potential increases with sugars and decreases with organic acids. Se speciation is closely related with soil properties, like pH, organic matter, and metal ion oxides, as mentioned above. Root exudates enhance the decomposition of soil organic matter and nutrient release in the rhizosphere soil [76,81]. In a review of the role of organic acids for soil Se bioavailability, Dinh et al. (2017) [75] summarized that many low molecular weight organic acids can increase Se bioavailability by reducing Se adsorption while promoting desorption. However, the amount and composition of plant root exudates depend largely on plant species and environments. The secretion of some organic acids, such as salicylic acid and citramalic acid, is increased by plants to solubilize phosphorus in phosphorus-deficient soil accompanied by decreasing soil pH [82]. The decreasing pH probably reduces soluble Se by promoting the adsorption of metals and organic matter to form complex compounds [32]. Plants varying in the ability of Se uptake have different influences on soil Se species, probably via root exudates. For instance, the soluble Se content in the rhizosphere soil of a Se-enriched *Oryza sativa* genotype was significantly higher than that of a non-Se-enriched rice genotype [83]. It is indicated that plants with a higher Se uptake have a stronger ability to convert insoluble Se species with a lower bioavailability to soluble Se with a high bioavailability than plants with a lower Se uptake.

Diverse microbes drive the steps of Se cycling, including reduction, oxidation, and methylation. The root exudates fuel soil microbes. Hyperaccumulators hold a greater propensity to take up and accumulate Se by transforming it into organic forms and transporting Se to root and shoot parts in seleniferous or Se-contaminated soils [70]. Se-reducing bacterial or fungal species can be recruited by plants via root exudates to immobilize selenite and selenate and to reduce these soluble anions [75,84,85]. Di Gregorio et al. (2006) [84] found that rhizobacteria contribute more

strongly to reducing selenite and selenate oxyanions into less bioavailable forms than does the plant (*Brassica juncea*). Two fungal species, *Alternaria seleniiphila* and *Aspergillus leporis*, within the rhizosphere soil of *Stanleya pinnata* are known to reduce selenate to elemental Se [85]. *Stenotrophomonas maltophilia*, *C. testosteroni* and other rhizobacteria reduce toxic Se(IV) and Se(VI) to nontoxic Se species [85]. Transforming stable Se species in soil by different soil microbes increases the content of bioavailable Se and Se uptake by plants.

We have reviewed the low oxidation rates by bacterial and fungal species and the interactions between microbe-driven cycling of carbon, nitrogen, and phosphorus. The abundance of AM fungi and actinomyces were found significantly positively correlated with available Se in the wheat rhizosphere soil [69]. The rhizosphere soil of the Se-enriched *O. sativa* genotype had a higher microbial biomass than that of the non-Se-enriched rice genotype [83]. The presence of AM fungi in the rhizosphere of crop roots has been verified to enhance Se bioavailability and uptake [59,69,86]. These studies imply the potential of increasing Se bioavailability by soil microbial communities recruited by plants (Fig. 2). The soil soluble Se content depends on the balance between adsorption and desorption, reduction, methylation, and oxidation as well as plant uptake. Phytoremediation, reduction, and methylation are primary pathways to reduce the soluble Se content, while Se oxidation driven by soil microbes, such as Se-oxidizing bacteria, may be weakened in Se-contaminated soils. By contrast, enhancing Se oxidation and Se desorption is crucial for the promotion of Se bioavailability and uptake, particularly in Se-deficient soils with Se supplements. Yet, the reduction and/or methylation processes would probably be impeded. However, so far, the crucial role of microbial communities in the plant–soil continuum on promoting Se bioavailability has not received much attention.

Selenium improves crop quality and resistance to environmental stresses

The soluble selenate, selenite, and a small proportion of organic Se, such as selenomethionine, are the available forms to plants in soils (Fig. 2). The Se uptake shares a common mechanism with, e.g. sulphur and phosphorus through anion channels and transporters [64]. As having highly similar chemical traits with sulfate, selenate species are absorbed by the sulfate transporters like Sultr1;1, Sultr1;2, and Sultr1;3 [58]. The symplasmic pathway delivers most acquired selenate via the plasmodesmata to adjacent root cells, then likely being transported from roots to shoots via sulfate transporters (including Sultr 2;1 and Sultr 2;2) after being released to xylem [58]. Higher expressions of Sultr 2;1 and Sultr 2;2 lead to a greater rate of Se root-to-shoot translocation and source-to-sink remobilization [87]. The selenite uptake and transport also take place via transporters and can be affected by phosphate transporters [64,88,89]. Different studies have demonstrated that phosphate transporters OsPT2 and OsPT8 are involved in selenite uptake [64,89,90]. A silicon transporter OsNIP2.1 in rice is also reported to increase Se uptake [64,65]. Unlike the transportation of selenate from roots to aerial parts via sulfate transporters, the majority of acquired selenite species accumulate in roots and convert into organic Se [91]. Selenomethionine in soil can enter roots via nitrate transporter NRT1.1B [58,64] and also probably via amino acid permeases located in the plasmamembrane, which mediates the movement of amino acids in a cell [92]. Then, the organic Se is transported to leaves to participate in the synthesis of Se proteins.

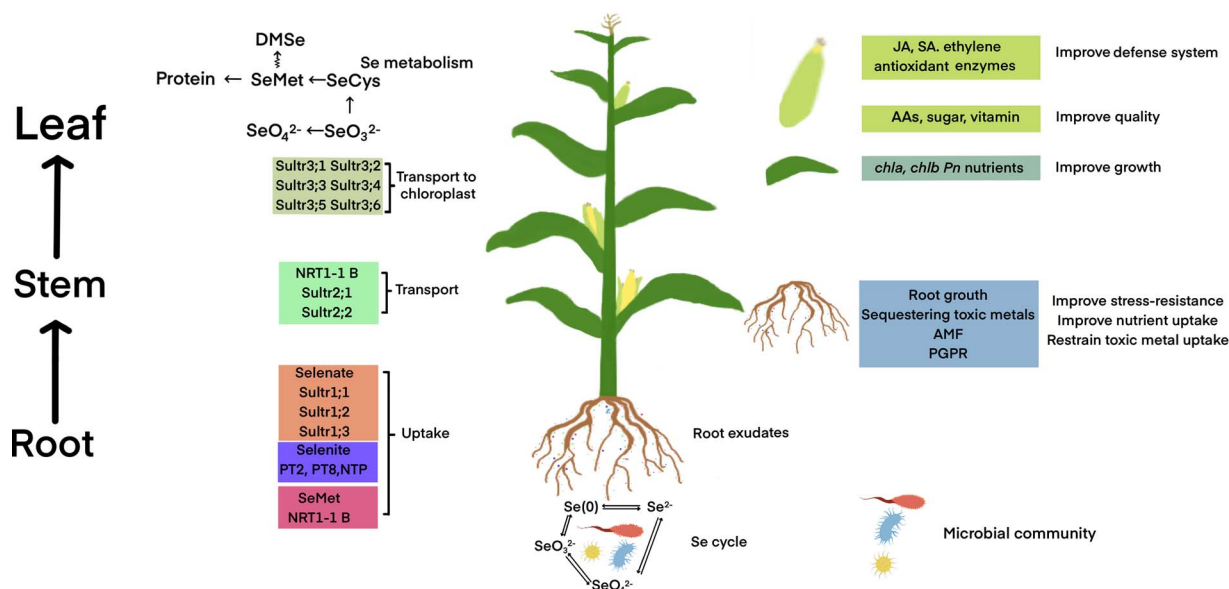


Figure 2. The uptake, transport, and metabolism of Se, and beneficial effects of Se on crop growth, defense, and quality. AAs: amino acids; AMF: arbuscular mycorrhizal fungi; JA: jasmonic acid; PGPR: plant growth promoting rhizobacteria; SA: salicylic acid. Se availability to crop plants depends on the balance between adsorption and desorption, reduction, methylation and oxidation, which are determined by interactions among soil properties, microbial communities and plants. Plants can affect Se fractions by root-derived compounds and by recruiting specific microbes like plant growth promoting rhizobacteria. Se is taken through transporters, including Sultr 2;1 and Sultr 2;2, and transported upward. Beneficial roles of Se in improving crop growth and quality, and enhancing protection against fungal diseases and abiotic stress.

Beneficial roles of the Se uptake are reported in terms of improving plant growth and crop quality and enhancing protection against fungal diseases and abiotic stresses (Fig. 2) [93–95]. The edible parts of crop plants like leaves, stems, roots, seeds, fruits, and flowers are the main source of dietary Se for humans and animals [96]. After Se uptake from soil, the selenate and selenite species are mainly transformed to selenocysteine (SeCys), selenomethionine (SeMet), and methylselenocystein (MeSeCys), which then can participate in protein synthesis. Cuderman *et al.* (2008) [97] reported that 30% of total Se is used to form Se-containing proteins in potato tubers, while this proportion reaches 60–74% in golden needle mushroom (*Flammulina velutipes*) [98]. A proper dose of Se fertilizer enhances Se accumulation in different plant parts but reduces the accumulation of heavy metals [64]. The application of Se promotes concentrations of nitrogen, phosphorus, potassium, calcium, and magnesium in citrus leaves [99] and also increases potassium and calcium concentrations of grape berries [100]. The nitrogen, potassium, and calcium uptake of wheat seedlings (*Triticum aestivum* L.) was enhanced by the application of 5 μM Na_2SeO_4 but the nitrogen uptake was significantly declined by 10 μM Na_2SeO_4 [101]. Drahoňovský *et al.* (2016) [102] investigated the effects of selenate on the uptake of many soil elements in 12 plant species and suggested that the improved nutrient uptake largely depends on the crop species and its growth environment.

Many studies have reported that Se fertilizer promotes the chlorophyll and photosynthesis rate [99,100,103]. The improved photosynthetic traits can supply sufficient carbon for the growth of roots, shoots and other edible parts [98,104]. For example, a 150 mg/L Na_2SeO_3 application increased the size and weight, and contents of total sugar and vitamins, but decreased the fruit acidity and the pericarp thickness of citrus fruit (*Citrus reticulata* Blanco cv. *Succosa*) [99]. Similarly, the grape berries showed an increase in sugars, vitamin C and soluble proteins, but a decline in organic acids after a proper Se fertilizer was applied [100]. In addition, the grape berries showed an increased acid invertase

activity, which plays an important role in sugar accumulation and could explain the increased soluble sugar content [105]. The carbohydrate content of rice grain is also promoted by a Se fertilizer [64]. Sugar transporter genes of tea plants (*Camellia sinensis*) were upregulated in response to a Se application [106]. All these results suggest a positive effect of proper Se on carbohydrate accumulation, which involves carbon fixation, transport, and metabolism.

Like nitrogen, potassium, and calcium, the Se metabolism of plants is closely associated with the metabolism of nitrogenous substances, especially with amino acids. Some studies have reported an increase in protein contents, such as those in rice grain, potato, and grape [64,100]. Ježek *et al.* (2011) [107] explored responses of 17 amino acids in potato tubers to Se application and reported significantly increased levels of phenylalanine, aspartic acid, glutamic acid, threonine, and tyrosine. Phenylalanine is reported to have an average increase of 46% [107]. Similarly, the increased Se level promotes protein and total amino acid contents of *F. velutipes*, indicating an increased nutritional quality [98]. In some crops, Se could be used as a regulator to manipulate the concentrations of amino acids that are essential for the quality. For example, the amount of amino acids is one of the most important traits in estimating the flavor and quality of tea, because amino acids supply umami and sweet taste and, thus, unique aroma to tea. An enhanced synthesis of diverse amino acids, including L-phenylalanine, L-lysine acid, L-glutamate, L-arginine, and increased epigallocatechin and epigallocatechin gallate contents (contributing to the tea quality) after Se application demonstrate a great improvement in the tea quality [108]. Li *et al.* (2021) [109] have reported a marked increase in theanine, glutamic acid, proline, and arginine by adjusting the GS-GOGAT cycle under Se application, and Se also promotes gene expression related to amino acid and protein metabolism in tea plants [106]. The enhanced nitrogen metabolism may be primarily driven by the increased nitrogen uptake under Se fertilization. However, the

specific mechanisms of how Se promotes nitrogen uptake is still lacking.

Crop species are vulnerable to various abiotic and biotic stresses, such as drought, heavy metals, herbivory, and diseases. Besides improving crop quality and plant growth, Se is a protective element for plants against toxic metals and pathogenic microbes, as explored in many studies [110–112]. Gui *et al.* (2022) [113] and Lai *et al.* (2022) [114] have summarized the crucial roles of Se in reducing metal toxicity to plants, for example, by reducing the mobility of metal ions by alternating soil pH and inhibiting upward transport by sequestering toxic metals inside the vacuoles. Many studies have reported that Se promotes plants' defense systems when facing diverse stresses [111,115]. Many amino acids play crucial roles in defense systems against stresses. For example, phenylpropanoids with significant antioxidant effects are derived from phenylalanine and tyrosine, which are promoted by Se fertilization in potato tubers [107]. Defense-related genes associated with the synthesis and signaling of jasmonic acid, salicylic acid and ethylene are more strongly expressed in *S. pinnata* (Se hyperaccumulator) than in *Stanleya elata* (nonaccumulator) when growing in a medium with 20 μM selenate [116]. Alleviating oxidative stress and regulating the activity of antioxidant enzymes are crucial Se-protective responses of crop plants to various stresses. Many studies have reported that exogenous Se application greatly reduces reactive oxygen species produced by crops exposed to stresses [95,115]. For example, by inducing disproportionation of O_2^- to produce H_2O_2 , which is then decomposed under antioxidant enzymes, mediating reduction in electrolytic leakage with improved cell integrity, Se can inhibit oxidative damage of plant cells [117,118].

The metabolism of Se increases antioxidant enzyme activities, including superoxide dismutase, peroxidase, and catalase, which further reduces oxidative damage caused by stresses [19,94–108]. Se can facilitate the biosynthesis of pigments, such as chlorophyll, by improving nutrient accumulation (e.g., Fe), thus being beneficial for the photosynthetic system (Fig. 2) [94,119]. SeCys constitutes the active glutathione peroxidase center, which catalyzes the synthesis of glutathione. While glutathione combines with ascorbic acid to decompose H_2O_2 , it is also involved in the synthesis of phytochelatin with a high ability of sequestering toxic metals [120]. Many studies have shown the effects of Se on heavy metal detoxification and accumulation reduction [94,95]. Most heavy metals can bind Se species to form complex compounds that cannot be absorbed by plants, thus indirectly reducing the toxicity of heavy metals [56,95,121]. Crop plants are healthier to humans and animals when Se reduces the accumulation of heavy metals.

Patel *et al.* (2018) [122] have suggested the enhancement of Se concentration via microorganisms (*Selenorhizobacteria*) as sustainable biotechnological tools to protect plants against stresses and to increase plants' nutrition and quality. Besides improving plants' defense systems, applying Se can help plants to recruit and boost beneficial microorganisms in the rhizosphere soil to protect them further [56]. For instance, many beneficial microbial species belonging to *Gammaproteobacteria*, *Alphaproteobacteria*, *Bacteroidia*, *Gemmatimonadetes*, *Deltaproteobacteria*, and *Anaerolineae* are enriched in the rhizosphere soil of pepper (*Capsicum annuum* L.) to protect against Cd stress after an exogenous Se application [56]. Root secretion fuels diverse microorganisms and shapes their communities [62,123]. It will be interesting to find out the role of Se in affecting soil microbial communities via altering root exudates.

Endophytes colonizing the interior of any plant part (such as roots, stems, and leaves), can improve plant growth and protect plants against environmental stresses [124–127]. It was recently discovered that a fungal endophyte *Alternaria tenuissima* isolated from the hyperaccumulator plant *A. bisulcatus* can transform Se species to Se(0) or methylated organic Se in the host, thereby removing Se toxicity to the host. This suggests the potential of endophytes to affect plant properties relevant for phytoremediation [125]. A tea plant-specific endophytic bacterium, *Herbaspirillum* sp. strain WT00C markedly enhanced Se enrichment [127], while it was reported to be capable of producing indole-3-acetic acid, ammonia and siderophores to improve plant growth [128]. Endophytic selenobacteria, such as *Alcaligenes faecalis* and *S. maltophilia*, and especially *Paraburkholderia megapolitana*, greatly improve the growth of *Glycine max* under drought because of exogenous Se application [126]. The endophytes successfully colonize plant roots and leaves probably through overcoming or escaping the plants' immune system [129]. Some studies suggest that the metabolism and immune-related traits of plants are key factors in regulating or selecting a specific microbiota that contribute to stress resistance [129,130]. The Se application largely influences plants' physiological and transcriptome traits [131,132], and probably imposes selective pressure to form specific endophytic communities related with stress resistance.

Conclusions and perspectives

In summary, the impact of soil properties, microorganisms and plant genotype on Se speciation and transformation along the soil–plant continuum has received increasing attention during recent years. This review highlighted the crucial roles of microorganisms and plants in driving the biochemical cycle of Se. The microbial isolates causing Se reduction and methylation rapidly immobilize or volatilize soluble Se species. These processes are important in reducing potential risks of highly soluble Se for non-hyperaccumulator plant species. These isolates are suggested to be recruited and enriched by plant root secretion in seleniferous and Se-contaminated environments. Plants recruit growth promoting microorganisms in soil and harbor diverse endophytes, including AM fungi. These microorganisms enhance Se absorption and accumulation, which, in turn, increase plant quality and stress resistance. Therefore, it is important to enhance Se accumulation in crop plants by increasing soil Se availability (e.g. via Se-oxidizing bacteria) in Se-limited areas.

Current understanding of the biochemical cycle pathways of Se relies on culture-based approaches, i.e. isolating the individual microorganism involved in Se species transformation. However, the pathways of the whole biochemical cycle of Se are poorly understood, although they have been shown to be closely connected with carbon, N, P, and S cycles. One of the main obstacles is that the functional genes involved in Se transformation have rarely been studied. It would be necessary to investigate how soil microbial communities differing in composition and function affect gene functions related to the Se cycle. Furthermore, there is a pressing need to explore specific mechanisms of plants that affect Se bioavailability by harboring different microbial communities. Nowadays, appropriate concentrations of exogenous Se are applied in Se-limited areas to increase crop yield, and to improve crop quality and stress tolerance. Understanding Se speciation and transformation along the plant–soil continuum is crucial for agricultural production and even for human health.

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Data availability

No new data was generated for the research reviewed in the article.

Conflict of interests

The authors declare that they have no conflict of interest.

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