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FOCUSED REVIEW

Selenium in Soil–Plant-Microbe: A Review

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Abstract

Selenium (Se) plays an important role in geochemistry and is an essential trace element for humans and animals. This review summarizes the transformation and accumulation of Se in the plant-soil-microbe system. As one of the important reservoirs of Se, soil is an important material basis of its entry into the food chain through plants. Soil with an appropriate amount of Se is beneficial for plant growth and plays a valuable role in a stress-resistant environment. Among the many migration and transformation pathways, the transformation of Se by microorganisms is particularly important and is the main form of Se transformation in the soil environment. In this review, the role and form transformation of Se in plants, soil, and microorganisms; the role of Se in plants; the form, input, and output of Se in soil; the absorption and transformation of Se by plants; and the role of microorganisms in Se transformation are presented. In addition to describing the migration and transformation laws of Se in the environment, this review expounds on the main directions and trends of Se research in the agricultural field as well as current gaps and difficulties in Se-related research. Overall, this reviews aims to provide necessary information and theoretical references for the development of Se-rich agriculture.

Keywords Se · Plant · Soil · Microbe · Function · Transformation

Selenium (Se) is a necessary trace element for human and animals that participates in many biological metabolic processes in the human body. Se deficiency can cause or induce many diseases, such as Keshan disease, skeletal muscle necrosis, and cardio-cerebrovascular disease (Vinceti et al. 2018). Although Se is not necessarily a necessary nutrient for plant growth, plants are the main source of Se intake for humans and animals (Natasha et al. 2018). Dietary Se supplement is the most common and important route of Se entry into the body. Se content and its existing form in crops determine the amount of Se absorbed by humans through food (Ekumah et al. 2021). The Se absorption and transformation abilities of plants and the transfer and enrichment abilities of the plant itself to its edible portion determine the Se enrichment effect of the plant (Guignardi and Schiavon 2017). According to the standards of the World Health Organization (WHO) and the International Food and Agriculture Organization (FAO), the global population with severe Se deficiency (daily intake of 7–11 μg) reached 0.5–1 billion, and the population with Se deficiency is markedly more than the population with excessive Se (Winkel et al. 2012). In China alone, nearly 2/3 of the planting soil is Se-deficient, posing health risks to people that live in these areas owing to insufficient Se intake (Zhang et al. 2014b). As in-depth research continues to be carried out, the important role of Se in humans has been discovered. Se can participate in the development of selenoprotein followed by glutathione peroxidase (GSH-Px), thioredoxin reductase (TrxR), iodothyroninedeiodinases, and a series of enzyme systems that display functions, such as anti-disease, anti-cancer, and inhibition of HIV development and other related immune system disorders (Ekumah et al. 2021).

Se can be found in different geographical features, such as the atmosphere, lithosphere, hydrosphere, and biosphere, and its basic fractions are affected by chemical processes (pH, redox properties, and organic matter content), physical processes (adsorption and deposition effects), and biological processes (microbial effects) (Sharma et al. 2015). The form of Se found in the soil of natural Se-rich areas is mainly antimonselite, supplemented by selenate. The form of Se in ores cannot be directly absorbed and utilized by

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plants. Further, Se salts are produced by long-term leaching and weathering of Se ores, which are highly toxic and unevenly distributed (Deng et al. 2018). The level of Se in plants is determined by the status of Se in the soil (Favorito et al. 2020). The form of Se, especially its effective content, is key to determining its mobility and toxicity (Galić et al. 2021). A series of environmental chemical reactions, such as (biological) oxidation–reduction, precipitation-dissolution, and adsorption–desorption, among others, occur between Se in the soil and soil components, such as iron and manganese oxidation, clay minerals, and organic matter (Wang et al. 2019). An appropriate amount of Se can increase the photosynthetic pigment content in plant leaves under stress, increase the activity of antioxidant enzymes in leaves and fruits, improve the osmotic adjustment ability, increase the organic acid content, and assist in plant growth under stress (Morales-Espinoza et al. 2019; Zahedi et al. 2019). Se is cycled in soil mainly through the microbial pathway (Mehdi et al. 2013). Microorganisms serve as the decisive factor of Se transformation (especially Se reduction) in soil as they participate in the formation and transformation of Se in various valence states (Gómez-Gómez et al. 2019; Fischer et al. 2020). The circulation of Se in the crop growth environment is shown in Fig. 1.

Understanding the migration and role of Se in plant-soil-microorganisms and clarifying the absorption of Se by plants are of particular importance. Moreover, understanding the process, influencing factors, and physiological functions of Se absorption and transformation by plants based on agro-ecology as well as the law of microbial transformation of Se and the migration of Se in soil can better guide production practices. Based on current studies on crop ecology in the development of Se-rich functional agricultural systems, the migration law and role of Se in plants, soil, and microorganisms are summarized in this review. The information presented herein is expected to serve as basic information for future research on the absorption and transformation of Se in agro-ecology and its physiological mechanism as well as a reference and basis for the development of Se-rich functional agricultural systems.

Se has various effects in plants, including promoting plant growth, enhancing plant resistance, and improving crop quality, among others (Table 1). An appropriate concentration of Se can promote the accumulation of starch in plant chloroplasts, which is beneficial to plant growth, as demonstrated in plant studies with lettuce (Rios et al. 2010), chicory (Germ et al. 2007), and potato (Turakainen et al. 2004). An appropriate amount of Se can increase the chlorophyll content in plants owing to the ability of Se to restore enzyme activity in the photoresponse and the electron transport chain of stressed plants (Diao et al. 2014). The addition of suitable concentration of Se could reduce the damage of chloroplast to some extent and increase the content of chlorophyll (Chu et al. 2010; Yao et al. 2011; Malik et al. 2012). Excessive Se application aggravates the damage to chloroplasts, which is not conducive to plant photosynthesis (Wang et al.

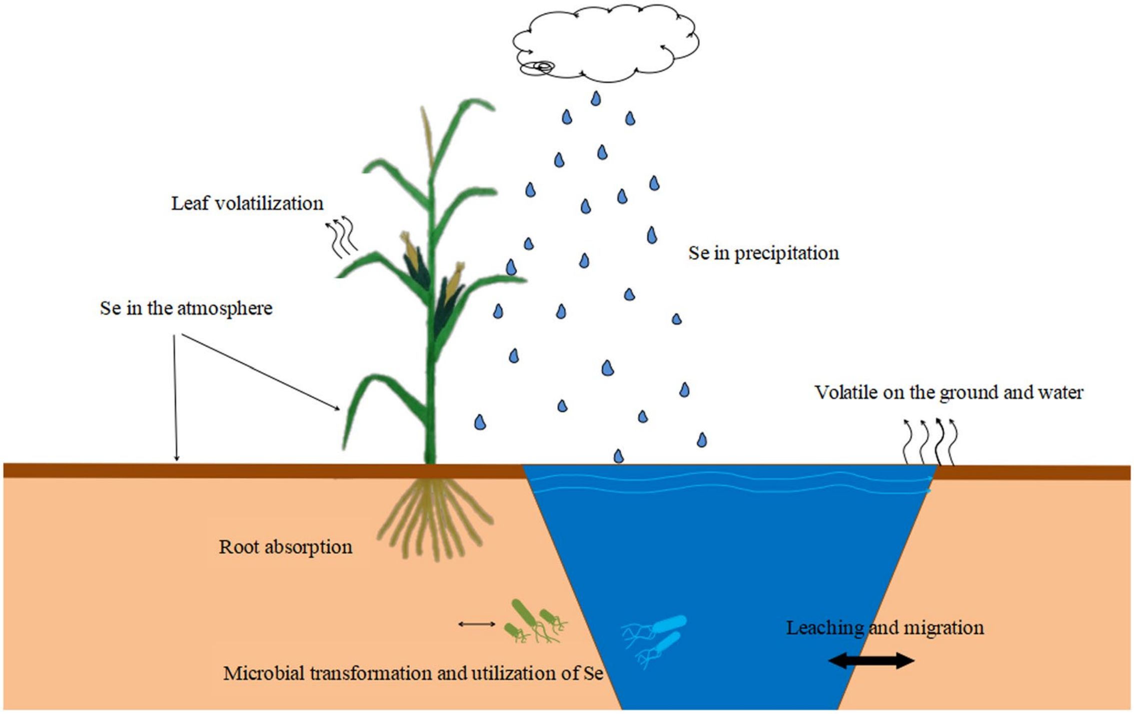

Fig. 1 The transfer and utilization of Se in the crop growth environment

Table 1 The role of Se in plant growth and physiology

Plant	Results after Se application	Mechanism	References
Wheat	Promote plant growth	Increase the dry weight of the above ground part and the yield of grains, and increase the concentration of organic selenium in the grains	Xia et al. (2020)
Wheat	Enhance cold resistance	Improve the antioxidant capacity of seedlings	Chu et al. (2010)
Wheat	Reduce the damage of UV-B to wheat seedlings	Significant increase in biomass, chlorophyll content, antioxidant content, and antioxidant enzyme activity	Yao et al. (2011)
Wheat	Improve the salt tolerance of wheat	Upregulate the antioxidant system, enhance the synthesis of the permeate, and prevent excessive Na^+ accumulation	Elkelish et al. (2019)
Wheat	Enhance the tolerance of wheat to NaCl stress	Improve antioxidant and sodium manipulation of AOX, SOS1, and NHX1 gene overexpression	Alla et al. (2020)
Tomato	Enhance resistance to salt stress	Regulate the antioxidant defense system in the chloroplast of tomato seedlings to reduce salt-induced oxidative stress	Diao et al. (2014)
Rice	Conducive to the production of rice with higher selenium content	Change the antioxidant enzyme activity and gas exchange in rice leaves	de Lima Lessa et al. (2019)
Rice	Reduce the adverse effects of salinity on the growth of rice plants	Enhance the antioxidant defense system and increase the transcription level of OsNHX 1	Subramanyam et al. (2019)
Rice	Reduce the toxicity of plant mercury	Inhibit the absorption and transport of mercury by plants	Zhang et al. (2012)
Rice	Change the energy metabolism of rice seedlings	Inhibit the growth of rice seedlings, stimulate the reactive oxygen species in rice seedlings, increase ethylene production, and reduce the auxin biosynthesis of rice seedlings	Malheiros et al. (2020)
Rice	Reduce the accumulation of Cd in rice	Increase soil pH, reduce Cd bioavailability, and inhibit Cd transport from roots to shoots	Huang et al. (2018)
Rape	Relieve cadmium toxicity	Increase the unsaturation of fatty acids in the cell and the fluidity of the cell membrane	Filek et al. (2010)
Potato	Positively affect production	Accumulate carbohydrates	Turakainen et al. (2004)
Pak choi	Maintain the stability of the microbial community in Cr-contaminated soil	Oxidation of Cr(VI) and reduction of Se reductases proportions, and increase the soil pH	Cai et al. (2019)
Mungbean	Relieve cadmium toxicity	Limit arsenic intake and enhance antioxidant activity	Malik et al. (2012)
Microalgae	Enhance photosynthesis	Regulate the photochemical properties of photosystem II (PSII) in chloroplasts	Zhong and Cheng (2017)
Maize	Alleviate the salt stress in corn	Improve photosynthetic capacity and antioxidant enzyme activity, and regulate Na^+ homeostasis	Jiang et al. (2017)
Lettuce	Increase nitrogen metabolism	Increase nitrate reductase, nitrite reductase, glutamine synthetase, and glutamate synthase	Rios et al. (2010)
Chinese flowering cabbage	Reduce the toxicity of plant cadmium	Increase SOD, CAT, and aseorbateperoxidase levels in plant tissues, and selectively induce glutathione reductase and dehydroascorbate reductase in plant tissues	Wu et al. (2018)
Chicory	Increase the respiratory potential in young plants	Exert a positive role on the photochemistry of PSII	Germ et al. (2007)

2012a). Zhang et al. (2014b) revealed that the application of Se (<50 g hm^{-2}) increased the photosynthetic rate (Pn), intercellular CO_2 concentration (Ci), electron transport rate (ETR), and chlorophyll fluorescence parameters, such as Fv, Fo, Fv/Fo, and Fv/Fo, in rice; however, the photosynthesis index decreased when 100 g hm^{-2} Se was applied. The photosynthetic physiology of plants is particularly sensitive to environmental stress. Further, the mechanistic effect of Se on plant photosynthesis may be similar to that of the antioxidant system; when electron transport is blocked during photosynthesis, reactive oxygen species (ROS) accumulation will be induced (Zhang et al. 2007). Se affects plant photosynthesis by inhibiting or inducing ROS accumulation and the photosynthesis-related enzyme system. Se may also affect electron transport and photosynthetic energy conversion by affecting Fe-S protein synthesis (Van Hoewyk et al. 2007; Feng et al. 2013). Freeman et al. (2010) compared the ETR between Se-hyperaccumulating plants and non-Se-hyperaccumulating plants under Se treatment. The ETR of Se-hyperaccumulating plants was significantly increased after treatment with 20 μmol selenate, whereas that of non-Se-hyperaccumulating plants decreased significantly under the same conditions. At present, only few studies have assessed the effects of Se on plant photosynthetic physiology, which must be further examined at the physiological level. Further, the molecular mechanism should be detected.

An appropriate amount of Se can promote plant growth and increase the yield of crops, such as rice (Zhang et al. 2014b), wheat (Nawaz et al. 2015), and lentils (Ekanayake et al. 2015), which is related to an increase in chlorophyll content, promotion of photosynthesis, enhanced antioxidant capacity of crops, and improved stress resistance of crops (Broadley et al. 2010; Jiang et al. 2015).

Drought stress can lead to abnormal accumulation of ROS in plant cells, resulting in different degrees of oxidative damage to biofilm, protein, and DNA, which in turn affects plant growth, respiration, and photosynthesis, and can even lead to death in severe cases (Mittler 2002). Feng et al. (2013) suggested that Se may control the ROS level of plants under stress via three ways: by mediating the disproportionation of superoxide anion ($O_2^{-\cdot}$) to H_2O_2; through the direct involvement of Se compounds in the scavenging activities of $O_2^{-\cdot}$ and hydroxyl radicals (·OH); and by regulating the antioxidant enzyme system. Se metabolism in plant cells controls the balance of ROS concentration by regulating the concentration of free metal ions (Fe^{2+}, Cu^{+}). Se can directly or indirectly regulate the formation of antioxidant enzymes in plants, especially GSH-Px (Feng et al. 2013). Akladious (2012) indicated that exogenous Se can increase the content of proline and reduce plant stress injury. Se plays an important role in increasing the growth rate of crops (Cartes et al. 2010), reducing ultraviolet radiation oxidative damage (Yao et al. 2013), increasing chlorophyll and carotenoid contents in plant leaves (Dong et al. 2013), increasing the activity of antioxidant enzymes, and regulating the content of osmotic substances under heavy metal stress (Kumar et al. 2012). In addition, Se alleviates the adverse effects of drought stress on wheat (Nawaz et al. 2015), barley (Habibi 2013), rape (Hasanuzzaman and Fujita 2011), and other crops by improving plant photosynthetic capacity, enhancing antioxidant capacity, and increasing the content of osmotic adjustment substances.

Heavy metals in the environment cannot be degraded, and the various forms of these metals will transform into each other as environmental factors change (Nagajyoti et al. 2010). The toxicity of different forms of heavy metals is quite different, which poses a great challenge to the treatment of heavy metal pollution (Yao et al. 2012). An appropriate amount of Se can inhibit the absorption and transport of heavy metals by crop roots (Zhang et al. 2012). Further, Se can directly react with heavy metals in the rhizosphere soil to inhibit its toxicity (Zeng et al. 2005). Se can affect the root surface iron plaque, soil solid phase, pH, microorganisms, root exudates and other possible indirect action pathways, convert heavy metals from a more toxic form to a less toxic form, complex/chelate with heavy metals, and reduce the mobility of heavy metals (Huang et al. 2018, 2015; Cai et al. 2019; Chen et al. 2019), to ultimately reduce the availability of heavy metals in the soil and the accumulation of heavy metals in crops. An appropriate addition of Se could significantly reduce the accumulation of heavy metals in crops. Se could inhibit the transport of As from underground to the shoot (Hu et al. 2014) and limit the transport of Hg from the root to shoot of garlic (*Allium sativum*), thereby reducing the accumulation of Hg in the shoot (Zhao et al. 2013). Selenate could repair damage caused by Cd to the chloroplast membrane structure (Filek et al. 2010). The antagonistic effect of Se on the accumulation of heavy metals is affected by many factors, including the concentration and form of Se and heavy metals. The inhibitory effect of Se on plant Cr (III) absorption was found to be significantly stronger than that on Cr (VI); however, the antagonistic effects of different fractions of Se on plant Cr absorption were similar (Srivastava et al. 1998). Se may also increase the heavy metal content in plants. For example, Se treatment increased As accumulation in *Thunbergia alata* (Bluemlein et al. 2009) and increased Cd and Cu contents in wheat shoots (Landberg and Greger 1994), which may be due to unreasonable Se addition or different crop varieties (Feng and Wei 2012). Se can alleviate the toxic and side effects of heavy metals in plants by: directly inhibiting or forming complexes with heavy metals to inhibit the absorption and transport of heavy metals in plants (Feng et al. 2011; Malik et al. 2012) or participating in the regulation of the plant antioxidant system to alleviate heavy metal poisoning (Belzile et al. 2006; Filek et al. 2010).

At present, only few reports have been published on the effect of Se on plants under temperature stress and salt stress. Both high and low temperature induce plant oxidative stress, affect the stability of many types of enzyme activities in plants, and interfere with the normal growth and development of plants (Chiang et al. 2015). After soaking in a suitable concentration of Se solution, the contents of auxin, chlorophyll, anthocyanin, proline, and the activities of related antioxidant enzymes under temperature stress increase in wheat seeds to reduce cell membrane damage (Akladious 2012). The application of exogenous Se can enhance the antioxidant system of crops, reduce the concentration of malondialdehyde (MDA), increase the content of proline, strengthen the protection of the mitochondrial electron transport chain, induce an increase in the protective substances in vivo, and alleviate the effects of temperature stress on plants (Djanaguiraman et al. 2018).

High salinity will destroy the structure of cytoplasmic membrane, hinder the absorption of mineral elements beneficial for growth, and cause secondary stress effects (Liang et al. 2017). Due to high osmotic pressure, osmotic stress occurs in plants, resulting in ultrastructural damage of chloroplasts, limited or even closure of the respiratory stomata, and a decrease in the rate of photosynthesis and respiration (Hanin et al. 2016). Under salt stress, Se acts as a coenzyme factor of antioxidant enzymes, such as superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT). The increase in Se concentration increases antioxidant enzyme activity, enhances antioxidant levels, and decreases ROS concentration and MDA content in plants. The main effect of exogenous Se is to scavenge ROS, improve plant antioxidation, and reduce the damage caused by salt stress (Hu et al. 2013). Under salt stress, exogenous Se increases the absorption of N, K, Ca, and induces more metabolites and stress signals in plants (Elkelish et al. 2019). In addition, exogenous Se inhibits the increase in cell membrane permeability of wheat under salt stress, which could effectively alleviate the damage caused by salt stress to plants (Yigit et al. 2012). It is inferred that exogenous Se may reduce the expression of Na^+ and K^+ transporter gene, thereby maintaining the balance of cell infiltration and improving the salt tolerance of plants. The comprehensive role of Se in plant stress shows that Se can improve the resistance of plants to abiotic stress by affecting ROS and the antioxidant system, interfering with the absorption and transport of heavy metals, changing the transformation process of heavy metals, and repairing the structure of cell membrane and chloroplast as well as the photosynthesis system (Feng et al. 2013). Crops are vulnerable to various diseases and insect pests and stress. Less free radicals and increased proline content can help plants resist stress, whereas Se can directly eliminate excessive free radicals, increase proline accumulation, enhance antioxidant enzyme activity, improve plant immunity, and increase its resistance to biotic and abiotic stresses (Kimani et al. 2013; Priyadarsini et al. 2013; Steinbrenner and Sies 2013; El-Demerdash and Nasr 2014).

Se inhibits the growth of pathogenic microorganisms in vitro. Further, it has a strong inhibitory effect on *Aspergillus funiculosus* isolated from banana and *Alternaria tenuis* and *Fusarium* sp. isolated from tomato; the growth of these pathogenic fungi was terminated in 10 mg kg^{-1} Na_2SeO_3 solution (Razak et al. 1991). The minimum inhibitory concentration of Se is very low, and it serves as a beneficial essential element at low concentration. If Se is used as an antifungal agent, it will certainly reduce the negative effects of similar pollutants on the environment. When treated with Na_2SeO_3, the level of ROS in the spores of a fungal pathogen, *Penicillium expansum*, increased, and the antioxidant system was destroyed, thereby weakening the cellular function of the pathogen and directly leading to plasma membrane damage of the pathogen, which inhibits the pathogen growth (Wu et al. 2014). Exogenous Se treatment can not only inhibit the growth of pathogenic microorganisms, but also achieve the effect of Se enrichment in fruits. The preharvest and postharvest treatment of apple and tomato with Na_2SeO_3 revealed that although Se delayed plant tissue senescence and inhibited blue mold disease occurrence, the Se content in apple and tomato was 6 and 5.5 times higher than that in the control fruits, respectively, and remained within the safe edible range (Wu et al. 2015; Wu et al. 2016). The use of exogenous Se helps the rape rhizosphere soil to accumulate beneficial rhizosphere microorganisms, thereby promoting plant growth (Cheng et al. 2021). Soil Se inhibits *Sclerotinia sclerotiorum* by affecting the dissolved organic matter in rape straw and upregulating antifungal pathway-related genes (Cheng et al. 2020).

Soil adsorption and fixation, leaching and migration, rice absorption, and gaseous volatilization are the four main processes of Se migration and transformation in the soil–plant system (Fernández-Martínez and Charlet 2009). Soil Se has different fractions, such as soluble state, exchange state and carbonate bound state, iron manganese oxide bound state, organic bound state and residue state (Wang et al. 2012b). The proportion of various fractions of Se in the soil is closely related to the physical and chemical properties of the soil, such as redox potential, pH, organic matter (Sharma et al. 2015). The Se form in the soil is the result of the combined effect of soil acidity and alkalinity and redox conditions (Neal et al. 1987). Changes in water content affect the redox conditions of soil (Tokunaga et al. 1996; Hefting et al. 2004), and changes in soil redox characteristics ultimately affect the form of Se in the soil (Gambrell 1994; Dwire et al. 2006). Soil drought, pH, clay content, and plant transpiration also play an important role in changing the soil's ability to fix Se (Jones et al. 2017).

There are five relatively stable valence states of Se in the environment: -2, -1, 0, $+4$, and $+6$ (Fernández-Martínez and Charlet 2009). In soil, the most common fractions of Se are inorganic, SeO_4^{2-} and SeO_3^{2-}, and the proportion of the two in the soil is controlled by the soil redox potential. When soil has alkaline and oxidizing conditions, SeO_4^{2-} is dominant; however, when soil has reducing conditions, SeO_3^{2-} is the main Se compound in the soil (Jacobs 1990). The aerobic soil mainly contains Se in the form of selenite; however, in anoxic soil (such as flooded paddy soil), Se mainly exists in the form of selenite (Zhu et al. 2009). The other organic fractions of Se in the soil depend on Se transformation by plants and microorganisms (Martens and Suarez 1996). The concentration of Se in most soils is 0.01–2 mg kg^{-1}, with an average value of 0.4 mg kg^{-1} (Fordyce 2013).

The Se in solid materials, such as rocks and soil, only accounts for 30–60% of the total Se in the environment, whereas a large proportion of Se exists in water systems, such as oceans (Zhang et al. 2004; Winkel et al. 2012). Therefore, Se in the atmosphere is mainly derived from the volatilization of marine substances (Blazina et al. 2017). Volatile Se is mainly dimethyl Se (DMSe) and dimethyl diselenide (DMDSe), which are easily soluble in water and can enter the soil via rainfall. Volatile Se is an important source of Se in soil (Amouroux et al. 2001; Wen and Carignan 2009). There is a significant positive correlation between Se content in soil and precipitation (Sun et al. 2016). When the total Se in soil is 0.08–0.12 mg kg^{-1}, water soluble Se accounts for 1–2%. According to the calculation of 100% loss of water-soluble Se in the rainy season each year, the amount of Se loss per hectare can reach 2–8 g a^{-1} (Wang and Gao 2001). Therefore, a large amount of rainfall can accelerate the loss of soluble Se in soil (Jones et al. 2017). Human farming activities also have an important influence on the migration cycle of Se on the surface (Bailey 2017). However, the aging process of exogenous Se fertilizer in soil markedly varies according to different soil types (Wang et al. 2017). In general, only 5–30% of Se fertilizers that are directly inputted into the soil can be absorbed and utilized by plants; 70–90% Se remains in the soil or is leached into the surrounding water (Sager 2006).

More studies have found that the distribution of Se in soil is not consistent with that of the parent material, and the distribution of Se in soil cannot be explained by soil parent material alone (Blazina et al. 2014; Sun et al. 2016). Climate and soil properties are the two most important factors affecting soil Se concentration globally (Winkel et al. 2012; Jones et al. 2017). The shading effect of plants on the soil, and surface vegetation can effectively reduce soil erosion by rainwater (Ravi et al. 2010), thereby reducing Se loss from surface soil. However, plants can also indirectly affect the Se content and the form of soil by changing the physical and chemical properties of the soil. Jones et al. (2017) found remarkable differences in soil organic carbon content under different vegetation types; the soil organic carbon content of farmland, woodland, and grassland increased, and the increase in organic carbon could fix soil Se to a certain extent, reduced Se loss, and indirectly increased soil Se retention. Therefore, there may be great differences in soil Se under different land use types (Pilon-Smits et al. 2017). Among different plants, Se-hyperaccumulating plants have a greater effect on soil Se, and they can effectively change the distribution of soil Se and soil Se fractions (Pilon-Smits et al. 2017). This is mainly achieved through the decomposition of litter and the action of root exudates of Se-hyperaccumulating plants (El Mehdawi and Pilon-Smits 2011). Soil and plants are thus an inseparable whole, and good vegetation coverage can play a positive role in the fixation of soil and its nutrients and the reduction of loss induced by leaching.

In the process of regulating the adsorption and desorption of Se and Fe, Al, Ca, Mg ions in the soil, the pH of soil affects the Se form (Goh and Lim 2004). When Se chelates with the iron in soil to form an insoluble selenite-iron complex, it is not easily used by plants and reduces the amount of Se migration (Peak and Sparks 2002). Compared with clay minerals, iron oxide has strong adsorption capacity, and its oxides can simultaneously adsorb Se (+4 and +6), of which, Se (+4) is the main type adsorbed. However, under alkaline conditions, the negative salts formed by iron oxide and Se converts selenite into soluble selenate, increasing the migration amount of Se, and form a more stable complex under acidic reduction conditions (Gustafsson and Johnsson 1992). After Se is applied to the soil, Se can be adsorbed or fixed in a short time, thereby transforming it into a form that is difficult to be absorbed by crops. In terms of the ability to fix Se, oxides are the strongest in all components of soil, followed by organic matter (Hawkes and Kutnink 1996).

Organic Se in soil is mainly recognized through the process of biodegradation and biosynthesis; however, the content of organically-bound Se in the soil is closely related to the content of soil organic matter. When the soil organic matter content is high, the content of organically-bound Se in the soil increases (Gustafsson and Johnsson 1992). Some related data show that organically-bound Se is related to its molecular weight. When the combination of soil organic matter and Se exists in the form of low molecular weight mixture, organically-bound Se can be directly absorbed and utilized by plants, whereas organically-bound Se with a larger molecular weight cannot be directly absorbed and utilized by plants (Zayed et al. 1998). Thus, the blind application of organic Se fertilizer and the pursuit of a high-Se-rich state in the soil to increase the Se content in plants are not desirable. At the same time, organic selenides in soil can be decomposed by microorganisms to form methylation fractions and cause gaseous volatilization. The products are mainly alkyl selenides, such as DMDSe and DMSe complexes, which reflect the loss pathway and quantity of soil Se (Gammelgaard et al. 2011). Inorganic selenides can also be methylated under the action of molds, and the methylation of Se may be related to the pH of soil (Zawislanski and Zavarin 1996).

Phosphorus has a similar structure to Se. Phosphate fertilizer regulates the migration of Se, which proves that the amount of phosphate fertilizer in the soil significantly changes the adsorption of Se in the soil (Altansuvd et al. 2014). When the phosphorus content is high, Se adsorption by soil is inhibited, thereby enhancing Se absorption by plants and further increasing Se mobility (Nakamaru et al. 2006; Altansuvd et al. 2014). The Se content in plants is related to the content of S amino acids in plants, where S in the structure of amino acids is often replaced by Se, resulting in an increase in Se content in plants (Ip and Ganther 1994).

The structure and chemical properties of Se are similar to those of S. Most plants are unable to distinguish between Se and S, resulting in the absorption of sulfate. Selenate in soil is transported by the S transport pathway through the transporters, SULTR1;1 and SULTR1;2, in plants (Barberon et al. 2008). SULTR2;1 and SULTR2;2 are involved in the selenate transfer process between roots, stems, and leaves, whereas SULTR4;1 and SULTR4;2 are mainly responsible for the phase transfer of Se between roots and stems (Zuber et al. 2010; Schiavon et al. 2015). SULTR3;1 transporters are mainly present in chloroplasts and are responsible for the transport of selenate across the membrane to chloroplasts (Cao et al. 2013). In summary, the pathway of plant absorption of selenate is highly related to the absorption of sulfate. Plant species and nutrition levels in the growing environment affect selenate transport efficiency in roots (White et al. 2004). Some plant species growing in Se-rich soil display Se accumulation, and their Se absorption capacity is more than 100 times higher than that of ordinary plants, up to 1–15 g kg^{-1} (dry matter); these plants are called Se-hyperaccumulating plants (Beath et al. 1939). Besides ordinary plants, there may be specific selenate transporters responsible for the transport and migration of Se in plants (Schiavon et al. 2015). The absorption of Se by plants is an active process, which occurs via two main routes: Se in soil and Se in the atmosphere. Selenate, selenite, and organic Se are the main uptake forms of Se by plants. When selenate is absorbed by plants, the valence state of Se does not change during transport. After being transported to leaves, it is reduced to + 4 valence state, converted into organic Se compounds, and finally distributed to other organs and tissues of plants (Li et al. 2010). After selenite is absorbed by plants, Se is converted into organic Se compounds in the roots, and most of the transformed organic Se compounds are retained in the roots, whereas a small portion is transported to the aboveground parts of plants (Keskinen et al. 2010).

Unlike plant selenate absorption, the mechanism of plant selenite absorption is not clear (Zhu et al. 2009). The transfer ability of plants to selenite is relatively poor, as selenite is easily converted into organic selenides after being absorbed by roots (Zhang et al. 2014a). Huang et al. (2016) found that the content of organic Se in wheat treated with selenite for 3 days was close to 90% of the total Se, and most of the substances produced were directly accumulated in the roots and could not be easily transferred to the aboveground parts of plants. The absorption of selenite by wheat is a metabolism-dependent active absorption process, which may be partially mediated by phosphorus transporters (Li et al. 2010). The silicon transport carrier, OsNIP2;1, in rice is also suggested to be related to the absorption of selenite. Selenite can enter the plant through OsNIP2;1, but this is regulated by environmental pH (Zhao et al. 2010). Some studies suggest that the absorption of selenite by plants is a passive diffusion process (Shrift and Ulrich 1969; Arvy 1989, 1993). In particular, Terry et al. (2000) reported that there is no evidence of membrane-mediated selenite uptake by plants. The studies on the absorption mechanism of selenite in plants are far less than that of selenate, which needs to be explored from the point of view of physiology and molecular biology.

Excessive Se has a toxic effect on plants, and there are remarkable differences in the symptoms of Se poisoning among different plants. When non-Se-hyperaccumulating crops are grown in high Se medium, normal growth and development of plants are inhibited. Further, withering and shedding of plant leaves, a decrease in protein synthesis, and dwarfism of plants occur (Trelease and Beath 1951; Mengel et al. 1982). Excessive Se leads to general inhibition in crops and reduces crop yield; however, phosphorus has a detoxification effect in a certain range (Singh and Singh 1978). Se poisoning has not been reported to occur in Se-hyperaccumulating crops after the absorption of a large amount of Se.

The accumulation of Se in plants will affect plant pollen development and fertilization. The accumulation of a large amount of non-toxic selenomethylcysteine (MeSeCys) in plant flowers inhibits pollen formation. Further, the maternal parents who accumulate a large amount of Se in flowers will have an important effect on their reproductive fertilization (Prins et al. 2011; Quinn et al. 2011).

Under the interaction of appropriate concentrations of S and Se, Se can inhibit or stimulate the absorption of S by plants (Cheng et al. 2016). When Se and S are combined, the resistance to cadmium stress is stronger than that of a single element. The ability of plants treated with S and Se to absorb Se was significantly higher than that of plants treated with Se alone (Golob et al. 2016). Si and Se have a strong synergistic effect on reducing Cd toxicity (Huang et al. 2020). Si-Se interaction increases the content of glutathione (GSH) and plant chelate (PC), causes more Cd to be distributed in the cell wall and organelles, and decreases the transport coefficient of Cd and accumulation in buds (Tang et al. 2015; Pereira et al. 2018).

The process of using plants to transfer Se from the Se-contaminated environment to alleviate soil Se pollution is called Se phytoremediation (Pilon-Smits 2005). There are more than 30 species of Se-hyperaccumulating plants, such as *Stanleya*, *Astragalus*, and *Symphyotrichum* (Cappa and Pilon-Smits 2014). Because of the Se enrichment characteristics of the above plants, they are often used in the phytoremediation of Se-contaminated soil (Salt et al. 1998; Pilon-Smits 2005). Phytoremediation has the advantage of ecological balance, but the prerequisite for phytoremediation of high Se soil is to screen plants that meet the tolerance conditions. Further, the area to be repaired should have the basic conditions of light, temperature, water, and heat needed for plant growth (Wu et al. 2015).

Microorganisms are the decisive factor of Se transformation (especially Se reduction) in soil (Yanke et al. 1995; Martens and Suarez 1996; Kessi and Hanselmann 2004). Therefore, understanding the role of soil microorganisms in Se transformation is particularly important to further clarify Se absorption by plants. The process of microbial transformation of Se generally involves dissimilatory reduction, assimilation reduction, oxidation, methylation, and demethylation (Dungan and Frankenberger 1999). Among them, dissimilatory reduction can reduce the toxic oxidized Se (SeO_3^{2-}, SeO_4^{2-}) to non-toxic Se^0 (Wen and Carignan 2007). As the synthesis method of the reduced product nano-Se is green, environmentally friendly, safe, and less toxic, nano-Se is widely used in electrochemical sensing and anticancer (Mehdi et al. 2013).

The reduction of selenate to selenite and the reduction of selenite to elemental Se are two separate processes (Kuroda et al. 2011). The mechanism of reduction of selenate to selenite has been thoroughly studied. In this process, there is a significant difference between the selenate reductase complex of gram-negative bacteria and gram-positive bacteria, which leads to a significant difference in the reduction process (Fig. 2). Membrane-bound molybdate plays an important role in the reduction of selenate to selenite. In Gram-positive bacteria, SrdBCA is a membrane-bound molybdenum enzyme. SrdA contains one [4Fe-4S] cluster, SrdB contains four [4Fe-4S] clusters, and SrdC contains two transmembrane domains, indicating that the protein is located on the cell membrane. The SeO_4^{2-} reduction process is related to the oxidation of hydroquinone. Hydroquinone

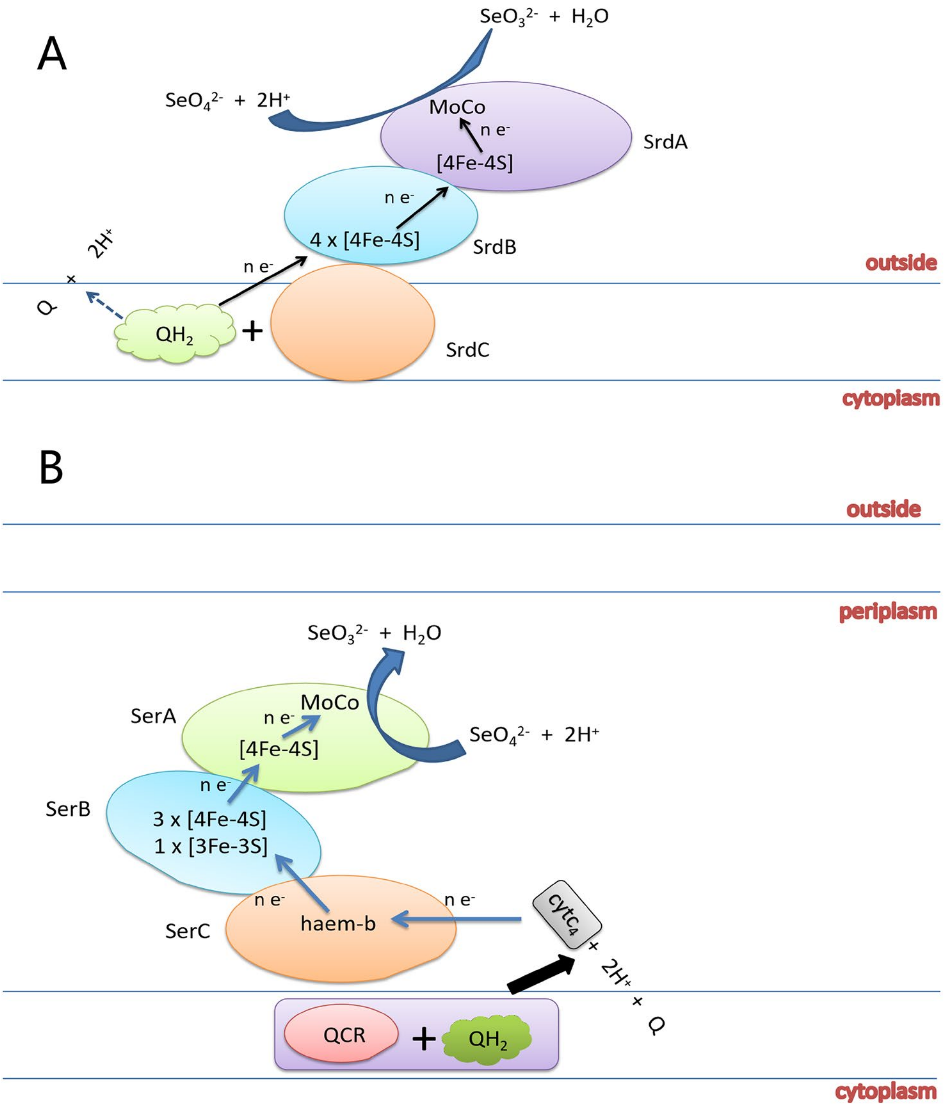

Fig. 2 Schematic of selenate reduction by gram-positive bacteria (**a**) and gram-negative bacteria (**b**). MoCo, molybdenum cofactor; SerABC, selenate reductase; SrdBCA, selenate reductase; cytc4, cytochrome c_4; QCR, quinol-cytochrome *c* oxidoreductase; Q, quinones; QH_2, quinols.Adapted from Nancharaiah and Lens (2015) and Kuroda et al. (2011)

combined with SrdC is oxidized to quinones, releasing 2 protons to the outside of the membrane and providing 2 electrons for SrdB (Nancharaiah and Lens 2015). Yee et al. (2007) inferred that the process of selenate reduction may be related to anaerobic respiration. In Gram-negative bacteria, SerABC is a soluble periplasmic molybdenum enzyme and SerA combines a molybdenum cofactor with catalytic activity and a subunit containing one [4Fe-4S] cluster. SerB contains three [4Fe-4S] clusters and one [3Fe-4S] cluster, and heme b (Nancharaiah and Lens 2015) is in SerC. SerABC accepts electrons from cytochrome c_4, combines with hydroquinone, and undergoes reduction under the catalysis of quinol-cytochrome *c* oxidoreductase (Lowe et al. 2010).

The mechanism of reduction of selenite to elemental Se has not been clarified. There are three well-recognized hypotheses regarding the SeO_3^{2-} reduction mechanism: (1) the role of selenite reductase in the periplasmic space (Li et al. 2014); (2) sulfide-mediated selenite reduction (Nelson et al. 1996); and (3) GSH-mediated selenite reduction (Kessi and Hanselmann 2004). Because GSH exists widely in a variety of microorganisms, this process is recognized by most people.

Compared with the dissimilation reduction of Se by microorganisms, there are few reports on other Se transformation methods. Based on microorganism-based Se methylation studies, some microorganisms can use selenate to form DMSe in the process of photoautotrophy as well as selenides to form DMSe (McCarthy et al. 1993). The Se methylating microorganisms isolated from soil and sediment include fungi and bacteria, whereas the Se methylating microorganisms in water are mainly bacteria (Swift 2002). The bacterial thiopurine methyltransferase (bTPMT) encoded by the *tpm* gene and the novel methylase encoded by the mmtA gene can convert selenite into DMSe and DMDSe (Ranjard et al. 2003, 2004, 2002). In anoxic sediments or anaerobic conditions, methylSe and dimethyl sulfides can undergo demethylation under the action of microorganisms; however, the current number of demethylated isolates is relatively small, and the types of reaction products have not been identified (Francis et al. 1974). In the study of Se assimilation by microorganisms, Se combines with amino acids through covalent bonds to form selenomethionine (Se-Met) and selenocysteine (Sec, U); Se-Met can non-specifically replace Met to participate in protein synthesis, and U specifically participates in protein synthesis (Böck et al. 2006). At present, few bacterial strains are known to be able to oxidize Se. As Se and S have similar chemical properties, the oxidation methods of Se and S are very similar (Blau 1961). Studies have shown that the oxidation of Se^0 to SeO_4^{2-} and SeO_3^{2} is mainly a biological process, and the speed is relatively slow (Torma and Habashi 1972; Dowdle and Oremland 1998). However, the oxidation mechanism of Se by microorganisms is still unclear and thus should be further examined.

Plant endophytes can also transform Se. Staicu et al. (2015) isolated the Se-tolerant endophytic strain, *Pseudomonas moraviensis*, from the Se hyperaccumulating plant, *Stanleya pinnata*, which can reduce the Se^{4+} of 790 mg L^{-1} to nanoscale Se^0 below the detection limit within 48 h, indicating that the endophytic strain has a strong ability to metabolize Se. Sura-de Jong et al. (2015) isolated a variety of Se-tolerant endophytes from the roots, stems, and leaves of *Stanleya pinnata* and *Astragalus bisulcatus* in Se-rich areas of California, which can reduce 15.8 g L^{-1} selenate and selenite to elemental Se. These endophytes can still grow in high Se medium containing 10 mg L^{-1} Se, whereas rhizosphere fungi isolated from non-Se hyperaccumulating plants in the same area cannot grow in high Se medium. Altogether, microorganisms participate in the transformation of Se in various valence states and the formation of organic Se. Further, the transformation of Se in nature cannot be separated from microorganisms.

In recent years, the physiological level and molecular mechanism of Se absorption and transformation in plants have been discovered. A certain basis exists for the study of plant absorption and transformation of selenate; however, the absorption and transformation of selenite and organic Se and the synergistic effect of environmental factors on Se absorption still need to be discussed. Se uptake by plants can induce a series of complex physiological responses in plants. Owing to many factors, such as environmental factors and Se levels, the accumulation of Se in plants can affect their own reproduction and development, and may also affect the habitat of plants. Therefore, it is of great significance to study the ecological effects of the interaction between Se and plants in the environment.

The absorption and metabolism of Se in plants are complex, but are closely related to the physical and chemical properties of soil. However, many related mechanisms are still unclear. From the viewpoint of human nutrition and health, how to improve the Se content in the edible part of crops must be urgently established. Se is unevenly distributed in various organs of plants and is mainly distributed in the unharvested parts of crops (Carvalho et al. 2003). With the development of molecular biology and by studying the mechanism of plant metabolism, it is possible to achieve the overexpression of target genes related to Se enrichment in specific plant tissues, such as grains, to increase the Se content of specific fractions in specific tissues of crops.

Although some progress has been made in the study of the interaction between Se and heavy metals, the mechanism of the interaction between Se and heavy metals is not clear. At present, research on the appropriate amount of Se that can alleviate the toxicity of heavy metals is mainly focused on the antioxidation of Se. However, the relationship between the plant antioxidant system and Se form and concentration under heavy metal stress and the relationship between the plant antioxidant system and heavy metal species must be clarified. In addition to activating the antioxidant system in plants, Se may also antagonize the toxic effects of heavy metals through other mechanisms; however, more experiments are needed to prove this hypothesis.

Further investigations are still needed to elucidate the mechanism of Se metabolism by microorganisms. Furthermore, more microbial resources involved in Se metabolism, especially the discovery of Se oxidizing bacteria, should be explored. However, the process of oxidation of elemental Se is markedly slower than the reduction process of Se. For the reduction and methylation of Se, much room still exists to explore the microbial resources. In addition, the reduction of Se is the most studied at present. However, the general law of selenate to selenite has not been fully clarified. The role of microorganisms in the transformation of soil Se is yet to be understood. The change in mode of microbial transformation of soil Se and how it affects the way plants absorb Se also need to be demonstrated. These questions need to be simultaneously resolved by researchers. The relationship between the existing fractions of Se in soil and the role of microorganisms must be understood to determine the status and ability of plants to absorb Se.

In this review, we discussed the migration and accumulation of Se in the plant-soil-microbe system. The physical and chemical properties of soil, microorganisms, and vegetation affect the migration of Se. Microbes play an important role in the transformation of Se. Se promotes plant growth and development and enhances plant resistance to adversity stress. Its metabolism in plants is an important physiological process. The circulation route of Se in the environment is relatively clear; however, there are still many aspects to be studied in depth. Understanding the distribution characteristics and migration rules of Se in the environment provides a reference and scientific basis for the development and utilization of Se resources and the development of Se-enriched agricultural systems.

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