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Review

Selenium-Mediated Rhizosphere Blocking and Control Network: Multidimensional Mechanisms for Regulating Heavy Metal Bioavailability

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Abstract

Soil heavy metal (HM) pollution poses a severe threat to ecological security and human health. Selenium (Se) is an essential trace element for the human body and can regulate crop growth and development as well as HM uptake in HM-contaminated soils. The regulatory mechanisms of Se on HMs are mainly reflected in four aspects: Geochemical immobilization promotes the formation of metal selenide precipitates and the adsorption of HMs by soil colloids by regulating the rhizosphere redox potential (Eh) and pH value. Rhizosphere microbial remodeling drives the enrichment of functional microorganisms such as Se redox bacteria, plant growth-promoting rhizobacteria (PGPR) and arbuscular mycorrhizal fungi (AMF) through the dual selective pressure of Se toxicity and root exudates, so as to synergistically realize Se speciation transformation and HM adsorption/chelation. Root barrier reinforcement constructs physical and chemical dual defense barriers by inducing the formation of iron plaques on the root surface, remodeling root morphology and strengthening cell wall components such as lignin and polysaccharides. Intracellular transport regulation down-regulates the genes encoding HM uptake transporters, up-regulates the genes encoding HM efflux proteins, and promotes the synthesis of phytochelatins (PCs) to form HM complexes and finally realizes vacuolar sequestration. Finally, we summarize current research gaps in the interaction mechanisms of different Se species, precise application strategies, and long-term environmental risk assessment, providing a theoretical basis and technical outlook for the green remediation of HM-contaminated farmlands and Se biofortification of crops.

Keywords: heavy metals; rhizosphere microorganisms; phytochelatins; regulatory mechanism; bioavailability

1. Introduction

Soil is the foundation of Earth's ecosystems and is critical for sustaining agricultural production and ensuring food security. However, with the rapid development of industrialization and intensive agriculture, soil heavy metal (HM) pollution has become increasingly severe[1]. Globally, approximately 14% to 17% of farmlands have toxic metal concentrations exceeding agricultural thresholds [2]. HMs such as cadmium (Cd), lead (Pb), and mercury (Hg) are highly biotoxic, persistent, and non-degradable [3], severely disrupting soil microbial community structure [4] and physicochemical properties [5], and reducing soil fertility. More critically, HMs easily transfer through the "soil-crop" system into the food chain-for example, rice's high Cd enrichment makes it the primary dietary source of Cd for humans [6], inducing various health risks including cardiovascular diseases [7], neurotoxicity [8], and cancer [9]. Therefore, effectively controlling the

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bioavailability of HMs in farmland soils and blocking their migration to crops is a major urgent issue in agricultural environmental science.

Selenium (Se) is an essential trace element for humans, with important biological functions such as antioxidant activity [10], anti-cancer effects [11], and cardiovascular protection [12]. Widespread Se deficiency globally increases the risk of diseases like Keshan disease [13] and type II diabetes [14]. Numerous studies have shown that agronomic biofortification measures (e.g., foliar Se spraying, soil Se fertilization) not only enhance crop Se content but also significantly reduce crop uptake and accumulation of HMs [15]. The realization of this "remediation-nutrition" dual effect highly depends on the rhizosphere-a dynamic microecological interface composed of plant roots and the closely associated surrounding soil [16]. The complex physicochemical environment (pH, redox potential (Eh))[17] and microbial activity [18] in the rhizosphere directly determine the interaction between Se and HMs. Thus, whether Se can effectively inhibit plant uptake of HMs largely depends on a series of chain reactions it triggers in the rhizosphere.

This paper focuses on the rhizosphere microdomain and systematically elaborates on the Se-mediated HM network from four dimensions: geochemical fixation, microbial synergy mechanisms, regulation of root structure and function, and molecular responses to intracellular immobilization and transport. The aim is to provide scientific support for constructing farmland pollution control strategies that balance "safe production" and "nutritional enhancement."

2. Geochemical Immobilization of HMs by Se

Before HMs directly interact with plant roots, Se first immobilizes HMs in the rhizosphere soil through geochemical processes, forming the first line of defense. This process primarily involves the formation of metal selenide precipitates and the adsorption of HMs by soil particles, which are strictly regulated by redox potential (Eh) and pH (Figure 1).

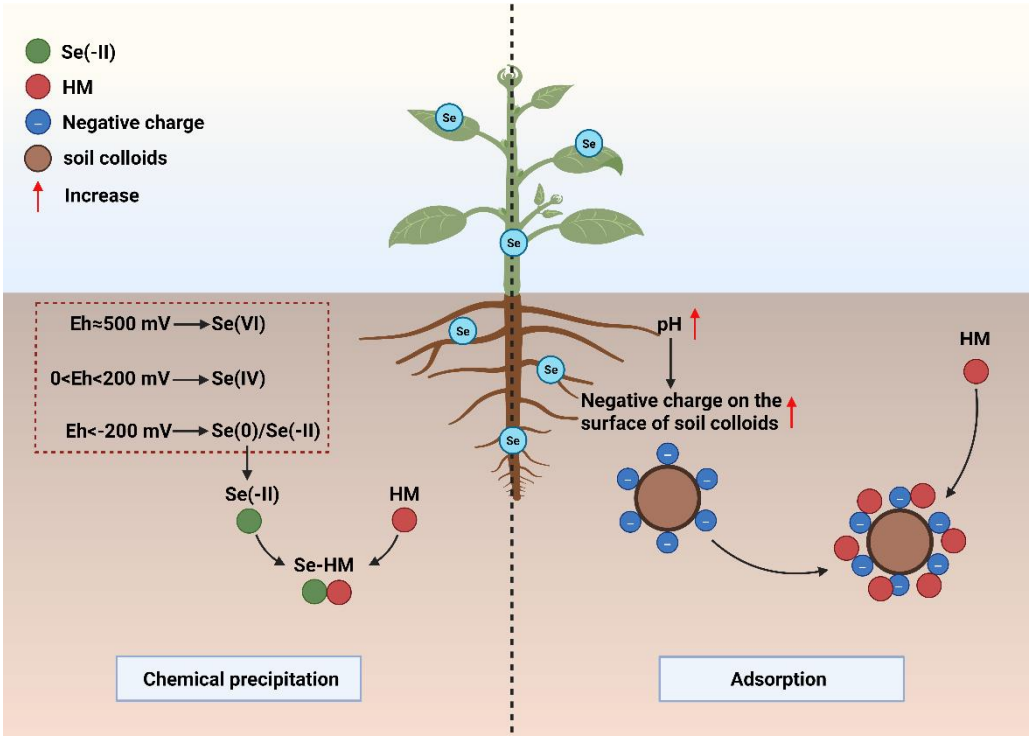

Figure 1. Se immobilizes HM through geochemical processes.Regulation of rhizosphere redox potentialand pH promotes metal selenide precipitation and HM adsorption by soil colloids. (HM: heavy metal; Eh: Redox Potential; Se(VI): selenate; Se(IV): selenite; Se(0): elemental Se; Se(-II): selenide; Se-HM: complexes formed by Se and HMs.

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2.1. Effect of Eh on Chemical Precipitation of Se and HMs

Chemical coprecipitation between Se and HMs is the most fundamental and long-lasting mechanism for Se-mediated HM immobilization. When Se exists in the Se(-II) form in soil, it rapidly reacts with HM ions to form insoluble metal selenide particles, thereby reducing the bioavailability of HMs [19]. Eh is the primary factor determining Se speciation transformation and is influenced by soil waterlogging conditions [20].

Soil Se exists in four main forms: **Selenate (Se (VI))**: Highly mobile due to high solubility and weak adsorption. **Selenite (Se (IV))**: Strongly adsorbed by soil minerals. **Elemental Se (Se (0))**: Chemically stable and insoluble. **Selenide (Se (-II))**: A highly reactive reduced form that precipitates with HMs [21].

Under high Eh conditions (≈500 mV), Se mainly exists as highly mobile Se(VI). As Eh decreases (0–200 mV), strongly adsorbed Se(IV) becomes dominant [22]. In strongly reducing environments (Eh < -200 mV, e.g., waterlogged conditions), high-valence Se is reduced to insoluble Se(0) and ultimately to Se(-II) [23]. For example, Mal J et al. found that in sludge systems with low Eh, Se(IV) was reduced to Se(-II) and reacted with Pb(II) to form insoluble PbSe precipitates. However, decreasing Eh may also affect the chemical precipitation of anionic HMs such as arsenic (As) [24]. Wan et al. showed that Se application reduced As uptake by rice under aerobic conditions but *promoted* As accumulation in rice under waterlogged conditions [25].

In addition to soil Eh, the bioavailable molar ratio of Se to HMs in soil is another critical factor affecting the formation of insoluble metal selenides. Studies have found that when the bioavailable molar ratio of Se to Cd exceeds 0.7, bioavailable Se can be reduced to Se(-II), followed by the formation of insoluble CdSe, which significantly reduces Cd content in crops. Conversely, Cd may be more efficiently absorbed by roots in the form of $CdSeO_3$ and $CdSeO_4$ [26]. Wang et al. also observed that an effective molar ratio of 1 between Se and Hg in soil leads to the formation of insoluble HgSe [27]. Therefore, when using Se to inhibit HM uptake by crops, soil Eh conditions should be adjusted based on soil pollution status to ensure optimal remediation effects.

2.2. Effect of Rhizosphere pH on HM Adsorption by Soil Colloids

Soil pH changes directly affect the solubility of HMs in soil. Se application can effectively regulate rhizosphere soil pH, and variations in soil pH directly influence the surface charge properties of soil colloids (e.g., clay minerals, organic matter), thereby altering the adsorption and desorption behaviors of HM ions. Studies have shown that the increase in pH generates hydroxide ions (OH^-), which enhance the negative charge content on the surface of soil colloids—this reduces the bioavailability of HM cations such as Cd, Pb, Mn, and Hg, but *increases* the mobility of oxyanions like As, Sb, and Se [28].

Thus, increasing soil pH can enhance the effect of Se on inhibiting cationic HM uptake. For example, Wan et al. found that elevated pH reduced the adsorption of Se(IV) by soil minerals by increasing the negative charge on their surfaces, thereby raising the effective concentration of Se in soil solution and ultimately enhancing the immobilization efficiency of Cd by Se [29]. Research on rice also clearly demonstrated that Se(IV) application significantly increased rhizosphere soil pH; this pH elevation directly reduced the mobility of Cd in soil and ultimately decreased Cd accumulation in plants [17]. This pH-regulating effect has important practical implications—for instance, combining Se with traditional soil amendments that increase pH (e.g., lime) can further immobilize Cd in soil, thereby strengthening the inhibition of Cd uptake by rice [30].

3. Rhizosphere Microbe-Mediated Immobilization of HMs by Se

The rhizosphere microbiome, known as the "second genome of plants," serves as the core hub connecting soil and plants [31]. Se can reshape the rhizosphere microbial community structure through dual selection pressures (self-induced selection pressure and regulation by root exudates).

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These communities can either directly immobilize HMs or achieve HM immobilization by transforming Se speciation [32] (Figure 2).

3.1. Se-Driven Construction of Rhizosphere Microbial Communities

Se exerts a significant selective enrichment effect on rhizosphere soil microbes. In the context of HM pollution, Se application can construct a functional microbial community capable of efficiently coping with HM stress. Microbes with both Se metabolism and HM detoxification capabilities—such as *Bacillus* [32], *Pseudomonas* [33], and *Sphingomonas* [34]—proliferate extensively and become dominant populations [35]. To reshape the composition and function of the rhizosphere microbial community, Se primarily acts through a dual pathway mediated by self-induced selection pressure and root exudates.

On one hand, Se at a certain concentration is toxic to many microbes, creating a strong environmental selection pressure. Only microbes with Se resistance or efficient detoxification mechanisms (e.g., reduction, methylation) can survive and become dominant. For example, in high-Se soils, the relative abundance of Proteobacteria and Firmicutes increases, with *Pseudomonas* and *Bacillus* becoming dominant genera [31].

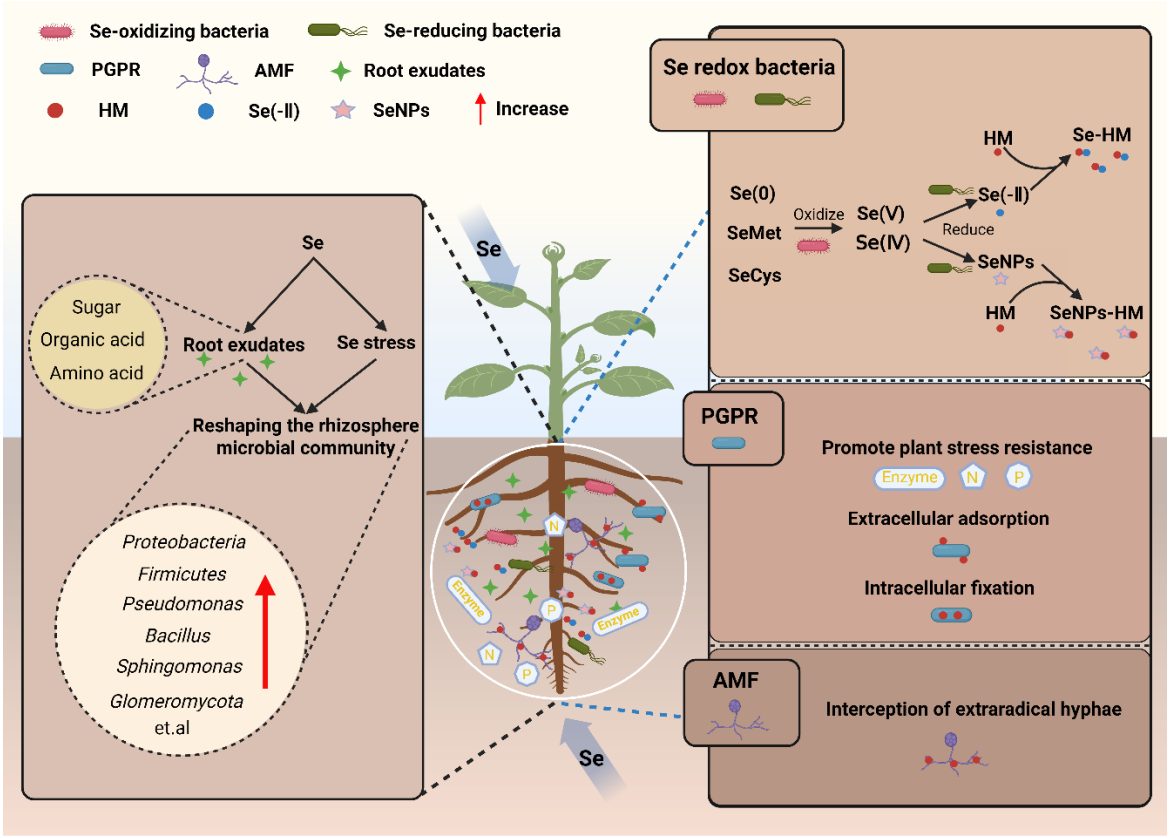

Figure 2. Rhizosphere microorganisms mediate Se-induced HM immobilization.Se remodels rhizosphere microbiota through its stress and root exudates; microbiota immobilize HM directly or through Se form transformation. (HM: heavy metal; Se(VI): selenate; Se(IV): selenite; Se(0): elemental Se; Se(-II) selenide; SeCys: Selenocysteine; SeMet: Selenomethionine; SeNPs: nano selenium; Se-HM: complexes formed by Se and HM; SeNPs-HM: complexes formed by nano selenium and HM; PGPR: plant growth-promoting rhizobacteria; AMF: arbuscular mycorrhizal fungi).

On the other hand, Se can alter the composition of root exudates by influencing plant physiological status. Root exudates (e.g., sugars, organic acids, amino acids) are not only the main nutrient source for rhizosphere microbes but also signal molecules mediating microbe-plant interactions; their changes directly drive shifts in microbial communities [36]. Metabolomics studies

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confirm that Se treatment increases the concentration of organic acids (citric acid, malic acid) and decreases sugars (glucose, fructose) in *Arabidopsis thaliana* root exudates, leading to a significant increase in the abundance of carbon source-preferring microbes (e.g., *Sphingomonas*) [37]. Li et al. [39] found that under Cd-contaminated conditions, nano-Se treatment significantly increased the release of sugars (e.g., glucose, fructose, sucrose) and phenolic acids (e.g., vanillic acid, p-hydroxybenzoic acid, and syringic acid) from pepper roots. These exudates effectively recruited and enriched beneficial microbes such as *Gammaproteobacteria*, *Alphaproteobacteria*, and *Bacteroidota* in the rhizosphere, thereby reducing the bioavailability of Cd and its accumulation in pepper plants [38].

3.2. Rhizosphere Microbe-Mediated Immobilization of HMs

3.2.1. HM Immobilization via Microbial Regulation of Se Speciation

Rhizosphere microbes can directly alter the chemical speciation of Se—the most direct manifestation of their regulatory role. Through a series of redox reactions, microbes convert highly toxic, soluble Se(IV)/Se(VI) into low-toxicity, insoluble Se(0), Se nanoparticles (SeNPs), and Se(-II), thereby indirectly achieving HM immobilization [39] (Table 1).

Table 1. Immobilization of HMs by rhizosphere microbe-mediated Se.

Microbial Species	Microbial Name	Core Function(s)	Reference
Se-reducing Bacteria	*Pseudomonas* spp	Reduces Se (VI)/Se (IV) to Se (0) or Se (-II)	[40]
	Rhizobium sp.	Reduces Se (IV) to SeNPs (selenium nanoparticles)	[41]
	Burkholderia fungorum	Reduces Se (IV) to SeNPs or Se (-II)	[42]
	Paenirhodobacter enshiensis	Reduces Se (IV) to SeNPs	[43]
	Comamonas testosteroni S44	Reduces Se (IV) to Se (0) or Se (-II)	[44]
	Bacillus megaterium	Reduces Se (IV)/Se (0) to Se (-II)	[45]
	Streptomyces sp. ES2-5	Reduces Se (IV) to Se (0) nanoparticles	[46]
	Thiobacillus ferrooxidans	Reduces Se (0) to Se (-II)	[47]
	Bacillus selenitireducens	Reduces Se (IV) to SeNPs	
Se-oxidizing Bacteria	*LX-1*	Oxidizes Se (0), SeMet (selenomethionine), and $SeCys_2$ (selenocystine) to Se (IV)	[48]
	LX-100	Oxidizes Se (0), SeMet, and $SeCys_2$ to Se (IV)	
	T3F4	Oxidizes Se (0), SeMet, and $SeCys_2$ to Se (IV)	
PGPR (Plant Growth-Promoting Rhizobacteria)	*Bacillus proteolyticus SES*	Enhances HM immobilization by secreting metabolites	[32]
	Bacillus cereus RC-1	Adsorbs Cd through the cell wall and chelates Cd via intracellular metallothioneins (MTs)	[49]
AMF (Arbuscular Mycorrhizal Fungi)	*Rhizophagus intraradices*	Physically intercepts and adsorbs HMs through hyphae	[50]

Microbial Se reduction is one of the most critical HM immobilization mechanisms in the rhizosphere. Se-reducing bacteria are widely distributed: currently known selenite-reducing bacteria mostly belong to Proteobacteria (e.g., *Pseudomonas* spp. [40], *Rhizobium* sp. [41], *Burkholderia fungorum* [42], *Paenirhodobacter enshiensis* [43], *Comamonas testosterone* [44]), Firmicutes (e.g., *Bacillus* spp. [45]), and Actinobacteria (e.g., *Streptomyces* sp. [46])—a pattern likely linked to the abundant thiol compounds in these phyla. These microbes reduce high-valence, mobile Se to low-valence Se(0),

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which is often further synthesized into SeNPs by microbes [51]. Se(0) may also be reduced to Se(-II): for example, the obligate acidophile *Thiobacillus ferrooxidans* and selenite-respiring bacterium *Bacillus selenitireducens* can convert Se(0) to Se(-II) [47]. Both SeNPs and Se(-II) reduce metal mobility and bioavailability. Microbe-synthesized SeNPs exhibit slow-release properties, stability, strong bioactivity, and environmental friendliness; they are typically spherical with high surface area and negative surface charge, enabling better adsorption of HMs [52]. Se(-II) forms stable metal selenides with HMs, and microbes tend to reduce Se to metal selenides in the presence of HMs [53]. This reduction mechanism allows Se fertilizers to act as efficient precipitants, forming highly insoluble metal selenides with HMs in soil solution and thus reducing the bioavailability of rhizosphere HMs.

While Se oxidation proceeds much slower than efficient Se reduction, it remains an important pathway to increase the concentration of bioavailable Se in soil [54]. Se(0) and organic Se (e.g., selenomethionine (SeMet), selenocystine ($SeCys_2$)) are naturally occurring Se forms in soil but have extremely low bioavailability: Se(0) cannot be directly absorbed by plants; SeMet and $SeCys_2$ are mostly bound to soil organic matter, making them difficult to release into soil solution for interaction with HMs [55]. Certain Se-oxidizing bacteria can oxidize low-valence, recalcitrant Se in soil to more mobile high-valence Se, thereby enhancing soil Se bioavailability [56]. High-valence Se is not only easily absorbed by plants but also readily reduced by Se-reducing bacteria to Se(-II) or SeNPs for HM binding and precipitation. Studies have shown that three Se-oxidizing bacteria (LX-1, LX-100, and T3F4) can oxidize soil SeMet, $SeCys_2$, and Se(0) to Se(IV), increasing the available Se content for rapeseed uptake while inhibiting Cd absorption and increasing Se content in aboveground plant parts [48]. In pak choi (*Brassica rapa* L.), application of the Se-oxidizing bacterium T3F4 was also shown to improve soil Se mobility, thereby promoting Se uptake and reducing As accumulation [57].

3.2.2. Other Microbe-Mediated HM Immobilization Mechanisms

Rhizosphere microbial communities co-selected by Se and HMs often include efficient plant growth-promoting rhizobacteria (PGPR). These microbes enhance plant stress resistance through multiple pathways—e.g., secreting ACC deaminase to reduce ethylene stress [58], and strengthening nutrient cycling (e.g., N, P)—thereby mitigating HM toxicity[59]. Additionally, some tolerant strains (e.g., *Bacillus cereus* RC-1) can immobilize HMs via two mechanisms: adsorption by hydroxyl-rich cell walls, and intracellular binding to proteins such as metallothioneins (MTs) after HM ions are transported into cells [49].

In addition to abundant PGPR, rhizosphere soil also contains mycorrhizal fungi [60]. Among them, arbuscular mycorrhizal fungi (AMF) are closely associated with plant tolerance to HM stress: their extraradical hyphae not only form a network to block HMs but also adsorb and immobilize HMs via cell wall components (e.g., polysaccharides, chitin), reducing HM migration to plant roots [61].

Based on the above-described interactions between Se and rhizosphere microbes, combining exogenous Se application with inoculation of specific microbial agents (e.g., PGPR, AMF) that have efficient HM resistance and transformation capabilities often produces a synergistic effect superior to single treatments. This strategy integrates the chemical and biological regulatory effects of Se with microbial bioaugmentation, making it the most promising application approach to date. Liu et al. found in a pot experiment that combined treatment of *Rhizophagus intraradices* (AMF) inoculation and Na_2SeO_3 application under Cd stress in wheat successfully reduced soil Cd bioavailability and wheat Cd content, alleviated wheat damage, and exhibited more significant effects than single treatments [50].

4. Regulation of Plant Root Structure and Function by Se

If rhizosphere chemical and microbial processes are “exogenous barriers,” then Se-mediated active regulation of plant roots constructs the second line of defense against HM uptake. Se can reduce root absorption of HMs by inducing iron plaque formation on root surfaces, reshaping root morphology, and strengthening cell wall components.

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4.1. Se-Induced Formation of Root Iron Plaque

Root iron plaque (IP) is a reddish-brown gelatinous film formed on the roots of wetland plants (e.g., rice) in waterlogged soil. Specifically, plants transport oxygen from aboveground tissues to roots via unique aerenchyma, then release it into the rhizosphere microenvironment through radial oxygen loss (ROL), creating an oxidizing environment that promotes the oxidation of soluble Fe(II) to Fe(III) and its deposition as amorphous iron oxide (FeOOH) and iron hydroxide ($Fe(OH)_3$) on root surfaces [62]. Iron plaque significantly restricts HM migration from soil to roots through two mechanisms: Tightly covered iron plaques directly block HMs from entering root cells [63]; Abundant hydroxyl groups (-OH) on the plaque surface immobilize HM ions via electrostatic interactions [64] (Figure 3a).

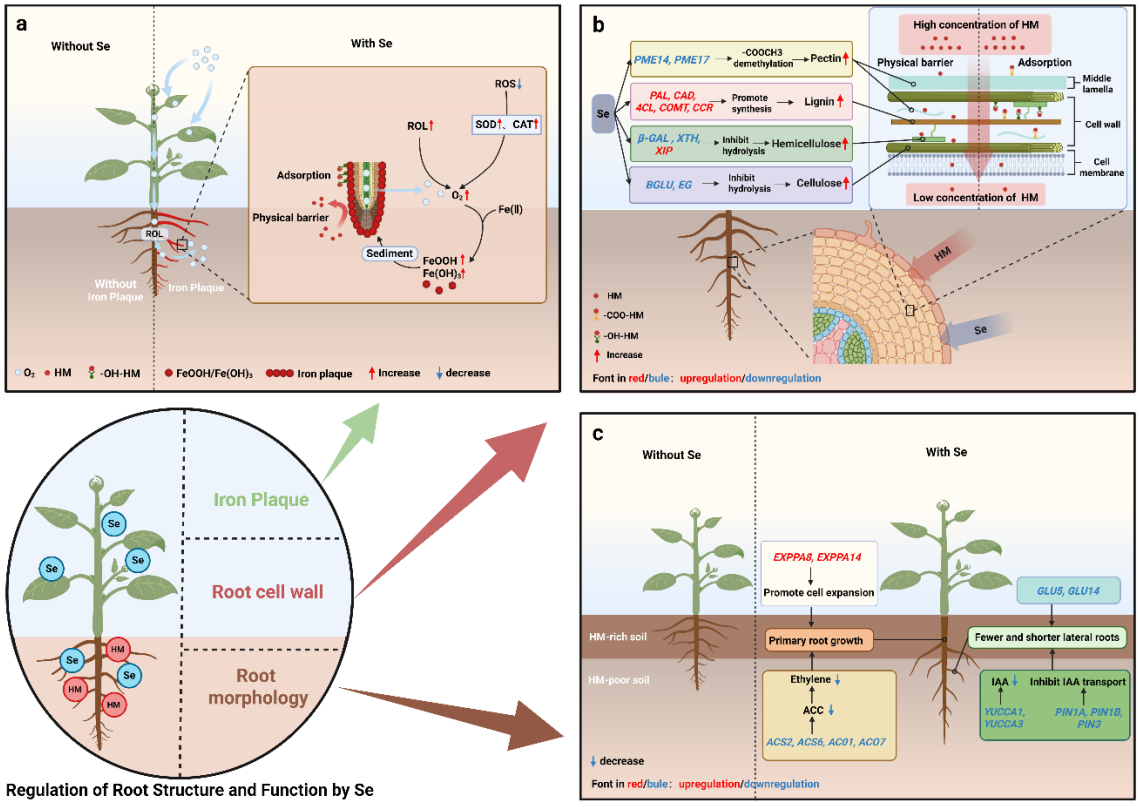

Figure 3. Se resists HM stress by regulating plant root structure and function.Se reduces root uptake of HM by inducing root surface iron plaque formation **(a)**, strengthening cell wall components **(b)** and remodeling root morphology **(c)**. (HM: heavy metal; -OH-HM: HM bound to hydroxyl groups; -COO-HM: HM bound to carboxylate groups; ROL: radial oxygen loss; ROS: reactive oxygen species; SOD: superoxide dismutase; CAT: catalase).

In the presence of Fe^{2+}, Se can influence root iron plaque formation by regulating root ROL levels, thereby blocking HM migration to roots [65]. Firstly, Se alleviates physiological damage to rice root aerenchyma caused by HMs, increasing root porosity and providing structural support for downward oxygen transport, which directly enhances ROL intensity at root tips [66]. Secondly, Se activates the activity of antioxidant enzymes such as superoxide dismutase (SOD) and catalase (CAT), accelerating the degradation of reactive oxygen species (ROS, e.g., O_2^-, H_2O_2) induced by HM stress. This process not only mitigates root damage but also produces O_2, indirectly increasing internal root oxygen content and providing an oxygen source for ROL [67].

The form of Se, application timing, and chemical form and content of HMs all affect the effect of Se on root iron plaque formation and HM immobilization. **Effect of Se forms**: Wang et al. found that

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Se(IV) promotes As transport from iron plaque to roots, while Se(VI) significantly inhibits this process—though the underlying mechanism remains unclear [68]. **Effect of application timing**: Huang et al. noted that Se application during the rice tillering stage (peak period of rhizosphere oxygen release via ROL) significantly induces extensive iron plaque formation on root surfaces at the heading stage, thereby maximizing inhibition of root Cd uptake[66]. **Effect of HM speciation and content**: Liu et al. found that Se only promotes iron plaque formation on rice roots under Sb(III) stress but has no significant effect on Sb(V)-exposed groups [69]. Huang et al. also confirmed that Se can immobilize Cd by promoting iron plaque formation only in low-Cd-contaminated soils, but fails to effectively induce iron plaque in high-Cd-contaminated soils [30].

4.2. Se Reshapes Root Morphology to Avoid HM Pollution

Root morphology plays a crucial role in plant resistance to HM toxicity and stress. A larger root surface area may lead to higher HM accumulation; thus, reducing lateral root number and increasing primary root dominance helps plants decrease HM uptake [70]. Additionally, plants can alter the spatial distribution of roots in HM-contaminated soil to avoid environments with high HM content [71].

Numerous studies have shown that Se can induce changes in plant root morphology, thereby reducing HM absorption and accumulation. For example, Ding et al. found that Se treatment in rice reduced the proportion of lateral roots, increased the proportion of primary roots, and significantly decreased Cd uptake [72]. The core mechanism of Se-regulated root morphology may involve the regulation of auxin (IAA) and ethylene biosynthesis, but there are significant differences in the regulatory mechanisms for primary and lateral roots. Se downregulates ethylene synthesis genes (ACS2/6, ACO1/7) to reduce the concentration of the ethylene precursor ACC, ultimately decreasing root ethylene levels; it also upregulates cell expansion genes (EXPA8/14, EXPB2/3) to promote primary root cell elongation, resulting in increased primary root length. For lateral roots: Se downregulates auxin synthesis genes (YUCCA1/3) to reduce IAA accumulation, while also downregulating auxin transport genes (PIN1A/B, PIN3) and key lateral root formation genes (GLU5/14), leading to reduced lateral root number and length [73] (Table 2).

Thus, Se treatment can both adjust the ratio of primary to lateral roots (reducing root surface area and thus HM uptake sites) and increase primary root length (guiding roots to migrate from the surface to deeper soil layers, actively avoiding HM-enriched topsoil and reducing exposure intensity) (Figure 3b).

Table 2. Influence of Se on the expression of genes related to root structure and function in crops.

Crop species	Gene	Gene function(s)	Gene expression after Se application	Reference
Oryza sativa L.	*EXPA8/14*	Promotes elongation of primary root cells	Upregulation	[73]
	EXPB2/3	Promotes elongation of primary root cells		
	ACS2/6	Synthesizes ethylene and promotes lateral root development		
	ACO1/7	Synthesizes ethylene and promotes lateral root development		
	YUCCA1/3	Synthesizes auxin and promotes lateral root development	Downregulation	
	PIN1A/B	Transports auxin and promotes lateral root formation		
	PIN3	Transports auxin and promotes lateral root formation		

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Capsicum annuum L.	*GLU5/14*	Promotes the formation and development of lateral root primordia, increasing the number and length of lateral roots	Upregulation	[74]
	XIP	Inhibits xylanase from cleaving xylan chains in hemicellulose		
	PME14/17	Catalyzes pectin demethylation to expose carboxyl groups	Downregulation	
	PAL	Catalyzes the conversion of phenylalanine to cinnamic acid, providing precursor substances for lignin synthesis	Upregulation	[75]
	CAD	Involved in lignin monomer synthesis		
	4CL	Catalyzes the conversion of coumaric acid to coumaryl-CoA, providing precursors for lignin synthesis		
	COMT	Catalyzes methylation reactions in lignin synthesis		
	CCR	Catalyzes lignin monomer synthesis		
Triticum aestivum L.	*β-GAL*	Hydrolyzes galactose residues in hemicellulose and participates in cell wall polysaccharide remodeling	Downregulation	[76]
	XTH	Hydrolyzes xyloglucan in hemicellulose		
	BGLU	Hydrolyzes cellobiose and decomposes cellulose		
	EG	Randomly cleaves cellulose polymer chains and degrades cellulose		

4.3. Se Enhances the HM Barrier Capacity of Root Cell Walls

The root cell wall is the last barrier for HMs entering plant cells, and changes in its components and structure directly determine its ability to block HMs. The cell wall is mainly composed of lignin, cellulose, hemicellulose, and pectin; the middle lamella adjacent to the cell wall is also pectin-based [77]. Se can intercept HMs from entering root cells through regulating genes related to root cell wall components and leveraging the cell wall's physical barrier and adsorption functions [76] (Figure 3c, Table 2).

4.3.1. Se Promotes Lignin Synthesis in Root Cell Walls

Lignin, synthesized via the phenylpropanoid pathway, is a hydrophobic polymer critical for plant resistance to HM stress [78]. HM stress induces phenolic compound accumulation, enhancing lignin deposition to form a physical barrier; additionally, carboxyl and phenolic hydroxyl groups in lignin can adsorb HMs [79]. Studies show that Se treatment significantly upregulates the expression of key lignin synthesis genes (e.g., *PAL*, *CAD*, *4CL*, *COMT*), activating the phenylpropanoid metabolic pathway, increasing lignin content in root cell walls, maintaining cell wall integrity, and hindering further infiltration of HM ions into the cytoplasm [75]. In wheat, key lignin synthesis genes *CAD* and *CCR* are also upregulated by SeNPs, thereby enhancing Cd barrier capacity [76].

4.3.2. Se Increases Cell Wall Polysaccharide Content

Se can significantly increase the content of cell wall polysaccharides (pectin, hemicellulose, cellulose).

Pectin: Composed mainly of galacturonic acid with abundant carboxyl groups. Pectin methylesterase (PME) catalyzes the hydrolysis of methyl ester bonds in pectin's galacturonic acid residues ("demethylation"), exposing free carboxyl groups (-COOH) for binding to HMs [80]. Se treatment downregulates the PME inhibitor genes *PME14* and *PME17*, reducing the synthesis of PME

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inhibitor (PMEI) and promoting pectin demethylation, thereby significantly enhancing the chemical binding capacity of cell walls for HMs [74].

Hemicellulose: A heteropolysaccharide composed of xylan, mannan, and other polymers, whose hydroxyl groups can adsorb a certain amount of HM ions. Studies show that Se regulates genes related to hemicellulose biosynthesis: it downregulates the β-galactosidase-encoding gene *β-GAL* to reduce hydrolysis of galactose residues in hemicellulose (ensuring binding stability between hemicellulose and other components), downregulates the xyloglucan hydrolase-encoding gene *XTH* to inhibit xyloglucan hydrolysis (avoiding hemicellulose structural damage) [76], and upregulates the xylanase inhibitor protein-encoding gene *XIP* to directly inhibit xylanase cleavage of the xylan backbone (blocking xylan degradation and maintaining hemicellulose stability) [74].

Cellulose: A fiber network formed by β-glucan chains via hydrogen bonds, serving as the framework component of the cell wall. Its hydroxyl groups can bind metals, and its tight cross-linking with hemicellulose increases overall specific surface area and HM binding sites, enhancing the cell wall's physical barrier function against HMs [81]. Research indicates that nano-Se inhibits cellulose degradation by downregulating the β-glucosidase-encoding gene *BGLU* and endoglucanase-encoding gene *EG*, thereby improving Cd immobilization capacity [76].

5. Se Regulates HM Transport in Root Cells

Despite the layered defenses constructed by geochemical immobilization, changes in plant root structure and function, and microbial synergistic interception in the rhizosphere, some HM ions inevitably enter root cells. At this stage, Se reduces HM entry into cells and sequesters HMs within root cells by precisely regulating the expression of genes related to HM uptake, transport, and compartmentalization in root cells, thereby blocking their translocation to aboveground edible parts (Table 3, Figure 4).

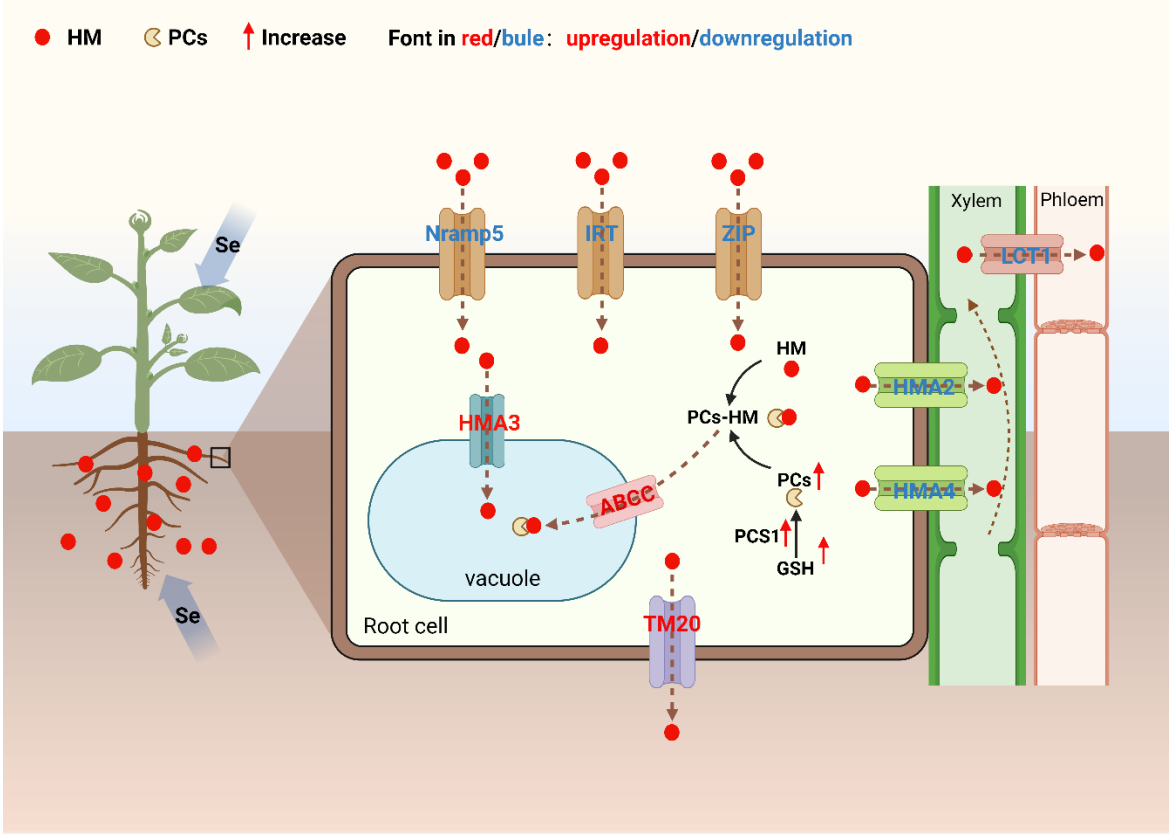

Figure 4. Se regulates HM transport in root cells.Se regulates the expression of root cell genes related to HM uptake, transport, and sequestration, reducing HM entry, retaining them in roots and blocking transport to

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shoots. (HM: heavy metal; PCs: phytochelatins; PCS1: phytochelatin synthase 1; PCs-HM: HM bound to phytochelatins; GSH: glutathione; Nramp 5: natural resistance-associated macrophage protein 5; IRT: iron-regulated transporter; ZIP: zinc-regulated transporter/iron-regulated transporter protein; TM20: transmembrane protein 20; HMA2/4: HM ATPase 2/4; HMA3: HM ATPase 3; ABCC: ATP-binding cassette subfamily C; LCT1: low-affinity cation transporter 1).

Table 3. Influence of Se on the expression of genes related to HM uptake, transport, and immobilization in crop roots.

Crop species	Gene name	Gene function (s)	Gene expression after Se application	Reference
Oryza sativa L.	*OsNramp5*	Mediates Cd uptake by root cells	Downregulation	[82]
	OsIRT1	Mediates Fe and Cd uptake by root cells		
	OsIRT2	Mediates Fe and Cd uptake by root cells		
	OsZIP1	Me diates Fe and Cd uptake by root cells	Downregulation	[83]
	OsPCS1	Promotes the synthesis of phytochelatins (PCs)	Upregulation	
	OsHMA2	Transports root Cd into the xylem	Downregulation	[84]
	OsHMA4	Transports root Cd into the xylem		
	OsLCT1	Transports Cd to leaves and grains	Downregulation	[85]
	OsHMA3	Transports Cd to vacuoles	Upregulation	[86]
Triticum aestivum L.	*TaTM20*	Mediates Cd efflux from root cells	Downregulation	[87]
Brassica juncea L.	*ABCC*	Transports PCs-Cd complexes to vacuoles	Upregulation	[88]

5.1. Se Inhibits HM Uptake and Transport in Root Cells

First, Se can inhibit HM uptake by plant root cells. Since HM ions such as Cd are physicochemically similar to certain essential mineral elements (Fe^{2+}, Zn^{2+}, Mn^{2+}), they often enter root epidermal cells by competing for and utilizing the transport channels of these essential elements. The manganese transporter Nramp5, a member of the natural resistance-associated macrophage protein (Nramp) family, has been identified as the primary transporter for Cd uptake in root cells [89]. iron-regulated transporters (IRT) such as IRT1, IRT2, and members of the zinc/iron-regulated transporter (ZIP) family such as ZIP1 in root cells also have Cd transport functions [90]. Existing studies show that Se treatment can downregulate the expression of these genes, thereby restricting Cd entry into root cells. Cui et al. found that Se treatment significantly inhibited the expression of OsNramp5, OsIRT1, and OsIRT2, directly reducing the Cd uptake rate of rice suspension cells [82]. Meanwhile, Barman et al. also found that Se treatment significantly downregulated the expression of OsZIP1, reducing Cd uptake in rice roots. In addition to inhibiting uptake, Se application can also stimulate the expression of the Cd efflux protein TM20[83]. In wheat roots, Se application significantly downregulated TaNramp5 while also upregulating TaTM20, which not only reduced Cd uptake but also promoted Cd efflux, further enhancing wheat tolerance to Cd [87].

Second, Se can inhibit the translocation of HMs from root cells to aboveground edible parts. HM ATPase (HMA) family members HMA2 and HMA4, mainly located on the plasma membrane of xylem parenchyma cells in plant roots, are responsible for pumping metal ions such as Zn and Cd from root stele parenchyma cells into the xylem, initiating their long-distance transport to aboveground parts [91]. In rapeseed (*Brassica napus*), Se inhibits the expression of HMA2 and HMA4, reducing the efficiency of Cd translocation from roots to aboveground parts [92], and the same

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conclusion has been found in rice [84]. The low-affinity cation transporter (LCT1), located on the plasma membrane of the root phloem, is responsible for transporting Cd from cells to leaves and grains [93]. In rice, Se treatment can also downregulate the expression of *OsLCT1*, leading to a decrease in Cd content in inflorescences and grains [85]. By inhibiting the expression of these key transport genes, Se effectively reduces the distribution of Cd from roots to stems, leaves, and grains, ensuring the safety of agricultural products.

5.2. Se Promotes Chelation and Compartmentalization of HMs in Root Cells

When HM ions inevitably enter root cells, plants immediately immobilize them within the cells. This process involves two synergistic mechanisms: (1) binding HM ions with chelators to form stable, low-toxicity complexes; and (2) pumping these complexes or free HM ions into vacuoles for compartmentalized storage via vacuolar membrane transporters.

5.2.1. Se Enhances HM Chelation Capacity of Root Cells

Se treatment significantly improves the chelation capacity of plant cells for HM ions. HM chelators in plants mainly include phytochelatins (PCs) and metallothioneins (MTs), which bind HM ions via abundant sulfhydryl groups (-SH) to form stable complexes, thereby reducing their biological activity [94]. Se increases intracellular PCs content by promoting the synthesis of PCs precursor glutathione (GSH) and activating the expression of the key PCs synthase gene *PCS1*, thus chelating HMs. In rice, Se treatment significantly increases GSH content and promotes *OsPCS1* expression in root cells, enhancing PCs levels to form stable PCs-Cd complexes, which are then transported into vacuoles for sequestration [83]. In tobacco, Se has also been shown to upregulate *PCS1* to chelate chromium (Cr) [95].

5.2.2. Se Activates Vacuolar Membrane Transporters to Enhance Compartmentalization Efficiency

Vacuoles are the primary organelles for storing and sequestering toxic substances in plant cells; efficient transport and compartmentalization of HM ions into vacuoles is a core mechanism for plants to cope with HM stress [96]. HM ATPase 3 (HMA3), a member of the HMA family, is a key transporter localized on the vacuolar membrane of root cells, specifically responsible for pumping HMs into vacuoles [97]. For example, in rice, Se treatment significantly activates *OsHMA3* expression, promoting Cd transport and sequestration into vacuoles of root cells [86]. Additionally, in mustard (*Brassica juncea*), Se treatment also activates genes of the ATP-binding cassette (ABC) transporter subfamily ABCC, whose members are confirmed to participate in transporting stable PCs-Cd complexes into vacuoles [88]. By activating these vacuolar membrane transporters, Se greatly enhances the ability of root cells to stabilize HMs in the cytoplasm and safely sequester them in vacuoles.

6. Conclusions

Se regulation of HM bioavailability in the rhizosphere system is a multi-dimensional, synergistic, and complex interaction network. Geochemically, Se reduces HM mobility at the source by regulating rhizosphere redox potential (Eh) and pH, inducing precipitation of metal selenides (e.g., CdSe, HgSe), and enhancing soil colloid adsorption. In terms of microbial synergy, Se reshapes the rhizosphere microbial community, indirectly immobilizing HMs by regulating Se speciation transformation and directly participating in HM sequestration via microbial adsorption and chelation. At the root structure and function level, Se induces root iron plaque formation, reshapes root morphology (reduces lateral root proportion, extends primary root), and strengthens root cell wall components (promotes lignin and polysaccharide synthesis), enhancing physical interception and adsorption of HMs. Intracellularly, Se inhibits the expression of HM uptake and transport genes (e.g., *Nramp5*, *HMA2*), promotes phytochelatin synthesis, and facilitates vacuolar compartmentalization of HM complexes, sequestering HMs in roots. This multi-level network not

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only effectively blocks HM migration to edible parts but also provides a theoretical basis for producing Se-enriched agricultural products.

Although the core mechanisms of Se regulation on rhizosphere HM bioavailability have been extensively elucidated, current research still faces key directions for breakthroughs. Future studies need to further focus on cross-interaction mechanisms between different Se species (e.g., Se nanoparticles, organic Se) and HMs, plant roots, and microorganisms in the rhizosphere microenvironment, especially clarifying molecular-level signaling pathways and gene co-regulation rules to improve the theoretical system. For actual scenarios such as soil type differences (acidic/alkaline) and combined HM pollution (e.g., Cd-Pb-As), it is necessary to optimize Se application forms, doses, and timing, and establish precise application schemes adapted to "soil-crop-HM type" to enhance the stability of field applications. Meanwhile, it is essential to strengthen the evaluation of potential impacts of long-term Se application on soil ecological functions (e.g., microbial diversity, enzyme activity) and agricultural product quality to avoid environmental risks. Additionally, accelerating the translation of laboratory results to field practice, combining the growth characteristics of major food and cash crops, and formulating standardized agricultural technical regulations that balance HM control efficiency and Se nutritional fortification effect will effectively provide technical support for ensuring food security and public health.

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