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Review

Progress in Elucidating the Mechanism of Selenium in Mitigating Heavy Metal Stress in Crop Plants

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Abstract: In the context of rapid industrialization and agricultural modernization, the issue of heavy metal (HM) pollution has surfaced as a critical concern, posing a substantial threat to human health and having a profound impact on agricultural cultivation. Selenium (Se), a beneficial micronutrient for crop growth and development, exerts numerous beneficial effects, including facilitating photosynthesis, enhancing physiological attributes, improving nutritional quality, strengthening antioxidant systems, and modulating the expression of stress-responsive genes. Notably, Se plays a pivotal role in alleviating HM stress in crops and effectively mitigating the accumulation of HMs in edible plant parts. This study investigates the physiological and molecular mechanisms underlying Se's capacity to alleviate HM stress in crops. Additionally, we discuss the application of Se-enriched fertilizers in agricultural practices, as well as the influence of environmental factors on their effectiveness. Our objective is to contribute to sustainable agricultural development and the production of safe, high-quality agricultural products, thereby providing valuable insights for the development of Se-functional industries and guiding agricultural practices in regions affected by HM pollution.

Keywords: heavy metal; reactive oxygen species; bioavailability; Se species; phytohormone

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1. Introduction

Selenium (Se) is an essential trace element for humans and a beneficial nutrient for plants. Research has shown that at moderate concentrations, Se promotes seed germination [1], accelerates seedling growth [2], enhances root development, and fosters flowering and fruiting [3], thereby augmenting crop yield and quality.

Moreover, Se has the capacity to enhance the photosynthetic rate of plants. This effect primarily stems from Se's ability to regulate the activity and expression levels of enzymes associated with photosynthesis in plant leaves [4]. Consequently, Se promotes chlorophyll synthesis while reducing its degradation, safeguarding photosystem II from photooxidative damage. This, in turn, elevates both the maximum photochemical quantum yield (Fv/Fm) and the actual photochemical quantum yield (ΦPSII), thereby improving the photosynthetic capacity and overall growth potential of plants [5]. Meanwhile, Cunha et al. found that Se can also enhance photosynthesis by increasing the synthesis of chlorophyll, carotenoids, and pheophytin through reducing the level of malondialdehyde (MDA) and increasing the activities of catalase (CAT) and ascorbate peroxidase (APX) [6].

Meanwhile, Se plays a pivotal role in nutrient transport and metabolism within plants. Tamaoki et al. observed that Se can influence sulfur transport and assimilation in *Arabidopsis thaliana* [7]. Shahid et al. discovered that Se promotes the accumulation of soluble sugars in potatoes, upregulating the activities of sugar metabolism, nitrogen metabolism, and glycolytic enzymes [8]. This not only enhances the stress tolerance of plants but also fosters the accumulation of nutrients. Moreover, Wang et al. observed that the foliar application of Se fertilizer positively impacts carbon and nitrogen metabolism in leaf tissues, resulting in a notable reduction in Cd content within grains [9]. This phenomenon further fosters the translocation of pertinent metabolites toward roots, thereby enhancing the distribution and abundance of nitrogen-metabolism-associated soil microorganisms.

Agricultural heavy metal (HM) pollution is a formidable environmental issue confronting the world today. Lead (Pb), cadmium (Cd), and mercury (Hg) are among the prominent HMs infiltrating agricultural ecosystems through diverse pathways such as industrial wastewater discharge [10], mining activities [11], excessive application of fertilizers and pesticides [12], and atmospheric deposition [13]. This contamination poses significant threats to agricultural productivity, impeding root development and nutrient absorption in crops [14], disrupting photosynthetic processes in chloroplasts [15], and ultimately leading to decreased crop yield and quality. Moreover, HM accumulation in crops can enter the food chain, posing health risks to animals and humans, including neurotoxicity [16], renal failure [17], and cancer [18], among others [19]. The ecological impacts of HM pollution are long-lasting, with natural remediation processes often taking decades [20], particularly for highly stable and persistent metals such as Cd and Hg [21].

Attributable to factors such as mineral exploitation and urbanization progress, the soil in central, southern, and southwestern regions of China suffers from relatively severe heavy metal contamination [22]. Among them, a sampling survey conducted in the rice-producing areas of the Yangtze River Basin reveals that among the collected rice grain samples, approximately 37% exhibit Cd contamination, and the proportions of samples contaminated with Pb and chromium (Cr) reach 60% and 70%, respectively [23]. It is reported that China loses 1,000,000 tons of crop output every year due to heavy metal pollution [24]. Therefore, resolving the issue of heavy metal pollution in agriculture is of utmost urgency and immediacy.

Under HM stress, the application of appropriate amounts of Se to crops enhances sulfur metabolism [25], sugar metabolism, and soluble protein content, ultimately increasing crop yield and selenoprotein levels [8]. Additionally, adequate Se stimulates the expression of the crop's antioxidant system, scavenges excess ROS, and upregulates the relative expression of PCs and metal transporter proteins [26]. Furthermore, Se improves the microbial community structure in soil, and increases microbial diversity and abundance, further enriching soil fertility and promoting root growth and development [27]. These mechanisms collectively mitigate the toxicity of HMs in crops (Figure 1).

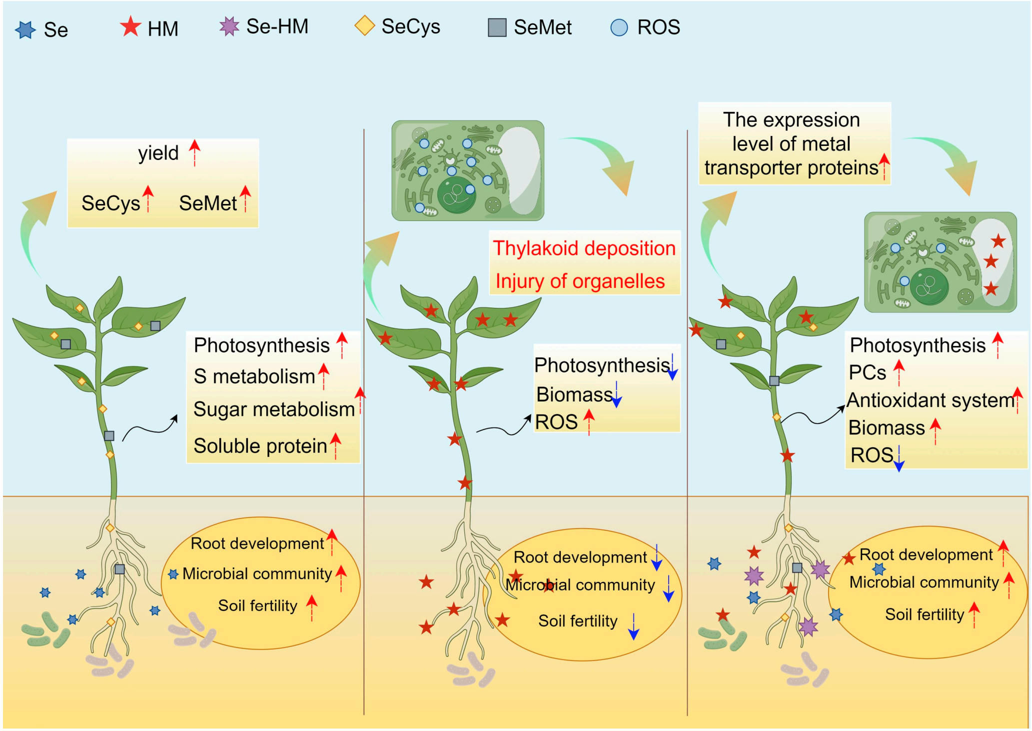

Figure 1. Enhancement of crop quality and mitigation of HM stress by Se. (Se–HM: complexes formed by Se and heavy metals; SeCys: selenocysteine; SeMet: selenomethionine; ROS: reactive oxygen species; PCs: phytochelatins).

2. Physiological Mechanism of Se in Alleviating HM Stress

2.1. Se Reduces the Bioavailability of HMs

The interplay between Se and HMs exerts a beneficial effect on mitigating HMs stress in plants. Se reduces the translocation of HMs from soil to plants by influencing their absorption and accumulation patterns [28]. It has been reported that applying Se fertilizer to crops under HM stress can reduce the contents of HMs in various parts of the plant, reduce the transfer coefficient of Cd in the plant, and reduce the absorption, transport, and accumulation of HMs by plants [29,30]. This may be due to the formation of non-toxic insoluble complexes between Se and HMs such as Cd–Se and Hg–Se in the plant, which reduces the mobility of HMs in the plant [31,32]. On the other hand, some studies have found that the exogenous application of Se fertilizer promotes the biosynthesis of phytochelatins (PCs) [33]. With abundant thiol groups, these PCs have a high affinity for HMs and chelate with them, reducing HMs' transfer coefficient in plants. In addition, rhizosphere exudates, pH, and electrical conductivity can also affect the absorption of HMs by plants by influencing the release of HMs [34,35], such as humic acid, which can reduce the release of Pb, Cu, and Cd [36]. Similarly, exogenous Se application modifies rhizosphere secretions, thereby altering soil metabolite distribution, improving soil quality, and decreasing HM bioavailability [9].

Furthermore, Se exerts its mitigating effects on HM toxicity in plants by modulating metabolic pathways. Research has demonstrated that Se promotes the formation of iron plaques in plants' root cells with a high affinity for HMs. These plaques act as chelators to sequester HMs, reducing their translocation to aerial parts and lessening their harm to plants [31,37]. Additionally, studies have found that the application of Se can activate PC synthase and promote the biosynthesis of the plant chelator precursor GSH, thereby increasing the synthesis of plant chelators and reducing the stress caused by HMs [32]. Studies have found that overexpressing the plant chelator synthase gene (*AtPCS2*) can improve the stress resistance of *A. thaliana* [38], but whether Se can promote the expression of this gene needs further research. In addition, metallothionein also plays an important role in alleviating the toxic effects of HMs in plants. It has been reported that low concentrations of Se can promote the expression of metallothionein genes, thereby helping plants tolerate HM stress [39].

2.2. Regulation of Plant Antioxidant Systems by Se

In response to HM stress, plants accumulate significant amounts of ROS, leading to detrimental effects on cellular proteins, lipids, and DNA [40]. Low concentrations of Se have been shown to bolster the antioxidant enzymes of plants such as superoxide dismutase (SOD), catalase (CAT), and glutathione peroxidase (GPx), mitigating ROS accumulation [33], thereby safeguarding them from oxidative stress-induced damage [41] (Table 1). By bolstering the antioxidant defense mechanisms, Se plays a pivotal role in protecting plants against the detrimental effects of HM exposure [42].

Se also has the ability to elevate the contents of non-enzymatic antioxidants in plants. Research has demonstrated that Se treatment significantly increases the levels of antioxidants such as GSH, AsA, proline, and flavonoids within plant tissues [33]. Furthermore, studies have revealed that the application of Se fertilizers markedly enhances the contents of non-enzymatic antioxidants such as ferulic acid, trehalose, ketohexose, and galactinol, which collaborate with the antioxidant system to eliminate excess free radicals [9]. This concerted effort maintains the redox balance within plants and safeguards cells against oxidative damage induced by HMs.

Furthermore, Se enhances plants' resilience to HM stress by regulating the expression of stress-responsive genes [43] and antioxidant protein-coding genes [44] such as *SOD*, *POD*, and *CAT*. This regulation subsequently elevates the antioxidant activity of plant cells [45]. In a transcriptome study conducted by Zhu et al. on *Oryza sativa* L., it was revealed that the application of 1 mg/kg of Se upregulated the expressions of genes related to oxidative stress, including *katE*, *CAT*, *catB*, and *Pox1*, thereby facilitating the elimination of excessive ROS [46]. Additionally, Zhu et al. observed in their study on *Solanum lycopersicum* L. that Se application downregulated the expression of the *Rboh1* gene, which is pivotal in plant ROS production [47]. Furthermore, Liu et al., in their research on *Malus pumila* Mill., found that Se application upregulated the expressions of *CYP73A*, *HCT*, and *CYP98A* genes. This upregulation promoted the synthesis of antioxidants such as chlorogenic acid, 5-O-caffeoylquinic acid, and 1-Sinapoyl-β-D-glucose, further augmenting the plant's antioxidant capacity [48].

Table 1. The influence of exogenous Se treatment on the expression levels and functionality of genes associated with the antioxidant system in crops subjected to HM stress.

Crop Species	Gene Name	Gene Function(s)	Gene Expression Trend After Se Application	Reference
Cucumis melo L.	*SOD*	Catalytic dismutation reaction of superoxide anion radicals, generating oxygen and hydrogen peroxide	Upregulation	[45]
	CAT	Decomposes hydrogen peroxide into water and oxygen to prevent the accumulation of hydrogen peroxide in cells		
	APX	Helps maintain the steady-state level of hydrogen peroxide in cells		
	POD	Catalyzes the reaction of hydrogen peroxide with other substrates to remove hydrogen peroxide and other peroxides		

Table 1. *Cont.*

Crop Species	Gene Name	Gene Function(s)	Gene Expression Trend After Se Application	Reference
Oryza sativa L.	*katE* *CAT* *catB* *srpA*	Related to oxidative stress response	Upregulation	[46]
Brassica juncea L.	*Pox1*	Participates in the process of oxidation and detoxification	Upregulation	[49]
	SAMS2	Related to S-adenosylmethionine biological processes/methionine adenosine transfer activity		
	NAD-ME2 *UCCR1-1*	Related to the oxidation–reduction process		
	FLCY *PLAT/LH2*	Participating in oxidative activity		
Solanum lycopersicum L.	*Rboh1*	Plays a major role in the production of ROS in plants	Downregulation	[47]
Nicotiana tabacum L.	*POX*	Encodes peroxidase to assist in clearing excess ROS	Upregulation	[50]
Malus pumila Mill.	*CYP73A* *HCT* *CYP98A*	Related to the antioxidant capacity of plants	Upregulation	[48]

2.3. The Effect of Se on the Stability of Plant Cell Membrane

HM stress can induce oxidative stress, resulting in the generation of excessive ROS, which in turn leads to decreased levels of unsaturated fatty acids, increased lipid peroxidation, and disruption of the structural and functional integrity of cell membranes [51]. Additionally, HMs may also affect the ion balance of cell membranes, further compromising their stability [52]. In recent years, a growing body of research has demonstrated that Se can mitigate the damage caused by HMs to plant cell membranes, to a certain extent, thereby enhancing the stress resistance of plants [53,54]. Studies have revealed that Se application reduces the accumulation of superoxide ions in rapeseed root cells, safeguarding the root tips from the assault of ROS and thereby maintaining the integrity and stability of cell membranes [54]. This protective effect is primarily attributed to the enhancement of antioxidant enzyme activities following Se application. These enzymes effectively scavenge excessively accumulated ROS, mitigate lipid peroxidation induced by HMs, and ultimately safeguard the stability of cell membranes [55].

It has been reported that HM ions (Zn^{2+}, Pb^{2+}, Cd^{2+}, Hg^{2+}) can enter plant cells through aquaporins (AQPs) and gate-control AQPs, reducing water permeability, and that the toxicity order of HMs toward AQPs has been determined as Hg > Cd > Pb > Zn [56]. Wang et al. found that organic Se fertilizers, specifically SeMet and SeOMet, can be absorbed by plants through AQPs [57]. However, the specific effects of Se on AQPs remain to be fully elucidated. Some studies suggest that certain AQPs can mediate the efflux and vacuolar sequestration of HMs, thereby alleviating HM stress in plants [58]. It is thus speculated that Se may also promote the expression of certain AQPs to mitigate HM stress. Additionally, membrane transporters are involved in the transport of HMs, and the influence of Se on these transporters warrants further investigation. Furthermore, Se's role in phospholipid metabolism represents a crucial pathway in protecting cellular membranes. Studies have shown that HM stress disrupts the synthesis and degradation processes of membrane phospholipids, leading to decreased lipid content in cellular membranes, increased levels of phosphatidic acid and free fatty acids, reduced membrane fluidity and, ultimately, membrane instability [59]. Se, on the other hand, can regulate enzymes and metabolic pathways associated with phospholipid metabolism, thereby maintaining phospholipid homeostasis and facilitating the repair and regeneration of cellular membranes.

In conclusion, the physiological mechanism of Se in alleviating HM stress encompasses multiple aspects: (1) Reducing the HM transfer factor by complexing with HMs in soil via Se and root-secreted organic acids and enhancing PC synthesis in root cells to sequester HMs in vacuoles. (2) Increasing the contents of photosynthetic pigments and enhancing the efficiency of photosynthesis. (3) Promoting antioxidant system expression by regulating enzymatic activities and increasing non-enzymatic antioxidant content to scavenge ROS and mitigate associated damages. (4) Improving soil microbial community structure, which promotes beneficial microorganism dominance, increases soil fertility, and consequently fosters crop growth (Figure 2).

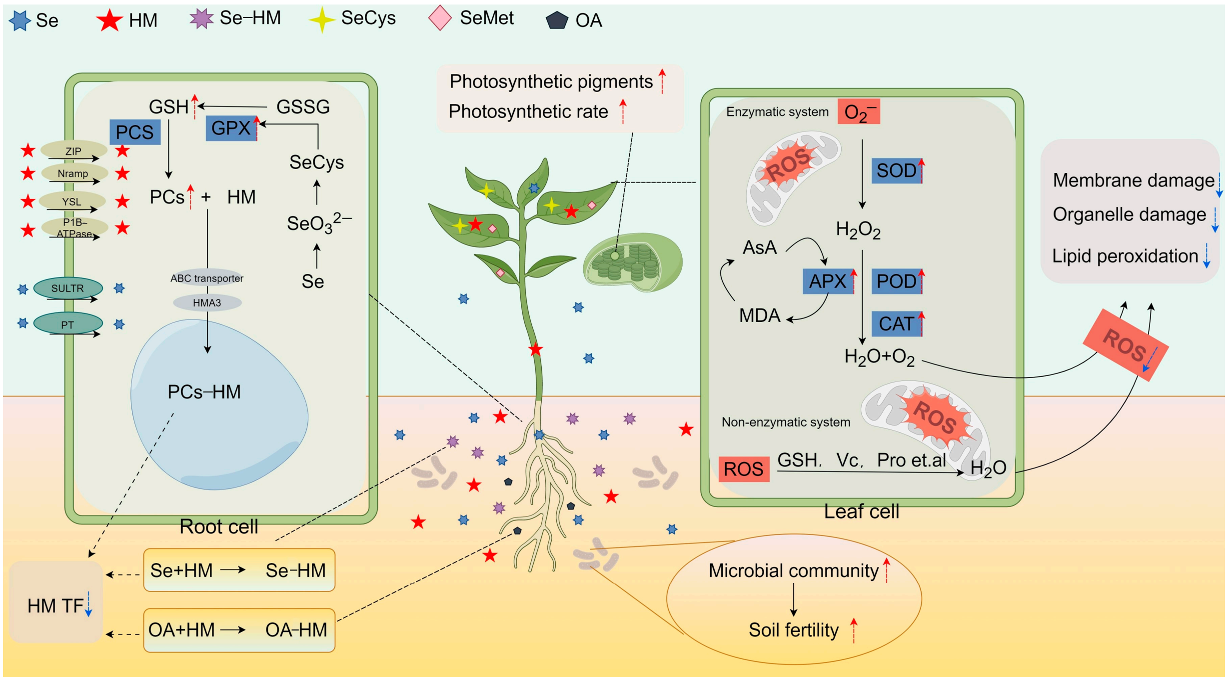

Figure 2. The physiological mechanism of Se in alleviating HM damage. (Se–HM: the complexes formed by Se and heavy metals; SeCys: selenocysteine; SeMet: selenomethionine; OA: organic acid; PCs: phytochelatins; PCS: phytochelatin synthase; GSH: glutathione; GSSG: oxidized glutathione; GPX: glutathione peroxidase; ZIP: zinc-regulated transporter/iron-regulated transporter protein; Nramp: natural resistance-associated macrophage protein; YSL: yellow stripe-like transporter; SULTR: sulfate transporter; PT: phosphate transporter; HMA3: HM ATPase3; HMTF: HM transfer factor; ROS: reactive oxygen species; SOD: superoxide dismutase; AsA: ascorbic acid; APX: ascorbate peroxidase; MDA: malondialdehyde; POD: peroxidase; CAT: catalase).

3. Molecular Mechanisms of Se in Alleviating HM Stress

3.1. Se and Plant Gene Expression Regulation

In crops, Se not only regulates the expression of genes related to antioxidant enzymes and antioxidant metabolism pathways but also protects crops from HM toxicity by regulating HM sequestration, phytohormone content, and photosynthesis [9,42,48]. Studies have demonstrated that Se can modulate the expression levels of various metal transporter families, including members of the ATP-binding cassette (ABC) transporter family [60], HM ATPases (HMA) [61], ZIP family [49], LCT transporter family [62], natural resistance-associated macrophage protein (Nramp) family [63], cation/hydrogen exchanger (CAX) family, and cation efflux (CE) family [64]. Additionally, Se upregulates the expression of genes related to lignin, cellulose, and hemicellulose, facilitating the sequestration of excess HM ions into vacuoles or cell walls in plants [50]. It has been reported that Se can upregulate the expression of genes related to lignin synthesis (*Os4CL3*, *OsHMA3* et al.)

and downregulate the expression of genes related to Cd uptake and transport (*OsLCT1*, *OsPAL*, *OsNramp5* et al.), thereby reducing the Cd content in rice seeds [63]. By regulating these genes (*TaHMA3*, *TaTM20*, *TaNramp5* et al.), HMs can be fixed in vacuoles and cell walls, reducing their transport and migration rate in plants, thereby alleviating the damage caused by HMs to plants [9,50]. Wang et al. found that applying a composite sol of Se and silica to rice leaves downregulated the expression of genes related to Cd transporters, such as *OsLCT1*, *OsCCX2*, and *OsHMA2*, subsequently reducing the contents of Cd and Pb in leaves and grains [62]. In the study of *Brassica juncea* L., Li et al. found that under Cd stress, Na_2SeO_3 application upregulated *PME3*, *4CL1*, and *DCT1* genes, promoting Cd fixation in vacuoles and cell walls, and downregulated genes related to Cd transporters such as *ABCC family10*, *ABCG39*, and *ZIP transporter 4* [49] (Table 2, Figure 2). This process reduces the concentrations of these HM ions in the cytoplasm, thereby mitigating their toxic effects.

Table 2. The effects of Se on the expression of genes related to HM absorption and transport in crops.

Crop Species	Gene Name	Gene Function(s)	Gene Expression After Se Application	Reference
Oryza sativa L.	*OsPAL*	Key enzyme in lignin synthesis process	Upregulation	[63]
	OsCoMT	Participates in the synthesis of lignin		
	Os4CL3	Participates in the synthesis of lignin		
	OsHMA3	Participates in the transport of Cd to vacuoles		
	OsLCT1	Participates in the transportation of Cd between grains and phloem	Downregulation	
	OsNramp5	Participates in the transportation of Cd from external solutions to root cells		
	OsNramp1	Participates in the uptake and transport of Cd		
	OsIRT1	May participate in the transport of Cd		
	OsIRT2	May be related to the transport of Cd		
Triticum aestivum L.	*TaHMA3*	Participates in chelating Cd from cytoplasm to vacuoles	Upregulation	[9]
	TaTM20	Enhances the output of Cd on the cell membrane		
	TaNramp5	Participates in the transportation of Cd from soil to root cells	Downregulation	
	TaLCT1	Participates in the transportation of Cd to wheat grains		
Nicotiana tabacum L.	*GAUT*	Participates in pectin biosynthesis	Upregulation	[50]
	GALE	Participates in polysaccharide biosynthesis		
	UGP	Related to cellulose biosynthesis		
	UGE	Related to the biosynthesis of hemicellulose		
	PAL	Related to lignin biosynthesis pathway		
	CCR	Related to lignin biosynthesis pathway		
	CAD	Participates in lignin biosynthesis		
	POX	Related to lignin biosynthesis pathway		
	XTH	Encoding xyloglucan endoglycosidase/hydrolase		
Oryza sativa L.	*OsLCT1*	Participates in the transportation of Cd from leaves to grains	Downregulation	[62]
	OsCCX2	Mediates the accumulation of Cd in grains		
	OsHMA2	Participates in the transport of Cd from roots to stems and its distribution to rice grains		
	OsPCR1	Related to the transport and accumulation of Cd in plants		
	TaCNR2	Participates in the regulation of heavy metal transport		
Saccharum officinarum L.	*MT*	Reduces the toxicity of heavy metal ions; antioxidant	Upregulation	[39]
Oryza sativa L.	*C4H1*	Involved in the biosynthesis pathway of phenylpropane, encoding functional proteins related to heavy metal ion binding, cell wall synthesis, and oxidative detoxification	Upregulation	[46]
	PRX			
	atp6			
	OsMYB60	Mainly involved in glycolysis, heavy metal ion transport, and stress response processes		
	PRX131			
	OsCDGSH			
	HXK7			
	OscytME2			
	FLS2	May participate in cell wall ion deposition		

Table 2. *Cont.*

Crop Species	Gene Name	Gene Function(s)	Gene Expression After Se Application	Reference
Brassica juncea L.	*PME3*	Related to cell wall modification/pectin esterase	Upregulation	[49]
	4CL1	Related to promoting lignin synthesis and reducing Cd transport to aboveground parts		
	DCT1	Related to the isolation and transport of Cd in root cell vacuoles		
	ABCC family10 *ABCG39* *ZIP transporter 4*	Related to Cd transporters	Downregulation	
	CAL1	Participates in the secretion of Cd between cells, which may be related to the chelation of Cd in the cytoplasm	Upregulation	
	RPS21 *NRT1*	Participating in the transportation of Se to the aboveground parts		
Cucumis melo L.	*CNGC9*	Plays a role in the binding motif of ion transport protein/IQ calmodulin	Upregulation	[45]
	PAL	Participates in the synthesis of various secondary metabolites, such as lignin, flavonoids, phenolic compounds, etc.		
Capsicum annuum L.	*C3H*	Possible involvement in phenylpropane metabolic pathways	Equal expression	[65]
	HCT	Regulating the biosynthesis of lignin		
	4CL	Regulating the biosynthesis of lignin		
	PAL	The initial steps involved in phenylpropane metabolism	Upregulation	
	CAD	Promotes the formation of lignin precursors		
	COMT	Catalytic methylation reaction of lignin precursor substances		

Moreover, studies have shown that Se fertilization enhances the expression of sulfate transporter genes in broccoli, stimulating sulfur metabolism in plants [66]. Notably, Sun et al., in their investigation of the *astol1* mutant in rice, found that this mutant exhibited enhanced sulfur metabolism and Se accumulation capabilities. This augmented sulfur metabolism, in turn, led to increased synthesis of sulfur-containing compounds such as GSH and PCs, which effectively inhibited the translocation of As—another toxic metalloid—within the plant [67]. However, the influence of exogenous Se on the expression of these genes and whether Se can indeed promote sulfur metabolism through the upregulation of these genes to alleviate HM toxicity remain largely unexplored and await further validation.

Furthermore, Se modulates the expression of genes associated with plant defense responses. These genes encode defensive proteins such as metallothioneins and PCs, which can directly bind to HM ions, reducing their bioactivity and, subsequently, mitigating their toxicity to plants [39]. By upregulating the expression of these defense genes, Se enhances the intrinsic defense mechanisms of plants, improving their survival under HM stress. Additionally, studies have shown that Se application can regulate the expression of genes involved in carbon, nitrogen, amino acid, and sugar metabolism, thereby increasing plants' resistance to HMs [48].

3.2. Se and Plant Signal Transduction Pathways

Se modulates metabolic pathways and signal transduction systems, and it orchestrates hormonal (auxin, abscisic acid, ethylene) balance and signaling molecule (nitric oxide, calcium ions, hydrogen sulfide) transduction, fine-tuning plants' physiological responses to HM stress [68]. According to reports, Se can upregulate the expression responses of auxin, ABA, and JA, activating intercellular synergies that collaboratively maintain homeostasis within the plant [46]. Furthermore, Se regulates ethylene biosynthesis, and studies have indicated that ethylene may participate in Se-induced defense responses, thereby enhancing the positive response of the antioxidant system and improving plant growth under Cd stress [69]. Several studies have revealed that Se can alter the expression of stress-related genes by influencing phytohormone signaling pathways, such as those involving IAA, abscisic acid (ABA), and jasmonic acid (JA) [46]. The products of these genes are often transcription factors, which further regulate the expression of downstream genes, forming intricate gene expression networks that contribute to the response to HM toxicity.

Additionally, Se regulates ion channels or channel proteins on plant cell membranes, thereby influencing the absorption and translocation of HMs. For instance, Se can modulate calcium ion channels, potassium ion channel proteins, AQPs [57], and several HM transporter proteins [60,61], ultimately reducing HM uptake while facilitating their excretion (Figure 3).

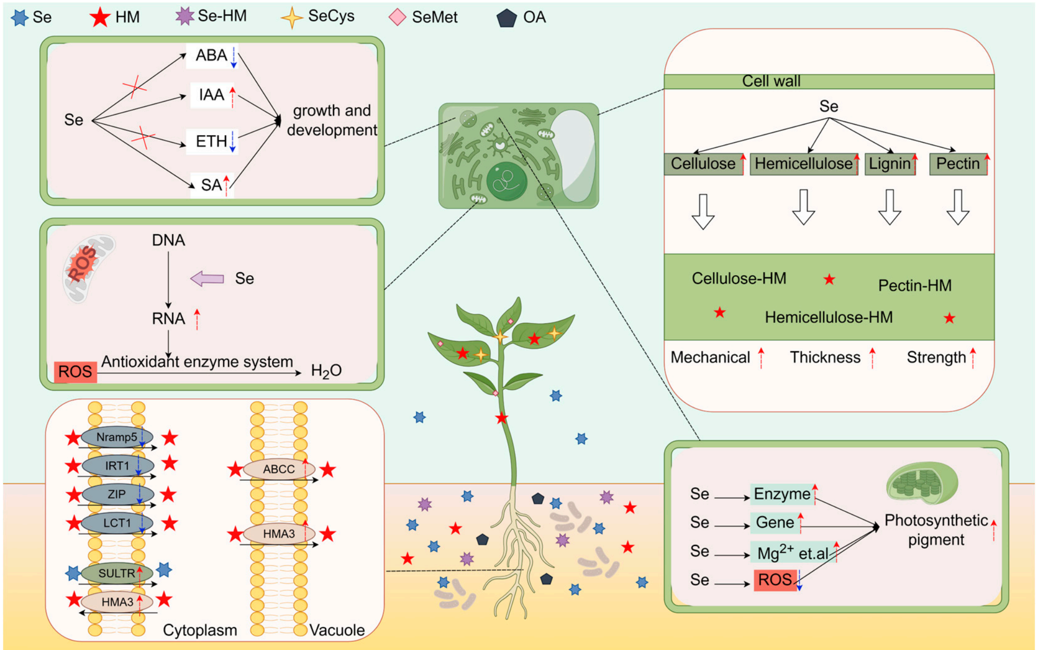

Figure 3. Molecular mechanisms of Se alleviating HM stress. (Se–HM: the complexes formed by Se and heavy metals; SeCys: selenocysteine; SeMet: selenomethionine; OA: organic acid; ABA: abscisic acid; IAA: indole-3-acetic acid; ETH: ethylene; SA: salicylic acid; ROS: reactive oxygen species; Nramp5: natural resistance-associated macrophage protein; IRT1: iron-regulated transporter 1; ZIP: zinc-regulated transporter/iron-regulated transporter protein; LCT1: lactate transporter 1; SULTR: sulfate transporter; HMA3: heavy metal ATPase 3; ABCC: ATP-binding cassette subfamily C). The molecular mechanism of Se in alleviating HM stress involves multiple aspects. It regulates plant hormone metabolic pathways, antioxidant system gene expression, transport protein genes, cell wall strength, and photosynthesis-related elements, thus helping crops cope with HM stress and maintain normal growth.

3.3. Regulation of Crop Metabolic Pathways by Se

The modulation of metabolic pathways by Se in crops plays a pivotal role in alleviating HM stress. Se's ability to regulate sulfur metabolism in plants stems from the chemical similarities between Se and sulfur. Studies have revealed that HM stress disrupts normal sulfur metabolism in plants [70], whereas the introduction of Se can partially maintain sulfur's metabolic balance [71]. Se enters plants via sulfate transporters and is metabolized into SeCys or SeMet via the sulfur assimilation pathway in chloroplasts [72]. This process reduces the binding of HMs to sulfur-containing ligands, thereby mitigating HM toxicity.

Furthermore, numerous studies have demonstrated that Se application affects plants' N metabolism, C metabolism, sugar metabolism, and amino acid metabolism, contributing to enhanced stress tolerance. Se plays a regulatory role in modulating the expression levels of photosynthesis-related genes in plants, including *Lhcb1*, *RbcL*, and *OsBTF3* [62]. In a study by Zhao et al. on *Oryza sativa* L., it was observed that Se application led to the upregulation of genes such as *HEMA1*, *OsBCH3*, and *GUN4*, while downregulating *OsRCCR1* and *PsaC*. This resulted in heightened synthesis and reduced degradation of photosynthetic pigments, thereby optimizing the pigment profile and potentially augmenting photosynthetic performance [4] (Table 3). Additionally, Se upregulates the synthesis of proteins involved in energy transfer processes within photosystem I and photosystem II, including *psbQ*, *psbO*, *psaG*, *atpG* et al. [46], or maintains their stability [7]. These actions collectively enhance photosynthetic efficiency and mitigate HM stress in plants (Table 3). Wang et al. discovered that foliar application of Se enhanced nitrogen metabolism in both the leaves and roots of rice, increasing the synthesis of nitrogen-containing organic compounds. This, in turn, promoted the growth of beneficial microorganisms in the rhizosphere, thereby mitigating Cd toxicity in rice [9]. Additionally, Rafael et al. observed that Se application facilitated carbon–nitrogen metabolism and other metabolic pathways in pepper plants, bolstering their tolerance to Cd [73]. In summary, the impacts of Se on N metabolism, C metabolism, sugar metabolism, and amino acid metabolism are significant, albeit with the detailed underlying mechanisms awaiting further elucidation.

Table 3. The effects of exogenous Se treatment on the expression of photosynthesis-related genes in crops under HM stress.

Crop Species	Gene Name	Gene Function(s)	Gene Expression After Se Application	Reference
Oryza sativa L.	*Lhcb1*	Plays a role in photosynthesis adapting to different light environments	Upregulation	[62]
	RbcL	The first step of carbon dioxide fixation in catalytic photosynthesis		
	OsBTF3	Plays an important role in the growth, development, and photosynthesis of rice		
	psbQ *psbO* *psaG* *psaD* *atpG* *PetH*	Participates in the energy metabolism processes of photosystem I and photosystem II	Upregulation	[46]
	LHCA *LHCB*	Upregulation of expression can enhance the photon capture ability and light utilization efficiency of plants		
Brassica juncea L.	*PSB27-1*	Participate in the repair product PSB27-H1 of photosystem II		[49]
Oryza sativa L.	*HEMA1* *Os10g0502450* *GUN4*	Related to the synthesis of chlorophyll a	Upregulation	[4]
	Os04g0692600	Prevents chlorophyll accumulation or activate chlorophyll decomposition metabolism		
	OsRCCR1	Participates in chlorophyll degradation	Downregulation	
	OsBCH3	Promoting the synthesis of carotenoids	Upregulation	
	OsFPPS1 *OsPSY2* *OsBCH2*	Participating in the synthesis of carotenoids		
	PsaC	Participating in the assembly of PSI complexes and P700 electron transfer	Downregulation	
	Fd1	Regulating the synthesis of FD plays an important role in maintaining Fe homeostasis in eukaryotic cells	Upregulation	

4. Soil Environmental Factors and Se in Alleviating HM Stress

The speciation and bioavailability of Se in soil are influenced by various factors. Based on its chemical form, Se in soil can be classified into two primary categories: organic and inorganic Se. Among inorganic Se, four main forms exist: elemental Se (Se^0), inorganic selenides (Se^{2-}), selenite ($SeO_3{}^{2-}$), and selenate ($SeO_4{}^{2-}$). Organic Se primarily comprises SeCys, SeMet, and their derivatives [74]. Soil pH exerts a multifaceted influence on the capacity of Se to alleviate HM stress in plants. Firstly, soil pH modulates the speciation and availability of Se in soil. In acidic soils, Se primarily exists in soluble inorganic forms such as selenite, whereas selenate predominates in alkaline soils [75].

Both selenite and selenate can be directly absorbed by plants, albeit selenite is the primary form preferred for plant utilization. Comparative studies on the application of sodium selenite (Na_2SeO_3) and sodium selenate (Na_2SeO_4) to crops have revealed that plants can better absorb Na_2SeO_3, leading to increased Se content in crops [76,77]. However, the preferential utilization of these two Se species by plants and their respective efficacies in mitigating HM stress remain controversial. Yu et al. compared the effects of Na_2SeO_3 and Na_2SeO_4 on alleviating Cd stress in *Brassica rapa* subsp. *chinensis* and found that Na_2SeO_3 significantly outperformed Na_2SeO_4 after 19 days of germination [78]. Similarly, Liao et al. observed that Na_2SeO_3 was more effective in mitigating Cd and As stress in rice, resulting in greater reductions in HM contents in grains, albeit with slightly inferior nutritional quality preservation compared to Na_2SeO_4 [79], while some studies indicate that Na_2SeO_4 is superior to Na_2SeO_3 in mitigating abiotic stress in tobacco [80]. Nevertheless, both forms can be employed to mitigate HM stress in agricultural systems. Na_2SeO_3 reduces Cd accumulation primarily by downregulating the expression of Cd uptake genes, whereas Na_2SeO_4 not only modulates gene expression but also enhances Cd sequestration in vacuoles [81]. Furthermore, studies suggest that selenite is more rapidly reduced and biologically transformed within plants, contributing to its superior performance in alleviating HM stress [82]. These findings underscore the complexity of Se-mediated HM stress mitigation and highlight the need for further research to elucidate the precise mechanisms underlying these effects.

Concurrently, soil pH exerts profound influences on the speciation and bioavailability of HMs. Soil acidification has been reported to markedly enhance the mobility of HMs, with Cd being particularly sensitive to this effect [83]. Studies have shown that, within a pH range of 3.40 to 8.97, the content of bioavailable Cd in calcareous soils decreases as pH increases [84]. This phenomenon is attributed to the fact that, under acidic conditions, HMs in soil more readily dissolve into ionic forms, thereby enhancing their mobility and bioavailability. Conversely, at higher pH values, the concentration of hydroxyl ions in soil increases, facilitating the formation of insoluble hydroxide precipitates with HM ions, which subsequently reduces their bioavailability.

Moreover, soil pH also modulates the community structure and functions of soil microorganisms. Soil microorganisms play a pivotal role in altering soil's physicochemical properties, nutrient cycling, and material transformation [85]. Variations in soil pH can influence the distribution of beneficial microbial communities, as well as the absorption and utilization of Se by plants. Specifically, soil harbors microorganisms involved in the reduction, oxidation, and assimilation of Se, which can convert organic Se and elemental Se into selenite [86] or reduce selenite to elemental Se [73]. These microbial activities impact the speciation and bioavailability of Se, subsequently influencing the absorption and utilization of Se fertilizers by plants. Therefore, soil pH, through its effects on both HM speciation and microbial activity, plays a crucial role in determining the efficacy of Se-mediated HM stress mitigation in agricultural systems. Future research endeavors should delve deeper into the intricate mechanisms governing the absorption, transformation, and utilization of various Se species by diverse plant species under varying soil pH conditions. This would include elucidating how these processes can be precisely regulated to more effectively mitigate HM stress.

5. Application of Se in Alleviating HM Stress in Agriculture

5.1. Application Technology of Se Fertilizer

The commonly utilized Se fertilizers encompass selenite, selenate, organic Se, and nano-Se fertilizers. The methods of application for these Se fertilizers primarily include soil application, foliar spraying, hydroponic application, and seed treatment. Among these methods, soil application involves directly incorporating the fertilizers—predominantly selenite, selenate, and organic Se fertilizers—into the soil as base fertilizers, thereby enabling plants to directly absorb and utilize them. This approach can modify the structure and distribution of soil microbial communities, which, through their metabolic activities, further influence the physicochemical properties and fertility of the soil. For instance, studies have demonstrated that soil application of Se can regulate the expression of genes related to rhizobia and nitrogen cycling in leguminous plants, thereby enhancing their biomass and nitrogen accumulation [87]. However, when implementing soil application of Se fertilizers, it is crucial to consider multiple factors, including the native Se content, fertility, and physicochemical properties of the soil, as these can significantly impact the efficacy of fertilization.

Foliar application of Se fertilizers involves preparing a solution of a specific concentration and spraying it onto both the upper and lower surfaces of plant leaves at a designated growth stage. The plant then absorbs the Se fertilizer through stomata on the leaf surface. Currently, nanoscale Se fertilizers are the most extensively studied for foliar application, as it is generally believed that this method allows for maximal efficacy of nano-Se. However, there are also studies indicating that soil amendment with nano-Se, rather than foliar application or seed soaking, can more effectively alleviate Cd stress in wheat [88]. Foliar application of Se fertilizers circumvents the impact of soil factors on fertilizer effectiveness, significantly reducing the amount of Se fertilizer required and enabling faster absorption and utilization by plants through stomata and cuticles, thereby accelerating the manifestation of beneficial effects. Furthermore, research has shown that foliar application of Se can modulate soil microbial community distribution through leaf and rhizosphere metabolites, enhancing plants' resistance to HMs and pests [9,89]. Currently, numerous studies have validated that foliar application is an effective agronomic measure, helping crops relieve heavy metal stress by inducing antioxidant defenses and enhancing the nutritional quality of edible parts via biofortification. Oliveira et al. compared soil and foliar applications of selenite and selenate. They found both could increase root Se content, with foliar application of selenite being the most effective [90]. Zhang et al. found that in wheat cultivation, selenate was more effective than selenite in fertigation and foliar applications, and foliar fertilization outperformed fertigation [91]. Li et al. found that foliar nano-Se application increases the Se content in the edible parts of *Brassica chinensis* L., boosting its nutritional value [92]. Zhang et al. foliar-applied selenite and selenate during potato tuber expansion and found that selenite could significantly increase the organic Se content in the edible parts. However, excessive foliar Se concentration may damage leaves and affect crop growth [93]. Rebecca et al. found that when the foliar spraying Se concentration exceeded 50 ppm, the yield of *Helianthus annus* L. decreased [94]. While foliar application of Se fertilizers is largely unaffected by soil conditions, it is susceptible to weather factors such as high temperatures, rainfall, and intense sunlight, which can negatively impact fertilizer efficacy.

Hydroponic application of Se fertilizers to crops similarly circumvents the influence of soil factors on fertilizer effectiveness, facilitating rapid absorption and utilization due to the direct contact between the plants' roots and the nutrient solution. Recent studies show that adding selenite, selenate, and nano-Se to hydroponic systems can alleviate HM stress on crops and improve their nutritional quality [77,95,96]. However, the practical implementation of hydroponic Se application requires significant investment in costs and technical expertise. Moreover, the stability of the system is a challenge, necessitating constant monitoring and adjustment of the Se concentration in the nutrient solution to maintain optimal conditions. These factors limit the widespread adoption of hydroponic Se application in commercial production settings.

Seed treatment involves soaking seeds in a solution containing a specific concentration of Se fertilizer to allow the seeds to absorb a certain amount of Se, thereby enhancing the crop's adaptability to HM stress. According to reports, pre-germination soaking of seeds in Se solutions can elevate the Se concentration in plant seedlings by several orders of magnitude, leading to an increase in the content of trace elements and the yield of crops. [97,98]. Furthermore, Se-treated seeds exhibit resilience against various environmental pressures and positively contribute to mitigating HM stress in plants [99]. Nonetheless, seed treatment also has its limitations. The efficacy of this method can be influenced by the inherent properties of the plant seeds, to ensure Se benefits seeds, treatment time and concentration must be set based on crop types to avoid harming germination and seedlings.

5.2. The Combined Application of Se and Other Biotechnologies

Se can be integrated with various biotechnological approaches to enhance its application in agriculture. Firstly, microbial synthesis of nano-Se particles offers advantages such as low toxicity, high bioavailability, and minimal environmental contamination [100]. These nano-Se particles, when applied through methods such as foliar spraying or rhizosphere application, can not only improve the nutritional quality of crops but also modulate plants' metabolic activities, thereby enhancing their stress tolerance [101]. Moreover, the utilization of carriers such as liposomes and epigallocatechin gallate Se can further enhance the efficacy of nano-Se particles, optimizing their role in improving the quality of agricultural products [102,103]. Additionally, Se can be combined with microbial remediation technologies. Studies have reported that exogenous Se application, in conjunction with Se-tolerant bacteria, can effectively inactivate Cd in soil, reducing its accumulation and transport in rice [104]. Furthermore, bacteria associated with Se-hyperaccumulator plant rhizospheres have been found to promote Se accumulation in non-accumulator plants, thereby enhancing crop quality [104]. The combined application of arbuscular mycorrhizal fungi and Se fertilizers not only improves soil microbial community distribution but also aids in alleviating Cd stress in wheat, underscoring the potential of this combined approach in sustainable agriculture [105].

It has been reported that Se, in conjunction with *Lysini bacillus* fusiformis SES, exerts a synergistic effect by recruiting microbial populations in the soil that possess plant-growth-promoting capabilities and rhizosphere HM resistance. This collaborative mechanism enhances the remediation of Cu-Cd-Cr composite-contaminated soil by ryegrass [106]. Beyond its synergy with microorganisms, recent studies have explored the combined application of Se and modified biochar. This integration has been found to increase the dissolved organic carbon, available silicon, and exchangeable magnesium contents in soil while reducing the bioavailability of HMs such as Cd, Pb, Zn, and Cu. Consequently, this approach promotes the growth of Chinese cabbage [107]. Additionally, the practice of intercropping has been suggested as a means to achieve HM pollution remediation [108]. However, further research is necessary to determine whether Se can augment the effectiveness of such remediation techniques. The potential role of Se in enhancing the efficacy of intercropping systems for HM remediation remains an area of active investigation.

6. Existing Problems and Challenges

Significant strides have been made in elucidating Se's role in mitigating HM stress in crop plants, yet numerous challenges persist that necessitate further inquiry. Although previous studies have documented Se's ability to alleviate HM stress through various mechanisms, such as reinforcing plant antioxidant systems, stabilizing cellular membrane structures, and modulating phytohormone levels [26,53], molecular-level validation remains elusive.

Moreover, while the modulating effects of soil environmental factors on Se's mitigation of HM stress have been briefly explored in existing research, systematic studies remain scarce [75,109]. For instance, issues that have not been fully elucidated include the influence of soil pH, organic matter content, and the presence of other trace elements on Se's availability, as well as the mechanisms by which Se alters the valence state of HM ions, impacts their bioavailability, interacts with HMs through complexation, and varies in its mitigating effects across different soil types. Furthermore, it is imperative to conduct studies under simulated agricultural conditions to investigate the efficacy and mechanisms of Se in alleviating multiple-HM co-contamination, thereby providing more practical guidance for agricultural production.

Se's influence on plant growth is akin to a "double-edged sword", where low concentrations promote plant growth and resilience, whereas high concentrations may induce toxicity [110]. It is reported that a selenite foliar application above 50 $g \cdot ha^{-1}$ on cowpea plants induces leaf lesions, disrupts physiological processes, and curtails yield and quality [111]. It has been reported that a 1.5 mM selenate causes rice growth retardation, lowers photosynthetic pigment content, impairs antioxidant metabolism, and induces chlorosis [112]. Saleem et al. discovered that 40 or 80 µM Se induces oxidative damage in tomatoes, leading to Se poisoning [113]. Cabral et al. also discovered that at a Se concentration of 1.5 mM, rice suffers reduced biomass and yield, accompanied by obvious phenotypic damage, which impacts its growth and productivity [114]. Consequently, the application rate of Se fertilizers must be meticulously controlled within an acceptable range for plants. Plants' HM resistance can be more effectively enhanced by tailoring the application of Se fertilizers in stages according to the specific needs and growth cycles of various crops and judiciously allocating the proportion of base- and top-dressing fertilizers.

7. Conclusions

In crop cultivation, Se mitigates HM stress through several mechanisms: (1) Se complexes with HMs such as Cd and Hg in soil, thereby reducing their bioavailability; (2) Se induces the expression of antioxidant systems to counter oxidative stress generated by HM stress; (3) Se regulates the expression of genes related to HM transport, decreasing the translocation of HMs within plants; (4) By upregulating the expression of genes associated with cell wall synthesis, Se enhances the mechanical strength of cell walls; (5) Se modulates the expression of genes involved in photosynthesis, bolstering photosynthetic efficiency; (6) Se adjusts metabolic pathways, including nitrogen, carbon, and amino acid metabolism, to enhance plant stress tolerance; and (7) through root exudates, Se influences the composition and distribution of soil microbial communities, aiding plants in coping with HM stress. With the development of functional agriculture, through in-depth research and technological innovation, it is possible to enhance the Se content of agricultural products while effectively alleviating HM stress and accumulation in crops, thereby contributing to sustainable agricultural development and ensuring the safety and high-quality production of agricultural products.

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