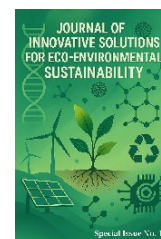




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Review Article

Mitigation Strategies for Cadmium Toxicity in Rice (*Oryza sativa* L.): A Comprehensive Review

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ABSTRACT

Cadmium (Cd) is a highly toxic heavy metal and a widespread environmental contaminant in paddy fields, where its accumulation in rice (*Oryza sativa* L.) poses significant risks to plant health, agricultural productivity, and human consumption. Cadmium toxicity adversely affects various physiological and biochemical processes in rice, including seed germination, root and shoot growth, nutrient homeostasis, photosynthetic efficiency, and grain yield. Additionally, Cd exposure induces oxidative stress by generating reactive oxygen species (ROS), leading to cellular damage and metabolic disruptions. To mitigate Cd toxicity, various agronomic, physiological, and biotechnological strategies have been explored. The application of essential nutrients such as zinc (Zn), iron (Fe), silicon (Si), and lime has been shown to alleviate Cd stress by modulating metal uptake and reducing Cd bioavailability in soils. Organic amendments, including compost and biochar, enhance soil properties and immobilize Cd, thereby limiting its translocation to rice tissues. Furthermore, the exogenous application of phytohormones, osmolytes, and signaling molecules has been demonstrated to improve rice tolerance by enhancing antioxidant defense mechanisms and stress response pathways. Genetic and breeding approaches, such as the development of low Cd-accumulating rice cultivars, offer a promising long-term solution for reducing Cd accumulation in edible plant parts. Additionally, utilizing beneficial rhizosphere microorganisms, including mycorrhizal fungi and plant growth-promoting rhizobacteria (PGPR), can further aid in mitigating Cd toxicity. This review provides a comprehensive synthesis of current mitigation strategies and highlights the need for an integrated approach combining soil amendments, genetic improvements, and sustainable agronomic practices to minimize Cd contamination in rice ecosystems.

1. Introduction

In recent decades, the issue of soil pollution has garnered significant attention, particularly concerning its impact on agricultural lands and food safety. Heavy metals such as lead (Pb), cadmium (Cd), and mercury (Hg) are especially problematic due to their persistence and bioaccumulation in the food chain. Among them, Cd poses one of the most serious threats to both soil and water quality. Cadmium concentrations in soil typically range between 0.01 and 1 mg/kg, with a global mean of about 0.36

mg/kg [1]. The bioavailability of Cd in soils depends on several physicochemical factors, such as pH, redox potential, and total Cd concentration. For example, decreasing soil pH enhances Cd mobility by converting it from stable forms (bound to carbonates, iron, and manganese oxides) to more soluble and plant-available forms [2, 3]. Anthropogenic activities, including the use of phosphatic fertilizers and irrigation with untreated wastewater, are major contributors to Cd accumulation in agricultural soils [3, 4]. Such contamination compromises soil health and, more importantly, threatens the safety of food crops.

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Cadmium toxicity is a growing concern in rice cultivation as it significantly affects plant growth, yield, and the grain quality. Rice plants are particularly vulnerable to Cd contamination due to their cultivation in waterlogged fields. Cadmium enters rice plants primarily through the roots, where it is subsequently transported to shoots and grains [5]. Once inside the plant, Cd disrupts key physiological processes including photosynthesis, nutrient uptake, and enzyme activities [5, 6]. Research has highlighted that Cd induces oxidative stress in rice plants, resulting in the excessive generation of reactive oxygen species (ROS), which damage cellular structures [7]. Furthermore, Cd accumulation in rice grains poses a health risk to humans because rice is a staple food for more than half of the world's population, sustaining over 2 billion people in Asia alone [8]. High levels of Cd contamination have been reported in rice-growing regions including India, Thailand, China, and Japan, with surveys in China revealing severe Cd accumulation in paddy soils and rice grains [8, 9]. Exposure to Cd poses severe health risks and can cause kidney damage, bone demineralization, and other toxic effects in humans [10].

Given the scale of the problem, there is an urgent need to develop effective mitigation strategies to limit Cd accumulation in rice. The feasible approaches include agronomic practices to regulate soil Cd mobility, genetic improvements to enhance rice tolerance and restrict grain Cd accumulation, and environmental management techniques to reduce Cd inputs. Such strategies are essential to ensure rice food safety, safeguard human health, and maintain sustainable agricultural production [11].

2. Cadmium (Cd) movement from soil to grain in rice plants

Cadmium (Cd) uptake and movement in rice involve interconnected processes: root absorption, xylem loading for upward translocation, redistribution at nodal junctions, and remobilization from leaves to the phloem, ultimately leading to grain accumulation [12]. Initial uptake occurs through both apoplastic and symplastic pathways, leading to Cd accumulation in root xylem tissues. From there, Cd is transported to shoots and grains via the xylem [13]. Cadmium shares transport routes with essential micronutrients such as Fe^{2+} , Zn^{2+} , Mn^{2+} , and Ca^{2+} . Transporter families involved include Zinc-regulated/Iron-regulated transporter-like proteins (ZIPs), Natural Resistance-Associated Macrophage Proteins (NRAMPs), Oligopeptide Transporters (OPTs), and Yellow Stripe-Like (YSL) proteins, which facilitate Cd movement across tissues [14]. Rice expresses high levels of the *OsNramp5* gene, a key player in Cd uptake and root accumulation [15]. Other transporters, including *OsIRT1*, *OsIRT2*, and *OsNramp1*, also contribute to Cd^{2+} uptake, though less effectively than *OsNramp5* [16, 17, 18]. *OsNramp1* also supports Cd uptake but plays a secondary role [19]. Other key players include *OsCd1* (a Major Facilitator Superfamily transporter), *OsZIP3* (a Zn- and Fe-regulated transporter), and *OsHIR1* (a hypersensitive-induced response protein), which also participate in Cd uptake [20, 21, 22].

Once absorbed, Cd may either be transported into the vascular system or sequestered in vacuoles by tonoplast-localized transporters, reducing its mobility and toxicity [23]. Approximately 95% of Cd absorbed by roots is stored in vacuoles, reducing immediate toxicity [24]. The transporters such as *OsZIP7*, *OsLCD*, and *OsMTP1* help sequester Cd in the cytosol or promote its secretion into extracellular spaces, lowering cytosolic Cd levels and reducing toxicity [17, 23]. Xylem loading and root-to-shoot translocation of Cd are mainly mediated by P-type heavy metal ATPases, including *OsHMA2* and *OsHMA4*, which facilitate Cd transport into the xylem [23]. During the reproductive stage, *OsHMA2* also aids in intervascular transfer at stem nodes, enhancing Cd movement via the phloem to panicles and grains. At the nodes, Cd is transported into the panicle and grains through phloem-mediated pathways. *OsLCT1*, located in

parenchyma cells of the phloem and vascular bundles, plays a key role in intervascular Cd transfer to grains [25]. Similarly, *CCX2* in xylem parenchyma cells supports Cd loading into the xylem and its movement into grains [26]. Once in the grains, Cd is fixed through cation distribution mechanisms, limiting further movement to other plant organs [17, 26].

Cadmium accumulation in plants depends on its bioavailability in soil. The release of organic acids and phytosiderophores in the rhizosphere mobilizes nutrients but also solubilizes Cd, increasing its bioavailability [27]. Conversely, iron plaque deposition on root surfaces acts as a barrier, immobilizing Cd and fitting its entry [27]. Within the vascular system, Cd moves upward through the xylem from roots to shoots and leaves, eventually reaching the rice grains [13]. The distribution of Cd in the plant depends on factors such as soil type, pH, competing ions, and the rice genotype [24].

3. Impact of Cadmium Toxicity on plants

3.1 Germination of seeds

Cadmium toxicity significantly reduces seed germination and early seedling growth by disturbing physiological and biochemical processes. Low Cd concentrations may cause little effect, but higher levels inhibit germination and seedling establishment. Radicle growth is more affected than plumule growth, especially in rice varieties with lower Cd tolerance [28, 29]. In general, heavy metal stress has a minor influence on germination percentage but strongly affects seedling vigor and growth. One of the major effects of Cd is hormonal imbalance. Cd disrupts the activity of phytohormones such as abscisic acid (ABA), auxins, and gibberellic acid (GA), which are essential for seed germination [30, 31]. Seed dormancy and germination are mainly regulated by the balance between GA and ABA. GA promotes germination, while ABA induces and maintains dormancy. Studies show that exogenous GA_3 promotes germination, whereas high ABA concentrations inhibit it [32]. The imbalance of hormones alters germination signaling and reduces seedling vigor [32].

Cadmium also restricts water absorption, limiting its availability for seedling development. It prevents the transfer of soluble sugars to the embryonic axis and hinders starch mobilization in the endosperm, processes essential for early growth [33, 34]. Another critical mechanism is the inhibition of hydrolytic enzymes. Cadmium reduces the activity of proteases and α -amylase, which are required to break down stored food reserves [35, 36]. It decreases α -amylase and acid invertase activity in rice seeds, restricting carbohydrate and mineral mobilization [33]. Sensitive rice varieties show stronger reductions in amylase activity compared to tolerant ones [28, 36].

Calcium (Ca^{2+}) plays a key role in early germination by activating metabolic pathways. However, Cd competes with Ca for binding sites on calmodulin and other Ca-binding proteins, disrupting signaling and metabolic regulation [31, 37]. Calcium deficiency further enhances Cd toxicity, while Ca supplementation reduces Cd availability to plants and uptake by competing for Ca-permeable channels [38] (Figure 1).

3.2. Water and Nutrient Absorption

Plant roots play vital roles in water and nutrient [39]. When soils are contaminated with Cd, the osmotic potential of the soil solution can drop below that of the root cell sap. This creates osmotic stress, reducing water uptake. The imbalance leads to water deficit conditions, which are worsened by structural changes in the root system [39]. Cadmium alters root morphology, causing reduced root hair density, impaired primary root elongation, increased dieback, and restricted secondary root development [40, 41].

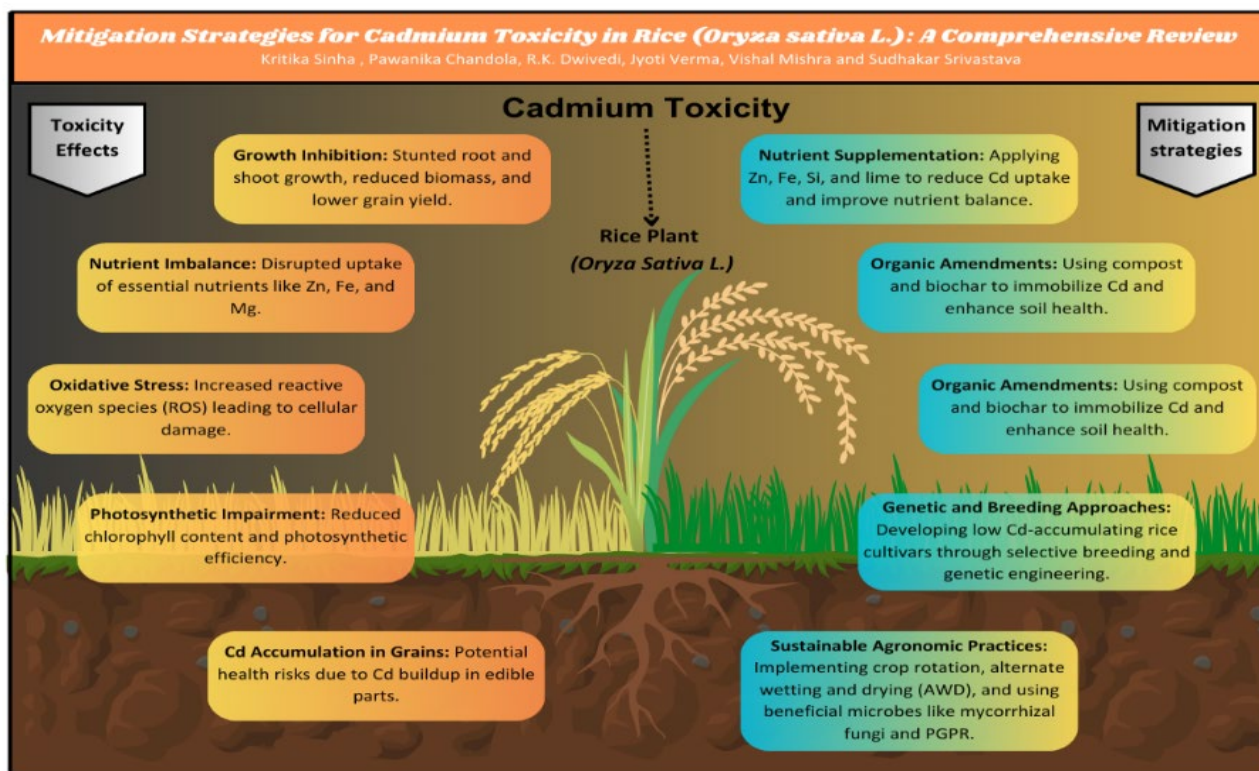


Figure 1. The mechanism of cadmium toxicity and potential mitigation strategies in plants

Prolonged exposure physically damages roots, making them soft, mucilaginous, and necrotic, which restricts root and shoot growth and limits water and nutrient uptake. At the molecular level, Cd disrupts the expression and function of auxin efflux transporter genes, which regulate auxin distribution. This disturbance inhibits lateral root formation and elongation, a process critical for root expansion in crops like rice [6].

Cadmium also causes cell wall thickening and deposition of incrusting compounds, which increase apoplastic resistance to water flow. In addition, Cd impairs aquaporin function, reducing water diffusion through membranes and hindering vascular transport. This lowers root sap exudation and decreases long-distance water movement [42]. As a result, aerial tissues like leaves experience dehydration, altered osmotic potential, vacuolar disruption, and reduced cellular water retention [43].

Besides water absorption, Cd strongly disrupts nutrient uptake and distribution. It competes with essential elements such as Ca, magnesium (Mg), phosphorus (P), and potassium (K), reducing their absorption and transport [44]. Cadmium exposure decreases uptake of iron (Fe), P, K, sulfur (S), Ca, zinc (Zn), manganese (Mn), and boron (B) limiting growth and development. Cadmium also blocks nitrate transport by inhibiting nitrate reductase activity in roots, reducing nitrate availability for shoots [44]. Elevated Cd levels, particularly under high temperatures, also disrupt the rhizosphere microbial community. This reduces nitrogen (N) availability and further compromises growth [45]. Furthermore, Cd interferes with iron chelation, limiting its loading into the xylem, and competes with calcium in alkaline soils, lowering its transport into roots [46].

3.3. Photosynthetic and Oxidative damage

Cadmium exposure disrupts essential physiological processes, including photosynthesis, resulting in reduced grain yield and overall productivity. The toxic effects are mainly linked

to oxidative stress and genotoxicity. Cadmium interferes with photosystem II (PSII) by blocking electron transfer, which disrupts chloroplast function and generates ROS [47]. In addition, Cd activates ROS production in the mitochondrial electron transport chain. Rice plants activate antioxidant enzymes to limit ROS; however, prolonged or high Cd exposure can suppress antioxidant defenses in both roots and shoots, worsening oxidative stress. Cadmium also stimulates plasma membrane-bound NADPH oxidase in peroxisomes, adding to ROS accumulation [44, 48]. Elevated ROS levels cause protein and lipid peroxidation, membrane disruption, nucleic acid degradation, and damage to photosynthetic proteins, undermining cellular integrity and metabolism [45, 49].

Cadmium accumulation in leaves further inhibits stomatal opening and disrupts Fe metabolism by suppressing iron reductase activity. This causes iron deficiency and reduces photosynthesis. Cadmium also interferes with chlorophyll biosynthesis, lowering chloroplast density and causing chlorosis. Stomatal conductance, cell size, and stomatal density in leaves also decline, affecting cell division and chloroplast differentiation [45]. At the biochemical level, Cd inhibits key enzymes of carbon fixation. It affects ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) and phosphoenolpyruvate carboxylase (PEPCase). Cadmium competes with Mg ions, essential cofactors for RuBisCO, substituting them with Cd ions. This alters RuBisCO activity, shifting it from carboxylation to oxygenation, which lowers photosynthetic efficiency [44]. Cd also induces irreversible dissociation of RuBisCO subunits, leading to enzyme inhibition [50]. In photosystem II, Cd displaces Ca in the Ca/Mn cluster of the oxygen-evolving complex (OEC) or modifies the Qb-binding site, further limiting photosynthesis [50]. These molecular and physiological changes reduce photosynthetic capacity, growth, and yield. Cd stress also affects nutrient uptake, enzyme activity, and metabolic processes, compounding its toxicity. Table 1 below summarizes some of the effects of chemicals on Cd stress in plants.

Table 1. Effect of Various Chemical Agents on Cd Stress Amelioration in Plants

S. No.	Plant name	Chemical agent and treatment details	Key Result of Amelioration	Ref.
Plant hormone				
1	Spanish needle (<i>Bidens pilosa</i>)	Foliar spraying with 6-Benzylaminopurine (30 mg/L), salicylic Acid (SA) (30 mg/L), and 24-epi-brassinosteroid (EBR) (10 mg/L) on plant leaves to enhance Cd accumulation and phytoextraction.	SA, 6-BA, and 24-EBR increased Cd in leaves, improved translocation and phytoextraction, boosted growth (dry weight), photosynthesis (chlorophyll), and antioxidant activity (reduced Malondialdehyde (MDA)). Best results with 30 mg/L SA spray.	51
2	Rapeseed (<i>Brassica napus</i>) (Youfei 1, Xiangyou 787 varieties)	Abscisic acid (ABA) Applied at 0, 0.5, 1, 5, or 10 $\mu\text{mol/L}$; treatment started after 1 week of Cd exposure and lasted for 2 weeks. Cd stress (10 $\mu\text{mol/L}$).	ABA application alleviated Cd toxicity in <i>Brassica napus</i> by improving growth traits (biomass, root/shoot length), enhancing chlorophyll content, and boosting photosynthesis through increased gas exchange. ABA established redox homeostasis via upregulation of antioxidant enzymes (Superoxide dismutase (SOD), Peroxidase (POD), catalase (CAT), reducing oxidative damage (lower MDA levels). It regulated Cd-related gene expression, promoting detoxification and tolerance signaling pathways.	52
3	Mung bean (<i>Vigna radiata</i>)	Foliar spray of 10 μM ABA applied to Cd-stressed mung bean seedlings to enhance tolerance in leaves, stems, and roots.	ABA improved plant growth, reduced Cd accumulation, and restored mineral content. It regulated 2241 differentially expressed genes (DEGs) involved in metabolism, stress responses, and photosynthesis. ABA upregulated transporter genes and enhanced photosynthetic activity to help plants cope with Cd stress.	53
4	Simple stone crop (<i>Sedum alfredii</i>)	Exogenous application of jasmonic acid (JA) in different concentrations; optimal effects observed at 1 $\mu\text{mol/L}$ under 100 $\mu\text{mol/L}$ Cd stress (100, 300, 500 $\mu\text{mol/L}$ Cd)	Jasmonic acid (JA) improves <i>Sedum alfredii</i> growth and photosynthesis under Cd stress by enhancing antioxidant enzyme activities, reducing oxidative stress, and mitigating ROS and MDA levels. JA promotes Cd uptake and accumulation while upregulating genes related to photosynthesis, antioxidant defense, and Cd transport.	54
5	Simple stone crop (<i>Sedum alfredii</i>)	100 $\mu\text{mol/L}$ SA applied exogenously	Enhanced growth and Cd accumulation. Best Cd remediation at 100 $\mu\text{mol/L}$. Upregulated genes related to photosynthesis and Cd uptake. Hormonal interactions crucial for stress resilience	55
6	Quick weed (<i>Galinsoga parviflora</i>)	Strigolactone (GR24) at 1 $\mu\text{mol/L}$ and 2 $\mu\text{mol/L}$, applied during Cd treatment at 0.1 mg/L.	1 $\mu\text{mol/L}$ GR24: Increased shoot Cd content (+8.75%), shoot Cd extraction (+12.35%), bioconcentration, and translocation factors. 2 $\mu\text{mol/L}$ GR24: Decreased shoot Cd content, shoot Cd extraction, and translocation factor.	56
Growth regulator and biostimulant				
7	Cotton (<i>Gossypium</i> sp.) (Guoxin 9 variety)	Melatonin (MT) (100 μM) applied through root irrigation and leaf spraying; applied weekly	MT alleviated Cd stress by enhancing root growth, prolonging root and root hair lifespan, and limiting Cd transport to shoots and bolls, reducing Cd bioconcentration in bolls by 61.17%. It also increased root volume, surface area, and length, while improving plant biomass and photosynthetic parameters.	57
8	Rapeseed (<i>Brassica napus</i>)	Melatonin was applied at 200 μM with a Cd concentration of 30 mg/kg, improving plant performance under Cd stress.	MT treatment improved growth (50%), biomass (45%), and Cd tolerance (45% Cd translocation). It increased phytochelators (8%) and metallothioneins (14%), reduced oxidative stress (lower hydrogen peroxide H_2O_2 , MDA), and regulated 1809 genes related to stress and plant-pathogen interactions.	58
9	Pepper (<i>Capsicum annum</i>)	Chitosan (CTS) was applied at 0.5 mg/L and 1.0 mg/L weekly for 3 weeks, with Cd concentrations of 0, 100, 150, and 200 mg/kg in the growth medium.	Decreased Cd uptake in plants. Increased plant growth and performance. Reduced oxidative stress (lower H_2O_2 , ABA, MDA). Enhanced amino acids and hormones (GA, IAA, SA).	59
10	Tobacco (<i>Nicotiana tabacum</i>)	Sodium Nitropursside (SNP) foliar spray of 150 μM applied to Cd-stressed tobacco seedlings to reduce oxidative stress and improve Cd tolerance.	Restored stress tolerance (MDA, H_2O_2 , proline) and reduced oxidative stress by enhancing antioxidants and enzymes (SOD, CAT, POD, ascorbate peroxidase (APX), glutathione reductase (GR). Improved Cd tolerance by increasing root accumulation, limiting shoot translocation, and promoting vacuolar sequestration. Upregulated genes like NtMT2F and NtPCS2 for Cd compartmentalization and increased residual Cd fraction. Boosted nitric oxide production and counteracted Cd's inhibition of NR activity.	60

Nutrient element				
11	Sweet Potato (<i>Ipomoea batatas</i>)	Potassium (K) hydroponic treatments: K0Cd0 (no K, no Cd), K0Cd1 (no K, 0.1 mg Cd/L), K1Cd0 (3 mM K, no Cd), K1Cd1 (3 mM K, 0.1 mg Cd/L). Seedlings treated for two weeks with nutrient solutions, changed every 3 days	K supply reduced Cd accumulation in roots and shoots, downregulated Cd uptake genes, and upregulated lignin/cellulose biosynthesis genes, enhancing Cd retention in roots and improving tolerance.	61
12	Tomato (<i>Solanum lycopersicum</i>)	Silicon (Si): 1 mM Na ₂ SiO ₃ solution applied as foliar spray.	Reduced Cd absorption, increased Cd efflux, enhanced antioxidant activity (SOD, CAT, APX, GR), lowered ROS and MDA, preserved chlorophyll and chloroplasts, improved seedling growth (root, weight), regulated hormones (IAA, GA, SA), boosted carbon-nitrogen metabolism.	62
Combinations and other agents				
13	Chickpea (<i>Cicer arietinum</i>)	Seeds were pretreated with effector solutions [MgCl ₂ (10 mM)], ascorbic acid (1 µM), Ethylenediaminetetraacetic acid, EDTA (100 µM), and citric acid (100 µM)] for 12 hours or exposed to a combination of 200 µM Cd and effectors for 6 days. Cadmium (Cd) stress ranged from 0 to 1000 µM, with key evaluation at 200 µM Cd.	Ascorbate (ASC) and EDTA reduced H ₂ O ₂ accumulation, alleviated Cd-induced growth inhibition, and increased epicotyl fresh weight by 28% (ascorbic acid) and 36% (EDTA). Ascorbic acid boosted APX activity and gene expression, while EDTA provided similar protection. Citric acid and magnesium chloride were less effective.	63
14	Ramie (<i>Boehmeria nivea</i>)	GA3 (Gibberellic Acid), BR (Brassinosteroids), Treatments applied every 15 days for 125 days. In Experiment A, five plant growth regulators GA3, brassinosteroids (BR), SA, putrescine (PA) and ethylene (ETH) were sprayed on ramie leaves at varying concentrations of 50, 100, and 200 mg L ⁻¹ for GA, ETH, and SA; 0.1, 1, and 10 mM for PAs; and 0.1, 1, and 10 mg L ⁻¹ for BR, with CK-1 as the control (0 mg L ⁻¹), while in Experiment B, a combination of GA ₃ , KNO ₃ , and KH ₂ PO ₄ was applied.	GA ₃ , BR, SA, and PA increased biomass and Cd accumulation by enhancing TF and BCF. ETH reduced biomass but improved translocation factor (TF) and bioaccumulation factor (BCF). GA ₃ was most effective, while GA ₃ +KNO ₃ or GA ₃ +KH ₂ PO ₄ inhibited Cd uptake.	64
15	Baby primrose (<i>Primula forbesii</i>)	24-EBR (0.1 µmol/L) and MT (100 µmol/L) applied via foliar spray on Cd-stressed plants (200 µmol L ⁻¹); treatments were done separately and combined for comparison. Cd	24-EBR alleviated Cd-induced growth inhibition, enhancing crown width, root length, shoot fresh weight, and other growth parameters. It boosted antioxidant enzyme activities and photosynthesis. EBR alone was more effective than in combination with MT, with both treatments improving plant growth and Cd tolerance.	65
16	Maize (<i>Zea mays</i>) ('Tiannong 9' and 'Fenghe 6' varieties)	Maize grown in nutrient solutions under Cd stress, Hemin applied to test its effects.	Hemin alleviated Cd stress in maize by enhancing sucrose and nitrogen metabolism (sucrose phosphate synthase (SPS), sucrose synthase (SS), nitrate reductase (NR), glutammin synthetase (GS), glutamine oxoglutarate aminotransferase (GOGAT), glutamate dehydrogenase (GDH) and balancing hormones by increasing IAA, zeatin riboside (ZR), GA, and their ratios to ABA while reducing ABA, methyl jasmonate (MeJA) and SA.	66
17	Maize (<i>Zea mays</i>)	Cadmium (Cd) stress (50 mg/L Cd in soil) -Seed priming: 450 ppm and 600 ppm zinc oxide nanoparticles (ZnO-NPs). - Foliar spray: 450 ppm and 600 ppm ZnO-NPs.	Seed priming (450 ppm) improved plant height (18.46%), total chlorophyll (80.07%), ascorbic acid (25.10%), and 2-2 diphenyl-1-picrylhydrazyl (DPPH) activity (26.66%). - Enhanced uptake of Mg ²⁺ (38.86%), K ⁺ (27.83%), and Zn ²⁺ (43.68%). - Foliar spray (450 ppm): Enhanced cob diameter (19.45%), kernels per cob (6.35%), total chlorophyll (73.59%), and yield.	67
18	Wheat (<i>Triticum aestivum</i>) and Rice (<i>Oryza sativa</i>)	Oxalic acid (OxA), Tartaric acid (TA); Citric acid (CA), Humic acid (HA) (Low and high molecular weight organic acids) OxA: 0.5 mM, TA: 0.5 mM; CA: 1 mM, HA: 10 g/kg soil. Exogenously applied to contaminated soil.	OxA and TA increased Cd bioavailability in soil and plants, with OxA showing maximum Cd uptake; HA decreased Cd bioavailability, leading to 41% and 48% reduction in Cd uptake in wheat and rice, respectively, while enhancing plant growth and yield.	68
19	Potato (<i>Solanum tuberosum</i>) ('Atlantic' variety)	500 µmol/L CdCl ₂ + 400 µmol/L glutathione (GSH); treatment duration: 96 h	Increased expression of PAL, CAD, POD genes, higher enzymatic activities (PAL, CAD, POD), and elevated lignin content. Hormonal changes: increased SA and JA, decreased IAA. Gene expression changes in TGA, PR1, Aux/IAA, JAZ, AUX, ARF.	69



Figure 2. The methods to reduce bioavailability of cadmium to plants

4. Mitigation of Cadmium (Cd) toxicity

Cadmium toxicity in rice can be reduced through several strategies that either limit Cd accumulation by altering bioavailability to plants (Figure 2) or enhance plant tolerance. 4.1 Soil Amendments

4.1 Soil Amendments

4.1.1 Inorganic Amendments

Recent studies highlight the critical role of inorganic substances in reducing Cd bioavailability in soils (Figure 3). Phosphorus-containing materials mitigate Cd bioavailability by direct adsorption, enhancing the negative charge of soil particles, and facilitating precipitation of Cd into stable metal phosphates like $\text{Cd}(\text{H}_2\text{PO}_4)_2$ and $\text{Cd}_3(\text{PO}_4)_2$ [9, 70, 71]. However, low recommended field application rates may not induce sufficient precipitation, making Cd immobilization largely dependent on adsorption [72]. High Cd concentrations in triple superphosphate (TSP) and phosphate rock (PR) fertilizers can release soluble Cd, increasing plant uptake [73]. Dissolution of adsorbed or precipitated Cd in the rhizosphere can further elevate Cd levels around roots, enhancing uptake by accumulator plants [74]. Therefore, the application and dosage of phosphate amendments should be tailored to soil physicochemical properties for effective Cd remediation.

Zinc can have antagonistic or synergistic effects on Cd accumulation; higher Zn activity reduces Cd levels in roots and shoots. Accordingly, soil and foliar Zn applications have been shown to decrease Cd accumulation in cereals [75, 76]. Zinc oxide nanoparticles have demonstrated feasibility in simultaneously reducing arsenic and cadmium accumulation in rice tissues under continuous flooding [77]. Similarly, Ca based supplements can be a solution to reduce Cd accumulation [78]. Silicon (Si) increases soil pH, reducing Cd solubility and availability. Calcium silicate treatments reduce Cd concentrations without altering soil pH [79]. Si also strengthens cell walls, limiting apoplastic Cd transport [80], and when combined with selenium (Se), it reduces Cd translocation from root to shoot. The integration of silicon with other treatments, such as nano-zinc oxide, has shown potential in alleviating Cd toxicity in rice plants [81].

Nitrogen (N) and potassium (K) fertilizers enhance growth and phytoextraction in Cd-contaminated soils [82]. Nitrogen supplementation improves Cd tolerance by enhancing photosynthesis, but NH_4^+ in soil can increase Cd uptake through rhizospheric acidification [83].

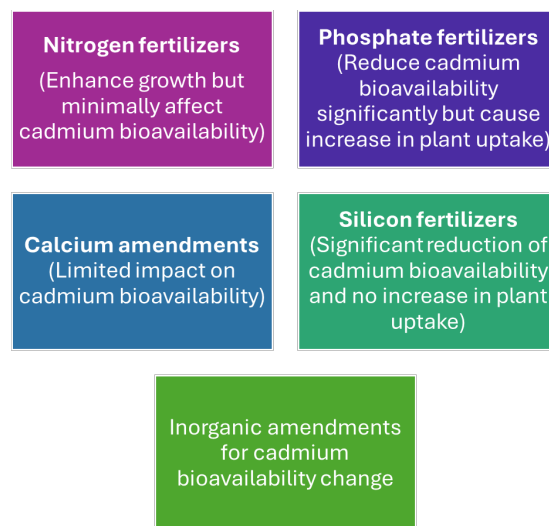


Figure 3. Potential inorganic amendments for cadmium toxicity mitigation

Iron (Fe) and manganese (Mn) oxides immobilize Cd through adsorption and redox reactions [84]. Zero-valent iron (Fe^0) reduces bioavailable Cd without affecting plant growth. $\text{EDTA-Na}_2\text{Fe}$ reduces Cd in rice when applied to soil, though foliar FeSO_4 and $\text{EDTA-Na}_2\text{Fe}$ can increase root and shoot Cd [85]. Zero valent iron (Fe^0) was found to be the most effective in decreasing the dynamic of Cd in spiked soil, showing significant reductions in Cd mobility compared to control treatments [86].

Innovative soil conditioning methods are being developed to reduce Cd accumulation in paddy rice. One such method involves uniformly spreading a soil conditioner (sulfite) over acid soil contaminated with heavy metal Cd before ploughing and fertilizing. Combining this with soil flooding during the rice growth period creates a low-electrochemical-potential reducing environment, which effectively adsorbs Cd and generates chemical precipitates, thereby controlling Cd contamination [87].

4.1.2 Organic Amendments

Biochar, derived from thermal combustion of organic material under anoxic conditions, effectively mitigates heavy metal pollution. Its high cation exchange capacity, porosity, fine particle size, elevated pH, carbon content, and functional groups enable Cd adsorption, reducing mobility and plant uptake [88]. Biochar efficacy depends on soil pH, moisture, organic matter, feedstock, and pyrolysis temperature [45]. Cadmium immobilization occurs via ion exchange, complexation with functional groups, π -bond interactions, oxygen group activity, pyrolysis-induced structural changes, and precipitation of metals on biochar surfaces [89]. Over time, mineral-organic layers on biochar further stabilize Cd. Reducing particle size enhances surface area and adsorption capacity. Biochar has shown significant effects in reducing rice grain Cd uptake. In a two-year field experiment, biochar amendments at 10, 20, and 40 t ha⁻¹ reduced grain Cd concentration by up to 61.9% and total plant Cd uptake by up to 54.2% [90]. The application of iron-modified biochar (FeBC) has been found to mitigate Cd toxicity and also the greenhouse gas emissions [91].

Compost immobilizes heavy metals through microbial decomposition, releasing humic substances rich in hydroxyl and phenolic groups that bind Cd [92]. Green waste compost increases soil cation exchange capacity, carbon, and nitrogen levels, enhancing fertility and reducing heavy metals [89]. Animal manures elevate soil pH, transforming Cd into less bioavailable forms. Organic amendments, rich in lignin, cellulose, tannins, and carbonates, coat soil particles and enhance dissolved organic

carbon (DOC), forming DOC-metal complexes that reduce Cd bioavailability [93]. Humic and fulvic acids in these amendments have carboxyl and hydroxyl groups that strongly bind Cd, lowering its mobility. Plant-based amendments like bamboo powder or charcoal, biosorb heavy metals and support sustainable remediation [94]. Applying 2% red mud has been shown to enhance soil iron and manganese oxide-cadmium proportions after soil drainage, which decreases the soil cadmium release maximum and rate. This amendment helps to reduce cadmium mobility in paddy soil [95]. Sepiolite, a clay mineral, has been reported to effectively reduce Cd mobility in soil and decrease Cd content in tobacco leaves by 32%–42% in yellow soil and 86% in red soil [96].

4.1.3 Chemical Amendments

Chemical amendments can alter Cd mobility and bioavailability, facilitating uptake or immobilization. EDTA is a common chelator that enhances Cd solubility, promoting translocation to shoots [34]. Its efficiency depends on soil properties; in calcareous soils, reaction with calcium carbonate reduces chelating efficiency, and its slow biodegradation poses environmental risks [97]. Alternatives like EDDS are more biodegradable and environmentally friendly while enhancing Cd phytoavailability [98]. Organic acids, including citric acid, mobilize Cd for phytoextraction at low concentrations. Humic acids increase Cd mobility through functional groups that facilitate transport. Soil acidification via fertilizers or direct acids increases Cd solubility for uptake [99, 100]. Acidified manure both supplies nutrients and lowers pH, enhancing Cd phytoavailability. Combining biochar with chemical amendments like EDTA or organic acids improves Cd sorption, retention, and uptake [101].

4.2 Agronomic Practices

Strategic fertilizer application plays a crucial role in modulating Cd dynamics in soil. Fertilizers, such as phosphate fertilizers, convert mobile Cd into more stable, less bioavailable forms [102]. Water management is another pivotal agronomic practice that influences Cd solubility through changes in redox potential and pH. Controlled water levels can limit Cd uptake and accumulation in rice grains. Flooding before and after the heading stage markedly reduces Cd in rice, while aerobic conditions increase Cd accumulation [103, 104]. Flooding raises soil pH and facilitates Cd immobilization, converting Cd^{2+} to cadmium sulfide (CdS), which is less soluble under anaerobic conditions. Tillage and crop rotation influence soil's physical, chemical, and biological characteristics, impacting Cd dynamics [105]. Rotating rice with high Cd-accumulating crops, such as oilseed rape, reduces Cd in subsequent rice crops. Reduced tillage decreases Cd levels in wheat grains compared to conventional practices, likely due to increased organic matter enhancing Cd adsorption and limiting microbial-driven Cd release [106]. Reduced tillage also stabilizes soil structure, reducing erosion and runoff of contaminated soil.

4.3 Phytoremediation

Phytoremediation uses hyperaccumulator plants to extract metals from soil. However, species selection is critical for the purpose, as root-to-soil surface area significantly influences metal accumulation. Naturally occurring hyperaccumulators demonstrate high efficiency [107]. Families such as Betulaceae, Brassicaceae, Carophyllaceae, Fabaceae, Fagaceae, Plumbaginaceae, and Poaceae can accumulate toxic metals, with Brassicaceae particularly prominent. Fast growth and high biomass are essential for phytoextraction [107]. Grasses and

weeds, including *Cyperus rotundus*, *Cyperus kylinga*, *Marsilea quadrifolia*, and *Ludwigia parviflora*, are effective for wetland rice remediation. Oilseed crops such as sunflowers provide dual benefits of field remediation and biofuel production. Rotating hyperaccumulators with crop plants strategically reduces Cd contamination. Aquatic macrophytes, including *Eichhornia crassipes*, *Lemna minor*, and *Pistia stratiotes*, can remove water-soluble Cd via rhizofiltration [108]. Other species like *Elatine hexandra*, *Althenia filiformis*, and *Monita rivularis* show potential for Cd removal in flooded fields [109]. Using algal biomass in flooded plains increases Cd removal efficiency threefold. Successive cropping and residue removal further reduce metal levels. Phytoremediation effectiveness improves with symbiotic associations such as mycorrhiza. Mycorrhizal symbiosis precipitates Cd as polyphosphate granules, binds Cd to fungal cell walls, and chelates Cd internally, enhancing soil cleanup [110]. Symbiosis extends root functional capacity, improving metal uptake, water use efficiency, and nutrient acquisition. Mycorrhiza also increases phosphorus uptake, precipitating Cd and reducing root entry, while tissue dilution decreases Cd translocation to grains [110].

4.4 Bioremediation

Microbes can either immobilize Cd or enhance its phytoextraction by plants in contaminated rice fields. Key factors include microbial cell wall binding, metal concentration, soil pH, calcium levels, ionic strength, and Cd methylation [111]. Functional groups on bacterial cell walls—carboxyl, phosphate, sulfhydryl, and hydroxyl—serve as active sites for Cd adsorption [111]. Microbial species such as *Bacillus subtilis* Tp8 and *Pseudomonas fluorescens* G9 produce biosurfactants that remove Cd efficiently. Sulfate-reducing bacteria precipitate Cd as insoluble sulfides, reducing bioavailability. Alginate carriers support microbial inoculation but require periodic renewal to prevent Cd release from degradation [112]. Siderophore-producing bacteria mobilizes metals via chelation improving remediation efficiency [113]. Bioaugmentation with strains like *Pseudomonas fluorescens* Pf27, *Variovorax paradoxus*, *Rhodococcus* sp., and *Flavobacterium* sp. increases water-soluble and exchangeable Cd, enhancing plant biomass and Cd uptake in *Brassica juncea* [114, 115]. Similar effects occur in soybean and canola using *Pseudomonas putida* 62BN, *Pseudomonas montelli* 97AN, *Pseudomonas tolaasii* ACC23, *Pseudomonas fluorescens* ACC9, *Alcaligenes* sp. ZN4, and *Mycobacterium* sp. [116, 117]. Certain bacterial strains, such as *Bacillus cereus*, can alleviate Cd toxicity and enhance the phytoremediation efficiency of rice seedlings by reducing Cd uptake and increasing antioxidant enzyme activities [118]. The use of *Serendipita indica* in combination with nano-zinc oxide (nZnO) has shown promise in alleviating Cd toxicity in rice plants [81].

4.5 Molecular and genetic approaches

Beyond conventional field-based remediation strategies, genetic modifications in rice crops that limit Cd uptake are crucial for ensuring food safety and mitigating economic losses associated with remediation efforts, particularly in moderately Cd-contaminated fields. Research indicates that the uptake and distribution of Cd in various plant tissues are governed by genetic factors [40]. Genes associated with Cd tolerance operate by either synthesizing metal chelators or excluding Cd via metal transporter-mediated processes). Genetic manipulation of these pathways facilitates targeted Cd sequestration within plant tissues, thereby regulating Cd accumulation in edible grains. Variation in Cd-controlling traits among different rice cultivars highlights the potential for genomic-level control in minimizing Cd content in rice grains [119].

4.5.1 Selection and breeding of low Cd accumulating rice plants

Differences in uptake and distribution of essential and nonessential trace elements, including Cd, among cultivars can lead to either deficiencies or toxicities, affecting food safety and nutritional quality. Plant breeding focuses on enhancing beneficial trace elements while minimizing Cd accumulation. Variation in Cd uptake and partitioning among rice cultivars provides a route to developing varieties with low Cd accumulation. Cd uptake and distribution in rice are controlled by heritable dominant traits [120]. Natural variation in grain Cd concentration ranges from 13- to 23-fold among diverse japonica germplasm [121]. Key factors influencing Cd accumulation include high root activity, elevated shoot-to-root ratio, and water consumption [122]. Quantitative Trait Loci (QTLs) for Cd accumulation have been mapped to chromosomes 2, 7, 3, 4, 6, 8, 5, 11, and 10, enabling marker-assisted selection for low-Cd traits [121, 122]. These traits remain stable across lowland and upland environments. Utilizing alleles linked to low-Cd accumulation can reduce grain Cd content with minimal management interventions. A Japanese temperate Japonica cultivar developed via carbon ion-beam irradiation exhibited undetectable Cd levels in grains while maintaining normal growth, yield, and quality [123].

4.5.2 Genetically Modified Cd Hyperaccumulation and Tolerance

Genetic engineering enables the development of hyperaccumulator plants with higher biomass and enhanced heavy metal sequestration. Introducing new genes or amplifying existing ones enhances heavy metal tolerance and accumulation. Overexpressed metal transport proteins can sequester metals in roots (phytostabilization) or shoots (phytoextraction). Manipulating genes involved in phytochelatin synthesis, such as

phytochelatin synthetase and γ -glutamylcysteine synthetase, further improves Cd tolerance and accumulation. Transgenic tobacco species, including *Nicotiana glauca* and *Nicotiana tabacum*, have shown increased Cd accumulation [124]. Plants overexpressing metallothionein genes also exhibit enhanced heavy metal tolerance. Gene silencing techniques offer additional precision, using small RNA molecules to suppress specific mRNA targets, thereby modulating heavy metal responses [125]. For example, silencing the phytochelatin synthase gene reduces grain Cd levels, while silencing the root-localized Cd transporter OsNRAMP5 increases Cd translocation to shoots, demonstrating versatility in controlling metal distribution [126]. A functional OsHMA3 allele limits Cd translocation from roots to above-ground tissues by sequestering Cd into root vacuoles [127]. Conversely, a loss-of-function mutation in OsHMA3 can lead to greatly elevated Cd translocation to rice shoots and grains [128]. CRISPR/Cas9 technology has been successfully employed to modify the regulatory region of OsNRAMP5, aiming to reduce Cd accumulation in rice [129]. Targeted expression of P-type ATPase genes encoding metallochaperones can direct Cd to non-edible tissues. Transgenic approaches using bacterial Cd efflux operons (CzcC, CzcB, CzcA) can prevent Cd accumulation in grains [130].

The Table 2 below summarizes genetic engineering strategies used to enhance Cd hyperaccumulation and tolerance in plants, highlighting key genes, mechanisms, and approaches for improved phytoremediation and environmental sustainability.

Despite these advances, challenges remain, including public acceptance and regulatory hurdles. Safety and environmental concerns regarding GMOs necessitate cautious adoption and rigorous testing for ecological safety and efficacy. Continued research and dialogue are needed to address these challenges and integrate genetically engineered plants into environmental management.

Table 2. Genetic engineering approaches to develop Cd hyper accumulation and tolerance in plants.

S.No.	Plant Name	Gene name and details	Transgenic plant key result only	Ref.
1	Thale cress <i>Arabidopsis thaliana</i>	WRKY33-ATL31-IRT1 regulatory cascade	WRKY33-ATL31-IRT1 module plays a crucial role in timely blocking Cd absorption to prevent metal toxicity in <i>Arabidopsis</i> .	131
2	Thale cress (<i>Arabidopsis thaliana</i>)	ApHIPP26 from <i>Arabis paniculata</i>	Overexpression of ApHIPP26 enhanced Cd tolerance and accumulation by boosting antioxidant enzyme activity and altering the expression of genes involved in plant hormone pathways.	132
3	Thale cress (<i>Arabidopsis thaliana</i>)	BcaSOD1 <i>Brassica carinata</i> superoxide dismutase gene from Purple <i>Brassica carinata</i>	BcaSOD1 overexpression led to higher Cd accumulation in roots but not shoots, suggesting its role in root-based Cd absorption.	133
4	Thale cress (<i>Arabidopsis thaliana</i>)	StWRKY6 (<i>Solanum tuberosum</i>) WRKY6 gene	Overexpression of StWRKY6 in <i>Arabidopsis</i> improved Cd tolerance, increasing reactive oxygen species scavenging enzyme activity and SAPD values.	134
5	Thale cress (<i>Arabidopsis thaliana</i>)	EcAGL	EcAGL enhances Cd tolerance in transgenic <i>Arabidopsis</i> by modulating metal transporter genes (AtHMA2, AtHMA3, AtNRAMP5) and affecting the ethylene biosynthesis pathway under Cd stress.	135
6	Barley (<i>Hordeum vulgare</i>)	HvNAT2	Overexpression of HvNAT2 in barley increased Cd tolerance and tissue Cd accumulation, while reducing oxidative damage.	136
7	Golden Rain Tree (<i>Koeleruteria paniculata</i>)	KpMIPS	Overexpression of KpMIPS in both <i>K. paniculata</i> and <i>Arabidopsis</i> increased Cd accumulation in roots while decreasing its transfer to stems and leaves. It regulates pectin and phytic acid contents, facilitating the immobilization of Cd in the root cell wall.	137
8	Desert poplar (<i>Populus euphratica</i>)	PePCR2	Overexpression of PePCR2 in poplar enhanced cadmium (Cd) tolerance by increasing Cd ²⁺ efflux from roots, regulating Cd ²⁺ transporter genes, and reducing cytosolic Cd toxicity	138
9	California poplar (<i>Populus trichocarpa</i>)	PtPLATZ3	enhanced cadmium (Cd) tolerance and accumulation, maintained chlorophyll content, membrane integrity, and upregulating Cd-related genes	139

10	Potato (<i>Solanum tuberosum</i>)	VvWRKY2TF <i>Vitis vinifera</i> WRKY2 Transcription Factor	VvWRKY2TF enhanced Cd stress tolerance by improving plant growth and activating defense mechanisms against oxidative stress.	140
11	Rice (<i>Oryza sativa</i>)	SQUAMOSA promoter binding-like transcription factor 7(SPL7)	MicroRNA miR535 influences Cd metabolism via its target gene SPL7, which negatively regulates Nramp5	141
12	Rice (<i>Oryza sativa</i>)	OsThi9	Overexpression of OsThi9 increased cell wall Cd binding, reduced Cd translocation to shoots, and decreased Cd accumulation in brown rice by $\geq 51.8\%$, without compromising yield or essential nutrient content.	142
13	Rice <i>Oryza sativa</i>	OsPDR20 (a Pleiotropic Drug Resistance 20 type ATP binding cassette transporter G family gene)	Knockdown of OsPDR20 (via RNA interference) resulted in reduced growth, biomass, and chlorophyll content in rice under Cd stress, but led to increased Cd accumulation in rice roots, shoots, and grains.	143
14	Rice (<i>Oryza sativa</i>)	OsNRAMP2 (a member of the Natural Resistance- Associated Macrophage Protein (NRAMP) family)	Knocking out OsNRAMP2 reduced grain Cd by 38%, while overexpressing it increased Cd by 50%, with Hap 1 of the gene linked to 45.3% lower Cd in grains, making OsNRAMP2 a potential target for low-Cd rice breeding.	144
15	Rice (<i>Oryza sativa</i>)	OsIRX10 (a gene involved in cell wall biosynthesis)	The fc19 mutants with OsIRX10 mutations exhibited improved lodging resistance, enhanced biomass saccharification, and increased cadmium resistance, with alterations in cell wall composition and genes related to carbohydrate and phenylpropanoid metabolism.	145
16	Kashgar tree (<i>Tamarix hispida</i>)	ThRAX2	enhanced Cd tolerance in <i>T. hispida</i> and Arabidopsis, ThRAX2 binds to the novel cis-element MYB-T (CTTCCA), the promoters of Cd-responsive genes (<i>ThSOS1</i> , <i>ThCKX3</i> , <i>ThCAX3A</i> , and <i>ThMYB78</i>), regulating their expression to maintain ion homeostasis and enhance antioxidant activity.	146
17	Tobacco (<i>Nicotiana tabacum</i>)	BADH (Betaine Aldehyde Dehydrogenase)	BADH-transgenic lines can synthesize Glycinebetaine in vivo; GB enhances cadmium tolerance	147
18	Tobacco (<i>Nicotiana tabacum</i>)	PePCR10, a cadmium resistance protein (PCR) from <i>Populus euphratica</i>	Overexpression of PePCR10, enhanced growth (height, root length, weight) and increased Cd/Al tolerance.	148
19	Tobacco (<i>Nicotiana tabacum</i>)	NtNRAMP3	Knockout of <i>NtNRAMP3</i> reduced Cd transport from the vacuole to the cytoplasm, reduced plant injury, and enhanced Cd tolerance.	149
20	Tobacco (<i>Nicotiana tabacum</i>)	NtNRAMP6c	CRISPR-Cas9 knockout of NtNRAMP6c reduced Cd accumulation, enhanced Cd resistance, altered gene expression related to metal ion transport and photosynthesis, modified phytohormone balance, and reshaped rhizosphere microbial communities	150
21.	Rice (<i>Oryza sativa</i>)	OsNramp1	Knockout of OsNramp1 reduces Cd accumulation in rice shoots and grains. In addition, compared to wild-type yeast, yeast expressing rice OsNramp1 suffers more serious toxicity under Cd stress	151
22.	Rice (<i>Oryza sativa</i>)	OsIRT1	Increased expression of OsIRT1 leads to increased Cd accumulation in rice.	152
23.	Rice (<i>Oryza sativa</i>)	OsCd1 (major facilitator superfamily; natural variation Val449Asp distinguishes <i>indica</i> vs. <i>japonica</i>)	<i>Japonica</i> allele OsCd1V449 reduces grain Cd accumulation; useful for breeding indica cultivars	22
24.	Rice (<i>Oryza sativa</i>)	OsZIP7 (plasma membrane- localized transporter for Zn and Cd; expressed in root and node parenchyma cells)	Knockout retained Zn and Cd in roots and basal nodes, reducing their delivery to upper nodes and grains; shows OsZIP7 is critical for Zn and Cd xylem loading and grain accumulation	153
25.	Rice (<i>Oryza sativa</i>)	OsMORC6a, OsMORC6b, OsMORC6c (Microrhizidia proteins regulating Cd response via DNA methylation)	Triple knockout (more6abc mutants) reduced Cd accumulation but increased Cd sensitivity; OsMORC6 proteins positively regulate Cd tolerance and uptake by modulating DNA methylation and stress-related genes	154
26.	Thale cress (<i>Arabidopsis thaliana</i>)	HIPP33–ATG8e module (HIPP33: metallochaperone, cargo receptor; ATG8e: core autophagy protein)	HIPP33 bound Cd and mediated autophagy-dependent vacuolar sequestration; loss of HIPP33 or autophagy mutants showed Cd hypersensitivity and reduced Cd tolerance	155
27.	Maize (<i>Zea mays</i>) / Tobacco (<i>Nicotiana tabacum</i>)	AGL8–ZmSKD1 module (ZmSKD1: AAA ATPase, vesicle trafficking; AGL8: transcription factor regulator)	Overexpression of ZmSKD1 in tobacco reduced Cd accumulation, enhanced antioxidant capacity, promoted vesicle trafficking, and improved Cd tolerance by reducing uptake and enhancing Cd excretion	156

28.	Potentilla (<i>Potentilla sericea</i>)	PsGSH2 (glutathione synthetase, Cd-inducible)	Overexpression in Arabidopsis enhanced antioxidant activity (SOD, POD, CAT, GR), reduced ROS and lipid peroxidation, lowered Cd translocation, and improved Cd tolerance	157
29.	Quinoa (<i>Chenopodium quinoa</i>)	CqNRAMP1 transporter with CqMYB26–CqbHLH162 regulators (CqNRAMP1: metal transporter; CqMYB26 & CqbHLH162: transcription factors promoting CqNRAMP1 expression)	Overexpression of CqNRAMP1 increased Cd uptake and sensitivity; CqMYB26 and CqbHLH162 enhanced CqNRAMP1 expression, further promoting Cd absorption	158
30.	Rice (<i>Oryza sativa</i>)	UCL23–WRKY51–miR528 module (UCL23: small copper protein regulating Cd via ROS signaling; WRKY51: transcription factor; miR528: post-transcriptional regulator)	Natural variation of UCL23 determines Cd accumulation differences; Japonica haplotype reduces Cd uptake and grain accumulation; WRKY51 and miR528 jointly regulate UCL23 expression in Cd response	159

5. Conclusions

Cadmium contamination in paddy fields represents a significant environmental and agricultural challenge, negatively impacting rice (*Oryza sativa* L.) growth, physiological processes, and grain quality. The toxic effects of Cd disrupt nutrient uptake, photosynthetic efficiency, and metabolic homeostasis while inducing oxidative stress through excessive ROS accumulation. Given its propensity to bioaccumulate in rice grains, Cd contamination poses severe risks to human health, necessitating the implementation of effective mitigation strategies. A multidisciplinary approach is essential to alleviate Cd toxicity in rice plants.

Agronomic strategies, including soil amendments with essential nutrients such as zinc (Zn), iron (Fe), silicon (Si), and lime, have been shown to reduce Cd bioavailability and modulate its uptake. Organic amendments, particularly biochar and compost, improve soil physicochemical properties and facilitate Cd immobilization, thereby limiting its translocation to aboveground plant tissues. Exogenous applications of phytohormones, osmolytes, and signaling molecules enhance antioxidant defense mechanisms and stress tolerance, mitigating Cd-induced oxidative damage. In addition to soil and nutrient-based approaches, genetic and biotechnological interventions, including the development of low Cd-accumulating rice cultivars through traditional breeding and molecular approaches, offer a long-term and sustainable solution for reducing Cd accumulation in grains. The utilization of beneficial microorganisms, including plant growth-promoting rhizobacteria (PGPR) and mycorrhizal fungi—play a critical role in reducing Cd uptake and enhancing plant resilience to heavy metal stress.

Given the complexity of Cd toxicity and its interaction with soil-plant systems, an integrated, multi-pronged approach combining soil amendments, biological interventions, and genetic improvements is imperative for effective Cd mitigation. Future research should focus on optimizing these strategies, exploring novel genetic modifications, and developing eco-friendly remediation techniques to ensure sustainable rice production in Cd-contaminated regions while minimizing risks to human health and food security.

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Competing interests

The authors declare there are no competing interests.

Authors' contributions

Kritika Sinha, Pawanika Chandola and Rakesh Kumar Dwivedi wrote the manuscript. Jyoti Verma and Vishal Mishra compiled the tables and references and Sudhakar Srivastava supervised and finalized the manuscript.

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