

Heavy Metal Stress In Plants: Mechanisms, Impacts, And Mitigation Strategies- A Comprehensive Review

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Abstract

The contamination of terrestrial and aquatic ecosystems by heavy metals (HMs) constitutes a pressing global environmental concern, particularly due to their toxicological impacts on plant systems, long-term persistence, and potential for food chain bioaccumulation. Both essential and non-essential HMs interfere with critical physiological and molecular pathways in plants, primarily through oxidative damage, disruption of enzymatic functions, nutrient imbalances, and genotoxic effects. Despite these challenges, plants possess an array of sophisticated defense systems—including enzymatic and non-enzymatic antioxidant responses, metal chelation, vacuolar sequestration, and hormonal signaling pathways—that enable mitigation of HM-induced toxicity. This review consolidates current knowledge on HM uptake, translocation, toxicity mechanisms, and plant adaptive responses, with an emphasis on phytoremediation technologies. Various remediation strategies, including phytoextraction, rhizofiltration, and phytostabilization, are critically evaluated based on their efficiency, limitations, and feasibility in practical applications. Emerging advancements such as molecular engineering, use of transgenic lines, and manipulation of rhizospheric microbiomes are also discussed as transformative approaches to enhance remediation outcomes. A systems-level understanding of plant–metal interactions is vital for the development of effective phytotechnologies and for mitigating the ecological and agronomic consequences of HM pollution.

Keywords: Heavy metals (HMs), Phytoremediation, Plant defense mechanisms, Toxicity mechanisms, Metal uptake and translocation.

1. INTRODUCTION

As immobile organisms, plants are continuously exposed to abiotic stressors, with heavy metal (HM) stress posing a major challenge to plant health and agricultural sustainability. Due to their non-biodegradable, persistent, and bioaccumulative nature, HMs disrupt key physiological functions. Heavy metals—defined as elements with atomic weights $>63.5 \text{ g mol}^{-1}$ and densities $>5 \text{ g cm}^{-3}$ —include both essential micronutrients (e.g., Fe, Cu, Zn) and toxic elements like Cd, Pb, Hg, and As (Alloway, 2013). Anthropogenic sources such as industrialization, mining, vehicular emissions, fossil fuel use, and agrochemical overuse are the primary contributors to HM pollution (Nagajyoti et al., 2010). These metals persist in soils and waters, entering food chains and threatening plant and human health through biomagnification (Clemens & Ma, 2016).

In plants, HMs induce oxidative stress, enzyme inhibition, ion imbalance, and nutrient disruption (Sharma & Dubey, 2005). Unlike organic pollutants, HMs cannot be degraded and must be detoxified via sequestration. Visible symptoms include chlorosis, necrosis, stunted growth, and reduced photosynthesis. At the molecular level, HMs disrupt nucleic acid synthesis, displace cofactors in metalloproteins, and alter gene expression (DalCorso et al., 2010). While natural processes like weathering contribute background levels, human activities such as electroplating and e-waste recycling are the primary sources (Wuana & Okieimen, 2011). These activities degrade soil quality, disrupt microbial communities, and promote HM accumulation in ecosystems. Chronic human exposure is linked to severe health issues including neurological and renal damage, and cancer (Clemens & Ma, 2016). Given their persistence and toxicity, understanding HM uptake, toxicity pathways, and plant defense responses is crucial. This review synthesizes recent advances in HM stress and phytoremediation, integrating knowledge from plant physiology, genomics, and environmental biotechnology to guide sustainable remediation strategies.

2. HEAVY METALS IN PLANTS: UPTAKE AND TOXICITY

Plants interact with heavy metals (HMs) through complex mechanisms influenced by environmental conditions and plant physiology. HM uptake and translocation are affected by soil pH, redox potential, organic matter, metal speciation, and genotype (Kabata-Pendias, 2011). Once inside the plant, the fate of metal ions—whether detoxified, sequestered, or toxic—depends on their chemical properties and the plant's tolerance capacity. Hyperaccumulator species can store high levels of HMs in tissues without toxicity, making them vital for phytoremediation (Rascio & Navari-Izzo, 2011).

At the cellular level, HMs cause phytotoxicity through multiple pathways: disrupting membrane integrity and permeability, binding to protein thiol groups and inhibiting enzymes, interfering with DNA processes, and disturbing ionic balance. These effects lead to visible symptoms such as chlorosis, necrosis, growth inhibition, and reduced fertility (Sharma & Dubey, 2005). Hormonal signals like ethylene, salicylic acid, and jasmonic acid help modulate gene expression under HM stress, enhancing plant defense responses (Kopyra & Gwóźdź, 2004). Advancements in molecular tools, including transgenic technologies and omics approaches, have provided insights into the genetic and biochemical networks governing metal tolerance. These findings support the development of HM-resilient crops and the refinement of phytoremediation techniques (Clemens et al., 2013).

3. RELEVANCE TO AGRICULTURE AND FOOD SECURITY

The proliferation of heavy metals (HMs) in agricultural soils presents a growing threat to crop production, food safety, and public health. Elevated HM concentrations in arable land negatively impact plant growth, yield, and physiological functionality, thereby undermining food security and the sustainability of agroecosystems. Numerous studies have linked chronic ingestion of HM-contaminated food to adverse health outcomes, including nephrotoxicity, neurodegenerative diseases, cardiovascular disorders, and carcinogenicity (Khan et al., 2015).

4. CLASSIFICATION

Heavy metals (HMs) are a diverse group of elements typically characterized by high

atomic mass (usually greater than 63.5 g mol^{-1}) and density exceeding 5 g cm^{-3} (Alloway, 2013). Their classification is primarily based on biological function and toxicity profile in plant systems. Accordingly, HMs are generally characterized into two primary groups: essential and non-essential elements.

4.1 Essential Heavy Metals

Essential heavy metals are micronutrients that play indispensable roles in plant physiological and biochemical processes when present at optimal concentrations. These elements are crucial cofactors in enzymatic reactions, contributors to redox reactions, and structural components of key biomolecules. However, their beneficial effects become deleterious when accumulated in excess, leading to toxicity through oxidative stress and metabolic dysfunction.

Key examples include: Copper (Cu), Zinc (Zn), Iron (Fe), Manganese (Mn) and Nickel (Ni): Required for urease activity and nitrogen metabolism (Marschner, 2011).

4.2 Non-Essential Heavy Metals Non-essential heavy metals are elements that have no recognized physiological function in plants and are typically toxic even at low concentrations. Their toxicity stems from their high reactivity, ability to mimic essential elements, and interference with enzymatic and genetic processes. These metals often induce oxidative stress, inhibit vital metabolic pathways, and cause irreversible cellular damage.

Prominent non-essential HMs include: Cadmium (Cd), Lead (Pb), Mercury (Hg), Arsenic (As) and Chromium (Cr) (notably in its hexavalent form)

These metals are predominantly introduced into the environment through anthropogenic sources such as industrial discharges, fossil fuel combustion, electroplating, and improper waste disposal (Clemens, 2006).

5. MECHANISMS OF PHYTOTOXICITY

Heavy metal (HM) phytotoxicity results from their interference with vital cellular processes, causing oxidative stress, metabolic disruption, and nutrient imbalance. These stressors lead to reduced growth, tissue damage, and impaired development.

5.1 Oxidative Stress and ROS Generation

HMs like cadmium (Cd), lead (Pb), and mercury (Hg) stimulate excessive reactive

oxygen species (ROS) such as superoxide (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($\bullet\text{OH}$), overwhelming antioxidant defenses (Gill & Tuteja, 2010). ROS induce: Lipid peroxidation, damaging membranes and increasing permeability; Protein oxidation, altering thiol (-SH) groups and enzyme activity; DNA damage, including strand breaks and chromatin cross-linking (Schützendübel & Polle, 2002).

5.2 Enzymatic and Metabolic Disruption

HMs bind functional groups or displace essential metal cofactors, inhibiting key enzymes. Cd and Hg substitute Zn in metalloproteins, disrupting redox regulation. Pb and Hg impair heme biosynthesis, nitrate metabolism, and Calvin cycle activity (Sharma & Dubey, 2005).

5.3 Nutrient Uptake Interference

Ionic mimicry allows HMs like Cd to compete with essential ions (Ca^{2+} , Fe^{2+}), inducing nutrient deficiencies and disturbing physiological functions (DalCorso et al., 2010).

5.4 Photosynthetic Impairment

HMs hinder chlorophyll biosynthesis, damage chloroplasts, reduce PSII efficiency, and limit CO₂ uptake through stomatal closure.

5.5 Genetic and Epigenetic Effects

HMs cause genotoxicity via direct DNA binding or ROS-mediated damage. They also trigger epigenetic changes—DNA methylation, histone modification, and chromatin remodeling—affecting gene expression and stress memory (Kovalchuk et al., 2001).

6. PLANT UPTAKE DYNAMICS

The uptake and internal distribution of heavy metals (HMs) in plants are regulated by soil properties, metal speciation, and specific transport mechanisms. Understanding these processes is key for assessing phytotoxicity, improving phytoremediation, and developing HM-tolerant crops.

6.1 Root Uptake Pathways

Roots are the main site for HM absorption, influenced by soil pH, redox conditions, cation exchange capacity, and organic ligands. Metals enter through two primary routes: the apoplastic pathway, involving passive flow through cell walls and intercellular spaces, and the symplastic pathway, requiring active transport across plasma membranes via metal-specific proteins.

Transporter families such as ZIP (ZRT/IRT-like Proteins) uptake Zn²⁺, Fe²⁺, Mn²⁺, and

Cd²⁺; NRAMPs transport Fe²⁺, Mn²⁺, Cu²⁺, and Cd²⁺; and HMAs (Heavy Metal ATPases) are involved in efflux and compartmentalization of Zn, Cu, Cd, and Pb. These transporters are tightly regulated to maintain metal homeostasis and prevent toxicity (Clemens, 2006).

6.2 Soil and Environmental Influences

Soil pH is a vital aspect in HM solubility and uptake. Acidic conditions enhance metal mobility, while alkaline soils reduce availability via precipitation (Alloway, 2013).

Organic matter can immobilize metals through complexation or enhance mobility by

forming soluble complexes. Competing cations like Ca²⁺ and Mg²⁺ can also reduce HM uptake through competitive inhibition.

6.3 Rhizospheric Interactions

Microbial associations, especially with arbuscular mycorrhizal (AM) fungi, modulate HM dynamics. AM fungi reduce metal toxicity by sequestering HMs, excreting chelators, and improving nutrient and water uptake (Glick, 2010). These interactions support plant health under metal stress.

6.4 Foliar Uptake

HMs can also enter through foliage in polluted environments. Atmospheric particles or gaseous forms like mercury vapor penetrate leaves via stomata or diffuse through the cuticle, especially under high humidity. This pathway enhances to HM load, mostly in industrial areas (Sharma & Dubey, 2005).

6.5 Translocation and Compartmentalization

Once inside, metals move via xylem to shoots, with some redistribution through phloem. Mobility varies: Cd, Zn, and Ni are mobile; Pb and Cu are less so. Plants detoxify metals by vacuolar sequestration, binding with ligands like phytochelatins/metallothioneins, or cell wall immobilization, limiting cellular damage.

7. PHYSIOLOGICAL IMPACTS

Exposure to heavy metals (HMs) imposes profound physiological stress on plants, affecting critical stages of growth and development. These impacts vary with metal species, concentration, duration of exposure, plant genotype, and environmental context. Typical symptoms include inhibited seed germination, reduced root and shoot elongation, chlorosis, necrosis, impaired photosynthesis, and reproductive failure (Sharma & Dubey, 2007; DalCorso et al., 2010).

7.1 Germination and Early Growth

HMs such as cadmium (Cd), lead (Pb), and mercury (Hg) hinder early developmental processes by disrupting cell division and elongation, increasing seedling mortality, and altering hormonal balances. These effects interfere with the establishment of a robust root system, ultimately reducing water and nutrient acquisition (Carrier et al., 2003).

7.2 Photosynthetic Efficiency

- Photosynthesis is a primary target of HM toxicity, with multiple disruptions observed:
- Chlorophyll biosynthesis is impaired due to restricted uptake of Mg^{2+} and Fe^{2+} , essential cofactors.
- Chloroplast structure is compromised, particularly thylakoid membrane disorganization.
- Photosystem II (PSII) function is reduced, lowering light energy conversion efficiency.
- Stomatal conductance decreases under HM stress, limiting CO_2 availability and reducing water-use efficiency (Sharma & Dubey, 2005).

7.3 Water Relations and Membrane Integrity

Heavy metal stress exacerbates membrane lipid peroxidation, leading to increased membrane permeability and ion leakage. Disruption of aquaporin function reduces cellular water transport, impairing turgor maintenance and cell expansion, especially under osmotic stress conditions.

7.4 Nutrient Imbalance

HMs hinder the uptake and distribution of essential nutrients for instance calcium (Ca^{2+}), potassium (K^+), magnesium (Mg^{2+}), and zinc (Zn^{2+}). This competition leads to deficiencies that compromise enzyme activity, protein synthesis, and structural stability. For instance, Cd can substitute for Zn in transcription factors, disrupting gene expression and cellular regulation (DalCorso et al., 2010).

7.5 Oxidative and Metabolic Stress

In addition to reactive oxygen species (ROS), HM exposure often results in the accumulation of toxic metabolites like methylglyoxal (MG), which exacerbate oxidative damage. Lipid peroxidation, protein carbonylation, enzyme inhibition, and DNA fragmentation are hallmarks of such stress, often culminating in genotoxicity, premature senescence, or programmed cell death (Schützendübel & Polle, 2002).

7.6 Reproductive Development

HMs impair reproductive structures and processes, including: Flower formation and morphology, Pollen viability and tube elongation and Fertilization success and seed development. These disruptions translate to reduced fecundity, poor seed quality, and compromised yield potential in contaminated environments (Nagajyoti et al., 2010).

7.7 Genetic and Epigenetic Modifications

At the genomic level, HMs can induce mutagenesis, chromosomal aberrations, and DNA- protein cross-linking. Epigenetically, exposure may alter DNA methylation and histone modification patterns, thereby modulating gene expression and potentially enhancing stress memory and transgenerational resilience (Kovalchuk et al., 2001).

8. ADAPTIVE RESPONSES

Plants have evolved a diverse repertoire of adaptive responses to cope with heavy metal (HM) stress, operating at molecular, cellular, physiological, and systemic levels. These mechanisms serve to mitigate toxicity, maintain cellular homeostasis, and ensure survival under adverse conditions.

8.1 Antioxidant Defense Systems

A central strategy against HM-induced oxidative stress is the upregulation of antioxidant defenses. These systems are composed of:

- Enzymatic antioxidants: Superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase (GR) play key roles in detoxifying ROS by converting superoxide radicals and hydrogen peroxide into water and molecular oxygen.
- Non-enzymatic antioxidants: Compounds such as ascorbic acid, glutathione, tocopherols (Vitamin E), and phenolic compounds act as redox buffers, directly scavenging ROS and protecting cellular structures (Gill & Tuteja, 2010).

8.2 Chelation and Sequestration

Plants mitigate HM toxicity through the chelation and subsequent sequestration of metal ions. Key players include:

- Phytochelatins (PCs): These glutathione-derived peptides bind to heavy metals like Cd^{2+} , Pb^{2+} , and Hg^{2+} , forming complexes that are transported into vacuoles.
- Metallothioneins (MTs): Cysteine-rich proteins with high metal-binding affinity, particularly for Cu, Zn, and As, contribute to intracellular detoxification (Clemens, 2006).

8.3 Vacuolar Compartmentalization

Sequestering metal-chelate complexes into vacuoles is a vital mechanism to limit cytosolic exposure. Transport across the tonoplast is facilitated by ATP-binding cassette (ABC) transporters and other vacuolar metal transport proteins.

8.4 Cell Wall Binding

The plant cell wall acts as a peripheral barrier to HM uptake. Functional groups such as carboxyl and hydroxyl residues in cell wall polysaccharides bind metal ions, reducing their mobility.

8.5 Hormonal Regulation

Plant hormones orchestrate a wide range of stress-responsive processes under HM exposure:

- Ethylene modulates antioxidant enzyme activity and stress gene expression.
- Salicylic acid (SA) improves defense signaling and redox homeostasis.
- Jasmonic acid (JA) subsidizes to systemic resistance and moderates ROS signaling

(Kopyra & Gwóźdź, 2004).

8.6 Symbiotic Associations

Symbiosis with arbuscular mycorrhizal (AM) fungi provides multiple protective effects:

- Binding metals within fungal structures
- Enhancing plant nutrient and water uptake
- Secreting chelators that limit metal bioavailability (Glick, 2010)

8.7 Genetic and Epigenetic Modulation

Plants respond to HM exposure through the transcriptional activation of genes encoding metal transporters (e.g., ZIP, NRAMP, HMA), detoxification proteins, and stress-associated factors. Epigenetic mechanisms, including DNA methylation and histone modifications, contribute to stress adaptation and may establish transgenerational tolerance (Kovalchuk et al., 2001).

8.8 Biotechnological Approaches

Genetic engineering has enabled the development of transgenic plants overexpressing metal-binding proteins, antioxidant enzymes, and transporters. These modified lines often exhibit enhanced tolerance and accumulation capacities (Clemens et al., 2013).

9. PHYTOREMEDIATION APPROACHES AND FUTURE PERSPECTIVES

Phytoremediation, the use of plants to mitigate environmental contaminants, represents an eco-friendly, cost-effective, and visually appealing strategy for remediating heavy metal (HM) pollution in soils and water bodies. This green technology capitalizes on the natural ability of certain plant species to absorb, accumulate, stabilize, or transform toxic metals into less harmful forms, thereby contributing to ecological restoration and agricultural recovery.

9.1 Core Phytoremediation Strategies

Phytoremediation comprises several distinct yet interconnected approaches, each operating via specific physiological and biochemical pathways:

- **Phytoextraction:** Plants absorb HMs through roots and transport them to shoots, allowing metal removal via harvested biomass. Hyperaccumulators like *Thlaspi caerulescens* and *Sedum alfredii* are especially effective.
- **Phytostabilization:** Involves immobilizing HMs in the rhizosphere via root adsorption, complexation, or precipitation, reducing their mobility and bioavailability to prevent leaching and uptake.
- **Phytovolatilization:** Some plants enzymatically convert toxic metals (e.g., Hg, Se, As) into volatile forms released into the atmosphere. This method requires careful ecological evaluation.
- **Rhizofiltration:** Working plant roots-terrestrial or hydroponic-to absorb and precipitate metals from water, valuable for treating wastewater and contaminated groundwater.
- **Phytodegradation & Phytotransformation:** Though primarily applied to organic pollutants, certain plants and rhizospheric microbes can degrade or transform metal complexes through metabolic activity.

9.2 Plant Selection Criteria

Successful phytoremediation depends heavily on plant traits, including:

- High biomass production
- Deep and extensive root systems
- Broad metal tolerance and accumulation capacity
- Rapid growth and adaptability to local conditions

Natural hyperaccumulators are valuable but often have low biomass. Conversely, high-biomass crops such as *Brassica juncea* and *Helianthus annuus* are increasingly being engineered or selected for improved HM uptake.

9.3 Technological Advancements

Enhancing phytoremediation efficiency requires integration with modern biotechnologies:

- Genetic Engineering: Introduction of genes encoding metal transporters, phytochelatin synthases, or antioxidant enzymes to improve uptake and detoxification.
- Rhizosphere Engineering: Utilization of plant growth-promoting rhizobacteria (PGPR) and mycorrhizal fungi to increase metal solubility and plant tolerance.
- Chelator-Assisted Phytoextraction: Application of synthetic (e.g., EDTA) or natural (e.g., citric acid) chelating agents to enhance HM availability, though this must be balanced against potential leaching risks.

9.4 Current Limitations

Despite its advantages, phytoremediation faces several constraints:

- Time-intensive, often requiring multiple cropping cycles
- Element specificity, with plants typically targeting only a subset of HMs
- Bioavailability challenges, especially in aged or strongly adsorbed metal forms
- Biomass disposal concerns, particularly with toxic residues

9.5 Future Directions

To overcome these limitations and expand phytoremediation's applicability, future efforts should prioritize:

- Identification and breeding of superior genotypes under field-relevant conditions
- Functional elucidation of regulatory networks involved in metal homeostasis
- Integration of omics technologies (genomics, transcriptomics, metabolomics) to uncover novel tolerance and accumulation pathways
- Development of site-specific decision-support systems for field implementation
- Conducting long-term, large-scale trials to validate laboratory successes

10. Comparative Analysis of Plant Species and Genetic Modifications Hyperaccumulators have received significant attention due to their inherent ability to concentrate astonishing amounts of definite metals in aerial tissues without exhibiting toxicity symptoms. However, their generally slow growth and low biomass output can limit their large-scale applicability.

10.1 Hyperaccumulator Species

Several naturally occurring hyperaccumulators have been identified and characterized for their metal-specific uptake capabilities

Table 1. Some hyperaccumulator plants used in phytoextraction

Species	Metal(s) Accumulated	Natural/Engineered	Biomass	Hyperaccumulation (mg/kg)	Reference
<i>Pteris vittata</i>	As	Natural	Medium	>2,000 (As)	Yan et al., 2020
<i>Thlaspi caerulescens</i>	Zn, Cd	Natural	Low	>30,000 (Zn)	Yan et al., 2020

Sedum alfredii	Cd, Zn, Pb	Natural	Medium	>1,000 (Cd)	Yan et al., 2020
Brassica juncea	Pb, Cr, Cd, Zn	Both	High	500–1,500 (Pb)	Ali et al., 2013
Arabidopsis halleri	Zn, Cd	Natural	Low	>10,000 (Zn)	Yan et al., 2020
Helianthus annuus	Pb, Cd	Engineered	High	500–1,000 (Pb)	Fasani et al., 2018

10.2 High-Biomass Engineered Crops

To address the limitations of hyperaccumulators, attention has shifted to fast-growing, high-biomass crops that can be genetically enhanced for HM tolerance and accumulation:

- *Brassica juncea* (Indian mustard): Engineered variants show enhanced accumulation of Pb, Cr, Cd, and Zn, making it suitable for moderate-to-heavy contamination scenarios.
- *Helianthus annuus* (sunflower): Genetically modified lines demonstrate improved uptake of Pb and Cd, combining rapid growth with phytoremediation potential (Fasani et al., 2018).

10.3 Genetic Engineering Strategies Genetic modifications include:

- Overexpression of metal transporter genes (e.g., HMA4 for Zn/Cd)
- Upregulation of genes involved in chelator biosynthesis (e.g., phytochelatin synthase)
- Enhancement of antioxidant pathways (e.g., SOD, CAT, GR)

10.4 Integration of CRISPR and Omics Tools

Recent advances in genome editing, particularly the use of CRISPR/Cas9, offer precise manipulation of HM-related genes to improve stress tolerance and uptake efficiency (Singh et al., 2023).

CONCLUSION

Heavy metal (HM) stress is a major abiotic threat that hampers plant growth, reduces crop yields, and degrades environmental quality. HMs interfere with key physiological functions such as photosynthesis, nutrient uptake, and water balance, primarily through

oxidative stress, enzyme inhibition, and genotoxic effects. In response, plants deploy complex defense mechanisms, including antioxidant activity, metal chelation, vacuolar sequestration, and hormonal regulation. At the molecular level, they adjust gene expression and epigenetic pathways to mitigate damage. Phytoremediation, a green and cost-effective approach to clean HM-contaminated soils, utilizes processes like phytoextraction, phytostabilization, and rhizofiltration. The use of hyperaccumulator plants and genetically modified high-biomass species has expanded its practical applications. However, limitations such as slow remediation and biomass disposal persist. Integrative approaches combining genomics, CRISPR, and microbiome engineering are essential to overcome these barriers. A deeper understanding of plant-metal interactions is crucial for developing resilient crops and advancing phytoremediation technologies.

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