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Heavy Metal Stress and Plant Metabolism: Physiological Insights and Mitigation Approaches

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ABSTRACT

Heavy metal contamination poses a serious threat to agricultural productivity and ecosystem health due to its persistence, bioaccumulation and toxicity. Excessive accumulation of metals such as cadmium (Cd), lead (Pb), mercury (Hg), arsenic (As) and chromium (Cr) disrupts plant growth and metabolism by inducing oxidative stress, impairing photosynthesis, altering nutrient uptake and disturbing cellular homeostasis. Heavy metal stress also affects enzyme activity, secondary metabolism, carbon and nitrogen metabolism resulting in reduced plant productivity. Plants employ various defense mechanisms to cope with metal toxicity including antioxidant activation, synthesis of metal-chelating compounds, osmolyte accumulation and intracellular sequestration of toxic ions. In addition, several mitigation approaches such as phytohormone application, soil amendments, microbial interventions, molecular breeding and other biotechnological strategies have also been explored to enhance plant tolerance. This review summarizes the effects of heavy metals on plant physiology and metabolism and highlights current strategies for alleviating heavy metal toxicity. Understanding these mechanisms is essential for developing sustainable approaches to improve crop performance in contaminated environments.

Introduction

Heavy metal (HM) contamination of soil and water has emerged as a major environmental concern. Toxic metals such as cadmium (Cd), chromium (Cr), lead (Pb), arsenic (As), mercury (Hg) and excessive concentrations of cobalt (Co), copper (Cu), nickel (Ni), zinc (Zn) and manganese (Mn) adversely affect plant growth, development and productivity. Heavy metal stress promotes the generation of reactive oxygen species (ROS), resulting in oxidative damage to cellular components and reduced crop yield (Ashfaque *et al*., 2016).

The surface layer of soil supplies essential nutrients for plant growth but also acts as a major sink for heavy metals originating from industrialization, urbanization and other anthropogenic activities. Upon entering plant tissues, these toxic metals disrupt cellular structures, impair nutrient and water transport, inhibit photosynthetic processes and induce oxidative stress. These effects disturb physiological and biochemical functions that ultimately reduce plant growth, biomass accumulation, and crop quality (Gill *et al*., 2022).Understanding the effects of heavy metal stress on plant metabolism is essential for developing effective mitigation strategies. Therefore, this review focuses on the impacts of heavy metals on plant metabolic processes and discusses potential approaches for alleviating their adverse effects.

Sources of Heavy Metals – The sources of heavy metals in the environment can be broadly classified into natural and anthropogenic sources. Human activities such as mining, smelting and agriculture have significantly increased heavy metal contamination in many regions of the world (Herawati *et al*., 2000).

Natural Sources – Heavy metals occur naturally in the Earth's crust enter the environment through processes such as rock weathering, volcanic eruptions, hydrothermal activities, soil formation and erosion. These processes introduce metals such as Cd, Pb, Ni, Cr, As and Hg into soil, water and air. Natural events including forest fires, desert dust storms and sea spray also contribute to their distribution. Although natural sources influence background metal levels their contribution is generally lower than that of human activities.

Anthropogenic Sources – Human activities are the major contributors to heavy metal pollution. Industrial activities such as mining, smelting, electroplating and manufacturing release large amounts of heavy metals into the environment. Fossil fuel combustion and intensive agricultural practices, including the excessive use of phosphate fertilizers, sewage sludge, manure and pesticides further increase heavy metal accumulation in soils (Yanqun *et al*., 2005). In addition, urbanization, vehicle emissions, industrial waste, wastewater, municipal waste and electronic waste contribute significantly to environmental contamination, posing risks to plants, animals and human health.

Table 1. Major Heavy Metals- Sources and Their Toxic Effects on Plants

Heavy Metals	Major Sources	Major Effects on Plants	References
Cadmium (Cd)	Mining, smelting, phosphate fertilizers, batteries	Chlorosis, root damage, Fe deficiency, reduced photosynthesis and growth	Guo *et al.*, (2008)
Lead (Pb)	Industrial waste, paints, batteries, vehicle emissions	Reduced seed germination, disturbed water balance, oxidative stress, altered mineral nutrition	Sharma and Dubey (2005a); Reddy *et al.*, (2005)
Mercury (Hg)	Coal combustion, mining, industrial waste	Stomatal closure, disrupted water transport, oxidative stress and metabolic damage	Israr *et al.*, (2006); Zhou *et al.*, (2007)

Arsenic (As)	Pesticides, contaminated groundwater, natural deposits	Compete with phosphate uptake, impaired transpiration, Photosynthesis, protein synthesis and metabolism	Ahmad *et al.*, (2020)
Chromium (Cr)	Electroplating, leather tanning industries	Reduced germination, impaired photosynthesis and enzyme activity	Davies *et al.*, (2002); Peralta *et al.*, (2001)
Nickel (Ni)	Mining, smelting, fertilizers, sewage sludge	Chlorosis, necrosis and growth inhibition	Rahman *et al.*, (2005)
Copper (Cu) (essential micronutrient) Harmful at high concentrations	Mining and industrial activities	Oxidative stress, chlorosis and reduced growth	Gang *et al.*, (2013); Lewis *et al.*, (2001); Stadtman and Oliver (1991)
Zinc (Zn) (essential micronutrient) Harmful at high concentrations	Industrial waste, fertilizers, galvanization	Growth inhibition, chlorosis and premature senescence	Malik *et al.*, (2011)

Responses of Heavy Metals on Growth, Physiology and Metabolism of Plants- Exposure to toxic concentrations of heavy metals causes significant physiological and metabolic disturbances in plants (Villiers *et al*., 2011). Although symptoms vary depending on the metal and plant species, common effects include reduced growth, chlorosis, necrosis, loss of turgor, poor seed germination, and impairment of the photosynthetic apparatus (DalCorso *et al*., 2010). These responses arise from structural, biochemical, and molecular damage induced by heavy metal accumulation in plant tissues (Gamalero *et al*., 2009).

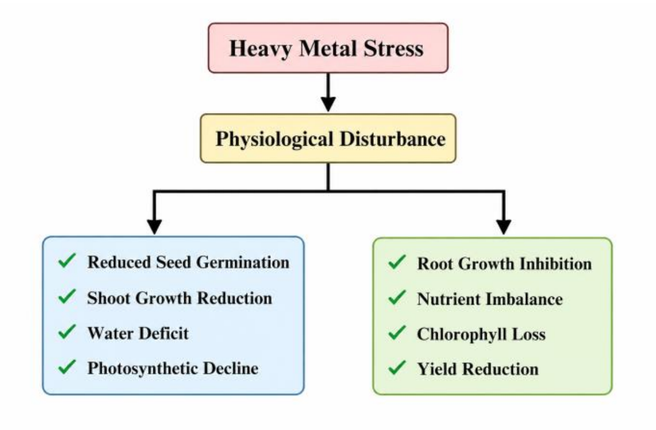

Fig 1: Physiological Consequences of Heavy Metal Stress in Plants-

Heavy metal stress also disrupts plant water relations, partly through the inhibition of aquaporins. Excess chromium (Cr) reduces water potential and transpiration rate while increasing resistance to water movement in cauliflower (Chatterjee, 2000). Similarly, elevated concentrations of Cu, Zn, and Mg inhibit seed germination and early seedling growth, whereas excess Fe, Pb, and Cu reduce germination in tomato seedlings (Mahmood *et al*., 2007; Mami *et al*., 2011). Heavy metals impair essential metabolic processes at toxic concentrations including photosynthesis, respiration and nitrogen metabolism (Maksymiec *et al*., 2007). They interfere with photosystems I and II, alter stomatal function and inhibit key carbon-fixation enzymes such as RuBisCO and phosphoenol pyruvate carboxylase (PEPC). Cadmium (Cd) reduces RuBisCO activity by replacing Mg^{2+} ions, while chromium damages chloroplast structure, thereby reducing photosynthetic efficiency.

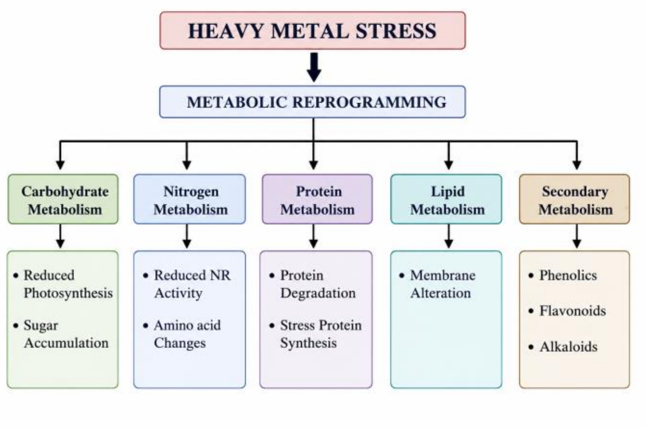

Fig 2: Effects of Heavy Metals on Plant Metabolism

Photosynthesis is further suppressed by metals such as Cu, Ni, Pb and Zn in maize (Vinit-Dunand, 2002). Respiration is also affected, with chromium showing strong inhibitory effects in pea plants (Bishnoi *et al*., 1993). In addition, heavy metals decrease the activity of nitrogen-metabolizing enzymes including nitrate reductase, nitrite reductase and glutamine synthetase, as reported in arsenic and aluminium exposed rice seedlings (Sharma and Dubey, 2005b).

Oxidative Stress and Antioxidant Defense

Heavy metals (HMs) disturb redox homeostasis in plants by increasing the production of reactive oxygen species (ROS) such as superoxide (O_2^-), hydroxyl radicals (OH•), singlet oxygen ($^1O_2$) and hydrogen peroxide (H_2O_2) (Anjum *et al*., 2012). These ROS react with important cellular components including DNA, proteins and lipids and cause oxidative stress and cellular damage (Hossain *et al*., 2012). Chloroplasts are one of the major sites of ROS production during photosynthesis (Asada, 2000).

Heavy metal stress also increases ROS generation through enhanced peroxisomal activity and the action of enzymes such as NADPH oxidases and cell-wall peroxidases (Seth *et al*., 2012; Mhamdi *et al*., 2010). For example, cadmium (Cd) stress increases H_2O_2 accumulation in leaf peroxisomes (Romero-Puertas *et al*., 2004). Excess ROS can damage cell membranes, proteins, enzymes and nucleic acids, leading to poor growth and metabolic disturbances in plants (Anjum *et al*., 2012; Miller *et al*., 2008).

To protect themselves from oxidative damage, plants activate both enzymatic and non-enzymatic antioxidant systems. Important antioxidant enzymes include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), glutathione peroxidase (GPX), monodehydroascorbate reductase (MDHAR) and dehydroascorbate reductase (DHAR) (Apel and Hirt, 2004). Plants also produce non-enzymatic antioxidants such as glutathione (GSH), cysteine (Cys), ascorbate (ASC), carotenoids and α-tocopherol, which help remove excess ROS and protect cells from oxidative injury (Gong *et al*., 2005).

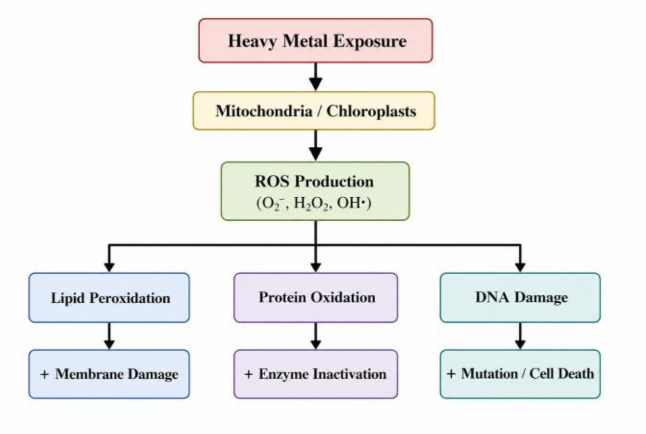

Fig 3: Heavy Metal-Induced Oxidative Stress Pathway

Mechanisms of Tolerance in Plants- Metal chelation (phytochelatins, metallothioneins) – Plants tolerate heavy metal stress by producing metal-binding compounds such as phytochelatins and metallothioneins. These cysteine-rich molecules bind and detoxify heavy metal ions, preventing them from interfering with important cellular processes and metabolic activities.

Transporters and compartmentalization – Plants also reduce heavy metal toxicity by transporting and storing excess metals in specific cellular compartments, particularly vacuoles. This process known as sequestration, prevents toxic metals from disrupting essential metabolic functions (Kanoun-Boulé *et al*., 2009). Several transporter proteins, including ABC, CDF, HMA, and NRAMP transporters, play important roles in metal transport and detoxification. Hyperaccumulator plants can store large amounts of metals in vacuoles; for example, Alyssum serpyllifolium can accumulate up to 72% of nickel (Ni) in vacuoles (Ernst *et al*., 1992).

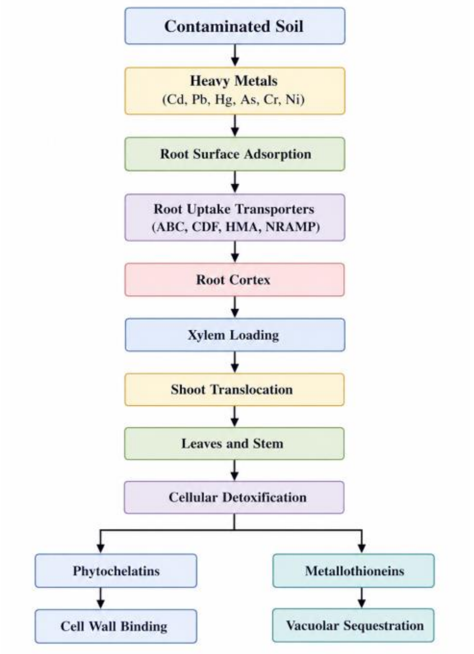

Fig 4: Mechanisms of Heavy Metal Uptake, Transport, and Sequestration in Plants

Hormonal regulation and signalling – Phytohormones play a crucial role in regulating plant responses to heavy metal stress. Hormones such as auxins, cytokinins, abscisic acid (ABA), gibberellins, ethylene and brassinosteroids help maintain growth, regulate stress-responsive genes and enhance tolerance under adverse conditions (Davies, 2012; Zluhan-Martínez *et al*., 2021). In particular, auxin influences root development and stress adaptation, while ABA is involved in the regulation of abiotic stress responses (Potters *et al*., 2007; Nambara *et al*., 2010; Danquah *et al*., 2014).

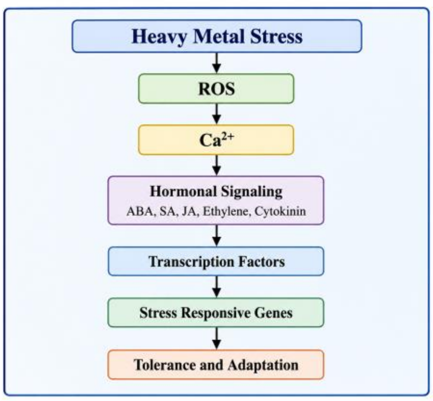

Fig 5: Phytohormone-Mediated Signaling Under Heavy Metal Stress

Mitigation Strategies- Heavy metal stress disrupts plant metabolism by inducing oxidative damage, impairing photosynthesis and disturbing nutrient balance. To counteract these effects, plants and researchers employ several mitigation strategies.

1. **Phytohormones**: Application of salicylic acid, jasmonic acid, brassinosteroids and cytokinins enhances antioxidant defense, maintains chlorophyll content and regulates stress-responsive metabolic pathways.
2. **Chelation and Sequestration**: Phytochelatins, metallothioneins and organic acids bind heavy metals and compartmentalize them into vacuoles, reducing their toxicity.
3. Soil Amendments: Biochar, compost, lime and phosphates reduce metal bioavailability and improve soil health, thereby limiting metal uptake.
4. **Microbial Assistance**: PGPR and arbuscular mycorrhizal fungi enhance nutrient uptake, improve antioxidant capacity and reduce metal translocation.
5. **Antioxidant Enhancement:** Strengthening enzymatic (SOD, CAT, APX, GR) and non-enzymatic (ascorbate, glutathione, proline, phenolics) antioxidants helps restore redox homeostasis and protect cellular metabolism.

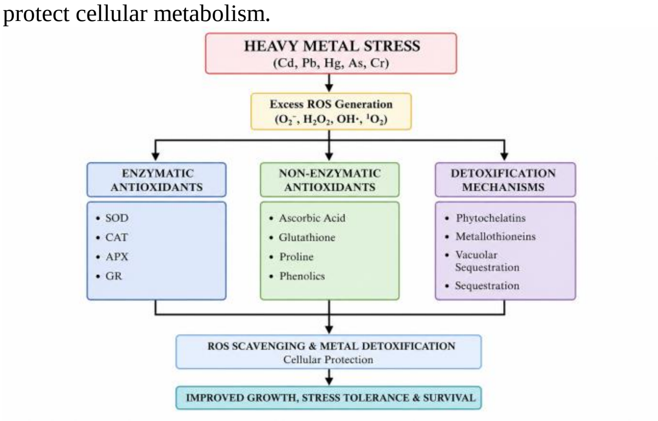

Fig 6: Plant Antioxidant and Detoxification Defense System Under Heavy Metal Stress

6. **Genetic and Molecular Approaches**: Overexpression of metal-binding proteins and modification of transporter genes improve tolerance and detoxification.
7. **Phytoremediation:** Hyperaccumulator plants such as Brassica juncea and Thlaspi caerulescens are used to extract or stabilize heavy metals from contaminated soils.

Overall, these strategies aim to restore physiological balance, maintain metabolic activity and enhance plant resilience under heavy metal stress.

Conclusion

Heavy metal stress is a major environmental problem that adversely affects plant growth, physiology and metabolism. Excess accumulation of metals such as Cd, Pb, Hg, As and Cr induces oxidative stress, damages cellular structures, impairs photosynthesis, disrupts nutrient balance and alters metabolic processes. To cope with these effects, plants activate antioxidant defense systems, produce metal-chelating compounds such as phytochelatins and metallothioneins, accumulate osmolytes and sequester toxic ions within cellular compartments.

Various mitigation approaches, including phytohormone application, antioxidant enhancement, soil amendments, microbial Assistance, nanotechnology-based interventions and genetic engineering have shown considerable potential in improving plant tolerance to heavy metal stress. A better understanding of plant responses and mitigation mechanisms will support the development of sustainable strategies for managing heavy metal toxicity and improving crop productivity in contaminated environments.

Future Perspectives

Despite significant progress, several gaps remain that require focused research:

Integrated Multi-Omics Approaches: Combining genomics, transcriptomics, proteomics and metabolomics will provide deeper insights into regulatory networks controlling heavy metal tolerance.

Molecular Regulation of Metal Transporters: Detailed functional characterization of metal transporter genes and signaling pathways is needed to improve selective uptake and sequestration.

Nanotechnology Safety and Optimization: Long-term ecological impacts and optimal dosages of nanoparticles must be evaluated before large-scale agricultural application.

Microbe-Plant-Soil Interactions: Understanding tripartite interactions under field conditions will enhance the reliability of microbial-assisted mitigation strategies.

Breeding and Genome Editing: CRISPR/Cas-based editing and marker-assisted breeding can accelerate development of metal-tolerant cultivars with minimal yield penalty.

Climate Change Interactions: Future studies should evaluate how combined stresses (heavy metals + drought/heat/salinity) affect plant metabolism.

Field-Level Validation: Most findings are laboratory-based; large-scale field trials are essential to translate physiological insights into practical agricultural solutions.

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