Review article
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Comparative analysis of heavy metal tolerance in Maize and strategies to enhance toxicity stress

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Abstract

Heavy metals pollute the ecosystem and negatively affect soil fertility, plant development, productivity and physiology. A plant's tolerance against heavy metal stress depends on its specie, heavy metal type, and period of exposure to that heavy metal. Plant hormones and organic compounds alleviate heavy metals stress in plants in various ways depending on plant species. Seed priming, plant growth regulator and osmoprotectants are a few latest techniques to alleviate heavy metal stress in various plants. These applications efficiently regulate the antioxidant enzyme activities to mitigate plant toxins, creditably enhancing the tolerance in plants through conserving cellular homeostasis and altering the adverse effects of toxic metals stress on plants. These novel techniques improve our understanding to enhance crop productivity and reduce global food security risks under heavy metal stress. Comparison between these strategies and maize genetic resistance arise new research questions.

Keywords: Maize, metal, toxicity, Seed priming, Plant growth regulators, plant, Chelation

Highlight

- Traditional techniques to hence heavy metal tolerance is compared with latest technology.
- Maize heavy metal tolerance mechanisms are compared with various plants at molecular level. Synthetic biology tools can be effective in regulating plants tolerance.
- Synthetic biology tools including CRISPR Cas9 system, TALENs and ZFNs are discussed against heavy metal stress.

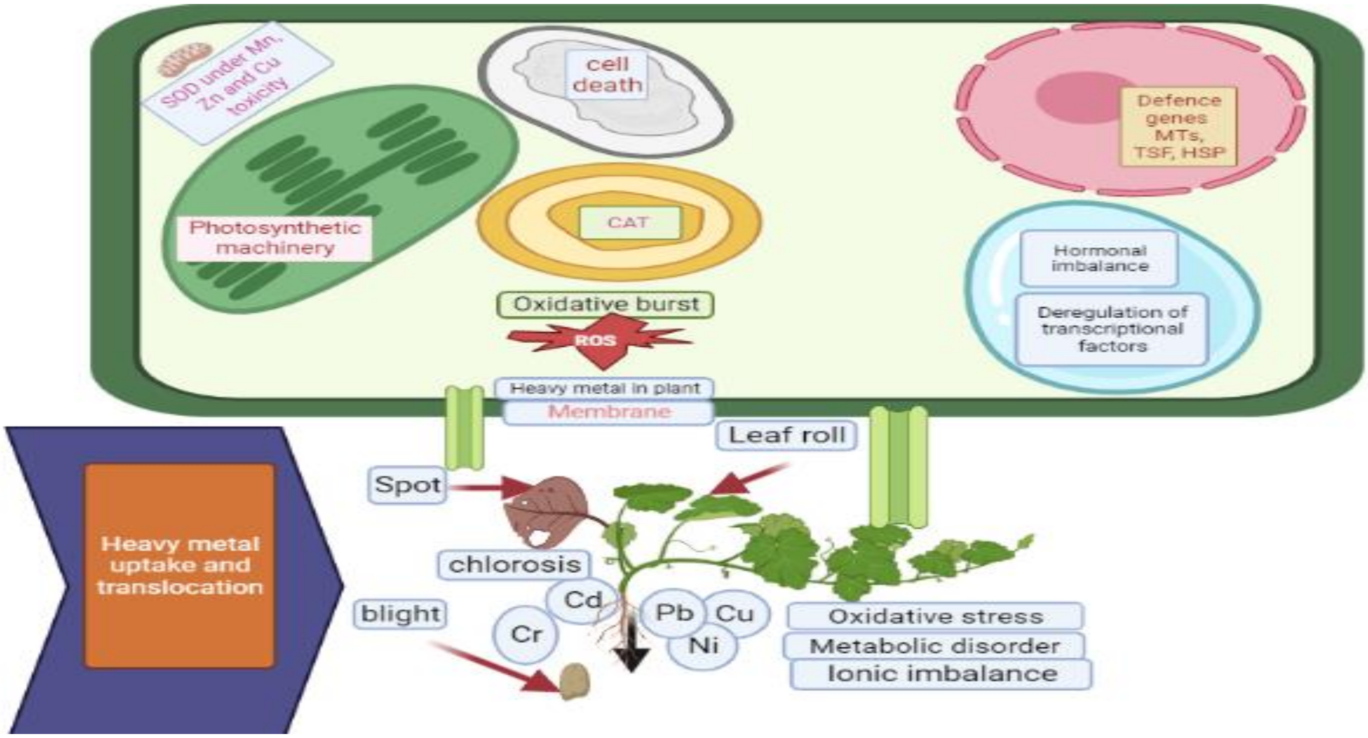

Figure 1. Schematic representation of plant heavy metal translocation and tolerance mechanisms in plant. Various receptors perceive heavy metals' signals, cause ROS production.

1. Introduction

1.1. Maize origin, history, and adaptation

Maize (*Zea mays* L.) is a multipurpose cultigen feed and crop worldwide and is highly susceptible to environmental perturbations that limit its yield (Ramazan 2022). About 9,000 years ago, Mexicans used generations of selective breeding to transform wild teosinte grass with small grains (corn) into a rich source of modern Zea food and as raw material in industries (Yang 2023). Maize spread from the Tehuacan Valley of Mexico to America and then to the rest of the world because of its ability to grow in diverse climates. Maize is a staple feed and annual grass in the family Gramineae. Among the six species of the genus, *Zea diploperennis* and *Zea maiz* are major and used in various forms e.g., popcorn, sweet corn and dent corn (Rathore et al., 2022). Maize is diploid with 20 chromosomes. An integrated approach to study plant responses to heavy metal stress. Maize a C4 cereal crop susceptible to heavy metal stresses (Nisar et al., 2023). Transcriptomics, Proteomics, Metabolomics, and genomics are useful tools that can help us to decipher and analyze active regulatory networks controlling heavy metal stress responses and tolerance in Maize. Polyamines regulate maize tolerance response under environmental stress. Moreover, polyamines catabolism determines the stress tolerance in plants (Ramazan 2022).

1.2 Heavy metals

Elements with a definite gravity greater than 5gcm^{-3} are known as heavy metals (Khanna et al., 2018), in which few are vital for plant growth (Cr, Co, Fe, Ni, Mn, Zn, Mo and Mo) at low concentrations, while As, Pb, Cd and Hg have no role in plants progression. These are toxic even at very low concentrations as they have no role in plant growth (Luo et al., 2020). Heavy metals, like Zn, Cu, etc., at low concentrations, are an integral part of plant enzymes and are involved in electron transport, metabolism of nucleic acids and redox reactions. Metals Fe, Cu, Mn, Ni and Zn are components of numerous plant proteins and enzymes vital for metabolic and growth processes. Plants growing in contaminated soils (containing heavy metals in excess) mostly faced physiological complications, including nutrient accumulation, gas changes and respiration. Higher concentrations of heavy metals affect physiological events and metabolism in plants. They ultimately cause oxidative stress in plants through reactive oxygen species (ROS production), increasing unsaturated lipid peroxidation and interrupting cell membrane function. Cell membrane disruption resulted in enzymatic activity imbalance and oxidative damage (Luo et al., 2020). Heavy metal accumulation considerably affects plants' viability, respiratory rates and carbohydrate level (Kumar et al., 2019). In Maize, the accumulation of metals is significantly affected by several factors such as plant structure, plant life cycle, plant vigour, soil pH, root system depth, temperature, partial oxygen pressure, carbohydrate level, respiration rate, nutrient interface and microbial presence, etc. (Chen et al., 2006).

1.3 Tolerance of Heavy Metals by Plants

Plants developed various mechanisms against heavy metal stress, including the exclusion of plasma membranes, immobilization, absorption and transport disruption, heavy metal carriers' production, stress proteins induction, and Chelation and sequestration of metals by ligand binding (Kumar et al., 2019; Yu et al., 2019; Luo et al., 2020). Under Cadmium, Copper and Lead stress *Psudomonas putida* (plant growth-promoting bacteria) solubilizes phosphorus and enhances Maize's IAA production (Marzban et al. 2016). Genome-wide association study and linkage analysis highlight Complex quantitative traits in Maize to recognize loci linked with Zn-deficiency tolerance (Xu et al., 2022).

1.4 Tolerance Mechanisms

1.4. 1 Organic Acids

Organic acids with one or more carboxyl groups can chelate with heavy metals to form a non-poisonous compound. Examples include citric acid (CA), oxalic acid (OA), malic acid, succinic acid and tartaric acid. Secretions of organic acid are higher under heavy metal stress; consequently, resistant diversities are observed (Fu et al., 2017; Xin et al., 2014). The early defence mechanism results in transcriptomic, signal transduction alternations and accumulation of metabolites (Dal et al., 2013).

1.4. 2 Root Exudates

Root secretions include high molecular weight, e.g., proteins and polysaccharides and low molecular weight, e.g., organic acids, amino acids, sugars and phenolics (Bais et al., 2006).

1.4. 3 Amino Acid

Under heavy metal stress, amino acids (lysine, histidine and methionine) discharge upsurges in the roots of various plants (Wang et al., 2016). These amino acids provide nutrition for plant growth-promoting bacteria (*pseudomonas stutzeri*) and fungi, sulphur bacteria (preventing heavy metals entrance into the plant).

1.4. 4 Soluble Sugar and Protein

Soluble sugar is an important plant component during respiration and photosynthesis, primarily involved in various metabolic reactions(Aldoobie and Beltagi, 2013). Protein acts as signalling molecules that regulate different genes. Those genes involve photosynthesis, sucrose metabolism, and osmolyte synthesis (Rosa et al., 2009). Plants under heavy metal stress accumulate more soluble proteins and sugars to maintain survival (Yu et al., 2019). Guangqiu et al. (2007) also reported that the soluble sugar content increase with increasing heavy metal concentration. Similar phenomena were observed in Maize, where various osmoprotectants, including proline, amino acids and antioxidants, enhance under heavy metal stress. Genetically modified maize varieties increase their yield and alleviate mycotoxins; examples include MON809, a gene that provides multiple stress tolerance, including heavy metal stress (Malenica et al., 2021).

1.5 Subcellular Structure

1.5.1 Cytoderm

Major components of the cell wall like cellulose, hemicellulose, proteins and pectin structure the cell wall. These functional groups also include hydroxyl, carboxyl, aldehyde, and amino groups that restrain heavy metal's entrance inside the cell. In cotton plants under stress, the cytodermin and the Casparian strip are thickened; thus, the transport of Cd ions is blocked, and toxicity symptoms are alleviated (Chen et al., 2019).

1.5.2 Cytomembrane

OsHMA3 overexpression increases the heavy metal tolerance of roots to cadmium (Sasaki et al., 2014). Moreover, Hg tolerance in numerous plants increases through *PtABCC1* overexpression (Sun et al., 2018).

1.6 Chelation

Amino acids show an affinity for metal ions, including histidine, Co^{2+}, Zn^{2+}, Cu^{2+} and $Ni^{2+,}$ which enhance heavy metals Chelation. High cadmium in the cell wall is transported to the vacuole, where it combines with organic acids, proteins and sugars to form macromolecular compounds via Chelation to reduce cadmium toxicity (Riyazuddin et al., 2021; Yang et al., 2021).

1.7 Metallothionein (MT)

Metallothionein (MT) is a cysteine-rich protein, small molecular weight, a metal-binding protein synthesized by mRNA transcription produced by heavy metal stress that enhances plant growth and developmental process and stress tolerance against heavy metals. Metallothionein protects against reactive oxygen species and heavy metal toxicity (Sato and Kondoh, 2002). ZmMT gene expression profiles were identified under Cu, Cd and Pb stress in Maize and analyzed. The results showed *ZmMTs* has the potential to regulate via hormones; moreover, metallothionein showed improvement in maize stress resistance under toxicity (Gao et al., 2022).

1.8 Phytochelatins (PC)

Phytochelatins bind various metals (e.g., As, Cd, Zn or Cu over carboxyl and sulfhydryl residues), then biosynthesis is controlled by metal Cd or metalloid As. Overexpression of phytochelatins synthase genes enhances Cd tolerance in bacteria and yeast (Gupta et al., 2013).

1.9 Reduced glutathione (GSH)

Reduced glutathione is an amino acid derivative composed of reduced glutathione, glutamic acid, cysteine, and glycine. It can also act as a ligand to chelate heavy metals and reduce their toxicity of heavy metals. Reduced glutathione application promotes the formation of phytochelatin in some plants, causing it to reduce Cadmium toxicity (Ding et al., 2017). Under conditions of HM stress, reduced glutathione helps to reduce ROS levels to maintain proper cellular homeostasis (Asgher et al., 2017).

1.10 Strategies for Heavy Metal Tolerance in Plants

Several strategies have been reported to mitigate the detrimental effects of heavy metal stress. Strategies that are used for the successful mitigation of heavy metal stress are given below.

1.10 .1 Seed Priming

Heavy metal stress in all phases of plant growth is toxic from early seedling to maturity, consequently decreasing crop yield. Sowing seeds in contaminated soils reduces germination, root development, and biomass. Seed priming is an instant method to mitigate the toxic effects of heavy metal stresses on plants (Chen et al., 2021). It comprises seed hydration to improve the plant metabolic process to increase crop germination rate and crop yield under stress (both abiotic and biotic) (Rhaman et al., 2020).

Seed priming upholds a momentary balance of ROS scavengers to alleviate the oxidative stress produced under stressful conditions (Hussain et al., 2017). It reduces malondialdehyde and hydrogen peroxide production and improves proline concentration (Hossain et al., 2015). In primed seeds signalling proteins are accumulated to become active soon after sensing the stressful conditions (Saboor et al., 2019). Various priming agents regulate stress-related physiological changes (Fariduddin et al., 2018). Seed priming with salicylic acid in *Trifolium vesiculosum* (annual) and *Trifolium repens* (perennial) resulted in upgrade germination and growth of seedlings against Al toxicity (Bortolin et al., 2020). Sodium hydrosulphide (NaHS) and Salicylic acid (SA) enhance lead tolerance in *Zea mays* L. through a reduction in Pb uptake to reduce Pb toxicity to the eatable crops (Zanganeh et al., 2020). Selenium (Se) primed rice seedlings enhanced the plant yield by limiting arsenic (As) translocation to the aerial parts. Under arsenic stress, mature plants with primed seeds showed higher shoot length and biomass, suggesting that seed priming effectively enhances plant growth against arsenic stress (Moulick et al., 2018).

Table 1. Seed priming with different agents for mitigation of heavy metal stress.

Priming compounds	**Heavy metal**	Plant	References
polyethylene glycol	Nano - ZnO	*Oryza sativa* L. (Paddy)	Sheteiwy et al., (2016)
Salicylic acid	Cd	*Triticum aestivum* L. (Wheat)	Gul et al., (2020)
		Lactuca sativa L. (Lettuce)	Šabanović et al., (2018)
		Nigella Sativa L. (Black Cumin)	Espanany et al., (2016)
		Hordeum vulgare L. (Barley)	Shahnawaz & Sanadhya (2017)
Silicon	Cd	*Lactuca sativa* L. (Lettuce)	Pereira et al., 2021
Purslane (extract)	Pb	*Triticum aestivum* L. (Wheat)	Sobhy et al., (2019)
Multiwall carbon nanotubes	Cd	*Zea mays* L. (Maize)	Chen et al., (2021)
Calcium chloride	Cd	*Faba bean* L. (Vicia faba)	Nouairi et al., (2019)
Sulfur Nanoparticles	Mn	*Helianthus annuus* L. (Sunflower)	Ragab & Saad-Allah (2020)
3-epibrassinolide	Cd	*Cucumis sativus* L. (Cucumbers)	Shah et al., (2020)
Brassinosteroids	Cr	*Oryza sativa* L. (Rice)	Basit et al., (2021)
Karrikinolide	Cd	*Vigna unguiculata* L. (Coriandrum sativum	Sardar et al., (2021)
Proline and Glycine Betaine		Cowpea	Sadeghipour, (2020)
Gibberellic acid, Citric acid, Potassium chloride, Sodium chloride, Iron and Zinc	As	Lepidium sativum L. (Garden cress)	Nouri and Haddioui, (2021)

1.10.2 Plant Growth Regulators

Plant growth regulators (PGRs) as Natural / organic or synthetic compounds affect plant development, metabolic processes, and hormonal states and are non-phytotoxic (Ranjan et al., 2021). Abscisic Acid (ABA) is a very important hormone that regulates the uptake of heavy metals in plants. Abscisic acid (ABA) application improves plant biomass and decreases Cd concentration in lettuce shoots (Tang et al. 2020). Thus, restricting the accumulation of toxic Cd concentration in edible parts of the plant. Similarly, in another study, the exogenous application of ABA also restricted the accumulation of Cd in *Arabidopsis,* increased growth, and improved photosynthesis under Cd stress (Pan et al., 2020). Salicylic acid application mitigates Cd stress through stimulation of antioxidant enzymatic pathways by decontaminating relative water, chlorophyll and proline content with a significant reduction in superoxide anion radicals (O_2^-), malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) in tomato under Cd stress (Li et al., 2019). Gibberellins (Gas) lessen the toxic effects of heavy metals and improve the expansion of different transition phases, cell division and cell extension in plants. Moreover, gibberellins reduce the harmful effects of copper in spinach seedlings by increasing proline and antioxidant enzyme activities (Gong et al., 2021).

1.10.3 Osmoprotectants

Using osmoprotectants effectively controls heavy metal toxicity in plants (Zulfiqar et al., 2020). Osmoprotectants, small, neutral molecules with low toxicity, possess low interference with metabolic pathways and high solubility. Osmoprotectants are compatible molecules that accumulate in plants when the growing state is inappropriate. Under these conditions, molecules preserve internal physiological practices to enhance plant survival (Seleiman, 2019). Examples include proline formed in plants under environmental stresses (Siddique et al., 2018) that perform an active role in osmotic adjustment to increase plant resistance and alleviate oxidative stress through ROS (Adejumo et al., 2015). Applying proline stabilizes plant's protein structure, increases chlorophyll content, and enhances antioxidant enzyme activities to mitigate heavy metal stress. Glycine betaine also alleviates the heavy metal stress in plants. It is metabolically stable among all other osmoprotectants (Jain et al., 2021). Glycine enhances nutrient uptake, limiting oxidative stress by controlling heavy metal uptake in plants (Ali et al., 2020). Under heavy metal stress, Glycine betaine improves plant growth by improving chlorophyll content and minimizing oxidative damage (Demidchik, 2015). It overcomes the oxidative stress under chromium stress in *Brassica oleracea* L (Zouari et al., 2018)

Soluble sugar like hexose, sucrose and trehalose acts as osmoprotectants to maintain cellular organizations, improve photosynthetic proficiency and scavenge ROS. They perform various physiological functions such as coordinating antioxidant activity, consolidating membrane integrity, and sustaining water requirements under heavy metal stress (Ahmad et al., 2020). Trehalose (TR) improves plant tolerance against heavy metal stress. It reduces Cd toxicity in rice via TR-CD chelate production (Wang et al. 2019). Exogenously applied TR restricts the accumulation of harmful Cd concentrations in roots and the rice seedling's shoots. *ZmAKINβγ1* gene regulated Pb tolerance in Maize by reducing root dry weight (RDW) and shoot dry weight (SDW) and use for soil phytoremediation (Li et al., 2023).

Table. 2. Bioremediation potential of plant growth regulators on various plants under heavy metal stress.

Phytohormones	Plants	HMs Alleviation effects	References
Jasmonic acid	*Avicennia marina* L. (Grey mangrove)	Alleviate Cd in leaves.	Yan et al., (2015).
	Vicia faba L. (Faba bean)		Ahmad et al., (2017)
Salicylic acid	Alyssum inflatum	ROS detoxification under Ni stress.	Kakavand et al., (2019)
	Brassica campestris L. (mustard)	Regulate the enzyme antioxidant defense system against Pb.	Hasanuzzaman et al., (2019).
	Triticum aestivum L. (wheat)	Enhance biochemical traits of Triticum aestivum aestivum to alleviate toxic effects of Pb.	Gillani et al., (2021).
	Phaseolus vulgaris L. (Bean)	Synthesis of methylglyoxal with lipid peroxidation to alleviate Cd stress.	Hediji et al., (2021).
		Minimize oxidative damage under Cd stress.	El Dakak and Hassan (2020).
	Zea mays L. (Maize)	Reduce Cd uptake	Jia et al., (2021)
	Tomato		
Cytokinin in 10 µM conc.	*Kosteletzkya pentacarpos* L. (Virginia saltmarsh mallow)	Increased resistance to Zn and Cd.	Zhou et al., (2019)
Abscisic acid	*Lactuca sativa* L. (Lettuce)	Enhance plant biomass, antioxidant enzymes activities and photosynthesis under Cd stress.	Dawuda et al., (2020)
Gibberellins	Vigna radiata L	Enhance photosynthesis and plant pigments under Cd stress.	Hakla et al., (2021)

2. Conclusions

Metals including aluminum, chromium, zinc and cobalt are essential for plant metabolic and growth processes but, at higher concentrations, show toxicity symptoms. There are two ways to enhance tolerance of heavy metals, including developing resistance in plants or controlling metal accumulation in Soil and uptake in plants. Plants developed numerous detoxification mechanisms to limit the toxic effects of heavy metals. Plant metal tolerance depends on chemical, physiological and biological adaptability. Seed priming and application of plant growth regulators and osmoprotectants are effective methods to alleviate heavy metal stress toxicity in plants. All these techniques efficiently regulate the antioxidant enzyme's activities to mitigate plant heavy metal stress and offer an understanding to boost crop productivity to decrease global food security risk under heavy metal stress.

Future perspectives

Maize is a potential high-biomass crop that can be introduced with guaranteed success to fulfill protein needs. Additional experimental approaches are needed at molecular and gene levels to explore plant cell death under heavy metal stress.

Conflicts of interest

It is declared that there are no conflicts of interest.

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