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Review

Molecular underpinning of heavy metal sequestration through advanced remediation strategies in higher plants

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ABSTRACT

Anthropogenic emissions, particularly from industrial and agriculture activities, have significantly elevated the concentrations of highly toxic Heavy Metals (HMs), such as lead (Pb), cadmium (Cd), and arsenic (As), in the soil, leading to their accumulation in plants. These HMs, when exceeding toxicity thresholds (e.g., Pb >10 mg/kg, Cd >0.5 mg/kg, As >1 mg/kg), disrupt the plant physiology and metabolism. To mitigate this toxicity, plants employ diverse detoxification and sequestration strategies, including mycorrhizal associations, root exudates, cellular compartmentalization, and the production of organic acids, phytochelatins, metallothioneins, proline, stress proteins, and plant hormones. This review aims to critically examine the molecular mechanisms by which key crop plants, such as rice, wheat, maize, and other higher plants, sequester these primary heavy metal contaminants. Additionally, it highlights the role of nanotechnology in enhancing plant resistance and facilitating nano-bioremediation under HMs stress conditions. This review provides valuable insights into innovative clean-up strategies for agriculturally important crops by exploring nanoparticle -mediated remediation mechanisms.

1. Introduction

The geosphere is made up of rocks, minerals, and heavy metals (HMs). It starts with soil surface and extends to sand beaches, mountain summits, and molten rock at the earth's center (Mukherjee et al., 2023). HMs are found in soil as natural components or by spontaneous occurrence such as volcanic eruptions. Moreover, it also occurred due to anthropogenic activities like mining or construction. These HMs enter the ecosystem and take part in biogeochemical processes, thereby increasing their spread in the earth's ecosystems (Zhang et al., 2010). According to reported literatures the most frequent contaminants that are toxic to human and animal health, even at low concentrations, are heavy metals like zinc (Zn), nickel (Ni), chromium (Cr), copper (Cu), mercury (Hg), arsenic (As), (metalloid), etc. (Lawal et al., 2021). Plants need some HMs like Zn, Cu, Ni, etc. as micronutrients to support normal growth and developmental activities. However, the quantity and concentration of both essential and non-essential nutrients must be carefully balanced to ensure their availability does not hinder plant development under natural circumstances (Hall, 2002) (Table 1).

Higher angiosperm and gymnosperm includes a diverse array of

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Table 1
Essential heavy metals (Play a Metabolic Role).

Sl. No	Metal	Metabolic Role in Plants	Refs.
1.	Zinc (Zn)	Enzyme cofactor, protein synthesis, auxin production	Mousavi et al. (2013)
2.	Copper (Cu)	Photosynthesis, respiration, oxidative stress protection	Droppa & Horváth (1990); Ravet & Pilon (2013)
3.	Iron (Fe)	Chlorophyll synthesis, electron transport, enzyme cofactor	Kroh & Pilon (2020)
4.	Manganese (Mn)	Photosynthesis (PSII cofactor), antioxidant defence	Ducic & Polle (2005) Takashima et al. (2012)
5.	Nickel (Ni)	Urease enzyme activation, nitrogen metabolism	Nim & Wong (2019); Lavres et al. (2016)
6.	Molybdenum (Mo)	Nitrate reduction, nitrogen fixation	Demtröder et al. (2019)
Non-essential Heavy metals (No metabolic Role)			
1.	Cadmium (Cd)	No known essential role; may induce stress response pathways.	Haider et al. (2021)
2.	Lead (Pb)	No beneficial role; can accumulate in root cell walls.	Zulfiqar et al. (2019)
3.	Mercury (Hg)	No beneficial role; highly toxic in ionic and methylated forms.	Clemens, (2013)
4.	Chromium (Cr)	Some plants show enhanced stress tolerance with Cr (III) at very low levels.	Cervantes et al. (2001)
5.	Aluminium (Al)	Some plants (e.g., tea, Camellia) accumulate Al to enhance defence mechanisms.	Poschenrieder et al. (2013); Panda et al. (2009)
6.	Arsenic (As)	Some plants can tolerate arsenic and use it in stress signalling.	Bali & Sidhu (2021)

plant species that serve as rich sources of staple foods, medicinal compounds, and fruits. Among them, angiosperms represent the most evolutionary advanced and ecologically dominant group of land plants. They play a central role in global food security by providing primary food crops such as rice, wheat, and maize, as well as widely consumed fruits including apples, oranges and bananas. However, these plants are increasingly threatened by the accumulation of toxic heavy metals, notably Cd, Pb, Hg, and As. The bioaccumulations of these metals in the edible plant tissues not only poses sever health hazards to consumers but also disrupts ecological balance by introducing contaminants into the food chain. Therefore, exploring the mechanism of heavy metals sequestration in the higher plants and developing eco-friendly or cost-effective remediation strategies is crucial for promoting sustainable agriculture (Kafle et al., 2022). The visual signs of HMs toxicity brought on by its high concentrations occur at the molecular level. This toxicity is due to the bonding between metal and proteins, which impairs the functionality of biomolecules like pigments and enzymes, compromising the cell membrane's integrity and suppressing essential plant processes like photosynthesis and respiration, etc. (Rubino, 2015). Moreover, HMs contributes to the production of free radicals, reactive oxygen species (ROS) i.e., superoxide ions ($O_2^{\cdot}$), hydroxyl ions (OH), and hydrogen peroxide ($H_2O_2^{\cdot}$). In addition, toxic compounds like methylglyoxal (MG) tend to accumulate under several stress conditions, including HMs exposure and elevated ROS levels (Aslam et al. 2021). This accumulation of MG and ROS in plants interferes with the metabolic and physiological functions like photosynthesis, by deactivating the antioxidant defense system and disrupting internal homeostasis (Sytar et al., 2013).

Additionally, it is essential to explore innovative and eco-friendly remediation strategies that not only mitigate soil contamination but also aid in restoring soil health. The integration of nanotechnology into agriculture marks a major breakthrough in addressing the complex challenges of global food production (Zhang et al., 2022). The extensive application of nanomaterials in precision agriculture, nutrient management, pest control, and soil health offers unprecedented opportunities for the adoption of sustainable and efficient farming practices (Yadav et al., 2023). In recent years, nanotechnology has gained significant recognition as an innovative and promising strategy for addressing the challenges associated with soil contamination in agricultural settings (Sable et al., 2024). The unique characteristics of nanomaterials, such as their large surface area, high reactivity, and ability to alter physicochemical properties, make them highly effective for soil remediation.

Nanotechnology has the potential to revolutionize traditional soil remediation techniques by offering more efficient, precise, and environmentally sustainable solutions for mitigating agricultural contamination (Dhanapal et al., 2024). This review aims to consolidate existing research on the application of nanotechnology in remediating contaminated agricultural soils. Through a detailed analysis of recent advancements, it explores various nanomaterials, nanocomposites, and nanotechnological methods used to remove, contain, and neutralize soil pollutants. Additionally, the review critically assesses the effectiveness, environmental implications, and possible risks associated with the use of nanotechnology in agricultural soil remediation.

To check the relevance of the topic we made a bibliometric analysis of the research papers published on the related topics and in the bibliometric data study, we retrieved a total of 24,597 articles between 2020 and 2024 from the Scopus database by searching the keywords "Heavy metals", AND "Bioremediation" or "bioaccumulation", or "biomagnification" or "Toxicity" Or 'Cd" or "Hg" or "Pb" or "Bacteria' or "Mycoremediation"or "Exopolysaccharides "or "Oxidative stress", or "Water" Pollution and created the bibliometric analysis using VOS viewer processing software (v1.6.9) by selecting 10,000 articles. The different colours present in the network showed linked terms; however, the size of the labels showed the number of publications, and the distances present between two nodes represent the degree through which they are associated (Fig. 1). This study explores the diverse strategies employed by plants to mitigate the effects of HMs contamination, with a particular emphasis on the molecular mechanisms underlying HMs sequestration in higher plants.

2. HM uptake, translocation and distribution in plants

The process of absorbing HMs by plants begins in the soil through their respective roots and proceeds through the root hairs. The metal crosses the root tissues apoplastically and makes its way in the symplast of the endodermis cell which later passes into the cells of stele, facilitated by the plasmodesmata (Grennan, 2009). Metal ions are transported to the shoots through a process known as transpiration pull, which is the mass upward flow of water. Plants passively absorb nutrients in one of two ways: assisted diffusion or simple diffusion (Annamalainathan et al., 2013). Plants inhabiting metal-contaminated soil have established three basic defense strategies. The first one is metals excluders; these types of plants restrict HMs uptake and maintain low concentration in their respective shoots over many different soil levels. A plant is considered an excluder for Cd if its shoot concentration is below 10 mg/kg, for Zn if it is below 100 mg/kg, and for Ni if it is below 50 mg/kg, even when these metals are present in higher concentrations in the soil (Backer and Brooks, 1989; Cobbett, 2000).The second type of plants captures metals in their aerial tissues and act as a good metal contamination indicator. Consequently, a plant is considered a metal contamination indicator for Cd if its shoot concentration exceeds 1–10 mg/kg, for Zn if it exceeds 200–300 mg/kg, and for Ni if it exceeds 50–100 mg/kg, signaling contamination in the environment (Cobbett, 2000; Raskin et al., 1997; Backer and Brooks, 1989).The third category includes accumulators or hyperaccumulators. In this group plants begin to concentrate HMs in the above ground tissues at levels higher than those found in the surrounding the soil (Verbruggen et al., 2009). Therefore, a plant is considered a hyperaccumulator if its shoot concentrations exceed 100 mg/kg for Cd, 1000 mg/kg for Zn and Ni (Backer and Brooks, 1989). Some examples of the common hyperaccumulators,

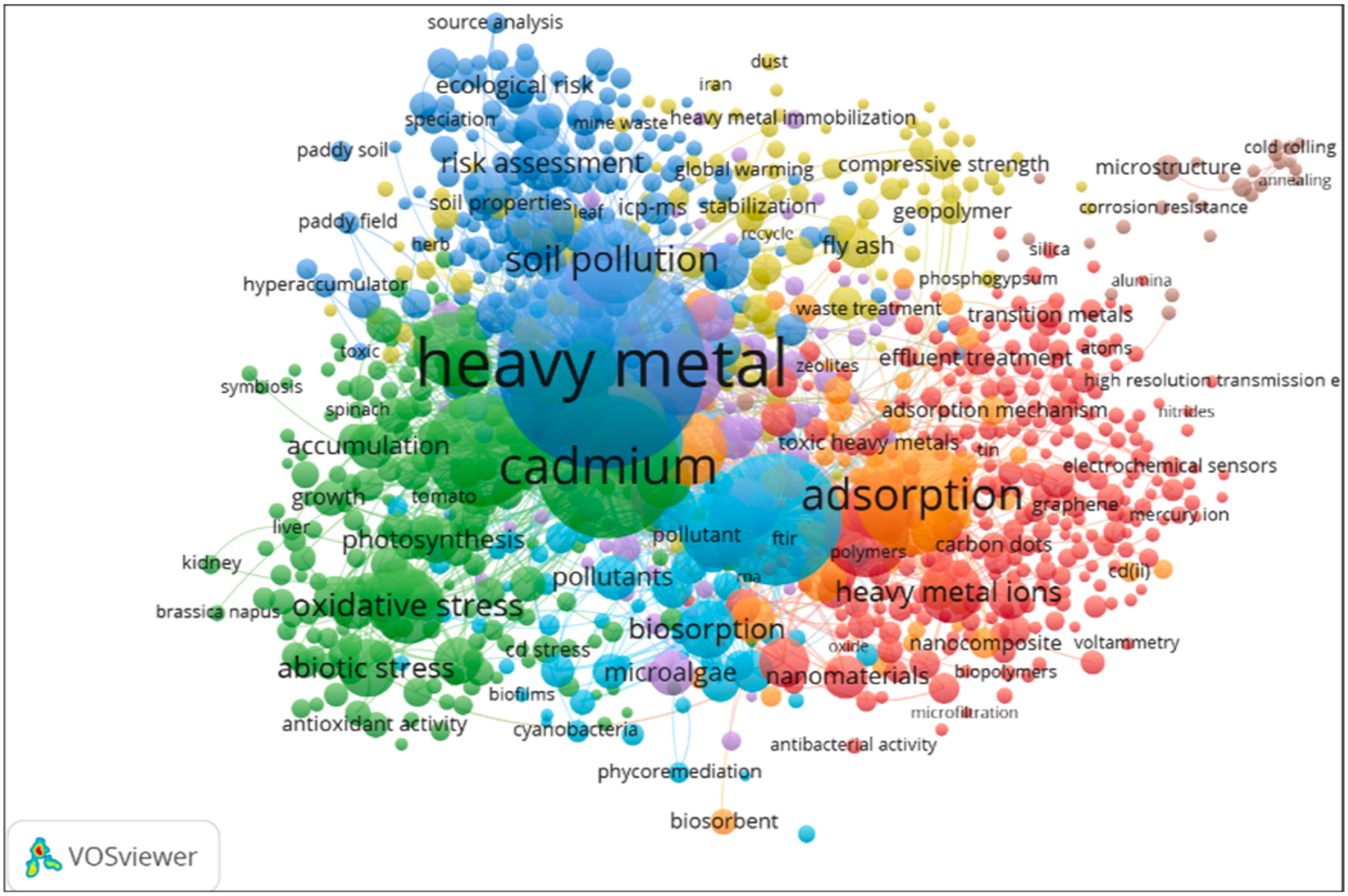

Fig. 1. Network visualization map displaying the key term present in the title and abstract of the published article related with the Metal Sequestration in higher plants. Nodes of the same color showed cluster of the interconnected phrases; however, the circle size indicates the number of publication larger the size indicates large number of publications. Network has been created using the software VOS viewer processing software (v1.6.9.).

metal excluders and metal indicators are given in Table 2.

Roots are crucial for nutrient absorption and regulate metal uptake with precision, while the translocation of HMs to the shoot, facilitated by selective transporters in the cortical or epidermal cell layer's plasma membrane, is a key process plants use to remediate polluted areas (Rutschow et al., 2011). In addition, nutrients move from the outer root layers through the stele to the pericycle, where selective membrane transporters facilitate their entry into the xylem for distribution throughout the plant, relying on a mix of membrane transporters and diffusion through plasmodesmata to ensure efficient nutrient flow within the root cell layers and effective symplastic pathway function (Miwa and Fujiwara, 2010). In the rhizosphere, solutes travel via apoplastic routes through extracellular gaps between cells and cell walls, while in endodermal tissues, the transition from apoplast to symplast is necessary due to the presence of the Casparian strip, a barrier that hinders diffusion. Further, Endodermal cells play a vital role in nutrient uptake from the rhizosphere to the xylem (AjM, 1989). Inside the cell for different HM's specific types of transporters are involved which either transports the HMs inside the cell or outside the cell. The manoeuvre of HMs from shoot to root are facilitated via chelating metals with ligands like thiols, amino acids and organic acids (Mehes-Smith et al., 2013). The chelation of Ni by histidine initiates a long-distance translocation mechanism, which was crucial in the hyperaccumulator *Alyssum lesbiacum,* where the xylem histidine level increased by 36 times compared to that in the non-accumulator *Alyssum montanum* (Krämer et al., 1996).

Root architecture refers to the spatial arrangement of the root system in growth medium, determining its three-dimensional dispersion. Whereas the first organ of the plant that comes in contact with polluted soil is the root. According to literatures the root architecture is sensitive to metal toxicity. In addition, the root system architecture (RSA) influences the soil volume and is an essential determinant for the absorption efficiency of water, nutrients and HMs. Although, at the morphological level, roots may modify many of their properties like root length and diameter, lateral root length and density, growth angle, and the presence and length of root hairs (Morris et al., 2017). The root morphology and anatomy plays an important role in HMs uptake. Huang et al. (2015) reported that the Jin fuzaohuangjiao (JFZ) hot pepper cultivar had longer root length, more root tips and greater surface area that resulted in increased Cd absorption. Romdhane et al. (2021) reported that branching index, root diameter and tip density of maize plants increased under artificially metal contaminated (Zn, Cu, Co, Cd, and Pb) soil whereas root length, fresh and dry weight of roots/shoots decreased considerably. The adaptation strategy used by maize plants is decreased fraction of finer roots and increased fraction of coarse root length.

3. HM speciation in plants

HM speciation refers to the various chemical forms in which a particular metal exists in the environment (example free ions, chelated, insoluble, organically complexed etc.) influencing their mobility, toxicity and bioavailability. Plants play a crucial role in the uptake, transformation, and sequestration of HMs, often influencing their speciation through various biological and chemical processes (Shahid et al., 2017; Millalleo et al., 2010). The process of speciation can be further classified as extracellular and intracellular speciation respectively.

Table 2
Examples of Metal excluders, metal indicators and metal hyperaccumulators.

Sl. no.	Defense strategies	Plant examples	Metals	Refs.
		Agrostis capillaris	Cu, Zn, Cd, and Pb	Dahmani-Muller et al. (2000)
		Bidens pilosa	As excluder	Sun et al. (2009)
		Commelina communis	Cd-excluders	Wei et al. (2005)
		Digitaria sanguinalis	Cd-excluders	Wang et al. (2020)
		Oenothera biennis,	Cd-excluders	Wei et al. (2005)
		O. biennis	Cu-excluder	Wei et al. (2005)
		Silene vulgaris	Cu, Zn, and Cd	Schat & Vooijs (1997)
		Taraxacum mongolicum	Zn-excluder	Wei et al. (2005)
		Thlaspi arvense	Cd-excluders	Martin et al. (2012)
2.	Metal indicators	*Ageratum conyzoides*	Pb, Cu, Cd and Zn	Deepalakshmi et al. (2014)
		Phragmites australis, Spartina maritima Typha capensis,	Cd, Cu, Pb, and Zn	Bonanno & Giudice (2010); Phillips et al. (2015)
3.	Metal hyperaccumulators	*Arabidopsis halleri*	Cd Zn	Zhao et al. (2000); Zhao et al. (2006)
		Amaranthus gangeticus	Cd	Zhou et al. (2013)
		Alyssum sp.	Ni	Mengoni et al. (2011); Broadhurst and Chaney (2016)
		Brassica juncea	Cd	Haag-Kerwer et al. (1999)
		Berkheya codii	Ni	Slatter (2013)
		Eichhhurnia crassipes	Cd	Wang et al. (2012)
		Helianthus annuus	Cd	Júnior et al. (2015)
		Microsorum pteropus	Cd	Lan et al. (2018)
		Noccaea sp.	Cd, Zn, Ni	Sterckeman et al. (2017)
		Phytolacca americana	Cd	Peng et al. (2008)
		Pteris vittata	As Pb	Kohda et al. (2021) Soongsombat et al. (2009)
		Pityrogramma calomelons	Ar Pb	Campos et al. (2018) Soongsombat et al. (2009)
		Salix caprea	Cd, Zn	Konlechner et al. (2013)
		Sedum sp.	Cd	Gao et al. (2013)

3.1. Extracellular speciation

Extracellular speciation refers to the interactions of HMs outside the cell, including in the rhizosphere, cell wall, and apoplastic space. Plants root release exudates with chelator properties into the rhizosphere which serves as the primary defense against the HMs uptake. In *Arabidopsis thaliana*, the uptake of Ni from soil was greatly reduced by the presence of Ni chelating histidine and citrate in root exudates (Nishida et al., 2011). However, the binding of HMs to plant cell wall components (pectin, cellulose and hemicellulose) is influenced by the availability of functional groups such as carboxyl (-COO^-), hydroxyl (-OH), amino (-NH_2), and sulfhydryl (-SH), thereby facilitating the toxic HMs ions to be immobilized and prevents their entry into the cytosol. Pectin has the highest metal binding capacity, particularly for Pb^{2+}, Cr^{3+}, and Cu^{2+}, due to its abundant carboxyl (-COO^-) groups. The cellulose and hemicellulose components bind to Cd^{2+}, Zn^{2+}, and Cr^{3+} through hydroxyl (-OH) groups, though with moderate efficiency (Krzesłowska, 2011). Whereas, bioavailability and speciation in plant- soil system are impacted by microbial activity in the soil matrix (Pierart et al., 2015). Some reports have shown an alteration in the phytoavailability of As in soil after microbial inoculation in soil, the microbes stimulate redox reactions between As(III) and As(V) (Gorny et al., 2015). Some bacterial species accountable for these interconversions are *Desulfotomaculum auripigmentum, Thermus thermophilus, Bacillus arsenicus, Geospirillum arsenophilus, etc.* The absorption sites of the cell wall are restricted, which accounts for its marginal impact on metal tolerance. Whereas, in *Arabidopsis halleri*, a negative correlation between Fe concentration and uranium uptake was studied, with Fe deficiency considerably increasing uranium uptake (Vaxevanidou et al., 2012; Yamamura and Amachi, 2014).

3.2. Intracellular speciation

In intracellular speciation, once HMs enter plant cells, they undergo intracellular detoxification and compartmentalization to minimize toxicity. HMs are promptly bounded by the intended cellular molecules upon arrival into the cytosol, eliminating the risk of toxicity brought on by metal ions freely available and enabling a number of synchronized metabolic activities including specialized integration in metalloproteins or vacuolar sequestration (Haydon and Cobbett, 2007). Nicotianamine (NA), a metal chelating agent, possess a high level of stability while binding transition metal ions along with some organic acids like citrates and is necessary for maintaining Fe, Zn and Cu homeostasis (Curie et al., 2009; Clemens et al., 2013). Furthermore, the formation of HM compounds in plants is aided by 1 mM GSH, a low-molecular-weight chelator, which triggers the production of PC's by phytochelatin synthase (M_w 95,000) that create metal-PC complexes, and these complexes are transported into vacuoles by an ABC-type transporter, thereby enhancing the plant's tolerance to HMs (Grill et al., 1989; Srivastava, 2016). In *A. thaliana*, upregulation of a critical enzyme in GSH production led to alleviate GSH concentration levels and improved tolerance of HMs like Co, Zn and Ni. Similarly, tolerance towards different HM's (Ni, Co, Zn, Cd) was seen in *A. thaliana* when *Thlaspi goesingense gene* serine acetyltransferase (TgSAT) was overexpressed in the former which led to three fold increase in GSH levels (Freeman et al., 2004).

4. Factors influencing metal uptake in plants

Thermodynamic activities and solubility of metal ions are vital factors that governs the HMs availability through rhizosphere in plants, because root uptake requires a soluble ion. In addition, thermodynamic activity refers to the effective concentration of a heavy metal ion in a system, considering its interactions with other ions and molecules whereas actual uptake refers to the amount of HMs absorbed by plant roots and translocated into tissues. This depends on metal bioavailability, root absorption mechanisms, and plant metabolism (Shukla et al., 2019). It has been observed that with an increase in thermodynamic activity the bioavailability thereby increasing the uptake of HMs (Kalis, 2006). Metal solubility is subjected to alterations due to the physiochemical properties of soil including composition of organic and inorganic solutes, oxidation–reduction potential and soil pH. Subsequently, soil Cation Exchange Capacity (CEC) plays a crucial role in determining the bioavailability of HMs by regulating their retention, mobility, and uptake in soil-plant systems. High CEC soils, such as those rich in clay minerals and organic matter, strongly adsorb HMs like Pb^{2+}, Cd^{2+}, and Zn^{2+}, reducing their solubility and plant availability. Conversely, low CEC soils, such as sandy soils, provide fewer binding sites, increasing metal mobility and bioavailability, which can lead to environmental contamination and plant toxicity (Alloway, 2012).

Additionally, soil pH significantly influences CEC, as acidic conditions reduce metal binding and enhance solubility, while alkaline conditions promote metal precipitation and adsorption onto soil particles. To mitigate HMs risks, soil amendments like biochar, compost, and lime can be applied to increase CEC and regulate metal availability, improving soil health and reducing toxicity (Kumpiene et al., 2008). These soil characteristics are quite diverse and depend on a number of different geographic elements, including terrain, biological processes, parent rock, climate, and anthropogenic activities. As soil pH rises above 5.5–6, the solubility of many metals like Cd, Pb, and Cu generally decreases, making chelating agents like Ethylenediaminetetraacetic acid (EDTA) useful for promoting metal translocation in plant tissues and enhancing phytoextraction over extended exposure (Roy et al., 2005). Moreover, EDTA, a synthetic ligand, binds to heavy metals like Cd^{2+}, Zn^{2+}, and Pb^{2+} through its carboxylate and amine groups, keeping them in their soluble form even at higher pH levels, preventing precipitation as insoluble hydroxides, and enhancing their mobility in soil for plant uptake, which is essential for phytoextraction (Shahid et al., 2014) A list of binding agents and their thresholds against heavy metals in various plant species is given in Table 3.

Temperature also determines the solubility and diffusion rates of HMs. It has been observed that elevated temperatures can stimulate root metabolic activity and transpiration, leading to greater metal translocation to aerial parts of the plant (Yu et al., 2010). However, excessive temperatures may disrupt membrane integrity and metal transport proteins, altering uptake efficiency. Conversely, lower temperatures reduce root permeability and enzymatic activity, restricting metal absorption and slowing translocation. The impact of temperature also varies by metal type; for instance, it has been observed that in rice Cd uptake tends to increase with temperature (Ge et al., 2016).

A variety of plant factors, including root characteristics, root-soil interactions, physiological processes, species-specific traits, growth stages, nutrient availability, environmental stress, mycorrhizal associations, and climate conditions, influence the uptake of HMs from the soil by affecting metal absorption, transport, and detoxification mechanisms. Plants possess very precise and efficient ways for obtaining critical micronutrients from their micro-environment. These pathways are also involved in the absorption, transport, and storage of harmful elements, playing a crucial role in the process of bioremediation. HMs including Zn, Cu, Mn, Pb, Ni, and Co can be captured and accumulated by metal-accumulating plant species up to 100–1000 times more than non–accumulating plant species (Sheoran et al., 2010). Certain plant species, such as *Thlaspi caerulescens*- a well-known zinc (Zn) hyperaccumulator, can accumulate up to 10,000 mg/kg in their leaves. This is approximately 1000 times more than the Zn levels typically found in normal plants, which usually contain <10 mg/kg. In contrast, non-accumulating plants growing in Zn -rich soils generally accumulate only about 30–100 mg/kg of Zn in their tissues (Asad, 2011).

5. Different types of metal transporters with their roles in HMs translocation

Hyperaccumulators use a range of metal transporter proteins, including those from the Zn regulated, Iron regulated transporter- like proteins **(**ZIP), Cation diffusion facilitator **(**CDF), Natural Resistance Associated Macrophage Protein **(**NRAMP) and P_{IB} – type HM ATPase (HMA) families, to facilitate metal uptake and maintain homeostasis, with these transporters playing a crucial role in regulating metal accumulation and tolerance at the cellular level (Fig. 2**)**.

5.1. ZIP family

The roots and shoots of several dicot plant species are known to utilize transporters from the ZIP family, such as Iron regulated transporter (IRT) and Zinc Regulated Transporter (ZRT) proteins (Grotz and Guerinot, 2006). ZIP proteins have eight transmembrane domains crossing the plasma membrane with both the amino (-NH2) and carboxy (-COO) terminal ends located on the outermost part of the membrane, and they vary in length from 309 to 476 amino acids due to a histidine-rich variable region, spanning from transmembrane domain III to domain IV, that resides in the cytoplasm (Guerinot, 2000). ***AtIRT1, OsIRT1***, and ***HvIRT1***, homologs of *A. thaliana, Oryza sativa*, and *Hordeum vulgare*, respectively, are crucial for Fe^{2+}/Fe^{3+} and Mn^{2+} uptake, being located on the plasma membrane; under Zn-limiting conditions, the transcript levels of *A. thaliana* ZIP family transporters, including *AtZIP1* to *AtZIP5, AtZIP9* to *AtZIP12*, and *AtIRT3*, are elevated (Wintz et al., 2003; Talke et al., 2006; Van De Mortel et al., 2006).

5.2. CDF protein family

The CDF proteins, belonging to the class of cation efflux transporters crucial for HMs maintenance and tolerance, include plant CDFs, typically Metal Tolerance Proteins (MTPs) transporting Mn^{2+}. Phylogenetic analysis divided the CDF family into three groups based on metal ion transport efficiency: (1) Mn^{2+}-transporting CDFs, (2) Fe^{2+}/Zn^{2+}-transporting CDFs, and (3) Zn^{2+} and other metal ion (except Mn^{2+} or Fe^{2+}) transporting CDFs. A study identified substrate-defined clades for Cd^{2+}, Ni^{2+}, and Co^{2+} transport within the CDF family using phylogenomic data (Montanini et al., 2007). CDF proteins play a role in binding or exporting cations like Zn from the cytoplasm to internal compartments through sequestration or efflux, affecting cation accumulation and tolerance, signal transduction, oxidative stress resistance, and protein

Table 3
Binding agents and their thresholds against heavy metals in various plant species.

S. No.	Plant species	Binding agents	Heavy metals	Concentration	Effect on plant	Refs.
1.	*Corchorus capsularis L*	citric acid (CA)	Cu	2.0 mmol kg− 1	Alleviate oxidative stress and Cu phytotoxicity	Parveen et al. (2020)
2.	*Helianthus annuus* L.	ethylenediamine-N,N'-disuccinic acid {(S, S)-EDDS}	Cd, U (Uranium)	5.0 mmol kg− 1	Enhanced oxidative stress	Chen et al. (2020)
3.	*Macleaya cordata*	citric acid (CA)	U	10.0 mmol kg− 1	Promoted dissolution of uranium, mitigated oxidative stress	Hu et al. (2019)
4.	*Oryza sativa* L.	Hydroxyiminodisuccinic acid (HIDS)	Fe, As	0.25 mmol	increased Fe uptake and growth of rice seedling As phytoextraction	Rahman et al. (2009)
5.	*Ricinus communis* L.	citric acid (CA)	Cr	5 mmol kg− 1	Enhanced Cr absorption, improved plant growth	Ali et al. (2022)
6.	*Solanum nigrum*	N, N-bis glutamic acid (GLDA)	Cd	3.0 mmol kg− 1	Improved Cd absorption	Teng et al. (2022)
7.	*Zea mays*	aspartate dibutyric acid ether (AES)	Cd	6.0 mmol kg− 1	Increased biomass above the ground	Yang et al. (2021)

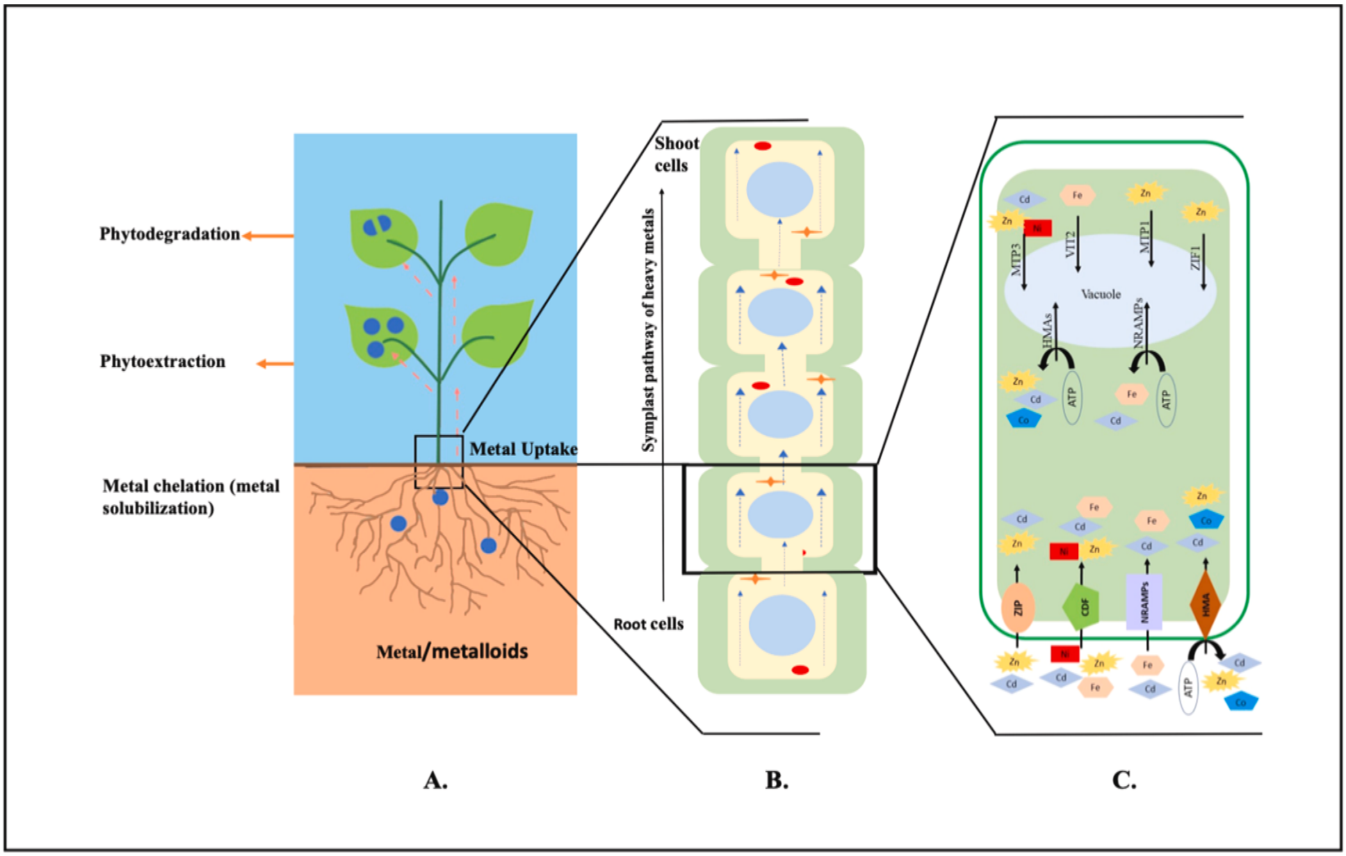

Fig. 2. Metal uptake and transport: Plants root cells take the heavy metals from the soil and through the symplast pathway. The heavy metals are transported to aerial parts of the plants using various types of transporters.

turnover (Barber-Zucker et al., 2019).

5.3. NRAMP family of proteins

The NRAMP family, which transports metal cations into the cytoplasm of plants, primarily functions to maintain iron homeostasis in *A. thaliana*, with several NRAMP genes in plants being expressed under Fe deficiency, indicating their role in nutrition, and are also expected to be present in intracellular membranes like the plastid envelope and vacuolar membrane (Thomine and Schroeder, 2004). Whereas, over-expression or disruption in *Arabidopsis NRAMP* genes results in alterations in sensitivity towards Fe or Cd. Transcriptomic analysis indicated *AtNRAMP3* upregulated at the time of leaf senescence, which implies its significant role in remobilization of HMs during leaf senescence (Zhu et al., 2021). *AtNRAMP1* demonstrates high affinity towards Mn and essential for a *Arabidopsis* growth in low Mn condition (Cailliatte et al., 2010). In addition, *A. helleri* and *T. caerulescens*, which are metal hyperaccumulating species, have significantly higher expression levels of *NRAMP3* and *NRAMP4* compared to their homologs in *A. thaliana* (Oomen et al., 2009).

5.4. HMAs

These HMs transporters use ATP molecules to efflux cytoplasmic cations through biological membranes. On the basis of phylogenetic studies, HMAs cluster is subdivided into two classes, namely the Pb/Cd/Co/Zntype and Ag/Cu type (Wang et al., 2011). Therefore, *AtHMA4* code for Zn/Co/Cd/Pb P_{1B}-type ATPase is the first HMAs that was cloned and characterized in plants (Colangelo and Guerinot, 2006). Whereas, in *A. thaliana, AtHMA2* and *AtHMA4* confers translocation of Zn utilizing the xylem loading process and are located on plasma membrane (Verret et al., 2004). *AtHMA4* homologs in *A. halleri* and *T. caerulescens* possibly execute a similar function, resulting in a dramatic increase of *AhHMA4* and *TcHMA4* expression in roots which accounts for the influx/efflux of Zn in accumulator species (Krämer et al., 2007). *T. caerulescens* and *A. helleri* utilize *HMA4* for the hyperaccumulation of Cd as well. Moreover, it has been affirmed that *HMA4* works as an efflux pump in roots and leaf cells conferring tolerance against Cd and Zn, which was confirmed by its heterologous expression in yeast (Colangelo and Guerinot, 2006).

6. Metal sequestration in vacuole by tonoplast

The vacuole in higher plants serves as a storage site for minerals, metabolites, and toxicants, while also playing a key role in long-term metal transport through its ability to dynamically modulate vacuolar sequestration capability (VSC), where it neutralizes and adjusts sequestration capacity in response to changing environmental conditions through the interaction of metal ion chelators and tonoplast-localized transporters (Clemens and Peršoh, 2009). Moreover, it paves the way for a successful biofortification of key nutrients or phytoremediation of the contaminants (Brunetti et al., 2011). Metal transporters in plants located in the tonoplast are imperative for the regulation of vacuolar sequestration capability and consequently the allocation of metal in different plant parts (Martinoia et al., 2012). When exposed with excess metal, metal transporters—identified in regulating metal sequestration in vacuoles—display increased cellular response. The enhanced expression of genes such as *MTP3* (Metal Transporter 3) (Arrivault et al., 2006), *VIT2* (Vacuolar Iron Transporter 2) (Zhang et al., 2012), *ZIF1* (Zinc- Induced Facilitator 1) (Haydon and Cobbett, 2007), *CAX4* (Cation Exchanger 4) (Mei et al., 2009), subsequently causes expansion in the VSC. The gene expression levels of *MTP1* increased significantly in various metal hyperaccumulators (Ricachenevsky et al., 2013).

A subclass of chelators, called PCs are potentially very crucial in HMs detoxification by formation of metal complexes which thereby get trapped in the vacuoles. NA a different metal chelator that is primarily found in higher plants, changes the VSC of Fe and Zn and consequently their respective distribution. The root biomass of *A. helleri* contains significant levels of NA which allows the metal allocation of Zn to shoots (Deinlein et al., 2012). The VSC regulation is mediated by chelators and can be categorized into two categories: 1) The metal chelators tend to translocate to vacuoles which leads to enlargement of VSC of certain metals. 2) As a consequence of metal chelation, the vacuolar sequestration is reduced, hence, reducing the VSC of certain metals (Deinlein et al., 2012). In some Ni hyper-accumulators, it has also been shown that Histidine (His) has a prominent role in detoxification and translocation of Ni. It is concluded in a study that Ni in the form of Ni-His complex when supplied increases the rate of uptake in tonoplast vesicles of hyper-accumulator *T. arvense.* According to their theory, His deposition in the roots of *T. caerulescens* declines Ni's cytosolic chelation potential, thereby, enhancing Ni transport and its hyperaccumulation in shoots (Maestri et al., 2010).

7. HMs sequestration mechanisms in plants

HMs accumulation in multicellular plants involves a complex interplay of metal uptake, intracellular metal binding, and detoxification processes, which is further complicated by cell proliferation and tissue-specific mechanisms that can disrupt the balance of essential metal homeostasis and redox systems, leading to increased metal-induced stress (Foyer and Noctor, 2005). Various processes are involved in the deposition of metals in plants, including the mobilization and uptake of HMs from the soil, their sequestration through the creation of metal complexes such as chelators and storage in vacuoles. Metal transport can occur via apoplastic or symplastic pathways to reach shoots, aided by effective xylem loading. Once transported to leaves, metal ions are confined within tissue layers, and ultimately, deposited metals are stored in structures like trichomes (Clemens et al., 2002). The absorption and movement of metals in plant leaves are aided by transporters and metallochaperones. Several mechanisms for HM sequestration in plants are detailed below.

7.1. Phytochelatins (PC's)

PC's are low molecular weight peptides containing thiol group. GSH serves as a PC precursor where GSH is acted upon by phytochelatin synthetase (Hasanuzzaman et al., 2017). Reports have found that PC's play a part in plant defense against metal-related challenges and other stress conditions like salt, intense heat, UV radiation, herbicides (Zagorchev et al., 2013). Additionally, in HMs stress diagnosis, PCs are used as biomarkers. Whereas, HMs like Hg, gold (An), Cu, silver (Ag), Cd and Zn induce biosynthesis of PCs. Further it has been observed that Cd is the strongest inducer in *Brassica napus* (Carrier et al., 2003). Moreover, PCs form complexes with metals, they are transported to the vacuoles. These complexes enable the extraction of HMs from cytoplasmic HMs sensitive enzymes. The transportation of metal-PC complexes from cytosol to vacuole is mediated by transporters of tonoplast which can be either ATP-dependent ABC transporters or metal/$H+$ antiporters (Kang et al., 2011). The sulfide and sulfite ions present in vacuoles are integrated in PC- HM complex, hence providing stability and stabilizing pH when dissociation of metal occurs. Roughly 90 % of total Cd of mesophyll cells remain in vacuoles in case of Cd-hyperaccumulator *Thlaspi caerulescens.* Vacuolar sequestration was therefore postulated in these plants as a key internal detoxifying mechanism for Cd in leaves (Ma et al., 2005).

7.2. Metallothionines (MTs)

MTs are cystine-rich, low molecular weight proteins that sequester HMs by forming metal-thiolate clusters, and are found abundantly in eukaryotes (including mammals, plants, and fungi) as well as prokaryotes, differing from PCs, which are enzymatically produced, whereas MTs result from the mRNA translation process (Verkleij et al., 2003). MTs in plants show affinity for a broader range of HMs, including As and Zn, playing a crucial role in detoxifying these metals by sequestering them, maintaining intracellular metal ion homeostasis, and regulating HM transport (Guo et al., 2013). They actively participate in cellular functions such as ROS scavenging, redox maintenance, cell proliferation, and DNA repair, while multiple factors including osmotic stress, nutritional deficiency, hormone secretion, naturally occurring or induced tissue senescence, infections, or wounds can lead to the expression of MTs (Kumar et al., 2017). MTs are classified into four types on the basis of order of Cysteine residues: Type 1 – root expressing MTs, Type 2-shoot expressing MTs, Type 3 and Type 4-leaf and developing seeds expressing MTs. Further these subgroups are divided into isoforms. In a study of *Arabidopsis* it was depicted that MT isoforms (Type 1a, 2a, 2b and 3) are responsible for copper chelation whereas Type 4a and 4b MT isoforms function as Zinc binders (Grennan, 2011).

7.3. Stress proteins

Upon subjection to metal toxicity, plants stimulate novel proteins production. These proteins, commonly known as "Stress proteins," belongs to heat shock protein family (HSPs). HSPs are molecular transporters and facilitate correct protein folding and assembly. In various plant species upon exposure to Cd, the DNA isolated from cells subjected to Cd stress produces certain mRNA transcripts, that control biosynthesis of stress related proteins. Cys-rich membrane protein (*Arabidopsis* plant cadmium resistance, (*AtPCRS*) were identified in *A.thaliana*. Its homologs were also found in *Oryza sativa* and *Solanum lycopersicum*, that provides resistance to Cd exposure (Song et al., 2004). The expression of proteins that are related to pathogenesis also called as PR proteins, which show metal selectivity in plants when metal toxicity increases. For instance, when exposed to Cd, Zn, and Cu, *Lupinus luteus* plants produce PR-10 family proteins that are associated to pathogenesis (Przymusiński et al., 2004).

7.4. Proline

Proline is the most ubiquitous 5-carbon α-amino acid, functioning like a suitable metabolic osmolyte, free radical scavenger and antioxidant. Elevation in proline levels is a non-enzymatic response of higher plants towards biotic and abiotic stress conditions like HMs, oxidative stress and increased salinity (Szabados and Savouré, 2010). HMs caused accumulation of proline in plants as a outcome of water imbalance, brought on by metal overload, rather than direct HM stress, hence proline working as an osmoregulator or osmoprotectant (Clemens, 2006). Primarily, proline acts as a ROS scavenger by hydroxyl radicles detoxification and singlet oxygen quenching. Experiments on *Brassica* sp. and lemongrass have demonstrated proline accumulation in roots after exposure to excessive concentration of HMs i.e., Pb, Cd, Hg and Cd (John et al., 2009; Handique and Handique, 2009).

8. Tolerance and toxicity to HMs at the cellular level

The exposure to HMs in plants can lead to genotoxic and oxidative stress responses, resulting in cellular damage and disruption. To counteract these harmful effects, plants have evolved two defense mechanisms: antioxidant enzymes (for example ascorbate peroxidase (APX), SOD, GR, and CAT) and the accumulation of various antioxidants like carotenoids, ascorbate, phenylpropanoids, GSH, proline, and alkaloids (Bhaduri and Fulekar, 2012). For example, it has been observed in

Sainfoin (*Onobrychis vicifolia*) the activity and function of three enzymes namely SOD, CAT and GPX increased in the leaves after contaminated with HM's like Cu and Pb (Beladi et al., 2011). However, HMs like Cd can still cause oxidative damage, disrupt lipid membranes, and contribute to reduced agricultural yield (Cho and Seo, 2005). Furthermore, ROS, despite their damaging potential, also play important roles as signalling messengers in various cellular processes, including cell development, differentiation, apoptosis, and stress response. Nevertheless, ROS-induced oxidative stress can lead to DNA damage and genome instability, further impacting plant development and agricultural productivity (Markkanen et al., 2012) (Fig. 3).

9. Environmental Implications of HMs

There is a widespread concern over HM contamination in both aquatic and terrestrial environments. HMs, originating from various sources (mining operations, industries, domestic sewage and agricultural runoff), are persistent and can accumulate in ecosystems, posing risks to organisms and human health (Singh and Steinnes, 2020). They enter the food chain, particularly affecting aquatic habitats, where sediments serve as reservoirs (Ali Azadi et al., 2018). Changes and reduction in pH can release HMs into water because reduction in pH causes a competition between metal ions and H^+ for binding sites in sediments which may dissolute the metal complexes into liberated metal ions in the water column (Nowrouzi et al., 2014). Soil contamination, often resulting from the use of fertilizers and various pollutants, highlights the importance of understanding the bioavailability of HMs in the soil to accurately assess their effects on ecosystems (Ali et al., 2019).

10. Nano-bioremediation of HMs contaminations

Significant amounts of pollutants have been dispersed around the world as a result of the world's rapid population increase, expanding industries, and developing urbanization. The main objective of scientific research is to create environmentally sustainable technologies that are also commercially feasible. Bioremediation has proved to be a more efficient, environmentally beneficial, and cost-effective technique (Patel et al., 2022). It exploits microbial ability to remove or degrade environmental pollutant (Sharma et al., 2024). Though, this process is not suitable for such sites which are highly contaminated with HMs and salts because they are harmful for microbial survival. So, there is a need for exploring innovative technologies which are highly beneficial compared to existing methods. The usage of nanomaterials is expanding rapidly to address environmental concerns as a result of the outstanding advances in the field of nanotechnology. There are numerous ways to create nanoparticles (NPs), including sonication, pulse wire discharge, radiation, spray pyrolysis, and electro-deposition. However, each of these approaches uses a different set of chemicals, is costly, and creates a range of hazardous byproducts (Abdel-Shafy and Mansour, 2018). It is therefore necessary to develop more affordable and environmentally friendly methods for synthesizing NPs. The synthesis of NPs through biological processes is more advantageous for bioremediation processes because it is both economical and environmentally beneficial (Sivaraj et al., 2015). During the biological or green synthesis of NPs, metabolites of living organisms reduce metal ions to stable nanomaterials by using NADPH-dependent enzymes via an electron shuttle enzymatic metal reduction mechanism (El-Seedi et al., 2019). These metal NPs or nanomaterials (NMs) minimize pollution by absorbing a sizable amount of contaminants owing to its high surface tension and surface area features, respectively. The bioremediation process is accelerated by these nanosized form of particles, which are able to reach contaminated areas more readily (Pete et al., 2021). Nanomaterials synthesized by fungi, bacteria, yeast and actinomycetes are widely used in industry, environmental remediation, remediation of uranium, solid waste remediation and HM remediation. Amongst all the microorganisms, fungi have been experimentally observed as the most momentous producer for NP synthesis, because fungal mycelia can tolerate harsh conditions and high pressure as compared to bacteria and plant extracts (Adebayo et al., 2021). Further fungi can grow easily and the extracellular secretions of fungi are composed of various reactive proteins which are easy to handle in

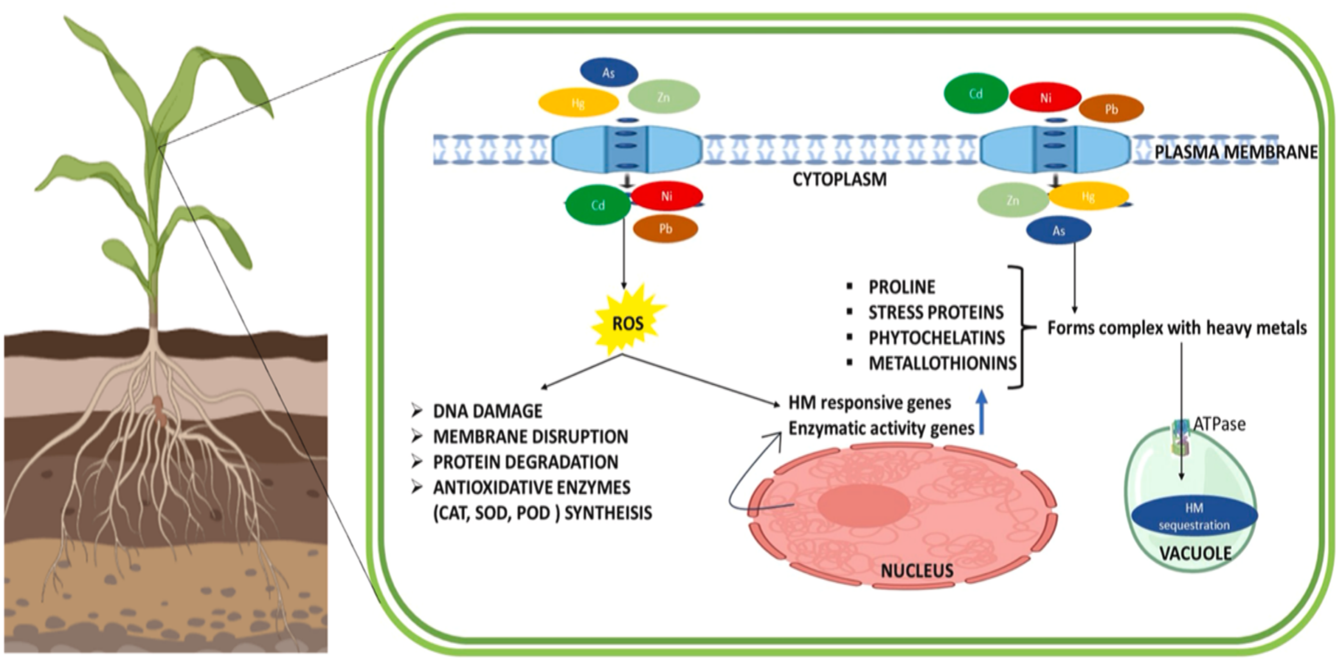

Fig. 3. Mechanisms involved in heavy metal sequestration: When heavy metals enter the plant system via transporters present in roots, they are distributed to whole plant body via symplastic and apoplastic mechanisms. At cellular level, these heavy metals enter the cell cytoplasm through plasma membrane. Upon reaching there, they tend to increase the ROS production that causes DNA damage, membrane disruption, increase in antioxidant enzyme synthesis. Also the expression of heavy metal responsive genes and enzymatic activity genes are upregulated in nucleus. Heavy metals forms complexes with stress proteins, phytochelatins, metallothionins and proline that are further transported to vacuole by ATPase transporters where heavy metal sequestration takes place.

downstream processing . It was reported that *Verticillium* sp. and *Fusarium oxysporum* on exposing with aqueous $AgNO_3$ solution produced intracellular and extracellular Ag NPs respectively (Khan et al., 2018; Yassin et al., 2021). Amongst all NPs, Ag-NPs, iron- NPs, carbon- NPs, nanoscale zero-valent iron (nZVI) are abundantly used in bioremediation experiment (Yadav et al., 2017). When utilized on heavily polluted sites containing persistent pollutants like Cr and As, zero valent nanoscale metal ions like Fe and bimetallic NPs like Fe/Ni and Fe/Pd have shown good results since they have very low toxicity and cost effective (Thomé et al., 2015). HMs pollution affects quality of aquatic bodies and soil. Although HMs are non-degradable, these can be modified by methylation, complexation, and absorption. Mostly the HMs polluted sites are found to be a good reservoir of various HMs tolerant microbes. Therefore, microbes are used to remediate and detoxify some metals and reduce metal pollution through bioremediation (Igiri et al., 2018). Fungi of the genera *Penicillium* and *Rhizopus* have been recognized to remove toxic HMs from solutions (Ghosh et al., 2023). As per reports, *Aspergillus niger* assist in removing lead and chromium ions from aqueous solutions (Li et al., 2016; Xu et al., 2021). Fungus based nanomaterials are more effective in remediation of various metal ions from aqueous and soil ecosystems. Fungi have biochemical and ecological capacity to remove environmental toxins associated with HM, radio nuclides and metalloids through chemical modifications (Fomina and Gadd, 2014). Agricultural pollution, a global concern, stems from practices such as fertilizer and pesticide application, soil tillage, and introduces harmful pollutants like nitrates, phosphates, pesticides, and HMs into the environment, posing significant hazards (Khan et al., 2018). Nano bioremediation is one such approach that exploits advantage of nanotechnology or nanomaterial along with bioremediation benefits. This combination of biotechnology and nanotechnology has proven to be a successful method for cleaning up pollutants. Additionally, it can be used in conjunction with bacteria or microbial enzymes.

11. Phytoremediation

Phytoremediation is the process whereby plants and their associated soil microbes collinearly work to reduce the concentrations or toxic effects of contaminants in the environment. It encompasses various methods, including phytoextraction, phytodegradation, phytovolatilization, and phyto-stabilization. Except for phytodegradation, which is employed only in the degradation of organic pollutants to non-toxic compounds, the other three methods can be employed for the removal of heavy metals from the soil (Kukreja and Goutam, 2012). Microbe-assisted phytoremediation is the decontamination of pollutants in the rhizosphere carried out by an interaction of plants and microbes. It can be carried out by one of the two ways: either by using natural existing population of microbes in the soil or by inoculation with the desired microbes that are able to break down pollutants (Asemoloye et al., 2019). To facilitate rhizospheric bacterial colonization, plants roots secrete copious amounts of bioactive chemicals such as root exudates (enzymatic and non-enzymatic) including flavanones, proteins, carbohydrates, enzymes, amino acids, nucleotides, organic acids and phenolics which are utilized by bacteria (Al-Ameeri and Al Sarawi, 2017). Bacteria release a variety of substances, including organic acids, polysaccharides, metal chelators (siderophores), organic acids, and biosurfactants. These substances all help in HMs detoxification by increasing bioavailability and reducing soil pH, which limits HMs mobility (Rajkumar et al., 2012). *Micrococcus luteus*, which is resistant to As, engaged in siderophore production, nitrogen sequestration, and phosphate solubilization, resulting in increased grapevine yield and reduced As toxicity, even under high arsenic concentrations (Pinter et al., 2017). The total dried weight and leaf surface area of pepper plants inoculated with AM fungus increased in response to high Cu in soil (Ruscitti et al., 2017). Mobilization and assimilation of Hg and As improved in *Brassica juncea* and *Lupinus albus* growing in soils contaminated with these metals when thiosulfate was added together with HM tolerant plant growth promoting (PGP) microorganisms (Franchi et al., 2017). AMF and rhizobacteria release cysteine-rich peptide molecules referred as MTs that are structurally identical to PCs and aid in the accumulation of HMs (Miransari, 2011). The application of AMF *Glomus mosseae* to the *Schedonorus arundinaceus* (tall fescue) plants lowers the movement of Ni to the plant and enhances the amount of *MT* and *ABC* gene expression (Shabani et al., 2016). Rhizosphere microbes produce extracellular polymeric substances (EPS) that contain a significant amount of anion functional groups, which aid in the biosorption and subsequent removal or recovery of metals, for example *Trichoderma harzianum* and *Bacillus subtilis* fungal-bacteria biofilms were able to reduce Zn, Pb and Cd assimilation in potato tissue which can be employed as viable solution in rhizoremediation of HMs (Henagamage et al., 2022). In one experiment, *Sesbania sesban* legume plant seedlings were subjected to HMs like Cr and Cd with the bacterium *Bacillus anthracis* PM 21. It was found that this bacterium promoted the growth of plants biomass by ACC-deaminase expression, Indole-3-acetic acid (IAA), exopolysaccharide production and elevated functions of antioxidants in HMs environments (Ali et al., 2021).

12. Genetic modified plant in HMs remediation

Utilizing transgenic plants for HMs removal is providing new direction in environmental clean-up. HMs can be removed by inserting gene specific promoters in plants enhancing the transcription of existing genes. For example, the overexpression of the *Vicia sativa* caffeoyl-CoA O-methyltransferase (*VsCCoAOMT*) gene in *Arabidopsis thaliana* showed the potential of genetically modified (GM) crops in phytoremediation applications, as these transgenics exhibit enhanced Cd tolerance and increased biomass production (Xia et al., 2018). Similarly, HMs ATPase (HMA5) is a Cd exchanger channel, present in plants for cadmium exchange between shoots and roots. Whereas, PtHMA5 isolated from *Populus trichocarpa*, when overexpressed in *Nicotiana tobaccum* leds to Cd accumulation suggesting its potential in phytoremediation (Wang et al., 2018). Additionally, Endophytic bacterial genes are quite useful for transforming plants to enhance their metal absorption. Endophytic bacterial genes, such as *CUP and bphC,* were used to produce first transgenic nettle (Urtica dioica) plants, which demonstrated a 33 % reduction in polychlorinated biphenyls and an 8 % reduction in HMs (Viktorova et al., 2016). Plants possess inherent detoxification mechanisms, notably glutathione (GSH) homeostasis; a potential redox compound, that links intracellular bioenergetic signaling pathways. Gamma- glutamyl-cysteine synthetase- glutathione synthetase gene (Gamma-GCS-GS) is recently discovered in *Sulfolobus thermophiles* that has high tolerance level for HMs (Liedschulte et al., 2010). Moreover, glutathione synthetase gene overexpressed in *Beta vulgaris* (sugar beet) had high ability to retain HMs like Cd, Cu, Zn, and showed high GSH and PC activities upon exposure to HM stress in comparison to wild type (Liu et al., 2015). There are also certain functional genes along with metal transporter proteins that could be targeted for remediation purposes. Furthermore, Nahar et al. (2017), successfully overexpressed the arsenic reductase*2* gene (*AtACR2*) in tobacco isolated from *A. thaliana* leading to high As accumulation in roots whereas lower concentration in the shoots. This indicates that the *ACR2* gene may be useful in As phytoremediation and in the production of transgenic crops. A list of genes involved in heavy metal uptake in plants is given in Table 4**.** However, the deployment of GM crops in environmental remediation raises biosafety concerns, ecological risks, and regulatory challenges. In addition, biosafety concerns include the potential for horizontal gene transfer to non-target organisms, the development of herbicide resistance in weeds due to gene flow, and the unintended effects of transgene expression on plant metabolism and ecological interactions. Ecological risks include the potential for altered plant-microbe interactions, changes in soil microbial communities, and the disruption of ecosystem services. Furthermore, regulatory frameworks for GM crops vary significantly across countries, posing

Table 4
Genes of plants involved in HM uptake.

Sl. No	Genes	Plants	HM	Refs.
1.	*Nramp*	*Arabidopsis* sp., *Oryza sativa*	Cd and divalent metals	Belouchi et al. (1995); Alonso et al. (1999); Thomine et al. (2003)
2.	*AtNRAMP6*	*Arabidopsis thaliana*	Fe	Li et al. (2019)
3.	*AhZIP6*	*Arabidopsis halleri*	Cd	Spielmann et al. (2020)
4.	*CAD1*	*Arabidopsis* sp.	Cd	Ha et al.(1999)
5.	*AtIRT1*	*Arabidopsis* sp.	Fe	DalCorso et al. (2008)
6.	*AtATM3*	*Arabidopsis* sp.	Pb and Cd	Kim et al. (2006)
7.	metallothionein (MT) genes	*Arabidopsis thaliana*	Cu	Khandekar & Leisner (2011)
8.	*COPT/Ctr (COPTR1–7)*	*Arabidopsis thaliana*	Cu	Jan et al. (2016)
9.	*CdR3*	*Arabidopsis* sp.	Cd	Sethy & Ghosh (2013)
10.	*VsCCoAOMT*	*Arabidopsis* sp.	Cd	Xia et al. (2018)
11.	TcHMA4	*Arabidopsis thaliana Thlaspi caerulescens*	Cd, Zn, Pb, and Cu	Papoyan & Kochian (2004)
12.	*TaHMA2*	*Arabidopsis* sp.	Zn and Cd	Qiao et al. (2018)
13.	*LuABCC9,*	*Arabidopsis* sp.	Cd	El-Sappah et al. (2023)
14.	*SlJMJ524*	*Arabidopsis* sp.	Cd	Li et al. (2022)
15.	*GGCT2*	*Arabidopsis* sp.	As	Paulose et al. (2013)
16.	*CaGrx*	*Arabidopsis thaliana*	As, Cr and Cd	Kumar et al. (2020)
17.	*AzMT2*	*Azolla filiculoides*	Ni and Cd	Schor-Fumbarov et al. (2005)
18.	*NRAMP*	*Brassica napus*	Zn, Mn, Cd and Pb	Meng et al. (2017)
19.	*GSHI and GSHII*	*Brassica juncea*	Cd	Liang Zhu et al. (1999)
20.	*HMA4*	*Brassica juncea*	Cd	Wang et al. (2019)
21.	*BjHMA4*	*Brassica juncea*	Cd	Wang et al. (2019)
22.	*BjYSL7*	*Brassica juncea*	Cd	Wang et al. (2013)
23.	*BjHO-1*	*Brassica juncea*	Hg	Li et al. (2012)
24.	*CsMTP8.2*	*Camellia sinensis*	Fe, Mn and Zn	Zhang et al. (2020)
25.	CaMYB	*Capsicum annuum*	Cd, Cu, and Pb	Xie et al. (2022)
26.	*GmHMA3*	*Glycine* max	Cd	Wang et al. (2018)
27.	*GmaMTPs*	*Glycine* max	Zn	El-Sappah et al. (2023)
28.	*HvHMA1*	*Hordeum vulgare*	Cu	Bernal et al. (2007)
29.	*LmSAP*	*Lobularia maritima*	Cd, Cu, Mn and Zn	Saad et al. (2018)
30.	*HMA4 PCS1*	*Liriodendron tulipifera*	Zn,	Adams et al. (2011)
31.	*HMA*	*Linum usitatissimum*	Cd	El-Sappah et al. (2023)
32.	*PvSR2*	*Nicotiana tabacum*	Cd	Chai et al. (2003)
33.	*TaPCS1*	*Nicotiana glauca*	Pb and Cd	Gisbert et al. (2003)
34.	*OsHMA3 OsMTP1 OsABCC1*	*Oryza sativa*	Cd, Zn and As	Menguer et al. (2013); Sasaki et al. (2014); Song et al. (2014)
35.	*HMA (HMA1 to HMA9)*	*Oryza sativa*	Zn, Pb and Cd	Takahashi et al. (2011)
36.	*OsHMA2* and *OsHMA3*	*Oryza sativa*	Cd and Cu	Kim et al. (2014)
37.	OsMTP1	*Oryza sativa* IR64	Cd	Das et al. (2016)
38.	*OsMTP11*	*Oryza sativa*	Mn	Zhang and Liu (2017)
39.	*H655* and *H767*	*Oryza sativa*	Hg	Wang et al. (2023)
40.	*RsMYB1*	*Petunia* sp.	Cu, Zn, Mn and Cr	Ai et al. (2018)
41.	*ScMT2–1–3,*	Saccharum officinarum	Cd and Cu	Guo et al. (2013)
42.	*SpHMA3*	*Sedum plumbizincicola*	Cd	Liu et al. (2017)
43.	*StMATE*	*Solanum tuberosum*	Cu	Huang & He (2021)
44.	*TcHMA3*	*Thlaspi caerulescens*	Cd	Ma et al. (2005); Ueno et al. (2011)
45.	ZIP family (*ZAT1, ZAT2, ZAT3*)	*Thlaspi caerulescens*	Cd, Zn and Mn	(Pence et al. (2000); Lombi et al. (2002)
46.	ZmHMA3	*Zea mays*	Cd	Tang et al. (2021)
47.	ZmST1	Zea mays	Cd, Zn, and Cu	Nocito et al. (2006)
48.	*ZjMT*	*Ziziphus jujuba*	Cd	Li et al. (2016)

challenges for the development and commercialization of these technologies. Public perception and acceptance of GM crops are also critical factors that can influence their adoption. Therefore, comprehensive risk assessments, stringent regulatory oversight, and transparent communication with stakeholders are essential to ensure the safe and responsible application of GM crops in HMs remediation. Whereas, future research should focus on developing strategies to mitigate these risks, such as the use of gene containment technologies and the development of site-specific and self-limiting transgenes. Additionally, the long-term ecological impacts of GM crops deployment should be thoroughly evaluated through field trials and monitoring studies.

13. Microbial based bioremediation of HMs

Heavy metal detoxification via microbial-based bioremediation has become popular as an cost effective and eco- friendly technique. This method uses of the innate ability of various microbes, such as bacteria, fungi, or algae, to degrade certain heavy metals from polluted areas. Since these microbes are flourishing in places affected by heavy metals, they are ideal candidates for microbial bioremediation due to their distinct metabolic characteristics. Microbial bioremediation can occur in several ways, including biosorption, bioaccumulation, biotransformation, and biomineralization (Tang et al., 2024; Priya et al., 2022; Pande et al., 2022).

According to Tripathi et al. (2023), biosorption is the process by which metal ions attach to microbial cell walls, containing functional groups with a high affinity for metal ions, such as carboxyl, amino, and hydroxyl. As this process is very effective and does not require the metabolic input from the cell so the dead cells can also be utilised for the process. A study demonstrated that dead cells of *Bacillus cereus* RC-1 shows higher Cd(II) biosorption capacity than live cells (Huang et al., 2013). Recent studies have highlighted the biosorption potential of green and red algae for heavy metals such as Pb, Cu, Cd, Zn, and Cr (Romera et al., 2007; Sarı and Tuzen, 2008). However, despite their ability to remove these metals from aqueous solutions, their performance is significantly lower compared to brown algae (such as *Sargassum* sp.) (He and Chen 2014).

In contrast to absorption, bioaccumulation is the process by which microbes absorb and accumulate metals within their cells using cellular energy with the involvement of metal-binding proteins and an efflux mechanism (Mishra and Malik, 2013). Microbes are also involved in the enzymatic conversion of hazardous metals into less dangerous or immobile forms by the process of biotransformation. For example, several bacteria have the ability to decrease the bioavailability of deadly hexavalent chromium (Cr^{6+}) by transforming it into less hazardous trivalent form Cr^{3+} (Juwarkar and Yadav, 2010).

Biomineralization is another process in which metals are immobilized in stable forms within the soils through microbial metabolic activities (Li et al., 2023). Microbes by lowering the toxicity, mobility, and bioavailability of HMs, help to lessen their negative impacts on the environment. There are various microbial species that has shown their remarkable capabilities in the HMs bioremediation. For example, strains of *Pseudomonas* show resistance towards the Cd as they are involved in the absorption of the cadmium (Chellaiah, 2018; Naz et al., 2016). *Bacillus* species are useful in the metal uptake and the transformation in the HMs contaminated environments (Wróbel et al., 2023; Butterfield et al., 2016). Whereas, *Aspergillus niger* and *Penicillium* exhibited the biosorption of HMs due to the nature of their cell walls that have the metal binding efficiency (El-Mahdy et al., 2021). Although, Use of microbe in a consortium can be utilized to detoxify several metals at once so it could be helpful in lethal contamination. Additionally, reduced levels of secondary pollutants, cost effective and recovery of metal for the industrial use are just a few benefits of microbial based bioremediation.

However, there are some limitations in the broad implementation of the microbial based bioremediation. There are several environmental elements that determine the effectiveness of microbial activity include pH, temperature, and the presence of other pollutants (Ayilara and Babalola, 2023). In addition, some HMs are poisonous to microbes, and this may restrict their ability to absorb and transform the metals into less harmful form. These constraints can be overcome by using adaptive evolution and genetic engineering practices to enhance metal-removal effectiveness and microbial resistance. To overcome these constraints, current studies have concentrated on using adaptive evolution and genetic engineering methods to improve metal-removal effectiveness and microbial resistance.

14. Conclusion and future outlook

The increasing concentrations of HMs in the environment poses a significant threat to the health and safety of the living organisms. As a result, it is crucial for plants to develop adaptive strategies that enhance their tolerance to HM stress and reduce the risk of HM transfer into the food chain. HMs appears to have diverse mechanisms to exert toxicity, while plants, in turn, deploy diverse defence responses to counteract their effects. When exposed to excessive HMs, plants exhibit distinct molecular and biochemical tolerance strategies. These strategies primarily aim to prevent the accumulation of toxic metals within the cells by the mechanisms such as apoplastic entrapment, chelation of metals by cytosolic ligands, and sequestrations into vacuole. Furthermore, the exogenous treatment of different organic or inorganic compounds has emerged as a promising approach to mitigate HM toxicity in plants. Exploring the interactions between these compounds and the plant systems, as well as their role in ameliorating HM stress, presents a potential area of future research.

CRediT authorship contribution statement

Himani Agarwal: Writing – original draft. **Divya Chaudhary:** Writing – original draft. **Himanshi Aggarwal:** Writing – original draft. **Chhavi Karala:** Writing – original draft. **Niharika Purkait:** Writing – original draft. **Neha Sharma:** Software, Investigation. **Arti Mishra:** Software, Methodology. **Vaibhav Mishra:** Software, Methodology. **Ajay Kumar:** Software, Methodology. **PrashantKumar Singh:** Visualization, Software, Investigation. **Laurent Dufossé:** Writing – review & editing, Supervision, Conceptualization. **NaveenChandra Joshi:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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