International Journal of
Innovative Scientific Research

Journal homepage: http://journals.worldbiologica.com/ijisr

World BIOLOGICA

Review paper

Zinc Uptake, Transport and Homeostasis in Plants: Implications for Sustainable Agriculture

Rubia Bukhari [a] *, **Azad Gull** [b]

[a] *PG Department of Sericulture, Poonch Campus, University of Jammu-185101, UT Jammu and Kashmir, India*
[b] *CSB- Central Sericultural Research and Training Institute, Mysore-570008, Karnataka, India*

KEYWORDS

- Defence
- Heavy metal
- Homeostasis
- Mechanisms
- Phytochelatins
- Zinc transporters

ABSTRACT

Zinc (Zn), a mineral that naturally occurs in soil in terrestrial environments, is essential for plant growth because it plays crucial roles in many metabolic pathways. However, the presence of potentially toxic levels of zinc in soils can affect plant growth, photosynthetic and respiratory rates, mineral nutrition and the amount of reactive oxygen species that are produced. The weathering of rocks, forest fires, volcanoes, mining and smelting operations, manure, sewage sludge and phosphatic fertilizers are only a few of the routes via which Zn enters soils. The scientific community has focused on Zn's impacts on plants and vital role in agricultural sustainability as a result of rising environmental alarm and the small window between Zn essentiality and toxicity in plants. Because of this, this review focuses on the most recent research on the numerous physiological and biochemical processes that are affected by high levels of zinc, as well as on the mechanisms of zinc uptake and transport and molecular aspects of excess zinc homeostasis in plants. This review also makes an effort to comprehend the mechanisms underlying Zn toxicity in plants and to give fresh viewpoints that aim to inspire more research into the subject. The review results will also provide light on different processes used by plants to deal with Zn stress, which will be very important to breeders who want to increase tolerance to Zn pollution.

Introduction

The group IIB transition element zinc (65.37Zn30) was named by the Swiss physician and alchemist Paracelsus after the German term Zinke. It comes in second place to iron, the most common transition element (Mir et al. 2015). There are five stable isotopic variants of zinc found in nature (Broadley et al. 2007). Zn has been described as having both light and heavy isotope enrichment in plant shoots and roots, respectively (Caldelas et al. 2010). Due to their similar sizes and + 2 oxidation states, Zn and magnesium (Mg) are chemically comparable.

*__Corresponding author__: Rubia Bukhari

DOI 105281/ijisr292324

N of histidine is the most prevalent, followed by S of cysteine, O of aspartate/glutamate and carbonyl O of peptide bond, glutamine/asparagine, and hydroxyl of tyrosine in proteins and enzymes. Zn^{2+} ions have high binding affinities for these amino acid residues (Leuci et al. 2020).

It is now widely acknowledged that the accumulation of toxic heavy metals in soil and streams is a serious environmental problem with detrimental effects on both plants and animals. Using the efficient, cost-effective and environmentally beneficial bioremediation technology known as phytoremediation, the harmful heavy metals in the contaminated ecosystem can be detoxified and collected in the plant. Hyperaccumulators exhale chemicals known as transporters, which are responsible for moving the heavy metals contained in the soil to different plant parts. The tissues of plants with hyperaccumulator genes may contain higher concentrations of toxic heavy metals. The nature of the rhizosphere, the characteristics of the rhizosphere microflora, the soil quality (pH and soil type), the amount of organic matter in the soil, the kind of heavy metal and more determine how efficient phytoremediation is.

According to Marschner (2012), most crops typically need between 30 and 200 g of zinc per dry weight (DW) to be healthy. Zn is an essential micronutrient that plays structural and/or catalytic roles in a number of processes, including protein synthesis, cell division and cell growth (Jain et al. 2010). According to Gai et al. (2017) and Noulas et al. (2018), it is essential for chromatin structure, gene expression and regulation, metabolism of nucleic acids, carbohydrates, lipids and proteins, as well as the conversion of pho-to synthetic carbon. Tryptophan, an amino acid that serves as a precursor to auxin, is synthesized using zinc as well (TsSonev and Lidon 2012).

The new study goes into great detail about the environmental toxicity of zinc as well as a number of phytoremediation mechanisms for the transport and accumulation of zinc from contaminated soil. This study gave detailed information on the tolerance of plants to elevated heavy metal concentrations, their responses to heavy metal accumulation and the many mechanisms behind heavy metal tolerance. The current state of the phytoremediation process and the distinctive traits that require improvement are also fully covered.

Recently, there has been a lot of interest in the physical and molecular underpinnings of interactions with agricultural plants and the environment at large. Abiotic stress factors as oxidative pressure, temperature, toxicity and salt from the ecosystem are the main contributors to the overall lower yields that imperil agricultural output (Raklami et al., 2021). The high population growth led to environmental damage and chemical toxicity problems. Toxins such heavy metals, oil-based chemicals, acids and pesticides have internalized in air, soil and water supplies as a result of rapid industrialization and urbanization projects, impacting the growth of plants, animals and the ecosystem itself. Lead, nickel, mercury, cadmium, zinc and chromium are a few of the heavy metals that have an impact on plants.

Physical, chemical and biological methods can all be used to clean up soils that have been contaminated with metals. The physical-chemical processes solidification, electro kinetics, encapsulation, soil cleaning and soil flushing all render the soil unfit for plant growth. These processes are frequently pricy. On contaminated soils, the biological remediation approach promotes plant growth and productivity (O'Sullivan et al., 2019). Because the process is biological, it is favourable for the environment. When compared to other clean-up techniques, bioremediation is another logical remediation option.

These metals are to blame for the agro-biological systems' damage and decreased profitability. They stress plants and have an impact on their physiology. Throughout their life cycle, plants are continuously exposed to unfavourable ecological conditions, which has a negative impact on their growth, development and product efficiency (Diaconu et al., 2020).

There are numerous methods, including physical, chemical and biological ones, for cleaning up metal-contaminated soils. Physical-chemical processes like solidification, electro kinetics, encapsulation, soil washing and soil flushing are typically expensive and render the soil unsuitable for plant growth. The restoration of plant growth and production on contaminated soils is energised by the biological remediation technology (O'Sullivan et al., 2019). Being biological, the procedure is environmentally beneficial. Compared to other remediation techniques, bioremediation is also a wise remediation option.

Table 1 Effects of zinc toxicity on different morpho-anatomical, physiological, biochemical and molecular traits in crop plants (reports cited 2010 onwards)

Plant	Zn concentration	Plant Zn content	Type of experiment	Effects	References
Brassica chinensis L.	2000–1000 mg kg−1		Pot	Small fronds, defoliation, a reduction in photosynthetic pigments, chlorosis and an increase in membrane permeability	Yang et al. (2012)
Brassica pekinensis	5–10 µM	5.49–7.93 µmol g−1 DW (Sh)	Hydroponic	Shoot biomass was more impacted than roots, there was chlorosis, an organ-dependent influence on nutrient concentrations, increased SO42 transporter activity and there was a higher amount of non-protein thiols.	Stuiver et al. (2014)
	5–10 µM	21.7–61.8 µmol g−1 DW (R)	Hydroponic	a decline in biomass; an increase in roots rather than shoots in cysteine, thiols, glucosinolates and transcript levels of CYP79B3, CYP83B1, ATPS and APR (genes catalysing glucosinolate production); increased content of SO42 in shoots	Aghajanzadeh et al. (2020)
Citrus reticulata Blanco	20 µM		Pot	Retardation of growth, defoliation, lower photosynthesis and transpiration, smaller stomata, disorder in the mitochondrial membranes, random distribution of cristae, decreased content of phenols, AsA, sugars and starches and oxidative stress; more active antioxidant enzymes	Subba et al. (2014)
Cajanus cajan (L) Millsp.	500 and 1000 mg kg−1		Pot	Reduced nodulation, nitrogen fixation, chlorophyll, and yield; disrupted mineral nutrition; increased oxidative stress; and an increase in antioxidant enzymatic and non-enzymatic defences	Garg and Kaur (2012, 2013a,b) Kaur and Garg (2017); Garg and Singh (2018)
Hibiscus esculentus cv. Hassawi	20–40 Mm		Pot	Decreased non-enzymatic antioxidants and increased lipid peroxidation, CAT, APOX, DHAR and GR activity.	Youssef and Azooz (2013)
Hordeum vulgare	500–4000 mg kg−1	800–2800 mg kg−1 (R) 200–300 mg kg−1 (Sh)	Pot	Negatively impacted the total biomass, dry weight of the roots and leaves and length of the roots and leaves.	Kherbani et al. (2015)
Lactuca sativa L. var. *longifolia*	100 mM	674.5 mg kg−1 (R)	Pot with peat-based substrate	decreased biomass; an unbalanced nutrition intake; The triggering of polyamines and polyamine conjugates	Rouphaelet al. (2016)
	100 mM	468 mg kg−1 (L)	Pot	Proline, hydroxycinnamic acids, ascorbate, sesquiterpene lactones and terpenoids biosynthesis; up-accumulation of HSP70 and HSP90; down-regulation of MatK (a protein involved in chloroplast development) and MYC2 (a transcription factor associated with ABA); up-accumulation of PAE and down-accumulation of CesA (enzymes of lignin biosynthesis); increased glycolytic supply of energy substrates; hormonal instability	Lucini and Bernardo (2015)

Lactuca sativa cv. Philipus	0.5 mM	34.95 ± 0.376 mg g−1 DW (Sh) 218.4 ± 35.7 mg g−1 DW (R)	Hydroponic	Proline and glycine betaine levels have increased whereas biomass has decreased	Paradisone et al. (2015)
Brassica oleracea cv. Bronco	0.5 mM	42.54 ± 0.234 mg g−1 DW (Sh) 382.4 ± 60.6 mg g−1 DW (R)	Hydroponic	Decrease in proline and glycine betaine levels; increase in GABA	
Lactuca sativa cv. Philipus	0.5 mM	34,949 ± 376 μg g−1 DW) (R) 218.4 ± 35.7 μg g−1 DW) (Sh)	Hydroponic	Decreased biomass, increased levels of anion superoxide, H2O2 and MDA, increased LOX activity, and increases in SAT, ECS, total GSH, APX, MDHRand GR, with a decline in DHAR.	Barrameda-Medina et al. (2014)
Brassica oleracea cv. Bronco	0.5 mM	42,540 ± 234 μg g−1 DW) (R) 382.4 ± 60.6 μg g−1 DW) (Sh)	Hydroponic	Reduced biomass; increased H2O2 and anion superoxide levels; decreased LOX, MDA and SAT; increased ECS, total GSH, APX and GR; and decreased MDHR and DHAR activities	
Oryza sativa L. cv. TY-167 (Zn-resistant) and cv. FYY-326 (Zn-sensitive)	2 μM	TY-167: 2500 μg g−1 DW (R) 7000 μg g−1 DW (L) FYY-326: 2600 μg g−1 DW (R) 6000 μg g−1 DW (L)	Hydroponic	genotype-dependent variations in growth, MDA and H2O2 levels, total root surface area, root length, chlorosis and the integrity of the root plasma membrane; antioxidant enzyme activities	Song et al. (2011)
Phaseolus vulgaris L	50 ppm	var. Sel 9: 440 μg g−1 DW (L)	Hydroponic	Chlorosis, a decrease in biomass, a rise in MDA, H2O2, proline and AsA levels, as well as increased SOD, POX and PPO activity are all seen.	Michael and Krishnaswamy (2011)
	150–500 μM		Hydroponic	Decrease dry matter, fresh weights, leaf area, RWC and increase in total protein content	Nejad et al. (2014)
Solanum lycopersicum	cv. PKM – 1: 150–250 mg kg−1		Pot	Reduced root length, shoot length, leaf area, root and shoot dry weights	Vijayarengan and Mahalakshmi (2013)
	50 μM	var. Arka Alok: 100 μg g−1 DW (R) 140 μg g−1 DW (L) Var. Arka Vikas: 110 μg g−1 DW (R) 120 μg g−1 DW (L)	Hydroponic	Reduction in shoot dry weight, total plant biomass and total chlorophyll content	Pavithra et al. (2016)
	50–150 μM	251–495 μg g−1 DW (R) 65.43-92.36 μg g−1 DW (Sh)	Hydroponic	Low total chlorophyll content, a decline in the rate of photosynthetic CO_2 fixation, a greater impact on shoot growth than on root growth, and an increase in MDA levels	Cherif et al. (2010)
	250–500 μM	23,000–44,000 μg g−1 DW (R)	Hydroponic	Chlorophyll levels decrease, CAT and APOX activities rise, GST activity declines and roots accumulate more metal than leaves do.	Sbartai et al. (2011)

		5000–10,000 μg g–1 DW (L)			
Triticum aestivum L	900 mg kg−1	160 mg kg−1 (Sh) 180 mg kg−1 (R)	Pot	decreased biomass, altered macro- and micronutrients, reduced chlorophyll and total sugar content and altered macro- and micronutrients; increase in proline and antioxidative enzyme activity (SOD, CAT, POX, APX)	Kanwal et al. (2016)
	0.5–3 mM	465.65-1129 μg g–1DW (R) 292.03–1124.45 μg g–1 DW (Sh)	Hydroponic	Reduced chlorophyll, oxidative stress, varying responses of antioxidant enzymes, increased soluble sugars and OAT but decreased GK activity and increased proline are all seen.	Li et al. (2013a)
	300 mg L−1	5,553.1±576.8 mg kg−1 (Sh) 32,205.2±8928.4 mg kg−1 (R)	Hydroponic	Ultra structural changes in the organelles of roots and mesophyll cells, decreased biomass, water content and mitotic index and an imbalance in nutrients	Glinska et al. (2016)
Triticum durum	600 μM		Hydroponic	Leaf necrosis; decrease in relative growth rate, net photosynthetic rate, photosynthetic pigments and electron transport processes; inactivation of photosystem II reaction centres	Paunov et al. (2018)
Vigna unguiculata	6-20 mg L−1	112.51–142.70 mg plant−1	Hydroponic	Decline in growth parameters (dry weight, number of roots, root length) and nutrient uptake	El-Kafafi and Rizk (2013)
Vitis vinifera	60–180 mg kg−1	320–490 mg kg−1 (Sh) 1500–1700 mg kg−1 (R)	Pot	Reduced plant growth; decreased pigments and photosynthetic efficiency; diminished SOD and POD activities in leaves	Tiecher et al. (2017)
	14–35 mM	3225.75–7553.35 μg g−1 DW (R) 6880.56–7224.84 μg g−1 DW (St) 1007.54–2982.97 μg g−1 DW (L)	Pot	Chlorosis; necrosis; suppression in daily height growth, daily stem diameter variation; alterations in nutrient contents; decrease in POD, CAT and PPO activities; enhanced ABA and MDA levels	Yang et al. (2011)
Zea mays	400 and 600 μM		Hydroponic	Increased EC, MDA, H2O2 contents and non-protein thiols; activities of antioxidant enzymes also increased	Hosseini and Poorakbar (2013)
	50 μM	150 mg g−1 DW (R) 180 mg g−1 DW (Sh)	Pot	Reduced plant height, leaf area and dry weight; roots that turned yellow-brown; altered root distribution; lessened levels of chlorophyll and total soluble protein; and increased levels of antioxidant enzyme activity and metabolites.	Islam et al. (2014)
	50–750 mg kg−1	Light soils: 94.97–1300.75 mg kg−1 DW (Sh) 288.31–2493.33 mg kg−1 (R) Heavy soils: 64.10–624.40 mg kg−1 (Sh) 155.75–1743.94 mg kg−1 (R)	Pot (light and heavy soils)	Greater phytotoxicity and Phyto availability in light soils compared to heavy soils; higher metal concentration in roots compared to aerial parts; higher bioaccumulation coefficient in roots compared to above ground portions	Baran (2012)

Understanding the genetic and molecular pathways of phytoremediation is essential for using plants to treat contaminated sites (Antoniadis et al., 2017; Wang et al., 2020). Depending on their oxidation levels, heavy metals can be highly reactive, which can cause issues in plant cells from a variety of perspectives (Rai et al., 2020). The diverse effects of heavy metals on plant cells and molecules include adjustments to their physiological cycles, including the inactivation of enzymes and protein denaturation, blocking the functional groups of molecules crucial for metabolism, removing or substituting essential metal ions from biomolecules and compromising membrane integrity. According to Manoj et al. (2020), these adjustments support changes in enzyme activity, suppression of photosynthesis and plant metabolism.

Additionally, heavy metals upset the balance of oxidation-reduction by restoring the generation of ROS and free radicals. In fact, even at low concentrations, heavy metals can affect a plant's physiological function (Sobariu et al., 2017). The uptake of metals by plants and their ascent up the food chain pose a major threat to the health of people, animals and plants.

One of the bioremediation methods is phytoremediation, particularly the botanical method, in which plants effectively eliminate poisonous heavy metals by absorbing them from contaminated soil. The heavy metals are transformed into non-toxic forms after absorption and either degraded or transferred to various areas of the plant where they accumulate on their own (Ahemad, 2019 and Jeevanantham et al., 2019). According to Niu et al. (2021); Pasricha et al. (2021) and Sharma et al. (2021) and others, accumulators and hyperaccumulators are plants that can accumulate hazardous heavy metals in their components, particularly roots and shoots. According to Reeves et al. (2017), 721 plant species from the Phyllanthaceae and Brassicaceae families have been identified as hyperaccumulators thus far. The heavy metals are transported and translocated from the soil to various areas of the plants via transporters or carriers in the plasma membrane of plant cells. The heavy metals are transferred and translocated from the soil to various areas of the plants by transporters or carriers in the plasma membrane of plant cells.

Heavy metals are uptaken from the soil by the transporters in the root cell, where they join forces with the chelators to produce a complex that allows them to be translocated into the plant's shoot. Even while a higher concentration of heavy metals is harmful to plants as well, once they enter the aerial system of a plant, they cause toxicity to its growth and metabolic processes. In hyperaccumulator plants, the important nutrition carrier is not the same as the heavy metal transporters or carriers. A significant amount of heavy metals accumulate in the hyperaccumulators' root or shoot systems (Guo et al., 2020 and Cui et al., 2021). Because the heavy metals were kept from entering the plants' aerial section, they did not interfere with or disrupt the basic mechanisms of the plant, such as growth and development (Shrivastava et al., 2019).

The ability to transmit heavy metals from the root to various plant components (shoot and leaves) at a higher metal uptake rate, as well as a higher metal tolerance, are the defining traits of hyperaccumulator plants. The amount of heavy metals that hyperaccumulator plants can absorb and accumulate depends on a number of variables, including soil pH, organic matter content, cation-exchange capacity, microbial community in the rhizosphere, soil type and type of heavy metal present in soil (Jung, 2008; Tangahu et al., 2011 and Chibuike and Obiora, 2014). Despite the fact that once the heavy metals have been removed from the soil, the hyperaccumulator plants detoxify or accumulate them.

Hyperaccumulator plants have some limitations, such as the fact that they are metal-specific, which means they do not accumulate all the heavy metals in the soil, that they can grow slowly and produce less biomass than other plants, and that they are typically uncommon and only occur in remote areas (Rascio and Navari-Izzo, 2011a; 2011b and Memon, 2016). If the quantity of heavy metals in the soil is excessive, this could interfere with the movement of important nutrients. They must be immobilized with the metal-chelators in the soil solution to avoid competition for nutrient delivery. Metal ions were immobilized by metal-chelating substances, including rhizosphere bacteria, several low molecular weight organic acids and phytosiderophores (Leitenmaier and Küpper, 2013).

Both the absorption of metals and the detoxification procedure are significantly influenced by the bacteria in the rhizosphere. The 1-aminocyclopropane-1-carboxylate (ACC) deaminase and indole acetic acid (IAA) are two examples of the metabolic products (enzymes and acids) that plant microflora produce in the rhizosphere to shield plants from abiotic stressors like salinity, antibiotics and heavy metal pollution and to enhance nutrient uptake. They can lessen the availability of heavy metals in soil, especially in the rhizosphere, by oxido-reduction reaction, adsorption, matrix formationand other mechanisms (Singh et al., 2018; Wang et al., 2019 and Liu et al., 2020).

The rhizosphere's microbiota has a significant impact on both the metal uptake and the detoxification process. In the rhizosphere, plant microflora creates a variety of metabolic products (enzymes and acids) like 1-aminocyclopropane-1-carboxylate (ACC) deaminase and indole acetic acid (IAA) to protect plants from abiotic stressors like salinity, antibiotics and heavy metal pollution and to improve nutrient uptake. Through oxido-reduction reaction, adsorption, matrix formation and other mechanisms, they can reduce the availability of heavy metals in soil, particularly in the rhizosphere (Singh et al., 2018; Wang et al., 2019 and Liu et al., 2020).

This article briefly addressed a biological technique for decontaminating soil that has been contaminated with heavy metals. This review discusses the harmful consequences of heavy metals on the environment and living beings. In-depth research is done on the removal of heavy metal from soil utilizing a variety of biological remediation techniques, including phytoremediation, bioremediation, cyanoremediation and mycoremediation. The primary focus of the current work is on specialized phytoremediation abilities as a critical tool for the removal of heavy metals that move and accumulate in plant parts like roots, shoots and leaves. Further research was conducted on the capacity of plants to withstand larger concentrations of heavy metals, as well as on how they respond to heavy metal accumulation and the many mechanisms at play.

- **The risks posed by heavy metals**

Heavy metal-induced soil pollution in the agricultural sector has developed into a significant ecological concern due to its harmful biological impacts. These hazardous contaminants are referred to as soil toxins due to their widespread availability and their severe and enduring detrimental effects on plants growing in such polluted soils. Each heavy metal has a different deleterious effect on plants (Rehman et al., 2020 and Clemens & Ma, 2016). prolonged contact with extremely dangerous cadmium metal levels.

- **Biological remediation methods**

Hazardous heavy metals in plants typically have harmful side effects in the majority of countries. Heavy metal discharges into the environment, whether indirect or direct, can have an effect on the food chain by affecting productivity, yield and food quality as well as soil quality. Remediation is the process of removing dangerous heavy metals from a contaminated or polluted environment. Other typical clean-up methods include dredging, which removes toxins and incinerating organic waste.

- **Transportation of heavy metals in plants**

To cope with the stress brought on by the accumulation of heavy metals, plants create biochemical systems in their bodies. Apoptosis is triggered by ROS, which are formed as a result of elevated soil metal ion concentration. The plants produce a few built-in defense mechanisms with the help of metal transporters or carriers, including chelation, restriction in metal absorption, the expulsion of metal from plant, compartmentalization, etc. (Page & Feller, 2015).

- **An accumulation of heavy metals in plants**

The harmful effects of heavy metals might present themselves in many ways depending on how they build up in plant cells. Metal carriers play a significant role in the transportation of heavy metals in plant cells. There are several different types of metal carriers in the plasma membrane. Because they are specific to the substrate, heavy metals are transported through the plasma membrane of plant cells alongside other essential nutrients (Sun et al., 2016).

- **Plant tolerance to heavy metal accumulation and its effects**

Heavy metal build-up alters the physiological and metabolic processes of plants. Although each heavy metal behaves differently in the plant, they all have negative impacts. The plant undergoes growth retardation, necrosis, chlorosis and a decrease in germination rate as a result of structural and molecular alterations heavy metals cause in plant cells (Villiers et al., 2011 and Khan et al., 2021).

- **The process by which plants can tolerate metal**

The molecular and physiological networks work together to regulate how tolerant plants are to heavy metals. Developing plants as the substrate for phytoremediation requires a detailed understanding of these interconnected processes. There are several heavy metal tolerance mechanisms displayed by different plants. Occasionally, a single plant may have several tolerance mechanisms.

- **Improvements to the plant's metal tolerance system**

Plants have in-built biochemical and molecular mechanisms for surviving high metal concentrations, depending on the growth conditions, such as soil type and water availability. Imtiaz et al. (2016) discovered that while the plant develops and provides yield while under stress, the nutritional value of edible plants is most severely compromised. In order to meet demand and maintain nutritional value, it is required to improve the mechanism of heavy metal tolerance in plants.

Conclusion and Prospective Future

The presence of toxic heavy metals in the ecosystem poses significant risks to humans, plants and animals. These elements are major contributors to substantial ecological contamination driven by human activities and population growth. Research indicates that utilizing high biomass-producing plants can enhance the effectiveness of phytoremediation, a technique that has seen increased demand in recent years.

Integrating high biomass-producing plants in phytoremediation strategies presents a promising approach to mitigating heavy metal contamination in the environment. By leveraging the natural capabilities of these plants to absorb and accumulate toxic metals, we can significantly reduce the ecological footprint of industrial and agricultural activities. Continued research and innovation in this field will be crucial for developing more efficient and sustainable phytoremediation techniques, leading to healthier ecosystems and improved public health outcomes.

Furthermore, fostering collaboration between scientists, policymakers and industry stakeholders will be essential in promoting the widespread adoption and implementation of phytoremediation practices. Such collaborative efforts will ensure the development of comprehensive strategies that address the challenges of heavy metal contamination and contribute to the restoration and preservation of our ecosystems for future generations.

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