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Microbe-mediated regulation in zinc-contaminated soils: the synergistic role of hyperaccumulator plants and zinc-tolerant rhizobacteria

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Zinc (Zn) contamination in soils is a serious environmental issue with adverse impacts on plant growth and crop productivity. High concentrations of Zn can induce toxicity in plants, leading to reduced growth, impaired nutrient uptake, and oxidative stress. However, some plants can resist and even collect Zn in their tissues, known as hyperaccumulators. Further, the utilization of rhizobacteria as a sustainable approach for mitigating Zn stress in plants and remediating Zn-contaminated soils has gained significant attention. The use of these hyperaccumulator plants and rhizobacteria can help overcome soil Zn contamination and improve soil fertility through phytostabilization, phytoextraction, and phytomining. Furthermore, the ability of rhizobacteria to enhance plant growth, alleviate Zn toxicity symptoms, and improve nutrient uptake efficiency makes them valuable allies in sustainable agriculture and soil remediation practices. The present review provides insights into the sources and impacts of Zn contamination, the noxious effects on plants, the mechanism of Zn hyperaccumulator plants, and the potential of rhizobacteria in alleviating Zn stress and remediating Zn contaminated soils.

KEYWORDS

hyperaccumulators plant, Zn-tolerant rhizobacteria, phytoextraction, phytostabilization, photosynthesis

1 Introduction

Soil contamination due to the presence of heavy metals has emerged as a significant environmental issue that affects not only the soil's health but also has implications for human health and the overall ecological balance (Okerefor et al., 2020; Alengebawy et al., 2021; Rajendran et al., 2022). Zinc (Zn) is one such heavy metal that is present in the environment naturally, but human activities such as industrialization, use of agrochemicals, mining, and smelting of metals can cause its excessive accumulation in soils (Singh et al., 2018; Kumari and Mishra, 2021). As Zn is an essential micronutrient for plant growth, it is present in both organic and inorganic forms in soil. However, its excessive metal concentration negatively impacts soil health, growth, and yield of crops. It also poses a threat to human health (Goyal et al., 2020).

The excessive accumulation of Zn in the soil leads to various issues in plants, such as toxicity, lower yield, less productivity, reduced cellular division, damage to cell membranes, reduced photosynthesis, stunted root development, and nutrient absorption, causing decreased crop productivity, and crop damage (Balafrej et al., 2020; Kaur and Garg, 2021). Additionally, Zn accumulation in edible plant parts can pose significant health hazards to humans upon consumption, causing grave health implications like nervous system dysfunction, gastrointestinal distress, nausea, and impaired immune function (Anuoluwa et al., 2021; Rahman et al., 2022). Zn over-concentration often leads to a reduced population of soil microbes that play a crucial role in soil nutrient cycling and plant-immune systems (Okerefor et al., 2020).

Costly and less effective traditional methods, which also have negative environmental impacts, have led to the need for sustainable and eco-friendly methods of Zn remediation (Kumar V. et al., 2022a; Sarker et al., 2023). Hyperaccumulator plants provide a cost-effective and environmentally sustainable solution because of their Zn toleration potential in their tissues (Li et al., 2019; Awa and Hadibarata, 2020). Balafrej et al. (2020) analyzed the characteristics and diversity of Zn hyperaccumulator plants and their possible applications in environmental remediation. Some species reported in the literature in Zn bioremediation include *Hydrocotyle umbellata* L., *Juncus effusus* L., *Carex buechananii* Berggr., *Salix viminalis* L., *Salix fragilis* L., and *Arabidopsis halleri* (L.) O'Kane & Al-Shehbaz (Archer et al., 2004; Rahman et al., 2022; Meers et al., 2007; Ladislav et al., 2014).

On the other side, rhizobacteria play an important role in the growth of plants and they are tolerant to heavy metals, including Zn, thus are valuable in Zn-contaminated soil remediation (Gavrilescu, 2022; Mondal et al., 2023). Interestingly, these rhizobacteria influence soil nutrient cycling and heavy metal availability, leading to improved nutrient absorption, reduced uptake, and translocation of heavy metals in plant systems (Kumar S. et al., 2022; Prasad et al., 2021). Several studies have examined the role of rhizobacteria in remediating Zn-contaminated soil. Liu et al. (2022) studied the potential of *Bacillus* sp. ZC3-2-1 in improving plant quality (yield and growth) in Zn and Cd-Zn contaminated soils, respectively, while Du et al. (2022) exhibited the use of *Rhodococcus qingshengii* in decontamination of heavy metals from soil via phytoremediation.

The possibility of microbial consortia in the rhizoremediation of Zn-contaminated water was also studied by Khan et al. in 2021

(Hussain et al., 2022). *Aspergillus brasiliensis*, *Penicillium citrinum*, and *Spirulina maxima* reduce the amount of Zn in contaminated water, while *Pseudomonas veronii*, *Bacillus licheniformis*, and *Escherichia coli* also increase the uptake of Zn by plants (Basha and Rajaganesh, 2014). Zn uptake and accumulation methods by plants were examined by Thakare et al. (2020), as well as the function of rhizobacteria in boosting the effectiveness of phytoremediation techniques.

The types of contaminants that commonly used macroplant species can tolerate, in addition to obstacles including slow growth, low biomass, a predilection for certain metals, and variable environmental needs, restrict their potential for phytoremediation. Adopting interdisciplinary approaches like genetic engineering and thorough biological system analysis (multi-omics) has the potential to produce hyperaccumulating plants that can produce substantial amounts of biomass in a variety of environmental settings (Moradpour and Abdulah, 2020).

It's intriguing to see how rhizobacteria and hyperaccumulator plants can work together to promote Zn uptake in plant systems, enabling effective remediation of soil contaminated with Zn. This review discusses soil Zn contamination, its consequences on plant health, and potential soil remediation strategies using rhizobacteria and Zn hyperaccumulator plants. It looks into the effects of these biological techniques for remediating contaminated soils as well as how rhizobacteria and hyperaccumulator plants help lower the concentrations of Zn in polluted soils.

2 Literature search and selection

To prepare this review, a comprehensive literature search has been conducted using electronic databases, including Web of Science, Scopus, PubMed, and Google Scholar, focusing on studies published from 2000 to 2024. Search keywords included combinations of terms such as "zinc hyperaccumulator," "phytoremediation," "rhizoremediation," "heavy metal tolerance," and "plant-microbe interactions." After screening for relevance and quality, a total of ~ 200 articles were selected for inclusion in this review, covering Zn accumulation, remediation mechanisms, and plant or microbial involvement. Additional studies were identified through reference lists of key papers. Only peer-reviewed articles published in English were included. This approach ensured a systematic and comprehensive review of the current knowledge on Zn bioremediation using plants and rhizospheric microbes.

3 Zinc contamination in soil

Numerous factors, such as natural weathering and geological processes, mining and smelting activities, industrial pollutants, and agricultural practices, have an impact on the concentration and composition of Zn in soil. Both natural and anthropogenic processes, including smelting and mining operations, galvanised structures, fertilizers, animal manures, sewage sludge, vehicle exhaust, and tyre wear, introduce Zn into the agro-ecosystem

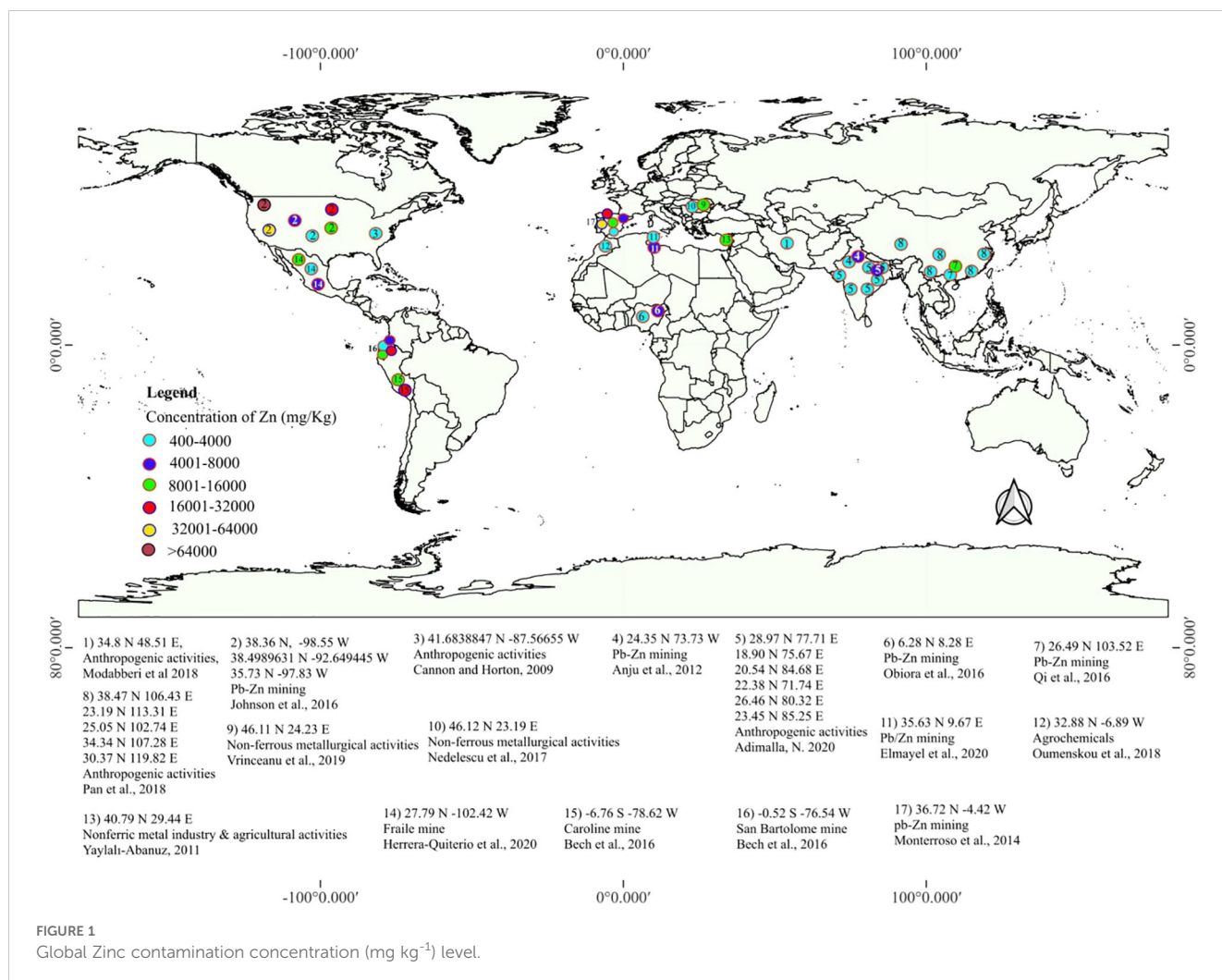
(Figure 1). According to Rani et al. (2023a), the usual range of Zn contents in uncontaminated soil is 5 to 50 mg kg⁻¹. However, soil Zn concentrations can reach as high as 5000 mg kg⁻¹, and the soil is considered Zn-contaminated soil (Rani et al., 2023b).

Zn contamination has been a challenging issue in several nations throughout the world, including Australia, China, India, and the United States (Ji et al., 2019; Rahman et al., 2021; Sankararamakrishnan et al., 2019). In Australia, overuse of Zn-containing fertilizers in dry land agriculture regions has resulted in soil contamination, poor soil health, and decreased crop productivity (Waldron et al., 2017). Extensive Zn mining activities in China and the United States, on the other hand, have resulted in widespread pollution of agricultural land (Li et al., 2021). India is also dealing with Zn contamination difficulties, notably in urban and industrial regions, as a result of inappropriate waste disposal practices and uncontrolled utilization of Zn pesticides and fertilisers (Sankararamakrishnan et al., 2019).

Zn is found naturally in rocks and minerals, and as these geological formations weather and erode, Zn is released into the environment (Alloway, 2012). Zn contamination can also be caused by geological events such as volcanic eruptions and tectonic

movements. Furthermore, sedimentation and erosion processes can move Zn-containing minerals, dispersing them in soils and potentially causing localized pollution. Further human activities, including mining and smelting, the use of agrochemicals, Industrial effluents, improper waste disposal, and atmospheric deposition, also contribute to Zn contamination (Cai and Li, 2022).

While Zn is not hazardous to mammals, its contamination in conjunction with toxic metals, mainly Pb and Cd poses considerable environmental concerns (Alengebawey et al., 2021). Hyperaccumulator plants are used in phytoremediation, a potential bioremediation technique, to help plants tolerate high amounts of Zn (Balafrej et al., 2020; Yaashikaa et al., 2022). Additionally, phytoremediation has the advantage of being adaptable to large areas of polluted land, giving it a workable solution for problems associated with widespread Zn contamination. Zn-tolerant rhizobacteria are becoming more and more popular as a long-term remedy for lowering Zn stress in plants and cleaning up Zn-contaminated soils in addition to phytoremediation (Okerefor et al., 2020). Rhizobacteria and hyperaccumulator plants work synergistically to reduce soil Zn contamination by increasing the effectiveness of Zn phytoremediation.



4 Zinc toxicity in plants

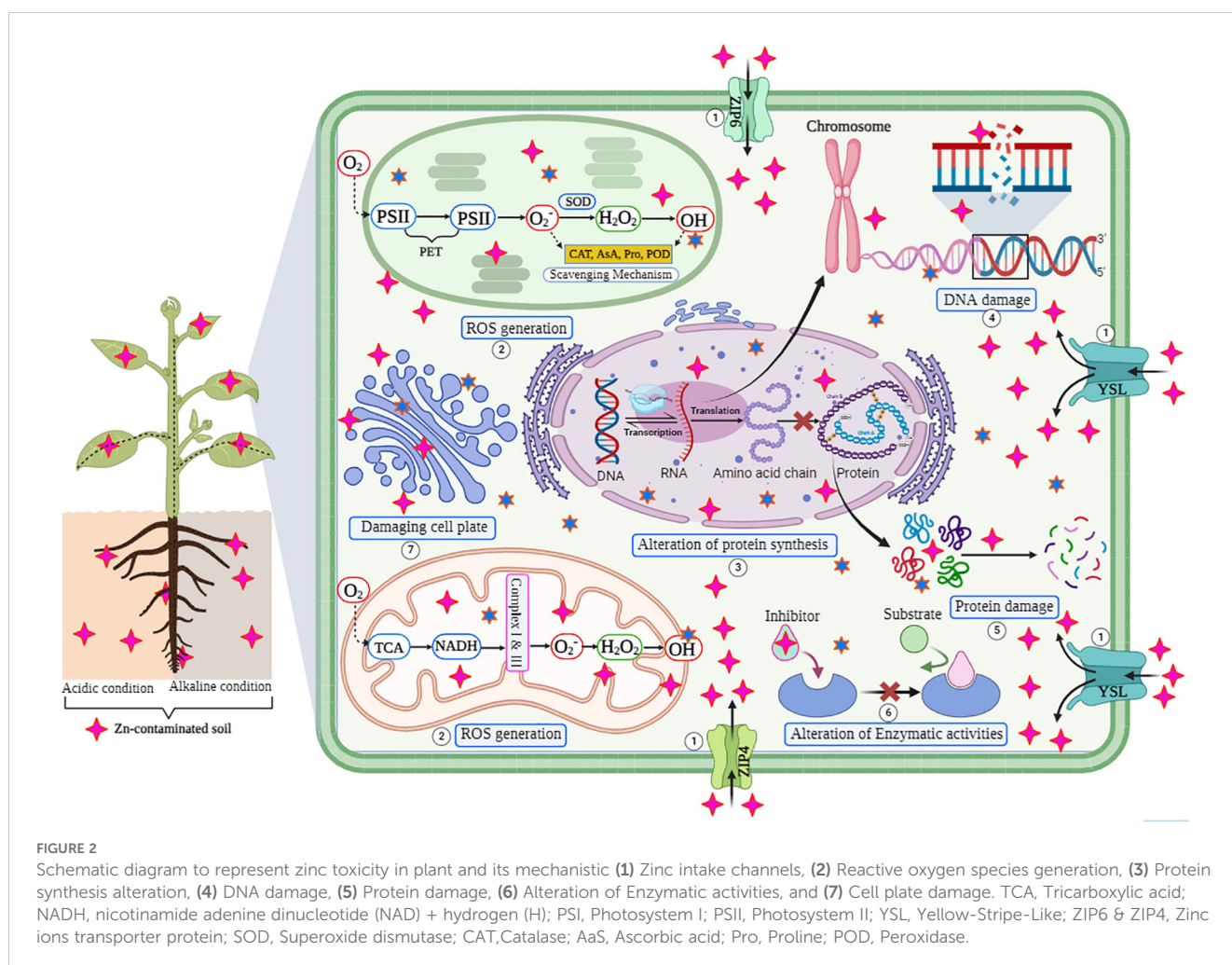
The total soil Zn concentration from pollution might rise to 3000 mg kg⁻¹ of dry soil (Kaur and Garg, 2021). This excessive amount of zinc in the soil has the potential to be poisonous, which would have a negative impact on plant development, photosynthesis, mineral nutrition, and antioxidant defense (Gjorgieva Ackova, 2018). Zn deficiency, on the other hand, happens when the soil doesn't have enough Zn for healthy plant growth. The optimal range of Zn in plant tissues is typically between 30 and 200 µg Zn g⁻¹ dry weight (Kaur and Garg, 2021). Deviations from this range can lead to either deficiency or toxicity symptoms (Figure 2). As per the figure, zinc (Zn) toxicity affects plants in different ways. Excessive Zn taken up through transporters causes it to build up in cells. High levels of Zn lead to the overproduction of reactive oxygen species (ROS) in chloroplasts, mitochondria, and the endoplasmic reticulum (ER), which creates oxidative stress. This can damage DNA, cause proteins to misfold, inhibit enzymes, and disrupt cell structures. Antioxidant defense systems, including catalase (CAT), ascorbic acid (AsA), proline (Pro), and peroxidase (POD), partially reduce these toxic effects. Therefore, Zn deficiency is a well-known issue affecting crop productivity; understanding Zn toxicity is also crucial for comprehensive nutrient management and sustainable agriculture.

4.1 Toxic effects of excessive Zn on growth

The impact of high Zn concentrations on seed germination varies according to Zn dose and plant species. While low Zn concentrations may have minimal effects on germination, higher levels can inhibit or delay the process. For instance, plant species like *Pinus sylvestris* and *Macrotyloma uniflorum* may exhibit delayed germination without significant inhibition. However, *Vigna unguiculata*, *Cassia angustifolia*, and *Glycine max* show reduced germination rates under high Zn concentrations (Balafrej et al., 2020).

Beyond germination, excess Zn significantly disrupts plant growth and development through multiple biochemical and physiological mechanisms. Elevated Zn concentrations interfere with root system architecture by reducing primary root length and suppressing cell division in the meristematic zone, thereby inhibiting root elongation (Małkowski et al., 2019). This reduction in root-specific surface area restricts water and nutrient uptake, further compromising plant growth. In species such as *Triticum aestivum*, *Jatropha curcas*, and *Citrus reticulata* Blanco, root development is severely impaired under Zn stress (Balafrej et al., 2020; dos Santos et al., 2020).

At the biochemical level, excess Zn disrupts membrane integrity and enzyme activities. High Zn induces the overproduction of



reactive oxygen species (ROS), such as hydrogen peroxide and superoxide radicals, which damage lipids, proteins, and nucleic acids, leading to oxidative stress. This oxidative imbalance interferes with cell elongation and expansion in both roots and shoots. Moreover, Zn toxicity competes with and displaces essential cations like Fe, Mg, and Ca from their binding sites, thereby inhibiting vital processes such as chlorophyll biosynthesis, photosynthesis, and cell wall stabilization. Inhibition of auxin metabolism and impairment of antioxidant defense enzymes (e.g., SOD, CAT, and POD) under Zn stress further exacerbate growth retardation.

Consequently, growth inhibition and reduced elongation of shoots and roots have been reported in *Phaseolus mungo*, *Bacopa monnieri*, and several grass species under high Zn exposure (Sidhu, 2016). Collectively, these findings indicate that Zn-induced growth suppression is not merely structural but also involves disruption of hormonal balance, oxidative homeostasis, and nutrient assimilation, ultimately compromising overall plant performance.

4.2 Photosynthesis disruption due to Zn excess

High Zn concentrations in plants can have adverse effects on photosynthesis, with the extent of damage varying among different plant species. Elevated Zn levels may limit stomatal conductance, reducing carbon dioxide fixation and affecting photosynthesis. Furthermore, the accumulation of Zn in mesophyll tissues can influence the size and number of stomatal cells. Increased Zn concentrations have been shown to retard the potential of photosystem II (PSII), leading to impaired plant growth and chlorosis (Balafrej et al., 2020). *Solanum lycopersicum*, *Halimione portulacoides*, *Populus*, and *Brassica rapa* are some examples of plants that have exhibited impaired photosynthetic activity due to excessive levels of Zn (Tiecher et al., 2016; Balafrej et al., 2020).

In *Populus* spp., hydroponic exposure to about 1 mM Zn can lower Fv/Fm and change chloroplast structure within days. This shows that PSII is impaired with relatively low ionic levels in solution culture (Neri et al., 2024). In *Brassica juncea* grown in soils with added Zn, approximately 200 mg Zn kg⁻¹ has been shown to reduce Fv/Fm and gas-exchange rates. This matches the PSII inhibition seen under typical field conditions, with thresholds varying based on soil chemistry and cultivar (Iqbal et al., 2024).

4.3 Induction of oxidative stress by excessive zinc

Excess Zn in plants can trigger oxidative stress, followed by the formation of reactive oxygen species (ROS). Such ROS cause oxidative damage to plants, affecting species like *Chenopodium murale* L., *Plantago major* L., *Carthamus tinctorius* L., and others (Zoufan et al., 2018; Goodarzi et al., 2020). Despite being a non-redox metal, Zn can indirectly promote ROS generation by stimulating ROS-producing enzymes or inhibiting enzyme activities (Figure 2). Plants respond to Zn stress by accumulating

proline, which has a major role in osmoregulation and protecting enzymes against denaturation. Proline helps reduce metal-induced oxidative stress by directly detoxifying ROS without relying on antioxidant enzymes (Balafrej et al., 2020). Additionally, plants produce various antioxidant enzymes, including peroxidase, superoxide dismutase, catalase, and ascorbate peroxidase to mitigate the effects of Zn-induced oxidative stress (Chen et al., 2017; Balafrej et al., 2020).

In addressing the challenges of soil Zn contamination and plant Zn toxicity, the potential of hyperaccumulator plants can be harnessed to remediate Zn-contaminated soils and mitigate the toxic effects of Zn toxicity in plants.

5 Hyperaccumulator plants: nature's metal detoxifiers for soil Zn contamination

Plants vary in their ability to tolerate and accumulate heavy metals and are generally classified into three groups. Non-accumulators restrict metal uptake or transport, keeping concentrations in shoots very low (<100 mg kg⁻¹ Zn). Accumulators store moderate metal levels in their shoots, above non-accumulators but below hyperaccumulator thresholds (up to 1000–3000 mg kg⁻¹ Zn). Hyperaccumulators are exceptional species that can amass extremely high concentrations in aboveground tissues, often exceeding 1% of dry weight (>3000 mg kg⁻¹ Zn).

Certain plant species have developed strategies to deal with high metal concentrations in soil, earning them the moniker “hyperaccumulators.” These plants can accumulate unusually high levels of metals in their aboveground parts, exceeding 1% of their dry weight, such as Zn, Ni, Mn, and Pb. Around 450 plant species have been identified as heavy metal hyperaccumulators (dos Santos et al., 2020). Hyperaccumulators primarily accumulate metals in their shoots, particularly the leaves. For instance, Zn hyperaccumulators exhibit a threshold of > 3000 mg kg⁻¹ dry weight (Table 1), with 21 species from 9 families and 12 genera recognized as Zn hyperaccumulators (Balafrej et al., 2020). The most widely studied Zn-tolerant plants include *Noccaea caerulescens* from Belgium and France, *Arabidopsis halleri* from France, Poland, Germany, and Italy. *Sedum alfredii* from China, *Minuartia verna* from Asia and the UK, and *Anthyllis vulneraria* from France. These plants are recognized for their ability to accumulate metals and withstand harsh conditions (Table 1).

Hyperaccumulator plants are not evenly distributed across all families but are particularly concentrated in certain groups. For Zn hyperaccumulation, the most well-studied species belong to the Brassicaceae family (e.g., *Noccaea caerulescens* and *Arabidopsis halleri*). Other families reported to include hyperaccumulators are Violaceae, Asteraceae, Caryophyllaceae, and Phyllanthaceae. Importantly, their distribution also depends on geography and climate. For example, most Zn hyperaccumulators described from Europe and North America belong to temperate families such as Brassicaceae, whereas tropical regions (e.g., Southeast Asia and Africa) report Zn hyperaccumulation in members of Phyllanthaceae

TABLE 1 List of Zn hyperaccumulator plants (>10,000 ppm in leaf dry weight).

Plant family	Genera	Location	References
Brassicaceae	<i>Arabis paniculata</i>	Yannan province, China	Tang et al., 2009
	<i>Arabs alpine</i>	Yunnan Province, China	Li et al., 2019
	<i>Noccaea caerulescens</i>	Belgium, France; western europe	Seregin et al., 2015; Sirguey et al., 2017
	<i>Noccaekakovatsii</i>	Balkans, southeast europe	Jakovljević et al., 2022
	<i>Arabis gemmifera</i>	Central Europe	Šrámková et al., 2019
	<i>Arabidopsis helleri</i>	Northern France, Poland, Germany and Italy	Claire-Lise and Nathalie, 2012
	<i>Noccaeaeburneosa</i>	Endemic to Turkey	Koch and German (2013).
	<i>Noccaecalaminare</i>	Endemic to Belgium	Koch and German (2013)
	<i>Noccaeaalpestre</i>	Europe	Koch and German (2013).
	<i>Noccaeastenopterum</i>	Endemic to Turkey	Koch and German (2013).
Caryophyllaceae	<i>Minuartia verna</i> ,	China, India, Nepal, Pakistan, Bhutan, Myanmar, united kingdom	Hodson, 2012
Crassulaceae	<i>Sedum alfredii</i>	China	Yang et al., 2002, 2004
	<i>Sedum plumbizincicola</i>	China	Wu et al., 2013
Dichapetalaceae	<i>Dichapetalumgelonioides</i> subsp. <i>Tuberculatum</i>	Sumatra, Indonesia	Nkrumah et al., 2018
	<i>Dichapetalumgelonioides</i>	Southeast Asia	Nkrumah et al., 2018
Fabaceae	<i>Anthyllis vulneraria</i>	France	Grisson et al., 2015
Violaceae	<i>Rinorealongiracemosa</i> ,	Sabah, Malaysia	Vanessa et al., 2022
	<i>Viola calaminaria</i>	Belgium	Balafrej et al., 2020
	<i>Viola baoshanensis</i>	China	Balafrej et al., 2020
Asteraceae	<i>Picris divaricata</i>	Subtropical China	Ying et al., 2010; Broadhurst et al., 2013
Rosaceae	<i>Potentilla griffithii</i>	Himalayas	Balafrej et al., 2020

and Euphorbiaceae. This indicates that hyperaccumulator flora is strongly shaped by local soil geochemistry and climate conditions.

Noccaea caerulescens was first identified as a high Zn accumulator in 1865. The so-called Zn hyperaccumulator plants contain at least 1% Zn in their dry leaves. Moreover, they can accumulate over 10,000 parts per million (ppm) of Zn in their aboveground parts, with *Arabidopsis helleri* and *Noccaea caerulescens* reaching concentrations of 13,620 ppm and 43,710 ppm, respectively (dos Santos et al., 2020). With only 28 species described so far, most of which are members of the Brassicaceae family, these Zn hyperaccumulators are relatively uncommon (Balafrej et al., 2020). In this discussion, we primarily emphasize members of Brassicaceae from temperate regions (e.g., *Noccaea*, *Arabidopsis*) as model species due to their extensive physiological and genetic characterization, while also acknowledging tropical families such as Phyllanthaceae that contribute to Zn hyperaccumulation in warmer ecosystems. These plants are crucial candidates for phytoremediation and the study of metal tolerance mechanisms due to their capacity to collect such extraordinarily high amounts of Zn.

Hyperaccumulator plants offer a safe and effective method of cleanup when present in contaminated soils. These plants possess the unusual capacity to withstand and amass significant concentrations of Zn, thereby lowering their mobility in the environment. Hyperaccumulator plants can aid in the process of phytostabilization, which immobilises metals to stop them from leaking into groundwater or spreading to other ecosystems, by absorbing too much Zn from the soil and storing it in their tissues (dos Santos et al., 2020). Furthermore, the ability of these plants to collect and mine important metals offers a sustainable and affordable method of cleaning up Zn-contaminated soils. Hyperaccumulator plants can be used in soil remediation to supplement more conventional techniques and lessen the need for costly, hazardous chemical treatments.

The mechanism of metal uptake, transport, and accumulation in plants is also greatly aided by the study of hyperaccumulator plants. Researchers can learn a great deal about the genetics of metal hyperaccumulation by examining the physiological and molecular processes of these organisms. This information can be used to

develop metal tolerance crop species with phytoremediation capacities. In metal-contaminated areas, using hyperaccumulator plants' inherent abilities to restore the environment and support sustainable agriculture may be possible.

6 Mechanisms of zinc hyperaccumulation in plants

Hyperaccumulator plants employ various strategies to enhance the bioavailability of Zn and efficiently accumulate high levels of this metal in their tissues. Hyper-accumulator plants can be examined with greater than one of the bio-concentration and translocation factors for specific metal/compound removal studies, as shown in Figure 3.

The bioconcentration factor (BCF) is defined as the ratio of the concentration of a metal in plant roots to its concentration in the soil. A BCF value >1 indicates effective uptake and accumulation of the metal from soil into roots, whereas a value <1 suggests poor accumulation. The translocation factor (TF), on the other hand, is defined as the ratio of metal concentration in the shoots to that in

the roots. A TF >1 indicates efficient transfer of metals from roots to aerial parts, while a TF <1 reflects metal retention in the roots. Thus, BCF is considered when evaluating root uptake efficiency, while TF is considered to determine the plant's capacity to redistribute and store metals in aboveground biomass. Together, these indices help classify plants as effective phytoextractors or phytostabilizers.

Translocation of metals/compounds in plants mainly depends on rhizoextraction mechanism that is directly involved in the removal of heavy metals from soil. One of these strategies involves the production of root exudates containing organic compounds and amino acids like histidine, which facilitate Zn mobilization from the soil through acidification or chelation secretion (dos Santos et al., 2020). For instance, *Sedum alfredii*, a Zn hyperaccumulator, exhibits higher Zn complexation and extraction capacity through dissolved organic matter in its exudates (dos Santos et al., 2020). Moreover, hyperaccumulator species like *Nocca caerulea* and *S. alfredii* employ additional mechanisms, such as the secretion of organic acids and antioxidants viz. ascorbic acid and glutathione, and antioxidant enzymes to counteract the synthesis of ROS induced by excess Zn (dos Santos et al., 2020).

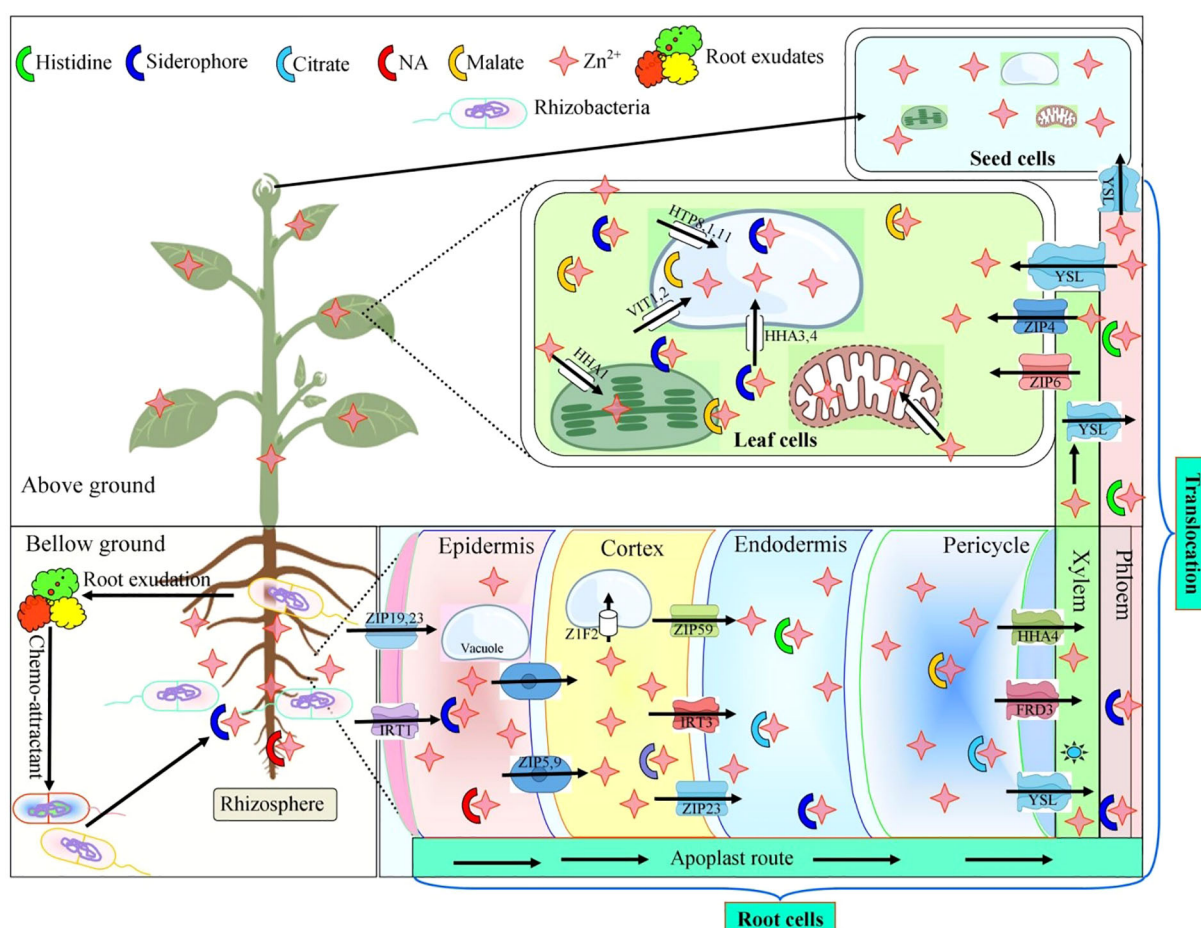


FIGURE 3

Zinc root uptake and their translocation induces attributes of hyperaccumulator plant added rhizospheric bacteria and CRISPR tool. [BCF, Bioconcentration factor of Zn; TF, Translocation factor of Zn; ZIP, Zinc/iron-regulated transporter-like protein; IRT, Iron-regulated transporter gene; YSL, Yellow stripe-1-Like; ZIP2, Zinc-induced facilitator 2; ZIP4, Zinc Transporter 4; FRD3, Ferric reductase defective 3; VIT1, Vacuolar iron transporter-1; HMA1, Heavy metal ATPase-1; MCU, Mitochondrial calcium uniporter; ZRT, Zinc regulator transporter.

Notably, glutathione and phytochelatins play crucial roles in Zn detoxification, with *N. caerulea* displaying a higher expression of metallothioneins (MTs) compared to non-accumulator species *Arabidopsis thaliana*. The overexpression of NcMT1 and NcMT2 in response to Zn exposure suggests their involvement in Zn hyperaccumulation (dos Santos et al., 2020). These metabolic processes contribute to the tolerance and metal detoxification mechanisms of hyperaccumulator plants, enabling them to thrive in Zn-contaminated environments.

As per the research, HMA4-mediated root-to-shoot loading is a key factor in zinc (Zn) and cadmium (Cd) hyperaccumulation in *Arabidopsis halleri*. This is mainly due to gene copy-number expansion and strong expression (Nouet et al., 2015). Vacuolar sequestration via MTP1 also plays an important role in providing Zn tolerance, although expression levels and subcellular location differ among groups and ecotypes. However, some details remain debated or specific to certain species. For example, while HMA4 is crucial in *A. halleri*, its effectiveness varies based on the ecotype. It also depends on the role of other transporters like zinc-regulated transporters (ZIP), natural resistance-associated macrophage proteins (NRAMP), and yellow stripe-like transporters (YSL). This is especially true for genera like *Noccaea* and *Sedum*, indicating that HMA4 acts as a species-specific module rather than a universal control (Krämer, 2025). Additionally, in *Noccaea*, MTP1-driven vacuolar storage seems to be the main sink mechanism compared to some other Brassicaceae relatives. This suggests that such patterns cannot be applied broadly without considering comparative transporter kinetics. For clarity, mechanisms are classified as either supported by consensus or disputed/variable, with specific genera clearly identified.

6.1 Root zinc uptake

In hyperaccumulator plants, Zn is primarily absorbed as Zn^{2+} ions by the roots. However, under high pH conditions, Zn can be absorbed as ZnOH after bioactivation in the rhizosphere, facilitated by mass flow and diffusion mechanisms (dos Santos et al., 2020). These plants possess zinc-regulated transporter (ZIP) or iron-regulated transporter-like proteins (ZRT-IRT-like proteins) located at the plasma membrane of the root, required in the transportation of Zn to the root stele, regardless of external Zn concentration (Figure 3). For instance, overexpression of such genes in *T. caerulea* (ZTN1 and ZTN2) and *A. halleri* (ZIP1 and ZIP6) enhances Zn uptake regardless of external Zn levels, unlike non-hyperaccumulator plants, where ZIP expression is Zn-mediated (Sytar et al., 2021). *Noccaea caerulea* expresses NcZNT1, a key Zn transporter, which, when overexpressed in *Arabidopsis thaliana*, increases Zn accumulation and enhances tolerance to excess Zn exposure (dos Santos et al., 2020).

6.2 Root to shoot Zn translocation

In hyperaccumulator plants, excess Zn is transported to xylem vessels after reaching the endodermis. Zn is chelated using low

molecular weight ligands, viz., nicotianamine (NA), malate, in the xylem parenchyma and citrate to prevent it from being retained by cell walls (dos Santos et al., 2020). The translocation of Zn relies on crucial transporters from ZIP, HMA, YSL, and MATE families (dos Santos et al., 2020). Genes such as NcZNT1, NcZNT2, NcZNT5, IRT3, ZIP19, ZIP23, NAS, HMA4, YSL, and FRD3 play essential roles in Zn uptake, loading into xylem, and shoot translocation, as shown in Figure 3 (dos Santos et al., 2020). The expression patterns of these genes significantly influence Zn uptake and translocation in hyperaccumulator plants, facilitating their ability to accumulate high Zn levels.

6.3 Vacuolar sequestration

Metal hyperaccumulators have effective mechanisms for detoxifying heavy metals by quickly chelating or sequestering metal ions into vacuoles or cell walls in above-ground organs (dos Santos et al., 2020). This leads to the accumulation of metal at higher concentrations in the leaf epidermis, trichomes, and cuticles while experiencing minimal inhibition of photosynthetic activities. Metal transporter proteins like MTP1 (Figure 3) reside in the tonoplast of Zn/Ni hyperaccumulators and are members of the cation diffusion facilitator (CDF) family. Also, their increased expression in leaves suggests a role in Zn sequestration within vacuoles, enhancing Zn tolerance through a systemic zinc deficiency response (dos Santos et al., 2020). ZIP transporters' upregulation can also facilitate increased Zn uptake. HMA3 and MHX proteins have also been linked to Zn compartmentalization or hyperaccumulation, with elevated gene expression in specific plant tissues (dos Santos et al., 2020).

7 Rhizoremediation and the dominant rhizospheric microbes

Soil microbes, particularly plant growth-promoting rhizobacteria (PGPR), play a significant role in the detoxification of heavy metals in contaminated soils. This process, known as rhizoremediation, has been widely studied to generally include the bacterial population in heavy metal-contaminated sites predominantly composed of Firmicutes, Proteobacteria, and Actinobacteria, with *Bacillus*, *Pseudomonas*, *Enterobacter*, and *Arthrobacter* being the most common genera (Verma et al., 2021; Khanna et al., 2022). These PGPRs possess a remarkable ability to facilitate nutrient and heavy metal absorption in plants through the synthesis of organic acids and metal chelates like siderophores (Khanna et al., 2022). Additionally, these PGPR strains can decrease heavy metals' availability in the soil through diverse processes, including biotransformation, complexation, biosorption, etc., thus significantly enhancing the efficiency of phytoremediation (Manoj et al., 2020).

Biotransformation refers to the enzymatic conversion of metals from one oxidation state to another, often reducing their toxicity or changing their solubility (e.g., microbial reduction of Zn^{2+} into less

mobile forms). Complexation involves the secretion of microbial metabolites, such as siderophores and organic acids, which form stable complexes with Zn, thereby altering its mobility and uptake by plants. Biosorption is a metabolism-independent process where microbial cell walls bind Zn through functional groups (carboxyl, hydroxyl, amine, sulfhydryl), immobilizing excess Zn in the rhizosphere. Together, these mechanisms regulate Zn speciation, decrease free ion toxicity, and influence whether Zn is mobilized for phytoextraction or immobilized for phytostabilization.

Their remarkable capacity for biosorption is attributed to their high surface-to-volume ratios and the presence of active chemisorption sites, including teichoic acid, in the cell wall (Sharma, 2021). Studies focused on eliminating cadmium, lead, and zinc metals from polluted soils have demonstrated the effectiveness of certain PGPR species like *Klebsiella* sp. and *Enterobacter* sp. due to their ability to resist metals and produce plant-stimulating compounds (Sharma, 2021).

Phytoextraction, a phytoremediation technique, exploits the natural ability of plants to take up heavy metals from contaminated soil and translocate them to their above-ground parts, facilitating their removal from the polluted site. PGPRs are instrumental in enhancing phytoextraction efficiency by altering various factors that affect heavy metal bioavailability, mobility, solubility, and transport (Mohammadzadeh et al., 2017). Through their intricate interactions with plants, PGPR contribute significantly to the successful remediation of Zn-contaminated soil. For instance, in a study conducted by Dąbrowska et al. (2017), it was found that certain bacteria, including Bacteroidetes bacterium, *Pseudomonas fluorescens*, and *Variovorax* sp., exhibited effectiveness in phytoextraction of Cd and Zn from the rhizosphere of *Brassica napus*, a plant growing in polluted soil. These bacteria were successful in lowering the levels of heavy metals in the rapeseed roots.

Heavy metals must be solubilized in order to be available for plant absorption, and this is where microbial siderophores, which are metal-chelating agents, come into play. According to studies (Manoj et al., 2020), inoculating siderophore-producing PGPR strains increases the accumulation of metals like lead (Pb), Zn, and iron (Fe) in host plants. In addition, PGPR strains create low molecular weight organic acids, including oxalic and citric acids, that, by forming complexes and lowering metal availability, aid in the solubilization and mobility of metals (Manoj et al., 2020; Rani et al., 2023b). Microbial biosurfactants produced by PGPR strains, such as *Acinetobacter*, *Pseudomonas*, *Bacillus*, and *Serratia*, interact with insoluble metals in the rhizosphere soil, promoting their desorption from the soil matrix and altering metal mobility and bioavailability (Manoj et al., 2020; Mondal et al., 2023). For instance, *Serratia* spp. show several plant growth-promoting traits that help with zinc bioavailability and stress reduction. These traits include zinc and phosphorus solubilization, ACC-deaminase activity, EPS or biofilm formation, and antioxidant support. They encourage growth during nutrient imbalances and abiotic stress (Wang and Xu, 2025). Recent studies and reviews report that *Serratia* can reduce heavy metals in the rhizosphere and improve crop performance. For example, *Serratia* sp. lowered rhizospheric

zinc in contaminated tea soils, and *S. marcescens* strains increased micronutrient levels like zinc and iron in cereals during pot and field trials. Therefore, we recommend testing *Serratia* in combination with traditional zinc-solubilizing bacteria (Kulkova et al., 2024).

Certain PGPR strains, as opposed to phytoextraction, can lessen the mobilisation and accumulation of heavy metals through particular mechanisms, such as adsorption, biosorption, bioaccumulation, biotransformation, precipitation, complexation, and alkalization (Ma et al., 2016; Manoj et al., 2020). Extracellular polymeric substances (EPS) and extracellular capsules, as well as anionic functional groups on bacterial cell surfaces such as sulfhydryl, sulfonate, carboxyl, hydroxyl, amine, and amide groups, are essential for the adsorption and immobilisation of heavy metals (Sessitsch et al., 2013). Bacteria can easily capture cationic charged heavy metals with their anionic charged EPS molecules. Microbial EPS has a general negative charge thanks to functional groups like hydroxyl, phosphate, amine, sulfhydryl, and carboxyl. These functional groups play a major role in the adsorption of heavy metals that are cationically charged, thereby lowering their availability and mobility in the rhizosphere. Table 2 lists the phytoextraction and phytostabilization of Zn that have been assisted by PGPR. Either metabolism-dependent active transport or metabolism-independent passive transport can be used by microorganisms to take up heavy metals. Metals can be immobilised after biosorption by a number of microbial processes, including precipitation, accumulation, sequestration, and transformation.

Fang et al. (2016) identified *Acinetobacter* sp. (FQ-44) as a Cu/Zn-resistant PGPR isolate with promising bioremediation capabilities. This strain showed significant potential for microbe-assisted phytoextraction, promoting plant growth and effectively mobilizing and adsorbing multiple metals from contaminated soils. In another study, Plociniczak et al. (2016) investigated the colonization potential of PGPR *Brevibacterium casei* MH8a in *Salix alba* plant tissues using rifampicin as a biomarker. The study revealed successful colonization of roots and leaves, leading to increased biomass and metal accumulation (Cd, Zn, and Cu) in the roots. Moreover, the presence of MH8a caused temporary alterations in the structure of native bacterial communities, highlighting its bioremediation potential and transient effects on indigenous microbial populations in the soil. Further, *Achromobacter piechaudii* E6S, a multi-metal resistant endophytic bacterium, promoted plant growth through IAA production and phosphate solubilization. In pot experiments, it increased plant biomass and accumulation of Cd, Zn, and Pb, while reducing Cd and Zn translocation, indicating its potential for metal rhizoaccumulation and phytostabilization improvement (Ma et al., 2016). According to Mousavi et al. (2018), *Helianthus annuus* accumulated more Pb and Zn after receiving microbial inoculation with the siderophore-producing bacterial strains *B. safensis* FO-036b (T) and *P. fluorescens*. The inoculation of the siderophore-producing PGPR strain *Streptomyces pactum* led to a significant increase in the accumulation of Zn, Pb, and Fe in the host plants, according to findings published by Amjad et al. (2017).

TABLE 2 A list of PGPR assisted phytoextraction and phytostabilization of Zn.

Strategies	Bacterial strains	PGP activities of the strains	Reference
PGPR assisted phytoextraction of Zn	<i>Klebsiella oxytoca</i> -JCM1665	ACCD, Ammonia, IAA, HCN	Arunakumara et al. (2015)
	<i>B. casei</i> -MH8a	ACCD, IAA, HCN	Plociniczak et al. (2016)
	<i>Enterobacter</i> -N9, <i>Serratia</i> -K120, <i>Klebsiella</i> -Mc173, <i>Escherichia</i> -N16	IAA, siderophores, ACCD, solubilization,	Carlos et al. (2016)
	<i>S. pactum</i> -Act12	Siderophore	Amjad et al. (2017)
	<i>Bacillus</i> sp. SC2b	Siderophore, IAA,	Ma et al. (2015)
	<i>B. safensis</i> -FO-036b(T) and <i>P. fluorescens</i> -p.f.169	IAA, siderophore, ACCD	Mousavi et al. (2018)
PGPR assisted phytostabilization of Zn	<i>Pseudomonas</i> - A3R3, <i>Psychrobacter</i> -SRS8	Siderophore	Ma et al. (2015)
	<i>B. aryabhattai</i> -RSO25, <i>Pantoea agglomerans</i> - RSO6, RSO7	IAA, siderophore, N fixation, P solubilization	Paredes-Páliz et al. (2016)
	<i>Rhodobactersphaeroides</i>	IAA production	Peng et al. (2018)

8 Utilizing GM bacteria for Zn phytoremediation

A successful strategy for creating plant-based phytoremediation techniques to address heavy metal contamination is genetic engineering. By using molecular biology techniques, it is possible to increase the biodegradability of microbes, which promotes the evolution of new procedures and the development of novel mechanisms through the assembly of catabolic segments (Zango Usman et al., 2020). Recombinant bacteria and plants with desired traits can be created through genetic modification, offering hope for the future of phytoremediation.

Bacterial surface structures, in particular, play a key role in the interaction between the environment's heavy metal ions and the inhabitant bacteria. Bacterial cell structures of both Gram-positive and Gram-negative types have a negative charge, allowing them to interact with metal ions successfully (Zango Usman et al., 2020). Microorganisms known as genetically modified bacteria (GMB) have had their genetic makeup changed through the use of processes like recombinant DNA technology. Activated sludge, groundwater, and soil bioremediation can effectively be treated by GMB, which has a better capacity to degrade various synthetic pollutants (Sayler and Ripp, 2000).

Various pathways can be utilized to produce GMB for bioremediation technologies. These pathways involve modifying enzymes to enhance their affinity and specificity, designing and regulating pathways, developing bioprocesses, and utilizing bio-affinity bioreporters for chemical sensing and toxicity reduction (Ramos-Cormenzana et al., 1995). Specific plasmids are designed for the degradation of different compounds, such as octane, xylene, toluene, camphor, and naphthalene. The creation of microbial strains that can break down various kinds of hydrocarbons is made possible by genetic engineering approaches.

Using genetic engineering, heavy metals from industrial effluent have been removed. For instance, recombinant *Rhodopseudomonas palustris* has been developed to remove Hg²⁺ from metal wastewater, whereas *Alcaligenes eutrophus* AE104 (pEBZ141) has been utilized for the removal of chromium (Srivastava et al., 2010; Deng and Jia, 2011). Additionally, genetically modified endophytic and rhizospheric

bacteria have shown promising results in the elimination of toxic substances from soils associated with plants, making them a pioneer solution for wastewater treatment in contaminated industrial areas (Divya and Kumar, 2011).

For genetic recombination and gene inoculation, acceptable strains must meet a number of requirements, including safety, high expression of the target genes, immunity or tolerance to contaminants, and compatibility with particular plant rhizospheres (Huang et al., 2004). *Escherichia coli*, *Deinococcus radiodurans*, *Pseudomonas putidia*, *Caulobacter* sp., and other strains have been genetically altered to effectively remove mercury, organophosphates, chlorinated organic compounds, chromium, cadmium, arsenic, and nickel from polluted environments (Barkay et al., 2003; Patel et al., 2018). Endophytic bacteria were genetically altered in a study by Liu et al. (2019) to improve Zn uptake and accumulation in maize plants. The modified bacteria successfully improved Zn absorption by the plant roots and facilitated its transport to the above-ground plant parts, leading to increased zinc build-up in plant tissues and encouraging effective zinc-contaminated soil phytoremediation.

The performance and persistence of microbial inoculants in a variety of field circumstances can be enhanced by formulation techniques such as the use of carriers, encapsulation methods, and osmoprotectants, as well as by biofilm development, exopolysaccharide (EPS) synthesis, and co-inoculation tactics. For monitoring, it is crucial to report persistence curves using colony-forming units (CFU) or quantitative polymerase chain reaction (qPCR) and to find the minimum effective agronomic dose. In the case of zinc (Zn) phytomining, standardized process chains include harvest, drying, ashing, and hydrometallurgical extraction, which should be documented along with life cycle assessment (LCA) and techno-economic analysis (TEA), paying attention to metal recovery efficiency and residue safety (Malecka et al., 2019). The environmental release of engineered microbes needs specific approval depending on the area. In the United States, this falls under the Environmental Protection Agency (EPA) Toxic Substances Control Act (TSCA), 40 Code of Federal Regulations (CFR) Part 725 for intergenic microorganisms. In the European Union, it is regulated by Directive 2001/18/EC, which governs the deliberate release of

genetically modified organisms (GMOs). In India, the Genetic Engineering Appraisal Committee (GEAC) oversees this under the 1989 Rules of the Environment (Protection) Act (EPA) along with the Department of Biotechnology (DBT) guidelines, which require multi-stage field trials and thorough risk assessments (Lea-Smith et al., 2025).

9 Limitations and factors affecting phytoremediation efficiency

Despite their effectiveness, phytoremediation and microbe-assisted remediation have certain limitations under realistic field conditions. Plant-based approaches can be slow, often requiring multiple growing seasons to significantly reduce metal concentrations, and may be limited by soil depth, metal bioavailability, and climate conditions. The efficiency of microbial remediation can also be influenced by soil pH, nutrient status, competition with native microorganisms, and environmental stresses. In the medium- to long-term, metals accumulated in plant biomass or microbial biomass must be properly managed to avoid secondary contamination. Furthermore, the success of decontamination depends on several factors, including the selection of suitable hyperaccumulator species, microbial strains with high metal tolerance and biosorption capacity, soil properties, metal speciation, and environmental conditions such as temperature and rainfall. Considering these factors is essential to ensure that phytoremediation strategies are both practical and sustainable in field applications.

10 Knowledge gaps and future directions

Transporter variability across species and ecotypes is an important area of research. While HMA4 copy-number expansion and overexpression are strongly linked to root-to-shoot zinc (Zn) and cadmium (Cd) loading in *Arabidopsis halleri*, this factor alone may not fully explain hyperaccumulation across different taxa. Accessory pathways that involve zinc-regulated transporters (ZIPs), natural resistance-associated macrophage proteins (NRAMPs), yellow stripe-like transporters (YSLs), and vacuolar sequestration through MTP1 show species- or ecotype-specific regulation, as seen in *Noccaea* compared to *Arabidopsis* (Krämer, 2024). To better understand these differences, there is a need of comparative single-cell transcriptomics and transporter kinetic studies across multiple genera (Nouet et al., 2015).

Moving from controlled environments to practical deployment brings additional challenges. Most evidence for zinc-solubilizing plant growth-promoting rhizobacteria (ZSB) and engineered strains is mainly from greenhouse experiments (Lea-Smith et al., 2025). To scale up, multi-site and multi-season field trials, better formulation strategies to improve microbial survival in non-sterile soils, and clear biocontainment and regulatory pathways for genetically modified microbes are required (Tang et al., 2024). Managing hyperaccumulator biomass is equally important. The standardized processes for drying, ashing, and hydrometallurgical recovery, along with life cycle assessment (LCA) and techno-economic analyses to ensure safety and feasibility (Malecka et al., 2019) are needed. Moreover, designing microbiome consortia that

integrate ZSB with traits like 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity and exopolysaccharide (EPS) production could improve performance, although the key factors for stability and optimization still require further study.

11 Conclusion

Soil contamination by heavy metals, including Zn, is a major concern for both the ecosystem and human health. A few ecotypes of metal hyperaccumulators and wild populations, as well as rhizobacteria (PGPR, endophytic bacteria, and mycorrhizae), can tolerate high heavy metal concentrations. The mechanism behind this involves genes such as *HMA*, *ZIP*, *YSL*, *MTP*, and others that facilitate Zn uptake, transfer to above-ground tissues, and subsequent chelation, as well as mitigating Zn stress in the environment. To achieve effective *in situ* bioremediation, a comprehensive approach involving microbiology, behavior, and environmental biotechnology is crucial.

Phytoremediation is considered a promising solution to remediate contaminated land and wastewater, but a proper understanding of plant-microbe intra-communication is crucial for its successful implementation. Studies of species relationships and their interactions provide valuable insights into plant and microbial dynamics, ecosystem responses to environmental changes, and the roles of important species. For genetically modified bacteria to be a viable alternative for bioremediation, specific guidelines for the degradation of toxic metabolites should be developed for each case. Ongoing research and an improved understanding of plant-microbe interactions are necessary to realize the maximum potential of phytoremediation in combating pollution and providing sustainable solutions for contaminated sites.

Author contributions

NR: Conceptualization, Formal Analysis, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing. AC: Data curation, Resources, Writing – original draft. NS: Conceptualization, Data curation, Formal Analysis, Project administration, Supervision, Validation, Writing – original draft, Writing – review & editing. VK: Data curation, Formal Analysis, Writing – original draft.

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